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A Floristic Assessment of Ecuador's Amazon Tree Flora

Juan E. Guevara, Hugo Mogollón, Nigel C. A. Pitman, Carlos Cerón,
Walter A. Palacios and David A. Neill

Abstract

Ecuadorian Amazonia has been catalogued as one of the most biodiverse regions on Earth and is particularly renowned for the highest peaks of plant diversity. This chapter addresses the observed tree species diversity and the expected number of tree species in Ecuadorian Amazonia. It examines whether the Ecuadorian Amazon is floristically heterogeneous or forms a big block of relatively homogeneous forests. The chapter provides a brief overview of the landscape characteristics of the historical centers of botanical collection and research in Ecuadorian Amazonia. It considers these areas because of historic sampling efforts and the high intensity of botanic collection rather than any specific ecological analysis. The chapter discusses the role of geomorphology and soils on the patterns of floristic change in Ecuadorian Amazonia. Plant-herbivore interactions have been hypothesized as the main drivers of speciation and co-existence in Amazonian forests.

Keywords *ecological analysis; Ecuadorian Amazonia; floristic changes; homogeneous forests; landscape characteristics; plant diversity; plant-herbivore interactions; tree species diversity*

2.1 Introduction

Ecuadorian Amazonia has been catalogued as one of the most biodiverse regions on Earth (Bass *et al.* 2010; Funk *et al.* 2012; Pitman *et al.* 2001) and is particularly renowned for the highest peaks of plant diversity (de Oliveira and ter Steege 2013; Kraft *et al.* 2008; Kreft *et al.* 2004; ter Steege *et al.* 2013; Valencia *et al.* 2004). Located in the so-called Piedemonte del Napo region, this area is also characterized by the highest levels of tree and shrub diversity across the Amazon Basin (Fine and Kembell 2011; Myers *et al.* 2000; Orme *et al.* 2005; Pitman *et al.* 2001; ter Steege *et al.* 2013; Valencia *et al.* 1994, 2004).

Despite a long history of data collection, a complete assessment of the tree flora across the region has remained elusive for both ecologists and botanists during the past 50 years. Historically, the centers of botanical exploration have been

Yasuní National Park (YNP) and to a lesser extent the Cuyabeno Reserve, where more than 50% of the collections have been carried out (Cerón and Reyes 2003; Jorgensen and León-Yáñez 1999; Valencia *et al.* 1994, 2004). This has left certain regions located to the south and northeast of these areas fairly unexplored and known from just a few collections and small-scale censuses. This lack of information is responsible for the partial picture of tree gamma diversity in Ecuadorian Amazon forests.

The first attempt to determine both floristic and abundance patterns in Ecuador's Amazonian tree flora was the work developed by Pitman *et al.* 2001 (see also Macía and Svenning 2005). Some of the most interesting conclusions of this work are that:

1. Forests are dominated by a small subset of species that represents almost 70–80% of the total number of individuals (see also ter Steege *et al.* 2013); and
2. This small subset of species forms predictable oligarchies, *sensu* Pitman *et al.* (2001), over large tracts of forests, if environmental conditions (soils particularly) are relatively homogeneous across the landscape.

On the basis of these conclusions, they suggested that Ecuadorean forests might represent a large block of forest dominated by the same oligarchic species due to the relative homogeneous soil composition across the region (Pitman *et al.* 2001, 2008)

Here we present the results of an extensive 1-ha plot network and herbarium data compilation to assess for the first time the number of tree species and the floristic patterns of lowland Ecuadorian Amazonia's hyper-diverse forests. In this section we address three basic questions:

1. what is the observed tree species diversity in Ecuador Amazonia?
2. what is the expected number of tree species? and finally
3. is Ecuadorian Amazonia floristically heterogeneous or does it form a big block of relatively homogeneous forests?

Ultimately, we discuss some potential factors and mechanisms that might be influencing the patterns we found.

2.2 Methods

To delimit lowland Amazonia, we followed a hierarchical-nested approach used in the *Vegetation Map of Ecuador* (Sistema de Clasificación de Ecosistemas del Ecuador Continental: Ministerio del Ambiente del Ecuador 2013). This approach uses seven levels of classification to define ecosystems; for the purposes of our work, the first five levels are relevant because they include parameters such as geomorphology, temperature, precipitation, biogeography and topography at local and landscape scales to define the major biogeographic regions (see Sistema de Clasificación de Ecosistemas del Ecuador Continental, 2013).

2.3 Study area

In this section, we provide a brief overview of the landscape characteristics of the historical centers of botanical collection and research in Ecuadorian Amazonia. We have chosen these areas because of the historic sampling efforts and the high intensity of botanic collection rather than any specific ecological analysis. Unfortunately, this bias has been considered in previous attempts to define these regions *a priori* as floristically distinct.

2.3.1 Yasuní

The focus of botanical exploration has been the northwestern portion of the YNP (Bass *et al.* 2010; Pitman 2000; Pitman *et al.* 2001; Valencia *et al.* 2004). The great majority of the information collected during the past 15 years makes this portion of YNP well known in floristic terms, regardless of the fact that there are many other areas inside the park that remain unexplored. The YNP covers almost 980,000 ha with an altitude range from 175 to 400 m a.s.l. (Pitman 2000; Valencia *et al.* 2004). The landscape is dominated by hilly terrain, with 50-m high hills interrupted by small valleys drained generally by small streams that occasionally flood the adjacent areas. This strong and abrupt topographic variation is almost ubiquitous in the northwestern portion of YNP. Nonetheless, flat areas with poor drainage are predominant in the floodplains of the major rivers that cross the park and swampy areas are also scattered across the region (Guevara obs. pers.; Pitman 2000; Pitman *et al.* 2014; Valencia *et al.* 2004).

Terra firme and swamp forests are the predominant habitat types in YNP and cover almost 80% and 20% of the area respectively (Pitman *et al.* 2014; Sistema de Clasificación de Ecosistemas del Ecuador Continental 2013). Swamp forests in Yasuní are divided in two well-differentiated types that previously have not been recognized: habitats dominated by the palm species *Mauritia flexuosa* (e.g. “moretales”) and the mixed swamp forests with higher species richness located in valleys adjacent to *terra firme* forests (Pitman *et al.* 2014).

2.3.2 Cuyabeno

The area between the Aguarico and Napo rivers, as well as the Cuyabeno and Lagartococha lacustrine systems, are part of Cuyabeno Reserve. This region is characterized by poorer soil conditions with respect to the Yasuní region or other areas of Ecuadorian Amazonia. On average, the clay:sand ratio in most of the landscape of the Cuyabeno Reserve is 2:8, while on average it is x:x in the Yasuní region is 48%. In addition, levels of aluminum are also higher in the Cuyabeno region compared with other areas of Ecuadorian Amazonia (Cerón and Reyes 2003; Guevara 2006; Poulsen *et al.* 2006; Saunders 2008).

The geomorphology in this region is remarkably different from the rest of the Amazonian lowlands in Ecuador. Most of the landscape is characterized by rolling plains with low hills that do not surpass 20 m in height. This area is also interrupted by small valleys, but the extent of swampy areas is low compared with the Yasuní region. Moreover, it has been reported that soil composition is

similar between this area and areas farther east in Amazonia such as the Yavari region in Peru (Pitman *et al.* 2003). On the northern banks of the Aguarico River, the landscape is dominated by extensive non-inundated alluvial terraces, rolling plains and few interspersed swamp areas. The extensive terraces of recent origin (e.g. Pleistocene) close to the margin of the river and under flooding regimes are interrupted only by high terraces with flat surfaces that have not suffered erosion of their surfaces (Saunders 2008; Wesselingh *et al.* 2006).

2.4 Herbarium collections

A preliminary compilation research of species records was performed based on the *Catalogue of Vascular Plants of Ecuador* (Jorgensen and León-Yáñez 1999). After this initial step, exhaustive research of collections of tree and shrub species collected in Ecuador's Amazonian lowland forests was carried out by Guevara from 2008 to 2013 from vouchers deposited in Herbario Nacional del Ecuador (QCNE), Catholic University Herbarium (QCA) and Alfredo Paredes Herbarium (QAP). We also include identified specimens cited in TROPICOS (<http://www.tropicos.org>) and material collected and cited in the virtual flora database of The Field Museum of Chicago (<http://fm1.fieldmuseum.org/vrrc/>). In both cases, we reviewed every specimen recorded in these databases to confirm that plant family circumscriptions follow APG III (APG III 2009; Chase and Reveal 2009). During this time we reviewed every voucher specimen of the previously recorded species and we added new records and corrected misidentifications. Most of the new records or new species have been confirmed by the specialists in each group, but in many other cases our extensive experience in Amazonian tree species identification allows us to be confident about the accuracy of the binomial name assignment. Together our experience in Amazonian tree species identifications totals more than 90 years.

2.5 Floristic inventories

In addition to the herbarium collections, we established a 70 1-ha plot network from 1980 to 2013 in Ecuadorian Amazonia lowland forests (Figure 2.1). This plot network includes the major habitat types across the region (e.g. *terra firme*, swamp mixed forests, palm-dominated swamp forests, *igapó* and *várzea*, white sands). Our plot network includes areas previously not visited by other botanical teams such as the lower portion of Cordillera del Condor and the Pastaza River watershed. In each plot we recorded, tagged and identified every single tree with diameter at breast height (dbh) above or equal to 10 cm. Botanical collections for every tree species were collected and duplicates were compared with and deposited as botanical specimens in the following herbaria: MO, QCNE, QAP, and F.

For every species recorded in the plot network and in the herbaria collections, we obtained information for their presence in Ecuadorian Amazonia, including information about records in every province of the Ecuador's Amazon region,

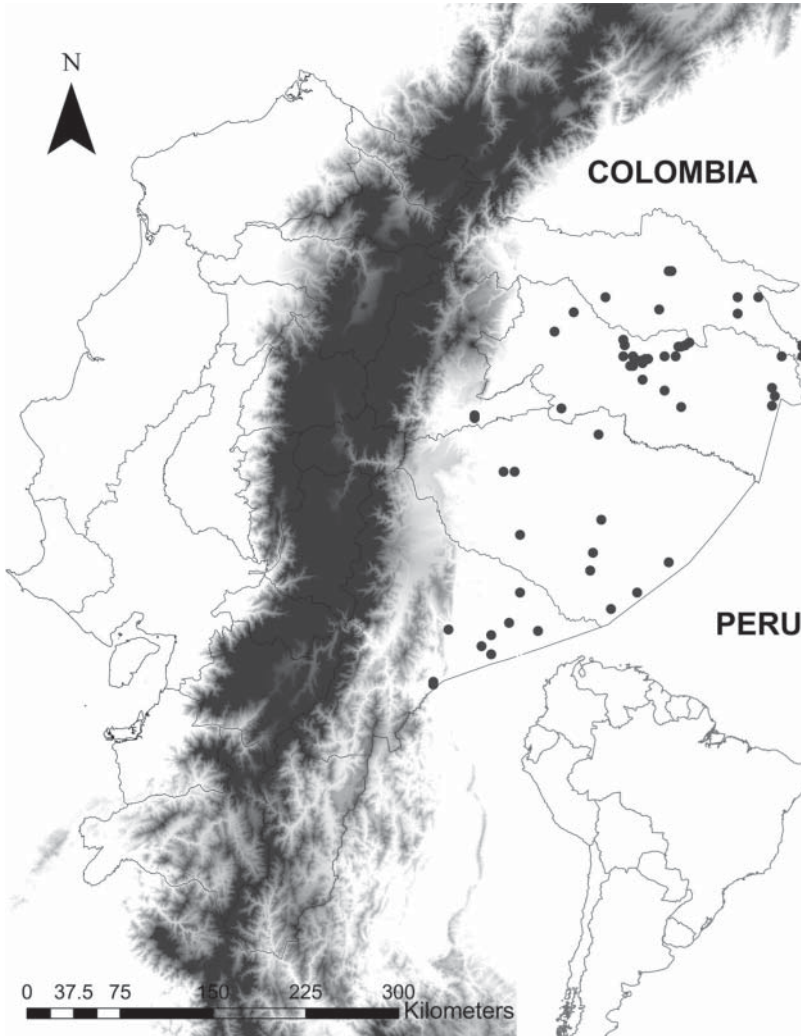


Figure 2.1 Map of the tree plot network established in the Ecuadorian Amazon.

habit, abundance and whether the species was previously recorded. All this information was gathered from the *Catalogue of Vascular Plants of Ecuador*.

2.6 Data analysis

We performed non-metric multi-dimensional analysis (NMDS) based on the Bray-Curtis dissimilarity index to establish the floristic relationships of the 1-ha plots we established across the Ecuadorian Amazon. NMDS is an ordination technique that forms groups of similar or dissimilar units in a bi-dimensional space based on abundance or presence-absence data. This technique allows us to group similar sampling units based on dissimilarity matrices without conserving

the original distance, but giving the best solution for the ordination based on those matrices.

2.6.1 Estimation of observed and expected tree species richness

In order to determine the observed number of species in Ecuadorian Amazon, we followed a two-step process. First, we counted the number of tree species with valid names in our plot network. Second, we added these species to the tree species published in the *Catalogue of Vascular Plants of Ecuador* (Jorgensen and Leon-Yanez 1999), the *Addition to the Flora of Ecuador* (Neill and Ulloa 2011) and new records that have not been formally published.

To estimate the expected number of tree species, we followed a similar approach used by Pitman *et al.* (2002) and ter Steege *et al.* (2013). Fisher's alpha index (α) was preferred over other extrapolation methods, due to two basic assumptions: the first one implies that species abundance follows a log series distribution and the second that the regional species pool is spatially homogeneous. Based on the results published in ter Steege *et al.* (2013), the first assumption is fulfilled while the second assumption is still a matter of debate. However, based on previous evidence, this could be a good approximation for Ecuador's Amazonian forests (Pitman *et al.* 2001, 2008).

Fisher's alpha is calculated as:

$$s = \alpha \ln \left(1 + \frac{n}{\alpha} \right) \quad (2.1)$$

where S is the number of species and n is the number of individuals in any community or meta-community. As a consequence, knowing α and the population size, one can easily estimate the expected number of species.

In order to obtain an estimate the number of trees in the Ecuadorian Amazon tree population size, we extrapolated the number of individuals from the 70 1-h plot networks to the 6,901,090 ha of original forest (Sierra 2013). Then, assuming a forest loss of 11% in the last 25 years for the Amazon region below 500 m (Mapa Histórico de Deforestación: Ministerio del Ambiente del Ecuador 2013a), we obtained the number of trees in the 6,551,700 ha of remnant forest. With this information we calculated the expected number of tree species and compared it with the combined observed data calculated as the mean of the individual plots alphas. In addition, we used the Chao 2 estimator, which incorporates Hill numbers or the effective number of species approach (Chao *et al.* 2014). Because Fisher's α is an asymptotic estimator of species richness while Chao's is a diversity index, we considered it appropriate to compare these two approaches in order to obtain the most accurate estimate of the expected number of tree species in lowland Ecuadorian Amazon.

2.7 Results

2.7.1 Observed patterns of tree species richness

In herbaria collections and the tree plot network we recorded 2,183 species of trees with taxonomic valid names. Forty-four percent of all species (964 spp)

were already present in Jorgensen and León-Yáñez (1999), while 56% (1,219 ssp) of all species with taxonomic valid names were present in the 1-ha tree plot network.

The three provinces with the highest numbers of records are Orellana, Sucumbíos and Pastaza, in that order. Orellana province with 1,848 tree species was the area with the highest number of records. Sucumbíos had 1,755 records, of which 110 species had been recorded only in this province, specifically in the Cuyabeno and Lagartococha lacustrine system and in the *terra firme* forests east of the Cuyabeno Reserve adjacent to Güeppí National Park in Peru.

Finally, the forests below 500 m in Pastaza province, with 708 records of tree species, is by far the least explored area in the Ecuadorian Amazon.

These results put in perspective the differences in sampling effort between areas adjacent to oil blocks or mining and those areas that remain inaccessible, even within a relatively well explored region such as Ecuadorian Amazonia.

The regional tree flora is characterized by a disproportionate number of taxa in families such as Fabaceae s.l. (222 ssp), Rubiaceae (163 ssp), Lauraceae (138 ssp), Annonaceae (110 ssp), Moraceae (110 ssp) and Euphorbiaceae (92 ssp) (Figure 2.2).

Low levels of endemism were detected in our analysis; approximately 3% of the total tree flora could be defined as endemic (Table 2.1). The families with the highest number of endemic species were Melastomataceae (15 ssp), Rubiaceae (10 ssp) and Fabaceae s.l. (7 ssp) (Figure 2.2). While some endemics are large trees, such as *Strypnodendron porcatum*, *Parkia balslevii*, *Andira macrocarpa*,

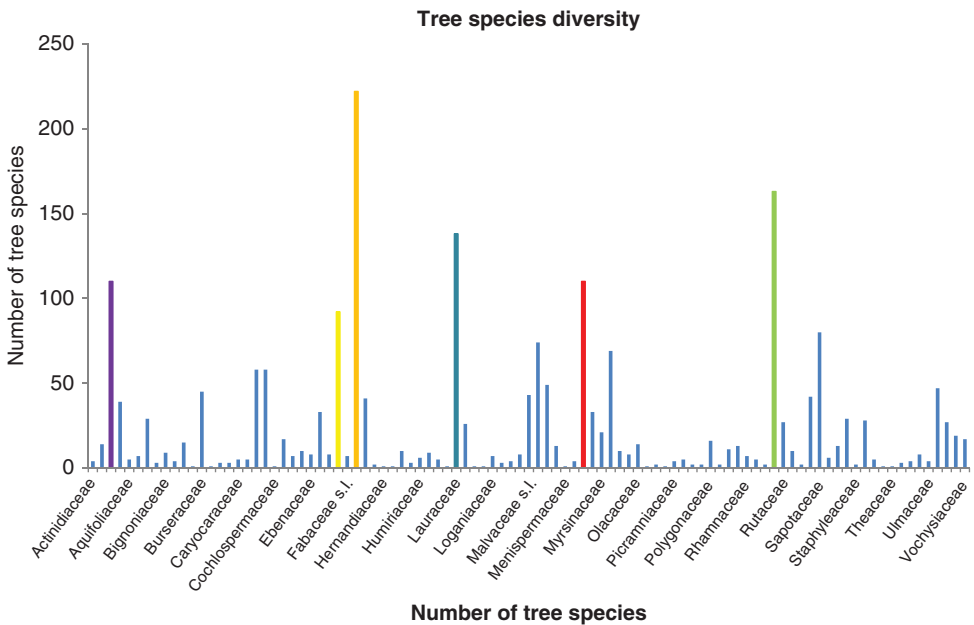


Figure 2.2 Patterns of diversity at the family level in the tree flora of the Ecuadorian Amazon.

Table 2.1 Estimates of tree species diversity, total number of trees and levels of endemism in Ecuador's Amazonian tree communities. Both values for Fisher's alpha and Chao's 2 metrics are shown.

	Original Area (ha)	Area remaining (ha)	Total number of trees	Fisher's alpha	Fisher's alpha(est)	Chao 2 Mean	Chao 2 95% CI Lower Bound	Chao 2 95% CI Upper Bound	Percent species that are endemic
Amazonian lowland forest	6.901.090	6.551.700	3.332.267.417	160.2	2.696	3.121	2.963.4	3.261.5	3.1

Swartzia bombycina, *S. aurosericea* and *Pentaplaris huaronica*, the majority of endemic species were small trees.

Both endemic trees and treelet species may exhibit small range size, restricted dispersal and sometimes clumped distributions at local scales, probably due to habitat specificity (see Duque *et al.* 2002; Guevara 2006; Pitman *et al.* 2001; Valencia *et al.* 2004). Particularly interesting is the fact that almost 90% of endemic species have been recorded close to the Andean foothills (Neill and Ulloa-Ulloa, 2011). In the cases, the endemics exhibit high relative abundance at local scales, in areas with unusual edaphic and geological particular conditions. For instance, the emergent endemic tree *Gyranthera amphibiolepis* (Malvaceae s.l.) has been reported in a narrow altitudinal band from 850 to 1,500 m on the eastern slopes of the Andes in Ecuador and Peru on calcareous limestones.

Five percent of the tree flora has also been recorded in Ecuador as treelets, while just 1% has been recorded as shrubs. In some cases these species change habit in response to changes in environmental gradients. A remarkable example of such plasticity is *Memora cladotricha* Sandwith, which can grow at the same locality as a tree or as a liana, depending on light availability.

2.7.2 Estimated number of tree species in Ecuadorian Amazonia

Based on our calculations, more than 3.3 billion adult trees co-exist in the Ecuadorian Amazon. We think our calculations are reasonable considering the 10 billion trees estimated for all of Ecuador (Crowther *et al.* 2015). Our estimate of tree species based on Fisher's α resulted in a mean of 2,696 species that may co-exist in the lowland Amazonian forests of Ecuador (Figure 2.3, Table 2.1). When we take into account the expected number of tree species based on Hill numbers, the estimate is significantly higher. Chao's estimation of tree species resulted in a mean of 3,121 tree species, almost 300 tree species more than the Fisher's α estimate.

The difference between estimates of tree species richness based on Fisher's α and Chao's algorithms may reflect the nature of both metrics. For instance, it is widely known that Fisher's α is a scale-independent non-parametric estimator that has a good discriminatory power to detect richness under the assumptions that communities sampled are characterized by a non-clustered spatial distribution of species and number of species tends to infinity (Schulte *et al.*

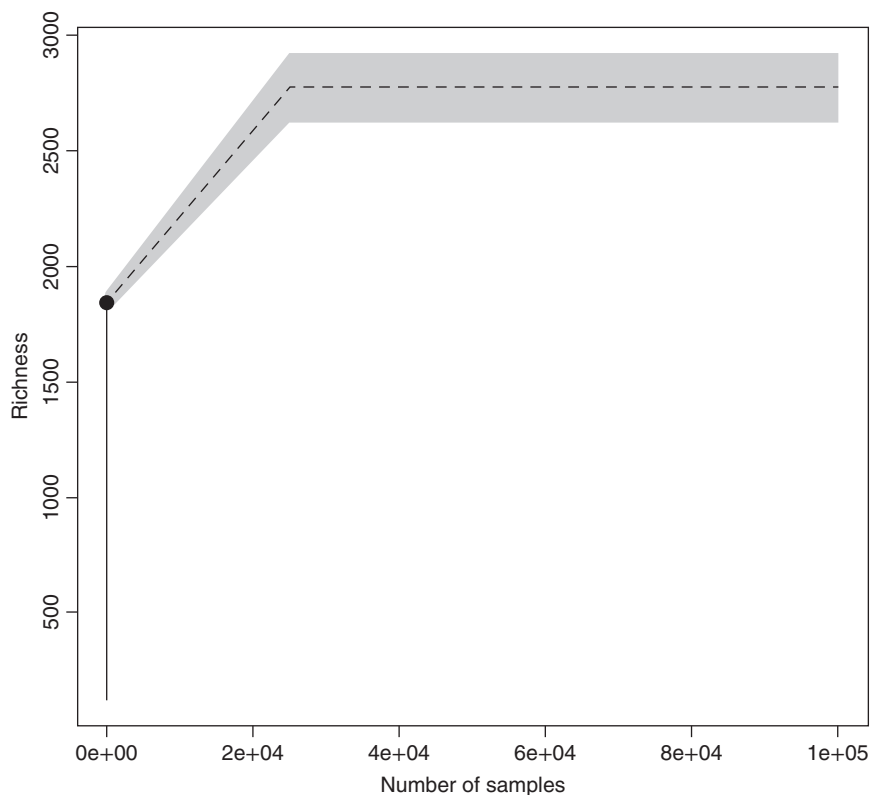


Figure 2.3 Species area curve and the estimated number of tree species expected for Ecuadorian Amazonia. Gray shaded area represents the 95% upper and lower bounds for the expected number of species with respect to area sampled. Data are based on a plot network of 70 one-hectare plots established across Ecuadorian Amazonia.

2005). In such cases, α might be underestimated. However, this could not be the case for the Ecuadorian Amazon, despite the fact that we assume *a priori* tree communities in this region follow this pattern. Meanwhile, Chao's 2 estimator works under the concept of the effective number of species (Hill numbers), which has been demonstrated to be a function of increasing sample effort and sample completeness.

Previous works have suggested an estimate of 3,370 species of woody plants including trees (Pitman *et al.* 2002). The most recent attempt to determine the expected number of tree species in the Ecuador Amazon predicts 6,827 tree species to occur in these hyperdiverse forests. This estimate was based on a fitting of tree species rank-abundance data to Fisher's log series distribution (ter Steege *et al.* 2013). However, ter Steege used a spatial model, with a relatively coarse span (1 degree grid cells = 111 km), to estimate the number of species based on the species rank-abundance curve. This could have resulted in the inclusion of areas that correspond to the Andean foothills above 500 m, which is considered the upper limit for lowland Amazonia. Therefore, we argue that this number might represent an overestimation of the real number of tree species

in Ecuador Amazon. This assumption is supported by the fact that increasing sampling area the probability of estimating a higher number of tree species will increase as well. In the case of ter Steege's estimation, this would result in the increase of the number of potential unsampled species in the right tail of the RAD distribution curve.

Our results could be interpreted as an underestimation of tree species diversity based on the work of Pitman *et al.* (2002). Nonetheless, we argue that this difference is artificial and lies in several factors. First of all, Pitman *et al.* (2002) estimates a regional species pool based on a sample of individuals with $\text{dbh} \geq 1$ cm, increasing the probability of sampling not just juveniles of the species that we could not record in our tree inventories, but also species with other life forms. In the list of species published by Romoleroux *et al.* (1997), the cornerstone for Pitman's analysis, one can find species of free-standing lianas, juveniles of treelets and vines and some species that can exhibit more than one life form. In addition, estimates of regional diversity following Pitman's approach do not consider habitats other than *terra firme* forests and were built upon a small sample size (2 ha). Differences in α diversity in contrasting environments (e.g. *terra firme* vs. swamp forests or *terra firme* vs. white-sand forests) have been well documented and they are one of the reasons why incorporating low tree diversity habitats into the analysis should lead to lower-overall Fisher's α values and consequently a lower than predicted regional species pool. Furthermore, we must consider that since the last time an estimate for woody plant species richness was done in Ecuador Amazon, there has been a reduction of almost 450,000 hectares of native forest (Sierra 2013; Pitman *et al.* 2002). Deforestation has direct negative effects on the overall number of Amazon trees, but particularly on the population sizes of rare, small-ranged tree species. Because the expected number of tree species is a function of the total number of trees, we consider our estimates to be accurate considering the regional context of deforestation.

While to our knowledge this is the first attempt to estimate regional tree species diversity based on an intensive sampling across Ecuadorian Amazonia, the number of species we present is just a proxy of the actual tree diversity. Based on the results discussed above, we can predict that approximately 3400 tree species with dbh above 10 cm might occur in Ecuador's Amazon lowland forests.

2.7.3 Floristic relationships and discontinuities at local and regional scales

Based on herbaria collections and the results from the NMDS (stress function = 0.145) based on plot data, we are able to define four floristically distinct sub-regions in Ecuadorian Amazonia. These are: (1) the Cuyabeno-Güepí region and the interfluvial area between the Napo and Aguarico rivers (Aguarico-Putumayo-Caqueta watershed), (2) the Napo-Curaray watershed, (3) the Pastaza watershed and (4) the lowland forests adjacent to Cordillera del Cóndor (Figure 2.3). We have named these biogeographic sub-regions based on the floristic differences between them, their floristic affinities with other Amazonian floras, and considering previous attempts that have incorporated geology, digital elevation models and climatic variables (see Sistema de Clasificación de los Ecosistemas del Ecuador Continental 2013).

2.8 Aguarico-Putumayo watershed

We found that the region of Güeppí-Cuyabeno has many elements of floras in Central Amazonia, including areas adjacent to the white-sand forests of the Iquitos and the Middle Caquetá region, the latter with a strong floristic influence of Guiana Shield forests. Genera such as *Sterigmapetalum*, *Chaunochiton*, *Neoptychocarpus*, *Macoubea*, *Podocalyx*, *Pogonophora*, *Antrocaryon*, *Botryarrhena*, *Clathrotropis*, *Adiscanthus*, *Ruizterania* and *Neocalyptocalyx* have been recorded only in the interlying region between the interfluvium of the Aguarico and Putumayo rivers and in the hill forest into the *terra firme* and on the high terraces of these two rivers' land.

Data from the network plots show us that the most diverse families in this region are, in order, Fabaceae s.l., Burseraceae, Chrysobalanaceae, Sapotaceae, Annonaceae, Lecythidaceae and Moraceae. In terms of abundance, the Burseraceae, Myristicaceae and Lecythidaceae are the most abundant families contrasting with the diversity patterns in forests on more fertile soils such as those ones located in Yasuní and near the foothills of the Andes, in which the diversity and abundance of families Moraceae, Arecaceae, Sapotaceae and Fabaceae s.l. are considerably higher. *Oenocarpus bataua*, *Neoptychocarpus killipi*, *Sterculia killipiana*, *Roucheria schomburgkii*, *Hebepetalum humirifolium*, *Swartzia racemosa*, *Dacryodes chimantensis*, *Couratari oligantha*, *Tachigali setifera*, *Eschweilera itayensis*, *E. rufifolia*, *Iryanthera lancifolia* and *I. laevis*, *Virola elongata*, *Licania octandra*, *L. cuyabenensis* and *Protium* have been reported with high local abundance in plots located in the Cuyabeno Güeppí region. Species of trees such as *Macoubea guianensis*, *M. sprucei*, *Rhigospira quadrangularis* and *Erythroxylum divaricatum* among others only have been recorded in our plots in this region. In several cases, the number of collections deposited in herbaria is much smaller than the abundance we have recorded in the plots. For example, *S. racemosa*, *C. oligantha*, *S. killipiana* and *N. killipi* are poorly represented in herbaria, but abundant in several of our plots located in the easternmost portion of the Ecuadorian Amazon.

Most of the new records in the Güeppí Cuyabeno area include species that are locally abundant in areas of the Middle Caquetá and certain areas near Manaus (De Oliveira and Daly 1999, De Oliveira and Mori 1999; Duivenvoorden 1995; Duque *et al.* 2002; Pitman *et al.* 2003). Thus, we think the northeastern portion of the Ecuadorian Amazon, the region of the triple border between Ecuador, Colombia and Peru, is the westernmost edge of Amazon with floristic influence of the Central Amazonia and Guiana Shield region. In the NMDS ordination, these plots established in the Aguarico-Putumayo–Caquetá region form a completely separate set of plots from the northwestern area of Yasuní.

2.9 Napo-Curaray basin

The Napo-Curaray basin region is characterized by high levels of tree alpha diversity, and the results of the tree inventory show that peaks of tree diversity can

be found in the forests located in the YNP area (Figure 2.5). Some groups, such as Arecaceae, Fabaceae, Moraceae, Rubiaceae, Sapotaceae and Melastomataceae are remarkably dominant in terms of abundance in this region. Fabaceae, Lauraceae, Myrtaceae, Rubiaceae, Melastomataceae and Sapotaceae exhibit high levels of diversity as well. Moreover, *Inga*, *Ocotea*, *Pouteria*, *Virola*, *Eugenia* and *Calypttranthes* are species-rich genera that exhibit peaks of diversity in the YNP.

Towards the south of this region, in the Curaray and Tigre river basins, most of the forests remain unexplored. Very few botanical works have been done in this vast region and the probability of finding new species and dozens of new records is high. However, based on the limited information available in herbarium collections and the results of the NMDS ordination and the indicator species analysis (ISA) (Appendix, Table 1), this region shares floristic affinities with the flora of Loreto in Peru, particularly with forests located on sandy-clayey soils in the upper Nanay and the high terraces of the Napo river close to Iquitos. *Marlierea umbraticola*, *Arachnotryx peruviana*, *Pterygota amazonica*, *Huberodendron swieteniioides*, *Cinchonopsis amazonica*, *Vatairea erythrocarpa* and *Ardisia huallagae* are conspicuous elements of the tree flora in this region. In addition, we recorded characteristic elements of the Central Brazilian Amazon. Species such as *H. humirifolium*, *Cassipourea guianensis*, *Licaria aurea*, *Septotheca tessmannii*, *Cleidon amazonicum*, *Compsonera lapidiflora*, *Conceveiba martiana* and *Hura crepitans* grow between high and low terraces and upland forests of the Tigre river basin.

The abundance data of the three plots established near the border with Peru show that in certain areas the flora of Yasuní, on richer soils, overlaps with elements of the flora of the Alto Nanay and high Arabela areas, with a mixture of white-sand and sandy-clayey soil species.

2.10 Pastaza basin region

Until a few years ago, the Pastaza basin region had remained unexplored. Our results demonstrate that the forests to the north of the Morona river and south of the Pastaza river change in species composition compared with the forest located on the adjacent sandstones at higher and lower elevations in El Cónдор (Figures 2.4 and 2.5). The confluence of several floras, including widely-distributed elements of the Amazon piedmont, the flora of Guyana Shield forests and the region of Iquitos on mixed soils, determines the patterns we found. Some Guyana Shield elements include *Chlorocardium rodiei*, *Zapoteca amazonica*, *Cochlospermum orinocensis* and *Calycophyllum obovatum* and species in the region of Loreto such as *Vantanea peruviana*, *Acacia lorentensis*, *Ruizterania trichantera*, *Chrysochlamys ulei* and *H. crepitans* have been also recorded in these plots and seem to be characteristic of the flora of this region.

In text, it is clear that the Ecuadorian Amazon is more heterogeneous than previously hypothesized. The overlapping of several regional floras in a relatively small area such as lowland Amazonian Ecuador proposes a new perspective on patterns of relative abundance and species diversity. The tree and shrub

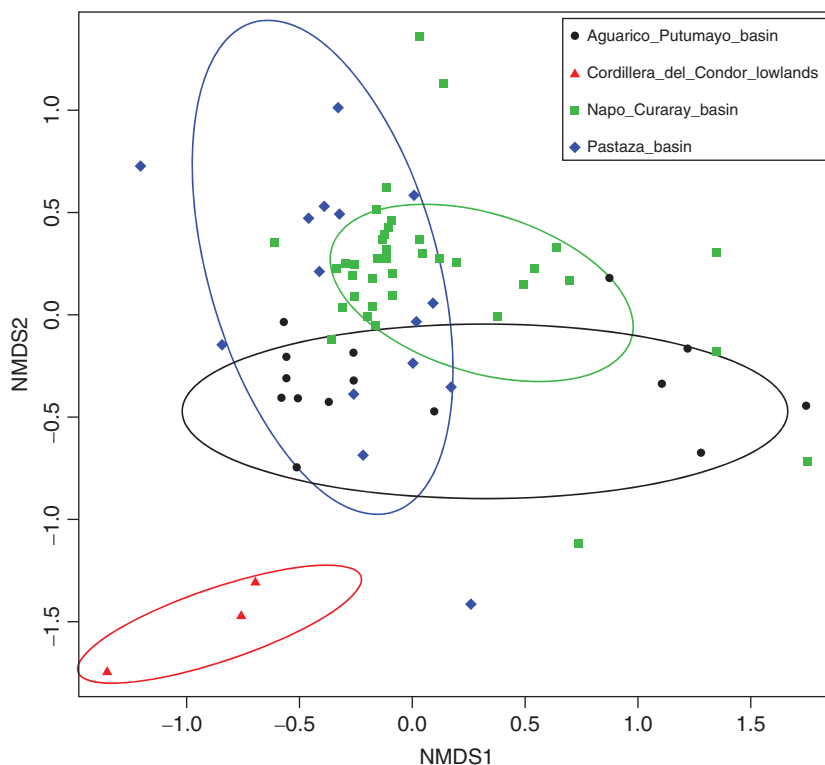


Figure 2.4 Non Metric Multidimensional ordination based on the species-level compositional dissimilarity matrix for 70 1-h plots in *terra firme* forests of the Ecuadorian Amazon. Ellipses represent the 95% confidence interval in grouping plots as part of a particular cluster of similar floristic units. Four floristically distinct regions are defined: triangle ellipse = forests in the lowlands of the Cordillera del C3n3rdor region; black ellipse = forests in the Aguarico-Putumayo watershed; square ellipse = forests in the hyperdiverse Napo-Curaray watershed; and diamond ellipse = forests in the Pastaza watershed.

community in the Ecuadorian Amazon reflects the influence of a number of forces, including historical evolutionary processes to current ecological processes, such as limited niche assembly and dispersal, the latter two believed to have happened simultaneously at different spatial scales (Antonelli *et al.* 2009; Cavender-Bares *et al.* 2009; Pennington and Dick 2010; Ricklefs 2006).

2.11 Cordillera del C3n3rdor lowlands

Finally, the forests below 500 m adjacent to the Cordillera del C3n3rdor and Cutuc3c3 could be considered as one of the areas of the Ecuadorean Amazon that remain floristically unexplored. A small number of works have focused on the floristic patterns of sandstone formations (called tepuis for their resemblance to Guyana Shield tepuis) and forests above 800 m; however, the forests below 500 m remain unexplored (Foster and Beltr3n 1997; Jadan and Aguirre 2011; Neill and Ulloa 2002).

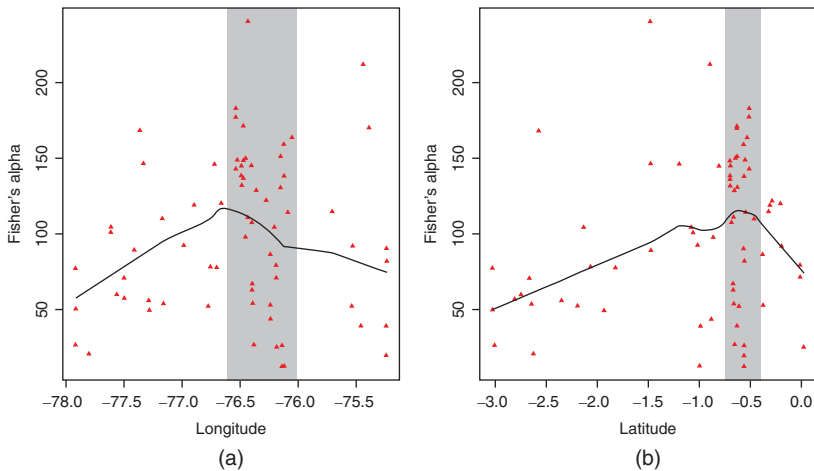


Figure 2.5 Tree alpha diversity (measured as Fisher's α) as a function of (a) longitude and (b) latitude. Loess regression is fitted to the data. The highest values of tree alpha diversity are found in the YNP region close to the Andean foothills and are probably related to climate and soil conditions. The gray bars highlight the Yasuni Park area.

In these studies, the authors have reported the presence of at least 16 genera with disjunct distributions that involve the Guyana Shield tepuis. Species such as *Stilnophyllum grandiflorum*, *Remija chelomophylla*, *Sterigmatopetalum obovatum*, *Pagamea duddeleyi* or *Dendrotrix yutajensis* and *Dacryodes uruts-kunchae* are diagnostic of forests on sandstone plateaus above 1,000 m in the C ndor–Cutuc  Cordillera. We believe, based on floristica data that comes from the few plots we established in the lowest part of this region, that some of the taxa mentioned above are part of the forests on sandstones below 500 m (Guevara *et al.* unpublished data). Moreover, some genera dominant in the white-sand forest of the surroundings of Iquitos and the upper Morona river watershed are also dominant in the low-elevation plateaus of El C ndor Cordillera. Some of these genera include *Pachira*, *Micrandra*, *Diclinanona*, *Parkia* and *Ilex*.

Despite the strong floristic patterns we report, there is a substantial number of plots (>50%) that lie in more than one cluster, representing overlap between the proposed biogeographic regions (Figure 2.4). This result might contradict the patterns of strong floristic turnover we describe; however, this pattern is in agreement with previous results that posit a non-mutually exclusive presence of strong floristic dissimilarities and dominance in Amazon tree communities (Pitman *et al.* 2014). Due to Bray-Curtis tending to preserve the abundance of species at each site or local community to obtain distances between them, the more abundant species should have a strong influence on the results of an NMDS ordination if these are widespread across the landscape. In other words, even if rare species are not shared between pairs of local communities, strong floristic similarities could arise as the result of the presence of widespread abundant species.

2.12 What factors drive gradients in alpha and beta diversity in Ecuador's Amazon forests?

2.12.1 Climate and latitudinal and longitudinal gradients

We observed a unimodal longitudinal gradient in the tree alpha diversity of *terra firme* forests, while species richness along latitude shows a unimodal gradient (Figure 2.4a). Forests close to the Andean foothills are remarkably more diverse with respect their counterparts to the east of the basin. However, a latitudinal gradient also appears to be strong in terms of tree alpha diversity, as the results of the Generalized Least Squares (GLS) analysis demonstrated (Table 2.2). We found the highest AIC when considering the interaction of Longitude, Latitude and Climate, therefore this was not considered as the optimal model. Longitude alone is implausible as the only predictor for the changes we observed in tree alpha diversity; climate shift along this longitudinal gradient appears to be the best predictor for this trend instead, as observed in the GAM results (Figure 2.5; Table 2.3).

Latitudinal gradients in species richness have been extensively described in the literature (Fine 2015; Jablonski *et al.* 2006; Mittelbach *et al.* 2007; Rohde 1992). This general pattern is observable in several taxa including mammals, plants, insects and marine biota, and the trend appears to be stronger at continental and regional scales (Mittelbach *et al.* 2007). This astonishing trend, nonetheless, has not been documented at smaller spatial scales including sub-regional and landscape scales. One of the reasons for this lack of information lies in the fact that processes such as extinction, speciation and dispersal are fundamental in the determination of the regional species pool. Therefore being more predominant at larger spatial scales.

Table 2.2 Generalized Least Squares analysis (GLS) comparing monthly mean precipitation values, maximum, minimum and mean temperature values condensed in the axis 1 of a Principal Components analysis (PC1), with respect Fisher's alpha values, Longitude and Latitude. Model selection to obtain the best model possible was performed applying a backward selection and a likelihood ratio test. Significance of the variables interactions for each model is coded as: * = significant at the 5% level; ** = significant at the 1% level.

	Model	df	AIC	BIC	logLik	Test	L.Ratio	p-value
Fisher_alpha~ Longitude+ Latitude+PC1	1	9	762.6473	782.1	-372			
Fisher_alpha~ PC1+Longitude	2	4	764.7193	773.7	-378	1 vs 2	12.07	0.034 *
Fisher_alpha~ PC1+Latitude	3	4	762.3509	771.3	-377			
Fisher_alpha~ PC1	4	3	769.1661	775.9	-382	3 vs 4	8.815	0.003 **

Table 2.3 Generalized Additive Model analysis (GAM) comparing climatic variables condensed in the axis 1 values of a Principal Components analysis (PC1), with Fisher's alpha values, Longitude and Latitude, to detect patterns of tree diversity in Ecuadorian Amazon forests. Significance of the variables interactions for each model is coded as: * = significant at the 5% level; ** = significant at the 1% level.

	Model	Estimate	Std. Error	t value	p-value	
(Intercept)		-3.52E+03	1.94E+03	-1.814	0.0743	*
PC1	1	1.75E+01	7.68E+00	2.276	0.0262	**
Longitude	2	4.78E+01	2.54E+01	1.88	0.0647	*
Latitude	3	2.78E+03	2.40E+03	1.158	0.2511	
PC1~Longitude	4	-2.28E-01	1.00E-01	-2.276	0.0262	**
PC1~Latitude	5	-1.03E+01	6.23E+00	-1.648	0.1042	
Longitude~Latitude	6	-3.67E+01	3.14E+01	-1.171	0.246	
PC1~Longitude+Latitude	7	1.34E-01	8.11E-02	1.655	0.1027	

We found that shifts in tree species diversity along latitudinal and longitudinal gradients can occur at smaller spatial scales, if environmental heterogeneity is strong enough to filter species from one region to another of the ecological space distributed over geographic space.

Examples of such longitudinal gradients occurring at smaller spatial scales than those repeatedly reported in the literature could occur in the Andean-Amazon transition from montane to lowland forests. In a study of aquatic communities across an Andean-Amazon fluvial gradient, Lujan *et al.* (2013) found a strong and non-linear shift in taxonomy and function of these communities and argued that strong turnover of basal food resources and inter-specific interactions was responsible for the change.

Although previous works have emphasized relatively homogeneous environmental conditions across lowland Amazonian in Ecuador (see Pitman *et al.* 2001; Tuomisto *et al.* 2003a), with respect to the more heterogeneous landscapes such as the forests surrounding Iquitos or the middle Caquetá, we believe that there is recent evidence to contradict this hypothesis.

Evidence for shifts in temperature and rainfall in an eastward direction has been reported for Ecuadorian Amazonia and could be responsible for the changes we detect, not just in diversity but also in composition (Figures 2.5 e,f).

Previously, Pitman *et al.* (2008) reported changes in tree species composition along a longitudinal gradient in a plot network from Yasuní to Yavarí along the Peruvian-Brazilian border. Strong and abrupt floristic changes were assumed to be produced by shifts in soil composition from richer soils in plots located in the Ecuadorian Amazon and poorer sandy soils in plots located on the northern bank of the Napo River.

We confirm these results but also posit that strong beta diversity along longitude might be correlated with climate and not just soil conditions.

2.13 The role of geomorphology and soils in patterns of floristic change in Ecuadorian Amazonia

There is an increasing number of studies showing the role of geology, geomorphology and soil heterogeneity in patterns of floristic change (beta diversity) at both landscape and regional scales in Amazonian forests (Figuereido *et al.* 2014; Fine *et al.* 2005; Higgins *et al.* 2011; Philips *et al.* 2003; Tuomisto and Poulsen 1996; Tuomisto *et al.* 2003a,b).

Higgins *et al.* (2011) reported a strong correlation between geological formations and their underlying soil conditions and fern and shrub species composition. Discontinuities in species composition therefore are tightly determined by geological history, which determines that forests are partitioned into large discrete floristic units. These changes instead follow a longitudinal gradient representing a complex history of deposition and erosion that predates the Pleistocene (Higgins *et al.* 2011; Hoorn *et al.* 1995; Hoorn 1996).

A strong correlation between abrupt floristic discontinuities, landforms and geological features has been also found in Central Amazonia. However, some caveats must be considered when interpreting this evidence. In both works, the authors test the role of geological control on Amazonian plant communities; however, the evidence relies on analysis done with groups of plants (Pteridophytes and Melastomataceae in Higgins *et al.* (2011) and Zingiberaceae in Figuereido *et al.* (2014)), which represent just a small fraction of total diversity. In both studies, the authors argue that focusing on these groups of plants helps to avoid taxonomic uncertainty, tall taxa and larger sample sizes, which involve a huge investment of time to demonstrate the patterns they reported. Although the authors predict the same patterns for the tree flora, we think this has to be tested instead of being assumed.

We found evidence for a correlation between geomorphology, soils and beta diversity in the Amazonian tree community. Towards the border with Peru, floodplains of the Napo, Putumayo and Aguarico rivers form high and low terraces with a fairly flat topography. The forest in this areas shows floristic affinities with plots established further east in the basin, registering families and monotypic genera present in areas of Central Amazonia (Alverson *et al.* 2008; Pitman *et al.* 2008).

For example, samples collected by Cerón and Montalvo (2009) in alluvial terraces of the Aguarico River correspond to species of monotypic genera such as *Podocalyx loranthoides* and *Pogonophora schomburgkiana*. These species are characteristic of poor soil forests in the Middle Caquetá and certain areas in Central Amazonia (Duivenvoorden 1996; Duque *et al.* 2002). In addition, in a rapid survey conducted in 2008 by the Field Museum in Chicago area in the Güeppí region, W. Palacios recorded the species *Chaunchiton kaplerii* (Alverson *et al.* 2008), a genus previously unknown for Ecuadorian Amazonia but with a widespread distribution.

Strong floristic affinities of forests along high terraces bordering the Napo River with forest eastwards of the Amazon Basin show a high abundance of species such as *R. quadrangularis*, *Mezilaurus sprucei*, *Rauvolfia polyphylla*,

Eriotheca longitubulosa, *Sloanea monosperma* and *V. peruviana* and high diversity and abundance of the genus *Protium*.

At the landscape scale, soils in this region are characterized by a very low pH and very high content of sand (Cerón and Reyes 2003; Saunders 2008).

Interestingly, studies in the Cuyabeno region have shown the predominance of certain taxa that are locally dominant and diverse in areas with poorer soils such as the sandy-clayey areas surrounding Iquitos (Fine *et al.* 2010; Valencia *et al.* 1994). Exceptional cases of family-level hyperdominance (*sensu* ter Steege *et al.* 2013) at the local scale (<1 km²) have been reported in the Ecuadorian Amazon, such as the unusual dominance of Burseraceae in an upland forest in the Cuyabeno region (Cerón and Reyes 2003; see also Vormisto *et al.* 2004).

2.14 Potential evolutionary processes determining differences in tree alpha and beta diversity in Ecuadorian Amazonia

Despite the increasingly number of works analyzing and describing patterns of alpha and beta diversity in Amazonian forests, a comparatively small fraction of these works have included an evolutionary perspective in their analysis. We think that differences in tree species richness and tree species turnover are intimately linked to evolutionary processes that operate at large spatial scales. Differences in species richness across a particular region may be the result of asymmetries in speciation and extinction rates. These asymmetries could be the result of multiple factors, including area population size relationships, geographic barriers promoting disruption in gene flow between populations, colonization of novel habitats, habitat specialization, floral and pollinator specialization, herbivory and plant defense mechanisms, low dispersal capabilities, productivity or high energy systems (Fine 2015).

For example, diversification rates might differ between two areas if there is colonization of areas outside the ancestral range by high dispersal capability clades. High extinction rates could be the result of physiological constraints if new colonizers do not evolve a particular trait or set of traits that allows adaptations to the new habitat. Conversely, high speciation rates might be produced by high phenotypic plasticity that allows successful colonization of novel habitats, as lineage divergence in this sense is produced by local adaptations.

On the other hand, population size and geographic range size may promote speciation and extinction rate asymmetries. For instance, large population size might involve more genetic diversity if genetic drift is not involved, because speciation rates should increase while extinction rates decrease (Fine 2015; Jetz and Fine 2012). Moreover, species with large population sizes can span different climatic or other environmental regimes, which increases the probability of parapatric or peripatric speciation (Kisel *et al.* 2011).

Here we described some examples of works which have tested plausible mechanisms for asymmetries in speciation and extinction in Amazonian forests, which could be responsible for the longitudinal and latitudinal gradients.

Plant–herbivore interactions have been hypothesized as the main drivers of speciation and co-existence in Amazonian forests (Coley and Kursar 2014; Fine *et al.* 2004; Kursar *et al.* 2009). Selection for divergence in anti-herbivore defenses should lead to differences in speciation rates, if different herbivore guilds exert selective pressure differentially across a geographic region. In addition, separate populations in different environments should exhibit different adaptations that eventually would result in reproductive isolation when the members of these populations re-unite and interbreed. In this case, hybrids may have lower fitness than members of the ancestral populations accentuating selection for reproductive isolation (Coley and Kursar 2014).

Fine *et al.* (2005) demonstrated that soil heterogeneity leads to edaphic specialization and consequently drives speciation. In this study, the authors reported that 21 of 25 species of the tribe Protiae in Burseraceae were confined to one edaphic habitat. In particular, the great majority of these specialists apparently have evolved habitat specialization very recently. Moreover, the role of historical processes such the geological history of the Amazon Basin apparently plays a fundamental role in speciation of the tribe Protiae and consequently in the distribution patterns of its species across Western Amazonia. Fine *et al.* (2005) argued that Miocene-rich sediments constitute the ancestral habitat for most current white-sand specialist species. White-sand habitats were extensive before the Miocene as some evidence suggests and the source of sediments were the Guiana and Brazilian shields. During the Miocene, as the Andean uplift started, the flux of sediments changed dramatically from a westward to an eastward direction, and the much richer sediments originating in the Andes were deposited over most of current Western Amazonia. This geological event produced an incredible edaphic heterogeneity in which parapatric (mosaic sympatry: *sensu* Mallet *et al.* 2009) speciation promoted by divergent natural selection for habitat specialization would have led to high rates of speciation in the northwestern Amazon forest (Fine *et al.* 2005, 2012; Hoorn *et al.* 2010).

Divergent natural selection should promote habitat specialization and should be involved in diversification processes if populations in contrasting environments (e.g. white sand soils vs. clay soils) evolve a different set of traits that promotes hybrids of the incipient species to have low fitness in both habitats resulting in lineages divergence (Endler 1977; Fine *et al.* 2005).

Despite the fact that we do not have knowledge of any work in Ecuador Amazon supporting this hypothesis, we think there is no reason to doubt the same mechanisms operate across the region (Figure 2.6).

On the other hand, turnover time has been posited as the driver of high diversification rates in Western Amazonia (Baker *et al.* 2014). Using demographic traits data from a plot network in Amazonian forests, the authors found that turnover time improved the estimates of species richness over models of diversification for 51 clades. Faster turnover rates are associated with higher diversification rates if species attain reproductive age faster than expected and populations exhibit short generation times. This could be associated with highly dynamic environments such as the western most part of the Amazon. The region shows a strong influence of Andean uplift, including recent events of deposition of sediments that have originated alluvial terraces, alluvial fans and

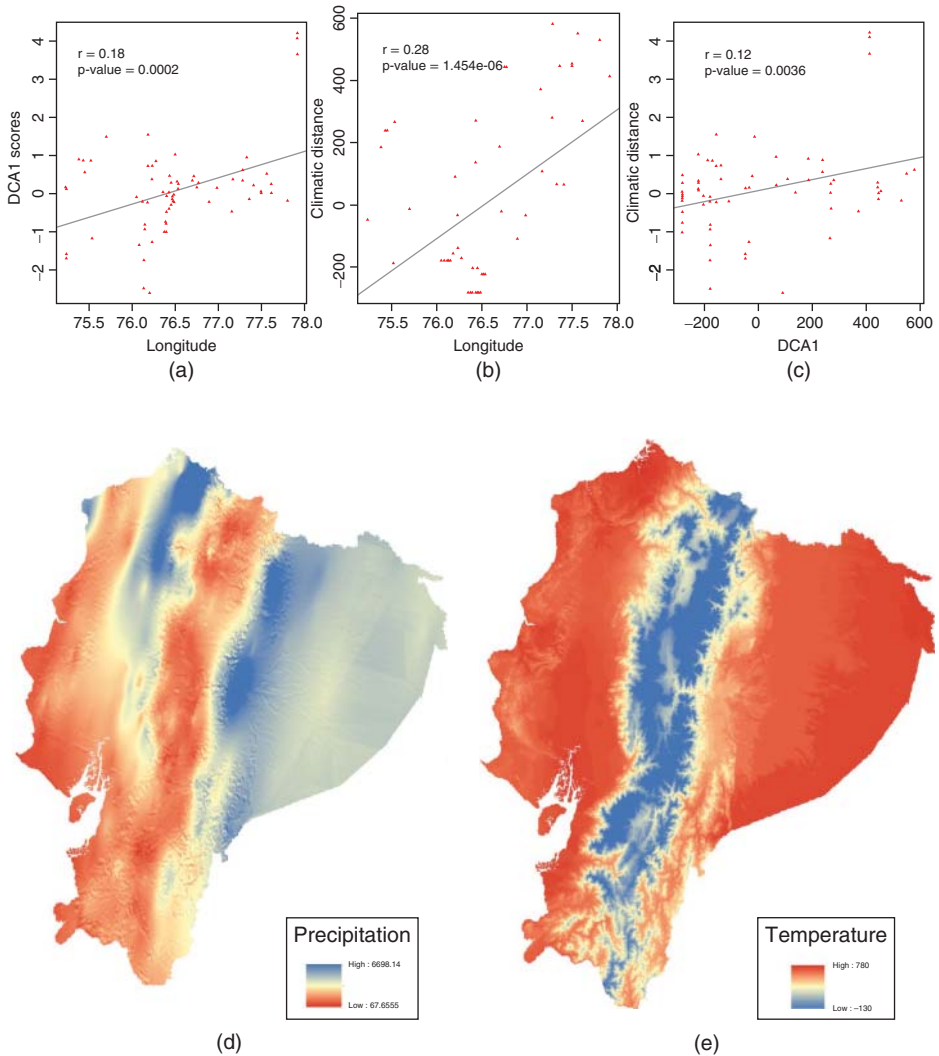


Figure 2.6 Floristic changes are correlated with shifts in climate along a longitudinal gradient in Ecuadorian Amazon forests. (a) Scores of DCA axis 1 against longitude. (b) Climatic distance against longitude; climatic differences were measured as score values of a PCA (principal component analysis) on the basis of monthly mean precipitation values and maximum, minimum and mean temperature values (see Ministerio del Ambiente del Ecuador 2013b). (c) Change in tree species composition as a function of climatic distance. (d) Spatial variation in precipitation across Ecuador. Interpolation of precipitation values was done using the kriging method on the basis of monthly mean precipitation values at 1 km² resolution. (e) Spatial variation in temperature across Ecuador. Interpolation of precipitation values were done using the kriging method on the basis of mean, maximum and mean temperature values at 1 km² resolution. A longitudinal gradient for temperature and precipitation at landscape scales is clear for (d) and (e).

other geomorphological units with specific underlying soil conditions. These novel edaphic habitats might have promoted high speciation rates in clades with the capability to exploit them efficiently by rapid occupancy and adaptation.

However, turnover times could be assumed to be a by-product of other traits directly involved in reproductive isolation that might promote high diversification rates. Species of the same clade may attain reproductive age faster than close relatives or members of a completely different clade co-existing in sympatry, only if they compete for the same set of potential pollinators. In other words, sympatric lineages that compete for the same pollinators may diverge in floral traits promoting increases in diversification rates (Armbruster and Muchala 2008; May and Sargent 2009). This floral isolation may be favored by natural selection after other traits involved in reproductive isolation have evolved.

On the other hand, pollination might reduce extinction rates for rare lineages, insuring that pollen transport between isolated populations could promote an increase in extinction rates if pollination syndromes have evolved through specialization.

In this way increasing turnover times is the result of the natural selection for different pollinators and not the ultimate cause of diversification rates increases.

2.15 Future directions

Regardless of the increasing number of studies that evaluate plant species richness in Western Amazonia, there are still few works concentrating on the Ecuadorean Amazon. Moreover, the lack of works linking taxonomy, phylogeny and traits constrains our ability to determine the potential factors that drive compositional and phylogenetic beta diversity in Amazonian tree communities. Therefore studies combining ecological and evolutionary approaches are necessary to understand the ecological and evolutionary processes acting together in the determination of local assemblages in Ecuador's Amazon forests. For instance, investigating the role of geological formations, soil conditions in the patterns of taxonomic and phylogenetic alpha and beta diversity will require a combination of plot network establishment, geological maps, soil sampling and community phylogenetics to elucidate the importance of these factors.

The inclusion of an evolutionary approach in any analysis of beta diversity is essential in order to improve scientific research-based conservation policies. Because species-centric conservation research takes into consideration a snapshot of the fractal nature of the tree of life, we miss all the information that genealogical relationships between organisms can give us. Evolutionary time plays a fundamental role in the origin and maintenance of biodiversity, because the rate of change in diversity is intrinsically linked to the rates at which a clade or taxa originate and become extinct. For the sake of argument, it is fundamental to consider that regions with extremely high levels of species richness do not necessarily represent areas with high phylogenetic diversity. Furthermore, because phylogenetic beta diversity measures how phylogenetic

relatedness changes across environmental and spatial gradients, we can make inferences about the different biogeographical histories of regional species pools with the strong analytical power that phylogenies give to us. Currently, many conservation priority-setting exercises tend to be focused on endemism, whereas many others are based on species information solely and have proved to be a poor predictor of both species richness and threatened species identification. In the light of climate change and human-induced extinctions, it is fundamental to include phylogenetic information in conservation priorities, even more so when the conservation research focus has reached the Noah's Ark dilemma when considering flagship, keystone and umbrella or restricted-range endemic species.

Ultimately, because physiological attributes are intimately related to habitat or ecological space occupancy, the inclusion of ecologically relevant traits is essential to understand both ecological and evolutionary causes of tree species diversity changes across space and environment. Therefore, the future of Western Amazonia's hyper-diverse forests depends on our capacity to develop multi-approach studies in order to understand the processes underlying the community assembly patterns of these systems.

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