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Biogeografia de Interações entre Eupatorieae (Asteraceae) e insetos endófagos de capítulos na Serra da Mantiqueira

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"Vivo de perguntas e respostas.

Enquanto eu tiver perguntas e não houver respostas,

continuarei a escrever."

Clarice Lispector

RESUMO

A presente tese analisou a estrutura de interações e a configuração regional de cinco comunidades locais de insetos endófagos de capítulos da tribo Eupatorieae (Asteraceae) na Serra da Mantiqueira, entre os anos de 1998 e 1999, em altitudes variando de 760m a 2460m: Ibitipoca (MG), Visconde de Mauá (RJ/MG), Itatiaia (RJ/MG), Passa Quatro (MG) e Campos do Jordão (SP). Ela é composta de quatro capítulos, que foram redigidos na forma de artigos independentes.

No primeiro capítulo a flora de Eupatorieae, a tribo mais diversa de Asteraceae na Serra da Mantiqueira foi comparada às floras da Serra do Espinhaço (Minas Gerais) e às serras de Santa Catarina e Rio Grande do Sul. Este estudo mostra que uma pequena fração das espécies de Eupatorieae se repete em diferentes regiões, e houve uma correlação espacial apenas na Serra do Espinhaço e para o pool de todas as serras, sendo as localidades mais próximas entre si também floristicamente mais semelhantes que localidades mais distantes.

O segundo capítulo trata dos insetos endófagos que se desenvolvem em capítulos de Eupatorieae na Serra da Mantiqueira. Estes insetos foram divididos em três guildas de acordo com o grau de endofagia e a sua relação com a planta hospedeira em Endófagos Estritos, Endófagos Móveis e Endófagos Facultativos. Analisamos seus elencos conhecidos de hospedeiras e sua distribuição geográfica. Espécies pertencentes à guilda de endófagos estritos são mais especialistas, sendo mais freqüentemente restritas a uma espécie, um gênero ou uma subtribo da planta hospedeira que as outras duas guildas. A composição da comunidade de Eupatorieae em cada localidade é o principal fator determinante da composição dos endófagos; a similaridade florística é mais importante que a proximidade geográfica para determinar a similaridade faunística entre localidades. Há indicações que diferentes guildas respondem diferentemente a pressões do ambiente, o que é em parte testado no capítulo seguinte.

O terceiro capítulo descreve a distribuição altitudinal das espécies de plantas e de endófagos separados por guildas e testa a hipótese do domínio médio de Colwell e co-autores em contraposição à regra de Rapoport de Stevens. Verificamos que em todas as localidades o máximo na riqueza de espécies ocorre em altitudes intermediárias - como previsto pela hipótese do domínio médio - mas raramente no centro do gradiente altitudinal, e cada guilda apresentou o mesmo padrão altiitudinal de distribuição de riqueza de espécies em cada localidade. O fato de as diferentes guildas responderem de forma semelhante às mesmas variáveis ambientais sugere que espécies ecologicamente semelhantes respondem de forma semelhante às limitações impostas por um ambiente austero. É a primeira vez que a hipótese do domínio médio é testada em mais de um nível trófico e em várias localidades de uma região.

O quarto e último capítulo apresenta teias tróficas quantitativas das comunidades locais e do conjunto regional da Serra da Mantiqueira, utilizando as freqüências de associações (incidências de espécies de insetos em amostras de plantas) como medidas quantitativas. Com exceção apenas de Itatiaia, as teias locais e regional se mostraram divididas em compartimentos de acordo com as guildas de endófagos, de modo que as espécies de uma guilda apresentam interações mais fortes entre si que entre guildas. Generalistas regionais também se alimentam de várias hospedeiras em cada localidade, entretanto entre 40% e 50% das interações foram direcionadas a uma única hospedeira, mostrando uma clara preferência local.

ABSTRACT

This thesis analysed the influence of regional factors in five local communities composed of endophagous insect species that feed on flower-heads from the tribe Eupatorieae (Asteraceae) in the Mantiqueira range, from 1998 to 1999, within altitudes varying from 760m to 2460m: Ibitipoca (Minas Gerais), Visconde de Mauá (Rio de Janeiro/Minas Gerais), Itatiaia (RJ/MG), Passa Quatro (MG) and Campos do Jordão (São Paulo). It is presented as four independent papers.

In the first chapter the Eupatorieae flora (the most diverse Asteraceous tribe in the region) present in the Mantiqueira range was compared to the flora of the Espinhaço range (MG) and Southern mountain ranges (Santa Catarina and Rio Grande do Sul). Only a small fraction of the Eupatorieae species occurs in more than one mountain range, and there is a significant spatial correlation for Espinhaço range and the pool of the three ranges, with adjacent localities being floristically more similar than more distant localities.

The second chapter examines the endophagous insects that develop in the Eupatorieae flower-heads in the Mantiqueira range. Endophagous species were divided in three guilds according to the degree of endophagy and relationship to the host plants: Strict endophages, mobile endophages and facultative endophages, and their geographic and host ranges were analysed. We show that strict endophages are more specialized and are more often restricted to a host species, genus or subtribe than the other two guilds. We suggest that different guilds show different responses to environmental pressures.

Chapter 3 describes the altitudinal distribution of plant and endophagous species grouped into feeding guilds, and tests the mid-domain hypothesis of Colwell and co-workers against Steven's Rapoport's rule. We observed that in all localities the peak in species richness occurs in mid-altitudes - as predicted by the mid-domain hypothesis - but seldom in the centre of the altitudinal domain, and each guild presented the same pattern of altitudinal richness distribution in each locality. The fact that different guilds respond similarly to the same environmental pressures suggests that ecologically similar species show the same response patterns to the limitations imposed by a harsh environment. This is the first time the mid-domain hypothesis is tested for more than a trophic level and in various localities within a region.

The fourth and last chapter presents quantitative trophic webs of the regional and local communities in the Mantiqueira range, using interaction frequency (insect incidence in plant samples) as quantitative measure. With the exception of Itatiaia, both the regional and local webs were divided into compartments according to the endophagous feeding guilds, with interactions within guilds being more intense than among guilds. Regional generalists were also localy generalists, but from 40% to 50% of interactions were directed to only one host species, indicating a clear local preference for a given host.

INTRODUÇÃO

"One cannot preserve interactions and ship them back home
to be cataloged and displayed in museums.
Interactions have no morphologies that can be studied side by side
as an aid to how they relate evolutionarily to one another.
Moreover, they rarely leave a direct fossil record."
(John N. Thompson, 1994, The Coevolutionary Process)

A subdivisão de sistemas ecológicos em partes cada vez menores e mais facilmente tratáveis, principalmente durante as décadas de 50 e 60, levou a uma era chamada de "determinismo local" (Ricklefs & Schluter, 1993b), "abordagem reducionista" (Maurer, 1999), ou até mesmo exageradamente de "eclipse da história" (Ricklefs, 1987). A abordagem reducionista concentra-se em recortes pequenos e locais de comunidades, passíveis de serem tratados através de manipulação experimental e modelagem matemática. Segundo esta abordagem, a diversidade local é determinada essencialmente por processos internos a cada comunidade. O estudo de comunidades e ecossistemas em nível exclusivamente local, entretanto, não é capaz de detectar processos que ocorrem em uma escala mais ampla, no nível regional (Ricklefs, 1987; Brown & Maurer, 1989; Ricklefs & Schluter, 1993a; Brown, 1995, 1999; Gaston & Blackburn, 1999; Maurer, 1999).

Influência de fatores locais e regionais na estruturação de comunidades

A partir do fim da década de 80 e por toda a década de 90, ecólogos voltaram a observar que processos imperceptíveis no nível local eram detectados na forma de padrões quando era usada uma abordagem com uma escala mais ampla, no nível regional. Esta abordagem regional, chamada de *macroecologia* por Brown e Maurer (1989) e Brown (1995), propõe a expansão de escalas não só espaciais (de locais para geográficas ou regionais) como também temporais (de imediatas para históricas), no estudo da ecologia de comunidades (Ricklefs, 1987; Ricklefs & Schluter, 1993a; Brown, 1995; Maurer, 1999; Hughes, 2000). Embora a análise de processos regionais atuando em comunidades locais tenha sido mais enfatizada a partir da década de 80, estudos anteriores já haviam sido capazes de entender sua importância. A teoria de biogeografia de ilhas (MacArthur & Wilson, 1963, 1967), estudando a diversidade em ilhas como o resultado de um equilíbrio entre colonização e extinção, é um exemplo de uma abordagem inicial da influência de processos locais e regionais atuando em comunidades.

Uma comunidade dificilmente é delimitável, possuindo uma estrutura espacial aberta, e as espécies que coexistem em uma dada localidade podem estender-se mais ou menos independentemente por outras localidades (por ex. Schluter & Ricklefs, 1993). Com a expansão da escala de estudo de local para regional, além dos processos de competição, predação e mutualismo que dominaram a era do "determinismo local", processos ocorrendo entre diferentes populações passaram a ser também estudados, como migração, colonização e extinção (Maurer, 1999). Enquanto os processos que ocorrem nos níveis locais estariam reduzindo a diversidade através da exclusão competitiva, da super-exploração de recursos e da extinção aleatória, os processos regionais estariam contra-balançando estes fatores, inserindo espécies na comunidade através do movimento de indivíduos entre habitats e manchas de habitat, especiação, e trocas de espécies entre regiões (Ricklefs, 1987; Ricklefs & Schluter, 1993b; Angermeier & Winston, 1998). Comunidades são estruturas hierárquicas, com indivíduos inseridos em populações, que estão inseridas em comunidades, que por sua vez estão inseridas em ecossistemas (Ricklefs & Schluter,1993b; Maurer, 1999). O comportamento e fisiologia dos indivíduos irão afetar não só a densidade populacional, como também das espécies presentes em uma comunidade. A composição da comunidade também responde a processos de escala mais ampla, no nível do ecossistema, com cada espécie participando de ciclos de nutrientes e também interagindo com outras espécies por meio de competição, predação e mutualismo. Como ecossistemas também não são sistemas fechados, escalas ainda mais amplas de observação abrangem a troca de nutrientes entre eles, assim como a entrada e saída de espécies da comunidade através dos processos de imigração e emigração (Figura i.1). Desta forma, há sempre uma relação entre o número de espécies no estoque (pool) regional de colonizadores potenciais e a riqueza de assembléias locais. O número de espécies presentes em uma comunidade local é uma fração do estoque regional de espécies e Ricklefs e Schluter (1993b) defendem que é impossível separar a diversidade local da regional, devendo-se considerar ambas como expressões diferentes de um sistema ecológico integrado em cada região.

O estudo da macroecologia entretanto não deve se limitar unicamente a uma abordagem em ampla escala, o que levaria a um determinismo em outro nível, o determinismo regional. Segundo Maurer (1999), deve-se também estudar a natureza dos processos que estão afetando as comunidades locais em pequena escala. Processos no nível populacional, principalmente resultantes de interações entre espécies, podem dar origem a padrões diferentes quando observados em escalas mais amplas, regionais ou continentais. É sempre importante conhecer bem os padrões locais, para se ter o entendimento necessário de como eles estão influenciando padrões em escalas regionais, ou pelo contrário, como são determinados por estes.

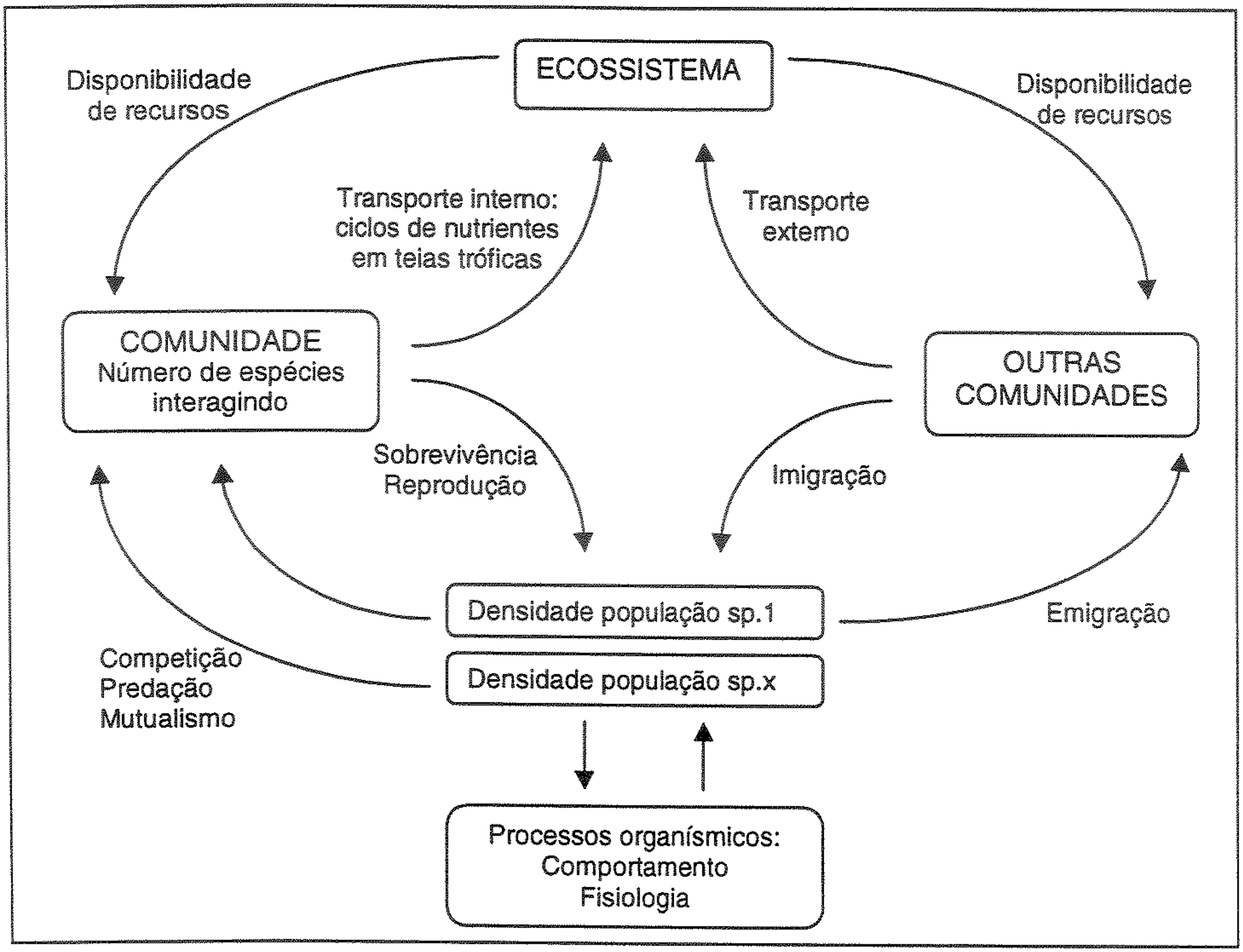

Figura i.1. Representação hierárquica de fatores que influenciam a dinâmica de comunidades, baseado em Maurer (1999).

Comunidades de endófagos de *Asteraceae* em campos rupestres brasileiros

Asteráceas constituem a maior família de angiospermas, com cerca de 23.000 espécies descritas, apresentando distribuição cosmopolita e ocorrendo em todos os continentes (com exceção do Antártico) (Bremer, 1994). A família é subdividida em várias tribos, que podem ser consideradas subdivisões naturais e bem estabelecidas (Bremer et al., 1992; Bremer, 1994). De maneira geral, as tribos de Asteráceas delimitam diferentes comunidades de insetos endófagos (Lewinsohn, 1991; Lewinsohn & Prado, no prelo).

Os capítulos (ou inflorescências) de asteráceas são estruturas delimitadas espacial e temporalmente, e insetos endófagos estão ao mesmo tempo mais protegidos de predadores generalistas e fatores abióticos, e também mais suscetíveis a predadores e parasitóides especialistas (Zwölfer, 1983). Em capítulos de asteráceas tropicais são encontrados vários grupos de insetos endófagos, que apresentam diferentes graus de endofagia e associação com as plantas hospedeiras : Cecidomyiidae (Diptera) galhadores de tubos florais; Tephritidae e Agromyzidae (Diptera) herbívoros que se alimentam de flores, óvulos e aquênios; Tortricidae, Pyralidae, Gelechiidae, Blastobasidae e Pterophoridae, assim como Geometridae e Lycaenidae (Lepidoptera), cujas larvas se alimentam de estruturas imaturas como aquênios e tubos florais, assim como estruturas de proteção como brácteas(Lewinsohn, 1991; Almeida, 1997; Prado, 1999).

Ricklefs e Schluter (1993b) chamam a atenção para a existência de poucos estudos macroecológicos comparando localidades semelhantes em regiões distintas. Desta forma, o estudo das comunidades dos topos de montanhas pertencentes a uma mesma serra são sistemas ideais para o estudo da macroecologia, pois apresentam localidades razoavelmente isoladas mas similares, e portanto comparáveis entre si (Lewinsohn et al., 2001).

Nas serras dos estados de São Paulo, Rio de Janeiro, Espírito Santo e Minas Gerais (e mais uma serra isolada em Santa Catarina) são encontradas formações chamadas de "campos de altitude", ou "páramos brasileiros" (Safford, 1999a, b) por possuírem algumas (poucas) analogias com os páramos andinos. Os campos de altitude são caracterizados por uma formação com elevado grau de endemismo de espécies vegetais, dominada por gramíneas, ervas e arbustos pequenos adaptados à sobrevivência em áreas com muito vento, geadas e queimadas ocasionais (Safford, 1999a,b; no prelo). No sul e sudeste do Brasil, estes campos estão restritos a uma área de menos de 350 km^2 e formam um arquipélago terrestre de habitats isolados de topos de montanha.

Embora se saiba que comunidades presentes em altitudes elevadas possuem um alto grau de endemismo e adaptações, seu estudo no Brasil tem sido restrito a comunidades locais e suas adaptações eco-fisiológicas para ocorrência em tais ambientes. Neste contexto o projeto "Diversidade de Espécies e de Interações em Plantas e Insetos Fitófagos", do qual o presente estudo faz parte, é uma exceção. Vários trabalhos anteriores, dentro do escopo do projeto, trataram das relações entre processos locais e regionais atuando sinergisticamente na estruturação de comunidades dos insetos endófagos de capítulos de asteráceas (Lewinsohn, 1988, 1991; Lewinsohn & Prado, no prelo; Almeida, 1997; Lewinsohn et al., 1997; Ortiz, 1997; Prado, 1999; Macedo, 2000; Prado & Lewinsohn 2000; Lewinsohn et al., 2001). O conjunto de trabalhos realizados e em realização no projeto estão evidenciando alguns padrões recorrentes dentro do sistema de insetos endófagos de capítulos de asteráceas tropicais. Parecem ser características gerais do sistema o fato de insetos da família Tephritidae serem mais especialistas, estando praticamente restritos a tribos de hospedeiras (Lewinsohn, 1988, 1991; Prado, 1999; Prado & Lewinsohn 2000; Lewinsohn & Prado, no prelo), assim como o fato de plantas hospedeiras estarem mais restritas a algumas localidades, enquanto as espécies de insetos endófagos são bem mais dispersas, ocorrendo em várias localidades (Lewinsohn, 1988; 1991; Prado, 1999; Prado & Lewinsohn 2000).

As comunidades de Eupatorieae e seus endófagos de capítulos na Serra da Mantiqueira

O presente estudo analisou a distribuição geográfica (vertical e horizontal) de asteráceas da tribo Eupatorieae e os insetos endófagos obtidos de seus capítulos em cinco localidades na Serra da Mantiqueira, estudando a estrutura local e regional das comunidades. Cada localidade foi estudada e descrita localmente e posteriormente relacionada com as demais.

A Serra da Mantiqueira foi escolhida por várias razões. Na Mantiqueira encontram-se o quarto e quinto pontos culminantes brasileiros (respectivamente Pedra da Mina com 2797m e o Pico das Agulhas Negras com 2789m), sendo considerada o orobioma mais frio do sudeste da América do Sul e com vários cumes apresentando campos de altitude (Mendes Jr. et al., 1991; Costa, 1994; Safford, 1999a, b). Aproximadamente um terço das espécies vegetais presentes em Itatiaia são endêmicas, entre elas várias espécies de asteráceas (Barroso, 1957; Safford, 1999a,b). A Serra da Mantiqueira encontra-se entre a Serra do Espinhaço e serras da região de Santa Catarina e Rio Grande do Sul, regiões anteriormente estudadas pelo Projeto, com os mesmos procedimentos utilizados neste estudo, tornando-as facilmente comparáveis. A tribo Eupatorieae foi escolhida por ser a tribo com maior número de espécies na região da Serra da Mantiqueira, e possivelmente no Brasil (Barroso, 1957).

Em 1998 e 1999 foram feitas seis viagens para coleta de amostras em cinco localidades da Serra da Mantiqueira: Ibitipoca (MG), Visconde de Mauá (MG/RJ), Itatiaia (MG/RJ), Passa Quatro (MG) e Campos do Jordão (MG/SP). Uma amostra corresponde a capítulos de vários indivíduos de uma espécie de planta hospedeira, que foram coletados e mantidos por um mínimo de 60 dias para emergência de adultos. Maiores detalhes sobre métodos de coleta e criação, assim como morfoespeciação e identificação dos organismos estudados estão descritos nos capítulos que se seguem. A obtenção de herbívoros através da criação de seus imaturos garante que os herbívoros não são "turistas", mas sim herbívoros associados àquela espécie vegetal (Lewinsohn et al., 2001). A determinação da comunidade de plantas hospedeiras e seus endófagos em várias localidades dentro de uma região perfaz um conjunto de dados que podem ser analisados de várias formas.

A presente tese está dividida em quatro capítulos, redigidos na forma de artigos independentes. O primeiro capítulo da tese trata da ocorrência e distribuição espacial das espécies de Eupatorieae em diferentes localidades na Serra da Mantiqueira e em relação a outras serras brasileiras. O segundo capítulo trata dos insetos endófagos obtidos dos capítulos de Eupatorieae na Serra da Mantiqueira. Endófagos foram divididos em três guildas segundo o grau de endofagia, e a relação entre o grau de endofagia/intimidade/especialização com a planta hospedeira e sua distribuição geográfica foi estudada. O terceiro capítulo descreve a distribuição altitudinal das espécies de plantas e endófagos distribuídos em guildas e testa a hipótese de domínio médio (*mid-domain*) de Colwell e colaboradores (Colwell & Hurtt, 1994; Colwell & Lees, 2000). O quarto e último capítulo trata de teias tróficas quantitativas das comunidades locais e da região da Serra da Mantiqueira, utilizando as freqüências de associações como medidas quantitativas. As teias quantitativas mostram graficamente como as composições de espécies e interações entre elas são diferentes entre as localidades estudadas, reforçando o argumento de que qualquer comunidade local está inserida e é bastante influenciada pelo estoque regional de espécies.

Ocorrência e distribuição de espécies entre localidades de uma região e sua relação com a especialização de insetos endófagos (capítulos 1 e 2)

Uma das ênfases da macroecologia é o estudo do tamanho e distribuição das áreas geográficas de ocorrência das espécies (Brown, 1995, 1999; Gaston & Blackburn, 1999; Maurer, 1999). As áreas geográficas de cada espécie são restritas, no seu limite inferior pelo tamanho mínimo da área necessária para manter uma população viável da espécie em questão; e no superior, pela área máxima disponível, como por exemplo o tamanho do continente para aves (Brown, 1987; 1995). O estudo das áreas geográficas de espécies pode ser difícil pois barreiras podem mudar com o tempo, sendo diferentes a cada estação do ano assim como entre anos (Yodzis, 1993). A delimitação geográfica de comunidades então é bem mais difícil pois as barreiras podem ser difusas e diferentes para as diferentes espécies que compõem uma comunidade.

Espécies com ampla distribuição geográfica são geralmente mais abundantes localmente (Brown, 1984, 1995). Este padrão pode ser explicado de várias formas; por exemplo, pela especialização de nichos, já que a abundância e distribuição das espécies são limitadas pela combinação de variáveis bióticas e ambientais que determinam seu nicho. Entre espécies com necessidades ecológicas semelhantes, as espécies generalistas serão mais abundantes em toda a sua área de distribuição, que será também mais ampla. Ao mesmo tempo, especialistas por serem menos tolerantes, devem ser ao mesmo tempo localmente mais raros e com distribuição mais restrita (Brown, 1984, 1995). Outras explicações propostas invocam mecanismos ecológicos alternativos, ou mesmo reduzem esta relação a uma conseqüência do processo de amostragem (Wright et al., 1998).

As interações entre as espécies de insetos associadas a capítulos podem ocorrer em três diferentes níveis. O primeiro nível ocorre dentro dos capítulos, onde ocorrem as interações entre imaturos que competem por espaço e recurso alimentar (Zwölfer, 1979). O segundo nível é formado pelas comunidades de plantas hospedeiras nas quais os endófagos adultos irão interagir na procura de sítios de oviposição e assim definir as arenas de interação entre imaturos (nível anterior) (Zwölfer, 1979). Um terceiro nível ocorre em uma dimensão regional, com o banco ou "pool" regional de espécies influenciando e delimitando o tamanho e composição da comunidade local.

Gaston e colaboradores (1992) sugerem que herbívoros endófagos, que se alimentam inseridos em estruturas da planta hospedeira, apresentam um alto grau de intimidade com a planta hospedeira, que pode se mostrar como uma maior especificidade de hospedeiros em relação a insetos ectófagos.

No primeiro capítulo, a flora de Eupatorieae amostrada na Serra da Mantiqueira é comparada à flora da Serra do Espinhaço meridional e das serras de Santa Catarina e Rio Grande do Sul. O segundo capítulo trata dos insetos endófagos obtidos dos capítulos de Eupatorieae coletados na Serra da Mantiqueira. Os insetos foram divididos em três guildas de acordo com o grau de endofagia: endófagos estritos (SE), endófagos móveis (ME) e endófagos facultativos (FE). O grau de especialização dos endófagos pertencentes às três guildas é analisado, juntamente com a distribuição espacial das espécies ao longo da Serra da Mantiqueira. A congruência de ocorrências entre espécies de hospedeiras e herbívoros é testada. É sugerido que diferentes guildas respondem diferentemente a pressões do ambiente, o que é em parte testado no terceiro capítulo para a distribuição altitudinal.

Ocorrência e localização de áreas geográficas de espécies em um gradiente altitudinal (capítulo 3)

Um padrão interessante que há muito chamou a atenção de ecólogos é o fato de os trópicos serem a região com maior riqueza de espécies do globo, apresentando um gradiente decrescente em número de espécies à medida que se aumenta a latitude. Várias hipóteses foram levatadas para explicar o gradiente latitudinal em diversidade (p. ex. Pianka, 1966; Rohde, 1992; Davidowitz & Rosenzweig, 1998). Neste capítulo analisaremos apenas uma das hipóteses levantadas para explicar este padrão, desenvolvida por Stevens (1989) e denominada "regra de Rapoport", a partir dos estudos de Eduardo Rapoport (1975). A regra de Rapoport se baseia em dois pontos. Primeiro, as amplitudes latitudinais de espécies que ocorrem em latitudes altas são em média maiores que as de espécies que ocorrem próximo ao equador, observado por Stevens (1989) para vários grupos vegetais e animais. Uma explicação levantada por Stevens (1989) seria que à medida em que aproximam os pólos, as espécies devem ser capazes de tolerar uma amplitude de condições climáticas cada vez maior, e assim seriam capazes de colonizar uma grande faixa latitudinal. Por outro lado, como nos trópicos as condições são mais homogêneas, os organismos não estariam adaptados a grandes mudanças no ambiente e por isso ficariam restritos a uma pequena faixa latitudinal. Desta forma, segundo a regra de Rapoport, indivíduos não-migratórios devem ser fisiologicamente ou comportamentalmente capazes de tolerar toda a amplitude de condições que as mudanças sazonais lhes impõe, e a seleção natural favorece maiores tolerâncias em altas latitudes (zonas temperadas). O segundo ponto se baseia no "efeito de resgate" (*rescue effect*), inspirado no "efeito de massa" (*mass effect*) de Shmida e Wilson (1985). Segundo este efeito, nas bordas da distribuição geográfica de cada espécie os indivíduos dispersam-se para áreas onde eles sobrevivem mas não se reproduzem devido a condições locais desfavoráveis e/ou insuficiência de recursos. Tais indivíduos são chamados "acidentais", e suas populações são mantidas inteiramente por migração contínua de indivídos das populações viáveis. São populações "escoadouro" (sink populations) conforme Pulliam (1988). Segundo Stevens (1989), o efeito de resgate aliado às pequenas áreas de ocorrência das espécies (regra de Rapoport) criariam a oportunidade de convivência de um número maior de espécies próximas ao equador. Ou seja, nos trópicos, distribuições geográficas mais restritas das espécies fazem com que mais indivíduos sejam encontrados fora de seus habitats ótimos, e uma entrada constante de "acidentais" vindos de habitats adjacentes iria inflar o número de espécies nos trópicos. A regra de Rapoport foi posteriormente ampliada para incluir gradientes altitudinais: "Se a explicação para a ocorrência da regra de Rapoport em um gradiente latitudinal é correta, então uma regra de Rapoport altitudinal deveria também ocorrer, já que a amplitude de condições climáticas experimentadas por habitantes de montanhas também aumenta com a altitude" (Stevens, 1992); e também para gradientes de profundidade em peixes no Oceano Pacífico (Stevens, 1996).

A regra de Rapoport foi examinada para uma grande quantidade de taxa em várias regiões, embora na maioria das vezes não tenha sido comprovada (por ex. Rohde et al., 1993; Roy et al., 1994; Mourelle & Ezcurra, 1997; Rahbek, 1997; Fleishman et al., 1998). Além destas refutações empíricas, Colwell e colaboradores (Colwell & Hurtt, 1994; Colwell & Lees, 2000) desenvolveram um modelo nulo geométrico e comprovaram que em qualquer gradiente com duas barreiras bem definidas (por ex. litoral e cume em montanhas, ou então os pólos para o globo) um máximo em número de espécies ocorre necessariamente no meio do gradiente. Quando o modelo nulo é aplicado a latitudes o pico ocorrerá nos trópicos, enquanto que se aplicado a montanhas o pico ocorrerá em altitudes intermediárias, e foi chamado de hipótese do domínio médio (*mid-domain*). Esta hipótese foi validada a partir de simulações em modelos geométricos nos quais o tamanho e a localização das áreas geográficas das espécies são distribuídos aleatoriamente dentro dos limites (domínios) das barreiras geográficas.

Posteriormente, Taylor e Gaines (1999) estenderam o modelo uni-dimensional de Colwell e Hurtt (1994) para uma esfera onde interações complexas entre vários fenômenos operam em uma escala global, e observaram que a presença de espécies com maiores áreas geográficas em direção aos pólos (zonas temperadas), quando aliada à competição interespecífica, é capaz de gerar um gradiente de diversidade igual ao previsto pela regra de Rapoport, tanto em escalas locais como regionais. Este artigo é importante pois voltou a dar ênfase à regra de Rapoport, desacreditada quando da sua publicação (por ex. Gaston, 1998).

A regra de Rapoport e a hipótese do domínio médio não podem operar ao mesmo tempo, já que prevêem diferentes distribuições na riqueza das espécies ocorrendo em um gradiente altitudinal. A hipótese do *mid-domain* cria um modelo nulo em que o máximo em riqueza de espécies é observado no centro do gradiente altitudinal, enquanto que pela regra de Rapoport o máximo deve ser na menor altitude. A comparação dos dados empíricos com o gradiente previsto pelo modelo nulo é uma forma bastante elegante de testar os resultados obtidos em um gradiente altitudinal.

O terceiro capítulo testou o efeito do mid-domain tanto para espécies de plantas como de insetos (divididos em guildas). Pela primeira vez a hipótese do domínio médio é testada em diferentes organismos, em mais de um nível trófico e em várias localidades dentro de uma região, assim como é a primeira vez que parâmetros biológicos são usados para explicar as assimetrias encontradas nos gradientes obtidos.

Descrição e comparação de comunidades através de teias tróficas quantitativas (capítulo 4)

Além da representação gráfica, teias tróficas são caracterizadas matematicamente por alguns parâmetros. Um dos parâmetros mais estudados e discutidos na estimativa de complexidade de teias tróficas é a conectância (C), ou seja, o número de interações presentes dividido pelo número de interações topologicamente possíveis em uma teia. Um modelo proposto por May (1972, 1973) estabelece que uma comunidade com S espécies possui um limite acima do qual deixa de ser estável, representado por $i\ (SC)^{1/2} < 1$, onde i é a "média da força da interações na teia". Este modelo prevê um decréscimo hiperbólico da conectância com o aumento da riqueza de espécies, ou seja, o produto SC é aproximadamente constante (Yodzis, 1980; Warren, 1990; Putman, 1994; Fonseca & John, 1996). Outros parâmetros calculados a partir de variáveis presentes nas teias também eram considerados constantes até pouco tempo, tais como a fração de espécies intermediárias, a razão do número de ligações tróficas (ou conexões) pelo número de espécies e a fração de conexões por espécies intermediárias (por ex. Briand & Cohen, 1984; Cohen, 1989; Sugihara et al., 1989). Cohen (1989) chega a comparar as proporções constantes em uma teia trófica com as proporções constantes de bases na molécula de DNA, e de como a descoberta desta proporção facilitou a descoberta da estrutura desta molécula. Warren (1990) explica a constância aparente em parâmetros da teia por três fatores: a. **Restrições na estabilidade da comunidade**, que iriam limitar muita da complexidade em sistemas; b. **Restrições Biológicas** onde a média de interações por espécie seria um valor constante, restrito pela anatomia, comportamento ou outras características biológicas dos organismos envolvidos; c. **Artefato** causado pela falta de ligações nas teias representadas, ou por não observância, ou por "conveniência artística", não incluindo na confecção das teias as interações menos importantes, para simplificação e melhor visualização.

Os descritores quantitativos de teias hoje não são mais considerados constantes, e sim dependentes de escala (esforço amostral e uso de agregados de espécies, como "grupos tróficos"), e passaram a ser usados com mais cautela recentemente (Warren, 1990; Martinez, 1992, 1993, 1994). Martinez e colaboradores (1999), entretanto, demonstram que o uso de grupos de espécies (trofoespécies) simplifica as teias e diminui consideravelmente o esforço amostral necessário para se chegar aos mesmos resultados obtidos em análises quantitativas das mesmas teias com maior resolução. Desta forma, a análise de teias simplificadas pelo uso de grupos tróficos necessitaria um esforço amostral muito menor que se a mesma teia tivesse todas as espécies presentes individualizadas.

Além da descrição das teias através de parâmetros matemáticos, duas outras características são procuradas e testadas em comunidades e conseqüentemente em teias tróficas: compartimentação e estabilidade. Uma comunidade compartimentada possui alguma forma de estruturação interna, tal que teias maiores são divididas em sub-unidades em que interações mais intensas ocorrem e que, ao contrário, interagem fracamente com outras sub-unidades (por ex. Pimm, 1979a; Pimm & Lawton, 1980; Rafaelli & Hall, 1992; Putman, 1994).

A compartimentação da comunidade é um mecanismo óbvio para manter a proporção SC constante, independente da escala (Putman, 1994), ou seja, independentemente do tamanho da comunidade, cada espécie estaria interagindo com um número fixo de outras espécies.

Comunidades podem se manter estáveis em dois sentidos distintos: *constância*, quando os sistemas tendem a um retorno exato ao ponto inicial após um distúrbio; e *resiliência*, quando os sistemas re-arranjam suas rotas (por ex. reestruturam suas redes) para buscar um outro ponto de equilíbrio após a ocorrência de um distúrbio (Pimm, 1979b; 1984).

A "força" das interações em uma comunidade pode interferir na sua estabilidade, embora a maioria das interações em uma teia sejam "fracas" (Bengtsson & Martinez, 1996; Raffaelli & Hall, 1996). Uma grande quantidade de interações fortes poderá afetar bastante a constância da comunidade, propagando qualquer distúrbio rapidamente e fortemente a outras partes do sistema. Por outro lado, também irá provocar um rápido tamponamento deste, resultando em uma alta resiliência (Putman, 1994).

Outro fator que pode estar influenciando a estabilidade das teias é a complexidade (alta conectância). Comunidades com alta conectância seriam teoricamente mais sensíveis à perda de espécies do topo da teia pois os efeitos da eliminação de um elemento de nível trófico mais alto seriam mais facilmente propagáveis em teias mais complexas. Por outro lado, comunidades mais simples seriam mais sensíveis à perda de espécies de plantas (base da teia), pois em comunidades com conectância mais baixa os consumidores estariam dependendo de poucas espécies (Pimm et al., 1991).

Três tipos de teias tróficas têm sido aplicadas ultimamente a comunidades onde plantas hospedeiras, seus herbívoros e os parasitóides destes (três níveis tróficos) são descritas (Memmott et al., 1994; Salvo, 1996; Godfray et al., 1999): **1. Teias de conectância**, mostrando apenas a presença/ausência de interações; **2. Teias semi-quantitativas**, onde a abundância relativa de um ou poucos níveis tróficos é mostrada graficamente; e **3. Teias quantitativas**, onde as densidades relativas de todos os níveis tróficos, assim como de suas ligações são mostradas graficamente em uma mesma escala.

Embora as teias tróficas pareçam estruturas estáticas, é muito comum sua mudança de estrutura em resposta às estações do ano e variações temporais em outras escalas de tempo maiores. Assim como ocorre com vários outros aspectos do estudo de comunidades, só nos resta torcer para que as teias estáticas representem algum tipo de média ou talvez a configuração mais importante do ano (Yodzis, 1993).

O quarto e último capítulo aplica a construção de teias tróficas quantitativas a comunidades locais e ao "pool" das localidades da Serra da Mantiqueira (variação regional). Em teias quantitativas, não apenas a informação de qual espécie se alimenta de qual, mas também com que freqüência, é representada em um mesmo gráfico, aumentando o poder descritivo e comparativo das teias. A variação temporal nas localidades (comparação entre início e fim do período reprodutivo das plantas hospedeiras) não foi analisada. Esta é a primeira vez que teias quantitativas são aplicadas à comparação de mais de duas localidades.

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CHAPTER 1

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

> "Las áreas geográficas de distribución son las sombras chinescas
> producidas por los taxones sobre la pantalla terrestre:
> es el medir, pesar y estudiar el comportamiento de fantasmas"
> (Rapoport, 1975)

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 collected for two years during the flowering period of the plants. Species composition in the Mantiqueira localities was then compared to previously obtained data from central (Espinhaço) and southern mountain ranges. The tendency of nearer localities to be more similar floristically was only significant for the Espinhaço range alone and for pooled ranges, as shown by a Mantel test. Both clustering and ordination separated localities from Mantiqueira, Espinhaço and Southern ranges. The dendrogram in the Mantiqueira range clustered Itatiaia and Campos do Jordão, two non-adjacent localities with similar physiognomy. Different processes may be influencing the structure and composition of the Eupatorieae flora in the different studied scales. Historical and biogeographical processes may be more important in determining the communities composition in different mountain ranges, whereas local characteristics such as climate and human impact may be determining differences among localities within each mountain range.

*Este capítulo, com pequenas modificações, será rapidamente submetido ao Journal of Biogeography.

INTRODUCTION

In recent years there has been a tendency to seek explanations for biogeographical patterns of community structure at the regional rather than the local scale (e.g. Ricklefs & Schluter, 1993; Brown, 1995; Brown et al., 1996; Caley & Schluter, 1997). Local communities are not isolated ecological units. They result from a variety of processes that span different spatial and temporal magnitudes. The scale at which the local community is defined will influence the number of species it contains, since local communities are inserted in a regional pool of potential species that sets an upper limit to local species richness. Regional and historical processes operating on larger temporal and spatial scales are necessary to explain the local abundance, distribution and diversity of species (Ricklefs & Schluter, 1993; Brown, 1995).

Brown (1995) proposes using "simultaneously a geographic and historical perspective in order to understand more completely the local abundance, distribution, and diversity of species, and to apply an ecological perspective in order to gain insights into the history and composition of regional and continental biota". A regional perspective on local communities may highlight processes that would not be detected otherwise.

The inability to derive global patterns of biodiversity from local environmental conditions alone has led researchers to search for other explanatory concepts. The theory that characterizes diversity on islands as a balance between colonization and extinction (MacArthur & Wilson, 1963, 1967) is an example of an early attempt to emphasize the influence of both local and regional processes on the diversity of local communities (Ricklefs & Schluter, 1993). With the same line of reasoning used in island biogeography, we can investigate the patterns of convergence of biodiversity among ecologically similar but geographically separate localities, which demands a regional perspective. This interesting problem deals with both community and species ranges.

Islands and mountaintops are ideal systems to address this problem. Mountaintops and islands have in common their 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 can be carried across the savannah by an agent equivalent to oceanic currents, and no plant species will survive in the intervening savannah valleys.

Within mountain ranges, plant species face three main problems. The first one derives from their altitudinal distribution. Abiotic factors differ in different altitudes, such as climatic (Bruijnzeel & Veneklaas, 1998; Safford, 1999a) and edaphic conditions (Smith, 1994; Sollins, 1998; Tanner et al., 1998). Thus, for species to disperse through various altitudes they will need to be habitat generalists to cope with those differences. The second one is the limited area for colonisation. Within a restricted altitudinal range of a particular mountain, sometimes confined to a single slope, populations are obliged to survive in strictly limited areas. This limited available area may not always be sufficient to support indefinitely a population, which will then depend on immigration to persist (the 'mass effect' (Shmida & Wilson, 1985)). The third one is the species geographical range. Unless the species is able to explore intermediate valleys or have extraordinary dispersal ability through air floatation (Hedberg, 1970), it will be restricted to an isolated mountaintop and become endemic.

The Serra da Mantiqueira is a mountain range that borders extensively on the three most populous and developed Brazilian States: São Paulo, Rio de Janeiro and Minas Gerais. It is the highest mountain range in Southeast Brazil, and above the treeline are found the *campos de altitude*. These tropical-subalpine grasslands, also called "Brazilian páramos" (Safford, 1999a), are among the most diverse natural communities in extra-Amazonian Brazil, with very high levels of endemism (Safford, 1999a,b); yet, up to now they have been relatively neglected by ecologists and conservation biologists in contrast to the Atlantic rainforest and the cerrado woodlands. Although Brazilian montane regions have been extensively collected over the years for a variety of taxa, they are still sorely lacking in biogeographic studies.

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), although 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) that set bounds to host ranges of many herbivorous insects (Lewinsohn, 1991; Prado & Lewinsohn, 1994; Prado & Lewinsohn, 2000).

The tribe Eupatorieae is the most diverse in Brazil, and within the country, the Mantiqueira range is presumed to have the highest Eupatorieae species richness (Barroso, 1957). Also, both Eupatorieae taxonomy and phylogeny has been recently reviewed and is now well established (King & Robinson, 1987). The tribe Eupatorieae is thus a promising choice to examine local assemblages and their variation across the region. In this study we present results of Eupatorieae collections in five localities of the Mantiqueira range and access intraregional variation and similarity with regard to other mountain ranges surveyed in previous studies. These collections follow a common protocol and were not designed as a floristic inventory in itself but form part of a larger project to study assemblages of flowerhead-feeding insects in South-east and Southern Brazil (Lewinsohn, 1991). Results on the insect assemblages associated with the tribe Eupatorieae in the Mantiqueira range are reported elsewhere (chapters 2, 3 and 4). To our knowledge, this is the first study using macroecological approaches to analyze and compare communities in such a broad scale in Brazilian mountains.

METHODS

Mantiqueira Range

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. 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. Frost occurs on average 56 days per year at 2200m in Itatiaia and at 1630m in Campos do Jordão, mostly during the dry winter. Drought may be partly offset by orographic fog, which in Itatiaia occurs 218 days per year at 2200m. In Itatiaia, monthly average free air humidity ranges from 65% to 90% (Safford, 1999a).

The Mantiqueira range is divided in two distinct geomorphologic 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 breaches 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.

The tree line in Itatiaia averages between 2000m and 2200m, which is considered low for its latitude (Körner, 1998). 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). According to Safford (1999b), the Brazilian *campos de altitude* are almost entirely restricted to an area of less than 350 Km^2 in the states of São Paulo, Rio de Janeiro, Minas Gerais and Espírito Santo with an outlier in Santa Catarina. The three largest families in Itatiaia are the Asteraceae, Polypodiaceae s.l. and Melastomataceae, summing about 40% of the plant species. In Itatiaia, the savannah-like associations dominated by the Asteraceae genus *Baccharis*, and the Asteraceae tribes Eupatorieae and Vernonieae are probably the most species-rich formation in the *campos*. About a third of the species in the Itatiaia *campos de altitude* appear to be endemic to this physiognomy (Safford, 1999a).

Sampling methods

For present purposes, we define *region* as one mountain range. *Locality* is a regional subdivision formed by a group of collection *sites*. A *site* is each point where a plant population was collected. With these definitions, the Mantiqueira range is considered a *region* and Ibitipoca is considered a *locality* with several collection *sites*.

In the Mantiqueira range, the following localities were collected (see Figure 1.1 for distribution of localities and Table 1.1 for coordinates):

1. **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.*
2. **VM** - The **"Visconde de Mauá"** locality is an important sampling area on the slope opposite to the "Itatiaia National Park". Since we could not reach the mountaintops, we collected only in open sites within the highland forest belt, and not in the *campos de altitude.* The locality straddles the border of Minas Gerais and Rio de Janeiro states.
3. **IT - "Itatiaia National Park"**, the first Brazilian National Park, which includes the Agulhas Negras peak, the second highest Mantiqueira summit with 2789m. On its southwestern slope and highland plateaus we had access to its *campos de altitude*, the most extensive in the Mantiqueira. The park also straddles the Minas Gerais and Rio de Janeiro State border.
4. **PQ - "Passa-Quatro"** in Minas Gerais. Sampling sites in this locality were spread apart, 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.
5. **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 highland forest and in *campos de altitude.*

Whenever possible, we preferred to travel between localities on dirt roads within the mountains, along which we could take additional collections. A total of 500 km of roads were collected, not counting areas that were only collected on foot, as in Ibitipoca. Linear distances between pairs of localities varied from 26 km between Visconde de Mauá and Itatiaia and 203 km between Ibitipoca and Campos do Jordão, the two extreme collected mountains.

Six field trips were carried out in the Mantiqueira range, from February to June in 1998 and 1999, encompassing the flowering and fruiting of all Eupatorieae, although not all localities were collected in all trips (Table 1.2). In each of the five localities a minimum of fifteen sites were chosen for collecting plants, with a minimum of 1km (exceptionally, 500m) spacing among them. In each site, all flowering and/or fruiting Eupatorieae species were collected. Although each collection 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.

Previous data obtained for the Espinhaço range in central and northern Minas Gerais and for south Brazilian ranges in 1995 and 1996 used the same collecting methods, but did not concentrate on a particular tribe (Prado & 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). Dr. Harold Robinson of the U.S. Natural History Museum (Smithsonian Institution) confirmed, corrected and completed our species identifications.

A set of six probably new Eupatorieae species, almost all from the Southern Brazilian range, was only identified to tribe (see Appendix). Since they are different morphospecies from all the other identified ones, they were included for analysis.

Data Analysis

The floristic dissimilarity between all pairs of localities was expressed by the relativized Euclidean distance of the occurrence of each plant species per locality (i.e. the number of sites the species was collected per locality). Floristic dissimilarity between localities was correlated to geographical distance with the Mantel test. It calculates the Mantel Z statistic and its standardized form r, equivalent to Pearson's correlation coefficient, and ranges from -1 to +1 (McCune & Mefford, 1999). The Mantel p value was achieved with a randomization (Monte Carlo) test for the pool of the three ranges, and with a Mantel's asymptotic approximation for isolated ranges, since five localities are considered 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 distance, namely the hypotenuse of a triangle formed by their northern and eastern UTM coordinates. 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 and Euclidean distances for standardized data for species frequencies within localities, with the UPGMA aggregation method (Digby & Kempton, 1987). The frequency of species within localities in the main matrix was standardized using the adjustment to standard deviate, with $b = (x - \overline{x}) / s_i$.

Localities were also subjected to ordination by detrended correspondence analysis (DCA), using also the occurrence of each plant species per locality. DCA is an improvement of ordinary Correspondence Analysis in which putative distortions are removed by rescaling of individual axis segments (Gauch, 1982; Digby & 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 rarer species on the final configuration (McCune & Mefford, 1999).

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

RESULTS

Eupatorieae species 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 subtribe with more species 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* and seven genera belonging to various subtribes were represented by only one species.

Not all subtribes and genera were present in all localities (Figure 1.2a,b). *Adenostemma brasilianum* was found only in Visconde de Mauá, while the subtribe Ayapaninae, with three species, was not collected 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 Mantiqueira range: *Ageratum fastigiatum, Austroeupatorium silphiipholium, Campovassouria cruciata, Campuloclinium purpurascens* and *Chromolaena laevigata* (see Appendix). With the exception of *C. purpurascens*, which seems to be restricted to humid Mantiqueira high elevation sites, the other four species are commonly widespread in other Brazilian mountains (Cabrera & Klein, 1989; Lorenzi, 1991; Prado, 1999).

The locality with more collections was Ibitipoca, with 157 collections and 33 species, followed by Visconde de Mauá with 144 collections and 24 species and Campos do Jordão, with 129 collections and 32 species. Substantially lower species richness was found in Passa Quatro, with 77 collections and 16 species, and in Itatiaia, with 89 collections and 19 species. The plant species richness recorded in each locality was strongly correlated with sampling effort. The total number of collections per locality accounted for 54% of local species richness ($r^2 = 0.543$; $p<0.05$).

Although we found 56 species altogether in the Mantiqueira localities, the maximum in one locality was 33 species in Campos do Jordão, 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 these 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 and five localities (Figure 1.2c).

It is worth noting that Praxelinae, the most widely distributed and second most speciose subtribe, was represented in Itatiaia by only one species with three collections (*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 species (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. We found one species, *Mikania vitifolia*, listed by Barroso (1957) in the Itatiaia, only once in Bom Jardim (in the Southern Brazil mountain ranges). A more recent paper without an intensive 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 two 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. Thus, *Ageratum conyzoides*, a widespread weed in Brazil (Lorenzi, 1991) listed by Barroso (1957) in the Itatiaia park, was not found in the sites collected 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*, which in the Mantiqueira range was found only once in Ibitipoca, is known to us from montane trails and open areas near Campinas, SP, respectively at 1000m and 600m altitude (Almeida, 1997).

The montane Eupatorieae flora in south-eastern and southern Brazil

A total of 2351 collections from 15 tribes and 534 species of Asteraceae were obtained for the three studied ranges. The tribe Eupatorieae represents almost half (1051 vouchered collections or 45%) of collections and more than a quarter of the species (144 species or 27%) collected in the whole project. 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 1.3). Since in the Mantiqueira we focused on Eupatorieae species, collections 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 (see Table 1.3).

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*, present in four localities in the Espinhaço range. 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 only one species: *Pseudobrickellia brasiliensis, Ophyosporus freyreysii, Campovassouria cruciata, Hatschbachiella tweediana, Stomatanthes polycephalus, Gyptis crassipes, Trichogoniopsis adenantha* and *Vittetia orbiculata.*

The Eupatorieae species turnover across the three mountain ranges is fairly high. From the entire pool of 144 Eupatorieae species recorded in the three ranges, 120 (83%) Eupatorieae species were found in a single mountain range, whereas only two species, *Mikania micrantha* and *Chromolaena laevigata* occurred in all three ranges (Figure 1.3). 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* occurred in the Espinhaço and Southern ranges but was not found in the Mantiqueira (see Appendix for details).

No subtribe was restricted to the Mantiqueira, but three genera, represented each by one species were found only in this mountain range: *Ophyosporus freyreysii, Adenostemma brasilianum* and *Trichogoniopsis adenantha* (=*Trichogonia gardneri*). The last two species are commonly found in other Brazilian open formations or in gaps and roadsides within midaltitude forests (e.g. Cabrera & 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, two of the 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* 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 in the three montane ranges, only 24 (17%) are shared among regions. Floristic dissimilarities increased with geographical distances among localities in the Espinhaço and pooled ranges (Figure 1.4). The Mantel test showed a positive significant 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 for the Mantiqueira ($r = 0.111$; $p > 0.70$) and South ($r = -0.041$; $p > 0.80$) ranges (Figure 1.4). Note that the plot for pooled ranges in Figure 1.4 shows two distinct groups: a first more dispersed group in relation to the relative Euclidean distance that encompasses pairs of localities that are less than 700km 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 1000km geographical distance. The first group shows mostly dissimilarities within the same mountain ranges, whereas the second group shows dissimilarities between each two localities present in different mountain ranges.

In the cluster analysis, localities of the three mountain ranges were clearly separated (Figure 1.5). In the cluster dendrogram, the Espinhaço is first grouped with the Mantiqueira and then with the South range. Within the Espinhaço range, Serra do Cabral was clustered with Diamantina and Serra do Cipó with Ouro Branco, with Grão Mogol alone. In the Mantiqueira, Visconde de Mauá is very similar to Passa Quatro and Itatiaia joins Campos do Jordão, while Ibitipoca joins the Mauá-Passa Quatro cluster at a higher floristic distance. In the Southern cluster, Matos Costa is grouped with Lages and then with Cerrito, while Bom Jardim stands close to Cambará. All of these joinings conform well to geographic distance (Figure 1.1), with the exception of Itatiaia - Campos do Jordão in the Mantiqueira and Lages - Matos Costa in the Southern range.

An alternative cluster analysis with Euclidean Distance on standardized data and UPGMA (not shown) joined first the Mantiqueira and Southern ranges and then both to Espinhaço. However, within each mountain range, localities were grouped exactly as in Figure 1.5. This shows that the floristic dissimilarity among the three ranges is sensitive to the used distance measure, but also 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 1.6). The first axis had an eigenvalue of 0.791 and grouped the localities from the three regions.

DISCUSSION

More than half of the Eupatorieae collections were obtained in the Mantiqueira range. With the exception of Vernonieae in the Espinhaço range (Prado, 1999), the tribe Eupatorieae was the one with most collections and species obtained in the three regions. These two tribes, followed by the Heliantheae and Asteraeae, are indeed the largest subdivisions of Asteraceae in Brazil (Barroso, 1986).

Within the Mantiqueira range the Itatiaia locality is the only one previously studied for its Asteraceae flora (Barroso, 1957). In Itatiaia we obtained 19 Eupatorieae species of which six (32%) were not yet assigned to this place, while 38% of the species previously recorded in this locality were not observed in the present study. The fact that some species were previously obtained for Itatiaia and were not detected in the present study may have several reasons. The first one is that Itatiaia National Park encompasses lower altitudes we did not collect and where probably are the *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). The flowering period for Asteraceae plants in this locality is probably narrower than for other localities with milder climate. Some Eupatorieae species may have been present in Itatiaia but were not flowering or fruiting during our field trips and therefore not detected (a sampling artifact to be expected according to Paine (1988), which again may explain the absence in our study of some previously recorded species. Plant species in mountaintops may show a reduced flowering period, as detected by Jonas and Geber (1999) for *Clarkia unguiculata* (Onagraceae) in the Sierra Nevada. They observed that the days to germination and flowering increased with elevation, showing that it is possible that elevation changes plant phenology.

High proportions of Eupatorieae species are singletons (collected only once) varying from 14% in the Mantiqueira to 38% in the Espinhaço. Since in the Mantiqueira range we were collecting preferentially Eupatorieae species - which was not true for the Southern and Espinhaço ranges, where all tribes were collected with the same intensity -, we always searched carefully for rare species in the collected sites, which may have reduced the number of singletons in this range.

Only two Eupatorieae species 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 studied mountain ranges, as shown by both clustering and ordination analyses. In the cluster dendrogram, the Mantiqueira range grouped first either with the Espinhaço or with the Southern range, depending on the distance measure used. This result reinforces the intermediate position of this range, which matches with its geographical position, between the Espinhaço and Southern ranges. Although the Mantiqueira is geographically much nearer to the Espinhaço range than to the Southern range, its flora is not more similar to one or the other range, but differs fairly equally from both ranges. It also suggests that within a same mountain range the locality distributions according to its Eupatorieae flora are better defined than at a higher level, among ranges.

Within each mountain range we also find the same pattern of many species restricted to only one or two localities. Species could be found occurring 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 result of the Mantel test, which detected no correlation between floristic and geographical distance in both Mantiqueira and Southern ranges. In these two mountain ranges the floristic dissimilarity between any pair of localities did not dependend on the geographical distance. The correlation of geographical and floristic distances was only significant in the Mantel test for the Espinhaço range alone. The same analysis conducted for the Vernonieae flora (another Asteraceae tribe) in the same Espinhaço localities was not significant (P. Prado, pers. com.), which shows that different groups respond differently to the same variables. The pool of the three ranges also showed more similar Eupatorieae flora in more proximate localities. The two distinct groups present in the Figure 1.4 for pooled localities shows that, in general, any pair of localities within a same mountain range show a more similar flora than pairs of localities from two distinct mountain ranges.

The cluster dendrogram grouped adjacent localities according to geographical distribution in the Espinhaço ranges. In the Mantiqueira range, Itatiaia was grouped with Campos do Jordão, both localities with collection sites in the *campos de altitude*, which did not occur in Visconde de Mauá and Passa Quatro, where only the highland forests borders were collected, because of the inaccessibility of the *campos de altitude* in these localities. Visconde de Mauá and Passa Quatro were also the most human-impacted localities, which may be affecting its flora. In the Southern range, Cerrito was also displaced in relation to its geographical position, probably because of the atypical Eupatorieae flora, with many exclusive species, found in this locality.

The geographical distance was a good predictor of floristic composition for both Espinhaço range and the pool of the three ranges. On the other hand, in the Mantiqueira range both clusters formed by Itatiaia and Campos do Jordão and also Visconde de Mauá and Passa Quatro joined non-adjacent localities but with similar physiognomies and human impact. This result suggests that environmental variables, such as climate, altitude and human impact may be influencing the floristic composition of localities in a more local scale. At least three previous studies in tropical montane forests observed that adjacent localities present more similar flora. 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 have been independently formed on each of the mountains concerned, the local populations of the species often having accumulated important ecological characters. Smith (1975) for the best known and collected New Guinea Mountains, 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 (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. In the high Andean flora, two families, 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 came to the same conclusion, that distance between localities is very important, but that climate can be as important as distance in determining the composition of adjacent montane floras.

In the Mantiqueira range other study using the same data analyzed here (chapter 3) reached two pertinent results. The first one is that for both Campos do Jordão and Itatiaia, the maximum species richness was detected above the treeline, showing that for Eupatorieae species the flora present in the *campos de altitude* contains more species, and a larger proportion of endemics, than the flora found in the lower highland forest zone. The second point is that more widespread Eupatorieae species present a wider altitudinal range, which means that species occurring in various localities are generalistic enough to occur in a wide variety of altitudes. These results direct us to the same conclusion as the three studies cited above. Campos do Jordão and Itatiaia are not geographically closest among the Mantiqueira localities, but the flora present in the *campos de altitude* are most similar in these two localities probably because of the similarity of suitable climatic and habitat conditions.

The processes structuring communities within a single locality may not be the same occurring within a mountain range, which may not be the same processes acting among mountain ranges. As already noted by some authors (e.g. Ricklefs & Schluter, 1993; Brown, 1995; Maurer, 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 species 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.

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Table 1.1. 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.

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'

Table 1.2. Eupatorieae voucher collections in the Mantiqueira range, per locality and field trip.

		Locality					
Field trips	Dates	IB	VM	IT	PQ	CJ	Total
1	15 - 19/02/1998		17	15	3	12	47
2	04 - 11/05/1998	25	45	10	23	27	130
3	20 - 22/06/1998	8	3				11
4	16 - 22/01/1999	28	18	1	7	14	68
5	02 - 09/03/1999	36	31	36	17	33	153
6	04 - 12/05/1999	60	30	27	27	42	187
Total		157	144	89	77	129	596

Table 1.3. Number of collections and species per Asteracean tribe for three Brazilian mountain ranges. Espinhaço and Southern ranges were collected in 1995 and 1996, while Mantiqueira was collected in 1998 and 1999. Eupatorieae tribe is in bold.

	Mantiqueira		Espinhaço		South	
Tribe	Collections	Species	Collections	Species	Collections	Species
Astereae	70	33	57	17	88	24
Barnadesioideae	1	1	10	4	2	1
Cardueae	0	0	0	0	13	3
Eupatorieae	**601**	**56**	**315**	**68**	**135**	**46**
Gnaphalieae	0	0	4	3	5	5
Heliantheae	15	7	89	39	20	9
Inuleae	6	6	0	0	0	0
Lactuceae	0	0	1	1	7	5
Mutisieae	10	7	93	21	38	14
Helenieae	0	0	12	2	0	0
Plucheae	0	0	2	1	5	2
Moquiniae	0	0	5	1	0	0
Senecioneae	23	15	31	7	67	15
Tageteae	0	0	0	0	1	1
Vernonieae	97	19	462	113	61	14
Indet.	5	5	0	0	0	0
Total	828	149	1081	277	442	139

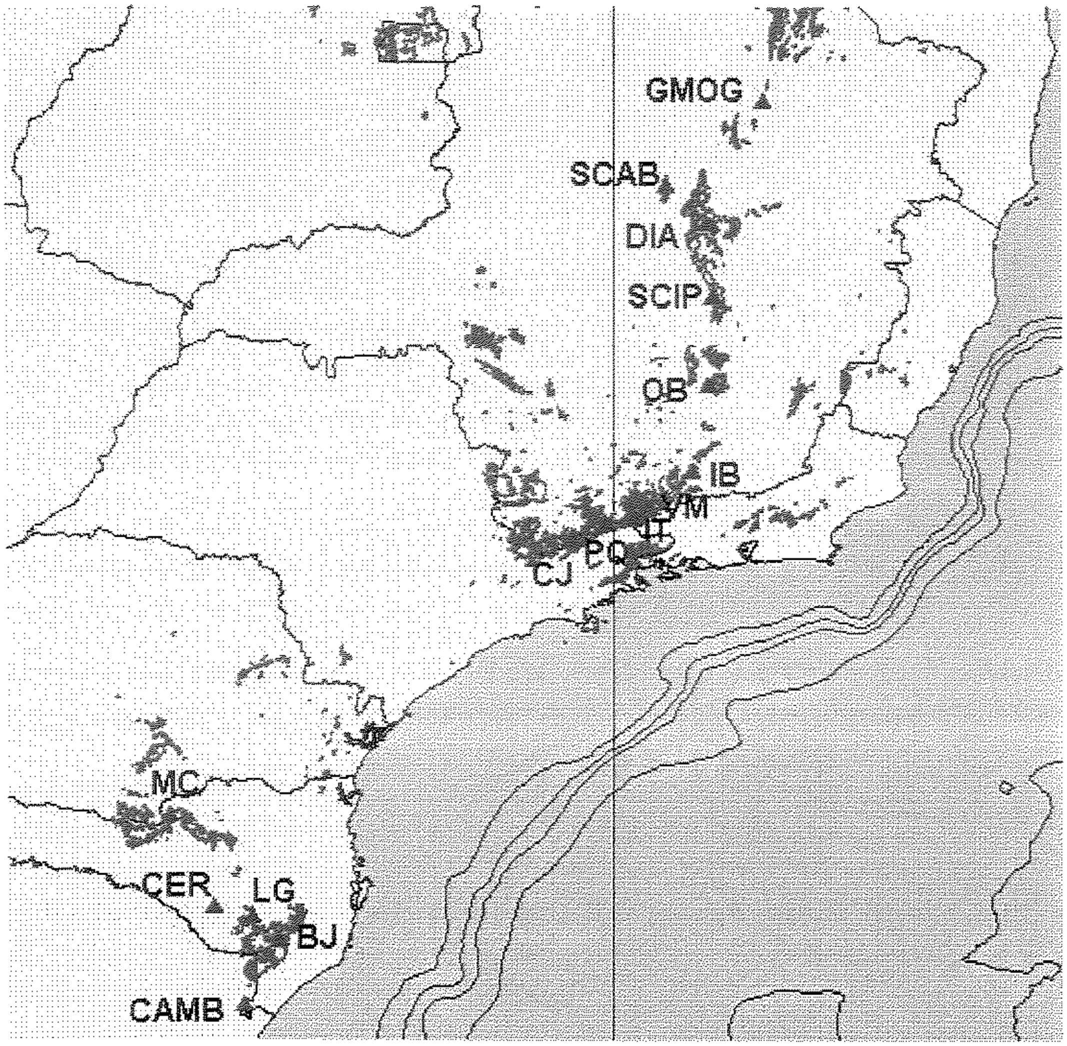
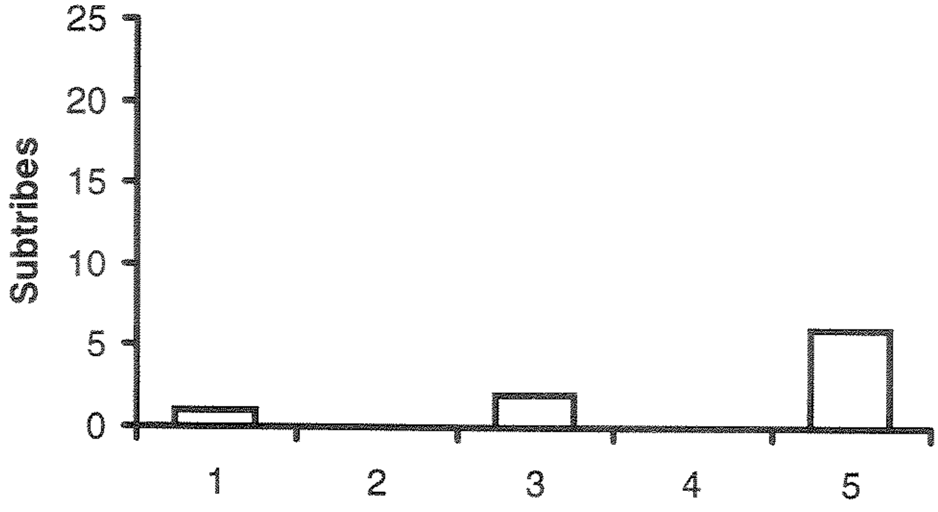
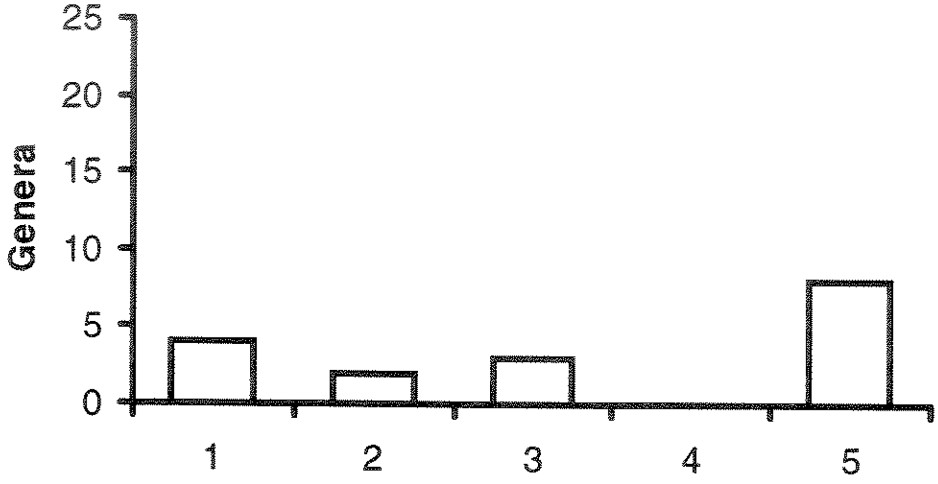


Figure 1.1. Sampling localities in the Espinhaço, Mantiqueira and Southern ranges. Areas in red present altitudes of more than 1,000m above sea level. Espinhaço localities are: **GMOG** - Serra do Grão Mogol, MG, **SCAB** - Serra do Cabral, MG, **DIA** - Planalto de Diamantina, MG, **SCIP** - Serra do 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). See Table 1.1 for coordinates of reference points.

a. Subtribes



b. Genera



c. Species

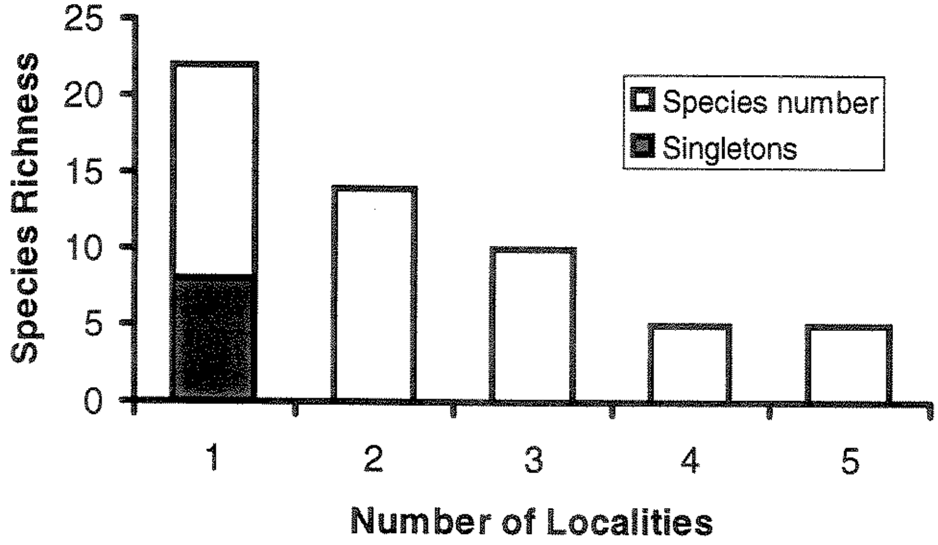


Figure 1.2. Occurrence of Eupatorieae subtribes (a), genera (b) and species (c) in localities of the Mantiqueira range. Note that the number of species that are singletons is higher than the number of species recorded in four or five localities.

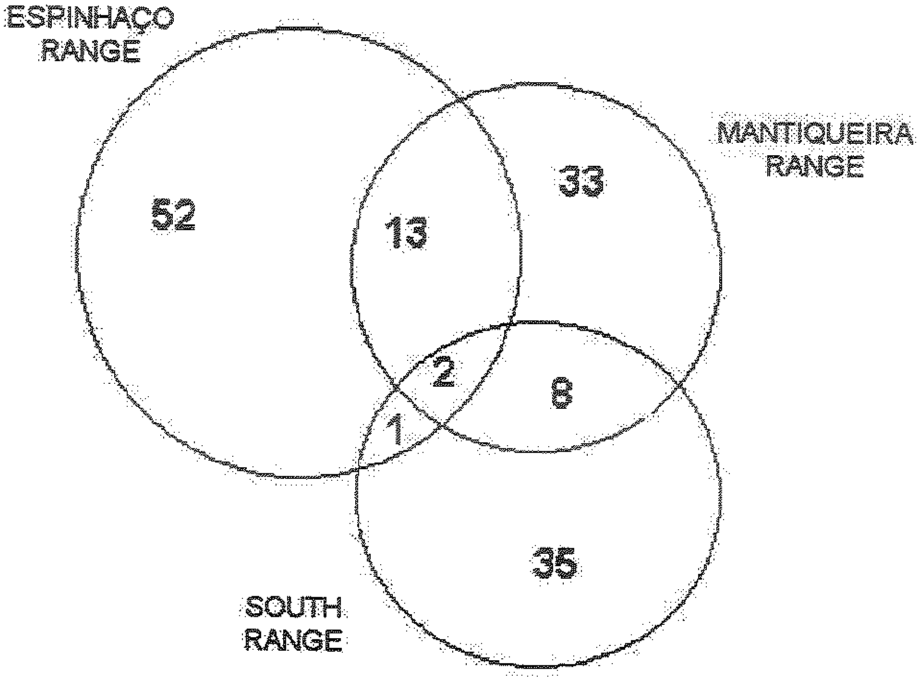


Figure 1.3. Venn diagram of the number of Eupatorieae species recorded in three Brazilian mountain ranges, showing species shared among ranges.

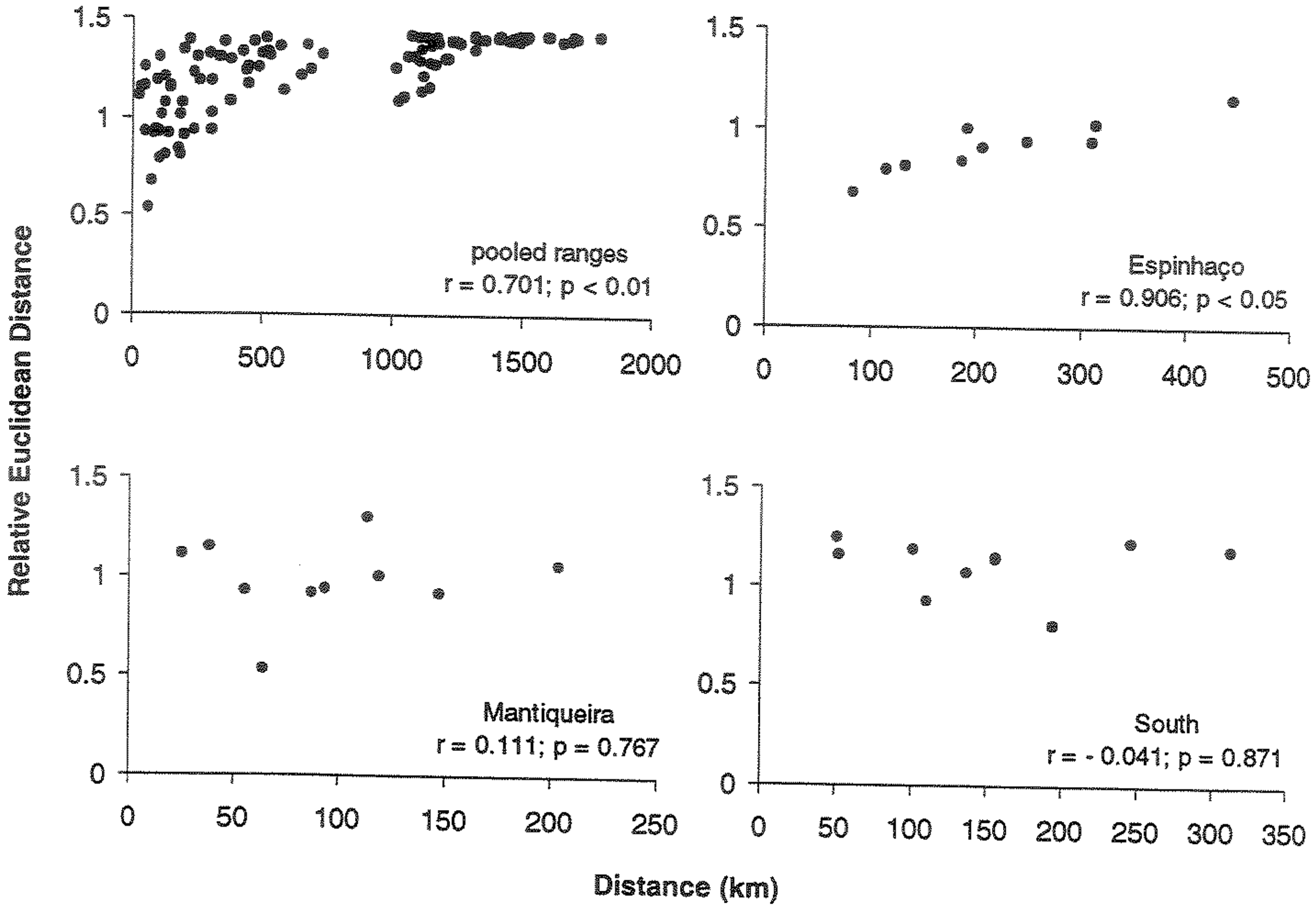


Figure 1.4. Floristic dissimilarity (determined by Relativized Euclidean distance of species composition) for pooled or individual mountain ranges plotted against geographical distance (km). The significance levels reported were obtained with a Mantel test. Note the difference in scale in the abcissa.

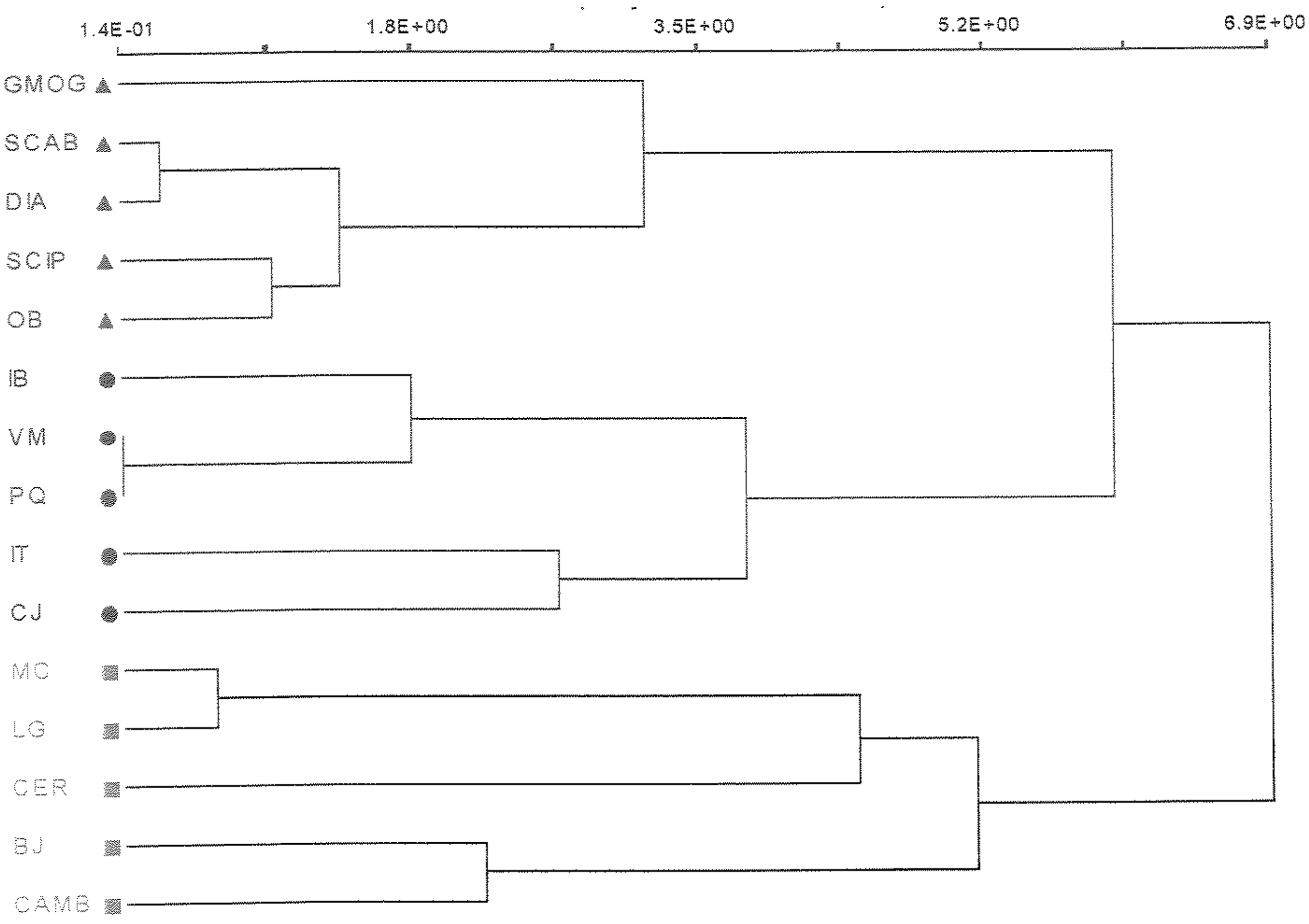


Figure 1.5. Hierarchical cluster diagram for localities from Espinhaço, Mantiqueira and Southern ranges. The clustering method used UPGMA with Relativized Euclidean Distance. Mountain ranges are assigned different colors and symbols: Espinhaço range, red triangles; Mantiqueira range, blue spheres and South ranges green squares. See Table 1.1 for locality codes.

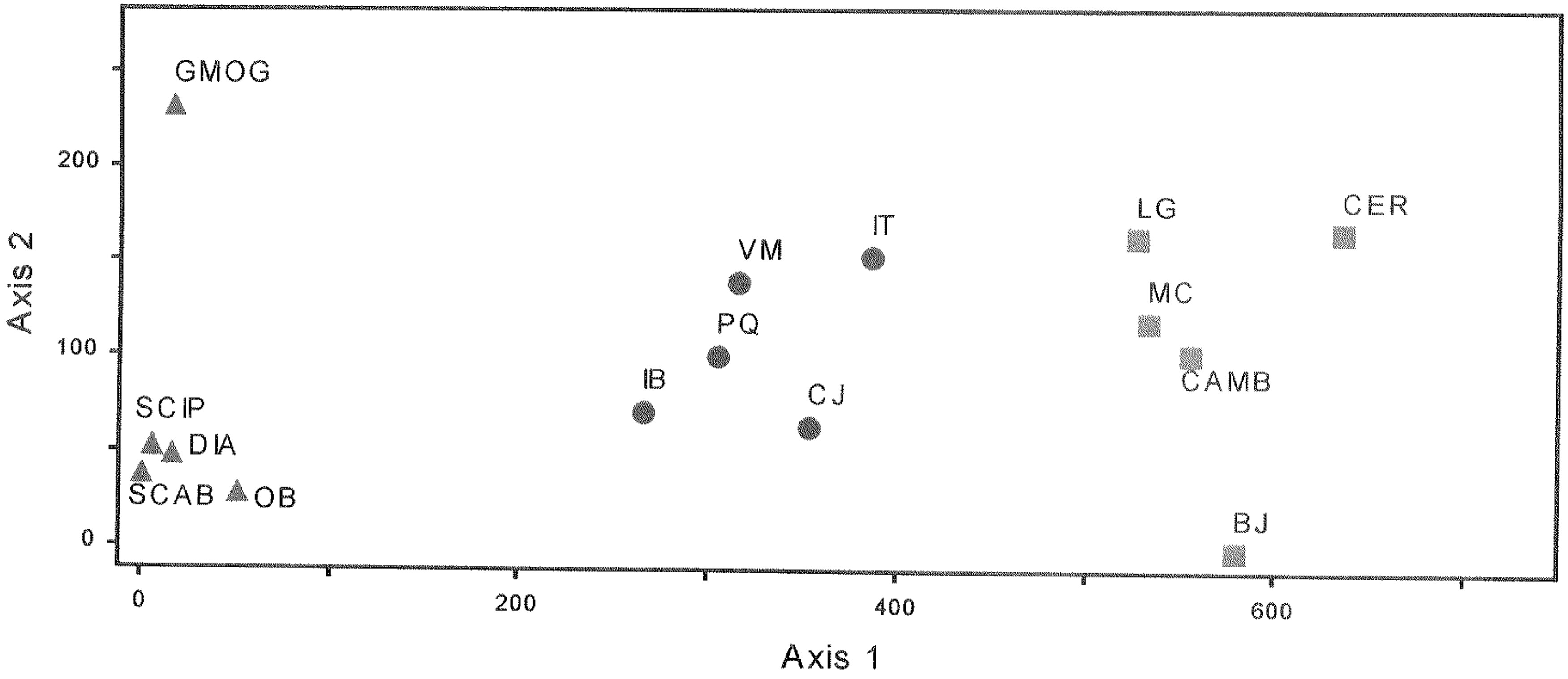


Figure 1.6. Ordination by DCA of collected localities in three Brazilian mountain ranges. Rare species were downweighted. Mountain ranges are assigned different colors and symbols: Espinhaço range, red triangles; Mantiqueira range, blue spheres and South ranges green squares. See Table 1.1 for locality codes

Appendix 1.1. Number of collections of each plant species per locality and per mountain range. Table 1.1 lists locality codes and coordinates. Abbreviations for subtribes are: Ad - Adenostemmatinae; Al - 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
Ad	Adenostemma brasilianum		12													
	Adenostemma verbesina											1				
Ageratinae	Acritopappus indet.						1									
	Acritopappus irwinii						5									
	Acritopappus longifolius							2	2							
	Ageratum conyzoides	6	25		11	5										
	Ageratum fastigiatum	30	24	2	11	7	7	2	8	3	1					
	Stevia commixta														1	
	Stevia crenulata	1		1		1										
	Stevia ophryophylla												1			
Al	Pseudobrickellia brasiliensis						2	1	3		1					
Ayapaninae	Ayapana amygdalina							2	1	4	3					
	Aypana aff. amygdalina									1						
	Heterocondylus alatus			1			4	1	4	3						
	Heterocondylus amphidictyus	5							2	2	4					
	Heterocondylus grandis												2			1
	Heterocondylus jaraquense	2				9										
Cr	Koanophyllon adamantium						1		1							
	Koanophyllon thysanolepis	1				3			2	1	2					
	Ophyosporus freyreysii		1													
Disynaphinae	Campovassouria cruciata	1	3	4	1	4						1	2	2	1	5
	Grazielia aff. serrata														3	
	Grazielia gaudichaudeana	3		5												4
	Grazielia gaudichaudeana var. bipinnata					2										
	Grazielia intermedia		8	15	3	16						2	3			
	Grazielia serrata												1	3		2
	Raulinoreitzia crenulata												1	1		
	Raulinoreitzia tremula							1					1			
	Symphyopappus aff. reticulatus									1						
	Symphyopappus angustifolius							1								
	Symphyopappus compressus		4	11		4										
	Symphyopappus cuneatus			3		2			3	2	1					
	Symphyopappus decussatus	5	1	1			1		1							
	Symphyopappus indet.															1
	Symphyopappus itatiayensis		4	10	2											
	Symphyopappus reticulatus								1							
	Symphyopappus sp.01						1									
	Symphyopappus viscosus							1	2							
Eupatoriinae	Austroeupatorium inulaefolium		1										1			
	Austroeupatorium laetevirens				1											
	Austroeupatorium neglectum		1	2		2										
	Austroeupatorium paulinum		1	7		3										
	Austroeupatorium picturatum											1	1		1	1
	Austroeupatorium silphiifolium	8	14	8	11	5										
	Hatschbachiella tweediana														1	2
	Stomathantes polycephalus							1								

Appendix 1.1 (continued).

ST	Species	Mantiqueira					Espinhaço					South				
		IB	VM	IT	PQ	CJ	GMOG	SCAB	DIA	SCIP	OB	MC	LG	CER	BJ	CAMB
Gyptidinae	Barrosoa betonicaeformis		1			5						1	2	1	5	7
	Barrosoa candolleana						4									
	Campuloclinium campuloclinoides							2								
	Campuloclinium chlorolepis							1								
	Campuloclinium indet.							1								
	Campuloclinium macrocephalum													2	5	1
	Campuloclinium megacephalum					2										
	Campuloclinium parvulum	2														
	Campuloclinium purpurascens	3	6	1	5	3										
	Gyptis crassipes													1		
	Trichogonia hirtiflora						10	2	6	4	2					
	Trichogonia salviaefolia						3	3								
	Trichogonia villosa	9					3	5	12	3	3					
	Trichogoniopsis adenantha	2														
	Vittetia orbiculata													2		
Mikaniinae	Mikania aff. lasiandrae									1						
	Mikania aff. leiolaena						1		1	1	1					
	Mikania aff. sessilifolia									1						
	Mikania bradei	1														
	Mikania burkelli															1
	Mikania campanulata			5		1										1
	Mikania cipoensis									3						
	Mikania citriodora						1									
	Mikania cordifolia					3		1								
	Mikania decumbens	3														
	Mikania elliptica	8			1	1										
	Mikania eriostrepta					2										
	Mikania glaziovii			1												
	Mikania hemisphaerica		1													
	Mikania involucrata														1	
	Mikania lasiandrae	3		1	4	8										
	Mikania leiolaena						5	3	2	2						
	Mikania lindbergii	2				3										
	Mikania linearifolia							1								
	Mikania micrantha	1	13	3	4		2	1				1	1			
	Mikania microcephala		1	5												
	Mikania microdonta	1			1											
	Mikania microphylla										1					
	Mikania neurocala							1								
	Mikania nitidula						1									
	Mikania oblongifolia									1						
	Mikania officinalis							4	7	1						
	Mikania orleansensis															1
	Mikania paraensis															1
	Mikania phaeoclados									2	1					
	Mikania pinnatiloba													1		
	Mikania pseudogracilis										1					
	Mikania purpurascens								1							
	Mikania ramosissima						1		1	1						
	Mikania retifolia						1		5							

Appendix 1.1 (continued).

ST	Species	Mantiqueira					Espinhaço					South				
		IB	VM	IT	PQ	CJ	GMOG	SCAB	DIA	SCIP	OB	MC	LG	CER	BJ	CAMB
Mi	Mikania salviaefolia											2	2			
	Mikania sessilifolia					2		1		2	1					
	Mikania sp.1	1				1										
	Mikania sp.12									1						
	Mikania sp.2		1													
	Mikania sp.31													1		
	Mikania sp.38											1				
	Mikania vitifolia														2	
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 1	2				1										
	Chromolaena ascendens	2				7									2	3
	Chromolaena barbacensis						1			1						
	Chromolaena chaseae						1	3	3	2	1					
	Chromolaena congesta	11				4									6	2
	Chromolaena cylindrocephala						2	3	6	2						
	Chromolaena decumbens	1									2					
	Chromolaena hookeriana	3	4													
	Chromolaena horminoides						1	4	4	2						
	Chromolaena laevigata	7	5	3	7	9	1	1	1	1	1	1	1	2		
	Chromolaena lineata								1							
	Chromolaena mattogrossensis						1	2								
	Chromolaena maximilianii	4	3		4	2										
	Chromolaena minasgeraesensis					2	3	1								
	Chromolaena multiflosculosa	15														
	Chromolaena odorata						2			1						
	Chromolaena pedalis	10	1			5										
	Chromolaena pedunculosa												1	1		
	Chromolaena pungens							1	2							
	Chromolaena sagittifera							1	2							
	Chromolaena sp.30													1		
	Chromolaena squalida	4	2		2		2	6	7	4	3					
	Chromolaena stachyophylla							2	1	2	1					
	Chromolaena verbenacea													1		
	Disynaphia aff. ligulaefolia													1		1
	Disynaphia ligulaefolia													1		
	Disynaphia spathulata													2		
	Praxelis capillaris									2						
	Praxelis clematidea		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			
	Sum	157	144	89	77	129	68	62	94	58	33	14	23	30	32	36

CHAPTER 2

Resource specialisation and geographical distribution of herbivorous insects in Eupatorieae (Asteraceae) flowerheads in Serra da Mantiqueira, Brazil*

Abstract. Endophagous insects feed inside host plant structures; and if on the one hand they are protected against climatic conditions and generalist predators and parasitoids, on the other hand they are food limited and more vulnerable to specialist predators and parasitoids. Interactions among flowerhead herbivores are often considered at two levels, the first among larvae within flower heads and the second the local community, in which adults interact for oviposition sites. A third level - the regional level - should also be considered, as a co-determinant of local community composition. In the Mantiqueira range (SE Brazil) we collected Eupatorieae flower heads from five localities to rear endophagous insect species. Endophagous species were divided into three guilds, according to feeding mode and degree of endophagy. The Strict Endophage (SE) guild is composed of more specialized and abundant species when compared to the other two guilds. In general, the three guilds present higher species richness in localities with higher host plant richness, suggesting that a richer host plant community supports a richer endophagous community. The endophagous community similarities among localities are not directly determined by either floristic composition in each locality or geographical distance among pairs of localities. The flower head endophagous insects in the Mantiqueira range present different strategies in host plant use, and respond differently to the same variables found in each studied locality. We suggest that local differences in environmental factors and habitat composition, allied to historical and biogeographical factors, all acting in each single locality are influencing differently the structure and composition of the different endophagous guilds in the studied system.

*Este capítulo, com pequenas modificações, será rapidamente submetido à Oecologia ou Journal of Animal Ecology.

Introduction

Structures such as Asteraceae flower heads and gall midges are discrete and complex microecosystems. They have measurable energy input, a fairly diverse infrastructure and distinct food chains with several trophic levels. Within these structures the interactions between plant, phytophagous insects and their entomophagous predators are relatively easy to access and offer an optimal object for the study of guild structures (Zwölfer, 1979; Freese & Günter, 1991). Flower heads are food resources with high structural diversity. In their early stages, they contain much meristematic tissue that facilitates gall formation and its external bracts provide some protection to its inhabitants. Flower heads are also a highly predictable resource, since most Asteraceae species occur in patches with high density and reliable seed production (Zwölfer, 1983; Straw, 1989a,b). On the other hand, exploiting flower heads involves particular costs. Being restricted to a discrete structure, endophagous insects not only have to cope with other competitor species, but also are easy and predictable targets for specialized natural enemies (Zwölfer, 1983).

According to Zwölfer (1979), the interactions of insect species associated with flower heads or plant galls take place at two different but mutually dependent ecological levels. The first level involves the individual flowerhead systems, which form discrete habitats with limited carrying capacity for the immature stages. This is the level where the interactions among immatures take place. The second level is the local host plant population and its community. At this level we find the arena for the activities among adult phytophagous insects, which with different oviposition strategies set the initial positions for the processes within the flower heads.

Although not considered by Zwölfer (1979), at a still higher level, the regional level is potentially important in determining local dynamics (Cornell & Lawton, 1992) and should also be taken into consideration. The regional level constitutes the pool from which the local community is formed. Communities are inserted in a regional pool of colonizer species that will influence the local species richness, setting an upper limit to it. Regional and historical processes, operating on large temporal and spatial scales will enable the understanding of the local abundance, distribution, and diversity of species. Although this approach has not received much attention in community studies until recently, it has now regained prominence in the ecological literature (e.g. Ricklefs and Schluter, 1993; Brown, 1995; Brown et al., 1996; Caley and Schluter, 1997).

A well-known pattern in the geographical distribution of species is the correlation of local abundance and wide geographical distribution (Hanski, 1982; Brown, 1984). Brown (1984) explains this pattern mainly by niche specialisation. He argues that the abundance and distribution of species are limited by the combination of physical and biotic environmental variables that determines the niche. He hypothesizes that among closely related, ecologically similar species, generalists should be abundant throughout their range and have a wide geographical distribution, since they are more tolerant than specialist species. Conversely, specialists should be both locally rare and have a restricted distribution.

Two other hypotheses are also used to explain the abundance-distribution relationship: resource availability and sampling artifact (Gaston et al., 1997). If the abundance and distribution of resources are positively correlated, then an observed abundance-distribution relationship may reflect that species are tracking their resources. On the other hand, species with a high average abundance will by chance be represented in more samples and then appear to be more widely distributed (sampling artifact hypothesis). The three hypotheses are not mutually exclusive, though. As pointed out by Hughes (2000), the total amount of resources available to a species may be related to its degree of resource specialization: specialists may have access to fewer resources, or alternatively, they may specialize on the most abundant resources.

The degree of specialisation can be influenced by the feeding mode of the herbivore insect. Internal feeders confined within plant structures for much of their life history would be more reliant on the host plant for microclimate and physical protection, and could be more exposed to plant chemical defenses, than external feeders for which the host plant is merely supplying space and food resource (Cornell, 1989; Gaston et al., 1992). In sum, endophagous insects would show a more intimate and complex interaction with the host plant, which could be reflected in a herbivore showing higher specificity in host plant use (Gaston et al., 1992).

The division of the studied community into guilds can be useful in studying regional differences among habitats, as proposed by MacNally (1994) for bird communities. The multiple ways in which flower heads can be used by endophagous species has led researchers to recognize distinct herbivore guilds. Zwölfer (1988) divided the herbivores of the European Asteraceae subfamily Cynaroideae into three trophic strategies according to their feeding niche. The first strategy consists of an early attack of the closed buds, usually combined with larval aggregation and the formation of structural galls or calluses. The second trophic strategy is characterized by the feeding on maturing or ripe achenes and on receptacle, without induced tissue growth. The third trophic strategy comprises polyphagous species with relatively mobile larvae, which are in effect omnivores (larvae can kill and eat other larvae inside the flower heads). Straw (1989b) divided the Paleartic flowerhead-inhabiting tephritids into three types of attack, according to particular phases of host development, and observed that each type of attack strategy is characteristic of a tribe or subfamily of Tephritidae. Lewinsohn (1991) studying flowerhead herbivores in Southeast Brazil divided species in endophagous and ectophagous groups. The division of flowerhead endophagous insects into feeding strategy guilds only makes sense if coexisting phytophagous species differ in parts of their ecological niches. The difference in feeding strategies is only the tip of the iceberg of the species niche, though. Species from different guilds belong to different genera, or higher taxa, which are in turn exposed to different mortality factors (e.g. different parasitoid species), host ranges, degree of larval aggregation, pupation and hibernation sites (in the case of temperate species) and so on (Zwölfer, 1985).

The present study on host specialisation is restricted to a single tribe, the tribe Eupatorieae within the Asteraceae. Previous studies in South and Southeastern Brazil (Lewinsohn, 1991; Lewinsohn and Prado, in press) have shown that flowerhead endophages do discriminate among Asteraceae tribes, and tribes or subtribes are "natural" boundaries for host ranges of many herbivores.

The Mantiqueira range is considered the coldest orobiome in eastern South America, and above the treeline we can find the *campos de altitude*, a physiognomy composed mainly by herbaceous species, with about a third of its species being endemic (Safford, 1999a). The Mantiqueira range is one of the South American regions with very high species richness of Eupatorieae (Barroso, 1957). Eupatorieae species composition in the Mantiqueira range is different among different mountaintops (localities), with few species occurring in various localities (chapter 1).

We have found different degrees of endophagy among flowerhead herbivores feeding on Brazilian Asteraceae (Lewinsohn, 1991; Almeida, 1997). In the present work we divided the insect species reared from Eupatorieae flower heads into three guilds according to their feeding mode and degree of endophagy, and examined how these guilds relate to host specificity and geographical distribution. The three guilds are designated as SE: *strict endophages* that spend their entire larval phase within one flower head; ME: microlepidoptera *mobile endophages*, whose larvae stay and feed within a flower head, but are capable of moving if necessary; and FE: microlepidoptera *facultative endophages* whose larvae normally burrow into flower heads to feed but are highly mobile and capable of feeding on other organs (e.g. apical meristems, new leaves). The three guilds show a gradient in endophagy and we hypothesized first a correspondence between the degree of endophagy and the specialization level; second, according to Gaston et al. (1992) an inverse relationship between geographical distribution and degree of endophagy.

Methods

The Mantiqueira Range

The Serra da Mantiqueira is a mountain range roughly in the NE-SW direction, spanning Rio de Janeiro, Minas Gerais and São Paulo states. Annual average precipitation is 1500mm, and the climate can be classified as sub-humid to humid. The maximum precipitation occurs in January (summer) while the minimum precipitation happens in July (winter). Drought may be partly offset by orographic fog, which in Itatiaia occurs 218 days per year at 2200m. In Itatiaia, monthly average free air humidities range from 65% to 90% Safford (1999a).

The treeline (timberline) in Itatiaia averages between 2000m and 2200m, which is considered low for its latitude (Körner, 1998; Safford, 1999a,b). Above the treeline we find the *campos de altitude*, "a series of humid, subalpine grasslands restricted to the highest peaks and plateaux of the Southeastern 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 families with most species in Itatiaia are the Asteraceae, Polypodiaceae sl. and Melastomataceae (about 40% of the species). In Itatiaia, the savanna-like associations, dominated by the Asteraceae genus *Baccharis* spp., and the Asteraceae tribes Eupatorieae and

Vernonieae (Asteraceae) are probably the most species-rich formation in the *campos*. In essence, about a third of the species in the Itatiaia *campos* appear to be endemic to the *campos de altitude* Safford (1999a).

Sampling methods

For present purposes, we define *region* as one mountain range. *Locality* is a regional subdivision formed by a group of collection *sites*. A *site* is each point where a plant population was collected. With these definitions, the Mantiqueira range is considered a *region* and Ibitipoca is considered a *locality* with several collection *sites*.

In the Mantiqueira range, the following localities were sampled (see Figure 2.1 for distribution of localities and Table 2.1 for coordinates):

1. **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*.
2. **VM** - The **"Visconde de Mauá"** locality is an important sampling area on the slope opposite to the "Itatiaia National Park". Since we could not reach the mountaintops, we collected only in open sites within the highland forest belt, and not in the *campos de altitude*. The locality straddles the border of Minas Gerais and Rio de Janeiro states.
3. **IT - "Itatiaia National Park"**, the first Brazilian National Park, which includes the Agulhas Negras peak, the second highest Mantiqueira summit with 2789m. On its southwestern slope and highland plateaux we had access to its *campos de altitude*, the most extensive in the Mantiqueira. The park also straddles the Minas Gerais and Rio de Janeiro State border.
4. **PQ** - **"Passa-Quatro"** - in Minas Gerais. Sampling sites in this locality were spread apart, 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.
5. **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 highland forest and in *Campos de Altitude*.

Whenever possible, we preferred to travel between localities on dirt roads within the mountains, along which we could take additional collections. A total of 500 km of roads were collected, not counting areas that were only collected on foot, as in Ibitipoca. Linear distances between pairs of localities varied from 26 km between Visconde de Mauá and Itatiaia and 203 km between Ibitipoca and Campos do Jordão, the two extreme collected mountains.

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

Insect Rearing

A sample consisted of flower heads from many individual plants of the same species; samples from individual plants were mostly too small to assess variation among individuals in any case. Samples were collected in plastic pots and were limited to a bulk volume of 500ml or 1000ml, depending on the flower head size, and/or its abundance in the field.

Each collected sample was kept in a transparent plastic pot covered with fine mesh screen to rear endophagous insects. Samples were kept in the laboratory for a minimum of 60 days and inspected every two days. To inspect rearing pots we used CO_2 to anaesthetize adult individuals, which could then be removed safely without harming immature insects. All adults were double mounted. Moths were mounted immediately and flies were refrigerated or frozen until mounted.

Morphospecies assignment and Singletons

Endophagous insects were first assigned to morphospecies or "OTU's" (operational taxonomic units) on the basis of external characters. For Lepidoptera, only adults were considered. All agromyzids belong to a species group in the genus *Melanagromyza*, with no clear difference in external characters since its taxonomy is based on the male genitalia, and were grouped in a species complex called *Melanagromyza* spp. We decided to exclude the Cecidomyiidae (Diptera) species from the present study, because of the difficulty of distinguishing species and of identifying the true herbivores. Asteraceae samples often contain a mixture of gallers, nongalling herbivores and predators of this group, which can only be sorted reliably to species with matched series of larvae, pupae and adults, demanding the rearing of adults of individual flower heads, not performed here.

Morphospecies assignment, hereafter 'species' for the sake of simplicity, was compared with specimens previously identified by specialists and about a third could then be assigned to a known species. Specialists (see Acknowledgements) confirmed most species and morphospecies assignment.

All the insects with only one obtained individual ("singletons", Colwell and Coddington, 1994), or two individuals reared from a single sample ("doubletons") were excluded from analyses. The exclusion of rare species eliminates errors in morphospecies assignment of individuals we were not familiar with, since confusion caused by lack of familiarity is most likely to occur among rare species. Also, singletons and doubletons may obscure host amplitude estimates, since they were obtained from one host species.

Some problems may still remain in decisions on morphospecies assignment and recognition. Two morphospecies, *Xanthaciura* sp.5 and *Xanthaciura* sp.6 are indeed two new species (Allen Norrbom, personal communication), however, *X. chrysura1* and *X. chrysura2* may turn out to be two variant morphs of *X. chrysura* (Allen Norrbom, personal communication). Adult Lepidoptera often lose wing scales in rearing containers, which can complicate sorting based on wing patterns. We did separate individuals on minor differences, which may have inflated species numbers in the Lepidoptera. Problems in morphospecies assignment are common in community studies, especially in the tropics, because a significant part of the obtained individuals are rare species, including many singletons, and also new species (e.g. Basset, 1997). However, we are confident that neither occasional rearing problems nor any remaing sorting mistakes are capable of altering our main results and conclusions, especially since our possible oversplitting of lepidopteran species would be compensated by omitting singleton and doubleton species from most analyses.

Feeding strategy guilds

A comparison of the feeding modes and behaviour of the flowerhead herbivores in the Mantiqueira range allowed us to divide this assemblage into three component guilds, with a gradient in degree of flowerhead endophagy (see Appendix 2.1 for species distribution within guilds, host plants per locality and number of individuals and of sites).

Strict endophages (SE) - The first guild is formed by endophagous species that oviposit directly into the flower head. The larvae hatch and complete development within a single capitulum, feeding on developing ovaries (e.g. Goeden, 1988; Almeida, 1997), without the induction of tissue growth (i.e. callus or gall formation). To this guild belong all the Diptera, both Tephritidae and Agromyzidae. This guild is the tropical equivalent to the second trophic strategy described for Cynaroideae (Asteraceae) flower head herbivores in the Paleartic region, also comprised by some Tephritid genera and a weevil genus (Zwölfer, 1988).

Mobile endophages (ME) - Members of this guild eat pollen and corollas, as well as ovaries and developing achenes while inserted into the flower heads. Since one Eupatorieae flower head often is not enough for complete development of a Lepidopteran larva, larvae can change capitula within shoots during development (e.g. Rogers, 1978; Almeida, 1997). In this guild we grouped the Lepidopteran families Tortricidae, Pterophoridae, Gelechiidae, Pyralidae, Blastobasidae and Pterophoridae. This guild is equivalent to the third trophic strategy described by Zwölfer (1988).

Facultative endophages (FE) - This guild groups the families Geometridae and Lycaenidae. Their larvae feed in flower heads by boring and inserting only their head or thorax, with most of the body remaining outside (Monteiro, 1990). For this reason they are not internal feeders in the strict sense. The difference from the previous guild is that the ME guild members are completely inserted within the flower head while eating and pupating, while the ectophagous Lepidoptera larvae remain outside this structure.

Data Analysis

Differences among guilds in the number of host taxa at different levels (species, genera and subtribes) were assessed through an Analysis of Covariance (ANCOVA) using number of samples (occurrence) as covariate, to correct for sampling effort. The number of samples per guild was transformed to deviations from the mean.

To compare the number of insect species restricted to different host plant taxonomic units across guilds, the insect species were charted by feeding guild and host taxonomic specificity in a contingency table, and the independence between these two variables were tested through Chi-square statistics.

Variations per feeding guild in the number of individuals, number of samples and number of individuals per sample and also geographical distribution were estimated with a non-parametric Kruskal-Wallis test (Sokal & Rohlf, 1995; Zar, 1996).

The differences in insect species composition among localities within the Mantiqueira range were represented as Euclidean distances, calculated from a matrix of species absolute occurrence (i.e. number of samples from which the herbivore species was obtained) in localities. Since there were some extreme values in this matrix, which could exert a strong influence on some multivariate analyses, the frequency of species was standardized, so that transformed values represent the number of standard deviations away from the mean. As an alternative, we used Relativized Euclidean distance (RED), which is similar to Euclidean distance, except that the data are normalized so that the sum of squares for each species equals one. Relative Euclidean distance excludes differences in total abundance among sample units. The range of RED is 0 to the square root of 2 given all non-negative data (McCune & Mefford, 1999).

A matrix of geographical distances (in km) between all pairs of localities was also produced. The geographical distance between two localities was calculated as a simple geometric distance, namely the hypotenuse of a triangle formed by their northern and eastern UTM co-ordinates. 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.

The matrix of relative Euclidean distances of endophagous species samples among localities was correlated to geographical distances and also to a matrix of relative Euclidean distances according to the Eupatorieae flora (chapter 1). The significance of correlations was evaluated through a Mantel's asymptotic approximation test (McCune & Mefford, 1999). The Mantel test measures the degree of congruence between two distance matrices, providing a probability value for the correlation between all corresponding pairwise distances among the matrices. The test is nonparametric, but is sensitive to skewness and nonlinearity, and for this reason we used Relativized Euclidean distances for floristic dissimilarity (McCune & Mefford, 1999).

To show graphically the relation between local endophagous faunas and their geographical location, we used a cluster analysis and compared the resultant dendrogram with the locality map in Figure 2.1. Localities were clustered using Euclidean distance for standardized data or Relativized Euclidean distance and the UPGMA aggregation method (Digby & Kempton, 1987).

Statistical analyses were carried out using Systat (SPSS, Inc. 1997) and PC-Ord (McCune & Mefford, 1999).

Results

Flowerhead herbivore species

In the Mantiqueira range we collected 596 voucher specimens, encompassing 56 Eupatorieae species from 9 subtribes (chapter 1). A total of 2032 individuals from 77 endophagous insect species were reared from 570 samples of Eupatorieae flower heads: 21 Tephritidae (Diptera), 1 Agromyzidae species group (Diptera) and 55 Lepidoptera. The tephritids belong to five genera: *Xanthaciura*, *Trupanea*, *Cecidochares*, *Dyseuaresta* and *Neomyopites*, while the agromyzids are in the genus *Melanagromyza*. Six Lepidoptera families were obtained: Tortricidae (16 species), Geometridae (14), Gelechiidae (7), Pyralidae (7), Pterophoridae (3), and Lycaenidae (8). Almost half of the obtained species were singletons (34 out of 77, or 44%) and when added to doubletons, 37 species (or 48%) were excluded from most analyses. Among the excluded species, seven are tephritids (31.8%) and, with the exception of one species of *Dyseuaresta*, all belong to the genus *Trupanea*. According to Foote et al. (1993) *Trupanea* species are of difficult identification because of both the large variation in wing pattern and also sexual dimorphism; and the genus needs to be completely revised. A greater proportion of Lepidoptera was rare (singletons and doubletons) and consequently excluded from subsequent analysis, encompassing 30 of 55 species (54.5%). Most Lycaenidae were very rare: only one *Erora* species was not a singleton or doubleton, and consequently maintained in the in analyses.

Feeding specificity

The number of host species increased linearly with the number of samples the flowerhead herbivore was reared from, for two out of the three guilds (Figure 2.2). In the SE guild the number of samples accounts for 97% of the variation in host species ($r^2 = 0.968$; $p < 0.001$; Figure 2.2a), or 70% if three species points with high leverage are excluded ($r^2 = 0.679$; $p < 0.01$). In the ME guild it explained 94% of variation ($r^2 = 0.938$; $p < 0.001$; Figure 2.2b) and 93% when two outlier species were excluded ($r^2 = 0.927$; $p < 0.001$). Note the ME guild's higher regression coefficient (0.32 versus 0.28), so that it would tend to accumulate host species somewhat faster across different population samples than the SE guild, as expected if the ME guild is more generalistic; however, the difference among slopes is nonsignificant, as shown from the interaction term of the ANCOVA (see bellow). The FE guild regression was not significant by itself ($r^2 = 0.255$; $p = 0.236$; Figure 2.2c). This is mainly due to two geometrid species that occurred in seven and ten samples, but from only two host species, a high degree of food specialization associated with a high degree of incidence. Without these two outlier species the regression is significant explaining 89% of variation ($r^2 = 0.891$, $p < 0.001$), and the regression coefficient is 0.603.

Endophagous species grouped in the SE guild are more restricted to one host plant genus than expected, while species of the other two guilds explore more subtribes than expected by chance (Heterogeneity contingency test, $\chi^2 = 11.031$; df = 4; $p < 0.05$; Table 2.2). The analysis of covariance showed that insect species of the SE guild have fewer host species, genera and subtribes than ME species, corrected for number of samples as covariate (Tables 2.3 and 2.4). Although the SE guild is more specialized than the ME guild, its species show a great variability of host ranges: in this guild we find *Xanthaciura mallochi*, obtained from three samples of the same host species, to *Xanthaciura chrysura*, the species with the highest number of host species and *X. biocellata*, the most abundant species.

More generalistic species, that is, with more recorded host species, within each guild, also occur in more localities and thus are geographically more widespread. The regression varies from explaining 46% of variation in SE species, through 53% in ME species to 69% in FE species, and is steeper for ME guild members (Figure 2.3).

Geographic occurrence and distribution

Ibitipoca was the region with the highest flowerhead herbivore species richness, with 41 species, followed by Visconde de Mauá with 39, Campos do Jordão with 37, Passa Quatro with 25 and Itatiaia with 14 species. The proportion of rare species (singletons and doubletons) varied from 12% in Passa Quatro to 29% in Itatiaia (Table 2.5). Itatiaia is the locality with lowest endophagous species richness, allied to lowest host plant richness (chapter 1) and highest sampled altitudes. In general, the number of endophagous species (for both isolated and pooled guilds) is in accordance to the number of its Eupatorieae host species in each locality (Figure 2.4). In general, localities with more Eupatorieae species present more endophagous species, independent of the observed guild.

The number of individuals per insect species showed no difference among guilds (Kruskal-Wallis = 4.274; df = 2; $p > 0.10$), which was also true for the number of samples the species was obtained from (Kruskal-Wallis = 3.170; df = 2; $p > 0.20$) (Table 2.4). On the other hand, the number of individuals per number of samples from which they were reared was higher for SE than for the other two guilds (Kruskal-Wallis = 7.278; df = 2; $p < 0.05$) (Table 2.4).

The three guilds are not present in the same proportion in all localities, considering either the number of species (with or without singletons and doubletons) or the number of individuals (Figure 2.5 and Table 2.5). For pooled localities, the ME guild showed highest richness and higher proportion of rare species than the other two; this also holds for Visconde de Mauá, Passa Quatro and Campos do Jordão (Figure 2.5a,b and Table 2.5). Ibitipoca was the only locality with higher proportion of species and rare species in the SE guild. Itatiaia, the locality with lowest species richness, was very different from the other localities; it had most species in the FE guild, and the SE guild had no rare species, whereas the ME guild had only one rare species (Figure 2.5a,b and Table 2.5).

The proportion of individual abundances per guild is very different from the species distribution (Figure 2.5c). First of all, the proportion of FE individuals is even lower than the species proportions, with highest abundance found for SE individuals. Species abundances show a gradient in species distribution, from Ibitipoca to Itatiaia and from Itatiaia to Campos do Jordão. From Ibitipoca to Itatiaia, there is a decrease in the number of SE and ME individuals with a slight increase in the number of FE individuals, and the reverse happens from Itatiaia to Campos do Jordão.

Different guilds seemingly have similar patterns of geographical distribution (Figure 2.6), with all three guilds containing species occurring from few to many localities. The number of localities each species is present was not significantly different among guilds (Kruskal-Wallis = 2.637; df = 2; $p > 0.25$; Table 2.4); nor did frequencies of species with different locality ranges differ significantly among guilds (G test on grouped data, G = 4.160; df=2, p=0.13; Figure 2.6).

The relationship between flowerhead herbivore composition and geographical distance was not significant either for isolated guilds (SE: r = - 0.126, p = 0.752; ME: r = 0.304; p = 0.473 and FE r = 0.218; p = 0.508) or for pooled guilds (r = - 0.125; p = 0.759) (Figure 2.7). The Eupatorieae floristic dissimilarity was not also correlated to faunistic differences among localities. Mantel tests showed that faunistic similarity does not covary with floristic similarity both for pooled (r = 0.487; p = 0.193) and for SE and ME guilds (SE: r = 0.502; p = 0.173; ME: r = 0.302, p = 0.429) (Figure 2.8). Although the FE guild showed a positive significant correlation in the Mantel test (r = 0.734, p = 0.02), this result is mainly due to an outlier point referent to the comparison between Passa Quatro and Visconde de Mauá, with comparatively low distances for both flora and fauna (Figure 2.8).

The grouping of localities by cluster analysis based on species frequencies in host samples varied among isolated and pooled guilds (Figure 2.9). None of the dendrograms mirrored the geographical placement of localities, or matched the similarity dendrogram of host plants (Figure 2.9e and chapter 1). The cluster diagrams for pooled guilds and SE and ME guilds showed different results, isolating either Itatiaia or Ibitipoca, which suggests that species from different guilds have different distributions throughout the Mantiqueira range.

Discussion

Feeding strategy guilds and food specialization

Zwölfer (1988) discusses that the three feeding strategy guilds he describes for Paleartic Cardueae (Asteraceae) are natural divisions of the herbivore fauna, since the same strategies are found throughout Europe and also in Californian *Cirsium* species. In the Mantiqueira range, flowerhead herbivores also follow the feeding strategies described by Zwölfer (1988): SE guild is equivalent to Zwölfer's second trophic strategy and our ME guild is equivalent to his third trophic strategy; with even the same European taxonomic groups within each guild. In the Mantiqueira flower heads the first trophic strategy described by Zwölfer is represented by galler Cecidomyiidae. Although the present study did not consider the Cecidomyiidae, Almeida (1997) and Rocha (1992) already observed and described Cecidomyiidae larvae galling floret tubes of other Eupatorieae species in São Paulo State (Brazil), and the presence of galled flowers in many Asteraceae species in Brazil confirms this assumption (Lewinsohn, Prado, Almeida, pers.obs.). On the other hand, Eupatorieae flower heads are very different from those of Cynaroideae: they are much smaller, have no spines in their bracts and we found no herbivore using exclusively the receptacle, which is common in Cynaroideae hosts (e.g. Zwölfer, 1988; Straw, 1989a,b). Zwölfer (1988) does not cite the strategy we described in the FE guild. The FE larvae stay with their body outside the flower head, and insert only their head into it (see methods for description), which is probably more difficult if the structure is surrounded by hard bracts. Since most tropical Asteraceae species have no hard bracts with spines, ectophagous species should be commoner in the tropics.

In the Mantiqueira range the number of hosts from which each endophagous species was reared increased with the number of samples from which the herbivore was obtained, both for SE and ME species. For the FE species this relationship is nonsignificant, presumably because the number of records we obtained in this study was not sufficient to define it for this guild. If SE are on average more host-specific than ME members (Tables 2.3 and 2.4), one might also expect a lower regression coefficient, reflecting a lesser accumulation of new hosts with additional occurrences; this, however, was not shown by the Analysis of Covariance in which no significant interaction of guild with sample number was found. Nonetheless, the same analysis shows that, for any given number of samples, an ME member has almost double the number of hosts than an SE insect (2.7 : 1.5) (Figure 2.2).

The high specialization of endophagous Diptera is in accord with previous data for tephritids in both Europe and Brazil. Zwölfer (1988) showed that within 77 specialized phytophagous species associated with Cynaroideae hosts, the transfer from an original host to other plant species belonging to the same genus or tribe is responsible for 88% of host relationships of oligophagous European thistle insects that kept their trophic preadaptations. Prado et al. (1999; in prep.) listed host species for the main flowerhead-feeding Tephritidae species in Brazil and found that 80% of tephritids have its main host species within a genus or a group of related genera.

The proportion of rare (singleton and doubleton) species ranged from 32% of the SE guild, through 53% of the ME species, to 56% of the FE species. Rare species were also very variable among localities, varying from 12% in Passa Quatro to 29% in Itatiaia, while 48% were rare when considering pooled localities.

Tephritids are more commonly found in aggregations within shoots and plants (Almeida, 1997) and singletons within tephritids should be rare. On the contrary, Lepidoptera larvae do not show a clumped distribution. In contrast to the Diptera larvae that are able to aggregate and complete development within a single flower head, each lepidopteran larva needs more than one flower head to complete development. This may limit the number of eggs a female lays in a patch or plant, to reduce risk of competition among larvae.

As we found in the Mantiqueira range, Basset (1997) using a different method and approach to study canopy-inhabiting insects in New Guinea, also found a higher proportion of rare species in the generalist than in the specialist category. To explain the high proportion of singletons he invokes the "mass effect" of Shmida and Wilson (1985). Basset proposes that rare species were presumably sampled in "marginal" habitats: "the proportion of rare insect species collected on the rainforest vegetation may be partly explained by high habitat diversity, the fact that a certain proportion of insects are able to exploit different habitats and by the limitation of sample procedures" (Basset, 1997). In the Mantiqueira range the higher proportion of rare generalist species may only in part be a sampling artifact. Since we focused on insects on one plant tribe, more generalistic species (as is the case of ME and especially of FE species) should be occurring also in other plant tribes (and possibly even families). Following Basset's argument, the Eupatorieae plants could be marginal host species especially for FE insects, which would then use them occasionally or, in any case, at a lower density.

Although all three guilds show a great variability in some species traits such as number of individuals, samples and host species, the SE guild is the one with greatest variation in these traits. This guild includes three congeneric tephritid species, *Xanthaciura mallochi,* obtained from three samples of the same host species; *Xanthaciura biocellata*, the most abundant species; and *X. chrysura*, obtained from more samples and more host species.

Gaston et al. (1992) compared host plant use by internal and external microlepidoptera in Britain, and found that internal feeders are more host specific than external feeders. Frenzel and Brandl (1998) tested and confirmed this hypothesis to endophagous and ectophagous herbivore insects on Brassicaceae in Poland. In the present study we found no statistical evidence that ME species would be more host specific than FE ones. The scarcity of FE species in Eupatorieae samples, though, suggests that they are also using hosts from other tribes or families, which explains why only one *Erora* species (Lycaenidae) was obtained from more than one sample in a total of 570 samples in a two-year study. Flower feeding Lycaenidae are well known for having a wide range of unrelated host plants, which is considered high even among butterflies (Robbins & Aiello, 1982; Monteiro, 1990). Host plant selection for Lycaenidae is highly related to ants presence, and non-myrmecophite plants are known to be sporadically selected (A.V.L.Freitas, pres. com.). If this assumption were correct, then FE species would be more generalistic than ME species, which are more commonly found on Eupatorieae samples and might be more restricted to them.

Occurrence and distribution

Brown (1984) suggested that for closely related, ecologically similar species, those with highest population densities tend to inhabit a greater proportion of sites within a region and have wider geographical ranges. He adapted this hypothesis to food specialization and suggested that specialists will be able to tolerate only a narrow range of conditions and will consequently be locally rare and with restricted distributions. On the other hand, generalist species will be both locally more abundant and show wider geographical distributions (but see Gaston et al., 1997; Hartley, 1998). This assumption is contrary to the postulated tradeoff between specialization and efficiency - "Jack-of-all-trades-master-of-none" - in which specialists with narrow tolerances should be more efficient in exploiting a limited range of resources and therefore should have more restricted distributions, but higher local abundances (if resource availability is similar to all), than generalists.

In the Mantiqueira range we found that within the three guilds, more widespread species occurred in more samples and are also more generalistic, which agrees with Brown's hypothesis. A previous study has shown that the Eupatorieae plant species in the Mantiqueira show little overlap among localities, but that (with the exception of Itatiaia) localities are spatially interrelated, with adjacent localities presenting more similar species composition (Eupatorieae dendrogram in Figure 2.9 and chapter 1). One could then expect that herbivore species would be changing host plants and using more host species as they occur in more localities. Even species from the SE guild, which tended to be most specialized, showed an increase in the number of host species as they occurred in more localities.

Mawdsley and Stork (1997) showed for a beetle community sampled with canopy fogging in Borneo that the regional host range of a species will be greater than that of local populations, and that host specialization is a property of both individuals and species. Many authors came to the same conclusion, that widely distributed "polyphagous" species may be locally much more specialized in their diet than host plant lists alone would suggest (e.g. Cates, 1981; Fox and Morrow, 1981; Thompson, 1994).

Although the turnover of host species through various localities contributed to increase the total number of used host plants, we also observed that regional generalists are also locally more generalistic (see also chapter 4). For instance, *Xanthaciura chrysura* was the endophagous species reared from the largest total number of host plants in the entire Mantiqueira region, and it also used many host plants in each locality. This is in accord with Brown (1984) and is also similar to what was found for Lycaenidae butterflies in the Rocky Mountains (Hughes, 2000).

The richness of both isolated and pooled guilds in general follows the richness of the local Eupatorieae flora (Figure 2.4), showing that localities with more Eupatorieae host species tend to support higher endophagous species richness, as in Ibitipoca and Visconde de Mauá. On the other hand, endophagous insects showed no significant convergence among localities of Eupatorieae host plant use. For both pooled and single guilds, Mantel tests showed no correlation between either flora and fauna similarities or faunistic composition and geographic distance among localities. The cluster dendrogram confirms this observation. First, dendrograms are not the same for pooled and single guilds, and none of them reproduced the dendrogram of localities based on their Eupatorieae host assemblages (chapter 1).

Prado and Lewinsohn (2000) showed that the composition of the Tephritidae fauna associated to Vernonieae (Asteraceae) host plants in the Espinhaço range (a northern, more central range, see chapter 1 for map) is in part determined by a passive mechanism. They showed that the lack of host-endophagous associations in the five studied localities is caused mainly because of the non-occurrence of the host plant. Although we did not address this specific question in the Mantiqueira, we included in the endophagous community more generalistic insects than they treated in their study (even species from our SE guild such as most *Xanthaciura* species are found in more host plant species than the *Tomoplagia* species studied in Espinhaço).

Different localities in the Mantiqueira range are composed by a multitude of habitats caused by differences in elevation and aspect and consequently of temperature, rainfall, cloudiness, edaphic conditions and so on. Hence, factors other than host plant communities do certainly influence the composition and abundance of the endophagous insects treated in the present study.

Erelli et al. (1998) showed that the same host plant species can have different degrees of palatability at different elevations of the same mountain. They showed that high-elevation trees tended to have higher leaf nitrogen, lower leaf tannins, and that macrolepidoptera larvae grew better on them than on conspecific trees from lower elevations. The authors concluded that "because herbivore species differ in their responses to dietary nitrogen and tannins, altitudinal patterns in nitrogen deposition could alter the community composition of herbivores in addition to altering the abundance of individual species". In the Mantiqueira range the faunal composition of Itatiaia, the locality with the highest sampled sites, was very different from the other localities. In Itatiaia the FE species richness was highest, whereas SE species richness was lowest. Some physiological plant traits due to higher altitude, allied with temperature, wind exposure, and frost may be influencing the host plant community (chapter 1) and consequently its endophagous insects.

The insects' physiology may also influence their presence in different habitats or altitudes. Eber and Brandl (1994) showed that for *Urophora cardui* - a common galler tephritid species in Europe - minor climatic fluctuations, represented basically by altitude, may be affecting this species and may influence its biogeographical distribution even on a short time-scale. They suggested that different genotypes are responsible for different physiological tolerances at various altitudes.

According to Angermeier and Winston (1998), an ideal region must be environmentally homogeneous, equally accessible to all species and with ecologically relevant boundaries. Large heterogeneous areas usually include many species not adapted for the habitat type being studied or unable to disperse to it. In the present study we tried to restrict our localities to similar habitats, but this was not always possible. In Ibitipoca, Itatiaia and Campos do Jordão we were able to reach summits and sample in the *campos de altitude* (chapter 1). Itatiaia showed the least flowerhead herbivore species richness, while in Campos do Jordão the herbivore species richness was high and in Ibitipoca it was highest. In Passa Quatro we collected samples in many sites bordering on agricultural areas, which may have limited insect species richness even because of pesticide effects, but it still had higher richness than Itatiaia, albeit at lower elevations.

The flower head endophagous insects in the Mantiqueira range present different strategies in host plant use, and respond differently to the same variables found in each studied locality. The endophagous community similarities among localities are not directly determined by either floristic composition in each locality or geographical distance among pairs of localities. We suggest that local differences in habitat composition and environmental characteristics, allied to historical and biogeographical factors acting in each single locality are influencing differently the structure and composition of the different endophagous guilds.

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TABLE 2.1. Localities within the Mantiqueira range, with its names, municipality, state, and position of the reference site, used to measure distances among localities. The altitudinal range (rounded to the nearest 50m) of collection sites is also provided.

Code	Name	Municipality	State	Lat (S)	Long (W)	Altitudinal Range
IB	Ibitipoca	Lima Duarte	MG	21° 41.58'	43° 52.73'	760 - 1784m
VM	Visconde de Mauá	Bocaina de Minas	MG	22° 14.38'	44° 29.21'	880 - 1480m
IT	Itatiaia	Itatiaia	RJ	22° 22.64'	44° 41.79'	1740 - 2460m
PQ	Passa Quatro	Virgínia	MG	22° 25.66'	45° 04.51'	960 - 1740m
CJ	Campos do Jordão	Campos do Jordão	SP	22° 39.48'	45° 33.41'	880 - 1920m

TABLE 2.2. Eupatorieae flowerhead herbivores categorized by guilds based on larval feeding behaviour and specificity. Observed and expected (in brackets) numbers of species are given. No single species was restricted to one subtribe or to one plant species ($\chi^2 = 11.031$ df = 4; $p<0.05$). Observed values exceeding expected ones are shown in bold.

	Feeding specificity			
	1 genus	2-5 subtribes	5-9 subtribes	Total
SE (strict endophages)	**5** (2.250)	8 (9.375)	2 (3.375)	15
ME (mobile endophages)	0 (2.250)	8 (9.375)	**7** (3.375)	15
FE (facultative endophages)	1 (1.50)	**9** (6.250)	0 (2.250)	10
Total	6	25	9	40

Table 2.3. Analyses of covariance for differences in host ranges among guilds for 40 endophagous insect species. Host range size is evaluated at three taxonomic levels (number of host species, genera and subtribes) and the covariate is number of samples, expressed in deviations from the mean. Note that the interaction term is not significant for any of the analyses. Post-hoc Tukey test showed differences between SE and ME guilds at the three host taxonomic levels. See Table 2.4 for mean and standard deviation of the analysed variables among guilds.

		Species		Genera		Subtribe	
Variable	df	F	p	F	p	F	p
Guild	2	4.503	0.018	5.511	0.008	5.951	0.006
N Samples	1	62.207	0.000	13.153	0.001	7.875	0.008
Guild * N Samples	2	0.754	0.478	0.506	0.607	0.461	0.634
Error	34						

TABLE 2.4. Mean and standard deviation of measures of feeding specialisation, occurrence and abundance and geographical distribution, for 40 species from the three studied flowerhead endophagous guilds. Results for Kruskal-Wallis non-parametric test, except for number of hosts in top panel (for which see Ancova in Table 3). Degrees of freedom = 2.

		GUILD				
		SE	ME	FE	Kruskal-Wallis	p
Feeding specialization	Number of host species	6.533 ± 6.770	8.333 ± 6.377	3.200 ± 1.687	*	
	Number of host genera	4.200 ± 4.092	6.133 ± 3.357	3.000 ± 1.563	*	
	Number of host subtribes	3.000 ± 2.330	4.933 ± 2.187	2.800 ± 1.317	*	
Occurrence and Abundance	Number of Individuals	87.333 ± 138.257	40.800 ± 66.287	7.000 ± 4.667	4.274	0.118
	Number of Samples	17.733 ± 23.478	17.800 ± 19.553	5.400 ± 3.026	3.170	0.205
	Individuals per sample	3.615 ± 2.910	1.636 ± 0.980	1.262 ± 0.371	7.278	0.026
Geographical Distribution	Localities	3.333 ± 1.345	3.133 ± 1.125	2.5 ± 1.269	2.637	0.268

TABLE 2.5. Total number of species of Eupatorieae flowerhead herbivores reared from single and pooled localities, per feeding guild. Numbers of singleton plus doubleton species (excluded from most analyses) are shown in brackets.

GUILD	LOCALITIES					Pooled Localities
	IB	VM	IT	PQ	CJ	
SE	19 (5)	14 (1)	3 (0)	9 (0)	11 (1)	22 (7)
ME	13 (4)	17 (4)	4 (1)	12 (2)	18 (5)	32 (17)
FE	9 (2)	8 (3)	7 (3)	4 (1)	8 (4)	23 (13)
Total	41 (11)	39 (8)	14 (4)	25 (3)	37 (10)	77 (37)

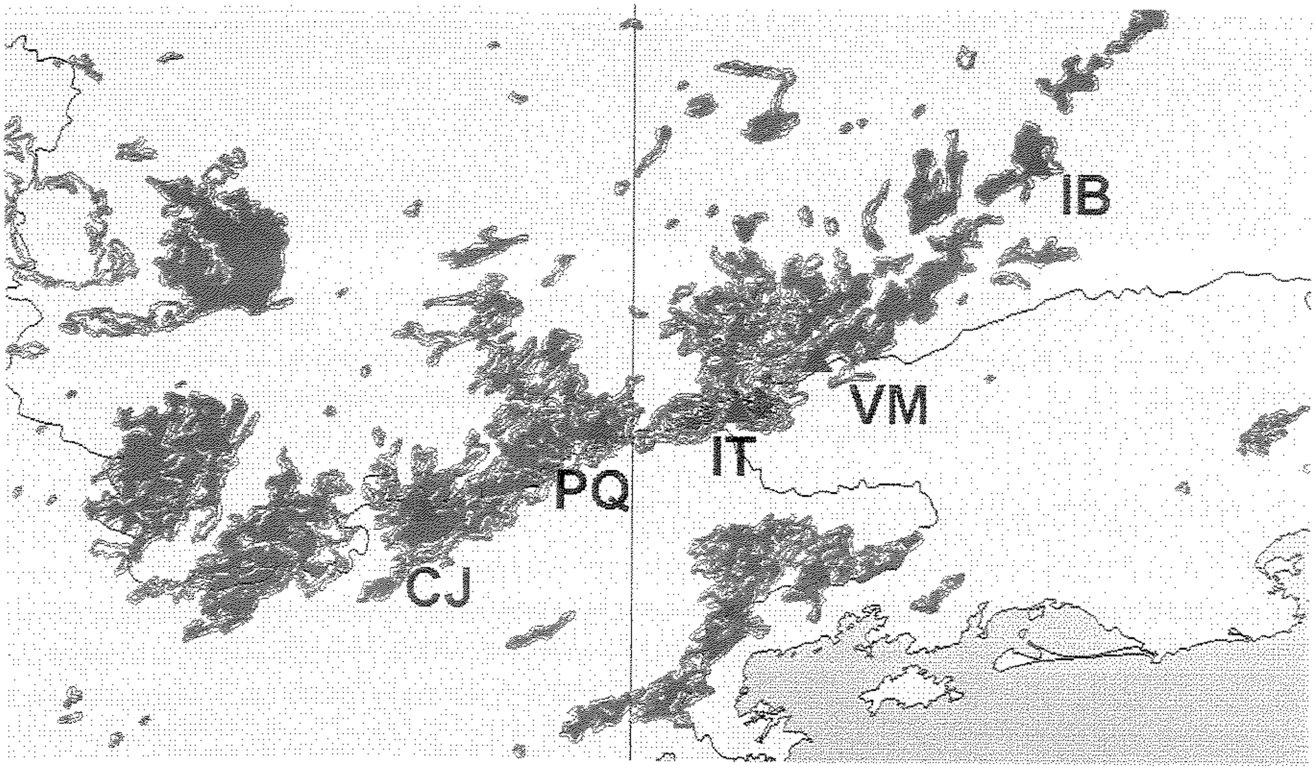


Figure 2.1. Sampling localities in the Mantiqueira range (Serra da Mantiqueira). Areas in red present altitudes of more than 1,000m, while areas in green present altitudes of more than 2,000m above sea level. Mantiqueira localities are: **IB** - Ibitipoca, MG; **VM** - Visconde de Mauá, MG/RJ; **IT** - Itatiaia, RJ/MG; **PQ** - Passa Quatro, MG; **CJ** - Campos do Jordão, MG/SP.

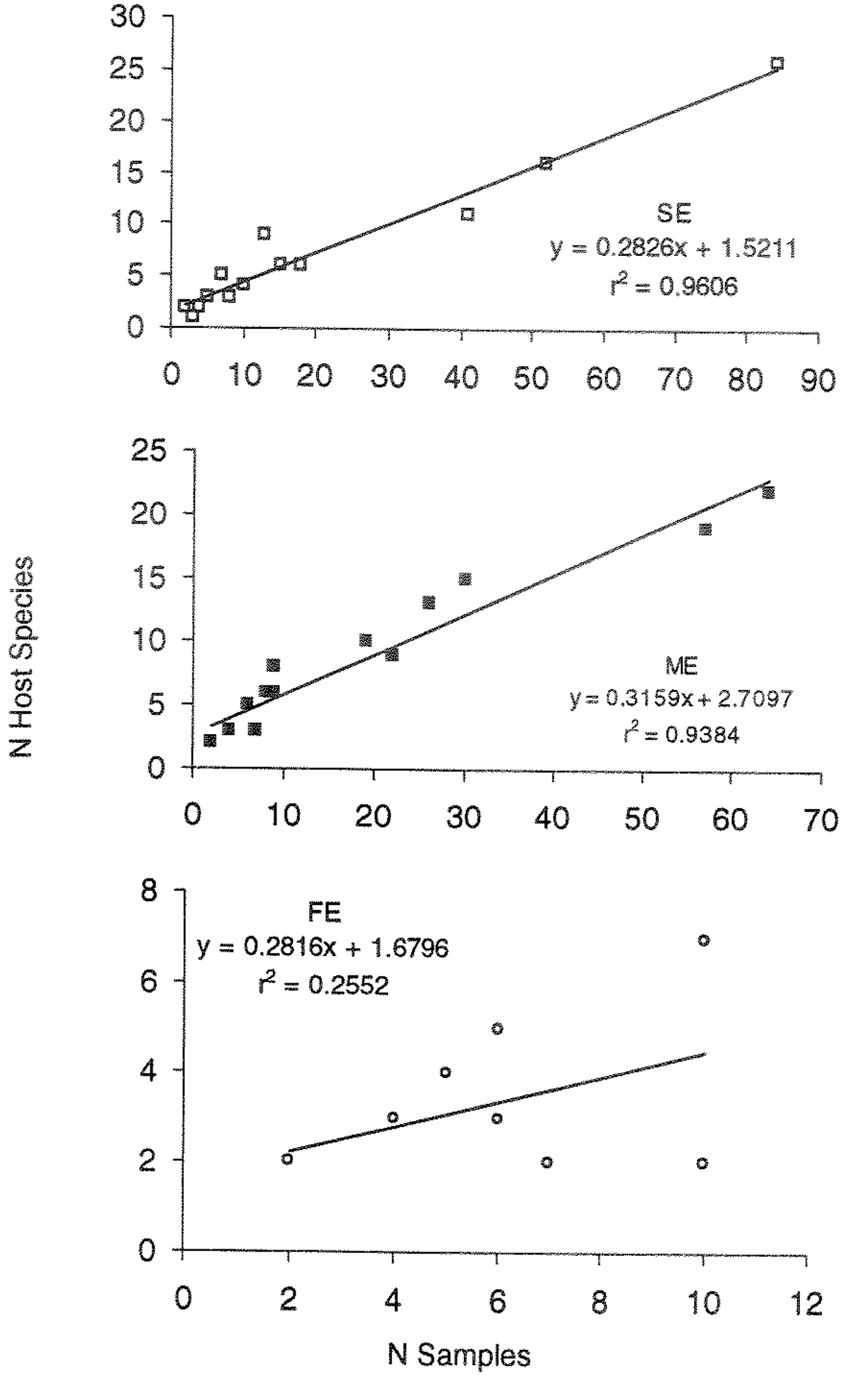


Figure 2.2. Number of host species against number of sample records of the endophagous species in each feeding guild, pooled for all Mantiqueira localities. Note different scales in both axes.

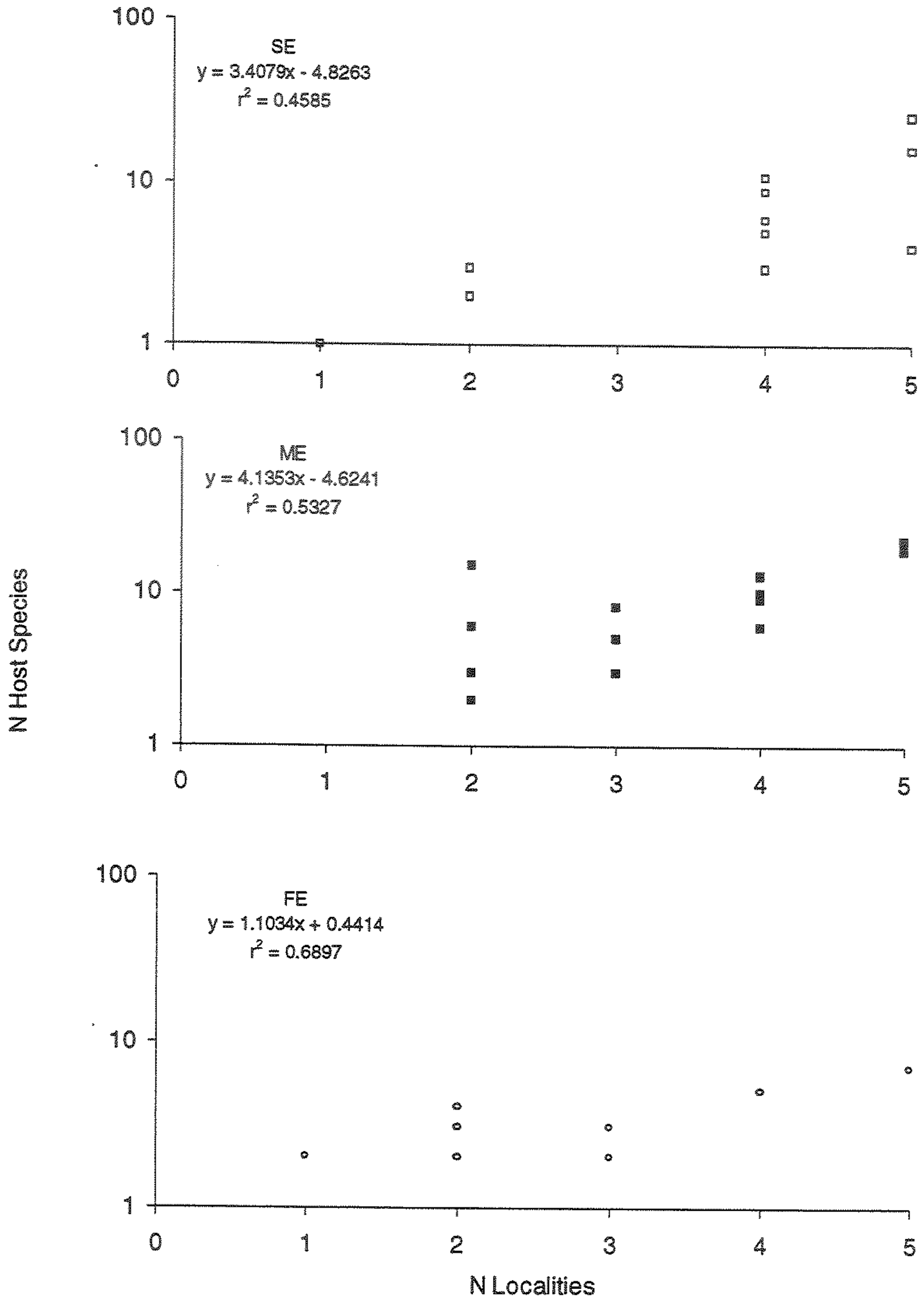


Figure 2.3. Number ($\log_{10}$) of host species per insect species of different feeding guilds, against the number of localities where the insect was recorded.

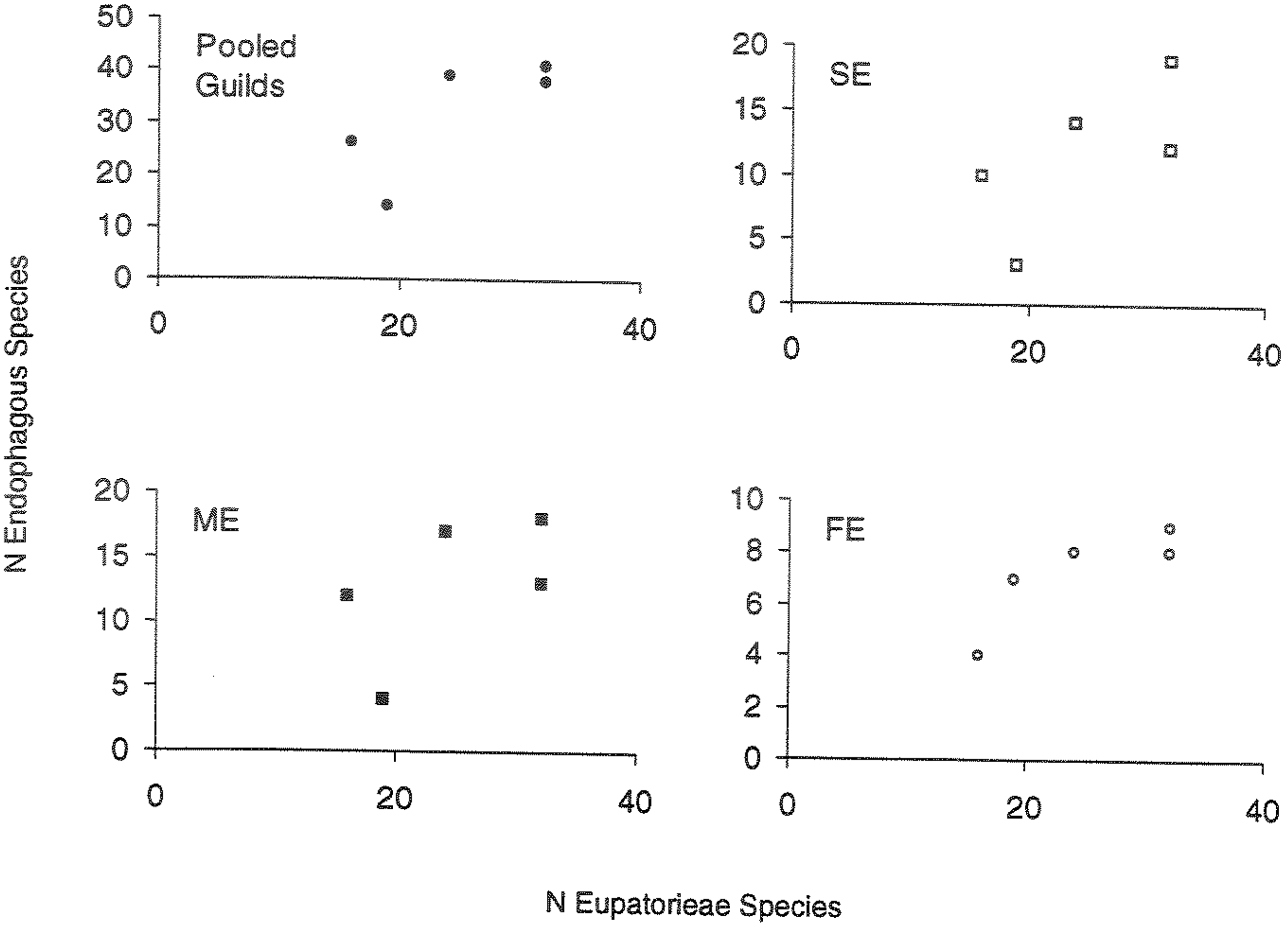
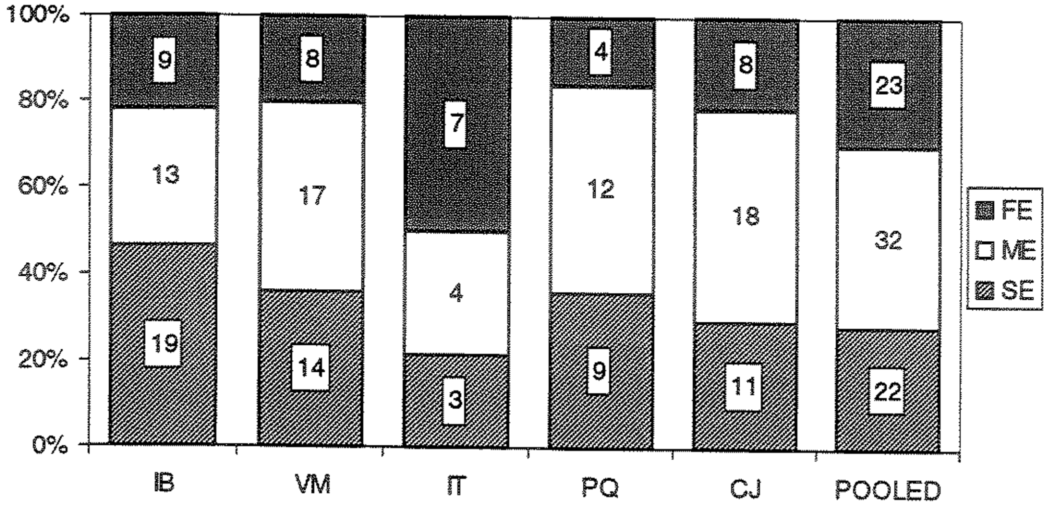
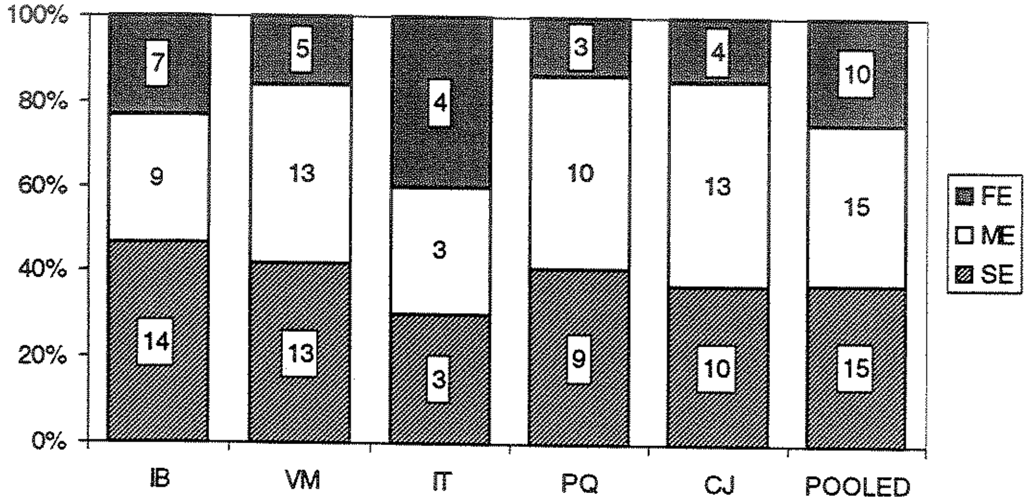


Figure 2.4. Number of endophagous species of different feeding guilds against the Eupatorieae species richness in the five studied localities.

a. Proportion of species (singletons and doubletons included)



b. Proportion of species (without singletons or doubletons)



c. Number of Individuals

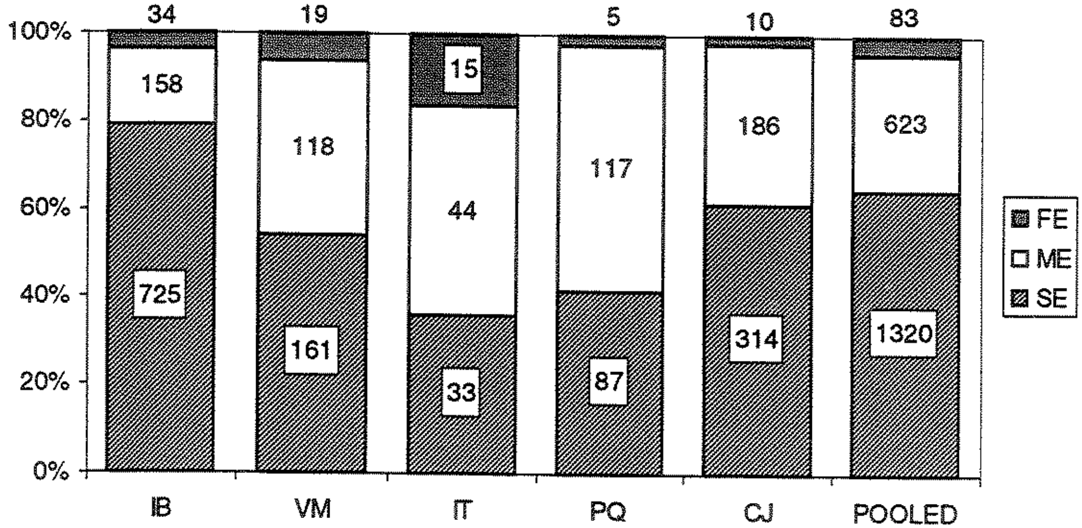


Figure 2.5. Proportion of the three feeding guilds per locality in relation to: (a) Number of species; (b) Number of species without singletons or doubletons; and (c) Number of individuals. The last bar shows pooled data for localities, for comparison.

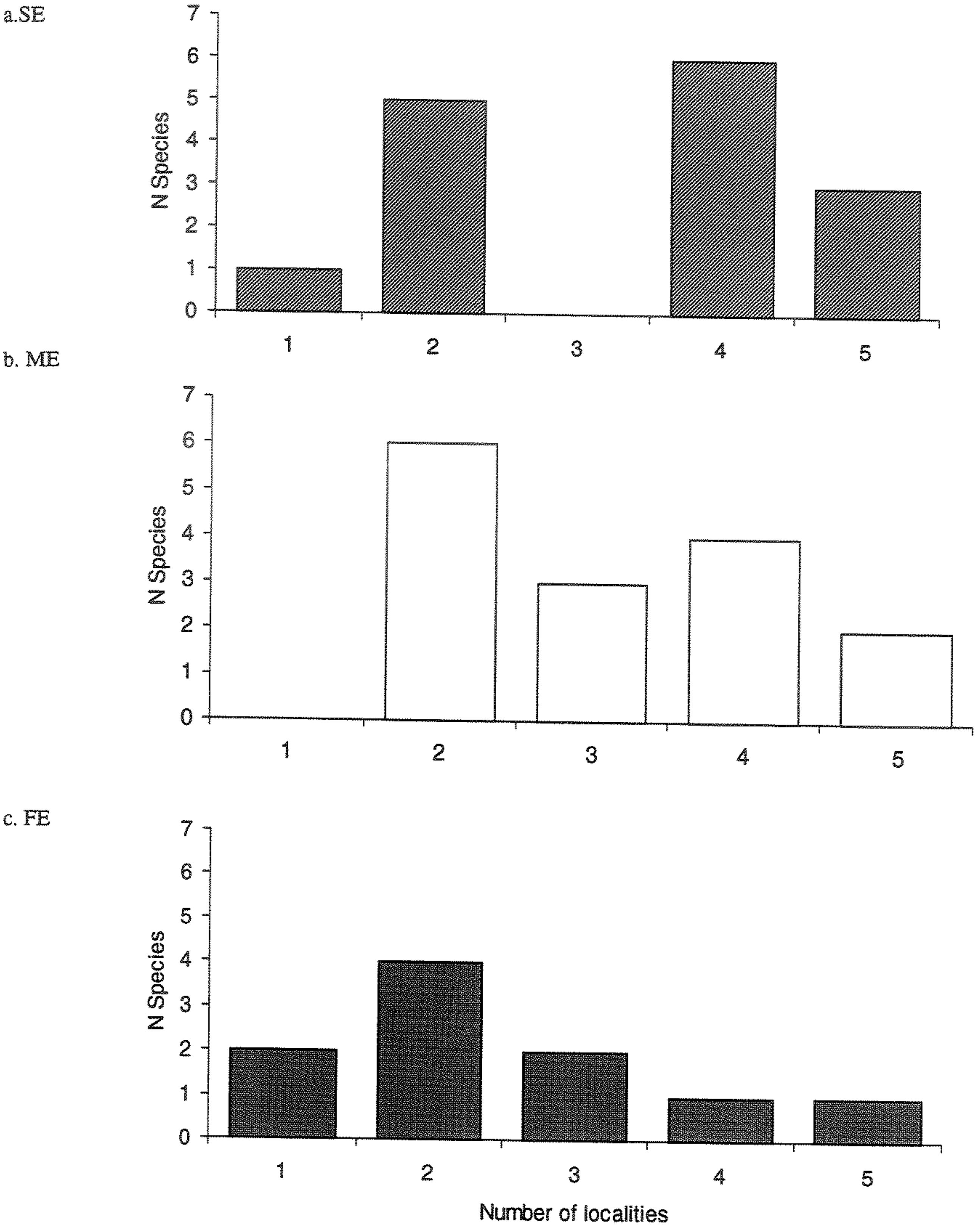


Figure 2.6. Number of species in each feeding guild per number of localities. Singletons and doubletons were excluded.

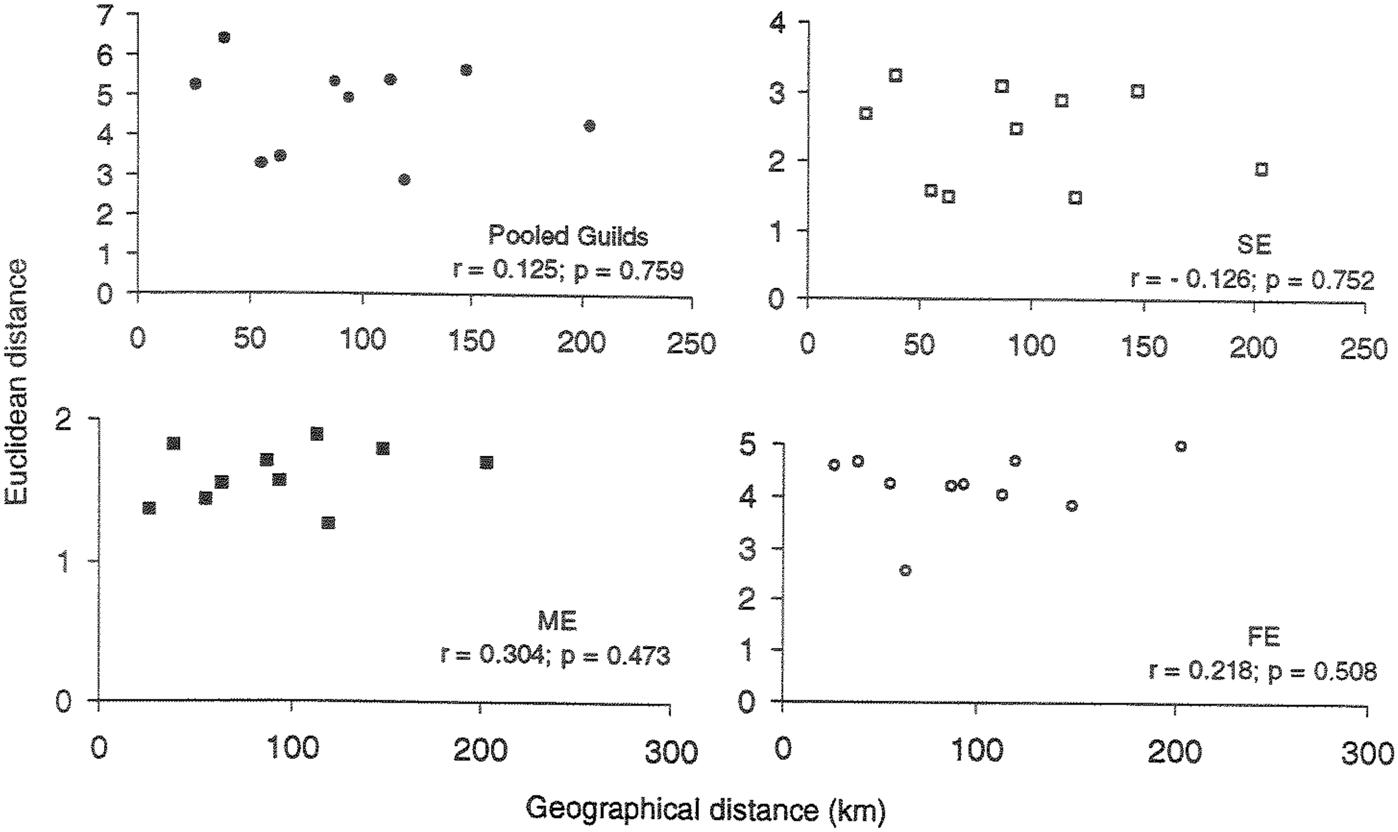


Figure 2.7. Euclidean distance of faunal composition among all locality pairs for pooled or isolated guilds plotted against geographical distance (km). Note the difference in scale in the ordinate.

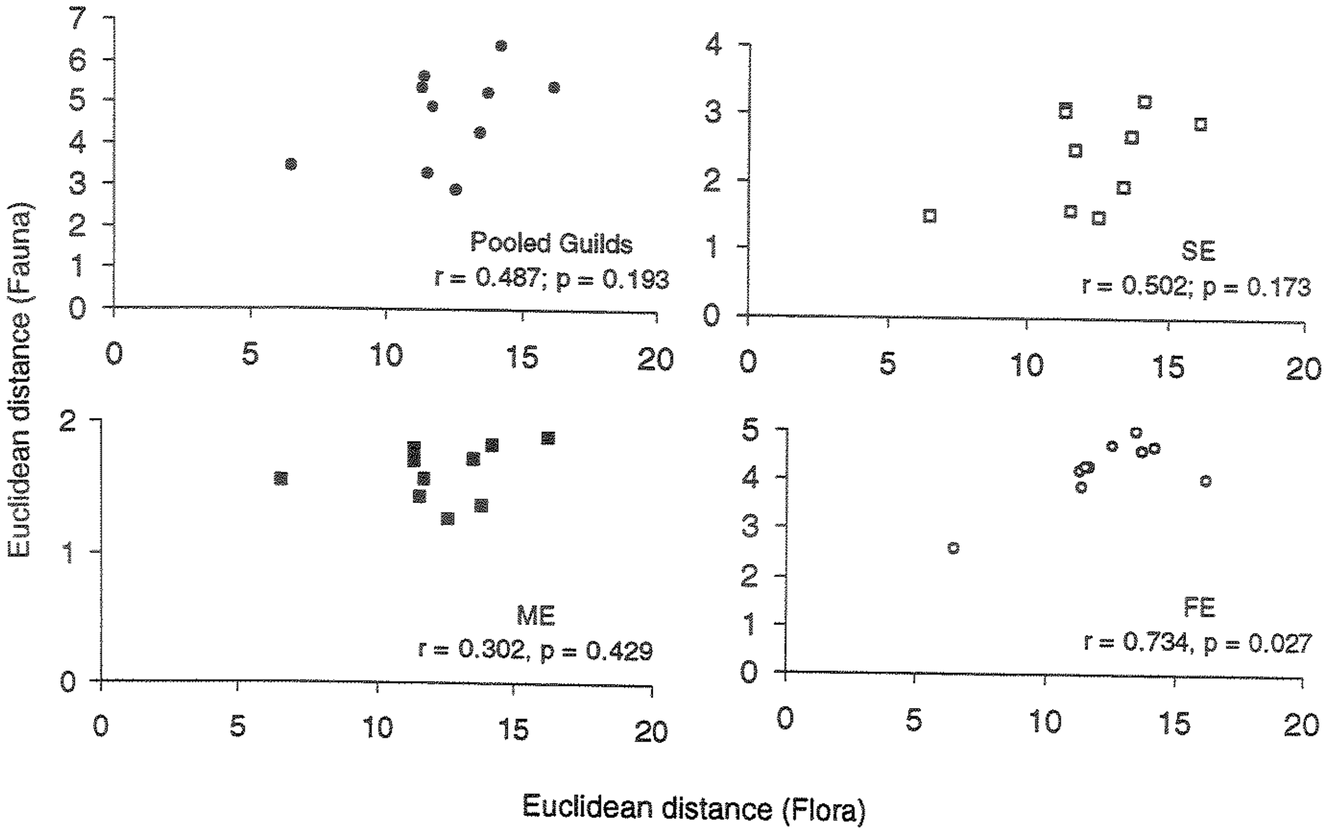
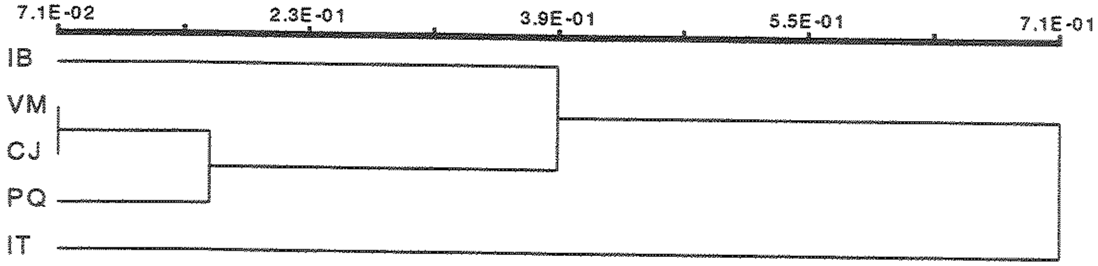
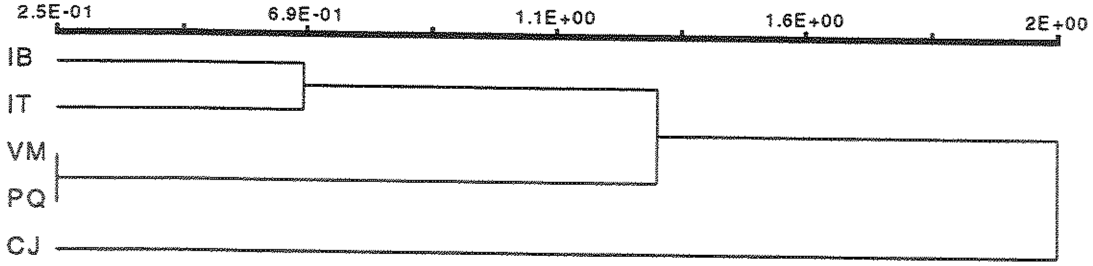


Figure 2.8. Euclidean distance among faunal composition for pooled or isolated guilds plotted against Euclidean distance for the Eupatorieae flora (analyzed in chapter 1). Note the difference in scale in the ordinate.

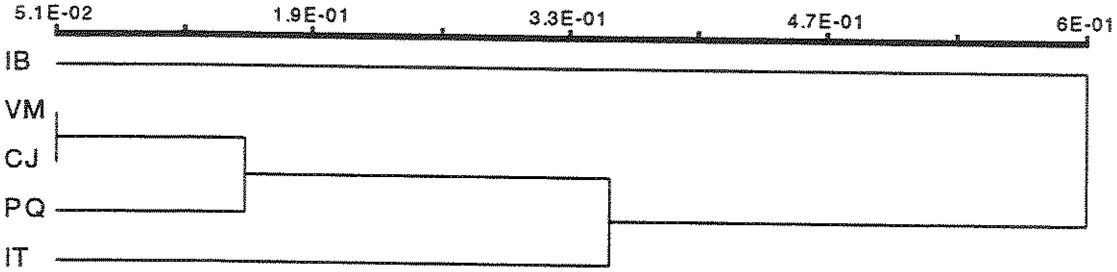
a. Pooled guilds



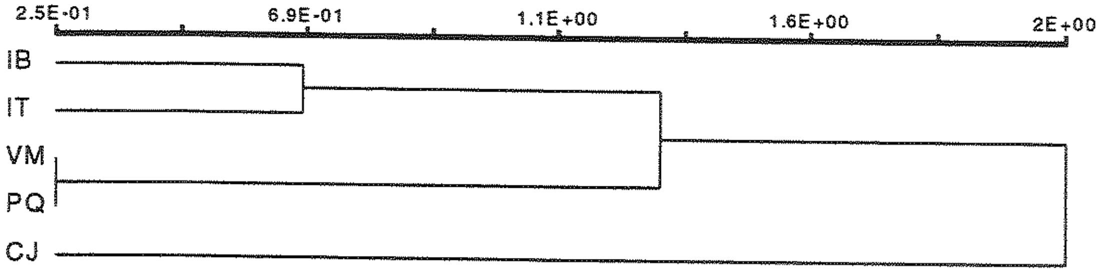
b. SE



c. ME



d. FE



e. Eupatorieae (host plants)

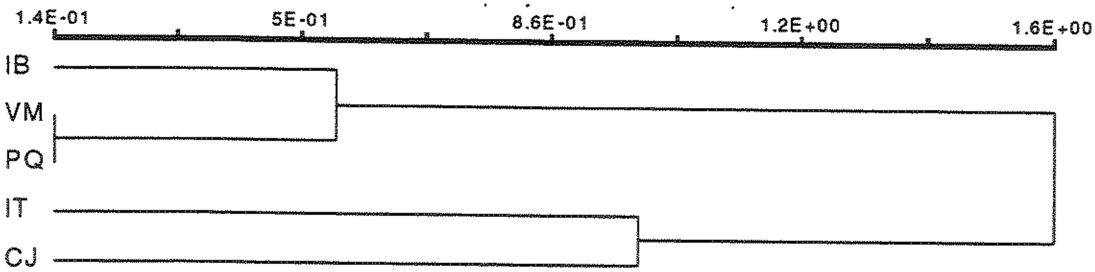


Figure 2.9. Dendrograms of similarity among Mantiqueira localities according to their flowerhead assemblages shown for all endophages (a) and separately by guild (b-d); similarity of host plant assemblages is shown in (e) for comparison. Cluster analyses used relative Euclidean distance and UPGMA. See table 1 for locality codes.

Appendix 2.1. Distribution of Eupatorieae endophagous species in the Mantiqueira range (Serra da Mantiqueira), its host plants and localities each interaction was found. Endophagous insects are grouped by feeding strategy guild and plants are grouped per subtribe. See Table 2.1 for locality codes. Codes for Subtribes are: Ad: Adenostemmatinae, Ay: Ayapaninae and Cr: Critoniinae.

		Ad	Ageratinae		Ay	Cr	Disynaphinae					
Guild	Endophagous	*Adenostemma brasilianum*	*Ageratum fastigiatum*	*A. conyzoides*	*Heterocondylus jaraguense*	*Koanophyllon thysanolepis*	*Campovassouria cruciata*	*Grazielia gaudichaudeana*	*G. gaudichaudeana var. bipinnata*	*G.intermedia*	*Symphyopappus compressus*	*S.cuneatus*
Strict Endophages (SE)	*Xanthaciura biocellata*		IB		IB,CJ							IT
	X. chrysura	VM	IB,VM,IT,PQ,CJ	IB,VM,PQ	CJ	IB	IT,CJ		CJ	VM,IT,PQ,CJ		
	Melanagromyza sp.		VM,CJ		IB,CJ					VM		
	X. chrysura sp.2						IB					
	Neomyopites paulensis									CJ		
	Cecidochares fluminensis											
	Trupanea sp.1						CJ				CJ	
	X. quadrisetosa		IB,PQ	IB,VM,PQ,CJ		CJ	VM,CJ			VM		
	Trupanea sp.2						VM					
	X. mallochi											
	C. conexa											
	Xanthaciura sp.5									VM,IT		
	Cecidochares sp.E											
	X. chrysura sp.1											
	Xanthaciura sp.6											
Mobile Endophages (ME)	*Phalonidia unguifera*		IB,VM,PQ,CJ	VM		CJ	VM	IB,IT		VM,IT,PQ,CJ	CJ	
	Adaina bipunctata	VM	IB,VM,PQ,CJ	IB,PQ,CJ		CJ	VM			CJ	CJ	
	Gelechiidae sp.1					CJ	IB			VM,PQ		
	Tortricidae sp.2		VM,CJ			CJ	IB				CJ	
	Tortricidae sp.7		VM				VM			VM,CJ	CJ	
	Tortricidae sp.1				CJ							
	Tortricidae sp.3		VM			CJ	CJ					
	Saphenista squalida	VM								VM		
	Tortricidae sp.6		VM,CJ							VM		
	Gelechiidae sp.7		CJ							CJ		
	Pyralidae sp.3											
	Gelechiidae sp.6											
	Pyralidae sp.2		VM									
	Tortricidae sp.11		VM									
	Tortricidae sp.4										CJ	
Facultative Endophages (FE)	*Geometridae sp.6*		VM				PQ			IT		
	Geometridae sp.4		IB									
	Geometridae sp.1		IB,VM,PQ									
	Geometridae sp.10		IB,IT									
	Geometridae sp.5		VM									
	Geometridae sp.7		IB									
	Geometridae sp.11		IB,VM							VM		
	Geometridae sp.13		VM									
	Geometridae sp.9											
	Erora sp.									CJ		

Appendix 2.1 (continued)

		Disynaphinae		Eupatoriinae				Gyptidinae					
Guild	Endophagous	*S.decussatus*	*S.italiayensis*	*Austroeupatorium inulaefolium*	*A.neglectum*	*A.paulinum*	*A.silphiifolium*	*Barrosoa betonicaeformis*	*Campuloclinium megacephalum*	*C.parvulum*	*C.purpurascens*	*Trichogoniopsis adenantha*	*Trichogonia villosa*
Strict Endophages (SE)	*Xanthaciura biocellata*	IB,VM,IT						CJ	CJ			IB	IB
	X. chrysura	IB	IT			IT,CJ	VM,IT,PQ	CJ			VM,PQ	IB	
	Melanagromyza sp.						IB			IB	VM,PQ,CJ	IB	
	X. chrysura sp.2												
	Neomyopites paulensis	IB											
	Cecidochares fluminensis												
	Trupanea sp.1						IB					IB	
	X. quadrisetosa						PQ						
	Trupanea sp.2						VM					IB	
	X. mallochi												
	C. conexa												
	Xanthaciura sp.5						IB,PQ						
	Cecidochares sp.E												
	X. chrysura sp.1												
	Xanthaciura sp.6		IT										
Mobile Endophages (ME)	*Phalonidia unguifera*	IB	PQ		IT	CJ			CJ		IB,VM,PQ,CJ	IB	IB
	Adaina bipunctata	IB,VM	PQ	VM			VM,IT,PQ,CJ				VM,PQ	IB	
	Gelechiidae sp.1						VM				VM,PQ		
	Tortricidae sp.2						VM,PQ,CJ				VM,PQ	IB	
	Tortricidae sp.7		IT,PQ				VM,IT,PQ,CJ				PQ		
	Tortricidae sp.1				CJ						PQ		
	Tortricidae sp.3		PQ				PQ				PQ		
	Saphenista squalida						CJ				IB,PQ		
	Tortricidae sp.6										VM		
	Gelechiidae sp.7						PQ				VM		
	Pyralidae sp.3	IB											
	Gelechiidae sp.6												
	Pyralidae sp.2										IB		
	Tortricidae sp.11						IB						
	Tortricidae sp.4												
Facultative Endophages (FE)	*Geometridae sp.6*						IB				IT		
	Geometridae sp.4						IT						
	Geometridae sp.1										VM,PQ		
	Geometridae sp.10						IB						
	Geometridae sp.5		IT		IT						IB		
	Geometridae sp.7					CJ					PQ		
	Geometridae sp.11										VM		IB
	Geometridae sp.13												
	Geometridae sp.9				IT		IT						
	Erora sp.					CJ							

Appendix 2.1 (continued)

		Mikaniinae								Praxelinae				
Guild	Endophagous	*Mikania bradei*	*M.campanulata*	*M.cordifolia*	*M.decumbens*	*M.elliptica*	*M.eriostrepta*	*M.lasiandrae*	*M.micrantha*	*Chromolaena aff. squalida1*	*C.congesta*	*C.hookeriana*	*C.laevigata*	*C.maximilianii*
Strict Endophages (SE)	*Xanthaciura biocellata*									IB		IB	IB,VM,PQ,CJ	IB,VM,CJ
	X. chrysura			CJ	IB			IB		IB		VM	PQ,CJ	IB,VM,CJ
	Melanagromyza sp.											IB,VM	VM,CJ	IB,VM,PQ,CJ
	X. chrysura sp.2												IB,PQ,CJ	VM
	Neomyopites paulensis												IB,VM	IB
	Cecidochares fluminensis											IB	PQ	IB,VM,PQ,CJ
	Trupanea sp.1											IB,VM	PQ,CJ	PQ
	X. quadrisetosa													
	Trupanea sp.2													IB,CJ
	X. mallochi													IB
	C. conexa													IB
	Xanthaciura sp.5													
	Cecidochares sp.E												CJ	IB
	X. chrysura sp.1													VM
	Xanthaciura sp.6													VM
Mobile Endophages (ME)	*Phalonidia unguifera*									IB	IB		PQ	IB,VM
	Adaina bipunctata			CJ				CJ					IB,VM,IT,PQ,CJ	IB
	Gelechiidae sp.1	IB				IB		IB					IB,VM,PQ	IB
	Tortricidae sp.2			CJ								VM	PQ	
	Tortricidae sp.7								VM,IT					VM
	Tortricidae sp.1													
	Tortricidae sp.3												PQ	PQ
	Saphenista squalida												CJ	IB
	Tortricidae sp.6							CJ	VM				CJ	
	Gelechiidae sp.7			CJ										
	Pyralidae sp.3													IB
	Gelechiidae sp.6												VM,CJ	
	Pyralidae sp.2													
	Tortricidae sp.11													
	Tortricidae sp.4	IB												
Facultative Endophages (FE)	*Geometridae sp.6*			CJ				IB						
	Geometridae sp.4													
	Geometridae sp.1													
	Geometridae sp.10													
	Geometridae sp.5						CJ							
	Geometridae sp.7													
	Geometridae sp.11													
	Geometridae sp.13									IB				
	Geometridae sp.9													
	Erora sp.													

Appendix 2.1 (continued)

		Praxelinae						
Guild	Endophagous	*C.multiflosculosa*	*C.pedalis*	*C.squalida*	*Praxelis clematidea*	N LOCALITIES	N SAMPLES	N INDIVIDUALS
Strict Endophages (SE)	*Xanthaciura biocellata*	IB	IB,CJ	IB	VM,PQ,CJ	5	52	489
	X. chrysura	IB	IB	IB,VM	PQ,CJ	5	84	264
	Melanagromyza sp.				VM,PQ,CJ	5	41	231
	X. chrysura sp.2			IB,VM		5	10	101
	Neomyopites paulensis			IB,VM	CJ	4	15	75
	Cecidochares fluminensis					4	8	36
	Trupanea sp.1			PQ	CJ	4	13	35
	X. quadrisetosa					4	18	29
	Trupanea sp.2				CJ	4	7	21
	X. mallochi					1	3	10
	C. conexa	IB		IB,VM		2	5	9
	Xanthaciura sp.5					2	4	4
	Cecidochares sp.E					2	2	2
	X. chrysura sp.1	IB				2	2	2
	Xanthaciura sp.6					2	2	2
Mobile Endophages (ME)	*Phalonidia unguifera*	IB	CJ	IB	VM,CJ	5	64	202
	Adaina bipunctata	IB			VM,PQ,CJ	5	57	185
	Gelechiidae sp.1			IB	CJ	4	26	95
	Tortricidae sp.2					4	19	29
	Tortricidae sp.7					4	22	29
	Tortricidae sp.1					2	7	14
	Tortricidae sp.3					3	9	14
	Saphenista squalida					4	9	13
	Tortricidae sp.6					2	8	10
	Gelechiidae sp.7					3	6	6
	Pyralidae sp.3				VM,PQ	3	4	5
	Gelechiidae sp.6					2	30	4
	Pyralidae sp.2					2	2	2
	Tortricidae sp.11					2	2	2
	Tortricidae sp.4					2	2	2
Facultative Endophages (FE)	*Geometridae sp.6*					5	10	14
	Geometridae sp.4	IB				2	6	13
	Geometridae sp.1					3	10	13
	Geometridae sp.10					2	7	7
	Geometridae sp.5					4	6	6
	Geometridae sp.7					3	4	5
	Geometridae sp.11					2	5	5
	Geometridae sp.13					2	2	3
	Geometridae sp.9					1	2	2
	Erora sp.					1	2	2

CHAPTER 3

The Mid-domain hypothesis applied to two trophic levels in the Mantiqueira range, Brazil*

> "In considering the distribution of organic beings over the face of the globe, the first great fact which strikes us, is that neither the similarity nor the dissimilarity of the inhabitants of various regions can be wholly accounted for by climatal and other physical conditions"
> (C. Darwin, The Origin of Species, 1859)

Abstract

This study deals with the altitudinal distribution of Eupatorieae (Asteraceae) plants and their flowerhead feeding insects in five localities in the Mantiqueira range, southeastern Brazil, from 760m to 2460m elevation, and sampled for two years in the peak flowering period of the plants. Most Eupatorieae species had their midpoint vertical distribution between 1420 and 1800m, while most endophagous insect species had their midpoint at lower elevations, between 1220 and 1400m. Both plant and insect species with wider altitudinal ranges were more widespread across localities as well. Species richness distributions for both plants and herbivore insects were all in accord with the mid-domain hypothesis, peaking in mid-elevations, although mostly the peak was displaced above or below the center of the altitudinal gradient. In localities where the *campos de altitude* were sampled, species richness peaked at higher altitudes, indicating that this physiognomy supports more Eupatorieae species than the highland Atlantic forest below it. For endophagous insects divided into feeding guilds, we found that for the Strict Endophage guild (Diptera with more specialized species) the peak in species richness was displaced to lower elevations, whereas species with midpoints in higher altitudes also tended to have wider altitudinal ranges. In contrast, the Facultative Endophage guild (more generalistic Lepidoptera species) had more species in the upper half of the altitudinal distribution, with species with midpoints in higher altitudes having narrower ranges. To our knowledge this is the first time the mid-domain hypothesis is applied and tested for various localities in a region and for more than a trophic level, advancing tentative biological hypotheses for the reported asymmetries in the mid-domain species distributions.

*Este capítulo, com pequenas modificações, será rapidamente submetido à American Naturalist, ou Journal of Biogeography, ou Ecography.

Introduction

One of the best known patterns in biogeography is the tendency of species richness to peak near the equator and decline toward the poles, forming a latitudinal gradient. Various hypotheses were developed to explain this pattern (e.g. Pianka 1966; Rohde 1992; Davidowitz and Rosenzweig, 1998). The first one was developed by MacArthur (1972) after Dobzhansky (1950), and states that biotic factors are more limiting in the tropics, whereas abiotic conditions are more important in higher latitudes, where species diversity is also lower and physical stress appears to be more severe (Brown 1995; Brown et al. 1996). In the present study we will analyze one of the raised hypothesis, developed by Stevens (1989) to explain the latitudinal gradient in species diversity using the tendency for species geographical ranges to decrease in size toward the equator. Stevens (1989) named it Rapoport's rule, after Eduardo Rapoport, the first one to describe this pattern (Rapoport 1975). Stevens argues that individuals must face a range of climatic conditions which becomes narrower with decreasing latitude (Stevens 1989), or altitude (Stevens 1992), or depth in aquatic environments (Stevens 1996). Natural selection would then favor broad tolerances in high latitudes (or altitudes or depth) because nonmigratory individuals would have to cope physiologically or behaviorally with the full range of conditions the seasonal changes impose on them.

As a part of Rapoport's rule to explain more species richness in tropical latitudes, Stevens (1989) used the "mass effect", after Shmida and Wilson (1985), and named it the "rescue effect". This hypothesis proposes that at the edge of a species geographical range, individuals disperse into areas where they survive but cannot reproduce because of inadequate local conditions or resources. Stevens calls these individuals "accidentals". Populations of accidentals do not reproduce and are maintained entirely by the rescue effect: dispersal from viable populations located closer to the center of the range; these are also known respectively as sink and source populations (Pulliam 1988; Pulliam and Danielson 1991).

Stevens proposed that if both Rapoport's rule and the rescue effect operate, a latitudinal, altitudinal, or bathymetric gradient in species richness would appear as a by-product. Toward the equator, where ranges are smaller, the ratio of rescue effect area to geographical range area increases, inflating species richness (Stevens 1989; Taylor and Gaines 1999). Even though Stevens (1989) cautioned that not all species will be in accord with Rapoport's rule, there are many studies questioning its generality as a 'rule' (e.g. Rohde 1992; Rohde et al. 1993; Colwell and Hurtt 1994; Roy et al. 1994; Rahbek 1995; Rohde 1996; Gaston et al. 1998; Colwell and Lees 2000). In considering only the rescue effect, Rohde et al. (1993) argue that in the tropics accidentals would also be tropical species and, although possibly increasing species numbers in a particular habitat, the rescue effect would not be responsible to inflate the number of tropical species as a whole. Secondly, random sampling may generate spurious Rapoport effects in range sizes, since species in high richness areas are relatively undersampled (Colwell and Hurtt 1994). Yet another factor causing spurious Rapoport effects would be the combined effect of smaller species numbers at high latitudes and of the wide latitudinal ranges of some species with their midpoint on the equator. With this effect, the rule would not result from wider latitudinal ranges of high-latitude species, but from the effect of some low-latitude species with wide ranges (Rohde et al. 1993).

Colwell and co-workers (Colwell and Hurtt 1994; Lees et al. 1999; Colwell and Lees 2000) investigated the geometry of species ranges in relation to geographical boundaries constructing null models with computationally intensive methods, to test Rapoport's rule. They found that in a global domain with hard boundaries in the poles, a latitudinal gradient in species richness, peaking at the equator, arises simply from the assumption of a random association between the latitudinal range and the latitudinal placement of ranges. The application of the same models to elevational gradients, with well-defined boundaries, predicts an unexpected peak in species richness at intermediate elevations (Colwell and Hurtt 1994; Colwell and Lees 2000). The prediction of a mid-gradient richness in altitudinal gradients "defies the longstanding dogma that species richness decreases monotonically with increasing elevation", and was called the 'mid-domain effect' (Colwell and Lees 2000).

Elevational gradients are somewhat different from latitudinal gradients. Colwell and co-authors (Colwell and Hurtt 1994; Colwell and Lees 2000) argue that elevational gradients possess two hard boundaries, at sea level and at mountaintops. Rahbek (1997) suggests that the latitudinal gradient encompass much longer distances, and consequently greater area, than the short elevational gradient. Also, montane regions show greater species richness when compared to flatlands. This pattern may arise because of the increased number of species distributed allopatrically on isolated mountains or in isolated valleys, the greater variety of habitats included within sampling areas of virtually any size, and the higher number of species coexisting within habitats (Ricklefs and Schluter 1993).

Within mountain ranges species face several problems. The first one is the altitudinal distribution of each population. Abiotic conditions in different altitudes are very different, from temperature, to edaphic conditions and air humidity (e.g. Smith 1994; Bruijnzeel and Veneklaas 1998; Sollins 1998; Tanner et al. 1998; Safford 1999a), and only more tolerant or plastic species can maintain themselves through a wide altitudinal range. The second one is the limited area for colonization. Within a given altitudinal range in a particular mountain, sometimes even restricted to one slope, many populations are obliged to survive in an area of limited extent. This restricted area may not always be sufficient to maintain a species population, which will then depend on dispersion to persist as a sink population (Shmida and Wilson 1985; Pulliam 1988; Stevens 1989; Pulliam and Danielson 1991). A third problem is the species' geographical range itself. Unless the species is able to explore intermediate valleys or has good dispersal ability (Hedberg 1970), it could be constrained to isolated mountains, becoming endemic.

The Serra da Mantiqueira is a mountain range that borders extensively on three of the most populous and developed Brazilian States: São Paulo, Rio de Janeiro and Minas Gerais. It is the highest mountain range in Southeast Brazil, considered the coldest orobiome in eastern South America, and above the tree line are the *campos de altitude*, which Safford (1999a;b) has characterized as Brazilian páramos. The tribe Eupatorieae (Asteraceae) is the most speciose in Brazil, and the Mantiqueira range is one of the South American regions with its highest species richness (Barroso 1957). For further explanations and details of the choice of system, see preceding chapters.

In the Mantiqueira range we sampled five localities (four mountaintops) above 760m above sea level. Eupatorieae flower heads were collected for two years to rear endophagous insets and determine insect-plant associations. The distribution and occurrence of plants and endophagous insects, as well as insect-plant interactions in the different localities are discussed elsewhere (chapters 1, 2 and 4). The present study compares the elevational ranges for both Eupatorieae plants and their endophagous insect species in the Mantiqueira range. Flowerhead endophages were divided in three feeding guilds, varying from Strict Endophages (Diptera, especially Tephritidae), Mobile Endophages (Lepidoptera), to Facultative Endophages (Lepidoptera), in a gradient of food specialisation (chapter 2).

The vertical distribution of species along an altitudinal gradient has two competing hypotheses: 'Rapoport's rule' and the 'mid-domain hypothesis'. While the first hypothesis predicts a monotonic decrease in species richness in increasing elevations, the second one predicts a humped curve with higher species richness at mid-elevations. In the Mantiqueira range we assessed species distributions along altitudinal gradients in the five sampled localities. As stated by Lees and co-authors (Lees 1996; Lees et al. 1999), before applying biological explanations to species gradients, the mid-domain null model should first be tested. Therefore, we first describe species richness variation along the studied collected elevational domain to detect which of the two hypotheses is best fit by observed patterns. We then test whether species with higher altitudinal midpoints tend to have larger altitudinal ranges, as expected by Rapoport's rule. The tests were carried out both on plants and on insects divided into feeding guilds, and biological factors are proposed to account for differences in the observed patterns among these groups.

Methods

Mantiqueira Range, Sampling methods, Plant Identification, Insect Rearing and Morphospecies assignment

The same as in chapter 2.

Feeding guilds

Endophagous insect species were divided into three guilds according to their feeding strategy (see chapter 2 for further details):

Strict Endophages (SE) - Tephritids and *Melanagromyza* (Diptera). The egg is laid in a flowerhead and the immature life cycle is completed within this single flowerhead.

Mobile Endophages (ME) - Tortricids, Gelechiids, Pyralids, Blastobasids, Pterophorids (Lepidoptera). The egg is laid in a flowerhead and if the larva needs more than a flower head to complete development, it is mobile enough to use more than a flower head within a shoot. The larva is completely inserted within the flower head while feeding.

Facultative Endophages (FE) - Lycaenids and Geometrids (Lepidoptera). Similar to the previous guild, the larvae are mobile and use many flower heads to complete development, being able to use also apical meristems and new leaves. The difference is that the larvae are larger and only their "head" or thorax is inserted within the flower head while feeding, with the body being exposed outside the structure.

A previous study (chapter 2) showed that the three guilds show a gradient of intimacy and specialisation, with strict endophages being more restricted to a single species, genus and subtribe than the other two guilds.

Vertical Distribution and Statistical Analyses

Coordinates for all sampling sites were obtained with a Magellan GPS receiver. Topographic maps were used to plot all collecting sites and verify their altitude to 20m precision (DSG 1981; IBGE 1971; IBGE 1974; IBGE 1976; IBGE 1981; IBGE 1983; IBGE 1986; IBGE 1988a; IBGE 1988b; IBGE 1991a; IBGE 1991b; IBGE 1992). The sampled localities within Mantiqueira range with its coordinates and the altitudinal range of sampled sizes is provided in Table 3.1.

Both vertical altitudinal ranges (AR) and their midpoints (MID) were calculated using the maximum and minimum altitudinal records for each species, where AR = (max-min), and MID = ((max+min) / 2) (Colwell and Hurtt 1994; Sklenár and Jorgensen 1999). Species only recorded at a single site were not assigned an AR value, but the elevation of their single record was taken as the species midpoint. The number of species records along the altitudinal range may also be skewed either upward or downward, in which case the midpoint may not be the best central measure of the species altitudinal distribution. Therefore, we also calculated the average altitude of where the species was recorded, which takes into consideration the frequency of records at each altitude. However, the average altitude showed no significant difference from midpoints for Eupatorieae plants (F= 0.020; df = 1, 110; p = 0.887), and we then kept the midpoint as the central location parameter in our analyses for both plant and insects, so that our results can be comparable to other studies.

To visualize the relation between the midpoint distributions and the species richness we used midpoint plots (Figure 3.1a,b) after Colwell and co-authors (Colwell and Hurtt 1994; Colwell and Lees 2000). In these plots the abscissa represents the location of the species within the domain, the ordinate shows the size of the altitudinal range, dots show the midpoint of each species distribution and horizontal lines (equal in length to the ordinate value of the dot) represent the species range. The two diagonal lines, setting both sides of the triangle, delimit the midpoint placement (within a bounded domain, midpoints will fall inside the triangle). In any location of the abscissa, the species richness is the number of horizontal range lines that intersect a vertical line from the stipulated location. Figure 3.1 uses the observed ranges of endophagous insects in pooled localities in the Mantiqueira range and changes midpoint placements to exemplify expected distributions according to the mid-point hypothesis (Figure 3.1a) and Rapoport's rule (Figure 3.1b). According to the mid-point hypothesis, in a fully stochastic null model with two hard boundaries, maximum proportional species richness (PSR) should be found at intermediate altitudes (Figure 3.1c) (Colwell and Hurtt 1994; Colwell and Lees 2000). In contrast, according to Rapoport's rule, species with wider altitudinal ranges will have midpoints in higher altitudes while species with narrow ranges will be more prone to be found in lower altitudes (Figure 3.1b), producing a monotonic decline in proportional species richness (PSR) in higher altitudes (Figure 3.1d, dots).

The predicted richness distributions for each group of empirical data according to the mid-domain hypothesis (continuous lines in Figures 3.1c,d) were generated by a Monte Carlo null model, where, for each species, a range size is first chosen, at random, from a given empirical range size/midpoint distribution. Then, the placement of the range midpoint for that species is chosen at random from among the feasible locations on the unit domain, given the chosen range size (Lees et al. 1999; Colwell, 2000; Colwell and Lees 2000). The analyses were done with RangeModel program (Colwell 2000), and the chosen model (model 4) corresponds to the analytical/empirical model of Lees et al. (1999) and, in most respects, to the Monte Carlo model of Pineda and Caswell (1998). The random sampling of ranges does not eliminates the sampled range, so that the same range value can be sampled many times. To generate the predicted distribution we inserted a set of 1,000 species within the domain envelope (as suggested by Colwell, 2000 to get smoother curves), and then compared their proportional species richness distribution (PSR) along the altitudinal domain with the proportional richness of empirical data. Proportional species richness is used so that both empirical and predicted distributions are plotted in the same dimensions. Figure 3.1 exemplifies species richness curves shapes (dots) expected according to the mid-point hypothesis (Figure 3.1c) and Rapoport's rule (Figure 3.1d) in contrast to the distribution generated by the null model (continuous line). This analysis was not done for data sets with less than three species, and some guilds in single localities could not be assessed. Kolmogorov-Smirnof two-sample tests were used to ascertain the goodness-of-fit of predicted and empirical distributions, as in Lees et al. (1999).

Stevens analyzed the variation in latitudinal range of species using the mean latitudinal range of all species present in each latitudinal band (Stevens 1989). Rohde et al. (1993) pointed out that Steven's method counted the same species several times and hence resulted in nonindependent samples. To circumvent this problem they suggested the 'mid-point method' that consists of calculating means only of species whose midpoints fall in a given latitudinal band. This method, though, does not overcome a further analytical complication because individual species do not themselves constitute independent data points due to their phylogenetic relatedness (but see Brown, 1999). Since species are phylogenetically related, they may share attributes such as range sizes (e.g. Taylor and Gotelli 1994; Blackburn and Gaston 1996; Gaston 1996; Gaston et al. 1998), although this has been not demonstrated to date. Stevens' and the mid-point method are not just different ways of quantifying the same relationship (Gaston et al. 1998): while the Stevens' method shows variation in the mean range size of all species present at any given altitude, the mid-point method relates altitudinal variation in range size to the position of species' midpoints distributions, with the advantage that each species is only considered once. Considering these problems, we compared the altitudinal range of species with the midpoint method, grouping species whose midpoints fell in every 100m of altitudinal band. Figure 3.1 shows graphically mid-point methods as expected by mid-domain hypothesis (Figure 3.1e) and Rapoport's rule (Figure 3.1f). According to the mid-domain hypothesis the species with wider altitudinal ranges will be concentrated in the center of the domain (Figure 3.1e), whereas Rapoport's rule predicts smaller altitudinal ranges in lower altitudes and wider ranges in higher altitudes (Figure 3.1f).

Results

Altitudinal distribution of Eupatorieae plants in the Mantiqueira range

In the Mantiqueira mountain range the sampling sites varied from 760m (Ibitipoca) to 2460m (Itatiaia) above sea level, with a maximum total altitudinal range (AR) of 1700m (Table 3.1). Ibitipoca and Campos do Jordão had ARs in excess of 1000m, while the samples in the other localities had ARs between 600m and 800m. All locality midpoints (MID) were above 1000m, the lowest one in Visconde de Mauá, and the highest in Itatiaia, a direct consequence of the sampling universe within each locality. More frequent species did not necessarily have wider altitudinal ranges, and the number of records explained only 34% of the size of the altitudinal range ($r^2 = 0.341$; $p < 0.001$). *Ageratum fastigiatum* was the most recorded species, but had the third widest range. *Austroeupatorium silphiifolium* had the widest elevational range, with an AR of 1600m in 47 samples, the second most frequent species. *Ageratum conyzoides* was also recorded 47 times but had only an AR of 880m, illustrating that altitudinal range is not a simple function of record number and therefore of geographical distribution. Another interesting point is that some species such as *Austroeupatorium neglectum*, restricted to altitudes above 1800m both in Itatiaia and Campos do Jordão, was recorded as low as 1280m in Visconde de Mauá, showing that different localities offer different conditions for plant growth and development. Eupatorieae species are listed in Appendix 3.1, with summary data of altitudinal records in each locality.

For the Mantiqueira as a whole, the distribution of species midpoints suggests a bimodal pattern, with more than half of species (62%) concentrated between 1420m and 1800m, fewer species between 1400m and 1220m, and then an increase in species numbers between 1020m and 1200m (Figure 3.2a). Only 14% of species had their midpoint above 2000m, but these altitudes were sampled only in Itatiaia and Campos do Jordão (Figure 3.2b-f). The species midpoint distribution did not reflect sampling intensity, though. Samples were concentrated in the 800m interval from 1020m to 1800m, with 75% of samples within this range (Figure 3.3a), although the curve is slightly bimodal with a minor peak with 6% of samples at 2220-2400m (Figure 3.3a).

Examining localities separately we note that all species have midpoint distributions included within the 800m interval which includes most samples, except for Itatiaia (Figure 3.2d). In Itatiaia most species had midpoints between 2220 and 2400m, which accounts for the minor peak in sample collections in Figure 3.3a. The distribution of species midpoints seems also slightly bimodal in Ibitipoca, Itatiaia and Campos do Jordão, whereas Visconde de Mauá and Passa Quatro were not sampled over an altitudinal range wide enough to show if they follow the same pattern. Even though samples and species midpoints may both have bimodal distributions, most samples are in the lower hump of the distribution (Figure 3.3a), whereas species midpoint curves peak at higher altitudes (Figure 3.2).

Most Eupatorieae species in the Mantiqueira showed a restricted altitudinal range, with 27 species out of 46 (59%) with recorded altitudinal ranges narrower than 600m. Few species (26%) showed an altitudinal range wider than 1000m, although there is a shallower peak in species distributions in the 1220m-1400m interval (Figure 3.4a). Since no single locality was sampled over such a wide range, this peak represents plants sampled in more than one locality. In fact, altitudinal range was significantly correlated with the geographical distribution, i.e. number of localities ($r^2 = 0.466$, $p<0.001$; Figure 3.5a).

The occurrence of Eupatorieae species richness peaks within the examined altitudinal domain differed among the five studied localities. Visconde de Mauá was the only locality in which observed distribution matched the distribution predicted by the null model, while Ibitipoca showed a marginally significant deviation, with species richness peaking ca. 1500m, slightly above the center of the altitudinal domain (Table 3.2 and Figure 3.6h-l). For the other three separate localities as well as the Mantiqueira as a whole, the observed richness distributions deviated significantly in a Kolmogorov-Smirnov test from the distributions predicted by the null model (Table 3.2). In Itatiaia and Campos do Jordão the peak in species richness was markedly beyond the predicted one, while in Passa Quatro the peak in species richness was lower than the predicted one (Figure 3.6h-l). When samples were pooled for the entire Mantiqueira, more species were found at intermediate altitudes as predicted by the mid-domain hypothesis, even though observed and expected distributions deviated significantly (Table 3.2), their maximum coincided (Figure 3.6g).

Vertical Distribution of endophagous insects

The distribution of flowerhead endophages in the Mantiqueira range varies according to their feeding guild. Strict endophages showed a lower altitudinal midpoint than facultative endophages ($F = 4.667$; $p = 0.016$; Table 3.3), which suggest that FE species are more diverse at higher elevations, while SE species are more diverse at lower elevations. Half the species from the strict endophage guild had midpoints between 1220 and 1400m above sea level; mobile endophages had 63% of their species with midpoints between 1220 and 1600m. In contrast, facultative endophages had their peak in midpoint distribution between 1620 and 1800m (Figure 3.7a).

The pattern of more specialized species peaking at lower elevations is clearly seen in Campos do Jordão (Figure 3.7f). In Ibitipoca a similar trend was found, with SE species occurring from 1220m to 1400m, while both ME and FE peaked from 1220m to 1600m (Figure 3.7b). In Visconde de Mauá and Passa Quatro this pattern was not evident (Figures 3.7c,e), while in Itatiaia SE species midpoints occurred all above 2000m and ME species midpoints were all below 2000m (Figure 3.7d). Appendix 3.2 shows the endophagous insect species grouped into guilds with summary data for each locality.

As seen for records of Eupatorieae species and their sample distributions, the altitudinal distribution of insect species does not match the distribution of samples from which they were reared (Figure 3.3b). More endophagous insects (total, SE or ME guilds) were reared from samples collected from 820m to 1800m, while most FE species were obtained from plant samples collected from 1020m to 1200m (Figure 3.3b).

The three insect guilds showed no significant difference in their altitudinal ranges (Table 3.3), though there are indications. More than half (53%) of mobile endophages showed ARs between 620 and 1000m, while strict endophages were more heterogeneous in their ranges, varying from 20m to 1680m and 80% of facultative endophages varied from 220 to 800m in altitudinal range (Figure 3.4b).

The geographical distribution of species was significantly correlated with their altitudinal range for each of the three guilds (Figure 3.5b-d).

As was shown by plant richness distributions, the richness distribution of endophagous insect species showed maximum distributions at mid-elevations, but rarely in the center of the domain. For the entire Mantiqueira the distributions of species richness all peaked below the center of the expected distribution according to the null model (Figure 3.8e-h and Table 3.4).

For pooled guilds in each locality, the observed distribution of species richness showed midpoints in the center of the altitudinal domain (Figure 3.9 and Table 3.4). Observed and predicted distributions matched in Passa Quatro and Campos do Jordão. In Itatiaia the species richness peaked at altitudes below the center of the distribution (note the few species considered in this locality), and in Ibitipoca and Visconde de Mauá, the richness peaks were just above the predicted ones (Table 3.4 and Figure 3.9).

The observed distribution of single guilds in each locality is very sparse, and will be exemplified graphically with the Ibitipoca locality, with more samples and species and consequently the best resolved patterns. The peak in species richness varied within the domain, according to the guild. Strict endophages tended to peak in richness at altitudes below the center of the distribution. For the SE guild, only in Ibitipoca no significant difference was found between observed and expected richness distributions (Table 3.4 and Figure 3.9). For mobile endophage species, in both Ibitipoca and Visconde de Mauá, the few analyzed species showed asymmetrical richness distributions that did not fit the predicted ones, mainly because of differences in shape (Table 3.3 and Figure 3.9 for Ibitipoca). The facultative endophage guild could only be analyzed in Ibitipoca and Visconde de Mauá, and in both localities the species richness tended to peak in higher elevations, differently from the predicted null model distribution (Table 3.3 and Figure 3.9).

The altitudinal range of species along the altitudinal gradient also varied substantially (Figures 3.8i-l and 3.9). All insects in the entire Mantiqueira mountain range with midpoints at intermediate altitudes showed comparatively broader ranges with the families Tephritidae, Agromyzidae and Tortricidae presenting comparatively wider ranges (Appendix 3.2). Facultative endophages showed a tendency of species with midpoints at higher altitudes to have narrower ranges (inverse to what expected by Rapoport's rule) (Figure 3.8l). Mobile endophagous species showed no trend in altitudinal range distribution across altitudinal bands (Figure 3.8k). For the Mantiqueira pooled localities, Rapoport's rule is in accordance only for the distribution of ranges from SE species (Figure 3.8j), which tended to show broader ranges in higher altitudes (Figure 3.8i-l, compare with Figure 3.1f).

Examining all endophages in each locality, no significant relation of AR with altitude was found (Figure 3.9q-y). Even though not strong, only Passa Quatro tended to be in accord to Rapoport's rule, with broader ranges in higher altitudes. Other localities showed no trend, or suggested either a reverse Rapoport trend or a unimodal distribution as expected from the mid-domain hypothesis. Data were mostly too sparse to examine these trends in each guild and locality. Some graphically discernible trends were a decrease of altitudinal ranges with increasing midpoints (FE in IB, ME in CJ) but none of these trends was strong by itself.

Discussion

On defining species boundaries

When assessing the mid-domain effect all the species considered must share the same "hard" boundaries, or boundary constraints, as stated by Colwell and Lees (2000). The environmental conditions that set the boundaries of a population or species range also define what biogeographers call barriers: the inhospitable areas that cannot sustain a population, so that dispersal across them must usually occur rapidly and during some resistant stage of the life cycle. The recognition of barriers implies that they separate areas that are at least potentially habitable (Brown 1995). The boundaries of the geographic range of a species are determined by ecological limits: by an interaction between the niche requirements of the organisms and the abiotic and biotic characteristics of the environment. Some abiotic restrictions may be absolute (or hard boundaries), such as the area of the continent over which the organisms are distributed (Brown et al. 1996), or the uppermost summit of a mountain (Colwell and Hurtt 1994; Colwell and Lees 2000).

Studying and defining, quantifying or even ranking barrier resistance depends on the temporal scale the study addresses (Colwell and Lees 2000). Mountains, like landmasses, may show many different boundaries depending on the studied group. Colwell and Hurtt (1994) argued that mountain summits, although not as absolute as the sea (for terrestrial species) are probably hard boundaries, since climatic regimes differ markedly on opposite slopes of mountain ranges, and the tree line can be considered a hard boundary for most forest animals and plants.

In the present study, localities were collected in different altitudes and altitudinal ranges, depending on both the locality's topography and accessibility. In no locality the sampling sites were situated in a linear altitudinal transect, but they followed dirt roads and pre-existing walking trails. In consequence, in Passa Quatro and Campos do Jordão the sampling sites were more dispersed than in Itatiaia and Ibitipoca, both parks where sampling sites are restricted in geographical extent and in road and trail access.

Albeit the problems cited above, localities in the Mantiqueira range were chosen based on physiographical similarity and proximity of collecting sites, and previous studies have proven these to be quite adequate criteria for the insects and plants of interest (chapters 1, 2 and 4). As to the altitudinal ranges of the study localities, even though we could not reach the higher summits in Visconde de Mauá and Passa Quatro, within the studied localities we can analyze how the studied organisms are distributed in our sampling universe, which is our sampled altitudinal domain.

Altitude and Species Richness

The distribution of species, per altitudinal midpoints, does not reflect the distribution of collected samples in the same altitudinal range, either for plants or their flowerhead endophages (Figures. 3.2, 3.3 and 3.7). Although for Eupatorieae species the two maxima in species richness are included in the major sampling maximum, the pattern seen on the graphs are very different. Most Eupatorieae species had their altitudinal midpoint in the Mantiqueira range peaking above the altitude where most samples were obtained, which suggests that at lower elevations prevail fewer locally more abundant species.

For Eupatorieae species in Itatiaia and Campos do Jordão - localities sampled both below and above the treeline - most species had their midpoint above the treeline. In Itatiaia most species had their midpoints ranging from 2220m to 2400m, whereas the treeline in this locality occurs from 2020m to 2200m (Safford 1999a). In Campos do Jordão, most species had midpoints from 1620m to 1800m, while the treeline is at 1630m (Safford 1999a). In Ibitipoca, the remaining locality sampled above the treeline, the major peak in species richness is also situated above the tree line, although the pattern is less clear.

Colwell and co-authors (Colwell and Hurtt 1994; Colwell and Lees 2000; Lees et al. 1999) have pointed out that there is a geometric effect in elevational gradients with two hard boundaries. According to the mid-domain effect, all constructed richness distributions based on null models show a near-parabolic unimodal peak in species richness. Therefore, species richness should peak in mid-elevations, at the center of the altitudinal gradient. According to Lees et al. (1999), if geometry underlies empirical species richness patterns as these models suggest, then it is the departure from mid-gradient species richness that requires explanation. In fact, all null distributions of species richness for both plants and insects in the Mantiqueira range predict a symmetrical unimodal curve with higher species richness at mid-elevations, whereas most empirical distributions showed humped curves asymmetric in relation to the center of the altitudinal domain (see Figures 3.6, 3.8 and 3.9).

The distribution of Eupatorieae species richness in pooled localities peaked in the middle of the distribution, but with a much higher hump than predicted. On the other hand, for single localities, only in Visconde de Mauá the species richness distribution followed the predicted distribution. In Ibitipoca, Itatiaia and Campos do Jordão - the three localities with sampling sites extending into the *campos de altitude* - species richness was higher at altitudes between the maximum altitude in the domain and their predicted center. Passa Quatro was the only locality in which species richness peaked below the predicted elevations. Safford (1999a) had already described that about a third of the plant species in the Itatiaia *campos* appear to be endemic to the *campos de altitude*. The peak in species richness above the middle of the distribution is probably due to the various endemic species in the *campos de altitude* physiognomy. These results suggest that, far from being the rule for plant species in altitudinal gradients, the monotonic decline in species richness with increasing altitudes - the central point of Rapoport's rule - does not hold, at least for Eupatorieae plant species in the Mantiqueira range.

A monotonic decline in tree species richness with elevation was described by Gentry (1988), for tropical forest plants, mainly within the Andes. He found a clear pattern of decreasing species richness with increasing altitudes from 1500m to 3100m up to the treeline. Although the forest data showed a decrease in species richness with altitude, the hemiepiphytic flora showed an increase in species at 1800m (mid-elevations) (Gentry 1988).

Turning now to endophagous insects, the peak in species midpoints distribution varies according to their feeding guild. Nonetheless, the overall pattern shows that for the three localities discussed above, where samples encompassed the *campos*, the peak in species midpoint distribution is lower than the peak in plant species distribution. This results indicates that the insect distributional patterns are not mirroring those of their host plants, and that most herbivores are not specialized on hosts endemic to the *campos de altitude*.

The distribution of endophagous insect species richness showed the same variability of results found for plant species. For pooled guilds in Mantiqueira, the species richness distribution peaked in the lower half of the elevational gradient, and each of the three guilds also peaked below the predicted center (Figure 3.8). When pooled guilds were examined in each separate locality, though, Passa Quatro and Campos do Jordão fit the predicted null model well, while in Ibitipoca and Visconde de Mauá species richness, though peaking at intermediate elevations, had markedly asymmetric distributions, and in Itatiaia species richness peaked below the predicted center (Figure 3.9). Ibitipoca exemplifies how species richness distributions of each guild differs in a given locality: SE species show a peak in species richness below the predicted altitudinal center, ME species fit the null distribution and FE species show a peak in species richness above the predicted altitudinal center.

Stevens (1992) tested several data sets for elevational decrease in species richness but, as Colwell and Hurtt (1994) noted, only two taxa (Colorado Orthoptera and regional data for Costa Rican trees) are in conformance with the predicted monotonic decline. The remaining ones, including trees, mammals, birds, amphibians and reptiles, show an increase in species richness at mid-elevations, although not in the center of the gradient, as expected by the null model. They conclude that although geometry is an important variable in determining species distributions in a bounded domain, the detected asymmetries in the species richness distributions are caused by other factors.

Rahbek (1997) analyzed bird species richness in an altitudinal gradient in the Andes, and found a hump-shaped curve with the highest species richness towards the lower end of the gradient, similarly to what we found for Eupatorieae plants in Passa Quatro and for strict endophagous species in most localities. Again, he concludes that the challenge in explaining unimodal species richness distributions is not their mid-elevational peak in itself, but to account for the asymmetries in the curves, with higher species richness below the predicted center.

The geometric null model is a very elegant way of testing species ranges within a bounded domain but it has no explicit biological assumptions, as befits a null model. The displacement of the curve's modes, found in the present study, in Rahbek's data (1997) and also when Colwell (1994) analyzed Stevens' (1992) data is probably caused by biological determinants, and will be discussed in the last section.

Species richness and altitudinal ranges

In the Mantiqueira, although most Eupatorieae species showed an altitudinal range narrower than 600m, the distribution was bimodal with a minor peak at 1400m. In the entire Mantiqueira data, the maximum recordable AR would span 1700m from the lowest site, in Ibitipoca, to the highest one, in Itatiaia. On the other hand, samples in Ibitipoca and Campos do Jordão extended over an altitudinal range of respectively 1024m and 1040m, so that species could show broad altitudinal ranges in a single locality.

At least two previous studies for tropical regions investigated plant species with altitudinal ranges exceeding 1000m. Smith (1975) found that for herbaceous angiosperms in New Guinea, with maximum collection sites of ca. 4500m above sea level, the great majority of species show altitudinal ranges exceeding 1000m. Sklenár and Jorgensen (1999) found that, for páramo plants in Ecuador with maximum altitudes of collection sites of also about 4500m above sea level, more than half of species show an altitudinal range wider than 1300m. Itatiaia encompasses the second highest summit of the Mantiqueira range that, at 2789m is much lower than the mountain ranges studied in both cited studies. The relatively narrow altitudinal range of most Eupatorieae species in the Mantiqueira range, then, is constrained by the low elevation of its mountains, explaining why the plants altitudinal ranges will necessarily fall below 1700m, a low range if compared to other tropical mountains in the Andes, Africa or New Guinea ranges (e.g. Hedberg 1970; Smith 1975; Rundel et al. 1994; Sklenár and Jorgensen 1999). Most Mantiqueira plants showed altitudinal ranges below 600m, though. In previous analyses of these data (chapter 1) we showed that 39% of the 56 Eupatorieae recorded in the Mantiqueira range are restricted to one locality. So, the fact that most plant species show a narrow altitudinal range, is a reflection of the geographical range among localities, with most species occurring in few localities.

The altitudinal ranges for endophagous insects differed among feeding guilds. The facultative endophages guild showed narrower ranges, most of them less than 800m in width. Most mobile endophages had ranges from 620 to 1000m. The greatest variation was found among strict endophages whose ranges varied from ca. 200m (*Xanthaciura mallochi*, recorded only in Ibitipoca) to the 1680m range out of the maximum possible of 1700m, recorded for *Xanthaciura chrysura*, present in all localities.

Another point worth attention is that more widespread species also showed a broader altitudinal range, both Eupatorieae and their flowerhead endophages. This relationship is partly a sampling artifact, since different localities were collected at different altitudes. Nonetheless, a species could be recorded over an altitudinal range of more than 1000m in a single locality. Smith (1975) and Sklenár and Jorgensen (1999) also found that more widespread species had broader altitudinal ranges. They concluded that it is more difficult for a plant species with a narrow range restricted to the top of a mountain to disperse among mountaintops, because it would have to overcome greater distances to reach other mountains, since it could not use intermediate areas as 'stepping stones'. On the other hand, species with a wide range easily migrate to adjacent areas (Sklenár and Jorgensen 1999).

The distribution of altitudinal ranges throughout an elevational gradient is the core explanation for Rapoport's rule (Stevens 1992), which states that the increase in the mean elevational range of species with elevation should result in a parallel, monotonic decrease of species richness with elevation caused by narrower environmental tolerance of genuine lowland species. Eupatorieae species with midpoints at higher elevations tended to have wider altitudinal ranges in Passa Quatro as well as over the entire Mantiqueira, whereas in Itatiaia there was an opposite trend. Endophagous insects suggested an intriguing pattern. Strict endophages with midpoints at higher altitudes showed broader ranges whereas the reverse narrower altitudinal ranges for species with higher-placed midpoints was shown by facultative endophages.

Rohde et al. (1993) found that marine teleost species with midpoints at lower latitudes have greater latitudinal ranges than species with midpoints at higher latitudes. In contrast, the same study found that, for freshwater fish, species with midpoints at higher latitudes also had higher ranges, only in latitudes above 40°N in both North America and Europe. Roy et al. (1994) argues that although their conclusions are very important, Rohde's (1993) marine data set involves pooled data from the Indo-Pacific and Atlantic oceans, regions that "could hardly be more disparate in climatic history and biogeographic structure". Roy et al. (1994) found that for molluscan species in the eastern Pacific Rapoport's rule does not apply and, if anything, species ranges decrease towards the poles. Mourelle and Ezcurra (1997) studied cacti distribution in Mexico (NAmerica) and Argentina (SAmerica) and found that although species richness increased toward the equator in both places, wider ranges at higher latitudes was only found in Mexico.

The fact that species richness in some groups increases towards the equator without an attendant decrease in species ranges contrasts with Stevens' hypothesis that decrease in species ranges could be the main explanation for the temperate-tropical gradient in species diversity (Rohde 1992; Rohde et al. 1993; Mourelle and Ezcurra 1997). Factors other than those invoked by Rapoport's rule must be acting to determine species richness in latitudinal and altitudinal gradients.

Biological determinants of mid-domain asymmetries

In the Mantiqueira range no studied group in any locality showed a clear Rapoport effect, with higher species richness in lower altitudes and wider altitudinal ranges for species with midpoints at higher altitudes. In contrast, most groups presented higher species richness at mid-elevations, as predicted by the 'mid-domain effect'. However, peaks in species richness were seldom in the middle of the sampled altitudinal domain, showing that species richness distributions are not only influenced by the random placement of midpoints and range sizes distributions, and other factors must be influencing species occurrence and range in Mantiqueira mountains.

In the present study we analyzed four distinct groups: host plants, strict endophages, mobile endophages and facultative endophage species. These groups encompass not only two trophic levels, but also a gradient in body size and larval mobility for the insect species. Differences in altitudinal distribution among groups can indicate how bionomic patterns of life histories affect species distributions. Some differences have indeed been found for different endophagous insect guilds. The present study has shown that strict endophagous species are more likely to present a peak in species richness below the predicted center of the altitudinal domain, as well as an increase in altitudinal ranges in higher altitudes. The opposite was found for facultative endophagous species, whose species richness peaked above the predicted distribution center, and altitudinal ranges that tended to decrease with increasing elevations. For Eupatorieae plant distributions we found both patterns. In Passa Quatro we found the same pattern described for the SE guild, while in Itatiaia the pattern was similar to that of a FE guild. Although the species richness distributions seem to be followed by a pattern of species range sizes, as described for the insect guilds, both patterns are not always linked. This was found for example for Eupatorieae plants in Ibitipoca, where species richness peaked at elevations above the predicted center of the distribution, whereas species ranges showed no detectable pattern.

Different distributions in the peak in species richness may reflect a sampling artifact, if central points are sampled more intensively. Lees et al. (1999) tested this hypothesis for various groups in Madagascar, eliminating all the empirical records for a central mountain range considered a 'hotspot'. They found no significant effect on the central tendency of the richness distribution, and concluded that although some points were oversampled, this did not influence the mid-domain effect found for the area. In the Mantiqueira range, although a sampling artifact may affect our results, this is certainly not the case for all localities. In Itatiaia, for example, more plant species were found above the predicted center, whereas endophagous insect distributions showed a peak below the predicted center.

For Eupatorieae plants in the Mantiqueira we found that although species richness showed a humped distribution similar to what predicted by the mid-domain null model, only in Visconde de Mauá predicted and observed distributions matched. In Visconde de Mauá and Passa Quatro, both localities where the *campos de altitude* were not sampled, the maximum in species richness is below the predicted center, while in Ibitipoca, Itatiaia and Campos do Jordão maximum species richness was found in the *campos de altitude* physiognomy. This pattern is in complete accordance to what expected to the *campos de altitude* and is also true for the Espinhaço mountain range (PIKL Prado, pers. comm.). Asteraceae plants are, together with Polypodiaceae sl. and Melastomataceae the three most important families in the *campos de altitude*, comprising about 40% of the species in Itatiaia (Safford, 1999a,b). The presence of a high richness of endemic species in the campos is probably the main factor displacing the observed peak in species richness above the predicted center. One other important factor that may be acting is that the areas below the *campos de altitude* in the Mantiqueira mountain range are mostly covered with highland Atlantic forest, with low richness of Asteraceae species. Localities like Visconde de Mauá and Passa Quatro are heavily human impacted. Asteraceae are commonly found in fields and meadows, since many are very invasive and mostly heliotropic. Impacted areas should have fairly high plant richness. Since lower altitude areas are comparatively more impacted, species richness would peak in lower altitudes. Both factors are biological processes that are probably determining the observed pattern of higher species richness above the treeline, in the campos de altitude.

For endophagous insects the peak in species richness can be related to their physiology, such as dietary preferences and/or tolerances to harsh climates. Facultative endophages are more often associated to the tribes Eupatoriinae and Gyptidinae (chapter 4), the tribes that presented higher altitudinal ranges. Facultative endophages are also large-bodied and may be more tolerant of the harsh conditions in the *campos de altitude*. Although strict endophagous immatures are protected within the flower head, adults of this group reach small sizes, and may be very sensitive to strong winds, for example. Plant characteristics may change along an altitudinal gradient. Erelli et al. (1998) have shown that the same plant species can have different degrees of palatability at different elevations of the same mountain, with high-elevation trees of three species from different families supporting a better performance of macrolepidoptera larval growth than conspecific trees from lower elevations. Phenology is equally important. Jonas and Geber (1999) showed that for *Clarkia unguiculata* in the Sierra Nevada, days to germination, flowering and node of first flower increased with elevation, whereas petal size tended to decrease with elevation. The fact that facultative endophagous insects show their peak in species richness and midpoint distributions at higher altitudes than strict endophagous insects is probably a function of dietary preferences, suitability, and tolerances to the different climatic conditions that occur in the observed altitudinal gradient.

In the Mantiqueira range the mid-domain effect seems to prevail, although most studied groups deviated from the predicted unimodal symmetrical curve centered on the middle of the altitudinal domain. As previously pointed out by many authors, these deviations are probably caused by biological determinants (Colwell and Hurtt 1994;Lees et al. 1999; Colwell and Lees 2000). The study of two trophic levels and the division of flowerhead endophagous insects into feeding strategies offer further insight into factors that may explain at least in part the observed patterns in species richness distributions along an altitudinal gradient.

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TABLE 3.1. Localities within the Mantiqueira range, with its names, municipality, state, and position of the reference site, used to measure distances among localities. The altitudinal domain (m) and range (m) of collection sites is also provided.

Code	Name	Municipality	State	Lat (S)	Long (W)	Altitudinal Domain	Atitudinal Range
IB	Ibitipoca	Lima Duarte	MG	21° 41.58'	43° 52.73'	760 - 1784m	1024m
VM	Visconde de Mauá	Bocaina de Minas	MG	22° 14.38'	44° 29.21'	880 - 1480m	600m
IT	Itatiaia	Itatiaia	RJ	22° 22.64'	44° 41.79'	1740 - 2460m	720m
PQ	Passa Quatro	Virgínia	MG	22° 25.66'	45° 04.51'	960 - 1740m	780m
CJ	Campos do Jordão	Campos do Jordão	SP	22° 39.48'	45° 33.41'	880 - 1920m	1040m
	Pooled ranges					760 - 2460m	1700m

TABLE 3.2. Kolmogorov-Smirnov two-sample test for agreement of observed to expected altitudinal species richness distributions of Eupatorieae plants in the Mantiqueira range. The results correspond to Figure 3.6, g-l (*$p < 0.05$; ✤ $0.05 < p < 0.10$).

	Kolmogorov-Smirnov two-sample test
Mantiqueira pooled data	0.267 *
Ibitipoca	0.233 ✤
Visconde de Mauá	0.167 ns.
Itatiaia	0.317 *
Passa Quatro	0.283 *
Campos do Jordão	0.300 *

TABLE 3.3. Mean and standard deviation of the altitudinal range and its midpoint (in meters) for 40 species from the three distinguished feeding strategy guilds (see methods for guild description). Probability values for one-tailed tests; degrees of freedom = 2, 37.

		GUILD				
		SE	ME	FE	F	p
Geographical Distribution	Midpoint (m)	1274.0 ± 242.98	1361.3 ± 142.22	1551.0 ± 285.91	4.67	0.016
	Altitudinal Range (m)	809.3 ± 443.23	669.3 ± 341.25	530.0 ± 288.64	1.72	0.194

TABLE 3.4. Kolmogorov-Smirnov two-sample test for agreement of observed to expected altitudinal species richness distributions of flowerhead endophages in the Mantiqueira range. The results correspond to Figures 3.8 and 3.9 (* $p < 0.05$; ** $p < 0.001$).

Locality	Guild			
	Pooled guilds	SE	ME	FE
Pooled Localities	0.300 *	0.300 *	0.267 *	0.350 *
Ibitipoca	0.267 *	0.183	0.417 **	0.267 *
Visconde de Mauá	0.283 *	0.350 *	0.467 **	0.400 **
Itatiaia	0.400 **			
Passa Quatro	0.150	0.317 *	0.300 *	
Campos do Jordão	0.167	0.400 **	0.283 *	

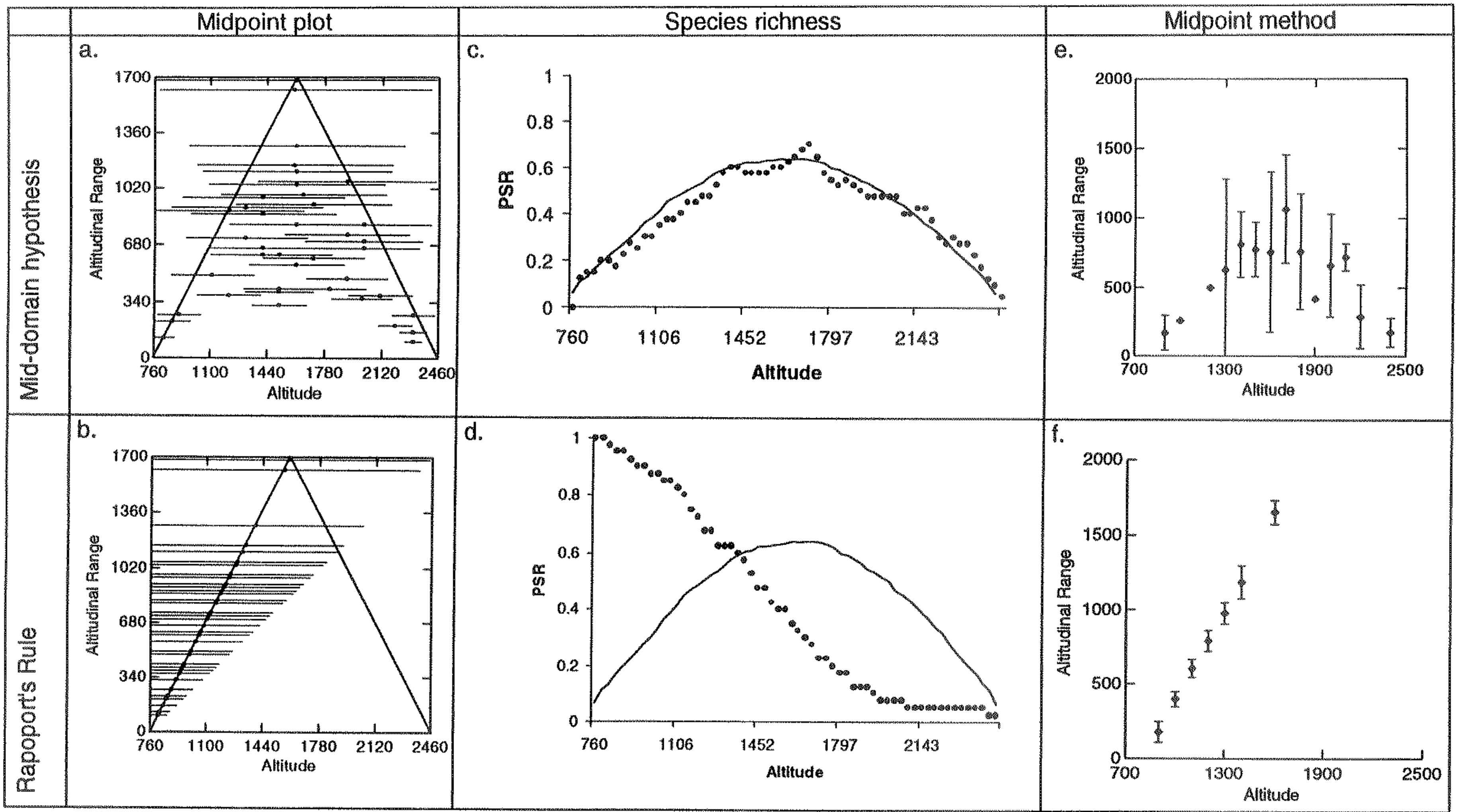


Figure 3.1. Three graphical tests to exemplify Rapoport's rule versus the mid-domain effect for modified midpoints in empirical ranges of endophagous insects in the Mantiqueira range (adapted from Figure 3.8a). Midpoint plots (a,b) : The abscissa represents the location of species within the domain, the ordinate represents the size of the altitudinal range. At any location of the abscissa, the species richness is the number of horizontal range lines that intersect a vertical line from the stipulated location (Colwell & Hurtt, 1994; Colwell & Lees, 2000). Observed (dots) proportional species richness (PSR) distributions (c,d) over the altitudinal gradient compared to predicted values from a Monte Carlo null model (line) (Colwell & Lees, 2000). Midpoint method (e,f) after Rohde et al. (1993): for each 100m altitudinal band, all species with their midpoint in that band were pooled and means (points) and SDs (bars) of the altitudinal ranges were calculated. The first series shows distributions pooled for the Mantiqueira range, followed by individual localities. Altitudes and altitudinal ranges in meters.

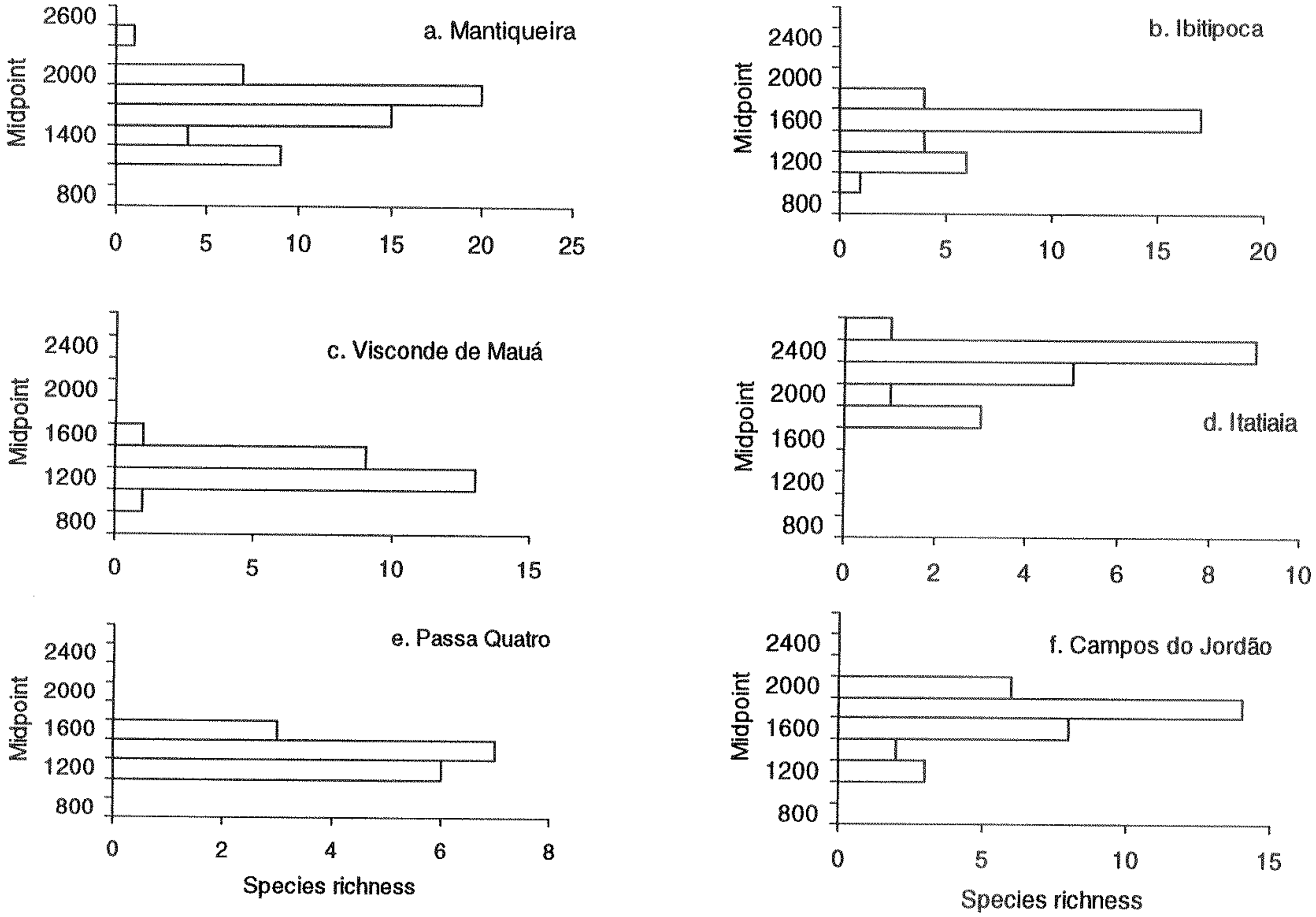
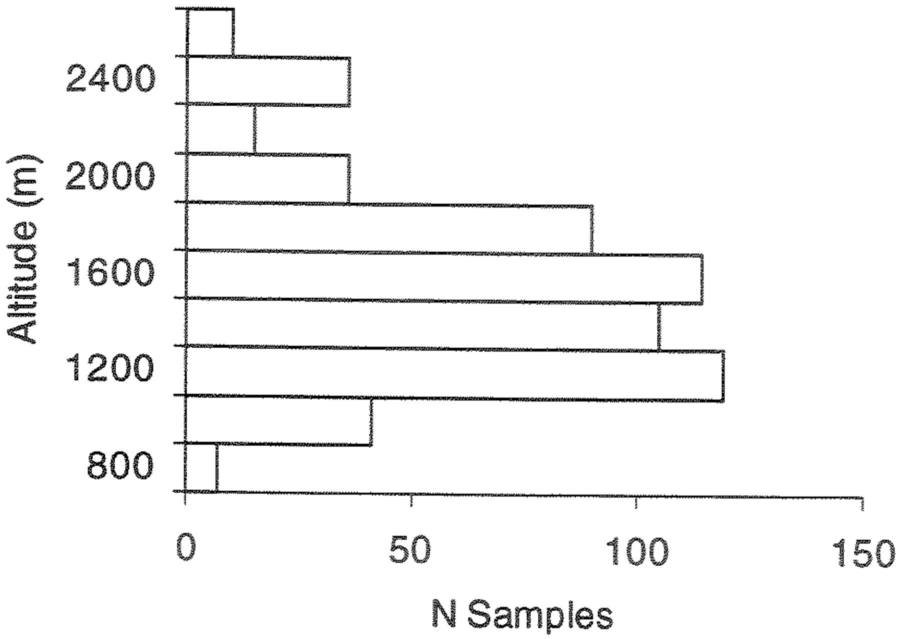


Figure 3.2. Distribution of midpoints of Eupatorieae species, showing peaks in species richness at intermediate elevations. Compare with Figure 3.3a for altitudinal distribution of samples. Refer to Table 3.1 for altitudinal range of samples per locality.

a. Eupatorieae Plants



b. Endophagous insects

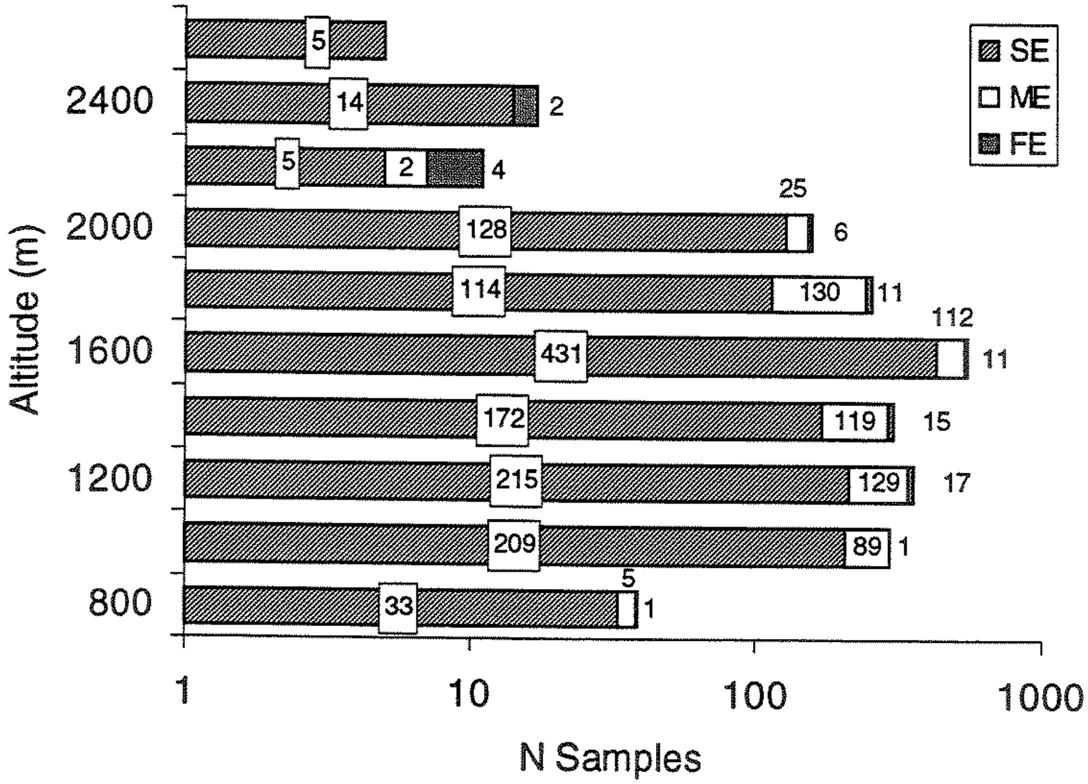
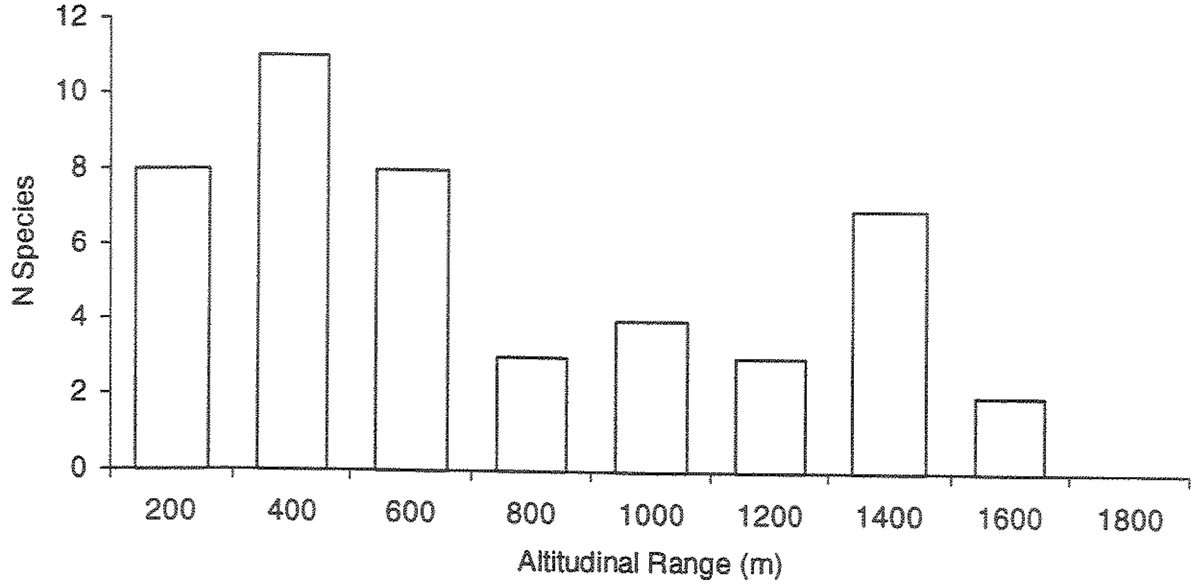


Figure 3.3. Total number of samples per altitudinal band in the Mantiqueira range for Eupatorieae plant species (a) and reared endophagous insect species (b). Endophagous insects are divided into feeding guilds (see text and chapter 2 for guild description).

a. Eupatorieae species



b. Endophagous insect species

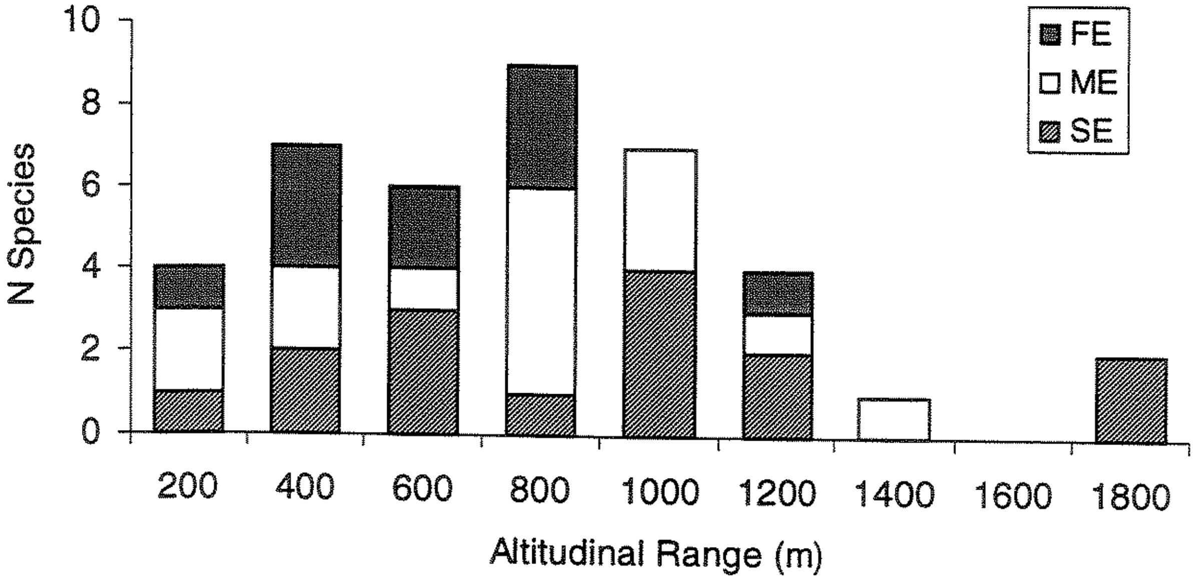


Figure 3.4. Frequency distribution of the width of the vertical altitudinal ranges for 46 Eupatorieae species (a) and 40 endophagous insect species (b) in the Mantiqueira range. Numbers in the abscissa scale are upper ends of class intervals.

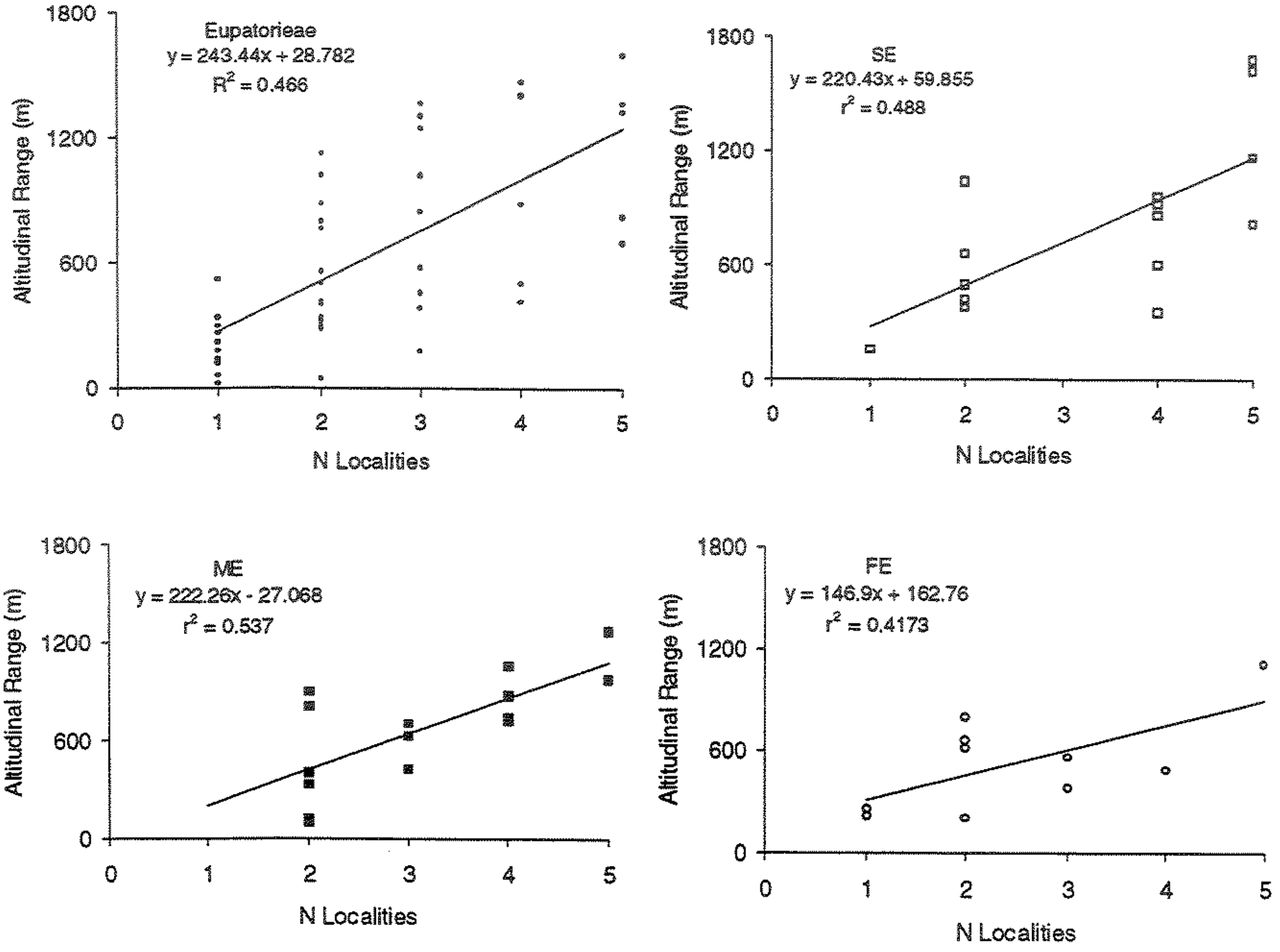
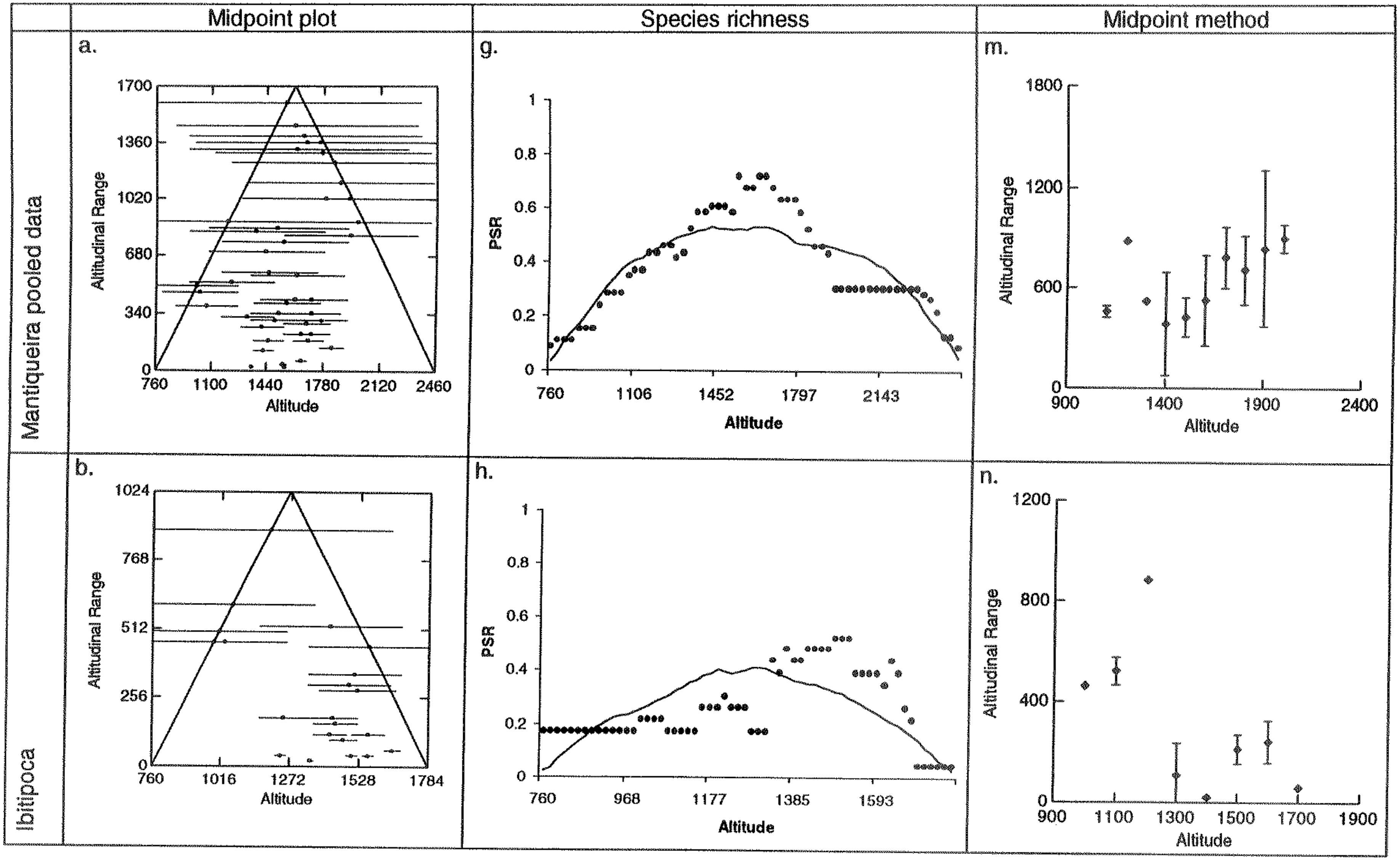
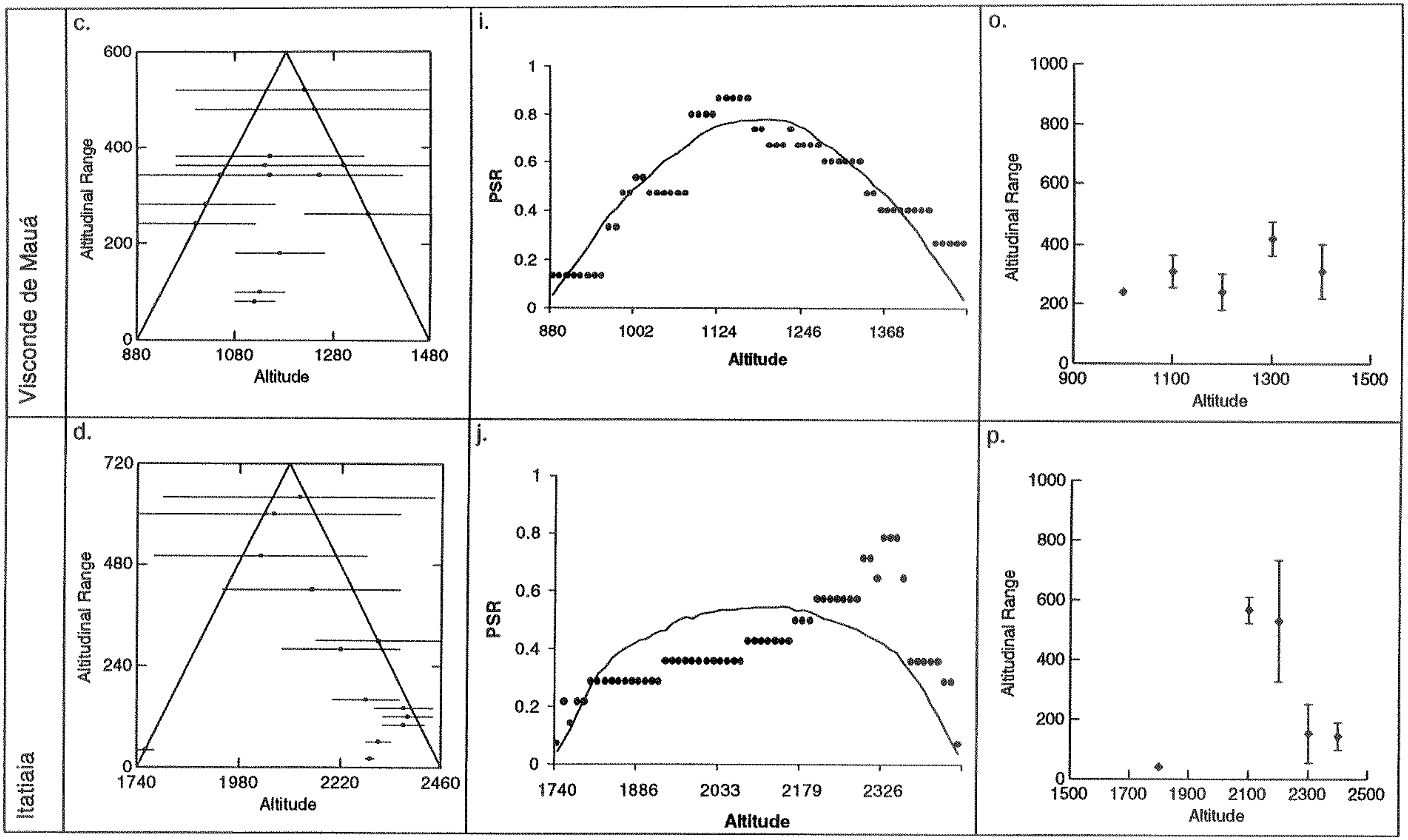


Figure 3.5. Altitudinal range of Eupatorieae host species and its endophagous insect guilds, against the number of localities they were recorded.


Midpoint plot
Species richness
Midpoint method
Mantiqueira pooled data
Ibitipoca
a.
Altitudinal Range
1700
1360
1020
680
340
0
760
1100
1440
1780
2120
2460
Altitude
g.
PSR
1
0.8
0.6
0.4
0.2
0
760
1106
1452
1797
2143
Altitude
m.
Altitudinal Range
1800
1200
600
0
900
1400
1900
2400
Altitude
b.
Altitudinal Range
1024
768
512
256
0
760
1016
1272
1528
1784
Altitude
h.
PSR
1
0.8
0.6
0.4
0.2
0
760
968
1177
1385
1593
Altitude
n.
Altitudinal Range
1200
800
400
0
900
1100
1300
1500
1700
1900
Altitude


Visconde de Mauá
Itatiaia
c.
Altitudinal Range
600
400
200
0
880
1080
1280
1480
Altitude
i.
PSR
1
0.8
0.6
0.4
0.2
0
880
1002
1124
1246
1368
Altitude
o.
Altitudinal Range
1000
800
600
400
200
0
900
1100
1300
1500
Altitude
d.
Altitudinal Range
720
480
240
0
1740
1980
2220
2460
Altitude
j.
PSR
1
0.8
0.6
0.4
0.2
0
1740
1886
2033
2179
2326
Altitude
p.
Altitudinal Range
1000
800
600
400
200
0
1500
1700
1900
2100
2300
2500
Altitude

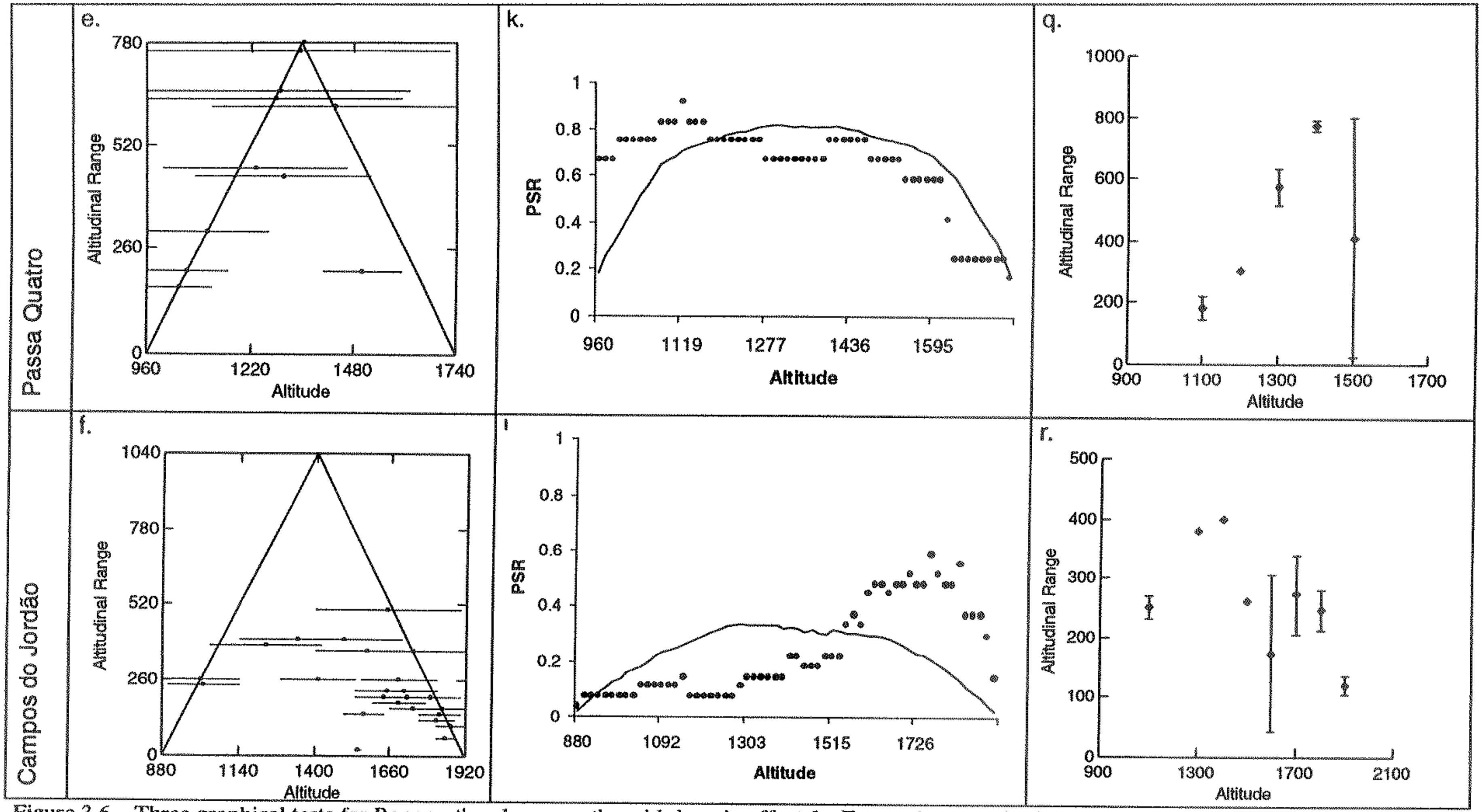


Figure 3.6. . Three graphical tests for Rapoport's rule versus the mid-domain effect for Eupatorieae species in the Mantiqueira range. See legend of Figure 3.1 for details.

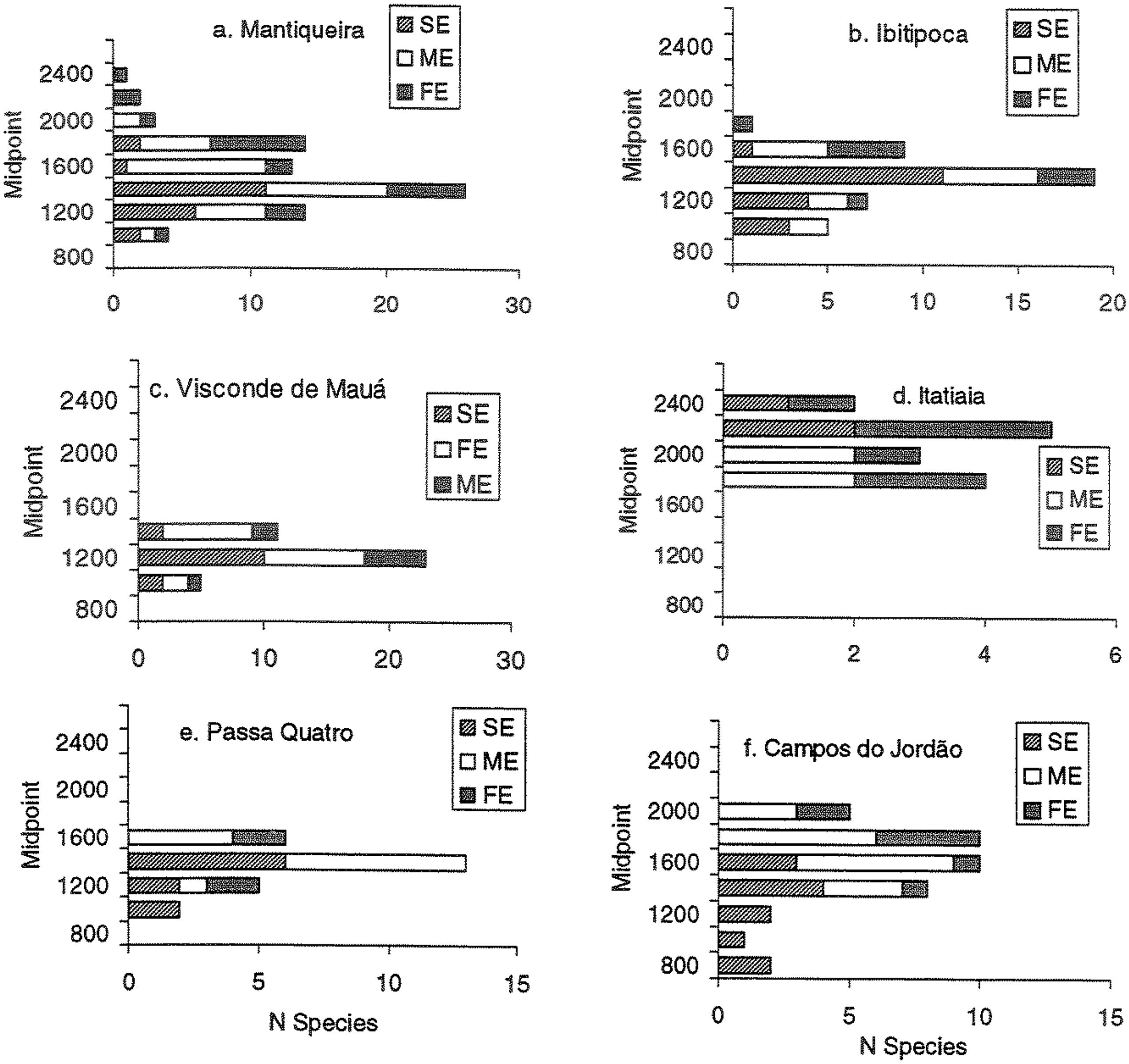
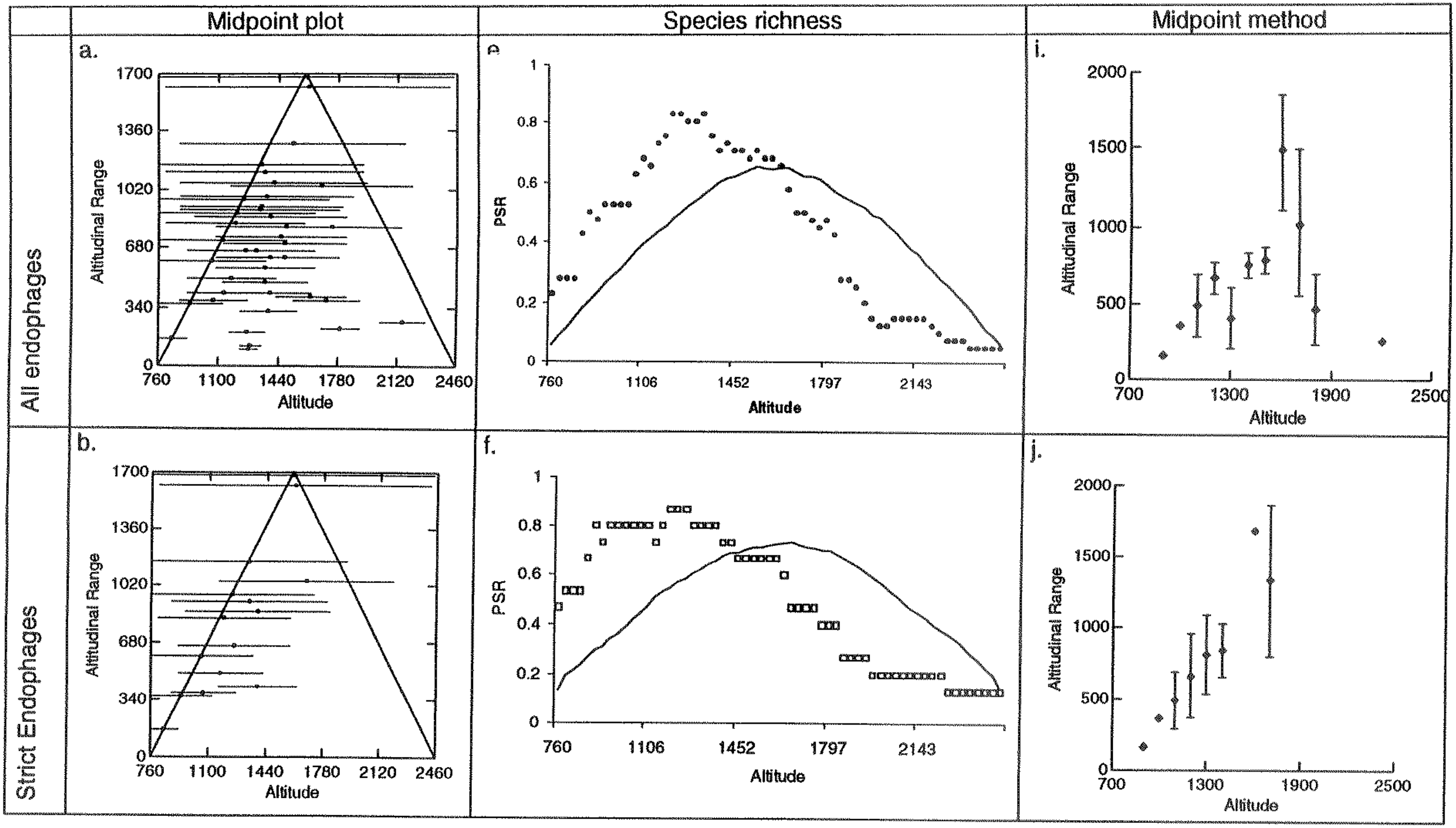


Figure 3.7. Distributions of midpoints of altitudinal distributions of flowerhead endophages showing peaks in species richness at intermediate elevations. Compare with figure 3.2b for altitudinal distribution of insect frequencies in samples, and with figure 3.1 for distribution of plants. Endophagous species are divided into feeding mode guilds.


Midpoint plot
Species richness
Midpoint method
All endophages
Strict Endophages
a.
b.
e
f.
i.
j.
Altitudinal Range
PSR
Altitude
1700
1360
1020
680
340
0
760
1100
1440
1780
2120
2460
1
0.8
0.6
0.4
0.2
1106
1452
1797
2143
2000
1500
1000
500
700
1300
1900
2500

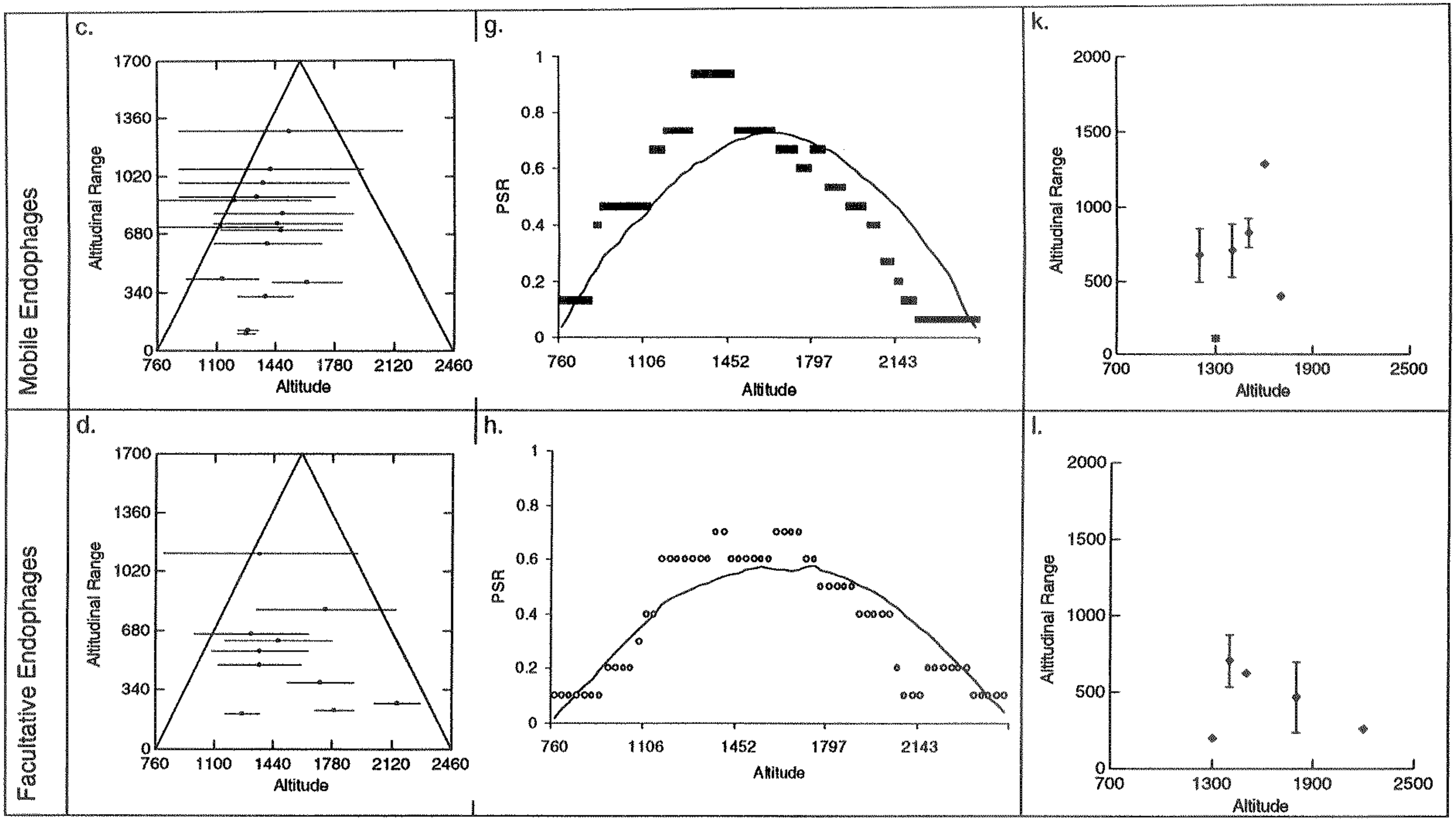
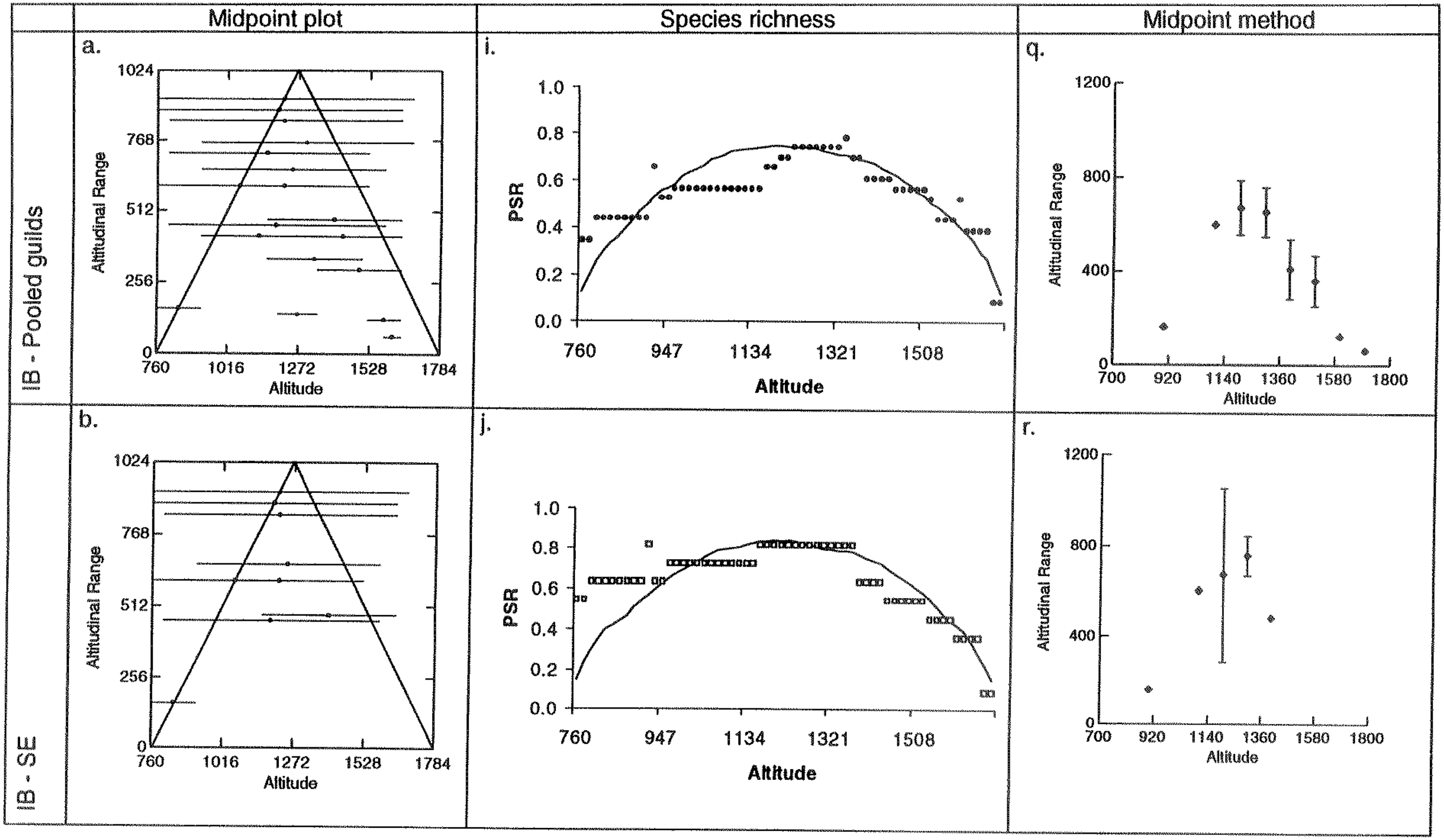
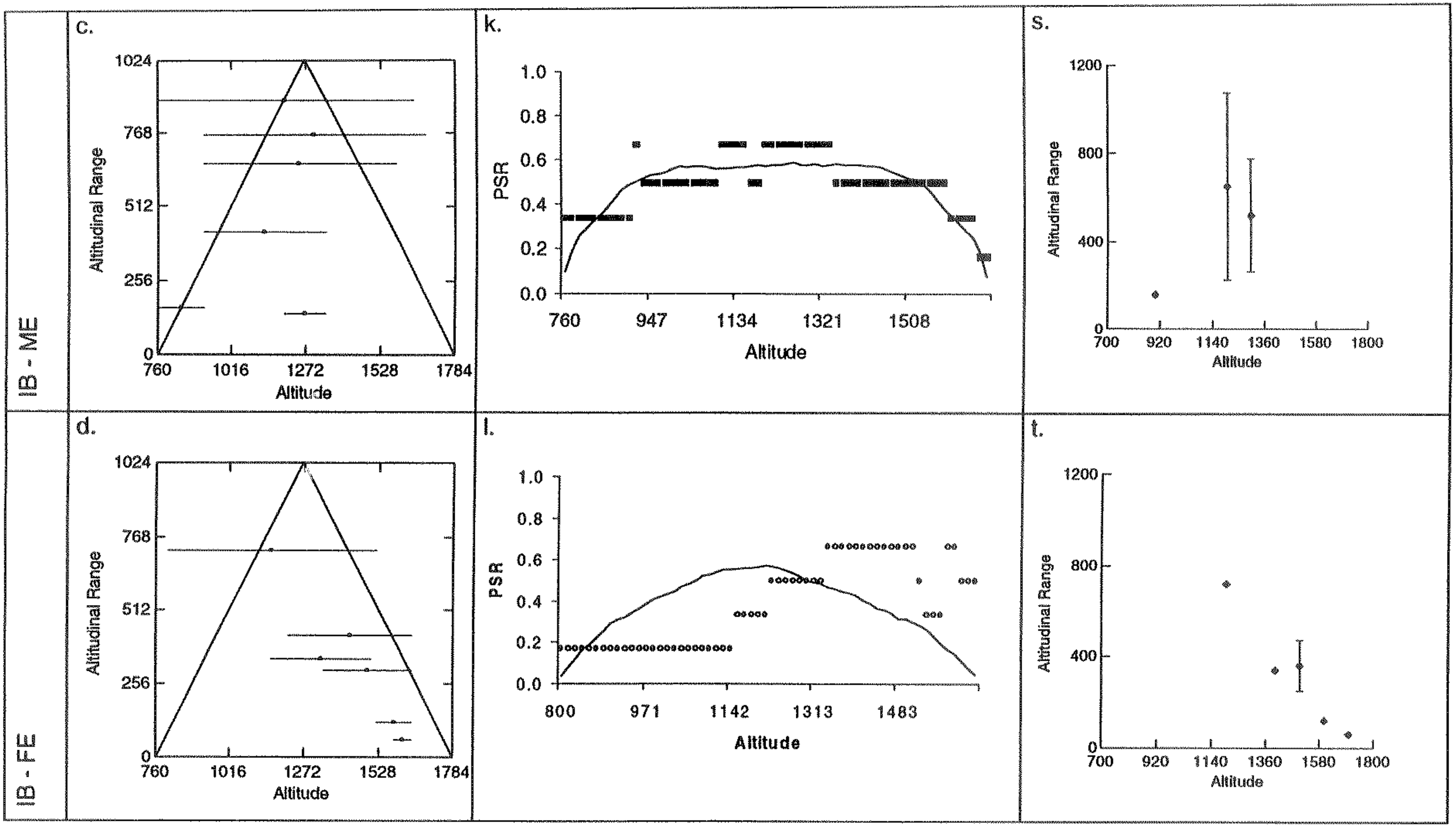
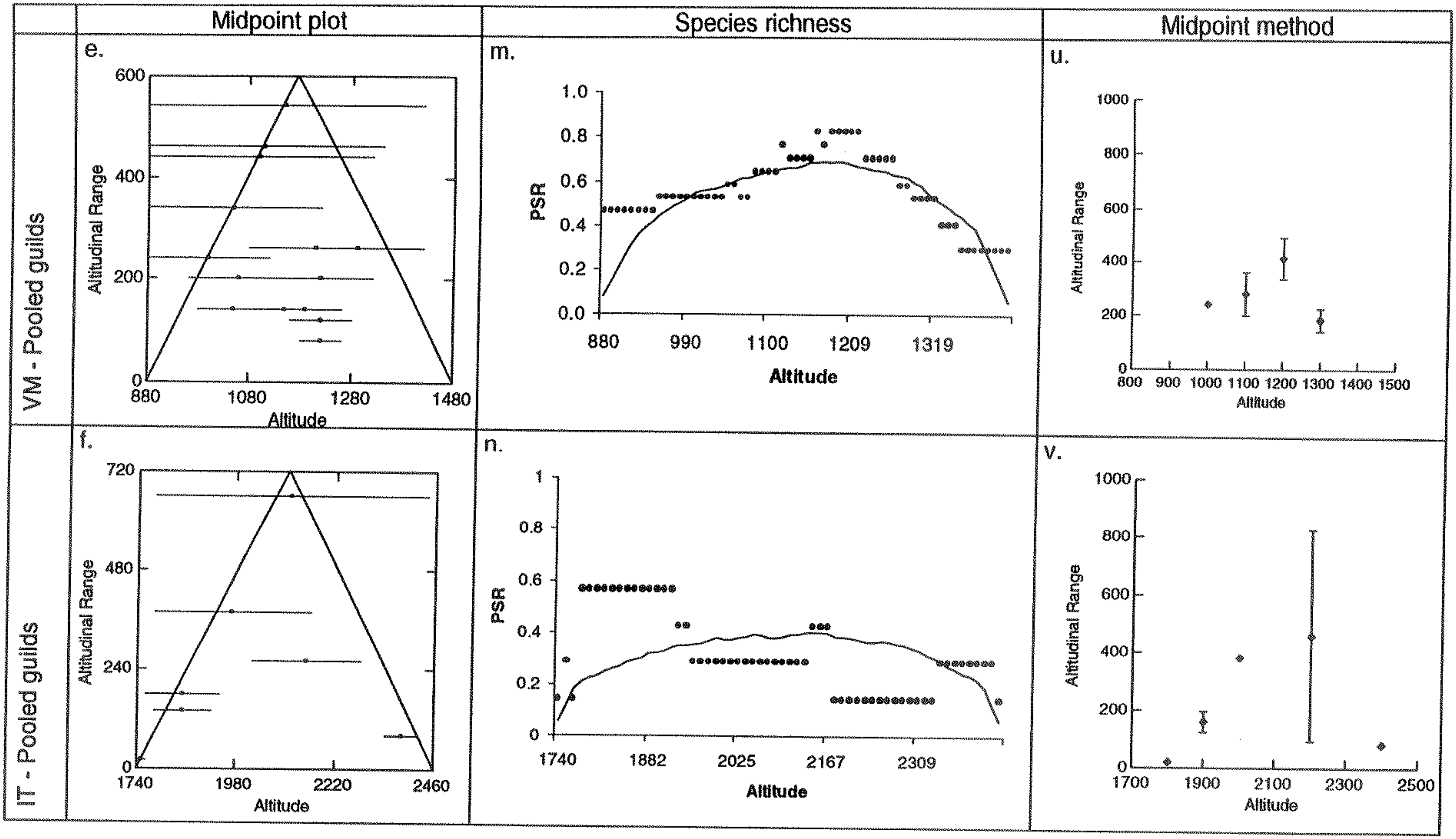


Figure 3.8. Three graphical tests for Rapoport's rule versus the mid-domain effect for flowerhead endophagous insect species in the Mantiqueira range. See legend of Figure 3.1 for details.


Midpoint plot
Species richness
Midpoint method
IB - Pooled guilds
IB - SE
a.
b.
i.
j.
q.
r.
Altitudinal Range
Altitude
PSR
1024
768
512
256
0
760
1016
1272
1528
1784
1.0
0.8
0.6
0.4
0.2
0.0
760
947
1134
1321
1508
1200
800
400
0
700
920
1140
1360
1580
1800


IB - ME
IB - FE
c.
Altitudinal Range
1024
768
512
256
0
760
1016
1272
1528
1784
Altitude
k.
PSR
1.0
0.8
0.6
0.4
0.2
0.0
760
947
1134
1321
1508
Altitude
s.
Altitudinal Range
1200
800
400
0
700
920
1140
1360
1580
1800
Altitude
d.
Altitudinal Range
1024
768
512
256
0
760
1016
1272
1528
1784
Altitude
l.
PSR
1.0
0.8
0.6
0.4
0.2
0.0
800
971
1142
1313
1483
Altitude
t.
Altitudinal Range
1200
800
400
0
700
920
1140
1360
1580
1800
Altitude


Midpoint plot
Species richness
Midpoint method
VM - Pooled guilds
IT - Pooled guilds
e.
Altitudinal Range
600
400
200
0
880
1080
1280
1480
Altitude
m.
PSR
1.0
0.8
0.6
0.4
0.2
0.0
880
990
1100
1209
1319
Altitude
u.
Altitudinal Range
1000
800
600
400
200
0
800
900
1000
1100
1200
1300
1400
1500
Altitude
f.
Altitudinal Range
720
480
240
0
1740
1980
2220
2460
Altitude
n.
PSR
1
0.8
0.6
0.4
0.2
0
1740
1882
2025
2167
2309
Altitude
v.
Altitudinal Range
1000
800
600
400
200
0
1700
1900
2100
2300
2500
Altitude

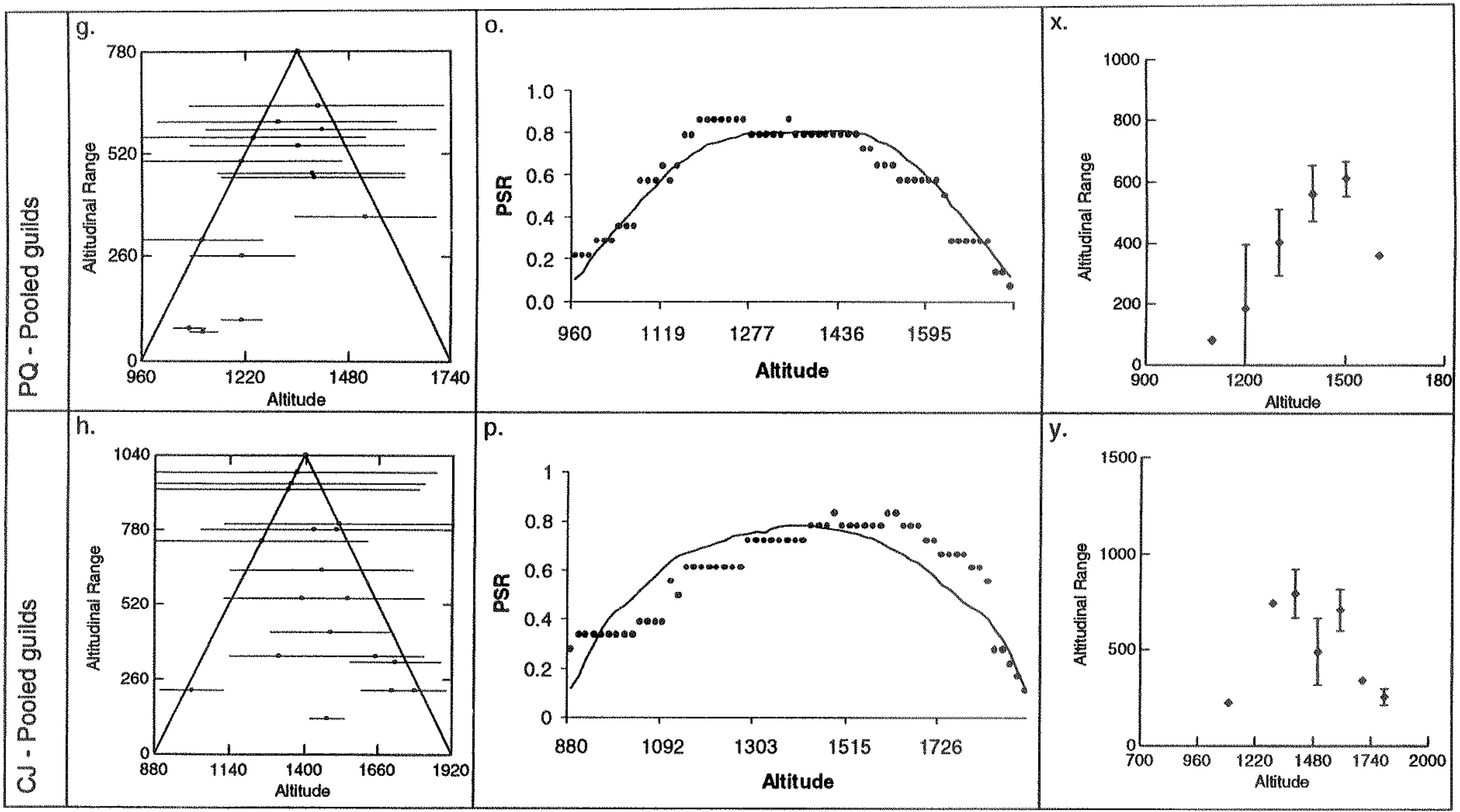


Figure 3.9. Three graphical tests for Rapoport's rule versus the mid-domain effect for flowerhead endophagous insect species in single localities within the Mantiqueira range. For Ibitipoca, graphs are also shown for each feeding guild. See legend of Figure 1 for details.

Appendix 1. Altitudinal distribution (DIST), midpoint (MID), altitudinal range (AR), altitudinal average (AVG) and number of samples for each locality. For species columns the number of localities sampled are also shown. Abbreviations for subtribes are: Ad - Adenostemmatinae; Ag - Ageratinae; Ay - Ayapaninae; Cr - Critoniinae; Eu - Eupatoriinae.

SubTb	Species	IBITIPOCA					VISCONDE DE MAUÁ				
		DIST	MID	AR	AVG	N	DIST	MID	AR	AVG	N
Ad	Adenostemma brasilianum	-					960 - 1480	1220	520	1173.3	12
Ag	Ageratum conyzoides	760 - 1640	1200	880	1224.0	6	960 - 1320	1140	360	1135.0	25
	Ageratum fastigiatum	1160 - 1680	1420	520	1493.3	30	960 - 1340	1150	380	1180.0	24
	Stevia crenulata	1360 - 1360	1360		1360.0	1	-				
Ay	Heterocondylus alatus	-					-				
	Heterocondylus amphidictyus	1360 - 1480	1420	120	1400.0	5	-				
	Heterocondylus jaraquense	1500 - 1620	1560	120	1560.0	2	-				
Cr	Ophyosporus freyreysii	-					1420 - 1420	1420		1420.0	1
	Koanophyllon thysanolepis	1540 - 1540	1540		1540.0	1	-				
Disynaphinae	Campovassouria cruciata	1200 - 1200	1200		1200.0	1	1080 - 1180	1130	100	1126.7	3
	Grazielia gaudichaudeana	1420 - 1520	1470	100	1453.3	3	-				
	Grazielia gaudichaudeana var. bipinnata	-					-				
	Grazielia intermedia	-					880 - 1220	1050	340	1110.0	8
	Symphyopappus compressus	-					1000 - 1480	1240	480	1215.0	4
	Symphyopappus cuneatus	-					-				
	Symphyopappus decussatus	1340 - 1520	1430	180	1416.0	5	1120 - 1120	1120		1120.0	1
	Symphyopappus itatiayensis	-					1220 - 1480	1350	260	1350.0	4
Eu	Austroeupatorium laetevirens	-					-				
	Austroeupatorium neglectum	-					1280 - 1280	1280		1280.0	1
	Austroeupatorium paulinum	-					1220 - 1220	1220		1220.0	1
	Austroeupatorium silphiifolium	760 - 1360	1060	600	1115.0	8	1080 - 1420	1250	340	1190.0	15
Gyptidinae	Barrosoa betonicaeformis	-					1160 - 1160	1160		1160.0	1
	Campuloclinium megacephalum	-					-				
	Campuloclinium parvulum	1680 - 1680	1680		1680.0	2	-				
	Campuloclinium purpurascens	1220 - 1260	1240	40	1240.0	3	1080 - 1420	1250	340	1196.7	6
	Trichogonia villosa	1340 - 1640	1490	300	1464.4	9	-				
	Trichogoniopsis adenantha	1340 - 1360	1350	20	1350.0	2	-				
Mikaniinae	Mikania bradei	1420 - 1420	1420		1420.0	1	-				
	Mikania campanulata	-					-				
	Mikania cordifolia	-					-				
	Mikania decumbens	1620 - 1680	1650	60	1646.7	3	-				
	Mikania elliptica	1340 - 1640	1490	300	1535.0	8	-				
	Mikania eriostrepta	-					-				
	Mikania glaziovii	-					-				
	Mikania hemisphaerica	-					1140 - 1140	1140		1140.0	1
	Mikania lasiandrae	1480 - 1520	1500	40	1493.3	3	-				
	Mikania lindbergii	1540 - 1580	1560	40	1560.0	2	-				
	Mikania micrantha	1160 - 1160	1160		1160.0	1	980 - 1320	1150	340	1141.5	13
	Mikania microcephala	-					1320 - 1320	1320		1320.0	1
	Mikania microdonta	1480 - 1480	1480		1480.0	1	-				
	Mikania sessilifolia	-					-				
	Mikania sp.1	1520 - 1520	1520		1520.0	1	-				
	Mikania sp.2	-					1080 - 1080	1080		1080.0	1
Praxelinae	Chromolaena aff squalida 1	1360 - 1520	1440	160	1440.0	2	-				
	Chromolaena ascendens	1620 - 1680	1650	60	1650.0	2	-				
	Chromolaena congesta	1340 - 1784	1562	444	1509.5	11	-				
	Chromolaena decumbens	1620 - 1620	1620		1620.0	1	-				
	Chromolaena hookeriana	760 - 1220	990	460	926.7	3	1080 - 1260	1170	180	1166.7	4
	Chromolaena laevigata	1160 - 1340	1250	180	1231.4	7	1120 - 1480	1300	360	1304.0	5
	Chromolaena maximilianii	760 - 1260	1010	500	965.0	4	880 - 1160	1020	280	1006.7	3
	Chromolaena minasgeraiensis	-					-				
	Chromolaena multiflosculosa	1340 - 1680	1510	340	1512.0	15	-				
	Chromolaena pedalis	1380 - 1660	1520	280	1506.0	10	1080 - 1080	1080		1080.0	1
	Chromolaena squalida	800 - 1260	1030	460	1055.0	4	1080 - 1160	1120	80	1120.0	2
	Praxelis clematidea	-					880 - 1120	1000	240	1000.0	7
	Total	760 - 1784	1272	1024	1414.5	157	880 - 1480	1180	600	1162.7	144

Appendix 1. Continued.

SubTb	Species	ITATIAIA					PASSA QUATRO				
		DIST	MID	AR	AVG	N	DIST	MID	AR	AVG	N
Ad	Adenostemma brasilianum	-					-				
Ag	Ageratum conyzoides	-					960 - 1620	1290	660	1141.0	11
	Ageratum fastigiatum	1780 - 2280	2030	500	2030.0	2	1120 - 1740	1430	620	1339.0	11
	Stevia crenulata	-				1	-				
Ay	Heterocondylus alatus	1920 - 1920	1920		1920.0	1	-				
	Heterocondylus amphidictyus	-					-				
	Heterocondylus jaraquense	-					-				
Cr	Koanophyllon thysanolepis	-					-				
	Ophyosporus freyreysii	-					-				
Disynaphinae	Campovassouria cruciata	2320 - 2440	2380	120	2385.0	4	1600 - 1600	1600		1600.0	1
	Grazielia gaudichaudeana	1800 - 2440	2120	640	2268.0	5	-				
	Grazielia gaudichaudeana var. bipinnata	-					-				
	Grazielia intermedia	1740 - 2340	2040	600	2161.7	15	960 - 1600	1280	640	1240.0	3
	Symphyopappus compressus	2080 - 2360	2220	280	2274.0	11	-				
	Symphyopappus cuneatus	2320 - 2420	2370	100	2360.0	3	-				
	Symphyopappus decussatus	2420 - 2420	2420		2420.0	1	-				
	Symphyopappus itatiayensis	1940 - 2360	2150	420	2200.0	10	1000 - 1460	1230	460	1230.0	2
Eu	Austroeupatorium laetevirens	-					1160 - 1160	1160		1160.0	1
	Austroeupatorium neglectum	2280 - 2300	2290	20	2290.0	2	-				
	Austroeupatorium paulinum	2160 - 2460	2310	300	2324.0	7	-				
	Austroeupatorium silphiifolium	1760 - 2360	2060	600	1967.5	8	960 - 1740	1350	780	1364.0	11
Gyptidinae	Barrosoa betonicaeformis	-					-				
	Campuloclinium megacephalum	-					-				
	Campuloclinium parvulum	-					-				
	Campuloclinium purpurascens	1780 - 1780	1780		1780.0	1	1080 - 1520	1300	440	1244.0	5
	Trichogonia villosa	-					-				
	Trichogoniopsis adenantha	-					-				
Mikaniinae	Mikania bradei	-					-				
	Mikania campanulata	2280 - 2340	2310	60	2312.0	5	-				
	Mikania cordifolia	-					-				
	Mikania decumbens	-					-				
	Mikania elliptica	-					1160 - 1160	1160		1160.0	1
	Mikania eriostrepta	-					-				
	Mikania glaziovii	2340 - 2340	2340		2340.0	1	-				
	Mikania hemisphaerica	-					-				
	Mikania lasiandrae	1740 - 1740	1740		1740.0	1	1400 - 1600	1500	200	1500.0	4
	Mikania lindbergii	-					-				
	Mikania micrantha	2200 - 2360	2280	160	2280.0	3	960 - 1620	1290	660	1246.7	4
	Mikania microcephala	2300 - 2440	2370	140	2360.0	5	-				
	Mikania microdonta	-					1160 - 1160	1160		1160.0	1
	Mikania sessilifolia	-					-				
	Mikania sp.1	-					-				
	Mikania sp.2	-					-				
Praxelinae	Chromolaena aff squalida 1	-					-				
	Chromolaena ascendens	-					-				
	Chromolaena congesta	-					-				
	Chromolaena decumbens	-					-				
	Chromolaena hookeriana	-					-				
	Chromolaena laevigata	1740 - 1780	1760	40	1766.7	3	960 - 1720	1340	760	1360.0	7
	Chromolaena maximilianii	-					960 - 1120	1040	160	1050.0	4
	Chromolaena minasgeraiensis	-					-				
	Chromolaena multiflosculosa	-					-				
	Chromolaena pedalis	-					-				
	Chromolaena squalida	-					960 - 1160	1060	200	1060.0	2
	Praxelis clematidea	-					960 - 1260	1110	300	1085.6	9
	Total	1740 - 2460	2100	720	2196.1	89	960 - 1740	1350	780	1248.8	77

Appendix 1. Continued.

SubT b	Species	CAMPOS DO JORDÃO					SPECIES					
		DIST	MID	AR	AVG	N	DIST	MID	AR	MT	AVG	N
Ad	Adenostemma brasilianum	-					960 - 1480	1220	520	1	1173.3	12
Ag	Ageratum conyzoides	1040 - 1420	1230	380	1188.0	5	760 - 1640	1200	880	4	1152.5	47
	Ageratum fastigiatum	1400 - 1760	1580	360	1528.6	7	960 - 2280	1620	1320	5	1387.3	74
	Stevia crenulata	1540 - 1540	1540		1540.0	1	1360 - 1540	1450	180	3	1450.0	3
Ay	Heterocondylus alatus	-					1920 - 1920	1920		1	1920.0	1
	Heterocondylus amphidictyus	-					1360 - 1480	1420	120	1	1400.0	5
	Heterocondylus jaraquense	1560 - 1920	1740	360	1782.2	9	1500 - 1920	1710	420	2	1741.8	11
Cr	Koanophyllon thysanolepis	1620 - 1820	1720	200	1753.3	3	1540 - 1820	1680	280	2	1700.0	4
	Ophyosporus freyreysii	-					1420 - 1420	1420		1	1420.0	1
Disynaphinae	Campovassouria cruciata	1560 - 1820	1690	260	1645.0	4	1080 - 2440	1760	1360	5	1715.4	13
	Grazielia gaudichaudeana	-					1420 - 2440	1930	1020	2	1962.5	8
	Grazielia gaudichaudeana var. bipinnata	1760 - 1900	1830	140	1830.0	2	1760 - 1900	1830	140	1	1830.0	2
	Grazielia intermedia	1400 - 1900	1650	500	1660.0	16	880 - 2340	1610	1460	4	1670.0	42
	Symphyopappus compressus	1660 - 1820	1740	160	1745.0	4	1000 - 2360	1680	1360	3	1921.1	19
	Symphyopappus cuneatus	1540 - 1740	1640	200	1640.0	2	1540 - 2420	1980	880	2	2072.0	5
	Symphyopappus decussatus	-					1120 - 2420	1770	1300	3	1517.1	7
	Symphyopappus itatiayensis	-					1000 - 2360	1680	1360	3	1755.0	16
Eu	Austroeupatorium laetevirens	-					1160 - 1160	1160		1	1160.0	1
	Austroeupatorium neglectum	1760 - 1880	1820	120	1820.0	2	1280 - 2300	1790	1020	3	1900.0	5
	Austroeupatorium paulinum	1700 - 1900	1800	200	1833.3	3	1220 - 2460	1840	1240	3	2037.8	11
	Austroeupatorium silphiifolium	1300 - 1700	1500	400	1460.0	5	760 - 2360	1560	1600	5	1383.6	47
Gyptidinae	Barrosoa betonicaeformis	1820 - 1920	1870	100	1888.0	5	1160 - 1920	1540	760	2	1766.7	6
	Campuloclinium megacephalum	1540 - 1760	1650	220	1650.0	2	1540 - 1760	1650	220	1	1650.0	2
	Campuloclinium parvulum	-					1680 - 1680	1680		1	1680.0	2
	Campuloclinium purpurascens	1500 - 1640	1570	140	1560.0	3	1080 - 1780	1430	700	5	1314.1	18
	Trichogonia villosa	-					1340 - 1640	1490	300	1	1464.4	9
	Trichogoniopsis adenantha	-					1340 - 1360	1350	20	1	1350.0	2
Mikaniinae	Mikania bradei	-					1420 - 1420	1420		1	1420.0	1
	Mikania campanulata	1540 - 1540	1540		1540.0	1	1540 - 2340	1940	800	2	2183.3	6
	Mikania cordifolia	1280 - 1540	1410	260	1373.3	3	1280 - 1540	1410	260	1	1373.3	3
	Mikania decumbens	-					1620 - 1680	1650	60	1	1646.7	3
	Mikania elliptica	1740 - 1740	1740		1740.0	1	1160 - 1740	1450	580	3	1518.0	10
	Mikania eriostrepta	1600 - 1780	1690	180	1690.0	2	1600 - 1780	1690	180	1	1690.0	2
	Mikania glaziovii	-					2340 - 2340	2340		1	2340.0	1
	Mikania hemisphaerica	-					1140 - 1140	1140		1	1140.0	1
	Mikania lasiandrae	1600 - 1820	1710	220	1700.0	8	1400 - 1820	1610	420	4	1613.8	16
	Mikania lindbergii	1820 - 1880	1850	60	1860.0	3	1540 - 1880	1710	340	2	1740.0	5
	Mikania micrantha	-					960 - 2360	1660	1400	4	1278.9	21
	Mikania microcephala	-					1320 - 2440	1880	1120	2	2152.0	6
	Mikania microdonta	-					1160 - 1480	1320	320	2	1320.0	2
	Mikania sessilifolia	1540 - 1560	1550	20	1550.0	2	1540 - 1560	1550	20	1	1550.0	2
	Mikania sp.1	1560 - 1560	1560		1560.0	1	1520 - 1560	1540	40	2	1540.0	2
	Mikania sp.2	-					1080 - 1080	1080		1	1080.0	1
Praxelinae	Chromolaena aff. squalida 1	1760 - 1760	1760		1760.0	1	1360 - 1760	1560	400	2	1546.7	3
	Chromolaena ascendens	1760 - 1920	1840	160	1854.3	7	1620 - 1920	1770	300	2	1808.9	9
	Chromolaena congesta	1760 - 1900	1830	140	1810.0	4	1340 - 1900	1620	560	2	1589.6	15
	Chromolaena decumbens	-					1620 - 1620	1620		1	1620.0	1
	Chromolaena hookeriana	-					760 - 1260	1010	500	2	1046.7	7
	Chromolaena laevigata	1140 - 1540	1340	400	1355.6	9	960 - 1780	1370	820	5	1360.0	31
	Chromolaena maximilianii	900 - 1140	1020	240	1020.0	2	760 - 1260	1010	500	4	1009.2	13
	Chromolaena minasgeraiensis	1140 - 1140	1140		1140.0	2	1140 - 1140	1140		1	1140.0	2
	Chromolaena multiflosculosa	-					1340 - 1680	1510	340	1	1512.0	15
	Chromolaena pedalis	1560 - 1920	1740	360	1760.0	5	1080 - 1920	1500	840	3	1558.8	16
	Chromolaena squalida	-					800 - 1260	1030	460	3	1072.5	8
	Praxelis clematidea	880 - 1140	1010	260	1064.0	5	880 - 1260	1070	380	3	1051.9	21
	Total	880 - 1920	1400	1040	1611.2	129	760 - 2460	1610	1700	5	1479.6	596

Appendix 3.2. Eupatorieae flowerhead herbivores listed by feeding strategy guild and collection locality. Altitudinal distribution (DIST), Midpoint (MID), and altitudinal range (AR) are shown per locality. See methods for guild description.

GUILD	SPECIES	IBITIPOCA			VISC. DE MAUA			ITATIAIA			PASSA QUATRO		
		DIST	MID	AMP	DIST	MID	AMP	DIST	MID	AMP	DIST	MID	AMP
Strict Endophages	Xanthaciura biocellata	800 - 1640	1220	840	880 - 1220	1050	340	2340 - 2420	2380	80	1150 - 1620	1385	470
	Xanthaciura chrysura	760 - 1640	1200	880	880 - 1420	1150	540	1780 - 2440	2110	660	960 - 1740	1350	780
	Melanagromyza sp.	760 - 1680	1220	920	880 - 1420	1150	540	-			960 - 1260	1340	300
	Xanthaciura chrysura sp.2	800 - 1260	1190	460	1160 - 1160	1160		-			1620 - 1620	810	
	Neo paulensis	920 - 1520	1220	600	1160 - 1280	1220	120	-			1160 - 1260	1210	100
	Cecidochares fluminensis	760 - 920	840	160	980 - 980	980		-			1040 - 1120	1080	80
	Trupanea sp.1	760 - 1360	1060	600	1160 - 1160	1160		-			1080 - 1720	1400	640
	Xanthaciura quadrisetosa	1160 - 1640	1400	480	960 - 1160	1060	200	-			960 - 1520	1240	560
	Trupanea sp.2	760 - 1360	1060	600	1180 - 1260	1220	80	-			1360 - 1360	1360	
	Xanthaciura mallochi	760 - 920	840	160	-			-			-		
	Cecidochares conex	920 - 1580	1250	660	1160 - 1160	1160		-			-		
	Xanthaciura sp5	1260 - 1260	1260		880 - 880	880		-			-		
	Trupanea sp.3	1360 - 1360	1360		-			-			-		
	Trupanea sp.4	1360 - 1360	1360		-			-			-		
	Trupanea sp.6	-			-			-			-		
	Cecidochares E	920 - 920	920		-			-			-		
	Xanthaciura chys1	1580 - 1580	1420		1160 - 1160	1160		-			-	810	
	Xanthaciura sp6	-			1160 - 1160	1160		2200 - 2200	2200		-		
	Diseuaresta sp.	-			1160 - 1160	1160		-			-		
	Trupanea sp.5	1220 - 1220	1220		-			-			-		
	Trupanea sp.8	1360 - 1360	1360		-			-			-		
	Trupanea sp.9	1360 - 1360	1360		-			-			-		
Mobile Endophages	Phalonidia unguifera (Tort.)	920 - 1680	1300	760	880 - 1420	1150	540	1780 - 2160	1970	380	1000 - 1600	1300	600
	Adaina bipunctata (Tort.)	920 - 1580	1250	660	880 - 1420	1150	540	1740 - 1760	1750	20	960 - 1460	1210	500
	Gelechiidae sp.1	760 - 1640	1200	880	1080 - 1220	1150	140	-			1160 - 1620	1390	460
	Tortricidae sp.2	1200 - 1340	1270	140	1160 - 1420	1290	260	-			1080 - 1620	1350	540
	Tortricidae sp.7	-			880 - 1340	1110	460	1760 - 1940	1850	180	1340 - 1700	1520	360
	Tortricidae sp.1	-			-			-			1080 - 1340	1210	260
	Tortricidae sp.3	-			1160 - 1160	1160		-			1120 - 1700	1410	580
	Saphenista squalida (Tort.)	760 - 920	840	160	880 - 1120	1000	240	-			1340 - 1340	1340	
	Tortricidae sp.6	-			880 - 1320	1100	440	-			-		
	Gelechiidae sp7	-			1080 - 1080	1080		-			1440 - 1440	1440	
	Pyralidae sp.3	920 - 1340	1130	420	1000 - 1000	1000		-			1260 - 1260	1260	
	Gelechiidae sp6	-			1220 - 1220	1220		-			-		
	Pyralidae sp.2	1220 - 1220	1220		1340 - 1340	1340		-			-		
	Tortricidae sp.11	1220 - 1220	1220		1320 - 1320	1320		-			-		
	Tortricidae sp.4	1420 - 1420	1420		-			-			-		
	Gelechiidae sp.2	1420 - 1420	1420		-			-			-		
	Gelechiidae sp.3	-			1280 - 1280	1280		-			-		
	Gelechiidae sp.4	-			-			-			-		
	Gelechiidae sp.5	-			-			-			1460 - 1460	1460	
	Pterophoridae sp.	-			-			-			-		
	Pyralidae sp.1	920 - 920	920		-			-			-		
	Pyralidae sp.4	-			-			-			1160 - 1160	1160	
	Pyralidae sp.5	-			1340 - 1340	1340		-			-		
	Pyralidae sp.7	-			-			-			-		
	Pyralidae sp.8	1520 - 1520	1520		-			-			-		
	Tortricidae sp.10	-			1280 - 1280	1280		-			-		
	Tortricidae sp.12	1580 - 1580	1580		-			-			-		
	Tortricidae sp.13	-			-			-			-		
	Tortricidae sp.14	-			1160 - 1160	1160		-			-		
	Tortricidae sp.5	-			-			1740 - 1740	1740		-		
	Tortricidae sp.8	-			-			-			-		
	Tortricidae sp.9	-			-			-			-		
Facultative Endophages	Geometridae sp.6	800 - 1520	1160	720	1080 - 1340	1210	260	1780 - 1920	1850	140	1600 - 1600	1600	
	Geometridae sp4	1340 - 1640	1490	300	-			2140 - 2140	2140		-		
	Geometridae sp1	1220 - 1640	1430	420	1120 - 1260	1190	140	-			1080 - 1150	1115	70
	Geometridae sp10	1160 - 1500	1330	340	-			1780 - 1780	1780		-		
	Geometridae sp5	-			1120 - 1320	1220	200	-			-		
	Geometridae sp7	1580 - 1640	1610	60	-			-			1520 - 1520	1520	
	Geometridae sp11	1520 - 1640	1580	120	980 - 1120	1050	140	-			-		
	Geometridae sp13	1360 - 1360	1360		1160 - 1160	1160		-			-		
	Geometridae sp9	-			-			2020 - 2280	2150	260	-		
	Erora sp. (Lycaenidae)	-			-			-			-		
	Geometridae sp14	-			-			-			1160 - 1160	1160	
	Geometridae sp15	-			-			-			-		
	Geometridae sp2	1520 - 1520	1520		-			-			-		
	Geometridae sp3	-			1000 - 1000	1000		-			-		
	Geometridae sp8	-			-			-			-		
	Lycaenidae sp.1	-			-			2340 - 2340	2340		-		
	Lycaenidae sp.3	1220 - 1220	1220		-			-			-		
	Lycaenidae sp.4	-			-			2140 - 2140	2140		-		
	Lycaenidae sp.5	-			1080 - 1080	1080		-			-		
	Lycaenidae sp.6	-			-			1780 - 1780	1780		-		
	Lycaenidae sp.7	-			1120 - 1120	1120		-			-		
	Lycaenidae sp.8	-			-			-			-		
	Lycaenidae sp.9	-			-			-			-		

GUILD	SPECIES	C. DO JORDAO			MANTIQUEIRA								
		DIST	MID	AMP	DIST	NMOUNT	MID	AMP	NHSpecies	Nsubtribes	Ngenera	Nsamples	Nindividuals
Strict Endophages	Xanthaciura biocellata	880 - 1820	1350	940	800 - 2420	5	1610	1620	16	5	10	52	489
	Xanthaciura chrysura	1120 - 1920	1520	800	760 - 2440	5	1600	1680	26	9	15	84	264
	Melanagromyza sp.	880 - 1920	1400	1040	760 - 1920	5	1340	1160	11	6	8	41	231
	Xanthaciura chrysura sp.2	1420 - 1420	710		800 - 1620	5	1190	820	4	2	2	10	101
	Neo paulensis	880 - 1800	1340	920	880 - 1800	4	1340	920	6	2	4	15	75
	Cecidochares fluminensis	900 - 900	900		760 - 1120	4	940	360	3	1	1	8	36
	Trupanea sp.1	1120 - 1660	1390	540	760 - 1720	4	1240	960	9	4	6	13	35
	Xanthaciura quadrisetosa	1040 - 1820	1430	780	960 - 1820	4	1390	860	6	4	5	18	29
	Trupanea sp.2	900 - 1120	1010	220	760 - 1360	4	1060	600	5	4	4	7	21
	Xanthaciura mallochi	-			760 - 920	1	840	160	1	1	1	3	10
	Cecidochares conex	-			920 - 1580	2	1250	660	3	1	1	5	9
	Xanthaciura sp5	-			880 - 1260	2	1070	380	2	2	2	4	4
	Trupanea sp.3	-			1360 - 1360	1	1360					1	2
	Trupanea sp.4	-			1360 - 1360	1	1360					1	2
	Trupanea sp.6	1120 - 1120	1120		1120 - 1120	1	1120					1	2
	Cecidochares E	1420 - 1420	1420		920 - 1420	2	1170	500	2	1	1	2	2
	Xanthaciura chys1	-	710		1160 - 1580	2	1390	420	2	1	1	2	2
	Xanthaciura sp6	-			1160 - 2200	2	1680	1040	2	2	2	2	2
	Diseuaresta sp.	-			1160 - 1160	1	1160					1	1
	Trupanea sp.5	-			1220 - 1220	1	1220					1	1
	Trupanea sp.8	-			1360 - 1360	1	1360					1	1
	Trupanea sp.9	-			1360 - 1360	1	1360					1	1
Mobile Endophages	Phalonidia unguifera (Tort.)	1120 - 1900	1510	780	880 - 2160	5	1520	1280	22	7	11	64	202
	Adaina bipunctata (Tort.)	880 - 1860	1370	980	880 - 1860	5	1370	980	19	8	11	57	185
	Gelechiidae sp.1	880 - 1620	1250	740	760 - 1640	4	1200	880	13	7	9	26	95
	Tortricidae sp.2	1280 - 1820	1550	540	1080 - 1820	4	1450	740	10	7	9	19	29
	Tortricidae sp.7	1480 - 1820	1650	340	880 - 1940	4	1410	1060	9	6	8	22	29
	Tortricidae sp.1	1560 - 1880	1720	320	1080 - 1880	2	1480	800	3	3	3	7	14
	Tortricidae sp.3	1600 - 1820	1710	220	1120 - 1820	3	1470	700	8	6	7	9	14
	Saphenista squalida (Tort.)	1140 - 1480	1310	340	760 - 1480	4	1120	720	6	5	5	9	13
	Tortricidae sp.6	1140 - 1780	1460	640	880 - 1780	2	1330	900	6	5	5	8	10
	Gelechiidae sp7	1280 - 1700	1490	420	1080 - 1700	3	1390	620	5	5	5	6	6
	Pyralidae sp.3	-			920 - 1340	3	1130	420	3	2	3	4	5
	Gelechiidae sp6	1420 - 1540	1480	120	1220 - 1540	2	1380	320	15	7	10	30	4
	Pyralidae sp.2	-			1220 - 1340	2	1280	120	2	2	2	2	2
	Tortricidae sp.11	-			1220 - 1320	2	1270	100	2	2	2	2	2
	Tortricidae sp.4	1820 - 1820	1820		1420 - 1820	2	1620	400	2	2	2	2	2
	Gelechiidae sp.2	-			1420 - 1420		1420					1	1
	Gelechiidae sp.3	-			1280 - 1280		1280					1	1
	Gelechiidae sp.4	1820 - 1820	1820		1820 - 1820		1820					1	1
	Gelechiidae sp.5	-			1460 - 1460		1460					1	1
	Pterophoridae sp.	1420 - 1420	1420		1420 - 1420		1420					1	1
	Pyralidae sp.1	-			920 - 920		920					1	1
	Pyralidae sp.4	-			1160 - 1160		1160					1	1
	Pyralidae sp.5	-			1340 - 1340		1340					1	1
	Pyralidae sp.7	1700 - 1700	1700		1700 - 1700		1700					1	1
	Pyralidae sp.8	-			1520 - 1520		1520					1	1
	Tortricidae sp.10	-			1280 - 1280		1280					1	1
	Tortricidae sp.12	-			1580 - 1580		1580					1	1
	Tortricidae sp.13	1900 - 1900	1900		1900 - 1900		1900					1	1
	Tortricidae sp.14	-			1160 - 1160		1160					1	1
	Tortricidae sp.5	-			1740 - 1740		1740					1	1
	Tortricidae sp.8	1640 - 1640	1640		1640 - 1640		1640					1	1
	Tortricidae sp.9	1640 - 1640	1640		1640 - 1640	1	1640		1	1	1	1	1
Facultative Endophages	Geometridae sp.6	1300 - 1300	1300		800 - 1920	5	1360	1120	7	5	6	10	14
	Geometridae sp4	-			1340 - 2140	2	1740	800	3	3	3	6	13
	Geometridae sp1	-			1080 - 1640	3	1360	560	2	2	2	10	13
	Geometridae sp10	-			1160 - 1780	2	1470	620	2	2	2	7	7
	Geometridae sp5	1600 - 1600	1600		1120 - 1600	4	1360	480	5	5	5	6	6
	Geometridae sp7	1900 - 1900	1900		1520 - 1900	3	1710	380	3	3	3	4	5
	Geometridae sp11	-			980 - 1640	2	1310	660	4	3	4	5	5
	Geometridae sp13	-			1160 - 1360	2	1260	200	2	2	2	2	3
	Geometridae sp9	-			2020 - 2280	1	2150	260	2	1	1	2	2
	Erora sp. (Lycaenidae)	1680 - 1900	1790	220	1680 - 1900	1	1790	220	2	2	2	2	2
	Geometridae sp14	-			1160 - 1160		1160					1	1
	Geometridae sp15	1700 - 1700	1700		1700 - 1700		1700					1	1
	Geometridae sp2	-			1520 - 1520		1520					1	1
	Geometridae sp3	-			1000 - 1000		1000					1	1
	Geometridae sp8	1700 - 1700	1700		1700 - 1700		1700					1	1
	Lycaenidae sp.1	-			2340 - 2340		2340					1	1
	Lycaenidae sp.3	-			1220 - 1220		1220					1	1
	Lycaenidae sp.4	-			2140 - 2140		2140					1	1
	Lycaenidae sp.5	-			1080 - 1080		1080					1	1
	Lycaenidae sp.6	-			1780 - 1780		1780					1	1
	Lycaenidae sp.7	-			1120 - 1120		1120					1	1
	Lycaenidae sp.8	1820 - 1820	1820		1820 - 1820		1820					1	1
	Lycaenidae sp.9	1640 - 1640	1640		1640 - 1640		1640					1	1

CHAPTER 4

REGIONAL VARIATION OF PLANT-HERBIVORE FOOD WEBS: EUPATORIEAE (ASTERACEAE) AND THEIR FLOWERHEAD FEEDERS IN THE MANTIQUEIRA RANGE, SE BRAZIL*

> "... plants and animals remote in the scale of nature,
> are bound together by a web of complex interactions"
> (Charles Darwin, The Origin of Species, 1859

> "A man may fish with the worm that hath eat of a king,
> and eat of the fish that hath fed of that worm"
> (William Shakespeare, Hamlet)

Summary

1. Food webs are always cited as being graphical representations of who eats whom in nature. Applying a macroecological approach to the study of food webs, and consequently amplifying its spatial and temporal perspective, we can say that food webs should show graphically who eats whom, where and when in nature (and how much or how often, in quantitative webs).

2. The present study compares quantitative food webs for five localities in relation to the community of species of the Eupatorieae (Asteraceae) and the endophagous insects reared from their flower heads along two years of study in the Mantiqueira range, Southeastern Brazil. The pooled, or regional web comprises a total of 79 taxa: 39 host plant species and 40 endophagous species belonging to the Diptera and Lepidoptera. There are 252 trophic links between these taxa in the pooled web.

3. Endophagous insects, grouped into three feeding guilds converge in host plant use, dividing the upper trophic level into three subunits, which does not reflect compartmentation, though. The connectance varied among localities, but the linkage density value was fairly constant for all local compartmented webs.

4. Regional generalist species were also local generalists, presenting interactions with many host species.

5. The average dominance of the strongest interaction varied from 40% to 50% of the interactions directed to one host species, in the regional and in local webs, showing that even local generalists show preferences for a certain host.

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*Este capítulo, com pequenas modificações, será rapidamente submetido ao Journal of Animal Ecology

Introduction

Food webs depict who eats whom in nature, and are one of the key concepts in community and ecosystem ecology (Lawton, 1989). As pointed out by Martinez (1994), studying food web structure is very important to the advancement of ecology, because it improves our ability to predict and to investigate fundamental processes responsible for the structure of all ecological systems containing consumers and their trophic resources. In the decade of 1990 community ecologists expanded their focus from a local to a regional one, comparing various localities within a region, and processes such as immigration and extinction engaged more attention together with local interspecific interactions (Ricklefs & Schluter, 1993; Brown, 1995; Ricklefs, 1987). In this context, Godfray et al. (1999) and Yodzis (1993) suggested the use of food web studies in comparing localities and habitats. Applying a regional perspective to food web studies has proven useful and some studies (e.g. Beaver, 1985; Kitching, 1987; Warren, 1989; Winemiller, 1990; Closs & Lake, 1994; Sota & Mogi, 1996; Sota et al., 1998) have shown that webs show different structures in different sites or at different time of the year. We could then broaden the standard food web always-cited quotation and say that food webs show graphically who eats whom, where and when (and how much or how often, if quantitative) in nature.

Food webs are graphical structures that can also be described mathematically by a variety of parameters, calculated from web data. In the 1980s many web parameters - such as the fraction of top, intermediate and bottom species, the ratio of number of links per species (linkage density) and the fraction of links between intermediate species - were considered to be constant and independent of scale (May, 1983; Briand & Cohen, 1984; Cohen, 1989; Pimm et al., 1991). In the 90s, most patterns previously thought to be invariant were shown to be scale-dependent and more variable than previously thought. The apparent constancy was a result of the use of trophic aggregations (trophospecies instead of biological species (but see Martinez et al. (1999) for evidences on the contrary) and/or low sampling effort (Sugihara et al., 1989; Pimm et al., 1991; Martinez, 1994; Martinez & Lawton, 1995; Wilson, 1996; Bersier et al., 1999). One other web parameter, the connectance, should be considered separately for its controversial history in web descriptions. Connectance is commonly taken as the number of observed (actual) direct interactions divided by the total number of possible interactions ($C = I_A / S(S-1)$), and was considered to be scale-invariant and to decrease hyperbolically with increased species richness, so that the product $S{*}C$ would always be constant (May, 1972, 1973; Rejmánek & Starý, 1979). In systems of a given interaction strength b, model webs would be stable when the term $b{*}(SC)^{1/2}$ remained below 1. As values approached or exceeded unity, such model systems suddenly became unstable (May, 1986). The search for empirical evidence of connectance and stability led researchers to analyze food webs with high-resolution data, which showed that the connectance value is constant and approximately independent of food-web size (Lawton, 1989; Warren, 1990; Martinez, 1992). Martinez (1991) proposed a modified index, "directed connectance" ($C_d = I_A / S^2$) including cannibalism and mutual predation, which was also expected to be constant among webs with variable species number, the constant connectance hypothesis (Martinez et al., 1999). Fonseca and John (1996) proposed a metric community allometry index, instead of connectance. Community allometry is calculated from the same values of actual and possible interactions as connectance, but does not have the problems that ratios, such as connectance, entail (Fonseca & John, 1996). Apart from this controversy, connectance is still used and advocated to compare linkage complexity among food webs (Memmott et al., 1994; Martinez et al., 1999). Patterns in food webs are not yet well established, but as stated by Lawton (1995), "far from being a sign of weakness in ecology, this interplay between preliminary patterns, theoretical explanations, revision of the patterns and the need to develop new theory is entirely healthy". At this stage, researchers contribute more to the debate by providing extensive and sound field data, than by adding entirely theoretical constructs.

The earlier findings of supposedly constant connectance in communities led to speculation that this might reflect some form of internal structuring within the web, and one of the most prominent hypotheses was that larger webs would be divided into compartments. A compartmented community would show some form of internal structuring within the web itself, such that larger food webs would be divided in subunits of intense interaction, weakly linked to other such subunits (Putman, 1994), maintaining constant connectance values. In earlier studies, compartments were found only in webs spanning habitat discontinuities (Pimm & Lawton, 1980), and authors concluded that compartments were caused by a sampling artifact. In this case, the presence of compartments would then be a reflection of the concentration of interactions within each sampled habitat, and samples taken inside one habitat would not be compartmented (Pimm & Lawton, 1980). On the other hand, Raffaelli and Hall (1992) later showed the presence of compartments in the same communities which Pimm and Lawton (1980) had not detected. Today it is known that most quantitative web descriptors are not constant but scale-dependent, but the division of communities into compartments is still found, as shown by at least two more recent studies (e.g. Raffaelli & Hall, 1992; Prado, 1999).

Since the study of all members in a community is not feasible, authors restrict their efforts to a subset of strongly interacting species. Recently, several studies (Memmott et al., 1994; Müller et al., 1999; Rott & Godfray, 2000) have focused on parasitoid webs (an assemblage of hosts with similar feeding strategies, their parasitoids and hyperparasitoids where present). Three different kinds of food webs have been used for describing parasitoid webs (Memmott et al., 1994; Salvo, 1996; Godfray et al., 1999): 1. **Connectance webs** showing trophic links as binary data; 2. **Semi-quantitative webs** showing quantitative information on the relative abundance of parasitoids on different hosts (not all trophic levels are described in a quantitative form); and 3. **Quantitative webs**, where the densities of all trophic levels and links are shown in the same units.

Quantitative food webs are proving useful in applied issues. Salvo (1996) used semi-quantitative and quantitative parasitoid webs to compare communities in a gradient of impacted areas and Valladares and Salvo (1999) applied the same webs of Salvo (1996) to detect more promising control agents for pest management in Argentina. Schönrogge and Crawley (2000) used quantitative parasitoid webs to investigate the impact of alien insects on the structure of a community of gall wasps in Britain. Recently, Godfray et al. (1999) suggested the use of quantitative food webs to describe and compare local inventories of insects in the tropics.

In the present study we built five quantitative local webs for distinct mountaintops (localities) within a mountain range in Southeastern Brazil and also a regional web for the pooled localities. The study focused on the community of endophagous insect species that feeds on flower heads of Eupatorieae, the most diverse Asteraceae tribe in this mountain range. An inventory based on internal feeders is a very suitable system to study interactions, since we can ensure that all obtained herbivore adults are actually interacting with the host plant (Lewinsohn et al., 2001). Also, as stated by Godfray et al. (1999), a web focusing on internal feeders will provide a relatively self-contained subsection of the whole food web from any one habitat. Unfortunately, parasitoids were not included in the webs because the adults rearing procedure does not allow parasitoids to be related to its exact host species, since all herbivores are potential hosts within a flower head sample. When observed in detail, the regional web is a complex result of spatial variation, and it is easily seen that only parts of the regional web are present in each locality. The spatial variation in web structure is studied in the present paper. These are, to our knowledge, the first time various local quantitative webs are analyzed in a regional perspective.

Methods

Mantiqueira Range, Sampling methods, Plant Identification, Insect Rearing and Morphospecies assignment, Feeding Guilds

The same as in Chapters 2 and 3.

Food Web Parameters

Plant-herbivore food webs were described and compared using the following quantitative food web parameters:

a. Maximum Trophic Interactions (I_{max})

$I_{max} = S * (S - 1)$, where S is the number of species in the web, and does not consider cannibalism and mutual predation.

b. Actual Trophic Interactions (I_A)

Is the number of observed interactions (or links) in the web.

c. Connectance (C)

$C = I_A / I_{max}$

Fonseca and John (1996) suggested an allometric procedure to scale the number of actual interactions in relation to the size of the community, where $I_A = a\,(I_{max})^b$, or in its logarithmic form, $\ln I_A = \ln a + b \ln I_{max}$. As in any regression model, this is only applicable to a series of independent communities or samples. The regression coefficient b estimates the rate of change of I_A in relation to I_{max}. When $b = 1$, the ratio I_A / I_{max} is a constant and communities are said to be isometric; when $b>1$, the ratio I_A / I_{max} increases with increasing I_{max} or community size, so that communities are positively allometric; and, conversely, when $b<1$ they are negatively allometric (Fonseca & John, 1996).

d. Directed Connectance (C_d)

$$C_d = I_A / S^2$$

This index was proposed by Martinez (1991) and includes cannibalism and mutual predation.

Rott and Godfray (2000) used in their study a more realistic measure of connectance taking into account the trophic constraints of the species in the community. With this approach, the number of maximum possible interactions was calculated by the number of insects multiplied by the number of host plants. In this connectance calculations host plants are not considered to be able to prey on each other or on their endophagous insects, as was considered in both previous connectance parameters.

e. Linkage Density (D)

$$D = I_A / S$$

f. Interaction Dominance (Dom)

$$\text{Dom} = (\text{frequency of interactions within the most frequent link}) / I_A$$

The interaction dominance is calculated for each web and is a measure of the dominance of the most frequent link in the web.

g. Importance (Import)

$$\text{Import} = \frac{(\text{frequency of interactions within the most frequent link}) * 100}{(\text{total frequency of all interactions for the species})}$$

The interaction importance is calculated for each insect species.

In the Mantiqueira range not all sites were sampled in every trip, and the complete set of data is composed of localities with more sampling effort than others (Table 4.1), which could affect comparison of the resultant webs. To avoid sample-size effects, a subset of the data containing only samples from the two last trips (March and May, 1999), in which sampling effort was uniform throughout localities, was analyzed and then compared to the regional (pooled) web. Slight differences in number of collections in the last two trips reflect the difference in availability of flowering/fruiting species in the two trips.

Food Web Construction

The first web to be constructed was the regional one pooling data from all localities, which was then used as a blueprint for the other webs. The regional web was constructed by adding the occurrences (frequencies) of each species and interactions from the constituent webs.

Plants and insects were ordered with a correspondence analysis (CA) (Digby & Kempton, 1987), minimizing trophic link overlap in web graphics. Plant species were then grouped by taxonomic criterion (subtribe) according to King and Robinson (1987) and endophagous insects were grouped by feeding guild (chapter 2). In each of these groups, species were ordered according to their scores in the first CA axis, and received a code, which is a direct reflection of its position in the trophic level. The regional trophic web was drawn separately for each insect guild for clarity. Insects were represented by rectangles, while plants were represented by ellipses. The relative widths of the rectangles and ellipses represent the relative abundance of samples for each species within that trophic level. The relative basal widths of the wedges linking insects to plants represent the relative interaction frequency. Species abundances and interaction frequencies were measured as the number of times they were sampled. All observed interactions (links) were reproduced in the graphs and kept in analysis.

Local webs were drawn using the pooled web as a template (or blueprint), but drawing in only those links defined by the particular set of species present at the place, so that the missing components could be more easily identified. When, in a specific locality, one host plant species was present but not attacked at all, it was both kept in the web and in the calculation of web parameters.

Subtribes and guilds as subunits of each trophic level

We tested if subtribes for plant species, and endophagous feeding guilds can be considered subunits within its trophic level with a Multi-Response Permutation Procedure (MRPP) (McCune & Mefford, 1999). MRPP is a non-parametric procedure for testing the hypothesis of no difference between two or more groups, defined *a priori*. Randomized groups with the same size of original groups are created by random permutations and the average distances among their elements are compared with the distance of those *a priori* groups. The probability value expresses the likelihood of getting an average within-group distance as extreme or more extreme than the observed distance. The metric A (chance-corrected within-group agreement) measures within-group homogeneity compared to that of random assemblages. The maximum value, $A = 1$ indicates that all items are identical within groups. For groups assembled by chance, $A = 0$. According to McCune and Mefford (1999), community ecology values for A are commonly below 0.1 and an $A > 0.3$ is fairly high.

MRPP was applied to the same quantitative matrixes used for food web construction, using number of times each interaction was found, for both single localities and the regional web. The distance measure used was Relativized Euclidean distance (RED), which is similar to Euclidean distance, except that the data are normalized so that the sum of squares for each species equals one. Relative Euclidean distance excludes differences in total abundance among sample units. The range of RED is 0 to the square root of 2 given all non-negative data (McCune & Mefford, 1999). Groups were weighted by **n_i/ sum (n_i)**, as recommended for MRPP (McCune & Mefford, 1999).

We tested the presence of groups within the Eupatorieae tribe, grouping them by subtribes, and of the endophagous insects, grouping species by feeding guilds, both in local webs and in the pooled, regional web. Plants were first grouped by subtribe. Since CA scores and plant codes in web construction were correlated (r_S = -0.803, Table 4.3), we considered subtribes natural groups and used them as *a priori* subdivisions. Since MRPP does not allow a group with one individual, subtribes with only one sampled plant species (Ayapaninae, Critoniinae and Adenostemmatinae) were discarded from analysis. Similarly, in local webs, other subtribes represented by a single species were excluded from analysis.

Endophagous insects were tested for the presence of groups, considering the guilds as the *a priori* groups, since CA scores and endophagous species codes, after guild grouping were also highly correlated (r_S = -0.890, Table 4.3).

Analyses were done in PC-Ord (McCune & Mefford, 1999).

Results

THE REGIONAL QUANTITATIVE FOOD WEB

In all, we recorded 40 endophagous insect species (after excluding singletons and doubletons, see Methods) reared from 39 Eupatorieae species. A total of 606 rearing records revealed 252 distinct trophic links, from which more than half (135 trophic links, or 54%) were found only once (Table 4.2).

Among the Eupatorieae, the subtribe with more species was Praxelinae, with nine species, whereas the subtribes Ayapaninae, Critoniinae and Adenostemmatinae were represented by one species each (see chapter 1 for a complete description of Eupatorieae occurrence and distribution). A list of endophagous insect species and their Eupatorieae host plants, with number of interactions is shown in Table 4.2.

The endophagous guilds were represented by similar species numbers. The guilds of strict endophages (SE) and mobile endophages (ME) were represented by 15 species each, while the facultative endophages (FE) guild was represented by 10 species (see chapter 2 for further details on guilds occurrence and distribution).

The correspondence analysis (CA) for the regional data set (see Table 4.3 for ordination of hosts and of endophages), evinced some general patterns of interactions among Eupatorieae host plants and flowerhead endophages, and was used as a template for web construction. The subtribes Eupatoriinae and Mikaniinae were placed on one end of the gradient, nearer to most lepidopterans (guilds FE and ME). Flower heads from these subtribes are of smaller size, with up to four or five achenes, and probably do not in general supply enough food for complete development of most strict endophagous larvae. Larvae from the SE guild complete development inside a single flower head and should prefer larger flower heads, although we seldom reared species from this guild in Mikania (Table 4.2), and P. Prado (pers. comm.) has noted that a tephritid species *Neomyopites* *paulensis* is commonly found in *Mikania* in other areas. The subtribes Dysinaphinae and Praxelinae were situated at the opposing end, specifically the Praxelinae have a closer relationship to *Xanthaciura* species, the majority of the SE guild members (Tables 4.2 and 4.3).

In the regional web the insect species with the largest number of hosts was *Xanthaciura chrysura* (a tephritid strict endophage), reared from 26 host species from all sampled subtribes (Table 4.2 and Figure 4.1a). Next comes *Phalonidia unguifera*, with 22 hosts from six subtribes and *Adaina bipunctata* with 19 host plants from eight subtribes (a tortricid and a pterophorid from the mobile endophage guild, see Table 4.2 and Figure 4.1b). In the facultative endophage guild, Geometridae sp.6 and Geometridae sp.5 had the highest record host numbers, respectively seven and five host plants from five subtribes (Table 4.2 and Figure 4.1c).

The number of rearing records for each endophagous species varied from a species observed in a single sample (*Xanthaciura mallochi* (SE), with three individuals) to *Xanthaciura chrysura*, present in 84 samples (Figure 4.3a). Most trophic links were scarce, occurring only once or twice, and the most frequent association occurred 18 times between *Ageratum fastigiatum* and *Xanthaciura chrysura* (Figure 4.3b).

Almost half of the studied endophagous species were associated with plants from more than four subtribes (18 out of 40, 45%), but only 17.5% (7 out of 40) were recorded in more than 10 plant species. The maximum number of endophagous species per host species (23) was found for *Ageratum fastigiatum*, also the most frequent species, followed by *Chromolaena maximiliani* (21 endophagous species), the fourth species in number of samples. The average number of endophages per plant species was 6.5 ± 6.19 (x ± SD) and did not differ among subtribes (Kruskal-Wallis = 7.367, df= 8; p = 0.498).

LOCAL QUANTITATIVE WEBS

Among local webs, Ibitipoca had the highest species richness, with 26 plant and 30 insect species, followed by Campos do Jordão, with 25 plant and 26 insect species (Table 4.3 and Figure 4.2). The poorest locality was Itatiaia, with 15 plant and 12 insect species (Table 4.3 and Figure 4.2).

Five plants were found in all five localities: *Austroeupatorium silphiipholium* (3), *Ageratum fastigiatum* (12), *Campuloclinium purpurascens* (17), *Campovassouria cruciata* (25), and *Chromolaena laevigata* (33) (numbers in parentheses are species codes used in Figures 4.1 and 4.2 and Tables 4.2 and 4.3).

Xanthaciura chrysura, the insect species with the highest number of hosts in the regional web, also had the highest number of host plants in all local webs, varying from 7 species in Itatiaia and Passa Quatro to 12 host species in Ibitipoca (Figure 4.2).

Ibitipoca presented some particularities with regard to other localities. First, only two plants in this community, *Mikania micrantha* and *Campuloclinium parvulum*, were not attacked by endophagous insects; endophagous species associated to these species in other localities are absent in Ibitipoca. Second, we reared no individual of *Melanagromyza*, one of the most frequent endophages elsewhere (Table 4.2). In Itatiaia also no *Melanagromyza* individual was obtained, nor were the two *Trupanea* species, although several host plants were available in Itatiaia. Another anomaly in Itatiaia is that *Symphyopappus compressus*, a common host plant, was quite abundant but no endophagous species was reared from its flowerheads, although three out of seven species attacking *S. compressus* in other localities occurred in this locality. Similarly, with *Mikania lasiandrae*, although three of its six endophagous species were found on other plants, none of them were reared from its flowerheads in Itatiaia (Figure 4.2).

In Visconde de Mauá and Campos do Jordão, the few plant species not attacked by any endophagous species were locally scarce, and some of their endophages were recorded in other hosts. In Passa Quatro, no *Mikania* species was attacked by flowerhead endophages, though endophagous species recorded elsewhere from these plants were present (Figure 4.2).

QUANTITATIVE WEB DESCRIPTORS

The locality with the highest potential trophic interactions, a direct function of species richness, was Ibitipoca (I_{max} = 2970) followed by Campos do Jordão (I_{max}=2550), whereas the lowest maximum links was found in Itatiaia (I_{max}=702) (Table 4.4).

The number of endophagous species associated to host plants among the studied areas was significantly different among localities (Kruskal-Wallis = 11.701; df = 4; $p<0.05$). In the regional web the values of average endophages per host plant were much higher, and almost identical for the average number of hosts by each insect species (6.3) to the number of insects per host plant (6.5) (Table 4.4).

The number of host plants of each insect species depends on the insect guild, with far fewer plants being used by facultative endophages than by strict endophages and mobile endophages (Kruskal-Wallis = 13.01; df = 2; $p< 0.001$), but did not vary among localities (Kruskal-Wallis = 1.029; df = 4; $p > 0.90$). Regionally, mobile endophages had an average of 8.1 host plants in contrast to 6.5 hosts for each strict endophage (Table 4.4).

Connectance (C) values varied from 0.029 in Ibitipoca to 0.046 in Passa Quatro. Ibitipoca, Visconde de Mauá (C = 0.034) and Campos do Jordão (C = 0.031) showed similar connectance values, whereas Itatiaia (C = 0.044), together with Passa Quatro, formed a second group with higher connectance. The regional web connectance (C = 0.041) was similar to the higher values for local webs (Table 4.4).

The community allometry regression showed a high correlation of 0.985 and resulted in the slope value of 0.704 ($\pm$ 0.070, 1 SD), significantly different from 1, which means a negatively allometric relationship (Figure 4.4). Itatiaia, followed by Passa Quatro showed more actual interactions per possible ones (or $\ln I_A$ / $\ln I_{max}$) than the other three localities, probably because of its lower species richness.

The values of linkage density (D) in local webs showed a small variation, between 1.5 and 1.7, with an only exception for Itatiaia, where the value of D was much lower (1.15). In the regional web, the interaction density increased to 3.23 (Table 4.4). This shows that, in pooling local webs, new links among existing species are added faster than new species.

Dominance varied from four to five percent of the most frequent interaction within the web converging on one host plant in local webs, except again for Itatiaia, where the most frequent interaction (*Xanthaciura chrysura* on *Grazielia intermedia*) encompassed 15% of all recorded association events. In Ibitipoca the strongest association occurred three times each of *Ageratum fastigiatum* and *Phalonidia unguifera, Xanthaciura chrysura* and *Xanthaciura biocellata,* each of which represented 5% of the recorded associations. The dominance value in the regional web for pooled localities was even lower than for local webs, encompassing 3% of the web interactions and was found for *X. chrysura* and *A. fastigiatum.* The absence of very frequent interactions (strong links) shows that interactions are diluted throughout the web in the Mantiqueira range, except in Itatiaia (see also Figure 4.2).

For the insects, the average importance of interactions varied from 41% to 54% of associations in samples directed to a particular host, in Passa Quatro together with Campos do Jordão and Ibitipoca, respectively (Table 4.4). The values of importance for endophagous insect species were significantly different among guilds (Kruskal-Wallis = 8.047; df = 2; $p < 0.05$) but not among localities (Kruskal-Wallis = 5.576; df = 4; $p > 0.20$), with strict endophagous species presenting significantly higher values (59.209 ± 17.000) than mobile endophages (42.066 ± 15.488) while facultative endophages did not differ from the other two (47.010 ± 15.429).

Except for Itatiaia, in all localities and also in the regional community, feeding guilds formed distinct subunits of endophagous insects , which were associated to a subset of plant species used less by the other guilds, as shown by the MRPP result (Table 4.5). Visconde de Mauá showed the highest values of A for both endophages and plants, and was the only locality to show significant subunits for plants grouped by subtribe. Itatiaia had the lowest species richness and most subtribes had a single species, so that only two subtribes could be compared; and this certainly influenced the non-significant result for this test. The fact that different guilds use different subsets of the host plants universe is not a direct indication of the presence of compartments, though.

The subset of data from the two last sampling trips, a more homogeneous data set spanning all sampling sites, showed the same patterns of the entire data set, with few exceptions (Table 4.6, compare with Table 4.4). The number of hosts per endophagous species differed among guilds (Kruskal-Wallis = 12.376, df = 2; $p < 0.05$) but not among localities (Kruskal-Wallis = 3.923, df = 4; $p > 0.40$) and the number of endophagous insects associated to each host plant did not differ among localities (Kruskal-Wallis = 7.041; df = 4; $p > 0.10$). Contrary to the entire data set, the values of connectance were higher for local webs than in the regional one. However, among localities trends were similar, with the lowest connectance in Ibitipoca and the highest values in Itatiaia and Passa Quatro (Tables 4.4 and 4.6). Community allometry also produced a negative relationship very similar to that of the entire data set ($b = 0.744$; $r^2 = 0.955$). In the last two samples dominance values were higher, varying from 6% of the recorded associations in a single link in Passa Quatro to 12% in Itatiaia, almost twice the figures in the entire data set (except for Itatiaia). As expected, the subset of samples had lower species richness in all localities, and higher connectance and dominance values, showing that there were proportionally more links among species, but that a higher frequency of records are concentrated in one link (dominance). In general, patterns in the more consistent subset of data from the last two trips were quite similar to the full data set, which can therefore be taken as a good descriptor of the system.

Discussion

This study presents the first description and comparative analysis of five local quantitative food webs and their comparison to the regional web. Food webs based on the inventory of internal feeders is the most secure form of evaluating trophic interactions (Lewinsohn et al., 2001) and also provide a relatively self-contained part of the entire food web from a given habitat (Godfray et al., 1999). The comparison of food webs with a macroecological perspective was suggested by Godfray et al. (1999) and Yodzis (1993).

Martinez et al. (1999), among others, showed that food web parameters are sensitive to sampling effort, especially in webs based on biological species, that need much more sampling effort than webs based on trophospecies. In the Mantiqueira, the quantitative web descriptors calculated for the last two sampling trips (in which sampling effort was uniform throughout localities) showed no major difference from parameters detected for the entire data set, (compare Tables 4.4 and 4.6). In the last two trips we obtained less endophagous species than in the full data set, and expected differences in connectance, since connectance and species number are expected to show a negative relation. Connectance values for the Mantiqueira are opposite to the expected, though. Since community parameters were not different between the two analyzed data sets, we will now discuss results for pooled data, used to construct the webs and summarized in Table 4.4.

Communities are not discrete and closed systems, and vary spatially and temporally with regard to local, biotic and abiotic conditions and history. Local communities can evolve different structures depending on their degree of isolation, species composition and history of colonization (Ricklefs & Schluter, 1993; Brown, 1995; Maurer, 1999). Some characteristics such as time of entry into the regional flora, taxonomic or biochemical isolation and clade membership are strongly related to plant history, and consequently will influence the community of herbivore insects in local communities (Brooks & McLennan, 1993; Farrell & Mitter, 1993). The successful establishment of a new herbivore species in a mountaintop (or other isolated area, such as an island) depends on many factors, from minimum area to maintain a viable population, to adequate climatic conditions (Bruijnzeel & Veneklaas, 1998; Safford, 1999) and genetic constraints that will restrict the insect species in the community to a subset of plant species they can eat (Brooks & McLennan, 1993; Farrell & Mitter, 1993; Thompson, 1994). Specialization has the potential to evolve in different directions among different populations of a species. The result will be a dynamic geographic mosaic created by the degree to which species are specialized to one another (Thompson, 1994).

Physiological, behavioral and even morphological restrictions of host plant use by endophagous flowerhead herbivores should result in more related species using related host plants, dividing the communities into compartments, even though these may change species composition among different localities. This is illustrated by the tephritid fly *Tephritis conura*, a flowerhead endophage with seven hosts within the genus *Cirsium* from the European Alps to Fennoscandia and with a geographically differentiated complex of populations, possibly including sibling species, adapted to different hosts (Zwölfer, 1988; Zwölfer & Romstöck-Völkl, 1991).

According to Kitching (1987), regional webs group organisms present in several localities and occasions and represent groups of species with overlapping ecologies at the population level and which have been in contact along an evolutionary time-scale. On the other hand, local webs lead to the understanding of the environment/community interactions on a more restricted scale. The simultaneous study of both local and regional webs addresses biogeographical questions, as well as the local trophic dynamics of the constituent species sets.

Recently, there has been increasing interest in compartmentation of food webs. For a community of herbivores, compartments occur when there is convergence in the use of host plants, in circumstances in which all insects in a compartment respond to the same plant characteristics (Futuyma & Gould, 1979). Two recent studies (Memmott et al., 1994; Salvo, 1996) searched for compartments in parasitoid food webs by visual inspection of connectance and concluded that the webs were not divided in subcompartments. Prado (1999) applied a procedure similar to the employed in this study to detect compartmentation to a community of endophagous tephritids associated with Vernonieae plants in the Espinhaço, the northern neighbouring range of the Mantiqueira (see chapter 1). Prado (1999) found that endophagous tephritids - grouped by guilds of host plant species use - form a highly compartmented community. He discusses this compartmentation as a consequence of specialization of endophages to the same plant species, forming natural groups, since even the few generalist species show most of their host plants in one compartment.

Two tribes of Asteraceae - Eupatorieae and Senecioneae - have palatability-affecting pyrrolizidine alkaloids (PAs) which are distinctive to each tribe (Hartmann & Witte, 1995). Although we have insufficient information until now, if different subtribes of Eupatorieae have different alkaloid composition or concentrations, subtribes could function as compartments restricting the insect species able to feed on them, from the whole community of endophagous. No such pattern is clearly discernible in the community of endophagous insects in the Mantiqueira range at this stage. Other morphological phenological differences among subtribes could entail similar differentiation among the insects. On the other hand, we did find that endophagous insects from the same guild interact more strongly and tend to use the same host plants. Endophagous insects show convergence in the use of host plants, but this was not related to the plants' subtribe classification. Other factors, such as local plant abundance, may also affect host plant use by different guilds.

The fact that endophagous insect guilds show convergence in host plant use does not necessarily mean that the community is compartmented. Compartmented communities are divided into blocks, with more interactions occurring within than among blocks. In this way, they should be easily visualized in a food web diagram and both Memmott et al. (1994) and Salvo (1996) concluded for the non-compartmentation of their food webs only on visual inspection. In the Mantiqueira range food webs, although the MRPP analysis showed that each endophagous guilds tend use different host plants, no compartments can be visualized in the web diagrams, either for the regional (Figure 4.1) or the local (Figure 4.2) webs.

Both the connectance and directed connectance of our local webs are much lower than most published webs. Martinez (1992) found an average directed connectance of 0.14 (SD = 0.06) when analyzing 175 food webs varying from 2 to 93 trophic species. Memmott et al. (2000) noted that many webs with predator top-species have directed connectance of approximately 0.1, while one well resolved parasitoid web (Martinez et al., 1999) has a directed connectance of 0.02, which is also much lower than other published webs; they surmise that parasitoid webs, in which both large and small organisms eat each other, would have an intermediate connectance in the range of 0.02 to 0.1. Salvo (1996) compared four leaf miner parasitoid webs in a gradient of disturbed areas and obtained directed connectance values varying from 0.03 to 0.1 (the last one from an agroecosystem), which agrees with Martinez (1999). On the other hand, Rott and Godfray (2000) found direct connectance values from 0.16 to 0.18 for a community of leaf miners and their parasitoids in England. As we see, hypotheses concerning connectance are not yet well established and further work is needed. The connectance of our local webs varied from 0.029 in Ibitipoca to 0.046 in Passa Quatro but our webs contain only two trophic levels and cannot be directly compared to parasitoid or predator webs.

Rott and Godfray (2000) propose that a more meaningful measure of connectance should take into account the trophic constraints of the species in the community, for example the fact that parasitoids must feed on hosts, and the hosts on plants. With this approach, Rott and Godfray (2000) obtained ditrophic connectance values in host-parasitoid associations of 0.41 and in herbivore-host associations to 0.25. This approach seems more reasonable to us, since host plants are unlikely to eat each other or their own herbivores. We applied this same approach to our data, where the connectance value for single localities varied from 0.11 in Ibitipoca to 0.19 in Passa Quatro, and to 0.16 in the regional web. This more realistic metric is directly comparable to Rott and Godfray (2000), and still substantially lower than their equivalent figure (0.25).

Connectance analysis is still controversial, and although Martinez et al. (1999) and Memmott et al. (2000) advocate their use in community studies, Fonseca and John (1996) have shown some intrinsic problems of connectance as a ratio, and suggest the use of community allometry regressions instead of the broadly used connectance parameter. Fonseca and John (1996) analyzed four published community datasets and found only one community set with isometry (slope value 1), the other three presenting negative allometry. They suggest that negative allometry can be a result of artifacts produced by sampling procedures (increasing difficulty in recording actual interactions in larger communities as stressed by Paine (1988)), or "at least partly representative of nature" (Fonseca & John, 1996), which we think will not affect good data. With the five localities in the Mantiqueira range, we obtained a slope value of 0.704, a negative allometric relationship, which means that the higher the maximum possible interactions (a simple function of species richness itself), fewer interactions will be found in the webs. Itatiaia was the locality with more actual links per maximum possible links, followed by Passa Quatro.

According to Bersier et al. (1999), while constant connectance implies that predators eat, on average, a constant proportion of the prey species available among webs of different sizes; they eat a fixed number of prey species in the case of constant link density. Equivalent to linkage density, the average number of links per species in trophic webs has also been assumed to take on constant values in webs, varying from 3-5 (Putman, 1994), or increasing with species richness with each species feeding on approximately 10% of the species in the web regardless of web size (Bengtsson & Martinez, 1996). In the Mantiqueira webs, we obtained similar linkage density values in four localities, but connectance was quite variable, suggesting that the herbivore species are in reality using a constant number and not a constant proportion of host plants in each locality. The average number of links per species varied widely in Mantiqueira local webs, some approximating the 10% rate of number of species in the web, and others not.

The only locality with a lower link density was Itatiaia. Goldwasser and Roughgarden (1997) found that a high level of sampling was necessary to reach the original values of several web properties, linkage density included. Although Itatiaia was the locality with least species richness (number of species), even when sampling effort was equalized for all localities, it still showed least linkage density. In Itatiaia, plant species also had the lowest number of associated endophagous insects, suggesting that the low value of link density is probably not a function of sampling effort, but of the low number of species present in this locality and possibly of biological constraints restricting host plant use by herbivore insects. The average number of links per species and link density will be influenced not only by species numbers, but also by the proportion of more specialist or generalist species, as we observed in Mantiqueira for the three feeding guilds.

Values of importance and dominance were lower for the regional web than for any single locality, showing that insects use more plant species overall than in any individual locality. This suggests that, for the majority of endophagous insects studied here, the number of host plants used will increase with increasing sampling localities. The importance of linkages varied from 40% to 50% of the strongest interactions per insect species directed to a single host. Although the present study shows that regional generalists are also local generalists (see also chapter 2), flowerhead endophages concentrate on a "preferred" host plant in local communities in the Mantiqueira range. This agrees with the theory of the Geographic Mosaic of Coevolution, which, broadly speaking, states that generalists will tend to be local specialists, depending on the conditions presented by the community it is inserted (Thompson, 1994).

Salvo (1996) was the first to use web parameters to analyze the environmental effects of impacted areas in two localities with different degrees of disturbance. In her study, the most disturbed area had fewer species and higher interaction strength and dominance. She discusses that the strength and dominance of interactions in a community will predict its "behaviour" after a disturbance: the deletion of a strong link in a community would result in serious effects in the community, while communities with numerous "weak" links should rapidly return to equilibrium; i.e. more resilient.

Web parameters of local webs in the Mantiqueira range proved useful in evaluating the structure and complexity of the regional assemblage and of its constituent local communities. The community allometry analysis showed that two localities show more links per species richness in the community: Itatiaia followed by Passa Quatro. In the other extreme of the community allometry analysis, we find Ibitipoca, with lowest rate of links per species number. Itatiaia is the locality with more interactions per number of species, which is a characteristic of resilience. On the other hand, interactions in this community are stronger than the ones found in the other four localities, and interaction importance is also high, which is not a characteristic of resilient communities. By the criterion of Salvo (1996) we would suggest that Itatiaia is the most impacted area. Itatiaia is a different community if compared to the other four localities, because it is at a much higher elevation, and subject to harsher climates than the other communities, which certainly limits the species able to survive and reproduce there, and is not strongly human impacted. Asteraceae are commonly found in fields and meadows, since many are very invasive and mostly heliotropic. Impacted areas should have fairly high plant richness and of their endophages, contrary to what Salvo (1996) found for agromyzid leaf miners and their host plants and parasitoids. The interpretation of food webs and their parameters must take into consideration the natural history of the focused species.

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Table 4.1. Eupatorieae voucher collections in the Mantiqueira range, per locality and field trip, showing similar sampling intensity in the last two field trips. From the total of 596 collected voucher specimens, 570 were sampled for rearing endophagous insects.

		Locality					
Field trips	Dates	IB	VM	IT	PQ	CJ	Total
1	15 - 19/02/1998		17	15	3	12	47
2	04 - 11/05/1998	25	45	10	23	27	130
3	20 - 22/06/1998	8	3				11
4	16 - 22/01/1999	28	18	1	7	14	68
5	02 - 09/03/1999	36	31	36	17	33	153
6	04 - 12/05/1999	60	30	27	27	42	187
Total		157	144	89	77	129	596

Table 4.2 (next page). Host associations recorded in the Mantiqueira range. Plant and endophagous species are listed in the same sequence as in the trophic diagrams. Code numbers are the ones used in the trophic webs. Values within the table are the number of samples in which an interaction was recorded. Value of N is the number of different associations found for each insect. Abbreviations for subtribes are: Ag - Agerantinae; Ay - Ayapaninae; Cr - Critoniinae; Ad - Adenostemmatinae.

Guild	Code	Species	Eupatoriinae				Mikaniinae							Ag		Ay	Cr	Ad	Gyptidinae						Disynaphiinae								Praxelinae									N	S
			1 Austroeupatorium neglectum	2 A.paulinum	3 A.silphiifolium	4 A.inulaefolium	5 Mikania eriostrepta	6 M.micrantha	7 M.cordifolia	8 M.lasiandrae	9 M.elliptica	10 M.decumbens	11 M.bradei	12 Ageratum fastigiatum	13 A.conyzoides	14 Heterocondylus jaraquense	15 Koanophyllon thysanolepis	16 Adenostemma brasilianum	17 Campuloclinium purpurascens	18 Trichogonia villosa	19 Campuloclinium parvulum	20 Trichogoniopsis adenantha	21 Barrosoa betonicaeformis	22 Campuloclinium megacephalum	23 Grazielia intermedia	24 Symphyopappus itatiayensis	25 Campovassouria cruciata	26 G.gaudichaudeana var.bipinnata	27 S.compressus	28 G.gaudichaudeana	29 S.decussatus	30 S.cuneatus	31 Chromolaena aff.squalida1	32 C. congesta	33 C. laevigata	34 C. pedalis	35 C. hookeriana	36 Praxelis clematidea	37 C.multiflosculosa	38 C.maximilianii	39 C.squalida		
Facultative Endophages	1	Geometridae sp.9	1		1																																					2	2
	2	Geometridae sp.7		1										2					1																							3	4
	3	Geometridae sp.1												8					2																							2	10
	4	Geometridae sp.5		1			1							2					1							1																5	6
	5	Lycaenidae sp.2		1																					1																	2	2
	6	Geometridae sp.10			1									6																												2	7
	7	Geometridae sp.11												2					1	1					1																	4	5
	8	Geometridae sp.6			3				1	1				2					1						1		1															7	10
	9	Geometridae sp.13												1																			1									2	2
	10	Geometridae sp.4			1									4																									1			3	6
Mobile Endophages	11	Tortricidae sp.1	1													2			4																							3	7
	12	Pyralidae sp.2												1					1																							2	2
	13	Tortricidae sp.11			1									1																												2	2
	14	Gelechiidae sp.7			1				1					2					1						1																	5	6
	15	Tortricidae sp. 6						2		1				2					1						1										1							6	8
	16	Tortricidae7			6			2						3					1						4	2	1		2											1		9	22
	17	Tortricidae3			1									1			1		1							1	2								1					1		8	9
	18	Tortricidae sp.2			6				1					2			1		3			1					1		2						1		1					10	19
	19	Saphenista squalida			1													1	2						2										1					2		6	9
	20	Gelechiidae sp.1			1					1	2		1	2			1		3						3		1								6			1		2	2	13	26
	21	Adaina bipunctata			9	1			1	1				5	4		1	1	6			2			1	2	1		2		2				7			8	2	1		19	57
	22	Phalonidia unguifera		2										17	1		3		8	4		2		1	9	1	1		1	2	1		1	1	1	1		3	1	2	1	22	64
	23	Tortricidae sp.4											1																1													2	2
	24	Gelechiidae sp.6											1	17			3		8						9	1	1		2						1			3		2	1	12	49
	25	Pyralidae sp.3																													1							2		1		3	4
Strict Endophages	26	Xanthaciura sp.5			2																				2																	2	4
	27	Xanthaciura quadrisetosa			1									3	9		1								1		3															6	18
	28	Melanagromyza			2									2		6			6		1	1			1										2		2	11		7		11	41
	29	Xanthaciura chrysura		4	3				1	1		1		18	7	3	1	2	2			2	3		11	1	5	1			1		1		2	1	1	2	1	5	4	26	84
	30	Trupanea sp.2			1																	2					1											1		2		5	7
	31	Xanthaciura sp.6																								1														1		2	2
	32	Trupanea sp.1			1																	2					1		1						2		2	1		2	1	9	13
	33	Xanthaciura biocellata												8		3				3		1	1	1							6	2	1		9	5	1	4	2	4	1	16	52
	34	Urophora paulensis																							2						1				5			2		1	4	6	15
	35	Xanthaciura Chrysura sp.2																									1								3					1	5	4	10
	36	Cecidochares fluminensis																																	1		1			6		3	8
	37	Cecidochares sp.E																																	1					1		2	2
	38	Xanthaciura Chrys1																																					1	1		2	2
	39	Cecidochares conexa																																					1	1	3	3	5
	40	Xanthaciura mallochi																																						3		1	3
		SUM	2	9	42	1	1	4	5	5	2	1	3	111	21	14	12	4	53	8	1	13	4	2	50	10	20	1	11	2	12	2	4	1	44	7	8	38	9	47	22	252	606

Table 4.3. Ordinations of host plants and endophages in the first axis of the correspondence analysis. Both hosts and endophages are ordered by their scores in the first axis of CA. Codes are the ranks of the species in Table 4.2 and the web figures (see Methods). Eigenvalue for Axis 1 = 0.422. Correlation between CA scores and ranks r_S (Hosts) = -0.803; r_S (Endophages) = -0.890).

Code	Score	Hosts	Code	Score	Endophages
1	481	*A.neglectum*	1	228	*Geometridae sp.9*
5	359	*M.eriostrepta*	11	178	*Tortricidae sp.1*
2	203	*A.paulininum*	2	176	*Geometridae sp.7*
17	170	*C.purpurascens*	3	162	*Geometridae sp.1*
6	157	*M.micrantha*	12	162	*Pyralidae sp.2*
12	153	*A.fastigiatum*	4	151	*Geometridae sp.5*
3	113	*A.silphiifolium*	5	151	*Lycaenidae sp.2*
7	106	*M.cordifolia*	6	133	*Geometridae sp.10*
23	100	*G.intermedia*	13	133	*Tortricidae sp.11*
8	75	*M.lasiandrae*	14	128	*Gelechiidae sp.7*
14	34	*H.jaraquense*	7	112	*Geometridae sp.11*
24	31	*S.itatiaiayensis*	26	106	*Xanthaciura sp.5*
15	14	*K.thysanolepis*	8	100	*Geometridae sp.6*
13	3	*A.conyzoides*	15	85	*Tortricidae sp.6*
16	-4	*A.brasilianum*	27	62	*X. quadrisetosa*
9	-5	*M.elliptica*	9	54	*Geometridae sp.13*
18	-13	*T.villosa*	16	48	*Tortricidae sp.7*
25	-14	*C.cruciata*	10	37	*Geometridae sp.4*
4	-16	*A.inulaefolium*	17	23	*Tortricidae sp.3*
19	-16	*C.parvulum*	18	17	*Tortricidae sp.2*
28	-38	*G.gaudichaudiana*	19	17	*S. squalida*
10	-38	*M.decumbens*	20	-2	*Gelechiidae sp.1*
27	-43	*S.compressus*	28	-6	*Melanagromyza*
31	-54	*C.aff.squalida*	21	-7	*A. bipunctata*
11	-60	*M.bradei*	29	-16	*X. chrysura*
26	-80	*G.gaudichaudiana var. bipinnata*	22	-33	*P. unguifera*
32	-80	*C.congesta*	23	-48	*Tortricidae sp.4*
20	-85	*T.adenantha*	15	-60	*Trupanea sp.2*
33	-108	*C.laevigata*	31	-71	*Xanthaciura sp.6*
34	-115	*C.pedalis*	32	-85	*Trupanea sp.1*
35	-128	*C.hookeriana*	33	-96	*X. biocellata*
21	-133	*B.betonicaeformis*	24	-108	*Gelechiidae sp.6*
36	-138	*P.clematidea*	34	-113	*N. paulensis*
37	-153	*C.multiflosculosa*	35	-122	*X. chrysura sp.2*
22	-154	*C.megacephalum*	36	-137	*C. fluminensis*
29	-169	*S.decussatus*	37	-141	*Cecidochares sp.E*
38	-175	*C.maximiliani*	25	-161	*Pyralidae sp.3*
39	-190	*C.squalida*	38	-164	*X. Chrysura sp.1*
30	-228	*S.cuneatus*	39	-173	*C. conexa*
			40	-175	*X. mallochi*

Table 4.4. Number of plant and insect species and Maximum Trophic Interactions (I_{max}), Actual Trophic Interactions (I_A), Connectance (C) (with Direct Connectance (C_d) in brackets), Linkage Density (D), Dominance (Dom), Average Importance (Import) of interactions, and average number of links per insect guild, pooled guilds and host plants, for local webs and the regional web. Numbers in parentheses are standard deviations. See Methods for formulae.

LOCALITY	Plant Species	Insect Species	I_{max}	I_A	C [C_d]	D	Dom (%)	Import	Avg links				
									FE	ME	SE	all insects	Plants
Ibitipoca	25	30	2970	87	0.0293 [0.0287]	1.582	5.063	53.716 (17.995)	1.500	3.375	3.692	3.000 (3.262)	3.954 (3.184)
Visconde de Mauá	21	29	2450	83	0.0339 [0.0332]	1.660	3.846	44.137 (14.341)	1.600	3.636	2.692	2.862 (2.489)	5.533 (3.758)
Itatiaia	15	12	702	31	0.0442 [0.0425]	1.148	15.385	49.800 (13.535)	1.600	3.000	3.500	2.583 (1.621)	2.0769 (1.498)
Passa Quatro	14	22	1260	56	0.0460 [0.0430]	1.556	4.598	44.579 (16.010)	1.333	3.000	2.667	2.636 (1.866)	5.273 (3.636)
Campos do Jordão	25	26	2550	80	0.0314 [0.0307]	1.569	4.132	41.495 (17.158)	1.000	3.583	3.800	3.360 (2.984)	4.000 (2.608)
Pooled Localities	39	40	6162	252	0.0409 [0.0404]	3.228	2.970	41.300 (17.702)	3.200	8.133	6.533	6.300 (6.189)	6.461 (5.889)

TABLE 4.5. Values of the test statistic A and associated probabilities for Multi-Response Permutation Procedure, testing for compartmentation in local and regional assemblages (see Methods). Values of A with a (*) had host species excluded from analysis because of only one species per subtribe. Values in bold are significant at $p < 0.05$.

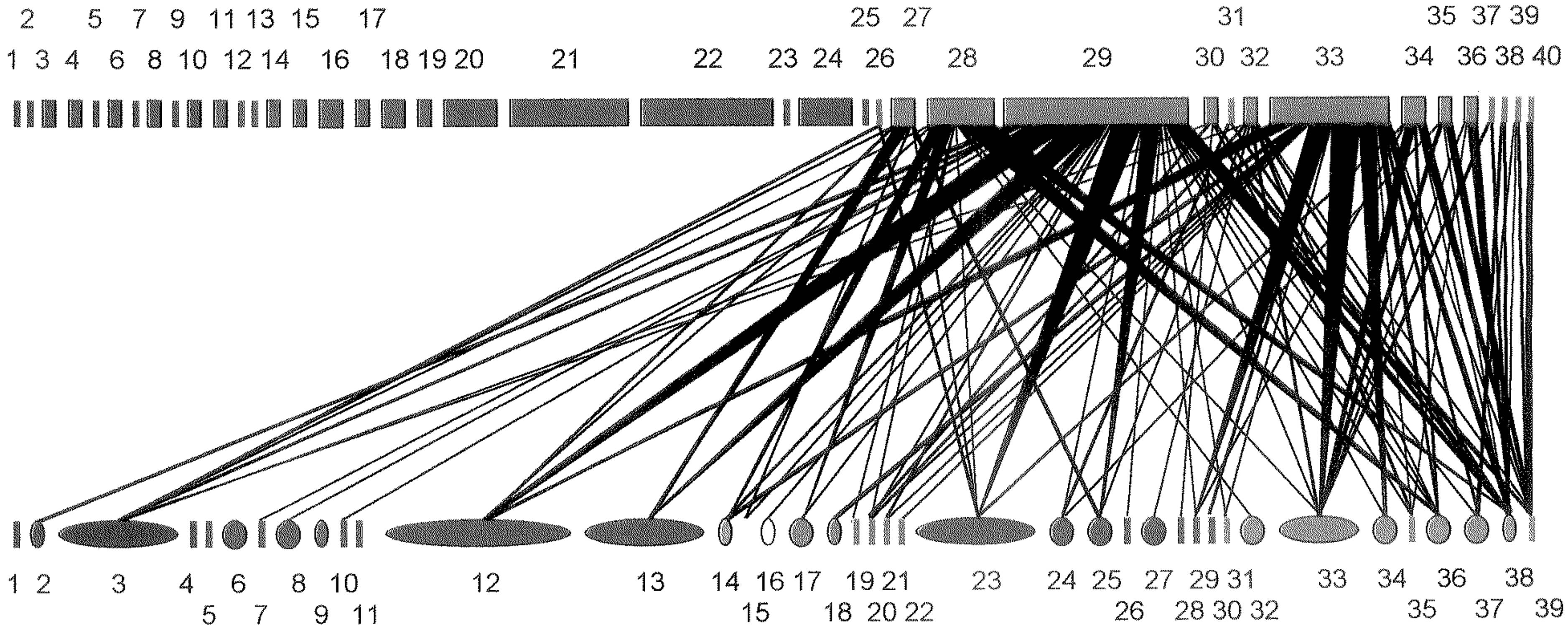
LOCALITY	Host Plant		Endophagous Species	
	A	p	A	p
Ibitipoca	0.0134 *	0.288	**0.0402**	**0.022**
Visconde de Mauá *	**0.1015 ***	**0.017**	**0.1232**	**0.000**
Itatiaia *	-0.0036 *	0.452	-0.0163	0.609
Passa Quatro *	0.0491 *	0.091	**0.0465**	**0.043**
Campos do Jordão	0.0131	0.303	**0.0374**	**0.013**
Mantiqueira	0.0199	0.122	**0.0822**	**0.000**

Table 4.6. Web parameters calculated for the last two collection trips, to homogenize collection areas. Number of plant and insect species and Maximum Trophic Interactions (I_{max}), Actual Trophic Interactions (I_A), Conectance (C) (with Direct Connectance (C_d) in brackets), Interactions Density (D), Dominance (Dom), Average Importance (Import) of interactions, and average number of links per guild, for pooled guilds and per host plants, for isolated and pooled localities. Numbers in parenthesis are standard deviations. Compare with Table 4.4. See Methods for formulae.

LOCALITY	Plant Species	Insect Species	I_{max}	I_A	C	D	Dom	Import	Avg links				
					[C_d]		(%)		FE	ME	SE	all insects	Plants
Ibitipoca	19	24	1806	67	0.0371	1.558	11.258	43.570	1.125	5.800	2.636	2.792	3.526
					[0.0362]			(20.987)	(0.353)	(7.563)	(3.042)	(4.118)	(2.480)
Visconde de	16	22	1406	62	0.0441	1.632	6.838	49.460	1.500	4.375	2.100	2.818	4.133
Mauá					[0.0429]			(19.150)	(0.577)	(4.534)	(1.663)	(3.096)	(3.440)
Itatiaia	15	10	600	30	0.0500	1.200	12.346	44.400	1.333	6.333	1.750	3.000	2.000
					[0.048]			(13.720)	(0.577)	(7.505)	(0.957)	(4.269)	(0.926)
Passa Quatro	13	20	1056	54	0.0511	1.636	6.316	45.066	1.500	3.200	2.375	2.700	4.154
					[0.0496]			(16.233)	(0.707)	(3.676)	(1.188)	(2.697)	(2.734)
Campos do	21	22	1806	72	0.0399	1.674	8.088	41.800	1.500	4.100	2.800	3.273	3.600
Jordão					[0.0389]			(15.560)	(0.707)	(5.782)	(2.573)	(4.233)	(2.062)
Pooled	36	36	5112	184	0.0360	2.556	6.034	42.200	2.200	7.580	5.070	5.111	5.111
Localities					[0.0355]			(15.667)	(0.920)	(9.390)	(5.570)	(6.632)	(4.301)

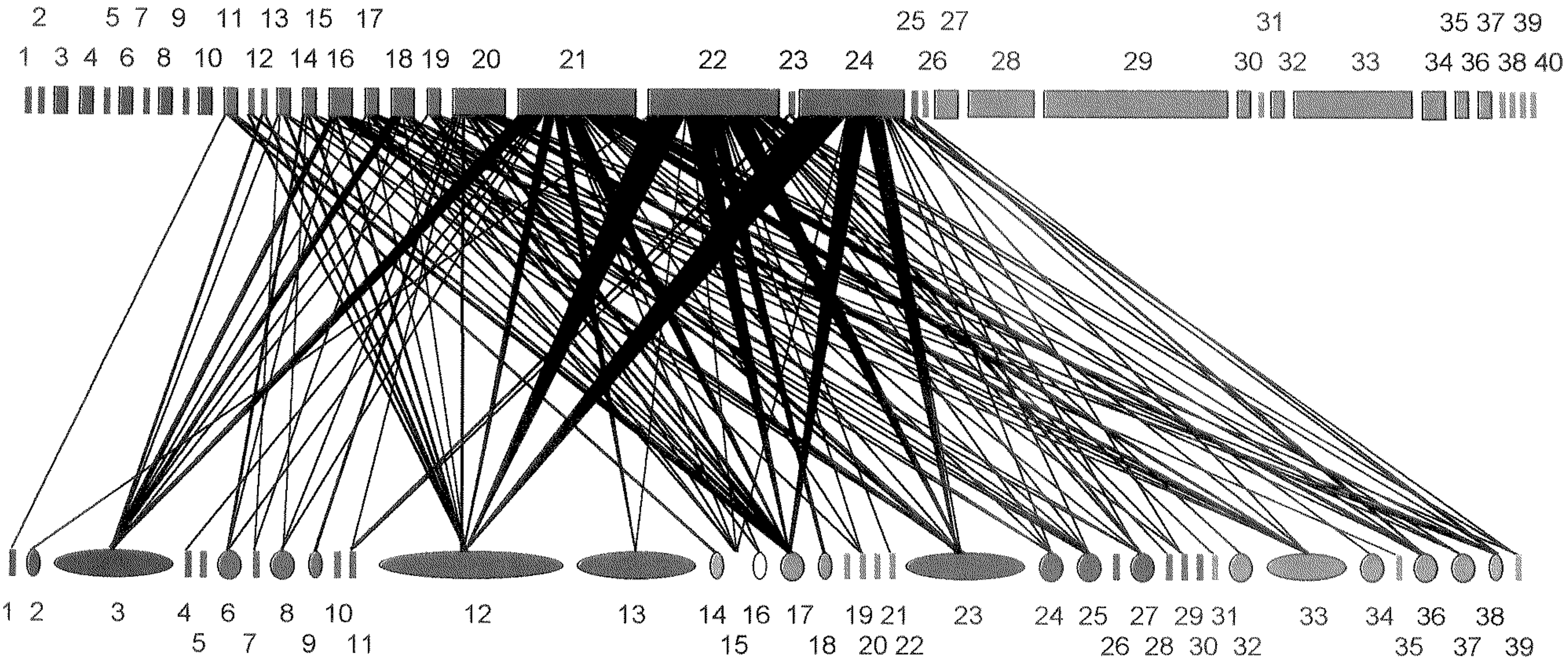
4.1a.

Strict Endophages (547 plant samples and 606 endophages records)



4.1b.

Mobile Endophages (547 plant samples and 606 endophages records)



4.1c.

Facultative Endophages (547 plant samples and 606 endophages records)

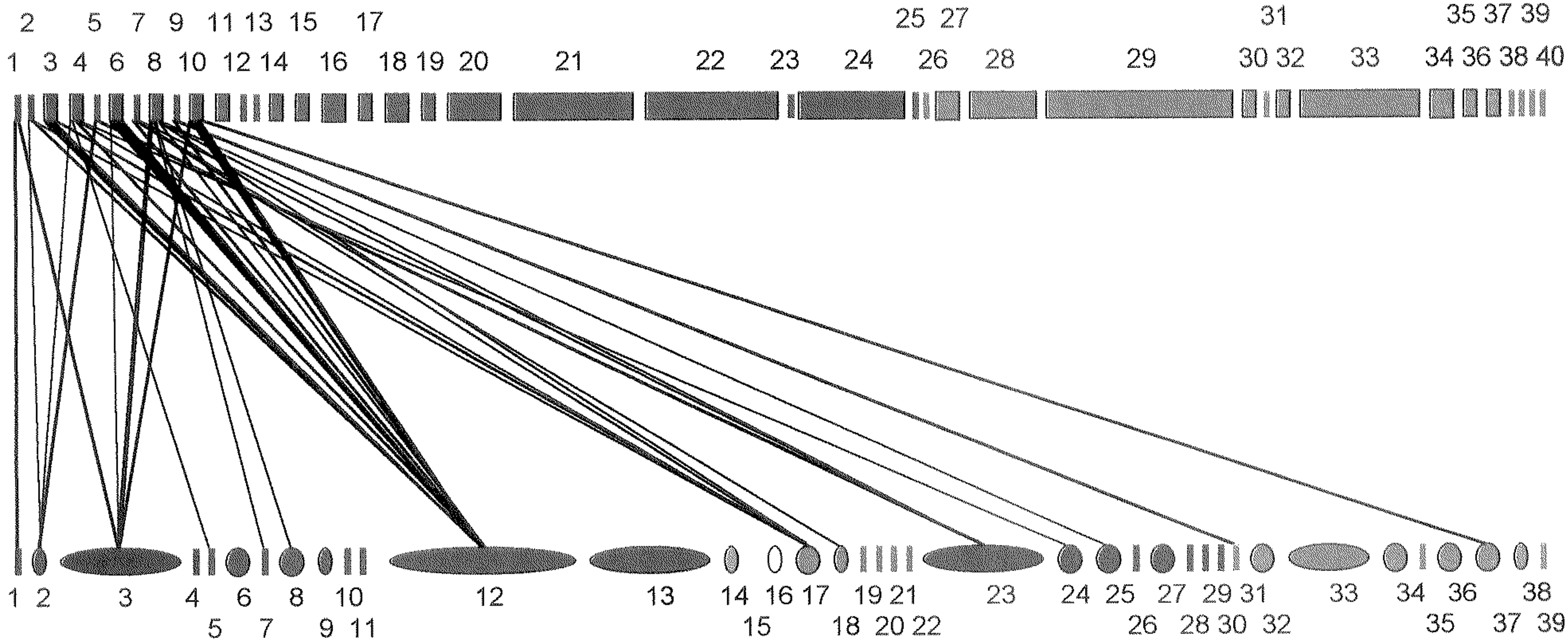
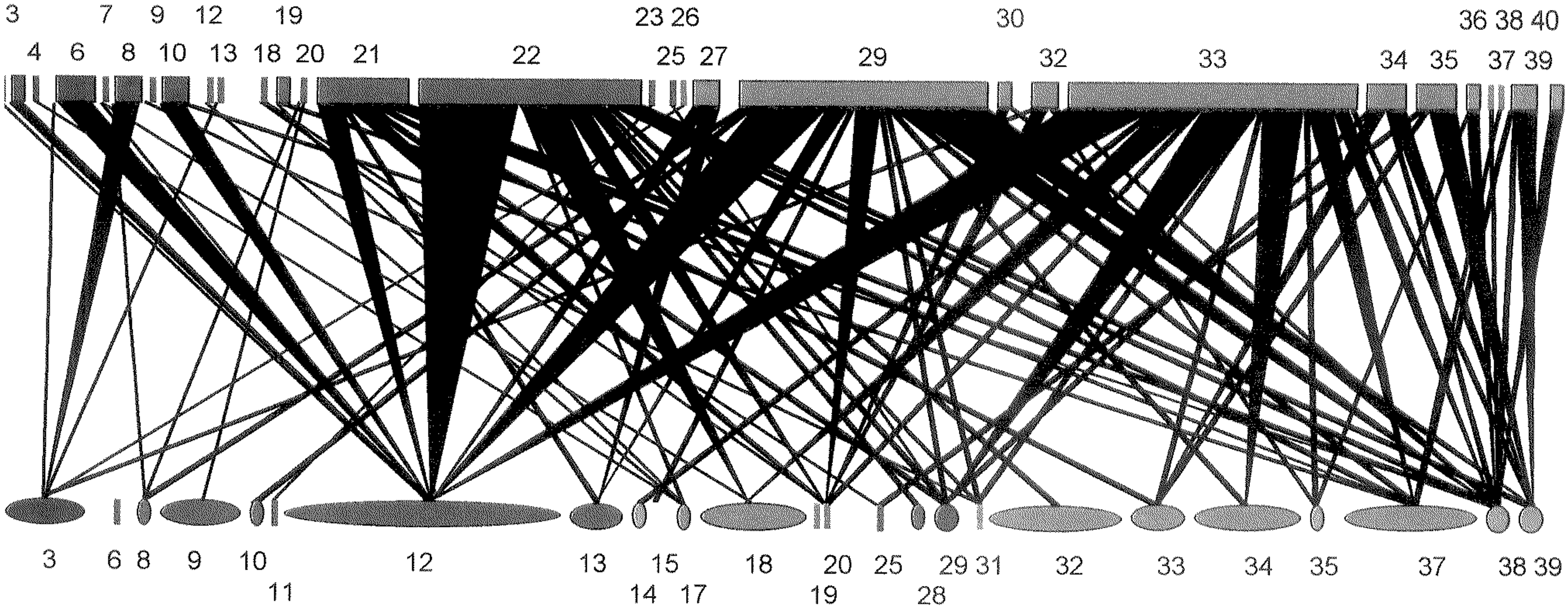
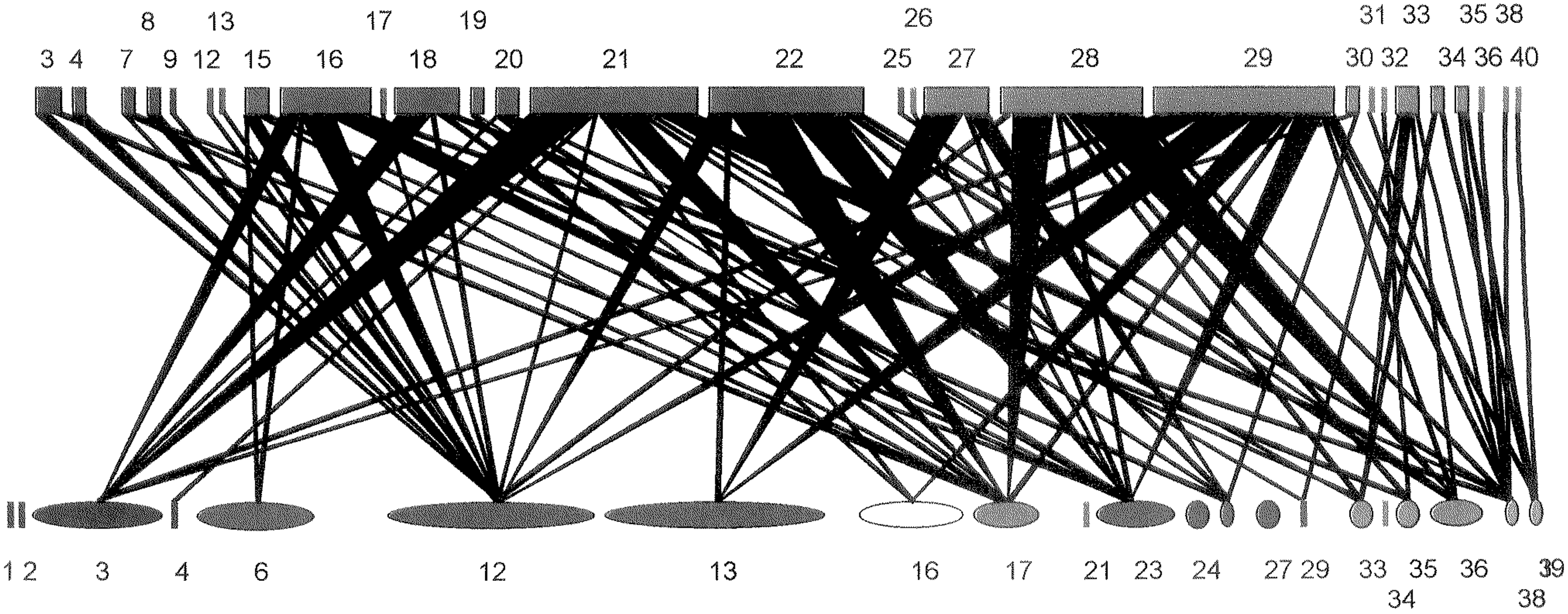


Figure 4.1. Trophic webs for Eupatorieae flowerhead endophagous insects in the Mantiqueira range. Insects are represented by rectangles, while host plants are represented by ellipses. For clarity, each guild is shown separately (a-c). The relative widths of the rectangles and ellipses represent the relative abundance of samples within that trophic level. The relative basal widths of the wedges linking insects to plants represent the relative interaction frequency. All observed interactions (links) were reproduced in the graphs. In insects different colours represent the three feeding guilds, while different colours for plants represents subtribes. Code numbers for plants and insects as in Table 4.1. Total number of plant samples was 547, while total endophages records in samples was 606. See text for further details.

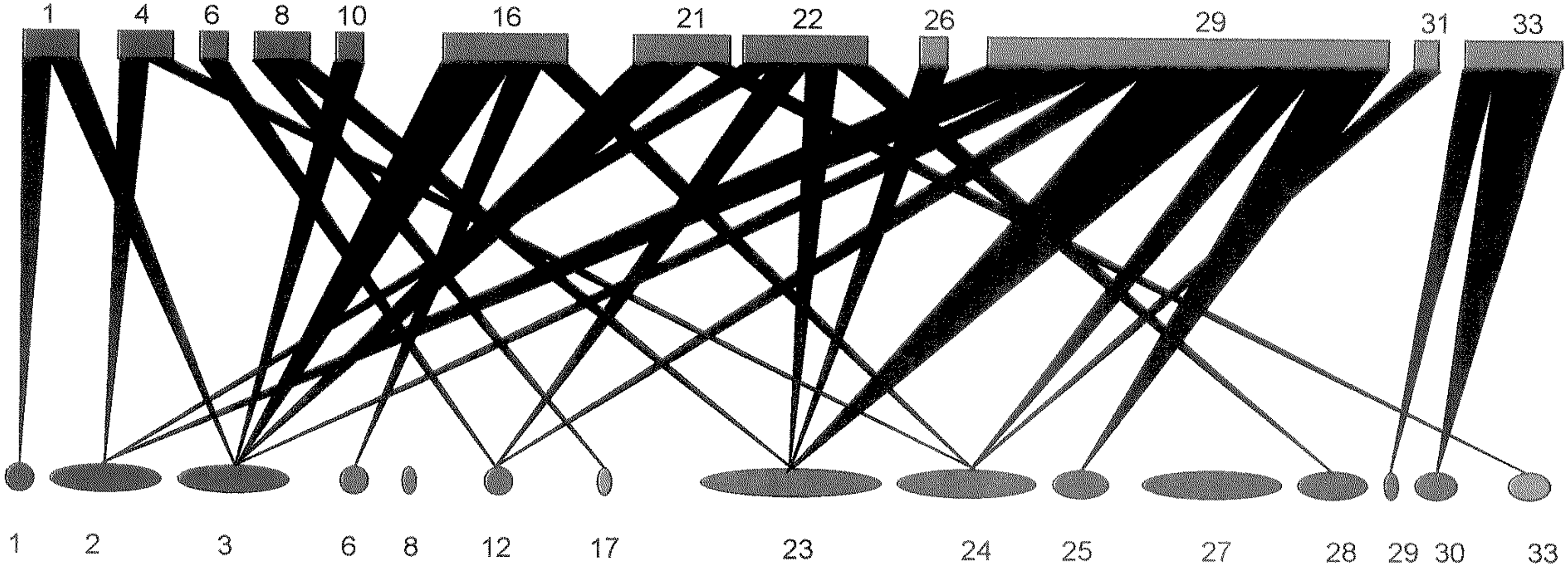
Ibitipoca (144 plant samples and 158 endophages records)



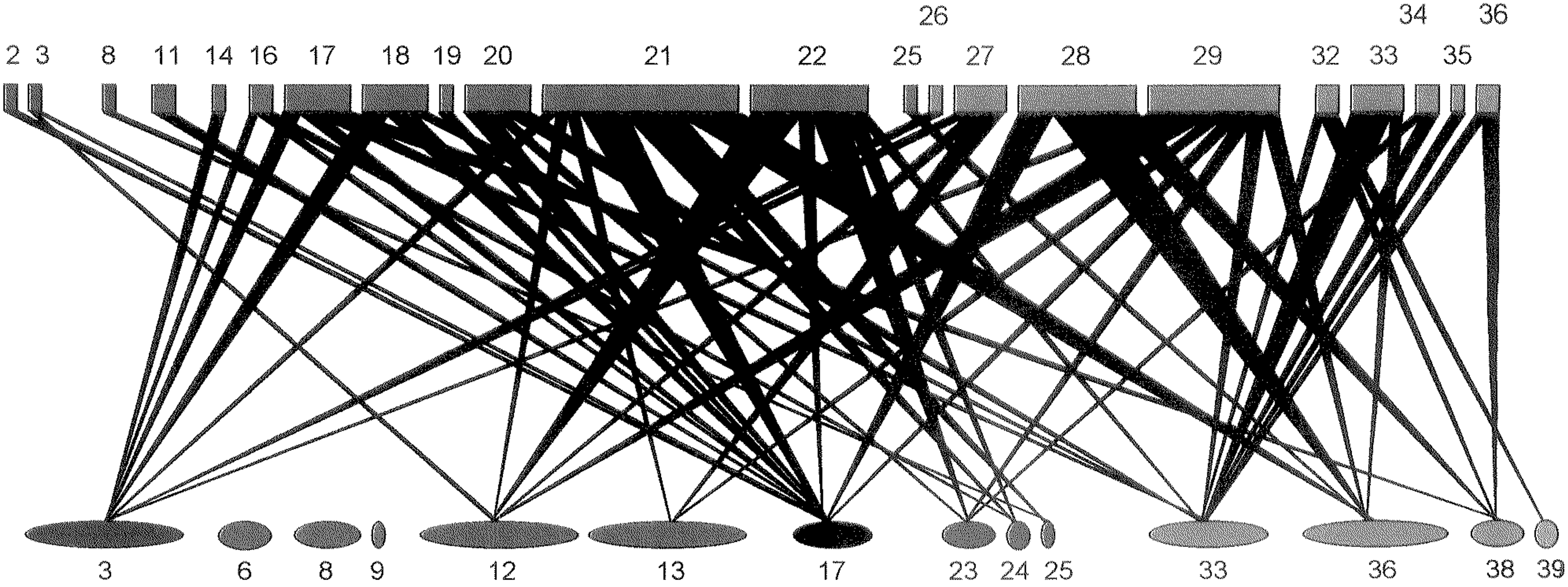
Visconde de Mauá (140 plant samples and 130 endophages records)

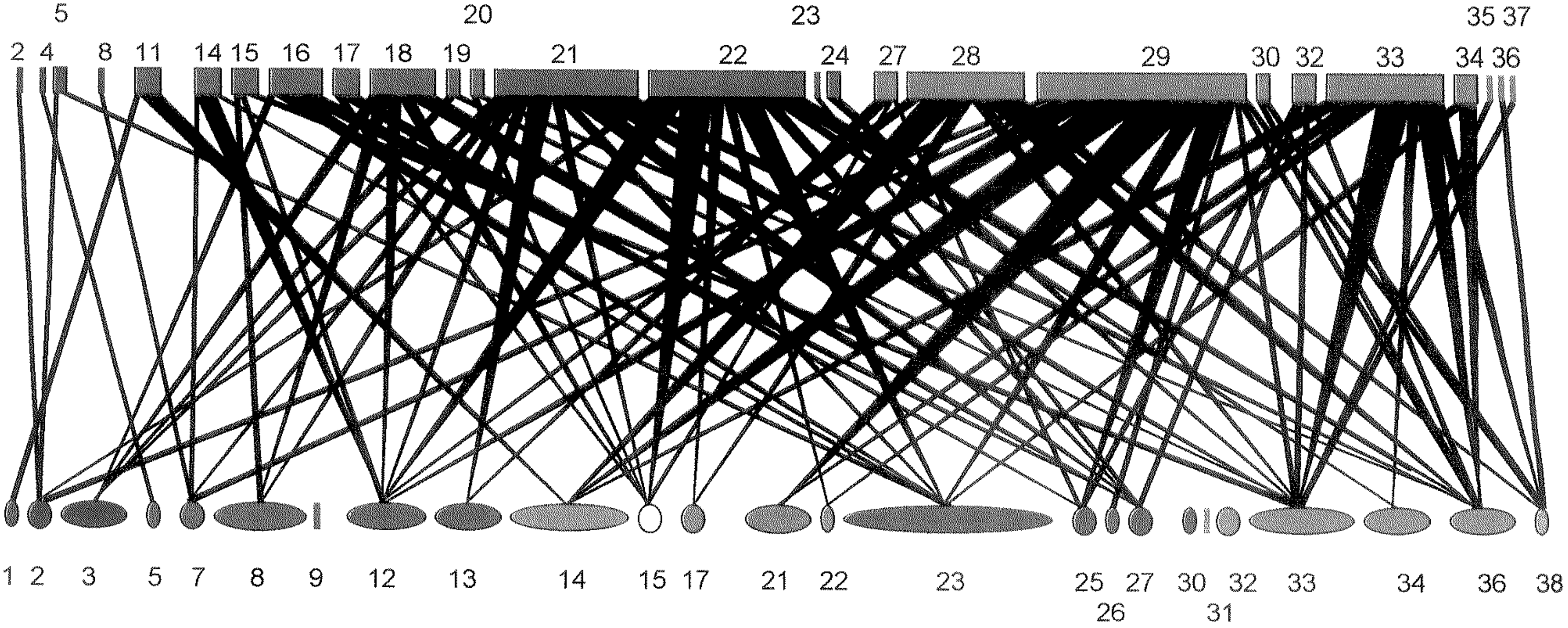


Itatiaia (76 plant samples and 39 endophages records)



Passa Quatro (75 plant samples and 87 endophages records)





Campos do Jordão (112 plant samples and 121 endophages records)

Figure 4.2. Trophic webs for Eupatorieae flowerhead endophagous insects in the Mantiqueira range. Total frequency of plant and endophagous samples was respectively for each locality: IB: 144 and 158; VM: 140 and 130; IT: 76 and 39; PQ: 75 and 87and CJ: 112 and 121. See legend of Figure 4.1 and text for further details.

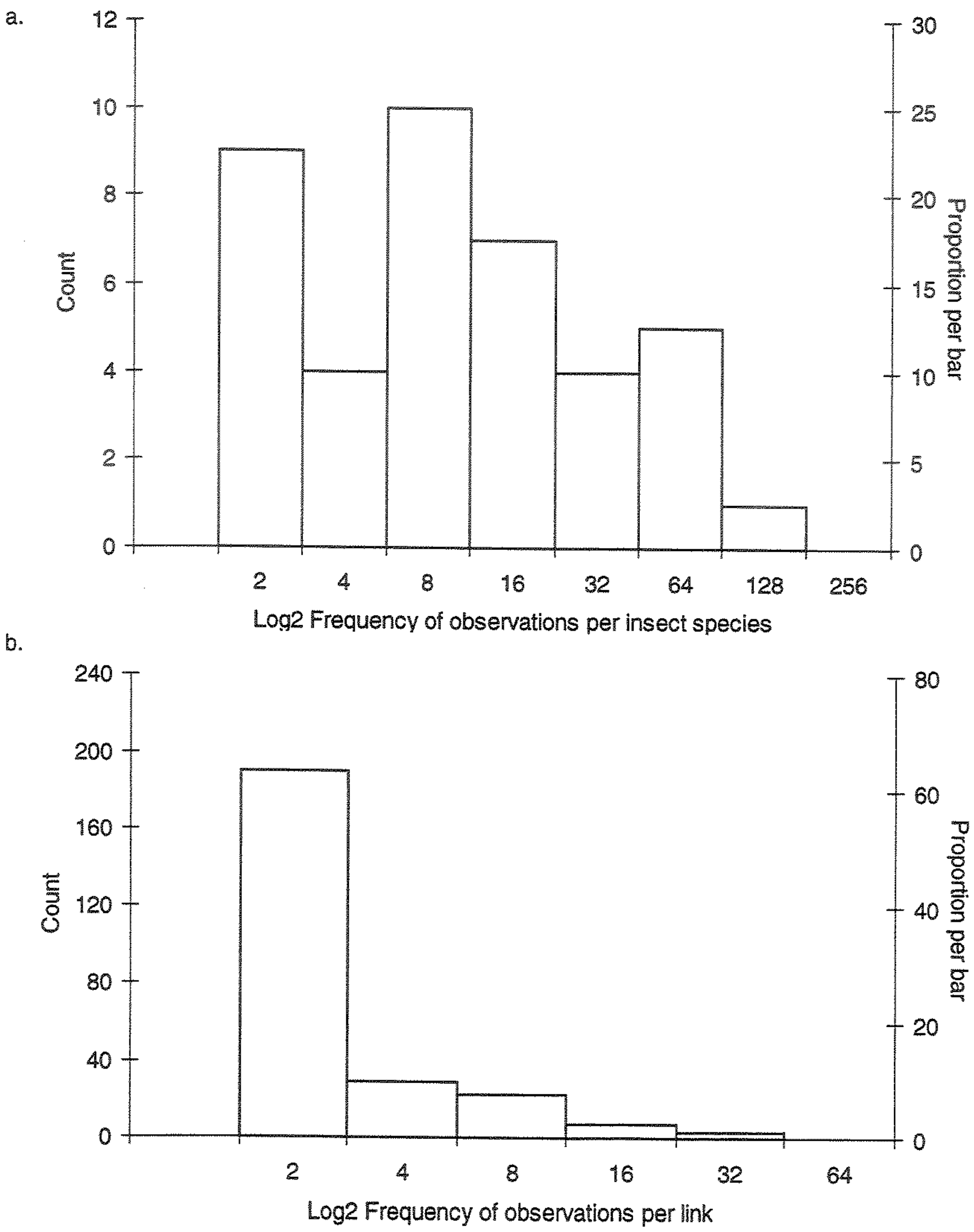


Figure 4.3. Distribution of the number of species (a) and links (b) in the food web for pooled localities (Figure 4.1) among classes (Log_2) of occurrence (number of times each species or link was observed) Singletons and doubletons (see methods for description) are excluded from this graph.

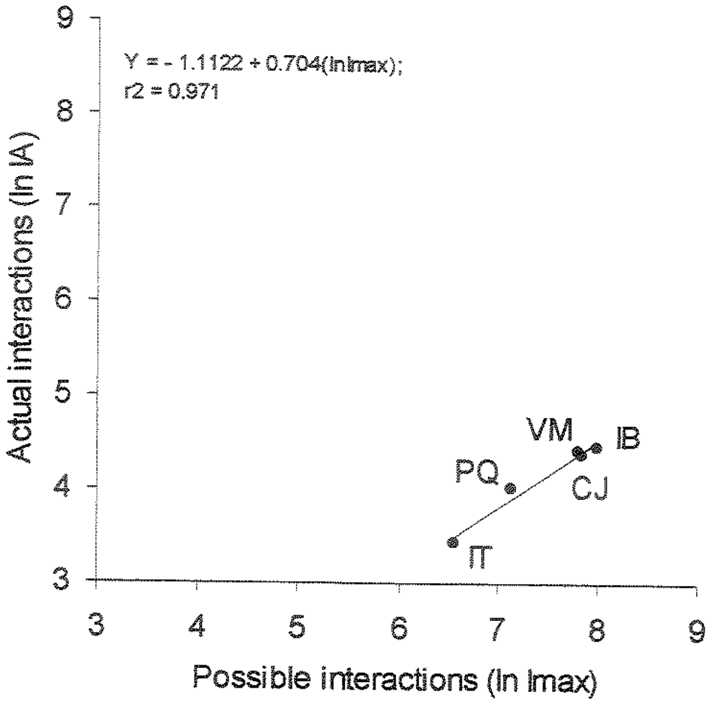


Figure 4.4. Community allometry of actual interactions (ln I_A) and possible interactions (ln I_{max}) for five communities of Eupatorieae flowerhead endophagous insects in Mantiqueira range after Fonseca (1996). Codes for localities are: IB - Ibitipoca; VM - Visconde de Mauá; IT - Itatiaia; PQ - Passa Quatro; and CJ - Campos do Jordão.

DISCUSSÃO

> "Even though we understand the laws of physics which govern
> the motion of falling objects, we do not expect physicists to predict
> where a feather will land after being lost from a soaring eagle"
> (Brown JH. 1999. Macroecology: progress and prospect. Oikos 87: 3-14)

> "It is likely that something very important is involved here,
> but for the present what it may be is a mystery,
> a very good thing with which to end a discourse"
> (Hutinson GE. 1953. The concept of pattern in ecology.
> Proc. Acad. Sci. Philadelphia 105: 1-12).

> "First get your facts straight, then you can distort'em"
> (Mark Twain a um repórter, em Cohen JE. 1989.
> Just proportions in food webs. Nature 341:104-105)

A estrutura e composição de comunidades locais é determinada tanto por processos locais de competição, predação, mutualismo, como processos regionais de especiação, imigração e emigração (Ricklefs, 1987; Ricklefs & Schluter, 1993a; Brown, 1995; Maurer, 1999). A maioria das teorias ecológicas, criadas para explicar o tamanho e a estrutura das comunidades foram formuladas tomando processos locais como determinantes, sem atentar aos processos regionais que determinam o pool de espécies presentes em uma área. Alguns autores, entretanto, já haviam percebido a importância de processos geográficos no estudo da ecologia, como por exemplo Robert MacArthur com sua teoria de biogeografia de ilhas (juntamente com Edward Wilson) e seus estudos com ecologia geográfica (MacArthur, 1963, 1967; 1972). A partir do fim da década de 80, como se nota pela publicação de dois artigos importantes (Ricklefs, 1987; Brown & Maurer, 1989) a influência de fatores regionais em comunidades locais voltou a ser estudada e analisada.

O número de artigos publicados com estudos macroecológicos vem aumentando progressivamente, e o interesse pela macroecologia levou à descrição de vários padrões que prevêem relações entre a variação na riqueza de espécies (e.g. Brown, 1988; Brown & Lomolino, 1988; Rohde, 1992; Shepherd, 1998), o tamanho das áreas geográficas (e.g. Rapoport, 1975; Stevens, 1989, 1992, 1996; Brown et al., 1996; Gaston, 1996b; Maurer, 1999), a abundância relativa de espécies (e.g. Brown, 1984; Brown et al., 1995; Gaston, 1996a) e o tamanho de corpo (e.g. Maurer et al., 1992; Marquet & Taper, 1998) em gradientes latitudinais, altitudinais e de profundidade (ver Brown, 1995, 1999; Gaston & Blackburn, 1999; Maurer, 1999 para lista mais completa de referências). Entretanto, a maioria destes artigos apenas descrevem os padrões observados, sem oferecer explicações de seus possíveis processos causadores, talvez porque os processos sejam tão complexos e englobem uma quantidade tão grande de fatores, que o corpo de dados existente hoje ainda não seja suficiente para entendê-los (como exceções ver p. ex. Rohde, 1992).

A análise da distribuição de espécies através do estudo geográfico de suas áreas de ocorrência, é uma das abordagens principais da macroecologia, embora o padrão vigente seja descrever a estrutura demográfica de espécies ou populações ao longo de sua área de ocorrência (Brown, 1984, 1995; Maurer, 1999).

Montanhas apresentam um gradiente altitudinal e as regiões de topo, com características ambientais bem mais severas que as áreas mais baixas, podem ser consideradas estruturas isoladas para a maioria dos organismos que ali vivem, duas características interessantes para um estudo macroecológico. A ocorrência de espécies em topos de montanha pode envolver três diferentes condições. Na primeira e mais óbvia as espécies presentes nos topos também ocorrem nos vales intermediários, e neste caso os topos não são regiões isoladas para as espécies em questão. Na segunda alternativa supõe-se que a distribuição geográfica destas espécies no passado englobava toda a área, incluindo os topos de montanhas e os vales intermediários e que no presente por alguma razão as espécies passaram a ser restritas apenas aos topos; neste caso, as distribuições atuais são relictos isolados. A terceira hipótese sugere que, de alguma forma a transmissão de adultos ou propágulos, pode ocorrer entre os topos, embora restrita, havendo transferência de material genético e a manutenção da espécie como uma unidade.

A Serra da Mantiqueira pode ser considerada uma região ótima para o estudo da relação entre padrões e fatores regionais e as comunidades locais. Nos topos de suas montanhas, são encontrados os campos de altitude, uma fisionomia que praticamente só ocorre na região sudeste brasileira. Regiões de campos de altitude podem ser consideradas fisionomias isoladas, ou ilhas de habitats e um terço de suas espécies vegetais são endêmicas (Safford, 1999a, b).

O sistema estudado na presente tese engloba grupos com características bionômicas distintas, incluindo as várias espécies de plantas hospedeiras e os vários grupos de insetos endófagos, que por sua vez pertencem a diferentes táxons superiores com características ecológicas e evolutivas bastante contrastantes. Como diferentes grupos possuem características biológicas próprias, é improvável que em uma comunidade como esta todas as espécies que a compõem respondam da mesma forma às pressões ambientais. Desta forma, cada espécie ou grupos de espécies podem apresentar diferentes padrões de distribuição e ocorrência, dificultando a detecção de padrões gerais. Para minimizar tal fator, os diferentes endófagos foram agrupados em três guildas de acordo com o grau de endofagia, reunindo assim espécies semelhantes troficamente.

Quando comparadas as distribuições geográficas das plantas e dos endófagos (capítulos 1 e 2), fica claro que as espécies de Eupatorieae são mais restritas a localidades individuais que qualquer guilda de insetos endófagos. Com relação à composição das espécies de Eupatorieae na serra da Mantiqueira (capítulo 1), embora localidades adjacentes tenham apresentado flora mais semelhante, Itatiaia se mostrou mais semelhante a Campos do Jordão, áreas com campos de altitude com composição semelhante, enquanto Passa Quatro foi mais semelhante a Visconde de Mauá, áreas com maior impacto antrópico e sem amostras nos campos de altitude. Ibitipoca é uma área ímpar na serra da Mantiqueira e, no que diz respeito à tribo Eupatorieae pode ser considerada como área de transição entre as serras da Mantiqueira e do Espinhaço. Uma grande parte das espécies de Eupatorieae é restrita a apenas uma localidade de coleta, confirmando o isolamento efetivo entre localidades no que concerne as plantas hospedeiras.

A distribuição espacial dos insetos endófagos (capitulo 2) não mostrou um padrão tão bem marcado como o encontrado para as plantas hospedeiras, o que é em parte o resultado de os insetos endófagos ocorrerem em mais localidades (serem mais amplamente dispersos) que a maioria das suas plantas hospedeiras. Este mesmo padrão já foi previamente observado para espécies de Tephritidae endófagas de capítulos de Vernonieae (Asteraceae) na Serra do Espinhaço (Prado, 1999); assim como para endófagos em capítulos de Asteraceae em áreas litorâneas (restingas) e montanhosas no sudeste brasileiro (Lewinsohn, 1988, 1991), e parece ser uma constante neste sistema.

A distribuição altitudinal das espécies tanto vegetais quanto animais são um objeto importante de estudos macroecológicos, em parte pelos gradientes altitudinais terem algumas analogias com gradientes latitudinais (Stevens, 1992; mas veja Rahbek, 1997 para várias diferenças entre os dois gradientes). Rahbek (1995) divide os fatores potencialmente causadores de gradientes altitudinais em primários e secundários. Fatores primários são abióticos, e incluem clima, área disponível em diferentes faixas de altitude, e históricos da área (por exemplo tempo desde a última perturbação, p. ex. glaciação). Fatores secundários são interações bióticas. Tanto fatores bióticos quanto abióticos podem variar entre diferentes épocas do ano, e ao longo dos anos, e diferentes táxons podem e devem então estar sendo afetados diferentemente por cada um destes fatores, fazendo também com que as espécies que habitam gradientes altitudinais apresentem distribuições de riqueza plásticas ao longo deste gradiente.

Nenhum dos grupos estudados na Serra da Mantiqueira, seja de plantas ou insetos (capítulo 3), apresentaram um decréscimo monotônico no número de espécies com o aumento da altitude, como seria esperado pela regra de Rapoport aplicada a um gradiente altitudinal (Stevens, 1992). Em vez disso, foram observados máximos de riqueza em altitudes intermediárias, como previsto e esperado pela hipótese do domínio médio (*mid-domain*) de Colwell e colaboradores (Colwell & Hurtt, 1994; Lees, 1996; Lees et al., 1999; Colwell & Lees, 2000), embora raramente ocorrendo exatamente no meio do gradiente. As espécies de Eupatorieae apresentaram diferentes distribuições de riqueza ao longo do gradiente altitudinal, que dependeu em parte da localidade estudada. Nas localidades onde áreas de campos de altitude foram incluídas na amostragem (Ibitipoca, Itatiaia e Campos do Jordão), esta fisionomia se mostrou mais rica que as regiões subjacentes de mata atlântica de altitude. Este resultado pode entretanto ter sido influenciado pela limitação de apenas se coletar em maiores elevações. O Parque Nacional de Itatiaia, por exemplo, foi amostrado acima de 1740m de altitude, excluindo grande parte da área de clareiras e bordas da mata de altitude presentes em áreas mais baixas do parque, conhecidamente possuidoras de várias espécies de *Mikania* não coletadas neste estudo (Barroso, 1957; Lewinsohn, com. pess.). A coleta em áreas mais baixas poderia ter afetado o formato da curva de distribuição, provocando o aparecimento de mais de um pico de riqueza, mas ainda assim se manteria a maior riqueza de espécies nos campos de altitude que nas áreas mais elevadas de mata de altitude, um padrão também observado na Serra do Espinhaço (Prado, com. pess.). Os insetos endófagos apresentaram também diferentes padrões de distribuições de riqueza, não em relação à área estudada, mas sim em relação à guilda a que pertencem. Endófagos estritos foram mais ricos em altitudes mais baixas, com maiores amplitudes altitudinais em espécies com pontos médios (*midpoints*) mais elevados. Por outro lado, os endófagos facultativos apresentaram um padrão inverso ao dos endófagos estritos, com maior riqueza em altas altitudes e maiores amplitudes altitudinais em espécies com pontos médios mais baixos, embora também tivessem o máximo de riqueza em altitudes intermediárias.

Colwell e colaboradores (Colwell & Hurtt, 1994; Lees et al., 1999; Colwell & Lees, 2000) afirmam que a hipótese do domínio médio é um modelo nulo, com o qual as distribuições empíricas devem ser comparadas, devendo-se posteriormente usar variáveis biológicas para explicar os desvios observados dos padrões previstos. Rahbek (1995) sustenta que ao se correlacionar a riqueza de espécies com variáveis de um gradiente altitudinal, devemos examinar se esta relação é de fato uma relação direta, ou se é um reflexo de interações de vários outros fatores. Embora esta tarefa seja das mais difíceis em ambientes naturais e em escalas geográficas, o fato de cada guilda responder de forma semelhante ao gradiente ambiental sugere que espécies semelhantes troficamente respondem de forma semelhante às limitações impostas por um ambiente "duro".

Teias tróficas são importantes instrumentos no estudo, descrição e análise de comunidades. Teias tróficas clássicas mostram de maneira facilmente visualisável e inteligível "quem come quem" em uma comunidade. Teias quantitativas, ainda pouco aplicadas a estudos de comunidades, são graficamente muito mais completas e descritivas que as teias usualmente construídas e publicadas, que representam todas as interações como equivalentes (Memmott et al., 1994; Salvo, 1996; Godfray et al., 1999; Müller et al., 1999; Valladares & Salvo, 1999; Rott & Godfray, 2000; Schönrogge & Crawley, 2000).

Na Serra da Mantiqueira, com a construção de teias quantitativas para cada localidade individual e sua comparação com a teia regional, alguns fatores que já haviam sido detectados e descritos em análises prévias foram melhor explicitados. O principal foi o fato de insetos endófagos presentes em várias localidades serem mais abundantes e estarem se alimentando de um maior número de plantas hospedeiras. As teias também acrescentaram novas informações ao sistema, como a de que embora as espécies generalistas regionais também sejam generalistas locais, algumas poucas hospedeiras foram usadas preferencialmente em relação às outras espécies. Um outro resultado importante é o fato de diferentes guildas de endófagos não só serem formadas por espécies que usam o recurso de forma semelhante, como também convergirem no uso espécies hospedeiras, dividindo o nível trófico superior em sub-unidades, o que entretanto não se reflete em compartimentação da comunidade.

A constância ou proporcionalidade de alguns parâmetros quantitativos usados como descritores de teias ainda não estão bem estabelecidos (Briand & Cohen, 1984; Cohen, 1989; Sugihara et al., 1989; Warren, 1990; Martinez, 1994; Martinez & Lawton, 1995; Bengtsson & Martinez, 1996; Martinez et al., 1999), mas isto não afeta a utilidade de teias tróficas como descritoras de comunidades. Pelo contrário, ao que parece, as teias tróficas prometem ser instrumentos ainda mais capazes e eficazes no estudo e comparação de comunidades. Brown (1999) sugere que o futuro da macroecologia está em entender que padrões cada vez mais gerais irão necessitar de leis científicas universais para explicá-los, o que inclui leis físicas e químicas e o estudo cada vez mais detalhado dos fluxos de energia e materiais entre comunidades e ecossistemas. Além do estudo de fluxos de energia e materiais em sistemas, a construção de teias locais e regionais também promete ser um instrumento ótimo em estudos de comparações entre comunidades semelhantes mas isoladas entre si, como proposto por Ricklefs & Schluter, (1993b) e Yodzis (1993) e tratado na presente tese.

A presente tese estudou comunidades de insetos endófagos de capítulos de Eupatorieae e suas hospedeiras, presentes em cinco localidades na Serra da Mantiqueira. Na descrição, estudo e comparação das cinco localidades foram aplicados conceitos e teorias recentes em macroecologia, como a hipótese do domínio médio e a aplicação de teias tróficas quantitativas. A divisão dos insetos endófagos em três guildas de acordo com o grau de endofagia (capítulo 2) mostrou-se efetiva para a divisão funcional de grupos que se reflete em padrões biogeográficos e estruturais, já que guildas diferentes apresentam diferentes distribuições de riqueza em gradientes altitudinais (capítulo 3) e tendem a se alimentar de hospedeiras diferentes (capítulo 4). A hipótese do domínio médio foi testada e comprovada para todos os grupos estudados, desde plantas à guilda de endófagos facultativos, e, embora as distribuições de riqueza não tenham sido exatamente as previstas pelo modelo nulo, fomos capazes de explicar biologicamente desvios encontrados.

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