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Areas of endemism and distribution patterns for Neotropical *Piper* species (Piperaceae)

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ABSTRACT

Aim The study aimed to establish areas of endemism and distribution patterns for Neotropical species of the genus *Piper* in the Neotropical and Andean regions by means of parsimony analysis of endemism (PAE) and track-compatibility analysis.

Location The study area includes the Neotropical region and the Northern Andean region (Páramo-Punan subregion).

Methods We used distribution information from herbarium specimens and recent monographic revisions for 1152 species of *Piper* from the Neotropics. First, a PAE was attempted in order to delimit the areas of endemism. Second, we performed a track-compatibility analysis to establish distribution patterns for Neotropical species of *Piper*. Terminology for grouping *Piper* is based on recent phylogenetic analyses.

Results The PAE yielded 104 small endemic areas for the genus *Piper*, 80 of which are in the Caribbean, Amazonian and Paranensis subregions of the Neotropical region, and 24 in the Páramo-Punan subregion of the Andean region. Track-compatibility analysis revealed 26 generalized tracks, one in the Páramo-Punan subregion (Andean region), 19 in the Neotropical region, and six connecting the Andean and Neotropical regions. Both the generalized tracks and endemic areas indicate that distribution of *Piper* species is restricted to forest areas in the Andes, Amazonia, Chocó, Central America, the Guayana Shield and the Brazilian Atlantic coast.

Main conclusions *Piper* should not be considered an Andean-centred group as it represents two large species components with distributions centred in the Amazonian and Andean regions. Furthermore, areas of greater species richness and/or endemism are restricted to lowland habitats belonging to the Neotropical region. The distribution patterns of Neotropical species of *Piper* could be explained by recent events in the Neotropical region, as is the case for the track connecting Chocó and Central America, where most of the species rich groups of the genus are found. Two kinds of event could explain the biogeography of a large part of the *Piper* taxa with Andean–Amazonian distribution: pre-Andean and post-Andean events.

Keywords

Andean region, biogeography, distribution patterns, Neotropical region, parsimony analysis of endemism, *Piper* clades, track analysis.

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INTRODUCTION

Piper (Piperaceae) is a Pantropical group with nearly 2000 species, constituting an important element of montane and

lowland forests. It is one of the 10 most speciose genera of basal Angiosperms found in the tropics (Gentry & Dodson, 1987). Most species of *Piper* appear to be restricted to altitudes ranging from 0 to 2500 m, and few occur above 3000 m. According to

Gentry (1990), *Piper* reaches its highest diversity in the lowlands of the Neotropical region. Here, most species have restricted distributions, and it is quite common to find numerous related endemic taxa occurring in small areas (Callejas, 1986). There is also a relatively small number of species with wide distributions. The Andean slopes, the Central American lowlands and Central Amazonia have been considered as centres of high species richness for *Piper* in the Neotropics (Callejas, 1986; Soltis *et al.*, 1999; Jaramillo & Manos, 2001).

A recent phylogenetic analysis for the genus suggests three major clades in *Piper* (Jaramillo & Manos, 2001), representing three large geographical regions: America (1300 sp.), Asia (600 sp.) and the South Pacific (100 sp.). Recent updates in *Piper* taxonomy and phylogeny, and the fact that the genus *Piper* in the Neotropics exhibits a wide distribution throughout most of the region, allow a new analysis of the group with regard to the history of the biota that shaped the Neotropical region.

Studies on the global distribution of *Piper* and its relationship to other genera in the Piperaceae were first conducted by Miquel (1844). Later, Trelease (1930) briefly summarized the geography of American pipers and indicated the distribution and abundance of major groups of the genus and related genera. He concluded that the origin of Piperaceae is rather obscure and that, according to fossil data, the group might have its origins in the Quaternary period. Raven & Axelrod (1974) suggested a Laurasian origin for the group, while Gentry (1982) and Graham (1995) proposed a Gondwanan origin, emphasizing that the genus was already established in South America by the Cretaceous period and extended into Central America via Panama. Callejas (1986), in his taxonomic revision of the subgenus *Ottonia*, analysed the distribution of the entire group and showed that *Ottonia* distribution patterns were related to 'Pleistocene refugia and isolated dispersal events'. Recently, a phylogenetic analysis by Jaramillo & Manos (2001) suggested that the presence of the genus in the Southern Hemisphere was a result of vicariance rather than dispersal.

The distribution patterns of *Piper* have not been studied in detail due to inadequate and often scarce sampling of some areas (e.g. Northern Andean region of Colombia, southern Guayana Shield, eastern Colombian Amazon, southern Bolivian Amazon) and to poor species descriptions. Therefore it was not known how each clade was distributed, and what the most important areas were in terms of endemism and for species richness.

The first step in a modern biogeographical study is delimitation of the study units or comparison areas (Nelson & Platnick, 1981). Morrone (1994) proposed that parsimony analysis of endemism (PAE) (Rosen, 1988) may be used to identify areas of endemism. Using Morrone's (1994) grid-based PAE approach, the congruence between distribution patterns of many different taxa can be optimized by employing quadrants of arbitrary size as operative units in relation to the prospective degree of resolution.

Our viewpoint is that the results obtained by using grid-based PAE do not allow us to distinguish the origin of spatial congruence among taxa, that is, these results fail to uncover the

extent of both historical and ecological influences (Posadas & Miranda-Esquivel, 1999; Brooks & Van Veller, 2003). When using PAE, we focus strictly on the demarcation of endemic areas, which accounts for the lack of an 'area cladogram' (which would assume historical or ecological relationships based on the distribution of the *Piper* species) in our results. An area of endemism is therefore defined as the area where the distribution patterns of at least two taxa overlap. These taxa may or may not be related phylogenetically.

Due to the large number of *Piper* species, and the lack of taxonomic resolution for some groups to date, it has been impossible to carry out a reliable and detailed analysis of current *Piper* distributions in order to postulate a hypothesis for their current distribution pattern in the Neotropical region. We used a panbiogeographical analysis as a first step to find distribution patterns that allow primary biogeographical homologies to be established, recognizing groups of organisms with currently disjunct distributions. These particular distributions might be part of one biota now fragmented by events of climatic or tectonic change (Craw, 1988; Craw *et al.*, 1999; Morrone, 2001).

Several authors have already recognized two stages in the proposition of homologies in systematics (Nelson, 1994), denominated 'primary' and 'secondary' homologies (de Pinna, 1991). Primary homology refers to the stage of hypothesis generation; secondary homology to the stage of evaluation. A primary homology statement is conjectural, reflecting an expectation of correspondence between parts of different organisms (in morphological characteristics, topological correspondence is the basic criterion of primary homology). Primary biogeographical homology refers to a common biogeographical history, which means that different taxa are spatio-temporally integrated into a single biota (Craw, 1988; Craw *et al.*, 1999; Morrone, 2001).

A panbiogeographical analysis allows comparison of individual tracks in order to detect generalized tracks (Craw *et al.*, 1999), and emphasizes the importance of spatial information, locality and position in life history as relevant factors for any evolutionary analysis (Craw, 1988; Craw *et al.*, 1999; Morrone, 2001). To improve our panbiogeographical analysis, we compiled a database of the largest available number of distribution records for the genus, covering 90% of Neotropical *Piper* species for which the taxonomy was carefully checked.

We used PAE and the panbiogeographical approach as two independent methods with two different purposes. The results of these analyses are complementary when analysing the distributions of Neotropical *Piper*, as both represent tools to postulate a hypothesis of primary biogeographical homology (Morrone, 2001); nonetheless, each employs a distinct method of data analysis.

MATERIALS AND METHODS

Study area

In this study we employed the biogeographical province scheme of Morrone (2002), based on the analysis of distribution

patterns of different taxa (fauna and flora). This allowed us to apply the primary biogeographical homology concept when establishing 'natural biogeographical areas', defined as areas supported by shared endemic species (Morrone, 2002). The study areas used in the analysis were the Neotropical region and the Páramo-Punan subregion belonging to the Andean region. The Neotropical region extends into the tropics from the north of Mexico to the centre of Argentina, and belongs to the Holotropical Kingdom. The Neotropical region is made up of the Caribbean, Amazonian, Chococoan and Paraná subregions. The Andean region belongs to the Austral Kingdom, and includes the Páramo-Punan, Central Chilean, Subantarctic and Patagonian subregions. The Andean area, where *Piper* is present, is part of the Páramo-Punan subregion, which extends from the Northern Cordilleras of Venezuela to Colombia, Ecuador and along the Puna of Perú and Bolivia.

Taxa

Despite the lack of a formal classification scheme for *Piper*, we opted to follow the cladistic analysis of Jaramillo & Manos (2001). In this study, a single unrooted parsimony network suggested that taxa representing major geographical areas could potentially form three monophyletic groups: Asia, the South Pacific and the Neotropics. Most clade names recognized by Jaramillo & Manos (2001) correspond to formal groups at generic or subgeneric levels previously identified by other authors, particularly Miquel (1844) and de Candolle (1923). Our sampling is more extensive than that of Jaramillo & Manos, as we include groupings not covered by them. Thus we include species belonging to *Peltobryon* (a clade of the *Schilleria* group); *Isophyllon* (a group first recognized by Miquel and belonging to *Schilleria*); and the *Carpunya* group. Following Jaramillo & Callejas (2004), the *Trianaepiper* group was split into three distinct clades, named temporarily as *Trianaepiper-trianae*, *Trianaepiper-filistylum* and *Trianaepiper-confertinodum* groups.

We mapped the distributions of 1152 species of *Piper*. Our primary sources came from the collection housed at the Herbario Universidad de Antioquia, which has the most complete holdings of Neotropical pipers, as well as specimens stored at the Botanical Institute of the Aarhus University (Denmark); Herbario Nacional Colombiano (Colombia); Herbario del Instituto Nacional de Biodiversidad (Costa Rica); Herbarium of the University of Texas (USA); Missouri Botanical Garden (USA); National Herbarium of the Netherlands (Netherlands); New York Botanical Garden (USA); and the United States National Herbarium (USA). As secondary sources, we employed the latest and most up-to-date taxonomic treatments of *Piper* for specific geographical areas (Yuncker, 1972, 1973; Steyermark, 1984; Callejas, 1986, 1999; Steyermark & Callejas, 2003) and revisions of specific clades (Burger, 1971; Callejas, 1986; Bornstein, 1989; Tebbs, 1993).

Sampling of *Piper* in the Neotropics has not been uniform across the region (many species are only found in single locations). We attempted to assemble the most complete data

base possible for Neotropical species, including almost 90% of all Neotropical species and 7500 records for the genus.

Parsimony analysis of endemism

Once taxa had been chosen and their taxonomy carefully checked, we proceeded to perform a PAE analysis (Morrone, 1994) using a sectoral search as well as a tree-drifting/tree-fusing strategy. For this analysis, we chose the relatively coarse 1° latitude, 1° longitude grid size, partly for the sake of data manipulation and partly to reduce the effects of sampling artefacts such as mapping errors and unsampled grids in sparsely inhabited areas (Crisp *et al.*, 2001; Morrone & Escalante, 2002). It is known that patterns of endemism are scale-dependent (Major, 1988; Anderson, 1994; Ruggiero & Lawton, 1998; Vilkenkin & Chikatunov, 1998; Crisp *et al.*, 2001). For this reason, it is important to clarify that the size of the square is totally operational. The size used in this study was chosen as a compromise between resolution and computational effort. Therefore an analysis using a different scale, with a higher number of records placed in a larger number of areas, could incorporate more functional square sizes than those used here.

All quadrants were numbered and a presence/absence matrix was constructed. A hypothetical taxon with 0 for all species (all species absent in that grid) was added to root the resulting tree (Morrone, 1994; Morrone & Crisci, 1995; Posadas & Miranda-Esquivel, 1999). A parsimony analysis was carried out using TNT ver. 1.0 (Goloboff *et al.*, 2004).

The trees were examined with WINCLADA 1.0 (Nixon, 2002). Groups of quadrants sharing at least two species were considered to represent an area of endemism (Platnick, 1991; Morrone, 1994). As the results consisted of multiple equally parsimonious solutions, these were summarized using strict consensus. Subsequently, the endemic areas were delineated and mapped.

Track analysis

The matrix used in the PAE analysis was subjected to a compatibility analysis (Craw, 1988, 1989) applying the same search as used for PAE. The cliques were examined using WINCLADA 1.0 (Nixon, 2002). The generalized tracks were detected and mapped according to the species distributions. In the resulting cliques, we searched for groups of species that supported particular generalized tracks. Each supporting species was revised to determine the group to which it belonged according to those proposed by de Candolle (1923), Callejas (1986), Bornstein (1989) and Jaramillo & Manos (2001).

RESULTS

A total of 661 quadrants out of 2000 were occupied by two or more species. *Piper* is found in almost all available habitats within its range. In the Neotropical region, two subregions contained areas with the highest species richness:

the Caribbean subregion in the provinces of Western Panamanian Isthmus (408 spp.), Chocó (378 spp.) and Eastern Central America (87 spp.); and the Amazonian subregion in the provinces of Ucayali (116 spp.) and Napo (69 spp.). In the Andean Region, the subregion with the highest number of species was the Páramo Punan in the provinces of Norandean Páramo and Puna (291 and 115 species, respectively).

The PAE analysis revealed 104 endemic areas (Fig. 1). It is interesting to observe that, since most of the species analysed exhibited a distribution restricted to specific areas such as Central America, the Andes and the Amazon, generalized tracks of great length were not established in the study area. A total of 24 (23.07%) areas correspond to the Andean region, distributed in the Páramo-Punan subregion: 16 areas in the provinces of Norandean Páramo and eight in Puna. In contrast, there are 80 (76.91%) areas corresponding to the Neotropical region: 48 distributed in the Caribbean, 28 in the Amazon and four in the Paranaense subregion (Table 1).

Eighty per cent of the endemic areas and of the generalized tracks are present in the subregions with the highest number of species per grid, while the remaining 20% of the endemic areas and tracks occur in zones with a small number of species (the Antilles, the Guayana shield and Manaus).

Twenty-six generalized tracks were obtained in the panbiogeographical analysis (Fig. 2). One generalized track was located in the Andean region, and 19 were restricted to the Neotropical region. Of these tracks, six were distributed in the Caribbean, 12 in the Amazon and one in the Paraná subregions. Finally, we found six generalized tracks that connect the Andean and Neotropical regions (Table 2).

Of the 1152 species examined, only 327 were informative. These species belong to the clades *Churumayu* (five spp.), *Enckea* (five spp.), *Isophyllon* (15 spp.), *Macrostachys* (45 spp.), *Ottonia* (five spp.), *Peltobryon* (63 spp.), *Radula* (127 spp.) and *Schilleria* (18 spp.). Three clades without formal ranking, and previously placed in the non-natural genus *Trianaeopiper* (polyphyletic according to Jaramillo & Manos, 2001; Jaramillo & Callejas, 2004), were informative and supported generalized tracks.

DISCUSSION

Endemic areas

Caribbean subregion, Magdalena and Chocó provinces

Our data indicate that *Piper* displays the highest number of species in the Neotropical region. This region, which presents 80 endemic areas as revealed by the endemism analysis, accounts for 77.44% of the endemic taxa. The Andean region exhibits a comparatively low level of endemism, with only 24 endemic areas, which represent 22.56% of the endemic species (Table 1).

In the province of Magdalena, only one area of endemism was detected, in the Sierra Nevada de Santa Marta (Fig. 1), a massif located in the north of Colombia and isolated from the Andean region (Harrington, 1962; Alemán & Ramos, 2000).

This area is home to nearly 50 species of *Piper* (Trelease & Yuncker, 1950), four of them endemic and the remainder mostly widespread taxa that are distributed in the Caribbean region, the Northern Andes or the Antilles.

The endemic areas with the highest number of known *Piper* species in the Neotropics were encountered in the very humid forests of the Chocó and Costa Rica provinces. *Piper* is not the only group that exhibits such a pattern; it is also seen in the family Ericaceae (Luteyn, 2002) and in the genus *Anthurium* (Araceae) (Croat, 1992). These results are congruent with the analysis of Marquis (2004), who found a high correlation between the number of species of *Piper* and annual precipitation in some Central American areas. We agree with the overall conclusion of Gentry (1982) that forested areas in lowland regions of the Neotropics with high precipitation hold the largest number of endemics for herbaceous genera. Although the Colombian Pacific slope area of the Chocó province is characterized by high rainfall, this region should not be considered an independent unit distinct from the neighbouring forests (Croizat, 1976; Gentry, 1982). Our track analysis supports the idea that the Chocó 'province' is rather a confluence area among different biogeographical elements, showing marked affinities with the lowland forests of Central America and the western slopes of the Western Cordillera.

It should be clarified that the western slopes of the Western Cordillera (up to 1000 m altitude) are not included in the Andean region; instead, they are an extension of the lowland biota of the Chocó and Cauca provinces. A mixed zone was delimited among these biotas, with species groups that occur within an altitudinal gradient between 0 and 1000 m.

Provinces of Chiapas, Eastern Central America and Western Panama

In the Neotropical region, the Caribbean subregion exhibits a great number of species of *Piper* and high levels of endemism for the Central American provinces of Chiapas, Eastern Central America (Costa Rica and Nicaragua) and the Western Panamanian Isthmus. With respect to the province of the Western Panamanian Isthmus, the lowland areas of Limón in Costa Rica and the Zelaya department of Nicaragua are well known for their high levels of endemism. Such differences are unlikely to be missed due to lack of sampling, since both provinces include areas with a long, continuous history of intensive collecting (Croat, 1997; Hammel *et al.*, 2003). The province of Western Panama shows a large number of species, but low endemism due to the fact that many species in the province cross over to the neighbouring areas of northern Chocó, or extend into southern Costa Rica. Despite the fact that Chiapas is an endemic area for *Piper*, it presents a small number of species. Some 80% of the endemic species belong to subgenus *Arctotonia*, a clade of *Piper* almost entirely restricted to Mesoamerica (Bornstein, 1989). This province has been previously recognized as an endemic area for various plant and animal taxa (Croizat, 1976; Halffter, 1978, 1987; Morrone, 1999; Luna-Vega *et al.*, 2001).

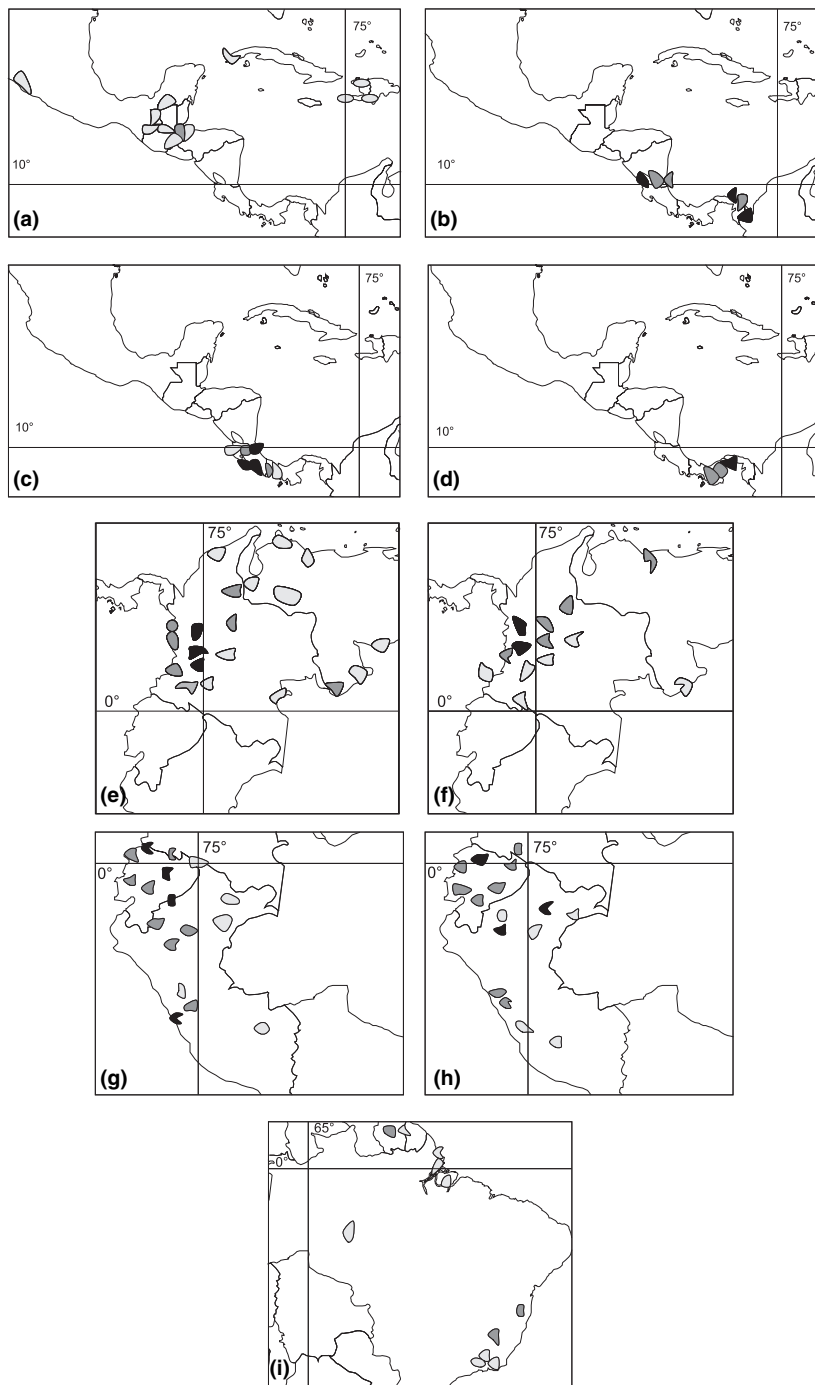


Figure 1 Endemic areas (104) delimited by parsimony analysis of endemicity (PAE) for the genus *Piper* in the Neotropics. The analysis using PAE is based on distribution data extracted from 7500 records (1152 species). Of the total species examined, 718 were endemic. The levels of saturation (increasing darkness) follow the scale: (2–10 endemic species), (10–20 endemic species) and (21–30 endemic species). (a–d) Endemism areas for Central America and the Caribbean, with the areas exhibiting the highest number of endemics located in: (a) Guatemala and north-eastern Nicaragua (prov. Chiapas); (b) north-eastern Panamá and Darien (prov. Chocó); (c) western Costa Rica (prov. Western Panamanian isthmus); (d) northern Panamá (prov. Eastern-Central America). (e–h) Endemism areas for South America, with areas exhibiting the highest number of endemics, located in: (e,f) north-western Colombia (prov. Cauca); (g) north-western Ecuador (prov. Chocó); north-eastern Ecuador (prov. Napo); southern Perú (prov. Puna); (h) northern Ecuador (prov. Norandean páramo) and north-eastern Perú (prov. Napo). (i) Endemism areas for western South America in Guianas (prov. humid Guyana) and south-eastern Brazil (prov. Brazilian Atlantic forest). Biogeographical scheme for Latin America and the Caribbean follows Morrone (2002).

Provinces of Antilles, Guayana Shield and the Atlantic forest of Brazil

Despite the low species count (Table 1) for the provinces of Chiapas, the Mexican Pacific coast, the Venezuelan coast, Cuba, arid Ecuador, the Mexican Gulf, Hispaniola, Magdalena, western Ecuador, Amapá, Imeri, Roraima, Ucayali, Antilles, Guayana Shield and the Atlantic forest of Brazil, the species here make up 15% of all endemic species. This figure indicates that areas can still have a high proportion of flora with restricted distribution ranges, despite species richness not being high (Crisp *et al.*, 2001).

There are relatively few species of *Piper* with Guayanian distribution, but three endemic areas were detected, two in Venezuela (in the states of Amazonas and Bolivar) and the third in Saramacca (Surinam). This is congruent with previous observations that such areas tend to have high values of endemism but low species richness (Steyermark, 1966, 1974, 1979, 1984; Maguire, 1970, 1979; Huber, 1988, 1990, 1992; Brako & Zarucchi, 1993; Cortés, 1996). It is likely that the extreme habitats often found in such areas, including rocky outcrops, dry forests, savannas, etc., tend to exclude most species of *Piper* which, in general,

Table 1 Summary of the results obtained by PAE

Region	Subregion	Province	Number of endemic areas	Percentage of endemic areas for subregion	Number of species	Number of species for subregion	Percentage of endemic species for subregion
Andean Region	Páramo Punan	Norandean Páramo	16	23.07	75	162	22.56
		Puna	8		87		
Neotropical Region	Caribbean	Cauca	4	46.15	32	381	53.08
		Chiapas	2		10		
		Chocó	13		72		
		Mexican Pacific Coast	3		13		
		Venezuelan Coast	2		6		
		Cuba	1		2		
		Arid Ecuador	2		5		
		Mexican Gulf	2		8		
		Hispaniola	3		13		
		Magdalena	2		7		
		Western Ecuador	1		2		
		Western Panamanian Isthmus	5		52		
		Eastern Central America	8		159		
	Amazonian	Amapá	1	26.92	2	160	22.28
		Guyana	4		11		
		Humid Guyana	2		5		
		Imeri	3		8		
		Madeira	1		2		
		Napo	15		127		
		Roraima	1		2		
Paraná	Ucayali	1		3			
	Brazilian Atlantic Forest	3	3.84	10	15	2.08	
	Parana Forest	1		5			

Endemic areas for the genus *Piper* in the Neotropics obtained by parsimony analysis of endemism. Areas are listed according to the biogeographical scheme for Latin America and the Caribbean proposed by Morrone (2002).

display a preference for humid and shady places (Marquis, 2004).

The Atlantic forest of Brazil, a belt of tropical rain forests along the coast of Brazil, has few species of *Piper*, comparable to the Antilles and the Guyana Shield, which is interesting if one considers the type of vegetation found in that area. It is well known that the area is home to a biota with a large endemic component, exhibiting close relationships with the Amazonian biota (Amorim, 2001; da Silva *et al.*, 2004). In the case of *Piper*, the Atlantic forests hold a lower number of taxa than the Amazon, but the Atlantic forests include all Neotropical clades of *Piper* (except *Arctotonia* and *Trianaeopiper*). For this reason, the Atlantic forest has a high phylogenetic information content.

Páramo-Punan Subregion, Norandean Páramo and Puna provinces

In the Andean region, the PAE analysis detected 24 endemic areas, 16 in the Páramo province and eight in the Puna province. In the Páramo province, six endemic areas are restricted to the North-eastern Cordillera of Colombia and to the neighbouring Andean zone in Venezuela, including two areas along the slopes of the Eastern Cordillera towards the Magdalena Valley. The latter is an area with a high number of species in many groups of angiosperms, and close affinities

with Amazonia (Croizat, 1976; Gentry, 1982, 1990; Gentry & Dodson, 1987). Two endemic areas were found, one in the Northern Central Cordillera in Antioquia, the other in the Central Andean region of the neighbouring departments of Tolima, Quindío and Caldas. Another two areas were located in the south of Colombia in the Central-Eastern Cordillera massif. In Ecuador the endemic areas are restricted to the Northern Andean zone, one close to the Colombian Massif in the state of Carchi, and the other two located on the eastern slopes, facing the Amazon, in the departments of Chimborazo and Morona-Santiago.

The eight endemic areas found in the Puna province are all restricted to Peru (provinces of Junín and Huánuco). They show 20 or more species per grid, richness values that are also evident for some plant groups in this province (Brako & Zarucchi, 1993).

The distribution patterns of *Piper* in the provinces of Norandean Páramo and Puna are congruent with the proposal of a transition area (Ruggiero & Ezcurra, 2003), which has been labelled by Morrone (2004) as 'The South American Transition Zone'. In these areas it was possible to identify distribution patterns in which some Neotropical *Piper* species presented distributions outside the Neotropical region. Similarly, some species of Andean *Piper* showed an extended distribution outside the limits demarcated by the Cordillera, as is the case of the western slopes of the Western Cordillera in

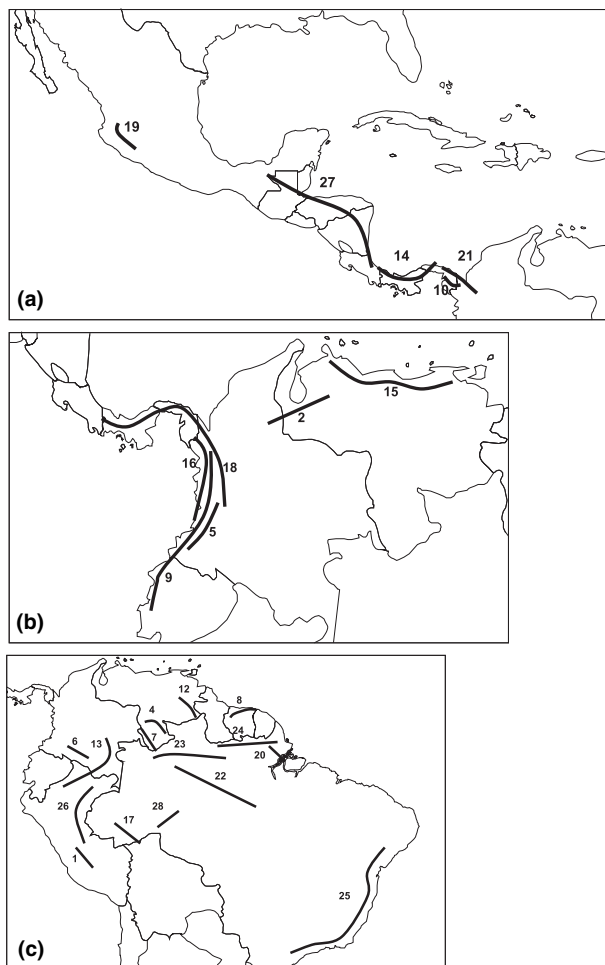


Figure 2 Generalized tracks for the Neotropical species of the genus *Piper*. Twenty-six tracks obtained in the panbiogeographical analysis are shown (a–c). One single track (track 1) is located in the Andean region; 19 tracks in the neotropical region (tracks 4, 6–8, 10, 12–15, 17, 19–25, 27, 28); and six tracks in the Andean-Neotropical regions (2, 5, 9, 16, 18, 26) (tracks connecting both regions). Biogeographical provinces scheme follows Morrone (2002).

Colombia and Ecuador. More than one static line among the Neotropical and Andean regions or ‘Subtropical Line’ (Rapport, 1968), the transition zone, could be an area where historical and ecological processes have allowed the evolution of a mixed biota. As the ‘Subtropical Line’ could vary according to the taxa analysed, we follow Morrone’s (2004) proposal of the recognition of a wider transition area.

Generalized tracks

The distribution patterns of *Piper* were congruent with several panbiogeographical analyses of the Neotropical region (Cortés & Franco, 1997; Contreras-Medina & Eliosa-Leon, 2001; Luna-Vega *et al.*, 2001). For instance, studies by Franco & Berg (1997) for the genus *Cecropia* revealed, among other aspects, generalized tracks in the slopes of the Northern Andean region of Colombia, Central America and the Atlantic forests of

south-eastern Brazil, all of which were also detected in our analysis. The coincidence in the distribution patterns established by the generalized tracks for these two genera could indicate that the current distributions of the species of these genera were influenced by shared vicariant events. This can be seen readily in areas such as southern Central America (Panama and Costa Rica), the slopes of the Andean region (Colombia, Ecuador, and Peru), the Guayana Shield (Guianas), Chocó (Colombia, Ecuador), and the Atlantic forest of Brazil (Rio de Janeiro and São Paulo), which in our analysis were areas of distributional congruence and high endemism.

Moreover, there seems to be a close agreement between our analysis and those using plants and animals to determine the nature of the Mexican Biota (Halffter, 1964; Rzedowski, 1978, 1991; Fa & Morales, 1998; Contreras-Medina & Eliosa-Leon, 2001; Morrone & Marquez, 2003). Our results include a generalized track that relates Central and South America, crossing the provinces of the Mexican Pacific Coast, the Mexican Gulf, the eastern region of Central America, the western Panamanian Isthmus, Magdalena, Cauca and Norendeán Páramo. This track underlies a pattern first proposed by Gentry (1982), which connected the floras of the lowland forests of Central America with those of northern South America.

The Neotropical region hosts the largest concentration of generalized tracks, corresponding to 73.07% of the total (Table 2). The presence of four tracks along the Chocó province is notable, suggesting a mixture of elements representing an apparently uniform biota (Fig. 2). One track extends from Darien province in Panama along the northern Pacific coast of Chocó, which includes sister taxa occurring on both sides of Darién Province and restricted to northern Colombia. A second track goes from the north-western slopes of the Western Cordillera in Colombia (Antioquia), to southern Calima, on the southern Pacific coast of the Chocó lowlands. This track includes taxa of *Piper* with restricted distributions in Chocó and affinities with Andean elements in northern Colombia. A third track, from southern Calima to the western slopes of the Western Cordillera, is supported by several endemic taxa with sister species in northern Chocó or neighbouring Andean slopes of the Western Cordillera in Colombia. Finally, there is a fourth track, extending from the northern Pacific coast of Chocó in Colombia to the province of Pichincha in Ecuador, which comprises a widespread presence of all *Piper* species with strong affinities for the Andean slopes of Ecuador and Colombia. Thus, based on the sampling of *Piper* for Chocó, we believe that the area should be considered not as a single unit, but rather as a compound biota with distinctive elements between north and south, bounded at Calima along the Pacific coast. Croat (1992) has detected similar discontinuous distributions in Chocó for *Anthurium* (Araceae).

The generalized tracks found in this study provide evidence for the composite nature of the Andean biota (Crisci *et al.*, 1991; Amorim & Tozoni, 1994; Katinas *et al.*, 1999). Three types of biogeographical pattern involving the Andean region are seen in Neotropical pipers. Firstly, there are areas in the

Table 2 Generalized tracks with their respective supporting species

Region	Subregion	Province	Number of generalized tracks for subregion	Track code	Species support	
Andean	Páramo Punan	Puna	1	1	<i>Piper carrapanum</i> , <i>P. brevestrigillosum</i> , <i>P. brevipedunculatum</i> , <i>P. cispontinum</i> , <i>P. edurumglaberimicaule</i> , <i>P. huantanum</i> , <i>P. perenense</i> , <i>P. planipes</i> , <i>P. pontis</i> , <i>P. scabricaule</i> , <i>P. serotinum</i> , <i>P. sidipilum</i> , <i>P. tardum</i>	
Neotropical	Caribbean	Mexican Pacific Coast	6	19	<i>Piper brachypus</i> , <i>P. cihuatlanense</i> , <i>P. mcvaughii</i>	
		Venezuelan Coast		15	<i>Piper schlimii</i> , <i>P. cumbotianum</i> , <i>P. nobile</i> , <i>P. marturense</i> , <i>P. sierra-aroense</i>	
		Eastern Central America		10	<i>Piper canaliculum</i> , <i>P. acutissimum</i> , <i>P. alstonii</i> , <i>P. amphibium</i> , <i>P. barbinerve</i> , <i>P. breve</i> , <i>P. cativalense</i> , <i>P. chagresianum</i> , <i>P. culebranum</i> , <i>P. diazanum</i> , <i>P. frijolesanum-grandifolium</i> , <i>P. gatunense</i> , <i>P. gonocarpum</i> , <i>P. humorigaudens</i> , <i>P. luciguadens</i> , <i>P. minute-scabiosum</i> , <i>P. non-retrorsum</i> , <i>P. panamense</i> , <i>P. persubulatum</i> , <i>P. portobellense</i> , <i>P. pseudocativalense</i> , <i>P. salamancaum</i> , <i>P. tabernillanum</i> , <i>P. tapianum</i> , <i>P. tecumense</i>	
		Mexican Pacific Coast, Eastern Central America, Western Panamanian Isthmus		14	<i>Piper affectans</i> , <i>P. agellifolium</i> , <i>P. altevaginans</i> , <i>P. amphoricarpum</i> , <i>P. arcte-acuminatum</i> , <i>P. barbirostre</i> , <i>P. biauritum</i> , <i>P. biseriatum</i> , <i>P. callibracteum</i> , <i>P. carminis</i> , <i>P. carpinteranum</i> , <i>P. casitense</i> , <i>P. chiriquinum</i> , <i>P. ciliatifolium</i> , <i>P. coronatibracteum</i> , <i>P. corrugatum</i> , <i>P. davidianum</i> , <i>P. davidsonii</i> , <i>P. fluvii-initii</i> , <i>P. fortunaensis</i> , <i>P. fusco-granulatum</i> , <i>P. glabrescens</i> , <i>P. goegeri</i> , <i>P. jubatum</i> , <i>P. magnilimum</i> , <i>P. subfuscum</i>	
		Chocó, Eastern Central America		21	<i>Piper daguanum</i> , <i>P. gamboanum-yapense</i> , <i>P. latibracteum</i> , <i>P. laxispicum</i> , <i>P. magnantherum</i> , <i>P. obaldianum</i> , <i>P. pallidibracteum</i> , <i>P. pervenosum</i> , <i>P. pinoganense</i> , <i>P. polyneurum</i> , <i>P. pseudohodgei</i> , <i>P. pseudoviridicaule</i> , <i>P. sambuanum</i> , <i>P. scabrilimum</i> , <i>P. sperdinum</i> , <i>P. subcaudatum</i> , <i>P. turbense</i> , <i>P. viridicaule</i>	
		Western Panamanian Isthmus, Mexican Gulf, Eastern Central America		27	<i>Piper barbulatum</i> , <i>P. donnell-smithi</i> , <i>P. flavidum</i> , <i>P. lanosibracteum</i> , <i>P. leptoneuron</i> , <i>P. luxii</i> , <i>P. matinatum</i> , <i>P. santa-rosanum</i> , <i>P. subcitrifolium</i> , <i>P. uspantanense</i> , <i>P. variable</i>	
	Amazonian	Guyana	Guyana	12	12	<i>Piper bolivarianum</i> , <i>P. sabanaense</i> , <i>P. tamayoanum</i> , <i>P. kegelianum</i> , <i>P. cernuum-perlongispicum</i> , <i>P. venamense</i> , <i>P. hippocrepiforme</i> , <i>P. politii-toronoense</i>
					20	<i>Piper schwackei</i> , <i>P. substilosum</i> , <i>P. glandulosissimum</i>
		Humid Guyana	8	<i>Piper nematanthera</i> , <i>P. gleasonii</i> , <i>P. paramaribense</i> , <i>P. poiteanum</i> , <i>P. regelianum</i> , <i>P. adenandrum</i> , <i>P. regelii</i> , <i>P. romboutsii</i> , <i>P. rudgeanum</i> , <i>P. insigne</i> , <i>P. saramaccanum</i> , <i>P. pulleanum</i>		
		Imerí	4	<i>Piper perciliatum</i> , <i>P. javitense</i> , <i>P. cililimum</i> , <i>P. pubivaginatum</i> , <i>P. liesneri</i> , <i>P. mosaicum</i>		
		Napo	6	<i>Piper corpuientispicum</i> , <i>P. calanyanum</i> , <i>P. florencianum</i> , <i>P. peculiare</i> , <i>P. statum</i> , <i>P. sucreense</i> , <i>P. purulentum</i>		
		Pantanal	17	<i>Piper moense</i> , <i>P. udisilvestre</i>		
Imeri	7	<i>Piper otto-huberi</i> , <i>P. para-peltobryumbryon</i>				
Imeri, Napo	13	<i>Piper japurense</i> , <i>P. maranyonense</i>				
Imeri, Napo	23	<i>Piper froesii</i> , <i>P. silvigaudens</i> , <i>P. uapesense</i>				
Imeri, Pantanal, Amapá	22	<i>Piper purusanum</i> , <i>P. coariense</i> , <i>P. limosum</i> , <i>P. subcostatum</i>				
Amapá, Roraima	24	<i>Piper carniconectivum</i> , <i>P. gurupanum</i> , <i>P. rupunianum</i> , <i>P. striatipetiolum</i> , <i>P. subglabrifolium</i>				

Table 2 continued

Region	Subregion	Province	Number of generalized tracks for subregion	Track code	Species support
		Madeira, Pantanal		28	<i>Piper brachypetiolum</i> , <i>P. madeiranum</i> , <i>P. tridentiphilum</i>
Parana	Brazilian Atlantic Forest		1	25	<i>Piper hayneanum</i> , <i>P. permucronatum</i> , <i>P. guimaraesianum</i>
Andean-Neotro	Paramo Punan, Caribbean	North Andean Páramo, Cauca, Chocó, Arid Ecuador, Western Ecuador	6	9	<i>Piper regale</i> , <i>P. bullosum</i> , <i>P. filistylum</i> , <i>P. killipii</i> , <i>P. pubes-tilis</i> , <i>P. bellowi</i> , <i>P. villosum</i> , <i>P. anisatum</i> , <i>P. peñasblancas</i> , <i>P. ambiguum</i> , <i>P. acaule</i> , <i>P. obovatilimum</i> , <i>P. altaqueri-ano</i> , <i>P. barbacoense</i> , <i>P. alejandrinum</i> , <i>P. cyphophyllose</i> , <i>P. cyphophyllose-brevipes</i> , <i>P. debilicaule</i> , <i>P. entradense</i> , <i>P. ignacioanum</i> , <i>P. parcum</i> , <i>P. poscitum</i> , <i>P. supernum</i> , <i>P. townsendii</i> , <i>P. mexiae</i> , <i>P. catripense</i> , <i>P. madisonii</i> , <i>P. cangapianum</i> , <i>P. arobense</i> , <i>P. tobarensis</i>
		North Andean Páramo, Venezuelan Llanos		2	<i>Piper deliciosanum</i> , <i>P. viridistachyum</i> , <i>P. pendentispicum</i>
		North Andean Páramo, Chocó		5	<i>Piper pseudoshupii</i> , <i>P. montanum</i> , <i>P. aguadulcense</i> , <i>P. veneralense</i> , <i>P. golondrinum</i> , <i>P. alwini</i> , <i>P. foreroi</i>
		North Andean Páramo, Chocó, Cauca		16	<i>Piper atrobaccum</i> , <i>P. bahiasolano</i> , <i>P. barklegi</i> , <i>P. basilobatum</i> , <i>P. blanquita</i> , <i>P. bolivar</i> , <i>P. brachypodon</i> , <i>P. caudefactum</i> , <i>P. certeguiense</i> , <i>P. condotoense</i> , <i>P. contraverrugosum</i> , <i>P. cordilimum</i> , <i>P. cristalinanum</i> , <i>P. diguaense</i> , <i>P. enganyanum</i> , <i>P. espejuelanum</i> , <i>P. espoliatum</i> , <i>P. exserens</i> , <i>P. frutescens</i> , <i>P. gesneroides</i> , <i>P. heterolrichum</i> , <i>P. ledezmae</i> , <i>P. lellingeri</i> , <i>P. lloro</i> , <i>P. mandinganum</i> , <i>P. monsalvianum</i> , <i>P. patoense</i> , <i>P. pedunculatum</i> , <i>P. pendulirameum</i> , <i>P. pilibracteum</i> , <i>P. pseudo oxistachium</i> , <i>P. pseudocordi</i> , <i>P. ramosense</i> , <i>P. roblalense</i> , <i>P. roldani</i> , <i>P. silvaticum</i> , <i>P. subconcinum</i> , <i>P. subnitidum</i> , <i>P. tutunendó</i> , <i>P. umbriculum</i> , <i>P. urrao</i> , <i>P. yatoensis</i> , <i>P. zingara</i>
		North Andean Páramo, Eastern Central America, Western Panamanian Isthmus, Mexican Pacific Coast, Magdalena, Cauca		18	<i>Piper amphioxys</i> , <i>P. annulatispicum</i> , <i>P. augustum-andino</i> , <i>P. betanii</i> , <i>P. borucanum</i> , <i>P. bullulaefolium</i> , <i>P. caeruleifolium</i> , <i>P. campamento</i> , <i>P. churruyacoanum</i> , <i>P. cocornanum</i> , <i>P. copacabanense</i> , <i>P. cyprium</i> , <i>P. divortans</i> , <i>P. domingense</i> , <i>P. dumeticola</i> , <i>P. el-bancoanum</i> , <i>P. epyginium</i> , <i>P. escobinifolium</i> , <i>P. falanense</i> , <i>P. fatoanum</i> , <i>P. fonnegrae</i> , <i>P. hermosanum</i> , <i>P. intersitum</i> , <i>P. jericóense</i> , <i>P. la-doradense</i> , <i>P. miramareense</i> , <i>P. multiforme</i> , <i>P. nigricaule</i> , <i>P. nodosum</i> , <i>P. nudifolium</i> , <i>P. pennellii</i> , <i>P. perpusillum</i> , <i>P. pseudo lagunaense</i> , <i>P. pseudovariabile</i> , <i>P. raizudoanum</i> , <i>P. scobinifolium</i> , <i>P. semitarium</i> , <i>P. semperflorens</i> , <i>P. sneidernii</i> , <i>P. soejartoi</i> , <i>P. subdilatum</i> , <i>P. subnudispicum</i> , <i>P. subtrinerve</i> , <i>P. taboganum</i> , <i>P. tolimae</i> , <i>P. vargasii</i> , <i>P. virgatum</i> , <i>P. zacatense</i>
	Paramo Punan, Amazonian	Puna, Pantanal, Napo, Ucayali		26	<i>Piper adreptum</i> , <i>P. albogranulatum</i> , <i>P. apodum</i> , <i>P. asclepiadifolium</i> , <i>P. barbicuspe</i> , <i>P. celer</i> , <i>P. circumspectantis</i> , <i>P. cupreatum</i> , <i>P. claudicans</i> , <i>P. epunctatum</i> , <i>P. ferruginispicum</i> , <i>P. indianonum</i> , <i>P. interitum</i> , <i>P. klugianum</i> , <i>P. mishuyacuense</i> , <i>P. paganicum</i> , <i>P. papillipetiolum</i> , <i>P. pernigricans</i> , <i>P. pervulgatum</i> , <i>P. rugosilimum</i> , <i>P. sanguineispicum</i> , <i>P. scapispicum</i> , <i>P. scapispicum</i> , <i>P. subsilvestre</i> , <i>P. villosispicum</i> , <i>P. vitaceum</i>

Andean region that show no relationship with any other areas, and that comprise the endemic Andean species of *Piper*, as is the case for species of the *Churumayu* clade, almost restricted to the Puna province. Second, there is a close relationship between areas of the Andean region and the Caribbean subregion (North Andean slopes/Chocó/Cauca/Magdalena/western Ecuador/eastern Central America/western Panama/Mexican Pacific Coast) (species of the *Radula*, *Macrostachys*, *Peltobryon* and *Trianaeopiper* groups). Third, there is a relationship between the Andean region and the Amazonian subregion (Andean slopes, Napo, Ucayali and Pantanal), which include a large number of species of *Isophyllon*, *Peltobryon* and *Radula*. These three patterns suggest a hybrid origin for Andean pipers.

Three altitudinal zones can be recognized for species of *Piper* in the Andes: the premontane-lower montane zone (0–1000 m); the sub-Andean montane zone (1000–2300 m); and the high Andean montane zone (2300–2800 m), with species richness diminishing at altitudes over 2000 m (Marquis, 2004). According to the scheme proposed by Van der Hammen (2000) to explain the history of Andean biodiversity, those species of *Piper* with Andean distribution originated in the tropical lowlands, probably during the Cretaceous and Palaeogene, reaching their full diversification by the Miocene and Pliocene. In this regard, it is relevant to cite the study by Wijninga (1996) on the Neogene sediments from the Bogotá Plains (2400 m present elevation), from which he reports (in his atlas of fossil plants from the Neogene) a set of unidentified seeds. Some of the seeds found by Wijninga (1996: plates 47, 48, 249, 285a and 285b) correspond, according to seed studies in *Piper* (Callejas, 1986, 2002), to species of subgenus *Ottonia*, a clade that is nowadays almost entirely restricted to the Atlantic forests of Brazil and the Central Amazon, with a single species on the western side of the Andes (*Piper darienense*). This suggests that Amazonian species of *Ottonia* (and probably of other clades) had a widespread distribution by the Pliocene in today's Andean region.

Distribution patterns such as those exhibited by *Piper* are difficult to treat using a dispersalist approach. We interpret these distributions based on our results, and on the ideas proposed by Croizat (1976), in terms of two types of vicariance event: Pre-Andean and Post-Andean events. The Andean uplift could have affected the distribution of *Piper* in various ways, as follows:

1. Certain species did not survive the alteration of their habitats and became extinct, leaving fossil evidence of their presence, or surviving only on the slopes of mountain ranges. This is the case for the species belonging to *Ottonia*, which support an endemism area in the western slopes of the Western Cordillera near the border between Colombia and Panama; and the generalized track in the Atlantic forests of Brazil.
2. Other species were able to adapt to environmental conditions produced by the Andean uplift, giving origin to groups that today are denominated Andean (such as the *Churumayu* clade, with endemic areas distributed in the Andes, which supports the only Andean generalized track demarcated in our analysis).

3. Some other species might have been able to survive with disjunct distributions in the intra-Andean valleys, but with Amazon affinities (such as the *Schilleria* and *Macrostachys* clades, both sustaining endemic areas in the Amazonian province of Napo, and a generalized track that connects the Andean slopes with the north of the Amazonian subregion).

With the formation of the Andes by the end of the Neogene, the vegetation of the Amazonian subregion was split into eastern and western elements, resulting in the formation of several areas currently recognized as centres of endemism for large portions of the Neotropical flora (Van der Hammen, 1960, 1961, 1974; Croizat, 1976; Callejas, 1999; Van der Hammen, 2000; Jaramillo & Callejas, 2004). Both the formation of the Andes and the relationship of a large part of its flora with the Amazon are revealed by generalized tracks that connect sub-Andean areas with the Amazonian provinces of Napo, Ucayali and Pantanal, and with the province of Chocó. Despite the fact that numerous elements of the flora in the north of Rio Magdalena valley in Colombia are related to species living in eastern Amazonia or the Guayana Shield (Gentry, 1982; Cortés & Franco, 1997), and that this sector is classified as one of the main biogeographical nodes of South America (Croizat, 1976), which made up part of a fluvial system that crossed over the Central Cordillera to Guayana Shield (Croizat, 1976; Alemán & Ramos, 2000), we did not detect a generalized track connecting the two areas. Moreover, there is no generalized track connecting the Andean areas in Colombia with the east Amazonian subregion because sampling in the area of Magdalena is incomplete, because *Piper* species are not informative on such connections, or because *Piper* species in the Magdalena Valley represent relictual distributions.

Just as the distribution patterns for species of *Piper* in the north of the Neotropical region are closely linked to the rising of the Andes, several different tectonic events in the southern portion of the Neotropical region (province of Paraná) could explain the current distribution patterns for the southern Neotropical species of *Piper*. One of these is the isolation of southern Amazonia from the Atlantic forest by the formation of a large, lacustrine area along the Paranaíba, São Francisco and Paraná rivers, (Petri & Fulfaro, 1983; Marroig & Cerqueira, 1997; Amorim, 2001) and the rise of Serra do Mar and Serra do Mantiqueira, producing several endemic areas along the Atlantic forests. For this zone, a single generalized track is revealed and supported by endemic species of the subgenus *Ottonia*, a group previously mentioned as having Amazonian and western Andean elements.

The distribution patterns and endemism areas of *Piper* species suggest that *Piper* should not be denominated an Andean-centred group, because the highest number of areas of endemism and species richness are located in the Neotropical region. In the present analysis, important areas in the distribution of the genus are the Atlantic forests of Brazil and the western Amazon, because they exhibit the vast majority of Neotropical *Piper* clades. It is also noteworthy that distributions of most *Piper* species are limited to small

areas or single sites, with a minority of widespread species, suggesting a distribution pattern fragmented through history by tectonic events.

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BIOSKETCHES

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