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Research article

Changes of the vegetation structure and composistion along an altitudinal and antropogenic gradiente

Cambios en la estructura y composición de la vegetación en un gradiente altitudinal y antrópico

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Abstract

Few studies have examined how human activities influence the structure and composition of vegetation ecological patterns along altitudinal gradients, to identify areas with different resilience or susceptibility. This study evaluated the impact of anthropogenic effects on the composition and structure of an *Abies religiosa* forest in the *Magdalena* River basin, near Mexico City. We established 15 plots, each measuring 30×30 m2, at three different altitudes: high (3 449 masl), intermediate (3 202 masl), and low (3 092 masl). Some environmental variables and calculated indexes of anthropogenic disturbances, including human activities, livestock presence and deforestation were assumed. Changes in composition and structure were analyzed using a dissimilarity model and multivariate analysis. Our findings recorded a total of 42 species, consisting of eight tree species and 34 herb species. Notably, mid-altitude plots, despite experiencing a high level of livestock activities, displayed greater species richness in both the understory and canopy. The trees in these plots, ranging from 20 to 40 m high, contributed to a larger basal area and showed a direct response to light and temperature. In contrast, the lower-altitude plots had the greatest basal area attributed to trees around 10 m tall. The results showed that altitude and anthropogenic disturbance are determining factors in the patterns of plant diversity and composition, in the canopy structure and in the understory.

Key words: Biomass, temperate forest, canopy, understory, dissimilarity, resilience.

Resumen

Son pocos los estudios que han evaluado cómo las actividades antropogénicas modifican los patrones de estructura y composición en la vegetación a lo largo de gradientes de altitud, para la identificación de zonas con distinta resiliencia y susceptibilidad. En este estudio se evaluaron los efectos antrópicos en la composición y estructura de un bosque de *Abies religiosa*, en la cuenca del río Magdalena, en la Ciudad de México. Se establecieron 15 parcelas de 30×30 m^2 en tres cotas altitudinales: alta (3 449 msnm), intermedia (3 202 msnm) y baja (3 092 msnm). Se determinaron variables ambientales e índices de perturbación antropogénicos (actividades humanas, de ganado y deforestación). A través de un modelo de disimilitud y un análisis multivariado, se evaluaron los cambios de composición y estructura. De acuerdo con los resultados se registraron 42 especies (ocho arbóreas y 34 herbáceas). Las parcelas de altitud media a pesar de tener una alta intervención del ganado mostraron mayor riqueza de especies, tanto para el sotobosque como para el dosel, con árboles de 20 a 40 m de altura que aportan mayor área basal y tienen una respuesta directa a la luz y la temperatura. Mientras que, en las parcelas de menor altitud, la mayor área basal correspondió a árboles de alrededor de 10 m de altura. Los resultados demostraron que la altitud y la perturbación antropogénica son factores determinantes en los patrones de diversidad y composición vegetal, tanto en la estructura del dosel como en el sotobosque.

Palabras clave: Biomasa, bosque templado, dosel, sotobosque, disimilitud, resiliencia.

Introduction

Temperate forests promote the provision of ecosystem services, such as water and climate regulation, in addition to supporting biodiversity (Castillo-Argüero et al., 2016). In these ecosystems, structure, defined as the vertical and horizontal configuration and distribution of vegetation (Pommerening, 2002), generates microhabitats for the coexistence of species (Smyčková et al., 2024). On the contrary, in areas with anthropogenic disturbance, the loss of tree biomass often favors a uniform structure that reduces species diversity. However, the relationship between disturbance and diversity is not always linear; the loss of tree cover can generate available niches for species (Silva-González et al., 2024a). According to the intermediate disturbance hypothesis, intermediate levels of disturbance can favor greater diversity, due to the competitive reduction between species (Connell, 1978). For example, in the state of *Durango*, Silva-González et al. (2024b) showed that forests subjected to silvicultural management present greater diversity, without significantly altering the structure (density, basal area, volume).

Along altitudinal gradients, it has been proposed that higher altitude areas exhibit lower species richness due to lower temperatures and decreased soil nutrient availability (Worku et al., 2023; Yirga et al., 2019). These trends suggest that higher altitude areas may be more prone to species loss due to disturbances (Worku et al., 2023; Yirga et al., 2019). However, recent empirical evidence demonstrates that the response of tree and understory vegetation is highly dependent on the elevational range (Worku et al., 2023). Different patterns have been documented along altitudinal gradients in Mexico. In a pine-oak forest in the state of *Oaxaca* (1 900-2 850 masl), tree structure in terms of basal area, height, and cover increases in relation to altitude (Velasco-Luis et al., 2023). On the other hand, along a broader altitudinal gradient in the state of *Guerrero* (450-2 800 m), a U-shaped pattern was recorded, where species richness was higher at the extremes of the gradient and lower at intermediate altitudes (Ávila-Sánchez et al., 2018).

Understanding the relationships between biomass and structure of temperate forests across elevational gradients is key to identifying areas more susceptible to changes in species composition (Worku et al., 2023; Yirga et al., 2019). While community assessments using species counts per site (species richness) and their incidence of individuals (abundance) have allowed for the description of community patterns, they do not include the contribution of species biomass and cover, which can be modified by anthropogenic disturbances (De Cáceres et al., 2013; Holopainen & Kalliovirta, 2006). Therefore, approaches that simultaneously assess diversity and structure are needed to fully characterize vegetation response. The statistical framework proposed by De Cáceres et al. (2013) allows for a joint assessment of vegetation composition, abundance, and structure, as it integrates data on dissimilarity between communities.

The *Abies religiosa* (Kunth) Schltdl. & Cham. temperate forest in the *Magdalena* River basin, Mexico City, is a strategic ecosystem in the study of disturbances, as it is one of the last remaining forests in the city (Ávila-Akerberg, 2004; Castillo-Argüero et al., 2016). Despite its importance, it experiences continuous disturbances due to its proximity to the urban area, which jeopardizes its role as a provider of ecosystem services (Ávila-Akerberg, 2004; Castillo-Argüero et al., 2016). Understanding how these plant communities respond to disturbance is key to anticipating changes in their structure and composition. Therefore, the objective of this study was to determine the environmental effect of altitude and the intensity of anthropogenic disturbances on species composition and structure, in terms of height, basal area, and canopy and understory cover. In this context, the study hypothesis is that altitude and the intensity of anthropogenic disturbances are limiting factors in vegetation composition and structure. Therefore, in higher altitude areas, the effects of anthropogenic disturbance are expected to promote lower species richness, basal area, cover, and height in the canopy and understory, compared to lower altitude areas.

Materials and Methods

Study area

The *Abies religiosa* temperate forest of the *Magdalena* River basin is located in the Southwest of the Valley of Mexico (between 19°13’53”-19°18’12” N and 99°14’50”-

99°20′30″ W) and covers 3 100 ha. This site has a temperate subhumid climate (C(w_2)(w)b(i')) with an average temperature of 13 °C. Annual precipitation ranges between 950 and 1 300 mm (Instituto Nacional de Estadística, Geografía e Informática [INEGI], 2010). It is located within Mexico City's designated conservation area, the site shows evidence of deforestation driven by the unauthorized timber extraction and land-use changes for livestock farming (Castillo-Argüero et al., 2016).

Sampling design

Anthropogenic disturbances. In the *A. religiosa* forest, 15 plots measuring 30×30 m (13 500 m^2 total) were randomly selected. At three altitudes (high=3 449 masl, plots 1 to 5; intermediate=3 202 masl, plots 6 to 10; low=3 092 masl, plots 11 to 15), the main agents of anthropogenic disturbance were classified: livestock (GA), human activity (HA), and habitat deterioration (HD). For the variable GA, the number of m^2 with cattle droppings, cattle roads (distance between roads and plots) and soil compaction were quantified by calculating the apparent density. For this, three independent soil samples were obtained with a corer (model SC900soil FieldScout®) (106.02 cm^3), each with an approximate weight of 250 g. The samples were oven-dried (model FM-392 Felisa®) (105 °C) for 24 h and then weighed (model 311-00 Ohaus Trimple Beam®). The apparent density was obtained using the Keller and Håkansson (2010) Equation:

$$DA = \frac{100 \times DS}{V} \times 100 \qquad (1)$$

Where:

DA = Bulk density (g cm^3)

DS = Weight of dry soil (g)

V = Volume of the cylinder (cm^3)

For the HD, the square meters with weeding (slashing) were quantified, measured as the number of square meters with bare soil and evidence of vegetation residues. Deforestation and canopy opening were measured as the number of square meters with stumps relative to areas without tree cover. For the HA, the number of square meters with inorganic litter, organic litter, and distance to roads were quantified (Martorell & Peters, 2005). The distance to nearby roads was quantified as the reciprocal of the distance (m) between plots and the two nearest human paths. The anthropogenic disturbance indices (GA, HA, and HD) were obtained by dimension reduction with a Principal components analysis (PCA) following the methodology proposed by Martorell and Peters (2005), in the statistical program R version 4.2 (R Development Core Team, 2024). The index of each disturbance agent was calculated from the sum of the scores in the first component. The sum of the indices of the three agents allowed obtaining the total disturbance index per plot.

Environmental variables. The following environmental variables were measured during both the rainy and dry seasons: daylight, temperature, and humidity, as well as soil chemical properties: N, P, K, pH, organic matter (*OM*), and electrical conductivity (*EC*).

To measure site temperature, a HOBO® Data Logger temperature sensor (model 2016, easy LogUSB-ONSET, Massachusetts, USA) was placed in the center of each plot for one year. Daylight was calculated by taking three hemispherical photographs per frame using a model D80 Nikon® camera with an EX SIGMA 4.5 1:28 DC HSM lens (model D80 Nikon® digital camera, fisheye lens EX SIGMA 4.5 2:28 DCHSM, Tokyo, JP) during the months of July–September (rainy season) and March–May (dry season). These photographs were taken at 8:00 a. m. with the upper part of the lens pointed toward geographic north. The photographs were analyzed using Gap Light Analyzer GLA 2.0 software (Frazer et al., 1999) to determine the amount of light transmitted by the global site factor (GSF; moles of light), defined as the percentage of total light transmission in moles (Frazer et al., 1999).

Two groups of soil samples were taken from each plot during the months of July (rainy) and May (dry): three samples for moisture analysis and three for soil chemical analysis. For each group of three samples, two were obtained from the corners of the plot and one from the center of the plot, systematically to a depth of approximately 30 cm using a corer (model SC900soil FieldScout®). It should be noted that these samples were taken independently from the GA soil compaction analysis. For soil moisture analysis, samples were weighed and oven-dried (model FM-392 Felisa®) at 100 °C for three days to record the dry weight (model 311-00 Ohaus Trimple Beam®). Soil moisture was determined using the Reynolds (1970) Equation:

$$H\% = \frac{PeHu - PeSe}{PeSe} \times 100 \qquad (2)$$

Where:

$H\%$ = Soil moisture

$PeHu$ = Weight of wet soil

$PeSe$ = Weight of dry soil

To determine the soil's chemical characteristics, the samples were sent to the Soil Fertility Laboratory of the *Colegio de Postgraduados* (*Colpos*) (Graduate Studies School) *Montecillo Campus*. The variables analyzed were: pH in water (1:2 ratio), electrical conductivity (*EC*) in water (1:5 ratio), measured with a conductivity bridge; percentage of organic matter (*OM*) by wet digestion; concentration of available inorganic phosphorus according to Olsen et al. (1954), extracted with 0.5 M $NaHCO_3$ at pH 8.5 and determined colorimetrically; and percentage of nitrogen, determined by wet digestion with sulfuric acid and semi-micro Kjeldahl steam distillation, followed by titration with 0.05 N sulfuric acid (Bradstreet, 1954).

Vegetation structure and composition

In each plot, the height, diameter at breast height (*DBH*, 1.30 m), and two perpendicular crown diameters (North-South and East-West) (model 14393 Truper$^{®}$ tape measure) of the trees were measured. Height was recorded with a pistol (model LaserAce 100 Trimble$^{®}$) and *DBH* was measured with a model 283D Forestry

Suppliers® diameter tape. For each tree species, biomass was determined using previously available allometric equations (Table 1), and basal area was determined using the following equation (Equation 3) (Mostacedo & Fredericksen, 2000):

Table 1. Formulas for estimating tree species biomass. The biomass formulas for each species are shown, considering the standard diameter (*SD*) at a height of 1.30 m, its reference area and location.

Tree species	Biomass formula	Reference	Location
Abies religiosa (Kunth) Schltdl. & Cham.	$(0.0754)\times(DAP^{\ 2.513})$	Avendaño-Hernández et al. (2009)	*Tlaxcala*
Buddleja cordata Kunth	$(260.343)\times\frac{(3.1416\times(DAP^{2}))}{4}^{1.036}$	Cano-Santana (1994)	Mexico City
Buddleja parviflora Kunth	$(258.487)\times\frac{(3.1416\times(DAP^{2}))}{4}^{0.968}$	Cano-Santana (1994)	Mexico City
Cupressus lusitanica Mill.	$0.5266\times(DAP^{1.7712})$	González-Iturbe (2019)	*Puebla*
Garrya laurifolia Hartw. *ex* Benth.	$e^{-2.14+2.23\times ln(DAP)}$	Gobierno del Distrito Federal (2000)	Mexico City
Pinus aff. ayacahuite C. Ehrenb. ex Schltdl.	$((0.5306\times DAP)^{2})-(2.2519\times DAP)+16.086$	Arias-Téllez and García-Martínez (2017)	State of Mexico
Salix paradoxa Kunth	$e^{-2.2094+2.3867\times ln(DAP)}$	Chojnacky et al. (2014) Jenkins et al. (2003)	North America
Sambucus nigra L.	$(0.180506\times DAP)^{0.7987}$	Dyderski and Jagodziński (2019) Jagodziński et al. (2019)	United States of America

DAP = Diameter at height 1.30 m; *ln* = Natural logarithm.

$$AB = \frac{\pi DAP^2}{4} \qquad (3)$$

Where:

π = 3.1416

AB = Basal area (m^2)

DAP = Diameter at breast height (*DBH*)

Tree, shrub, and herbaceous species were identified by comparing them with specimens from the microherbarium of the Community Dynamics Laboratory of the Graduate School of Sciences at *Universidad Nacional Autónoma de México* (*UNAM*) and using the descriptions of Calderón de Rzedowski and Rzedowski (2001). The understory included tree seedlings resulting from natural regeneration and herbaceous and shrub species less than 1.57 m tall, while the tree stratum was characterized by trees taller than 1.57 m. The species cover of the understory was determined based on the assumption that the canopy cover of each individual tends to be a circle: the two perpendicular diameters of the species' canopy (D1 and D2) were calculated using Equation 4 (Mueller–Dombois & Ellenberg, 1976).

$$C = \pi\frac{D1+D2^2}{4} \qquad (4)$$

Where:

D1 = Crown diameter 1

D2= Crown diameter 2

π = 3.1416

Statistical analysis

A Canonical correspondence analysis (CCA) with 999 permutations ($P<0.05$) was performed to observe the relationship between species abundances and environmental factors, and a Principal components analysis (PCA) was performed to determine the environmental effect on structure. These analyses were performed using the statistical package Vegan 2.7-2 (Oksanen et al., 2025).

A structure and composition dissimilarity analysis was applied according to the method proposed by De Cáceres et al. (2013) with the vegclust package version 1.1, which considers the structure values of each species weighted by the overall structure in the sampled community. Thus, species-specific structural variables are simplified into *s*-ordered size classes (or vertical strata), and the abundance of each species within each size class is relative to the basal area for canopy species and to the understory cover ($t=1, \ldots, s$). CAP is defined as the vector of values defined by *s*, and the value for a given class *t* is the sum of the species abundances across all classes (Equation 5).

$$CAP = \sum_{u=t}^{s} x(u) \qquad (5)$$

Where:

CAP = Vector of values

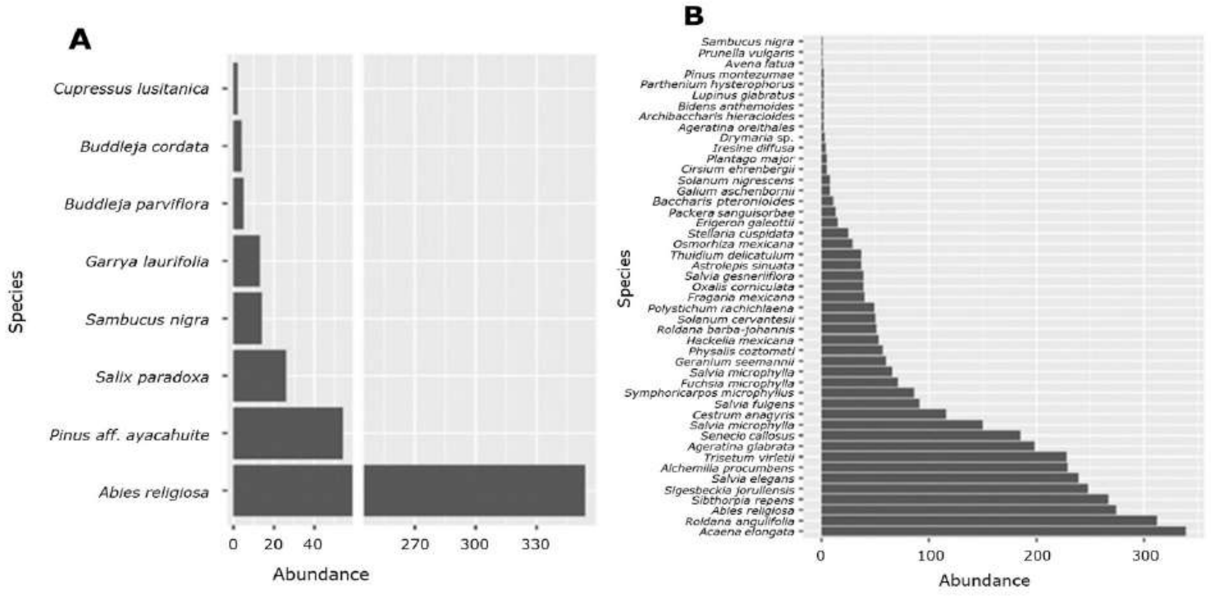
x(u) = Recorded abundance of the target species in the size class

All analyses were performed using the statistical software R version 4.2 (R Development Core Team, 2024).

Results

Composition of the *Abies religiosa* forest

Eight tree species were identified in the study area, the most dominant being *Abies religiosa* with 356 individuals, *Pinus aff. ayacahuite* C. Ehrenb. *ex* Schltdl. with 54 individuals, and *Salix paradoxa* Kunth with 26 individuals (Figure 1A). In the understory, 34 species were recorded, with the most abundant being the shrubs *Acaena elongata* L., with 339 individuals and *Roldana angulifolia* (DC.) H. Rob. & Brettell, with 312 individuals, as well as the herbaceous species *Sibthorpia repens* (L.) Kuntze, with 267 individuals and *Sigesbeckia jorullensis* Kunth, with 248 individuals. The species distribution is shown in Figure 1B.

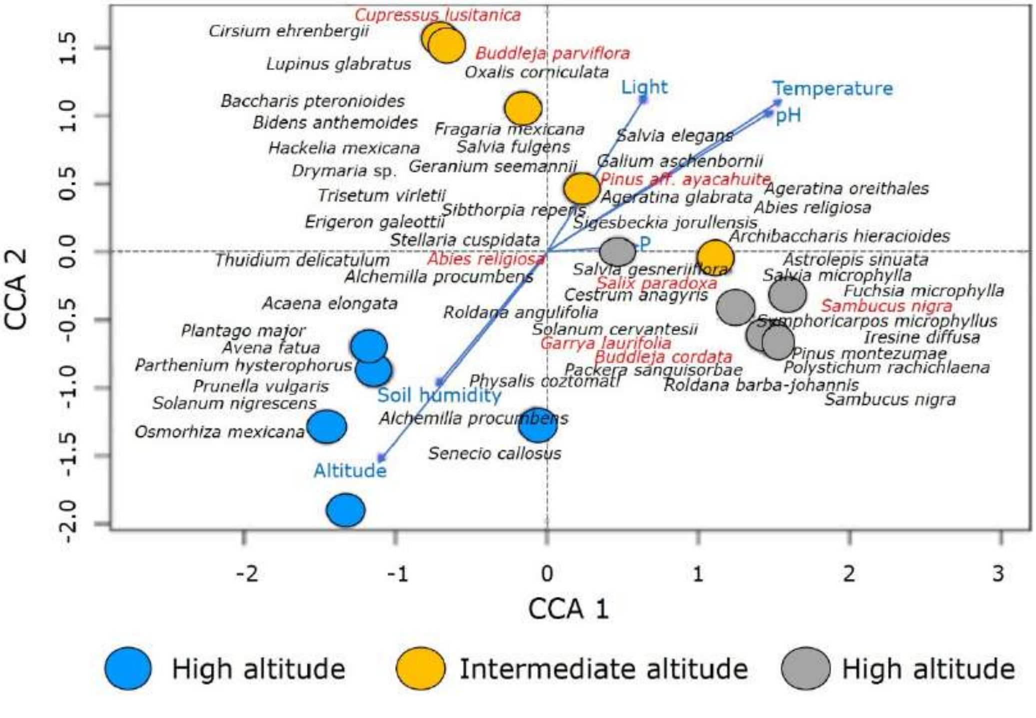


A = Abundance of canopy species; B = Abundance of understory species.

Figure 1. Species abundances (number of individuals).

Species richness and abundance at the three altitudinal levels

The CCA showed a significant relationship between understory and canopy species composition and altitude, temperature, light, phosphorus, pH, and soil moisture ($p<0.005$). Accordingly, at the highest altitude site, a positive association was observed between altitude and soil moisture with the abundance of herbaceous and shrubby weed species, such as *Acaena elongata*, *Plantago major* L. and *Avena fatua* L. (Figure 2), the latter being the most abundant species (Table 2).



P = Phosphorus.

Figure 2. Canonical correspondence analysis (CCA) showing the relationship between significant environmental variables and the species composition of the canopy and understory.

Table 2. Study sites description.

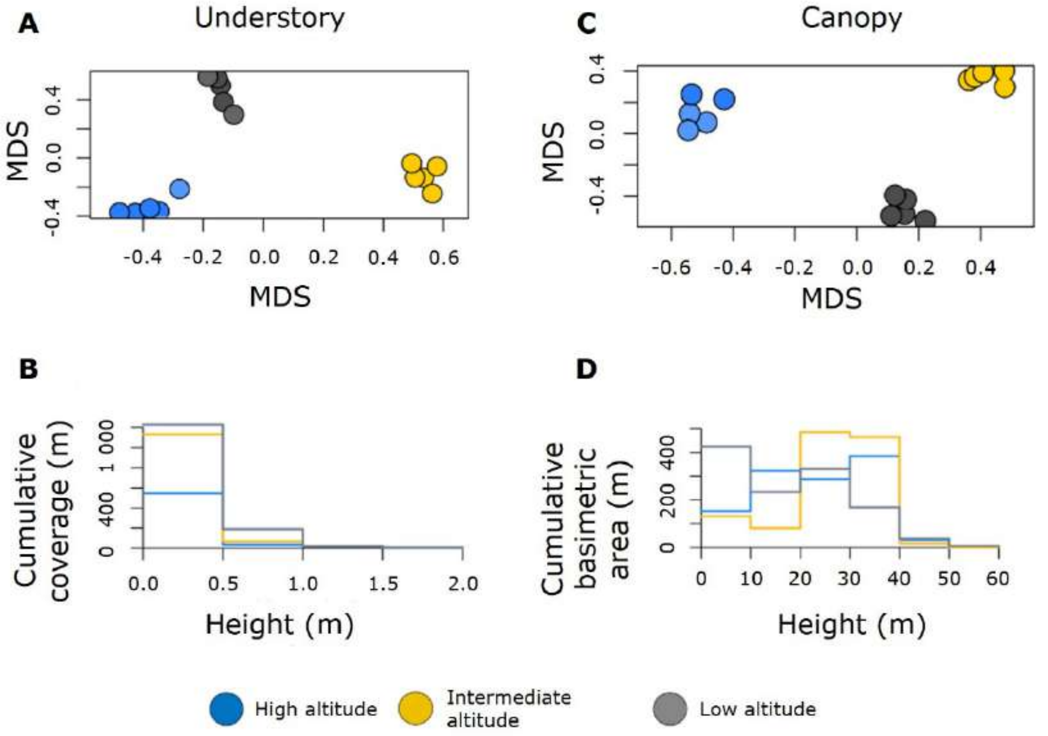
	Site 1: high altitude	**Site 2: Intermediate altitude**	**Site 3: Low altitude**
	Environmental variables		
Altitude	3 449	3 202	3 092
HD	0.933-47.02	-27.48-42.10	-40.1-40.55
HA	-5.67-3.42	-2.57-5.45	-3.55-2.18
GA	-21.80-5.56	18.48-50.67	-19.67-21.95
Temperature	6.73±0.003	9.30±0.093	10.07±0.18
Humidity	48.11±1.79	42.88±3.34	42.54±2.80
	Canopy (abundance-frequency)		
Species richness	2	4	6
Densities of specimens	140	192	139
Species of greatest dominance	*Abies religiosa* (Kunth) Schltdl. & Cham. (trees, 136)	*Abies religiosa* (Kunth) Schltdl. & Cham. (138) *Pinus aff. ayacahuite* C. Ehrenb. *ex* Schltdl. (26)	*Abies religiosa* (Kunth) Schltdl. & Cham. (68) *Pinus aff. ayacahuite* C. Ehrenb. *ex* Schltdl. (6)
	Understory (abundance-frequency)		
Species richness	21	25	22
Densities of specimens	1 050	1 372	1 032
Dominant species	*Abies religiosa* (Kunth) Schltdl. & Cham. (seedlings, 30) *Acaena elongata* L. (206) *Senecio callosus* Sch. Bip. (185)	*Abies religiosa* (Kunth) Schltdl. & Cham. (138) *Sibthorpia repens* (L.) Kuntze (159)	*Abies* religiosa (Kunth) Schltdl. & Cham. (seedlings, 68) *Roldana angulifolia* (DC.) H. Rob. & Brettell (103)

HD = Habitat deterioration; HA = Human activity; GA = Livestock activities.

At the intermediate altitude site, despite a greater predominance of livestock activities (GA), a high richness and abundance of species was recorded (Table 2). In these intermediate-altitude plots, the CCA showed a positive relationship between light, temperature, and soil pH with tree species (*Cupressus lusitanica* Mill., *Buddleja* *parviflora* Kunth and *Pinus aff. ayacahuite*) (Figure 2). A high abundance of *Abies religiosa* seedlings, resulting from natural regeneration, was also observed (Table 2). Meanwhile, the lowest-altitude site exhibited higher temperature values, greater tree species richness, and a direct association with the tree weed *Sambucus nigra* L. (Figure 2).

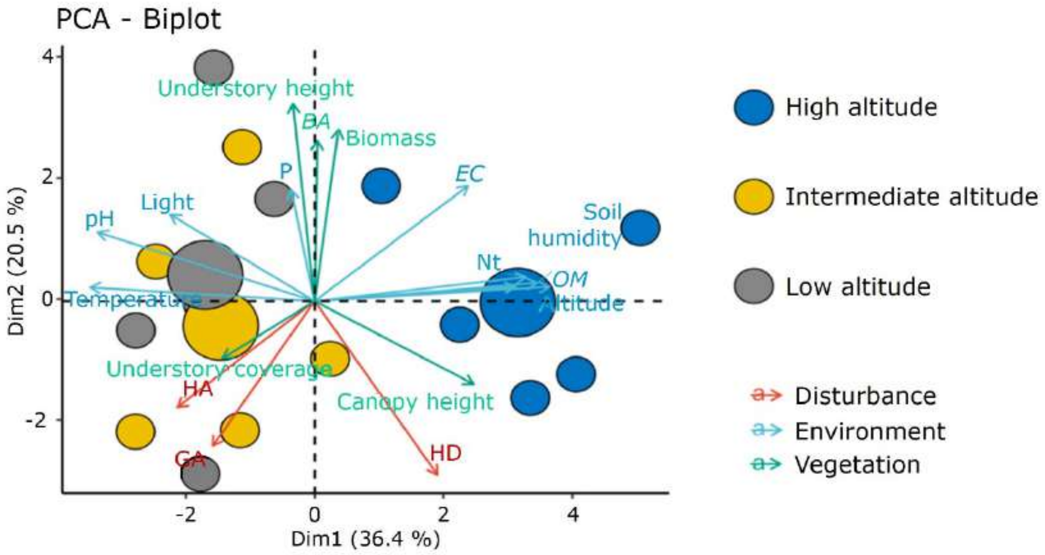
Structural changes along the altitudinal gradient

The dissimilarity analysis by De Cáceres et al. (2013) showed that in all three study sites, seedlings, herbaceous plants and understory shrubs with 0.03 to 0.5 m high of had the greatest cover (Figure 3A and 3B). Significant differences ($P<0.05$) were confirmed in the canopy at the highest altitude site. Trees measuring between 10 and 40 m in height showed higher basal area values (Figure 3C and 3D), while the intermediate altitude site showed a greater contribution of basal area in individuals between 20 and 40 m tall (Figure 3C and 3D), a trend that contrasts with the lowest altitude site, where a greater contribution of basal area was observed in shorter individuals, measuring 1.8 to 10 m (Figure 3C and 3D). The PCA demonstrated that the height of understory species, biomass and basal area of the canopy layer were positively correlated with environmental variables and negatively correlated with anthropogenic activities. Tree height has a positive relationship with habitat degradation (HD) (Figure 4). Meanwhile, the cover of understory species showed a direct relationship with human activities (HA) and livestock grazing (GA).



A = Multidimensional scaling (MDS) of the understory; B = Understory cover and height profile; C = Multidimensional scaling (MDS) of the canopy; D = Canopy basal area and height profile.

Figure 3. Vegetation structure of the understory and canopy.



HD = Habitat deterioration; HA = Human activity; GA = Livestock activities; *OM* = Organic matter; Nt = Total nitrogen; *EC* = Electrical conductivity; P = Phosphorus; *BA* = Basal area.

Figure 4. Principal component analysis (PCA) of the relationship between canopy and understory vegetation structure and environmental and anthropogenic disturbance variables.

Discussion

The species richness of the *Abies religiosa* forest, with 42 species (eight tree species and 34 herbaceous and shrub species), was higher than that recorded in other forests in Mexico, such as those in the state of *Michoacán*, with 39 species (Cornejo-Tenorio

& Ibarra-Manríquez, 2017), and the *Nevado de Toluca* with 33 species (Mejía-Canales et al., 2018) or 36 species (Zepeda-Gómez et al., 2023). This difference can be attributed to the intensity of sampling, as well as the altitudinal ranges considered. In *Michoacán* and *Nevado de Toluca*, the sampling range varies between 2 400 and 4 680 masl, while the altitudinal range in this study was more restricted, between 3 092 and 3 449 masl. However, the richness recorded in this forest was lower than that of other sites in the state of *Jalisco*, with 64 species (Cuevas-Guzmán et al., 2011) and 84 species respectively (Guerrero-Hernández et al., 2014). This is because temperate forests in *Jalisco* have been described as having higher humidity and intermediate disturbance conditions, factors that favor both species richness and vegetation structure.

Regarding species composition, despite the presence of anthropogenic activities, there was a high dominance of native species, among which *Abies religiosa* stands out (356 individuals), both in the tree component and in natural regeneration (seedlings). However, in the understory, the highest abundance values were for *Acaena elongata*, a species considered a native weed and an indicator of anthropogenic disturbance. In addition to other species, such as *Plantago major*, an introduced herbaceous plant (Castillo-Argüero et al., 2016) and the tree weed *Sambucus nigra* (Bonilla-Valencia et al., 2022).

Along the altitudinal gradient, abiotic conditions vary considerably and influence the structure and composition of temperate forests (Silva-González et al., 2024a). In this study, although the mid-altitude site exhibited high levels of livestock activity, these conditions favored high species richness in the understory and canopy, as well as a high abundance of *Abies religiosa* seedlings, suggesting the presence of natural regeneration (Cruzado-Vargas, 2017). This may be due to the greater heterogeneity of mid-altitude regions, resulting from the intersection of microclimates, which promotes the coexistence of species of Nearctic and Neotropical origins and ecological requirements (Worku et al., 2023).

This result is consistent with the findings in the CCA, where a positive relationship was observed between temperature, light, and soil pH with native tree species such as *Cupressus lusitanica*, *Buddleja parviflora* and *Pinus aff. ayacahuite*. Furthermore, livestock can contribute to some extent to nutrient input through the deposition of feces and urine, enriching the soil with nitrogen, phosphorus, and organic matter (Dorrough et al., 2006; Trejo-Escareño et al., 2013).

It was expected that, at the highest altitude site, biomass and basal area would be limited by factors such as low temperatures; however, the dissimilarity analysis showed that individuals between 10 and 40 m in height contribute significantly to the basal area at this site, suggesting a dominance of individuals with greater investment of resources in biomass (Weemstra et al., 2021). Conversely, at the lowest altitude site, a greater basal area was observed in shorter trees (1.8-10 m). The dominance in biomass of small trees could be associated with an adaptive growth strategy, in which they prioritize trunk widening to maximize stability and resource storage (Weemstra et al., 2021).

The PCA analysis showed that tree biomass and the height of understory species have a negative relationship with livestock grazing and human activities at the lower-altitude site. This could be due to soil compaction from livestock trampling, which reduces the ability of roots to penetrate the soil and access nutrients and water. These impacts lead to a decrease in total biomass, partly due to consumption by livestock, as the plant species do not have sufficient resources to grow and accumulate biomass (Dorrough et al., 2006; Trejo-Escareño et al., 2013).

From an ecological perspective, the mid-elevation areas with greater species diversity may function as diversity hotspots in this site. In the lower elevation areas, where short tree species dominate in terms of biomass, an average height of 2.11 m was recorded for *Abies religiosa* and 4.30 m for *Pinus aff. ayacahuite*.

Therefore, forest management with selective thinning should be implemented to allow for increased tree biomass growth.

The higher elevation areas should be under a constant monitoring of natural regeneration processes, with a selective forest management approach that ensures the establishment and protection of young individuals, which may have difficulty surviving in an environment with competition from larger trees and under restrictive environmental conditions with low temperatures and higher solar radiation.

Conclusions

The results reveal that intermediate altitudes support both elevated species richness and suitable environmental conditions for *Abies religiosa* regeneration, even under pressures from activities like livestock farming. This highlights the ecological significance of these areas and their contribution to the conservation of temperate forest biodiversity in Mexico.

Acknowledgments

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Conflict of Interest

Leticia Bonilla Valencia y Marisela Cristina Zamora-Martínez declare that they did not participate in the editorial process of the article

Contribution by author

Leticia Bonilla-Valencia: methodological design, modeling and statistical analysis, manuscript preparation; Silvia Castillo-Argüero: research design and supervision, fieldwork, and document revision; Efraín Velasco Bautista: results analysis, review; Marisela Cristina Zamora-Martínez: results interpretation and revision of the manuscript; Yuriana Martínez Orea: research supervision, fieldwork, document revision; Alma Delia Ortiz-Reyes: revision, results interpretation.

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