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Article

Estructura y composición del bosque de *Pinus hartwegii* Lindl. en su distribución altitudinal en el Nevado de Toluca

Pinus hartwegii Lindl. forest, structure and composition along of its elevational distribution in the *Nevado* of *Toluca*

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Abstract

Knowledge of the structure and composition of a forest makes it possible to understand the dasometric attributes of trees and ecosystem processes along altitude-derived vegetation gradients. The structure of the *Pinus hartwegii* forest was analyzed at an altitude of 600 m on the *Nevado* of *Toluca*. Clusters of 1 ha were established at each altitude; dasometric variables were registered. The vertical and horizontal structure was assessed based on the tree density (*TD*), basal area (*BA*), and structural parameters and indices. The latter showed that *P. hartwegii* maintains its abundance and dominance along the studied altitudinal gradient, mainly between 3 700 and 4 000 m, where it forms monospecific forests. The contribution to the tree structure decreased from 100 % at 3 900 and 4 000 m to 45 % at 3 500 m. The dasometric parameters indicated a higher *TD* in individuals in diameter classes of 5–15 cm at altitudes below 3 800 m; this showed that regeneration may be more limited at higher altitudes, possibly due to irregular tree removal. We conclude that the structural composition of the *P. hartwegii* forest shows an important change in its structure depending on the altitude, as a result of the environment-society interaction through altitude-related land use management, which compromises the structure and function of this ecosystem. We recommend incorporating altitude as a decisive variable in management plans for high-mountain forests.

Keywords: Altitude, temperate forests, tree composition, tree density, ecosystem processes, ecological importance value.

Resumen

Conocer la estructura y composición de un bosque, permite entender los atributos dasométricos de los árboles y los procesos ecosistémicos a lo largo de gradientes de vegetación derivados de la altitud. Se analizó la estructura del bosque de *Pinus hartwegii* en un gradiente de 600 m en el Nevado de Toluca. Se establecieron conglomerados de 1 ha en cada altitud y se registraron variables dasométricas. La estructura vertical y horizontal se evaluó con la densidad arbórea (*DA*), área basal (*AB*) y parámetros e índices estructurales. Estos últimos mostraron que *P.*

hartwegii mantiene su abundancia y dominancia a lo largo del gradiente altitudinal estudiado, principalmente de los 3 700 a 4 000 m donde forma bosques monoespecíficos. La contribución en la estructura arbórea disminuyó de 100 % a 3 900 y 4 000 m, a 45 % en los 3 500 m. Los parámetros dasométricos indicaron mayor *DA* en individuos de clases diamétricas de 5-15 cm, y fue superior por debajo de los 3 800 m; ello evidenció que la regeneración puede ser más limitada a grandes altitudes, posiblemente debido a una extracción irregular del arbolado. Se concluye que la composición estructural del bosque de *P. hartwegii* presenta un cambio importante en su estructura de acuerdo con la altitud, lo que resultaría de la interacción ambiente-sociedad mediante la gestión del uso del suelo asociada a la altitud, y que compromete la estructura y función del ecosistema. Se recomienda incorporar la altitud como una variable determinante en planes de manejo para bosques de alta montaña.

Palabras clave: Altitud, bosques templados, composición arbórea, densidad arbórea, procesos ecosistémicos, valor de importancia ecológica.

Introduction

The three-dimensional (3D) arrangement of plant elements in a forest ecosystem depends on the combination of climatic, topographic, and hydrological variables, among others, which generate great structural heterogeneity (of size, shape, and spatial distribution) (Gadow *et al.*, 2012; Sharma *et al.*, 2017). However, patterns are also generated in patches of vegetation across the landscape that can be useful as indicators of the stability and integrity of the forest, enabling it to function and provide multiple ecosystem services (carbon sequestration, water capture and purification, climate regulation, etc.) (McElhinny *et al.*, 2005; Gadow *et al.*, 2012; Seidler, 2017).

Forest structure is dynamic and is constantly changing as trees grow, through primary allocation processes that promote increases in diameter, height, and overall biomass (Gadow *et al.*, 2012; Hu *et al.*, 2020), depending on the prevailing environmental conditions. Changes in structure are generally attributed to the interaction of environmental variations and the influence of land use history (Báez *et al.*, 2015), including logging disturbances, selective tree harvesting, or harvesting in the case of forest plantations (Gadow *et al.*, 2012).

One of the most obvious indicators of disturbance to the structure of a forest is the establishment of different types of vegetation, such as shrubs and herbs (Baéz and Collins, 2008; Waddell *et al.*, 2020). This, in combination with habitat functions, growth, and ecosystem stability —the main underlying processes—, contribute to the characterization of a site and of the patterns of past land use practices, which provide insight into the type of disturbance existing in it (Gadow *et al.*, 2012).

Mountain areas are sites of great ecological importance, occurring under various environmental contexts (Körner and Paulsen, 2004; Ramírez-Huerta *et al.*, 2016); most of these sites exhibit significant environmental changes over short distances as one ascends in altitude (Körner and Paulsen, 2004; Buthia *et al.*, 2019). In relation to the structure, tree density and basal area are indicators of the changes and stability of the forest (Gadow *et al.*, 2012). Altitude-related increases in tree density and basal area have been reported in mid-altitude Andean forests (Unger *et al.*, 2012), with subsequent decreases (Homeier *et al.*, 2010) or absence of apparent effect (Girardin *et al.*, 2010).

In Mexico, most mountain areas have been incorporated into protected natural areas (Ramírez-Huerta *et al.*, 2016); these have been subject to strong anthropic pressures derived from urban expansion and the selective extraction of trees (Regil *et al.*, 2014; Gómez and Villalobos, 2020), with the consequent fragmentation of habitat, forest cover and forest diversity (Durán-Medina *et al.*, 2005).

Pinus hartwegii Lindl. is a dominant forest species in the Mexican mountains, distributed within an altitudinal gradient of 2 800 to 4 300 m (Alpine line in Mexico) (Farjón *et al.*, 1997). From 3 000 m upwards, it forms pure subalpine forests (Manzanilla-Quiñones *et al.*, 2019). It has great ecological value, particularly for its adaptability to the low temperatures that dominate at high altitudes, as well as a high timber value. Therefore, it has been exploited for commercial purposes, an activity that has had great impact on the extension and functioning of its forests (Franco *et al.*, 2006; Endara *et al.*, 2012; Pérez-Suárez *et al.*, 2022).

The *Nevado* of *Toluca* Wildlife Protection Area (WPA) is an area that has been protected for more than 50 years, exhibiting a zoning pattern that divides the territory according to the various prevailing environmental, physical, economic, and social conditions (Granados *et al.*, 2018), along with a participatory conservation model that provides legal permission to carry out diverse economic activities such as cattle ranching, agriculture, natural resource exploitation, tourism, and selective tree extraction. These activities implicitly decrease in relation to the altitudinal gradient; thus, as one approaches the buffer and core zones (close to the volcanic cone), the use of the land becomes restricted or protected (Semarnat, 2016). Yet, neither the zoning nor the allowable economic activities are planned according to the altitude (Granados *et al.*, 2018), however, they do determine the distribution, functioning, and accessibility of the forests. Therefore, if *P. hartwegii* forests are subjected to more anthropic pressure than allowed (i.e., to other than exclusively low-impact economic activities), they will exhibit differences in their structure and composition as a function of altitude.

The objective of this study was to evaluate the structure and composition of the *P. hartwegii* forest at an altitudinal gradient of 600 m in the *Nevado de Toluca* WPA, under the expectation that the information generated will serve as a basis for understanding the functioning of the forest and its resilience to various factors of global change.

Materials and Methods

Study area

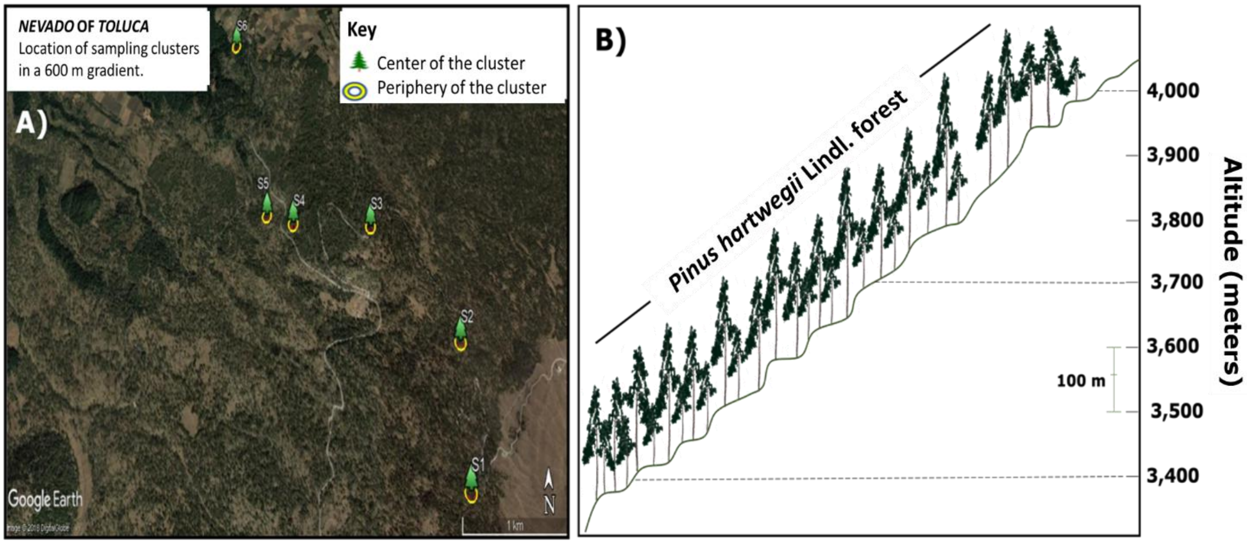
The study was conducted in the *Nevado de Toluca* WPA in the State of Mexico, located between the valleys of *Toluca* and *Tenango*, within an altitudinal range of 3 000 to 4 680 m (Körner and Paulsen, 2004). The predominant climate is cold, with semi-cold-sub-humid variants C(E)wig and cold E(T)Hwig, and an annual average temperature range of -2 °C to

7 °C (García, 2004). The region has an isothermal behavior and the highest temperature occurs before the summer solstice. Although there are precipitation events at any time of the year, the rainy season is from May to October, July is the wettest month; the average precipitation varies from 200 to 1 800 mm, with snowfall from December to February (Challenger and Soberón, 2008).

The soil type in 90 % of the area is Andosol and, in smaller proportions, Phaeozem, Regosol, Cambisol, and Litosol (Körner and Paulsen, 2004). The *Nevado* of *Toluca* WPA is an important biogeographic area at the national level, as it harbors temperate pine (*Pinus* spp*.*)*,* fir (*Abies religiosa* (Kunth) Schltdl. & Cham.), and oak (*Quercus* spp.) forests located between 3 000 and 4 100 m of altitude. From 3 500 to 4 000 m, particularly, the *P. hartwegii* forest dominates (Challenger and Soberón, 2008), while between 4 100 and 4 500 m, the high mountain grassland is dominated by the following genus *Festuca* and *Calamagrostis* (Calderón de Rzedowski and Rzedowski, 2010).

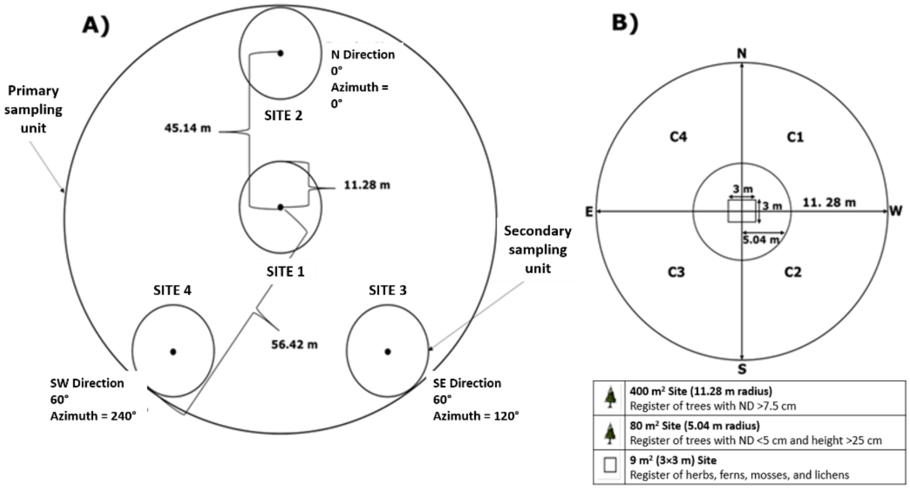
Characterization of the tree structure

In ordinalr to characterize the tree structure in the *Nevado* of *Toluca* WPA along an altitudinal gradient of *P. hartwegii* forest, an altitudinal elevation of 600 m (3 400-4 000 m) was established using satellite images and contour lines (Figure 1A). Along this gradient, six permanent sampling sites (PSS) were established at every 100 m, similar to those of the National Forest and Soil Inventory (*INFyS*) (Figure 1B), which is based on systematic stratified sampling (Figure 2). Each PSS consisted of a circular cluster of 1 ha (56.42 m radius) (Figure 2A) comprising four secondary sampling sites (SSS) with a surface area of 400 m^2 (11.28 m radius), geometrically arranged in an inverted "Y" shape with respect to the north (Conafor, 2012).



A) S1 corresponds to the lowest sampled altitude (3 400 m), and S6, to the highest sampled altitude (4 000 m); B) Vertical scheme of the sampled altitudinal gradient (Prepared by the authors).

Figure 1. Altitudinal gradients where the permanent sampling sites for characterizing the structure of the *Pinus hartwegii* Lindl. forest are located within the *Nevado* of *Toluca* WPA.



A) circular sites similar to those established by the National Forest and Soil Inventory, and B) secondary sampling sites for the characterization of the structure of the *Pinus hartwegii* Lindl. forest in the *Nevado* of *Toluca* WPA (Conafor, 2012).

Figure 2. Design of permanent sampling sites.

Each SSS was numbered from 1 to 4. SSS 1 was placed in the central part of the cluster (Figure 2A), and the rest (2, 3, and 4), as peripheral to 1. Starting from the center of each site, a circular plot with a surface area of 80 m^2 (5.04 m radius) (Figure 2A) and a further plot with a surface area of 9 m^2 (3×3 m) were marked to compensate for the slope of the terrain.

The trees recorded and measured in the 400 m^2 SSS corresponded to those with a normal diameter (*ND*) greater than or equal to 5 cm. All individuals were counted and marked starting from the tree closest to north (0º) and continued clockwise; their scientific or common name, normal stem diameter (model 283D/5m Forestry Suppliers Inc® diameter tape), and total height (model FP550 Nikon Forestry Pro II laser hypsometer) were recorded.

Characterization of the shrub and herbaceous structure

In order to characterize the shrub stratum in the 80 m^2 sites, individuals with a normal diameter (*ND*) of over 2.50 cm but under 5 cm were considered. The herbaceous stratum was characterized in the 9 m^2 sites, where a cover of grasses, ferns, mosses, lichens and herbs was registered. The percentages of these were calculated in relation to the occupied area in the site; therefore, they did not necessarily add up to one hundred.

Data analysis and processing

The horizontal structure along the altitudinal gradient of the *P. hartwegii* forest was characterized by calculating abundance (number of trees), dominance (basal area) and frequency (presence of the species per site). These variables were estimated in absolute and relative (%) values, and the Importance Value Index (*IVI*) and Forest Value Index (*FVI*) were obtained based on them. The *IVI* defines the species that contribute most to ecosystem structure (Mostacedo and Fredericksen, 2000), was determined by the sum of abundance, dominance and relative frequency, dividing the result by three. The *FVI* determines the two-dimensional structure of the tree and it was calculated on the basis of two factors: 1) the sum of *DN* and crown cover in the horizontal plane, and 2) the total height in the vertical plane (Corella *et al.*, 2001).

Statistical analysis

The analysis of the forest structure of the *P. hartwegii* forest considered the comparison of the distribution of tree density (*TD*) and basal area (*BA*) along the altitudinal gradient evaluated. For the tree stratum, the *TD* and *BA* were compared between the different trees diameter classes (10 cm intervals), at each altitudinal level. The shrub and herbaceous stratum considered the same dasometric variables (*TD* and *BA*), but were compared between the different altitudinal levels. All statistical analyses were performed in the statistical package SAS/ETS®SAS Inc. (Statistical Analysis System, 2009), through an analysis of variance (ANOVA) and Tukey's comparison of means ($p<0.05$) between the dasometric variables evaluated.

Results and Discussion

Tree structure and composition

The tree community in the *Nevado* of *Toluca* WPA along the assessed altitudinal gradient was composed mainly of two tree species: *P. hartwegii* and *A. religiosa* (Table 1). Other taxa present were *Quercus* sp., *Cupressus* sp., and *Pinus ayacahuite* C. Ehrenb. ex Schltdl., but with less than two individuals in a single cluster of four sites. In this regard, *P. hartwegii* was the most abundant and dominant taxon in the entire gradient; its greatest abundance was registered at 3 800 masl (59 individuals), with a 100 % dominance between 3 900 and 4 000 masl. This dominance decreased at lower altitudes, although only by 9 %, i.e., it went from 100 % at the two highest altitudes to 91 % at 3 400 masl (Table 1).

Table 1. Estimated structural parameters and indices for tree species recorded along an altitudinal gradient of 3 400 to 4 000 m in the *Nevado* of *Toluca* WPA.

Structural parameter	**Species**	**Altitude (m)**						
		3 400	**3 500**	**3 600**	**3 700**	**3 800**	**3 900**	**4 000**
Absolute abundance (No. of individuals)	*Pinus hartwegii* Lindl.	11.3	18.0	27.0	52.0	59.0	10.0	12.0
	Abies religiosa (Kunth) Schltdl. & Cham.	6	0.3	0.3	0.0	0.0	0.0	0.0
	Others	0.0	1.0	2.0	0.0	0.1	0	0
Relative abundance (%)	*Pinus hartwegii* Lindl.	61	96	91	99	99	100	100
	Abies religiosa (Kunth) Schltdl. & Cham.	39	2	1	1	0	0	0
	Others	0	2	8	0	1	0	0

Absolute dominance (m^2)	*Pinus hartwegii* Lindl.	0.69	0.56	0.64	0.51	1.21	0.54	0.68
	Abies religiosa (Kunth) Schltdl. & Cham.	0.06	0.05	0.00	0.01	0.00	0.00	0.00
	Others	0.00	0.01	0.01	0.00	0.01	0.00	0.00
Relative dominance (%)	*Pinus hartwegii* Lindl.	91	93	99	99	99	100	100
	Abies religiosa (Kunth) Schltdl. & Cham.	9	6	0	1	0	0	0
	Others	0	1	1	0	1	0	0
Absolute frequency (%)	*Pinus hartwegii* Lindl.	100	100	100	100	100	100	100
	Abies religiosa (Kunth) Schltdl. & Cham.	100	25	25	25	0	0	0
	Others	0	25	50	0	50	0	0
Relative frequency (%)	*Pinus hartwegii* Lindl.	50	67	57	80	67	100	100
	Abies religiosa (Kunth) Schltdl. & Cham.	50	17	14	20	0	0	0
	Others	0	17	29	0	33	0	0
IVI (Importance Value Index) (%)	*Pinus hartwegii* Lindl.	67	85	82	93	88	100	100
	Abies religiosa (Kunth) Schltdl. & Cham.	33	8	5	7	0	0	0
	Others	0	6	12	0	11	0	0
FVI (Forest Value Index) (%)	*Pinus hartwegii* Lindl.	66	45	54	58	64	100	100
	Abies religiosa (Kunth) Schltdl. & Cham.	34	43	22	42	0	0	0
	Others	0	11	23	0	36	0	0

These results confirm that *P. hartwegii* continues to maintain its abundance and dominance along the sampled altitudinal gradient, specifically, between 3 700 and 4 000 m, where it forms monospecific forests (Challenger and Soberón, 2008). Meanwhile, in the range of 3 400 to 3 600 m, the presence of *A. religiosa* increased, so that the highest frequency occurred at 3 400 m, but in the same proportion as *P. hartwegii* (50% in absolute frequency) (Table 1).

The Importance Value Index (*IVI*) and Forest Value Index (*FVI*) reinforce the above statement that *P. hartwegii* is the tree species that contributes most to the tree structure, both vertically and horizontally, along the sampled altitudinal gradient, being the species that exhibited the highest percentages in these two indexes (Table 1), mainly at 3 900 and 4 000 m (100 %). However, below this altitude range (3 400–3 800 m), both the *IVI* and *FVI* of *P. hartwegii* decreased to 45 % at 3 500 m, where the contribution of this species to the tree structure was practically equal to that of *A. religiosa*, whose *FVI* was 43 %.

These results would indicate that, although, as previously cited, *P. hartwegii* maintains its abundance and dominance along the entire sampled altitudinal gradient in the *Nevado* of *Toluca* WPA (Farjon and Filer, 2013; Jobbágy and Jackson, 2000) it exhibits important changes in its structural composition below 3 900 masl. This could be related to the economic activities permitted in the *Nevado* of *Toluca* WPA, such as harvesting and selective logging, which have a greater impact on the *P. hartwegii* forest structure located between 3 400 and 3 800 masl (Jafari *et al.*, 2013).

The assessed dasometric parameters indicate that the distribution of *TD* for the *P. hartwegii* forest exhibited significant differences ($p<0.05$) between the different diameter categories for the entire altitudinal gradient, except for the *TD* observed at 3 900 m (Table 2). It should be noted that the *TD* was higher for the 5-15 cm diameter class below 3 800 masl, with a maximum of 1 287.5 trees ha^{-1} at 3 800 masl (Table 2), whereas at 3 900 and 4 000 masl, the *TD* for this diameter class was 15 to 7 times lower (81.2 and 181.2 trees ha^{-1}, respectively).

Table 2. Tree density (*TD*, trees ha^{-1}) and basal area (*BA*, m^{2} ha^{-1}) by diameter class (in 10 cm intervals) and altitude for *Pinus hartwegii* Lindl. forests at a 600 m gradient in the *Nevado* of *Toluca* WPA.

Altitude (m)	Variable	Diameter class intervals (cm)							
		5-15	15-25	25-35	35-45	45-55	55-65	65-75	75-85
3 400	*BA*	1.59	0.74	0.00	5.84	1.00	9.39	0.00	0.00

		±0.44	±0.47	±0.00	±2.36	±1.00	±3.48	±0.00	±0.00
	TD	300.00	18.75	0.00	43.75	6.25	31.25	0.00	0.00
		±62.08	±11.96	±0.00	±18.75	±6.25	±11.96	±0.00	±0.00
3 500	*BA*	1.79	0.12	0.94	3.37	5.69	3.62	0.00	0.00
		±0.82	±0.12	±0.57	±2.30	±2.95	±2.10	±0.00	±0.00
	TD	331.25	6.25	12.50	25.00	31.25	12.50	0.00	0.00
		±175.70	±6.25	±7.21	±17.67	±5.72	±7.21	±0.00	±0.00
3 600	*BA*	3.50	1.75	0.55	4.05	3.84	1.69	0.00	0.00
		±1.96	±1.58	±0.55	±1.11	±2.52	±1.69	±0.00	±0.00
	TD	525.00	62.50	6.25	31.25	18.25	6.25	0.00	0.00
		±301.73	±54.49	±6.25	±6.25	±11.97	±6.25	±0.00	±0.00
3 700	*BA*	5.42	0.69	0.00	0.00	0.00	3.50	0.00	3.18
		±2.16	±0.40	±0.00	±0.00	±0.00	±2.02	±0.00	±3.18
	TD	1 193.75	31.25	0.00	0.00	0.00	12.50	0.00	6.25
		±502.33	±18.75	±0.00	±0.00	±0.00	±7.22	±0.00	±6.25
3 800	*BA*	6.00	0.00	0.98	0.65	6.04	9.19	4.25	3.12
		±3.19	±0.00	±0.57	±0.65	±3.38	±3.52	±2.45	±3.12
	TD	1 287.50	0.00	12.50	6.25	31.25	31.25	12.25	6.25
		±649.16	±0.00	7.22	6.25	15.73	11.97	7.22	±6.25
3 900	*BA*	0.81	3.34	0.85	0.94	2.34	5.32	0.00	0.00
		±0.62	±0.95	±0.50	±0.94	±1.37	±3.29	±0.00	±0.00
	TD	81.25	112.50	12.50	6.25	12.50	18.75	0.00	0.00
		±57.17	±33.07	7.22	6.25	7.22	11.97	0.00	±0.00
4 000	*BA*	0.96	1.22	2.11	2.07	4.83	2.11	2.99	0.00

	±0.44	±1.02	±1.20	±1.27	±2.86	±2.11	±2.99	±0.00
TD	181.25	43.75	31.25	12.50	18.75	6.25	6.25	0.00
	±94.30	±35.90	±15.73	±7.22	±11.97	±6.25	±6.25	±0.00

It is important to point out that, for both altitudinal levels, the highest *TD* corresponded to the diameter class of 15 to 25 cm, which indicates that regeneration occurs mainly below 3 800 masl; at higher levels, regeneration is limited.

The regeneration of *P. hartwegii* forest at higher altitudes may be limited by anthropogenic activities such as overexploitation of natural resources, which in turn modify the biotic and abiotic conditions in these forests, and which, together with the low viability and germination of its seed, may have a negative impact on the regeneration of *P. hartwegii* (Iglesias *et al.*, 2000) may limit natural regeneration at these altitudes (Ramírez-Contreras and Rodríguez-Trejo, 2009). These conditions may account for the fact that the structure of *P. hartwegii* forest at these altitudes is changing significantly (according to the estimated *FVI*). Therefore, the results encourage the promotion of strategies to recover the forest structure of *P. hartwegii* based on studies such as that of Ramírez-Contreras and Rodríguez-Trejo (2009), who point out that the survival of *P. hartwegii* seedlings increases when nurse plants are used to promote a more favorable microclimate at these altitudes, both for germination and survival. Therefore, the use of *Lupinus montanus* Kunth nurse plants integrated to reforestation programs in the *Nevado* of *Toluca* WPA is recommended in this type of forests.

In terms of tree diameter, the present study highlights the absence of the 65-75 cm and 75-85 cm diameter classes within the altitudinal range of 3 400 to 3 600 m, which suggests the presence of some natural or anthropogenic disturbance. Baéz *et al.* (2015) document that regional patterns in the structure and dynamics of high mountain forests at various altitudinal gradients are due to the interaction of biotic and abiotic factors with land use history. This would corroborate that, in general, *P. hartwegii* forests in the *Nevado* of *Toluca* WPA are exposed to degradation by activities such as legal and illegal logging, overgrazing, and burning of pastures, among others (Endara *et al.*, 2012; Pérez-Suárez *et al.*, 2022), which bring about alterations in their structural patterns.

Regarding the distribution of *BA*, significant differences ($p<0.05$) were only observed between the different diameter classes at 3 400 masl (Table 1), with the highest record at that altitude and at 3 800 m, with a *BA* of approximately 9 m^2 ha^{-1} for the diameter class of 55 to 65 cm. This coincides with the fact that, at the same altitude (3 800 m), the highest *TD* value was obtained for individuals of the smallest diameter class (5-15 cm), which is characteristic of sites where such silvicultural practices as reforestation are applied. This was confirmed *in situ* (in field) by the symmetrical arrangement observed in the smaller trees and the presence of a few individuals with larger diameters.

The few trees with larger diameters (of over 55 cm in diameter) along the entire sampled altitudinal gradient were the parent or seed trees, which had the best dasometric and phenotypic characteristics; however, they may also be the trees that are being extracted illegally. This is inferred from the damage observed in the remaining individuals in the study sites as indicative of inadequate cutting, such as extreme detachment of the bark, loss of branches and new foliage, which have been observed before in the study area (Regil *et al.*, 2014). This would limit seed production and dispersal, a fact observed in other studies for the same area (Endara, 2007). And, undoubtedly, it would directly affect the forest structure along the altitudinal gradient, generating a less complex tree structure, due to the low regeneration derived from urban expansion and the selective extraction of trees (Regil *et al.*, 2014).

Shrub and herbaceous structure and composition

The shrub stratum, characterized in the sampling area by two main diameter classes: a) 2.5 to 5.0 cm and b) greater than 5.0 cm in diameter, showed that only the *TD* of shrubs with diameters of the second diameter class differed significantly (p<0.05) between altitudinal levels (Table 3). The greater value observed in *TD* was at 3 700 masl, both for shrubs of the first and second diameter class, with 44 and 31 individuals ha^{-1}, respectively. A similar behavior was observed for *BA*, that is, the highest value for both diameter classes was recorded at the same altitudinal level (3 700 m). The absence of shrubs belonging to these two diameter classes between 3 800 and 4 000 m of altitude is noteworthy (Table 3). This would indicate that the shrub structure may be compromised by disturbance events such as grazing, fatwood extraction, reforestation, or by management practices.

Table 3. Tree density (*TD*, trees ha^{-1}) and basal area (*BA*, m^2 ha^{-1}) of shrubs between 2.5–5.0 cm and above 5 cm in diameter per altitudinal level established at every 100 m between 3 400 and 4 000 m, in the *Nevado* of *Toluca* WPA.

Diameter category range	**Variable**	**Altitude (m)**						
		3 400	**3 500**	**3 600**	**3 700**	**3 800**	**3 900**	**4 000**
2.5-5.0 cm	*BA*	0.03	0.07	0.01	0.27	0.00	0.00	0.00
		±0.01	±0.06	±0.01	±0.01	±0.16	±0.00	±0.00
	TD	13.00	6.00	6.00	44.00	0.00	0.00	0.00
		±7.21	6.25	6.25	±29.53	±0.00	±0.00	±0.00
>5 cm	*BA*	0.00	0.04	0.17	0.23	0.00	0.00	0.00
		±0.00	0.03	0.16	±0.08	±0.00	±0.00	±0.00
	TD	0.00	13.00	0.00	31.00	0.00	0.00	0.00
		±0.00	12.50	0.00	±11.96	±0.00	±0.00	±0.00

In the herbaceous stratum, different types of vegetation cover were observed: grasses, ferns, mosses and herbs in general, which were present at all altitudinal levels, with the exception of ferns (Table 4). The plants that exhibited the highest proportion were grasses for all altitudinal levels (Table 4), in a proportion of approximately 80 %, indicating that this type of plants has a high association with the *P. hartwegii* forest in the *Nevado* of *Toluca* WPA along the sampled altitudinal gradient, without resulting in significant changes in the structure of the forest. This coincides with Calderón de Rzedowski and Rzedowski (2010), who point out that the pastures that are mainly associated with *P. hartwegii* are *Calamagrostis tolucensis* (Kunth) Trin. ex Steud., *Muhlenbergia macroura* (Kunth) Hitchc. and *Festuca tolucensis* Kunth, all of which were found the study area (Royo and Carson, 2006).

Table 4. Percentages of various plant covers (%) found in association in the herbaceous stratum along an altitudinal gradient of 3 400 to 4 000 masl in the *Nevado* of *Toluca* WPA.

Altitude (m)	Gramineae (%)	Ferns (%)	Moss (%)	Lichens (%)	Herbs (%)
3 400	73	0	18	10	3
3 500	70	1	2	0	25
3 600	84	0	3	4	11
3 700	31	0	8	8	14
3 800	49	0	8	13	10
3 900	80	0	14	3	8
4 000	73	0	18	10	3

Conclusions

Pinus hartwegii forests in the *Nevado* of *Toluca* WPA continue to maintain their abundance and dominance within the altitudinal range of 3 400 to 4 000 m, specifically between 3 700 and 4 000 m, where they continue to form monospecific forests. This species contributes 100 % to the structural composition of the forest only between the altitudes of 3 900 and 4 000 m. Below this interval, its value and importance in the forest structure are significantly reduced (by up to 45 %), which is evidence of an important altitude-related structural change, mainly due to extreme anthropic activities. Therefore, we suggest a differential management based on the structure and permissible activities by altitude that will affect neither the dynamics of the forest and its regeneration nor the sustainability of the forest that has been compromised by the accumulated deterioration in its structure and function. We conclude that altitude is an important variable to be considered in management plans for high mountain forests.

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Conflict of interest

The authors declare that they have no conflicts of interest.

Contribution by author

Griselda Chávez-Aguilar and Marlín Pérez-Suárez: original idea of the study, supervision and field work, data analysis and writing of the manuscript; Gisela Virginia Campos-Ángeles: data analysis, writing and revision of the document.

References

Báez, S. and S. L. Collins. 2008. Shrub invasion decreases diversity and alters community stability in northern Chihuahuan Desert plant communities. PLOS ONE 3(6):e2332. Doi: 10.1371/journal.pone.0002332.

Báez, S., A. Malizia, J. Carilla, C. Blundo, … and K. J. Feeley. 2015. Large-scale patterns of turnover and basal area change in Andean forests. PLOS ONE 10(5):e0126594. Doi: 10.1371/journal.pone.0126594.

Bhutia, Y., R. Gudasalamani, R. Ganesan and S. Saha. 2019. Assessing forest structure and composition along the altitudinal gradient in the State of Sikkim, Eastern Himalayas, India. Forests 10(8):633. Doi: 10.3390/f10080633.

Calderón de Rzedowski, G. y J. Rzedowski. 2010. Flora fanerogámica del Valle de México. Instituto de Ecología, A. C. y Comisión Nacional para el Conocimiento y Uso de la Biodiversidad. Xalapa, Ver., México. 975 p.

Challenger, A. y J. Soberón. 2008. Los ecosistemas terrestres. In: Soberón, J., G. Halffter y J. Llorente-Bousquets (comps.). Capital natural de México, Vol. I: Conocimiento actual de la biodiversidad. Comisión Nacional para el Conocimiento y Uso de la Biodiversidad (Conabio). Tlalpan, D. F., México. pp. 87-108.

Comisión Nacional Forestal (Conafor). 2012. Inventario Nacional Forestal y de Suelos, Manual y procedimientos para el muestreo de campo, re-muestreo 2012. Comisión Nacional Forestal y Secretaría de Medio Ambiente y Recursos Naturales. Zapopan, Jal., México. 140 p.

Corella J., F., J. I. Valdez H., V. M. Cetina A., F. V. González C., A. Trinidad S. y J. R. Aguirre R. 2001. Estructura forestal de un bosque de mangles en el noreste del estado de

Tabasco, México. Ciencia Forestal en México 26(90):73–102. http://cienciasforestales.inifap.gob.mx/index.php/forestales/article/view/914. (12 noviembre de 2021).

Durán-Medina, E., J. F. Mas and A. Velázquez. 2005. Land use/cover change in community-based forest management regions and protected areas in Mexico. In: Bray, D. B., L. Merino-Pérez y D. Barry (eds.). The Community Forests of Mexico, Managing for Sustainable Landscapes. University of Texas Press. Austin, TX, USA. pp. 215-238.

Endara A., A. R. 2007. Estructura forestal de *Pinus hartwegii* en el Parque Nacional Nevado de Toluca. Tesis de Maestría. Centro de Investigación en Ciencias Agropecuarias y Rurales, Universidad Autónoma del Estado de México. Toluca, Edo. Méx., México. 76 p.

Endara A., A. R., S. Franco M., G. Nava B., J. I. Valdez H. and T. S. Fredericksen. 2012. Effect of human disturbance on the structure and regeneration of forests in the Nevado de Toluca National Park, Mexico. Journal of Forestry Research 23(1):39-44. Doi: 10.1007/s11676-012-0226-8.

Farjon, A. and D. Filer. 2013. An atlas of the world's conifers: An analysis of their distribution, biogeography, diversity and conservation status. Brill. Leiden, ZH, The Netherlands. 512 p.

Farjon, A., J. A. Pérez de la R. y B. T. Styles. 1997. Guía de Campo de los Pinos de México y América Central. The Royal Botanic Gardens, Instituto Forestal de Oxford y Universidad de Oxford. Grimbergen, BF, Bélgica. 151 p.

Franco M., S., H. H. Regil G., C. González E. y G. Nava B. 2006. Cambio de uso del suelo y vegetación en el Parque Nacional Nevado de Toluca, México, en el periodo 1972-2000. Investigaciones Geográficas, Boletín del Instituto de Geografía, UNAM (61):38–57. http://www.scielo.org.mx/scielo.php?script=sci_arttext&pid=S0188-46112006000300004. (3 enero de 2022).

Gadow, K. v., C. Y. Zhang, C. Wehenkel, A. Pommerening, … and X. H. Zhao. 2012. Forest Structure and Diversity. In: Pukkala, T. and K. v. Gadow (eds.). Continuous Cover Forestry. Managing Forest Ecosystems. Springer. Dordrecht, ZH, The Netherlands. pp. 29–83.

García, E. 2004. Modificaciones al sistema de clasificación climática Köppen. Serie Libros, Núm. 6. Instituto de Geografía, Universidad Nacional Autónoma de México. Coyoacán, D. F., México. 91 p.

Girardin, C. A. J., Y. Malhi, L. E. O. C. Aragão, M. Mamani, … and R. J. Whittaker. 2010. Net primary productivity allocation and cycling of carbon along a tropical forest elevational transect in the Peruvian Andes. Global Change Biology 16(12):3176–3192. Doi: 10.1111/j.1365-2486.2010.02235.x.

Gómez D., J. A. y F. Villalobos. 2020. Montañas: cómo se definen y su importancia para la biodiversidad y la humanidad. CIENCIA ergo-sum 27(2):e88. Doi: 10.30878/ces.v27n2a9.

Granados R., G. R., A. Toscana A. y A. Villaseñor F. 2018. Recategorización del Nevado de Toluca: Elementos escénicos y turismo. Teoría y Praxis (26):36-66. http://www.teoriaypraxis.uqroo.mx/doctos/numero26/Granados_etal.pdf. (10 de septiembre de 2022).

Homeier, J., S. W. Breckle, S. Günter, R. T. Rollenbeck and C. Leuschner. 2010. Tree diversity, forest structure and productivity along altitudinal and topographical gradients in a species-rich Ecuadorian Montane Rain Forest. Biotropica The Scientific Journal of the ATBC 42(2):140-148. Doi: 10.1111/j.1744-7429.2009.00547.x.

Hu, M., A. Lehtonen, F. Minunno and A. Mäkelä. 2020. Age effect on tree structure and biomass allocation in Scot pine (*Pinus sylvestris* L.) and Norway spruce (*Picea abies* [L.] Karst.). Annals of Forest Science 77(3):90-104. Doi: 10.1007/s13595-020-00988-4.

Iglesias A., L. G., J. Alba L. y J. L. Enríquez. 2000. Estrategias para la conservación de la población de *Pinus hartwegii* Lindl. en la región del Perote, Veracruz. Cuadernos de Biodiversidad 4:4-8. Doi: 10.14198/cdbio.2000.04.01.

Jafari, S. M., S. Zarre and S. K. Alavipanah. 2013. Woody species diversity and forest structure from lowland to montane forest in Hyrcanian forest ecoregion. Journal of Mountain Science 10(4):609–620. Doi: https://doi.org/10.1007/s11629-013-2652-2.

Jobbágy, E. G. and R. B. Jackson. 2000. The vertical distribution of soil organic carbon and its relation to climate and vegetation. Ecological Applications: Ecological Society of America 10(2):423–436. Doi: 10.1890/1051-0761(2000)010[0423:TVDOSO]2.0.CO;2.

Körner, C. and J. Paulsen. 2004. A world-wide study of high altitude treeline temperatures. Journal of Biogeography 31(5):713–732. Doi: 10.1111/j.1365-2699.2003.01043.x.

Manzanilla-Quiñones, U., Ó. A. Aguirre-Calderón, J. Jiménez-Pérez, E. J. Treviño-Garza y J. I. Yerena-Yamallel. 2019. Distribución actual y futura del bosque subalpino de *Pinus hartwegii* Lindl en el Eje Neovolcánico Transversal. Madera y Bosques 25(2):e2521804. Doi: 10.21829/myb.2019.2521804.

McElhinny, C., P. Gibbons, C. Brack and J. Bauhus. 2005. Forest and woodland stand structural complexity: its definition and measurement. Forest Ecology Management 218(1-3):1–24. Doi: 10.1016/j.foreco.2005.08.034.

Mostacedo, B. y T. S. Fredericksen. 2000. Manual de métodos básicos de muestreo y análisis en ecología vegetal. BOLFOR. Santa Cruz de la Sierra, SC, Bolivia. 87 p. https://pdf.usaid.gov/pdf_docs/PNACL893.pdf. (10 diciembre de 2018).

Pérez-Suárez, M., J. E. Ramírez-Albores, J. J. Vargas-Hernández and F. U. Alfaro-Ramírez. 2022. A review of the knowledge of Hartweg's Pine (*Pinus hartwegii* Lindl.): current situation and the need for improved future projections. Trees 36(1):25-37. Doi: 10.1007/s00468-021-02221-9.

Ramírez-Contreras, A. y D. A. Rodríguez-Trejo. 2009. Plantas nodriza en la reforestación con *Pinus hartwegii* Lindl. Revista Chapingo Serie Ciencias Forestales y del Ambiente 15(1):43–48. http://www.scielo.org.mx/scielo.php?script=sci_arttext&pid=S2007-40182009000100005. (30 enero de 2022).

Ramírez-Huerta, L., C. M. López-Guzmán, V. J. Arriola-Padilla, Z. Trejo-Sandoval, R. Pérez-Miranda y C. L. Jiménez-Sierra. 2016. La investigación en las Áreas Naturales Protegidas de la Región Centro y Eje Neovolcánico Transversal de México. Áreas Naturales Protegidas Scripta 2(2):37–66. Doi: 10.18242/anpscripta.2016.02.02.02.0003.

Regil G., H. H., S. Franco M., J. A. B. Ordóñez D., G. E. Nava B. y C. Mallén R. 2014. Procesos de deforestación y reducción de densidad del arbolado del parque nacional nevado de Toluca. Revista Mexicana de Ciencias Forestales 5(23):42–62. Doi: 10.29298/rmcf.v5i23.341.

Royo, A. A. and W. P. Carson. 2006. On the formation of dense understory layers in forests worldwide: consequences and implications for forest dynamics, biodiversity, and succession. Canadian Journal of Forest Research 36(6):1345-1362. Doi: 10.1139/x06-025.

Secretaría de Medio Ambiente y Recursos Naturales (Semarnat). 2016. Acuerdo por el que se da a conocer el Resumen del programa de Manejo del Área Natural Protegida con categoría de Protección de Flora y Fauna Nevado de Toluca. Diario Oficial de la Federación, Segunda y Tercera secciones, 21 de octubre de 2016. https://www.conanp.gob.mx/que_hacemos/pdf/programas_manejo/RESUMEN_NEVADO_TOLUCA.pdf. (1 de enero de 2017).

Seidler, R. 2017. Patterns of biodiversity change in anthropogenically altered forests. In: Roitberg, B. D. (ed.). Reference Module in Life Sciences. Elsevier. Amsterdam, NH, The Netherlands. pp. 1–17.

Sharma, J., S. Upgupta, M. Jayaraman, R. K. Chaturvedi, G. Bala and N. H. Ravindranath. 2017. Vulnerability of forests in India: A national scale assessment. Environmental Management 60(3):544–553. Doi: 10.1007/s00267-017-0894-4.

Statistical Analysis System. 2009. SAS© Web Report Studio 4.2: User´s Guide. SAS Institute Inc. Cary, NC, USA. 310 p.

Unger, M., J. Homeier and C. Leuschner. 2012. Effects of soil chemistry on tropical forest biomass and productivity at different elevations in the equatorial Andes. Oecologia 170(1):263–274. Doi: 10.1007/s00442-012-2295-y.

Waddell, E. H., L. F. Banin, S. Fleiss, J. K. Hill, … and D. S. Chapman. 2020. Land-use change and propagule pressure promote plant invasions in tropical rainforest remnants. Landscape Ecology 35(9):1891-1906. Doi: 10.1007/s10980-020-01067-9.