



How deforestation and forest use affect tree diversity in a conifer forest from central Mexico

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Abstract

Aim of study: To assess the association of deforestation and forest use with tree diversity and dominance of pine species.

Area of study: La Malinche National Park, central Mexico.

Material and methods: Three forest stands were selected on each of four slopes in La Malinche National Park, in which the percent forest cover was determined using a concave spherical densitometer. Additionally, we estimated logging, firewood, and *ocoteo* as indirect measures of forest use. In each forest stand, we set five 0.1-ha circular plots and we recorded tree species, diameter at breast height, and height of all individuals ≥ 1.5 m. We estimated diversity using Hill numbers (qD). We identified dominant species from rank-abundance curves, and explored the dissimilarity between forest stands for the three q orders. Using generalized linear mixed-effects models, we evaluated the relationships of deforestation and forest use with species diversity and pine dominance, and studied the effect of pine dominance on the abundance of other tree species through generalized linear models.

Main results: We recorded a total of 16 tree species; a pine (*Pinus montezumae*) was the dominant species. The diversity of tree species was not associated with forest use or deforestation, but deforestation increased *Pinus* dominance, with a strong slope effect.

Research highlights: Regulation and control of forest use should be prioritized to avoid further deforestation and the transformation of species-diverse forests into monospecific forests, further increasing the dominance of *P. montezumae*. We also suggest reforestation with native species and those scarcely represented to increase forest cover and maintain tree diversity.

Additional key words: Hill numbers; human activities; conservation; community ecology; pine-dominated forest.

Abbreviations used: AICc (corrected Akaike Information Criterion); Cov (Coverage); 0D (species richness); 1D (common species); 2D (dominant species); DBH (diameter at breast height); %FC (percentage of forest cover); G_{dind} (total basal area); J (Jaccard's index); MH (Horn index); m asl (meters above sea level); RD_{dind} (relative density of damaged individuals); %SC (percentage of sampling coverage); S_j (Jaccard's similarity index); $S_{\text{M-H}}$ (Morisita-Horn similarity index); TD (total density); TG (total basal area).

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Introduction

In addition to the serious effect of deforestation on biodiversity loss, deforested ecosystems lose their ability to provide multiple ecological services, such as erosion control, wind protection, carbon sequestration, and air purification (Imai et al., 2012; Adekunle et al., 2013). Deforestation is the conversion of forests to non-forest land uses (e.g., agriculture or housing); in this process, forest cover is gradually lost until only 10 % or less of the original cover is conserved (Chakravarty et al., 2012). The ecological consequences of deforestation on plants through selective logging, firewood extraction, grazing, and land clearing for permanent agriculture involve changes in succession patterns and species composition. Deforestation favors pioneer species due to their ability to colonize recently disturbed sites, while late successional species are more sensitive to disturbance, which considerably reduces their populations, even to the point of local extinction (Figueroa-Rangel et al., 2008; Chakravarty et al., 2012; Pessoa et al., 2017).

In conifer forests, many species of *Pinus* are considered invasive and colonizers in areas with severe deforestation or disturbance because they can germinate and establish successfully in open areas (Richardson & Bond, 1991; Galindo-Jaimes et al., 2002). Previous investigations have reported an increase in pine abundance in conifer forests due to land clearance for logging and agriculture; as a result of deforestation, drier environments have a positive effect on pine dominance (Figueroa-Rangel et al., 2008). Furthermore, pine-dominated forests are characterized by drier and hotter conditions along with more compact, less acidic, and less fertile soils, which reduce microbial biomass, deteriorate the microhabitat, and restrict the establishment of other tree species (Galindo-Jaimes et al., 2002).

Mexican conifer forests cover 16 % of the country, with a deforestation rate of 0.8 % per year, being the second-most-affected vegetation type from original cover loss (27 %), only after tropical forests (42 %) (Guerra-De la Cruz & Galicia, 2017). The conifer forests of central Mexico are particularly important in terms of biodiversity due to the environmental conditions conferred by the convergence of the Nearctic and Neotropical zones (Morrone, 2005). However, it is one of the areas of Mexico with the greatest conversion of forest cover to different land uses (Reyes-González & Rhodes, 2015; FAO & PNUMA, 2020).

La Malinche National Park has been a Protected Natural Area since 1938 and has 206.07 km² of conifer forest in central Mexico (Rojas-García & Villers-Ruiz, 2008). Although the La Malinche National Park management plan indicates restricted land-use changes and controlled extraction of forest resources (Rojas-García & Villers-Ruiz, 2008), these guidelines have not been observed and deforestation has increased since 1985; to date, about 54 % of its area includes cropland, induced pastures, and human settlements (Rojas-García & Villers-Ruiz, 2008). La Malinche National Park is an area of great ecological importance for the conservation of conifer forests in central Mexico because it maintains the diversity and endemism

unique to the Trans-Mexican Volcanic Belt. However, tree diversity has only been partially described, and the effects of constant deforestation and conversion of forest use have not yet been explored (SEMARNAT & CONANP, 2013).

This study aimed to describe the diversity of trees in the La Malinche National Park, identify its association with deforestation and forest use, explore whether pine dominance increases with forest cover loss and forest use, and assess whether this pine dominance determines the abundance of other tree species. We expected to find a negative relationship of deforestation and forest use with tree diversity, a positive relationship with pine abundance, and a lower abundance of non-pine trees in areas with higher dominance of *Pinus* species.

Material and methods

Study area

La Malinche National Park is located in central Mexico, in the states of Tlaxcala and Puebla, between coordinates 19°08'–19°20' N and 98°08'–97°55' W (Fig. 1a,b); it comprises a total of 461.12 km² across an altitudinal range between 2,200 and 4,461 m asl, which includes conifer forest, broadleaf forest (e.g. *Quercus* spp. and *Buddleja cordata*) and alpine grassland (Rojas-García & Villers-Ruiz, 2008; SEMARNAT & CONANP, 2013).

The climate in La Malinche National Park changes with altitude, but the one that prevails is temperate subhumid, with a mean annual temperature of 14 °C to 16 °C and summer rains, which are more intense from June to September (Rojas-García & Villers-Ruiz, 2008). Vegetation also varies with altitude, slope, and orography. The dominant vegetation types are pine forest, fir forest, and pine-oak forest, all of which can be classified as conifer forests (Rzedowski, 2006).

The altitudinal belt sampled represents a bioclimatic transition zone that ranges between 2,800 m and 3,200 m asl (~158 km², 34 % of La Malinche National Park; SEMARNAT & CONANP, 2013); therefore, this area harbors the highest species diversity. Above this altitude, *Abies religiosa* and *Pinus hartwegii* dominate with monospecific forests at different elevations; below this range, deforestation is more prevalent (Rojas-García & Villers-Ruiz, 2008).

The land-use changes in La Malinche National Park that have caused the greatest forest loss are agriculture and grazing (Valdez et al., 2016). From 1995 to 2020, La Malinche National Park has been subjected to sustained deforestation, with an annual loss of continuous forest of 0.41 km² and an increase of 0.38 km² of discontinuous forest and 0.10 km² of urban areas (Table S1 [suppl]).

Sampling

We spatially located three forest stands on each of four slopes in La Malinche National Park (North, East, Southeast,

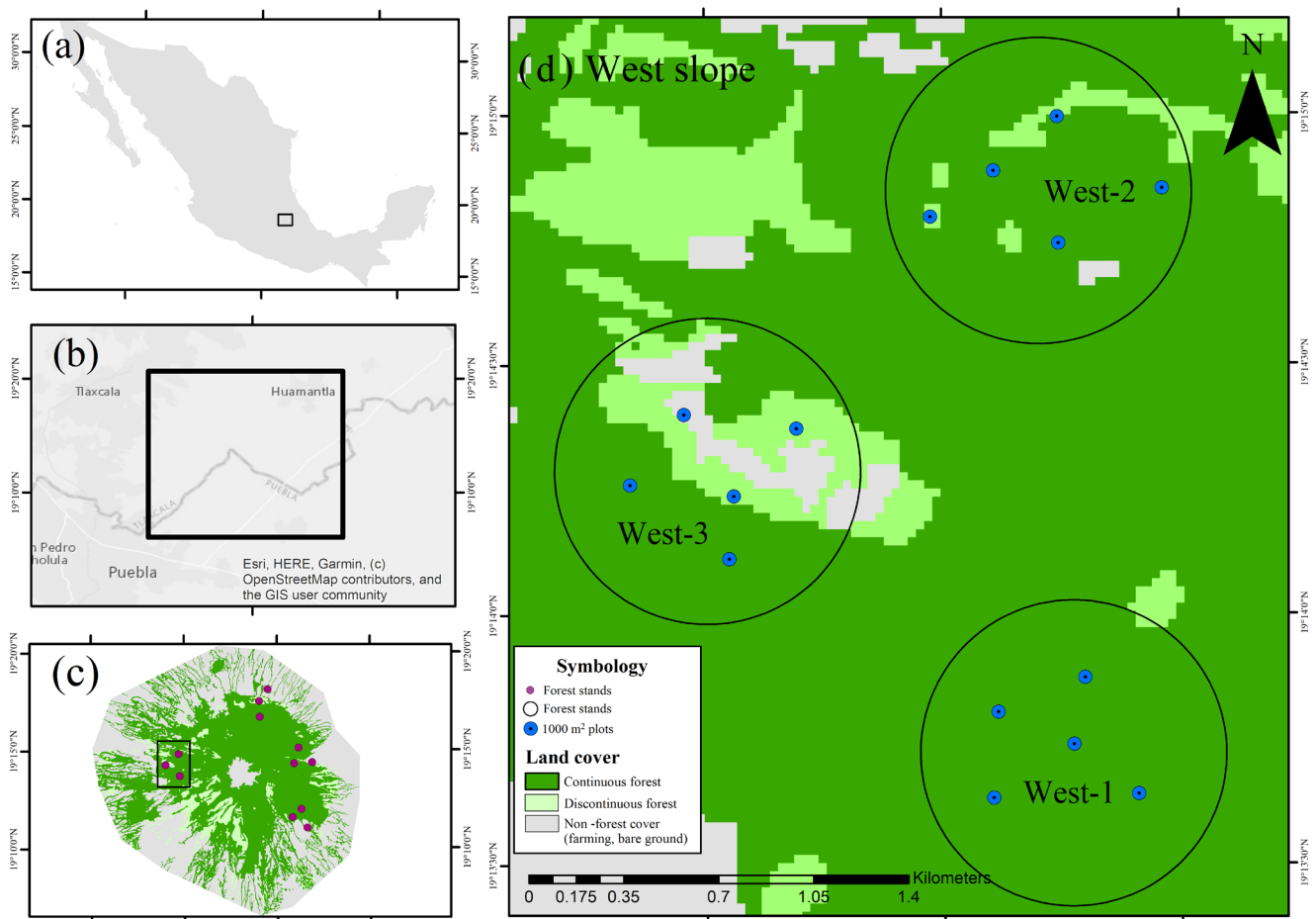


Figure 1. Study area for sampling the composition of tree species in La Malinche National Park. Location of: (a) the study area in Mexico, (b) La Malinche National Park, (c) forest stands on each slope in La Malinche National Park, (d) sampling plots within West slope forest stands.

and West) (Fig. 1c). We randomly established five 1,000 m² circular plots (17.8 m radius) in each forest stand (Fig. 1d), with a minimum distance of 50 m between plots. In each plot, we measured the diameter at breast height (DBH) at 1.3 m above the ground for all trees ≥ 1.5 m in height. We taxonomically identified each tree by comparing specimen samples with herbarium material deposited at the TLXM Herbarium of the Universidad Autónoma de Tlaxcala (Thiers, 2024).

Deforestation and forest use

We obtained the percentage of forest cover (%FC) as an approximation of deforestation measured with a convex spherical densitometer (Model A) at four points within each plot (i.e., North, South, East, and West) at a distance of 11 m from the plot center. We estimated the percentage of forest cover in each stand as the average value of the respective plots.

Knowing that deforestation is directly related to forest use (Vieilledent et al., 2018) but that the latter (forest use) is a continuous and historical process (Table S1 [suppl])

for which we have no record, we used three indicators of forest use to obtain current values and assess how they affect species diversity and dominance. These indicators are: logging, *ocoteo* (cuttings of pine wood fragments that are impregnated with resin and used by local human populations to light fires), and firewood extraction. To this end, we used the relative density and basal area of damaged individuals (juveniles and adults), compared to undamaged trees, for each indicator (Sapkota et al., 2010). We measured firewood extraction as the number of tree stumps < 20 cm DBH, while logging considered tree stumps > 20 cm DBH, and *ocoteo* included the number of individuals of *Pinus* spp. with cut marks in the bark.

To estimate the extent of each type of forest extraction, we first calculated the relative density and basal area of damaged individuals per plot with the following formulas:

$$RD_{\text{dind}} = \Sigma RD_{\text{dind}} / TD \quad (1)$$

$$G_{\text{dind}} = \Sigma G_{\text{dind}} / TG \quad (2)$$

where RD_{dind} is the relative density of damaged individuals, ΣRD_{dind} is the sum of the relative density of damaged

individuals, TD is the total density; G_{dind} is the relative basal area of damaged individuals, ΣG_{dind} is the sum of the relative basal area of damaged individuals, and TG is the total basal area. Subsequently, we estimated relative values by dividing the values of the plot of interest by the lowest value (density and basal area) for the entire La Malinche National Park. Then, we calculated the overall value for each forest stand as the arithmetic mean of the respective plots, representing the sum of density and basal area (Sapkota et al., 2010).

Tree composition

We estimated diversity for each forest stand by obtaining rarefaction curves and Hill numbers (Hill, 1973) of order q , or the effective number of species, defined as ${}^qD = (\sum_{i=1}^S P_i^q)^{1/(1-q)}$, where qD is the effective species richness, and q indicates the relative abundance of species i . When $q = 0$, species abundances are not considered, so 0D is species richness. If $q = 1$, species are weighed proportionally to their frequencies (common or typical species), so 1D is equivalent to the exponential of Shannon's entropy (Shannon's diversity index). Finally, for $q = 2$, diversity (2D) represents the dominant species and is equivalent to the inverse of Simpson's diversity index (Chao et al., 2014). We constructed interpolation or extrapolation curves relative to the sample size at each sampling site with a 95 % confidence level and 1,000 bootstrap replicates. Additionally, we estimated the completeness of the sampling (coverage) for species.

We identified dominant species through rank-abundance curves for each species. Furthermore, we determined the dissimilarity between forest stands according to the order

q using Jaccard's index (J) for $q = 0$ with the formula: $J = \frac{\bar{S}/S - 1/N}{1 - 1/N}$, where $\bar{S}$ is the average species richness of the plots in the forest stand, S is the species richness of all forest stands pooled, and N is the number of forest stands (Chiu et al., 2014). For $q = 1$, the Horn index (R_o) was used: $R_o = \frac{H_{\text{max}} - H_{\text{obs}}}{H_{\text{max}} - H_{\text{min}}}$, where H_{max} is the value when the forest stands (X and Y) have no species in common; H_{obs} are the species observed in the forest stands ($X + Y$); and H_{min} is the value of the forest stands that have the same species in equal proportion. For $q = 2$, the Morisita-Horn index (MH) was used: $MH = 1 - \frac{H_{GS,Y} - H_{GS,X}}{(1 - 1/N)(1 - H_{GS,\alpha})}$, where H_{GS} is gamma (γ) and alpha (α) diversity with the Gini-Simpson index, and N is the number of forest stands (Chiu et al., 2014).

Effect of deforestation or forest use on species diversity

We assessed the relationship of total tree species diversity (0D , 1D , 2D) with deforestation (forest cover percentage; %FC) and forest use indicators (firewood extraction, logging, *ocoteo*) as explanatory variables using generalized linear mixed-effects models and the Poisson family for richness, and Gaussian family for abundant and dominant species, and whose random variable was the stand (i.e., 0D , 1D or ${}^2D \sim (\text{Logging, ocoteo, Firewood, or \%FC}) * \text{Slope} + (1|\text{stand})$). With the same models using the plot as random variable and the Poisson distribution, we also studied the effect of deforestation and forest use on pine abundance (only *Pinus* spp.), which included the five species recorded at La Malinche National Park (*Pinus ayacahuite*, *P. hartwegii*, *P. leiophylla*, *Pinus pseudostrubus*, and *P. teocote*) (i.e., *Pinus*

Table 1. Deforestation and forest use indicators and tree diversity of 12 forest stands on the four slopes of La Malinche National Park.

Forest stand	Firewood extraction	Logging	Ocoteo	%FC	0D	1D	2D	%SC
East-1	10.6	10.0	17.4	74.4	5	2.6	2	100
East-2	16.1	0.0	0.0	70.0	11	4	3.2	100
East-3	2.0	18.4	51.7	52.2	4	1.5	1.3	98
West-1	11.7	25.0	9.1	72.9	5	2.3	1.8	99
West-2	11.9	0.0	0.0	54.9	6	1.9	1.5	100
West-3	0.0	0.0	127.6	49.6	8	2	1.5	98
North-1	45.6	11.7	0.5	68.0	11	1.7	1.3	100
North-2	7.4	20.2	32.7	59.9	2	1.1	1.0	100
North-3	5.0	16.1	179.2	70.9	3	1.3	1.1	98
Southeast-1	1.1	10.8	23.5	55.2	6	2.5	2.2	99
Southeast-2	0.0	20.6	99.0	63.9	7	3	2.4	98
Southeast-3	29.2	1.1	61.6	35.8	6	2.5	1.7	100
Average	11.7	11.2	50.2	60.6	6.2	2.2	1.8	99.2

%FC: percentage of forest cover. 0D , observed species richness. 1D , observed diversity of common or typical species. 2D , observed diversity of the dominant species. %SC, relative sampling coverage, in percentage.

spp. $\sim$ (logging, *ocoteo*, firewood, or %FC)*Slope+(1|stand)). We tested the statistical significance of each model by contrast with the null model (dependent variable $\sim 1+(1|\text{stand})$) (Gualchi, 2019). For those response variables with more than one model, we used the corrected Akaike Information Criterion (AICc) to identify the model with the best fit to the data (Hurvich & Tsai, 1991). Finally, we assessed the contribution of each variable of the statistically significant and optimal models (according to the AICc) with a Permuted Multivariate Analysis of Variance (PERMANOVA).

In addition, to evaluate whether pine dominance (*Pinus* spp.) determines the abundance of other tree species, we performed generalized linear models using the Poisson family (i.e., other non-pine trees $\sim$ *Pinus* spp.). As *P. montezumae* was the dominant conifer in almost all forest stands, we explored whether its abundance alone governs the abundances of other tree species (i.e., other non-pine trees $\sim$ *P. montezumae*). We determined the statistical significance of all generalized linear models using a likelihood-ratio test. We performed all the analyses with the R v. 4.1.1 program, using the following libraries: AICmodavg, Biodiversity, car, corplot, lme4, lattice, MASS, MuMIn, permute, Vegan, vegdist, and iNEXT (R Core Team, 2023).

Results

Deforestation and forest use

Forest cover values ranged between 35.8 % and 74.4 % (Table 1); Southeast-3 and East-1 were the forest stands with the lowest and highest percent cover values. In general, there were differences in intensity of use according to slope exposure; on average, there was higher *ocoteo* (50.2) than firewood extraction (11.7) and logging (11.2); there was no firewood extraction in West-3 and Southeast-2, while no logging was detected in East-2, West-2, and West-3, and we did not record *ocoteo* (0.0) in East-2 and West 2.

Tree composition

We recorded a total of 16 tree species: *Alnus jorullensis*, *Abies religiosa*, *Arbutus xalapensis*, *Buddleja cordata*, *Comarostaphylis discolor*, *Cupressus benthamii*, *Pinus ayacahuite*, *Pinus hartwegii*, *Pinus leiophylla*, *Pinus mon-*

Table 2. Generalized linear mixed-effects models that evaluated the effect of deforestation and forest use on total tree diversity (a), and on pine abundance (b) in La Malinche National Park. The statistically significant and best model is highlighted in bold.

	Model	r ² m	r ² c	AICc	p
(a) Diversity $\sim$ deforestation/forest use					
⁰ D	$\sim$ Logging*Slope+(1 stand)	0.58	0.58	19.08	0.07 ^{ns}
	$\sim$ <i>Ocoteo</i> *Slope+(1 stand)	0.62	0.62	18.80	0.07 ^{ns}
	$\sim$ Firewood*Slope+(1 stand)	0.48	0.48	24.25	0.07 ^{ns}
	$\sim$ %FC*Slope+(1 stand)	0.01	0.01	19.84	0.75 ^{ns}
¹ D	$\sim$ Logging*Slope+(1 stand)	0.88	0.88	20.23	0.44 ^{ns}
	$\sim$ <i>Ocoteo</i> *Slope+(1 stand)	0.94	0.94	20.08	0.42 ^{ns}
	$\sim$ Firewood*Slope+(1 stand)	0.82	0.82	20.33	0.45 ^{ns}
	$\sim$ %FC*Slope+(1 stand)	0.01	0.01	14.92	0.65 ^{ns}
² D	$\sim$ Logging*Slope+(1 stand)	0.92	0.92	20.11	0.75 ^{ns}
	$\sim$ <i>Ocoteo</i> *Slope+(1 stand)	0.98	0.98	20.03	0.75 ^{ns}
	$\sim$ Firewood*Slope+(1 stand)	0.76	0.76	20.41	0.79 ^{ns}
	$\sim$ %FC*Slope+(1 stand)	0.48	0.48	21.17	0.87 ^{ns}
(b) <i>Pinus</i> spp. $\sim$ deforestation/forest use					
<i>Pinus</i> spp.	$\sim$ Logging*Slope+(1 plot)	0.34	0.92	363.98	0.003**
	$\sim$ <i>Ocoteo</i> *Slope+(1 plot)	0.37	0.91	369.01	0.026*
	$\sim$ Firewood*Slope+(1 plot)	0.50	0.91	344.23	0.000***
	$\sim$ %FC*Slope+(1 plot)	0.49	0.92	335.14	0.000***

⁰D: observed species richness. ¹D: typical or common species diversity. ²D: dominant species diversity. %FC: percent forest cover. r²m: determination coefficient of the model without the effect of the random variable. r²c: determination coefficient of model including the effect of the random variable. AICc: corrected Akaike Information Criterion (Hurvich & Tsai, 1989). p: p-value relative to the null model (dependent variable $\sim 1+(1|\text{stand or plot})$); *: p<0.05; **: p<0.01; ***: p<0.001; ^{ns}, not significant.

Table 3. Generalized linear models that evaluated the influence of the abundance of pine species (*Pinus* spp.) (a), and of the dominant pine species (*Pinus montezumae*) (b), on the abundance of non-pine trees, in La Malinche National Park. The statistically significant models are highlighted in bold.

Model	r ²	p
(a) Other trees ~ <i>Pinus</i> spp.		
<i>Alnus jorullensis</i> ~ <i>Pinus</i> spp.	0.09	0.00***
<i>Abies religiosa</i> ~ <i>Pinus</i> spp.	0.02	0.00***
<i>Arbutus xalapensis</i> ~ <i>Pinus</i> spp.	0.02	0.00***
<i>Buddleja cordata</i> ~ <i>Pinus</i> spp.	0.27	0.00***
<i>Comarostaphylis discolor</i> ~ <i>Pinus</i> spp.	0.00	0.77 ^{ns}
<i>Cupressus benthamii</i> ~ <i>Pinus</i> spp.	0.02	0.46 ^{ns}
<i>Pinus pseudostrobus</i> ~ <i>Pinus</i> spp.	0.05	0.08 ^{ns}
<i>Quercus laurina</i> ~ <i>Pinus</i> spp.	0.01	0.19 ^{ns}
<i>Quercus crassipes</i> ~ <i>Pinus</i> spp.	0.02	0.24 ^{ns}
<i>Quercus dysophylla</i> ~ <i>Pinus</i> spp.	0.04	0.50 ^{ns}
(b) Other trees ~ <i>Pinus montezumae</i>		
<i>Alnus jorullensis</i> ~ <i>Pinus montezumae</i>	0.10	0.00***
<i>Abies religiosa</i> ~ <i>Pinus montezumae</i>	0.05	0.00***
<i>Arbutus xalapensis</i> ~ <i>Pinus montezumae</i>	0.02	0.00***
<i>Buddleja cordata</i> ~ <i>Pinus montezumae</i>	0.29	0.00***
<i>Comarostaphylis discolor</i> ~ <i>Pinus montezumae</i>	0.00	0.98 ^{ns}
<i>Cupressus benthamii</i> ~ <i>Pinus montezumae</i>	0.02	0.41 ^{ns}
<i>Pinus pseudostrobus</i> ~ <i>Pinus montezumae</i>	0.03	0.14 ^{ns}
<i>Quercus laurina</i> ~ <i>Pinus montezumae</i>	0.02	0.16 ^{ns}
<i>Quercus crassipes</i> ~ <i>Pinus montezumae</i>	0.00	0.58 ^{ns}
<i>Quercus dysophylla</i> ~ <i>Pinus montezumae</i>	0.06	0.42 ^{ns}
<i>Pinus teocote</i> ~ <i>Pinus montezumae</i>	0.04	0.00***
<i>Pinus ayacahuite</i> ~ <i>Pinus montezumae</i>	0.00	0.93 ^{ns}
<i>Pinus hartwegii</i> ~ <i>Pinus montezumae</i>	0.57	0.00***
<i>Pinus leiophylla</i> ~ <i>Pinus montezumae</i>	0.00	0.78 ^{ns}
<i>Pinus pseudostrobus</i> ~ <i>Pinus montezumae</i>	0.00	0.73 ^{ns}

r²: determination coefficient of the model; p: p-value obtained using a likelihood-ratio test, *: p<0.05; **: p<0.01; ***: p<0.001; ^{ns}, not significant.

tezumae, *Pinus pseudostrobus*, *Pinus teocote*, *Prunus serotina*, *Quercus laurina*, *Quercus crassipes*, and *Quercus dysophylla*; of these, *P. montezumae* was the dominant species (Abundance = 2219 individuals in total), and *Q. dysophylla* and *P. ayacahuite* were the least abundant (1 individual of each species) (Table S2 [suppl]).

Tree species richness ranged from ⁰D = 2 in North-2 to ⁰D = 11 in East-2 and North-1. Common species ranged from ¹D = 1.1 in North-2 to ¹D = 4.0 in East-2. The dominant species were more diverse in East-2 (²D = 3.2) and less diverse in North-2 (²D = 1.0) (Table 1). Unlike the diversity of common and dominant species, species richness did not

reach the asymptote in all forest stands. The closest curves corresponded to East-1, East-2, North-1, and West-2 (Fig. 2), but the %SC was never below 98 % (Table 1).

Regarding dissimilarity for the order $q = 0$, Jaccard's similarity index (S_j) showed a higher dissimilarity between East-2 and North-3 ($S_j = 0.923$), while East-1 and East-3 were less differentiated ($S_j = 0.200$) (Table S3a [suppl]). When the common ($q = 1$) and dominant species ($q = 2$) were weighted, the similarity index showed high similarity between North-2 and North-3 ($S_H = 0.001$, $S_{MH} = 0$) and greater dissimilarity between East-1 and Southeast-1 ($S_H = 0.741$, $S_{MH} = 0.740$) (Table S3b,c [suppl]).

Effect of deforestation and forest use on species diversity

Of the 12 models constructed to assess the influence of deforestation and forest use on total tree diversity, none was statistically significant (Table 2a). In contrast, pine dominance (*Pinus* spp.) was affected by the interaction of slope with forest use and with percentage of forest cover; the latter was chosen as the optimal model according to AICc (*Pinus* spp. $\sim$ FC*Slope+(1|stand); Table 2b), however the PERMANOVA did not show significant differences between groups (stands), with a marginal contribution of forest cover ($r^2 = 0.01$; Table S4 [suppl]). Nonetheless, the data showed a trend of higher pine dominance in forest stands with lower forest cover (Fig. 3).

Finally, *P. montezumae* alone and all pine species combined (*Pinus* spp.) affected the abundance of *B. cordata* (Table 3b; Fig. 4a); furthermore, when we assessed only the influence of *P. montezumae* on the abundance of the rest of the species, we also detected an effect on *P. hartwegii* (Table 3b; Figure 4b). In the remaining four species (*A. jorullensis*, *A. religiosa*, *A. xalapensis*, *P. teocote*), we detected a significant relationship and optimal models according to AICc, but the explanation of the data by the model was very low ($r^2 = 0.2\text{--}0.10$) (Table 3a,b); therefore, we deemed these relationships inconclusive.

Discussion

Forest use did not influence tree diversity, but did influence pine dominance, and forest stands with higher deforestation showed a higher pine dominance; therefore, our predictions were partially consistent with these findings. The strong effect of slope on pine dominance in La Malinche National Park is remarkable and agrees with previous studies in other mountain systems that have also reported the high contribution of slope on species composition (e.g., Yang et al., 2020).

We also observed the effect of slope in the levels of dissimilarity. We observed the greater affinity in species richness between the forest stands East-1 and East-3, while we found a greater dissimilarity between East-2 and West-3. The greater species turnover between these forest stands is possibly a result of historical local disturbance processes that have modified and reduced ecological niches for various species (Monárrez-González et al., 2018), which has probably affected the distribution of species between stands. The same pattern was detected in 1D and 2D , that is, the lowest dissimilarity between North-2 and North-3, and a strong differentiation between East-1 and Southeast-1, apparently due to the loss of common and dominant species (e.g., *P. teocote*, *Q. laurina*).

The dissimilarity between pairs of communities describes how communities respond to different factors, such as anthropogenic influences (e.g., deforestation; Hubbell, 1997), climate change, and environmental gradients (Myers et al., 2013), conditions that are highly variable between the slopes

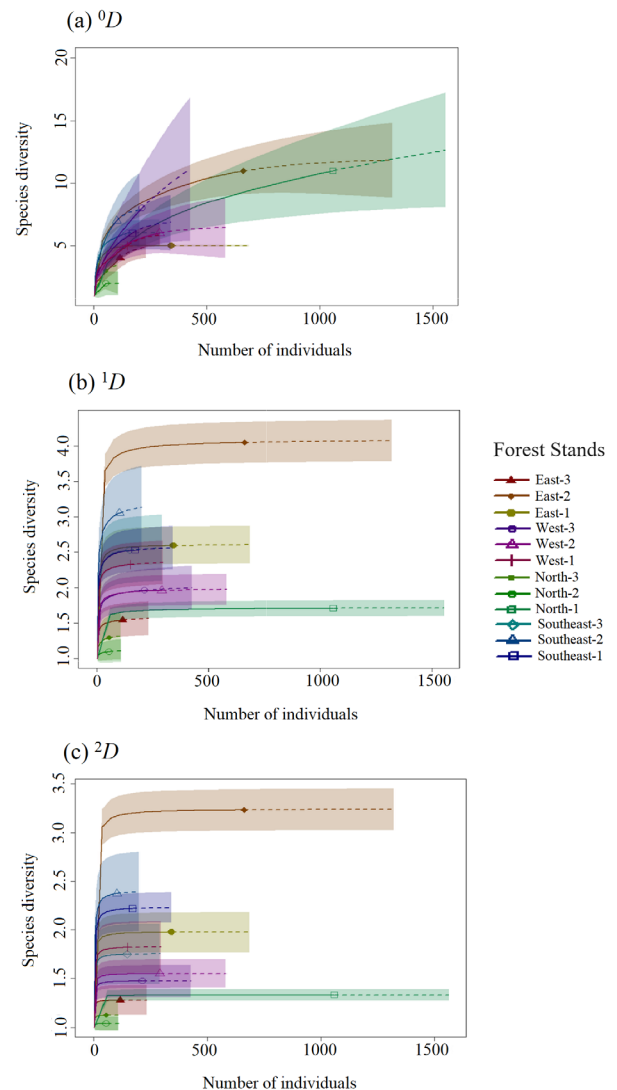


Figure 2. Interpolation curves (rarefaction) and extrapolation of Hill numbers of 12 tree forest stands on the four slopes of La Malinche National Park. (a) Species richness (0D); (b) diversity of common or typical species (1D); (c) diversity of the dominant species (2D).

of La Malinche National Park. Despite this, our results did not find a significant effect of deforestation and forest use on tree diversity, possibly due to the need to increase the sample size (i.e., the number of sampling plots) to improve statistical power or include other potential drivers of diversity change (e.g., selective logging, distance to human settlements, main economic activity) that could help better explain the distribution of diversity. This is the case of selective logging, which drastically reduces population density until entire populations are lost (Galindo-Jaimes et al., 2002). Therefore, further studies should consider other variables potentially affecting tree diversity.

Although deforestation and forest-use variables did not affect tree diversity, they are important indicators of forest deterioration. For example, logging can lead to the

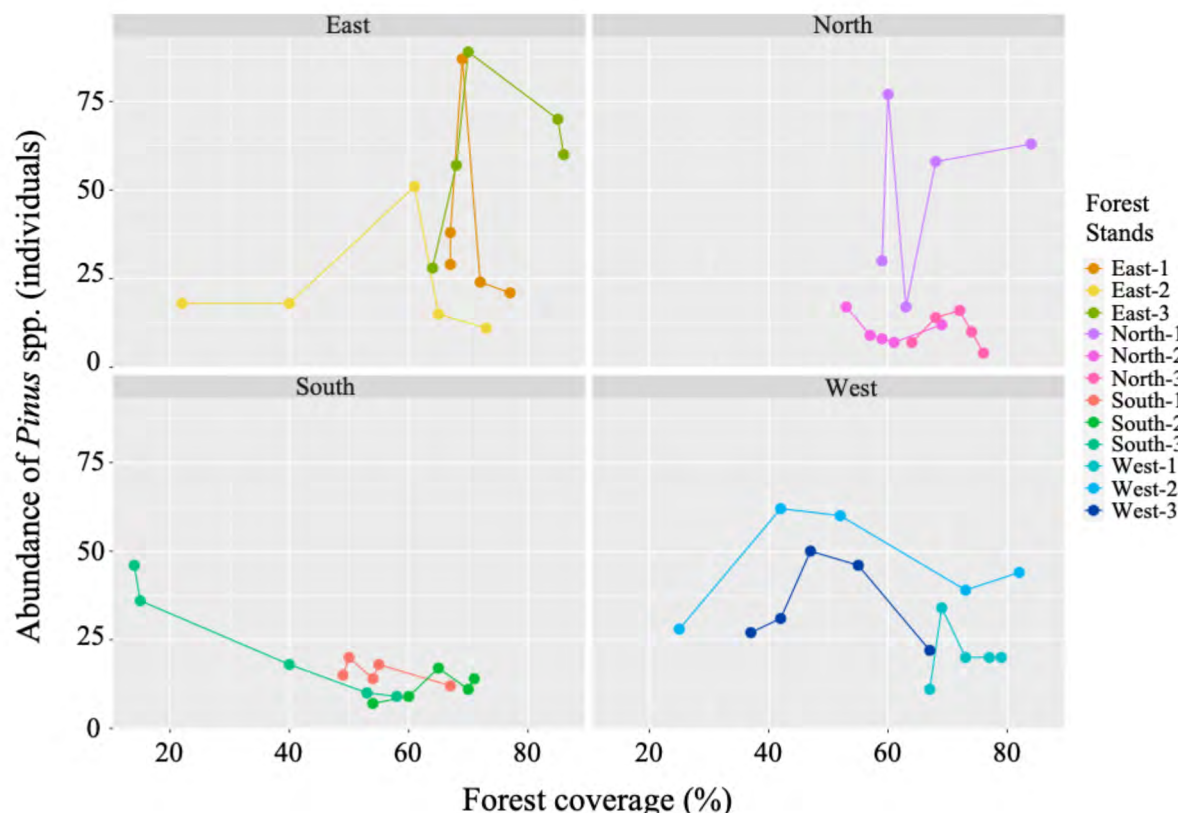


Figure 3. Relationships of abundance of *Pinus* spp. with deforestation (percent forest cover, %FC) of La Malinche National Park (LMNP) obtained with linear mixed-effect models, using the plot as random variable.

homogenization of communities (McKinney & Lockwood, 1999) by ecological drift, as it induces the loss of under-represented species and drastically decreases richness by random fluctuations (Gilbert & Levine, 2017). Unlike logging or firewood extraction, *ocoteo* has no apparent effect on the structure of pine populations since it does not eliminate trees; nevertheless, it can significantly affect populations by weakening the vigor of trees in the long term until they die or are felled by the wind (Díaz-Carranza et al., 2022). In La Malinche National Park, *P. montezumae* is the pine species most intensively exploited by *ocoteo* (Díaz-Carranza et al., 2022), and, according to Acuña (1984) and González (2006), oak trees in La Malinche National Park have been used for carbon, firewood, and wood for construction since the conquest. Therefore, the evaluation of the effect of these types of forest use on tree diversity was a necessary aspect to study for the conservation of the remaining forests, and its effect on the abundance of pine species is relevant to report.

It has already been shown that areas cleared by deforestation favor the establishment and dominance of pioneer species, such as pine, while shade-tolerant species are lost (McKinney & Lockwood, 1999; Pessoa et al., 2017; Monárrez-González et al., 2018). Our results showed a pattern of higher dominance of *Pinus* species associated with lower percent forest cover, which coincides with the findings reported by other authors who have documented

the prevalence of these species in deforested areas (Galindo-Jaimes et al., 2002; Figueroa-Rangel et al., 2008).

Specifically, *P. montezumae* was the dominant species in most forest stands. Ern (1976) proposed that *P. montezumae*, like other pine species, has historically benefited from fires and forest burning in La Malinche National Park, favoring its high dominance between 2800 m and 3200 m asl. Nevertheless, the dominance of this pine species is relatively recent; Ern (1976) indicated that in the past, the climax forest communities between 2300 m and 2700 m asl were *A. religiosa*, *Cupressus lindleyi*, and *P. pseudostrobus*. Even *A. religiosa* was present from 2400 m asl with large populations outside ravines of the wettest slopes — the only sites where it currently occurs (S. George-Miranda, pers. obs.; Rzedowski, 2006). In addition, Acuña (1984) reported the abundant presence of firs and cypresses in 1577, indicating a major shift in the floristic composition in La Malinche National Park that favored the dominance of *Pinus* species. Moreover, the scarcity we found of *B. cordata*, *Quercus crassipes*, *Q. laurina*, and *P. serotina* may be explained because the study area is above the optimal altitudinal limit reported for these species (<2700 m asl; Ern, 1976). Another aspect that may account for the dominance of *P. montezumae* is the expansion of dry environments, which has intensified due to the historical increase of fires, deforestation, and climate change (Figueroa-Rangel et al., 2008; Richardson & Bond, 1991).

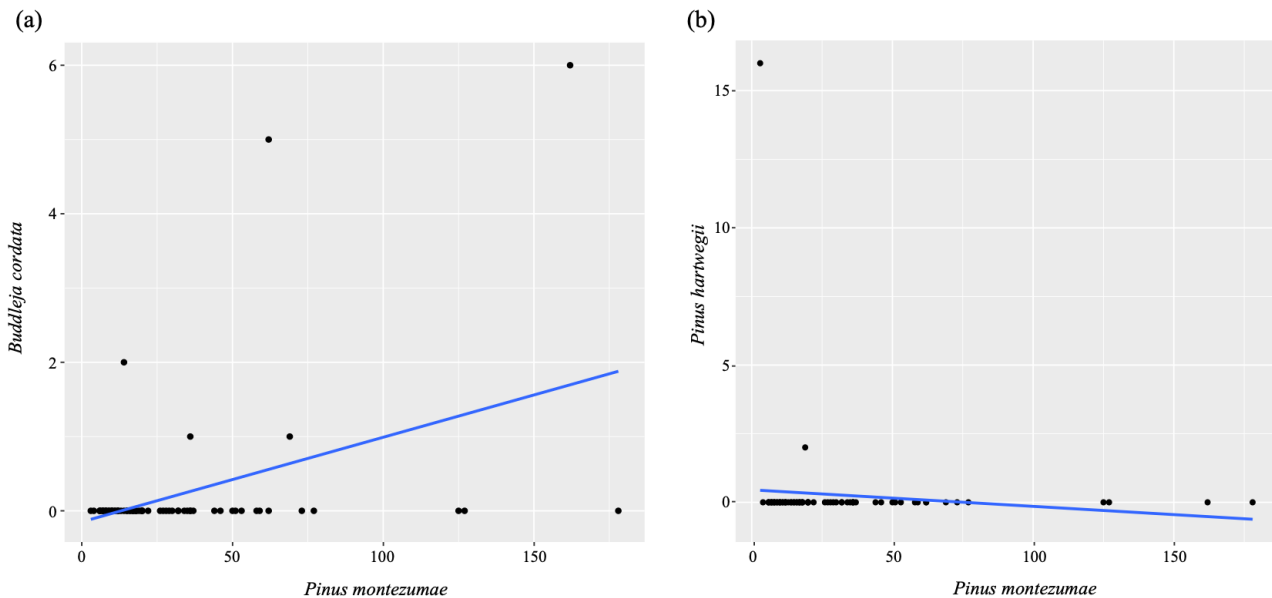


Figure 4. Relationships between the abundance of *Pinus montezumae* and the abundance of *Buddleja cordata* (a) and *Pinus hartwegii* (b) in La Malinche National Park (LMNP) obtained with generalized linear models.

Our study detected a positive association between *P. montezumae* and *B. cordata*, possibly due to their high tolerance to degraded soils (Mendoza-Hernández et al., 2010). In contrast, the abundance of *P. hartwegii* decreased when the dominance of *P. montezumae* increased, this is potentially explained because fire exerts a strong adverse impact on *P. hartwegii* while it seems to favor *P. montezumae* (Endara et al., 2012). Nevertheless, it is worth mentioning that the altitudinal distribution of *P. hartwegii* (3000–4300 m asl; Manzanilla-Quñones et al., 2019) barely covered a small part of the study area (2800–3200 m asl). Likewise, the altitudinal displacement of *P. montezumae* resulting from climate change probably causes the observed relationship – a hypothesis that should be tested in a future study. The case of species that showed a low explanation of their models (*A. jorullensis*, *A. religiosa*, *A. xalapensis*, and *P. teocote*) deserves to be studied in further detail with a greater sampling effort and considering additional factors that may influence diversity (e.g., environmental characteristics, nutrients) since the negative relationships of *P. montezumae* with *A. religiosa* and *P. teocote* suggest an incipient displacement that should be identified to preserve forest diversity in La Malinche National Park.

The low abundance of other species in the National Park, such as *Q. dysophylla*, highlights the importance of La Malinche National Park as a diversity reservoir of tree species and the need to establish immediate strategies to increase the abundance of underrepresented species. A suggestion to address this aspect is to plan reforestation with these species, including monitoring over at least two years to improve success, promote increased tree cover, and preserve tree diversity. An issue with this approach is that the species produced in Mexican nurseries are those

characterized by rapid and easy growth, and these species are not always suitable for reforestation. Therefore, additional studies are required to improve the propagation of tree species found in low abundance for use in reforestation projects. The case of *P. ayacahuite* is especially interesting because, according to Ern (1976), this species was not part of the local forest vegetation in La Malinche National Park; therefore, the few recorded individuals might have resulted from reforestation efforts in the area.

Although the altitudinal belt where the sampling was carried out has always been covered by conifer forests, the results of our study indicate a trend of shift toward the dominance of *Pinus* spp. and a major effect of slope on species composition. Even though the forest use indicators do not consider the history of continuous use of forest resources in La Malinche National Park (Table S1 [suppl]), these quantified the intensity of use at the time of the study; therefore, they provide valuable information to achieve our objectives. Nevertheless, given the lack of this important information, we do not rule out the need to measure the variation of forest use over time in future research.

Although we found that not only forest use modifies tree diversity, the adverse effects of forest use and deforestation on species composition warn of the need to implement immediate measures to protect it in La Malinche National Park. We propose the following actions: (1) control human activities that promote deforestation in La Malinche National Park (e.g., logging, *ocoteo*, firewood extraction, and changes in land use) and (2) promote reforestation using native and poorly represented species (e.g., *Q. dysophylla*), along with long-term monitoring (>2 years), to increase forest cover and maintain species diversity. Otherwise, the advance of the agricultural frontier and illegal deforestation

(e.g., logging) will cause the loss of species diversity, the conversion to monospecific forests, and the deterioration of ecosystem services in the region (e.g., Cayuela et al., 2006). The present study contributes relevant knowledge on the effect of deforestation in an extremely threatened ecosystem of great importance in Mexico, which could be useful to define forest management actions for La Malinche National Park and other Mexican conifer forests.

Supplementary material (Tables S1-S4) accompanies the paper on *Forest System's* website

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