Title: DISTRIBUTIONAL PATTERNS AND ENDEMISM AREAS OF THE NEOTROPICAL SPECIES OF *Piper* (PIPERACEAE)[*].

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Keywords: Neotropical Region, Andean Region, biogeography, track analysis, parsimony analysis of endemicity, distribution patterns, *Piper* Clades.

Description

Here we present a panbiogeographic and endemicity analysis of the Neotropical species of the genus *Piper,* with the purpose of establishing its distributional patterns and to locate its endemic areas in the Neotropical and Andean regions. We also examined the distribution of every single clade recognized in *Piper* for the Neotropics, to determine whether the generalized tracks are congruent with the endemic areas for specific clades. We used information on distributions, extracted from herbarium specimens and recent monographic treatments for 1152 species of *Piper* from the Neotropics, and subjected it to a parsimony analysis of endemicity and to a track compatibility analysis. Patterns of distribution for the different clades were described trying to stablish to what extent the different generalized tracks coincide with monophyletic

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groupings. The parsimony analysis of endemicity revealed 104 endemic areas for the genus *Piper* in the Caribbean, Amazonian and Paranensis subregions of the Neotropical region (80) and the Páramo-Punan subregion of the Andean region (24) (Table 1). Track compatibility analysis resulted in 26 generalized tracks, one in the subregion Páramo-Punan (Andean Region), 19 tracks in the Neotropical region and 6 tracks connecting the Andean and Neotropical regions (Table 2). There is not a single clade for *Piper* restricted or endemic to the Andean region, since the species in that area are all derived from the Caribbean and Amazonian subregions. Higher richness and/or endemic areas are restricted to lowland habitats, in the Pacific coast of Colombia and Ecuador in the Chocó Province, the Atlantic forests of Brazil, and the lowlands of Eastern Central America.

Título: PATRONES DE DISTRIBUCION Y AREAS DE ENDEMISMO DE LAS ESPECIES NEOTROPICALES DE *Piper* (PIPERACEAE)[*].

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Palabras Claves: Región Neotropical, Región Andina, Biogeografía,

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Análisis de trazos, Análisis de Simplicidad de Endemismos, Patrones de Distribución, Clados de *Piper*.

Descripción

Se presenta un análisis panbiogeográfico y de endemismos de las especies Neotropicales del género *Piper*, con el propósito de establecer sus patrones de distribución y localizar sus áreas endémicas en la región Neotropical y Andina. También se examino la distribución de todos los clados conocidos de *Piper* en el Neotropico, para determinar si los trazos generalizados son congruentes con áreas endémicas para clados específicos. Se utilizó información de distribución, extraída de especímenes de herbario y recientes tratamientos monográficos, para 1152 especies de *Piper* Neotropicales las cuales se sometieron a un análisis de simplicidad de endemismos y a un análisis de compatibilidad de trazos. Los patrones de distribución para los diferentes clados fueron descritos, tratando de establecer cuales de los trazos generalizados coincidían con grupos monofiléticos. El análisis de simplicidad de endemismos reveló 104 áreas endémicas para el género *Piper* en las subregiones Caribeña, Amazónica y Paranaense de la región Neotropical (80) y en la subregion Paramo Puneña de la región Andina (24) (Tabla 1). El Análisis de Compatibilidad de trazos produjo 26 trazos generalizados, uno en la subregión Paramo Puneña, 19 trazos en la región Neotropical y 6 trazos conectando la región Andina y

Neotropical (Tabla 2). No hay un clado de *Piper* restringido a la región Andina, pues las especies de esta área son todas derivadas de las subregiones Caribeña y Amazónica. Las áreas más ricas y/o endémicas, están ubicadas en tierras bajas de la Costa Pacifica de Colombia y Ecuador, en la provincia del Chocó, el Bosque Atlántico del Brasil y las tierras bajas del oriente de América central.

INTRODUCTION

Piper (*Piper*aceae) is a Pantropical group with nearly 2000 species, which are often an important element of mountain and lowland forests and one of the 10 most speciose genera of basal Angiosperms found in the tropics (Gentry & Donson, 1987). Most species of *Piper* appear restricted from 0 to 2500 m, few species occur above 3000 m. According to Gentry (1990) *Piper* reaches its higher diversity in the lowlands of the Neotropical region. There, most species exhibit restricted distributions and is rather common to find numerous related endemic taxa occurring in small size areas, and there is a relatively low number of species that have wide distributions. The Andean slopes, Central America lowlands and Central Amazonia are often cited as centers with high species richness for *Piper* in the Neotropics (Callejas, 1986; Soltis *et al.,* 1999; Jaramillo & Manos, 2001).

Taxonomy of the genus has been hampered by numerous nomenclatural problems, poorly described species, a misinterpretation of floral structure and tree architecture (Trelease, 1930; Trelease & Yuncker, 1950; Tebbs, 1993) and scarce sampling for many areas (Northern Andean region of Colombia, Southern Guianan shield, Colombian Eastern Amazonia and Southern Bolivian Amazonia, among others). However recent advances on the general biology of *Piper* (structure, ontogeny, evolution of flowers, pollination biology, tree architecture analysis, seed coat structure, seed dispersal, physiological ecology), revisionary studies for specific groups and for large geographic areas (Tucker, 1982; Tucker *et al.,* 1993) and phylogenetic analyses have paved the way for constructing a natural classification for the genus (Callejas, 1986; Jaramillo & Manos, 2001; Jaramilo & Callejas; 2004)

The recent phylogenetic analysis (Jaramillo & Manos, 2001) suggests three major clades in *Piper*, a Neotropical, a Paleotropical and a South Pacific, representing three large geographical components, America (1300 sp.), Asia (600 sp.) and South Pacific (100 sp.). Given that species of *Piper* in the Neotropics attains a wide distribution in practically all areas of the region, and that we have access to an updated taxonomy and phylogeny, it is worthwhile to look for the information content of the group regarding the history of the biotas that conform the Netropical Region.

Miquel (1844) was the first author who provide at global scale an account for the genus in *Piper*aceae and their distribution, indicating a possible ancestral group related to *P. nigrum*. Trelease (1930), long time specialist of *Piper*aceae for the Neotropics examined the geography of American pipers in a short summary where he indicated the distribution and abundance of major groups of the genus and allied genera. He concluded that the history of the origin of Piperaceae is rather obscure and that according to fossil data the group has an origin in the Quaternary. Raven and Axelrod (1974) suggested a Laurasian origin for the group, while Gentry (1982) and later Graham (1995) proposed a Gondwanic origin emphasizing that the genus *Piper* was already established in South America by the Cretaceous and it extended into Central America via Panamá. Callejas (1986) in his taxonomic revision for the subgenus *Ottonia* analyzed the distribution of the entire group and of several species pairs showing that for *Ottonia* distribution patterns were related to Pleistocene refuges and isolated dispersal events. Recently Jaramillo & Manos (2001) suggested, based on phylogenetic evidence, the ancestral presence of the genus in the Southern Hemisphere as a result of vicariance rather than dispersal.

Here we delimited the patterns of distribution for the Neotropical species of *Piper* by means of a panbiogeographic analysis, to define the localization of the endemic areas for the genus and to analyze what extent the group is congruent regarding to the history of biotas in the Neotropics.

MATERIALS & METHODS

Study Area.

For the purpose of this study we choose the scheme of Biogeographic provinces of Morrone (2002). The study areas present in the analysis were the Neotropical region and the subregion Páramo-Punan belonging to the Andean region. The Neotropical region extends in the tropics from the North of Mexico to the center of Argentina and belongs to the Holotropical Kingdom. The Neotropical region is divided in the Caribbean, Amazonian, Chaqueña and Parana subregions. The Andean region belongs to the Austral Kingdom and includes Páramo-Punan, Central Chile, Subantartic and Patagonian subregions. The Andean area where there is presence of species of *Piper* belongs to the Páramo-Punan subregion, which extends from the Northern Cordilleras of Venezuela through Colombia, Ecuador and along the Puna of Perú and Bolivia.

Taxa

Despite the lack of a formal scheme of classification for *Piper*, we chose to follow the cladistic analysis of Jaramillo & Manos (2001). Most clade names recognized in Jaramillo & Manos (2001) correspond to formal group at the generic or subgeneric level previously recognized by others, particularly De Candolle (1923) and Miquel (1844). Since our sampling is far more extensive than Jaramillo and Manos one, we include groupings no sampled by them. Thus we include taxa belonging to *Peltobryon*, a clade at the interior of *Schilleria*, *Isophyllon*, a group recognized first by Miquel and belonging to *Schilleria*, and *Carpunya*, at the interior of *Radula* but not sampled previously by Jaramillo and Manos.

Also, *Trianaeopiper* is here split in three distinct clades, named temporarily by Jaramillo & Callejas (2004) as the *Trianaeopier-Trianae*, the *Trianaeopiper-filistylum* and the *Trianaeopiper-confertinodum* groups.

Ours source of data for mapping netropical pipers included 1250 species, using as primary source herbarium collections at Herbario Universidad de Antioquia, with the most complete holdings of

Neotropical pipers as well as specimens of particular groups stored at: AAU, COL, F, INBIO, L, MO, NY, TEX, US, U. Secondary sources were latest and up to date taxonomic treatments of *Piper* for specific geographic areas, (Yuncker, 1972, 1973; Steyermark, 1984; Callejas 1986, 1999; Steyermark & Callejas, 2003) and treatments for specific clades (Bornstein, 1989; Burger, 1971; Callejas, 1986; Tebbs, 1993).

As previously noticed sampling of *Piper* in the Neotropics is not uniform across the region (i.e. many species are known only from single localities). Being aware of the problems of paralogy for ancient groups with widespread distributions, caused by poor sampling (Amorim, 2001), we procured to assemble for Neotropical pipers the most complete data base possible, which includes almost 95% of all Neotropical species of the genus and 7500 registers.

Parsimony Analysis of Endemicity

Once taxa were chosen, and their taxonomy carefully checked we proceed to perform a PAE analysis. For this analysis, we chose the relatively coarse 1° latitude 1° longitude grid size, partly for ease of data manipulation and partly to reduce the effects of sampling artifacts, such as mapping errors and unsampled grids in sparsely inhabited areas

(Crisp, 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, 2001). For this reason is important to clarify that the size of the square is totally operational and was chosen because, a wider and handled range of resolution was needed, from the methodological and computational point of view. So, for this reason, an analysis using other scale, with a bigger number of registers placed in a larger quantity of areas, could be incorporate square sizes more functional than the ones used.

All grids were numbered and a presence/absence matrix was built, where columns represent the taxa and rows represent the areas (quadrants) (If a taxon is present in the area, the entry is 1 and if it is absent, the entry is 0). A hypothetical grid with 0 for all species (all species absent in that grid) was added for the purposes of rooting the resulting tree (Morrone, 1994; Morrone & Crisci, 1995; Posadas & Miranda-Esquivel, 1999). The matrix was subjected to parsimony algorithms by using TNT 1.0b (Goloboff *et al*., 2003), applying option *New Technology Search* (*sectorial searches, tree-drifting and tree-fusing*), because this software is more efficient to analyze large data matrices.

The trees were examined using Winclada 1.0 (Nixon, 2002). Groups of quadrants that share at least two species were considered as diagnosing of an area of endemism, which was delimited and mapped (Fig. 1). In case several cladograms result, was obtained a strict consensus cladogram.

Track analysis

The matrix used in the PAE analysis was subjected to a track compatibility analysis (Craw, 1988, 1989) by using a compatibility approach implemented in TNT 1.0b (Goloboff *et al*., 2003), applying option *new technology search* (*sectorial search, tree-drifting and tree fusing,* using implied weight function) (Goloboff *et al*., 2003). The trees were examined using Winclada 1.0 (Nixon, 2002). In case several trees result, was obtained a strict consensus cladogram. The Generalized tracks (groups of terminal areas connected on the basis of unique component of sharing species) were detected and according to the species distributions mapped. Finally we search for those groups of species than support particular generalized tracks and that correspond to clades proposed at a phylogenetic analysis of Jaramillo and Manos (2001) or previously recognized as subgenera by other authors (de Candolle, 1923; Callejas, 1986; Bornstein, 1989).

Results

661 grids of a total of 2000 were occupied by at least one species. *Piper* occurs in practically all habitats available within the range of the genus. In the Neotropical region the following subregions exhibited the grids with the highest species number. The Caribbean subregion, in the provinces of Western Panamanian Isthmus (408 spp.), Chocó (Pacific Coast of Northern Ecuador, Colombia and Panamá) (378 spp.) and Eastern Central America (87 spp.); the Amazonian subregion, in the provinces of Ucayalí (116 spp.) and Napo (69 spp.). In the Andean Region, the subregion with the highest species number was the Páramo Punan, in the provinces of Norandean Páramo and Puna (291 and 115 species, respectively).

80% of the endemic areas and of the generalized tracks occur in the subregions with the highest species number per grid and 20% of the endemic areas and tracks occurred in zones with low number of species (Antilles, the Guyanian shield and Manaus).

The PAE analysis revealed 104 endemic areas (Fig. 2). A total of 24 (23.07%) areas correspond to the Andean region, distributed in the Páramo-Punan subregion in the provinces of Norandean Páramo (16 areas), Puna (8 areas) and 80 (76.91%) corresponding to the

Neotropical Region, distributed in the Caribbean (48), Amazonian (28) and Parana (4) subregions (Table 1).

26 generalized tracks were obtained (Fig. 2): one generalized track was located in the Andean Region, 19 tracks were restricted to the Neotropical Region, of those 6 distributed in the Caribbean, 12 in the Amazonian and one in the Parana subregions, and finally, 6 generalized tracks that connect the Andean and Neotropical regions (Table 2).

For the 1250 species examined, only 327 species of *Piper* belonging to the following clades: *Churumayu* (5 spp.), *Enckea* (5 spp.), *Isophyllon* (15 spp.), *Macrostachys* (45 spp.), *Ottonia* (5 spp.), *Peltobryon* (63 spp.), *Radula* (127 spp.), *Schilleria* (18 spp.), and three clades without formal ranking and previously placed under genus *Trianaeopiper* (polyphyletic according to Jaramillo & Manos, 2001 and Jaramillo & Callejas, 2004) (42 spp.) were informative and supported generalized tracks.

DISCUSION

ENDEMISM

Gentry (1982) stated that in regard to the Neotropical Flora, plant taxa exhibit two types of distribution affinities, species with distribution centers restricted to the Amazonia and those with distribution centers restricted to the Andean region, which he termed respectively Amazonian-Centered and Andean-Centered taxa.

Gentry (1982) suggested that Andean-Centered species exhibit high endemism along the low elevation humid slopes of the Andes and the montane forests of Central America. Such observation is in part congruent with our findings for the distribution of *Piper* in the Neotropics. *Piper* can hardly be assigned to Andean-Centered species groups, because species of this genus are not only concentrated in the Andean region (including the provinces of Norandean Páramo and Puna) but also in the Neotropical region, specially in the Antilles, Central America, the Pacific Province, Amazonia and the Atlantic forests of Brazil; thus Gentry's perception of the biogeography of Neotropical flora (Gentry, 1982; Gentry & Dobson, 1987) was rather simplistic and poorly resolved for explaining the endemism levels of *Piper* in the Neotropical region.

Endemic Areas of the Neotropical Region

The number of species and endemism for *Piper* as revealed by PAE in this study coincide with those formulated by Van der Hamen (2000) when comparing biotas of the Andean Region with those of the Amazonia, accordingly the areas with the highes values for richness and endemism were the western slope of the Western Cordillera and the lowland forests of the Pacific region (Chocó) (Fig. 1).

Caribean subregion, the Magdalena and Chocó Provinces.

Our data indicate that *Piper* displays the highest species number in the Neotropical region, but also that this region, with 80 endemic areas as revealed by the PAE analysis, accounts for 77.44% of the endemic taxa. On the other hand, the Andean region exhibits comparatively a low level of endemism with only 24 endemic areas, what represent 22.56% of the endemic species (Table 1).

For the Magdalena Province, only one area of endemism was detected in the Sierra Nevada de Santa Marta (Fig. 1), which is a massif located at the north of Colombia isolated from the Andean region, and with a puzzling geological history (Harrington, 1962; Aleman & Ramos, 2000). This area has nearly 50 species of *Piper* (Trelease & Yuncker, 1950) four of them endemic, and the others mostly widespread taxa that are distributed either along the Caribbean region, the Northern Andes, or the Antilles. The lack of phylogenies for distinct clades in *Piper* restricts an explanation for the significance of the endemism in the area.

The very humid forests of the Chocó and Costa Rica provinces included the endemic areas with the highest number of species known for the genus in the Neotropics, where *Piper* is not the only group that exhibits such pattern, also seen in the family Ericaceae (Luteyn, 2002) and in the genus *Anthurium* (Araceae) (Croat, 1992). These results coincide with the analysis of Marquis (unpublished data), who found a high correlation values between the *Piper* species richness and the precipitation on some Central American areas. We suspect, as did Gentry (1982), that forested areas from the lowland regions of the Neotropics with high precipitation hold for herbaceous genera the largest number of endemics.

It should be clarified that the western slopes of the Western Cordillera (until 1000 m of altitude) are not to be included in the Andean region, but rather are an extension of the lowland biota of the Chocó and Cauca provinces. As the endemism analysis show, for these areas there are not *Piper* species that belong to the low zones of the Chocó and Cauca Provinces neither to the Andean Region. Instead it was delimited a transition zone between this biotas, whit sister species groups which occur within an altitudinal gradient between 0 and 1000 m.

Provinces of Chiapas, Eastern Central America and Western Panamá

In the Neotropical region, the Caribbean subregion exhibits a high species number for *Piper* and high endemic values for the provinces of Chiapas, Eastern Central America (Costa Rica y Nicaragua) and Western Panamanian isthmus. It is notorious the high endemism of the lowland areas of Costa Rica in Limón and neighboring the Zelaya department of Nicaragua, as compared to the Province of Western Panamanian isthmus. Such differences are unlikely due to sampling, since both provinces include areas with a long continuous history of intensive collecting (Croat, 1997; Hammel *et al*., 2003). The province of Western Panamá shows high species number but low endemic values due to, many species in the province crosses into neighboring Northern Chocó, or extends into Southern Costa Rica. Chiapas is an endemic area for *Piper* but with low species number, since the 80% of the endemic species belongs to subgenus *Arctottonia,* a clade of *Piper* almost entirely restricted to Mesoamerica (Bornstein, 1989). This province has been previously recognized as an endemic area for a diverse number of plant and animal taxa (Croizat, 1976; Halffter, 1978, 1987; Morrone, 1999; Luna *et al*., 2001)

Provinces of Antilles, Guyana Shield and Atlantic East forest of Brazil.

Even though in the provinces of Chiapas, Mexican Pacific Coast, Venezuelan Coast, Cuba, Arid Ecuador, Mexican Gulf, Hispaniola, Magdalena, Western Ecuador, Amapá, Imeri, Roraima, Ucayali, Antilles, the Guyana Shield, and the Atlantic Forest of Brazil, there are low species number (Table 1), these include 15% of the total of endemic species. It emphasizes areas that, not necessarily high in species richness, have a high proportion of flora with restricted distribution range (Crisp, 2001). The correlation between species richness and endemism is an empirical observation that reflects a roughly similar lognormal distribution of species-range sizes over a wide range of biota and over scales from the regional to the global (Gaston *et al.*, 1998). However, as it is shown with *Piper* this corelation varies among areas (Marquis, unpublished data), and these deviations from the more general relationship are the most interesting ones in the study of endemism (Crisp, 2001).

In the case of the Guyana Shield our data indicates that species number for *Piper* tends to be very low, however three endemic areas were detected, two in the Venezuelan territory, in the states of Amazonas, Bolivar, and a third one in Saramaca (Suriname). This is congruent with observations that such areas tend to have high values of endemism, but low species richness (Brako & Zarucchi, 1993; Cortes, 1996; Huber, 1988, 1990, 1992, 1999; Maguire, 1970, 1979; Steyermark, 1966, 1974, 1979, 1984). It is likely that the extreme habitats often found in such areas, including rocky outcrops, dry forests, savannas, etc, are a restriction for most species of *Piper*, which in general display a preference for humid and shady places (Marquis, unpublished data).

The Atlantic forest of Brazil, a belt of tropical rain forests along the coast of Brazil, exhibits low species number for *Piper*, comparable to those of the Antilles and Guyana shield, which is somehow surprising for the genus if one considers the type of vegetation of that area. The tropical rainforests in this region are at present reduced to nearly 10% of its original cover (Amorim, 2001), and it should not be underestimated the impact of deforestation as a process distorting values for species number in the area, even if the available herbarium records comprise collections since 1840, because deforestation in the area backs since 1500 (Hoehne, 1942).

Why then an area larger than the Chocó region, exhibits such a low species number for *Piper*? Not ignoring a sampling bias, the answer might be more related to the ancient history of the area, differential speciation rates for different clades and extinction. It is well known that the area represents a biota with a large endemic component, exhibiting close relationships to the Amazonian biota (Amorim, 2001; da Silva *et* *al*., 2004*).* In the case of the genus *Piper*, the Atlantic Forests holds less number of taxa than the Amazonia for the different clades here recognized, but present all Neotropical clades of *Piper* (except *Arctottonia* and *Trianaeopioper*), translating this area into one with a high phylogenetic information value for the genus.

Andean Region:

Subregion Páramo-Punan, Norandean Páramo and Puna provinces

In the Andean Region the PAE analysis detected 24 endemic areas, 16 in the Páramo province and 8 in the Puna province. In the Páramo province 6 endemic areas are restricted to Northern Eastern Cordillera of Colombia and neighboring the Andes of Venezuela, including two areas along the slopes of the Eastern Cordillera towards the Magdalena valley. The valley of “Rio Magdalena” is an area with a high number of species in many groups of Angiosperms, with close affinities to Amazonian elements (Gentry, 1982, 1990; Gentry & Dondson, 1987; Hernandez *et al.,* 1992). Two endemic areas were founded in the Northern Central Cordillera in Antioquia and Central Andean region of neighboring departments of Tolíma, Quindío and Caldas; two other areas were located in the South of Colombia, in the Central-Eastern Cordillera massif. In Ecuador the endemic areas are restricted to the Nothern Andean zone, one near the Colombian Massif, in the state of

Carchí, and two others toward the eastern slopes, facing the Amazonia, in the departments of Chimborazo and Morona-Santiago.

The eigth endemic areas found along the Puna province are all restricted to Perú (departments of Junín and Huanuco), and show 20 o more species per grid, richness values for this province that are also evident for some plant groups in Brako & Zarucchi's (1993) checklist for the Flora of Perú. These authors found for Cactaceae 247 species of which 176 are endemics, and for Asteraceae, 729 endemic species from a total of 1432 species known for the country. Other authors have found similar results for plant genera such as *Barnadesia* (Asteraceae), *Brunellia* (Bruneliaceae), *Cecropia*, (*Cecropia*ceae), *Ilex* (Aquifoliaceae), *Peperomia* (*Pipera*ceae), *Solanum* (Solanaceae) *Styrax* (Styracaceae) and *Symplocos* (Symplocaceae), (Franco & Berg, 1997; Knapp, 2002; Urtubey, 1999; Young & Leon, 2001).

Given that the final uplifting of Northern Andes occurred near the middle Pliocene (Aleman & Ramos, 2000; Van der Hammen, 2000), we argue, as others before (Bates & Zink, 1994; Fjedlsa & Rahbek, 1998; Johns & Avise, 1998; Garcia Moreno *et al.,* 1999; Tassinari *et al*., 2000; Bates & Demos, 2001) that the species and endemism levels found in the Andean region for *Piper* are of recent origin as compared to those found in the Neotropical region; even more endemic areas in the Amazonia have lower number of endemic species and those occupy basal positions in the phylogeny of the genus. It seems then that recently formed habitats, and also stable, in terms of their climate and geology, have a higher number of endemic species of more recent origin (Moritz *et al*., 2000). It will be more interesting to search for the composition and genetic distances among sets of species pairs form the Amazonia versus the Andean Region to corroborate the hypothesis stated above.

GENERALIZED TRACKS.

The distribution patterns of *Piper* were congruent with several panbiogeographic analysis of the Neotropical region (Cortes & Franco, 1997; Luna *et al*., 2001*;* Contreras-Medina & Eliosa-León, 2001). For instance, the studies of Franco & Berg (1997) for the genus *Cecropia* revealed in part generalized tracks in the slopes of the Northern Andean region of Colombia, Central America and the Atlantic Forests of southern Brazil, all of whom were also detected in our analysis.

Also, it 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, 2001). Our results include a generalized track relating Central and South America, crossing the provinces of the Mexican Pacific Coast, Mexican Gulf, Eastern region of Central America, Western Panamanian Isthmus, Magdalena, Cauca and Norandean Páramo. This track underlies a pattern first proposed by Gentry (1982) relating the floras of the lowland forest of Central America with those of Northern South America.

As with the analysis of endemism, the Neotropical Region concentrates the largest percentage of generalized tracks, corresponding to the 73.07% of the total (Table 2). It is notorious the presence of four tracks along the Chocó Province, suggesting a mixture of elements for a biota apparently uniform (Fig. 2). One track is extended from Darién Province in Panamá along the Northern Pacific coast of Chocó, which includes sister taxa occurring on both sides of the Darién province, and restricted to Northern Colombia. A second track goes from North western slopes of the Western cordillera in Colombia (Antioquia), south to Calima in the Southern Pacific Coast of the Chocó lowlands, which includes taxa of *Piper* with a restricted distribution in Chocó and affinities with Andean elements in Northern Colombia. A third track, from Calima south to the western slopes of Western Cordillera, is supported by several endemic taxa with sister species in Northern Chocó or neighboring Andean slopes of 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 comprise all *Piper* species widespread and with strong affinities to Andean slopes of Ecuador and Colombia. Thus, based on the sampling of *Piper* for Chocó the area should not be considered as a single unit but rather a composite of several biota, with a distinctive Northern and Southern elements, bounded at Calima area along the Pacific Coast. Croat (1992) has detected similar discontinuous distributions in Chocó, for the *Anthurium* genus.

Both, the phylogenetic analysis of Jaramillo & Manos (2001) as well as the generalized tracks of the present study evidence the composite nature of the Andean biota (Crisci *et al*., 1991; Amorim & Tozoni, 1994; Katinas *et al.,* 1999). Three types of Biogeographic patterns involving the Andean region are seen in Neotropical *Piper*s. First, there are areas in the Andean region showing no relationship to any other areas and which comprise the endemic Andean species of *Piper*, as it is the case with species of the *Churumayu* clade, almost restricted to the Puna Province. Secondly, there is close relationship among areas in the Andean region with the Caribbean subregion (Norandean slopes / Chocó/ Cauca/ Magdalena/ Western Ecuador / Eastern Central America/ Western Panamá/ Mexican Pacific Coast) (species of the

Radula, Macrostachys, Peltobryon and *Trianaeopiper* groups). Third, there is a relationship among the Andean region and the Amazonian subregion (Andean slopes, Napo, Ucayali, Pantanal), which includes a large number of species of *Isophyllon, Peltobryon* and *Radula*. These three patterns suggest a hybrid origin for Andean pipers.

BIOGEOGRAPHIC HYPOTHESIS

Andean Orogeny

Two main events have been put forward to explain the general patterns of distribution in the Neotropical flora: The uplifting of the Andes and the Quaternary glaciation events (Prance, 1978, 1982; Gentry, 1982; Whitmore & Prance, 1987; Katinas *et al*., 1999; Van der Hammen, 2000; Amorin, 2001; Haffer, 2001; Hooghiemstra & Van der Hammen, 2001).

The Andean formation begins in the Tertiary and coincides with the breaking up of Africa and South America (Van der Hammen, 1960, 1961; Aleman & Ramos, 2000; Lopez-Ramos, 2001), marking the first major vicariant event that shaped the present distribution of Neotropical and Paleotropical *Piper* species (Callejas, 1986; Jaramillo & Manos, 2001). The Northern Andes reached its present elevations during the Pliocene (3-5 mya), when it occurred the main uplifting (Harrington, 1962; Van der Hammen, 1974; Van der Hammen, 1995).

Three altitudinal zones can be recognized for species of *Piper* in the Andes: A premontane-lower montane zone (0-1000 m), a subandean montane zone (1000-2300 m) and high Andean montane zone (2300-2800 m), with species richness diminishing with elevations above 2000 m (Marquis, unpublished data). According to the scheme proposed by Van der Hammen (2000) for explaining the history of the Andean Biodiversity, those species of *Piper* with an Andean distribution center have an origin in the lower tropical lowlands, likely during the Cretaceous and Paleogene, reaching their full diversification by the Miocene and Pliocene. Regarding to this it is relevant the study of Wijninga (1996) on the Neogene sediments from the Bogotá Plains (2400 m present elevation), where he reports in his atlas of fossil plants from the Neogene a set of unidentified seeds. Some of seeds found by Wijninga (1996; plates 47, 48, 249, 285a and 285b) correspond, according to the seed studies in *Piper* (Callejas, 1986, 2002), to species of subgenus *Ottonia*, a clade that at present is almost entirely restricted to the Atlantic Forest of Brazil and the Central Amazonia with a single species in the Western side of the Andes (*Piper dariense*). This suggests that Amazonian species of *Ottonia* (and likely of other clades) had a widespread distribution by the Pliocene, but also supports the recent origin of Andean *Piper*s from Amazonian ancestors. It emphasizes the general consensus that the Andean flora was developed, at least in part, from the rich Neogene Neotropical lowland vegetation of the Amazonia. Jaramillo & Manos (2001) phylogeny of *Piper* backs the above hypothesis by showing that the Andean species of *Piper* do not conform a monophyletic group and our Panbiogeography study indicates additionally the existence of generalized tracks connecting the Andean and Neotropical regions.

With the formation of the Andean mountain chain by the end of the Neogene vegetation of the Amazonian subregion became divided in East and West elements and concluded in the formation of several areas today recognized as endemic for large portions of the Neotropical flora (Van der Hammen, 1960, 1961, 1974; Callejas, 1999; Van der Hamen, 2000; Callejas & Jaramillo, 2004). The formation of the Andes and the conectedness of much of its flora with the Amazonia is revealed by generalized tracks that relate subandean areas with the Amazonian provinces of Napo, Ucayali and Pantanal, and with the Chocó province. Despite the fact that numerous elements of the Flora from the North of "Rio Magdalena" valley in Colombia have been related to species occurring in Eastern Amazonia or Guiana Shield (Gentry, 1982; Hernandez *et al.,* 1992; Cortes & franco, 1997), we did not detect a generalized track connecting the two areas. Moreover there is not a generalized track connecting the Andean areas in Colombia with the east Amazonian Subregion; because sampling in the area of Magdalena is incomplete, *Piper* species are not informative on such connection and/or because *Piper* species in the Magdalena valley represent relict distributions.

Just as the patterns of distribution for the species of *Piper* in the North of the Neotropical region are closely linked to the uplifting of the Andes, several different tectonic events in the Southern portion of the Neotropical region (Province of Paraná) could explain the actual patterns of distribution for the southern Neotropical species of *Piper*; specially the isolation of Southern Amazonia from the Atlantic forest by the formation of a large lacustrine area along the Paranaiba, São Francisco and Paraná rivers, (Petri & Fulfaro, 1983; Marroig & Cerqueira, 1997; Amorim, 2001) and the rise of Serra do Mar, and Serra do Mantiqueira, giving place to several endemic areas along the Atlantic Forests. For this region a single generalized track is revealed and supported by endemic species of the subgenus *Ottonia*, a group afore mentioned as having Amazonian and West Andean elements.

Pleistocene Refuges and present day patterns of distribution in the Neotropical species of *Piper*.

Callejas (1986), in his taxonomic revision of the subgenus *Ottonia*, analyzed the distribution of several species pairs in the Atlantic Forest and the Amazonian region (*Piper hoffmannseggianum, P. piscatorum; P. Ottonoides, P. klotzchianum*) and concluded that such disjunctions were likely to be explained in the framework of the theory on Pleistocene refuges.

The theory of refuges of the Pleistocene has been often used as a major explanation for the present day patterns of diversity and endemism of biotas in the Neotropical region (Haffer, 1969; Vanzolini & Wiliams, 1970; Vanzolini, 1973; Ab Saber, 1977; Simpson & Haffer, 1978; Dixon, 1979; Absy, 1979, 1982; Brown, 1976, 1977, 1982; Gentry, 1982; Prance, 1978, 1982; Van der Hammen, 2000).

Eventhough, it has been shown that the theory has serious limitations at the theoretical level (Amorin & Pires, 1996; Lynch, 1982; Amorin, 2001), but anyway several authors still insist in a major role for the glaciation event in shaping actual patterns (i.e. Haffer, 1974, 1977; Prance, 1982; Van der Hammen, 2000), by assuming that climatic changes pushed speciation rates in the region.

Although it has been shown that during the Quaternary the Neotropical regions were subjected to climatic changes (Ab Saber, 1977; Absy, 1979, 1982; Van der Hammen, 1972, 1974, 2000; Prance, 1982), it is not that clear that those changes resulted in large fragmented areas; even, it will be hard to explain how a group as *Piper*, a very basal one in the Angiosperms, and with a gondwanan origin (Raven & Axelrod, 1974; Gentry, 1982; Graham, 1995), could have attained his present richness and distributions in the last two thousand years; thus previous events of Pleistocene should also be called for explaining the distribution pattern of Neotropical pipers.

The endemism areas here recognized by the panbiogeographic analysis suggest other ancient tectonic events, occurring during the Tertiary and Cretaceous, as was proposed by Gentry (1982) and Graham (1995), whom stated that the Piperaceae was a plant family first established in the Cretaceous in South America and then its distribution was extended into Central America much before the formation of the Isthmus of Panamá (Pindell & Barret, 1990; Taylor, 1995).

The presence of a generalized track connecting the lowland forest areas of Central America and those of the Pacific lowlands of Northern South America, makes sense with a range expansion of *Piper* before the formation of the Isthmus of Panamá and its more recent closure, giving place to an endemic element in Chiapas area and the high richness and endemisms in Eastern Central America and Western Panamá. Thus, and for an ancient group as *Piper*, the theory of Pleistocene refuges does not explain satisfactorily the present day patterns of distribution of this plant group in the Neotropics, by ignoring tectonic process previous to the Quaternary.

TRACKS AND CLADES

The most recent phylogenetic analysis for *Piper*, which was based on molecular data (Jaramillo & Manos, 2001), recognizes 3 monophyletic groups, the Neotropical, Paleotropical and South Pacific groups, a hypothesis first proposed by Callejas (1986), but also somehow implicit in the de Candolle's key of the *Piper*aceae (1923). Within the Neotropical clade Jaramillo & Manos (2001) recognized several clades that coincide with infrageneric groups of de Candolle (1923). Is important to emphasize the later reanalysis done to the data from the Jaramillo & Manos (2001) using cladistic parsimony (Quijano *et al*., unpublished data) and the following options outlined by Nixon & Carpenter (1996), an unrooted cladogram was produced similar to the one that they obtained. Nevertheless when the analysis was repeated using the out-groups proposed (*Houttuynia cordata*, *Peperomia elongata*, *Sarcorhachis naranjoana*, *Sarcorhachis Sydowii* and *Saururus* *cernuus*), the obtained results were different, due to the Neotropical Clade, was not monophyletic. The justification for this incongruity, is explained by Jaramillo and Manos as a methodological artifact, because it is well known that moderate to high levels of sequence divergence between in-group and out-group could potentially lead to spurious rooting of the ingroup topology (wheeler, 1990). Therefore the alignment of very divergent sequences, would be less informative and could to recover few consistent results.

Is important to argue, that although the morphological phylogenetic analysis made by Callejas (1986), has equally showed the monophyly of this clade it would be interesting to make an analysis of total evidence (Quijano *et al*., unpublished data), to develop an alternative phylogenetic hypothesis about the phylogenetic relationships of the neotropical pepers.

In our analysis the generalized tracks for *Piper* were supported by several species belonging to the clades present in the phylogeny of Jaramillo & Manos (2001): *Pothomorphe* (2 species), *Churumayu* (5 spp.), *Arctottonia* (5 spp.), Enckea (1 sp.), *Isophyllon* (15 spp.), *Macrostachys* (45 spp.), *Ottonia* (5 spp.), *Peltobryon* (63 spp.), *Radula* (127 spp.), *Schilleria* (18 spp.) and the three groups of "*Trianaeopiper*"

(42 spp.). Among these clades, species of *Radula* supported nearly 70% of the tracks. *Radula*, still loosely defined, holds the largest number of species in the Neotropics, but sampling in the Jaramillo & Manos (2001) phylogeny is far from being adequate.

Among the clades present in the Neotropical Region, those with most species distributed to the Eastern Amazonia (*Ottonia*) tend to be basal, while those with most species in Western Amazonia tend to be in more derived positions within the phylogeny (*Macrostachys, Radula, Schilleria*). Also, when comparing the generalized tracks with the proposed phylogenies for the genus (Callejas, 1986; Jaramillo & Manos, 2001), it can be shown that in some cases sister groups support the same tracks; that is the case of *Macrostachys-Radula-Schilleria*, whose endemic species display congruent distributions for the provinces of Norandean Páramo, Puna, Venezuelan Coast, Imerí and Napo.

No specific generalized track is supported by a specific *Trianeopiper* clade; probably because there was not variation in the species distribution for the three groups; rather *"Trianaeopiper"* as a single unit supports a generalized track in the province of Chocó, the Andean slopes, the Ecuadorian Pacific and the province of Loreto. *"Trianaeopiper"* is a polyphyletic group conformed by at least three unrelated clades (Jaramillo & Callejas, 2004), that include a rather characteristic type of *Piper* species in Chocó, mostly low stature plants with simple stems and axial inflorescences, often individual plants being less tan 10 cm tall. Dwarfing in *Piper* seems to have occurred only in the pluvial forests of the Chocó region and in three distinct clades.

The generalized track of the Puna province is supported by species of *Churumayu*, a small group of 10-15 species with an apparent center of diversity in the Peruvian Andes (Callejas, 1986). This clade also supports generalized tracks in the Andean slopes of the Western Cordillera of Colombia. *Churumayu* is not included in the phylogenetic analysis of Jaramillo & Manos (2001), but according to Callejas (1986) it is a monophyletic group (supported by long stylose fruits and banched hairs), close to the *Trianeopiper -triane* group of Jaramilo & Callejas (2004).

For other clades, the support for generalized tracks by sister groups is not that straightforward, as it is illustrated by the clade of *Enckea, Arctottonia* and *Ottonia*. *Ottonia*, with 35 species is almost entirely (30 spp.) restricted to the Atlantic Forest (five species present in the Central Amazon and one west of the Andes). *Arctottonia* exhibit its largest concentration of species in Central America (30 endemic species with most species clustered in Southern Mexico), while *Enckea* has five species distributed in Central Amazonia, four species in North Andean subregion and one species in Southern Panamá.

Different hypothesis (mostly based on floral development) have been put forward for the relationships of subgenus *Ottonia* and *Enckea* (Presl, 1849; Kunth, 1839) and *Arctottonia* (Trelease, 1930; Callejas, 1986; Bornstein, 1989) suggesting that *Enckea* is most closely related to *Arctottonia* and that both are the sister group to *Ottonia*. Jaramillo & Manos (2001) corroborated the above hypothesis and indicated that this clade is the most basal one in the phylogeny of Neotropical *Piper*s. Our analysis reveals several important issues refering to the biogeography of the clade *Ottonia, Enckea y Arctottonia*, which are most revealing for explaining why the present patterns of distribution of Neotropical species of *Piper* do not match the geological history of the area, as a whole. 1) *Ottonia* species support a generalized track in the Atlantic forests of Brazil, while its sister group, the clade of *Arctottonia* and *Enckea*, supports two generalized tracks in Central America, one by *Arctottonia* in Colima, Southern Mexico and a second one in the Darién Province of Panamá. 2) Thus the most basal clades of *Piper* in the Neotropics support generalized tracks unconnected and located in the most Northern and Southern portions of the distribution range for the genus

Piper. 3) Geographic distribution and phylogenetic relationships indicates that the pattern seen in this clade is the result of ancient widespread distribution in the Neotropical region by species of *Piper* belonging to *Ottonia -Arctotonia-Enckea.* 4) Widespread ancient gondwanic groups as *Piper* exhibit distributions that reflect ancient tectonic events and recent cladogenesis in several groups, triggered by most recent vicariant processes. Therefore the track analysis is able to detect most recent cladogenetic events (like those by tracks connecting Central America and Chocó regions) but not very ancient ones. The issues exposed above explain to some extent why there is a partial corological and geological correspondence between the patterns of distribution of *Piper* and the geology of the Neotropics.

Finally the analysis suggest that for the genus *Piper*, the Atlantic Forest of Brazil, an area isolated from the South Western Amazonia since the mid Cretaceous (Amorim & Pires, 1996), might harbor answers regarding the early evolution of the genus in the Neotropics. Eighth of ten clades of Neotropical pipers have species present in the Atlantic Forest and in several instances as in the clade *Macrostachys*, all species present are endemics. We should look whether the species component in the Atlantic Forest, of each clade present, conform monophyletic groups, basal in every clade, otherwise widespread in the

Neotropical regions.

The basal position of *Piper*aceae clade in the Angiosperms (Donoghue & Doyle, 1989; Loconte & Stevenson, 1991; Jud *et al*., 2003) and its significance for understanding the radiation of the group has renewed the interest on this plant family. This study is a first attempt to unveil the biogeographic history of *Piper* in the Neotropics. Needless to say we are aware that despite of including in our sample 96% of the species, only 366 were informative, thus more sampling is needed. Moreover, in order to explain the track analysis it is required a more resolved phylogeny for *Piper*. With this additional information, we could asses to what extent ancient gondwanic groups as *Piper* can be fully informative about the history of a region like the Neotropics. Also it will be worthwhile to apply to our data an analysis of cladistics Biogeography, based on events and not patterns, which may allow to consider dispersal events on the cladogram and to explain firmly to what extent vicariance or dispersal underlines present distributions (Ronquist, 1997).

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Figures Caption.

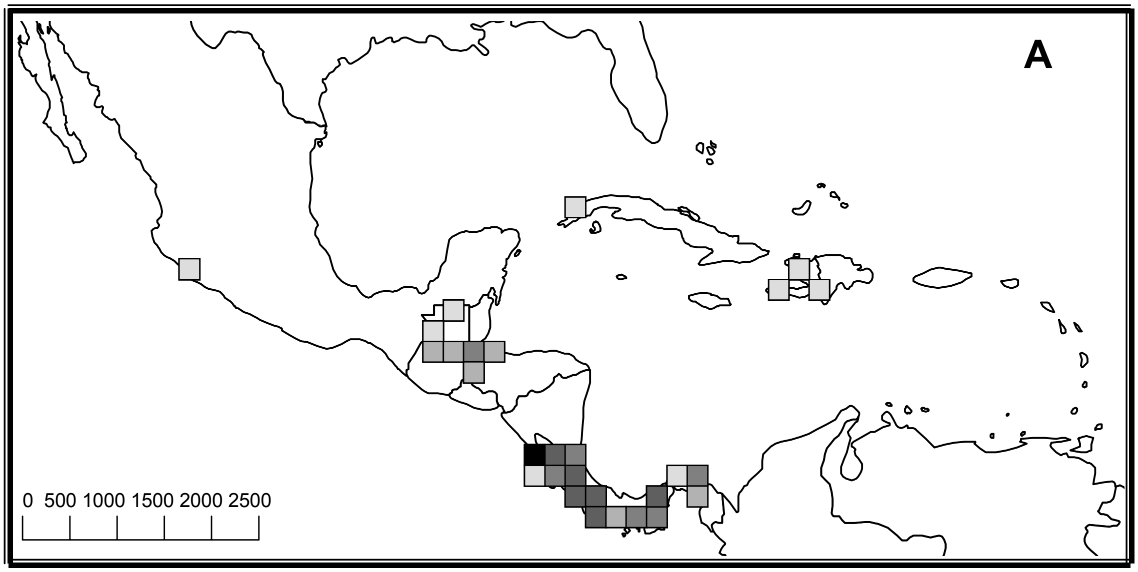
Figure 1.

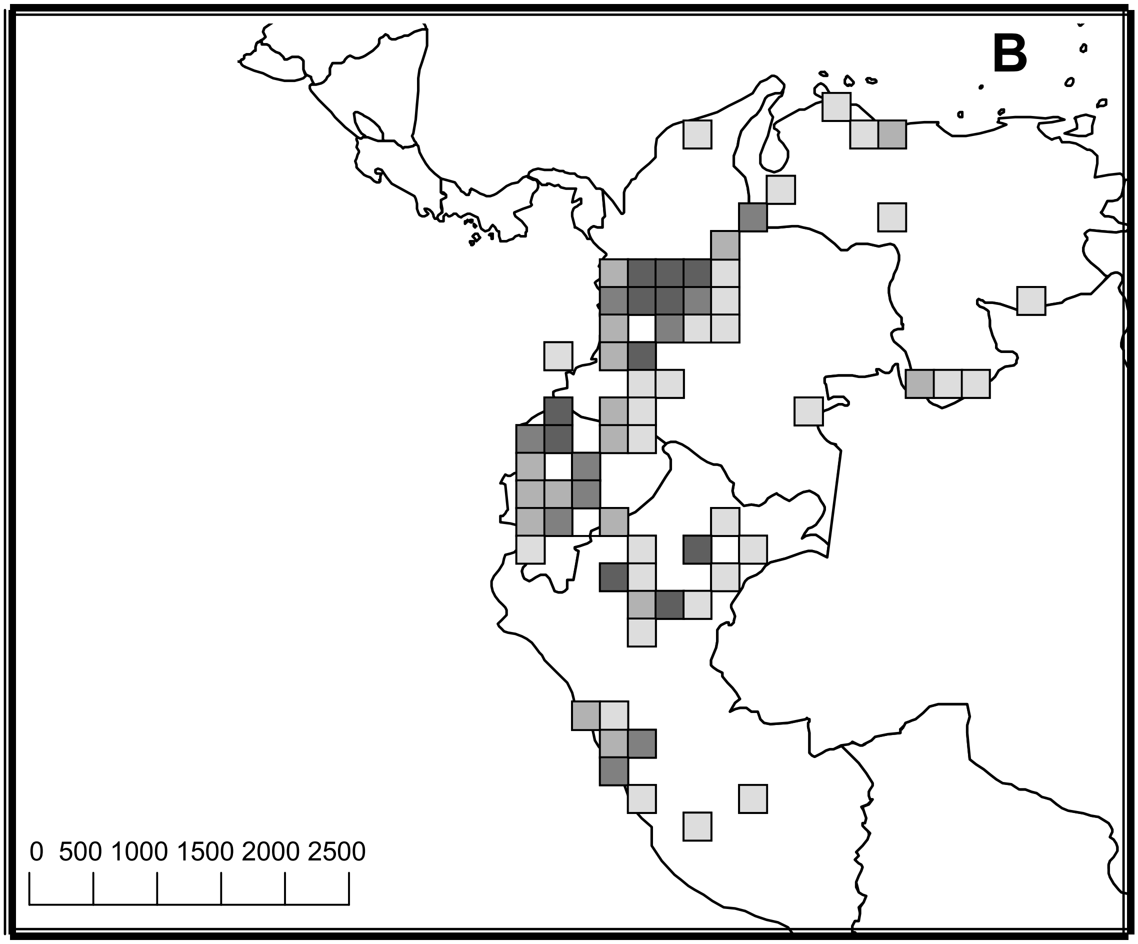
A, B, C. Endemic areas delimited by the PAE. Densities of endemic species to the study area. The levels of saturation (increasing darkness) follow the scale: (1 to 10 endemisms), (11 to 20) and (21 to 30).

Figure 2.

A, B, C. Generalized Tracks of the Genus *Piper.*

Figure 1.

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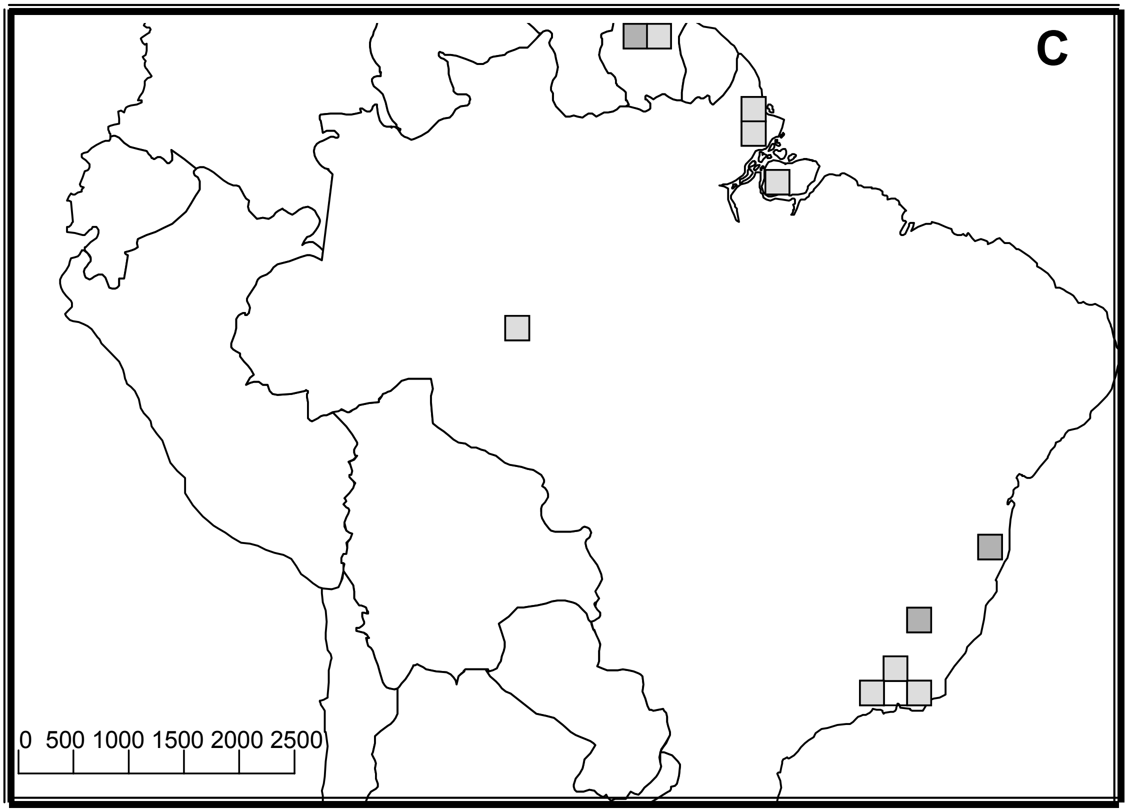
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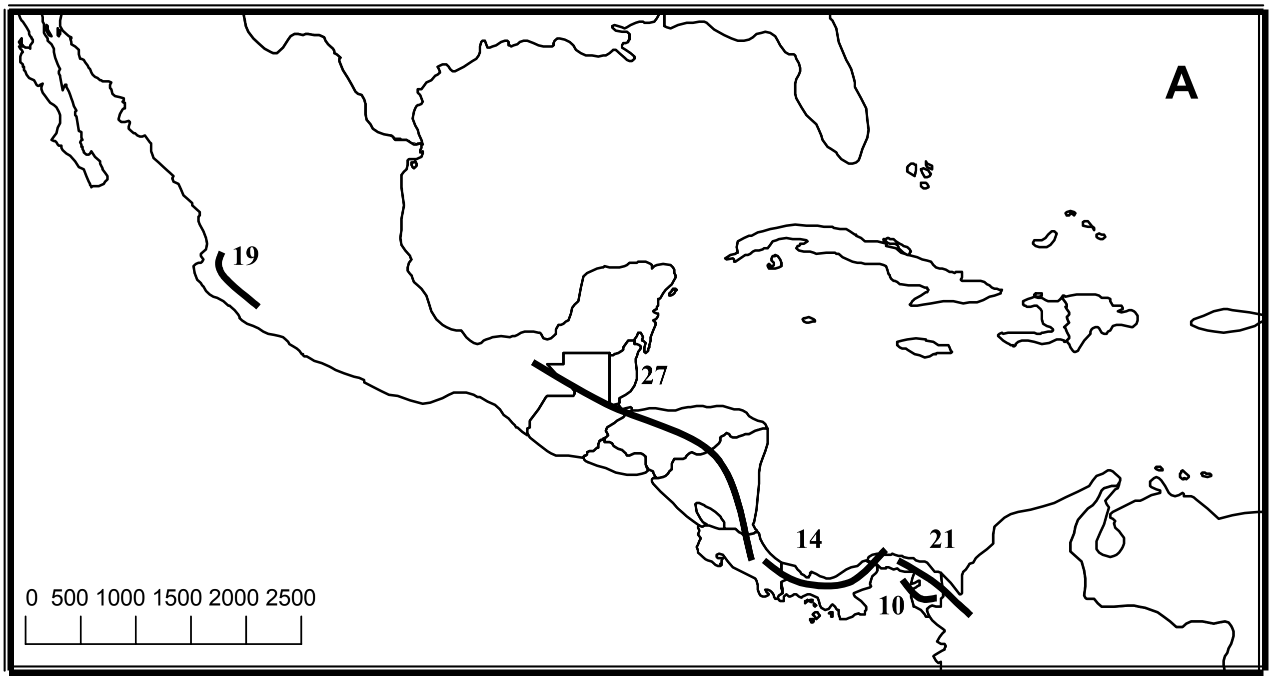
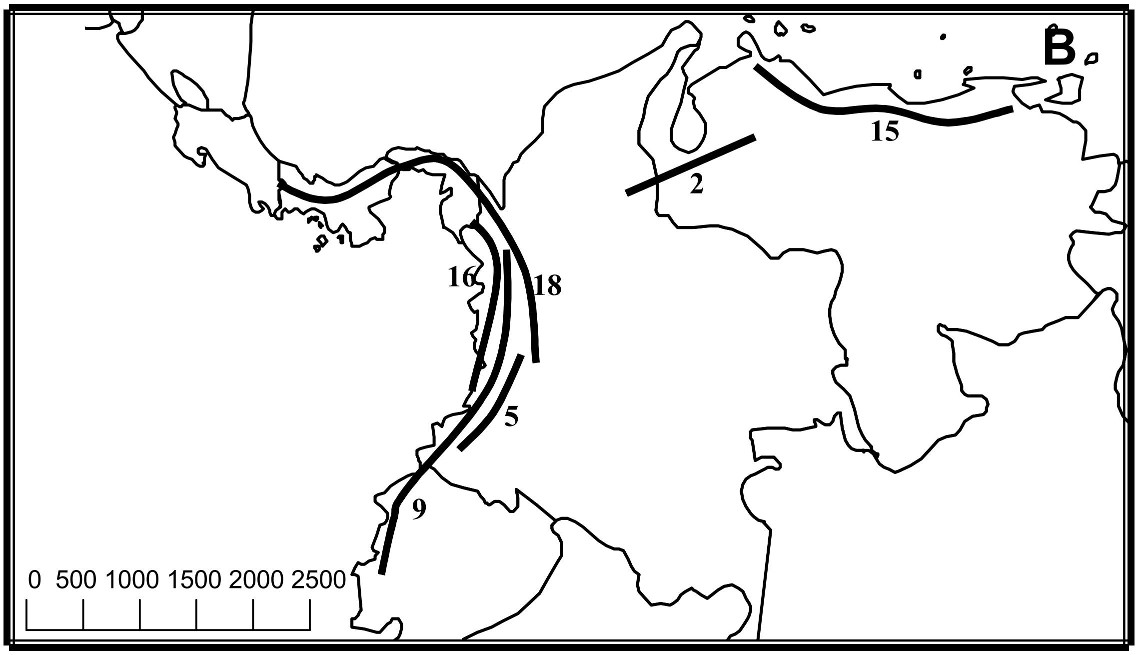
Figure 2

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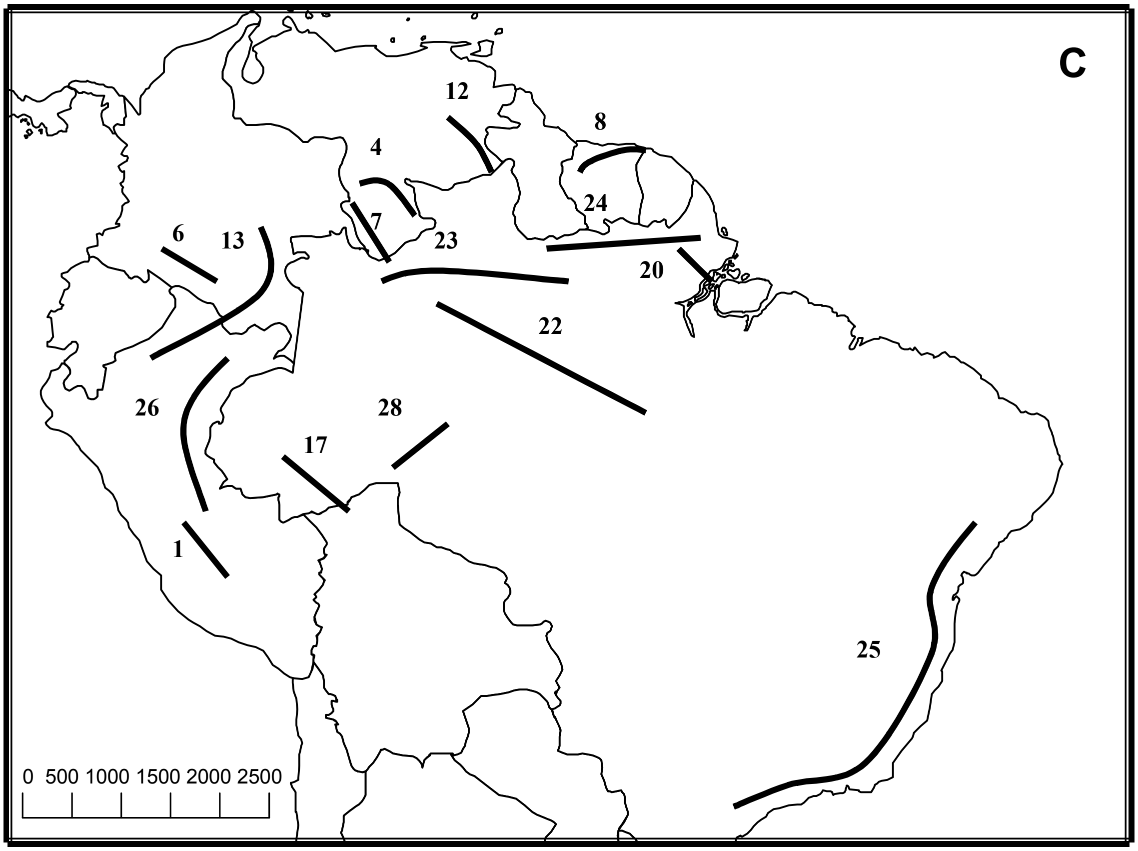
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Table 1. Summary of the results obtained in the PAE.

Region	**Subregion**	**Province**	**Number of Endemic Areas.**	**% of endemic areas for the subregion.**	**Number of species.**	**Number of species for the Subregion.**	**% of endemic species for the subregion.**
Andean Region	Paramo Punan.	Norandean Paramo	16	**23.07**	75	162	**22.56**
		Puna	8		87		
Neotropical Region	Caribbean.	Cauca	4	**46.15**	32	381	**53.08**
		Chiapas	2		10		
		Choco	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		
		Ucayali	1		3		
	Parana.	Brazilian Atlantic Forest.	3	**3.84**	10	15	**2.08**
		Parana Forest.	1		5		

Table 2. Generalized tracks with their respective supporting species.

Region	Subregion	Province	Number of Generalized Tracks for the subregion	Track code	Species support
Andean	Paramo Punan.	Puna.	1	1	*Piper carrapanum, P. brevestrigillosum, P. brevipedunculum, P. cispontinum, P. edurumglaberimicaule, P. huantanum, P. perenense, P. planipes, P. pontis, P. scabricaule, P. serotinum, P. sidipilum, P. Tardum*
	Caribbean	Mexican Pacific Coast.	6	19	*Piper brachypus, P. cihuatlanense, P. mcvaughii*
		Venezuelan Coast.		15	*Piper schlimii, P. cumbotianum, P. nobile, P. marturense, P. sierra_aroense*
		Eastern Central America.		10	*Piper canaliculum, P. acutissimum, P. alstonii, P. amphibium, P. barbinerve , P. breve , P. cativalense, P. chagresianum , P. culebranum , P. diazanum, P. frijolesanum_grandifolium, P. gatunense , P. gonocarpum ,P. humorigaudens, P. luciguadens , P. minute_scabiosum , P. non_retrorsum, P .panamense, P. persubulatum , P. portobellense, P. pseudocativalense, P. salamancanum, P. tabernillanum , P. tapianum, P. tecumense*
		Mexican Pacific Coast, Eastern Central America, Western Panamanian Isthmus.		14	*Piper affectans, P. agellifolium, P. altevaginans, P. amphoricarpum, P. arcte_acuminatum, P. barbirostre, P. biauritum, P. biseriatum, P. callibracteum, P. carminis, P. carpinteranum, P. casitense, P. chiriquinum, P. ciliatifolium, P. coronatibracteum, P.corrugatum, P.davidianum, P.davidsonii, P. fluvii-initii, P. fortunaensis, P. fusco_granulatum, P. glabrescens, P. goergeri, P. jubatum, P. magnilimbum, P. subfuscum*
		Choco, Eastern Central America.		21	*Piper daguanum, P. gamboanum_yapense, P. latibracteum, P. laxispicum, P. magnantherum, P. obaldianum, P. pallidibracteum, P. pervenosum, P. pinoganense, P. polyneurum, P. pseudohodgei, P. pseudoviridicaule, P. sambuanum, P. scabrilimbum, P. sperdinum, P. subcaudatum, P. turbense, P. viridicaule*

	Western Panamanian Isthmus, Mexican Gulf, Eastern Central America.		27	*Piper barbulatum, P. donnell_smithi, P. flavidum, P. lanosibracteum, P. leptoneuron, P. luxii, P. matinanum, P. santa-rosanum, P. subcitrifolium, P. uspantanense, P. variabile*
Amazonian	Guyana.	12	12	*Piper bolivarianum, P. sabanaense, P. tamayoanum, P. kegelianum, P. cernuum_perlongispicum, P. venamoense, P. hippocrepiforme, P. politii_toronoense*
			20	*Piper schwackei, P. substilosum, P. glandulosissimum*
	Humid Guyana.		8	*Piper nematanthera, P. gleasonii , P. paramaribense , P. poiteanum, P. regelianum, P. adenandrum, P. regelii, P. romboutsii , P. rudgeanum, P. insigne , P. saramaccanum, P. pulleanum.*
	Imerí.		4	*Piper perciliatum, P. javitense, P. cililimbum, P. pubivaginatum, P. liesneri, P. mosaicum*
	Napo.		6	*Piper corpuientispicum, P. calanyanum, P.florencianum, P. peculiare, P. statum, P. sucreense, P. purulentum*
	Pantanal.		17	*Piper moense, P. udisilvestre*
	Imeri.		7	*Piper otto_huberi, P. para-peltobryumbryon*
	Imeri, Napo.		13	*Piper japurence, P. maranyonense*
	Imeri, Napo.		23	*Piper froesii, P. silvigaudens, P. uapesense*
	Imeri, Pantanal, Amapá.		22	*Piper purusanum, P. coariense, P. limosum, P. subcostatum,*
	Amapá, Roraima.		24	*Piper carniconectivum, P. gurupanum, P. rupunianum, P. striatipetiolum, P. subglabrifolium*
	Madeira, Pantanal.		28	*Piper brachypetiolatum, P. madeiranum, P. tridentiphilum*
Parana	Brazilian Atlantic Forest.	1	25	*Piper hayneanum, P. permucronatum, P. guimaraesianum*

Andean-Neotro	Paramo Punan, Caribbean.	North Andean Paramo, Cauca, Choco, Arid Ecuador, Western Ecuador.	6	9	*Piper regale, P. bullosum, P. filistylum, P. killipii, P. pubestilis, P. bellowi, P. villosum, P. anisatum, P. peñasblancas, P. ambiguum, P. acaule, P. obovatilimbum, P. altaqueriano, P. barbacoense, P. alejandrinum, P. cyphophyllopse, P. cyphophyllopse_brevipes, P. debilicaule, P. entradense, P. ignacioanum, P. parcum, P. poscitum, P. supernum, P. townsendii, P. mexiae, P. catripense, P madisonii, P. cangapianum, P. arobense, P. tobarensis*
		North Andean Paramo, Venezuelan Llanos.		2	*Piper deliciasanum, P. viridistachyum, P. pendentispicium.*
		North Andean Paramo, Choco.		5	*Piper pseudoshupii, P. montanum, P. aguadulcense, P. veneralense, P. golondrinum, P. alwini, P. foreroi*
		North Andean Paramo, Choco, Cauca.		16	*Piper atrobaccum, P. bahiasolano, P. barklegi, P. basilobatum, P. blanquita, P. bolivar, P. brachypodon, P. caudefactum, P. certeguiense, P. condotoense, P. contraverrugosum, P. cordilimbum, P. cristalinanum, P. diguaense, P. enganyanum, P. espejuelanum, P. espoliatum, P. exserens, P. fructescens, P. gesneroides, P. heterolrichum, P. ledezmae, P. lellingeri, P. lloro, P. mandinganum, P. monsalvianum, P. patoense, P. pedunculatum, P. pendulirameum, P. pilibracteum, P. pseudo oxistachium, P. pseudocordi, P. ramosense, P. roblalense, P. roldani, P. silvaticum, P. subconcinum, P. subnitidum, P. tutunendó, P. umbriculum, P. urrao, P. yatoensis, P. zingara*

	North Andean Paramo, Eastern Central America, Western Panamanian Isthmus, Mexican Pacific Coast, Magdalena, Cauca.	18	*Piper amphioxys, P. annulatispicum, P. augustum_andino, P. betanii, P. borucanum, P. bullulaefolium, P. caeruleifolium, P. campamento, P. churruyacoanum, P. cocornanum, P. copacabanense, P. cyprium, P. divortans, P. domingense, P. dumeticola, P. el_bancoanum, P. epyginium, P. escobinifolium, P. falanense, P. fatoanum, P. fonnegrae, P. hermosanum, P. intersitum, P. jericoense, P. la_doradense, P. miramarense, P. multiforme, P. nigricaule, P. nodosum, P. nudifolium, P. pennellii, P. perpusillum, P. pseudo lagunaense, P. pseudovariabile, P. raizudoanum, P. scobinifolium, P. semitarium, P. semperflorens, P. sneidernii, P. soejartoi, P. subdilatatum, P. subnudispicum, P. subtrinerve, P. taboganum, P. tolimae, P. vargasis, P. virgatum, P. zacatense*
Paramo Punan, Amazonian.	Puna, Pantanal, Napo, Ucayali.	26	*Piper adreptum, P. albogranulatum, P. apodum, P. asclepiadifolium, P. barbicuspe, P. celer, P.circumspectantis, P. cupreatum, P. claudicans, P. epunctatum, P. ferruginispicum, P. indianonum, P. interitum, P. klugianum, P. mishuyacuense, P. paganicum, P. papillipetiolatum, P. pernigricans, P. pervulgatum, P. rugosilimbum, P. sanguineispicum, P. scapispicum, P. scapispicum, P. subsilvestre, P. villosispicum, P. vitaceum*