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Research article

Riqueza de especies, estructura horizontal y diversidad arbórea en un gradiente altitudinal en cafetales de *Chiapas*

Tree richness, structure, and diversity in an altitudinal gradient in coffee plantations in *Chiapas*

Edwin Geyner Verdugo Morales¹, María Inés Yáñez Díaz¹, Eduardo Alanís Rodríguez^{1*}, Humberto González Rodríguez¹, Fortunato Garza Ocañas¹, Luis Alfredo Rodríguez Larramendi²

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¹Facultad de Ciencias Forestales, Universidad Autónoma de Nuevo León. México.

²Facultad de Ingeniería, Universidad de Ciencias y Artes de Chiapas. México.

*Autor para correspondencia; correo-e: eduardo.alanisrd@uanl.edu.mx

*Corresponding author; e-mail: eduardo.alanisrd@uanl.edu.mx

Abstract

The richness, horizontal structure and diversity of the tree component were compared in three altitudinal intervals in shade-grown coffee: Lower from 800 to 1 200 masl, Intermediate 1 200-1 600 masl, Upper from 1 600-2 000 masl, in *Motozintla*, state of *Chiapas*. 1 736 trees of 146 species were recorded. Species richness was significantly higher in the Lower and Upper intervals (91 sp.) and lower in the Intermediate (59 sp.). The Shannon-Wiener index values were 3.37, 3.25 and 3.90 for the Lower, Intermediate and Upper ranges with a significant difference for the Upper interval, equivalent to 29, 26 and 50 effective species respectively. The Intermediate and Upper ranges showed a similarity of 40 % of species in the Jaccard index, while both only shared 28 % with the Lower interval. The basimetric area and the density of individuals per hectare were 17.97 ± 4.9 , 10.91 ± 4.5 and 17.05 ± 10 m² ha⁻¹ in the Lower, Intermediate and Upper parts, being significant for the Lower one ($p=0.04$). Tree density per hectare was not significant in the altitudinal gradient analyzed. *Pinus maximinoi*, *Inga vera* and *Chamaedorea tepejilote* were the species of greatest ecological importance. The variables studied did not present a linear pattern along the gradient as occurs with forest ecosystems. The coffee plantations that overlap with Mesophilous forest and Medium-sized evergreen forest maintain a great diversity of trees as shade.

Keywords: Coffee, diversity, *Inga vera* Willd., *Pinus maximinoi* H. E. Moore, species richness, similitude.

Resumen

Se comparó la riqueza, estructura horizontal y diversidad del componente arbóreo en tres intervalos altitudinales en cultivo de café bajo sombra: Inferior 800 a 1 200 msnm, Intermedio 1 200-1 600 msnm, Superior de 1 600-2

000 msnm, en Motozintla, Chiapas. Se registraron 1 736 árboles de 146 especies. La riqueza de especies fue significativamente mayor en los intervalos Inferior y Superior (91 spp.), con menos registros en el Intermedio (59 spp.). Los valores del Índice de *Shannon-Wiener* fueron de 3.37, 3.25 y 3.90 para los intervalos Inferior, Intermedio y Superior, respectivamente; con diferencia significativa para el Superior, equivalentes a 29, 26 y 50 especies efectivas, respectivamente. Los intervalos Intermedio y Superior presentaron una similitud de 40 % de especies en el Índice de *Jaccard*, mientras que ambos solo compartieron 28 % con el intervalo Inferior. El área basal y la densidad de individuos por hectárea fueron de 17.97 ± 4.9 , 10.91 ± 4.5 y 17.05 ± 10 m² ha⁻¹ en la parte Inferior, Intermedio y Superior, para la parte Inferior fue significativa ($p=0.04$). La densidad de individuos por hectárea no fue significativa en el gradiente altitudinal analizado. *Pinus maximinoi*, *Inga vera* y *Chamaedorea tepejilote* fueron las especies de mayor importancia ecológica. Las variables estudiadas no presentaron un patrón lineal a lo largo del gradiente como ocurre en los ecosistemas forestales. Los cafetales que se traslapan con bosque mesófilo y selva mediana mantienen gran diversidad de árboles como sombra.

Palabras clave: Café, diversidad, *Inga vera* Willd., *Pinus maximinoi* H. E. Moore, riqueza de especies, similitud.

Introduction

A good number of research studies have revealed that there is a correlation between environmental factors and changes in the composition, structure and diversity of forest ecosystems in an altitudinal gradient (Ávila-Sánchez et al., 2018; Sánchez-González & López-Mata, 2005).

There are few studies of this type of intervened ecosystems, such as in agroforestry systems that, although they are not complete forests, conserve much of the complexity of the structure and its functionality (Farfán, 2014; Soto-Pinto et al., 2001). For example, coffee plantations located in mesophilous forests in the state of *Veracruz*, preserve up to 89 % of the species of all life groups (Manson et al., 2018).

Moguel and Toledo (1999) did not determine a correlation between the species richness of the tree canopy in traditional coffee plantations and altitude, and they mention that the existing diversity is a product of management. However, they recognize that their data were limited.

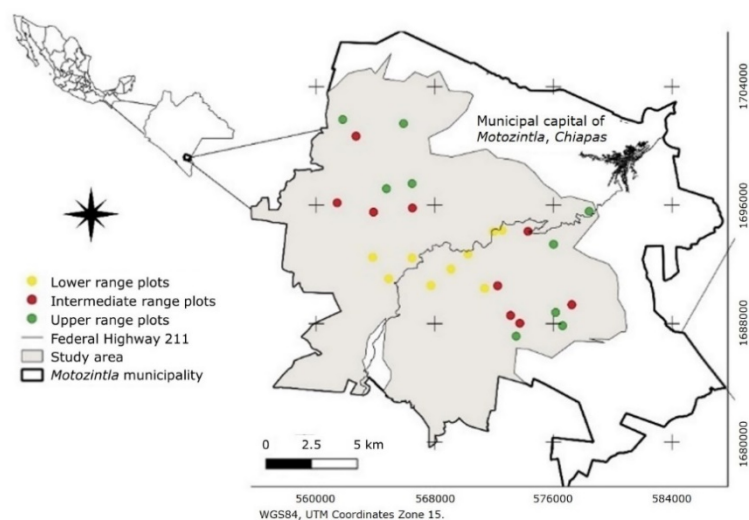
The coffee plantations located in the *Sierra Madre* region of the state of *Chiapas* were established under the shade of primary forests, preserving a large part of the native tree species (*Comisión Nacional para el Conocimiento y Uso de la Biodiversidad* [Conabio], 2015). With this base, the work described below was carried out to

describe the tree canopy of the coffee plantations in the region, following an altitude gradient. The proposed hypothesis is that, in the tree component associated with coffee cultivation in agroforestry schemes, there are changes in species richness ($q=0$), diversity ($q=2$) and horizontal structure, in a linear pattern similar to native forests.

Materials and Methods

Study area

The study was conducted in *Motozintla* municipality, *Chiapas* (566515.64 m W, 1691655.35 m N), in coffee plantations with Arabica coffee (*Coffea arabica* L.) located between 2 000 and 800 masl (Figure 1). This gradient was divided into three intervals: Lower from 800 to 1 200 masl, Intermediate from 1 200 to 1 600 masl, and Upper from 1 600 to 2 000 masl.



Source: Prepared by the authors using data from the *Instituto Nacional de Estadística y Geografía* (Inegi, 2023).

Figure 1. Study area with location of sampling plots.

In the area, the average annual rainfall ranges between 3 000 and 3 500 mm (INEGI, 2006). The average annual temperature in the Lower range is 24 °C, in the Intermediate range it is 22 °C and in the Upper range it is 20 °C (INEGI, 2007). In the Lower part, the coffee plantations are intertwined with Medium forest; in the Intermediate range with pine-oak vegetation and Low deciduous forest, in the Upper range with Mesophilous mountain forest (INEGI, 2017; field observation).

In the Lower part, the coffee plantations are of varieties resistant to orange rust (*Hemileia vastatrix* Berk. & Broome 1869) such as *catimores* (Julca-Otiniano et al., 2023). In the Intermediate and Upper areas, typical, *bourbon* and *caturras* are also grown, mainly. Planting densities range from 1 600 to 3 000 plants per hectare. Management activities such as pruning productive tissue, shade regulation, weed control and nutrition are carried out manually.

Materials and Methods

Nine circular plots of 2 000 m² were randomly established at each altitude interval. In the plots, the normal diameter (cm) of the plants that cast shade on the coffee trees was quantified and measured with a model 283d Forestry Suppliers® diameter tape. They were taxonomically identified with the support of specialists from the Inaturalistmx platform (iNaturalist, 2024), and corroborated in *Enciclovida* (Conabio, 2024a) and World Flora Online (2024).

The formulas to obtain the variables are described in Table 1. For sampling, the sample coverage method based on rarefaction and extrapolation -which is independent of the size of the sampled area- was used in order to determine the richness of tree species in the altitude ranges (Chao & Jost, 2012) (Formula 1). López-

Mejía *et al.* (2017) used this method in various biological groups, considering a 90 % minimum coverage. The calculations were performed with the iNEXT program version 2024 (Chao *et al.*, 2024).

Table 1. Formulas used to calculate the variables.

Variable	Formula	Citation
Species richness ($q=0$)	$\hat{C} = 1 - \frac{f_1}{n} \left[\frac{(n-1)f_1}{(n-1)f_1 + 2f_2} \right] \quad (1)$	Chao and Jost (2012)
<p>Where:</p> <p>\hat{C} = Sample coverage estimation (%)</p> <p>f_1 = Singletons</p> <p>f_2 = Doubletons</p> <p>n = Number of observed individuals</p>		
Alpha diversity ($q=2$)	$H' = -\sum_{i=1}^n pi \times (\ln pi) \quad (2)$	Shannon (1964)
<p>Where:</p> <p>H' = Shannon-Wiener Index</p> <p>\ln = Natural logarithm</p> <p>pi = Proportion of species $pi=(ni \times N^{-1})$</p> <p>ni = Number of individuals of the i species</p> <p>N = Total number of individuals</p>		
	$D^1 = \exp (H') \quad (3)$	Moreno <i>et al.</i> (2011)
<p>Where:</p> <p>D^1 = Effective number of species or first order diversity ($q=1$)</p> <p>H' = Shannon-Wiener Index</p>		
Beta diversity	$I_j = \frac{c}{a+b-c} \quad (4)$	Moreno (2001)
<p>Where:</p> <p>I_j = Jaccard Coefficient</p> <p>c = Species present in both intervals</p> <p>a = Species present in interval a</p> <p>b = Species present in interval b</p>		
Horizontal structure	$AB_{na} = \left[\sum_{i=1}^n \left(\frac{\pi}{4} \times dn^2 \right) \right] \times n \quad (5)$	Alanís <i>et al.</i> (2020)

Where:

AB_{ha} = Basimetric area per hectarea ($m^2 ha^{-1}$)

dn = Normal diameter (m)

$$n = \frac{10\,000\ m^2}{\text{Surface of the sampling plot (m}^2\text{)}}$$

$$d_{ha} = \left(n_p \times \left(\frac{10\,000\ m^2}{t} \right) \right) \quad (6)$$

Where:

d_{ha} = Density of individuals per hectarea (individuals ha^{-1})

n_p = Observed individuals in sampling plot

t = Size of sampling plot (m^2)

$$IVI = \frac{\sum_{i=1}^n (AR_i \times DR_i \times FR_i)}{3} \quad (7) \quad \text{Curtis and McIntosh (1951)}$$

Where:

IVI = Importance Value Index

AR_i = Relative abundance

DR_i = Relative dominance

FR_i = Relative frequency

Species richness was calculated with an extrapolation of 96.7 % with a confidence level of 95 % (Chao & Jost, 2012).

With the species richness and abundance values, alpha diversity was determined using the Shannon-Wiener Index (Formula 2), with the support of the Species-richness Prediction and Diversity Estimation in R (SPADE) software (Chao et al., 2024). The procedure considered the Bias-corrected Shannon diversity estimator, which corrects for undersampling (Chao & Shen, 2003). The values obtained were expressed in effective number of species (Jost, 2006; Moreno et al., 2011) (Formula 3), based on a 95 % confidence interval resulting from the application of the Bootstrap method (Chao & Shen, 2003).

To determine the similarity of species, an Unweighted Pair Group Method with Arithmetic Means (UPGMA) dendrogram was created, based on the Jaccard Coefficient (Formula 4), and with the support of the PAST 4.17 software (Hammer *et al.*, 2001).

To describe and compare the horizontal structure, the values of basimetric area per hectare (Formula 5) and density of individuals per hectare (Formula 6) were calculated. The results were compared in an ANOVA at 95 % confidence with the IBM SPSS Statistics 22.0 program (International Business Machines Corp. [IBM], 2021).

To determine the importance of the species in the plant community, the Importance Value Index (Formula 7) was created (Alanís *et al.*, 2020).

Results

Species richness

A total number of 1 736 trees were recorded, corresponding to 146 species (Table 2). In the Lower interval, 782 individuals and 90 species were recorded, corresponding to a coverage of 96.42 % of the estimated species richness. In the Intermediate interval, 457 individuals in 59 tree species were recorded, equivalent to a coverage of 96.73 %. In the Upper interval, 497 individuals in 82 species were recorded, which implies a coverage of 94.98 %.

Table 2. List of tree species associated with coffee plantations.

No.	Scientific name	Intervals			Total	No.	Scientific name	Intervals			Total
		1	2	3				1	2	3	
1	<i>Acaciella angustissima</i> (Mill.) Britton & Rose			1	1	74	<i>Inga inicuil</i> G. Don	1			1
2	<i>Aiouea</i> sp.	2		4	6	75	<i>Inga paterno</i> Harms	25	2	5	32

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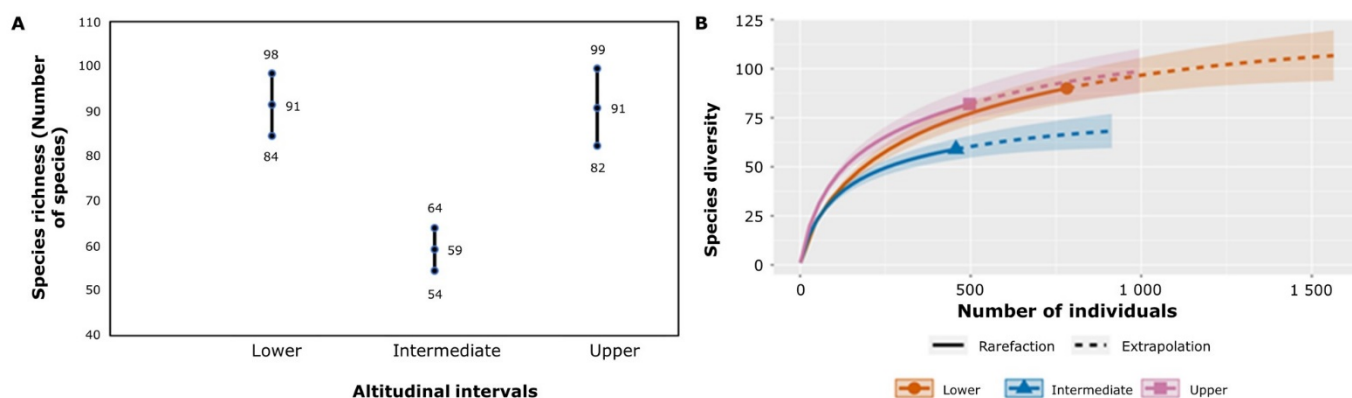
3	<i>Alchornea latifolia</i> Sw.	1	2	2	5	76	<i>Inga punctata</i> Willd.	15	31	11	57
4	<i>Alnus acuminata</i> Kunth			7	7	77	<i>Inga vera</i> Willd.	46	127	49	222
5	<i>Alstonia longifolia</i> (A. DC.) Pichon	1			1	78	<i>Lasianthaea fruticosa</i> (L.) K. M. Becker		1	1	2
6	<i>Anacardium occidentale</i> L.	2			2	79	<i>Lepidaploa polypleura</i> (S. F. Blake) H. Rob.			7	7
7	<i>Annona cherimola</i> Mill.	1		1	2	80	<i>Lippia</i> sp.	1		8	9
8	<i>Annona muricata</i> L.	5	1		6	81	<i>Lonchocarpus heptaphyllus</i> (Poir.) DC.	54	2		56
9	<i>Aphananthe monoica</i> (Hemsl.) J.-F. Leroy		1	1	2	82	<i>Lonchocarpus minimiflorus</i> Donn. Sm.	5			5
10	<i>Ardisia</i> sp.		2	6	8	83	<i>Lonchocarpus rugosus</i> Benth.	1			1
11	<i>Ardisia paschalis</i> Donn. Sm.	5			5	84	<i>Machaerium</i> sp.	6			6
12	<i>Ardisia verapazensi</i> Donn. Sm.			1	1	85	Malvaceae			1	1
13	<i>Averrhoa carambola</i> L.	1			1	86	<i>Mangifera indica</i> L.	4	1	2	7
14	<i>Bambusa vulgaris</i> Schrad. ex J. C. Wendl. var. <i>vulgaris</i>	1			1	87	<i>Matayba oppositifolia</i> (A. Rich.) Britton	5			5
15	<i>Bixa orellana</i> L.	2			2	88	<i>Miconia xalapensis</i> (Bonpl.) M. Gómez		9		9
16	<i>Brosimum alicastrum</i> Sw.	4			4	89	<i>Montanoa</i> sp.			2	2
17	<i>Brugmansia aurea</i> Lagerh.			1	1	90	<i>Muntingia calabura</i> L.			1	1
18	<i>Bunchosia</i> sp.	8			8	91	<i>Musa × paradisiaca</i> L.	63	15	9	87
19	<i>Byrsonima crassifolia</i> (L.) Kunth			1	1	92	<i>Myrsine coriacea</i> (Sw.) R. Br. ex Roem. & Schult.			3	3
20	<i>Calliandra houstoniana</i> (Mill.) Standl.	2			2	93	<i>Ocotea sinuata</i> (Mez) Rohwer	8			8
21	<i>Carica papaya</i> L.			1	1	94	<i>Oreopanax echinops</i> (Schltdl. & Cham.) Decne. & Planch.			4	4
22	<i>Casimiroa edulis</i> La Llave			2	2	95	<i>Oreopanax sanderianus</i> Hemsl.	1		1	2
23	<i>Cecropia obtusifolia</i> Bertol.	3	3		6	96	<i>Ostrya virginiana</i> (Mill.) K. Koch			14	14
24	<i>Cedrela odorata</i> L.	27			27	97	<i>Persea americana</i> Mill.	9	5	25	39
25	<i>Cestrum guatemalense</i> Francey	1		1	2	98	<i>Perymenium grande</i> Hemsl.	1	3	6	10
26	<i>Cestrum nocturnum</i> L.	4			4	99	<i>Phyllanthus acuminatus</i> Vahl	4			4
27	<i>Cestrum tomentosum</i> L. f.		2		2	100	<i>Pinus devoniana</i> Lindl.		4		4
28	<i>Chamaedorea tepejilote</i> Liebm.	221	7	4	232	101	<i>Pinus maximinoi</i> H. E. Moore		1	23	24
29	<i>Chionanthus</i> sp.	1			1	102	<i>Pinus teocote</i> Schltdl. & Cham.			7	7
30	<i>Chrysophyllum cainito</i> L.	7			7	103	<i>Piper aduncum</i> L.	1			1
31	<i>Citrus deliciosa</i> Ten.	1			1	104	<i>Piper auritum</i> Kunth	2			2
32	<i>Citrus × aurantium</i> L.	2			2	105	<i>Platymiscium dimorphandrum</i> Donn. Sm.	1			1

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33	<i>Citrus × limetta</i> Risso	4	1	5	106	<i>Podachaenium eminens</i> (Lag.) Sch. Bip.	2	2			
34	<i>Citrus × limon</i> (L.) Osbeck	2		2	107	<i>Prunus</i> sp.		3	3		
35	<i>Citrus × limonia</i> (L.) Osbeck		7	1	8	108	<i>Psidium guajava</i> L.	2	7	2	11
36	<i>Citrus medica</i> L.	11	5	5	21	109	<i>Quercus acutifolia</i> Née	1		1	
37	<i>Clethra pachecoana</i> Standl. & Steyerl.	2	4	9	15	110	<i>Quercus segoviensis</i> Liebm.		3	3	
38	<i>Clibadium arboreum</i> Donn. Sm.			1	1	111	<i>Quercus calophylla</i> Schltld. & Cham.	3	12	15	
39	<i>Coccoloba</i> sp.	3			3	112	<i>Quercus peduncularis</i> Née	3		3	
40	<i>Cordia alliodora</i> (Ruiz & Pav.) Oken	9	1		10	113	<i>Quercus sapotifolia</i> Liebm.	5	1	6	
41	<i>Cordia collococca</i> L.	12	6	3	21	114	<i>Quercus skinneri</i> Benth.		3	3	
42	<i>Coussapoa purpusii</i> Standl.			6	6	115	<i>Quercus vicentensis</i> Trel.	3	7	10	
43	<i>Crateva tapia</i> L.	2			2	116	<i>Ricinus communis</i> L.	1		1	
44	<i>Critonia morifolia</i> (Mill.) R. M. King & H. Rob.	25	43	11	79	117	Rubiaceae	2		2	
45	<i>Croton draco</i> Schltld. & Cham.		6	8	14	118	Rubiaceae 2		1	1	
46	<i>Croton guatemalensis</i> Lotsy	3		1	4	119	<i>Sapindus saponaria</i> L.	3		3	
47	<i>Cupania dentata</i> DC.	8	9	3	20	120	<i>Saurauia kegeliana</i> Schltld.	2	29	31	
48	<i>Dendropanax arboreus</i> (L.) Decne. & Planch.	2		4	6	121	<i>Saurauia madrensis</i> B. T. Keller & Breedlove		1	1	
49	<i>Diphysa americana</i> (Mill.) M. Sousa	1	7	9	17	122	<i>Sideroxylon capiri</i> (A. DC.) Pittier	2		2	
50	<i>Dombeya × cayeuxii</i> André		1		1	123	<i>Sinclairia andrieuxii</i> (DC.) H. Rob. & Brettell	1	6	7	
51	<i>Eremosis leiocarpa</i> (DC.) Gleason			6	6	124	<i>Solanum aphyodendron</i> S. Knapp	1		1	
52	<i>Eremosis triflosculosa</i> (Kunth) Gleason	13	2		15	125	<i>Solanum mauritianum</i> Scop.	1	6	14	21
53	<i>Eriobotrya japonica</i> (Thunb.) Lindl.	4	13	9	26	126	<i>Spondias purpurea</i> L.	1	1	2	
54	<i>Erythrina americana</i> Mill.	2		1	3	127	<i>Symplocos limoncillo</i> Bonpl.		4	4	
55	<i>Erythroxylum macrophyllum</i> Cav.	1			1	128	<i>Syzygium jambos</i> (L.) Alston	11	1	1	13
56	<i>Eugenia axillaris</i> (Sw.) Willd.	6			6	129	<i>Tabebuia rosea</i> (Bertol.) DC.	3		3	
57	<i>Eugenia</i> sp.	5			5	130	<i>Tabernaemontana donnell smithii</i> Rose	2		2	
58	<i>Eysenhardtia adenostylis</i> Baill.		4	2	6	131	<i>Terminalia oblonga</i> (Ruiz & Pav.) Steud.	5		5	
59	Fabaceae	2			2	132	<i>Ternstroemia tepezapote</i> Schltld. & Cham.		3	3	
60	<i>Ficus costaricana</i> (Liebm.) Miq.	5	1		6	133	<i>Theobroma cacao</i> L.	8		8	
61	<i>Ficus</i> sp.			1	1	134	<i>Trema micrantha</i> (L.) Blume	1	14	15	30
62	<i>Frangula discolor</i> (Donn. Sm.) Grubov		2	2	2	135	<i>Trichilia martiana</i> C. DC.	6	1	7	
63	<i>Fuchsia paniculata</i> Lindl.		4	4	4	136	<i>Trichilia</i> sp.	1		1	

64	<i>Gliricidia sepium</i> (Jacq.) Kunth ex Walp.	1	3	4	137	<i>Trichospermum mexicanum</i> (DC.) Baill.	11	11
65	<i>Gonzalagunia tacanensis</i> Lundell	3	3		138	<i>Turpinia</i> sp.	1	1
66	<i>Guazuma ulmifolia</i> Lam.	3	3		139	<i>Ulmus mexicana</i> (Liebm.) Planch.	3	2
67	<i>Hauya elegans</i> DC.	1	1		140	<i>Urera caracasana</i> (Jacq.) Gaudich. ex Griseb.	1	2
68	<i>Heliconia collinsiana</i> Griggs	3	4	7	141	<i>Verbesina</i> sp.	3	2
69	<i>Heliocarpus donnellsmithii</i> Rose	4	5	9	142	<i>Vernonanthura patens</i> (Kunth) H. Rob.	3	15
70	<i>Hesperocyparis lusitanica</i> (Mill.) Bartel	3	7	10	143	<i>Viburnum hartwegii</i> Benth.	1	14
71	<i>Hymenaea courbaril</i> L.	1	1		144	<i>Wimmeria concolor</i> Schtdl. & Cham.	1	1
72	<i>Inga calderonii</i> Standl.	1	1		145	<i>Witheringia solanacea</i> L'Hér.	1	9
73	<i>Inga edulis</i> Mart.	5	5		146	<i>Yucca gigantea</i> Lem.	32	11

When extrapolating and comparing species richness at 96.7 % coverage, 91 species were estimated for the Lower and Upper intervals and 59 species for the Intermediate interval (Figure 2A). The ratio of species richness between the Lower and Upper intervals is 1:1. The Lower interval contains 1.54 times more species than the Intermediate interval. If the completeness of the sample is extrapolated to 98 %, the significant differences remain (Figure 2B).

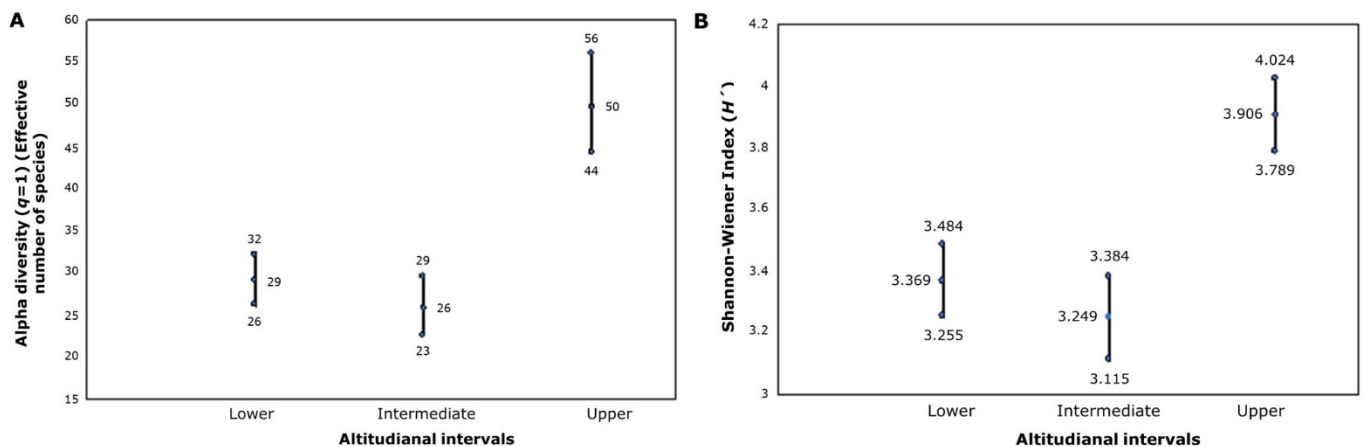


A = Comparison of species richness at 96.73 % sample coverage; B = Extrapolation of species richness at twice the sample size.

Figure 2. Species richness.

Alpha diversity

The Shannon-Wiener diversity indexes were H' : 3.37, 3.25 and 3.90 in the Lower, Intermediate and Upper intervals, with a significant difference for the Upper interval (Figure 3). In effective numbers of species (Jost, 2006), this means that the Lower interval has a diversity equivalent to 29 equally abundant species, the Intermediate 26 and the Upper 50. The Upper interval is 1.72 times more diverse than the Lower interval and 1.92 times more diverse than the Intermediate interval.



A = Effective number of species; B = Shannon-Wiener Index.

Figure 3. Alpha diversity with confidence intervals.

Beta diversity or species similarity

The UPGMA dendrogram shows that the Intermediate and Upper intervals have a similarity of 40 %. This first group and the Lower interval share about 28 % of the species (Figure 4).

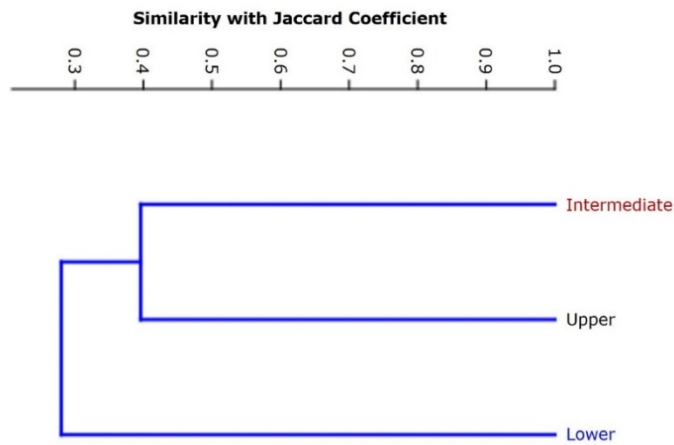


Figure 4. Dendrogram showing the similarity between altitude intervals, using the Jaccard presence/absence method.

Structure

The densities of individuals per hectare were 434 ± 251 ($\mu \pm$ Standard Deviation), 254 ± 80 and 276 ± 195 ind ha⁻¹ for the Lower, Intermediate and Upper intervals. The ANOVA showed that there are no significant differences ($p=0.07$).

The distribution of individuals in diameter categories was graphed, by making a comparison between the three intervals (Figure 5). The graph reveals that, in all categories, the Lower interval has more individuals per hectare.

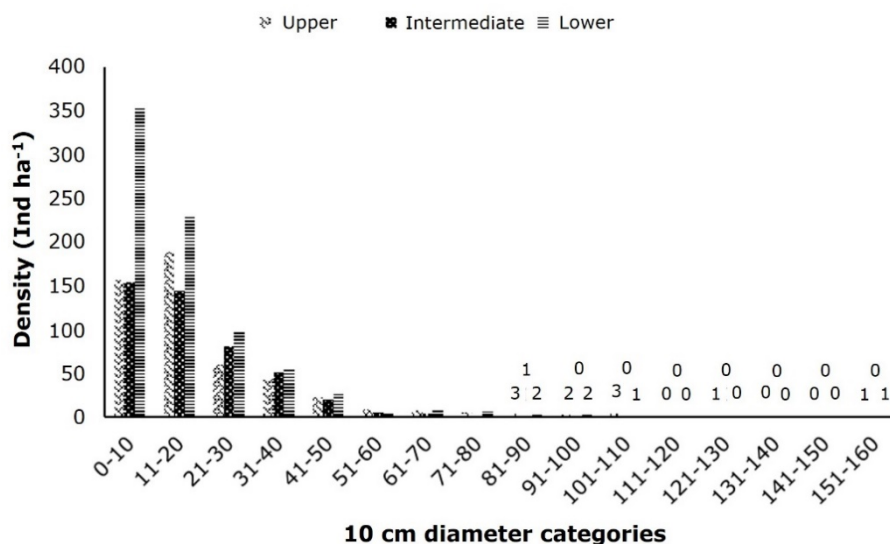


Figure 5. Distribution in diameter classes of the individuals recorded in the three altitudinal intervals.

In the basimetric area, values of 17.97 ± 4.9 , 10.91 ± 4.5 and 17.05 ± 10 $m^2 ha^{-1}$ were recorded in the Lower, Intermediate and Upper intervals, with significant differences ($p=0.04$).

Importance Value Index (IVI)

The way in which the species were ordered helped to interpret the weighted result of the abundance, dominance and frequency of the species in a single number (Table 3).

Table 3. Species with the highest Importance Value Indices (IVI) for each altitude interval.

Interval	Species	AR	DR	FR	IVI
Upper	<i>Pinus maximinoi</i> H. E. Moore	4.6	22.9	2.0	29.5
	<i>Inga vera</i> Willd.	9.9	6.0	4.7	20.5
	<i>Yucca gigantea</i> Lem.	9.1	2.5	1.4	12.9

Intermediate	<i>Inga vera</i> Willd.	27.8	38.1	7.7	73.6
	<i>Critonia morifolia</i> (Mill.) R. M. King & H. Rob.	9.4	2.3	6.8	18.6
	<i>Inga punctata</i> Willd.	6.8	5.1	6.0	17.9
Lower	<i>Chamaedorea tepejilote</i> Liebm.	28.3	28.3	3.5	60.1
	<i>Musa × paradisiaca</i> L.	8.1	8.1	2.0	18.1
	<i>Lonchocarpus heptaphyllus</i> (Poir.) DC.	6.8	6.8	3.5	17.1

AR = Relative abundance; *DR* = Relative dominance; *FR* = Relative frequency; *IVI* = Importance Value Index.

In the Upper interval, *Pinus maximinoi* H. E. Moore (Red pine) was the one with the greatest ecological value, due to its dominance. In the Intermediate interval it was *Inga vera* Willd. (*Chalun*) for its dominance, abundance and frequency. In the Lower interval, *Chamaedorea tepejilote* Liebm. (*Pacaya*) stood out for its abundance and dominance values.

Discussion

Tree species richness

Species richness ($q=0$) was higher in the Upper and Lower intervals. The Upper part of the study area overlaps with one of the ecosystems with the greatest biodiversity: the Mountain cloud forest (*BMM* for its acronym in Spanish) (Conabio, 2014). Verdugo-Morales et al. (2022) described that between 1 800 and 2 000 masl of *BMM* in this region, the range of greatest tree species richness is located with 44 ± 5 taxa in a 1 000 m² site.

The coffee plantations in the Lower interval overlap with the Medium forest, which is also an ecosystem of great floristic richness (Secretaría de Medio Ambiente y Recursos Naturales [Semarnat], 2014). It has been documented that trees of this type of vegetation are functional as shade in coffee plantations (García *et al.*, 2015).

The Intermediate interval recorded lower richness of tree species; one of the factors that can explain this is the types of vegetation with which it overlaps, which are pine-oak forests and Low deciduous forest (INEGI, 2017; field observations).

Lowland forests have a high species richness and endemism (Gallardo-Cruz *et al.*, 2005); in contrast to the tropical forests and the *BMM*, pine-oak forests have a lower richness of tree species (Barrios-Calderón *et al.*, 2022; Castellanos-Bolaños *et al.*, 2010; Méndez *et al.*, 2018). Many tree species of both vegetation types are deciduous; therefore, they are not highly valued as shade in coffee plantations and have been replaced by evergreen species, mainly by individuals of the *Inga* sp. genus, which has historically been promoted as shade in coffee plantations (Jarquín, 2003), and has become one of the most used genera for shade in traditional coffee plantations in Mexico (Sánchez *et al.*, 2017). Based on the above, the distribution of species richness along the altitudinal gradient did not show a descending or ascending pattern, as in natural ecosystems (Ávila-Sánchez *et al.*, 2018; Sánchez-González & López-Mata, 2005). In addition, the 146 tree species identified in this work are greater than those reported in traditional coffee plantations in the state of *Veracruz* (Ramos *et al.*, 2020) and *Guerrero* (Silva *et al.*, 2024).

Alpha diversity

The diversity measured with the Shannon-Wiener Index ($q=1$), as well as the effective number of species, did not show a linear pattern along the altitude gradient. The value of the Shannon-Wiener Index for the Upper interval is classified as high diversity (Medrano *et al.*, 2017), and is due to the high tree richness and because there were

no dominant species (Jost, 2006; Pla, 2006). The most abundant species only concentrated 9.9 % of the individuals.

In the Lower and Intermediate intervals, diversity is classified as medium (Medrano et al., 2017). This is explained because in both there were dominant species (Jost, 2006; Pla, 2006), which gathered 27.7 % of the individuals in each range mentioned.

The diversity values expressed in effective number of species facilitate their understanding and allow to establish a relationship of diversity between the intervals (Jost, 2006).

The alpha diversity values ($q=1$) of this study are similar to those obtained in coffee plantations in *Ixhuatlán* (3.59), *Amatlán* (3.04) (Ramos et al., 2020) and *Atoyac* (3.56) (García et al., 2015) in *Veracruz*. Alpha diversity does not show a correlation with the altitudinal gradient as has been recorded in natural ecosystems (Ávila-Sánchez et al., 2018; Verdugo-Morales et al., 2022).

Beta diversity or species similarity

In natural forests with little human intervention, similarity indices are usually low because the structure of the forest changes in response to variations in environmental factors (Mazzola et al., 2008). In the mesophilous forests adjacent to the coffee plantations, it was identified that, in 700 m of altitudinal gradient, the similarity between the Upper and Lower interval was 16 % (Verdugo-Morales et al., 2022). Williams-Linera et al. (1996) report 10 % similarity between a site located at 2 050 masl and another at 1 250 masl in *Cofre de Perote, Veracruz*.

This work, in 1 200 m of altitudinal gradient, recorded 28 % similarity between the Upper and Lower interval. This high percentage is influenced by the species cultivated in the coffee plantations such as *Citrus* sp., *Inga* sp., *Musa × paradisiaca* L., *Persea*

americana Mill., *Chamaedorea tepejilote*, *Yucca gigantea* Lem. and *Critonia morifolia* (Mill.) R. M. King & H. Rob.

Structure

The behavior of the density values (individuals ha⁻¹) did not define an ascending or descending trend as has been recorded in forest ecosystems (Bauters *et al.*, 2017; Gairola *et al.*, 2008; Silva-García *et al.*, 2022).

The number of trees per hectare is not homogeneous between plots, and is determined by the agricultural management of each producer. In an adjacent Mountain mesophyll forest, the number of trees per hectare presented coefficients of variation ($CV = \frac{\mu}{SD}$) of 10.34 and 7 % in the altitudinal ranges (Verdugo-Morales *et al.*, 2022). In this work, the values were 71.31 and 58 % Coefficient of Variation in the altitude intervals.

The tree density of this work is lower than the 928, 428, and 678 ind ha⁻¹ recorded in traditional coffee plantations in *Veracruz* (García *et al.*, 2015).

The basimetric area as well as density, exhibit distribution patterns in forest ecosystems as recorded by Bauters *et al.* (2017), Kharal *et al.* (2014) and Silva-García *et al.* (2022). In this study, a linear pattern was not recognized.

The results of basimetric area per hectare of this research are lower than those located in portions of adjacent mesophilous forests of 34, 53 and 55 m² ha⁻¹ in the Upper, Intermediate and Lower intervals (Verdugo-Morales *et al.*, 2022), and lower than the 22, 27 and 25 m² ha⁻¹ in traditional coffee plantations of *Veracruz* (García *et al.*, 2015).

Importance Value Index

In the Upper interval, *Pinus maximinoi* was the species with the greatest ecological weight due to its dominance, since individuals with a normal diameter above 100 cm were recorded.

In the Intermediate interval, *Inga vera* was the most important. This is because it is preferred as shade because it is perennial, adapts to dry climates, generates leaf litter, and is used as firewood (Carrera et al., 2022; Conabio, 2024b; Reyes et al., 2022), because in its adult state it projects shade for coffee trees. Its importance is due to the fact that it is cultivated and appreciated for its nutritional and ornamental importance (Rodríguez et al., 2024), since pre-Hispanic times (Meléndez et al., 2013).

Conclusions

There are significant differences in the forest structure in the variables of richness, alpha diversity, and basimetric area, but these differences did not follow a linear pattern in the altitudinal gradient as occurs in forest ecosystems. The modification of the ecosystem, accentuated in the Intermediate interval, occurs to adapt it to the needs of coffee cultivation (shade). Therefore, the proposed hypothesis is rejected.

Coffee plantations conserve tree richness and diversity, mainly those that overlap with ecosystems of high biodiversity.

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Conflict of interest

There is no conflict of interest in the realization of this research work. Eduardo Alanís Rodríguez declares not to have participated in the editorial process of the document

Contribution by author

Edwin Geyner Verdugo Morales: field work, data analysis, and manuscript preparation; María Inés Yáñez Díaz and Eduardo Alanís Rodríguez: data analysis, writing and review of the manuscript; Humberto González Rodríguez, Fortunato Garza Ocañas and Luis Alfredo Rodríguez Larramendi: field work, review and correction of the manuscript. All authors participated in the conception of the research and approval of the final version of this paper.

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