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Aboveground Biomass Along an Elevation Gradient in an Evergreen Andean–Amazonian Forest in Ecuador

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The aim of this research was to assess how aboveground biomass (AGB) changes along an altitudinal gradient in evergreen Andean–Amazonian forests [Evergreen Lower Montane Forest, northeastern Cordillera of the Andes; Evergreen Piedmont Forest (EPF), northeastern Cordillera of the Andes; and Evergreen Lowland Forest (ELF), Napo–Curaray] from 373 to 1,826 m above sea level (m.a.s.l.). All trees measured in nine permanent 0.36-ha plots (60 × 60 m) were $\geq$ 10-cm (diameter at breast height) in the aforementioned ecosystems. We assessed tree density, basal area, species richness, and AGB. In the tree inventory, we measured 2,132 trees (Lower Montane Forest 687, Piedmont Forest 773, and Lowland Forest 672). AGB (Mg ha^{-1}) increases with decreasing elevations: 310.26 ± 81.59 (SD) for the Evergreen Lower Montane Forest, 347.73 ± 90.38 (SD) for the EPF, and 377.39 ± 42.73 (SD) for the ELF. *Otoba glycycarpa* and *Alchornea latifolia* were the species with the highest biomass importance value (BIV) in the Evergreen Lower Montane Forest (1,421–1,826 m.a.s.l.), *Spirotheca rosea* and *Pouteria glomerata* in the EPF (892–1,195 m.a.s.l.), and *Otoba glycycarpa* and *Iriartea deltoidea* in ELF (373–394 m.a.s.l.). Biomass contribution along the altitudinal gradient in the evergreen Andean–Amazonian forests is concentrated in few species. This has implications in forest management and reforestation programs where the main focus is on carbon sequestration.

Keywords: aboveground biomass, Ecuadorian Amazon, tree diversity, elevation gradient, Lower Montane Forest, Piedmont Forest, Lowland Forest

INTRODUCTION

Tropical forests act as a large carbon sink (Lal, 2005; Pan et al., 2011). Although these forests provide the ecosystem service of carbon sequestration, they suffer degradation as a result of selective logging (Eguiguren et al., 2020) or total removal due to changes in land uses for agriculture and livestock. Deforestation is responsible for much of the greenhouse gas emissions in South America (Sy et al., 2015; Erb et al., 2018). In tropical forests, carbon stored in aboveground biomass (AGB) depends on multiple factors and scales. At large scales, the main drivers of AGB in South American subtropical forests are climate (temperature annual range) and large-sized trees but not diversity

(Bordin et al., 2021). In African Tropical forests, AGB is mediated by climate (precipitation and temperature) and soils (Lewis et al., 2013). In Amazonian lowland forest, AGB correlates with forest structure, soil, and climate variables (Baraloto et al., 2011), and Poorter et al. (2015) found that AGB is driven by rainfall, forest attributes (tree density, tree size), and rarefied species richness.

Regarding variation in AGB stocks in the Andes, studies report that there is no relationship between temperature/altitude and biomass stocks (Peña et al., 2018); in contrast, several studies report that the basal area increases with elevation, whereas the species richness decreases (González-Caro et al., 2020; Malizia et al., 2020); the maximum of the basal area is between 1,800 and 2,000 m above sea level (m.a.s.l). This could be due to the contribution of temperate-affiliated species (González-Caro et al., 2020) or the effect of climate change that forces tree species to migrate to higher areas, a phenomenon known as "thermophilization" (Fadrique et al., 2018; Peña et al., 2018). At small spatial scales, the drivers of AGB are taxonomic forest attributes, such as species richness, rarefied richness, and Shannon diversity (Chisholm et al., 2013), and forest attributes, such as tree density, tree size, and soil properties (Unger et al., 2012; Poorter et al., 2015). Concerning the AGB productivity, it is influenced by mortality patterns due to natural disturbance in the forest (Peña et al., 2018; Duque et al., 2021) and mycorrhizal associations (Duque et al., 2021). AGB productivity and phylogenetic diversity are negatively correlated in Andean forests (Duque et al., 2021), and woody growth declined with elevation at this latitudinal zone, but the basal area increased in Lower Montane Moist Forests (Báez et al., 2015).

Most of the studies related to the floristic diversity and structure of the forests of the Ecuadorian Amazon Region (EAR) have been developed in the lowland forests of the Amazon (Valencia et al., 1994, 2004); therefore, areas of the Amazon closer to the Andes have not been studied with the same intensity. Moreover, only few studies have been carried out along an altitudinal gradient in the Ecuadorian Evergreen Andean–Amazonian forests (e.g., Homeier et al., 2010; Torres et al., 2020), in contrast to a greater number of studies conducted in the South American tropical forests region (e.g., Malhi et al., 2017; Fadrique et al., 2018; Peña et al., 2018; González-Caro et al., 2020; Malizia et al., 2020; Blundo et al., 2021). Studies of forest structure, diversity, biomass, and carbon stocks along an altitudinal gradient are important because the record and distribution of tree species in the tropics are poorly represented in studies that seek to predict the impact of disturbances on forest dynamics, including the effects of climate change (Feeley et al., 2015). The forests of the EAR have a high diversity of tree species per hectare (Valencia et al., 1994, 2004). This diversity implies a heterogeneity of wood densities (Chave et al., 2005, 2009, 2014; Poorter, 2007) that influence the variability of carbon stocks per hectare in the different types of forest.

Our study aims to study the floristic diversity and to elucidate which species contributes the most to AGB in forests at different altitudes and could therefore provide a framework for forest restoration projects aimed at maximum carbon sequestration in Ecuador, along an altitudinal gradient (350–1,850 m.a.s.l.) in an Evergreen Andean–Amazonian Forest. Based on previous experiences, we hypothesize that Evergreen Andean–Amazonian Forest has, in general, a high diversity of species, but only few species concentrate the majority of biomass. We expect a decline in AGB as well as tree height and diameter with elevation.

MATERIALS AND METHODS

Study Area

The study was conducted in three ecosystems of the EAR: (a) Evergreen Lower Montane Forest (ELMF), northeastern Cordillera of the Andes; (b) Evergreen Piedmont Forest (EPF), northeastern Cordillera of the Andes; and (c) Evergreen Lowland Forest (ELF), Napo–Curaray, according to the Ecosystem Classification of Continental Ecuador (Ministerio de Ambiente del Ecuador (MAE), 2013). The study sites were located within and in the buffer zone of the Colonso–Chalupas Biological Reserve and the Lowland Forest in the Protective Forest of the Runashito Community, respectively (**Figure 1**). Mean annual temperatures and mean annual rainfall range from 17.9 to 24.2°C and from 3,229 to 3,986 mm, respectively, and elevation varies between 373 and 1,826 m.a.s.l. (**Table 1**). The ELF plots are classified as megathermal and hyperhumid with no water deficit, whereas the EPF and ELMF sites are classified as mesothermal and humid with little water deficit (Thornthwaite, 1948; **Table 1**).

Forest Inventory

A cluster of three 60 × 60-m permanent plots was installed in each type of forest according to the National Forest Inventory methodology (MAE and FAO, 2015). The three plots in the ELF were installed in an "L" shape. EPF and the Evergreen Lower Montane Forest plots were installed equidistant along the altitudinal gradient because in mountainous areas, with steep slopes, it is not achievable to install plots in an "L" shape (Casanoves et al., 2014). Each plot was divided into a "grid" of 20 × 60 m delimited by plastic tubes and nylon rope. All trees $\geq$ 10-cm diameter at breast height (DBH) were labeled (numbered and barcoded). The variables DBH and spatial location of each individual were recorded. Tree species were identified by a dendrologist either in the field or by comparing collected samples in Ecuador's National Herbarium (QCNE). The project data will eventually be part of the "Red de Bosques Andinos" network.[1]

Aboveground Biomass Estimation and Floristic Diversity

A scientific name verification process was carried out using the fdiversity software (Casanoves et al., 2011) and the Plant List database version 1.1 (The Plant List, 2013). In addition, with the generation of a Python Script, the scientific names of the project database were verified with the trees registered in the Ecuadorian Amazon (Andino et al., 2019). The number of stems, basal area, and AGB (Eq. 1, 2 in **Table 2**) were then calculated per species and forest type.

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[1] https://redbosques.condesan.org

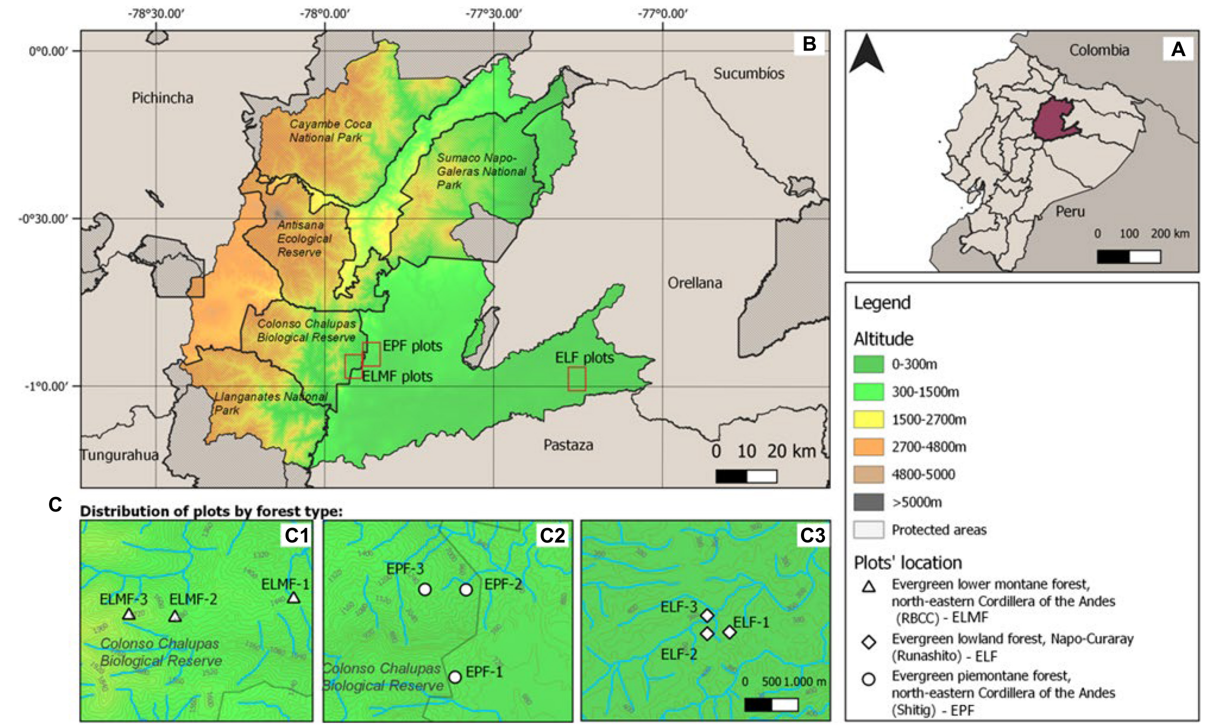

FIGURE 1 | Study area and plot location. **(A)** Location of Napo province in Ecuador. **(B)** location of plot areas in Napo province; and **(C)** location of plots per forest types: **(C1)** ELMF—Evergreen Lower Montane Forest; **(C2)** EPF—Evergreen Piedmont Forest; and **(C3)** ELF—Evergreen Lowland Forest.

We used allometric equations of Chave et al. (2005) to calculate AGB (**Table 2**). Equations were used for the Moist Forest (Eq. 1 in **Table 2**) and Wet Forest (Eq. 2 in **Table 2**); these equations require DBH and wood specific gravity (ρ) values for each tree.

Specific gravity values (ρ in g cm^{-3}), required for allometric equations, were obtained from Baker et al. (2004). When ρ was not available, the mean of 0.623 g cm^{-3} (SD = 0.178) for tropical South America was used (Chave et al., 2009); this value is obtained from the Global Wood Density database (Zanne et al., 2009). A biomass importance value (BIV) was calculated as the average of the relative density, relative basal area, and relative AGB values (Torres et al., 2020).

As indicators of biodiversity, the total richness, species richness per unit area, Fisher α, Shannon, and Simpson indices were calculated. Total richness (S) was taken as the count of total species per unit area. Species richness was calculated through the Margalef Index, MI = (NS - 1)/ln (N), where MI = Margalef Index, NS = number of species, and N = total number of individuals (Margalef, 1957).

All measurements by ecosystem were calculated as the average of the data obtained by the three established plots. Standard deviations are also provided to understand variations among plots of the same forest type (**Table 3**).

Statistical Analyses

To analyze the differences in height, DBH, and AGB between forest types and plots, we used non-parametric test Kruskal–Wallis as our data were not normal. In order to observe differences between forest types we applied Mann–Whitney *post-hoc* test. To assess differences in species composition, we calculated Bray–Curtis dissimilarity Index between all studied plots. A Pearson correlation matrix between environmental variables was developed to remove statistically redundant variables. All correlation values > 0.8 were considered strongly related (e.g., $r > \pm 0.8$). Based on the selected variables, we tested mixed models [AGB = scale (var$_1$) +. + scale (var$_n$) + random effect (site)] and simple linear regressions to assess the relationship between AGB and abiotic factors, such as altitude, temperature, and precipitation. All statistical analyses were performed using R 4.0.5 (R Core Team, 2021).

RESULTS

Structure and Diversity

In this study, the total species richness per 0.1 hectare was recorded in the Evergreen Lower Montane Forest (21.11 ± 4.15), in the EPF (27.22 ± 0.96), and in the ELF (22.69 ± 2.36). In relation to the biodiversity indices calculated, the highest values for all of them were found in EPF (892–1,195 m.a.s.l). The lowest values were found in ELMF (1,421–1,826 m.a.s.l.) for total richness (21.11) and Margalef Index (13.59) and in ELF for Fisher α (37.60) and Shannon–Wiener Index (3.78).

Trees are concentrated in the first diameter class (10–20 cm), with few trees with large diameters. The density of trees per

TABLE 1 | Geographical and climatic data.

Forest type	Evergreen lower montane forest, northeastern Cordillera of the Andes			Evergreen Piedmont Forest, northeastern Cordillera of the Andes			Evergreen lowland forest, Napo–Curaray		
Closest town	**Alto Tena**			**Shitig**			**Runashito**		
	Plot 1	**Plot 2**	**Plot 3**	**Plot 1**	**Plot 2**	**Plot 3**	**Plot 1**	**Plot 2**	**Plot 3**
Altitude (m)	1,421	1,576	1,826	892	1,007	1,195	394	389	373
Latitude	−0.933	−0.93619	−0.93583	−0.92415	−0.90925	−0.90921	−0.9763	−0.97657	−0.97347
Longitude	−77.90826	−77.92835	−77.93615	−77.88578	−77.88394	−77.8909	−77.25376	−77.25753	−77.25755
Slope (%)	> 25–40	>40–70	> 70–100	>40–70	> 40–70	>40–70	> 5–12	>5–12	> 5–12
Soil type	Andosols			Andosols			Cambisols		
Mean temperature (°C)	20	18.8	17.9	21.7	21.3	21.3	24.2	24.2	24.2
Max. temperature (°C) (BIO5)	24.3	25.0	25.3	26.4	27.0	27.4	30	30	29.9
Min. temperature (°C)	13.3	12.9	11.6	16.2	15.7	15.0	18.8	18.8	18.7
Annual precipitation (mm)	3,913	3,663	3,288	3,986	3,972	3,970	3,229	3,229	3,229
Precipitation of the wettest month (mm)	462	452	417	444	443	450	376	373	373
Precipitation of the driest month (mm)	218	208	171	241	241	242	171	168	168
Climate type (Thornthwaite, 1948)	Humid with Little water deficit Mesothermal			Humid with Little water deficit Mesothermal			Hyperhumid with no water deficit. Megathermal		

Climatic data derived from Fick and Hijmans (2017).

TABLE 2 | Equations.

Number	Equation	Description
Eq. 1	Moist forest, Chave et al. (2005)* $\text{AGB}_{\text{est}} = \rho \times \exp(-1.499 + 2.148\ln(\text{DBH}) + 0.207(\ln(\text{DBH}))^2 - 0.0281(\ln(\text{DBH}))^3)$	AGB = aboveground biomass (kg) ρ = Wood specific gravity (g cm^{-3}) DBH = diameter at breast height (cm)
Eq. 2	Wet forest, Chave et al. (2005)** $\text{AGB}_{\text{est}} = \rho \times \exp(-1.239 + 1.980\ln(\text{DBH}) + 0.207(\ln(\text{DBH}))^2 - 0.0281(\ln(\text{DBH}))^3)$	AGB = aboveground biomass (kg) ρ = Wood specific gravity (g cm^{-3}) DBH = diameter at breast height (cm)
Eq. 3	Richness (S) count of total species per unit area	Richness (S) = total richness (N ha^{-1})
Eq. 4	$\text{MI} = \frac{(\text{NS}-1)}{\ln(\text{N})}$	*MI* = Margalef Index *NS* = number of species *N* = total number of individuals

**Used to calculate AGB in the Evergreen Lowland Forest (ELF). **Used to calculate AGB in the Evergreen Piedmont Forest (EPF) and the Evergreen Lower Montane Forest (ELM).*

TABLE 3 | Means and standard deviations of forest structure characteristics, total live aboveground biomass (AGB), richness, and biodiversity indices by forests type along an altitudinal gradient.

Variable	Evergreen Lower Montane forest	Evergreen Piedmont forest	Evergreen Lowland forest
Stem density (1 ha^{-1})	687 ± 100.21	773 ± 127.30	672 ± 37.92
Basal area (m^2 ha^{-1})	36.15 ± 7.65	42.01 ± 8.39	32.47 ± 1.86
Average DBH (cm)	21.35 ± 2.70	22.32 ± 1.59	20.97 ± 0.60
Maximum DBH (cm)	134	96	135
AGB (Mg ha^{-1})	310.26 ± 81.59	347.73 ± 90.38	377.39 ± 42.73
Richness (S) (N 0.1 ha^{-1})	21.11 ± 4.15	27.22 ± 0.96	22.69 ± 2.36
Margalef Index (MI)	13.59 ± 2.39	17.27 ± 0.78	14.70 ± 1.55
Fisher's α	43.85 ± 8.16	55.16 ± 8.99	37.60 ± 8.95
Simpson Index	0.96 ± 0.003	0.98 ± 0.0009	0.96 ± 0.01
Shannon–Weaver Index	3.89 ± 0.07	4.18 ± 0.05	3.78 ± 0.25

hectare in the Evergreen Lower Montane Forest was 687, 773 in the EPF, and 672 in ELF (**Table 3** and **Figure 2**).

Families with most species per hectare are Fabaceae (17), Rubiaceae (17), Moraceae (15), and Lauraceae (11) in the ELMF; Fabaceae (16), Moraceae (14), Lauraceae (13), and Rubiaceae (13) in the EPF; Fabaceae (16), Meliaceae (13), Moraceae (13), and Sapotaceae (10) in the ELF. The most abundant species in the ELM forest are *Mabea standleyi* (7%), *Otoba glycycarpa* (4.7%), *Miconia* sp. (4.6%), and *Eschweilera coriacea* (3.6%); in the EPF *Pouteria* sp. (3.7%), *Pseudolmedia laevigata* (3.6%), in the ELF *Iriartea deltoidea* (10.9%), *Otoba glycycarpa* (4.4%), and *Grias neuberthii* (4.1%) (**Table 4**).

Bray–Curtis dissimilarity Index maximum value can be found between ELF-1 and ELMF-3 (0.97) and minimum value between ELF-2 and ELF-3 (0.55). Close value to 1 means that the two sites hardly share species and close to 0 that the two plots have

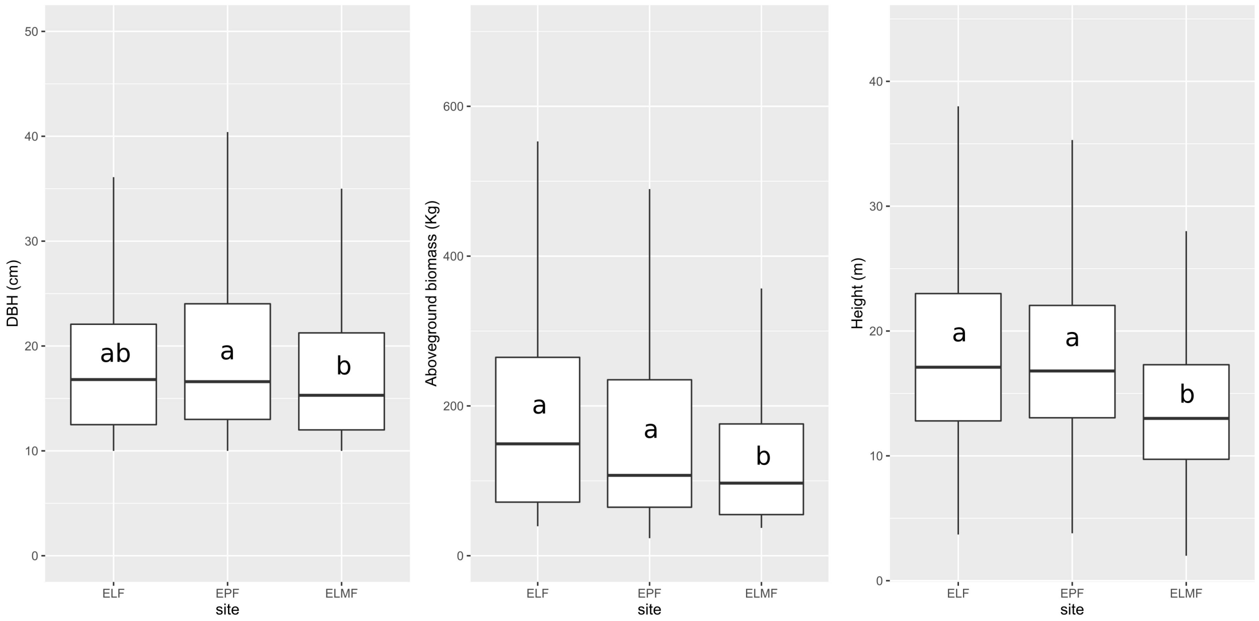

FIGURE 2 | Boxplot of dbh, total height, and AGB of all trees measured per forest type: Evergreen Lowland Forest (ELF), Evergreen Piedmont Forest (EPF), and Evergreen Lower Montane Forest (ELMF). Center line and outside edge of each box indicate the median and interquartile range (IQR = Q3–Q1), respectively. Vertical lines (whiskers) represent values falling within 1.5-IQR value from the upper and lower quartiles. Outliers are not shown due to visualization purposes. Letters show significant differences between forest types according to Mann–Whitney *post-hoc* test results.

very similar composition. In general, lower values can be found between plots of the same site (**Table 5**).

Aboveground Biomass

We found a higher tree density in moderate altitudes (892–1,195 m.a.s.l.), EPF (773), and lower in the Evergreen Lower Montane Forest (687) and ELF (671), but no significant differences were found according to Kruskal–Wallis ($p = 0.547$). Between forest types, significant differences according to Kruskal–Wallis test were found in all the metrics studied: tree height, dbh, and AGB (**Table 6** and **Figure 2**).

Within forest types, plots are more homogeneous in ELF (where only significant differences in height were found $p < 0.001$), followed by EPF (ns for dbh, $p < 0.001$ for height and $p = 0.042$ for AGB). In ELMF is where we found more differences among plots ($p = 0.002$ for dbh, $p < 0.001$ for height, and $p = 0.0052$ for AGB; **Table 7**).

The 10 most common species concentrate 51, 47, and 41% of AGB, respectively (**Table 4**). *Otoba glycycarpa* and *Alchornea latifolia* were the species with the highest BIV in the Evergreen Lower Montane Forest (1,421–1,826 m.a.s.l.); *Spirotheca rosea* and *Pouteria glomerata* in the EPF (892–1,195 m.a.s.l.); and *Otoba glycycarpa* and *Iriartea deltoidea* in the ELF (373–394 m.a.s.l.) (**Table 4**). The highest BIV is for *Otoba glycycarpa* in the Evergreen Lower Montane Forest (9.21%) and ELF (8.13%) and *Spirotheca rosea* (8.15%) in the EPF. Also, least abundant tree species contributed with a high percentage of the AGB, that is, *Alchornea latifolia* 11.64% (1,421–1,826 m.a.s.l.), *Vochysia braceliniae* 8.15% (892–1,195 m.a.s.l.), *Guarea kunthiana* 7.84% (373–394 m.a.s.l.).

As a result of the correlation matrix, we found that temperatures T (min, max, and mean) are highly correlated with altitude ($> |0.9|$) and annual precipitation (P) with the wettest and driest month. From seven variables, we finally selected two: elevation and annual P. We scaled these independent variables and tested mixed models. We use scaled P, elevation, and richness independent variables as fixed effects and forest type as random effect [AGB = scale (elevation) + scale (annualP) + scale (richness) + random effect (site)], but none of them had a significant effect.

In order to show the positive relationship (although not significant) between elevation (or mean temperature as they are highly correlated) and biomass, in the next figure a linear regression is presented with total AGB per plot by site and elevation.

DISCUSSION

Amazon tropical forests are characterized by their high diversity (Valencia et al., 1994, 2004); however, diversity varies greatly, depending on various factors, such as soils, historical events, altitudinal range, topography, or level of isolation or fragmentation (ter Steege et al., 2000). Diversity in the Ecuadorian Amazon is spatially heterogeneous because of its proximity to the Andes, differences in soil composition, and topography (Unger et al., 2012). Therefore, a wide range of richness values can be found in this region. ter Steege et al. (2000) compared α diversity levels from 268 plots in Amazonian Forests, six of them in Ecuador, and found a Fisher α from 3.6 to 221.8 in

TABLE 4 | Relative density, Relative basal area, Relative live aboveground biomass (AGB) and biomass importance value (BIV) of the 10 most important tree species along the study gradient, ordered according the BIV in each forest.

Family	Species	Rel. Den. (%)	Rel. BA (%)	Rel. AGB (%)	BIV (%)
Evergreen Lower Montane Forest					
(1,421–1,826 m.a.s.l.)					
Myristicaceae	*Otoba glycycarpa*	4.72	10.94	11.97	9.21
Euphorbiaceae	*Alchornea latifolia*	1.35	9.46	11.64	7.48
Euphorbiaceae	*Mabea standleyi*	7.01	3.99	3.3	4.77
Lecythidaceae	*Eschweilera coriacea*	3.64	5.12	5.26	4.67
Anacardiaceae	*Tapirira guianensis*	1.35	4.58	5.42	3.78
Phyllanthaceae	*Hieronyma asperifolia*	2.83	3.58	3.68	3.36
Melastomataceae	*Miconia sp.*	4.58	1.92	1.46	2.65
Meliaceae	*Guarea kunthiana**	2.02	2.53	2.51	2.36
Sapotaceae	*Micropholis venulosa*	0.67	2.68	3.26	2.21
Burseraceae	*Protium amazonicum*	1.21	2.56	2.63	2.14
Subtotal		29.38	47.36	51.13	42.63
Evergreen Piedmont forest					
(892–1,195 m.a.s.l.)					
Malvaceae	*Spirotheca rosea*	3.11	9.82	11.51	8.15
Sapotaceae	*Pouteria glomerata*	2.28	6.2	7.55	5.34
Vochysiaceae	*Vochysia braceliniae*	1.08	6.4	8.15	5.21
Moraceae	*Pseudolmedia laevigata**	3.59	3.3	3.24	3.38
Myristicaceae	*Virola flexuosa*	1.92	3.73	4.23	3.29
Lecythidaceae	*Eschweilera coriacea*	3.11	2.77	2.84	2.91
Vochysiaceae	*Vochysia ferruginea**	3.11	3.5	2.08	2.9
Sapotaceae	*Pouteria* sp.*	3.71	2.36	2.36	2.81
Sapotaceae	*Pouteria reticulata**	1.32	2.83	3.45	2.53
Myristicaceae	*Otoba glycycarpa*	1.92	2.14	2.12	2.06
Subtotal		25.15	43.05	47.53	38.58
Evergreen Lowland Forest					
(373–394 m.a.s.l.)					
Myristicaceae	*Otoba glycycarpa*	4.41	8.98	11.01	8.13
Arecaceae	*Iriartea deltoidea*	10.9	6.04	4.24	7.06
Meliaceae	*Guarea kunthiana* *	0.69	5.59	7.84	4.71
Myristicaceae	*Virola pavonis*	3.03	3.05	3.11	3.06
Fabaceae	*Cedrelinga cateniformis**	0.28	4.19	4.68	3.05
Lecythidaceae	*Grias neuberthii*	4.14	2.43	1.83	2.8
Violaceae	*Leonia glycycarpa*	4	2.23	2.14	2.79
Fabaceae	*Brownea ucayalina*	3.59	2.38	1.89	2.62
Myristicaceae	*Virola elongata*	2.34	2.71	2.67	2.57
Arecaceae	*Oenocarpus bataua*	2.21	2.16	1.82	2.07
Subtotal		35.59	39.76	41.23	38.86

**Species with wood specific gravity based on Baker et al. (2004). Rel. Den., relative density (%); Rel. BA, relative basal area (%); Rel. AGB, relative live aboveground biomass (%); BIV, biomass importance value (mean of relative density, relative basal area, and relative live aboveground biomass).*

TABLE 5 | Bray–Curtis dissimilarity Index between plots.

	ELF-1	ELF-2	ELF-3	EPF-1	EPF-2	EPF-3	ELMF-1	ELMF-2
ELF-2	0.562							
ELF-3	0.651	0.550						
EPF-1	0.810	0.775	0.827					
EPF-2	0.800	0.779	0.853	0.625				
EPF-3	0.789	0.851	0.891	0.672	0.648			
ELMF-1	0.797	0.866	0.862	0.867	0.811	0.858		
ELMF-2	0.862	0.869	0.819	0.823	0.847	0.826	0.743	
ELMF-3	0.969	0.958	0.917	0.877	0.888	0.793	0.898	0.823

TABLE 6 | Kruskal–Wallis results for height, dbh, and aboveground biomass between forest types.

Numeric variable	*n*	χ^2	*df*	*p*	Significance level
dbh (cm)	2,302	14.01	2	0.000907	****
Height (m)	2,302	180.56	2	<0.001	****
AGB (kg)	2,302	33.879	2	<0.001	****

*Significance level of p-values by number of asterisks (****$\alpha < 0.001$).*

TABLE 7 | Kruskal–Wallis results for height, dbh, and aboveground biomass between plots within forest types.

Site	Numeric variable	*n*	chi-square	*df*	*p*	Significance level
ELF	dbh (cm)	725	0.63105	2	0.7294	ns
ELF	Height (m)	725	16.38	2	<0.001	****
ELF	AGB (kg)	725	0.64217	2	0.7254	ns
EPF	dbh (cm)	835	4.38	2	0.1119	ns
EPF	Height (m)	835	23.435	2	<0.001	****
EPF	AGB (kg)	835	6.3438	2	0.042	**
ELMF	dbh (cm)	742	11.841	2	0.002683	***
ELMF	Height (m)	742	172.96	2	<0.001	****
ELMF	AGB (kg)	742	10.5	2	0.005246	***

*Significance level of p-values by number of asterisks (****$\alpha < 0.001$, ***$\alpha < 0.01$, ** $\alpha < 0.05$). ns, Not significant ($\alpha > 0.1$).*

general and from 39.2 to 211.0 in Ecuador. Our results for Fisher α (ELMF: 43.85 ± 8.16, EPF: 55.16 ± 8.99, ELF: 37.60 ± 8.95) are within this interval (**Table 3**).

In our study area, the species composition varies considerably from one plot to another. These variations are greater when differences in elevation are also higher. Thus, according to the Bray–Curtis index (**Table 5**), within the same forest type, plots located at the same altitude have a similar composition, and those located on a gradient present greater difference. The highest Bray–Curtis values are therefore found between the lowland plots and the last plot of the low montane forest (**Table 5**). Largest difference in species composition between plots of the same site is found in the Evergreen Low Montane Forest.

In general, richness values (ELMF: 21.1 ± 4.15 N 0.1 ha^{-1}, EPF: 27.2 ± 0.96 N 0.1 ha^{-1}, ELF: 22.69 ± 2.36 N 0.1 ha^{-1}) (**Table 3**) are similar to those found in other studies conducted in Amazon forests within an elevation range of 350 and 1,000 m.a.s.l. For example, Torres et al. (2020) carried out a study in the Napo Province and obtained richness values that ranged from 23.80 to 32.00 N 0.1 ha^{-1}. The maximum detected by Torres et al. (2020) were in plots located at 900–1,000 m.a.s.l. (32.0 ± 3.39 N 0.1 ha^{-1}), which corresponds to the same elevation of our richest plot (EPF: 272.22 ± 9.62 N ha^{-1}) (**Table 3**). Also, Patiño et al. (2015) conducted a floristic composition and forest structure study in the EPF (600–700 m.a.s.l.) with similar Simpson (0.94) and Shannon (3.52) values to the ones we found in our study (**Table 3**). Huamantupa-Chuquimaco (2010) carried out a study in southeastern Peru and, although the number of families and the density of individuals are lower, the number of species found (68 in 5,000 m^2) is comparable with our results, especially in the EPF (27.2 ± 0.96 N 0.1 ha^{-1}) and ELF (22.69 ± 2.36 N 0.1 ha^{-1}). However, the number of species recorded in this study are lower than in other parts of Ecuadorian Amazon such as Cuyabeno or Yasuní National Park (Valencia et al., 1994; Pitman et al., 2002), which corresponds to one of the most important biodiversity hotspots in the world (Ramsar, 2018).

Comparing the different ecosystems, we found 33 families that are present in the three types of ecosystems, whereas five (Combretaceae, Cannabaceae, Caricaceae, Bignoniaceae, Polygonaceae) are found only in the ELF, five (Ochnaceae, Ebenaceae, Caryocaraceae, Sabiaceae, Solanaceae) in the EPF, and six (Picramniaceae, Piperaceae, Icacinaceae, Chloranthaceae, Aquifoliaceae, Cunoniaceae) in the Evergreen Lower Montane Forest. There are two of these families (Cunoniaceae and Chloranthaceae) that are not present in any of the 1,170 plots studied by ter Steege et al. (2013). These families were found in the highest plot in the Evergreen Lower Montane Forest (1,826 m.a.s.l.). This may be due to the fact that the studied plots in other studies are located in a lower altitudinal range.

Fabaceae is the most diverse family in all plots studied: 17 sp. in ELMF and 16 sp. in EPF and ELF. This is consistent with other studies in the Peruvian (Gentry and Ortiz, 1993; Huamantupa-Chuquimaco, 2010) and Ecuadorian Amazon (Valencia et al., 1994; Quizhpe et al., 2019) and seems to be a common pattern in the Amazon Basin according to the results of ter Steege et al. (2013). The other more diverse families are Rubiaceae, Moreaceae, Meliaceae, Lauraceae, and Sapotaceae that are included by Gentry and Ortiz (1993) in the group of the most diverse families in neotropics. *Iriartea deltoidea* was found to be the most abundant species, which agrees with our results of ELF.

Aboveground Biomass

Our AGB values (ELMF: 310.26 ± 81.59 SD Mg ha^{-1}, EPF: 347.73 ± 90.38 SD Mg ha^{-1}, ELF: 377.39 ± 42.73 SD Mg ha^{-1}) (**Table 3**) are within the ranges of studies carried out in similar ecosystems. Biomass records for Evergreen Lower Montane Forest have been reported between 216.09 and 359.95 Mg ha^{-1} in an altitude range from 1,421 to 1,826 m.a.s.l. (Nadkarni et al., 2004; Sierra et al., 2007; Unger et al., 2012; Girardin et al., 2014). Higher biomass values (270.37–447.08 Mg ha^{-1}) were reported for EPF values in altitude ranges between 892 and 1,195 (Moser et al., 2011; Unger et al., 2012; Torres et al., 2020; García et al., 2021). Biomass records for ELF values between 349.39 and 426.57 Mg ha^{-1} in altitude range between 373 and 426 (Girardin et al., 2014; Cabrera Quezada et al., 2019; Tierres et al., 2020).

Significant differences were found in AGB between ELMF and the other two forest types. No significant differences were found between ELF and EPF; however, a trend can be observed of lower biomass as elevation increases (**Figure 2** and **Table 6**). Future studies should focus on investigating specific gravity values for all species and developing local allometric models that include the height variable for accurate biomass calculations (Báez et al., 2015; Phillips et al., 2016).

Forest biomass variability could be linked to the interaction of abiotic factors, such as temperature, precipitation, and nutrient availability (Rutishauser et al., 2015); or factors that influence plant regeneration, such as landslides (Myster, 2020); or species-inherent factors, such as wood density (Keeling and Phillips, 2007). In the mixed models, none of these variables were significant, which casts doubt on the effect of these abiotic factors on biomass in our study plots. However, this may be due to the sample size. The observed trend of biomass increasing with decreasing altitude, or with increasing temperatures, is confirmed in other studies (González-Caro et al., 2020). This also is in agreement with the results obtained for differences between plots (**Table 7**). Those plots of the same forest type in which there is a greater difference in elevation (ELMF) are those where significant differences were found for all variables (DBH, height, and AGB) (**Table 7**). Furthermore, in the linear regression between aboveground elevation and altitude, although the relationship is not significant, there is a clear trend (**Figure 3**). The lowest significance values were found for precipitation, practically ruling out that this is a factor influencing the amount of biomass. This is because the study area does not have significant water deficits.

Most biomass (**Figure 2**) belongs to individuals that are between 10 and 20 cm in diameter. This corresponds to a negative exponential diametric distribution, commonly known as reverse J–shaped curve. This type of curve is typical of mature stages in low-disturbed forest (Imaña et al., 2011).

The use of mixed models for the present study is a good choice as our data are nested (plots are nested within forest types). The fact that none of the variables are significant may be due to the level of resolution of environmental layers. As we do not

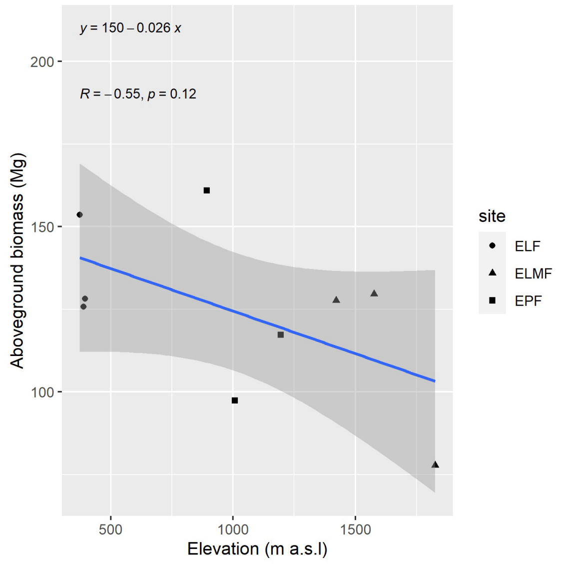

FIGURE 3 | Linear regression of mean AGB and elevation. Gray shadow represents confidence interval.

have specific meteorological data for the plots studied, we used climatic information from WorldClim, which offers these data at a resolution of 1 km^2, which may be too low for our study plots. In addition, WorldClim data were calculated from interpolation, including elevation (Fick and Hijmans, 2017), which makes the independence of the variables studied even less likely.

Land Management Implications

Ecuador has relatively low greenhouse gas emissions (Ritchie and Roser, 2020). However, the country made a strong commitment to reduce these within the framework of Nationally Determined Contributions (Samaniego et al., 2019). Two national strategies stand out to meet the objectives. The first strategy is focused on avoiding forest degradation through the national program "Socio Bosque," where the state pays an economic incentive to forest owners for their conservation (Jones et al., 2020). The second strategy is focused on increasing carbon stocks through the national restoration program (Wiegant et al., 2020). Forest restoration is the mechanism to increase carbon stocks and counteract greenhouse gas emissions from deforestation and forest degradation (UNFCCC, 2008). The forest restoration is one of the priorities of the world environmental agenda because of its potential for reducing greenhouse gases emissions (Silver et al., 2000; Hawes, 2018). Active restoration helps accelerate the reestablishment of the original biomass (Wheeler et al., 2016; Hietz et al., 2019). For a successful restoration, it is necessary to consider native species with genetic variability (Di Sacco et al., 2021) and its "ecological niche" (Silvertown, 2004; Poorter, 2007). The restoration approach changes, depending on the ecosystem service to be restored. The objectives of restoration could be carbon storage, forests products, biodiversity, and hydrologic ecosystem services (Di Sacco et al., 2021); if the objective of the restoration program is to recover the original carbon stocks, species with potential for carbon sequestration should be used (Cerullo and Edwards, 2019) that maximizes the highest amount of biomass per type of forest and be based on a reference ecosystem that supports the restoration (Gann et al., 2019). This consideration is important for future restoration programs in Ecuador, and this study identified the species with the highest biomass by forest type. Forest restoration in ELM, EPF, and ELMF with a focus on carbon sequestration should prioritize planting of the 10 most significant native species.

CONCLUSION

In this study, an assessment of the differences in forest structure (i.e., AGB, DBH, height) and floristic composition between three forest types in the Andean–Amazonian region of Ecuador is presented. We used a total of nine plots (three per forest-type) and a combination of non-parametric Kruskal–Wallis test and diversity indicators to elucidate these differences in detail. We found significant differences for all forest structure metrics studied. Higher AGB is found in the lowland forests compared with the other sites, especially with the Evergreen Lower Montane Forest, which is located at higher altitudes.

We also investigated how different environmental variables affect AGB, but only temperature was found to be significant. This is probably due to the relatively low sample size, the closeness of the plots, and the low resolution of the environmental layers (1 km^2), as no weather stations are available in the study area.

In relation to the floristic composition, we found that different species dominate the amount of AGB in these forests, which can have important implications in forest management.

Our objective is to expand the sample size in future studies in order to deepen our understanding of the interaction between environmental variables, forest structure, and floristic composition.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/**Supplementary Material**, further inquiries can be directed to the corresponding author/s.

AUTHOR CONTRIBUTIONS

MR-B and ER: data processing. BM and MR-B: writing the article. All authors contributed to the article and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/ffgc.2022.738585/full#supplementary-material

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