THERYA, 2023, Vol. 14(2):269-280 DOI:10.12933/therya-23-1022 ISSN 2007-3364

Taxonomic, functional, and phylogenetic diversity of primate communities in Ecuador

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One of the fundamental objectives of ecology is to study the relative importance of ecological, evolutionary, and stochastic processes in determining local community structure. Many studies have focused on taxonomic diversity, paying relatively little attention to other dimensions of biological diversity, such as phylogenetic and functional diversity. Little is known about how these dimensions relate to each other, and the ecological processes that influence their variation. In this study, we characterize these three dimensions of biodiversity in 14 primate communities from different ecosystems in Ecuador to understand possible mechanisms responsible for their assembly. Results show that coastal communities are taxonomically less diverse than those from the Amazon and present different functional groups. On the other hand, phylogenetic diversity is higher in Amazonian communities, showing a tendency for overdispersion (high values of MPD_{PD} = mean phylogenetic distance per pair and low PSC = degree to which coexisting species are related). This indicates a possible influence of biological factors, such as competition, on community assembly. For all three dimensions, climatic variables were the most significant predictors of community structure, while vertical forest structure contributed significantly to variation in the phylogenetic dimension. The high functional diversity reported in this study highlights the importance and vulnerability of this group and the ecosystems they inhabit. Macroecological studies, such as the one presented here, allow a better understanding of community structure and provide important information for the development of conservation strategies.

El estudio de la importancia relativa de los procesos ecológicos, evolutivos y estocásticos en la determinación de la estructura de las comunidades es un objetivo fundamental de la ecología. Muchos de los estudios se han centrado en la diversidad taxonómica y prestan relativamente poca atención a otras dimensiones de la diversidad biológica, tales como la filogenética y la funcional. Se conoce poco sobre cómo se relacionan estas dimensiones entre sí, y sobre cuáles son los procesos ecológicos que influyen sobre su variación. En el presente trabajo se caracterizan estas tres dimensiones de la diversidad en 14 comunidades de primates de diferentes ecosistemas del Ecuador, buscando entender los posibles mecanismos responsables de su ensamblaje. Los resultados muestran que las comunidades de la costa son taxonómicamente menos diversas que las de la Amazonia y presentan grupos funcionales diferentes. Por otro lado, la diversidad filogenética es mayor en las comunidades amazónicas, mostrando una tendencia a la sobre dispersión (altos valores de MPD_{PD} y bajo PSC), lo que indica la posible influencia de factores biológicos, y particularmente la competencia como posibles determinantes del ensamblaje de esas comunidades. Para las tres dimensiones, el factor climático influencia la estructura de las comunidades de primates, mientras que para la dimensión filogenética la estructura vertical del bosque afecta en gran parte su variación. La gran diversidad funcional reportada en este estudio pone en evidencia la importancia y vulnerabilidad de los primates y los ecosistemas que habitan. Los estudios macroecológicos permiten comprender mejor los factores que influyen en la composición de las comunidades animales y proveen información importante para el desarrollo de estrategias de conservación.

Keywords: Community structure; functional traits; Neotropical primates; phylogenetic relationships; predictive variables.

Introduction

One of the main objectives of ecology is to understand the coexistence patterns of species and identify the mechanisms regulating the assembly of biological communities (Llorente-Bousquets and Morrone 2003). In this context, several hypotheses have been proposed regarding the relative importance of deterministic and stochastic processes in community assembly (Schöener and Haken 1986; Hubbell 2001) which varies depending on the spatial and temporal scales of measurement (Gavilanez and Stevens 2013; Plasencia-Vázquez *et al.* 2014; Stevens and Gavilanez 2015; Aguirre *et al.* 2016). Deterministic hypotheses propose that community composition is determined by niche differentiation according to the principles of competitive exclusion. This hypothesis prioritizes deterministic biotic interactions or abiotic filtering mediated by niche conservatism (Weiher *et al.* 2011). Environmental filtering (stress tolerance) proposes that the similarity of species within a given community increases due to abiotic restrictions (Cornwell *et al.* 2006). On the other hand, ecological differentiation (niche partitioning, limitation of similarities) proposes that ecological interactions prevent similarities between coexisting species (MacArthur and Levins 1967; Chesson 2000). On the other hand, stochastic models consider processes such as dispersal limitation and demographic drift, which produce assemblage patterns that can explain spatial autocorrelation in the presence of species, regardless of environmental variables. Particularly, dispersal limitation proposes that the presence of species in a community is limited by their ability to reach the site (Hurtt and Pacala 1995; Beaudrot and Marshall 2011).

Recently, studies focused on the multiple dimensions of diversity have been developed (Webb *et al.* 2002; Petchey and Gaston 2006; Cadotte *et al.* 2011; Srivastava *et al.* 2012) to better understand the mechanisms underlying local community assembly, as well as distribution and diversity patterns at broader scales (Jarzyna and Jetz 2016; Brum *et al.* 2017). Additionally, approaches that directly consider the effect of species on ecosystems, such as functional diversity, have been developed (Tilman *et al.* 1997; Gómez-Ortiz and Moreno 2017). Likewise, new strategies to evaluate the evolutionary relationships of species through their phylogeny have been proposed (Webb *et al.* 2002). These new approaches for assessing diversity, such as functional and phylogenetic diversity, aim for a comprehensive quantification of biodiversity (Rosenzweig 1995; Cadotte *et al.* 2011; Rattis *et al.* 2018). However, few studies have assessed diversity using these approaches simultaneously (Weinstein *et al.* 2014; Stevens and Gavilanez 2015; Brum *et al.* 2017).

Studies on mammals and the multiple dimensions of biodiversity seek to understand the processes involving these vertebrates within ecosystems. Several of these studies consider characteristics such as body size, relating them to the functions provided by mammals within their natural habitats (Smith and Lyons 2011). Safi *et al.* (2011) suggested that phylogenetic diversity and species richness increase in relation to mean annual temperature, while functional diversity decreases along with a higher seasonality. González-Maya *et al.* (2016) reported that functional diversity in mammal communities within the Neotropics decreases with the degradation of ecosystems and the loss of threatened species. On the other hand, Oliveira *et al.* (2016) found that species richness and functional diversity are decoupled in various regions of the world, and that species richness is closely correlated with environmental conditions while functional diversity depends mainly on non-equilibrium factors, including the evolutionary time to overcome the conserved niche. According to this analysis, species-rich regions (especially the Neotropics) could have many species that may be functionally redundant.

Primates are one of the most seriously threatened animal groups in tropical areas, mainly due to habitat loss, deforestation, and fragmentation (Stevenson 2016; Brum *et al.* 2017; Roncancio *et al.* 2010; Bueno *et al.* 2013; Rattis *et al.* 2018). They play central ecological roles in ecosystems as dispersers, pollinators, predators, and prey. Additionally, they are part of the diet of various native cultures in the region (Cueva 2005; de la Torre 2010; de la Montaña 2013). In Ecuador, primates have been studied in aspects such as conservation status, demography, diversity, diet, distribution, and survival in forest patches under anthropic pressure (Lizcano *et al.* 2016; Cervera *et al.* 2017). Although these studies are an important contribution to the knowledge of primates, they have favored a one-dimensional perspective of diversity (*i. e.*, taxonomic diversity) without considering their evolutionary history and ecological function (Cisneros *et al.* 2014; Brum *et al.* 2017).

The present study focuses on characterizing in multiple dimensions of diversity Ecuadorian primate communities inhabiting different ecosystems of Ecuador, and evaluating the influence of environmental, structural, and spatial factors as possible assembly mechanisms of these communities.

Materials and methods

The characterization of primate communities of Ecuador was conducted through a systematic survey of literature, using databases such as Scopus, Google Scholar, and ISI Web of Science, using the following keywords (in English and Spanish): "primate community + Ecuador", "primate diversity + Ecuador", "primates + Ecuador". We also reviewed theses and unpublished reports issued between 1989 and 2017. Studies that met our selection criteria were used to ensure data comparability (Table 1). Primate community composition (incidence) for the selected study sites were obtained from the papers. Spatial coordinates were projected in UTMs and later converted to WGS 84. This procedure allowed for the spatial reference to be compatible with the raster files containing altitude data and type of ecosystem (MAE 2013).

Taxonomic diversity was characterized using presence/absence data for each study site. Functional diversity was estimated based on morphological, ecological, and behavioral data of the recorded species based on the information available in PanTHERIA (Jones *et al.* 2009) and All the World's Primates (Rowe and Myers 2016) databases. We included variables related to body weight, body size, home range, and population density, which are related to how individuals interact with each other and the environment (Lefcheck *et al.* 2015). In addition, niche breadth of each species was estimated based on the number of ecosystems they inhabit in Ecuador, which was determined using species range maps and a layer with information on the ecosystems of mainland Ecuador (MAE 2013), usingQGIS version 2.10 (QGIS Development Team2015).

Information regarding primate species diet was obtained from the database published in the database All the World's Primates by Rowe and Myers (2016). We also conducted a thorough literature search regarding diet of each of the species reported. Based on this information, the following functional characteristics were determined:

Trophic breadth: Maximum number of food categories used by a species, with 13 being the highest number. For this category we grouped species in three levels: low (between 1 and 4 categories), medium (between 5 and 9 categories), and high (between 10 and 13 categories).

Percentage of fruit in the diet: Percentage of fruit in the total food consumed was calculated based on the food records reported in the All the World's Primates database (Rowe and Myers 2016).

Table 1. Criteria considered for the study selection regarding primate communities of Ecuador.

N	Criteria	References
1	Actual sightings, indirect records not considered.	Gavilánez and Stevens 2013
2	Study duration (≥21 days).	Buckland *et al.* 2010
3	Methodology, 10 km transects considering important areas in each ecosystem, flexibility in ravines and rivers, among others.	Buckland *et al.* 2010
4	Works covering 5 % of the study surface.	Gavilánez and Stevens 2013
5	Data from long-term studies with available information (presence/absence).	This study
6	Communities separated from each other by 10 km (avoiding pseudo-replicate samples), considering different ecosystems and biogeographical and anthropogenic barriers.	Ayres and Clutton-Brock 1992; Naka and Brumfield 2018
7	Nocturnal monkeys (*Aotus* spp.) excluded due to their different habits.	Gavilánez and Stevens 2013

Trophic guilds: Trophic guilds used in this study were adapted from those proposed by Benchimol and Peres (2014). Five trophic guilds were defined: 1 = Folivore-facultative frugivore: species that consume leaves and some fruits according to availability; 2 = Frugivore-folivore: species that feed mainly on fruits and leaflets; 3 = Frugivore-insectivore: species that feed mainly on fruits, insects, and sometimes leaflets; 4 = Granivore-frugivore-insectivore: species with a wide food range, mainly seeds, fruits, and insects according to their availability; 5 = Insectivore-frugivore-gummivore: species that mainly consume insects, fruits, bark, and exudates.

We calculated the Gower index using functional characteristics to build a distance matrix. This matrix was used to estimate the functional diversity indexes FD, FDISP, MPD_{FD}, and $MNTD_{FD}$, which characterize the diversity and dispersion of species in the functional space (Table 2).

Finally, phylogenetic diversity was characterized using the phylogeny by Kuhn *et al.* (2011), updating the nomenclature to Tirira *et al.* (2020). The phylogenetic diversity indexes PD, PSC, MPD_{PD}, and $MNTD_{PD}$ (Table 2) were calculated based on metrics by Webb *et al.* (2002) and Helmus *et al.* (2007).

Similarity between communities was evaluated via cluster analysis, which also served for comparing the diversity between the resulting groups (functional and phylogenetic). Gower distance was used for functional diversity and divergence times, in millions of years, for phylogenetic diversity. This analysis was performed to assess whether different functional and phylogenetic groups of primates could be identified. All analyses were performed in R.

To determine the influence of different assembling mechanisms on the variability of the taxonomic, functional, and phylogenetic structure of primate communities, three groups of predictor variables were defined (environmental/environmental filtering - X1, spatial/ dispersal limitation - X2, and structural/competition - X3). These variables are key to diversity and composition patterns of mammal communities, including Neotropical primates (Plasencia-Vázquez *et al.* 2014; Aguirre *et al.* 2016; Gavilanez and Stevens 2013). Lastly, a variance partitioning analysis was applied (Borcard *et al.* 1992; Legendre and Legendre 1998; Legendre and Gallagher 2001) to discriminate the extent to which the variables contribute to the variation in the taxonomic, functional, and phylogenetic dimensions of primate community structure and whether they do so in isolation or synergy.

Environmental data were obtained from the BioClim database using a 30s (~1 km^2) spatial resolution (Hiijmans *et al.* 2005) using the coordinates of each locality using QGIS (QGIS Development Team 2015). A principal component analysis (PCA) of 19 bioclimatic variables was performed to obtain a subset of orthogonal axes (Legendre and Legendre 1998). Based on this analysis, six representative environmental variables (that represented more than 90% of variability in environmental data) were selected to evaluate their influence on community structure (Table S4). The influence of spatial processes associated with dispersal limitation (Beaudrot and Marshall 2011) was assessed with a matrix of Euclidean distances between the identified communities. Forest structure elements, particularly canopy height (Oliveira and Scheffers 2019), are variables related to the availability of resources and niches (Gouveia *et al.* 2014), therefore associated with competition. Canopy height data were obtained from the layers created by Simard *et al.* (2011), which resulted from the use of a "LIDAR" device. This information for each community identified was obtained by overlapping the corresponding raster layer.

Statistical analyses were performed in R version 4.1.1 (R Core Team 2017) using the packages Vegan (Oksanen *et al.* 2018), FD (Laliberté *et al.* 2014), picante (Kembel *et al.* 2010), and spatstat (Baddeley and Turner 2005).

Results

Of the 192 studies reviewed, 46 were conducted in Ecuador, and 14 primate communities that met the established requirements were selected. Four of these communities were distributed in the coastal region and ten in the amazon region. The total number of species recorded was 17, representing 80 % of the diversity of primates in Ecuador. The community with the highest richness was located in the surroundings of the Kiwcha settlements in the northern region of the Yasuní National Park (Amazon region), with 12 species. In contrast, communities with lowest rich-

Table 2. Functional and phylogenetic diversity indexes selected for the analysis of primate community structure in Ecuadorian communities.

	Index	Characteristic	Reference
Functional	FD	Sum of the length of branches of a functional dendrogram built through a cluster analysis.	(Petchey and Gaston 2006)
	FDISP	Mean distance of each species to the centroid of the community in the functional trait space.	(Laliberté *et al*. 2014)
	MPD_{FD}	Calculates the mean distance per pair that separates taxa based on a matrix of functional distances between species.	(Webb *et al.* 2002)
	$MNTD_{FD}$	Calculates the mean distance of the nearest taxon for each species pair based on a matrix of functional distances.	(Webb *et al.* 2002)
Phylogenetic	PD	Calculates the sum of the total phylogenetic branch length for species coexisting in a community.	(Helmus *et al*. 2007; Kuhn *et al*. 2011)
	PSC	Measurement of the degree to which coexisting species are related by comparing with the expected variance of a hypothetical trait that evolves neutrally.	(Helmus *et al*. 2007)
	MPD_{PD}	Mean phylogenetic distance per pair between all possible pairs of species coexisting in a community.	(Webb *et al*. 2002)
	$MNTD_{PD}$	Mean minimum phylogenetic distance of the nearest taxon for a community.	(Webb *et al*. 2002)

ness were in western part of Ecuador, near the coast, Jama Coaque and Pacoche, with two species each (Table 3). The 14 communities covered nine ecosystems, three in the coastal region and six in the amazonn (Figure 1).

A marked variation was found in the functional attributes (Table S2). Average weight for the species registered was 3,088.4 ± 2,807.4 g (range: 123.94 to 9,067.9 g). Average size (head and body) was 387.6 ± 118.1 (154.6 to 576.3) mm. Of the recorded species, *Cebus aequatorialis* was found in the largest variety of ecosystems. Furthermore, we observed variations between communities in functional characteristics related to diet. The primate community with the highest number of trophic guilds was Kichwa, with five guilds. The most common guild was granivore-frugivore-insectivore, with 13 species, while the least common was frugivore–insectivore, with two species. Most of the recorded species had a narrow trophic breadth. The "high" trophic breadth was the least represented category, absent in six communities. The community near the Kichwa settlements had the highest number of fruit-eating species in their diet (See Table S3).

Again, the community with the highest diversity in all dimensions was the Kichwa community in the Amazon (Table 4), which showed a wide range of coexisting functional groups and evolutionary lineages. On the other hand, some coastal communities showed low functional diversity values, although functional diversity indexes such as MPD_{FD}, were relatively high since the species that compose

Table 3. Geospatial data. richness (S). and composition of primate communities used for the analyses.

Community	Latitude	Longitude	Elevation (m)	S	*Alouatta palliata*	*Alouatta seniculus*	*Ateles belzebuth*	*Ateles fusciceps*	*Plecturocebus discolor*	*Cheracebus lucifer*	*Cebuella pygmaea*	*Cebus aequatorialis*	*Sapajus macrocephalus*	*Cebus capucinus*	*Lagothrix lagotricha*	*Pithecia napensis*	*Pithecia milleri*	*Leontocebus lagonotus*	*Leontocebus nigricollis*	*Leontocebus tripartitus*	*Saimiri cassiquiarensis*	References
Kichwa	-0.4538	-76.4406	248	12	0	1	1	0	1	0	1	1	1	0	1	1	1	1	0	1	1	Cueva 2005
Cuyabeno	-0.5874	-75.4706	221	8	0	1	0	0	0	1	1	1	0	0	1	0	1	0	1	0	1	de la Torre *et al*. 1995
Kutukú Foothills	-2.585	-77.7672	315	7	0	1	1	0	0	0	0	1	1	0	1	0	1	0	0	0	1	Zapata Ríos *et al*. 2006
Jama Coaque	-0.1158	-80.1249	294	2	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	Whyte 2005
Oglán	-1.3202	-77.6193	477	5	0	1	1	0	0	0	0	0	0	0	1	0	0	1	0	0	0	Carrillo-Bilbao y Martín-Solano 2010
Pacoche	-1.0334	-80.8333	292	2	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	Cervera *et al*. 2015
Payamino	-0.5097	-77.2796	318	5	0	1	0	0	1	0	0	1	0	0	0	0	0	0	1	0	1	Gavilánez-Endara 2013
South Pompeya	-0.7021	-76.4383	250	6	0	0	0	0	1	0	1	1	0	0	0	0	1	0	0	1	1	Pozo 2004
Colonso-Chalupas Reserve	-0.7017	-77.9691	300	4	0	0	0	0	0	0	1	1	0	0	1	0	0	0	1	0	0	Álvarez-Solas *et al*. 2016
Cayapas River	0.9156	-78.9113	111	3	1	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	Madden y Albuja 1989
San Miguel River	0.2778	-76.3928	286	6	0	1	0	0	0	0	1	1	0	0	1	0	0	0	1	0	1	Zapata Ríos 2001
Tesoro Escondido	0.5419	-79.1449	280	3	1	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	Miller *et al*. 2016
Tiputini	-0.6167	-76.1667	246	9	0	1	1	0	1	0	1	1	0	0	1	1	0	0	0	1	1	Blake *et al*. 2010
Station Tiputini	-0.6379	-76.1497	220	9	0	1	1	0	1	0	1	1	0	0	1	1	0	0	0	1	1	Marsh 2004

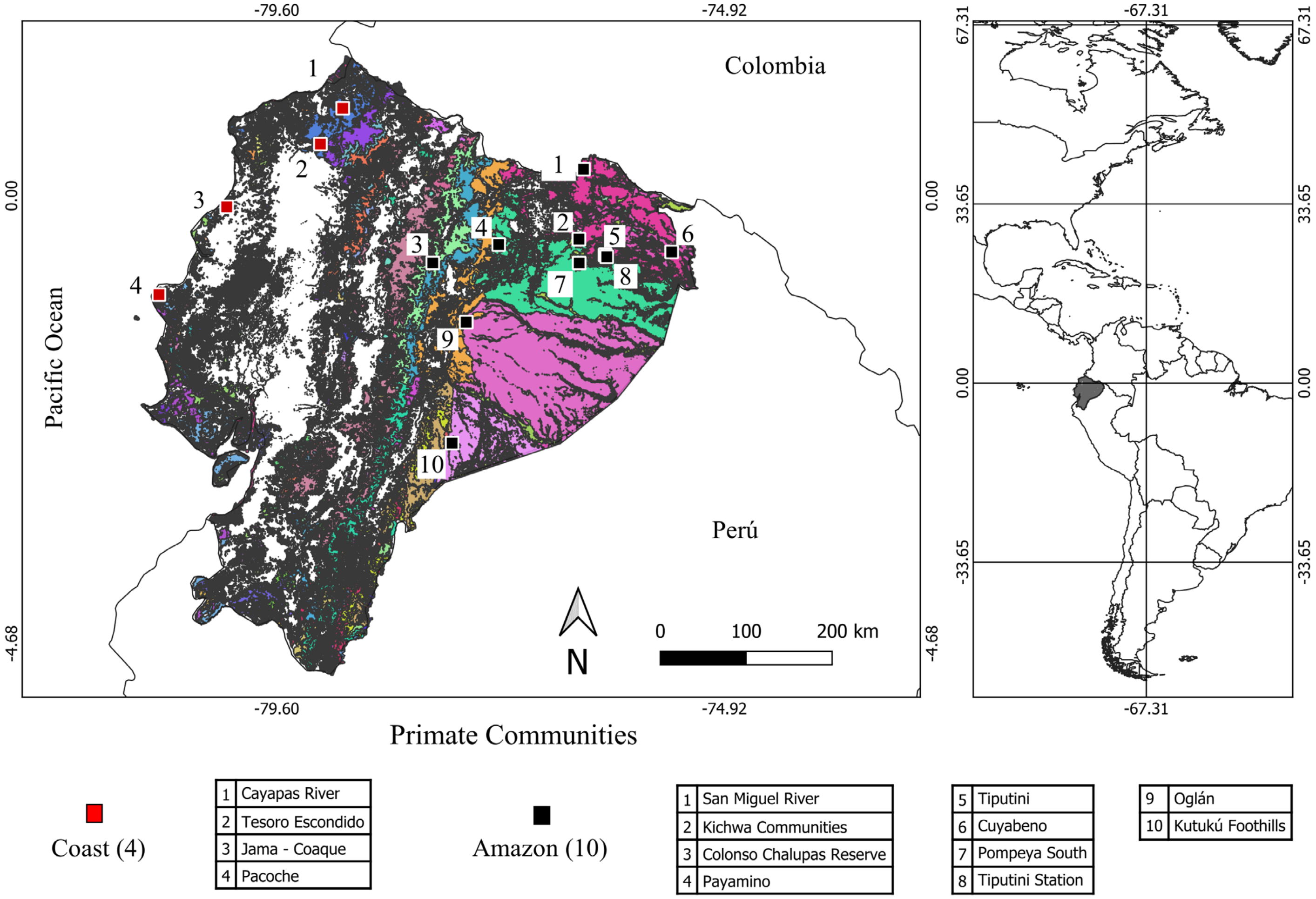

Figure 1. Ecuador map indicating the 14 primate communities considered in the study.

them differ functionally. Despite having an intermediate richness, the community of the San Miguel River showed the greatest functional dispersion (FDISP; mean distance of each species to the centroid of the composition), with a high MPD_{FD} value. The primate community in Pompeya Sur had the lowest functional dispersion and was composed of functionally similar species (low $MNTD_{FD}$ values).

The 17 species identified in the 14 communities were grouped into four primate families (Figure 2). The Kichwa community showed the greatest phylogenetic diversity (Table 4), with a PD value of 163.2. The MPD_{PD} index, representing the mean phylogenetic distance between species pairs, was higher for Pacoche and Jama-Coaque communities since the species in them belong to different and phylogenetically distant families ($MPD_{PD} = 40.5$). By contrast, the primate community inhabiting the foothills of Kutukú had the most phylogenetically related species ($MNTD_{PD} = 0.19$). The Phylogenetic Species Clustering (PSC) index indicated that the communities with the phylogenetically closest species were Rio Cayapas and Tesoro Escondido, which are geographically close in the northwest of the country, within the equatorial Chocó.

Five functional groups were identified (Figure 2). Species of the family Atelidae were clustered into two functional groups. *Ateles fusciceps, Alouatta palliata,* and *A. seniculus* were more closely related in terms of body weight, body size, and trophic breadth, while the group of *Ateles belzebuth* and *Lagothrix lagothricha* shared the same trophic breadth and guild. The representatives of the family Pitheciidae formed two functional groups. The species of the genus *Pithecia* were functionally similar to *Cebus aequatorialis* in terms of body weight and body size, and shared almost the same trophic guild. The titi monkeys of the genera *Cheracebus* and *Plecturocebus* were functionally related to *Sapajus macrocephalus* and *Saimiri cassiquiarensis*, sharing the same trophic guild and a similar home range. The species of the family Callithrichidae formed a single functional group with a similar home range, trophic guild, size, and weight. The phylogenetic clustering showed that pitheciids and atelids are the oldest families in the study area.

As for taxonomic diversity, both environmental (X1) and spatial (X2) variables separately explained the highest variation (X1 = 28 % and X2 = 24 %, respectively) in the taxonomic composition of the communities. On the other hand, structural variables (X3) only accounted for 1 % of the variation. Functional diversity, environmental variables (X1), and forest structure (X3) were associated with a

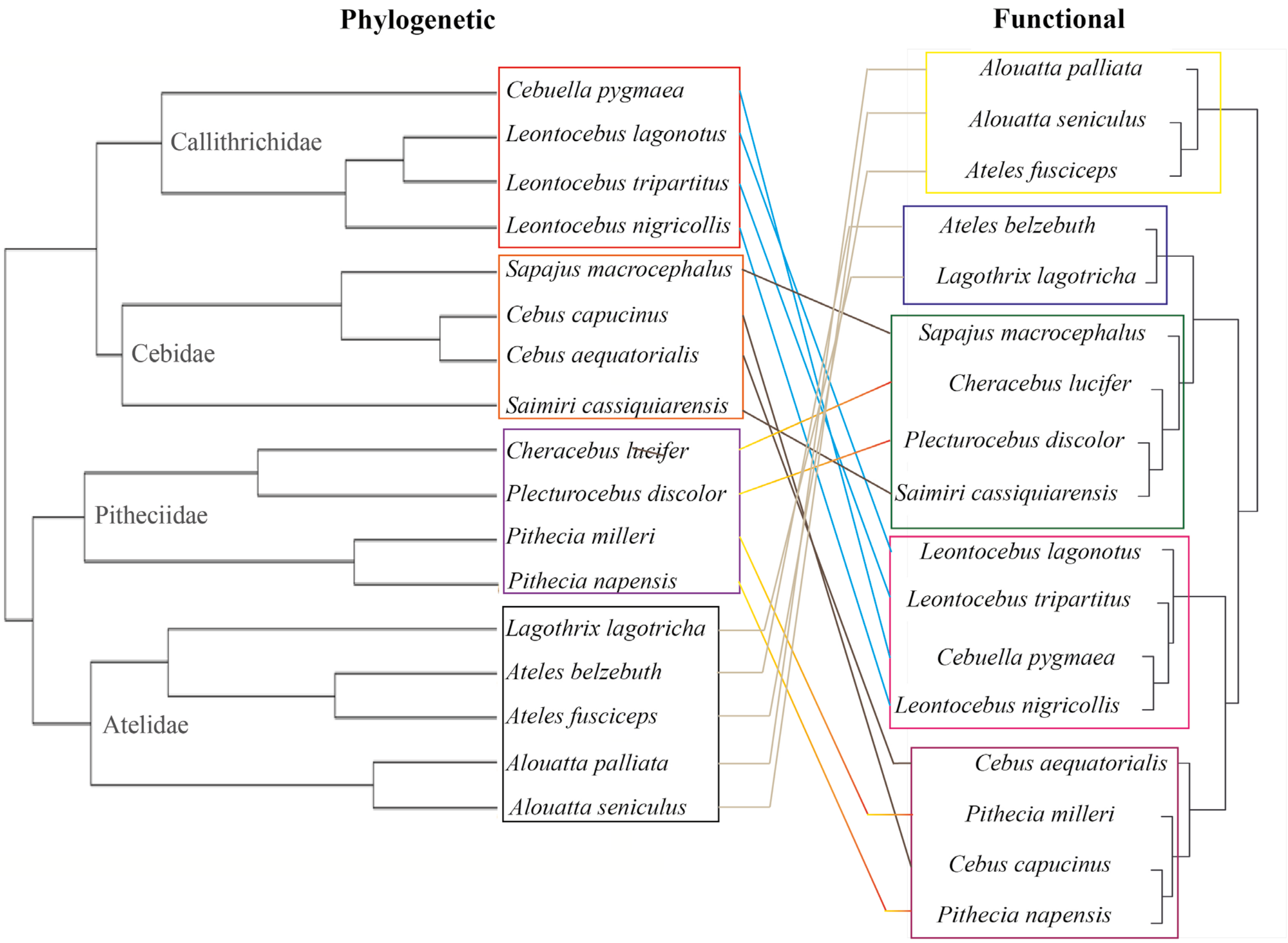

Figure 2. Contrast of phylogenetic and functional diversity between groups. Squares mark groups; lines indicate the distribution based on functional traits.

greater variation in the functional diversity of communities (25 %). Finally, the cluster that included the three predictor variables explained 25 % of the variation in phylogenetic diversity (Figure 3).

Discussion

The taxonomic diversity recorded in the present study is consistent with the one reported by Sampaio *et al.* (2018) in communities of the southern Amazon, Purus state, Brazil, reflecting the high diversity of mammals that characterizes the western Amazon (Voss and Emmons 1996). This great diversity has been related to the large rivers that limit species dispersal (Ayres and Clutton-Brock 1992; Van Roosmalen *et al.* 2002). It has also been reported that the high diversity of primate species in the Amazon region is associated with high fruit production levels (Stevenson 2016; Camaratta *et al.* 2017) and structural complexity that creates microhabitats due to the different orography in the region (Homeier *et al.* 2010).

Communities of the western region show a low diversity (S = 4) and are represented by endemic, and highly threatened species such as *Ateles fusciceps* and *Cebus capucinus*, which inhabit the easternmost section of the tropical Andes hotspot in the Chocó area. These areas, and the primate communities that inhabit them, are subject to environmental, biotic, and anthropic pressures that influence at the local (behavior) and macro (distribution) levels, affecting their composition, diversity patterns, and roles in the ecosystems (Kamilar and Beaudrot 2018; Kaisin *et al.* 2020).

At the functional level, the variety of guilds ($n = 5$) and broad trophic niche of the species were important, mainly in Amazonian communities. Multiple species presented complementary functional traits that are important in the functioning of ecosystems (Pereira-Bengoa *et al.* 2010; Córdova-Tapia and Zambrano 2015). The most common trophic breadth category was low (1 to 4 food types in the diet), indicating that most registered species have a level of specialization in their diet, which can make species sensitive to forest conversion (Cervera *et al.* 2017). On the other hand, species with broad trophic niche (*e. g.*, *Sapajus macrocephalus*) were recorded to include between 10 to 14 food types in their diet. These were common in Amazonian regions where resource availability may be higher. In some cases, when a generalist species becomes locally extinct, its ecological role may be assumed by another species (Galetti *et al.* 1994; Stoner *et al.* 2003; Link *et al.* 2006; Gómez-Posada 2012).

Table 4. Functional diversity (FD) and phylogenetic diversity (PD) indexes of the 14 primate communities analyzed in the study.

	Fuctional				**Phylogenetic**			
Comunidades	**FD**	**FDISP**	**MPD$_{FD}$**	**MNTD$_{FD}$**	**PD**	**PSC**	**MPD$_{PD}$**	**MNTD$_{PD}$**
Kichwa	3.463	0.230	0.335	0.168	163.227	0.4268	36.554	23.252
Cuyabeno	2.940	0.237	0.352	0.195	139.328	0.223	37.882	31.535
Kutukú Foothills	2.541	0.220	0.332	0.198	111.976	0.356	36.699	26.125
Jama Coaque	1.194	0.169	0.338	0.338	40.562	0	40.562	40.562
Oglán	2.234	0.237	0.367	0.252	70.898	0.209	35.979	32.100
Pacoche	1.194	0.169	0.338	0.338	40.562	0	40.562	40.562
Payamino	2.214	0.220	0.343	0.233	91.726	0.154	37.876	34.319
South Pompeya	1.933	0.199	0.299	0.153	103.406	0.239	36.625	30.875
Colonso-Chalupas Reserve	1.519	0.222	0.345	0.222	70.922	0.205	35.912	32.235
Cayapas River	1.497	0.202	0.351	0.305	57.319	0.116	38.213	35.864
San Miguel River	2.562	0.247	0.374	0.252	103.149	0.243	36.590	30.703
Tesoro Escondido	1.497	0.202	0.351	0.305	57.319	0.116	38.213	35.864
Tiputini	3.082	0.235	0.347	0.168	152.906	0.252	37.785	30.342
Station Tiputini	3.082	0.235	0.347	0.168	152.906	0.252	37.785	30.342

Coastal communities comprise the same trophic guilds (facultative folivore - frugivore and granivore - frugivore - insectivore), indicating lower interspecific competition levels associated with resource availability. Differences in the diet of coexisting species (howler, capuchin, and spider monkeys) have been attributed to historical competition events that led to divergent dietary choices or foraging techniques (Fleming 1979; Arcos *et al.* 2013; Cervera *et al.* 2015). However, it is worth highlighting that all coastal species include at least a low proportion of fruit in their diet, contributing to the ecological role of this functional trait (seed dispersers) in these ecosystems. Therefore, these species, and their disappearance can have a long-term impact on western tropical ecosystems, which are highly disturbed in Ecuador (Urbina 2010).

Although functional characteristics of species suggest how they interact with each other and with the environment (Cadotte *et al.* 2011; Meachen and Roberts 2014; Gómez–Ortiz and Moreno 2017), it is necessary to analyze the other dimensions of diversity. The comparison between the phylogenetic and functional clustering of primate species in the communities analyzed in this study showed that relationships between species are defined by the way in which they use the resources, creating cohesive functional groups that reflect an important phylogenetic dispersion, as in the case of Cebidae and Pithecidae. However, callitrichids had a conserved trophic niche, because they are very similar in body size, trophic niche breadth, and trophic guild. These species use the same resources, potentially reducing their coexistence; this is confirmed by analyzing the distribution maps of the species (IUCN 2016), which show no overlap. Furthermore, the atelids formed two subgroups with different functional characteristics.

Communities with high taxonomic diversity, such as those in the lower Amazon, showed patterns of phylogenetic overdispersion (high MNTD$_{PD}$ and MPD$_{PD}$ and low PSC values). This illustrates the coexistence of species representative of ancient (pitheciids and atelids) and recent taxa (cebids and callitrichids), as well as a high functional diversity (high FD and FDISP), indicating that the resources available for use by primate species are diverse (Cooper *et al.* 2008; Kamilar and Guidi 2010).

For the phylogenetic dimension, the best predictor of community structure was structural variability associated with strata diversity, which may be related to a high environmental heterogeneity and niche partitioning among different primate species in a community. Structural variation can foster the coexistence of species with similar requirements and functions, contributing to highly diverse communities, such as those reported in the Amazonian region (Arcos *et al.* 2013; Gómez-Ortiz and Moreno 2017).

Kamilar *et al.* (2015) suggested that zones with climatic stability favor a higher speciation rate. This could be reflected in the communities inhabiting the lower Amazon, which show high phylogenetic diversity. By contrast, the structure of communities within the dry seasonal forests of the Coast, where diversity is lower, seems to be governed by processes related to limited dispersal due to the Andes Mountain range barrier (Beaudrot and Marshall 2011). However, these ecosystems may harbor higher endemism in some groups, including vertebrates (Olguín-Monroy *et al.* 2013).

Our results suggest that both deterministic (environment and habitat structure) and stochastic processes (dispersal) play central roles in the structuring of equatorial primate communities (Cadotte *et al.* 2009; Flynn *et al.* 2011). Part of the variation not explained in this study could be addressed by considering interspecific interactions, spatial scale, and seasonality (Belmaker and Jetz 2013; Stevens and Gavilanez 2015; Weinstein *et al.* 2017).

Regardless of other factors, predictions considering the spatial dimension were the most important to explain taxo-

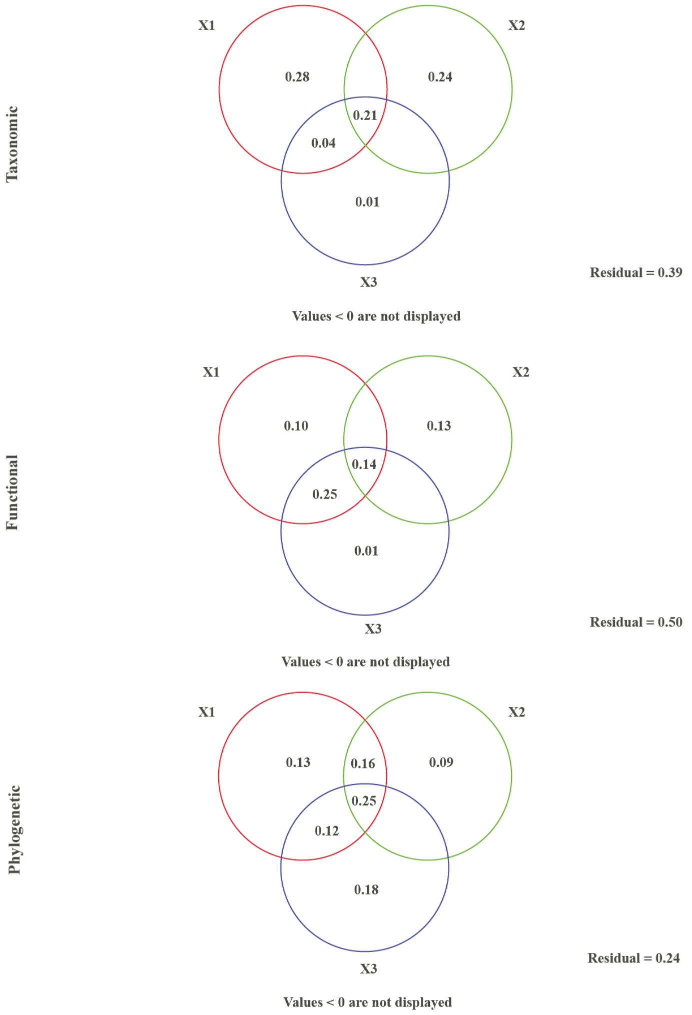

Figure 3. Representation of the variance partitioning analysis with a Venn diagram for the three dimensions of biodiversity: X1 = environmental, X2 = spatial (dispersal), X3 = structural (canopy strata).

nomic diversity. These results are supported by Beaudrot and Marshall (2011), who state that dispersal limitation is the primary mechanism in structuring primate communities. Neutral processes (Hubbell 2001) related to spatial factors were important for the taxonomic and phylogenetic dimensions of biodiversity. Our findings show that the distribution of closely related species in communities may be controlled by stochastic factors, such as random speciation, extinction, and ecological drift (Pavoine and Bonsall 2011).

There is an urgent need to understand community diversity patterns and their assembling mechanisms from a perspective encompassing beyond the taxonomic dimension. Our study highlights the complementarity of the information provided by different dimensions of biodiversity. Therefore, diversity should be assessed in a multidimensional way to better understand the mechanisms responsible for the establishment and persistence of communities and their ecological functions in ecosystems. Our findings support the importance of conducting diversity analyses on a spatial scale broader than local communities to make inferences on the ecological processes that influence the assembling and persistence of diversity, particularly in highly diverse communities such as those of Neotropical primates in Ecuador. This study shows that a varied resource availability (structure) could partly define the composition of these communities by reducing competition between species. Finally, our results provide valuable information to develop conservation strategies for Ecuadorian primates, as the roles of spatial processes and environmental and structural variables, and their association with the multiple dimensions of biodiversity, should be considered to set priority areas of conservation in a better way and ensure their maintenance over time. In this way, the environmental issues currently facing these communities and ecosystems can be comprehensively addressed.

Acknowledgments

To Universidad Central del Ecuador, Facultad de Ciencias Biológicas, particularly I. Jácome-Negrete, J. Torres, and J. F. Rivadeneira for their valuable comments and recommendations to the manuscript. To P. Guarderas and B. Medina for their help with maps and the use of the computer laboratory. Finally to the editor and the anonymous reviewers for their constructive comments on the manuscript. M. E. Sánchez-Salazar translated the manuscript into English.

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Associated editor: Eduardo Mendoza
Submitted: August 15, 2020; Reviewed: August 31, 2020
Accepted: November 17, 2022; Published on line: May 8, 2023

Supplementary material

https://www.revistas-conacyt.unam.mx/therya/index.php/THERYA/article/view/1022/1022_Supplementary_material