

## ORIGINAL RESEARCH ARTICLE

# Forest communities in secondary high Andean forests (Azuay, Ecuador)

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### ABSTRACT

In the mountains of southern Ecuador there are areas occupied by high Andean secondary forests formed as a result of anthropogenic activities. Here we identified different secondary forest communities located above 2,900 m a.s.l., based on their floristic similarity. In each community the floristic composition was described by total, exclusive and shared species. Estimation curves were used to provide richness and diversity metrics. Structure was analyzed according to abundance and basal area. In addition, the role of environmental variables in explaining floristic conformation and structure was evaluated through principal component and redundancy analysis. Three forest communities were identified. The highest value in diversity and basal area was for the community located at the highest altitude and lowest temperature. Variation in species composition was explained by climatic and geographic environmental variables, density by edaphic and climatic variables, and basal area by topographic variables. Species richness and basal area did not show a similar altitudinal distribution pattern with other Andean tropical forests. Therefore, it was deduced that floristic variation, species richness and basal area are also explained by the chronological age of secondary succession, as shown by indicator species belonging to different ecological groups. It was concluded that floristic composition, richness and vegetation structure in forest communities of high Andean secondary forests are influenced by climatic, topographic, physiographic and geographic variables linked to the age of succession.

**Keywords:** Altitude; Floristic Composition; Ecological Guilds; Structure; Succession; Tropical Forests

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## 1. Introduction

The Andean tropical forests, due to their high biodiversity and endemism, are among the richest plant centers in the world<sup>[1]</sup>. On the western slopes, they form part of the hotspots of the planet. Here, a large number of microhabitats and the rugged topography favor the existence and biological adaptations including different plant communities<sup>[2]</sup>.

In some Andean areas of southern Ecuador, there are sparse patches of primary forests as a result of deforestation, linked to regional anthropogenic pressure<sup>[3]</sup>. There are also considerable areas of secondary forests at altitudes above 1,000 m as a result of the abandonment of agricultural lands, which are currently undergoing natural regeneration or secondary succession processes<sup>[4]</sup>.

In young secondary forests, species richness, basal area and biomass are lower than in primary forests under similar environmental

conditions<sup>[5]</sup>. Nevertheless, secondary forests chronologically recover taxonomic, structural and functional parameters depending on the type and intensity of disturbance, distance to the original forest, presence of dispersing fauna, topography and local climate<sup>[3,4,6]</sup>. Another indicator parameter of recovery is the variation in floristic composition to which species belonging to different ecological guilds are chronologically linked<sup>[7]</sup>. Indicator parameters of recovery in secondary vegetation are positively related to the provision of wood, seeds and ecosystem services linked to hydrological regulation, conservation of local biodiversity, physical and chemical fertility of soils<sup>[8]</sup>. Globally, secondary forests are efficient in mitigating climate change through their higher carbon fixation rates compared to primary forests<sup>[9]</sup>.

In primary and secondary forests, forest communities have been identified based on floristic composition and quantitative vegetation parameters<sup>[10,11]</sup>. To understand ecologically the magnitude and variation in vegetation composition, diversity and structure parameters, relationships with environmental variables have been described. For example, at the local level in Zamora Chinchipe, it is reported that floristic composition and species richness is influenced by altitude<sup>[2]</sup>. This result is also evidenced at the regional level, in broad Andean gradients in Peru and Bolivia<sup>[12]</sup>. Castellanos-Castro and Newton<sup>[11]</sup> found that soil potassium, pH, nitrogen and sodium significantly explain floristic variation and altitudinal distribution of tree species<sup>[13]</sup>. This floristic variation is also explained by geographic distance, which influences the limitation or facilitation of species dispersal<sup>[10,14]</sup>. In the Andean forests of South America, the increase in basal area is negatively related to altitude and possible effects of low temperatures that influence the photosynthetic metabolism of plants<sup>[15]</sup>.

No studies have been reported on vegetation attributes in high Andean secondary forest communities in Ecuador (2,900 m altitude) or their relationships with environmental factors. The description of forest communities would allow us to understand their functionality and the provision of ecosystem

goods and services, especially in ecologically important areas. Against this background, the objectives of this research are: (1) to identify forest communities and describe their floristic composition, diversity and structure; (2) to evaluate relationships between floristic composition, vegetation structure and environmental variables. Based on similar works carried out in the tropical region, it is expected to identify more than one forest community and establish positive relationships between floristic composition, density and basal area with environmental variables.

## 2. Methods

**Description of the study area.** The study area is located in southern Ecuador, Azuay province, Cuenca canton, in an agricultural matrix of 150,000 hm<sup>2</sup> (**Figure 1**). Ecologically, it belongs to the high montane evergreen forest<sup>[6]</sup>. Altitudinally, it is distributed in patches of secondary forests between 2,900 and 3,500 m a.s.l. in sectors of the inter-Andean slopes. Average annual temperatures here were recorded between 6 and 12 °C, and annual rainfall between 800 and 1,500 mm<sup>[17]</sup>.

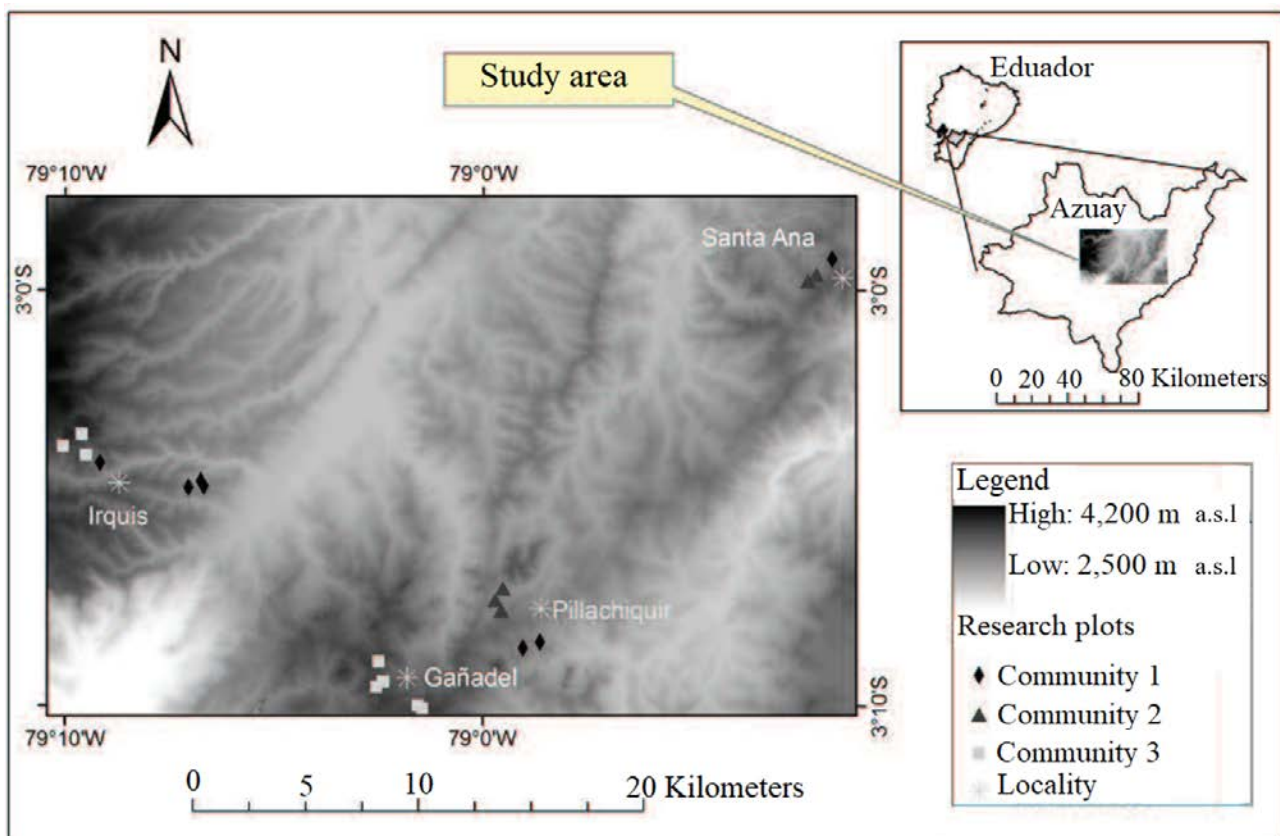
**Sampling.** Twenty permanent research plots of 500 m<sup>2</sup> (25 m × 20 m) were randomly installed in patches of secondary forests with areas >1 hm<sup>2</sup> distributed between 2,900 and 3,500 m a.s.l. (**Figure 1**); these forests were identified through vegetation cover maps and exploratory sampling where the presence of pioneer and intermediate species considered as secondary succession indicators<sup>[7]</sup> was evaluated. Secondary forest was considered to be those areas that registered values ≥25% in the richness of species indicative of secondary succession, with respect to the total number of species registered, in an area of 500 m<sup>2</sup>. The agricultural past of the forest was also investigated with local people or field guides. These plots were installed within four areas of hydrological importance, in the localities of Pillaquichir, Gañadel, Irquis and Santa Ana (**Figure 1**); the average distance between plots was 3,000 m.

Within each plot, dasometric variables such as dap (diameter at 1.3 m above the ground) were counted and measured in all trees, palms and ferns

in individuals with  $dap \geq 5$  cm. All sampled individuals were taxonomically identified to species level.

Three types of variables were taken. The topographic variables were taken in each plot and are: slope, altitude and spatial geographic variables (UTM-WGS 84 coordinates). The environmental variables were extracted with the values of the coordinates of the plots and are minimum, average and maximum annual temperature, average annual

and monthly precipitation from the raster format digital database generated by the Vegetation Map for Ecuador project<sup>[16]</sup>. The edaphic variables were determined through composite soil samples in each plot at 30 cm depth that were sent to the Agrocalidad laboratory in Quito, Ecuador, for chemical analysis and to describe available elements: pH, organic matter (OM), nitrogen (N), phosphorus (P), potassium (K), calcium (Ca), magnesium (Mg), iron (Fe), manganese (Mg), copper (Cu) and zinc (Zn).



**Figure 1.** Location of the study area and plots in the Province of Azuay, Ecuador.

Study area and plots in the Azuay province, Ecuador.

**Determination of forest communities.** As part of the first objective, forest communities were identified by means of cluster analysis (Ward separation method and Bray Curtis distance). First, matrices were designed with the species composition and the sum of the relative abundance and dominance values. Second, the optimal number of resulting clusters was exploratorily selected based on plot clustering and ANOSIM similarity analysis (Bray Curtis;  $P < 0.05$ ). The resulting clusters formed by plot clustering were named forest communities.

**Floristic composition, diversity, and structure.** An indicator species analysis was performed to identify characteristic species within each identified community. From this analysis, species with an indicator value  $\geq 0.7$  and  $P < 0.05$  were considered. The floristic composition was described by the species recorded, rare (those present in a single plot or with a single individual) shared, and exclusive to the identified communities. The importance value index (IVI) was calculated for all species at the community level, based on the sum of the relative values of density, dominance, and frequency.

Diversity was analyzed through differences in

species richness and alpha diversity among the three sites by constructing rarefaction and extrapolation curves, using the probability distribution model according to Colwell *et al.*<sup>[18]</sup>. For species richness, rarefaction curves were constructed with data by plots and individuals. For alpha diversity the curves were constructed with the exponential values of the Shannon index and the inverse of Simpson's index, with data by plots. Beta diversity was estimated using the Chao-Sorensen similarity index and the sum of relative abundance and dominance values, categorized by forest community. Relationships between plots according to relative values and species composition were explored by non-metric multidimensional scaling ordination (Bray Curtis) using the Queco statistical program<sup>[19]</sup>.

Vegetation structure was analyzed using the parameters of density ( $N\text{ hm}^{-1}$ ) and basal area ( $G, \text{m}^2\text{ hm}^{-1}$ ). Comparisons of means between forest communities were performed using the non-parametric Kruskal-Wallis test ( $P < 0.05$ ) by applying the statistical program Infostat<sup>[20]</sup>.

Relationship between vegetation parameters and environmental variables. First, the environmental variables that characterize the forest communities, differentiated into topographic, climatic and edaphic, were described by means of mean comparison and the Kruskal-Wallis nonparametric test ( $P < 0.05$ ). Secondly, as a specific relationship analysis, the environmental values were explored under correlations and associations with the forest communities identified by means of principal component analysis.

Thirdly, a redundancy analysis expressed by variance partitioning was performed under procedures applied in tropical forests by Chust *et al.*<sup>[14]</sup> and Castellanos-Castro and Newton<sup>[11]</sup>. This analysis allowed explaining the relative importance of environmental variables differentiated into topographic, climatic and edaphic variables on floristic composition, density and basal area. The spatial location of the plots was incorporated into this analysis to analyze the similarity of floristic composition and structure based on their geographic location. The geographic coordinates of each plot were trans-

formed to distance using principal coordinate analysis of neighboring matrices (PCNM; logarithmic transformation and Euclidean distance). The Forward Selection procedure was applied to groups of standardized environmental variables separately, to select which ones contribute significantly to the variation in floristic composition, density and basal area (999 random permutations and  $P < 0.05$ ). Analyses were performed using the Vegan package in the R environment from the Queco program<sup>[19]</sup>.

### 3. Results

Determination of forest communities. Cluster analysis based on the similarity of floristic composition and IVI values identified three forest communities (**Figure 2**). ANOSIM similarity analysis significantly confirmed the separation of identified communities ( $P = 0.001$ ). Community 1 grouped seven plots, community 2 five plots, and community 3 eight plots.

The cluster of forest communities identified in plots of  $500\text{ m}^2$  in High-Andean secondary forests, Azuay province.

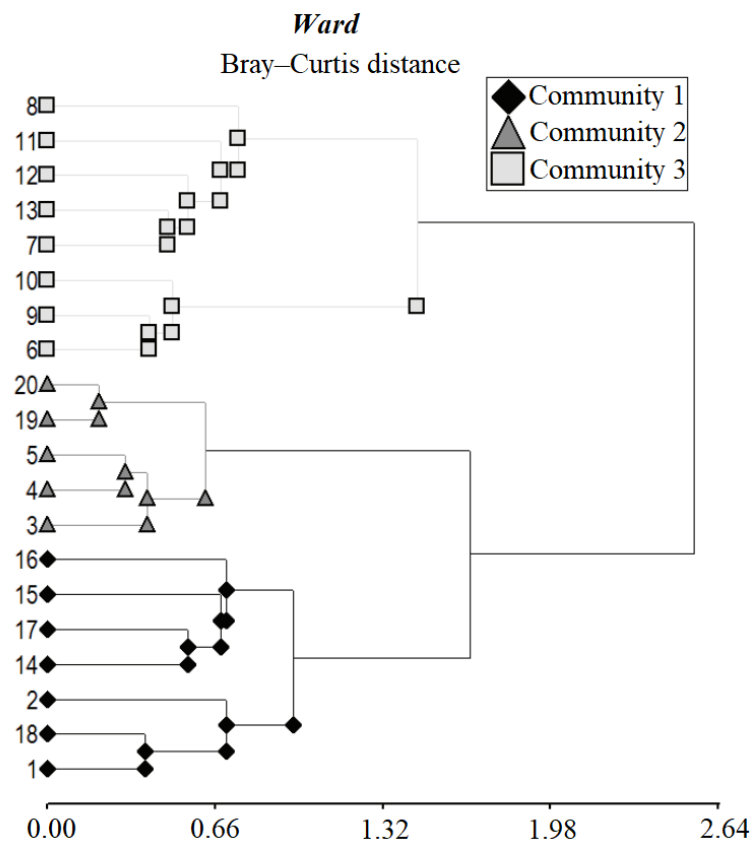
Floristic composition. Twelve species were recorded as strong indicators ( $VI \geq 0.7$ ;  $P < 0.05$ ) of Andean secondary forests (**Table 1**). Of these, six belong to community 1, eight to community 2 and five to community 3. Also recorded were, one species exclusive to community 1, two to community 2, three to community 3 and the remaining seven species are shared among the three communities.

A total of 108 species and 37 botanical families were recorded throughout the study area. Of these, 49 are considered rare species because they are found in only one plot and 12 present only one individual; 60 species belong to community 1 (mean value  $29 \pm 8.58$  standard deviation); 47 to community 2 ( $27.6 \pm 7.83$ ) and 73 to community 3 ( $37.13 \pm 6.96$ ). The highest number of total and exclusive species was observed in community 3 (32 species) (**Annex 1**). Species with the highest IVI values were also recorded as indicator species (**Annex 1**).

**Table 1.** Indicator values ( $VI \geq 0.7$ ) for indicator species and their botanical family in the forest communities identified in secondary high Andean forests, Azuay province.

Indicator species	Family	VI		
		Community 1	Community 2	Community 3
<i>Gaiadendron punctatum</i> (Ruiz et Pav.) G.Don	Loranthaceae		0.82*	0.82*
<i>Hedyosmum cumbalense</i> H. Karst	Chloranthaceae			0.99**
<i>Hesperomeles ferruginea</i> (Pers.) Benth	Rosaceae	0.95*	0.95*	
<i>Lomatia hirsuta</i> (Lam.) Diels ex J.F.Macbr.	Proteaceae	0.87*	0.87*	
<i>Maytenus andicola</i> Loes.	Celastraceae		0.78*	
<i>Morella parviflora</i> (Benth.) C. Parra-O	Myricaceae	0.76*		
<i>Myrsine dependens</i> (Ruiz et Pav.) Spreng	Mysinaceae	0.99**	0.995**	
<i>Ocotea infrafoveolata</i> van der Werff	Lauraceae			0.78*
<i>Oreocallis grandiflora</i> (Lam.) R. Br.	Proteaceae	0.87**	0.87**	
<i>Palicourea amethystina</i> (Ruiz et Pav.) DC.	Rubiaceae	0.70*		
<i>Piper andreanum</i> C. DC.	Piperaceae			0.79*
<i>Weinmannia fagaroides</i> Kunth	Cunoniaceae		0.96*	0.96*

\* $P < 0.05$ ; \*\* $P < 0.001$ .



**Figure 2.** Dendrogram of forest communities identified in 500 m<sup>2</sup> plots in the secondary high Andean forests, Azuay province.

Richness. Accumulation curves showed significantly ( $P < 0.05$ ) higher and similar estimated values for species richness in communities 1 and 3. These two communities were significantly different from community 2, both in the relationship rich-

ness—number of plots (**Figure 3A**) and richness—number of individuals (**Figure 3B**). In both relationships, the curves showed a steep increasing pattern initially, but decreased in the first plots or low number of individuals. Species richness be-

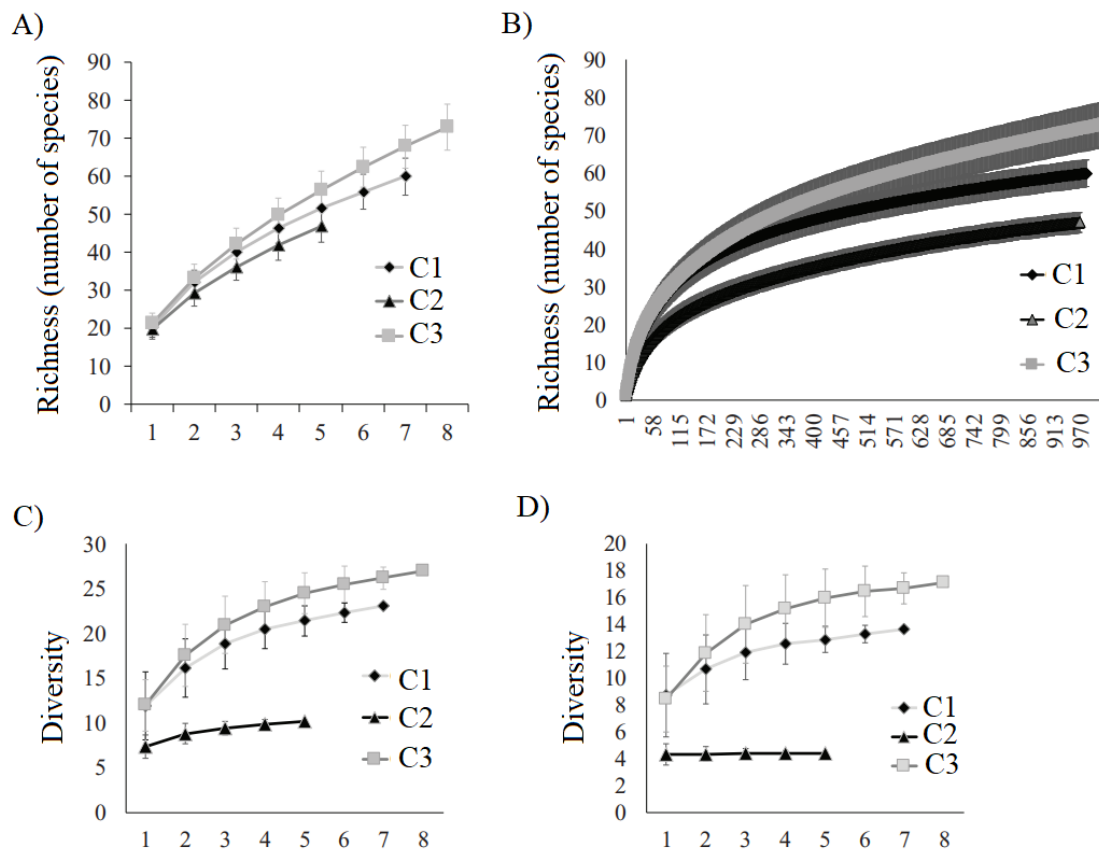


tween community 1 and 3 ceased to be significantly similar as the number of plots and individuals increased, according to the overlap of the standard deviations, so community 3 presented the highest estimated values in species richness.

**Diversity.** Diversities, according to Shannon's index (**Figure 3C**) and Simpson's inverse (**Figure 3D**), were significantly higher for communities 1 and 3, compared to community 2, which was less diverse. Between communities 1 and 3, diversity according to these two indices was similar. As with species richness, as the number of plots increased, the diversity between communities 1 and 3 were no longer significantly similar, so community 3 had the highest estimated values for alpha diversity.

The similarity of floristic composition in combined samples of plots (averages) according to the

Chao-Sorensen index was highest in community 2 (0.89) and equal for communities 1 and 3 (0.56 in each). The lowest similarity results were found in community 1 (0.13) and the highest in community 2 (0.97). According to these results, the ordination of the plots based on floristic composition and IVI value presented species similarity in communities 1 and 2 located to the left in the first ordering axis non-metric multidimensional (**Figure 4**). On the contrary, the plots of the third community, to the right of the first axis, were located with greater dispersion and were, therefore, floristically different from the other two communities. In the second axis of ordination, a separation of communities 1 and 2 was observed, marking a variation in their floristic composition.



**Figure 3.** Species accumulation curves in the relationships: plots – species (A) and individuals – species (B). Accumulation of diversity: plots – Shannon index (C) and Simpson index (D) recorded in 500 m<sup>2</sup> plots of secondary high Andean forests, Azuay province. Vertical lines represent standard deviation; C: forest community.

**Structure.** Density was significantly higher in community 2 as opposed to communities 1 and 3, which were equal (**Figure 5A**). Basal area was significantly higher in community 3 compared to communities 1 and 2 (**Figure 5B**).

Relationship between vegetation parameters and environmental variables. The average altitude was higher ( $P = 0.0009$ ) in community 3, in contrast to communities 1 and 2, which presented the lowest values (**Table 2**). Oppositely, all tempera-

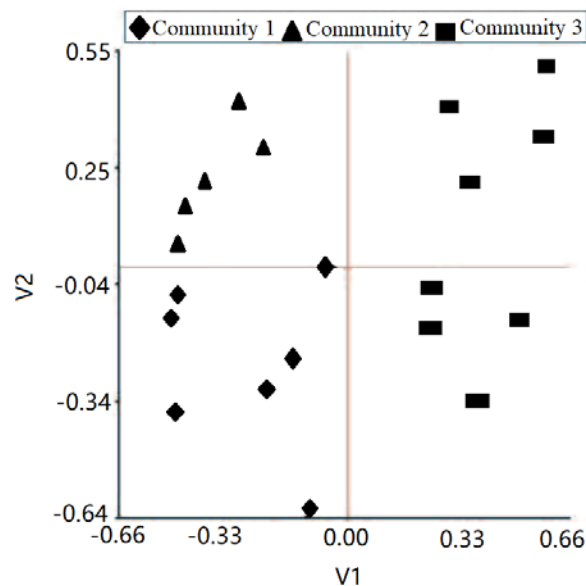
tures registered higher values in communities 1 and 2 ( $P < 0.05$ ). Annual and monthly rainfall were statistically similar, as were the edaphic variables.

Only copper was significantly higher for communities 1 and 2.

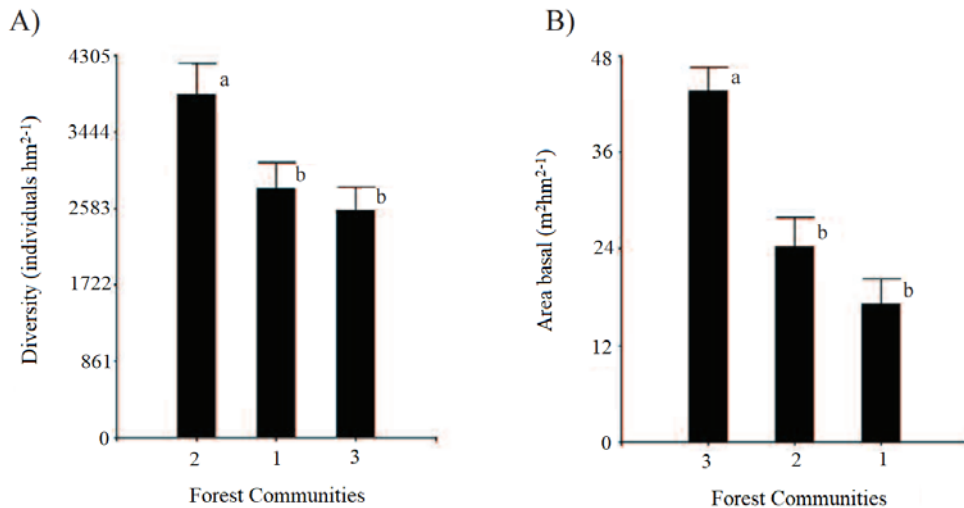
**Table 2.** Averages of environmental variables recorded in 500 m<sup>2</sup> plots within secondary high Andean forests, Azuay province

Variables		C1	C2	C3	P
Topographic	Altitude (m a.s.l.)	3.080 a	3.112 b	3.362 b	0.0009
	Slope (%)	13.0 a	17.8 a	26.4 a	0.1683
Weather	Average annual temperature (°C)	10.4 a	10.4 a	8.8 b	0.0014
	Maximum annual temperature (°C)	16.3 a	16.2 a	14.0 b	0.0007
	Minimum annual temperature (°C)	5.1 a	5.2 a	3.8 b	0.0003
	Average monthly temperature (°C)	10.3 a	10.0 a	8.9 b	0.0011
	Annual precipitation (mm)	841.4 a	828.5 a	802.0 a	0.1218
	Average monthly precipitation (mm)	75.0 a	80.9 a	74.2 a	0.0678
	Edaphic	pH	4.81 a	4.28 a	4.49 a
Organic matter-OM (%)		24.27 a	11.92 a	20.99 a	0.1127
Nitrogen-N (%)		1.21 a	0.59 a	1.05 a	0.1125
Phosphorus-P (mg kg <sup>-1</sup> )		15.89 a	11.34 a	15.13 a	0.7600
Potassium-K (cmol kg <sup>-1</sup> )		0.28 a	0.22 a	0.62 a	0.5838
Calcium-Ca (cmol kg <sup>-1</sup> )		4.98 a	2.55 a	7.17 a	0.8873
Magnesium-Mg (cmol kg <sup>-1</sup> )		1.03 a	1.08 a	0.96 a	0.4943
Iron-Fe (mg kg <sup>-1</sup> )		1.342,67 a	1.061,12 a	1.222,24 a	0.9056
Manganese-Mn (mg kg <sup>-1</sup> )		15.30 a	25.70 a	41.00 a	0.7949
Copper-Cu (mg kg <sup>-1</sup> )		6.00 a	3.38 ab	1.73 b	0.0325
Zinc-Zn (mg kg <sup>-1</sup> )		3.35 a	2.43 a	4.75 a	0.1789

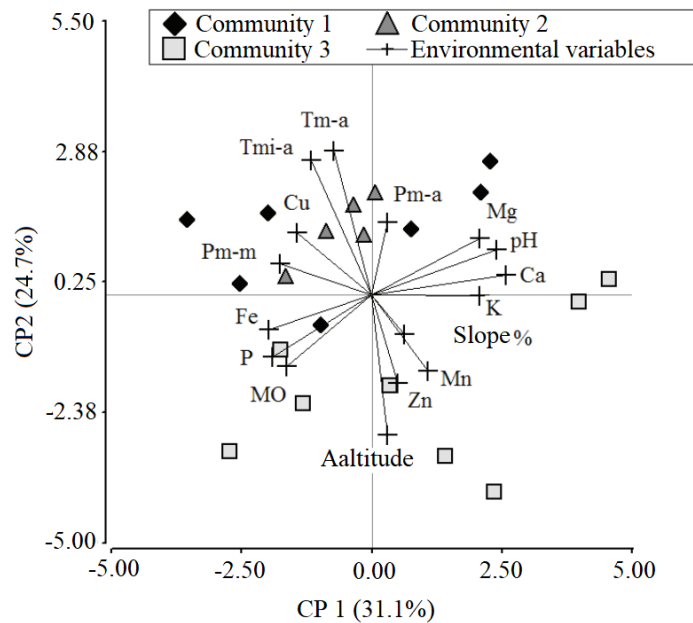
C: forest communities.



**Figure 4.** Non-metric multidimensional scaling to measure similarity in floristic composition in 500 m<sup>2</sup> plots of secondary high Andean forests, Azuay province.



**Figure 5.** Average density (A) and basal area (B)  $\pm$  standard error recorded in 500 m<sup>2</sup> plots of forest communities identified in secondary high Andean forests, Azuay province.



**Figure 6.** Principal component analysis for the ordering, correlation and association with environmental variables in secondary high Andean forests, Azuay province. Tmi-a: minimum annual temperature; Tm-a: mean annual temperature; Pm-m: mean monthly precipitation and Pm-a: mean annual precipitation.

The principal component analysis explained with 56% of variation the association of the environmental variables with the identified communities, in two components (**Figure 6**). Edaphic variables such as magnesium, pH, calcium and potassium were positively associated, with greater intensity and partially with plots of community 3, in the first component. In the second component, although with a lower percentage of explanation, copper was associated with communities 1 and 2, and was negatively correlated with altitude and edaphic variables such as zinc and manganese. In this same component, altitude was more strongly associated with community 3 and negatively correlated with

temperature and precipitation variables, which were positively associated with community 1 and 2.

The analysis of redundancy or variance partitioning showed that the topographic, climatic, edaphic and geographic variables selected under *Forward Selection*, significantly explained proportionally the variation of vegetation parameters such as: floristic composition, density and basal area (**Table 3**). Mean annual temperature and mean monthly precipitation explained more proportionally the variation in floristic composition. Organic matter and potassium explained with greater proportion the variation in the density of individuals and altitude explained the variation in basal area.



**Table 3.** Variance partition values (F;  $P < 0.05$ ) of environmental variables and their relative explanation (%) on floristic composition, density and basal area in secondary high Andean forests of the Azuay province.

Environmental variables	Floristic composition				Density				Basal area			
	Variable	%	F	P	Variable	%	F	P	Variable	%	F	P
Topographic	Al	0.12	3.56	0.002					To	0.49	19.06	0.003
Weather	Tm-a, Pm-m	0.21	3.59	0.001	Tm-a, Tm-m	0.42	7.88	0.003	Tmax-a	0.23	6.58	0.018
Edaphic	pH, Ca, Mg, Mn, Cu	0.16	1.72	0.015	MO, K	0.52	11.36	0.002				
Geographic		0.11	3.39	0.003								
All		0.28	1.84	0.001		0.61	8.41	0.003		0.50	10.69	0.0020
Waste		0.72				0.39				0.50		

Al: aluminum; Ca: calcium; Cu: copper; K: potassium; Mg: magnesium; Mn: manganese; MO: organic matter; Pm-m: mean monthly precipitation; Tm-a: mean annual temperature; Tm-m: mean monthly temperature; Tmax-a: maximum annual temperature.

## 4. Discussion

Studies on the variation in floristic composition and vegetation structure have not been reported for the study area. Multivariate analysis and vegetation parameters such as IVI allowed us to determine different forest communities based on the dissimilarity of floristic composition in plots located in secondary, high Andean forests (**Figure 2**). The IVI has been used in other tropical contexts for its robustness in assessing species in diverse forests<sup>[5]</sup>. Thus, this index, in addition to considering abundance, links the dominance expressed in basal area and the presence or frequency of species in plots differentiated into communities or forest types<sup>[12]</sup>.

The presence of exclusive and shared indicator species within and between forest communities (**Table 1**) consolidate the floristic composition, their similarity and interchange (beta diversity) to form floristically differentiated forest communities. All indicator species have been recorded throughout the Andean region in Ecuador above 2,000 m a.s.l.<sup>[21]</sup>, which allows us to deduce that they are exclusive species of this region. The nonmetric multidimensional scaling graph (**Figure 4**) shows strong patterns of spatial differentiation, with a greater similarity in floristic composition between communities 1 and 2, which are completely differentiated from community 3. This shows that floristic variation (beta diversity) is explained by the exchange of floristic composition as stated by Chust *et al.*<sup>[14]</sup>.

Through redundancy analysis, certain climatic variables of temperature and precipitation selected with Forward selection explained most of the variation in floristic composition, which was also ex-

plained by altitude (**Table 3**). Although the altitudinal ranges are moderate and do not exceed 600 m altitudinal difference, a negative correlation between altitude and temperature is evident according to the principal component analysis (**Figure 6**). This association is common in wide or moderate altitudinal gradients within the tropical region<sup>[10,15]</sup>. Under this variation, higher values in richness and diversity (**Figure 3**) were described in community 3, located in sites with lower temperatures and higher altitudes.

Regarding structure, temperature variables explained the variation in vegetation density and altitude explained the variation in basal area. Thus, the highest values described in density were for communities 1 and 2 located at lower altitudes. Conversely, the highest values of basal area were for community 3 located at higher altitudes. Results on the influence of altitude and temperature on floristic composition and structure have been reported historically, but in recent decades have been described conclusively under technical and scientific procedures<sup>[12]</sup>. Under the application of these procedures, the results differ from those obtained in other studies in Andean forests at local<sup>[2]</sup> and regional levels<sup>[12,15]</sup> where the highest values in species richness and basal area are recorded in sites of lower altitudes.

In the absence of association patterns similar to those recorded in other contexts, the results obtained could possibly be explained by the age of the secondary succession. This is deduced by considering indicator and exclusive species as has been done in other tropical ecosystems<sup>[5,11]</sup>. In community 3, *Hedyosmum cumbalense* (heliófitas durables), *Piper*

*andreaenum* and *Ocotea infrafoveolata* (esciófitas) stand out as indicator and exclusive species whose ecological characteristics are linked to species of advanced succession<sup>[7]</sup>, so it is inferred that this community is formed by species of secondary forests of advanced succession.

However, in community 1 and 2, *Mollela parviflora*, *Oreocallis grandiflora*, *Lomatia hirsuta* and *Mysine dependens* belonging to the ephemeral heliophytes (short-aged pioneers) stand out as exclusive indicator species, so these communities and their floristic composition would correspond to secondary forests of early succession. These associations in ecological guilds linked to floristic variation are the effect of natural succession processes, where environmental variables and time make a difference in vegetation parameters<sup>[5,6]</sup>. Similarly, the age of secondary forests is positively associated with diversity values<sup>[22]</sup> and, especially, structure with basal area<sup>[4,7]</sup>.

The floristic similarity in communities 1 and 2 is associated with the distance of contiguous sites located at lower altitudes (**Figure 4**). Here we add the significant explanation of geographic distance in the variation of floristic composition and species exchange, shown in the non-metric multidimensional ordination analysis (**Figure 4**) and redundancy analysis (**Table 3**). According to Günter *et al.*<sup>[3]</sup>, species exchange and natural regeneration are positively associated with the proximity of forest edges, since seed dispersal is facilitated, which will later contribute to the similarity of floristic composition. Likewise, they agree with the results recorded by Chust *et al.*<sup>[14]</sup>, Chain-Guadarrama *et al.*<sup>[10]</sup> and Castellanos-Castro and Newton<sup>[11]</sup> where geographic distance significantly explains floristic composition. They also agree with Phillips *et al.*<sup>[23]</sup> and Chust *et al.*<sup>[14]</sup> who express that environmental factors should be considered to explain beta diversity, with strict inclusion of geographic distance because of its high intrinsic relationship with surrounding environmental variables.

After the climatic variables, certain edaphic chemical parameters explained the variation in floristic composition (pH, calcium, magnesium, manganese and copper) according to the redundancy

analysis (**Table 3**). The positive correlations observed in the principal components (**Figure 6**) between calcium, magnesium and potassium with low pH (<5); the latter not correlated with copper, manganese and zinc, agree with the comparisons reported by John *et al.*<sup>[24]</sup> for tropical forests. Here it is stated that low pH influences the lower availability of calcium, magnesium, potassium and phosphorus, while aluminum, copper, manganese and zinc cations become more soluble and available for tree root uptake. Thus, the availability of copper cations associated with communities 1 and 2 (**Figure 6**) would be influencing their floristic composition. The same happens with the availability of manganese and zinc, which are associated with the largest number of plots in community 3. In this community, the addition of organic matter provides stability to the soil aggregates<sup>[25]</sup>. The availability of these chemical elements in the soil could possibly be facilitating the processes of seed germination and root growth and initial seedling growth, especially of indicator and exclusive species in the different forest communities.

The organic matter that explained the variation in vegetation density according to the redundancy analysis (**Table 3**) was associated with all plots in community 2 (**Figure 6**). In this community the highest density values were recorded, contrasting with few plots of community 1 and 3, where density was lower (**Figure 5**). By means of principal component analysis, the positive correlations between organic matter with phosphorus, iron and copper elements were added; the latter were also associated with community 2 (**Figure 6**). These associations allow us to deduce that the organic matter is formed by these elements, whose availability would probably facilitate the processes of germination and initial root growth of seedlings of all the species that emerge abundantly in this community. Likewise, organic matter was negatively correlated with potassium, whose quantities are insignificant within the organic component of the soil<sup>[25]</sup>, so this last chemical parameter would not be positively influencing vegetation density.

## 5. Conclusions

The floristic composition and structure within the identified forest communities are associated with climatic variables such as temperature and topographic variables such as altitude. In the forest communities located at lower altitudes there is greater floristic similarity. This is not the case between these communities and the community at higher altitudes, where the floristic composition is different. To this association is added the geographic distance through the spatial location of the plots that facilitate the exchange of species or beta diversity. The highest richness and diversity of floristic composition was recorded in the forest community located at the highest altitude, which marked an atypical pattern of association compared to lowland tropical forests. In the identified communities, the variation of the evaluated parameters can be explained through secondary succession processes based on the presence of indicator species belonging to different ecological groups, which should be evaluated in further studies.

## Conflict of interest

The authors declared no conflict of interest.

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**Annex 1.** Relative importance value index (%) for the plant species found in the three high Andean secondary forest communities determined by this study

Family	Species	Community 1	Community 2	Community 3
Actinidaceae	<i>Saurauia</i> sp.			0.2
Actinidaceae	<i>Saurauia tomentosa</i> (Kunth) Spreng.	0.6		
Aquifoliaceae	<i>Ilex myricoides</i> Kunth		0.5	0.6
Aquifoliaceae	<i>Ilex rupicola</i> Kunth	0.7	0.7	0.3
Araliaceae	<i>Oreopanax andreanus</i> Marchal	2.4	1.3	1.9
Araliaceae	<i>Oreopanax avicennifolia</i> (Kunth) Decne. et Planch.	2.8	2.6	
Araliaceae	<i>Oreopanax ecuadorensis</i> Seem.			0.2
Asteraceae	<i>Baccharis elaeagnoides</i> Steud. ex Sch.Bip.	0.3		0.2
Asteraceae	<i>Baccharis</i> sp.	0.3		0.3
Asteraceae	<i>Critoniopsis pycnantha</i> (Benth.) H. Rob.	0.3		0.2
Asteraceae	<i>Critoniopsis</i> sp.	0.3		0.2
Asteraceae	<i>Ferreyranthus verbascifolius</i> (Kunth) H. Rob. et Brettell	2.4		
Asteraceae	<i>Gynoxys azuayensis</i> Cuatrec.	2.4	0.8	5.8
Asteraceae	<i>Gynoxys buxifolia</i> (Kunth) Cass.	0.9		0.6
Asteraceae	<i>Gynoxys hallii</i> Hieron.	1.8		2.2
Asteraceae	<i>Gynoxys laurifolia</i> (Kunth) Cass.			0.3
Asteraceae	<i>Gynoxys validifolia</i> Cuatrec.	0.3		0.3
Asteraceae	<i>Lepidaploa sordipaposa</i> (Hieron) H. Rob		0.4	
Asteraceae	<i>Pappobolus acuminatus</i> (S.F.Blake) Panero		0.4	
Asteraceae	<i>Verbesina klattii</i> B.L. Rob. et Greenm.		0.4	
Asteraceae	<i>Verbesina lloensis</i> Hieron.	0.8		1.2
Berberidaceae	<i>Berberis rigida</i> Hieron.	0.7		
Boriganaceae	<i>Tournefortia brevilobata</i> K. Krause			0.4
Boriganaceae	<i>Tournefortia scabrida</i> Kunth.			0.4
Caprifoliaceae	<i>Viburnum pichincheense</i> Benth.	1.9	0.5	4.6
Caprifoliaceae	<i>Viburnum triphyllum</i> Benth.	1.6	0.8	1.3
Celastraceae	<i>Maytenus andicola</i> Loes.	1	2.5*	0.3
Celastraceae	<i>Maytenus</i> sp.	0.6	0.9	
Chloranthaceae	<i>Hedyosmum cumbalense</i> H. Karst.			11.6*
Chloranthaceae	<i>Hedyosmum goudotianum</i> Solms		0.4	
Chloranthaceae	<i>Hedyosmum racemosum</i> (Ruiz et Pav.) G. Don		1.1	0.2
Clethraceae	<i>Clethra ferruginea</i> Ruiz et Pav.	0.6		
Clethraceae	<i>Clethra fimbriata</i> Kunth.	1	3.1	0.8
Clethraceae	<i>Clethra ovalifolia</i> Turcz.	1.2	1.7	
Clethraceae	<i>Clethra revoluta</i> (Ruiz et Pav.) Spreng.	0.3	1.4	
Cornaceae	<i>Cornus peruviana</i> J.F. Macbr.	0.3		
Cunnoniaceae	<i>Weinmannia fagaroides</i> Kunth	3.7	31.4*	4.3*
Cunnoniaceae	<i>Weinmannia rollottii</i> Killip			1.2
Cyatheaceae	<i>Cyathea caracasana van maxonii</i> (Underw.) R.M. Tryon			6.9
Elaeocarpaceae	<i>Vallea stipularis</i> L. f.	4.7	2.4	1.7
Ericaceae	<i>Gaultheria reticulata</i> Kunth			0.2

**Annex 1. (Continued)**

<b>Family</b>	<b>Species</b>	<b>Community 1</b>	<b>Community 2</b>	<b>Community 3</b>
Ericaceae	<i>Macleania rupestris</i> (Kunth) A.C. Sm.	1	2.9	1.1
Euphorbiaceae	<i>Alchornea glandulosa</i> Poepp. et Endl.			0.2
Euphorbiaceae	<i>Croton</i> sp.			0.2
Grossuralaceae	<i>Escallonia myrtilloides</i> L. f.	3.8		1.4
Lamiaceae	<i>Lepechinia mollis</i> Epling			0.4
Lauraceae	<i>Aiouea dubia</i> (Kunth) Mez	0.3		
Lauraceae	<i>Aniba riparia</i> (Nees) Mez		0.5	1
Lauraceae	<i>Aniba</i> sp.		0.4	
Lauraceae	<i>Nectandra laurel</i> Klotzsch ex Nees		0.4	
Lauraceae	<i>Nectandra lineata</i> (Kunth) Rohwer			0.2
Lauraceae	<i>Ocotea heterochroma</i> Mez et Sodiro		0.5	0.8
Lauraceae	<i>Ocotea infrafoveolata</i> van der Werff	0.3	0.4	10*
Lauraceae	<i>Ocotea rotundata</i> van der Werff	0.3		
Lauraceae	<i>Ocotea</i> sp.		0.4	
Lauraceae	<i>Persea brevipes</i> Meisn.	1		0.8
Lauraceae	<i>Persea caerulea</i> (Ruiz et Pav.) Mez.	0.3		
Lauraceae	<i>Persea mutisii</i> Kunth	0.3		
Lauraceae	<i>Persea</i> sp.	0.6		
Loranthaceae	<i>Gaiadendron punctatum</i> (Ruiz et Pav.) G. Don	0.3	1.9*	3.2*
Melastomataceae	<i>Axinaea macrophylla</i> (Naudin) Triana	0.5	0.4	3.2
Melastomataceae	<i>Miconia cladonia</i> Gleason			0.6
Melastomataceae	<i>Miconia crocea</i> (Desr.) Naudin	0.8		0.3
Melastomataceae	<i>Miconia lutescens</i> (Bonpl.) DC.			0.5
Melastomataceae	<i>Miconia poortmannii</i> (Cogn.) Wurdack.	5	6.3	4.5
Melastomataceae	<i>Miconiapunctata</i> (Desr.) D. Don ex DC.			0.6
Melastomataceae	<i>Miconia salicifolia</i> Naudin	0.3		
Melastomataceae	<i>Miconia theaezans</i> (Bonpl.) Cogn.	0.4	0.4	0.6
Melastomataceae	<i>Tibouchina lepidota</i> (Bonpl.) Baill.		0.4	
Monimiaceae	<i>Siparuna tomentosa</i> (Ruiz et Pav.) A. DC.			0.3
Myricaceae	<i>Morelia parvifolia</i> (Benth.) Parra-Os.	5.7*		
Myrsinaceae	<i>Cybianthus marginatus</i> (Benth.) Pipoly	0.6	0.4	0.2
Myrsinaceae	<i>Geissanthus andinus</i> Mez			0.8
Myrsinaceae	<i>Geissanthus</i> sp.			0.2
Myrsinaceae	<i>Myrsine andina</i> (Mez) Pipoly	2.6	0.7	0.7
Myrsinaceae	<i>Myrsine dependens</i> (Ruiz et Pav.) Spreng.	9.9*	8.7*	0.6
Myrsinaceae	<i>Stylogyne</i> sp.			0.2
Myrtaceae	<i>Myrcianthes discolor</i> (Kunth) McVaugh	1.3	3.2	0.3
Myrtaceae	<i>Myrcianthes rhopaloides</i> (Kunth) McVugh	0.4	1	
Myrtaceae	<i>Myrcianthes</i> sp.			0.2
Piperaceae	<i>Piper bogotense</i> C. DC.	0.3		
Piperaceae	<i>Piper andreanurn</i> C. DC.			2.9*
Polygalaceae	<i>Monninia arbuscula</i> Chodat			0.2
Proteaceae	<i>Lomatia hirsuta</i> (Lam.) Diels	1.8*	1.8*	



**Annex 1. (Continued)**

Family	Species	Community 1	Community 2	Community 3
Proteaceae	<i>Lomatia obliqua</i> R.Br.		0.4	
Proteaceae	<i>Oreocallis grandiflora</i> (Lam.) R. Br.	10.9*	2.6*	
Rhamnaceae	<i>Rhamnus granulosa</i> (Ruiz et Pav.) Weberb. ex M.C. Johnst.	1.5	0.8	
Rosaceae	<i>Hesperomeles ferruginea</i> (Pers.) Benth.	8.1*	6.4*	0.5
Rosaceae	<i>Hesperomeles obtusifolia</i> (Pers.) Lindl.			0.2
Rosaceae	<i>Prunus opaca</i> (Benth.) Walp.	0.3		
Rosaceae	<i>Prunus ovalis</i> var <i>nummularia</i> Koehne		0.4	
Rubiaceae	<i>Guettarda aromatica</i> Poepp. et Endl.			0.4
Rubiaceae	<i>Palicourea amethystina</i> (Ruiz et Pav.) DC.	1.2*		
Rubiaceae	<i>Palicourea</i> sp.			0.7
Solanaceae	<i>Cestrum</i> sp.		0.4	
Solanaceae	<i>Cestrum tomentosum</i> L. f.			0.4
Solanaceae	<i>Iochroma cornifolium</i> (Kunth) Miers			0.3
Solanaceae	<i>Iochroma</i> sp.			0.2
Solanaceae	<i>Solanum asperolanatum</i> Ruiz et Pav.	0.3		0.9
Solanaceae	<i>Solanum cutervanum</i> Zahlbr.			0.5
Solanaceae	<i>Solanum hypacrarthrum</i> Bitter	0.3	0.4	
Styracaceae	<i>Styrax foveolaria</i> Perkins			0.2
Styracaceae	<i>Styrax loxensis</i> Perkins	1.2		
Symplocaceae	<i>Symplocos canescens</i> B. Stahl	1.6	0.4	0.2
Symplocaceae	<i>Symplocos quitensis</i> Brand	2.4	2.1	4.6
Verbenaceae	<i>Aegiphila monticola</i> Moldenke			0.3
Verbenaceae	<i>Duranta mutisii</i> L. f.			0.2
Verbenaceae	<i>Duranta obtusifolia</i> Kunth	0.3		

\* Indicator species in forest communities.