

Article

Distribution of the Genus *Passiflora* L. Diversity in Colombia and Its Potential as an Indicator for Biodiversity Management in the Coffee Growing Zone

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Abstract: Analysis was made of 3,923 records of 162 wild *Passiflora* specimens to assess the distribution of their diversity in Colombia, identify collection gaps, and explore their potential as indicator species. Despite variable collecting density among and within biogeographic regions, the Andean region clearly presents a higher species richness, particularly in the central coffee growing zone and the departments of Antioquia, Cundinamarca and Valle del Cauca. The elevational distribution of diversity shows a small peak below 500 m, and two higher ones between 1,000–2,000 and 2,500–3,000 m. This pattern corresponds to divergent adaptive trends among infrageneric divisions. The analysis on 19 climatic variables showed that the two principal variance components, explaining 77 percent of the total, are respectively associated with temperature and precipitation, without influence of seasonality. Distribution parameters allow recognizing more than 36 narrow endemics. Prediction of species distribution showed nine areas with very high richness (predicted sympatry of 41 to 54 species) in the Andean region, three of which correspond to collection gaps. Endemics were not particularly frequent there, so a

prioritization of protected areas based on species richness would not favor their conservation. The sites with high *Passiflora* diversity are poorly represented in the current system of protected areas. Instead, their striking correspondence with ecotopes of the coffee growing zone imposes a conservation strategy integrating agricultural and environmental management at the landscape level. Reciprocally, several traits of *Passiflora* species make them particularly suited as indicators for any effort of conservation or restoration in this region of importance for the country.

Keywords: Andes; coffee growing zone; Colombia; biodiversity indicators; endemism; geographic information systems

1. Introduction

Colombia is divided into five main biogeographic regions [1]. The Andean region presents a highly diverse topography (100–5,400 m), with three mountain ranges, the Eastern, Central and Western Cordilleras, separating two main inter-Andean valleys from the other regions. The uplift of the Andes created new habitats and increased local isolation, favoring high speciation rates in many taxa [2]. The continuously humid climate of the Amazonian and Orinoquian lowlands and the extremely wet climate of the Pacific region contrasts with the drier and more seasonal climate of the Caribbean. As a result, the Colombian flora includes some of the world's most diverse groups of vascular plants, with 51,220 documented species [3–5]. It is hoped that most of this floristic richness is located in the protected areas that cover 365,120 km², approximately 32 percent of the territory [6], falling under different categories of protection, including Natural National Parks, Flora and Fauna Sanctuaries, Natural National Reserves, Unique Natural Areas, Park Ways and Indigenous Areas, among others. Smaller forest reserves have also been created to protect river basins for water supply. On the other hand, destruction of many natural habitats has drastically affected species, often reducing their historical ranges to a set of small, fragmented populations. Such alteration is predicted to lead to substantial extinction in the near future [6]. Within the field of conservation biology as a whole, and protected area management in particular, it is becoming increasingly urgent to develop spatial and temporal predictions of how significant environment changes, and, particularly, multiple anthropogenic threats, may affect the abundance and distribution of species [7,8]. Bioclimatic modeling can provide first-cut estimates of risk of biodiversity loss even where species distribution data are relatively poor [8].

Many conservation biologists have focused their attention on areas presenting high levels of endemism and diversity, and experiencing a high rate of loss of ecosystems. Such regions concentrating biodiversity under threat are defined as biodiversity hotspots, representing priorities for conservation actions [9]. The tropical Andes are considered one of these hotspots, as they support almost half of the Neotropical biodiversity [10]. However, the application of this concept in the case of Colombia implies the development of wide studies to investigate the distribution of biodiversity, at an operational resolution level across the country. Complete inventories are not realistic at that scale, so other approaches have been taken to exploit incomplete biodiversity data, combining remote sensing and field sampling/inventories of indicator taxa at different scales [11]. We proposed the use of

climatic niche modeling and tested the potential of *Passiflora* as an indicator of biodiversity in Colombia, as Passifloraceae represent several interesting traits in terms of diversity, adaptation and evolution.

Indeed, Colombia is particularly rich in Passifloraceae, with 167 species from *Ancistrothyrsus* (2), *Dilkea* (4) and *Passiflora* (162) genera, mostly in the Andean region (123 species). The country has 57 endemic species, 95 percent of them Andean, implying a high extinction risk as this region is the most densely populated and disturbed, particularly the coffee growing zone [12]. According to the Von Humboldt Institute, the Universidad Nacional de Colombia [13], and Ocampo *et al.* [12], more than 100 Colombian Passifloraceae species are threatened to some degree, and three species are considered extinct.

Neotropical Passifloraceae include about 650 species from the genera *Ancistrothyrsus*, *Dilkea*, *Mitostemma* and *Passiflora* [14]. The largest one is *Passiflora*, with *ca.* 575 species distributed in a wide range of habitats, from humid rain forests to semi-arid subtropics. Most of them are herbaceous or woody vines, while a few are trees or shrubs. More than 80 species produce an edible fruit, the most interesting ones belonging to subgenera *Passiflora* and *Tacsonia* [15,16]. Among them, are the yellow and purple maracuja, *P. edulis* Sims, with a world production estimated at more than 805,000 tons [17], and more than 13 species/forms present on the national or local markets of Colombia [12]. *Passiflora* species also present ornamental and pharmaceutical interest [16]. Killip's [18] classification divided *Passiflora* into 22 subgenera. It was amended by Escobar [19,20], who merged two subgenera and proposed a new one, and by MacDougal [21], who revised subgenus *Plectostemma*, restoring its ancient name *Decaloba*. In 2003, Feuillet and MacDougal [22] proposed a deeper revision, recognizing only four subgenera, *Astropheia*, *Decaloba*, *Deidamioides* and *Passiflora*. This proposal has been partially justified by molecular data [23-26], however further studies are still needed for understanding Passifloraceae diversity and evolution.

As vines, most *Passiflora* species have adapted to many different habitats, particularly for their support. They are medium-lived organisms depending on longer-lived trees and shrubs, which makes them responsive to both medium and long-term changes. They also show high levels of co-evolution with their herbivores, particularly *Heliconius* butterflies [27], and some species even exhibit elements of the carnivory syndrome [28]. They have developed mutualism with protector insects as nectar-feeding ants [29], and with a wide range of pollinators, including small and large insects, birds and bats [30,31]. Finally, given its economic importance, the genus *Passiflora* constitutes an important genetic resource, and the characterization of wild and cultivated populations is seen as a priority for Andean countries because of its potential for development and crop diversification [32]. Strategies for conservation and improvement are needed to optimize the use and conservation of this resource.

Biodiversity data have been traditionally produced through a variety of complementary approaches using field survey and sampling, museum records, botanical collections, and, in recent times, spatial analysis of data integrated within Geographical Information Systems (GIS). In each area, the combination of geological, edaphic, climatic, ecological, historical and anthropic factors produces a unique range of constraints defining patterns of diversity [33]. GIS allow building maps of species richness, potential distribution and endemism, prioritizing areas for conservation based on principles such as complementarity, and assessing the completeness of existing protected areas networks [34].

Several methods use climatic variables as the principal drivers of herbarium or collecting data, generating information for diversity studies and conservation actions [35,36]. Such modeling tools have been applied to problems of phytogeography [37,38], conservation [39,40], evolutionary ecology [41], invasive or endemic species management [42–44], potential areas for plant collection [45,46] and the effect of climate change on crop wild relatives [47]. In *Passiflora*, Segura *et al.* [48] mapped the potential distribution of five species of the subgenus *Tacsonia* and produced evidence of intra-specific variation in climatic adaptation along the Andes, from Colombia to Peru.

The present study was conducted through (1) assessing the geographic distribution of Colombian Passifloraceae; (2) analyzing it in terms of species richness across the territory; (3) inferring the potential distribution of each species with predictive distribution models; (4) summing these spatial predictions to produce a map of potential diversity; and (5) locating collecting gaps by detecting those areas where *Passiflora* species are likely to occur but have not yet been collected. Combining these results permits an analysis of the current status of *in situ* and *ex situ* conservation of *Passiflora* in Colombia. It also provides elements to evaluate the potential of this group as an indicator for the detection of biodiversity hotspots and monitoring of conservation/restoration efforts.

2. Material and Methods

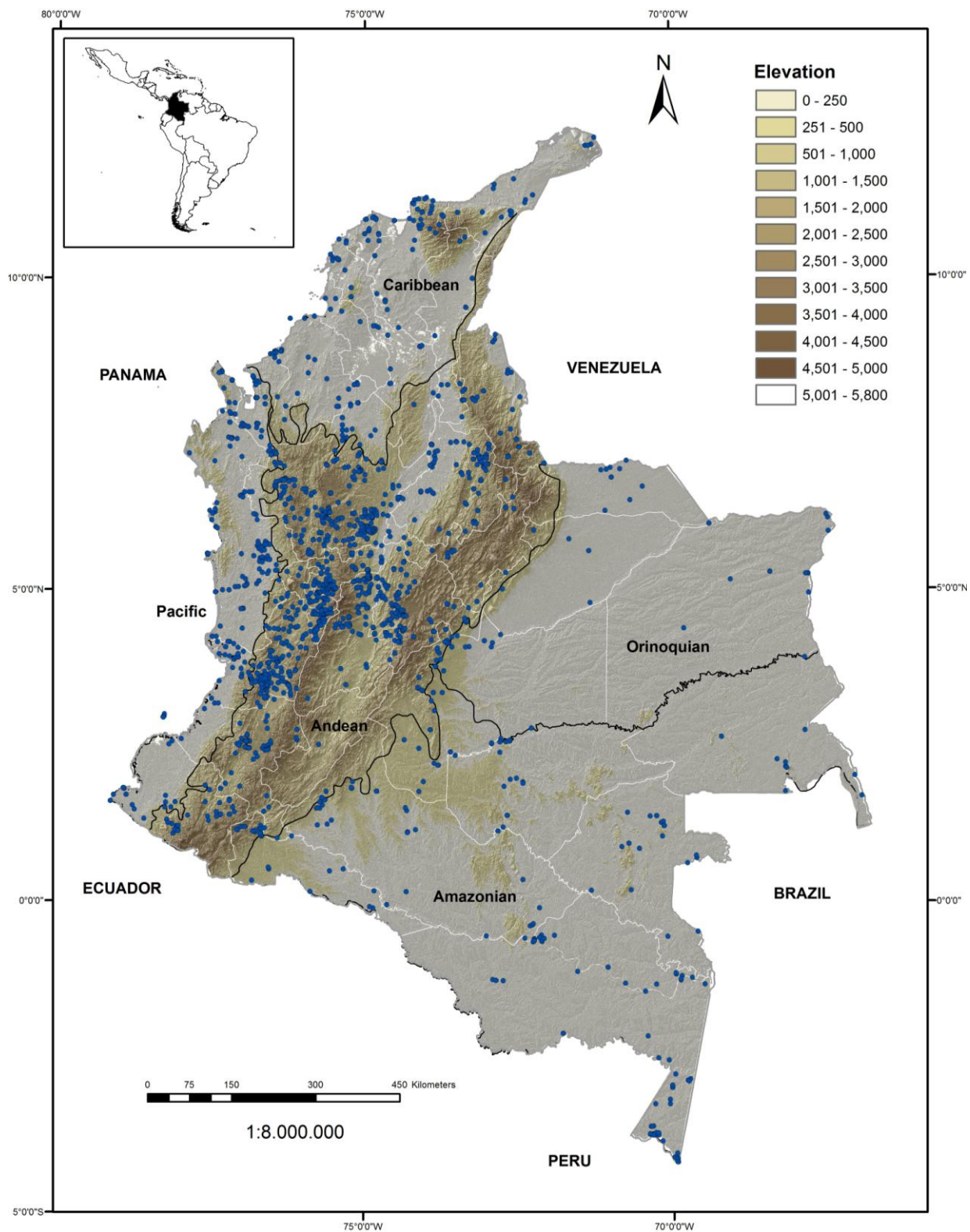
2.1. Geography and Climate

Colombia is located in the north of South America, between 12°26'46" N and 4°13'30" S and between 66°50'54" W and 79°02'33" W, covering an area of 1,141,748 km², with altitudes ranging from the sea level to 5,775 m [1]. It is divided in 32 departments (see Supplementary Figure 1: Colombia's geopolitical division in 32 departments and biogeographic division in five regions.). Figure 1 shows their distribution among the five biogeographic regions of the country [1]. Colombian climates are tropical, with relatively uniform temperatures throughout the year. Precipitations vary greatly, with some of the wettest parts of the world in the Pacific lowlands (average annual rainfall reaching 10,000 mm) contrasting with extremely dry areas in the coast (<500 mm per year), and show a tendency to increase with altitude.

2.2. Species Distribution and Richness

The original plant dataset consists of the information gathered and georeferenced by Ocampo *et al.* [12] from 3,930 individuals of 167 Passifloraceae species, consisting of 3,330 herbarium specimens (AFP, CAUP, CDMB, CHOCO, COL, COAH, CUVV, FAUC, FMB, HUA, HUQ, JAUM, K, MA, MEDEL, MO, NY, P, PSO, SURCO, TOLI, VALLE and UIS), 555 field records, and 45 records from Killip [18,49], Uribe [50] and Escobar [19,20,51]. The few specimens from genera *Ancistrothyrus* (three) and *Dilkea* (four) brought too limited information, as compared to *Passiflora*, so they were not taken into account in the analysis presented here.

Figure 1. Collection localities (blue dots) of *Passiflora* specimens used in this study among 32 Colombian departments and five biogeographic regions (see Supplementary Figure 1).



Species distribution was plotted on dot-maps using the DIVA-GIS software and quantified by their maximum distance (MaxD) and circular area (CA_r) according to Hijmans *et al.* [52]. For each species,

MaxD is the longest distance between any pair of observations, and CA₅₀ was calculated by assigning a circle of radius 50 km to each observation and calculating the area covered by all circles. As in a previous paper [12], we used the following threat criteria: a number of observations under six characterizes rare species, MaxD under 100 km and CA₅₀ under 20,000 km² characterize narrow endemics.

Species richness was calculated as the number of species within a defined area, superimposing species location maps, using the point-to-grid richness analysis tool in DIVA-GIS with a $0.1 \times 0.1^\circ$ grid (*i.e.*, 12×12 km at the Equator). The circular neighborhood option was applied with a 2° radius [37] to eliminate border effects due to assignation of the grid origin.

2.3. Climatic Adaptation and Modeling

Climatic models were developed to predict species occurrence, with DIVA-GIS. This package uses WorldClim data [52], consisting of global climate surfaces with a $30''$ grid resolution (*i.e.*, 1×1 km at the Equator), derived from a network of over 12,500 meteorological stations across Latin America, 1,479 of them in Colombia. For each collection site, 19 bioclimatic variables (derived from 12 monthly means for temperature, rainfall and diurnal temperature range according to Busby [53]) were extracted. Principal components analysis (PCA) was performed on the resulting dataset, applying a varimax normalized rotation. For readability, the centroid, *i.e.*, the arithmetic average of the factor scores, was used to represent each species climatic preferences.

Potential species distributions were mapped by extrapolation, using the 19 bioclimatic variables and the DIVA-GIS BioClim method for the 80 species with more than 10 observations. BioClim was chosen because it is a robust methodology, requiring presence-only data [54]. Unfortunately, many of the omitted 85 native species, too poorly represented for reliable results, are endemic and/or rare species. Finally, an analysis of complementarity [55] was applied to identify the lowest number of protected areas needed for the conservation of native *Passiflora* species.

3. Results and Discussion

3.1. Distribution of Observations and Species Richness/Diversity

Figure 2 and Table 1 show the distribution of collection/observation points. The Andean region of Central Colombia is by far the most densely explored, particularly the central coffee growing zone (Quindío, Caldas and Risaralda; 18.93 to 77.20 observations/1,000 km²) and the three large departments of Antioquia, Valle del Cauca and Cundinamarca (12.45 to 19.82 observations/1,000 km²). By comparison, the northeastern Andes (Boyacá, Santander, and Norte de Santander) and the central department of Tolima appear less well explored (3.59 to 9.39 observations/1000 km²). The situation is more difficult to appreciate in the southern Andes, as the southern departments of Cauca and Nariño also belong in good part to the Pacific region. However, they show a collection density only slightly superior to that of Chocó, which indicates that they have also been less explored than the central Andes. The situation is heterogeneous in the Caribbean, with only two of its seven departments exhibiting more than three observations/1,000 km² (excluding the atypical case of the small San Andrés and

Providencia islands). Finally, the Amazonian and the Orinoquian are by far the least explored biogeographic regions of the country, although they cover half of its area.

The mean number of observations per species also reflects variation in exploration among departments (Table 1), confirming the much denser exploration in the Andes of Antioquia, Cundinamarca and Valle del Cauca (more than seven observations/species) and in the Pacific region, while this ratio takes much lower values in the other regions. However, the relation between exploration density and this indicator is not simple, as the numerous observations in the central coffee growing zone are distributed among a very wide diversity of species, so the mean number of observations/species is not as high as could be expected for such densely explored areas.

Figure 2. Species richness observed for *Passiflora* in $0.1 \times 0.1^\circ$ grid cells in Colombia (162 species). Points on the map represent sites of collection.

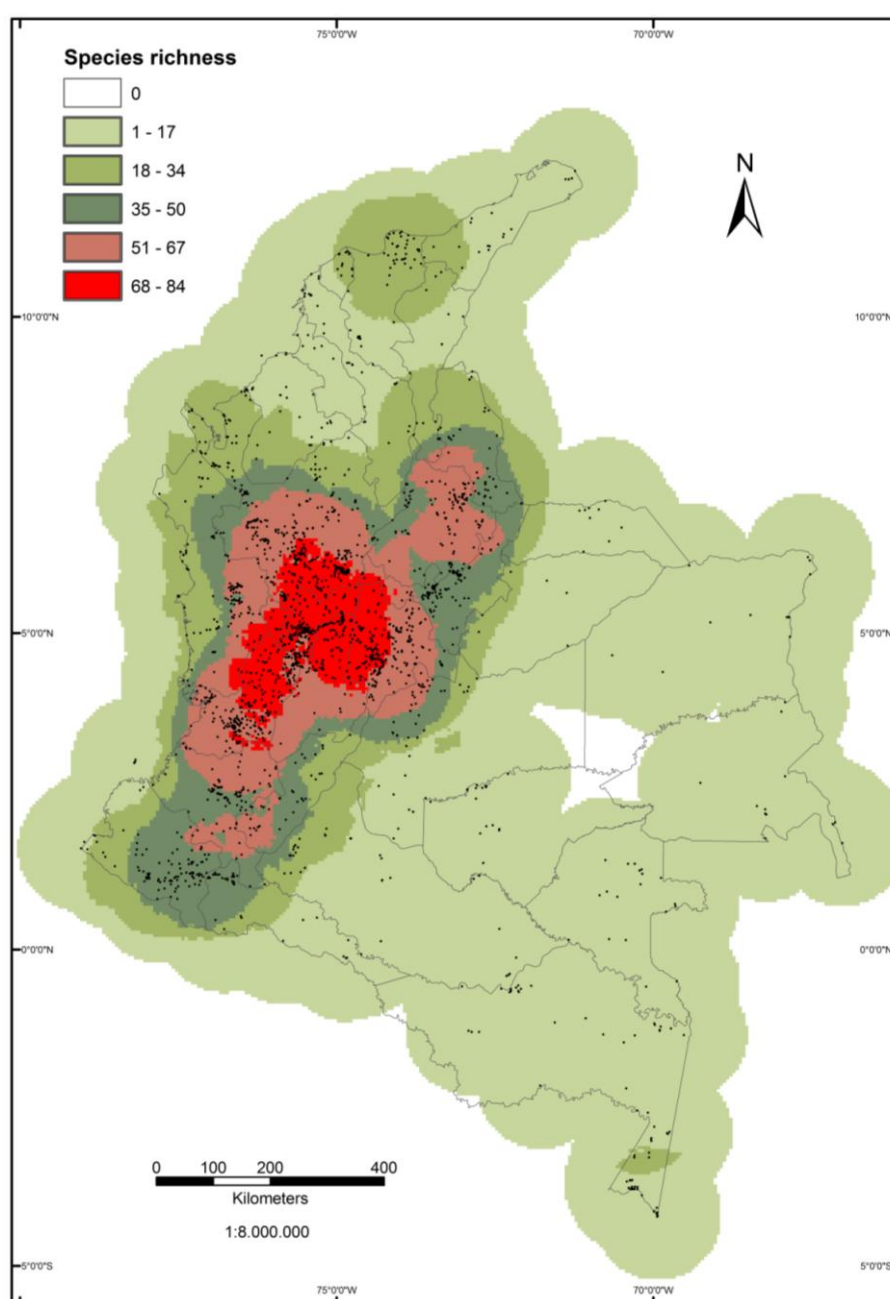


Table 1. Number of observations, species, rare and endemic *Passiflora* species by Colombian division (see Supplementary Figure 1).

<i>Biogeographic region/ department</i>	Area (km ²)	Nb. observ.	Nb. observ./ 1,000 km ²	Total Species	Total species/ 1,000 km ²	Total species/ Log. area	Observ./ species	Rare species	Endemic species
<u>Andean</u>									
Antioquia	62.869	783	12.45	68	1.08	14.171	11.51	28	6
Boyacá	23.012	145	6.30	36	1.56	7.502	4.03	14	1
Caldas	7.291	245	33.60	36	4.94	7.502	6.81	14	1
Cundinamarca	23.942	419	17.50	53	2.21	11.045	7.91	23	0
Huila	18.331	62	3.38	22	1.20	4.585	2.82	18	0
Quindío	1.943	150	77.20	38	19.56	7.919	3.95	25	0
Norte de Santander	22.007	79	3.59	36	1.64	7.502	2.19	25	0
Risaralda	3.592	68	18.93	24	6.68	5.002	2.83	20	0
Santander	30.537	207	6.78	48	1.57	10.003	4.31	31	3
Tolima	22.672	213	9.39	43	1.90	8.961	4.95	27	4
<u>Andean and Pacific</u>									
Cauca	30.985	161	5.20	42	1.36	8.753	3.83	24	1
Nariño	32.046	170	5.30	44	1.40	9.170	3.79	27	0
Valle del Cauca	21.195	420	19.82	56	2.69	11.670	7.38	28	1
<u>Pacific</u>									
Chocó	46.530	210	4.51	39	0.84	8.356	5.38	23	1
<u>Caribbean</u>									
Atlántico	3.319	18	5.42	7	2.11	1.459	2.57	5	0
Bolívar	26.469	33	1.25	15	0.57	3.126	2.20	9	1
Cesar	22.213	13	0.59	10	0.45	2.084	1.30	9	0
Córdoba	25.020	33	1.32	9	0.36	1.876	3.67	6	0
La Guajira	20.848	21	1.01	12	0.58	2.501	1.75	9	0
Magdalena	22.742	84	3.69	31	1.36	6.460	2.71	19	1
S. Andrés y Providencia	53	4	75.47	2	37.74	0.417	2.00	2	0
Sucre	10.917	6	0.55	3	0.27	0.625	2.00	2	0
<u>Orinoquian</u>									
Arauca	23.393	10	0.43	6	0.26	1.250	1.67	3	0
Casanare	44.428	4	0.09	4	0.09	0.834	1.00	4	0
Meta	85.286	85	1.00	24	0.28	4.930	3.56	14	0
Vichada	100.242	16	0.16	9	0.09	1.876	1.78	6	0
<u>Amazonian</u>									
Amazonas	109.665	85	0.75	16	0.15	3.175	5.31	14	0
Caquetá	91.725	46	0.50	17	0.20	3.425	2.71	13	0
Guainía	70.691	16	0.23	10	0.14	2.084	1.60	9	0
Guaviare	55.391	27	0.49	14	0.25	5.418	1.93	11	0
Putumayo	24.885	56	2.25	26	1.04	2.918	2.15	20	0
Vaupés	54.135	34	0.63	19	0.36	4.014	1.79	10	0

This variation in exploration of the Colombian territory is partly due to difficulty of access and/or social conflict. Data are poor and misleading in lowland forests, collections being limited along rivers in the Orinoquian and Amazonian and rare roads in the Pacific. Social conflict is the prevalent cause in the less explored Andean departments (Tolima, Santander, Norte de Santander and part of Boyacá) and in the Caribbean. Conversely, populated areas, particularly around main cities and their universities (Bogotá Medellín, Cali, central coffee growing zone), have been densely explored.

However, despite this sampling bias among departments, all observation parameters point to a concentration of *Passiflora* collecting in the central Andes and, within these departments, in the coffee growing zone, a situation explained by both easier access and higher species richness.

Indeed, departments of the Andean region present clearly higher species richness (Table 1). The only non-Andean department showing a comparable richness is Chocó. In the Andes, Antioquia has by far the highest number of species (68), followed by Valle del Cauca and Cundinamarca. Concerning rare species, Santander (northeast) occupies the first place, with 31 species, followed by Valle del Cauca and Antioquia (28), and Nariño and Tolima (27). Thus, there is little doubt that a more thorough exploration north of the Eastern Cordillera (Santander) and south of the Central Cordillera (Tolima) would discover more specimens per species and/or more species. This is even more obvious for the Amazonian, Orinoquian and Pacific departments, given their poor richness/surface and observation/species ratios.

When species richness is related to department size, the most diverse area corresponds to the central coffee growing zone, as this ratio appears to be several times higher in Caldas, Risaralda and Quindío than in the other Andean departments. A precise comparison with departments of other regions is only possible if the species are equally sampled, *i.e.*, if the number of observations per species is equivalent. This is the case for Chocó, Amazonas, and Córdoba, all of them showing a much lower diversity. The map of observed *Passiflora* diversity, as produced by the GIS analysis (Figure 2), confirms the importance of the Andes and the special contribution of the central coffee growing zone.

3.2. Altitudinal Distribution

Ancistrothyrsus and *Dilkea* reach altitudes of 800 m, mostly in the Amazon [12]. In contrast, *Passiflora* is distributed between sea level and 3,700 m. Figure 3 shows a trimodal relationship between elevation and species diversity for this genus, with maximal values below 500 m and in the ranges 1,000–1,500 and 2,500–3,000 m. The species number decreases sharply after 3,500 m until the limit of 4,000 m. To understand better this particular repartition, we have taken into account the complexity of *Passiflora*, gathering its Colombian species into five groups defined on morphological and molecular grounds, and resumed the analysis on these species subsets. This grouping is similar to the four subgenera proposed by Feuillet and MacDougal [22], except that Killip's subgenera *Rathea* and *Tacsonia* are maintained as a distinct fifth group, because of their elongated, red or pink flowers and reduced crown, specifically adapted to pollination by the sword-hummingbird. The four others correspond to (1) subgenus *Astrophea* (trees and shrubs), (2) subgenus *Decaloba sensu* Feuillet and McDougal (Killip's subgenera *Apodogyne*, *Decaloba*, *Murucuja*, *Porphyroanthanthus*, *Pseudomurucuja* and *Psilanthus*; mostly species with laminar nectaries, small apetalous flowers, small fruits, and pollinated by bees and small insects, (3) subgenus *Deidamioides sensu* Feuillet and

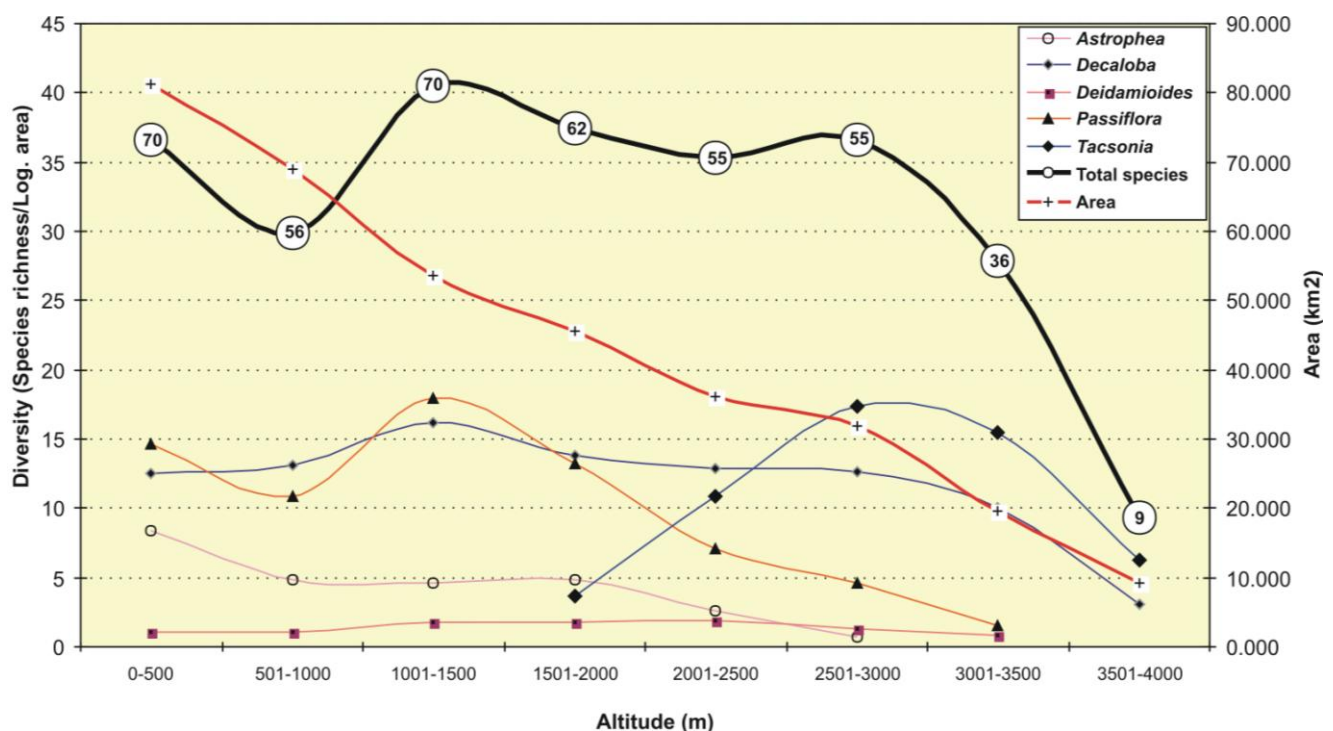
MacDougal (Killip's subgenera *Deidamioides* and *Tryphostemmatooides*), and (4) a *Passiflora*-like group gathering Killip's subgenera *Calopathanthus*, *Distephana*, *Dysosmia*, *Dysosmioides*, *Passiflora*, and *Manicata*, i.e., species with large flowers and fruits, pollinated by large bees or hummingbirds. The comparison between partial curves shows three distinct patterns in the adaptive potential of these groups. *Astropheia* and the *Passiflora*-like group present a bimodal distribution with a first cohort of species adapted to lowlands, below 500 m, with 16 and 28 species respectively, a second one adapted to medium elevations (1,000–2,000 m), and very few species at higher altitudes, with only one record of *P. lindeniana* near 2,700 m for subgenus *Astropheia*, and seven species for the *Passiflora*-like group. The opposite is true for the *Tacsonia* group, showing exclusive adaptation to cool highland climates, as it is typically concentrated above 2,500 m, with a peak at 2,500–3,000 m. Its fast radiation is clearly the cause of the third peak of the global curve. Another pattern is that of the *Decaloba* group, whose range of adaptation extends from 0 to more than 3,000 m, with no lowland peak and a slight peak around 1,000–1,500 m. The few species of the *Deidamioides* group also show a quite uniform distribution from 0 to 3,150 m, mostly in the Pacific and Andean regions. An interrogation remains concerning the first inflexion of the global curve and those of *Astropheia* and *Passiflora*-like groups in the range of 500–1,000 m. Interestingly, Jørgensen [56] reports a bimodal altitudinal distribution of vines in the Ecuadorian flora, with maximal diversity below 500 m and in the 2,000–3,000 m range, and a maximal diversity for *Passiflora* at 2,500–3,000 m. Taking latitudinal variation into account (*Tacsonia* species usually show a higher distribution in Ecuador, with a difference of 300–500 m), this corresponds very well with our observations in Colombia. Considering all Passifloraceae, the variation in number of Ecuadorian species with altitude [57] follows the same pattern as in Colombia. The Ecuadorian richness and high endemism level for *Tacsonia* is another strong point of convergence with the Colombian situation. According to Jørgensen [56], bimodality in altitudinal vine diversity distribution might be due to differential collecting intensity. However, there is no reason to expect a more continuous pattern. Indeed, Kessler [57] showed that there is no common elevational pattern for diversity, but a wide variety of independent patterns at all taxonomic levels, and that endemism appeared highest in the narrowest and most fragmented elevational belts: “The degree to which these influences become visible along the elevational gradient are determined by which combination of species is analyzed”. The same conclusion may be drawn within *Passiflora*, taking into account infrageneric divisions. This result restricts the potential use of *Passiflora* species as an indicator group to the Andean region, where they have developed most of their diversity.

3.3. Climatic Requirements

The PCA on the 19 climatic variables evidenced a first factor accounting for half of the variation (49%), strongly correlated with temperature variables (maximum, mean and minimal, but not seasonality in temperature), and a second one explaining 28 percent of the variation, related with precipitation in the whole year and in particular seasons (but again, not for their seasonality) (Table 2). Thus, in the principal plane (Figure 4), the first axis differentiates Andean species adapted to temperatures below 15 °C (i.e., >2,000 m), on the left side from those growing below 2,000 m, on the right side. Characteristically, these rightmost species originate from the Amazonian and Orinoquian. The second axis separates the species according to precipitation. Thus *P. arbelaezii*, *P. costaricensis*,

P. chocoensis, *P. lobata*, *P. occidentalis*, *P. pacifica*, *P. palenquensis* and *P. tica* show preferences for high precipitation, a predominant condition in the Pacific region, and all are predicted to exist sympatrically. At the other extreme of the second axis, are species adapted to lower precipitation levels, specifically to the marked dry season of the Caribbean, such as *P. bicornis*, *P. serrulata*, *P. guazumaefolia* and *P. pallida*. Amazonian species take intermediate positions. The species repartition in the principal plane consistently reflects the potential for climatic adaptation of the groups that were defined for the analysis of altitudinal distribution. Thus, the *Tacsonia* group shows adaptation to cool conditions, while subgenus *Astrophea* and the *Passiflora*-like group show higher potential in hot and mild climates. The *Decaloba* group shows a much broader adaptation range, explaining its quite constant presence across the different biogeographic regions.

Figure 3. Distribution of total species richness (within circles) and species relative diversity in relation to altitude in Colombia, for genus *Passiflora* and five infrageneric groups.



3.4. Areas of Distribution and Endemism

Distribution parameters (MaxD and CA₅₀) have been given for each native species in Ocampo *et al.* [12]. Figure 5 shows a good correspondence between them, and their comparison provides information on species dispersion. For instance, a high MaxD and relatively low CA₅₀ indicate low density, resulting from biological rarity and/or under-collection. The species with the widest distributions in Colombia (more than 1,100 km MaxD) are those showing a wide Neotropical distribution, such as the common *P. foetida*, *P. auriculata*, *P. quadrangularis*, *P. laurifolia*, *P. suberosa*, *P. serratodigitata*, *P. capsularis*, *P. rubra*, *P. misera*, and others of still considerable regional distribution, such as *P. vitifolia*, *P. coccinea*, *P. spinosa*, *P. nitida*, *P. subpeltata*, *P. maliformis*, *P. menispermifolia*, and *P. biflora*. Only *P. arborea* (Panamá to Ecuador) and

P. cumbalensis (Colombia to Peru) show a more restricted distribution. These high-MaxD species are concentrated at low to medium elevations, the only exception being *P. cumbalensis*. According to IUCN [58] criteria, they are not threatened (Least Concern category), except for *P. arborea* (Near Threatened; [12]). Between 200 and 1,100 km of MaxD, are species of regional importance, such as *P. mixta*, *P. ligularis*, and endemics with a relatively wide distribution, such as *P. sphaerocarpa* (96,244 km³), *P. lehmanni* (91,156 km³), *P. antioquiensis* and *P. mollis*. The latter displays a relatively high CA₅₀ in its group, as its 17 observations are quite scattered along the Cordillera Occidental. The position of *P. coriacea* in this group of medium dispersion is surprising, as it is found in all Neotropical countries. The 71 species with MaxD values below 225 km include 34 narrow endemics, 21 of which are exclusive to nine departments, particularly Antioquia (six species), Tolima (four) and Santander (three). The 15 others show similar MaxD and CA₅₀ but live across administrative divisions. Only four of these 36 narrow endemics are represented by 10 or more observations while 10 are only known from the type collection. The situation of 33 non-endemic species with a MaxD under 100 km must be examined in relation to their distribution in neighboring countries. *P. truxillensis*, shared with Venezuela, is a narrow endemic living around the border. The distribution of 14 species extends to farther places in neighboring countries, and 18 species present a wide distribution, extending to non-neighboring countries. For example, *P. tricuspis* is only reported once, in the Andean foothill, so it has a null MaxD, however its distribution extends south to Bolivia. Sixteen of these 33 species are adapted to lowland conditions, which suggests that their apparent rarity is in fact due to the poor collecting in the corresponding regions.

Figure 4. Distribution of *Passiflora* species centroids in the PCA principal plane for climatic variables.

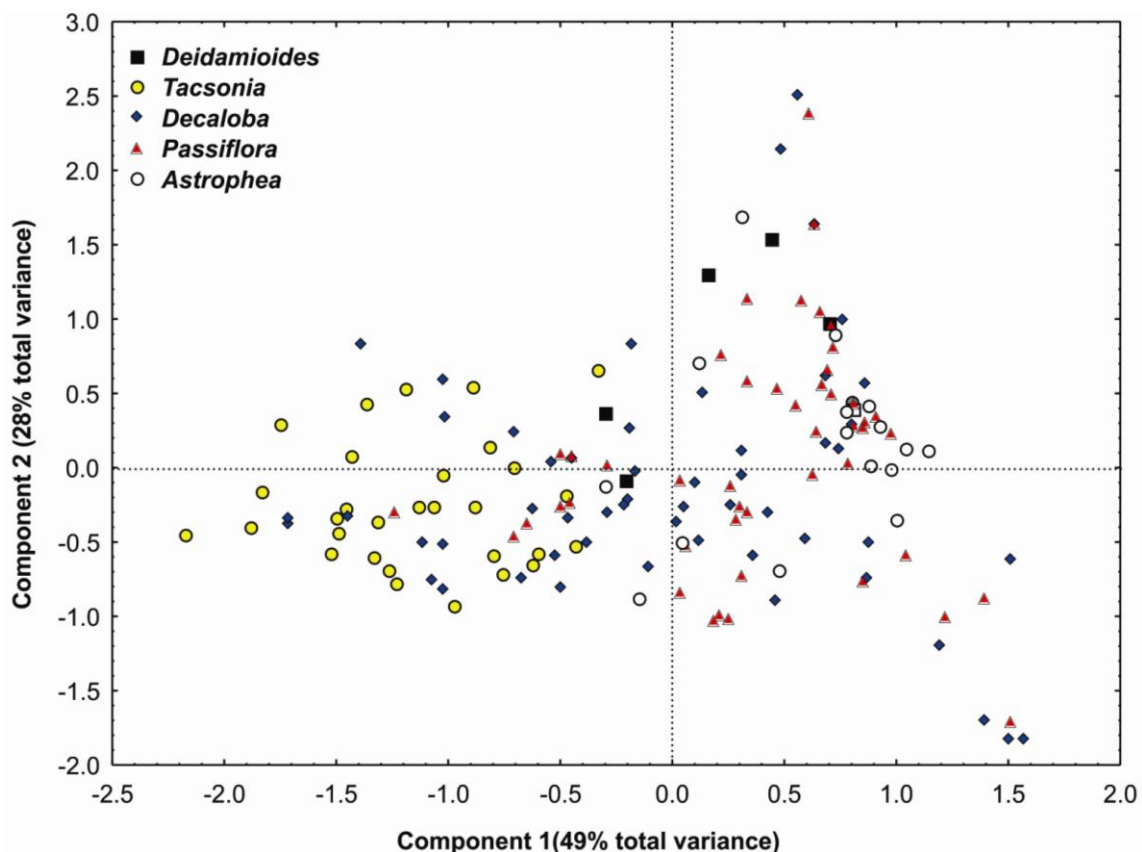
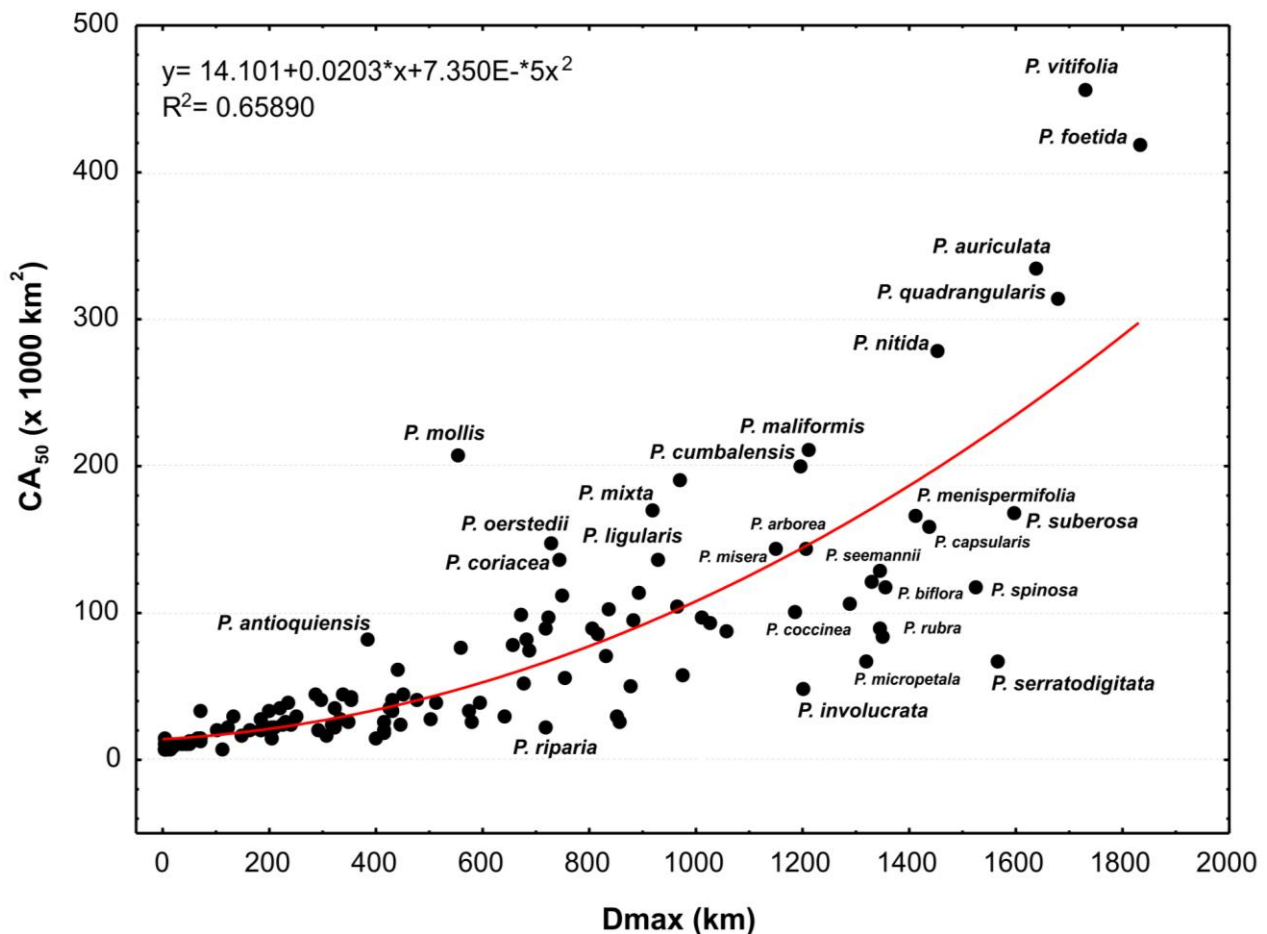


Figure 5. *Passiflora* species distributions in Colombia: circular area (CA₅₀) vs. maximum distance (MaxD).



3.5. Modeling Distributions and Species Assemblages

The predicted distributions of the 80 species with more than 10 observations cannot be presented here, but are available upon request. Figure 6 presents the potential distribution of richness obtained by assembling them. The areas of highest predicted richness (41 to 54 predicted sympatric species) are mostly located in the center of the country, on the slopes of the three cordilleras, between an elevation of 1,000 and 2,000 m. Despite collection intensity in these areas, the correspondence is not perfect between observed and modeled distribution. While the species-rich areas of Antioquia, Caldas, Quindío, Cundinamarca and eastern Boyacá and even the poorly explored but promising Santander, are well represented on the map (areas 2, 5, 3, 4 and 1 respectively), only very small richness spots are drawn for Valle del Cauca (area 7), and none for Cauca and southern Huila. Conversely, predicted richness spots 6, 8 and 9 (eastern Tolima-northern Huila-southern Cundinamarca, western Caquetá, Nariño) were not detected in the analysis of observed diversity, suggesting collecting gaps. The model predicts a poor representation of *Passiflora* in the lowlands of the Caribbean, Orinoquian and part of the Pacific, as well as in the Sierra Nevada de Santa Marta, an isolated mountain range on the Caribbean Coast, reputed for its high level of endemism. In both cases, this may be attributed to the poor exploration of these areas (low densities of observations) and poor representation of their species (few observations/per species), resulting in them not having sufficient observations to be used in the

predictive modeling. This bias can be corrected by further collecting in these regions. Alternatively, materials of Colombian species collected in border regions of neighboring countries, belonging to the same biogeographic entities (e.g., the Venezuelan Llanos for the Orinoquian, Costa Rican and Ecuadorian Pacific, Brazilian, Ecuadorian and Peruvian Upper Amazonian) might be used to refine these models and increase the number of observations per species under analysis.

Table 2. Factor loadings, eigenvalues and percentages of variance for the first four components, resulting from the PCA analysis on 19 bioclimatic parameters for the 3,923 collection points.

<i>Bioclim Parameters</i>	Principal components			
	1	2	3	4
Annual Mean Temperature	0.98	0.17	0.09	−0.03
Mean Monthly Temperature Range	0.08	−0.21	−0.16	−0.96
Isothermality	0.00	0.06	−0.95	−0.01
Temperature Seasonality	0.45	0.03	0.77	−0.18
Max, Temperature of Warmest Month	0.97	0.16	0.12	−0.12
Min, Temperature of Coldest Month	0.98	0.20	0.06	0.04
Temp, Annual Range	0.08	−0.22	0.37	−0.89
Mean Temperature of Wettest Quarter	0.98	0.17	0.09	−0.02
Mean Temperature of Driest Quarter	0.98	0.18	0.10	−0.04
Mean Temperature of Warmest Quarter	0.98	0.17	0.11	−0.04
Mean Temperature of Coldest Quarter	0.98	0.17	0.07	−0.03
Annual Precipitation	0.24	0.96	0.04	0.10
Precipitation of Wettest Month	0.29	0.91	0.15	0.10
Precipitation of Driest Month	0.09	0.91	−0.28	0.13
Precipitation Seasonality	0.23	−0.55	0.60	0.00
Precipitation of Wettest Quarter	0.28	0.91	0.17	0.09
Precipitation of Driest Quarter	0.09	0.93	−0.25	0.13
Precipitation of Warmest Quarter	0.10	0.87	−0.20	0.12
Precipitation of Coldest Quarter	0.29	0.89	0.05	0.02
Eigenvalue	9.24	5.35	1.74	1.50
Percentage of variance	48.71	28.28	9.13	7.95

3.6. Conservation of *Passiflora* species and their Habitat

The biodiversity hotspot concept not only considers diversity but also endemism. Analyzing the distributions of New Zealand ferns, Mexican gymnosperms, or European butterflies, Lehmann *et al.* [36], Contreras-Medina and Luna-Vega [59], and Werner and Buszko [60] observed a poor correlation between both parameters. At the genus level, Jaramillo [61] found some correspondence between them for *Piper* diversity in the Chocó region, however there was a negative correlation between phylogenetic diversity and the proportion of endemics. For *Passiflora* in Colombia, we could not establish rigorously their correspondence, as the analysis was not designed for rare species, however we compared their spatial repartition, distinguishing four categories among the 56 endemics: those with a relatively wide distribution (MaxD > 100 km, 19 species), the narrow endemics

(11 species), the rare endemics (three species), and the rare narrow endemics (23 species). Six of the 11 narrow endemics, seven of the 23 rare narrow endemics, and none of the three rare endemics live in one of the areas defined by our analysis. Indeed, seven endemics are adapted to lowlands, and two belong to the Sierra Nevada de Santa Marta, an area of endemism not sufficiently taken into account for reasons explained previously. In any case, of the 37 living Andean rare/narrow endemics, only 13 live in one of the “hotspots”. This proportion must be compared with more than 54 sympatric species out of 80 non-rare species whose distribution determined those hotspots. Thus, preserving these nine areas should have a less positive impact on the conservation of narrow endemics than on the general *Passiflora* diversity, which appears to limit the application of the biodiversity hotspot concept.

According to the analysis of complementarity for reserve selection, 52 sites of 25×25 km would suffice to represent all 162 native species throughout the country. The best five sites, in Caldas, Risaralda, Norte de Santander, southern Antioquia and Boyacá capture a total 64 species. In just seven sites, 50 percent of all species could be conserved, though many of the endemic/rare species are not captured in these sites.

Figure 6 also shows a general lack of correspondence between the estimated distribution of *Passiflora* diversity and that of protected areas in the Colombian Andes, concentrated around the summits, obviously targeting páramo ecosystems. Very few small protected areas harbor a high *Passiflora* diversity: the watershed forest reserves of Sierra del Peligro (Boyacá 16.5 km²), Ró Nare (Antioquia, 118.8 km²), Ró San Francisco, Cuchillas Peñas Blancas, and Cerro Quininí (Cundinamarca, 28.8, 16.3 and 18.0 km²). The Parque Nacional Farallones (Valle del Cauca) is the only reserve of national importance to protect part of a small *Passiflora* hotspot, on its eastern fringes. This poor coverage is not good news, neither for a genus including 71 percent threatened species, nor for the habitats where these species have developed numerous interactions with many other organisms.

Figure 7 shows a striking general superposition of areas of high *Passiflora* diversity on certain coffee growing zone ecotopes [62] whose conservation is of the utmost importance for Colombia. This is not surprising, as the corresponding elevation belts include or enclose those of major diversity. Clearly, efforts for the conservation of *Passiflora* habitats and genetic resources must be integrated in the more general management of the coffee growing zone environment at the landscape level.

Figure 6. Modeled distribution of Colombian *Passiflora* species diversity based on data from 80 species presenting more than 10 observations. Ellipses individualize high richness spots mentioned in the text. Distribution of protected areas in Colombia, showing poor correspondence with areas of high *Passiflora* diversity.

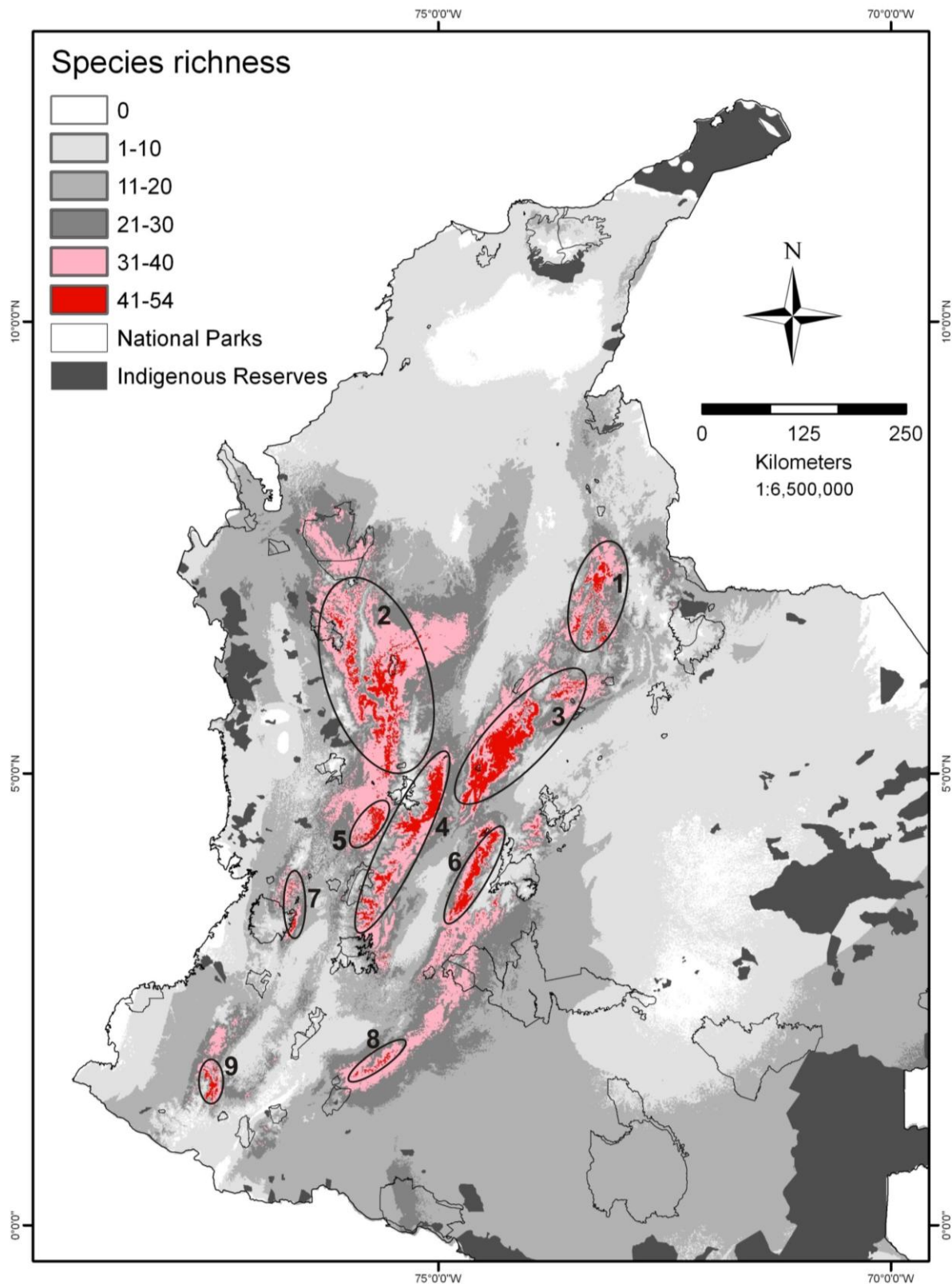
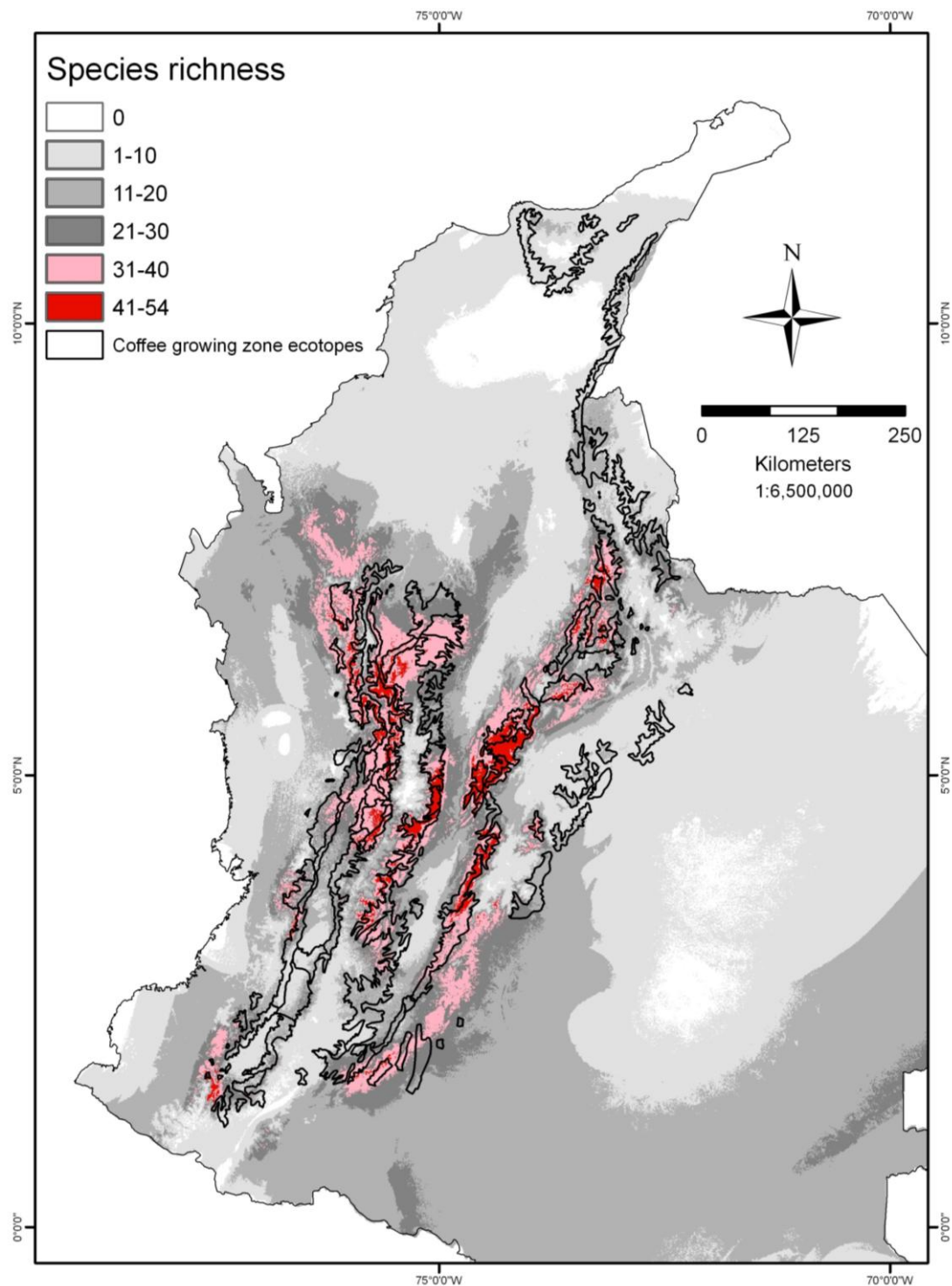


Figure 7. Correspondence between *Passiflora* species high richness spots and coffee growing zone ecotopes.



3.7. *Passiflora* as Indicators of Biodiversity

According to Pearson [34], an ideal indicator taxon should cumulate seven criteria: (i) a well-known and stable taxonomy, (ii) well-known natural history, (iii) readily surveyed and manipulated, (iv) higher taxa broadly distributed geographically and over a breadth of habitats, (v) lower taxa

specialized and sensitive to habitat changes, (vi) patterns of diversity reflected in other taxa, and (vii) potential economic importance. *Passiflora* clearly fills the fifth and seventh criteria, though we must keep in mind that several common species are indicators of more or less disturbed habitats. Concerning the fourth criterion, our analyses have repeatedly underlined that Colombian *Passiflora* species distribution is concentrated in the Andean region, so their use as indicators should be restricted to the corresponding elevation belts. Lianas growing in high trees are not always easily surveyed (third criterion), however their typical structures, showy flowers and interesting fruits make them easy to identify as a group, catching the attention of local populations and specialists, who can thus help localize the different species in particular places. The application of molecular techniques should produce important progress in the complex taxonomy of this group and further, in understanding its natural history. The sixth criterion is particularly important. The numerous interactions of *Passiflora* species with other organisms (surrounding vegetation, pollinators, and herbivores) constitute a first indication that their diversity is necessarily related to that of other ecosystem components. Another indication came from a preliminary study, where we found an excellent correspondence between the distributions of diversity of *Passiflora* and *Vasconcellea* (mountain papayas), another plant group whose diversification is clearly related to the rise of the Andes [38]. Similar results must be obtained with more plant taxa before considering unequivocally *Passiflora* as a reliable surrogate for floral diversity in Andean ecosystems. However, given the excellent correspondence between *Passiflora* diversity maps and coffee growing zone ecotope maps, we may already recommend them as useful indicators of habitat degradation or of restoration in this environmentally and economically very important region. They could complement other indicators working at the landscape level, such as birds, whereas insect diversity indicators work better at a smaller scale [63].

4. Conclusions

Collections of *Passiflora* have not been uniform as a consequence of difficulty of access and/or chronic social conflict in many areas. They have been much denser in the central coffee growing zone, Antioquia, Valle del Cauca and Cundinamarca. The southern and northeastern Andes, and the Caribbean have been little explored. For the lowland forests of the Pacific, the Orinoquian and the Amazonian, data are so poor that they are misleading. Despite the resulting sampling bias, collecting parameters clearly point to the concentration of observed *Passiflora* diversity in the Andes, and more particularly the central coffee growing zone.

The modeled species richness map allowed identifying nine richness spots of variable size, three of which, located in the southern and southeastern Andes of Colombia, correspond to collection gaps, as they were not detected in the analysis of observed diversity. Another probable collection gap, not detected by diversity modeling, corresponds to the Sierra Nevada de Santa Marta, an isolated mountain range with both high diversity and endemism. The proportion of endemics living in high richness spots is lower than the proportion of all species used for modeling, confirming the lack of relation between diversity concentration and endemism reported in other studies. If this is further substantiated in different groups of organisms, it could limit the application of the biodiversity hotspot concept, as the best-protected areas for diversity would not necessarily provide protection to a high proportion of narrow endemics.

Passiflora diversity is not conserved by the current network of Colombian protected areas. On the contrary, it is particularly concentrated on certain ecotopes of the coffee growing zone, *i.e.*, highly disturbed habitats, so any conservation effort must be integrated in local management strategies at the landscape level. *Passiflora* may provide an interesting indicator to evaluate the outcome of such efforts.

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