Plant Ecology **174:** 163–181, 2004.

Geographical distribution of *Eupatorieae* (*Asteraceae*) in South-eastern and South Brazilian Mountain Ranges

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Received 17 July 2002; accepted in revised form 18 August 2003

Key words: Biogeography, Brazilian mountain ranges, Mantiqueira range, Mountaintops, Species distribution, Species occurrences

Abstract

This study deals with the geographical distribution of Eupatorieae species in South-eastern and Southern Brazilian mountain ranges, with special emphasis on the Mantiqueira range (Serra da Mantiqueira). In the Mantiqueira range, five localities were sampled for two years during the flowering period of the plants. Species composition in the Mantiqueira localities was then compared to data from a central range (the Espinhaço) and a southern coastal range. Cluster and ordination analyses showed clear floristic differences among the three ranges. Nearer localities were more similar floristically only within the Espinhaço range and across all ranges, as shown by Mantel tests. The dendrogram in the Mantiqueira range clustered Itatiaia and Campos do Jordão, two non-adjacent localities with similar environment, landscape and topography. Different processes may be influencing the structure and composition of the Eupatorieae flora at different geographical scales. Historical and biogeographical processes may be more important in determining community composition of different mountain ranges, whereas factors such as climate and human impact may be determining differences among localities within each mountain range.

Introduction

In recent years ecologists seeking for patterns of community structure have shifted their attention from the local to the regional scale (e.g., Ricklefs and Schluter 1993; Brown 1995; Brown et al. 1996; Caley and Schluter 1997). Local communities are not isolated ecological units. Regional and historical processes operating on larger temporal and spatial scales are required to explain the local abundance, distribution and diversity of species (Ricklefs and Schluter 1993; Brown 1995).

The inability derive global patterns of biodiversity from local environmental conditions alone has led researchers to search for other explanatory concepts. Following the reasoning of island biogeography (MacArthur and Wilson 1963; MacArthur and Wilson 1967), one can investigate the patterns of convergence of biodiversity among ecologically similar but geographically separate localities, setting local assemblages into the context of regional processes (Ricklefs and Schluter 1993).

Islands and mountaintops are outstanding systems in which to address this problem, both showing the imprint of physical isolation. In some cases, such as tropical East Africa, where some mountains reach more than 4000m above sea level, mountaintops are more effectively isolated than oceanic islands (Hedberg 1970); no diaspore of a mountain plant will normally be carried across the savannah by an agent equivalent to oceanic currents, and no plant species will survive in the intervening savannah valleys.

Plant species occurring in mountain ranges face certain problems that restrict the occurrence areas of most species. Abiotic factors *e.g.,* climate (Bruijnzeel and Veneklaas 1998; Safford 1999a) or soil conditions (Smith 1994; Sollins 1998; Tanner et al. 1998) change along with altitude. Small areas with homogeneous conditions are limited colonization targets, often restricting species to a small altitudinal range of a particular mountain, sometimes even to a single slope. Thus, a species able to disperse through various altitudes is of necessity a habitat generalist. Furthermore, to disperse among different mountains, a species must be capable of colonizing intermediate valleys (habitat generalists), have extraordinary dispersal ability through air flotation (Hedberg 1970) or long-distance dispersing agents. Suitable areas for high-altitude specialists are often too small to support indefinitely a population, which will then depend on immigration to persist (the ‘mass effect’ of Shmida and Wilson 1985).

The present study is centred in *campos* (= fields), open physiognomies that occur above treeline (*c.a.* 1,000m) in three Brazilian mountain ranges that extend from the state of Bahia to northern Rio Grande do Sul: the Espinhaço range (in the states of Bahia and Minas Gerais, but we studied only in the latter), the Mantiqueira range (in Minas Gerais, Rio de Janeiro and São Paulo) and the Southern Coastal range (studied in Santa Catarina and Rio Grande do Sul). Within each mountain range the *campos* are separated by deep and extensive river valleys in numerous patches and so present a discontinuous distribution.

Botanists and phytogeographers distinguish “campos de altitude” – high altitude grasslands – from “campos rupestres” – rocky grasslands – from “campos de cima da serra” – fields above *Araucaria* forests. The first term is reserved for plateaus mainly in the Mantiqueira range above treeline (Safford 1999a); the second is used for fields or higher slopes and mountaintops in central Brazilian mountain ranges, especially in the Espinhaço range (Giulietti and Pirani 1988); the last term is used for fields above *Araucaria angustifolia* (Bertol.) O.Kuntze forests in Santa Catarina and Rio Grande do Sul, with common frosts in winter (Menezes 2000).

Although recognized as different physiognomies, these montane campos have much in common. They are composed basically of herbaceous vegetation with xeromorphic perennials, mainly grasses and herbaceous Asteraceae and Melastomataceae, with many endemic species (*e.g.,* Safford 1999a, b). According to Safford (1999a) the *campos de altitude* (or “Brazilian páramos”) in the Mantiqueira range are among the most diverse natural communities in extra-Amazonian Brazil, with very high numbers of endemic species (Safford 1999a,b); yet, till now they have been relatively neglected by ecologists and conservation biologists in contrast to the Atlantic rainforest and the cerrado (savannah) woodlands.

These areas have been visited and collected by many botanists, which has resulted in an extensive literature comprised of local species lists and taxonomic descriptions of particular families. The distinction of the *campos* in the southern Brazilian mountain ranges into distinct vegetation formations is based on geographical location, their underlying geology and their floristics, especially their unique or typical taxa (e.g., Martinelli 1989; Rizzini 1995). Brazilian montane regions are thus still largely lacking in biogeographic studies and, in the Neotropical domain, they are far less known than several ranges in Mexico and within the Andes (*e.g.,* Rundel et al. 1994). This paper, to our knowledge, presents the first comparison among areas based on a common taxon that is well represented in all areas. Moreover, our data come from comparable samples that, although not strictly standardised, can be investigated by multivariate methods commonly used in vegetation ecology.

Asteraceae is the largest family of dicotyledonous plants with about 23,000 described species widely dispersed through all environments and continents except Antarctica (Bremer 1994), though they are more abundant and diverse in open and /or non-forested areas. The tribes of Asteraceae are well established natural subdivisions (Heywood et al. 1977; Jansen et al. 1991; Bremer et al. 1992; Bremer 1994). The tribe Eupatorieae is pantropical and the most diverse in Brazilian open areas, and its taxonomy has recently been reviewed and is now well established (Barroso et al. 1986; King and Robinson 1987). The tribe Eupatorieae is therefore well-suited to examine local assemblages and their variation in our region of interest.

Methods

Study areas

The Mantiqueira range is divided in two distinct geomorphological units, the Campos do Jordão and Itatiaia massifs (Gatto et al. 1983). The Campos do Jordão massif encompasses the states of Minas Gerais and São Paulo; our sampling locality of Campos do

Jordão and part of the sites of Passa Quatro are included in this unit. The Itatiaia massif reaches the states of Minas Gerais and Rio de Janeiro; it includes the sampling localities of Ibitipoca, Visconde de Mauá, Itatiaia and part of Passa Quatro (see sampling methods for a description of collection sites).

The Serra da Mantiqueira extends roughly in the NE-SW direction, bordering on the states of Rio de Janeiro, Minas Gerais and São Paulo. The climate is sub-humid to humid. The tree line in Itatiaia averages between 2000m and 2200m, which is considered low for its latitude (Körner 1998). Above treeline, annual precipitation ranges from 1500-2000mm in the *campos de altitude* of São Paulo and Minas Gerais, to 2000-3000mm in Rio de Janeiro. Maximum precipitation occurs in January (mid-summer) and minimum precipitation in July (winter). The dry season is characterized by less than 50mm precipitation and lasts from one to three months (June-August) in all the southeastern mountains of Mantiqueira (Safford 1999a,b). Although it has been speculated that the Itatiaia summits suffered glaciation during the Pleistocene, there is no solid evidence for this (Safford 1999a). Frost occurs on average 56 days per year at 2200m in Itatiaia and at 1600m in Campos do Jordão, mostly during the dry winter (July). Drought may be partly offset by orographic fog, which in Itatiaia occurs 218 days per year at 2200m. In Itatiaia, monthly average of air humidity ranges from 65% to 90% (Safford 1999a).

Above the tree line we find the *campos de altitude*, “a series of humid, subalpine grasslands restricted to the highest peaks and plateaus of the South-eastern Brazilian Highlands. Comprising a classic terrestrial archipelago of isolated, mountaintop habitats, these systems form the highest, coldest orobiome in eastern South America” (Safford 1999a, b). The three largest families in Itatiaia and presumably in the entire Mantiqueira are the Asteraceae, Polypodiaceae s.l. and Melastomataceae, summing about 40% of the plant species. In Itatiaia, the savannah-like associations dominated by Asteraceae, especially the genus *Baccharis* and tribes Eupatorieae and Vernonieae, are probably the most species-rich formation in the *campos*. About a third of the vascular plant species in the Itatiaia *campos de altitude* appear to be endemic to this physiognomy (Safford 1999a).

The Serra do Espinhaço (Espinhaço Range) extends from Northern Bahia southward to the Serra do Ouro Branco in the state of Minas Gerais. Its upper reaches are covered by *campos rupestres* lying between 700 and 2,000m in elevation (Giulietti and Pirani 1988). The climate is mesothermic with mild summers accompanied by a rainy season. The dry winter season lasts 3 to 4 months, in which frosts can occur, but not as frequent as in Mantiqueira or the Southern range. The average annual temperature varies from 17° to 20 °C. The *campos rupestres* are interspersed with cerrado patches with denser shrubs and sparse treelets (Davis et al. 1997). As in the Mantiqueira, the *campos rupestres* vegetation is composed mainly of grasses and asteraceans.

In Southern Brazil the *campos de cima da serra* vegetation occurs in montane areas above 1000m in elevation, above *Araucaria angustifolia* forests, extending through the states of Santa Catarina and north-eastern Rio Grande do Sul. These regions present frosts very often during winter (Menezes 2000).

Sampling methods

For present purposes, we define *region* as one mountain range. *Locality* is a regional subdivision that includes a group of sampling *sites*. A *site* is each point where the Eupatorieae assemblage was sampled. For instance, Mantiqueira range is considered a *region* and Ibitipoca is called a *locality* with several sampling *sites*.

Five localities were sampled in each mountain range (see Figure 1 for localities’s codes and geographical distribution and Table 1 for coordinates). Since Mantiqueira flora will be described in more detail, we detail here only the five localities sampled within this mountain range:

IB – Ibitipoca State Park, in the State of Minas Gerais. This is the northernmost part of the Mantiqueira and also the locality closest to the Espinhaço range. Our sampling sites mostly comprised *campos de altitude*.

VM – The *Visconde de Mauá,* on the border between the States of Minas Gerais and Rio de Janeiro, is an important sampling area on the slope opposite to the Itatiaia National Park. Since we could not reach the mountaintops, we sampled only in open sites within the highland forest belt, close to but not within the *campos de altitude* proper.

IT – Itatiaia National Park, which also lies on State border between Minas Gerais and Rio de Janeiro, includes the Agulhas Negras peak, the second highest Mantiqueira summit at 2789m. On its southwestern slope and highland plateaus we had access to its

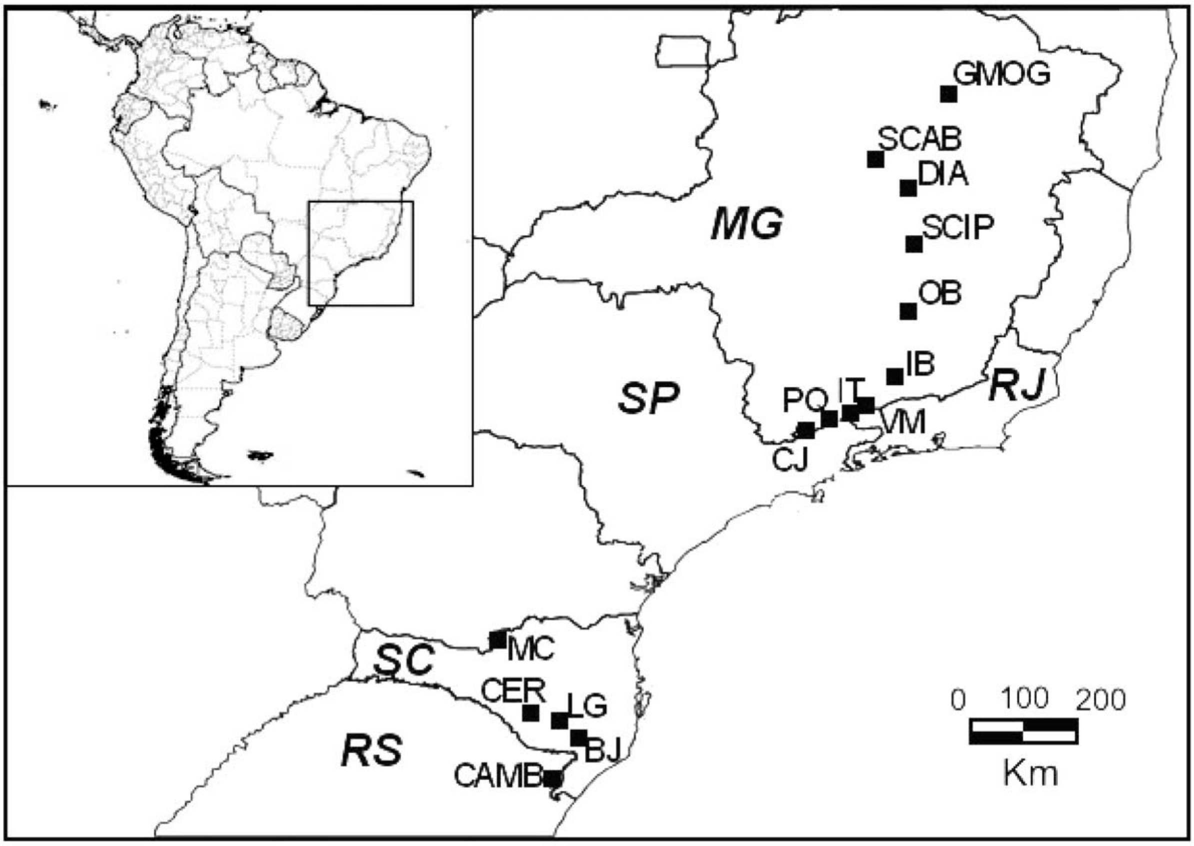


Figure 1. Sampling localities in the Espinhaço, Mantiqueira and Southern ranges. Espinhaço localities are: *GMOG* – Serra do Grão Mogol, MG, *SCAB* – Serra do Cabral, MG, *DIA* – Planalto de Diamantina, MG, *SCIP* – Serra do Cipó, MG and *OB* – Serra do Ouro Branco, MG. Mantiqueira localities are: *IB* − Ibitipoca, MG; *VM* − Visconde de Mauá, MG/RJ; *IT* − Itatiaia, RJ/MG; *PQ* − Passa Quatro, MG; *CJ* − Campos do Jordão, MG/SP. Southern localities are: *MC* – Matos Costa (SC); *LG* – Lages (SC); *CER* – Cerrito (SC); *BJ* – Bom Jardim (SC); *CAMB* – Cambará do Sul (RS). States are: *MG* – Minas Gerais, *RJ* – Rio de Janeiro, *SP* – São Paulo, *SC* – Santa Catarina, *RS* – Rio Grande do Sul. See Table 1 for coordinates of reference points.

campos de altitude, the most extensive in the Mantiqueira.

PQ – Passa-Quatro in Minas Gerais. Sampling sites in this locality were spread out, along dirt roads and tracks in the mountains. This area is more inhabited and the landscape is dominated by secondary highland forest and small-cultivated holdings.

CJ – The *Campos do Jordão* locality is situated in São Paulo state, intruding slightly into Minas Gerais in the direction of Itajubá. Our sampling sites were in *campos de altitude* or in highland forest.

Whenever possible, we preferred to travel between localities on dirt roads within the mountains, along which we could take additional samples. Linear distances between pairs of localities varied from 26 km between Visconde de Mauá and Itatiaia, to 203 km between Ibitipoca and Campos do Jordão, the two extreme sampled mountains.

Six field trips were carried out in the Mantiqueira range, from January to June in 1998 and 1999, encompassing the flowering and fruiting of all Eupatorieae. In only one trip not all localities were surveyed. In each of the five localities a minimum of fifteen sites were chosen for sampling plants, with a minimum of 1km (exceptionally, 500m) spacing among them. In each site, all flowering and/or fruiting Eupatorieae species were sampled. Although each sample site was chosen for the presence of Eupatorieae, all flowering and/or fruiting Asteraceae species present in the site had at least one voucher specimen collected. Exact geographical coordinates of each site were obtained with a GPS receiver.

Data analysed for the Espinhaço range in central and northern Minas Gerais are from 1995-1996 samples in February, April, July and September, and for south Brazilian ranges in February, April and Oc-

Table 1. Codes for the localities within three Brazilian mountain ranges, with their name, main county, state, and reference coordinate of the locality centroid, used to measure distances among localities. States are: MG – Minas Gerais, RJ – Rio de Janeiro, SP – São Paulo, SC – Santa Catarina, RS – Rio Grande do Sul.

Mountain Range	Code	Name	Municipality	State	Lat (S)	Long (W)
Espinhaço	GMOG	Grão Mogol	Grão Mogol	MG	16° 32.64'	42° 54.87'
	SCAB	Serra do Cabral	Joaquim Felício	MG	17° 42.95'	44° 14.51'
	DIA	Diamantina	Diamantina	MG	18° 15.20'	43° 41.10'
	SCIP	Serra do Cipó	Santana do Riacho	MG	19° 17.29'	43° 35.45'
	OB	Ouro Branco	Ouro Branco	MG	20° 30.05'	43° 39.71'
Mantiqueira	IB	Ibitipoca	Lima Duarte	MG	21° 41.58'	43° 52.73'
	VM	Visconde de Mauá	Bocaina de Minas	MG	22° 14.38'	44° 29.21'
	IT	Itatiaia	Itatiaia	RJ	22° 22.64'	44° 41.79'
	PQ	Passa Quatro	Virgínia	MG	22° 25.66'	45° 04.51'
	CJ	Campos do Jordão	Campos do Jordão	SP	22° 39.48'	45° 33.41'
South	MC	Matos Costa	Matos Costa	SC	26° 29.18'	51° 07.63'
	CER	São José do Cerrito	Lages	SC	27° 47.09'	50° 29.61'
	LG	Lages	Lages	SC	27° 55.30'	49° 59.30'
	BJ	Bom Jardim	Bom Jardim da Serra	SC	28° 14.76'	49° 36.91'
	CAMB	Cambará do Sul	Cambará do Sul	RS	29° 08.61'	50° 04.77'

tober in the same years. In these regions we used the same sampling methods, but focused on the five major Brazilian tribes of Asteraceae, including the Eupatorieae (*e.g.,* Prado 1999; Prado and Lewinsohn 2000).

Species assignment

Voucher specimens were first compared and assigned to morphospecies and later to species, with nomenclature following King and Robinson (1987) and references therein. Although in the field we collected separate vouchers for any difference noted, slight morphological variants were later grouped and treated as single species, so that our operational taxonomy was mostly conservative (to avoid undue splitting and inflating differences among sites and localities). Specialists (see acknowledgements) confirmed, corrected and completed our species identifications.

Six probably new Eupatorieae species, almost all from the Southern Brazilian range, were only identified to tribe (see Appendix). Since they are different morphospecies from all the other identified ones, they were included in the analyses.

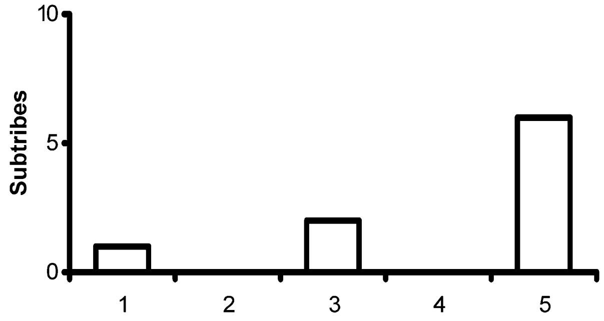
Data analysis

The floristic dissimilarity between all pairs of localities was expressed by the relativized Euclidean distance of the incidence of each plant species per locality (i.e., the number of sites where the species was sampled per locality). Correlation of floristic dissimilarity and geographical distance among localities was evaluated with the Mantel test (McCune and Mefford 1999). The Mantel p value was obtained with a randomisation (Monte Carlo) test for the pool of the three ranges, and with Mantel's asymptotic approximation for each range, since five localities is a small sample size, resulting in a small number of possible permutations of the data. The geographical distance between two localities was calculated as a simple geometric linear distance. The centroid of sampling sites for each locality was used as reference point for that locality. Over the range of distances considered and the precision of the data set, geodesic correction was not deemed necessary.

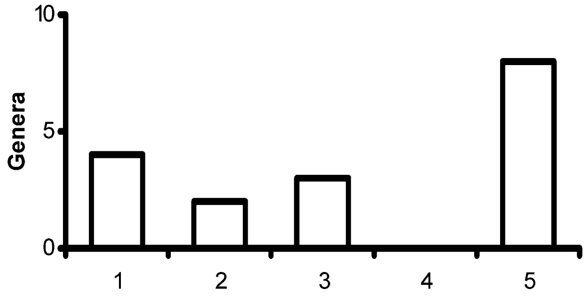
Localities were clustered using relativized Euclidean distances for species frequencies within localities, with the UPGMA aggregation method (Digby and Kempton 1987).

Localities were also subjected to ordination by detrended correspondence analysis (DCA), using the occurrence of each plant species per locality as a surrogate measure of local abundance. DCA is an improvement of ordinary Correspondence Analysis in which putative distortions are removed by rescaling of individual axis segments (Gauch 1982; Digby and Kempton 1987). Since DCA is sensitive to low values, species were selectively weighted: abundances of all species rarer than 20% of the frequency of the commonest species were downweighted in proportion to their frequency, thus reducing the effect of these

a. Subtribes



b. Genera



c. Species

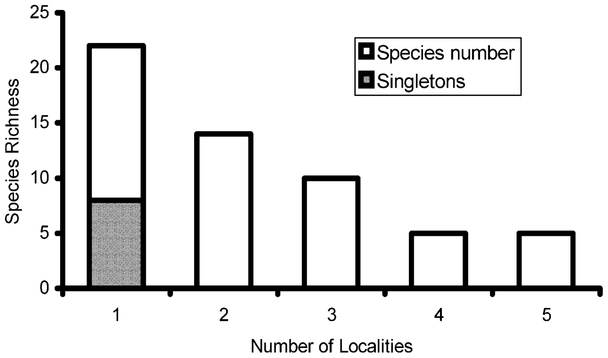


Figure 2. Occurrence of Eupatorieae subtribes (a), genera (b) and species (c) in localities of the Mantiqueira range. Note that the number of species that are singletons is higher than the number of species recorded in four or five localities.

rarer species on the final configuration (McCune and Mefford 1999).

Analyses were performed with Systat© (SPSS Inc. 1997) and PC-Ord© (McCune and Mefford 1999).

Results

Eupatorieae in the Mantiqueira range

In the Mantiqueira range we obtained a total of 596 Eupatorieae collections from 56 species, within an overall elevational range from 760m to 2460m. The 56 species belong to 9 subtribes and 17 genera. The most speciose subtribe and genus in the area was Mikaniinae, with 16 *Mikania* species. The second subtribe in species number was Praxelinae, with 12 species, 11 in the genus *Chromolaena*. At the other extreme, the tribe Adenostemmatinae was represented by a single species, *Adenostemma brasilianum* Cass. and seven genera belonging to various subtribes were represented each by a single species (Appendix).

Not all subtribes and genera were present in all localities (Figure 2a,b). *Adenostemma brasilianum* was found only in Visconde de Mauá, while the subtribe Ayapaninae, with three sampled species, was not sampled in Visconde de Mauá and Passa Quatro, and the subtribe Critoniinae, with two species was not found in Itatiaia and Passa Quatro. Eight genera (47%) occurred in all localities, whereas four genera occurred in only one locality. Only five species (9%) occurred in all localities throughout the Mantiqueira: *Ageratum fastigiatum* (Gardner) R. King and H. Robinson, *Austroeupatorium silphiipholium* (Martius) R. King and H. Robinson, *Campovassouria cruciata* (Vell. Conc.) R. King and H. Robinson, *Campuloclinium purpurascens* (Schultz- Bip. ex Baker) R. King and H. Robinson and *Chromolaena laevigata* (Lam.) R. King and H. Robinson (see Appendix for a complete list of species and their localities). The five species are widespread in other Brazilian mountains (Cabrera and Klein 1989; Lorenzi 1991; Prado 1999).

The richest localities were Ibitipoca, with 157 collections and 32 species, and Campos do Jordão, with 129 collections and 32 species, followed by Visconde de Mauá with 144 collections and 25 species. Substantially lower species richness was found in Itatiaia, with 89 collections and 20 species, and in Passa Quatro, with 77 collections and 16 species. The plant species richness recorded in each locality tended to stabilize with greater sampling effort. The log of total number of records per locality accounted for 78% of local recorded species richness ($r^2 = 0.785$; $p < 0.05$).

Although we found 56 species altogether in the Mantiqueira localities, the maximum in one locality was 32 species in Campos do Jordão and Ibitipoca, which suggests a fairly high species turnover among localities. In fact, a high proportion of the species (22 species, 39%) was found in a single locality, eight of which were singletons – were collected only once – in the Mantiqueira range. Most species showed a restricted distribution and only 10 species (18%) were found in four or five localities (Figure 2c).

It is worth noting that Praxelinae, the most widely distributed and second most speciose subtribe in the studied ranges, was represented in Itatiaia by only one species with three records (*Chromolaena laevigata*), while on the opposite slope of the same mountain, in Visconde de Mauá, we obtained six species from this subtribe (Appendix).

Some common and widespread species were not found in one or more localities in the Mantiqueira range. Itatiaia was the only locality previously surveyed for Asteraceae, where Barroso (1957) listed 42 Eupatorieae species. Sixteen of these species (38%) were not found in the localities we surveyed (from which more than half (56%) belong to the genus *Mikania*); 15 species were collected in Itatiaia and 10 were collected in the Mantiqueira range but not in Itatiaia itself. *Mikania vitifolia* DC., listed by Barroso (1957) in the Itatiaia, was recorded by us only once in Bom Jardim (in the Southern Brazil mountain ranges). A more recent paper with a non-comprehensive floristic survey (Barros et al. 1998) cites eight Eupatorieae species occurring in Itatiaia, all of them previously cited by Barroso (1957). On the other hand, we collected six species in Itatiaia that were not cited by either of the preceding studies.

Barroso's (1957) pioneering paper was based on specimens amassed in a number of botanical excursions that covered the Itatiaia Park more widely and encompassing more habitats than we did; thus, several of the species we did not detect are vines in rainforest gaps or edges at lower elevations. For instance, *Ageratum conyzoides* L., a widespread weed in Brazil (Lorenzi 1991) listed by Barroso (1957) in the Itatiaia park, was not found in the sites sampled for this study, although it was previously noted in roadside clearings, camp sites and other disturbed areas in the lower part of Itatiaia (Lewinsohn, unpublished). Another widespread species, *Trichogoniopsis adenantha* (DC.) R. King and H. Robinson (=*Trichogonia gardneri*), which in the Mantiqueira range was found only once in Ibitipoca, is a common and fairly widespread species (Lewinsohn, unpublished).

The montane Eupatorieae flora in south-eastern and southern Brazil

A total of 2351 records of 534 species in 15 Asteraceae tribes were obtained in the three studied ranges. The tribe Eupatorieae represents almost half (1051 vouchered collections or 45%) of samples and more than a quarter of the species (144 species or 27%) recorded. Both the Espinhaço and the Southern ranges had a high proportion of singletons, respectively 40% and 41% of the Eupatorieae species recorded. When the three ranges are considered, the Eupatorieae singleton species in the Mantiqueira are reduced to six species, or four percent of species from the three ranges.

In the Espinhaço range we obtained 1081 Asteraceae collections belonging to 277 species, while in the Southern mountains we obtained 442 collections and 139 species and in the Mantiqueira range we obtained 828 collections and 149 species (Table 2). Since in the Mantiqueira we focused on Eupatorieae

Table 2. Number of collections and species of the main Asteracean tribes in three Brazilian mountain ranges. Espinhaço and Southern ranges were collected in 1995 and 1996, whereas Mantiqueira was collected in 1998 and 1999. Eupatorieae tribe is in bold. "Others" include the tribes Cardueae, Gnaphalieae, Inuleae, Lactuceae, Helenieae, Plucheae, Moquiniae, Tageteae and the subfamily Barnadesioideae.

	Mantiqueira		Espinhaço		Southern Range	
Tribe	Collections	Species	Collections	Species	Collections	Species
Astereae	70	33	57	17	88	24
Eupatorieae	**601**	**56**	**315**	**68**	**135**	**46**
Heliantheae	15	7	89	39	20	9
Mutisieae	10	7	93	21	38	14
Senecioneae	23	15	31	7	67	15
Vernonieae	97	19	462	113	61	14
Others	12	12	34	12	33	17
Total	828	149	1081	277	442	139

species, records for this tribe represented almost 75% of all collections in this range, while in both the Espinhaço and Southern ranges Eupatorieae collections represent about 30% of plant collections. Proportional Eupatorieae species richness, on the other hand, varied less, from 24.5% of species in the Espinhaço to 33% in the South and 37.6% in the Mantiqueira ranges (Table 2).

The tribe Eupatorieae in the three mountain ranges is represented by 10 subtribes and 26 genera. The subtribe Alomiinae is the only one not represented in the Mantiqueira, and is represented by one species, *Pseudobrickellia brasiliensis* (Sprengel) R. King and H. Robinson, present in four localities in the Espinhaço range. This genus is restricted to mountains in Minas Gerais and Goiás (King and Robinson 1987). The most speciose subtribe is Mikaniinae with 43 *Mikania* species, followed by the subtribe Praxelinae with 29 *Chromolaena* species. Conversely, eight genera from various subtribes are represented by single species: *Pseudobrickellia brasiliensis, Ophryosporus freyreysii* (Thunb. and Dallm.) Baker, *Campovassouria cruciata, Hatschbachiella tweediana* (Hook and Arn.) R. King and H. Robinson, *Stomatanthes polycephalus* (Schultz-Bip. Ex B. Robinson) H. Robinson, *Gyptis crassipes* (Hieron.) R. King and H. Robinson, *Trichogoniopsis adenantha* and *Vittetia orbiculata* (DC.) R. King and H. Robinson.

The Eupatorieae species turnover across the three mountain ranges is fairly high. From the entire pool of 144 Eupatorieae species we found, 120 (83%) Eupatorieae species were found in a single mountain range, whereas only two species, *Mikania micrantha* H. B. K. and *Chromolaena laevigata* occurred in all three ranges (Figure 3). Only 13 species (9%) are shared solely between the Mantiqueira and Espinhaço, eight (5.5%) co-occur only in the Mantiqueira and Southern ranges, and a single species, *Raulinoreitzia tremula* (Hook and Arn.) R. King and H. Robinson occurred in the Espinhaço and Southern ranges but was not found in the Mantiqueira (Figure 3, and see Appendix for details).

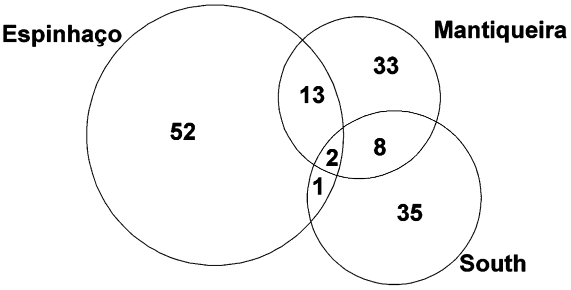


Figure 3. Venn diagram of the number of Eupatorieae species recorded in three Brazilian mountain ranges, showing species shared among ranges.

No subtribe was restricted to the Mantiqueira, but three genera, each represented by one species were found only in this mountain range: *Ophryosporus freyreysii, Adenostemma brasilianum* and *Trichogoniopsis adenantha*. The last two species are commonly found in other Brazilian open formations or in gaps and roadsides within midaltitude forests (e.g., Cabrera and Klein 1989; Lorenzi 1991).

Few species were widespread throughout different localities, within and among mountain ranges. *Chromolaena laevigata* occurred in 13 localities (but not in Bom Jardim and Cambará, the two southernmost localities), followed by *Ageratum fastigiatum* and *Campovassouria cruciata*, each of which occurred in 10 localities. While *A. fastigiatum* was collected in all localities in the Espinhaço and Mantiqueira ranges but was not found in the Southern range, *C. cruciata*

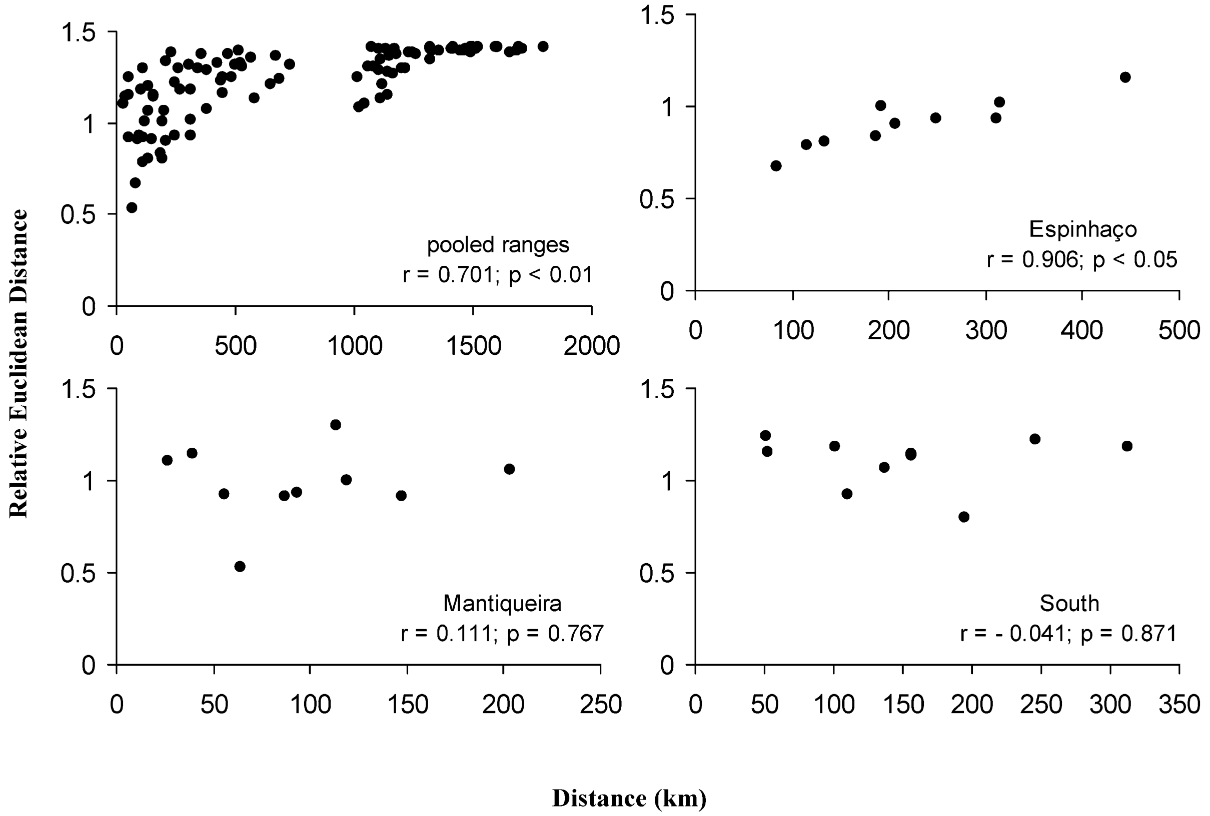


Figure 4. Floristic dissimilarity (determined by Relativized Euclidean distance of species composition) for pooled or individual mountain ranges plotted against geographical distance (km). The significance levels reported were obtained with a Mantel test. Note the difference in scale in the abscissa.

occurred in all localities in the Mantiqueira and Southern ranges but not in the Espinhaço range.

Intra and interregional similarity of Eupatorieae assemblages

From a total of 144 Eupatorieae species found, only 24 (17%) are shared among regions. Floristic dissimilarities increased with geographical distances among localities in the Espinhaço and across all ranges (Figure 4). The Mantel test showed a significant positive correlation between floristic and geographical distances, in the Espinhaço range ($r = 0.906$, $p < 0.05$) and also for the pool of the three mountain ranges ($r = 0.701$; $p < 0.001$). No correlation was found in the Mantiqueira ($r = 0.111$; $p > 0.70$) and Southern ($r = -0.041$; $p > 0.80$) ranges (Figure 4). Note that the plot for pooled ranges in Figure 4 shows two discrete groups: a first more dispersed group in relation to the relative Euclidean distance that encompasses pairs of localities that are less than 700 km apart. The second group forms a more concentrated group of points in relation to floristic distance, and includes all pair of localities with more than 1,000 km geographical distance. The first group shows mostly dissimilarities within mountain ranges, whereas the second group shows dissimilarities between localities belonging to different mountain ranges.

In the cluster analysis, localities of the three mountain ranges were clearly separated (Figure 5). In the cluster dendrogram, the Espinhaço clusters with the Mantiqueira and then with the Southern range. All the joinings found within single mountain ranges conform well to geographic distance (Figure 1), with the exception of Itatiaia – Campos do Jordão in the Mantiqueira, non-adjacent localities with similar physiognomies and human activity, and Lages – Matos Costa in the Southern range. In the Southern range, Cerrito was also displaced in relation to its geographical po-

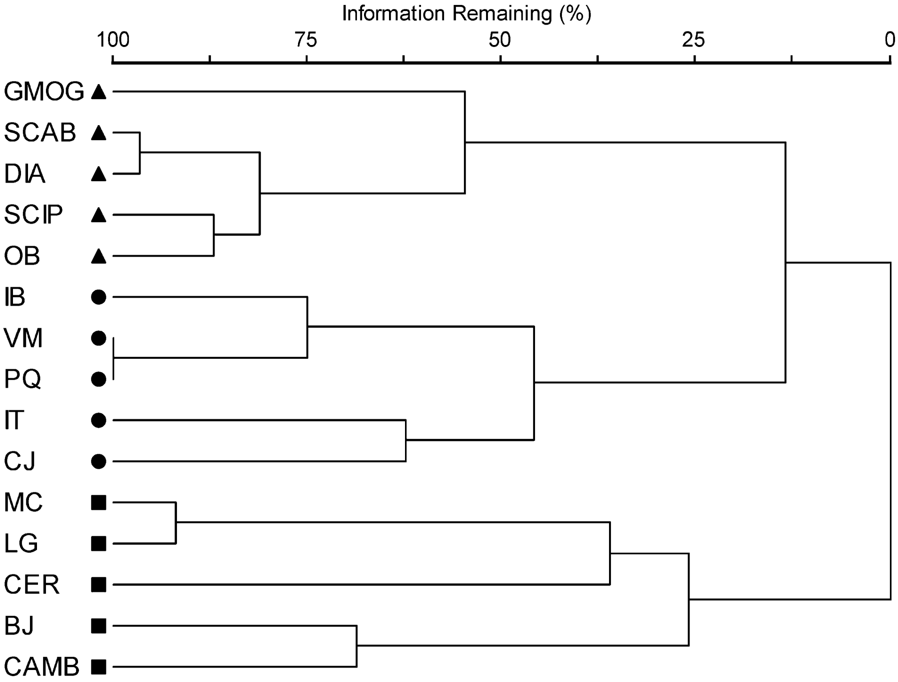


Figure 5. Hierarchical cluster diagram for localities from Espinhaço, Mantiqueira and Southern ranges. The clustering method used UPGMA with Relativized Euclidean Distance. Mountain ranges are assigned different symbols: Espinhaço range, triangles; Mantiqueira range, spheres and South ranges, squares. See Table 1 for locality codes.

sition, probably because of the many exclusive Eupatorieae species found in that locality.

An alternative cluster analysis with Euclidean Distance on standardized data using the adjustment to standard deviate, with $b = (\bar{x}) * s_i^{-1}$ and UPGMA (not shown) clustered with the Mantiqueira and Southern ranges and then to Espinhaço. However, within each mountain range, localities were grouped exactly as in Figure 5. This shows that the floristic dissimilarity among the three ranges is sensitive to the distance measure used, and reinforces the intermediate position of the Mantiqueira between the Espinhaço and Southern ranges.

Ordination by DCA also split localities clearly among the three mountain ranges according to their Eupatorieae flora (Figure 6). The first axis had an eigenvalue of 0.791 and grouped the localities from each region.

Both cluster and ordination analysis clearly separated the *campos* of the three mountain ranges according to its Eupatorieae flora, reinforcing the splitting of the *campos* in three physiognomies.

Discussion

Within the Asteraceae, the tribe Eupatorieae had the highest number of records and species in the three regions, with exception of the Vernonieae in the Espinhaço range (Prado 1999). These two tribes, followed by the Heliantheae and Asteraeae, are indeed the largest Asteraceae tribes in Brazil (Barroso et al. 1986).

Within the Mantiqueira range, only Itatiaia had been previously studied for its Asteraceae flora (Barroso 1957). In Itatiaia we obtained 19 Eupatorieae species of which six (32%) were previously unrecorded, whereas 38% of the species previously listed in this locality were not observed in the present study. This is mainly due to the fact that Barroso (1957) also collected in lower altitudes occupied by humid forests; these probably harbour the many *Mikania* species we did not observe. In comparison with the other four Mantiqueira localities, the Itatiaia higher slope and plateau has the harshest climate, presenting lower temperatures with recurrent winter frost and strong winds (Barros et al. 1998; Safford 1999a). For that reason the flowering period for Asteraceae in this locality is probably narrower than in other localities

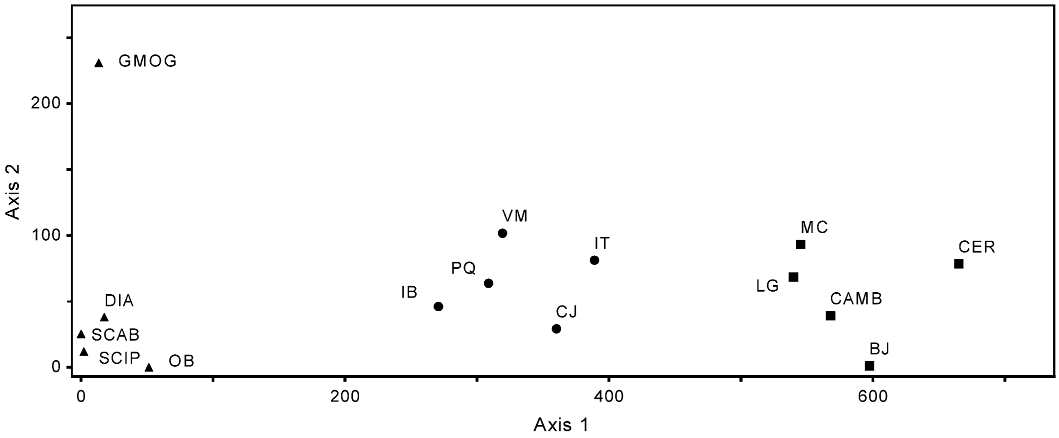


Figure 6. Axis 1 and 2 of a Detrended Correspondence Analysis (DCA) applied to Eupatorieae species collected in localities from three Brazilian mountain ranges. Rare species were downweighted. Mountain ranges are assigned different symbols: Espinhaço range, triangles; Mantiqueira range, spheres; South ranges, squares. See Table 1 for locality codes.

with milder climate, and therefore some Eupatorieae species may have eluded us by not flowering or fruiting during our sampling periods. Such a reduced flowering period was shown by Jonas and Geber (1999) for *Clarkia unguiculata* Lindl. (Onagraceae) in the upper Sierra Nevada.

A high proportion of Eupatorieae records are singletons, varying from 14% in the Mantiqueira to 38% in the Espinhaço. Since in the Mantiqueira range we were sampling preferentially Eupatorieae species we always searched carefully for rare species in the sampled sites, which may have reduced the number of recorded singletons in this range compared to the other sites. However, since the sampling protocol was consistent among regions, we have no indication that this was the case.

Only two Eupatorieae were shared among the three studied mountain ranges, and even the two closest ranges, Mantiqueira and Espinhaço have only 15 species (14%) in common. With few species shared among mountain ranges, the Eupatorieae flora was clearly differentiated among the ranges, as shown by both clustering and ordination analyses. In the cluster dendrogram, the Mantiqueira range grouped either with the Espinhaço or with the Southern range, depending on the distance measure used. This result reinforces the intermediate position of this range, and matches its geographical position as well. Although the Mantiqueira is geographically much closer to the Espinhaço range than to the Southern range, its flora turned out to differ fairly equally from both ranges.

The *campos* vegetation present in the studied mountain rages harbours discrete and distinct sets of Eupatorieae species, which are not directly related to geographical distance. This result suggests that each mountain range is a discrete ecological unit. Although biogeographers have considered the campos areas of each mountain range a distinct phytophysiognomy, their classification is somewhat controversial. According to Safford (1999b), the Brazilian *campos de altitude* proper are almost entirely restricted to an area of less than 350 km^2 in southeastern Brazil with an outlier in the state of Santa Catarina. This outlier includes what we consider here as *campos de cima da serra*, and is not distinguished by Safford. The present study helps to clarify this distinction.

Within each mountain range we find the same pattern of many species restricted to only one or two localities. Species could be found in adjacent mountains or not. For example, for the group of species occurring in only two localities in the Mantiqueira range, the proportion of species in adjacent localities is 14%, while the proportion of species occurring only in the two most extreme localities (Ibitipoca and Campos do Jordão) is 50%. This is corroborated by the Mantel test, which detected no correlation between floristic and geographical distance in either the Mantiqueira or Southern range. In these two mountain ranges the floristic dissimilarity between any pair of localities did not depend on the geographical distance. The correlation of geographical and floristic distances was only significant within the Espinhaço range. However, the same analysis on the tribe Vernonieae in the same Espinhaço localities was not significant (P. Prado, unpublished), which shows that different groups respond differently to the same variables. Moreover, pooling localities among the three ranges showed the Eupatorieae flora to be more similar in nearer localities. The two distinct groups in Figure 4 for pooled localities shows that, on average, any pair of localities within a mountain range is floristically more similar than pairs of localities from different mountain ranges. This shows up even more clearly in ordination (Figure 6).

The cluster dendrogram showed that geographical distance was a good predictor of floristic composition both for the Espinhaço range and for the pool of the three ranges. In the Mantiqueira range, Itatiaia was grouped with Campos do Jordão, both localities with sampling sites in the *campos de altitude* proper, which did not occur in Visconde de Mauá and Passa Quatro. These two localities are most affected by human activity, which may reflect on its flora. In the Southern range, Cerrito was a unique locality, with many exclusive Eupatorieae species. This result suggests that environmental variables such as climate, altitude and human impact may be influencing the floristic composition of localities at the more local scale.

At least three previous studies in tropical montane forests observed adjacent localities have more similar floras. Hedberg (1970) studied the alpine flora in Africa and concluded that the constituent species dispersed one by one, in stepping-stone "jumps" from one mountain to another, and that the associations were independently formed on each mountain. Smith (1975), in the best studied New Guinea ranges, showed that adjacent mountains have a higher herbaceous angiosperm similarity than more distant sites. Simpson and Todzia (1990) compared four localities in the high Andean flora in South America and two high-elevation floras in North America and detected that, at a generic level, the alpine flora is most similar to that of the nearest locality within the same continent. Two families in the high Andean flora, Asteraceae and Poaceae, constitute over one-third of all the species in the studied localities. Although both families characteristically have wind-dispersed fruits, successful colonization of the Andes by north temperate genera depended on similarities in climate as much as, or more than, distance. The three studies concluded that, though distance between localities is of prime importance, climate could be equally influential in determining the composition of adjacent montane floras.

Nekola and White (1999) studied the distance decay hypothesis for plant species divided into growth form and dispersal type classes in Northern North America. They found that wind-dispersed species had lower rates of distance decay than larger fruited species, being more widely dispersed and more variable in their occurrence. They also found the highest rates of similarity loss with distance in herbs compared to other growth forms. These results may not apply in our case. The Eupatorieae have plumose wind-dispersed fruits, but encompass different growth forms, from herbs (*e.g., Ageratum conyzoides*) and vines (*e.g., Mikania* spp.) to trees (*e.g., Austroeupatorium silphiifolium*. The occurrence and distribution of Eupatorieae across the Brazilian mountain ranges seems to be more related to individual species characteristics and restrictions than to growth form.

In the Mantiqueira range another analysis using the same data (Almeida 2001; Almeida and Lewinsohn, unpublished) produced two relevant results. First, both in Campos do Jordão and in Itatiaia the maximum species richness was detected above the treeline, showing that for Eupatorieae the *campos de altitude* have a richer flora, and a larger proportion of endemics, than the lower highland forest zone. The second point is that more widespread Eupatorieae have a wider altitudinal range, which means that species occurring in various localities are generalistic enough to occur in a wide variety of altitudes. Campos do Jordão and Itatiaia are not geographically closest among the Mantiqueira localities, but the flora is most similar between these two localities probably because of the similarity of suitable climatic and habitat conditions.

Processes that structure communities within a particular locality may differ from those acting across an entire mountain range, and again from those acting among mountain ranges. As already noted by several authors (e.g., Ricklefs and Schluter 1993; Brown 1995; Maurer 1999; Nekola and White 1999), the wider the study scale the more the chance that biogeographical and historical factors will be influencing the observed results. The high turnover rate of Eupatorieae in Brazilian mountain ranges, with few species present in more than a region, suggests that different processes are occurring in the more local scale, within mountain ranges, and in the regional mesoscale, among mountain ranges.

Acknowledgements

Most of this work was conducted by Adriana M Almeida in partial fulfilment of the PhD degree in the Unicamp Graduate Program in Ecology. We thank two anonymous reviewers for valuable comments on the manuscript. We are very grateful to Drs. Harold Robinson, Nelson I. Matzenbacher, Roberto L. Esteves and João Semir for help with plant identifications. Antônio Carlos Macedo, Umberto Kubota, Érika P. Anseloni, Soraia de A. Ferreira, Antônio M. Rosa, Bruno D. Buys, Vinícius N. Mota, Flavia Q. Batista, Marcelo A. B. Lopes, Adalberto J. Santos and José C. Silva for their invaluable help in field trips. Rafael L. G. Raimundo produced the locality map. C. Jacobi, A.V.L. Freitas, L.B. Klaczko read and commented an earlier version of the manuscript. IEFMG and IBAMA permitted collections at Ibitipoca and Itatiaia parks, respectively. The staff of the Parque Estadual de Ibitipoca and Parque Nacional de Itatiaia helped with access and facilities within the parks. This project was supported by Fapesp (grant 98/05085-2), as part of the Biota/FAPESP program, and by CAPES and Fapesp with graduate and post-doctoral scholarships for A. Almeida.

Appendix

Table A1. Number of collections of each plant species per locality and per mountain range[1]. Table 1 lists locality codes and coordinates. Abbreviations for subtribes (ST) are: Ad – Adenostemmatinae; A1 – Alomiinae; Cr – Critoniinae; Gy – Gyptidinae; Mi – Mikaniinae.

ST	Species	Mantiqueira					Espinhaço					South				
		IB	VM	IT	PQ	CJ	GMOG	SCAB	DIA	SCIP	OB	MC	LG	CER	BJ	CAMB
Adenostemmatinae	*Adenostemma brasilianum* Cass.		12													
	Adenostemma verbesina (L.) Kuntze											1				
Ageratinae	*Acritopappus* indet.						1									
	Acritopappus irwinii K&R						5									
	Acritopappus longifolius (Gardner) K&R							2	2							
	Ageratum conyzoides L.	6	25		11	5										
	Ageratum fastigiatum (Gardner) K&R	30	24	2	11	7	7	2	8	3	1					
	Stevia commixta B. Robinson														1	
	Stevia crenulata Baker	1		1		1										
	Stevia ophryophylla B. Robinson												1			
Alomiinae	*Pseudobrickellia brasiliensis* (Sprengel) K&R						2	1	3		1					
Ayapaninae	*Ayapana amygdalina* (Lam.) K&R							2	1	4	3					
	Aypana aff. amygdalina									1						
	Heterocondylus alatus (Vell. Conc.) K&R			1			4	1	4	3						
	Heterocondylus amphidictyus (DC.) K&R	5							2	2	4					
	Heterocondylus grandis (Schultz-Bip.ex Baker)K&R												2			1
	Heterocondylus jaraguensis (B. Robinson) K&R	2				9										
	Koanophyllon adamantium (Gardner) K&R						1		1							
Critoniinae	*Koanophyllon thysanolepis* (B. Robinson) K&R	1				3			2	1	2					
	Ophyosporus freyreysii (Thunb. and Dallm.) Baker		1													
Disynaphinae	*Campovassouria cruciata* (Vell. Conc.) K&R	1	3	4	1	4						1	2	2	1	5
	Grazielia aff. serrata														3	
	Grazielia gaudichaudeana (DC.) K&R	3		5												4
	Grazielia gaudichaudeana var. *bipinnata* (DC.) K&R					2										
	Grazielia intermedia (DC.) K&R		8	15	3	16						2	3			
	Grazielia serrata (DC.) K&R												1	3		2
	Raulinoreitzia crenulata (Sprengel) K&R												1	1		
	Raulinoreitzia tremula (Hook and Arn.) K&R							1					1			
	Symphyopappus aff. reticulatus									1						
	Symphyopappus angustifolius Cabrera							1								
	Symphyopappus compressus (Gardner) B. Robinson		4	11		4										
	Symphyopappus cuneatus (DC.) Schultz-Bip. ex Baker			3		2			3	2	1					
	Symphyopappus decussatus Turcz.	5	1	1			1		1							
	Symphyopappus indet.															1
	Symphyopappus itatiayensis (Hieron.) K&R		4	10	2											
	Symphyopappus reticulatus Baker								1							

Table A1. Continued.

ST	Species	Mantiqueira					Espinhaço					South				
		IB	VM	IT	PQ	CJ	GMOG	SCAB	DIA	SCIP	OB	MC	LG	CER	BJ	CAMB
	Symphyopappus sp.01						1									
	Symphyopappus viscosus Schultz-Bip.							1	2							
Eupatoriinae	*Austroeupatorium inulaefolium* (H. B. K.) K&R		1										1			
	Austroeupatorium laete-virens (Hook and Arn.) K&R				1											
	Austroeupatorium neglectum (B. Robinson) K&R		1	2		2										
	Austroeupatorium paulinum (DC.) K&R		1	7		3										
	Austroeupatorium picturatum (Malme) K&R											1	1		1	1
	Austroeupatorium silphiifolium (Martius) K&R	8	14	8	11	5										
	Hatschbachiella tweediana (Hook and Arn.) K&R														1	2
	Stomathantes polycephalus (Schultz-Bip. ex B. Robinson) H. Robinson							1								
Gyptidinae	*Barrosoa betonicaeformis* (DC.) K&R		1			5						1	2	1	5	7
	Barrosoa candolleana (Hook and Arn.) K&R						4									
	Campuloclinium campuloclinoides (Baker) K&R							2								
	Campuloclinium chlorolepis (Baker) K&R							1								
	Campuloclinium indet.							1								
	Campuloclinium macrocephalum (Lees.) (DC)													2	5	1
	Campuloclinium megacephalum (Martius ex Baker) K&R					2										
	Campuloclinium parvulum (Glaz.) K&R	2														
	Campuloclinium purpurascens (Schultz-Bip. ex Baker) K&R	3	6	1	5	3										
	Gyptis crassipes (Hieron.) K&R													1		
	Trichogonia hirtiflora (DC.) Schultz-Bip. ex Baker						10	2	6	4	2					
	Trichogonia salviaefolia Gardner						3	3								
	Trichogonia villosa Schultz-Bip. ex Baker	9					3	5	12	3	3					
	Trichogoniopsis adenantha (DC.) K&R	2														
	Vittetia orbiculata (DC.) K&R													2		
Mikaniinae	*Mikania aff. lasiandrae*									1						
	Mikania aff. leiolaena						1		1	1	1					
	Mikania aff. sessilifolia									1						
	Mikania bradei B. Robinson	1														
	Mikania burchellii Baker															1
	Mikania campanulata Gardner			5		1										1
	Mikania cipoensis G Barroso									3						
	Mikania citriodora n.species						1									
	Mikania cordifolia (L.f.) Willd					3		1								
	Mikania decumbens Malme	3														
	Mikania elliptica DC.	8			1	1										
	Mikania eriostrepta B. Robinson					2										
	Mikania glaziovii Baker			1												
	Mikania hemisphaerica Schultz-Bip. ex Baker		1													
	Mikania involucrata Hook and Arn.														1	

Table A1. Continued.

ST	Species	Mantiqueira					Espinhaço					South				
		IB	VM	IT	PQ	CJ	GMOG	SCAB	DIA	SCIP	OB	MC	LG	CER	BJ	CAMB
	Mikania lasiandrae DC.	3		1	4	8										
	Mikania leiolaena DC.						5	3	2	2						
	Mikania lindbergii Baker	2				3										
	Mikania linearifolia DC.							1								
	Mikania micrantha H. B. K.	1	13	3	4		2	1				1	1			
	Mikania microcephala DC.		1	5												
	Mikania microdonta DC.	1			1											
	Mikania microphylla Schultz-Bip. ex Baker										1					
	Mikania neurocaula DC.							1								
	Mikania nitidula Baker						1									
	Mikania oblongifolia DC.									1						
	Mikania officinalis Martius							4	7	1						
	Mikania orleansensis Hieron.															1
	Mikania paranensis Dusen															1
	Mikania phaeoclados Martius ex. Baker									2	1					
	Mikania pinnatiloba DC.													1		
	Mikania pseudogracilis K&R										1					
	Mikania purpurascens Schultz-Bip ex. Baker								1							
	Mikania ramosissima Gardner						1		1	1						
	Mikania retifolia Schultz-Bip ex. Baker						1		5							
Mi	*Mikania salviaefolia* Gardner											2	2			
	Mikania sessilifolia DC.					2		1		2	1					
	Mikania vitifolia DC.														2	
	Mikania sp.1	1				1										
	Mikania sp.12									1						
	Mikania sp.2		1													
	Mikania sp.31													1		
	Mikania sp.38											1				
Praxelinae	*Chromolaena aff. ascendens*									1						
	Chromolaena aff. congesta											2	1	2	2	1
	Chromolaena aff. hirsuta											1		2	1	
	Chromolaena aff. pedunculosa										1					
	Chromolaena aff. squalida								1							
	Chromolaena aff. squalida sp.1	2				1										
	Chromolaena ascendens (Schultz-Bip. ex Baker) K&R	2				7									2	3
	Chromolaena barbacensis (Hieron.) K&R						1			1						
	Chromolaena chaseae (B. Robinson) K&R						1	3	3	2	1					
	Chromolaena congesta (Arn. and Hook) K&R	11				4									6	2
	Chromolaena cylindrocephala (Schultz-Bip. ex Baker) K&R						2	3	6	2						
	Chromolaena decumbens Gardner K&R	1									2					
	Chromolaena hookeriana (Griseb.) K&R	3	4													

Table A1. Continued.

ST	Species	Mantiqueira					Espinhaço					South				
		IB	VM	IT	PQ	CJ	GMOG	SCAB	DIA	SCIP	OB	MC	LG	CER	BJ	CAMB
	Chromolaena horminoides DC. K&R						1	4	4	2						
	Chromolaena laevigata (Lam.) K&R	7	5	3	7	9	1	1	1	1	1	1	1	2		
	Chromolaena linearis (Malme) K&R								1							
	Chromolaena mattogrossensis (Hieron.) K&R						1	2								
	Chromolaena maximilianii (Schrader ex DC.) K&R	4	3		4	2										
	Chromolaena minasgeraesensis (Hieron.) K&R					2	3	1								
	Chromolaena multiflosculosa (DC.) K&R	15														
	Chromolaena odorata (L.) K&R						2			1						
	Chromolaena pedalis (Schultz-Bip. ex Baker) K&R	10	1			5										
	Chromolaena pedunculosa (Hook and Arn.) K&R												1	1		
	Chromolaena pungens (Gardner) K&R							1	2							
	Chromolaena sagittifera (B. Robinson) K&R							1	2							
	Chromolaena sp.30													1		
	Chromolaena squalida (DC.) K&R	4	2		2		2	6	7	4	3					
	Chromolaena stachyophylla (Sprengel) K&R							2	1	2	1					
	Chromolaena verbenacea (DC.) K&R													1		
	Disynaphia aff. ligulaefolia													1		1
	Disynaphia ligulaefolia (Hook and Arn.) K&R													1		
	Disynaphia spathulata (Hook and Arn.) K&R													2		
	Praxelis capillaris (DC.) Schultz-Bip.									2						
	Praxelis clematidea (Griseb.) K&R		7		9	5			1		1					
	Eupatorieae indet.										1					
	Eupatorieae sp.05													1		
	Eupatorieae sp.15														1	
	Eupatorieae sp.21															1
	Eupatorieae sp.31													2		
	Eupatorieae sp.32												2			
	Total	157	144	89	77	129	68	62	94	58	33	14	23	30	32	36

[1] The abbreviation K&R in most species names refers to R. King and H. Robinson.

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