The Centre–Periphery Model, a Possible Explanation for the Distribution of Some *Pinus* spp. in the Sierra Madre Occidental, Mexico

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Abstract: Genetic diversity is key to survival of species. In evolutionary ecology, the general centre–periphery theory suggests that populations of species located at the margins of their distribution areas display less genetic diversity and greater genetic differentiation than populations from central areas. The aim of this study was to evaluate the genetic diversity and differentiation in six of the main pine species of the Sierra Madre Occidental (northern Mexico). The species considered were *Pinus arizonica*, *P. cembroides*, *P. durangensis*, *Pinus engelmannii*, *P. herrerae* and *P. leiophylla*, which occur at the margins and centre of the geographic distribution. We sampled needles from 2799 individuals belonging to 80 populations of the six species. We analysed amplified fragment length polymorphisms (AFLPs) to estimate diversity and rarity indexes, applied Principal Coordinate Analysis (PCoA), and used the Kruskal–Wallis test to detect genetic differences. Finally, we calculated Spearman's correlation for association between variables. The general centre–periphery model only explained the traits in *P. herrerae*. The elevation gradient was an important factor that influenced genetic diversity. However, for elevation as partitioning criterion, most populations showed a central distribution. This information may be useful for establishing seed collections of priority individuals for maintenance in germplasm banks and their subsequent sustainable use.

Keywords: AFLPs; elevation; gene flow; geographic location; genetic diversity

1. Introduction

Ecological research focuses on how environmental conditions and population processes regulate the abundance and distribution of species [1], which reach their highest abundance at the centre of their range and decrease towards the edges [2]. In addition, peripheral populations often become more patchy, isolated and transient [3,4]. Although abiotic and biotic aspects are not always consistent with geographical components (latitude, longitude and altitude) [5], the location is considered a key factor in species conservation because it greatly influences the capacity of any living system to persist in response to environmental changes [6].

Moreover, the centre–periphery theory suggests that peripheral or marginal populations will diverge over time from central or core populations as a result of two important processes: genetic drift and natural selection [7], because they are more fragmented and

less likely to receive immigrants from other populations than central populations [7,8]. Thus, marginal areas are ecologically less favourable for species development [1,9–12], and the probability of extinction is therefore relatively high in these areas [13].

However, in some specific cases, the geographical and ecological areas are not congruent [5,7,9,10]. This incongruent pattern may be explained by one of the three main hypotheses concerning trends in genetic diversity across the central–peripheral clines, each of which has different spatial implications [14]. The first hypothesis, developed by Carson [15], argues that genetic diversity will increase from the periphery of the distribution range towards the centre. Carson suggested that the more continuous, denser and central populations undergo balancing selection and are therefore expected to display higher levels of within-population genetic diversity [15,16].

The second hypothesis, proposed by Fisher [17], predicts that genetic diversity will decrease from the periphery towards the core of the range of distribution of a species. Accordingly, peripheral populations will sustain higher levels of genetic diversity due to fluctuating selection in spatially heterogeneous and unpredictable environments, while central populations will experience stabilising selection, which maintains genetic diversity [17–20].

The third hypothesis, proposed by Mayr [16], considers homogeneous diversity from the periphery to the core and suggests that gene flow from the core may compensate for the effects of local selection and genetic drift at the periphery. In such cases, genetic diversity may be homogeneous throughout the species range [16,21,22].

Numerous studies have tried to test this theory in animals and plants, comparing the genetic diversity in central and peripheral populations of species by using morphological markers, allozymes, RAPD (Random Amplified Polymorphic DNA), ISSR (Inter-simple Sequence Repeats), AFLPs (Amplified Fragment Length Polymorphisms) and microsatellites [9,14,22–27].

Contrasting results have been obtained. Some authors have concluded that genetic diversity is similar, and differentiation is greater in peripheral than in central populations [28,29]. However, in some cases, no evidence was found in peripheral populations for the greater genetic differentiation, lower genetic diversity and asymmetric genetic flow predicted by the central–peripheral hypothesis [30–33]. Therefore, results of empirical research remain ambiguous and limited [8,32,34,35].

One motivation for the conservation of species is to understand the patterns and the processes associated with the geographical variation in the genetic structure of the population, through the distribution ranges of the species of interest [8,36–40]. It is also stated that when a species is in danger of extinction, its geographic range will contract inwards, with central populations persisting until the final stages of decline [41].

Consequently, the species adaptation will not decrease gradually from the centre towards the periphery but will decrease dramatically once an environmental tipping point is exceeded, as with abrupt changes in climate, land use and/or biotic interactions [5,42]. Accordingly, some authors suggest that peripheral populations are also gaining importance for the conservation of genes, as under climate change conditions, they may possess genotypes of future adaptive potential on which natural selection can act [9,37,43].

Summarising, populations at the edge of a species distribution range may differ substantially from central populations, in the context of current climate and geography. Therefore, the aim of the present study was to examine whether the centre–periphery theory helps to explain the genetic diversity and differentiation in six of the main pine species in the pine-oak region of the Sierra Madre Occidental (northern Mexico). In this region, the species considered were *Pinus arizonica, P. cembroides, P. durangensis, Pinus engelmannii, P. herrerae* and *P. leiophylla*, which are located at the margins and centre of the geographic distribution. Many communities depend on the services and products provided by the forests with these endemic pine species.

2. Materials and Methods

2.1. Species and Study Area

Eighty populations (seed stands) of six pine species were randomly selected in the Sierra Madre Occidental (SMO), in the states of Durango and Chihuahua. The SMO is the longest and most continuous mountain system in Mexico (Figure 1). The sampling points (locations) were randomly selected from the potential distribution maps of the six pine species studied [44].
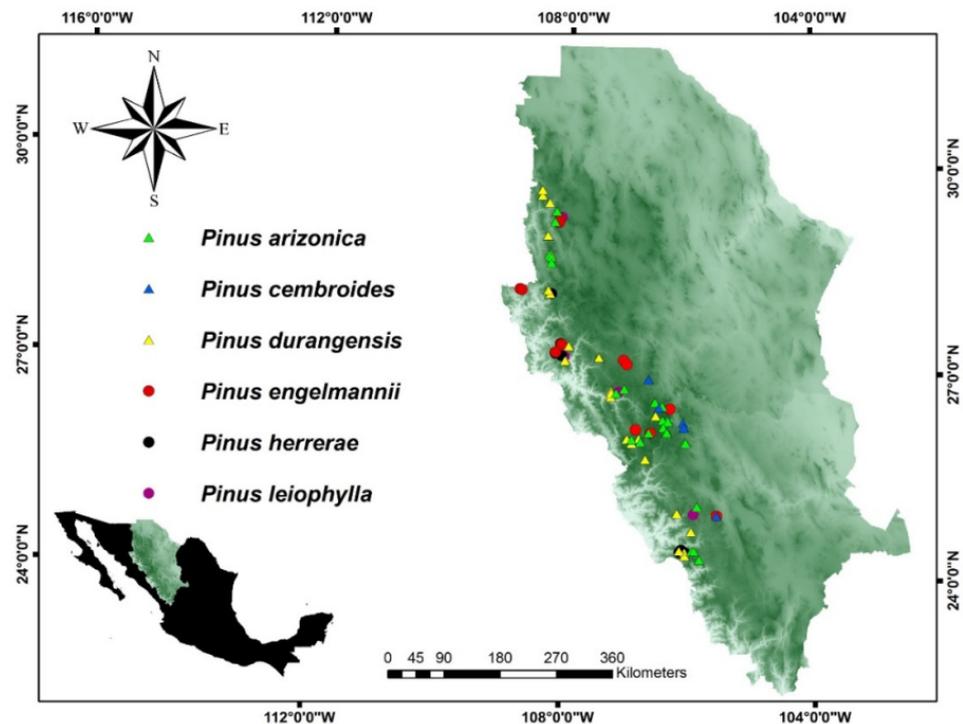
Figure 1. Location of the 80 populations of *Pinus arizonica, P. cembroides, P. durangensis, P. engelmannii, P. herrerae* and *P. leiophylla* in the Sierra Madre Occidental in Durango and Chihuahua, Mexico.

Needles were sampled from 877 *Pinus arizonica* (PA) trees, 174 *P. cembroides* (PC) trees, 908 *P. durangensis* (PD) trees, 420 *P. engelmannii* (PE) trees, 280 *P. herrerae* (PH) trees and 140 *P. leiophylla* (PL) trees. The sampled populations were grouped into two categories: central and peripheral (Table 1). For analysis of genetic diversity, 35 needle samples were randomly selected from each study population; for selection criteria see Wehenkel et al. [45].

2.2. Species Distribution and Identification of Central and Peripheral Populations

Species distribution models (SDM) were used to identify the habitat where each pine species under study was located [44]. Rather than detecting isolated populations from main continual populations, the first partitioning criterion applied was the distance from the margin of the range, to avoid any possible bias. First, the distance (in km) between the sampled stands and the closest edge where the distribution of each species ends (range margin) was measured. The central populations, defined as those geographically farthest from all the distribution edges, and peripheral populations, defined as those closest to the edges, were then identified (Figures S1–S6). The partitioning point for separating central and peripheral groups was established in the range of populations of species separated by the greatest distance (wide gaps, in km), as a function of the population distribution, which varied between species. The partitioning point was therefore different for each species under study.

Table 1. Comparison of the differences between central and peripheral populations according to the nonparametric Kruskal–Wallis test using criterion 1.

	Location	v_2	*% Poly*	DW	GD	PopGD	Elevation (m)
				Pinus arizonica			
M_e	Central	1.314	0.682	0.093	65.674	70.177	2801
	Peripheral	1.319	0.715	0.102	67.254	71.332	2640
	p-value	0.5333	0.411	0.365	0.496	0.396	0.005 *
				P. cembroides			
M_e	Central	1.376	0.849	0.392	82.204	92.299	2434
	Peripheral	1.373	0.802	0.318	80.735	90.576	2588
	p-value	0.564	0.083	0.248	0.564	0.248	0.564
				P. durangensis			
M_e	Central	1.332	0.7245	0.108	70.632	75.504	2561
	Peripheral	1.324	0.725	0.116	69.010	74.517	2439
	p-value	0.853	0.853	0.673	0.257	0.673	0.2154
				P. engelmannii			
M_e	Central	1.314	0.715	0.123	66.874	70.351	2344
	Peripheral	1.299	0.684	0.098	64.091	67.527	2176
	p-value	0.781	0.781	0.517	0.781	0.644	0.309
				P. herreae			
M_e	Central	1.329	0.742	0.21	69.600	72.639	2399
	Peripheral	1.285	0.621	0.14	59.839	68.661	1858
	p-value	0.025 *	0.051	0.101	0.025 *	0.1797	0.025 *
				P. leiophylla			
M_e	Central	1.3215	0.764	0.255	68.555	73.2575	2356
	Peripheral	1.3420	0.778	0.239	72.578	75.5045	2268
	p-value	0.4386	1	0.4386	0.4386	0.4386	0.4386

Note: PopGD = average genetic distance within populations; GD = average genetic distance between populations; elevation in metres above sea level; v_2 = genetic diversity measured through the effective number of variants; *% Poly* = percentage of polymorphic fragments; DW = frequency of down-weighted marker; M_e = median; * = significant difference ($p < 0.05$).

The second partitioning criterion was the elevation. The data were stratified in quartiles. The first and the last quartile corresponded to peripheral populations, while those within the 2nd and 3rd quartiles were grouped as central populations.

2.3. Genetic Analysis

DNA was extracted using the QIAGEN DNeasy 96 plant kit (Qiagen, Venlo, The Netherlands) and digested with the restriction enzymes EcoRI and MseI. Double-stranded EcoRI and MseI adaptors were amplified by Polymerase Chain Reaction (PCR) and ligated to the end of the restriction fragments, to produce template DNA. In pre-AFLP amplification, the PCR products were treated with the primer combination E01/M03 (EcoRI-A/MseI-G).

Extracted DNA was analysed by the Amplified Fragment Length Polymorphisms (AFLPs) technique, according to the protocol described by Vos et al. [46] and modified by Ávila-Flores et al. [47], in order to yield genetic data.

Selective amplification was carried out with the fluorescent-labelled (FAM) primer pair E35 (EcoRI-ACA-3) and M63 + C (MseI-GAAC). All PCR reactions were carried out in a Peltier thermocycler (PTC-200 version 4.0, MJ Research). The amplified restriction products were electrophoretically separated in a genetic analyser (ABI 3100 16 capillaries), along with the internal standard size GeneScan 500 ROX (ROX fluorescent dye) from Applied Biosystems (Foster City, CA, USA).

The size of the AFLP fragments was resolved with the GeneScan 3.7 and Genotyper 3.7 software packages (Applied Biosystems). Quality and reproducibility were checked by including reference samples in each plate and by independent analysis (replicate PCRs) of at least 16 samples (i.e., a minimum of 16 individuals per randomly chosen tree species). All replicates showed the same AFLP patterns as in the first analysis [47,48].

Finally, six binary AFLP matrices (one per species) were produced from the presence (code 1) or absence (code 0) at potential band positions. Detection of a band indicates a dominant genetic variant (the "plus phenotype") [49,50]. Conversely, absence of a band

reflects the recessive genetic (allelic) variants at the given position (locus) (the "minus phenotype").

2.4. Diversity and Genetic Differentiation

GenALex® 6.501 software [51] was used to estimate the mean pairwise genetic distance between populations (GD) and average genetic distance relative to the rest of the population—within populations (PopGD)—by generating several matrices with the genetic distances between pairs of populations. Thus, paired combinations of all populations were run for all species. In addition, the AFLP matrix was used to conduct Principal Coordinate Analysis (PCoA). The analysis was conducted, along with graphical representation of individual species and populations of species, to detect any dissimilarities or homogeneity in the sampled groups. Genetic diversity indices were calculated with Microsoft Excel® software (2013) according to the protocol described by Gregorius [52] and modified by Wehenkel et al. [53]. Hill's number (v_a) was considered, with the subscript a = 2, referred to as the "effective number" of variants or the average genetic diversity and its characteristic of Simpson's diversity [54].

The percentage of polymorphic fragments (% *Poly*) was also calculated and used to measure interpopulation diversity. The frequency-down-weighted marker (DW) values were calculated as a measure of differentiation [55,56]. Higher DW values indicate greater differentiation and vice versa.

We also conducted an analysis of molecular variance (AMOVA) based on genetic distances across all 376 loci with 10,000 permutations, to identify whether most of the genetic variation was partitioned within or among populations [57]. For purposes of comparison, pairwise FST values (proportion of genetic variance in a subpopulation) were evaluated in AFLP-SURV 1.0 [58].

The AFLP-SURV software estimates genetic diversity and population genetic structure from population samples analysed with the AFLP method and computes genetic distance matrices between populations. Hierarchical cluster analysis (HCA) was also conducted for both criteria. The grouping method chosen was the Ward's linkage algorithm with Manhattan (Cityblock) distances.

Finally, a nonparametric Kruskal–Wallis test was performed in R software [59], to determine the presence of any significant differences in the genetic variables in central or peripheral population.

2.5. Geographic Central and Peripheral Populations

Nonparametric Spearman correlation coefficients were also calculated in R software [59]. The following data were used: the closest edge distance (km), the elevation (m), and the results obtained for the average genetic distance within the populations (PopGD), average genetic distance between populations (GD), genetic diversity measured through the effective number of variants (v_2), percentage of polymorphic fragments (% *Poly*) and the scores of the frequency-down-weighted marker (DW).

3. Results

3.1. Diversity and Genetic Differentiation (Criterion 1)

Amplification of AFLP molecular marker fragments of the 2799 individual trees of the six *Pinus* species yielded 376 loci with 75 to 450 base pairs (bp). Location, genetic diversity and differentiation indexes calculated for each population are shown in Table S1 and the elevation partitioning criterion (second criterion) and the indices of genetic diversity and differentiation are shown in Table S2. See relevant results in Section 3.3 and thereafter.

For criterion 1, the genetic diversity, measured according to Gregorius [52] and Wehenkel et al. [53], was generally similar in all the populations analysed; the lowest v_2 value of 1.250 corresponded to a central population of *Pinus arizonica*, while the highest v_2 value of 1.414 corresponded to a peripheral population of *P. durangensis*. The % *Poly* varied from 57.8% in a central population of *P. arizonica* to 87.3% in a central population of *P. durangensis*.

The rarity index (DW) [56] reached values ranging from 0.051 in a peripheral population of *P. durangensis* to 0.426 in a peripheral *P. cembroides* population. The Pop GD varied from 66.677 to 93.638 in central populations of *P. herrerae* and *P. cembroides*, respectively. The lowest and highest GD values of 52.027 and 89.388 corresponded to central populations of *P. arizonica* and *P. durangensis*, respectively.

The geographic distance varied from 0.06 to 31.45 km in peripheral populations of *P. arizonica* and *P. durangensis*, respectively. The lowest recorded elevation, 1820 m, corresponded to a peripheral population of *P. engelmannii*, and the highest (3062 m), to a central population of *P. arizonica*.

Regarding the PCoAs, the populations of species were closer to one another, and more similar than those detected further away, at the boundaries of the map (Figure 2). No definite pattern of grouping central or peripheral populations was observed in *P. arizonica*. However, a tendency for groups of peripheral populations separated from the central populations of *P. cembroides* was observed.
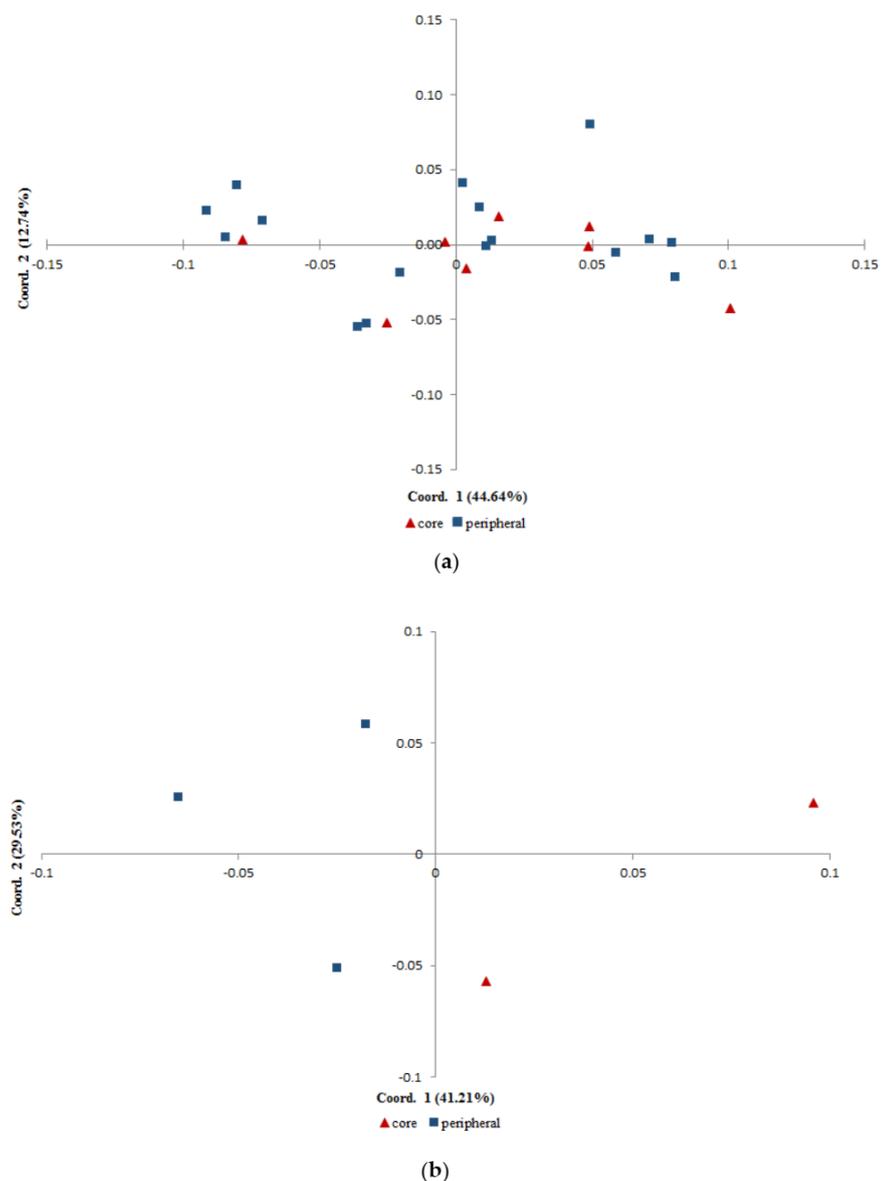
Figure 2. Results of Principal Coordinate Analysis (*PCoA*) of the individual trees of *Pinus arizonica* (**a**) and *P. cembroides* (**b**).

The Kruskal–Wallis test did not reveal any significant difference in diversity and differentiation variables in the six species analysed, as the *p* values were generally greater than 0.05. This result indicates that geographic location was not a determining factor in diversity and differentiation measures, except in *P. herrerae*, for which significant differences ($p < 0.05$) were found in v_2, GD and elevation. In this regard, we observed that the number of effective genetic variants, the average genetic distances and the elevation were important factors influencing the geographical location and helped to discriminate the central from the peripheral populations (Table 1).

The results of the analysis of molecular variance (AMOVA) for the AFLP fragments evaluated in the six species showed higher levels of variation within than between populations (FST ranged from 0.019 for *P. cembroides* to 0.067 for *P. herrerae*, with values of 0.05 for *P. arizonica*, 0.054 for *P. durangensis*, 0.047 for *P. engelmannii* and 0.041 for *P. leiophylla*). All FST values were significant ($p \leq 0.001$).

3.2. Geographic Central and Peripheral Populations (Criterion 1)

Several significant correlations between different diversity indexes were detected in the six *Pinus* spp. studied (Tables 2–7). However, in *Pinus arizonica*, *P. cembroides*, *P. durangensis* and *P. engelmannii*, there were no significant correlations between genetic variants, elevation and geographical distance (Tables 2–5).

Table 2. Correlations between genetic and geographical variants of *Pinus arizonica* and the different peripheral and central populations of this species.

Variable	v_2	*% Poly*	DW	GD	PopGD	Elevation	DGEO
v_2	1	**0.878**	**0.849**	**0.996**	**0.945**	0.0162	0.046
% Poly	**0.878**	1	**0.936**	**0.911**	**0.840**	0.027	0.046
DW	**0.848**	**0.936**	1	**0.880**	**0.862**	0.085	−0.007
GD	**0.996**	**0.911**	**0.879**	1	**0.948**	0.041	0.065
PopGD	**0.949**	**0.840**	**0.862**	**0.947**	1	0.055	0.025
Elevation	0.016	0.027	0.085	0.041	0.056	1	0.655
DGEO	0.046	0.046	−0.007	0.065	0.025	0.655	1

Statistically significant correlations ($p < 0.005$) are highlighted in bold. Note: PopGD = average genetic distance within populations; GD = average genetic distance between populations; DGEO = distance to the nearest edge (km); elevation in metres above sea level (m); diversity and divergence indexes: v_2 = genetic diversity measured through the effective number of variants; *% Poly* = percentage of polymorphic fragments; DW = frequency down-weighted marker.

Table 3. Significant and non-significant correlations between genetic and geographic variants of *Pinus cembroides* and the different peripheral and central populations of this species.

Variable	v_2	*% Poly*	DW	GD	PopGD	Elevation	DGEO
v_2	1	0.574	0.443	**0.978**	−0.112	−0.274	0.632
% Poly	0.574	1	**0.891**	0.665	−0.589	0.069	0.747
DW	0.443	**0.891**	1	0.458	−0.877	0.368	0.449
GD	**0.978**	0.665	0.458	1	−0.070	−0.325	0.757
PopGD	−0.112	−0.589	−0.877	−0.070	1	−0.724	−0.125
Elevation	−0.274	0.069	0.368	−0.325	−0.724	1	−0.018
DGEO	0.633	0.747	0.450	0.757	−0.125	−0.018	1

Statistically significant correlations ($p < 0.005$) are highlighted in bold. Note: PopGD = average genetic distance within populations; GD = average genetic distance between populations; DGEO = distance to the nearest edge (km); elevation = metres above sea level (m); diversity and divergence indexes: v_2 = genetic diversity measured through the effective number of variants, *% Poly* = percentage of polymorphic fragments, DW = frequency down-weighted marker.

Table 4. Correlations between genetic and geographical variants of *Pinus durangensis* and the different peripheral and central populations of this species.

Variable	v_2	*% Poly*	DW	GD	PopGD	Elevation	DGEO
v_2	1	**0.914**	0.775	**0.997**	0.618	−0.238	−0.111
% Poly	**0.914**	1	**0.867**	**0.930**	0.499	−0.111	−0.040
DW	0.775	**0.867**	1	0.785	0.460	0.016	−0.156
GD	**0.997**	**0.930**	0.785	1	0.609	−0.238	−0.109
PopGD	0.618	0.499	0.460	0.609	1	−0.046	0.022
Elevation	−0.238	−0.111	0.016	−0.238	−0.046	1	0.156
DGEO	−0.112	−0.040	−0.156	−0.109	0.022	0.156	1

Statistically significant correlations ($p < 0.005$) are highlighted in bold. Note: PopGD = average genetic distance within populations; GD = average genetic distance between populations; DGEO = distance to the nearest edge (km); elevation in meters above sea level (m); diversity and divergence indexes: v_2 = genetic diversity measured through the effective number of variants; *% Poly* = percentage of polymorphic fragments; DW = frequency down-weighted marker value.

Table 5. Correlations between genetic and geographic variants of *Pinus engelmannii* and the different peripheral and central populations of this species.

Variable	v_2	*% Poly*	DW	GD	PopGD	Elevation	DGEO
v_2	1	**0.907**	**0.849**	**0.990**	**0.936**	0.434	0.107
% Poly	**0.901**	1	**0.967**	**0.913**	**0.897**	0.316	0.079
DW	**0.849**	**0.967**	1	**0.861**	**0.849**	0.265	0.274
GD	**0.990**	**0.913**	**0.861**	1	**0.898**	0.331	0.120
PopGD	**0.936**	**0.897**	**0.849**	**0.897**	1	0.602	0.092
Elevation	0.434	0.316	0.265	0.331	0.602	1	0.076
DGEO	0.107	0.078	0.274	0.120	0.092	0.076	1

Statistically significant correlations ($p < 0.005$) are highlighted in bold. Note: PopGD = average genetic distance within populations; GD = average genetic distance between populations; DGEO = distance to the nearest edge (km); elevation in metres above sea level (m); diversity and divergence indexes: v_2 = genetic diversity measured through the effective number of variants; *% Poly* = percentage of polymorphic fragments; DW = frequency down-weighted marker.

Table 6. Correlations between genetic and geographical variants of *Pinus herrerae* and the different peripheral and central populations of this species.

Variable	v_2	*% Poly*	DW	GD	PopGD	Elevation	DGEO
v_2	1	**0.938**	**0.919**	**0.994**	0.761	**0.895**	−0.281
% Poly	**0.938**	1	**0.922**	**0.958**	**0.855**	0.791	−0.076
DW	**0.919**	**0.922**	1	**0.944**	**0.898**	0.663	0.099
GD	**0.994**	**0.958**	**0.944**	1	0.799	**0.853**	−0.202
PopGD	0.761	**0.855**	**0.898**	0.799	1	0.474	0.316
Elevation	**0.895**	0.791	0.663	**0.853**	0.474	1	−0.594
DGEO	−0.281	−0.077	0.099	−0.202	0.316	−0.594	1

Statistically significant correlations ($p < 0.005$) are highlighted in bold. Note: PopGD = average genetic distance within populations; GD = average genetic distance between populations; DGEO = distance to the nearest edge (km); elevation in metres above sea level (m); diversity and divergence indexes: v_2 = genetic diversity measured through the effective number of variants; *% Poly* = percentage of polymorphic fragments; DW = frequency down-weighted marker p.

By contrast, for *P. herrerae*, significant correlations were found between elevation and some variables (v_2 and GD) in peripheral and central populations (Table 6). Thus, the peripheral populations tend to be less diverse and with a greater degree of differentiation relative to the central populations only in *P. herrerae*.

Although there were significant correlations between genetic (DW) and geographic (DGEO) variants of *P. leiophylla* and its different peripheral and central populations, the differences might not be considered statistically significant due to the small number of populations sampled (Table 7). However, the trend observed was very consistent.

Table 7. Correlations between genetic and geographic variants of *Pinus leiophylla* and the different peripheral and central populations of this species.

Variable	v_2	*% Poly*	DW	GD	PopGD	Elevation	DGEO
v_2	1	0.780	0.195	**0.999**	**0.956**	0.616	−0.088
% Poly	0.780	1	0.478	0.793	**0.921**	0.455	0.167
DW	0.195	0.478	1	0.207	0.262	0.753	**0.945**
GD	**0.999**	0.793	0.207	1	**0.962**	0.615	−0.079
PopGD	**0.956**	**0.921**	0.262	**0.962**	1	0.510	−0.057
Elevation	0.616	0.455	0.753	0.615	0.510	1	0.657
DGEO	−0.088	0.167	**0.945**	−0.079	−0.057	0.657	1

Statistically significant correlations ($p < 0.005$) are highlighted in bold. Note: PopGD = average genetic distance within populations; GD = average genetic distance between populations; DGEO = distance to the nearest edge (km); elevation in metres above sea level (m); diversity and divergence indexes: v_2 = measured genetic diversity through the effective number of variants; *% Poly* = percentage of polymorphic fragments; DW = frequency down-weighted marker value.

3.3. Diversity and Genetic Differentiation (Criterion 2)

According to the Kruskal–Wallis test based on the altitude for centre–periphery partition, the genetic diversity measured according to Gregorius [52] and Wehenkel et al. [53] in all the analysed populations, was similar; the lowest v_2 value (1.3015) corresponded to peripheral populations of *P. engelmannii*, while the highest value (1.376) corresponded to peripheral populations of *P. cembroides* (Table 8). The *% Poly* varied from 69.4% in central populations of *P. engelmannii* to 81.6% in peripheral populations of *P. cembroides*. The rarity index (DW) ranged from 0.051 in peripheral populations of *P. durangensis* to 0.426 in peripheral *P. cembroides* populations. The PopGD varied from 69.3 to 91.8 in peripheral populations of *P. arizonica* and *P. cembroides*, respectively. The lowest (64.1) and highest (81.7) GD values corresponded to peripheral populations of *P. arizonica* and *P. cembroides* respectively (Table 8).

The geographic distance varied from 3.72 to 12.522 km in peripheral populations of *P. engelmannii* and *P. arizonica*, respectively. The lowest recorded elevation (1820 m) corresponded to a peripheral population of *P. engelmannii*, and the highest (3062 m), to a peripheral population of *P. arizonica*.

Finally, the Kruskal–Wallis test applied to diversity and differentiation variables in the six species analysed only revealed significant differences in *P. arizonica* (Table 8). The elevation appeared to be a determining factor in diversity and differentiation measures.

In terms of the diversity and differentiation measures, Manhattan distance was used with Ward's linkage to construct dendrograms. The Manhattan distance was preferred for high dimensional and categorical data. Similar cluster groupings were observed in all the populations of the six species under study. Clustering results for central and peripheral populations of *P. arizonica* are shown in Figure 3.
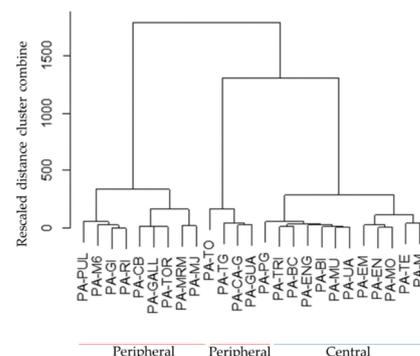
Figure 3. Hierarchical cluster analysis (HCA) of the 25 populations of *Pinus arizonica* forest communities in the Sierra Madre Occidental. The populations (sampling points) are represented with their abbreviated names.

Table 8. Comparison of the differences between central and peripheral populations according to criterion 2 using the non-parametric Kruskal–Wallis test.

	Location	v_2	% *Poly*	DW	GD	PopGD	DGEO (km)
				Pinus arizonica			
M_e	Central	1.330	0.745	0.114	70.347	73.752	6.447
	Peripheral	1.305	0.682	0.089	64.097	69.326	12.522
	p-value	0.072	0.016 *	0.047 *	0.064	0.038 *	0.414
				P. cembroides			
M_e	Central	1.3555	0.8155	0.338	79.18460	89.5215	7.215
	Peripheral	1.3760	0.8160	0.372	81.66629	91.7780	7.710
	p-value	0.08326	0.5637	0.248	0.08326	0.2482	0.563
				P. durangensis			
M_e	Central	1.320	0.7065	0.104	68.2490	73.823	6.24
	Peripheral	1.334	0.7435	0.116	71.4285	75.854	9.61
	p-value	0.1567	0.08461	0.3412	0.1108	0.1108	0.2367
				P. engelmannii			
M_e	Central	1.3065	0.694	0.1025	65.4825	68.939	5.0390
	Peripheral	1.3015	0.679	0.0955	64.1815	68.426	3.7205
	p-value	0.8728	0.6884	0.7488	0.7488	0.5218	0.4233
				P. herreae			
M_e	Central	1.3105	0.6820	0.1695	64.6470	70.836	6.74
	Peripheral	1.3070	0.7025	0.1760	64.7195	72.700	9.69
	p-value	0.5637	0.6631	1	0.5637	0.7728	0.3865
				P. leiophylla			
M_e	Central	1.3300	0.7545	0.2435	70.1495	73.5915	8.035
	Peripheral	1.3335	0.7875	0.2505	70.9835	75.1705	9.025
	p-value	1	0.2207	1	1	1	1

Note: v_2 = genetic diversity measured through the effective number of variants; % *Poly* = percentage of polymorphic fragments; DW = frequency down-weighted marker; GD = average genetic distance between populations; elevation in metres above sea level; PopGD = average genetic distance within populations; DGEO = distance to the nearest edge (km); M_e = median; * = significant difference ($p < 0.05$).

Ward's method was used for hierarchical clustering of *P. arizonica* populations. Three main groups were formed within central and peripheral populations. The peripheral group from PA-TO to PA-GUA was more similar to the central group than the peripheral group formed by PA-PUL to PA-MJ. This pattern may depend on the elevation.

4. Discussion

In this study, we determined and evaluated the genetic diversity in 80 populations of six important *Pinus* spp. located in the centre and periphery of their natural distribution in the Sierra Madre Occidental, in the states of Durango and Chihuahua, Mexico. The main goal of the study was to determine whether the Centre–Periphery Theory could explain the distribution of some pine species, for the purposes of conservation and subsequent sustainable use.

According to the first partitioning criterion (the distance to the closest range edge), there were no significant differences among species' populations, except for *P. herrerae* populations. The number of effective genetic variants, the average genetic distances and the elevation were important factors influencing the geographical location and helped to

discriminate the central from the peripheral populations. On the other hand, the quartile stratification of elevation (second criterion) did not show significant differences between centre and peripheral populations, except for *P. arizonica* in which the elevation appeared to be a determining factor in diversity and differentiation measures. However, the hierarchical cluster analysis revealed that genetically, peripheral and central populations of *P. arizonica* are very similar. Therefore, genetic diversity of the six pine species evaluated is good, and it may be inferred that all the populations assessed were central.

In detail, analysis of 376 loci from AFLPs markers revealed non-significant differences between the genetic diversity of central and peripheral populations of four of the six species analysed (*P. arizonica*, *P. cembroides*, *P. durangensis* and *P. engelmannii*), according to proximity to the closest range border (criterion 1). These findings contrast with those of Schwartz et al. [60], who stated that genetic diversity is expected to be greater in central than in peripheral populations, for two reasons. On the one hand, peripheral populations are usually smaller than central populations, and heterosygosity, allelic diversity and gene flow are therefore lower. On the other hand, genetic variation may be reduced in peripheral populations due to limited and poor connectivity with other populations. In addition, the actual pattern of genetic variation observed may be a result of historical and actual ecological forces [5,61–63], as well as the current population dynamics.

Population dynamics are related to the size of populations and the factors involved in their maintenance, decline or expand considering the limits of the distribution ranges of species related to emerging issues, such as biotic invasions and epidemic diseases under conditions of climate change [64–67]. Several studies have focused on native species borders and central–peripheral processes in natural settings [2,36,68,69]. The Sierra Madre Occidental is home to 46% of the Mexican native pine species [70], including those evaluated in the present study. However, in four of the six species studied, i.e., *P. arizonica*, *P. cembroides*, *P. durangensis* and *P. engelmannii*, genetic variables were not correlated with either the central or peripheral location (criterion 1). In the context of climate change and emerging issues, it may be necessary to carry out a further examination of the central–peripheral patterns and processes of invasive species, partly due to their highly dynamic populations and management implications [64,67,68,71,72]. This issue may raise questions as to the dynamics of the six *Pinus* spp. analysed in the present study and their probability of being invaded by foreign species.

Traditionally, most central–peripheral comparisons, including the present study, have been conducted on native species, especially for conservation purposes [36,73–77]. However, many patterns and processes in central and peripheral populations are often non-linear, as pointed out by Sexton and Dickman [67]. In addition, marginal populations located in different directions are often structurally and dynamically very different [64,67,78,79]. Consequently, the underlying mechanisms may be key to explaining the patterns of distribution of at least three of the six *Pinus* spp. considered in the present study. The population sizes may also be important factors, as populations of *P. arizonica* (Figure S1) and *P. durangensis* (Figure S3) have higher densities and number of individuals in comparison with the other four species tested, and according to Lázaro-Nogal et al. [78], population size can at least partly override the effects of geographical periphery.

The highest values of genetic diversity of the six *Pinus* species analysed, measured as the effective number of variants v_2 [52,80–82], were (1.387) for *P. arizonica* and (1.414) for *P. durangensis*. The differences in average gene diversity between central and peripheral populations were not significant for any of the two species under the centre–periphery partitioning (criterion 1). This behaviour may be explained by Mayr's hypothesis, whereby the gene flow from the core may compensate for the effects of local selection and genetic drift at the periphery. In such cases, genetic diversity may be homogeneous throughout the species range [16]. Nonetheless, in other cases, such as those mentioned by Pironon et al. [5], geographical and environmental gradients do not strictly overlap and therefore the abundance should not systematically follow a geographical or ecological central–peripheral pattern [5,66].

The rarity index (DW) showed that *P. cembroides* was the most strongly differentiated species of the six evaluated, but only five populations of this species were sampled; however, given the distribution range of this pine, these observations were probably insufficient to analyse the dynamics and genetic diversity that contribute to the distribution patterns. Moreover, ecological, and genetic factors are closely related to each other, and their interactions regulate population dynamics over space and time [83,84]. For example, for many species, climate conditions can limit species distribution, but whether the species can expand its range (birth > death) may be affected by the genetic pool and evolutionary potential of its component populations, especially peripheral populations [85,86].

However, small population size and spatial isolation can promote inbreeding in natural populations, driving excess of homozygote frequencies in subsequent generations [87,88], and the possibility that recessive deleterious or lethal alleles will be expressed [89]. According to criterion 1, this may be the case in species with fewer and smaller populations, where the DW value may be higher and populations occur at higher elevation, as the possible case in *P. leiophylla* and *P. cembroides,* with four and five populations, respectively. However, the highest DW value of 0.426 in *P. cembroides*, together with the high and stable number of mean genetic variants of 1.380 and the 86.6% of polymorphic loci make this species the most differentiated and well-adapted to its growth conditions, across its range. This finding is similar to that of Sexton et al. [83], who reported that adaptation of individuals in marginal populations may be high if these individuals reside in favourable habitats, even though such habitats may be scarce toward the range edge; therefore, it is important to conserve front-edge populations that may contribute to species adaptation [68].

These findings contradict the hypothesis that species with small ranges generally exhibit lower genetic variation than more widespread species [87]. The distribution of *P. cembroides* is more consistent with Fisher´s hypothesis, which predicts that peripheral populations sustain higher levels of genetic diversity due to fluctuating selection in spatially heterogeneous and unpredictable environments [17–19,67,68,83,84].

As conifers are self-compatible plants, homozygosity may arise from self-fertilisation and biparental inbreeding, affecting the mating system. A study of reproductive traits and mating systems in *Pinus strobus* revealed significantly lower reproductive adaptation in small, peripheral stands than in large, central populations [88]. Conifers have one of the highest known numbers of lethal equivalents [89,90], and an increase in homozygosity is likely to have strong negative effects on offspring. Salzer and Gugerli [90] found that around 76% of the fully developed seeds collected in the peripheral stands of *Pinus cembra* were empty, while seeds from large central populations only showed an average embryo abortion of 30%, which may lead to better survival of individuals in central populations. This scenario provides a possible explanation for the trend observed in the *P. leiophylla* species evaluated here using criterion 1.

In the present study, based on criterion 1, the lack of significant differences in genetic diversity between central and peripheral populations in 66% of the species under study indicates the possibility that longevity and large enough population sizes could reduce the negative effects of genetic drift in peripheral populations [79,85]. In summary, the absence of statistically significant correlations between genetic variants and geographical distances (criterion 1) was evident in five of the six species under study. Therefore, this distribution pattern was not explained by the general centre–periphery hypothesis [2,7,8]; the same finding has been demonstrated in other studies with conifers [26,31] and the endemic *Lilium pomponium* [91].

By contrast, the general centre–periphery hypothesis supported and explained the pattern observed in *P. herrerae* [2,7,8,37], based on criterion 1. Statistically significant correlations between genetic and geographic variants and the different peripheral and central populations were found in this species, showing that the existing diversity and differentiation depended on elevation, as they were slightly more pronounced at higher elevations. Therefore, the establishment of greater number of effective allelic variants will

appear in populations occurring at higher elevations, due to the extreme climatic conditions to which they have adapted [92–95].

Regarding standard diversity measures, such as FST, and the results of the AMOVA using the AFLP markers, the main source of variation was within populations for all the species evaluated [58,93]. In addition, considering the very low FST values, it is likely that two key genetic parameters: the effective number of migrants among populations (Nm) and the rate of gene flow (m), will be homogeneous, and genetic diversity will therefore be evenly distributed in the centre and at the margins of the range. As a result, geographically peripheral populations were not detected in this study; according to criterion 1, populations of the six species studied can be considered central populations because they all exhibit higher genetic diversity and extremely low genetic differentiation.

By contrast, according to results of the non-parametric Kruskal–Wallis test using genetic diversity indexes from Gregorius (1978) [52] based on criterion 1, we verified that the peripheral populations of *P. herrerae* are less diverse and more differentiated than the central population. This finding is consistent with those reported in other studies that also show greater genetic diversity in central populations [35,94], and larger genetic differentiation in peripheral populations [37,78].

The evolutionary theory suggests that, in virtue of their isolation, peripheral populations should adapt more closely to their environment than central populations. The degree to which a population can adapt to its environment not only depends on the rate of environmental change, but also on how much maladaptive gene flow a population receives [95]. Therefore, from ecological and evolutionary perspectives, individuals in peripheral populations of *P. herrerae* are worth conserving in face of climate change as new arguments for their conservation importance may be provided [68].

Although we found a correlation between geographic distance (DGEO) and DW for *P. leiophylla*, the relationship was not statistically significant because of the small number of observations. However, the observed trend indicates the probable differentiation that may be occurring in this species. The adaptive trajectory of the population types with respect to climate by means of population size, population connectivity and climatic environment may be responsible for this trend [68,78].

For criterion 2, by using elevation as a partitioning criterion for distinguishing between central and peripheral populations, a similar pattern was observed in all the populations of the six species studied. There is an ecological gradient from the sampling points, which was adequate for classifying central and peripheral populations derived from elevation.

The current pattern observed in *P. arizonica*, in which central populations are more diverse (Table 8) may be explained by pollination processes and seed dispersion traits. Moreover, populations are widely distributed and sufficiently dense to compensate for any disturbing phenomenon that may occur. In this regard, the altitude range in central populations seems to be optimal. The difference between central and peripheral populations may be due to a lack of homogeneous bidirectional gene flow.

In this study, three groups of plots were visible in the *P. arizonica* distribution pattern: two plots of peripheral populations and one of central populations (Figure 3). However, one peripheral population was more similar to the central group than to the other peripheral group, with distinctly different forest traits in the Sierra Madre Occidental. In addition, forest structural attributes, such as number of trees and average tree size, may be affected by elevation.

Tree species diversity was similar in central and peripheral populations of all the six species evaluated. This general result may indicate that elevation is a better partitioning criterion than the distance to the closest edge. However, in *P. herrerae* the pattern seems to correspond to both partitioning criteria. In addition, the data trend is related to the elevation, although this species shows a closer relation with the geographic distance (criterion 1).

Regarding diversity, the results are consistent with those of Corral–Rivas et al. [96], who reported that the diversity profile of forest species may be characterised by a number of attributes, including the distribution of species and sizes of individuals.

The lowest peripheral population recorded belongs to *P. engelmannii*, at an elevation of 1820 m; however, diversity was very similar in both central and peripheral populations. This may be a good indicator of adaptation, as studies by Bickford et al. [97] have shown that increasing frequency and severity of drought predicted for the lowest regions of the Sierra Madre Occidental in the coming decades will reduce growth of *P. engelmannii*, with a greater impact on low-elevation populations of *P. engelmannii*.

The findings of the present study rule out differences in central and peripheral populations of *P. leiophylla* as the diversity measures are very similar in both types of populations at different elevations. These findings are consistent with those reported by Castellanos-Acuña et al. [98], who reported that growth decreases when populations shift to sites that are colder (at higher elevation) than the sites of origin. However, no differences were found at an elevational shift of 300 m for *P. leiophylla* populations. This shift would not lead to severe maladaptation and may thus represent a viable management strategy for *P. leiophylla* populations in scenarios of climate change [98].

Finally, the importance of traits differs depending on ecosystem conditions. One of the basic requirements appears to be grouping species into cohorts with similar traits, such as *P. arizonica* and *P. durangensis*. This is an important factor to consider for developing more advanced methods of harvest control in the forests in the Sierra Madre Occidental [99]. Therefore, it is important to know that these two species are genetically diverse and have ample distribution.

5. Conclusions

The levels of genetic diversity and differentiation observed in this study suggest that isolation or proximity to marginalisation, probable wood exploitation due to the economic value of these species, together with population decline and fragmentation, may have little effect on the short-term or immediate-term evolutionary potential of central or peripheral populations of five of the six pine species under study.

However, although genetic diversity was high and evenly distributed within populations of all the pine species evaluated, the geographically peripheral populations set a priori did not coincide with the genetic diversity expected for peripheral populations because all populations displayed a predominantly central distribution after running all the analyses; therefore, considering the central–marginal theory, it is possible that the populations of the six species studied are central populations because they all exhibit higher genetic diversity and extremely low genetic differentiation.

Whether the geographically central populations differ in their genetic diversity and levels of genetic differentiation relative to marginal populations remains an open question as our findings were not conclusive.

Given the limited information on patterns of genetic diversity and genetic differentiation in central and peripheral Mexican pine populations, the study findings contribute to a better understanding of the genetic pattern in terms of the central–peripheral evolutionary theory in Mexican pines of the Sierra Madre Occidental.

The results of the present study according to both partitioning criteria may be useful for making decisions regarding the collection and preservation of seeds, either from central or peripheral populations from the six pine species studied, noticing that after analysis of both partitioning criteria, there are predominantly central populations.

Despite the ecological and economical characteristics of these species, population level studies are scarce. We therefore suggest reinforcing our findings by conducting more population studies using different types of molecular markers of codominant nature and nuclear origin to complement the present findings.

Supplementary Materials: The following are available online at https://www.mdpi.com/article/10.3390/f13020215/s1, Figure S1: Map showing the location of the 25 populations of *P. arizonica*. Figure S2: Map showing the location of the five populations of *P. cembroides*. Figure S3: Map showing the location of the 26 populations of *P. durangensis*. Figure S4: Map showing the location of the 12 populations of *P. engelmannii*. Figure S5: Map showing the location of the eight populations of

P. herrerae. Figure S6: Map showing the location of the four populations of *P. leiophylla*. Table S1: Geographic location of the 80 populations of six *Pinus* spp. and results of diversity and divergence indexes calculated using GenAlEx 6.501 (criterion 1). Table S2: Geographic location of the 80 populations of six *Pinus* spp. and results of diversity and divergence indexes calculated using GenAlEx 6.501 (criterion 2).

Author Contributions: C.L.R.-O. compiled and analysed the field data, designed the tables, figures, and wrote the original draft of the manuscript. C.A.L.-S. provided the data for the species natural distribution models and revised the original draft of the manuscript. C.W. coordinated the project, designed the experiments and conducted the fieldwork. J.C.H.-D., A.C.-P. and C.Z.Q.-P. reviewed and edited the original draft of the manuscript. C.E.B.-S. coordinated the work, carried out the data analysis and wrote most of the text. All authors have read and agreed to the published version of the manuscript.

Funding: This paper presents a portion of the results of the research projects "Proyectos de PROFOS-CONAFOR 2012–2015" granted to Christian Wehenkel.

Acknowledgments: We thank the Consejo Nacional de Ciencia y Tecnología (CONACYT) for the scholarship granted to Claudia Lizbeth Ramírez Orozco to complete her master's studies and for the scholarship granted to Claudia Edith Bailón Soto for completion of her post-doctoral studies, which allowed her to coordinate the present work. Finally, we thank scientists, rangers and students for their assistance in field work. We also acknowledge the Comisión Nacional Forestal (CONAFOR) for funding this research. We also thank the three anonymous reviewers whose comments helped us to improve this research paper.

Conflicts of Interest: The authors declare no conflict of interest.

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