Six forests in one: Tree species diversity in the Bosque Protector Chongón Colonche, a lowland mountain range in coastal Ecuadorian

Oswaldo Jadán [a,b,*], David A. Donoso [c], Edwin Ponce-Ramírez [d], Franz Pucha-Cofrep [e,f], Omar Cabrera [g]

[a] Facultad de Ciencias Agropecuarias, Universidad de Cuenca, 12 de Octubre y Diego de Tapia, Cuenca, 010107, Ecuador
[b] Programa de Doctorado en Conservación de Recursos Naturales, Escuela Internacional de Doctorado, Universidad Rey Juan Carlos, Móstoles, Madrid, ES- 28933, Spain
[c] Departamento de Biología, Escuela Politécnica Nacional, Ladrón de Guevara E11·253, Quito, 170525, Ecuador
[d] Geoforest S.A, 12 de febrero y Av. Franklin Vega, Macas, 140150, Ecuador
[e] Grupo de Investigación Hidrología y Climatología, Universidad Técnica Particular de Loja, San Cayetano Alto S/N, Loja, 110101, Ecuador
[f] Brandenburg University of Technology (BTU) Cottbus-Senftenberg, 03044, Cottbus, Germany
[g] Departamento de Ciencias Biológicas y Agropecuarias, Universidad Técnica Particular de Loja, San Cayetano Alto S/N, Loja, 110101, Ecuador

ARTICLE INFO

ABSTRACT

Tropical mountain ranges shape the structure of tree communities and promote highly diverse natural habitats. The "Bosque Protector Chongón-Colonche" (BPCC), an 86,000-ha mountain formation situated on the coast of Ecuador, is biogeographically important for the region by connecting floristic elements of the wet Choco and the dry Tumbesian forests. Our understanding of the factors that model tree and palm diversity and distribution in this mountain range are limited. We measured and identified all trees and palms (DBH $\geq$10 cm) in 289 plots of 0.2 ha, distributed throughout BPCC. We used generalized linear models to explain the relationship between forest diversity and structure and climatic variables (temperature, rain, aridity), and altitude. We then used cluster and non-metric multidimensional scale (NMDS) analyses to search for distinct forest communities within the BPCC. Variance partition (varpart) was used to determine which predictor variables best explained these distinct forest communities. A species indicator analysis identified the species most likely to define these distinct forest communities. Finally, we carried out a niche modeling approach to identify the potential distribution of these forest communities within BPCC. In total, we identified 220 tree and palm species in our survey. The average number of species per plot was 17.8 $\pm$ 5.8, ranging from 3 to 40 species. Classification methods sorted the 289 study plots into six different forest communities, three communities in the dry forest and three in the semi-humid Garúa forest. Precipitation and temperature, but not altitude or aridity, explained floristic composition. These results emphasize the high but little cataloged diversity in the lowland mountain rainforests of coastal Ecuador.

1. Introduction

In the tropics, two contrasting theories have been proposed to explain the assembly of forest communities: niche and dispersion assembly (Pennington et al., 2009; Swenson and Enquist, 2009; Chain-Guadarrama et al., 2012). The first one assumes that floristic composition and abundance result from specific adaptations of species to environmental conditions and predicts a correlation between floristic composition and climatic variables. The second one states that floristic similarity (or beta diversity) between sites decreases with increasing geographic distance (spatial correlation) due to limited dispersion, regardless of any environmental difference (Hubbell, 2001). Both theories have been empirically confirmed throughout studies of the environmental influence on taxonomic and functional aspects of vegetation (Sesnie et al., 2009; Veintimilla et al., 2019; Jadán et al., 2021).

The floristic composition and frequency of trees at a given site are important in understanding the ecological drivers of tropical forest diversity and identifying forest communities of high value for conservation. The latter task can be facilitated by computer tools that predict the potential species distribution (de la Cruz-Uc et al., 2019). For example, niche modeling allows us to determine the current status of threatened species and their relationship with changes in land use (De Cauwer et al., 2014). In addition, occurrence models using absolute frequencies have provided predictions about species' current and potential distribution.

These occurrence models use current or future climatic variables (Vessella and Schirone, 2013) to explore species distribution based on the niche theory. In cases of extreme deforestation, niche models have been used to design synthetic arboreal communities based on the maximum potential distribution shown by a group of native species (de la Cruz-Uc et al., 2019).

The western coastal Cordilleras are isolated from the Andes and have unique environmental characteristics of climate, soil, and seasonality (Astudillo-Sánchez et al., 2019). These unique environmental conditions produce particular plant formations, dominated mainly by dry forests (Banda et al., 2016). As in other dry forests, the number of species per area unit is low (Banda et al., 2016), but endemism (Josse and Balslev, 1994; Leal-Pinedo and Linares-Palomino, 2005; Hernández et al., 2016; Quintana et al., 2017a) and the percentage of tree species used by humans (Uslar et al., 2004; Sánchez et al., 2006; Quintana et al., 2019) are high. Scattered among these dry habitats, there are also humid and semi-humid ecosystems with distinct vegetation (Bonifaz and Cornejo, 2004; Astudillo-Sánchez et al., 2019). In these ecosystems, species richness and structure of forest communities are driven by climatic variables such as temperature (Espinosa et al., 2011), precipitation (Muenchow et al., 2013), edaphic variables, spatial effects (Rasal Sánchez et al., 2011; Castellanos-Castro and Newton, 2015), and geographical barriers (Linares-Palomino et al., 2011; Quintana et al., 2017b). Ecological niche and its climatic divergence are also responsible for the species richness patterns (Stevens, 1989; Liu et al., 2020).

In Ecuador, coastal mountain ranges in Guayas, Manabí, and Santa Elena provinces within the "Tumbesian" endemism bioregion and the Chocó-Darién hotspot are characterized by their high richness of timber trees (Aldrich et al., 1997; Bonifaz and Cornejo, 2004). These coastal mountain ranges are less than 20 km from the coast and more than 200 km apart from the main Andean branches. Studies of diversity (Neill et al., 1999; Bonifaz and Cornejo, 2004; Clark et al., 2006; Linares-Palomino et al., 2010; Palacios and Pérez, 2012) and taxonomy (Cornejo and Bonifaz, 2005; Cornejo and Iltis, 2005; Cornejo, 2009) confirm that the western mountain ranges of Ecuador host a high floristic diversity. At the same time, this area bears intense anthropogenic pressures that have caused the loss of more than 40% of its original vegetation (Berg and Horstman, 1996; Gibson et al., 2000). Therefore, structural characterization of these understudied forests and the development of potential distribution maps are key for guiding the conservation efforts in this area.

Here, we study the ecology of Ecuadorian coastal forests within a protected area called "Bosque Protector Chongón-Colonche" (BPCC), combining a phytosociological approach with niche modeling to determine the number and spatial distribution of forest communities. We answered the following questions: 1) what is the relationship between forest diversity and structure with climatic variables (temperature, precipitation, aridity) and altitude? 2) are there distinct forest communities along BPCC, and if so, which climatic variables best explain them? We identified indicator species that best describe these forests; 3) what is the potential distribution of these distinct forest communities within BPCC?

2. Materials and methods

2.1. Study area

BPCC is located in the lowland mountain range called "Cordillera Chongón-Colonche" in the Ecuadorian Pacific region, approximately 200 km from the western foothills of the Andes, in Guayas, Manabí, and Santa Elena provinces (Fig. 1). It has 86,000 ha and is altitudinally distributed between 0 and 900 m. Orography is very irregular, which leads to climatic heterogeneity over short distances (García-Garizábal, 2017). BPCC bioclimates range from semi-arid to sub-humid. Semi-humid forests, known as Garúa forests (GF), are present at altitudes above 400 m, while dry forests (DF) occur in the lower zones (Astudillo-Sánchez et al., 2019). Mean annual temperature ranges from 21 °C to 25 °C, and mean annual precipitation is 590–1289 mm (Appendix 1). In BPCC two types of vegetation coverage have been identified by local authorities: 1) semi-humid forest or Garúa forest (GF) and 2) dry forest (DF) (Ponce,
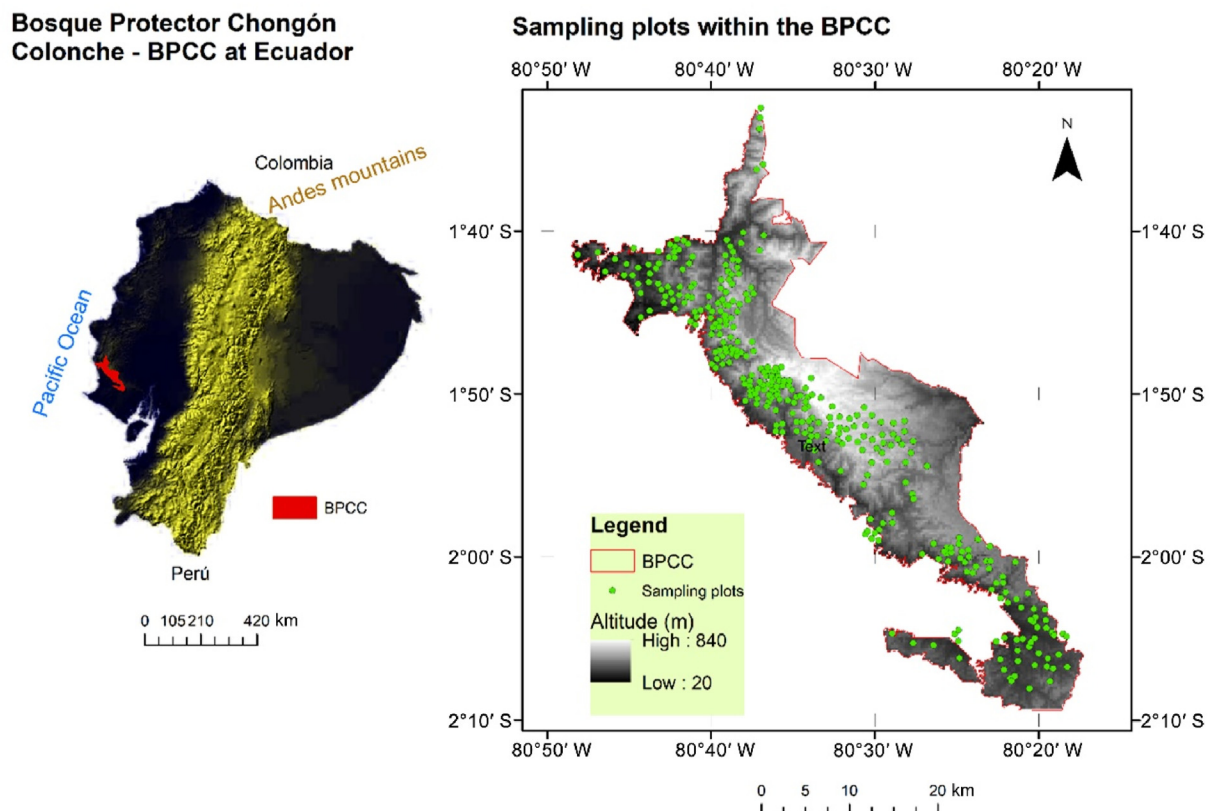

Fig. 1. Location of the Bosque Protector Chongón Colonche (BPCC) at Ecuador and spatial distribution of 289 sampling plots.

2009). These forests are subdivided into non-intervened and intervened mature forests. Previously, Garúa forests (undisturbed and intervened) were characterized by descriptive and conventional methods, using an incomplete database for taxonomic identification (Jadán et al., 2014). Four years ago we evaluated the dry forests and completed the taxonomic identification of all the sample plots. In this context, the present study corresponds to an exhaustive analysis with complete taxonomic and climatic data of the two types of coverage. In addition, we only consider undisturbed forests to evaluate parameters in native vegetation, expecting to obtain the highest values, compared to disturbed areas.

2.2. Sampling and data collection

For this research, we randomly established 289 sampling plots of 2,000 m^2 (or 0.2 ha; 50 m × 40 m), covering the entire study area (Fig. 1). In DF we installed 172 plots and GF 117 plots. The presence of these two forest types was verified through field trips, and only mature forests with few or no anthropogenic disturbances were chosen. To reduce the topographic influence, all the plots were set on sites that did not exceed 90% slope. Although it was impossible to perform a stratification by altitude, our plots were well distributed across the altitudinal range (Appendix 1). Within each plot, all trees and palms ≥10 cm DBH were counted, measured (total and dominant heights), and taxonomically identified at the species level, directly in the field or by comparison with specimens of LOJA and GUAYAS herbaria.

We used altitude and 20 climate variables as environmental predictors (Appendix 1). Climate variables were taken from the Worldclim global climate database (https://www.worldclim.org/) using the central geographic coordinates of each plot. Evapotranspiration was taken from the CGIAR-CSI Global-PET and Global Aridity Index (Global-Aridity) database (http://www.cgiar-csi.org) at five arcsec. The aridity index, a measure of available water, was calculated as the ratio between mean annual precipitation and potential evapotranspiration (Mazón et al., 2020). All environmental predictors were described by their mean, standard deviation, and range (Appendix 1).

2.3. Relationship between forest diversity and structure and environmental predictors

As quantitative response variables, we used plot diversity (i.e., species richness for each plot) and three structural variables: tree density, basal area, total height, and dominant height. Total height is the average of the total height that was measured for all trees within each plot. Dominant height is the average of the total height that was measured in the ten tallest trees within each plot. To avoid collinearity between the environmental predictors, we performed a correlation analysis using the "find Correlation" function in the R package "Caret" (Kuhn et al., 2018). When pairs of predictors showed a correlation of $r > 0.7$, one of the predictors was eliminated. Pearson's correlations between all variables are shown in Appendix 2. The selected environmental predictors were: mean annual temperature (°C), mean diurnal range of temperature (°C), precipitation of wettest month (mm), precipitation of driest month (mm), precipitation of driest quarter (mm), aridity index, and altitude (m).

Generalized Linear Models (GLMs) with Negative Binomial distribution and logarithmic link function were fitted to determine which environmental predictors influenced the variation in the four quantitative response variables, using the "glm" function in R package "Stats" (R Core Team, 2013). We chose GLMs for the potential lack of independence between the plots and heteroscedasticity, as Finegan et al. (2015) suggested. The distribution and link used did not present overlapping errors, which was verified with the test of goodness of fit of models for count data, using the "gof" function in R package "Aods3" (Lesnoff et al., 2018).

2.4. BPCC forest communities

To determine if the vegetation sampled within the BPCC formed distinct forest communities we applied the beta diversity approach as a function of distance and species dissimilarity (Sesnie et al., 2009; Castellanos-Castro and Newton, 2015). For this, a cluster analysis was performed using the Ward method and Bray-Curtis distance ($p < 0.05$), using the floristic composition, abundance, and the "hclust" function in the "Stats" R package (R Core Team, 2013). We considered a similarity distance of over 25% as the threshold to separate the groups of plots. These groups were statistically differentiated by ANOSIM similarity analysis ($p < 0.05$) using the "vegdist" function in the "Vegan" R package (Oksanen et al., 2020). The resulting groups were considered different forest communities. Non-metric multidimensional scaling (NMDS) was performed to show the multivariate dissimilarity between forest communities. The species turnover or beta diversity between communities was calculated using the Chao-Jaccard-Raw index (Chao et al., 2005).

2.5. Forest community's indicator species

After determining the presence of forest communities, an indicator species analysis (Indicspecies, $p < 0.05$) was performed according to their frequencies and abundances per plot, using the "Indicspecies" R package (De Cáceres et al., 2012). This analysis identified those species strongly associated with each forest community. We scored their endemic status for all indicator species identified using the red book of endemic plants of Ecuador (Valencia et al., 2004) and the red list of the International Union for the Conservation of Nature (https://www.iucnredlist.org/).

Differences among forest communities in species richness (alpha diversity), density, basal area, total height, and dominant height were tested using Kruskal-Wallis's test ($p < 0.05$) since variables were not normally distributed.

2.6. Floristic composition in forest communities and environmental variables

A variation partition analysis (varpart) was performed to determine which environmental predictors better explained the variation in floristic composition, using the "varpart" function in the "Vegan" R package (Dray et al., 2012). For this analysis, the effect of spatial correlation was also included as a predictor variable. This variable was calculated using geographic distance through the function "principal coordinates of proximity matrices – PCNM" in the "Vegan" R package (Oksanen et al., 2020). Geographic distance was calculated using the central geographic coordinates of each plot. We applied the forward selection procedure to select the climate and PCNM variables most associated with the matrix of floristic composition and abundance per plot.

2.7. Potential distribution of forest communities within BPCC

Using spatial distribution models, maps of the potential distribution of communities were generated. Sampling plots were used as geographical distribution points corresponding to each forest community. The environmental predictors used for this analysis (mean annual temperature, mean diurnal range of temperature, precipitation of wettest month, precipitation of driest month, precipitation of driest quarter, and altitude) were the same climatic and altitude variables that influenced community formation and explained floristic composition.

The Maxent software version 3.3.3 was used to model the potential distribution of each forest community following the same methodological protocols used by de la Cruz-Uc et al. (2019) and Phillips et al. (2006). The models were run with default parameters, such as 10,000 background points and a maximum of 500 iterations. As test data, 25% of the points were randomly selected. The "threshold" and "hinge" options were not considered to avoid overfitting the response curves. Environmental predictors that did not contribute significantly to the model or were repetitive in each model for each forest community were eliminated.

To evaluate the performance of Maxent in the calculation of potential

distributions, the Area Under the Curve (AUC) and ROC (Receiver Operating Characteristic) were used (Franklin, 2010). The ROC curve represents the sensitivity based on false positives and is a parameter that evaluates the goodness of fit with values between 1 "perfect test" or 0.5 "weak test" (Navarro-Cerillo et al., 2016). The goodness of fit of the models obtained was assessed following the criteria of Thuiller et al. (2005) and Navarro-Cerillo et al. (2016): unsatisfactory AUC <0.80; satisfactory $0.80 \leq$ AUC <0.90; good $0.90 \leq$ AUC <0.95, and very good AUC $\geq$0.95.

The layers obtained were exported in a raster format to the free program GVSIG (http://www.gvsig.org). The potential distribution maps were made with the probability of occurrence values using this classification: very low (<25%), low (25%–42%), medium (43%–59%), high (60%–74%), and very high (75%–100%) (de la Cruz-Uc et al., 2019). The areas with a high and very high probability of occurrence were reported as those with the greatest potential. To show sequence in the analysis carried out in this study, we present the distribution maps together with the cluster that was carried out in objective two.

3. Results

Overall, 20,000 individuals were sampled. They belonged to 60 botanical families and 222 species. The five most diverse families were Fabaceae (35 species), Moraceae (17 species), Lauraceae (12 species), Rubiaceae (11 species), and Meliaceae (10 species). The remaining families (55 species) were represented by 1–9 species each. The average number ($\pm$S.D.) of species per plot was 17.8 $\pm$ 5.8 (range 3–40). The average number of individuals per plot was 72 $\pm$ 34 (range 8–206).

3.1. Forest diversity, structure, and environmental predictors

Species richness was negatively related to mean diurnal temperature range and aridity index and positively related to altitude (Table 1). All four forest structure variables tree density, basal area, total height, and dominant height were explained by at least one environmental predictor (Table 1). Tree density was negatively influenced by temperature, precipitation, and aridity index and positively by altitude (Table 1). The basal area was negatively affected by precipitation of driest month and positively by precipitation of driest quarter (Table 1). Total height was negatively influenced by mean annual temperature, mean diurnal range of temperature, precipitation of wettest month, precipitation of driest month, and aridity index, and positively by precipitation of driest quarter and altitude (Table 1). The dominant height was negatively influenced by the precipitation of wettest month and positively by altitude (Table 1).

3.2. Classification of forest communities from BPCC

The cluster analysis grouped the 289 plots into six forest communities (FC) (Appendix 3). These FC were statistically different (ANOSIM: $r = 64$;

$p = 0.001$). In the NMDS ordination, FC1, FC2, and FC3 were located to the right along the first ordination axis, within the dry forest biozone (Fig. 2). In contrast, FC4, FC5, and FC6 were located to the left of the first ordination axis, within the semi-humid Garúa forest biozone (Fig. 2). Beta diversity ranged from 0.01 to 0.75 (Fig. 2). FC2 and FC5, FC3 and FC5, and FC3 and FC6 shared the lowest number of species (1), while FC2 and FC3 shared the highest (29) (Fig. 2).

3.3. Indicator species

We identified 30 indicator species for different FCs (Table 2). FC1 and FC3 had more indicator species than FC4 and FC6 (Table 2). Indicator species *Erythrochiton giganteus*, *Phytelephas aequatorialis*, and *Matisia grandifolia* are endemic to the western Ecuador Coastal region. Other Ecuadorian endemic species found in the FC1, FC2, and FC3 were *Clavija eggersiana*, *Compsoneura mutisii*, *Caryodaphnopsis theobromifolia*, *Chrysochlamys dependens*, *Prestoea decurrens*, and *Couepia platycalyx*; the last is an endangered species.

3.4. Differences in response variables among the six forest communities

FC2 had the highest number of plots (Table 3). Mean species richness was significantly higher in FC1, FC2, and FC3 ($p < 0.0001$) compared to FC4, FC5, and FC6 (Table 3). All four structural variables had higher values in FC1, FC2, and FC3 than in FC4, FC5, and FC6 ($p < 0.0001$) (Table 3).

3.5. Floristic composition and environmental predictors

The varpart analyses (Table 4) showed that climatic variables, altitude, and spatial correlation explained 14% of the variation in the floristic composition of trees. Climate, altitude, and space explained 13%, 4%, and 0.5% of the variation, respectively (Table 4). The pure effects of individual predictor matrices, though significant ($p = 0.001$), were all much smaller, with $R^2_{adj} = 0.09$, 0.01, and 0.01, respectively, for climatic variables, altitude, and spatial correlation (Table 4). Shared effects between two variables when controlling for the third one were $R^2_{adj} = 0.04$ for climate and altitude, 0.01 for climate and spatial correlation (Table 4). Altitude and space control over climate was not significant.

### 3.6. Potential distribution models of forest communities

The potential distribution models of FC1, FC2, and FC3 reached satisfactory AUC values (Table 5). FC5 presented a very good AUC value and FC6 a good value. On the other hand, the potential distribution model of FC4 did not reach satisfactory AUC values. Mean diurnal range of temperature was the most important in the potential distribution of the FC1 and FC2 (Table 5). Precipitation of driest quarter and month were significant for FC3 and FC4, respectively. Mean annual temperature was

Table 1
Results of GLM evaluating the relationship between species richness and vegetation structure parameters and environmental predictors in 2,000 m² plots within the BPCC. Estimates (Est.) and their *p*-value (z(*p*)) are shown. Values in bold were significant.

Environmental predictors	Richness		Structure								
			Tree density		Basal area		Total height		Dominant height	
	Est.	z(*p*)	Est.	z(*p*)	Est.	z(*p*)	Est.	z(*p*)	Est.	z(*p*)
(Intercept)	**12.6**	**7.3*****	**18.0**	**7.5*****	5.2	1.7	**10.3**	**6.7*****	**6.1**	**5.3*****
Mean annual temperature (°C)	−0.05	−1.5	**−0.1**	**−2.9****	−0.1	−1.7	**−0.1**	**−3.2****	−0.04	−1.7
Mean diurnal range of temperature (°C)	**−0.9**	**−5.2*****	**−0.9**	**−3.3****	−0.03	−0.11	**−0.5**	**−3.1****	−0.2	−1.4
Precipitation of wettest month (mm)	0.002	1.7	**−0.004**	**−1.9***	−0.002	−0.7	−0.002	−1.7	**−0.002**	**−2.3***
Precipitation of driest month (mm)	−0.05	−1.7	−0.1	−1.8	**−0.3**	**−3.5****	**−0.1**	**−2.5***	−0.06	−1.9
Aridity index	**−1.1**	**−3.3****	**−1.3**	**−2.7****	−0.3	−0.5	**−0.8**	**−2.8***	−0.2	−0.9
Precipitation of driest quarter (mm)	0.01	0.9	0.03	1.3	**0.1**	**4.9*****	**0.02**	**2.1***	0.02	1.9
Altitude (m a.s.l.)	**0.001**	**4.2*****	**0.001**	**2.7****	0.0004	1.5	**0.0004**	**2.7***	**0.0004**	**3.2****

*$p < 0.05$; **$p < 0.001$; ***$p < 0.0001$.
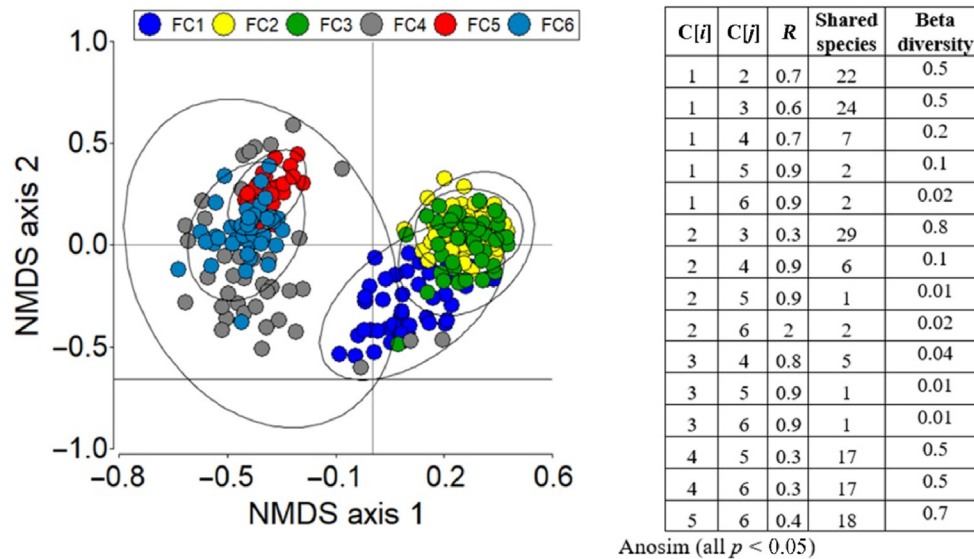
Fig. 2. To the left, is an NMDS plot showing the multivariate dissimilarity between the six forest communities (FC). To the right, a table with ANOSIM pair-wise comparisons indicated that all FC were statistically different (C[*i*], C[*j*]). Higher *R* values indicate greater dissimilarity in floristic composition. The table also shows the species shared between FCs and their beta diversity values according to the Chao-Jaccard-Raw index.

important for FC5 and FC6. FC3 had the largest potential distribution (1,794 ha), with a probability of occurrence >75% (Table 5; Fig. 3c), while FC4 did not reach this probability of occurrence in any grid square (Table 5; Fig. 3d). However, considering the percentages of occurrences >60%, FC4 presented the largest potential occurrence area, followed by FC2, unlike FC5 which presented the lowest values (Table 5; Fig. 3d, b, e, respectively). The potential distributions of the forest communities and their relationship with the cluster analysis (cluster) within the BPCC are shown in Fig. 3.

4. Discussion

4.1. Relationships between richness, structure, and environmental predictors

Even though altitudinal variation in BPCC is not as marked as in other tropical areas (Girardin et al., 2014; Veintimilla et al., 2019), altitude significantly impacted four of the five response variables (except basal area). The highest values for all response variables were recorded at higher altitudes, corresponding to the semi-humid Garúa forest (FC1, FC2, and FC3). Here, mean annual temperature, mean diurnal range of temperature, aridity, and precipitation seasonality (all negatively and significantly correlated with altitude) are lower than those in the dry forests (FC4, FC5, and FC6). The high climatic divergence explains these results in the BPCC, which is more marked at the higher altitudes of the western slope of the Cordillera (Ayerza, 2019). This climatic divergence and its influence on richness are linked to the narrow environmental niche that conditions high variation of species richness in small geographic spaces (Stevens, 1989). In FC1, FC2, and FC3, temperature is lower but still moderate in terms of plant physiological thresholds when compared to the conditions in high-altitude forests (Jadán et al., 2021). These complex climatic conditions facilitate efficient ecophysiological processes such as seed germination and initial seedling growth. Also, climatic seasonality would be an important factor for the formation of microhabitats that favor efficient biomass accumulation, resulting in higher values of basal area and height of the trees.

Our results also can be explained by interspecific interactions. For example, herbivorous predation could limit monospecific development in low-density forests (Janzen, 1970; Malizia et al., 2020). The positive relationship between species richness, density, and basal area with altitude is similar to what was recorded by Cueva et al. (2019) in a dry forest

with a shallower altitude gradient. On the other hand, our results are different from those recorded in the Andes and rain forests, where species richness (Homeier et al., 2010), basal area (Báez et al., 2015), and density (Schwarzkopf et al., 2011; Girardin et al., 2014) generally follow a contrasting pattern with altitude.

4.2. Forest communities, floristic composition, and their relationship with environmental variables

Combined multivariate analysis of floristic composition and abundance allowed us to determine six forest communities, reinforced by the presence of indicator species in each of them. Indicator species are ecologically important because they are susceptible to environmental changes (Bakker, 2008). Two indicator species are endemics: *Phytelephas aequatorialis* and *Matisia grandifolia* (Valencia, 2000); they were present in high abundance and frequency compared to other species, suggesting a good conservation status. Therefore, these forest communities have high ecological importance for conserving species with restricted distribution.

The varpar analysis suggested that climatic predictors drive the variation in floristic composition in BPCC. Temperature and precipitation are the main determinants of plant ecophysiological processes, such as seed production, germination, and growth (Peng et al., 2019; Rosbakh and Poschlod, 2015). This finding is consistent with the niche assembly theory (Hubbell, 1979; Jones et al., 2006). These results are similar to those reported in the Tumbesian dry forest over a moderate altitude gradient (Espinosa et al., 2011) and a broader gradient in the humid forests of Mesoamerica (Veintimilla et al., 2019).

The combined effect of climate and altitude in controlling spatial correlation was the strongest of the three combined effects ($R^2_{adj} = 0.4$). Given the small altitudinal gradient sampled, this interaction between climate and altitude is remarkable (Appendix 2). Several studies have found altitude to be a strong predictor of qualitative and quantitative changes in vegetation (Báez et al., 2015; Malizia et al., 2020). This is due to the combined effects of climate variables and other environmental factors, such as the soil (not evaluated), that generate an ideal setting at the habitat level for establishing specialized floristic groups (Geml et al., 2014; Jadán et al., 2015).

In addition, climate showed the highest pure effect (0.09), which suggests the community assembly is highly influenced by the predictor variable (Chain-Guadarrama et al., 2012; Veintimilla et al., 2019). For example, higher temperature and humidity promote the decomposition

Table 2
Indicator species in the forest communities of the BPCC. IV: indicator value.

Forest communities	Species	Family	IV	p
1	*Cordia alliodora* (Ruiz & Pav.) Oken	Boraginaceae	0.8	0.001
1	*Erythrochiton giganteus* Kaastra & A.H. Gentry	Rutaceae	0.7	0.001
1	*Hyeronima alchorneoides* Allemao	Phyllanthaceae	0.6	0.001
1	*Mauria suaveolens* Poepp. & Endl.	Anacardiaceae	0.7	0.001
1	*Phytelephas aequatorialis* Spruce.	Arecaceae	0.5	0.003
1	*Triplaris cumingiana* Fisch. & C.A.Mey. ex C.A.Mey.	Polygonaceae	0.6	0.001
1	*Urera caracasana* (Jacq.) Gaudich. ex Griseb.	Urticaceae	0.7	0.001
2	*Aegiphila haughtii* Moldenke	Verbenaceae	0.7	0.001
2	*Grias peruviana* Miers.	Lecythidaceae	0.7	0.001
2	*Matisia grandifolia* Little	Malvaceae	0.8	0.001
2	*Rauvolfia tetraphylla* L.	Apocynaceae	0.6	0.001
3	*Aniba hostmanniana* (Nees) Mez	Lauraceae	0.7	0.001
3	*Carapa guianensis* Aubl.	Meliaceae	0.8	0.001
3	*Cecropia angustifolia* Trécul	Urticaceae	0.6	0.001
3	*Cupania latifolia* Kunth	Sapindaceae	0.5	0.001
3	*Dendropanax arboreus* (L.) Decne. & Planch.	Araliaceae	0.6	0.001
3	*Dussia lehmannii* Harms	Fabaceae	0.6	0.001
3	*Garcinia macrophylla* Mart.	Clusiaceae	0.5	0.001
3	*Nectandra cissiflora* Nees	Lauraceae	0.6	0.001
3	*Sapium glandulosum* (L.) Morong	Euphorbiaceae	0.6	0.001
4	*Gallesia integrifolia* (Spreng.) Harms	Phytolaccaceae	0.6	0.001
5	*Caesalpinia glabrata* Kunth	Fabaceae	0.6	0.001
5	*Cochlospermum vitifolium* (Willd.) Spreng.	Bixaceae	0.6	0.001
5	*Eriotheca ruizii* (K. Schum.) A. Robyns.	Bombacaceae	0.6	0.001
5	*Erythrina megistophylla* Diels	Fabaceae	0.5	0.001
5	*Pisonia aculeata* L.	Nyctaginaceae	0.5	0.001
5	*Handroanthus chrysanthus* (Jacq.) S.O. Grose	Bignoniaceae	0.8	0.001
6	*Capparis scabrida* Kunth	Capparaceae	0.6	0.001
6	*Citharexylum poeppigii* Walp	Verbenaceae	0.7	0.001
6	*Guazuma ulmifolia* Lam.	Ulmaceae	0.5	0.001

Table 4
Variation partitioning results for trees and palms ≥10 cm DBH sampled in 289 0.2-ha plots in the studied landscape. R^2_{adj} and F statistics are presented for all measured factors. The effect of factors controlling for any combinations of other factors is denoted by symbol.

Variables	R^2_{adj}	F	p
Cl: These variables were described in 2.7	0.13	8.0	0.001
Al	0.04	14.4	0.001
SC	0.005	2.3	0.003
All	0.14	7.1	0.001
Cl | Al + SC*	0.09	6.0	0.001
Al | Cl + SC*	0.01	6.0	0.001
SC | Cl + Al*	0.01	3.0	0.001
Cl + Al | SC	0.04		
Cl + SC | AL	0.01		
Al + SC | CL	0		

Cl: climatic variables; Al: altitude; SC: spatial correlation. *Pure effects.

highest AUC values, indicating an important effect of the predictor variables, with mean annual temperature the most important. The models for FC1 and FC2 showed good values, the mean diurnal range of temperature being the most critical predictor in these cases. However, the potential distribution model for FC4 did not reach the satisfactory prediction level (AUC < 0.7), which suggests that the chosen environmental variables had limited predictive power.

Mesoscale climate patterns are important for modeling ranges geographical distribution of species (Navarro-Cerillo et al., 2016). This is because climatic parameters documented at this scale have strongly impacted plant dispersal and growth (Neuvonen et al., 1999). Temperature, in particular, has a strong impact on the potential area of distribution for species, its effect being more evident at lower latitudes and altitudes (Wrege et al., 2016). Also, each species has optimal temperature thresholds, which are essential for an efficient internal metabolism (Malhi, 2012). In FC3 and FC4, the precipitation during the driest quarter and monthly precipitation were the most important environmental variables. This significant impact of weather conditions in specific months suggests that tree species in FC3 and FC4 are sorting themselves across gradients of temperature and precipitation (Khurana and Singh, 2001). However, in forests with high environmental heterogeneity, it is stated that temperature seasonality is more important than precipitation seasonality in explaining distribution patterns (Gaikwad et al., 2011).

In this research, we evaluated plant communities by combining phytosociological methods with an assessment of potential distribution maps. The merge of these two approaches allows a better understanding of ecological processes at the species (floristic composition) and community (climate composition) levels. Although our objective was not to compare the methods and algorithms to determine the potential distribution of forest communities, the performance of Maxent in our dataset reached quite good evaluation indices for the resulting models. This was possible due to the large number of plots that formed the forest communities. The models were based on predictor variables that explained to a large extent variation in the floristic composition in the study area. Also, they allowed to identify and spatially define the forest communities in BPCC.

and mineralization of organic matter, generating nitrates and ammonium, which are essential for various ecophysiological processes of arboreal plants (Robertson, 1989; Yang and Chen, 2009).

4.3. Potential distribution of forest communities

Models represented by distribution maps were made for the six forest communities identified in the BPCC. The models showed high predictive capacity (AUC > 0.8) for five of the six forest communities in a heterogeneous environmental gradient. The FC5 and FC6 models presented the

Table 3
The number of plots, species richness, and forest structure metrics registered in 2,000 m^2 plots across the six forest communities (FC) in the BPCC. Average values with different letters were significantly different ($p \leq 0.05$).

Variables	FC1	FC2	FC3	FC4	FC5	FC6	p
Number of plots	49	79	44	41	33	43	
Mean richness	18.1(a)	19.2(b)	20.8(b)	11.2(c)	12.7(c)	13.4(c)	<0.001
Tree density (individuals·ha^{-1})	408.9(a)	455.1(a)	510.7(b)	210.9(c)	241.8(c)	206.6(c)	<0.001
Basal area (m^2·ha^{-1})	17.8(a)	30.7(b)	27.2(b)	14.1(c)	13.5(c)	14.9(ca)	<0.001
Total height (m)	18.3(a)	19.9(b)	19.2(a)	11.5(c)	11.2(c)	11.5(c)	<0.001
Dominant height (m)	29.1(a)	30.9(b)	29.7(ab)	22.2(c)	22.5(c)	22.6(c)	<0.001

Table 5

Forest communities and their percentage of potential distribution in the BPCC. Values are in hectares. AUC: Area Under the Curve; FC: Forest community. <25%: very low; 25%–42%: low; 43%–59%: medium; 60%–74%: high; 75%–100%: very high. * Variables and their contribution to the potential distribution. MAT: Mean annual temperature; MDR: Mean diurnal range of temperature; PDQ: Precipitation of driest quarter; PDM: Precipitation of driest month; PWM: Precipitation of wettest month.

Community	AUC (test data)	*Variables (%)	Potential distribution and probability of occurrence (ha)					
			<25%	25%–42%	43%–59%	60%–74%	>75%	>60%
FC1	0.80	MDR (94.5)	36,217	23,661	16,058	7,858	940	8,798
		MAT (5.5)						
FC2	0.80	MDR (60)	39,548	20,756	15,119	8,371	940	9,311
		MAT (33.8)						
		PDM (2.8)						
		PDQ (1.5)						
		PWM (1.2)						
FC3	0.88	PDQ (42.2)	45,869	17,938	11,702	7,431	1,794	9,225
		MDR (36.3)						
		MAT (9.8)						
		PWM (7.9)						
		PDM (3.8)						
FC4	0.70	PDM (72.3)	6,833	37,071	28,358	12,471	0	12,471
		Altitude (27.7)						
FC5	0.94	MAT (72.2)	72,092	4,869	3,758	3,417	598	4,015
		PWM (18.3)						
		PDM (6.7)						
		PDQ (2.7)						
FC6	0.90	MAT (64.2)	53,129	13,581	10,165	7,602	256	7,858
		PWM (25.5)						
		PDM (9)						
		PDQ (0.8)						
		MDR (0.5)						
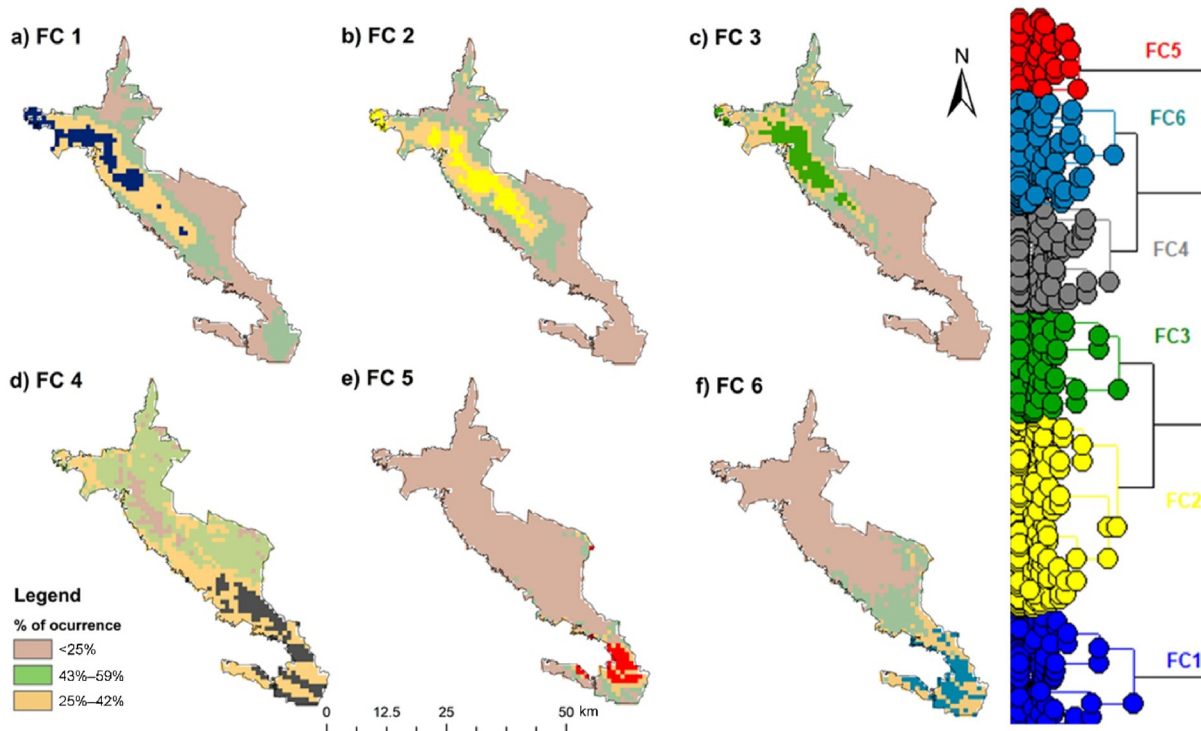
Fig. 3. Potential distribution of six forest communities (FC) for different categories of percentages of occurrence: very low (<25%), low (25%–42%), and medium (43%–59%). High (60%–74%) and very high (75%–100%) percentages in a single color are present on the map, and correspond to each FC in the cluster. The complete cluster is shown in Appendix 3. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

5. Conclusions

Six forest communities were found within the BPCC area. Each of these six forests has a distinct floristic composition, structure, and environmental optima. These forest communities add a new dimension to forest diversity in this area. Although the effect of altitude on vegetation is a well-known ecological phenomenon, its study in areas with marked rain seasonality is essential to define forest communities and their respective indicator species.

Authors' contributions

OJ and EPR did the fieldwork. OJ, DAD, OC, and FP performed the data analysis and writing of the document. OJ, DAD, and OC did the final

editing of the document.

Ethics approval and consent to participate

Not applicable.

Declaration of competing interest

Acknowledgments

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.fecs.2022.100069.

References

Aldrich, M., Billington, C., Edwards, M., Laidlaw, R., 1997. Tropical montane cloud forests: an urgent priority for conservation. WCMC Biodiver. Bull. 2, 1–14.

Astudillo-Sánchez, E., Pérez, J., Troccoli, L., Aponte, H., Tinoco, O., 2019. Flora leñosa del bosque de garúa de la cordillera Chongón Colonche, Santa Elena-Ecuador. Ecol. Appl. 18, 155–169. https://doi.org/10.21704/rea.v18i2.1334.

Ayerza, R., 2019. Importancia hídrica de los bosques de la cordillera Chongón-Colonche para las tierras áridas del noroeste de Santa Elena. Bosques Latitud Cero 9, 16–30.

Báez, S., Malizia, A., Carilla, J., Blundo, C., Aguilar, M., Aguirre, N., Aquirre, Z., Álvarez, E., Cuesta, F., Duque, Á., 2015. Large-scale patterns of turnover and basal area change in Andean forests. PLoS One 10, e0126594. https://doi.org/10.1371/journal.pone.0126594.

Bakker, J.D., 2008. Increasing the utility of indicator species analysis. J. Appl. Ecol. 45, 1829–1835. https://doi.org/10.1111/j.1365-2664.2008.01571.x.

Banda, K., Delgado-Salinas, A., Dexter, K.G., Linares-Palomino, R., Oliveira-Filho, A., Prado, D., Pullan, M., Quintana, C., Riina, R., Rodríguez, G.M., 2016. Plant diversity patterns in neotropical dry forests and their conservation implications. Science 353, 1383–1387. https://doi.org/10.1126/science.aaf5080.

Berg, K.S., Horstman, E., 1996. The Great Green Macaw *Ara ambigua guayaquilensis* in Ecuador: first nest with young. COTINGA 5, 53–54.

Bonifaz, C., Cornejo, X., 2004. Flora del Bosque de Garúa (árboles y epífitas) de la comuna Loma Alta, cordillera Chongón Colonche, provincia del Guayas, Ecuador. Universidad de Guayaquil, Guayaquil.

Castellanos-Castro, C., Newton, A.C., 2015. Environmental heterogeneity influences successional trajectories in Colombian seasonally dry tropical forests. Biotropica 47, 660–671. https://doi.org/10.1111/btp.12245.

Chain-Guadarrama, A., Finegan, B., Vilchez, S., Casanoves, F., 2012. Determinants of rain-forest floristic variation on an altitudinal gradient in southern Costa Rica. J. Trop. Ecol. 28, 463–481. https://doi.org/10.1017/S0266467412000521.

Chao, A., Chazdon, R.L., Colwell, R.K., Shen, T.J., 2005. A new statistical approach for assessing similarity of species composition with incidence and abundance data. Ecol. Lett. 8, 148–159. https://doi.org/10.1111/j.1461-0248.2004.00707.x.

Clark, J.L., Neill, D.A., Asanza, M., 2006. Floristic checklist of the mache-chindul mountains of Northwestern Ecuador. Contrib. U. S. Natl. Herb. 1–180.

Cornejo, X., 2009. *Amyris centinelensis* and *Zanthoxylum bonifaziae*: two new species of Rutaceae from western Ecuador. Harv. Pap. Bot. 14, 161–166. https://doi.org/10.3100/025.014.0207.

Cornejo, X., Bonifaz, C., 2005. *Inga colonchensis* (Fabaceae, Mimosoideae), una Nueva Endémica del Bosque Seco Tropical en Ecuador. Novon St. Louis Mo 15, 270–273. http://www.jstor.org/stable/3393333. (Accessed 12 January 2022).

Cornejo, X., Iltis, H.H., 2005. Studies in the Capparaceae XXVI. *Capparis bonifaziana*, a new species and western ecuadorian sister to the mostly amazonian *C. macrophylla*. Novon St. Louis Mo 15, 393–404. https://biostor.org/reference/63898. (Accessed 12 January 2022).

Cueva, E., Lozano, D., Yaguana, C., 2019. Efecto de la gradiente altitudinal sobre la composición florística, estructura y biomasa arbórea del bosque seco andino, Loja, Ecuador. Bosque 40, 365–378. https://doi.org/10.4067/S0717-92002019000300365.

De Cáceres, M., Legendre, P., Wiser, S.K., Brotons, L., 2012. Using species combinations in indicator value analyses. Methods Ecol. Evol. 3, 973–982. https://doi.org/10.1111/j.2041-210X.2012.00246.x.

De Cauwer, V., Muys, B., Revermann, R., Trabucco, A., 2014. Potential, realised, future distribution and environmental suitability for *Pterocarpus angolensis* DC in southern Africa. For. Ecol. Manag. 315, 211–226. https://doi.org/10.1016/j.foreco.2013.12.032.

de la Cruz-Uc, X., Valdés-Manzanilla, A., Barradas, V.L., Cámara Cabrales, L.d.C., 2019. Comunidades sintéticas arbóreas: una alternativa al deterioro forestal en la parte baja de la cuenca del río Usumacinta en Tabasco, México. Bosque 40, 117–127. https://doi.org/10.4067/S0717-92002019000200117.

Dray, S., Pélissier, R., Couteron, P., Fortin, M.-J., Legendre, P., Peres-Neto, P.R., Bellier, E., Bivand, R., Blanchet, F.G., De Cáceres, M., Dufour, A.-B., Heegaard, E., Jombart, T., Munoz, F., Oksanen, J., Thioulouse, J., Wagner, H.H., 2012. Community ecology in the age of multivariate multiscale spatial analysis. Ecol. Monogr. 82, 257–275. https://doi.org/10.1890/11-1183.1.

Espinosa, C.I., Cabrera, O., Luzuriaga, A.L., Escudero, A., 2011. What factors affect diversity and species composition of endangered Tumbesian dry forests in Southern Ecuador? Biotropica 43, 15–22. https://doi.org/10.1111/j.1744-7429.2010.00665.x.

Finegan, B., Peña-Claros, M., de Oliveira, A., Ascarrunz, N., Bret-Harte, M.S., Carreño-Rocabado, G., Casanoves, F., Díaz, S., Eguiguren Velepucha, P., Fernandez, F., Licona, J.C., Lorenzo, L., Negret, B.S., Vaz, M., Poorter, L., 2015. Does functional trait diversity predict above-ground biomass and productivity of tropical forests? Testing three alternative hypotheses. J. Ecol. 103, 191–201. https://doi.org/10.1111/1365-2745.12346.

Franklin, J., 2010. Mapping Species Distributions: Spatial Inference and Prediction. Cambridge University Press, Cambridge. https://doi.org/10.1017/CBO9780511810602.

Gaikwad, J., Wilson, P.D., Ranganathan, S., 2011. Ecological niche modeling of customary medicinal plant species used by Australian Aborigines to identify species-rich and culturally valuable areas for conservation. Ecol. Model. 222, 3437–3443. https://doi.org/10.1016/j.ecolmodel.2011.07.005.

García-Garizábal, I., 2017. Rainfall variability and trend analysis in coastal arid Ecuador. Int. J. Climatol. 37, 4620–4630. https://doi.org/10.1002/joc.5110.

Geml, J., Pastor, N., Fernandez, L., Pacheco, S., Semenova, T.A., Becerra, A.G., Wicaksono, C.Y., Nouhra, E.R., 2014. Large-scale fungal diversity assessment in the Andean Yungas forests reveals strong community turnover among forest types along an altitudinal gradient. Mol. Ecol. 23, 2452–2472. https://doi.org/10.1111/mec.12765.

Gibson, C.C., McKean, M.A., Ostrom, E., 2000. Explaining Deforestation: the Role of Local Institutions. People and Forests: Communities, Institutions, and Governance. MA. MIT Press, Cambridge, pp. 1–26.

Girardin, C.A., Farfan-Rios, W., Garcia, K., Feeley, K.J., Jørgensen, P.M., Murakami, A.A., Cayola Pérez, L., Seidel, R., Paniagua, N., Fuentes Claros, A.F., Maldonado, C., Silman, M., Salinas, N., Reynel, C., Neill, D.A., Serrano, M., Caballero, C.J., de los Angeles La Torre Cuadros, M., Macía, M.J., Killeen, T.J., Malhi, Y., 2014. Spatial patterns of above-ground structure, biomass and composition in a network of six Andean elevation transects. Plant Ecol. Divers. 7, 161–171. https://doi.org/10.1080/17550874.2013.820806.

Hernández, L., Parés-Jiménez, V., Reyna, C., Lizcano, D.J., Martínez, C.E.C., 2016. Woody plants of the machalilla National park, Ecuador: a check list. Arnaldoa 23, 363–392.

Homeier, J., Breckle, S.W., Günter, S., Rollenbeck, R.T., Leuschner, C., 2010. Tree diversity, forest structure and productivity along altitudinal and topographical gradients in a species-rich Ecuadorian montane rain forest. Biotropica 42, 140–148. https://doi.org/10.1111/j.1744-7429.2009.00547.x.

Hubbell, S., 1979. Tree dispersion, abundance, and diversity in a tropical dry forest. Science 203, 1299–1309. https://doi.org/10.1126/science.203.4387.1299.

Hubbell, S., 2001. The Unified Neutral Theory of Biodiversity and Biogeography. Princeton University Press, Princeton.

Jadán, O., Cifuentes, M., Torres, B., Selesi, D., Veintimilla, D., Guenter, S., 2015. Influence of tree cover on diversity, carbon sequestration and productivity of cocoa systems in the Ecuadorian Amazon. Bois. et Forets des. Trop. 325, 35–47. https://doi.org/10.19182/bft2015.325.a31271.

Jadán, O., Donoso, D.A., Cedillo, H., Bermúdez, F., Cabrera, O., 2021. Floristic groups, and changes in diversity and structure of trees, in tropical montane forests in the southern Andes of Ecuador. Diversity 13, 400. https://doi.org/10.3390/d13090400.

Jadán, O., Veintimilla, D., Ponce, E., González, M., Waise, H., Aguirre, Z., 2014. Identificación y caracterización florística de bosques naturales en el Bosque Protector Chongón Colonche, Ecuador. Bosque Latitud. Cero. 4, 7–14.

Janzen, D.H., 1970. Herbivores and the number of tree species in tropical forests. Am. Nat. 104, 501–528. https://doi.org/10.1086/282687.

Jones, M.M., Tuomisto, H., Clark, D.B., Olivas, P., 2006. Effects of mesoscale environmental heterogeneity and dispersal limitation on floristic variation in rain forest ferns. J. Ecol. 94, 181–195. https://doi.org/10.1111/j.1365-2745.2005.01071.x.

Josse, C., Balslev, H., 1994. The composition and structure of a dry, semideciduous forest in western Ecuador. Nord. J. Bot. 14, 425–434. https://doi.org/10.1111/j.1756-1051.1994.tb00628.x.

Khurana, E., Singh, J., 2001. Ecology of tree seed and seedlings: implications for tropical forest conservation and restoration. Curr. Sci. 80, 748–757.

Kuhn, M., Wing, J., Weston, S., Williams, A., Keefer, C., Engelhardt, A., 2018. Classification and Regression Training. R Package Version 6.0–81.

Leal-Pinedo, J., Linares-Palomino, R., 2005. The dry forests of the Biosphere Reserve of Northwestern (Peru): tree diversity and conservation status. Caldasia 27, 195–211.

Lesnoff, M., Lancelot, R., Lancelot, M.R., 2018. Package 'aods3'. CRAN. https://cran.r-p roject.org/web/packages/aods3/aods3.pdf. (Accessed 5 May 2021).

Linares-Palomino, R., Kvist, L.P., Aguirre-Mendoza, Z., Gonzales-Inca, C., 2010. Diversity and endemism of woody plant species in the Equatorial Pacific seasonally dry forests. Biodivers. Conserv. 19, 169–185. https://doi.org/10.1007/s10531-009-9713-4.

Linares-Palomino, R., Oliveira-Filho, A.T., Pennington, R.T., 2011. Neotropical seasonally dry forests: diversity, endemism, and biogeography of woody plants. In: Dirzo, R., Young, H.S., Mooney, H.A., Ceballos, G. (Eds.), Seasonally Dry Tropical Forests. Island Press, Washington, DC. https://doi.org/10.5822/978-1-61091-021-7_1.

Liu, H., Ye, Q., Wiens, J.J., 2020. Climatic-niche evolution follows similar rules in plants and animals. Nat. Ecol. Evol. 4, 753–763. https://doi.org/10.1038/s41559-020-1158-x.

Malhi, Y., 2012. The productivity, metabolism and carbon cycle of tropical forest vegetation. J. Ecol. 100, 65–75. https://doi.org/10.1111/j.1365-2745.2011.01916.x.

Malizia, A., Blundo, C., Carilla, J., Osinaga Acosta, O., Cuesta, F., Duque, A., Aguirre, N., Aguirre, Z., Ataroff, M., Baez, S., 2020. Elevation and latitude drives structure and tree species composition in Andean forests: results from a large-scale plot network. PLoS One 15, e0231553. https://doi.org/10.1371/journal.pone.0231553.

Mazón, M.M., Klanderud, K., Finegan, B., Veintimilla, D., Bermeo, D., Murrieta, E., Delgado, D., Sheil, D., 2020. How forest structure varies with elevation in old growth and secondary forest in Costa Rica. For. Ecol. Manag. 469, 118191. https://doi.org/10.1016/j.foreco.2020.118191.

Muenchow, J., von Wehrden, H., Rodríguez, E.F., Rodríguez, R.A., Bayer, F., Richter, M., 2013. Woody vegetation of a Peruvian tropical dry forest along a climatic gradient depends more on soil than annual precipitation. Erdkunde 67, 241–248. https://doi.org/10.3112/erdkunde.2013.03.03.

Navarro-Cerillo, R., Clavero, I., Lorenzo, A., Quero, J., Duque-Lazo, J., 2016. Integración de datos de inventario y modelos dehábitat para predecir la regeneración de especies leñosas mediterráneas en repoblaciones forestales. Ecosistemas 25, 6–21. https://doi.org/10.7818/ECOS.2016.25-3.02.

Neill, D.A., Clark, J.L., Vargas, H., Nuñez, T., 1999. Botanical Exploration of the Mache-Chindul Mountains, Northwestern Ecuador. Final report presented to the National Geographic Society, Washington, DC, USA (unpublished).

Neuvonen, S., Niemelä, P., Virtanen, T., 1999. Climatic change and insect outbreaks in boreal forests: the role of winter temperatures. Ecol. Bull. 47, 63–67.

Oksanen, J., Blanchet, F., Kindt, R., Legendre, P., Minchin, P., O'Hara, R., Simpson, G., Solymos, P., Stevens, M., Wagner, H., 2020. vegan: Community Ecology Package. R package version 2.6-2. https://CRAN.R-project.org/package=vegan. (Accessed 15 August 2022).

Palacios, W., Pérez, J., 2012. Ecología, Usos y Manejo de la Tagua (Phytelephas aequatoriales Spruce) en la Cordillera Chongón Colonche. Int. Symp. Med. Plant. Nat. Prod. 1030, 39–48.

Peng, L., Cheng, F., Hu, X., Mao, J., Xu, X., Zhong, Y., Li, S., Xian, H., 2019. Modelling environmentally suitable areas for the potential introduction and cultivation of the emerging oil crop Paeonia ostii in China. Sci. Rep. 9, 1–10. https://doi.org/10.1038/s41598-019-39449-y.

Pennington, R.T., Lavin, M., Oliveira-Filho, A., 2009. Woody plant diversity, evolution, and ecology in the tropics: perspectives from seasonally dry tropical forests. Annu. Rev. Ecol. Evol. Syst. 40, 437–457. https://doi.org/10.1146/annurev.ecolsys.110308.120327.

Phillips, S.J., Anderson, R.P., Schapire, R.E., 2006. Maximum entropy modeling of species geographic distributions. Ecol. Model. 190, 231–259. https://doi.org/10.1016/j.ecolmodel.2005.03.026.

Ponce, E., 2009. Línea base para la estimación de la cantidad de carbono fijado y para la planificación forestal comunal y grupal al futuro del bosque protector Chongón Colonche. In: Natura, F. (Ed.), Fundación Natura - KFW, Santa Elena, Ecuador, p. 35.

Quintana, C., Girardello, M., Barfod, A.S., Balslev, H., 2017a. Diversity patterns, environmental drivers, and changes in vegetation composition in dry inter-Andean valleys. J. Plant Ecol. 10, 461–475. https://doi.org/10.1093/jpe/rtw036.

Quintana, C., Pennington, R.T., Ulloa, C.U., Balslev, H., 2017b. Biogeographic barriers in the Andes: is the Amotape—huancabamba zone a dispersal barrier for dry forest plants? Ann. Mo. Bot. Gard. 102, 542–550. https://doi.org/10.3417/D-17-00003A.

Quintana, C., Girardello, M., Balslev, H., 2019. Balancing plant conservation and agricultural production in the Ecuadorian Dry Inter-Andean Valleys. PeerJ 7, e6207. https://doi.org/10.7717/peerj.6207.

R Core Team, 2013. R: a Language and Environment for Statistical Computing. Vienna, Austria. http://www.R-project.org/. (Accessed 15 August 2022).

Rasal Sánchez, M., Troncos Castro, J., Lizano Durán, C., Parihuamán Granda, O., Quevedo Calle, D., Rojas Idrogo, C., Delgado Paredes, G.E., 2011. Características edáficas y composición florística del bosque estacionalmente seco la menta y timbes, Región Piura, Perú. Ecol. Apl. 10, 61–74.

Robertson, G., 1989. Nitrification and denitrification in humid tropical ecosystems: potential controls on nitrogen retention. In: Proctor, J. (Ed.), Mineral Nutrients in Tropical Forest and Savanna Ecosystems. Cambridge, Massachusetts, USA, pp. 55–69.

Rosbakh, S., Poschlod, P., 2015. Initial temperature of seed germination as related to species occurrence along a temperature gradient. Funct.l Ecol. 29, 5–14. https://doi.org/10.1111/1365-2435.12304.

Sánchez, O., Kvist, L.P., Aguirre, Z., 2006. Bosques secos en Ecuador y sus plantas útiles. In: Morales, M., Ollgaard, B., Kvist, L.P., Borchsenius, F., Balslev, H. (Eds.), Botánica Económica de los Andes Centrales. Universidad Mayor de San Andrés, La Paz, Bolivia, pp. 188–204.

Schwarzkopf, T., Riha, S.J., Fahey, T.J., Degloria, S., 2011. Are cloud forest tree structure and environment related in the Venezuelan Andes? Aus. Ecol. 36, 280–289. https://doi.org/10.1111/j.1442-9993.2010.02160.x.

Sesnie, S.E., Finegan, B., Gessler, P.E., Ramos, Z., 2009. Landscape-scale environmental and floristic variation in Costa Rican old-growth rain forest remnants. Biotropica 41, 16–26. https://doi.org/10.1111/j.1744-7429.2008.00451.x.

Stevens, G.C., 1989. The latitudinal gradient in geographical range: how so many species coexist in the tropics. Am. Nat. 133, 240–256.

Swenson, N.G., Enquist, B.J., 2009. Opposing assembly mechanisms in a Neotropical dry forest: implications for phylogenetic and functional community ecology. Ecology 90, 2161–2170. https://doi.org/10.1890/08-1025.1.

Thuiller, W., Lavorel, S., Araújo, M.B., Sykes, M.T., Prentice, I.C., 2005. Climate change threats to plant diversity in Europe. Proc. Natl. Acad. Sci. USA 102, 8245–8250. https://doi.org/10.1073/pnas.0409902102.

Uslar, Y.V., Mostacedo, B., Saldias, M., 2004. Composición, estructura y dinámica de un bosque seco semideciduo en Santa Cruz, Bolivia. Ecol. Boliv. 39, 25–43.

Valencia, R., 2000. Libro rojo de las plantas endémicas del Ecuador. Herbario QCA, Pontificia Universidad Católica del Ecuador, Quito, Ecuador.

Valencia, R., Foster, R.B., Villa, G., Condit, R., Svenning, J.C., Hernandez, C., Romoleroux, K., Losos, E., Magård, E., Balslev, H., 2004. Tree species distributions and local habitat variation in the Amazon: large forest plot in eastern Ecuador. J. Ecol. 92, 214–229.

Veintimilla, D., Ngo Bieng, M.A., Delgado, D., Vilchez-Mendoza, S., Zamora, N., Finegan, B., 2019. Drivers of tropical rainforest composition and alpha diversity patterns over a 2,520 m altitudinal gradient. Ecol. Evol. 9, 5720–5730. https://doi.org/10.1002/ece3.5155.

Vessella, F., Schirone, B., 2013. Predicting potential distribution of Quercus suber in Italy based on ecological niche models: conservation insights and reforestation involvements. For. Ecol. Manag. 304, 150–161. https://doi.org/10.1016/j.foreco.2013.05.006.

Wrege, M.S., de Sousa, V.A., Fritzsons, E., Soares, M.T.S., de Aguiar, A.V., 2016. Predicting current and future geographical distribution of Araucaria in Brazil for fundamental niche modeling. Ecol. Environ. Conserv. 4, 269–279. https://doi.org/10.13189/eer.2016.040506.

Yang, X., Chen, J., 2009. Plant litter quality influences the contribution of soil fauna to litter decomposition in humid tropical forests, southwestern China. Soil Biol. Biochem. 41, 910–918. https://doi.org/10.1016/j.soilbio.2008.12.028.