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I. B.

BIOLOGIA DA POLINIZAÇÃO EM CAMPOS DE ALTITUDE NO PARQUE NACIONAL DA SERRA DA BOCAINA, SP

Leandro Freitas

Orientadora: Profa. Dra. Marlies Sazima

Este exemplar corresponde à redação final
da tese defendida pelo(a) candidato(a)
Leandro Freitas
e aprovada pela Comissão Julgadora.

Marlies Sazima

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SUMÁRIO

Resumo. Este estudo apresenta informações sobre a biologia da polinização em uma área de campos de altitude no estado de São Paulo. Campos de altitude são formações frias e úmidas com vegetação aberta, as quais ocorrem nas partes mais altas das serras costeiras do sudeste e sul do Brasil. Atributos florais e a fenologia de floração foram registrados em 124 espécies pertencentes a 37 famílias e os agentes de polinização foram determinados em 107 destas espécies. Flores pequenas que secretam néctar predominaram na comunidade. Abelhas e vespas, seguidas por sirfídeos, foram os principais agentes polinizadores da comunidade, sendo que a maioria das espécies foi polinizada por mais de um grupo funcional. As tendências gerais das interações planta-polinizador nos campos estudados se assemelham àquelas em ecossistemas com afinidades biogeográficas, tais como o "morichal" venezuelano, campos cerrados e campos rupestres. Entretanto, o grau de generalização dos sistemas de polinização tende a ser mais elevado nos campos de altitude em comparação com estes outros ecossistemas, o que reflete a predominância de espécies da família Asteraceae na área estudada. A polinização por diversos agentes (sistemas de polinização generalista) pode ser vantajosa para plantas de campos de altitude, devido às condições climáticas severas que se refletem nas baixas taxas de visitação de polinizadores às flores. Este estudo é complementado por estudos de caso com três espécies típicas dos campos de altitude. A biologia floral e a polinização por abelhas do gênero *Anthrenoides* (Andrenidae) em *Viola cerasifolia* (Violaceae) foi estudada. A produção de néctar foi escassa e polem constituiu o principal recurso floral desta espécie, diferindo assim das flores de néctar que predominam entre espécies boreais do gênero. O segundo caso trata do padrão de florescimento diário e da polinização por moscas Syrphidae em *Sisyrinchium vaginatum* (Iridaceae). As flores duraram de um a quatro dias, porém fechavam ao final de cada dia e voltavam a abrir no dia seguinte. As flores não secretam óleo como em outras espécies do gênero. Sirfídeos e, em menor grau, abelhas pequenas em busca de polem polinizaram esta espécie. Por último, a produção de néctar das flores polinizadas por beija-flores de *Esterhazya macrodonta* (Scrophulariaceae) foi estudada. O néctar é produzido continuamente nos três primeiros dias da flor que dura cinco-seis dias. A remoção de néctar afeta a sua secreção e isto parece estar ligado à baixa taxa de visitação às flores pelos beija-flores.

Palavras-chave: abelhas, beija-flores, biologia floral, biologia da polinização, campos de altitude, *Esterhayia*, fenologia, Mata Atlântica, moscas, *Sisyrinchium*, vespas, *Viola*.

Abstract. Here we studied the pollination biology in high altitude grasslands at São Paulo State, southeastern Brazil. These grasslands are a series of cool/humid, grass-dominated formations, which are restricted to the highest parts of the coastal mountain ranges in southern-southeastern Brazil. We registered floral traits and flowering phenology for 124 species in 37 families. Pollinators were determined in 107 of these species. Small nectar-secreting flowers dominated in the community, and bees and wasps, followed by hoverflies, were the most important pollinator groups. Most plant species were pollinated by two or more pollinator groups. The general trends of the plant-pollinator interactions in these grasslands resemble results from some biogeographic-connected ecosystems, such as the Venezuelan "morichal", and the Brazilian "campos cerrados" and "campos rupestres". But the degree of generalization in the pollination systems at the grasslands here studied is higher than in these other ecosystems, reflecting the dominance of Asteraceae species in the study area. Pollination by several agents may be advantageous for plants of the high altitude grasslands, due to the harsh climatic conditions and the low visitation rates of pollinators to the flowers in this habitat. This study is completed by study cases involving three typical species of these grasslands. We studied the floral biology of *Viola cerasifolia* (Violaceae) and its pollination by Andrenidae bees of the genus *Anthrenoides*. Nectar secretion was poor, and pollen was the chief floral resource in this species, which differs from nectar-flowers of the boreal species of this genus. The second case reports the daily blooming pattern of *Sisyrinchium vaginatum* (Iridaceae) and its pollination mainly by Syrphidae flies. Flowers lasted one to four days, but they closed at the end of the day, to re-open in the following day. Flowers do not bear oil-secreting glands as other species in the genus. Hoverflies - and in a minor degree small bees - in search of pollen pollinated this species. At last, we studied the nectar production of the hummingbird-pollinated flowers of *Esterhazya macrodonta* (Scrophulariaceae). Nectar was continuously secreted for the first three days of flower lifetime (five-six days). Nectar removal negatively affected its production, and this seems to be related to the low floral visitation rates by the hummingbirds.

Key words: Atlantic Forest, bees, *Esterhayia*, flies, floral biology, high altitude grasslands, hummingbirds, phenology, pollination, *Sisyrinchium*, *Viola,* wasps.

INTRODUÇÃO GERAL

Desde o trabalho seminal de Sprengel em 1793 (q.v. Vogel 1996), os estudos em biologia da polinização expandiram e diversificaram muito. Nas últimas décadas, em particular, as pesquisas sobre as interações planta-polinizador têm sido norteadas por enfoques diversos, tais como ecologia de comunidades, genética de populações e comportamento animal, e exibem uso crescente de experimentos quantitativos e técnicas analíticas modernas (e.g., determinação da composição química do néctar e de odores florais através de cromatografia líquida) (q.v. Kearns & Inouye 1993, Endress 1994, Lloyd & Barret 1996, Waser et al. 1996, Waser 1998, Johnson & Steiner 2000, para uma síntese das tendências teóricas e metodológicas na área). O desenvolvimento e a ramificação dos estudos na área implicaram no surgimento de linhas de pesquisa distintas, as quais têm ajudado a elucidar questões em vários campos, tais como sistemática e filogenia vegetal (Armbruster 1991, 1993, McDade 1992, Ollerton 1996), biologia evolutiva e da adaptação (Vogel, 1969, 1990, Stebbins 1970, Campbell 1989, 1996, Grant 1994, Sazima et al. 2001), ecologia de populações (Campbell 1985, Feinsinger et al. 1986, Waser & Price 1989, Feinsinger & Tiebout III 1991), biologia reprodutiva (Waser & Price 1991, Gibbs et al. 1999, Oliveira & Gibbs 2000) e biologia da conservação (Aizen & Feinsinger 1994, Allen-Wardell et al. 1998, Corbet 2000).

Em adição, como destacado por Johnson & Steiner (2000), o estudo da biologia da polinização tem sido revitalizado por um debate corrente sobre o grau de especialização das interações planta-polinizador e a validade do conceito de "síndromes de polinização" (cf. Faegri & van der Pijl 1979). Nesta discussão, a visão clássica que sistemas de polinização especializados refletem uma tendência evolutiva geral (Grant & Grant 1965, Faegri & van der Pijl 1979) é contrabalançada pela idéia que sistemas mais generalizados seriam predominantes (Herrera 1996, Ollerton 1996, Waser et al. 1996). Outro debate, que constitui um tema recente e crítico em biologia da conservação, trata do declínio de polinizadores e suas prováveis conseqüências na conservação da biodiversidade e da estabilidade agrícola (Allen-Wardell et al. 1998). Devido a esta natureza abrangente e dinâmica, a biologia da polinização permanece notavelmente vigorosa para um campo com mais de dois séculos de história (Johnson & Steiner 2000).

Processos reprodutivos das plantas têm sido reconhecidos como determinantes da composição, estrutura e dinâmica das comunidades (Heithaus 1974, Moldenke & Lincoln 1979, Bawa 1990, Vogel & Westerkamp 1991, Oliveira & Gibbs 2000). Entre estes processos, as relações planta-polinizador, em particular, são fundamentais para a caracterização das comunidades, uma vez que a maioria das plantas depende dos agentes de polinização para sua reprodução sexuada e, em contrapartida, recursos florais constituem as principais fontes de alimento para diversos grupos de animais. Neste sentido, estudos sobre a biologia da polinização em nível de comunidades vêm sendo desenvolvidos na região neotropical abrangendo vários tópicos, por exemplo, diversidade e distribuição dos organismos envolvidos nas interações, estrutura de guildas de polinizadores e de plantas, fenologia de floração, sobreposição de nicho e partilha de recursos (e.g., Feinsinger 1976, 1978, Bawa et al. 1985, Silberbauer-Gottsberger & Gottsberger 1988, Ramirez 1989, Ormond et al. 1993, Kress & Beach 1994, Barbosa 1997, Buzato et al. 2000, Oliveira & Gibbs 2000).

Em relação à Mata Atlântica (*sensu lato*), diversas pesquisas em polinização vêm sendo realizadas em áreas florestais, envolvendo tanto grupos pequenos de espécies de plantas (e.g., Sazima & Sazima 1989, Fischer et al. 1992, Araújo et al. 1994, Passos & Sazima 1995, Figueiredo & Sazima 1997, Singer & Cocucci 1999, Singer & Sazima 1999, Machado & Loiola 2000, Machado & Lopes 2000, Pombal & Morellato 2000, Santos 2000) quanto conjuntos de espécies associadas a certo grupo de polinizadores (Sazima et al. 1995, 1996, 1999, Arruda & Sazima 1996, Alves-dos-Santos 1999, Buzato et al. 2000), as quais se somam a estudos em diversas disciplinas (q.v. Morellato & Haddad 2000 para uma síntese recente). Porém, ainda pouco se conhece sobre este bioma (Prance & Campbell 1988, Morellato & Haddad 2000), destacadamente em relação aos campos de altitude - uma vegetação aberta pertencente ao domínio da Mata Atlântica - para a qual dados botânicos, ecológicos e biogeográficos são muito limitados e fragmentários (Ab'Saber 1989, Safford 1999a), em que pese os artigos recentes de Safford (1999a, b, c, 2001). Em relação à biologia da polinização, os únicos registros conhecidos para estes campos estão restritos a comentários anedóticos em artigos devotados a outros assuntos (e.g., Zikán & Zikán 1940, Brade 1956).

Os campos de altitude formam um arquipélago de formações frias e úmidas entre Minas Gerais/Espírito Santo e Santa Catarina, as quais ocupam as partes mais altas (a partir de 1500-2000 m) das principais cadeias de montanhas justamarítimas do sudeste/sul do Brasil (Safford 1999a, q.v., Semir 1991 para um tratamento dos campos rupestres e campos de altitude como complexos vegetacionais, então denominados complexos rupestres de quartzito e de granito, respectivamente). Este tipo de vegetação está representado em áreas bem conhecidas da Serra do Mar e da Serra da Mantiqueira, tais como a Serra do Caparaó, Serra dos Órgãos, Pico do Itatiaia, Serra da Bocaina e Campos do Jordão, as quais abrigam unidades de conservação estaduais e nacionais, embora permaneçam sujeitas a pressões antrópicas com diferentes graus de intensidade (Safford 1999a). Os campos de altitude são formados por espécies de ervas e arbustos de diversas famílias e também por arvoretas, as quais se encontram distribuídas em estratos contínuos de gramíneas e ciperáceas. Esta vegetação apresenta características muito peculiares, tais como flora rica, numerosos casos de endemismo, muitas espécies com populações pequenas, conexões biogeográficas com hábitats (sub-)alpinos dos Andes e condições climáticas adversas para uma área tropical (q.v., Martinelli 1989, Safford 1999a, b), as quais a tornam particularmente interessante para estudos em biologia da polinização.

Este estudo apresenta informações sobre a biologia da polinização em campos de altitude no Parque Nacional da Serra da Bocaina, estado de São Paulo. O enfoque principal do estudo foi o levantamento das interações planta-polinizador em nível de comunidade, o que englobou a composição florística, fenologia de floração e atributos florais das espécies de plantas polinizadas por animais, bem como, a determinação de seus agentes de polinização (capítulo I). Os dados obtidos para a comunidade permitiram: i. o reconhecimento de grupos de espécies de plantas de acordo com seus sistemas de polinização, ii. a identificação dos principais agentes polinizadores, iii. determinação do grau de especialização dos sistemas de polinização e iv. a comparação de padrões gerais com o registrado em outras comunidades campestres (e.g., “páramos” venezuelanos, Ramirez 1989). Devido à carência de informações para os campos de altitude, particularmente na Serra da Bocaina (para a qual os estudos prévios parecem ser restritos a Brade 1951 e Martinelli 1989), a proposta do capítulo I é fornecer uma primeira descrição das interações planta-polinizador nesta comunidade, a qual possa servir como base para estudos futuros.

Este estudo é completado por três estudos de caso (capítulos II a IV). O primeiro caso trata da biologia floral e da polinização por abelhas da família Andrenidae em uma espécie do gênero *Viola* (Violaceae) (capítulo II). Este gênero com mais de 500 espécies está representado por apenas quatro espécies no Brasil, as quais são restritas a ambientes frios. A morfologia das flores da espécie estudada (*V. cerasifolia*) é complexa e difere em certo modo da morfologia floral típica do gênero, apresentando estruturas adaptadas para a coleta de polem pelas abelhas.

O capítulo III aborda a dinâmica de abertura floral e a polinização principalmente por moscas em uma espécie da família Iridaceae (*Sisyrinchium vaginatum*). Esta espécie não secreta óleo, como é típico no gênero, sendo que polem é seu único recurso floral. As flores duram de um a quatro dias, porém as tépalas invariavelmente se fecham ao final do dia, podendo abrir no dia seguinte. Embora descrito para outros taxa, este fenômeno é incomum e parece estar relacionado, ao menos nesta espécie, com fatores climáticos e com o período de atividade dos agentes polinizadores mais freqüentes.

As flores grandes e vermelhas de *Esterhazya macrodonta* (Scrophulariaceae) são supostamente muito atrativas para seus polinizadores, os beija-flores. Entretanto, visitas de polinizadores foram raramente observadas. Baseado nestas observações, a produção de néctar das flores desta espécie foi estudada para verificar possíveis relações entre as características do néctar e a baixa frequência de visitas (capítulo IV).

A escolha em apresentar estes estudos de caso, em particular, está baseada no fato das três espécies pertencerem a gêneros de plantas típicos dos campos de altitude e serem polinizadas por agentes que pertencem a três dos principais grupos de polinizadores da comunidade, respectivamente, abelhas, sirfídeos e beija-flores. Além disso, estes casos foram estudados sob enfoques distintos e, consequentemente, com técnicas diferentes, fornecendo uma amostra das possíveis abordagens em estudos de biologia da polinização.

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CAPÍTULO I: POLLINATION BIOLOGY IN A TROPICAL HIGH-ALTITUDE GRASSLAND IN BRAZIL: INTERACTIONS AT THE COMMUNITY LEVEL

Contents

POLLINATION BIOLOGY IN A TROPICAL HIGH-ALTITUDE GRASSLAND IN BRAZIL: INTERACTIONS AT THE COMMUNITY LEVEL[1]

ABSTRACT

A survey of plant-pollinator interactions was carried out in an area of high-altitude grasslands ("campos de altitude") in southeastern Brazil. Such grasslands are restricted to mountain tops, and thus, constitute diminutive island-distributed formations surrounded by rain forest, which belong to the Atlantic Forest Domain. We registered floral traits of 124 species belonging to 37 families (excluding Poaceae and Cyperaceae), and determined the pollinator agents on 107 of them. Most families are represented by a few species, but Asteraceae and Melastomataceae are prominent (40 and 10 species respectively). The predominant floral traits are dish or short-tubular shape, nectar as resource, and pale or violet as the main color. These features permit flower exploration by different pollinator groups, and in fact, most species were pollinated by more than one functional group. Small bees, wasps and large bees (mainly due to the bumblebee species) were the most important pollinator groups in the community. Butterflies, beetles, oil-collecting bees and hummingbirds were poorly represented, and we failed in detecting some pollinator groups which are present in the surrounding forest areas, such as bats and odor-collecting bees. Floral visitors were uncommon in many species, and several cases of spontaneous self-pollination combined to the biotic agents seem to occur. The general trends of the floral traits and plant-pollinator interactions in the high-altitude grasslands resemble those of biogeographic-connected ecosystems, such as the Venezuelan "morichal", and the Brazilian "cerrados" and "campos rupestres". However, pollination systems in these grasslands tend to be less specialized than in those ecosystems. The marked presence of more generalized systems reflects the prevalence of Asteraceae species. The possibility of pollination by several agents may be interesting for plants in such habitat, because of the general climatic conditions and low rates of pollinator visitation.

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[1] Following the *Annals of the Missouri Botanical Garden* format

Plant reproductive processes are believed to be among the determinants of the composition and structure of communities (Heithaus 1974, Bawa 1990, Oliveira & Gibbs 2000). Among such processes, the plant-pollinator interactions form a dynamic, yet somewhat cohesive, ecological subunit of a community, which can be studied in terms of, for example, species diversity and distribution, resource utilization, and niche packing (Moldenke & Lincoln 1979). Pollination biology at the community level in the Neotropics has been studied in forest areas (Bawa et al. 1985, Kress & Beach 1994), and also in savanna-like vegetation (Silberbauer-Gottsberger & Gottsberger 1988, Ramirez 1989, Barbosa 1997, Oliveira & Gibbs 2000). Concerning the Brazilian Atlantic Forest Domain, there are several studies on pollination biology in forest areas on both individual species and flower assemblages (e.g., Sazima et al. 1995, 1996, 1999, Buzato et al. 2000 and references therein). However, for the high altitude grasslands - a subtype of the Atlantic Forest Domain - there is no information on plant-pollinator interactions but a study on nectar features of *Esterhazya macrodonta* (Freitas & Sazima 2001).

The Brazilian Atlantic Forest is one of the most endangered ecosystems on earth (see Morellato & Haddad 2000), and comprises different vegetation types, such as semi-deciduous forest, *Araucaria* mixed forest and coastal rainforest (Oliveira-Filho & Fontes 2000). The high altitude grasslands ("campos de altitude") comprise an archipelago of mountaintop formations, which show strong floristic similarities to the Andean and Central-American (sub-)alpine habitats and also to the Central-Eastern Brazilian rupiculous and grassy habitats ("campos rupestres") (Safford 1999a, see also Giulietti & Pirani 1988). These grasslands are found along the main mountain ranges of the southeastern Brazil, and for such restricted areas of habitat, these formations harbor extraordinarily rich floras and many endemisms. For example, about a third of the ca. 400 species in the Itatiaia plateau (< 50 km^2) appears to be endemic to the high altitude grasslands (Martinelli 1989, Safford 1999a). However, many species on high-altitude grasslands present few populations, and even few individuals, especially in human-disturbed areas. Due to their several particularities - richness of species and small populations, many endemisms, "island-type" occurrence, biogeographic connections, and harsh climatic conditions for a tropical place - the Brazilian high-altitude grasslands are interesting communities for studies on pollination biology.

A current debate on pollination biology focuses on the degree of specialization in plant-pollinator relationships, in which the traditional view based on syndrome concept (cf. Faegri &

van der Pijl 1979) has been counterbalanced by skepticism about the specialized nature of pollination systems (Johnson & Steiner 2000 and references therein). Surveys of entire local assemblages of plant and pollinators are suitable to evaluate the specialization degree among pollination system (Waser et al. 1996), since specific plant-pollinator interactions may be examined in a broad ecological context (Moldenke & Lincoln 1979). In this paper we report on plant-pollinator interactions at the community level of a high altitude grassland area ("campos de altitude") in southeastern Brazil. The specific goals were: i. to study floral biology of the plant species (sexual system, flower shape, dimensions, resource and color) and their pollinators; ii. to register the flowering phenology, and the flower resource availability along the year for the main pollinator groups; and iii. to group plant species in accordance to their pollination systems. Then, we provide a discussion about general patterns of plant-pollinator interactions at the high altitude grasslands in relation to other ecosystems, which have strong biogeographic connections to such grasslands.

AREA AND VEGETATION STUDIED

The Parque Nacional da Serra da Bocaina (PNSB) - with about 100,000 hectares in area - is located between Rio de Janeiro and São Paulo States in southeastern Brazil. The PNSB includes different vegetation types of the Brazilian Atlantic Forest biome from the sea level till the highest peaks in the Serra da Bocaina (ca. 2100 m). The lower areas are covered mainly by lowland and sub-montane rainforest, followed by montane and high-altitude forest. The high-altitude grasslands (Fig. 1) probably began only above 1700-1800 m. Nowadays these fields can be found from ca. 1450 m on, due to human disturbances on forest areas. Brazilian high-altitude grasslands resemble an archipelago of grassy fields isolated between them by continuous areas of forest or by human settlements. The origin of this vegetation is connected to glaciating episodes at least since the Late Pleistocene, when it is supposed that grassland areas had suffered expansion and retraction events (Ledru et al. 1998). Present grasslands have strong biogeographic connections with other high-altitude ecosystems in South America, such as the Andean alpine vegetation in Argentina and Chile, the Venezuelan "páramos" and the Brazilian "campos rupestres" (Safford 1999a and references therein). High-altitude grasslands are also connected to the Central Brazilian savannas ("cerrados") (Silveira & Cure 1993, see also Modenesi 1988 for cerrado components in palinofloras from the grasslands). Grasslands are composed by a matrix of Poaceae and Cyperaceae species mixed with shrubs and herbs from many families, mainly Asteraceae and Melastomataceae. Scattered small trees can be found in more preserved fields, mainly several species belonging to the genus *Eremanthus* (e.g., *E. erythropappus* and *E. mollis*, Asteraceae), which are popularly called "candeia".

Figure 1. High altitude grasslands at the Parque Nacional da Serra da Bocaina. The area in the foreground (study site 1) was burned in the previous year (Aug, 1997), and had been used for cattle breeding. Note the trampling marks, and the abrupt limit between grassland and adjacent forest at this site. The area in the middle ground (study site 3) was a well preserved area before to be burned in Sep, 1999.

Montane areas in southeastern Brazil encompass two Köppen (1948) climate regions. Grasslands at the highest summits (above ca. 2000 m) are Cwb, with ≤ 12° C mean annual temperature, cool summers, moderately cold winters with frequent frost, and rare snow. Montane areas below can be classified Cfb, i.e., mesothermic, with 12-20° C average annual temperature, moderate winters, and mild, wet summers (Segadas-Vianna & Dau 1965, Nimer 1977, Safford 1999a, b). Most grasslands areas at Serra da Bocaina are Cfb. Annual precipitation is up to 2100 mm (Fig. 2). Rains are concentrated on summer, mainly from Dec to Mar. Dry season is stronger from Jun to Aug, with precipitation < 50 mm per month. The effects of seasonal drought on vegetation are partially offset by thick banks of orographic fog that shroud most Serra da Bocaina grasslands for much of the year, mainly early in the morning (see Safford 1999a). Annual mean temperature is ca. 15° C at 1500-1600 m, and minimum temperatures around 0° C are common during winter (pers. obs.). Frosts occurred more than thirty days a year (pers. obs., 1998-1999). General information about the vegetation, climatic and topography of southeastern Brazil is available in Eiten (1970, 1992), Hueck (1972), Alonso (1977), Nimer (1977), Moreira & Camelier (1977), and Safford (1999a, b).

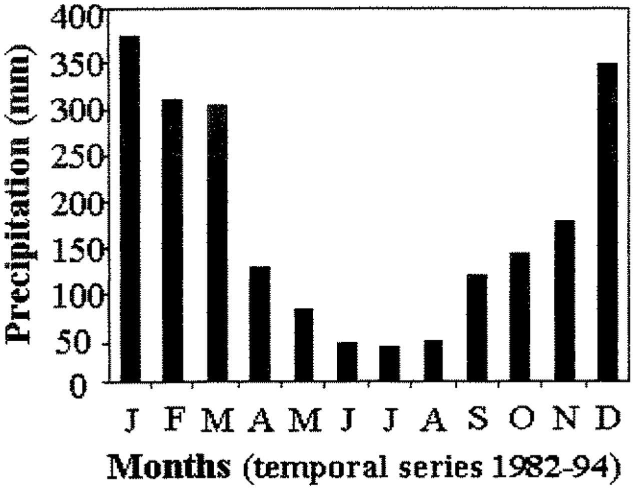

Figure 2. Mean monthly precipitation at the Serra da Bocaina grasslands from 1982-1994. Data from DAEE-SP (Posto Pluviométrico Bocaina).

Serra da Bocaina highlands have a long history of human disturbances, but human impact was low until the beginning of 20th century. In the middle of that century, Brazilian government tried to established colonists in the area to cultivate orchards (e.g., pear, peach, persimmon), but the attempt failed. Then, it was decided to plant exotic pines to replace native Araucarian forest. The idea of pine-wood extraction was abandoned, but its remains are still present in the PNSB. Finally, the Park was established in the beginning of the 70's, with a precarious logistic. Many people live in small farms inside and surrounding the PNSB, including legal owners and leaseholders, and general economic and social condition of that people is precarious. The primary economic source of the inhabitants on grassland areas comes from livestock. The traditional way of cattle breeding in Serra da Bocaina includes the use of fires in grasslands during the winter, permitting grasses to sprout after rains. Areas of forest are devastated to expand the grasslands and, consequently, the area for livestock. There are no studies measuring the effects of fires and grazing in grasslands but that of Safford (2001). However, it is supposed that regular fires and grazing have negative impacts on physical environment, vegetation structure and dynamics (see Fig. 1), and welfare of some of the small and endemic plant populations of these grasslands (see Safford 1999a). It is possible that plant demises have occurred due to the regular fires, in special those species that are restricted to mesic habitats, but many of the typical high-altitude taxa exhibit capacity to sprout, apparently as a pre-adaptation against the frost, which work against the fire pressure (e.g., geophytes). The occurrence of natural fires is apparently a rare event on grasslands, and it would be basically restricted to the wet season - when lightning occurrence is frequent - in contrast to anthropogenic fires during the dry season.

This study was carried out in three sites harboring grasslands, which were submitted to different fire regimes along the years. There is no official register of fire occurrences, and information was obtained with both the PNSB staff and inhabitants in the region, covering the last 45-50 years. The first area (22°43'57'' S, 44°37'06'' W) is up to a private farm (Fazenda Mariana), which has been burned each two-three years (Fig. 1). The last fire in that area occurred ca. five months before the beginning of this study. The second area (22°44'50'' S, 44°36'57'' W) is close to the Santo Izidro's waterfall and has suffered eventual fires at intervals of five-ten years. The last fire in this area occurred five years before the beginning of our observations, but was burned again in 1998. At the beginning of this project, there was no register of fire in the third area (22°44'12'' S, 44°36'55'' W), which presented marked differences in structure, with many treelets and large shrubs (Fig. 1). This area was burned during this study in Sep, 1999. In accordance with the older residents, this latter area was the only large one at Serra da Bocaina that did not have been burned at least once in the last 50 years.

We carried out the floristic survey by monthly collections in the three areas, in addition to non-systematic collections in other grassland areas located between 1450 m and 2100 m. We collected ca. 260 plant species belonging to 47 families. The most representative families are Asteraceae (ca. 70 spp.), Poaceae (ca. 30 spp.), Cyperaceae (ca. 20 spp.), and Melastomataceae (18 spp.). Orchidaceae, Iridaceae, Rubiaceae and Solanaceae are also well represented. The majority of families presented a few species. Most species were herbs or (sub)shrubs, with small leaves, often lignified and hairy. Many species have leaves with cupressoid or rosette arrangement. Several perennial plants (e.g., *Tibouchina minor*, *Microlicia isophylla*, *Esterhazya macrodonta*, *Escallonia farinacea*) presented well-developed underground organs. These vegetative features are typical of plants living in high altitude tropics (Smith & Young 1987), and are related to some environmental factors, such as water and temperature stress (Camerik & Werger 1981), acid soils (Safford 1999a) and regular fires (Laegaard 1992).

MATERIAL AND METHODS

We made 25 field trips to Serra da Bocaina between Dec 1997 and Feb 2000, totaling 211 days of field work. The pollination biology at the community level was studied along a transect ca. 1 km long in each of the three study sites. We studied all plant species, but Cyperaceae and Poaceae, located until 5 m right or left of the transects. The following floral attributes were registered in field: shape, symmetry, dimensions, odor presence, color and rewards. We classified the flowers along eight different types (after Faegri & van der Pijl, 1979 and Endress, 1994): inconspicuous, dish (bowl), brush, bell (funnel), flag, gullet, tube, and revolver. Tube type included both salverform and spurred flowers. The florets in Asteraceae were included in the tube type, and the capitula as a whole was classified as dish or brush type. Floral measures were taken, in accordance to the flower shape, by a caliper in at least five fresh flowers (see Table 1). The main flower color was determined using a color guidebook (Kornerup & Wanscher, 1963). We grouped the flowers in six color sets to the analysis at community level. The color groups are: i. *violet* - showy combinations of blue and red, such as purple and magenta; ii. *pink* - light colors based on blue or red, such as rose, lavender and lilac; iii. *red* - orange and red; iv. *yellow* - bright and deep yellow; v. *pale* - sallow colors with greenish, yellowish or brownish tonalities, such as cream; and vi. *white* - bright, apparently pure, white. For many species, pollen viability was estimated by its cytoplasmic stainability, using the acetic carmine test (Radford et al. 1974), and the stigmatic receptivity was verified with the H_2O_2 catalase activity test (Zeisler 1938). In some cases, flowers were tagged and bagged in bud stage, and in the following day, nectar was extracted with a graduated microliter syringe (Hamilton, USA). Nectar volume was registered immediately, and nectar sugar concentration was measured with a hand refractometer (Atago).

Sexual systems were determined through the presence of both functional stamens and ovary. Flowers were divided in hermaphroditic (monoclinous) and unisexual (diclinous). Plants with unisexual flowers were classified as monoecious or dioecious. Other information about sexual systems - such as presence of dichogamy and heteromorphy - were registered in part of the species. Breeding systems were studied for some of the species by hand-pollination experiments using bagged flowers, and fluorescence microscopy (Martin 1959). Plants along the transects were monthly accompanied from Dec 1998 to Feb 2000, and two phenology parameters were registered: *flowering time* - months in which each species was in flower; and *blooming peak* - months in which more than 50% of the individuals of each species presented flowers.

Pollinator groups on each species were determined through focal observation on flowers for at least four hours. In general, observations were distributed along sessions lasting one-two hours, but longer sessions (three-eight hours) were done for some species, usually in those ones that we have observed for more than 12 hours (see Appendix). For each species, we tried to concentrate the focal observation on the most probable period of visitation. For this, most observation sessions were done at the middle of the day, because in general insects were more active at this day period at the study sites. Only observations under good climatic conditions and during the flowering peak of each species were considered for the total time of observation. Visitors with pollen grains adhered on their body, which touched the stigmas during their visits, were considered pollinators. Hummingbirds were identified in field or through photographs. Insects visiting the flowers were collected as far as possible by means of an entomological net. Insect specimens were identified by specialists. The non-captured insect visitors were grouped in different hierarchical categories, at least at the order level (e.g., Diptera, Coleoptera), and in a few cases, until the genus (e.g., *Bombus*). For the broad community study, we divided both captured and non-captured insect visitors along seven functional groups (after Root, 1967; Cummins, 1973): large bees, small bees, wasps, syrphids, other dipterans, butterflies and beetles. Large bees are those larger than 12 mm. Plant species were grouped in pollinating systems, which were determined using a number of common floral traits of plants pollinated in a similar way by one or two animal groups. A large fraction of species were pollinated by three or more groups, but in some of them, one or two groups were clearly identified as main pollinators by means of frequency of visits, behavior of agents, and flower morphology. In these species, other than the main pollinators were called additional agents. Plant species pollinated either exclusively by one group or in which main pollinators may be accessed were named specialists. It was not possible to determine main pollinators in the remaining species, which were put together in the pollination system by several insect groups. These latter plant species were named generalists. However, there may be noticeable differences in the pollination systems of the generalists that may be detected in further studies at the populational level.

RESULTS

We studied a total of 124 species from 37 families. Forty species belonged to Asteraceae (32%), followed by Melastomataceae (10 spp., 8%). Nineteen (51%) and seven (19%) families were represented, respectively, by one and two species.

FLORAL BIOLOGY AND POLLINATOR AGENTS AT THE COMMUNITY LEVEL

A. FLORAL TRAITS

The most common flower color groups were violet (29.8%) and pale (28.2%), followed by yellow (17.0%). Pink, white and red groups, in such order, were less represented. Most flowers were tubular (47.6%), followed by dish-shaped (28.2%). Considering the shape of the capitula as a whole instead of the florets for Asteraceae, dish-shaped blossoms were the most frequent (43.6%), followed by brush (16.9%) and tube type (15.3%). Bell flowers (11.3%), and gullet, inconspicuous, flag, and revolver flowers (12.8% together) were less represented. Most plants had actinomorphic flowers (69.4%), and the remaining species had zygomorphic ones (25.8%) or both types of flowers (4.8%). Small flowers were predominant, for example, from the 65 species with tubular or gullet flowers, 55.4% had corolla tubes ≤ 5 mm long, and only 13.8% had >10 mm long tubes. Nectar was the exclusive or main resource for 71.0% of the species. Although we have carefully measured nectar production only in a few species, low nectar production (i.e., less than 2 µl) was prevalent. In general, high nectar production was restricted to some species with tubular flowers, which were pollinated by hummingbirds or large bees, and also among the species adapted to moth-pollination (see below).

The great majority of species had hermaphroditic flowers (82.3%), and a few were either monoecious (3.2%) or dioecious (8.9%). The latter group was represented by the eleven species of the genus *Baccharis* (Asteraceae). Other seven species of Asteraceae (5.6%) presented both hermaphroditic and unisexual (ligulate) flowers (gymnomonoecism). We detected spontaneous self-pollination in several species, including plants that were pollinated by animals (Table 1).

Table 1. Floral features and pollinator groups of 124 plants in the high-altitude grasslands at Serra da Bocaina. *Gyno/Andro* = pistil height from the corolla base x stamen height from the corolla base (or spur base in spurred flowers). *Res.* = floral resource. Flower measures are the mode.

Family Species	Sexual system	Flower shape[1]	Flower symmetry and size[1, 2]	Gyno/ Andro	Flower color[3]	Res.	Pollinators
Amaryllidaceae							
*Hippeastrum glaucescens**	H	tube	Zy, 14 (82) x 7	114 x 96	RE	N	Hb
Apiaceae							
Eryngium canaliculatum	H, Pa	incons.	Ac, d1	1 x 1	PA	N P	Co .
Eryngium horridum	H, Pa	incons.	Ac, d1	2 x 4	PA	N P	Bs, Di, Le, Sy, Wa
Apocynaceae							
Mandevilla erecta	H, K	tube	Ac, 13 x 3	5 x 8	PA	N	undet.
Aquifoliaceae							
Ilex amara	U-M, Td	bell	Ac, 4 x 2	2 x	PA	N	Bs, Wa
			Ac, 4 x 2	x 2		N P?	
Asclepiadaceae							
Gonioanthela hilariana	H	dish	Ac, d1	1 x 1	PA	N	Wa
Oxypetalum appendiculatum	H	revol.	Ac, 8 x 3	2 x 2	PA	N	Wa
Oxypetalum sublanatum	H	revol.	Ac, 8 x 5	5 x 5	PA	N	Bl
Tassadia subulata	H	dish	Ac, d1	1 x 1	PA	N	Sy
Asteraceae							
Achyrocline satureioides	H, Pa, 2a	tube (dish)	Ac, 4 x <1 (14)	5 x 5	PA	N	Bs, Di, Sy, Wa
	U		Ac, 6 x <1	10 x		N	
Baccharis aphylla	U-D	tube (dish)	Ac, 5 x <1 (2)	6 x	PA	N	Di, Wa
			Ac, 4 x 1 (5)	x 6		N	
Baccharis curitybenses	U-D	tube (dish)	Ac, 5 x <1 (7)	5 x	PA	N	Wa
			Ac, 5 x <1 (6)	x 6		N	

Baccharis dracunculifolia	U-D	tube (dish)	Ac, 2 x <1 (1)	3 x	PA	N	Di, Wa (Le?, Sy?)
			Ac, 2 x <1 (4)	x 3		N P	
Baccharis intermixta	U-D	tube (dish)	Ac, 2 x <1 (2)	4 x	PA	N	Wa
			Ac, 3 x <1 (4)	x 4		N	
Baccharis leptocephala	U-D	tube (dish)	Ac, 2 x <1 (2)	3 x	PA	N	Sy, Wa
			Ac, 3 x <1 (3)	x 4		N	
Baccharis pentziifolia	U-D	tube (dish)	Ac, 3 x <1 (2)	5 x	PA	N	Co, Di, Sy, Wa
			Ac, 3 x <1 (4)	x 5		N P	
Baccharis platypoda	U-D	tube (dish)	Ac, 3 x <1 (5)	7 x	PA	N	Bs, Di, Wa
			Ac, 4 x 1 (6)	x 6		N P	
Baccharis tarchonanthoides	U-D	tube (dish)	Ac, 3 x 1 (7)	4 x	PA	N	Bs, Co, Di, Sy, Wa
			Ac, 2 x 1 (5)	x 3		N	
Baccharis sp. 1	U-D	tube (dish)	Ac, 3 x <1 (2)	7 x	PA	N	Wa
			Ac, 4 x <1 (4)	x 7		N	
Baccharis sp. 2	U-D	tube (dish)	Ac, 4 x <1 (2)	5 x	PA	N	Bs, Di, Wa
			Ac, 4 x 1 (6)	x 5		N	
Baccharis sp. 3	U-D	tube (dish)	Ac, 2 x <1 (1)	4 x	PA	N	Wa
			Ac, 2 x <1 (2)	x 3		N	
Barrosoa betonicaeformis	H, Pa, 2a	tube (brush)	Ac, 3 x <1 (10)	6 x 5	VI	N	Bs, Co, Le
Chaptalia integerrima	H, Pa, 2a	tube (brush)	Ac, 10 x 1 (22)	14 x 3	WH	N P	Bs, Co, Le, Wa
	U. Li		Zy, 2 x <1	3 x		N	
Chaptalia runcinata	H, Pa, 2a	tube (dish)	Ac, 3 x <1 (12)	4 x 4	YE	N P	Bs, Di, Le, Sy
	U, Li		Zy, 2 x <1	3 x		N	
Chromolaena megacephalum	H, Pa, 2a	tube (brush)	Ac, 4 x <1 (16)	9 x 8	VI	N	Bs, Bl, Co, Di, Le, Wa
Chromolaena xylorhiza	H, Pa, 2a	tube (dish)	Ac, 4 x 1 (4)	6 x 4	VI	N	undet.
Erigeron maximus	H, Pa, 2a	tube (dish)	Ac, 4 x 1 (35)	8 x 7	YE	N P	Bs, Co, Di
	U, Li		Zy, 3 x <1	7 x		N	
Eupatorium cf. *decumbens*	H, Pa, 2a	tube (dish)	Ac, 5 x <1 (9)	7 x 6	VI	N	Bl
Eupatorium sp. 1	H, Pa, 2a	tube (brush)	Ac, 7 x <1 (10)	15 x 13	WH	N P	Bl, Le
Eupatorium sp. 2	H, Pa, 2a	tube (dish)	Ac, 6 x <1 (8)	8 x 7	VI	N	Bs, Bl, Co, Di, Le, Wa
Eupatorium sp. 3	H, Pa, 2a	tube (brush)	Ac, 9 x 1 (12)	19 x 18	VI	N	Bs, Le
Eupatorium sp. 4	H, Pa, 2a	tube (brush)	Ac, 6 x 1 (8)	9 x 8	WH	N P	Bs, Co, Di, Le, Sy, Wa
Gochnatia paniculata	H, Pa, 2a	tube (brush)	Ac, 3 x <1 (10)	8 x 7	PA	N P	Sy, Wa

Graziela gaudichaudeana	H, Pa, 2a	tube (brush)	Ac, 3 x <1 (5)	7 x 5	WH	N P	Bs, Co, Di, Le, Wa
Hypochaeris gardnerii	H, Pa, 2a, U,	tube (brush)	Ac, 7 x <1 (16)	10 x 9	YE	N	Bs, Bl
	Li		Zy, 5 x <1	11 x			
Lucilia lycopodioides	H, Pa, 2a	tube (dish)	Ac, 6 x 1 (3)	7 x 6	PA	N	Wa
	U, Li		Zy, 6 x 1	7 x			
Mikania nummularia	H, Pa, 2a	tube (brush)	Ac, 4 x 1 (3)	5 x 4	WH	N	Le, Wa
Mikania sessilifolia	H, Pa, 2a	tube (dish)	Ac, 2 x 1 (5)	4 x 3	PA	N	Di, Sy, Wa
Mikania lundiana	H, Pa, 2a	tube (brush)	Ac, 8 x <1 (4)	11 x 9	PA	N P	Bs, Le, Wa
Senecio oleosus	H, Pa, 2a	tube (brush)	Ac, 7 x 1 (40)	10 x 9	YE	N P	Bs, Bl, Sy
	U, Li		Zy, 7 x 1	7 x			
Stevia myriadenia	H, Pa, 2a	tube (brush)	Ac, 5 x <1 (10)	7 x 6	PK	N P	Bs, Bl, Di, Sy
Symphyopappus compressus	H, Pa, 2a	tube (brush)	Ac, 6 x 1 (7)	12 x 11	WH	N P	Bs, Bl, Di, Le, Wa
Vanillosmopsis erythropappa	H, Pa, 2a	tube (brush)	Ac, 5 x <1 (14)	10 x 8	VI	N P	Bs, Bl, Di, Le, Sy, Wa
Vernonia herbacea	H, Pa, 2a	tube (brush)	Ac, 5 x <1 (15)	11 x 10	VI	N	Bs, Bl
Vernonia megapotamica	H, Pa, 2a	tube (brush)	Ac, 2 x 1 (12)	5 x 4	VI	N P	Bs, Di, Le, Wa
Vernonia aff. *rosea*	H, Pa, 2a	tube (brush)	Ac, 10 x 1 (21)	15 x 14	VI	N	Bl
Vernonia tomentella	H, Pa, 2a	tube (brush)	Ac, 9 x <1 (20)	15 x 14	VI	N P	Bs, Bl, Le
Vernonia tragiaefolia	H, Pa, 2a	tube (brush)	Zy, 4 x <1 (9)	9 x 7	VI	N	Bs, Bl
Vernonia westiniana	H, Pa, 2a	tube (brush)	Ac, 6 x <1 (11)	10 x 7	VI	N P	Bs, Bl, Di, Le, Wa
Bromeliaceae							
Dyckia tuberosa	H, K	tube	Zy, 13 x 5	10 x 12	RE	N	Hb
Campanulaceae							
Wahlenbergia brasiliensis	H, Pa, 2a	bell	Ac, 3 x 3	5 x 4	PK	N P	Bs, Sy
Clethraceae							
Clethra scabra	H	bell	Ac, 2 x 2	2 x 2	PA	N	Bs, Co, Di, Le, Wa
Convolvulaceae							
Convolvulus crematifolius	H, A	bell	Ac, 12 x 14	7 x 7, 6	PK	N P	Bs, Sy
Ipomoea procumbens	H, A, K	bell	Ac, 38 x 11	26 x 25, 21	PK	N P	Bl
Jacquemontia glandiflora	H, K	bell	Ac, 18 x 23	14 x 11	VI	N P?	Bs, Bl, Wa

Cunoniaceae							
Weinmania organensis	H	dish	Ac, d3	2 x 2	PA	N	Co, Le, Wa
Droseraceae							
Drosera montana	H	dish	Ac, d10	3 x 2	PK	P	Sy
Ericaceae							
Agarista hispidula	H, 2a	tube	Ac, 11 x 2	8 x 7	RE	N	Hb (SSP)
Gaylussacia chamissonis	H, 2a	bell	Ac, 7 x 3	7 x 5	WH	N	Bs, Wa
Gaylussacia jordanensis	H	bell	Ac, 9 x 6	10 x 5	WH	N P	Bs, Bl, Wa
Eriocaulaceae							
Paepalanthus paulensis	U-M	incons.	Ac, d1	2 x	PA	N	Bs, Co, Di, Le, Sy, Wa
		incons.	Ac, d1	x 2		N P	
Paepalanthus polyanthus	U-M	incons.	Ac, d1	2 x	PA	N	Co, Di, Le, Sy, Wa
		incons.	Ac, d1	x 2		N P	
Erythroxylaceae							
Erythroxylum microphyllum	H, S	dish	Ac, d7	5 x 2, 2 x 5	PA	N	Bs, Wa
Euphorbiaceae							
Croton dichrous	U-M, Td	dish	Ac, d2	2 x	PA	N	Bs, Di, Sy, Wa
		dish	Ac, d3	x 2		N P	
Gentianaceae							
Deianira nervosa	H, Pg, K	dish	Ac, d15	3 x 2	PK	P	Sy (SSP)
Irlbachia oblongifolia	H, Pa	tube	Zy, 20 x 3	16 x 15	PA	N	undet. (SSP)
Irlbachia pedunculata	H, Pa	tube	Zy, 32 x 12	30 x 29	RE	N?	undet. (SSP)
Irlbachia pendula	H, Pa, Pg	tube	Zy, 25 x 9	22 x 20	VI	N?	undet. (SSP)
Zygostigma australe	H, Pg	dish	Ac, d20	3 x 2	VI	P?	Bs, Sy (SSP)
Gesneriaceae							
Sinningia allagophylla	H, Pa, K	tube	Zy, 14 x 3	11 x 14	RE	N	Hb
Grossulariaceae							
Escallonia farinacea	H, Pa, K	bell	Ac, 3 x 2	5 x 4	WH	N	Bs

Hipericaceae							
Hipericum brasiliense	H, Ax	dish	Ac, d22	4 x 3	YE	P	Bs, Bl, Di, Sy
Hipericum ternum	H, Ax	dish	Ac, d22	4 x 3	YE	P?	undet.
Iridaceae							
Alophia geniculata	H, K	bell	Ac, 20 x 14	23 x 12	VI	P N?	Bs, Bl, Sy
Alophia sp. 1	H, K	bell	Ac, 20 x 12	10 x 8	PK	P N?	Bs, Sy
Calydorea campestris	H	dish	Ac, d28	5 x 4	VI	P	Bs, Sy
Sisyrinchium micranthum	H	tube	Ac, 5 x 2	3 x 3	VI	P O	Bs, Sy
Sisyrinchium vaginatum	H	dish	Ac, d26	6 x 5	YE	P O	Bs, Sy
Lamiaceae							
Hyptis lippioides	H, Pa	gullet	Zy, 4 x 2	12 x 8	VI	N	Bs, Bl
Hyptis plectranthoides	H, Pa	gullet	Zy, 2 x 1	6 x 5	VI	N	Bs, Bl
Hyptis umbrosa	H, Pa	gullet	Zy, 3 x 1	5 x 5	VI	N	Bs, Wa
Peltodon radicans	H, Pa	gullet	Zy, 5 x 1	8 x 6	VI	N	undet.
Leguminosae							
Chamaecrista sp. 1	H, K, A	bell	Zy, 12 x 7	12 x 12,4	YE	P	Bl
Crotalaria breviflora	H, 2a, A	flag	Zy, k12 x f12	11 x 10	YE	N P	Bs, Bl
Lupinus velutinus	H, 2a, A	flag	Zy, k13 x f16	12 x 12	VI	P	Bl (SSP)
Lobeliaceae							
Lobelia camporum	H, Pa, 2a	gullet	Zy, 8 x 3	14 x 12	PK	N	Bs, Bl
Lythraceae							
Cuphea glutinosa	H, Pa	tube	Zy, 8 x 2	9 x 9	VI	N	Bs, Bl, Le, Sy, Wa
Malpighiaceae							
Byrsonima variabilis	H	dish	Zy, d13 x 10	3 x 3	YE	O P	Bs, Bl
Malvaceae							
Pavonia cf. *reticulata*	H, K	bell	Ac, 9 x 9	7 x 6	YE	N P	Bs
Sida sp. 1	H, K	bell	Ac, 18 x 25	17 x 9	PK	N	Bs

Melastomataceae							
Leandra erostrata	H	dish	Ac, d7	6 x 6	PK	P?	undet. (Ax?)
Leandra sp. 1	H	dish	Ac, d6	5 x 5	WH	P?	undet. (Ax?)
Leandra sp. 2	H	dish	Ac, d7	14 x 12	PK	P?	undet. (Ax?)
Leandra sp. 3	H	dish	Ac, d8	15 x 13	PK	P?	undet. (Ax?)
Microlicia isophylla	H, A	dish	Zy, d20	3 x 4	VI	P	undet. (Ax?)
Tibouchina frigidula	H, A	dish	Zy, d44	14 x 16	VI	P	Bl
Tibouchina martialis	H, A	dish	Zy, d55	15 x 20	VI	P	Bl
Tibouchina minor	H, A	dish	Zy, d30	6 x 7	VI	P	Bs, Bl
Trembleya parviflora	H, A	dish	Zy, d18	5 x 5	PK	P	Bs
Trembleya phlogiformis	H, A	dish	Zy, d22	4 x 4	VI	P	Bs, Bl
Ochnaceae							
Ouratea semiserrata	H, Pa	dish	Ac, d16	6 x 5	YE	P	Bs, Bl
Orchidaceae							
Epidendrum secundum	H	tube	Zy, 5 x <1	6 x 6	VI	N	undet. (Bl?)
Habenaria parviflora	H	tube, spur	Zy, 8 x <1	9 x 9	PA	N	undet.
Oncidium barbaceniae	H	dish	Zy, d22 x 19	3 x 2	YE	O?	undet. (Bs?, Bl?)
Oncidium blanchetii	H	dish	Zy, d24 x 15	2 x 2	YE	O?	undet. (Bs?, Bl?)
Oncidium sp. 1	H	dish	Zy, d15 x 11	2 x 2	YE	O?	undet. (Bs?, Bl?)
Polygalaceae							
Polygala brasiliensis	H, Pa?	flag	Zy, k2 x f3	2 x 2	VI	N P?	Bs (SSP?)
Polygala cneorum	H, Pa?	flag	Zy, k3 x f4	3 x 3	VI	N P?	Bs (SSP?)
Rubiaceae							
Borreria capitata	H, Pg?, K	tube	Ac, 3 x 1	4 x 4	WH	N	Bs, Sy, Di, Wa
Borreria tenella	H, Pg, K	tube	Ac, 2 x 1	3 x 3	VI	N	Bs, Wa
Declieuxia cordigera	H, S	tube	Ac, 7 x 1	8 x 6, 6 x 8	VI	N	Bs, Bl, Le, Wa
Galianthe angustifolia	H, S	tube	Ac, 3 x 1	4 x 2, 2 x 4	PA	N	Bs, Bl, Di, Le, Sy, Wa
Galianthe brasiliensis	H, S	tube	Ac, 3 x 1	4 x 3, 3 x 4	WH	N	Bs, Di, Le, Sy, Wa

Galium hypocarpium	H, S?	dish	Ac, d1	2 x 1	PA	N	Di, Wa
Scrophulariaceae							
Esterhazya macrodonta	H, Pa, K	gullet	Zy, 24 x 10	38 x 34	RE	N	Hb
Solanaceae							
Solanum aculeatissimum	H, Am	dish	Ac, d12	10 x 8	YE	P	Bs
Solanum americanum	H	dish	Ac, d4	1 x 1	YE	P	Bs
Solanum pseudocapsicum	H	dish	Ac, d11	4 x 3	YE	P	Bs
Solanum swartzianum	H	dish	Ac, d17	5 x 4	YE	P	Bs
Solanum viarum	H, Am?	dish	Ac, d16	10 x 8	PA	P	Bs
Verbenaceae							
Verbena hirta	H, A, K	tube	Ac, 6 x 1	3 x 4, 5	VI	N	Bs, Bl, Le, Sy, Wa
Violaceae							
Viola cerasifolia	H, K	tube	Zy, 6 x 3	6 x 4	VI	P N	Bs
Xyridaceae							
Xyris asperula	H	dish	Ac, d13	4 x 4	YE	P	Bs, Sy
Xyris tortulla	H, K	dish	Ac, d22	3 x 3	YE	P	Bs, Sy

Abbreviations - Floral traits: A = heterandrous, Ac = actinomorphic, Am = andromonoecious, Ax = apomictic, D = dioecious, H = hermaphroditic, K = herkogamous, Li = ligulate floret, M = monoecious, N = nectar, O = oil, P = pollen, Pa = protandrous, Pg = protogynous, S = heterostylic, SSP = spontaneous self-pollination, Td = temporal dioecious, U = unisexual (diclinous) flower, Zy = zygomorphic, 2a – secondary pollen presentation. Pollinator groups: Bl = large bees, Bs = small bees, Co = beetles, Di = flies but syrphids, Hb = hummingbirds, Le = butterflies, Sy = hover flies (syrphids), Wa = wasps. ? = information to be confirmed.

[1] The shape of the blossom in Asteraceae (head) and its width are given in brackets, in addition to the measures of the tubular florets.

[2] Flower size for tube, gullet, bell and revolver type is effective corolla length vs. opening width, for dish, brush, and inconspicuous is the flower width (diameter - d), and for flag is keel (k) vs. flag (f) length.

[3] Main color of corolla, but Solanaceae (anthers) and Cunoniaceae (sepals). Color groups: PA = pale, PK = pink, RE = red, VI = violet, WH = white, YE = yellow.

* Hummingbirds perch on the corolla of the large *Hippeastrum* flowers (corolla tube length in brackets) during the visits. Nectar is concealed in a tube at the corolla base, whose size is the effective corolla length.

B. POLLINATOR AGENTS

A wide array of pollinator agents was observed (Appendix), although pollinator visits were scarce in many species, and some typical Neotropical pollinator groups were not detected. Hymenopterans followed by dipterans were the most important pollinators (Table 2). Hummingbirds were the only vertebrate group observed. Only 33.6% of the plant species (36 out 107 species) were pollinated by just one pollinator group. However, for 50 out 71 species pollinated by two to six pollinator groups, it was possible to determine one or two insect groups - respectively for 33 and 17 plant species - acting as the main pollen vectors. The remaining 21 (19.6%) species were generalists, since there was not a dominant pollinator agent. All insect groups but large bees acted in more species as additional agents than as exclusive and main agents (Table 2).

Table 2. Number of plant species pollinated by each pollinator group in the high altitude grasslands at Serra da Bocaina. Percentages are given in brackets (n = 107 plant species). As many species are pollinated by two to six pollinator groups, the totals exceed 100%.

Pollinator Groups	**Role in the pollination**			
	Exclusive	**Main***	**Additional**	**Total**
Small bees §	12 (11.2)	21 (19.6)	39 (36.5)	72 (67.3)
Wasps	7 (6.5)	15 (14.0)	26 (24.3)	48 (44.9)
Large bees §	8 (7.5)	18 (16.8)	10 (9.4)	36 (33.6)
Syrphids	3 (2.8)	8 (7.5)	23 (21.5)	34 (31.8)
Other flies	0	3 (2.8)	26 (24.3)	29 (27.1)
Butterflies	0	2 (1.9)	24 (22.4)	26 (24.3)
Beetles	? 1 (0.9)	0	13 (12.2)	14 (13.1)
Hummingbirds	5 (4.7)	0	0	5 (4.7)

* - plant species presenting one or two main pollinator groups;
§ - *Apis mellifera* not included;
? - doubtful status

HYMENOPTERANS: Bees and/or wasps were among the pollinator agents in 98 out of 102 plant species pollinated by insects. In addition, hymenopterans were the pollinators of three fourths of the plants pollinated by only one group (Table 2). We registered at least 55 native species of bees, in addition to *Apis mellifera*. The families Apidae (including "Anthophoridae"), Halictidae, and Megachilidae were well represented (28, 16, and 10 species, respectively). Andrenidae and Colletidae each presented only one species. Halictidae bees - mainly due to Augochlorini species - were among the pollinators of ca. a half of the species in the community. Meliponini bees played a minor role on pollination, acting as pollen thieves in several species (e.g., in *Baccharis* and Melastomataceae species, Fig. 3I) and occasionally as pollinators in some generalist plant species. However, *Melipona bicolor* - which is a markedly larger than other Meliponini bees in the area - was an important pollinator for several species (Fig. 3B). Small and large bees belonging to Megachilidae pollinated 13 species from six families. The large Apidae bees belonging to the genera *Bombus*, *Xylocopa* and *Centris* were very important pollinators in the community. The three bumblebee species - mainly *Bombus atratus* - pollinated at least 29 species, and they were either the most frequent or the exclusive pollinators in twelve of them.

Apis mellifera visited flowers of 32 species (Appendix), and probably acted as pollinator in most of them. These bees were frequent visitors in some mainly bee-visited species (see "Pollination systems" below), such as *Ilex amara*, *Gaylussacia chamissonis*, *G. jordanensis*, and *Cuphea glutinosa*. Honeybees were the most important pollinators for the three *Hyptis* species (Lamiaceae), being the only observed flower visitors in the remaining species of this family, *Peltodon radicans*.

We observed at least 47 species of wasps acting as pollinators. The most important family is the predominantly social Vespidae - in special *Polistes* species - followed by Pompilidae and Sphecidae. Many social species were in activity year round and were particularly important pollinators during the cold season (see "Flowering Phenology" below).

DIPTERANS: Syrphids constituted a noticeable group of pollinators in the community, feeding on both nectar and pollen flowers. They were associated to small bees in the pollination of many flowers, and also acted as pollinators in several generalist species. Species of the genus *Toxomerus* (Syrphidae) were particularly important, for example, *T. watsoni* acted as pollinator of 21 species. Flies other than syrphids were represented mainly by Tachinidae and Bombyliidae (bee-flies), and were in general co-pollinators (i.e., one among other pollinator groups with similar importance) of generalist plant species (Fig. 4B).

LEPIDOPTERANS: Pollination by lepidopterans was poorly represented (Fig. 4I). In general, butterflies ("Rhopalocera") and diurnal moths ("Heterocera") played a secondary role in plants pollinated mainly by bees. They were among the most frequent pollinators only in a few Asteraceae species. Butterflies belonging to the genus *Vanessa* (Nymphalinae) were the most frequent flower visitors of this group. In spite of the scarcity of visits to flowers, many different butterflies were observed during the summer and fall, and small butterflies belonging to Hesperiinae (probably species of *Corticea*) were very common in all seasons at the study sites.

COLEOPTERANS: Beetles pollinated a few species, and in general as occasional agents. We observed only beetles visiting *Eryngium canaliculatum* flowers. However, this species is possibly pollinated by other animal groups too, as observed in *E. horridum*, which presents a generalist pollination system (see "Pollination systems" below). Species belonging to the family Cantharidae (Fig. 4H) set the only beetle group with a noticeable importance in pollination at the community level, especially Cantharidae sp. 1 which pollinated ten species.

VERTEBRATES: The interactions between hummingbird-pollinated plants and their agents were the most specialized at the community level. We observed five Trochilinae species in the study area, *Chlorostilbon aureoventris*, *Clytolaema rubricauda*, *Colibri serrirostris*, *Leucochloris albicollis* and *Stephanoxis lalandi* (Fig. 5). These species may be observed year round in the high-altitude areas (forest and grasslands), with the exception of *Colibri serrirostris* which seems to migrate to these highlands on the wet season.

POLLINATION SYSTEMS

A. NECTAR-FLOWERS POLLINATED MAINLY BY SMALL AND LARGE BEES

Here are grouped the species in which large or small bees mainly in search of nectar were the most important pollination agents (Fig. 3A-C). This group presents a high variability of floral traits, and we observed distinct associations of pollination agents among its species. As a whole, this group is the most representative pollination system in the community.

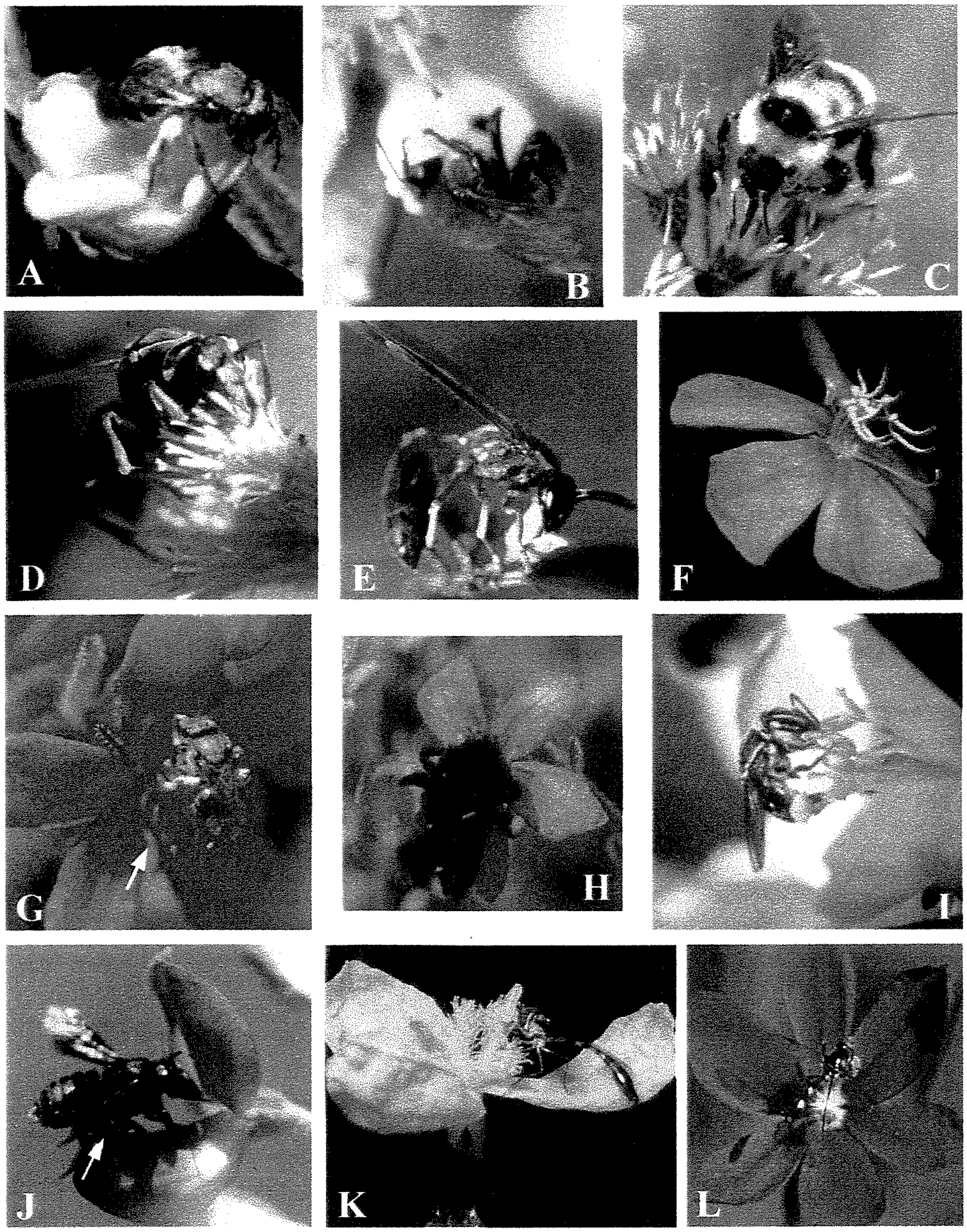

Figure 3. Flowers and pollinators at the Serra da Bocaina grasslands. -Bee nectar-flowers: A. *Augochloropsis* aff. *cognata* (Halictidae) visiting a flower of *Pavonia* cf. *reticulata* (Malvaceae). B. A stingless bee *Melipona bicolor* (Apidae) entering a bell-shaped flower of *Gaylussacia chamissonis* (Ericaceae). C. *Bombus brasiliensis* (Apidae) visiting a head of *Vernonia westiniana* (Asteraceae). -Wasp/fly flowers: D. *Polistes billardieri* (Vespidae) visiting a head of *Gochnatia paniculata* (Asteraceae), which is also pollinated by syrphids. E. *Polybia sericea* (Vespidae) visiting a flower of *Gonioanthela hilariana* (Asclepiadaceae). Bee pollen-flowers: F. A flower of *Tibouchina minor* (Melastomataceae). Note the long poricidal anthers.→

This plant group includes firstly five species pollinated exclusively by small bees. Species of Malvaceae (Fig. 3A) and Polygalaceae were pollinated by Ceratinini or Halictidae bees, and *Escallonia farinacea* was pollinated only by *Colletes* sp. 1 (Colletidae). An important sub-group comprises species predominantly pollinated by small bees, in which wasps were either rare - *Mikania lundiana*, *Hyptis umbrosa*, and *Gaylussacia jordanensis* - or secondary agents - *Ilex amara* and *Gaylussacia chamissonis* (Fig. 3B). The latter three species have white, bell-shaped flowers.

Large bees were the exclusive pollinators of the large flowers of *Ipomoea procumbens* and *Oxypetalum sublanatum*, and also, of two Asteraceae species with showy flowers, *Eupatorium* cf. *decumbens* and *Vernonia* aff. *rosea*. In a similar way, *Lobelia camporum* and *Hyptis lippioides* were mainly pollinated by large bees, whereas small bees acted as eventual pollinators. The typically melittophilous flowers (sensu Faegri & van der Pijl 1979) of *Cuphea glutinosa* and *Verbena hirta* were each pollinated by five different agents, however large bees were by far the most frequent. In addition to data on frequency, in *C. glutinosa*, the pollen load deposited on stigma in a single visit by a large bee was significantly higher than that deposited by either a small bee, a wasp, or a syrphid (unpubl. data). Both *Cuphea glutinosa* and *Verbena hirta* bloom for several months and are among the most common plants in the studied area.

Some of these species closely related to large bees produced high quantities of nectar in relation to the other insect-pollinated species, which typically secreted less than 2 μl of nectar per flower. For example, *Oxypetalum sublanatum* and *Lobelia camporum* flowers secreted 5.5-8 μl and 4-7 μl of nectar per day, respectively.

Another sub-group in this system is composed by species in which both large and small bees seemed to be the most important pollinators - *Hypochaeris gardnerii*, *Vernonia herbacea*,

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G. *Augochloropsis* sp. 1 collecting, by buzzing, pollen from a single anther of a *Trembleya phlogiformis* (Melastomataceae) flower. This bee only occasionally touches the stigma (arrow). H. *Bombus atratus* collecting pollen by buzzing in *Trembleya phlogiformis*, which is mainly pollinated by this bee. I. *Paratrigona subnuda* (Apidae) collecting pollen of a flower of *Trembleya parviflora*. This bee removes pollen from the anther by inserting the proboscis and, in general, acts as pollen thief of this species that is mainly pollinated by other stingless bee, *Melipona bicolor*. J. *Megachile iheringi* (Megachilidae) collecting pollen of the keel-shaped flower of *Lupinus velutinus* (Leguminosae). See text for description of pollen collection mechanism. Note the bee abdomen touching the keel petals (arrow). -Syrphid/small bee pollen-flowers: K. L. Syrphids species feeding directly on pollen of flowers of *Xyris tortulla* (Xyridaceae) and *Calydorea campestris* (Iridaceae), respectively.

V. tragiaefolia, *Jacquemontia glandiflora*, *Hyptis plectranthoides*, *Crotalaria breviflora*, and *Declieuxia cordigera*. Pollination system of some species of Asteraceae diverge slightly from this sub-group since butterflies were either important agents - *Eupatorium* sp. 3 and *Vernonia westiniana* (Fig. 3C) - or secondary agents - *Eupatorium* sp. 1 and *V. tomentella* - in addition to small or large bees as their main pollinators.

B. NECTAR-FLOWERS POLLINATED EITHER BY WASPS OR BY WASPS AND DIPTERANS

This group includes species from several families, in which wasps were the exclusive pollinators, or were the most frequent pollinators in general associated with flies, such as *Gonioanthela hilariana* (Fig. 3C), *Oxipetalum appendiculatum*, *Erythroxylum microphyllum*, *Croton dichrous*, *Clethra scabra* (Fig. 4H), and *Borreria tenella*. Wasps were also observed as the main or exclusive pollinators in many asterids - *Achyrocline satureioides*, *Gochnatia paniculata* (Fig. 3D), *Lucilia lycopodioides*, *Mikania nummularia*, and all species of the genus *Baccharis* but *B. tarchonanthoides* (see “generalist system” below) and *B. dracunculifolia*. In the latter species, and also in *Mikania sessilifolia* and *Galium hypocarpium*, pollination by flies and wasps was important in a similar way. Most species in this group are monoecious or dioecious, or present heterostyly (Table 1).

Flowers of this group typically have easily accessible nectar and in general are pale colored. Short tube (e.g., *Mikania*) or dish (e.g., *Gonioanthela, Erythroxylum*) are the predominant flower shapes, but flowers may be large in width favoring the insect to penetrate in it to reach the nectar (e.g., *Oxypetalum appendiculatum*). In *Gochnatia paniculata*, the corolla tube is ca. 7-8 mm long but the petals are slightly fused. Thus, part of the petals becomes free during the anthesis so that the effective tube length is reduced to 2-3 mm, becoming more suitable for wasps to visit these flowers. In general, wasps presented few pollen grains on their bodies and it is possible that some species belonging to this pollination system are additionally pollinated by the wind (see Discussion below).

C. POLLEN-FLOWERS POLLINATED BY SMALL AND LARGE BEES

Nectarless flowers with poricidal anthers are the most characteristic of this system, including species of Melastomataceae and Solanaceae among others (Fig. 3F-I). Plants of this group were pollinated by large and small bees, which collect pollen by vibration. The large Apidae bees - belonging to the genera *Bombus*, *Xylocopa*, and *Centris* - were the exclusive pollinators of *Tibouchina frigidula*, *T. martialis*, and *Chamaecrista* sp. 1. Large bees were also pollinators of *Tibouchina minor* (Fig. 3F), *Trembleya phlogiformis* (Fig. 3G-H), and *Ouratea semiserrata*, in addition to small bees, such as *Melipona bicolor* and some Halictidae species. The remaining plant species with poricidal anthers - *Trembleya parviflora* (Fig. 3I) and the five *Solanum* species - bear relatively small flowers, which were pollinated only by small bees. Four species of *Solanum* were exclusively pollinated by the same Halictidae species - *Augochloropsis cyanea*. This bee species (Fig. 4C) is an endemic in Brazilian coastal range, and was markedly larger (mean body length 10.1 ± 0.99 mm, range 9-12 mm, n = 10) than other Halictidae species in the study area.

Some flowers without poricidal anthers also belong to this system. The elaborated *Viola cerasifolia* flowers have five anthers opening longitudinally, but the androecium is arranged in such a way to work like a single poricidal anther. This species was mainly pollinated by the small bee *Anthrenoides* aff. *meridionalis* (Andrenidae), which, in addition to vibration, showed a singular pollen collecting behavior on these flowers (see Chapter II for details).

The nectarless flag-shaped flowers of *Lupinus velutinus* were pollinated only by large bees, belonging to the genera *Bombus* (bumblebees) and *Megachile* (leafcutter bees) (Fig. 3J). During the bumblebee visits, the wing petals were flexed downward by the weight of the bee, and thereby pollen was pressed out in portions at the tip of the keel ("macaroni pump" type of pollen presentation, sensu Endress 1994) and contacted the bee's abdomen. Pollen collection by bumblebees was usually improved by vibration on flowers. Leafcutter bees seem to lack the weight necessary for flexing the wings, in such a way pollen could be pressed out the keel. During the visit to a flower, these bees used the head as a lever and thus, the wings were depressed with the front and middle legs (Fig. 3J). The hind legs stroked the sides of the keel, forcing a stream of pollen out of the keel beak, and then, pollen was packed on the bee's ventral abdomen (milking action, sensu Wainwright 1978). Additionally, leafcutter bees, in some occasions, caught on the wing petals using their mandibles and then dug the pollen out of the keel, using their hind legs.

Although its visits were infrequent, *Bombus atratus* collecting pollen by vibration was the effective pollinator of *Alophia geniculata* flowers, which have anthers opening longitudinally.

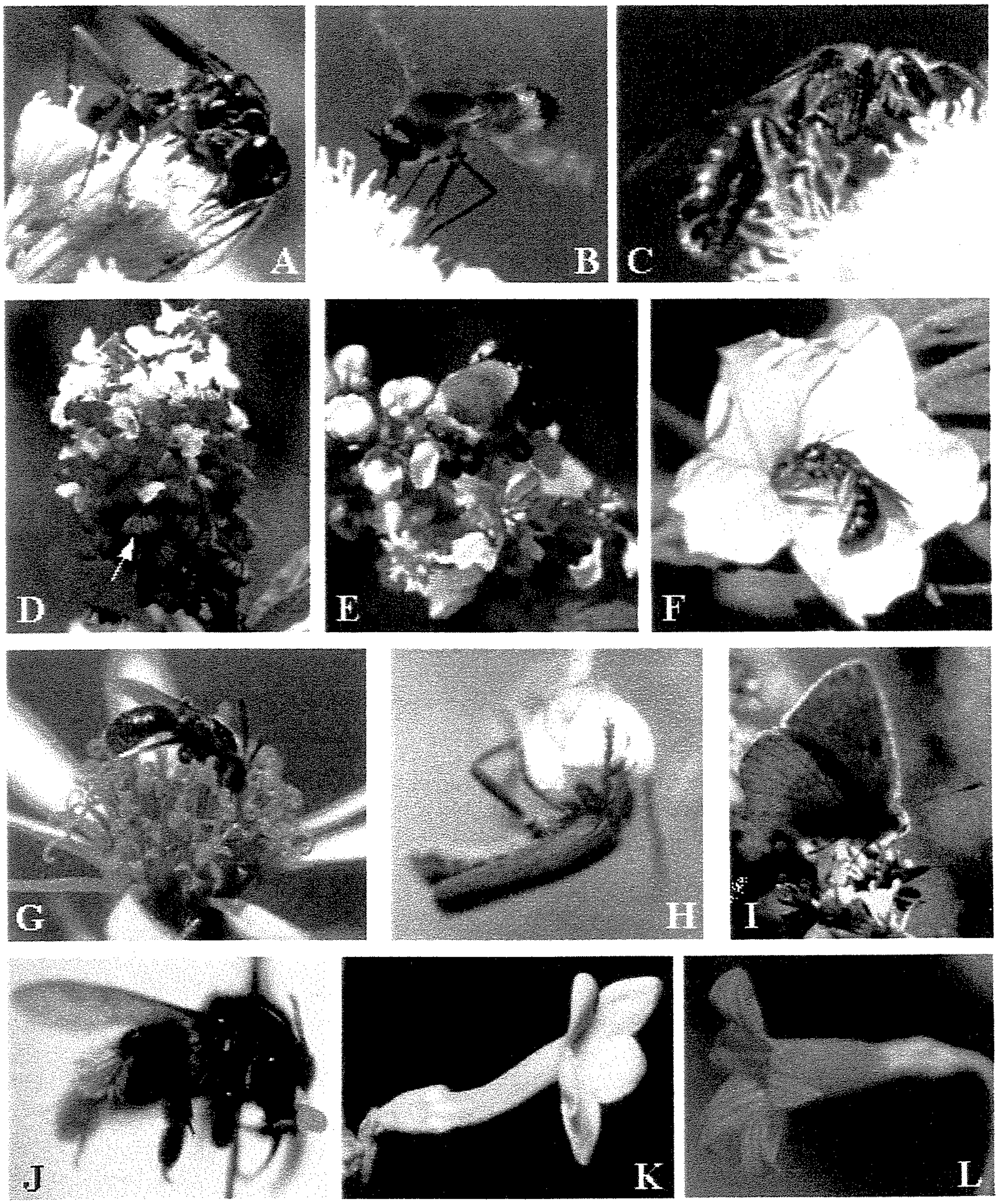

Figure 4. Flowers and pollinators at the Serra da Bocaina grasslands. -Generalist flower: A-C. Species of three distinct pollinator groups visiting the heads of *Eupatorium* sp. 4 (Asteraceae), respectively, a sphecid wasp (*Sphex opacus*, Sphecidae), a beefly (Bombyliidae), and a small bee (*Augochloropsis cyanea*, Halictidae). Oil- flower: D. Inflorescence of *Byrsonima variabilis* (Malpighiaceae). Note the flower oil-glands (elaiophores, arrow). E. *Centris* cf. *insularis* (Apidae) collecting oil of a flower of *B. variabilis*. Syrphid/small bee nectar-flowers: F. *Ceratina* sp. 2 (Apidae) visiting a flower of *Convolvulus crematifolius* (Convolvulaceae). G. *Pseudagapostemon cyaneus* (Halictidae) visiting a head of *Senecio oleosus* (Asteraceae). Minor pollinator agents: H. A beetle (Cantharidae sp. 2) visiting a flower of the mainly wasp-pollinated *Clethra scabra* (Clethraceae). →

Small bees and syrphids frequently fed on pollen of this species, but they only occasionally pollinated its large flowers. A similar pollination system is expected to *Alophia* sp. 1, although we failed to observe large bees on their flowers.

D. POLLEN-FLOWERS POLLINATED EITHER BY SYRPHIDS OR BY SMALL BEES AND SYRPHIDS

Syrphids were particularly connected to some species with pollen flowers, in which they were the exclusive pollinators - *Drosera montana* and *Deianira nervosa* - or co-pollinators in association with small bees - *Zygostigma australe*, *Calydorea campestris*, *Sisyrinchium micranthum* (but see "Other cases" below), *Sisyrinchium vaginatum*, *Xyris asperula*, and *Xyris tortulla* (Fig. 3K-L). Species in this group typically bear small, dish-shaped, actinomorphic, and vivid colored flowers. Pollen grains are easily accessible to pollinators in these species, since the anthers open longitudinally.

E. NECTAR-FLOWERS POLLINATED BY SEVERAL INSECT GROUPS (GENERALIST SYSTEM)

Here are grouped species pollinated by three or more pollinator groups, in which no pollinator agent acted as the most important (generalists). This group includes firstly some species with very small, pale flowers - *Eryngium horridum* (probably also *E. canaliculatum*), *Paepalanthus paulensis*, *P. polyanthus*, and *Weinmannia organensis* - which fit in the diverse small insects (d.s.i.) syndrome (sensu Bawa et al. 1985).

Remaining generalists at Serra da Bocaina are mainly represented by Asteraceae species of several genera: *Baccharis tarchonanthoides*, *Barrosoa betonicaeformis*, *Chaptalia integerrima*, *C. runcinata*, *Chromolaena megacephalum*, *Eremanthus erythropappus*, *Erigeron maximus*, *Eupatorium* sp. 2, *Eupatorium* sp. 4 (Fig. 4A-C), *Graziela gaudichaudeana*, *Stevia myriadenia*,

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I. A butterfly *Thecla* sp. 1 (Lycaenidae) visiting the generalist flowers of *Galianthe brasiliensis* (Rubiaceae). Doubtful pollination systems: J. A female of *Monoeca* sp. 1 (Apidae) with a pollinarium of a species of *Oncidium* (Orchidaceae) attached to the clipeus. This Tapinotaspidini bee was captured while collected oil on flowers of *Byrsonima variabilis*, and its role in the pollination of *Oncidium* species is uncertain. K. Flower of *Irlbachia oblongifolia* (Gentianaceae). Floral traits point to pollination by nocturnal moths, but pollinators were not observed. L. Flower of *Irlbachia pedunculata*. The attractive flowers of this species seem to be adapted to pollination by hummingbirds, but they are nectarless and spontaneously self-pollinated.

Symphyopappus compressus, and *Vernonia megapotamica*. This group is complemented by three Rubiaceae species: *Borreria capitata*, *Galianthe angustifolia*, and *G. brasiliensis* (Fig. 4I). Large insects like bumblebees and Pompilidae wasps may be among the pollination agents in the generalist species of Asteraceae and Rubiaceae, differently of the generalist species of Apiaceae, Eriocaulaceae and Cunoniaceae, which fit in the d.s.i. syndrome (see Appendix).

Although generalist flowers, but d.s.i. species, were restricted to two families (Asteraceae and Rubiaceae), they embody a certain variability in floral traits, for example color, size, pollen presentation and heterostyly, and also in their flowering phenology. Furthermore, genera belonging to the generalist group also present species with specialized pollination systems, e.g., wasp pollination in *Baccharis* and *Borreria*; and bee/butterfly pollination in *Vernonia* and *Eupatorium* (including *Barrosoa*, *Chromolaena*, and *Graziela*). The floral characteristics related to the attraction of a few or several pollinator groups to the flowers of, respectively, specialists or generalists, are uncertain among species in those genera at the study community.

F. HUMMINGBIRD-POLLINATED FLOWERS

Hummingbirds pollinated five species from five families, and were the exclusive pollinators of them. The hummingbird-pollinated species bear tubular/urceolate flowers, which may easily be separated from flowers of other species in the community (Fig. 5). For example, all species with red-orange flowers, but the nectarless spontaneous self-pollinated *Irlbachia pedunculata* (Fig. 4L) were pollinated by hummingbirds.

Plant species each were pollinated by one to four hummingbird species (Appendix). *Leucochloris albicollis* was the main visitor in the study area, pollinating four plant species and being the single pollinator of *Hippeastrum glaucescens* and *Esterhazya macrodonta*. This *Hippeastrum* species is a small herb, which grows close to the forest edges. It bears very large flowers (tepals ca. 140 cm long), and the birds needed to perch on one of the inferior tepals to reach the nectar at the flower base (Fig. 5A). Pollen was deposited mainly on the bird wings. The *Esterhazya* species is a perennial herb with protandrous flowers (Fig. 5B) that last up to 6 days. Nectar removal in the first days of anthesis strongly affects nectar production (see Chapter IV for details).

Sinningia allagophylla is a herb with a long hairy inflorescence with more than 40 flowers, which last up to seven days and present partial herkogamy combined with protandry. This gesneriad was mainly pollinated by *Leucochloris albicollis* and *Stephanoxis lalandi*, but also by *Colibri serrirostris* and *Clytolaema rubricauda* (Fig. 5C). The flower disposition along the inflorescence of the rare terrestrial bromeliad *Dyckia tuberosa* resembles strongly that one in *Sinningia* (Fig. 5C-D). In addition, *Dyckia tuberosa* flowered just before *Sinningia allagophylla* (Fig. 7), suggesting some mimetic relationship between these species. We observed only *Colibri serrirostris* females pollinating this bromeliad (Fig. 5D). *Agarista hispidula* is a shrub that - differently of the previous species - bears dozens of flowers arranged in dense inflorescences (Fig. 5E). The urceolate flowers with poricidal anthers are short, and pollen is secondarily presented in hairs at the corolla opening. It was pollinated very early in the morning, mainly by the small *Chlorostilbon aureoventris* (Fig. 5E), but also by *Leucochloris albicollis*.

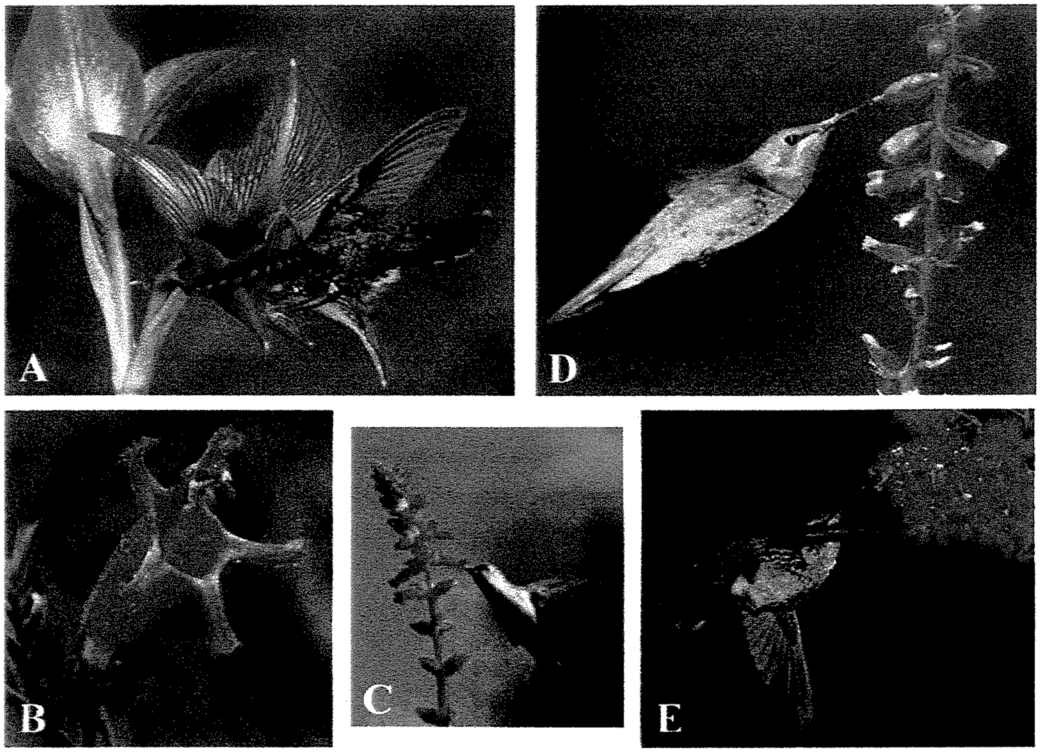

Figure 5. Hummingbirds and their flowers at the Serra da Bocaina grasslands. A. *Leucochloris albicollis* visiting the very large flower of *Hippeastrum glaucescens* (Amaryllidaceae). Note the hummingbird's foot gripping on the inferior tepal. B. Flower of *Esterhazya macrodonta* (Scrophulariaceae), which is also pollinated by *Leucochloris albicollis*. C. A female of *Stephanoxis lalandi* visiting flowers of *Sinningia allagophylla* (Gesneriaceae). D. A female of *Colibri serrirostris* visiting flowers of *Dyckia tuberosa* (Bromeliaceae). Note pollen on bird's bill and forehead, and the similar inflorescence arrangement of *Sinningia* and *Dyckia*. E. A female of *Chlorostilbon aureoventris* visiting flowers of *Agarista hispidula* (Ericaceae).

In general, the ornithophilous species were rare in grasslands. We found only four, seven and eight flowering individuals of *Agarista hispidula*, *Dyckia tuberosa*, and *Hippeastrum glaucescens*, respectively, in the studied areas. *Esterhazya macrodonta* plants were commonly less than ten along each transect, but we found exceptionally 55 flowering individuals along one transect where we also studied its nectar features (see Chapter IV for details). In contrast, *S. allagophylla* was common in many places at Serra da Bocaina. In general, individuals of this species were distributed in small clusters (three to eight plants), which were separated each other by many meters. However, *Sinningia* plants - probably due to clonal reproduction - occurred in large clusters in some areas, with dozens of individuals per ca. 100 m^2. *Esterhazya*, *Agarista* and *Dyckia* plants were scarcely visited, with respectively 0.05, 0.18 and 0.20 visits per hour. Each plant of *Hippeastrum glaucescens* received ca. one visit each two hours. Plants of *Sinningia* growing in small clusters received ca. one visit each three hours, but in large clusters, hummingbirds visited each patch three to six times per hour. In such circumstances, most individuals were visited at intervals of one to two hours, although some plants were neglected for the hummingbirds.

Because of the low flower availability, hummingbird species acted basically as low-reward trapliners in the studied grasslands (foraging strategies after Feinsinger & Colwell 1978). Territorial foraging behavior was observed only in the large clusters of *Sinningia allagophylla*. *Clytolaema rubricauda* and *Stephanoxis lalandi* behaved territorially in these circumstances, and *Leucochloris albicollis* sometimes acted as parasite in territories set by *Clytolaema rubricauda*. Thus, *Leucochloris albicollis* may alternate its foraging strategy from low-reward traplining to territory-parasitism in some instances.

G. OTHER CASES

Many oil-collecting bees - mainly large bees belonging to *Centris* - were observed pollinating the flowers with oil glands (elaiophores) of *Byrsonima variabilis* (Fig. 4D-E). The mechanism for oil-collection by the bees in this species was similar to that observed in other Malpighiaceae species (see Vogel 1990). *Byrsonima variabilis* was also pollinated by small bees belonging to Apidae (Meliponinae) and Halictidae in search of pollen, but in a minor degree. Some oil-collecting bees also collected pollen on this *Byrsonima* species. Flowers of *Sisyrinchium micranthum* bear oil-secreting trichomes on the base of the column built by the fusion of their filaments (see Cocucci & Vogel 2001). However, we failed to detected oil-collecting bees in these flowers, which worked as pollen flowers being pollinated by syrphids and small bees. Other three species - belonging to the genus *Oncidium* - have flowers with elaiophores (see below).

The nectar flowers of *Tassadia subulata* were pollinated exclusively by syrphids, which carried the pollinia on their head. The elaborated, small, ruby flowers of this species are typically myiophilous (sensu Faegri & van der Pijl 1979). Small bees were also associated to syrphids in the nectar secreting flowers of *Senecio oleosus*, *Wahlenbergia brasiliensis*, and *Convolvulus crematifolius* (Fig. 4F-G). The latter two species bear bell-shaped, lilac/lavender flowers. Pollinators firstly fed on nectar in these three species, although they also searched for pollen on them. Syrphids and small bees seemed to be co-pollinators of these species.

The distribution of the pollination systems at the community level is given at the Table 3.

Table 3. Number of plant species belonging to each pollination system in the high altitude grasslands at Serra da Bocaina.

Pollination System	No. plant species	% plant species
Bee nectar-flowers	30*	28.0
Wasp/fly nectar-flowers	22	20.6
Bee pollen-flowers	16	15.0
Syrphid/small bee pollen-flowers	8	7.5
Several insect groups (generalists)	21	19.6
Hummingbird flowers	5	4.7
Other cases	5	4.6
Total	107	
Undetermined	17	

* include the four species of Lamiaceae pollinated mainly or exclusively by *Apis mellifera*.

Floral traits, relation among pollinator groups, and additional subdivisions for each pollination system are given in the text.

SPECIES IN WHICH POLLINATION SYSTEMS ARE DOUBTFUL

Flowers of 17 species were not visited during the focal observation sessions or the visitor role in pollination was unclear. The results and brief discussions of these cases are jointly presented in the present section.

We did not observe oil-collecting bees visiting the flowers of any of the three *Oncidium* species in the studied area (total 47 h of observation), including observations in plants growing close to individuals of *Byrsonima variabilis* in flower. However, an individual of *Monoeca* sp. 1 (Tapinotaspidini, "Anthophoridae") - collected while visiting *B. variabilis* flowers - had one *Oncidium* pollinarium attached to its head (Fig. 4J). An individual of *Megachile aureiventris* (Megachilidae) - collected while landing on a branch - also had one *Oncidium* pollinarium attached to its head. During an observation session on *Lupinus velutinus* flowers, a female individual of *Bombus* (probably *B. atratus*) - after collecting pollen on *Lupinus* flowers - visited quickly a flower of *Oncidium barbaceniae*, which grew close to the *Lupinus* cluster. During this visit to *O. barbaceniae*, the bee held on the flower with its legs, and then vibrated in a missed attempt to collect pollen. This bee was not collected, but the visited flower had no pollinia, indicating that this bee could have removed it. Thus, these observations indicate that bees in search of pollen could be acting as pollinators in these populations of *Oncidium*. In this sense, *Oncidium* flowers would be pollinated by deceit by pollen-collecting bees, in addition to the expected system involving oil-collecting bees (see Singer & Cocucci 1999). So, the following aspects point to a pollination system by deceit in the studied populations of *Oncidium*: i. bees in search of pollen visiting the flowers; ii. bees of the "Anthophoridae" group intensively collected oil on *Byrsonima* flowers, but they were not observed on flowers of the *Oncidium* species growing in the same patch; iii. visits by bees from any group on *Oncidium* flowers were scarce, and the fruit production was very low in the three species.

Pollination by nocturnal moths (Noctuidae and Sphingidae) was not observed. However, we found three species, in which the floral features point to pollination by nocturnal moths (phalaenophily and sphingophily, after Faegri & van der Pijl 1979, see also Endress 1994): *Mandevilla erecta*, *Habenaria parviflora*, and *Irlbachia oblongifolia* (Fig. 4K). These species flowered in the middle of the wet season, and their flowering period overlapped (Appendix). The flowers have narrow greenish or yellowish tubes (spurs in *H. parviflora*), presenting both odor and nectar at night. *Irlbachia oblongifolia* occurs in clusters in wet-soil areas and its long-lived flowers produce 4-8 µl of nectar per night (sugar concentration 14-21%) and are spontaneously self-pollinated at the end of anthesis. The other two species were rare in the studied areas. *Mandevilla erecta* is a plant with large inflorescences and dozens of flowers, which secrete 10-25 µl nectar (sugar concentration 41-44%), but we observed only one fruit produced during three subsequent blooming periods (from 1998 to 2000). Several *Habenaria* *parviflora* plants produced fruits in the studied areas. This species is self-compatible, but spontaneous self-pollination is improbable (Singer 2001). It is pollinated by crepuscular crane-flies and nocturnal moths in an area at the sea level in São Paulo coast (Singer 2001). Results indicate that moths did not frequently use floral resources from grassland plants, but it is expected that these agents occasionally visit these three species.

Similarly to the other two species of the genus, *Irlbachia pendula* flowers were not visited. The tubular flowers are lilac to pale violet, and in general do not produce floral nectar, excepting some rare flowers with diminute nectarioles (sensu Vogel, 1998) on the petals. The flowers show some degree of protandry or, in a few cases, protogyny. In most flowers, as soon as they open, the pollen (in tetrads) is exposed, and the style is short and the stigmatic lobes are closed. After two-three days, the style is elongated, and the stigmatic lobes are deflected, in such a way that the receptive papillate portion faces the corolla opening. At this stage, pollen grains are in contact with the non-receptive stigmatic surface, and both male and female functions overlap. Stigma lobes follow the curving movement, in such a way that late in the flower lifetime (ca. eight days), the receptive surfaces touch the pollen on anthers. Pollen viability is high (> 85%) in all floral stages. Self-pollen grains deposited on stigma grew and reached the ovules. In addition, all observed flowers in the field set fruits, including 18 bagged blossoms. Delayed self-pollination seems to ensure the reproduction of this species, as well as of the other four studied gentians of Serra da Bocaina. Anyway, it is expected that bees may occasionally pollinate flowers of *I. pendula* by deceit.

The two studied species of *Hipericum* have extended flowering periods, with individual plants flowering in different months year round. Flowers of both species are similar; actinomorphic, dish-shaped, with ca. 2.5 cm in diameter, and polyandrous. Corolla, stamens and styles are bright yellow. The fourteen individuals of *Hipericum ternum* observed in the study area had flowers that did not produce pollen, but all flowers developed fruits with seeds. Emasculated flowers examined by microscope showed well developed seeds. Similar results were found for the ca. 40 individuals of *Hipericum brasiliense*. However, we found two individuals of the latter species producing flowers with pollen grains (ca. 95% viability) in Dec 1998. One of these plants was followed since Jan 1998, and curiously, it had produced only flowers without pollen until Dec 1998. The capacity for sexual and apomictic reproduction within the same individual (facultativism) may be environmentally influenced and is probably rarer among plants than animals (Asker and Jerling, 1992). In the pollen-producing flowers of *Hipericum brasiliense*, self- and cross-pollen tubes grew down the style, but only crossed ones seemed to penetrate the ovule. We observed these pollen-producing individuals in Dec 1998 and Jan 1999, and found that several insects searched for pollen and pollinated the flowers (Appendix). Empty anthers were also observed in herbarium specimens of *Hipericum* species from forest areas (V. Bittrich, pers. comm.). It is expected that *H. ternum* also produces pollen in any occasion. Thus, these two species seem to be predominantly apomictic, and some genetic recombination would occur after sporadic pollen production and consequent cross-fertilizations.

No floral visitor was registered along 28 h of observation on the four *Leandra* species. Although we did not study any aspect of their breeding system, there are records of apomixis in species of this genus (e.g., Goldenberg and Shepherd 1998), and it is possible that the *Leandra* species at Serra da Bocaina are also apomictic. Another Melastomataceae, *Microlicia isophylla*, was also not visited. This species is very common on grasslands and bears attractive flowers, with magenta petals and vivid yellow anthers. The smooth pollen grains are highly viable and produced in large quantity. Bees collecting pollen by vibration are the expected pollinators of this species, although it could be also apomictic.

Epidendrum secundum is a common orchid in southeastern Brazil. It bears showy, long-lived flowers - with a narrow tube analogous to a spur - that are pollinated mainly by butterflies, but also by bumblebees in forest sites at São Paulo State (E. R. Pansarin, pers. comm.). We failed to detect pollinators in the focal observations, but we sighted a probable *Bombus* visit one occasion and so, it is possible that bumblebees may be pollinating this species at Serra da Bocaina.

FLOWERING PHENOLOGY

Mean flowering period in grasslands was high - 5.5 months (sd = 2.92 , n = 124) - and the mean flowering peak was 2.6 months (sd = 1.56, n = 124). Flowering pattern in this community was seasonal, with a peak during the middle of the wet season (Fig. 6A). More than 60% of the species flowered in Jan and Feb, and ca. one third of the species was in flowering peak during these two months. There was a drastic reduction on flowering during the end of the dry season/beginning of the wet season (Aug, Sep or Oct). Blooming pattern of species close related to small and large bees followed the pattern observed in the community (Fig. 6A-C).

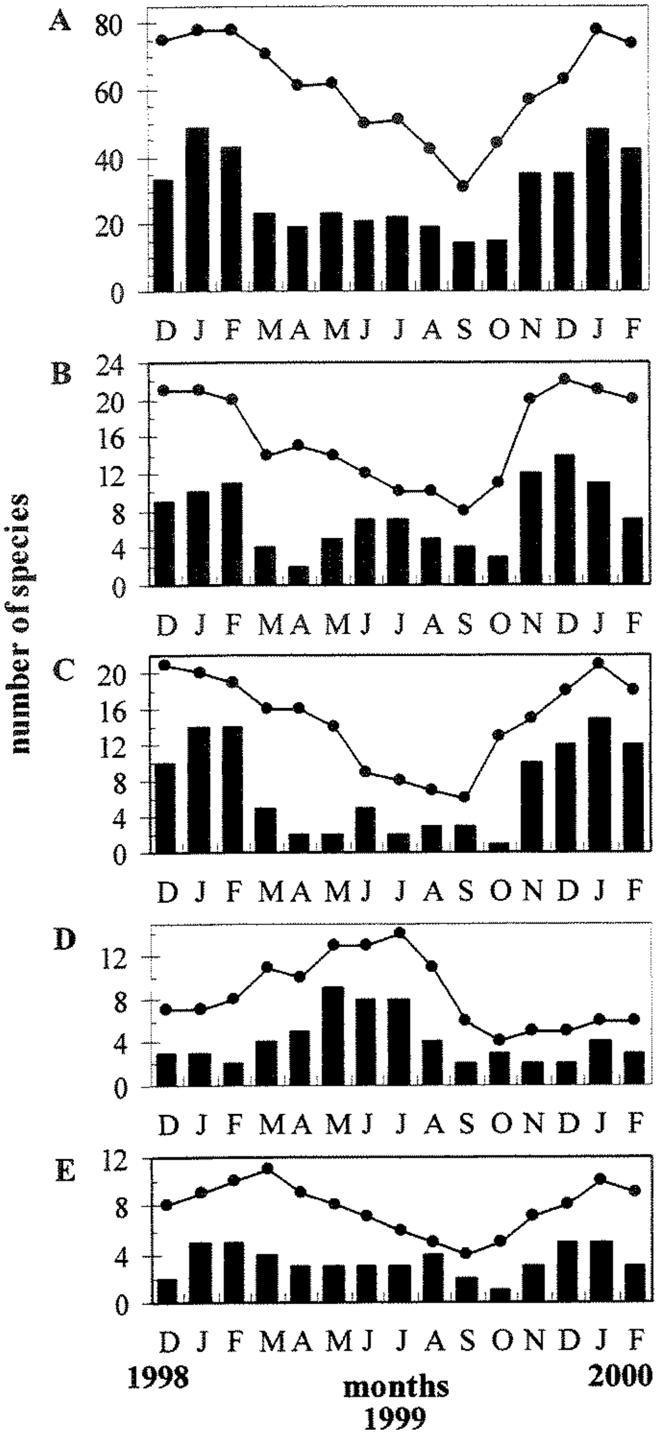

Fig. 6. Number of species blooming (line) and in flowering peak (bars) from Dec 1998 to Feb 2000 at the Serra da Bocaina grasslands. A. Distribution at the community level (n = 124). B to E. Distribution of plant species close related to each pollinator group. B. Small bees (n = 31). C. Large bees (n = 26). D. Wasps (n = 19). E. Syrphids and other dipterans (n = 15).

However, species related to small bees showed a bimodal flowering peak pattern, with a drastic reduction of species in peak during the end of the wet season (Apr) (Fig. 6B). In contrast, most species related to wasp pollination flowered, and also presented their peak of flowering, during the dry season (Fig. 6D). Wasps are very important during that season, for example, eight or nine out of 21 to 23 species in flowering peak during May to Jul 1999 are exclusively or mainly pollinated by wasps (Fig. 6A, D). Flowering pattern of species related to dipterans was more constant along the year, although there is a peak in the hottest months (Fig. 6E).

Flowering patterns of the five hummingbird-pollinated plants was sequential (Fig. 7). However, there were no species flowering in Apr and May, and there was absence of species in flowering peak for several months.

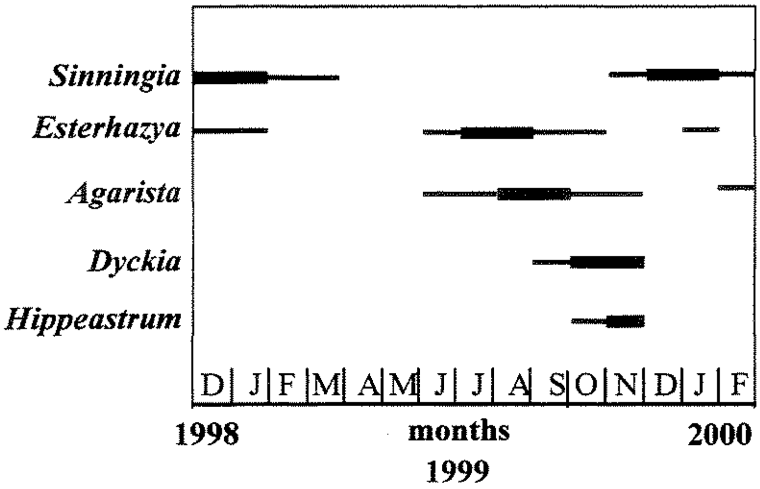

Fig. 7. Flowering patterns of the five hummingbird-pollinated species at the Serra da Bocaina grasslands. Thin and thick lines indicate, respectively, flowering period and peak of flowering. Species are abbreviated by the genus names.

DISCUSSION

We collected ca. 260 species in the Serra da Bocaina grasslands, whereas Martinelli (1989) quoted a total of 215 flowering species to these grasslands, but he studied more restricted areas. About one fifth of the species in this community - belonging to the families Poaceae, Cyperaceae, and Juncaceae - are anemophilous. Thus, this study encompassed about 60% (124) of the animal-pollinated species, and pollinators were determined in ca. a half of the species (107) - excepting wind-pollination - in the community. In addition, ca. 80% of the 47 plant families that we found at the Serra da Bocaina grasslands are represented in this study, thus, our sample is fairly representative of the high-altitude grasslands in the area.

There are no data on floral biology and pollination biology in other areas harboring high-altitude grasslands in southeastern Brazil, which would permit comparative analysis for this ecosystem. However, data on pollination at the community level from ecosystems with strong biogeographic connections with such grasslands are available, for example, for the high temperate Chilean Andes, in special at the subandean scrub zone (Arroyo et al. 1982), the Venezuelan Guayana Highlands, hereafter "morichal" (Ramirez 1989), the Brazilian open savannas, hereafter "cerrado" (Barbosa 1997, and also Silberbauer-Gottsberger & Gottsberger 1988, Oliveira & Gibbs 2000 for other cerrado physiognomies), and to some extend to the Brazilian "campos rupestres" (Faria 1994). Here our discussion is focused on comparison between these ecosystems and the studied grasslands.

FLORAL TRAITS

Flowers with light colors - considering pale, pink, and white color groups together - are well represented at Serra da Bocaina, resembling somehow morichal and cerrado communities, in which light colored flowers predominate (Silberbauer-Gottsberger & Gottsberger 1988, Ramirez 1989, Barbosa 1997). However, more than a half of the species have showy flowers (violet, yellow and red color groups) at Serra da Bocaina. The dominance of Asteraceae and Melastomataceae seems to be connected to the expressive quantity of showy violet-colored flowers in such grasslands. Further, pale flowers were more continuously distributed along the year, in contrast to violet flowers which are more concentrated on wet months. We detected only a weak relation between floral color and frequency of each pollinator group for the community, by means of canonical analysis (unpubl. res.). Strong relation was restricted to hummingbirds and red flowers, and in a minor degree to beetles and wasps with pale flowers. Although we use the human color spectrum, such results for insect responses to flower color resemble the general trends detected by Chittka et al. (1994) and Waser et al. (1996), i.e., there were no statistical differences among insect pollinator groups (at the order level) in the colors of flowers visited, although flies and beetles visited slightly more human white, whereas large bees and butterflies visited more human blue, purple, violet and pink.

The prevalence of nectar as the main floral resource - as observed at the Serra da Bocaina grasslands - was registered in other grassy communities (Arroyo et al. 1982, Ramirez 1989, Faria 1994, Barbosa 1997), and also in forest areas (e.g., Momose et al. 1998). In fact, nectar-flowers are the most important flower class among angiosperms because most pollinator groups are nectar consumers (Endress 1994). The percentage of pollen flowers at Serra da Bocaina was similar to that registered at the campos rupestres (Faria 1994) and open cerrados (Barbosa 1997). Melastomataceae species are the most important pollen-flowers at Serra da Bocaina, as well as in the campos rupestres (Faria 1994). Species of this family are also important pollen sources in the morichal (Ramirez 1989). However, in open cerrados, species of other families (e.g., Leguminosae and Myrtaceae) constitute the chief sources of pollen (Barbosa 1997). Malpighiaceae is represented by several species at the campos rupestres and cerrados (Faria 1994, Barbosa 1997), thus, oil-flowers are more frequent in those communities than at the Serra da Bocaina grasslands.

Although small flowers predominate in morichal and cerrado (Ramirez 1989, Barbosa 1997), flowers in these two communities are even larger than those at Serra da Bocaina. Here again, the noticeable presence of Asteraceae exerts a direct influence on floral patterns. In fact, the distribution of the floral features at the community level is markedly influenced by phylogenetic constraints at the Serra da Bocaina grasslands. The prevalence of small tubular flowers secreting nectar reflects largely the head morphology of the Asteraceae species in this area, independently of their pollinator agents. General floral characteristics at Serra da Bocaina also resemble to some extent those observed for floras on oceanic islands (e.g., Webb & Kelly 1993, Anderson et al. 2001). Such similarity may be related to the island-kind distribution of the high altitude grasslands in southeastern Brazil (see Safford 1999a), since oceanic islands are far from mainland and vegetation at the mountaintops on the Atlantic coastal range is isolated of close-related floras.

The prevalence of hermaphroditic flowers is typical for angiosperms, and consequently characteristic of most communities (Ramirez 1993). Our results hold this tendency for the Serra da Bocaina flora, however, many hermaphrodites presented spatial/temporal separation of the male and female functions, by dichogamy, herkogamy, or heterostyly. In fact, high frequency of dichogamy (protandry) is expected in a flora dominated by Asteraceae, due to the frequent presence of secondary pollen presentation on the style among the Campanulales (see Lloyd & Webb 1986). Further, the female ray-florets of many Asteraceae species confer a state of "protogyny" to the head as a whole. Dioecy has been specially associated to the generalist mode of pollination, carried out by several opportunistic and small insects, primarily small bees (Bawa 1994, but see Renner & Feil 1993). All dioecious species here belong to the genus *Baccharis*, which is primarily connected to wasp-pollination. Thus, phylogenetic constraints seem to be the main factor affecting dioecy distribution in the studied community.

The percentage of monoecism and dioecy in the grasslands at Serra da Bocaina is certainly higher than the here represented because of the presence of many species of Cyperaceae and Poaceae in these areas. Hence, considering the latter families in addition to *Baccharis*, dioecy is perhaps more strongly connected to wind pollination than to generalist pollination systems in this community. The open vegetation, frequent winds, and dry weather during the winter provide favorable conditions to the evolution of anemophily in the high altitude grasslands. Although this study was not focused on abiotic pollination, there was some evidence of ambiphily among the studied taxa, in which the wind could be a pollen vector in addition to insects. The species of *Baccharis* may fit on this category, as female heads have well exposed stigmata, and the male flowers produce small pollen grains. In addition, during some exploratory experiments at the study sites, we found pollen grains of *Baccharis* species adhered on microscope slides covered by glycerol. Most species of this genus are flowering during the winter, when environmental conditions for wind pollination are more favorable and insect activity is reduced. Ambiphily has been registered in species of *Croton* in southeastern Brazil (Passos 1995), and perhaps, *C. suberosus* could present such pollination system at Serra da Bocaina.

Floral traits - and consequently pollination systems - are generally similar among species belonging to the same genus (or family) at Serra da Bocaina, for example the species of *Eryngium*, *Baccharis*, *Eupatorium*, *Paepalanthus*, *Hipericum*, *Tibouchina*, *Galianthe*, *Solanum*, and *Xyris*. However, some interesting cases of floral radiation were observed. Species of Asclepiadaceae fit on three different pollination systems. The small flowers of *Gonioanthela* and *Tassadia* are pollinated by wasps and syrphids, respectively, and the two *Oxypetalum* species are pollinated by wasps or large bees each one. The three *Irlbachia* species fit on three different pollination syndromes - sphingophily, melittophily, and ornithophily - although we failed to detect pollinators in these species, which are spontaneously self-pollinated. In fact, the five gentian species in this study presented self-pollination mechanisms, which seem to be frequent in the family (e.g., Petanidou et al. 1998, Luijten et al. 1999). Differences in flower dimensions seem to be the main segregating factor in the pollination of the Convolvulaceae species here studied. Differences in the tube size also seem to be determinant for the pollination mainly by wasps or by small bees among the three *Mikania* species. The two species of *Sisyrinchium* differ markedly in the offered resource, tepal color, flower shape, and anther morphology. Oil-collecting bees of the genus *Lanthomelissa* are the expected pollinators of

Sisyrinchium micranthum (see Cocucci & Vogel 2001), in contrast to the pollination mainly by syrphids in *S. vaginatum* (see Chapter III). However, we registered only small pollen-collecting bees and syrphids pollinating both species. Another interesting case of floral radiation on Serra da Bocaina highlands (montane forest and grasslands) is among the eleven species of Ericaceae. Species belonging to the genus *Agarista*, *Gaylussacia*, and *Gaultheria* are pollinated exclusively or mainly by either hummingbirds or bees/wasps - but the endemic *Gaultheria sleumeriana* is pollinated equally by both agents. Floral characters related to one or another of these agents are similar within the three genera (unpubl. res.).

POLLINATION AGENTS

Hymenopterans, markedly small bees, are the predominant pollination agents at the Serra da Bocaina grasslands, as well as for cerrado, morichal, and subandean zone (Arroyo et al. 1982, Ramirez 1989, Barbosa 1997). Bees have been reported as the main pollinators for most studied communities (Moldenke 1976, Kevan & Baker 1983, Roubik 1989, Bawa 1990, Momose et al. 1998), and different patterns - for example dominance by dipterans - seem to be restricted to very singular habitats, such as Arctic areas, high elevation mountain areas, and oceanic islands (e.g., Kevan & Baker 1983, Primack & Inouye 1993, Anderson et al. 2001). However, certain communities with similar percentages of bee-pollination may present marked differences among their pollination patterns, since several other factors are determinants of the plant-pollinator relationships. Bees belonging to different groups show great variation, for example, in preferences, abilities, and behavior on flowers (see Roubik 1989), and this variation is expected to lead to different pollination patterns among communities with distinct bee fauna.

The two main functional groups of bees that may be recognized at the Serra da Bocaina grasslands are the large bumblebees (mainly *Bombus atratus*) and small Halictidae bees. Agents of one or both of these groups were among the pollinators in 67 out of 107 species (62.6%). *Bombus* and Halictidae species pollinated, respectively, 80% of large bee-pollinated species (28 out 35), and 75% of small bee-pollinated species (54 out 72). Both groups of bees presented a generalist foraging behavior, visiting flowers of different shapes, sizes and colors, which in many cases may be pollinated by some other groups. For an illustrative example, an individual of *Bombus atratus* was observed visiting flowers of seven species - belonging to Asteraceae (five spp.), Lamiaceae, and Rubiaceae - with violet flowers (including purple and magenta) in a single round (for ca. three min) on Apr 1999 (see Chittka et al. 1999 for general considerations on flower constancy by bees). There was another violet-colored flower species in the patch, the nectarless *Irlbachia pendula*, which was the only species not visited by that bumblebee. Such generalist behavior is typical for the Brazilian species of *Bombus* (Alves-dos-Santos 1999, Barbola et al. 2000, see also Wesselingh et al. 2000 for inconstancy by the Costa Rican *Bombus ephippiatus*). In contrast, individual bumblebees of temperate species usually specialize on one flower species, with occasional visits to other species (Heinrich 1976, 1979, but see Macior 1994). Bumblebees pollinated the majority of the large bee-pollinated species at Serra da Bocaina, and prevailed over almost a half of them, including the nectar-richest ones (e.g., *Oxypetalum sublanatum*, *Lobelia camporum*, *Cuphea glutinosa*, and *Verbena hirta*). Further, these bees showed a trapline behavior, favoring pollen dispersal at large distances. Taken together, the variety of visited flowers (including nectar and pollen flowers), the year-round activity, and the foraging behavior make bumblebees as the main pollinators among the studied species related to large bee-pollination. As bees are the most important pollinator group at the Serra da Bocaina grasslands, bumblebees may even be the most important pollinators in the whole community, acting as general organizer in these grasslands (see Sazima et al. 1995 for a similar role filled by the Saw-billed Hermit among hummingbirds in lowland forest areas).

Pollination by wasps has been classically claimed in some highly specialized and infrequent cases (e.g., *Ophrys*, *Ficus*), and also among generalists plants pollinated by several insects (Faegri & van der Pijl 1979). Hence, wasps were detected as minor agents in most communities (e.g., Arroyo et al. 1982, Bawa et al. 1985, Silberbauer-Gottsberger & Gottsberger 1988, Momose et al. 1998, Oliveira & Gibbs 2000). In contrast, considering all wasp-pollinated species in the Serra da Bocaina grasslands (ca. 45% of the species in the community), they acted as exclusive or main pollinators in almost a half of them, i.e., more than 20% of animal-pollinated species (Table 2). Pollination by wasps has some importance at the opened cerrado and the morichal vegetation, although they act as exclusive pollinators only in a few species in these communities (Ramirez 1989, Barbosa 1997). In fact, such importance of wasps in the pollination as observed at the Serra da Bocaina grasslands, as far as we know, has not been registered in any other ecosystem. Whether wasps are minor pollinators or their role in the pollination has been neglected in Neotropical communities is still an inadequately explored question, which deserves further studies. However, at least in some subtropical habitats, the rates of floral visitation by wasps, and probably their importance as pollinators at the community level, seem to have been underestimated (P. Feinsinger, pers. comm.).

Lepidopterans were, in general, co-pollinators in species with a generalist pollination system or eventual agents in species pollinated mainly by bees at Serra da Bocaina. Similar results were found at cerrados and morichal (Ramirez 1989, Barbosa 1997, Oliveira & Gibbs 2000). In spite of the scarcity of visits to flowers, butterflies (mainly Hesperiidae) may have an important role in gene flow for many species, transferring pollen at long distances due to their traplining behavior. In contrast to pollination relations, interactions between grassland plants and butterfly larvae seems to be noticeable. During their larval stage, species of Hesperiidae feed on plants of Asteraceae and Poaceae species (Brown, 1992), which are the most abundant plant families on grasslands. As a general trend, increasing in pollination by lepidopterans seems to occur from open to close vegetation types (Barbosa 1997). However, butterflies are very important pollinators in the open vegetation at the Chilean Andes, in special at the subnival zone (Arroyo et al. 1982).

Fly pollination has been considered mostly unspecialized, since flies do not feed their young and may have other food sources than flowers (Kearns 1992, Proctor et. al. 1996, but see Chapter III for a discussion on pollen importance to syrphids). In fact, most species pollinated by the three most important fly groups at Serra da Bocaina - Syrphidae, Tachinidae, and Bombyliidae - bear small nectar flowers, which were pollinated by several agents. However, syrphids were associated to small bees in many species, particularly in some species with pollen-flowers. These latter species present specialized pollination systems, in which syrphids are the exclusive or main agents. Percentage of species close related to flies at Serra da Bocaina - considering the pollination by syrphids and other dipterans together - is similar to those from cerrados and morichal (Ramirez 1989, Barbosa 1997), but in Chilean Andes myiophily is fairly well represented (Arroyo et al. 1982). Higher importance of flies and butterflies in Chilean Andes, in relation to the other ecosystems here compared, probably reflect the unfavorable climatic conditions for bee activity in the Andes (Arroyo et al. 1982, see also Kevan 1975, Kearns 1992). At the Serra da Bocaina grasslands, climatic conditions are not that harsh to limit the development of bees, which dominate the pollination in this community.

The frequency of hummingbird pollination at Serra da Bocaina is inferior than in other high altitude communities, such as morichal (12%) (Ramirez 1989) and campos rupestres (10%)

(Faria 1994), but it is similar to that observed in opened cerrado areas (Barbosa, 1997). The ornithophilous species in such grasslands constitute secondary nectar sources to hummingbirds, which have their main nectar sources in the surrounding high altitude forest (Sazima et al. 1996, Freitas & Sazima 2001). There are at least two factors supporting this idea. First, there are no ornithophilous species in blooming peak during Feb and Jun in the grasslands. So, this community could not support hummingbirds year round. The second point is that the five ornithophilous species, in general, were scarcely visited by hummingbirds, but in contrast hummingbirds fed intensively on many species (ca. 30 spp.) of the surrounding forest (Sazima et al. 1996, Buzato et al. 2000, pers. obs.). Hence, the continued replacement of forest areas by grasslands, mainly because of fires, is a risk factor to the populations of the five observed hummingbird species and also to *Phaethornis eurynome*, which is the only hermit hummingbird at highlands at São Paulo State (Sazima et al. 1996, Buzato et al. 2000). This Phaethorninae species ranges from coastal to mountain areas, however, at least its highland populations, forage almost exclusively in forest areas (Sazima et al. 1996, pers. obs.), and we never observed it in grasslands at Serra da Bocaina. Thus, preservation of high-altitude forest is essential to maintain the hummingbird populations of this species. A similar situation involves the hummingbird species, *Stephanoxis lalandi lalandi*, which lives exclusively in some high-altitude areas (grasslands and forest) in southeastern Brazil (see Grantsau 1989, Sazima et al. 1996). Forest plant species with short-tubed flowers, for example Ericaceae species of the genera *Gaultheria* and *Gaylussacia*, *Buddleja brasiliensis*, *Collaea speciosa*, *Salvia arenaria*, *Fuchsia regia*, and *Cestrum corymbosum*, form the main floral resources for this hummingbird species (Sazima et al. 1996, see also Buzato et al. 2000). The forest replacement by grasslands probably represents a serious danger for the maintenance of this sub-species (*Stephanoxis l. lalandi*) at Serra da Bocaina, and hence for some plant species pollinated almost exclusively by this bird, such as the ericaceous *Gaultheria eriophylla* and *G. serrata*.

The absence of some plant taxa in the grasslands - which are typically specialized for pollination by insects other than hymenopterans - could be among the factors of the very high frequency of bees and wasps as exclusive pollinators in the community. For example, the presence of *Bulbophyllum* species (Orchidaceae) - that are frequent in the campos rupestres - would increase the pollination exclusively by flies, more specifically Milichiidae (Sazima 1978, Borba & Semir 1998). In a similar way, representatives of Annonaceae and Araceae - families predominantly connected to beetle pollination in Brazilian savannas and forests - would affect frequency of beetle pollination, specifically Dynastinae beetles (Gottsberger 1986). Grasslands at Serra da Bocaina also do not harbor perfume flowers, which exhibit a highly specialized pollination system. Such flowers have fragrance-secreting glands which attract male euglossine bees (e.g., Sazima et al. 1993). Euglossine bees have restrict altitudinal limits of distribution (Roubik 1989). Furthermore, we failed, by means of aromatic compounds traps (after Campos et al. 1989), to detected such bees at the high altitude grasslands and forest at Serra da Bocaina. In fact, altitudinal limits of euglossine bees seem to be ca. 1200 m around 22° S latitude (R. B. Singer, pers. comm.).

We observed pollination by neither bats or other mammals at the Serra da Bocaina grasslands. Moreover, no species were collected with floral features in accordance with the mammal pollination syndromes, suggesting absence of such pollination systems in these grasslands. In fact, we know of no published register of mammal-pollinated species occurring on mesic habitats of the high-altitude grasslands (see Sazima et al. 1994 for *Siphocampylus sulfureus* growing on marshes). In contrast, bat pollination is well represented in areas of high altitude forest, which surround grasslands (Sazima et al. 1999). Further surveys on other areas - such as Pico do Itatiaia and Serra dos Órgãos - are necessary to expand the idea of the absence of pollination by mammals at the high-altitude grasslands as a whole. Anyway, the most important genera bearing bat-pollinated species on the surrounding high altitude forest - such as *Vriesea* (Bromeliaceae), *Lafoensia* (Lythraceae) and *Abutilon* (Malvaceae) - are not present at Serra da Bocaina grasslands (see Sazima et al. 1999). In addition, bat- and hummingbird-pollinated flower assemblages in the Atlantic rainforest seem to share several features (Sazima et al. 1999). In this sense, the absence of bat pollination could have some, yet unexplored, relation to the scarcity of hummingbird pollination on grasslands, in comparison to rainforest, in southeastern Brazil.

In contrast to bats, nocturnal pollination by moths was expected since grasslands harbor at least three species adapted to pollination by such agents. However, we failed to observe these pollinator agents, and the low fruit set in *Mandevilla erecta* indicate low - perhaps unpredictable - rates of flower visits by nocturnal moths in these habitats. Strong winds at the studied areas may be harmful to the moth pollinating species, as suggested for the cerrado (Oliveira & Gibbs 2000). Furthermore, the restricted flowering period of the supposedly moth-pollinated species at

Serra da Bocaina grasslands may be linked to migrating pollinator agents, which is an additional difficult for their observation.

FLOWERING IN RELATION TO POLLINATORS

Flowering showed a drastic reduction at the end of the dry season at Serra da Bocaina. Most species flowering in the rainy season have been detected in the seasonal Neotropics (e.g., Monasterio & Sarmiento 1976). Climatic conditions are apparently unfavorable for flowering during winter months, due to low temperatures, low precipitation, and occasional frosts. In addition, this period is marked by anthropogenic fires in grasslands at the study areas. Fires may have been fundamental for the strong flowering reduction in Sept-Oct, at both levels, the whole community and species groups connected to each pollinator agent. We observed mass-flowering a few months after fires in several species, such as *Sinningia allagophylla*, *Microlicia isophylla*, *Tibouchina frigidula*, *T. minor*, *Galianthe angustifolia*, and *Xyris asperulla*. Flowering controlled by fires is a well-known and widespread phenomenon among cerrado species (Coutinho 1990), but is not characteristic of the Brazilian high altitude grasslands according to Safford (2001), based on his observation at the Serra do Caparaó grasslands. Similarities between cerrado and high altitude grasslands may be more pronounced for Serra da Bocaina than for other grassland areas in southeastern Brazil, since fire regimes are more intense in the former (see Safford 1999a, 2001, and also Martinelli 1989 for floristic comparisons). In this sense, Serra da Bocaina grasslands may be pyrogenic to a greater extent than other grassland areas, such as those from Pico do Itatiaia, Serra dos Órgãos and Serra do Caparaó.

The activity of bees of all families was reduced during the dry season at Serra da Bocaina. The reduction in the number of bee species and individuals in activity during the winter was also observed in connected ecosystems in southern Brazil (e.g., Alves-dos-Santos 1999, Barbola et. al. 2000). This reduction is related to several factors, such as reproductive phenology of bee species, climatic restriction for flying, and flower availability. Flowering pattern of species closely related to bee pollination followed the pattern of the whole community. Hence, there was a reduction on flower resource for bees during the cold season, especially for large bees. The floral nectar of some long-flowering species - *Cuphea glutinosa*, *Galianthe brasiliensis*, and *Verbena hirta* - and the winter-flowering *Eremanthus erythropappus* constitutes keystone plant resources (sensu van Schaik et al. 1993) for pollinators during the winter. These four species are large shrubs - or treelet (*E. erythropappus*) - which produce many flowers during this period of low flower availability, and are particularly important for bumblebees. A similar role is carried out by *Lupinus velutinus* among species bearing large pollen-flowers. This species is the only one of the latter group in flowering peak at the end of the dry season, and its pollen may be fundamental for bumblebees and also for *Megachile laeta*.

In contrast to bees, social wasps showed more constant activity patterns along the year, and the pollination by wasps was prominent during the dry season at Serra da Bocaina. Small bees, especially Halictidae, and wasps may have similar abilities to obtain nectar on flowers. These two groups may be playing complementary roles in pollination at the community level in Serra da Bocaina grasslands, since flowering for species groups closely related to either bees or wasps was sequential. Competition could be one of the forces driving the displacement in flowering of species pollinated by each group (Mosquin 1971), although other factors could also be decisive (e.g., floral architecture, Murcia & Feinsinger 1996), in special at Serra da Bocaina, because many plants are generalists and many pollinators are inconstant foragers (see Motten 1986). Anyway, sequential flowering as a central factor in pollination structure of communities has been pointed out for different pollinator groups in Neotropical communities (see Newstrom et al. 1994).

POLLINATION SYSTEMS OF TAXA IN DIFFERENT HABITATS

We carried out intensive pollinator observations for some plant species and brief ones for many other species. Such situation is expected in studies of plant-pollinator interactions at the community level, which embody many species with low population density (see Momose et al. 1998). Because of the low observation time, in addition to the general low visitation rates to the flowers, we may have failed in assigning the habitual pollination system in some species at the Serra da Bocaina grasslands (see Waser et al. 1996 for possible biases in pollinating community surveys). However, it is possible - since we used broad categories to describe the pollination systems - to draw general trends in the interactions at this community, and also, establish general comparisons.

Close related species - or even distinct populations of a same species - which occur in different habitats may present different pollination systems. For example, many butterfly- or fly-pollinated species in Chilean Andes at 3200-3600 m are derived from genera pollinated by bees at lower altitudes, and among *Senecio francisci* populations, pollination shifts from a generalist system to a fly-pollination system with increasing altitude (Arroyo et al. 1982). Such phenomenon could be expected in the high-altitude grasslands in southeastern Brazil since they constitute the highest plant communities in eastern South America, and also, because these communities have few phytogeographic connections with the surrounding forest areas, i.e., they are far from the related ecosystems. However, for the groups that we have information, the pollination systems of most species from the Serra da Bocaina grasslands were similar to co-generic species in other ecosystems (Table 4). Similarities are found among species with markedly diverse pollination systems, such as the specialized oil-flowers of Malpighiaceae, hummingbird-pollinated flowers, and generalist flowers pollinated by several agents.

Contrasting the examples above, we detected differences on pollination of some species occurring in the studied grasslands and in other areas. Pollination by large bees is prevalent among species of *Solanum* (e.g., Buchmann et al. 1977, Coleman & Coleman 1982), and accordingly, the ruderal *Solanum aculeatissimum* is mainly pollinated by large bees (*Bombus*, *Centris*, *Oxaea*, and *Xylocopa*) - but also by some small bees - in urban areas (Avanzi & Campos 1997, and also our observations). In contrast, this latter species and the others of this genus at Serra da Bocaina were exclusively pollinated by small bees belonging to Halictidae, which vibrate on these flowers. The pollination of *Solanum* species in the studied area only by small Halictidae bees, particularly *Augochloropsis cyanea*, is a curious event, since it would be expected that large bees also acted as pollinators of these species.

Although pollination systems of some Asteraceae taxa at Serra da Bocaina coincide with observations in an open cerrado area (Barbosa 1997, Table 4), we observed more generalized pollination systems in some species of *Vernonia*, which were pollinated by butterflies, wasps and flies, in addition to bees. Moreover, the three species of *Eupatorium* studied by Barbosa (1997) were closely related to Bombyliidae flies, and in a minor degree to small bees. Among the eight species of *Eupatorium* alliance at Serra da Bocaina, five were generalists and the others were mainly bee-pollinated. Five out seven species pollinated by Bombyliidae flies at Serra da Bocaina were Asteraceae, but only two of them belong to *Eupatorium*. Thus, it seems that there is no especial connection between this family of flies and the *Eupatorium* species at Serra da Bocaina. Anyway, a probable new beefly species (genus *Euprepina*, C. Campaner, pers. comm.) was collected while was visiting *Chromolaena megacephallum* flowers.

Table 4. Examples of either disjunct populations of a certain species or co-generic species, which present similar pollination systems at the Serra da Bocaina grasslands and in other habitats.

Taxa at Serra da Bocaina	**Comparable taxa**	**Habitat or place**	**Pollinator agents**	**Source**
-Oxypetalum appendiculatum	*O. appendiculatum*	Southeastern Brazil	-*Polybia* wasps	10
-Achyrocline satureioides	*A. satureioides*	cerrado	-wasps (main), flies (secondary)	1
-Baccharis dracunculifolia	*B. dracunculifolia*	cerrado	-flies and wasps	1
-Byrsonima variabilis	*Byrsonima* spp.	cerrado, forest	-oil-collecting bees, mainly *Centris* spp.	2, 8, 9
***-Chamaecrista* sp. 1**	*C. campestris,* *C. cathartica*	cerrado	-large bees (main), small bees (secondary)	4
***-Vernonia* spp.**	*Vernonia* spp.	cerrado	-small and large bees	1
-Erythroxylum microphyllum	*Erythroxylum* spp.	cerrado	-wasps (main), bees (secondary)	1, 3
-Mikania nummularia	*M. psilostachia*	Venezuelan shrubland	-wasps (main), bees (secondary)	7
-Borreria capitata	*Borreria* spp.	cerrado	-generalist (bees, butterflies and wasps)	1
-Hippeastrum glaucescens	*H. moreliano,* *H. psittacinum*	rocky outcrops	-hummingbirds	6
-Dyckia tuberosa	*D. leptostachya*	cerrado	-hummingbirds	9
-Esterhazya macrodonta	*E. splendida*	coastal shrubland	-hummingbirds	5

Source: 1. Barbosa 1997, 2. Barros 1992, 3. Barros 1998, 4. Gottsberger & Silberbauer-Gottsberger 1988, 5. Ormond et al. 1998, 6. Piratelli 1997, 7. Ramirez 1989, 8. Rêgo & Alburquerque 1989, 9. Silberbauer-Gottsberger & Gottsberger 1988, 10. Vieira & Shepherd 1999.

We found five species bearing flowers with oil glands (elaiophores) in the community. The expected pollinators of these species are small and large bees belonging to the "Anthophoridae" group (Centridini, Exomalopsini and Tapinostapidini), which collect oil on flowers to provide their larvae or to apply as lining on brood cells (see Neff and Simpson 1981, Cane et al. 1983). The pollination of *Byrsonima variabilis* at Serra da Bocaina mainly by oil-collecting bees belonging to *Centris* is in accordance to the observed in other species of this genus from different ecosystems (Table 4). However, we did not observe the large oil-collecting bees belonging to the genus *Epicharis* on *B. variabilis* at the Serra da Bocaina grasslands, which are frequent pollinators of oil-producing Malpighiaceae in areas at lower altitudes (see Sazima & Sazima 1989). Concerning to *Oncidium*, pollination biology of the species at Serra da Bocaina is not clear, although pollen-collecting bees seem to be involved in a pollination system by deceit. Many *Oncidium* species bear flowers that produce nonvolatile oils, which have a chemical composition suitable to larvae nurturing by "Anthophoridae" bees (A. D. Faria, pers. comm.). However, only a single observation of a bee actively collecting oils on flowers in this genus is reported up to moment (Singer & Cocucci 1999). Thus, further more comprehensive studies are required to clear the pollination biology in the genus (see Nilsson 1992 for trends in orchid pollination).

Irlbachia pedunculata flowers (Fig 4L) are in accordance to the syndrome of ornithophily (cf. Faegri & van der Pijl 1979), but they did not produce floral nectar in the studied population at Serra da Bocaina. We failed to observe floral visitors in this species, which invariably was spontaneously self-pollinated at the end of the flower's lifetime, through stigma movements toward the anthers. However, hummingbirds visiting *I. pedunculata* flowers were observed at Serra do Cipó, Minas Gerais State (Vogel 1998). Further, flowers of *I. pedunculata* from Serra do Cipó had floral nectaries (St. Vogel, pers. com.). In another locality in Minas Gerais State (S. Tomé das Letras), *I. pedunculata* flowers produced nectar, which may reach more than 15 µl in volume (pers. obs.). These results indicate that nectar presence/absence may be a plastic character among populations of this *Irlbachia* species. The scarcity of hummingbirds on studied grasslands may have influenced the selection of this character, once the seed production is assured by the self-pollination mechanism.

Pseudagapostemon cyaneus (Halictidae) visited only flowers of *Mikania lundiana* and *Senecio oleosus* (Asteraceae) at Serra da Bocaina (Fig. 4G). Similarly, this bee species is an oligolectic, strongly associated to *S. oleosus* flowers, in a grassland area in Lapa, Paraná State, southern Brazil (Barbola et. al. 2000). *Pseudagapostemon cyaneus* occurs from the southernmost Brazil to São Paulo State, and in the latter it is known only above 1000 m at Serra da Bocaina and Campos do Jordão (Cure 1989). Furthermore, the species of *Pseudagapostemon* from highlands in southeastern Brazil are closely related to the species of the genus found in cool areas from southern regions of the country (Cure 1989). Such biogeographic relation between these regions also seems to be reflected among some *Senecio* species (M. D. Moraes, pers. comm.). The strong interaction between *Senecio oleosus* and *Pseudagapostemon cyaneus* in both Serra da Bocaina and Lapa is one of the most illustrative examples about the biogeographic connections between the mountain ranges of southeastern Brazil and the cool lowland areas in southernmost regions (see Behling 1997).

In spite of the similarity in pollinator agents among co-generic species (Table 4), pollinator visits are less frequent at Serra da Bocaina than in other habitats (pers. obs.). Similar, and perhaps correlated, results were observed for flower longevity. For example, flowers of *Esterhazya splendida* last ca. 2 days on coastal shrublands ("restinga") in contrast to the 5 to 6-days flowers of *E. macrodonta*, and also, hummingbird visitation rates are markedly lower in *E. macrodonta* than in *E. splendida* (Ormond et al. 1998, Freitas & Sazima 2001). Differences on pollination ecology - at both co-generic and community levels - between the Serra da Bocaina grasslands and communities at lower altitudes will probably be more clearly perceived in relation to flower longevity, flowering time (43.5% of the species flowered for six or more months), spontaneous self-pollination mechanisms or apomixis, and generalization degree on pollination systems (see below). Such effects may be responses to low visitation rates by pollinators, due to harsh climatic conditions, for a tropical habitat, on these grasslands.

GENERALIST POLLINATION SYSTEMS

Generalist pollination systems have been classically connected to small and pale flowers pollinated by small insects, the also called diverse small insect (d.s.i) syndrome (Bawa et al. 1985). However, some of the small pale flowers at Serra da Bocaina present highly specialized pollination systems (e.g., the asclepiad *Gonioanthela hilariana*), and moreover, some highly generalist pollination systems involve large insects, for example, species of the "generalist group" were pollinated by large bees, wasps, and butterflies, in addition to small insects. In fact, only a few species fit in the d.s.i. syndrome (e.g., species of *Paepalanthus* and *Eryngium*), although many species present a highly generalist pollination system in this community. Therefore, generalist pollination system - in contrast to Bawa et al. (1985) purpose - should not be inferred from size of both flowers and pollinators, as previously postulated by Ramirez (1989) taking in consideration observations at morichal (see also Waser et al. 1996). In addition to the species here placed in the generalist group, many other species presented generalist systems to a certain extent. For example, many species had two main pollinator agents, and further, the majority of the species in the community was pollinated by both main and additional agents. Although additional agents seem to have a minor importance in pollinating such species, they carried out some pollination, which may have ecological and evolutionary implications. On the other hand, the several agents of generalists may have quite different abilities in pollinating, in such a way that those plants may effectively be specialists on the most efficient visitor (Ollerton 1996, see Schemske & Horvitz 1984 for a clear example).

The traditional view in pollination studies - based on the syndrome concept (cf. Faegri & van der Pijl 1979) - supports that pollination systems tend toward specialization. Such view has been questioned a few years ago, based on evidences for widespread generalization in pollination systems (e.g., McDade 1992, Waser et al. 1996, Herrera 1996, Ollerton 1996). Johnson and Steiner (2000) call our attention to the fact that such dichotomy between generalization and specialization is a simplification - for purposes of debate - of a continuum of plants pollinated by one to hundreds of pollinator species. Many factors - such as plant life history, phylogenetic constraints, vegetation strata, successional status, plant abundance, breeding system, and local fauna - may influence the degree of specialization/generalization of the pollination systems (Stebbins 1970, Vogel & Westerkamp 1991, Waser et al. 1996, Ollerton 1996, Johnson & Steiner 2000).

Generalization is predicted as long as temporal and spatial variance in pollinator quality is appreciable, different pollinator agents do not fluctuate in unison, and they are similar in their pollination effectiveness (Waser et al. 1996). Such conditions seem to be more frequent in naturally inclement or unstable areas, in the modern agricultural-urban mosaics or human surroundings and among short-lived plants (Vogel & Westerkamp 1991, Johnson & Steiner 2000). The climatic conditions and the island-type distribution of high altitude grasslands may naturally favor the prevalence of generalists at the Serra da Bocaina grasslands in comparison to surrounding forest areas. Presently, fires in this community may be an additional factor in making the environment more severe for specialists (both plants and animals).

CONCLUDING REMARKS

The correlation between certain taxa and particular ecological conditions may enhance the abundance of some plant groups. Thus, ecological attributes of the community - not related to reproduction - may promote certain taxonomic groups with particular reproductive traits, and hence may bias the frequency distribution of these traits in the community (Ramirez 1993). Grasslands at Serra da Bocaina are - beside the abiotic-pollinated species of Poaceae and Cyperaceae - strongly dominated by species of Asteraceae, and pollination systems at the community level reflect much of the Asteraceae floral characteristics (i.e., short tubular flowers with exposed reproductive parts, and that offer nectar). In such grasslands, the distribution of the pollination systems, with high frequency of unspecialized pollination systems, may be connected to phylogenetic floral trends of species with certain abilities - not necessarily related to pollination - to occupy these habitats, such as short living-cycles, adaptations to frost, low mean temperature, high daily temperature variation, and acidic soils, and more recently, some kind of adaptation to fire (see Safford 1999a). Thus, despite local adaptations for specific pollinators, the pollination modes are regionally coined by kinship-dependent species properties and random in their presence, because certain taxa may have became members of the community by historical fortuity (Vogel & Westerkamp 1991).

High altitude grasslands in southeastern Brazil are linked to episodes of expansion and retraction due to glacial events during the Quaternary (Behling 1997, Safford 1999a). Such situation may have favored species with the ability to occupy new habitats fast. The dependence by a few specialized pollinators could be less suitable than more generalist pollination systems in the occupation of a new habitat, since previous pollinator agents may be left behind. In fact, generalized pollination systems might have been of ecological advantage for plants colonizing post-glacial landscapes (Johnson & Steiner 2000). Biogeographic and palynologic studies indicate that high altitude grasslands has to be understood as a relict of the Pleistocene cold and dry climates and of the early- and mid-Holocene warm and dry climates (Behling 1997). Because their probable relatively recent origin, these grasslands unlikely have produced highly coevolved plant communities. Eventually some relictual plant-pollinator interactions could be kept, in cases that both plant and pollinator colonize the mountain tops (*Senecio oleosus* and *Pseudagapostemon cyaneus* could be a probable example). Most bee species from the Serra da Bocaina grasslands are also found in lower forest areas of the Atlantic Forest Domain (J. M. F. Camargo and S. R. M. Pedro, pers. comm.), and the wasp community is represented by even wider-distributed species (O. T. Silveira, pers. comm.). Such data support the view that the pollination of many plants that colonized these grassland areas has been carried out by elements of the local forest fauna.

In addition to generalist pollination system, other common floral traits at Serra da Bocaina, such as spontaneous self-pollination mechanisms and extent flower longevity, may be advantageous to both plant establishment and maintenance in those high altitude grasslands, which are characterized by unpredictable and scarce pollinators.

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APPENDIX

A. The studied plant species at the Serra da Bocaina's grasslands and the pollinator animals captured or observed on their flowers. The number of the collector (L. Freitas) of the plant specimens deposited at the UEC and the total time of observation are given in brackets. The main flower color, the plant habit, and the flowering period and flowering peak (in italic) from Jan to Dec 1999 are given after pollinator data. Some species were found only in the area that was burned in Sep 1999, and are indicated by (f). Abbreviations are BS - small bees, BL - large bees, CO - beetles, DI - dipterans other than syrphids, LE - butterflies, SY - syrphids, WA - wasps, HB - hummingbirds, uncoll - uncollected, undet - undetermined. Non-pollinating visitors were excluded.

AMARYLLIDACEAE: **1. *Hippeastrum glaucescens*** Martins (773) (18h30'): HB - *Leucochloris albicollis* (Vieillot). Dark red. Herb. Out-Nov, *Nov*.

APIACEAE: **2. *Eryngium canaliculatum*** Cham. & Schlchtdl. (792) (4h): CO - Cantharidae sp. 1. Yellowish green. Herb. Nov-Dec, *Dec*. **3. *Eryngium horridum*** Malme (140) (4h): BS - *Plebeia saiqui* (Friese, 1900) (Meliponini); DI - *Jurinella* aff. *corpulenta* (Townsend, 1927) (Tachinidae), Culicidae sp. 1, Curtonotidae sp. 1, Tachinidae sp. 9, Diptera sp. 1; LE - Riodininae sp. 1 (Lycaenidae); SY - uncoll (1 sp.); WA - uncoll (1 sp.). Yellowish green. Herb. Jan-Mar, *Jan*.

APOCYNACEAE: **4. *Mandevilla erecta*** (Vell.) Woodson (86, 509) (18h): not visited. Pale yellow. Sub-shrub. Jan-Feb, *Jan*.

AQUIFOLIACEAE: **5. *Ilex amara*** (Vell.) Loes. (656, 797) (4h30'): *Apis mellifera* Linnaeus, 1758; BS - *Augochloropsis* aff. *cognata* Moure, 1944, *Ceratalictus* sp. 1 (Augochlorini), *Plebeia saiqui* (Meliponini); WA - *Mischocyttarus drewseni* Saussure, *Polistes billardieri* Fabricius (Vespidae), uncoll Vespidae (1 sp.), Pompilidae (1 sp.). Yellowish white. Sub-shrub. Nov-Dec, *Nov-Dec*.

ASCLEPIADACEAE: **6. *Gonioanthela hilariana*** (E. Fourn.) Malme (329) (5h30'): WA - *Polistes cinerascens* Saussure, *Polybia sericea* (Olivier) (Vespidae). Pale yellow. Vine. Mar-July (f), *Mar-May*. **7. *Oxypetalum appendiculatum*** Mart. (123) (7h30'): WA - *Polybia sericea* (Vespidae). Greenish lilac. Vine. Jan-Aug (f), *Apr-June*. **8. *Oxypetalum sublanatum*** Malme (13, 491) (11h): BL - *Bombus atratus* Franklin, 1913 (Bombini). Pale green. Vine Jan, Mar-May, Out-Dec, *Jan, Apr, Nov-Dec*. **9. *Tassadia subulata*** (Vell.) Fontella & E.A. Schwarz (686) (15h): SY - *Palpada rufipedes* Thompson, 1976, *Toxomerus watsoni* (Curran, 1930), *Toxomerus* sp. 1, uncoll (1 sp.). Dark ruby. Vine. May-Aug, *June*.

ASTERACEAE: **10. *Achyrocline satureioides*** (Lam.) DC. (276, 330) (6h): BS - *Plebeia droryana* (Friese, 1900) (Meliponini); DI - Tachinidae sp. 8; SY - *Toxomerus watsoni*, *Toxomerus* sp. 1, uncoll. (2 spp.); WA - *Mischocyttarus drewseni*, *Polistes billardieri* (Vespidae), Larrinae sp. 1 (Sphecidae), undet sp. 1, sp. 7, sp. 8, sp. 9, uncoll (1 sp.). Light yellow. Shrub. Jan-Aug, Dec, *Mar-June*. **11. *Baccharis aphylla*** (Vell.) DC. (707) (7h): DI - Sciaridae sp. 1; WA - *Mischocyttarus drewseni* (Vespidae), undet sp. 4, uncoll (1 sp.). Greenish white. Sub-shrub. Sep-Nov, *Sep-Oct*. **12. *Baccharis curitybenses*** Heering (498) (4h): WA -

Protonectarina sylveirae (Saussure). Pastel yellow. Sub-shrub. Jan-Mar, Dec, *Jan.* **13. *Baccharis dracunculifolia*** DC. (372) (7h30'): *Apis mellifera*; DI - *Jurinella* aff. *corpulenta* (Tachinidae), Tachinidae sp. 8, undet sp. 4; WA - *Mischocyttarus drewseni*, *Polistes cinerascens* (Vespidae), *Pryonyx thomaz* (Fabr.) (Sphecidae), Chrysididae sp. 1, undet sp. 14. Yellowish green. Shrub. Mar-Oct, *Apr-May, Aug.* **14. *Baccharis intermixta*** Gardn. (418) (4h): WA - *Agelaia vicina* (Saussure) (Vespidae), Leucospidae sp. 1, uncoll (1 sp.). Pale yellow. Shrub. May-Aug, *July.* **15. *Baccharis leptocephala*** DC. (392, 443, 688) (4h): SY - *Syrphus phaeostigma* Wiedemann, 1830, *Toxomerus watsoni*; WA - uncoll (2 spp.). Pale yellow. Herb. Apr-Sept, *May-Aug.* **16. *Baccharis pentziifolia*** Sch.Bip. ex Baker (589, 691, 728) (9h30'): *Apis mellifera*; CO - Cantharidae sp. 1; DI - uncoll (1 sp.); SY - *Toxomerus watsoni*, undet sp. 3; WA - *Mischocyttarus drewseni* (Vespidae), undet sp. 5, sp. 10, uncoll (1 sp.). Yellowish green. Shrub. Jan-Dec, *Feb, May-Aug, Oct-Nov.* **17. *Baccharis platypoda*** DC. (334, 863) (4h): *Apis mellifera*; BS - uncoll Augochlorini? (1 sp.); DI - *Jurinella* aff. *corpulenta* (Tachinidae), Curtonotidae sp. 1; WA - *Polistes cinerascens*, *Polybia fastidiosuscula* Saussure (Vespidae), Braconidae sp. 1, Pompilidae sp. 2. Grayish yellow. Shrub. Mar-June, *May.* **18. *Baccharis tarchonanthoides*** DC. (733) (4h): BS - uncoll Augochlorini (1 sp.); CO - Cantharidae sp. 1; DI - Sciaridae sp. 1, uncoll. Tachinidae (2 spp.); SY - *Toxomerus watsoni*, uncoll (1 sp.); WA - *Polybia scutellaris* (White) (Vespidae). Whitish yellow. Sub-shrub. Oct-Nov, *Oct-Nov.* **19. *Baccharis* sp. 1** (407) (4h): WA - uncoll (1 sp.). Pale yellow. Shrub. July-Aug, *July.* **20. *Baccharis* sp. 2** (441, 689) (7h): *Apis mellifera*; BS - *Schwarziana quadripunctata* (Lepeletier, 1836), *Trigona spinipes* (Fabricius, 1793) (Meliponini); DI - Tachinidae sp. 4; WA - *Mischocyttarus drewseni*, *Polistes billardieri*, *Polybia fastidiosuscula*, *Protopolybia sedula* (Saussure) (Vespidae), Pompilidae sp. 1, sp. 3, sp. 4, Tiphiidae sp. 1, uncoll Vespidae (2 spp.). Greenish yellow. Shrub. May-July, *June-July.* **21. *Baccharis* sp. 3** (108) (4h): WA - *Brachygastra lecheguana* (Latreille), *Polistes billardieri* (Vespidae). Pale yellow. Shrub. Jan-Mar, *Jan.* **22. *Barrosoa betonicaeformis*** (DC) King & Robins (512, 591) (4h): *Apis mellifera*; BS - *Augochloropsis cyanea* (Schrottky, 1901) (Augochlorini); CO - Cantharidae sp. 1; LE - *Sarbia* cf. *damippe* Mab. & Boul, 1908 (Hesperidae), uncoll Sphingidae (1 sp.). Purple. Herb. Jan-May, *Feb-Mar, May.* **23. *Chaptalia integerrima*** (Vell.) Burkart (744) (5h): BS - *Paratrigona subnuda* Moure, 1947 (Meliponini), *Paroxystoglossa* sp. 1 (Halictini), uncoll Halictidae (2 spp.); CO - Cantharidae sp. 1; LE - Pyrrhopyginae sp. 1 (Hesperidae), uncoll Lycaenidae (1 sp.); WA - *Mischocyttarus drewseni* (Vespidae), uncoll Eunemidae (1 sp.), Vespidae (1 sp.). White. Herb. Jan-Feb, Oct-Dec, *Oct-Nov.* **24. *Chaptalia runcinata*** H.B.K. var. *graminifolia* (Dus. ap. Malme) Burkart (406, 697) (13h30'): BS - *Augochloropsis cyanea* (Augochlorini), *Dialictus* sp. 2 (Halictini); DI - *Paravilla* sp. 1 (Bombyliidae), undet sp. 2, sp. 3, uncoll Bombyliidae (1 sp.); LE - *Thecla* sp. 1 (Lycaenidae), uncoll Hesperidae (1 sp.); SY - *Toxomerus watsoni*, *Toxomerus* sp. 1, undet sp. 6. Yellow. Herb. May-Nov, *July-Aug.* **25. *Chromolaena megacephalum*** (Mart. ex Baker) King & Robins (101, 596) (11h30'): *Apis mellifera*; BS - *Melipona quadrifasciata anthidioides* (Lepeletier, 1836) (Meliponini), *Augochloropsis cyanea*, *A. iris* (Schrottky, 1902), *A.* aff. *cognata* (Augochlorini), uncoll Augochlorini (1 sp.); BL - *Bombus atratus* (Bombini); CO - Cantharidae sp. 1; DI - *Euprepina* sp. 1, *Paravilla* sp. 1 (Bombyliidae), uncoll Bombyliidae (2 sp.); LE - *Sarbia* cf. *damippe*, *Thespeius* sp. 1 (Hesperidae), *Vanessa myrinna* (Dbldy., 1849) (Nymphalidae), uncoll *Vanessa* (1 sp.), Hesperidae (1 sp.) Sphingidae (1 sp.); WA - uncoll Pompilidae (1 sp.), Sphecidae (1 sp.). Reddish purple. Herb. Jan-May, *Feb-Apr.* **26. *Chromolaena xylorhiza*** (Sch-Bip. ex Baker) King & Robins (835) (4h): not visited. Purple. Herb. Jan-Feb, *Jan.* **27. *Eremanthus***

erythropappus Sch.-Bip. (403) (5h): *Apis mellifera*; BS - *Melipona bicolor bicolor* Lepeletier, 1836, *M. quadrifasciata*, *Paratrigona subnuda*, *Schwarziana quadripunctata* (Meliponini); BL - uncoll *Bombus* (1 sp.); DI - Tachinidae sp. 5; LE - uncoll Hesperidae (1 sp.), *Vanessa* (2 spp.); SY - uncoll (1 sp.); WA - uncoll Pompilidae (1 sp.), Sphecidae (1 sp.). Purple. Treelet. Jul-Aug (f), *Aug.* **28. *Erigeron maximus*** Link. & Otto (64) (4h): BS - *Coelioxys* sp. 1 (Megachilini), uncoll Augochlorini (1 sp.); CO - Cantharidae sp. 1; DI - undet sp. 6. Vivid yellow. Shrub. Jan-Mar, Oct-Dec, *Jan-Feb, Dec.* **29. *Eupatorium decumbens*** (Gardn.) Baker (100) (7h30'): BL - *Bombus atratus* (Bombini). Reddish violet. Herb. Jan-July, *Jan-Mar.* **30. *Eupatorium* sp. 1** (60, 61) (6h): BL - *Megachile iheringi* Schrottky, 1913, *M. terrestris* Schrottky, 1902 (Megachilini); LE - *Vanessa myrinna* (Nymphalidae), uncoll Lycaenidae (1 sp.). White. Shrub. Jan, Nov-Dec, *Nov.* **31. *Eupatorium* sp. 2** (99) (9h30'): *Apis mellifera*; BS - *Augochloropsis* sp. 1 (Augochlorini); BL - uncoll *Bombus* (1? sp.); CO - Cantharidae sp. 1; DI - Tachinidae sp. 1; LE - uncoll Hesperidae (2 spp.); WA - undet sp. 6, uncoll (1 sp.). Violet. Herb. Jan-July, Dec, *Jan-Feb.* **32. *Eupatorium* sp. 3** (326) (4h): BS - *Melipona bicolor* (Meliponini); LE - *Vanessa* sp. 1 (Nymphalidae). Purple. Herb. Mar-June, *Apr-May.* **33. *Eupatorium* sp. 4** (374) (6h): BS - *Schwarziana quadripunctata* (Meliponini), *Augochloropsis cyanea* (Augochlorini); CO - Tenebrionidae sp. 1; DI - uncoll Bombyliidae (1 sp.), Tachinidae (1 sp.); LE - *Vanessa myrinna* (Nymphalidae); SY - uncoll (1 sp.); WA - *Mischocyttarus drewseni* (Vespidae), *Sphex opacus* Dahlbom (Sphecidae). White. Herb. Apr, *Apr.* **34. *Gochnatia paniculata*** (Less.) Cabrera (438, 705) (4h): SY - *Toxomerus watsoni*, uncoll (2 sp.); WA - *Mischocyttarus drewseni*, *Polistes billardieri* (Vespidae), uncoll Pompilidae (1 sp.), Vespidae (2 spp.). Greenish yellow. Subshrub. Aug-Nov, *Sep-Oct.* **35. *Graziela gaudichaudeana*** (DC.) King & Robins (226, 590) (5h): *Apis mellifera*; BS - *Melipona bicolor*, *Schwarziana quadripunctata* (Meliponini), *Augochloropsis cyanea* (Augochlorini) ; CO - Cantharidae sp. 1, uncoll (1 sp.); DI - *Cylindromyia dorsalis* (Wiedemann, 1830) (Tachinidae); LE - Hesperiinae sp. 1 (Hesperidae); WA - undet sp. 13, uncoll (1 sp.). White. Shrub. Jan-June, *Jan-Feb.* **36. *Hypochaeris gardnerii*** Baker (481) (5h30'): *Apis mellifera*; BS - *Colletes* sp. 1 (Colletini); BL - *Centris klugi* Friese, 1899 (Centridini). Vivid yellow. Herb. Jan-Feb, Oct-Dec, *Jan-Feb, Nov-Dec.* **37. *Lucilia lycopodioides*** Less. (398, 838) (12h30'): WA - undet sp. 2, uncoll Vespidae (3 spp.). Yellowish white. Herb. June-Sep, *July-Aug.* **38. *Mikania lundiana* DC.** (393) (4h30'): *Apis mellifera*; BS - *Melipona bicolor*, *M. quadrifasciata*, *Paratrigona subnuda*, *Schwarziana quadripunctata* (Meliponini), *Pseudagapostemon cyaneus* Moure & Sakagami, 1984 (Halictini); LE - uncoll *Vanessa* (1 sp.); WA - uncoll Pompilidae (1 sp.). Yellowish white. Vine. May-Jul, *May.* **39. *Mikania nummularia*** DC. (440, 690) (7h): LE - *Thecla* sp. 1 (Lycaenidae), uncoll Hesperidae (1 sp.); WA - Cercerini sp. 2 (Sphecidae), undet sp. 1, sp. 2. White. Shrub. May-Aug, *June-Aug.* **40. *Mikania sessilifolia*** DC. (318, 417, 871) (6h30'): DI - *Jurinella* aff. *corpulenta* (Tachinidae), Curtonotidae sp. 1, uncoll Curtonotidae (1 sp.), Tachinidae (3 spp.); SY - *Toxomerus watsoni*, undet sp. 5; WA - *Polistes billardieri* (Vespidae), undet sp. 3, uncoll Vespídae (2 spp.). Yellowish white. Shrub. Mar-May, *Apr.* **41. *Senecio oleosus*** Vell. (391, 409) (5h): BS - *Ceratina* cf. *asuncionis* Strand, 1910 (Ceratinini), *Pseudagapostemon cyaneus* (Halictini), *Coelioxys* sp. 1 (Megachilini), uncoll Halictini (1 sp.); BL - uncoll *Bombus* (1 sp.); SY - *Toxomerus watsoni*, uncoll (2 spp.). Vivid yellow. Shrub. Jan, Mar-Sep, Nov, *Mar, July-Aug.* **42. *Stevia myriadenia*** Sch. Bip. ex Baker (88, 291) (23h): *Apis mellifera*; BS - *Paratetrapedia (Lophopedia)* cf. *pygmaea* (Schrottky, 1902), *P. (Trigonopedia)* sp. 1 (Tapinotaspidini), *Augochloropsis* sp. 1 (Augochlorini), *Epanthidium autumnale* (Schrottky, 1909) (Anthidiini), *Coelioxys* sp. 2 (Megachilini), uncoll Augochlorini (1 sp.); BL - *Bombus* *atratus*, *B. brasiliensis* Lepeletier, 1836 (Bombini), uncoll *Centris* (1 sp.); DI - *Paravilla* sp. 1 (Bombyliidae), uncoll Bombyliidae (1 sp.); SY - undet sp. 5, uncoll (1 sp.). Pink. Shrub. Jan-May, *Feb-Mar*. **43. *Symphyopappus compressus*** (Gardn.) B.L. Rob. (57) (5h): *Apis mellifera*; BS - *Melipona quadrifasciata* (Meliponini), *Melissoptila aureocincta* Urban, 1968 (Eucerini), *Agapostemon* sp. 1 (Halictini), *Megachile* cf. *anthidioides* Radoskowski, 1874 (Megachilini); BL - *Bombus atratus* (Bombini), *Xylocopa brasilianorum* (Linnaeus, 1767) (Xylocopini); DI - Tachinidae sp. 8; LE - *Yphthimoides ochracea* (Butler, 1867) (Nymphalidae), uncoll Nymphalidae (2 sp.), Pieridae (1 sp.); WA - Scoliidae sp. 1, uncoll (1 sp.). White. Shrub. Jan-Feb (f), *Jan*. **44. *Vernonia herbacea*** (Vell.) Rusby (741) (8h30'): BS - *Ceratina* cf. *asuncionis* (Ceratinini); BL - uncoll *Bombus*. Purplish magenta. Herb. Oct-Dec, *Nov-Dec*. **45. *Vernonia megapotamica*** Spreng. (36, 536) (12h): BS - *Melipona bicolor* (Meliponini), uncoll Meliponini (2 spp.), Halictidae (3 spp.); DI - *Paravilla* sp. 1 (Bombyliidae); LE - *Agraulis vanillae maculosa* (Stichel, 1907) (Nymphalidae); WA - uncoll Pompilidae (1 sp.), Vespidae (2 spp.). Purple. Herb. Jan-Apr, *Jan-Feb*. **46. *Vernonia* aff. *rosea*** Mart. ex DC. (275, 592, 844) (4h): BL - *Centris klugi* (Centridini), uncoll *Bombus*. Purple. Sub-shrub. Jan-Feb, *Feb*. **47. *Vernonia tomentella*** Mart. ex DC. (67, 588) (8h): BS - *Melipona bicolor* (Meliponini), *Mesonychium caerulescens* Lepeletier & Serville, 1825 (Ericrocidini), *Ceratina* cf. *asuncionis* (Ceratinini), *Augochloropsis* aff. *cognata*, *A. cyanea* (Augochlorini), uncoll Halictini (1 sp.); BL - *Bombus atratus* (Bombini), *Centris klugi* (Centridini), *Megachile iheringi*, *M. terrestris* (Megachilini), uncoll *Bombus*; LE - *Vanessa myrinna* (Nymphalidae). Purple. Sub-shrub. Jan-May, Oct-Dec, *Jan-Feb, Nov-Dec*. **48. *Vernonia tragiaefolia*** DC. (626) (4h): BS - *Gaesischia nigra* Moure, 1948 (Eucerini); BL - uncoll *Bombus*. Magenta. Sub-shrub. Jan-Feb, Apr, *Feb*. **49. *Vernonia westiniana*** Less. (92) (8h): *Apis mellifera*; BS - *Melipona bicolor*, *Plebeia saiqui* (Meliponini), *Ceratalictus* sp. 1 (Augochlorini), uncoll Meliponini (1 sp.), Halictidae (2 spp.); BL - *Bombus atratus*, *B. brasiliensis*, *B. morio* (Swederus, 1787) (Bombini), uncoll *Centris* (2 spp.); DI - Tachinidae sp. 6, uncoll Tachinidae (2 spp.); LE - *Sarbia* cf. *xanthippe* Spixii (Plotz, 1879), Pyrrhopyginae sp. 1 (Hesperidae), *Thecla* sp. 1 (Lycaenidae), *Hesperocharis erota* (Lucas, 1852) (Pieridae), uncoll Hesperidae (1 sp.), Nymphalidae (5? spp.), Pieridae (1 sp.), Sphingidae (1 sp.) ; WA - Scoliidae sp. 1, uncoll Pompilidae (1 sp.), Vespidae (1 sp.). Reddish purple. Shrub. Jan-June, *Feb*.

BROMELIACEAE: **50. *Dyckia tuberosa*** (Vell.) Beer. (495) (10h): HB - *Colibri serrirostris* (Vieillot). Reddish orange. Herb. Sep-Nov, *Oct-Nov*.

CAMPANULACEAE: **51. *Wahlenbergia brasiliensis*** Cham. (232, 280) (15h): *Apis mellifera*; BS - uncoll Augochlorini (2 spp.); SY - *Allograpta exotica* (Wiedemann, 1830), *Toxomerus watsoni*, uncoll (2 spp.). Lilac. Herb. Jan-Dec, *Feb, June-Sep*.

CLETHRACEAE: **52. *Clethra scabra*** Pers. var. *scabra* (332) (7h30'): *Apis mellifera*; BS - *Melipona bicolor*, *Scaptotrigona bipunctata* (Lepeletier, 1836), *Schwarziana quadripunctata* (Meliponini), *Augochloropsis* aff. *cognata* (Augochlorini), uncoll Meliponini (2 spp.), Halictidae (3 spp.); CO - Cantharidae sp. 2, *Rhinotragus festivus* Perty 1832 (Cerambicidae); DI - Tachinidae sp. 2, undet sp. 7, uncoll Sarcophagidae (1 sp.), Tachinidae (1 sp.); LE - *Yphthimoides ochracea* (Nymphalidae); WA - *Mischocyttarus drewseni*, *Synoeca cyanea* (Fabricius), *Polybia fastidiosuscula*, *P. minarum* Ducke (Vespidae), Cercerini sp. 1, sp. 2 (Sphecidae), undet sp. 10, uncoll (1 sp.). Yellowish white. Treelet. Feb-Aug (f), *Mar-May*.

CONVOLVULACEAE: **53. *Convolvulus crematifolius*** Ruiz & Pav. (37, 89) (4h): *Apis mellifera*; BS - *Ceratina* sp. 2 (Ceratinini), uncoll *Ceratina* (1 sp.); SY - uncoll (1 sp.). Lavender. Vine. Jan-Feb, Dec, *Jan, Dec.* **54. *Ipomoea procumbens*** Mart. (76) (6h): BL - *Bombus atratus* (Bombini), *Xylocopa brasilianorum* (Xylocopini), uncoll *Bombus*. Pink. Vine. Jan-Mar, *Feb.* **55. *Jacquemontia glandiflora*** Meisn. (118) (9h): BS - uncoll Meliponini (1 sp.), Tapinotaspidini (1 sp.), Halictidae (3 spp.); BL - *Bombus atratus* (Bombini), uncoll *Bombus*, *Centris* (1 sp.); WA - uncoll Vespidae (1 sp.). Violet. Vine. Jan-Aug, Nov-Dec, *Jan-Feb, May-July, Dec.*

CUNONIACEAE: **56. *Weinmania organensis*** Gardn. (54, 125) (8h): CO - Cantharidae sp. 2; DI - uncoll (1 sp.); WA - *Polybia minarum* (Vespidae). Pale yellow. Treelet. Jan-Aug (f), *Feb-Mar, May.*

DROSERACEAE: **57. *Drosera montana*** St. Hil. (127) (6h): SY - *Toxomerus watsoni*, undet sp. 1, uncoll (1 sp.). Pink. Herb. Jan-Feb, Nov-Dec, *Jan, Dec.*

ERICACEAE: **58. *Agarista hispidula*** (DC.) J. D. Hook ex Nied. (23, 431) (38h30'): HB - *Chlorostilbon aureoventris berlepschi* Pinto, *Leucochloris albicollis*. Red. Shrub. Jun-Nov, Aug-Sep. **59. *Gaylussacia chamissonis*** Meisn. (469) (16h30'): *Apis mellifera*; BS - *Melipona bicolor* (Meliponini), *Augochloropsis* sp. 1 (Augochlorini), uncoll Meliponini (1 sp.); WA - uncoll *Polybia* (2 spp.). White. Sub-shrub. Apr-Dec, *Oct-Dec.* **60. *Gaylussacia jordanensis*** Sleum. (370, 432) (31h30'): *Apis mellifera*; BS - *Plebeia saiqui* (Meliponini), *Augochloropsis cyanea*, *Augochloropsis* sp. 1, *Ceratalictus* sp. 1 (Augochlorini), *Dialictus* sp. 1 (Halictini), uncoll Meliponini (1 sp.), Halictidae (1 sp.); BL - *Megachile iheringi* (Megachilini); WA - uncoll Vespidae (1 sp.). White. Sub-shrub. Jan-May, Aug-Dec, *Sep-Oct.*

ERIOCAULACEAE: **61. *Paepalanthus paulensis*** Ruhland (706) (8h): BS - *Trigona spinipes* (Meliponini); CO - Buprestidae sp.1, Cantharidae sp. 3; DI - Sarcophagidae sp. 2, Sciaridae sp.1, Tachinidae sp. 3, uncoll (1 sp.); LE - uncoll Hesperiidae (1 sp.); SY - *Toxomerus watsoni*, *Toxomerus* sp. 1, uncoll (3 spp.); WA - uncoll Vespidae (1 sp.). Yellowish white. Herb. Sep-Dec, *Sep-Nov.* **62. *Paepalanthus polyanthus*** (Bong.) Koern. (18) (4h): CO - Cantharidae sp. 1; DI - undet sp. 5, sp. 8, uncoll Bombyliidae (1 sp.); LE - uncoll (1 sp.); SY - *Toxomerus watsoni*; WA - *Agelaia vicina* (Vespidae). Greenish white. Herb. Jan-June, Nov-Dec, *Jan-Apr, Dec.*

ERYTHROXYLACEAE: **63. *Erythroxylum microphyllum*** St. Hil. (373, 496) (6h): BS - *Ceratalictus* sp. 1 (Augochlorini), uncoll Meliponini (1 sp.), Augochlorini (2 spp.); WA - *Mischocyttarus drewseni*, *Polistes billardieri* (Vespidae), undet sp. 2, uncoll Pompilidae (1 sp.), Vespidae (2 spp.). Pastel yellow. Shrub. Jan-May, Nov-Dec, *Jan-Feb, Dec.*

EUPHORBIACEAE: **64. *Croton dichrous*** Muell. Arg. (17, 619) (6h): *Apis mellifera*; BS - *Augochloropsis* aff. *cognata*, *A. cyanea* (Augochlorini); DI - uncoll Tachinidae (2 spp.); SY - *Toxomerus watsoni*; WA - *Mischocyttarus drewseni*, *Polybia scutellaris* (Vespidae), Gasteruptiinae sp. 1 (Gasteruptiidae), uncoll Vespidae (2 spp.). Yellowish white. Shrub. Jan-Dec, *Mar-Jul, Nov-Dec.*

GENTIANACEAE: **65. *Deianira nervosa*** Cham. & Schlecht. (348) (6h): SY - undet sp. 5.

Reddish lilac. Herb. Feb-Apr, June, *Feb-Mar.* **66. *Irlbachia oblongifolia*** (Mart.) Maas (1, 95) (20h): not visited. Yellowish green. Herb. Jan-Mar, *Jan-Feb.* **67. *Irlbachia pedunculata*** (Cham. & Schlecht.) Maas (430, 520) (19h30'): not visited. Deep red. Herb. Jan-Apr, Dec, *Jan-Feb.* **68. *Irlbachia pendula*** (Mart.) (80, 264) (38h30'): not visited. Violet. Herb. Jan-May, July, *Feb.* **69. *Zygostigma australe*** (Cham. & Schltdl.) Griseb. (622) (8h30'): BS - *Ceratalictus* sp. 1 (Augochlorini); SY - *Allograpta exotica*, uncoll (1 sp.). Purple. Herb. Feb-Apr, *Feb-Mar.*

GESNERIACEAE: **70. *Sinningia allagophylla*** (Mart.) Wiehler (9) (27h): *Apis mellifera*; HB - *Clytolaema rubricauda* (Boddaert), *Colibri serrirostris, Leucochloris albicollis, Stephanoxis lalandi lalandi* (Vieillot). Reddish orange. Herb. Jan-Mar, Nov-Dec, *Jan, Dec.*

GROSSULARIACEAE: **71. *Escallonia farinacea*** St. Hil. (507) (6h): BS - *Colletes* sp. 1 (Colletini). White. Shrub. Nov-Dec, *Nov.*

HIPERICACEAE: **72. *Hipericum brasiliense*** St. Hil. (218, 508) (8h): BS - *Schwarziana quadripunctata* (Meliponini), Halictini sp. 1; BL - *Megachile iheringi* (Megachilini); DI - *Cylindromyia dorsalis* (Tachinidae); SY - uncoll (1 sp.). Vivid yellow. Shrub. Jan-May, Dec, *Jan.* **73. *Hipericum ternum*** Choisy (71, 494): apomictic. Vivid yellow. Herb. Jan-Mar, May-Aug, Oct-Dec, *Jan-Feb, Nov-Dec.*

IRIDACEAE: **74. *Alophia geniculata*** Klatt (376) (11h): BS - *Melipona bicolor, Plebeia saiqui* (Meliponini), *Augochloropsis iris, Paroxystoglossa* aff. *jocasta* (Schrottky,1910) (Augochlorini), *Dialictus* sp. 1, Halictini sp. 2, uncoll Tapinotaspidini (1 sp.); BL - *Bombus atratus* (Bombini); SY - *Toxomerus watsoni*, undet sp. 2. Violet. Herb. Mar-Apr, Nov-Dec, *Mar, Nov.* **75. *Alophia* sp. 1** (235) (7h): BS - *Ceratalictus* sp. 1 (Augochlorini); SY - *Allograpta exotica*. Lilac. Herb. Jan-Feb, *Jan.* **76.*Calydorea campestris*** (Klatt) Baker (236, 368) (8h30'): BS - *Plebeia saiqui* (Meliponini), *Augochloropsis* aff. *cognata* (Augochlorini), *Dialictus* sp. 1 (Halictini); SY - undet sp. 5, uncoll (2 spp.). Purplish violet. Herb. Jan-Mar, Oct-Dec, *Jan, Nov-Dec.* **77. *Sisyrinchium micranthum*** Cav. (762) (5h): BS - *Dialictus* sp. 1 (Halictini); SY - *Allograpta exotica*. Purple. Herb. Jan-Feb, Nov-Dec, *Nov-Dec.* **78. *Sisyrinchium vaginatum*** Spreng. (346, 434, 515) (21h30'): *Apis mellifera*; BS - uncoll Augochlorini (2 spp.); SY - *Toxomerus watsoni*, *Toxomerus* sp. 1, uncoll (1 sp.). Vivid yellow. Herb. Jan, Mar-Dec, *May-Oct.*

LAMIACEAE: **79. *Hyptis lippioides*** Pohl ex Benth. (399, 423) (7h): *Apis mellifera*; BS - *Melipona bicolor, Plebeia saiqui, Trigona spinipes* (Meliponini), *Augochloropsis* aff. *cognata*, *Ceratalictus* sp. 1 (Augochlorini); BL - *Bombus atratus* (Bombini). Grayish violet. Herb. July-Oct, *July.* **80. *Hyptis plectranthoides*** Benth. (5, 606) (6h30'): *Apis mellifera*; BS - *Ceratalictus* sp. 1 (Augochlorini); BL - *Bombus atratus* (Bombini), uncoll *Bombus*. Violet. Herb. Jan-May, Oct-Dec, *Jan, Dec.* **81. *Hyptis umbrosa*** Salzm. ex Benth. (310) (4h): *Apis mellifera*; BS - *Augochloropsis* sp. 1, *Ceratalictus* sp. 1 (Augochlorini); WA - uncoll Vespidae (2 spp.). Violet. Shrub. Jan-Apr, *Feb-Mar.* **82. *Peltodon radicans*** Pohl (313, 625) (4h): *Apis mellifera*; not visited. Bluish violet. Herb. Mar-May, *Mar-Apr.*

LEGUMINOSAE: **83. *Chaemaecrista* sp. 1** (85) (6h): BL - *Centris klugi* (Centridini). Vivid yellow. Sub-shrub. Feb-Mar, Oct-Dec, *Nov-Dec.* **84. *Crotalaria breviflora*** DC. (308, 818) (7h):

BS - *Anthidium sertanicola* Moure & Urban, 1964 (Anthidiini); BL - *Bombus atratus*, *B. brasiliensis* (Bombini). Vivid yellow. Sub-shrub. Jan-Apr, Dec, *Jan-Mar.* **85. *Lupinus velutinus*** Benth. (427) (27h): BL - *Megachile iheringi*, *M. laeta* Smith, 1853 (Megachilini), *Bombus atratus* (Bombini), uncoll *Bombus*, *Megachile* (1 spp.). Violet. Sub-shrub. July-Oct, Dec, *Aug-Sep.*

LOBELIACEAE: **86. *Lobelia camporum*** Pohl (41) (7h): BS - *Ceratina* cf. *asuncionis* (Ceratinini); BL - *Bombus atratus* (Bombini), *Centris burgdorfi* Friese, 1901 (Centridini), uncoll *Bombus*. Lilac. Herb. Jan-June, Nov-Dec, *Jan-Feb, June, Dec.*

LYTHRACEAE: **87. *Cuphea glutinosa*** Cham. & Schlechtd (20) (24h): *Apis mellifera*; BS - *Ceratina* sp. 1 (Ceratinini), *Mesonychium caerulescens* (Ericrocidini), *Augochloropsis cyanea*, *Augochloropsis* sp. 1 (Augochlorini), *Anthidium sertanicola* (Anthidiini), *Megachile* cf. *anthidioides* (Megachilini); BL - *Bombus atratus*, *B. brasiliensis*, *B. morio* (Bombini), *Centris klugi* (Centridini); LE - *Eurema nise tenella* (Bdvl., 1836) (Pieridae); SY - *Toxomerus watsoni*; WA - undet sp. 3, sp. 11. Purple. Sub-shrub. Jan-Dec, *Jan, Apr-June, Aug, Nov-Dec.*

MALPIGHIACEAE: **88. *Byrsonima variabilis*** A. Juss. (112, 490) (16h): BS - *Plebeia saiqui* (Meliponini), *Augochloropsis* aff. *cognata* (Augochlorini), *Monoeca* sp. 1, *Paratetrapedia (Xanthopedia)* sp. 1 (Tapinotaspidini), *Centris* cf. *insularis* Smith, 1874 (Centridini); BL - *Centris discolor* Smith, 1874, *C. klugi*, *C. tarsata* Smith, 1874, *Centris (Melacentris)* sp. 1 (Centridini), uncoll *Centris* (2 spp.). Vivid yellow. Sub-shrub. Jan-Feb, May, Oct-Dec, *Nov-Dec.*

MALVACEAE: **89. *Pavonia* cf. *reticulata*** (105) (4h): BS - *Augochloropsis* aff. *cognata* (Augochlorini). Yellow. Vine. Jan-Feb, Dec, *Feb.* **90. *Sida* sp. 1** (24, 456) (6h): BS - *Ceratina* cf. *asuncionis* (Ceratinini), uncoll *Ceratina* (1 sp.). Pastel pink. Herb. Jan-Mar, Oct-Dec, *Jan, Nov-Dec.*

MELASTOMATACEAE: **91. *Leandra erostrata*** Cogn. (113) (5h): not visited, apomictic? Pink. Herb. Jan-Feb, Oct-Dec, *Jan, Nov-Dec.* **92. *Leandra* sp. 1** (19) (6h): not visited, apomictic? White. Herb. Jan-Feb, Nov-Dec, *Jan, Nov-Dec.* **93. *Leandra* sp. 2** (401) (11h): not visited, apomictic? Pink. Shrub. July-Oct, *Aug-Sep.* **94. *Leandra* sp. 3** (402) (6h30'): not visited, apomictic? Pink. Shrub. July-Dec, *Oct-Nov.* **95. *Microlicia isophylla*** DC. (103) (14h30'): not visited, apomictic? Magenta. Sub-shrub. Jan-Mar, July-Aug, Dec, *Jan-Feb.* **96. *Tibouchina frigidula*** (DC.) Cogn. (25, 419) (24h): BL - *Bombus atratus* (Bombini), *Xylocopa brasilianorum* (Xylocopini), *Centris discolor* (Centridini), uncoll *Bombus*, *Centris* (2 spp.). Deep violet. Shrub. Jan-Dec, *Jan-Mar, Dec.* **97. *Tibouchina martialis*** (Chamisso) Cogn. (369) (4h): BL - *Xylocopa brasilianorum* (Xylocopini), uncoll *Centris* (1 sp.). Reddish violet. Shrub. Apr-June, *June.* **98. *Tibouchina minor*** Cogn. (32) (10h): BS - uncoll Augochlorini (1 sp.); BL - *Bombus atratus* (Bombini), *Centris klugi* (Centridini), uncoll *Centris* (2 spp.). Violet. Herb. Jan-Apr, Dec, *Jan-Feb.* **99. *Trembleya parviflora*** (Don) Cogn. (341, 420) (6h): BS - *Melipona bicolor*, *Paratrigona subnuda* (Meliponini). Pink. Shrub. Feb-July, *June-July.* **100. *Trembleya phlogiformis*** DC. (44, 74) (7h): BS - *Augochloropsis* sp. 1 (Augochlorini); BL - *Bombus atratus* (Bombini). Purple. Sub-shrub. Jan-Mar, *Jan-Mar.*

OCHNACEAE: **101. *Ouratea semiserrata*** (Mart. & Nees) Engl. (425) (7h): BS - *Melipona bicolor*, *Trigona spinipes* (Meliponini), *Dialictus* sp. 1 (Halictini); BL - uncoll *Centris* (1 sp.). Vivid yellow. Treelet. June-July, *June.*

ORCHIDACEAE: **102. *Epidendrum secundum*** Jacq. (150) (14h): not visited. Purple. Herb. Jan-Aug (f), *Jan, Apr-May.* **103. *Habenaria parviflora*** Lindl. (82, 804) (5h day, 13h night): not visited. Grayish green. Herb. Jan-Mar, Dec, *Jan-Feb.* **104. *Oncidium barbaceniae*** Lindl. (282, 305) (19h30'): uncoll *Bombus*? Vivid yellow. Herb. Jan-Mar, May-Dec, *Jan, May, July, Sep-Dec.* **105. *Oncidium blanchetii*** Rchb.f. (611) (14h): not visited. Vivid yellow. Herb. Jan-Dec, *July-Nov.* **106. *Oncidium* sp. 1** (501) (14h): not visited. Vivid yellow. Herb. Jan, Dec.

POLYGALACEAE: **107. *Polygala brasiliensis*** L. (309, 366, 683) (6h30'): BS - uncoll Augochlorini (1 sp.). Reddish purple. Herb. Feb-Sep, Nov-Dec, *Mar, June-Aug, Dec.* **108. *Polygala cneorum*** A. St.-Hil. (390) (10h): BS - *Augochloropsis* sp. 1 (Augochlorini). Grayish magenta. Herb. Apr-Sep, Nov, *May-Aug.*

RUBIACEAE: **109. *Borreria capitata*** (R. & P.) DC (322) (8h30'): *Apis mellifera*; BS - *Augochloropsis* aff. *cognata*, *Ceratalictus* sp. 1 (Augochlorini); DI - *Exoprosopa* sp. 1 (Bombyliidae), uncoll Sarcophagidae (1 sp.); SY - *Pseudodoros clavatus* (Fabricius, 1794), *Toxomerus watsoni*, *Toxomerus* sp. 1, uncoll (1 sp.); WA - undet sp. 2, uncoll Vespidae (1 sp.). White. Herb. Feb-July, *Mar-Apr.* **110. *Borreria tenella*** Cham. & Schltdl. (192, 667) (5h): BS - *Ceratalictus* sp. 1 (Augochlorini); WA - *Polybia sericea* (Vespidae), undet sp. 2, uncoll Vespidae (2 spp.). Purple. Herb. Mar-Jul, *May-June.* **111. *Declieuxia cordigera*** var. *angustifolia* M. Arg. (6, 727) (7h): BS - Augochlorini sp. 1, uncoll Augochlorini (1 sp.); BL - *Bombus atratus* (Bombini), *Centris burgdorfi* (Centridini), uncoll *Bombus*; LE - uncoll Hesperidae (1 sp.); WA - uncoll Vespidae (1 sp.). Purple. Herb. Jan-Dec, *Jan-Feb, June, Aug-Sep.* **112. *Galianthe angustifolia*** (Cham. R.Schltdl.) E.L. Cabral (50) (24h): *Apis mellifera*; BS - *Mesonychium caerulescens* (Ericrocidini), *Augochloropsis cyanea* (Augochlorini), uncoll Augochlorini (2 spp.); BL - *Bombus atratus*, *B. morio* (Bombini), uncoll *Centris* (2 spp.); DI - Curtonotidae sp. 2, Sarcophagidae sp. 1, Tachinidae sp. 7; LE - uncoll Hesperidae (1 sp.); SY - *Allograpta exotica*, uncoll (2 spp.); WA - *Bicyrtes paranae* Bohart, *Sphex dorsalis* Lepeletier (Sphecidae), *Polybia fastidiosuscula* (Vespidae), undet sp. 15, uncoll Vespidae (2 spp.). Yellowish white. Sub-shrub. Jan-May, July, Sep-Dec, *Jan-Feb, Dec.* **113. *Galianthe brasiliensis*** Spreng. (618) (8h): *Apis mellifera*; BS - *Augochloropsis* aff. *cognata*, *Augochloropsis cyanea*, *Augochloropsis* sp. 1, *Ceratalictus* sp. 1 (Augochlorini); DI - Tachinidae sp. 1, sp. 4; LE - *Thecla* sp. 1 (Lycaenidae); SY - *Pseudodoros clavatus*, *Toxomerus watsoni*, uncoll (1 sp.); WA - *Mischocyttarus drewseni*, *Polistes billardieri* (Vespidae), Tenthredinidae sp. 1, undet sp. 12, uncoll Pompilidae (1 sp.), Sphecidae (1 sp.), Vespidae (3 spp.). White. Shrub. Jan-Aug, Oct-Dec, *Jan-July, Nov.* **114. *Galium hypocarpium*** (L.) Endl. ex Griseb. (371, 802) (11h30'): DI - *Trupanea* sp. 1 (Tephritidae), WA - Eurytomidae sp. 1. Greenish yellow. Sub-shrub. Jan-July, Oct-Dec, *Jan, Apr-May, Nov-Dec.*

SCROPHULARIACEAE: **115. *Esterhazya macrodonta*** (Cham.) Benth. (244) (72h30'): *Leucochloris albicollis*. Reddish orange. Shrub. Jan, June-Oct, *July-Aug.*

SOLANACEAE: **116. *Solanum aculeatissimum*** Jacq. (483) (9h30'): BS - *Augochloropsis* *cyanea* (Augochlorini). Vivid yellow. Herb. Jan-Feb, May, Oct-Dec, *Jan-Feb, Oct-Dec.* **117.** ***Solanum americanum*** Mill. (488, 675) (8h30'): BS - uncoll Augochlorini (1 sp.). Vivid yellow. Herb. Jan, Nov-Dec, *Nov.* **118.** ***Solanum pseudocapsicum*** L. (768) (5h30') : BS - *Augochloropsis cyanea, Augochloropsis* sp. 1 (Augochlorini). Vivid yellow. Sub-shrub. Jan-Feb, Nov-Dec, *Jan-Feb, Nov.* **119.** ***Solanum swartzianum*** Roem. & Schug. (538, 659) (4h30'): BS - *Augochloropsis cyanea* (Augochlorini). Vivid yellow. Shrub. Jan, Apr-June, Aug (f), *Apr-May.* **120.** ***Solanum viarum*** Dunal (559, 742) (13h): BS - *Augochloropsis cyanea* (Augochlorini). Yellowish green. Herb. Jan-Mar, Aug-Dec, *Feb, Sep, Nov-Dec.*

VERBENACEAE: **121.** ***Verbena hirta*** Spreng. (31, 243) (10h): *Apis mellifera*; BS - *Mesonychium caerulescens* (Ericrocidini), *Ceratina* cf. *asuncionis* (Ceratinini), *Pseudaugochlora* aff. *graminea* (Fabricius, 1804) (Augochlorini), Halictini sp. 2; BL - *Bombus atratus, B. brasiliensis, B. morio* (Bombini), *Xylocopa brasilianorum* (Xylocopini), *Centris tarsata* (Centridini), *Megachilie laeta* (Megachilini); LE - *Urbanus* sp. 1 (Hesperidae), *Eurema nise* (Pieridae), uncoll *Vanessa* (Nymphalidae) (1 sp.); SY - uncoll (2 spp.); WA - uncoll Vespidae (1 sp.). Purplish violet. Sub-shrub. Jan-Dec, *Jan, Sep-Dec.*

VIOLACEAE: **122.** ***Viola cerasifolia*** A. St.-Hil. (124) (27h): BS - *Anthrenoides* aff. *meridionalis* (Schrottky, 1906) (Panurginae), *Augochlorodes turrifaciens* Moure 1958 (Augochlorini), *Dialictus* sp. 1 (Halictini). Violet. Herb. Jan-Feb, Dec, *Jan, Dec.*

XYRIDACEAE: **123.** ***Xyris asperula*** Mart. (846) (4h): BS - *Augochloropsis cyanea* (Augochlorini), uncoll Meliponini (1 sp.), Augochlorini (1 sp.); SY - *Toxomerus watsoni*, undet sp. 1, uncoll (2 spp.). Vivid yellow. Herb. Feb-Mar, *Feb.* **124.** ***Xyris tortulla*** Mart. (2, 350) (6h): BS - *Paratetrapedia* cf. *pygmaea* (Tapinotaspidini); SY - *Toxomerus watsoni*, undet sp. 4, uncoll (2 spp.). Deep yellow. Herb. Jan-May, Dec, *Jan-Mar.*

B. Pollinator insects at the Serra da Bocaina's grasslands arranged by their taxonomy.

COLEOPTERA

1. **BUPRESTIDAE**: sp.1
2. **CANTHARIDAE**: sp. 1, sp. 2, sp. 3
3. **CERAMBICIDAE**: *Rhinotragus festivus* Perty 1832
4. **TENEBRIONIDAE**: sp. 1

DIPTERA

1. **BOMBYLIIDAE**: *Euprepina* sp. 1, *Exoprosopa* sp. 1, *Paravilla* sp. 1
2. **CULICIDAE**: sp. 1
3. **CURTONOTIDAE**: sp. 1, sp. 2
4. **SARCOPHAGIDAE**: sp. 1, sp. 2
5. **SCIARIDAE**: sp. 1

6. **SYRPHIDAE**: *Allograpta exotica* (Wiedemann, 1830), *Palpada rufipedes* Thompson, 1976, *Pseudodoros clavatus* (Fabricius, 1794), *Syrphus phaeostigma* Wiedemann, 1830, *Toxomerus watsoni* (Curran, 1930), *Toxomerus* sp. 1, Syrphidae sp. 1, sp. 2, sp. 3, sp. 4, sp. 5, sp. 6

7. **TACHINIDAE**: *Cylindromyia dorsalis* (Wiedemann, 1830), *Jurinella* aff. *corpulenta* (Townsend, 1927), Tachinidae sp. 1, sp. 2, sp. 3, sp. 4, sp. 5, sp. 6, sp. 7, sp. 8, sp. 9

8. **TEPHRITIDAE**: *Trupanea* sp. 1

9. **UNDETERMINED FAMILIES**: 8 species

HYMENOPTERA

Apoidea

1. ANDRENIDAE, PANURGINAE

a. Panurgini: *Anthrenoides* aff. *meridionalis* (Schrottky, 1906)

2. APIDAE, APINAE

a. Apini: *Apis mellifera* Linnaeus, 1758

b. Bombini: *Bombus (Fervidobombus) atratus* Franklin, 1913, *B. (Fervidobombus) brasiliensis* Lepeletier, 1836, *B. (Fervidobombus) morio* (Swederus, 1787)

c. Centridini: *Centris (Centris)* cf. *insularis* Smith, 1874, *C. (Hemisiella) tarsata* Smith, 1874, *C. (Melacentris) discolor* Smith, 1874, *C. (Paracentris) burgdorfi* Friese, 1901, *C. (Paracentris) klugi* Friese, 1899, *C. (Melacentris)* sp. 1

d. Ericrocini: *Mesonychium caerulescens* Lepeletier & Serville, 1825

e. Eucerini: *Gaesischia (Gaesischia) nigra* Moure, 1948, *Melissoptila (Ptilomelissa) aureocincta* Urban, 1968

f. Meliponini: *Melipona bicolor bicolor* Lepeletier, 1836, *M. quadrifasciata anthidioides* (Lepeletier, 1836), *Paratrigona subnuda* Moure, 1947, *Plebeia droryana* (Friese, 1900), *P. saiqui* (Friese, 1900), *Scaptotrigona bipunctata* (Lepeletier, 1836), *Schwarziana quadripunctata* (Lepeletier, 1836), *Trigona spinipes* (Fabricius, 1793)

g. Tapinotaspidini: *Monoeca* sp. 1, *Paratetrapedia (Lophopedia)* cf. *pygmaea* (Schrottky, 1902), *P. (Trigonopedia)* sp. 1, *P. (Xanthopedia)* sp. 1

XYLOCOPINAE

a. Ceratinini: *Ceratina (Crewela)* cf. *asuncionis* Strand, 1910, *Ceratina* sp. 1, *Ceratina* sp. 2

b. Xylocopini: *Xylocopa (Neoxylocopa) brasilianorum* (Linnaeus, 1767)

3. COLLETIDAE, COLLETINAE

a. Colletini: *Colletes* sp. 1

4. HALICTIDAE, HALICTINAE

a. Augochlorini: *Augochlorodes turrifaciens* Moure 1958, *Augochloropsis* aff. *cognata* Moure, 1944, *A. cyanea* (Schrottky, 1901), *A. iris* (Schrottky, 1902), *Augochloropsis* sp. 1, *Ceratalictus* sp. 1, *Paroxystoglossa* aff. *jocasta* (Schrottky,1910), *Paroxystoglossa* sp. 1, *Pseudaugochlora* aff. *graminea* (Fabricius, 1804), Augochlorini sp. 1

b. Halictini: *Agapostemon* sp. 1, *Dialictus* sp. 1, *Dialictus* sp. 2, *Pseudagapostemon cyaneus* Moure & Sakagami, 1984, Halictini sp. 1, sp. 2

5. MEGACHILIDAE, MEGACHILINAE

a. Anthidiini: *Anthidium (Anthidium) sertanicola* Moure & Urban, 1964, *Epanthidium autumnale* (Schrottky, 1909)

b. Megachilini: *Coelioxys* sp. 1, *Coelioxys* sp. 2, *Megachile* cf. *anthidioides* Radoskowski, 1874, *M. aureiventris* Schrottky, 1902, *M. iheringi* Schrottky, 1913, *M. laeta* Smith, 1853, *M. terrestris* Schrottky, 1902

"Wasps"

1. BRACONIDAE: sp. 1

2. CHRYSIDIDAE: sp. 1

3. EURYTOMIDAE: sp. 1

4. GASTERUPTIIDAE: Gasteruptiinae sp. 1

5. LEUCOSPIDAE: sp. 1

6. POMPILIDAE: sp. 1, sp. 2, sp. 3, sp. 4

7. SCOLIIDAE: sp. 1

8. SPHECIDAE: *Bicyrtes paranae* Bohart, *Pryonyx thomaz* (Fabr.), *Sphex dorsalis* Lepeletier, *Sphex opacus* Dahlbom, Cercerini sp. 1, Cercerini sp. 2, Larrinae sp. 1

9. TENTHREDINIDAE: sp. 1

10. TIPHIIDAE: sp. 1

11. VESPIDAE: *Agelaia vicina* (Saussure), *Brachygastra lecheguana* (Latreille), *Mischocyttarus drewseni* Saussure, *Polistes billardieri* Fabricius, *P. cinerascens* Saussure, *Polybia fastidiosuscula* Saussure, *P. minarum* Ducke, *P. scutellaris* (White), *P. sericea* (Olivier), *Protonectarina sylveirae* (Saussure), *Protopolybia sedula* (Saussure), *Synoeca cyanea* (Fabricius)

12. UNDETERMINED FAMILIES: 15 species

LEPIDOPTERA

1. HESPERIDAE: *Sarbia* cf. *damippe* Mab. & Boul, 1908, *Sarbia* cf. *xanthippe* Spixii (Plotz, 1879), *Thespeius* sp. 1, *Urbanus* sp. 1, Hesperiinae sp. 1, Pyrrhopyginae sp. 1

2. LYCAENIDAE: *Thecla* sp. 1, Riodininae sp. 1

3. NYMPHALIDAE: *Agraulis vanillae maculosa* (Stichel, 1907), *Vanessa myrinna* (Dbldy., 1849), *Vanessa* sp. 1, *Yphthimoides ochracea* (Butler, 1867)

4. PIERIDAE: *Eurema nise tenella* (Bdvl., 1836), *Hesperocharis erota* (Lucas, 1852)

CAPÍTULO II:

Floral Biology and Pollination Mechanisms in *Viola cerasifolia* - from nectar to pollen flower?[1]

The genus *Viola* is represented by four related species in Brazil belonging to *Leptidium*, one of the most basal sections in the genus. We studied floral biology and pollination by bees in *Viola cerasifolia* A. St.-Hil. in a high-altitude grassland in southeastern Brazil. The flower is pentamerous, zygomorphic and spurred. The five stamens are joined through papillae, and are arranged in a cuff around the ovary. Each connective bears a membranous apical projection. Pollen is released by means of the superior and lateral connective projections, which form a cone surrounding the base of the style. The connective projections of the inferior stamens are elongated and curved in a hook-shaped structure. The two inferior stamens each bear a basal connective appendage, which projects into the spur. The apices of these appendages form a nectar secreting tissue, where traces of nectar can be detected. The stigma is simple and truncate. Pollinators are solitary bee species of the families Andrenidae and Halictidae, which search mainly for pollen. During visits, the bees obtain large amounts of pollen by vibrating the flowers or by moving the hook repeatedly backward and forward. The basic floral structure in the genus *Viola* fits that of "nectar flowers". The uncommon hook-shaped projections, scanty nectar production, and behavior of pollinators suggest that *V. cerasifolia* may be shifting its reward for pollinators from nectar to pollen. Based on floral morphology, this shift may be widespread in section *Leptidium*.

Key words: Andrenidae, bee pollination, buzz pollination, floral biology, Halictidae, melittophily, nectary, pollen flower.

INTRODUCTION

Viola is a large genus, containing ca. 525-600 species. The genus is distributed mainly in the Northern Hemisphere despite its probable Andean origin (Ballard, Sytsma and Kowal, 1999). *Viola* plants have attracted the attention of pollination biologists since Sprengel (1793), due the

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[1] Following the *Annals of Botany* format

presence of cleistogamous flowers and by the singularity of its chasmogamous flowers. Floral biology and pollination mechanisms have been studied in several North-American and European species of *Viola* (e.g., Knuth, 1904; Beattie, 1969*a, b*, 1971, 1972; Herrera, 1988), but we know of no published information about South American species.

In Brazil, there are only four *Viola* species, which belong to the predominantly austral *Viola* section *Leptidium*. Species of this section occur mainly in the Andes, and constitute one of the two most basal groups of *Viola* (Ballard *et al.*, 1999). In spite of considerable divergence in vegetative morphological traits, the four Brazilian species of *Viola* are closely related and apparently reflect a single evolutionary relict lineage, which is probably the most basal within the section *Leptidium* (H. E. Ballard, pers. comm.). These *Viola* species occur mainly in shady parts of both upper-montane forests and high-altitude grasslands at the coastal mountain ranges in southeastern Brazil.

The high-altitude grassland is a subtype of Brazilian coastal rainforest (Atlantic Forest), which is one of the most endangered ecosystems on earth (Mori, Boom and Prance, 1981, Morellato and Haddad, 2000). These grasslands form an archipelago of mountaintop formations, which show strong floristic similarities to the Andean and Central-American alpine habitats (Safford, 1999). For such restricted areas of habitat, grasslands harbor extraordinarily rich floras with high endemism. For example, about a third of the ca. 400 species in the Itatiaia plateau (< 50 km^2) appears to be endemic to high altitude grasslands (Martinelli, 1989; Safford, 1999). Due to several particularities - richness of species, endemism, "island-type" occurrence and biogeographical connections - the Brazilian high-altitude grasslands are interesting places for studies on pollination biology. However, plant-pollinator interactions are poorly known in these habitats.

In this paper we report observations on floral biology and pollination mechanisms of *Viola cerasifolia* A. St.-Hil. Based on floral morphology and the type and behavior of pollinators, we suggest that this *Viola* species could be shifting its reward for pollinators from nectar to pollen, and thereby would be moving away from the basal condition of "nectar flower" which characterizes the family.

Study System

We studied a *Viola cerasifolia* population in a grassland area (ca. 1600 m a.s.l.) at the

Parque Nacional da Serra da Bocaina (PNSB) in the Serra do Mar range, southeastern Brazil (ca. 22°44'S, 44°36'W). This montane area is covered mainly by high altitude grasslands, which are surrounded by mixed broadleaf and Araucarian forest (Eiten, 1970, Safford 1999). Annual rainfall is up to 2100 mm, with a rainy season mostly from October to March and monthly rain lower than 50 mm from June to August. Average annual temperature is approximately 15°C and temperatures may fall below 0°C during the winter, with the presence of frost. The vegetation of the grassy fields is a mosaic of shrubs (mainly species of Asteraceae and Melastomataceae) set within a matrix of species of Poaceae and Cyperaceae. Human disturbances, mainly fires during the winter season, are common in grassland areas at the PNSB.

Viola cerasifolia is a small perennial herb (ca. 10 cm in length) with clonal reproduction and grows in small clusters. It prefers shaded and sheltered spots on the grassy fields, mainly in slits of exposed granite rocks. We found only ca. 40 individuals of this species and we failed to find others in more disturbed areas. The flowering period of *V. cerasifolia* was from Dec. to Feb. at the study site. Cleistogamous (CL) flowers were not detected, neither in plants studied at the PNSB nor in material examined in herbaria. However, it is possible that CL flowers occur during the winter season. Voucher specimens of *V. cerasifolia* (L. Freitas, 124 and 783) were deposited in the Herbarium of the Universidade Estadual de Campinas (UEC).

MATERIALS AND METHODS

We spent a total of 21 hours watching floral visitors mainly in morning and occasionally in afternoon periods during the 1999-2000 flowering season. We recorded the frequency on visits by each insect species, and behavior when searching for floral resources during the visits. Pollen viability was estimated by cytoplasmic stainability, using the aceto-carmine technique (Radford *et al.*, 1974). Stigma receptivity was tested by H_2O_2 catalase activity method (Zeisler, 1938).

For scanning electron microscopy, 12 flowers were fixed in 2.5% glutaraldehyde in 0.05 M sodium cacodylate buffer, pH 7.0; then dehydrated with a graded ethanol/acetone series. Flowers were critical point dried in a Balzers CPD 030 instrument using CO_2 as the replacement fluid. Dried specimens were mounted on stubs and coated with gold in a Balzers SCD 050 sputter coater. Material was examined with a Phillips 505 scanning electron microscope at 25 KV to study the floral morphology.

RESULTS

Floral Biology

Flowers are horizontal in position at the beginning of anthesis (Fig. 1A), but the pedicel elongates during and after anthesis, changing its position in such a way that the young fruits are placed on the ground. Flower morphology follows, in general lines, the description given by Beattie (1969a, 1971) for three British *Viola* species. The zygomorphic, pentamerous and spurred flowers of *V. cerasifolia* are ca. 15 x 12 mm in diameter. The corolla tube is 3-4 mm in length and the corolla opening is 2-3 mm in diameter. Petals are smooth, without the tufts of hairs, which are common in other species of the genus. The spur of the inferior petal is short, ca. 1-2 mm in length. The main color of the petals is violet with their distal parts pale violet to white, and with dark violet ribs forming nectar guides. The base of the inferior petal is vivid yellow and white, providing a contrasting pattern (Fig.1A). During anthesis, the petals gradually lose their color, becoming completely pale lilac or white by the end of anthesis. We detected a sweet fragrance, especially during the morning hours. The flowers last about 6 days.

The androecium is the most elaborate floral part in *V. cerasifolia* (Fig. 2A). The five stamens have short and broad filaments. Anthers are introrse and fused longitudinally through many papillae (Fig. 2B), in such a way that they form a cuff around the ovary. The basal part of the two inferior anthers have ca. 1 mm long connective appendages projecting into the corolla spur. Nectar is produced at the distal parts of these appendages by a mesenchymal nectary and exuded by modified stomata (Fig. 2C, see Vogel, 1998). We could only detect a thin layer of secretion covering the tips of the appendages, and as nectar production was very low, we could not measure its volume. In many flowers we observed neither stomata at the connective appendages (eight out twelve flowers examined by SEM) nor any indication of nectar secretion (sixteen out twenty flowers at field).

Connectives also have projections at their distal part. The projections of the superior and lateral stamens (1-2 mm long) form a hollow cone around the style (Fig. 2A, 3A). The projections of the inferior stamens are joined to the lateral ones through papillae in their proximal part. The inferior projections are especially elongate, ending in a hook-shaped tip (ca. 1 mm long), hereafter called simply "hook" (Fig. 2A, 3A). Each anther (ca. 2.5 mm) opens longitudinally; however the fusion between them leads the pollen to be presented at the inferior part of the cone. Dehiscence of the anther valves begins at their distal end and then the suture opens up, zipper-like, down to the anther's base (see Beattie, 1969*b*). The dehiscence of the five anthers follows a superior-lateral-inferior sequence in such a way the pollen is gradually deposited on the cone, and thus, pollen is progressively available to pollinators during the anthesis period.

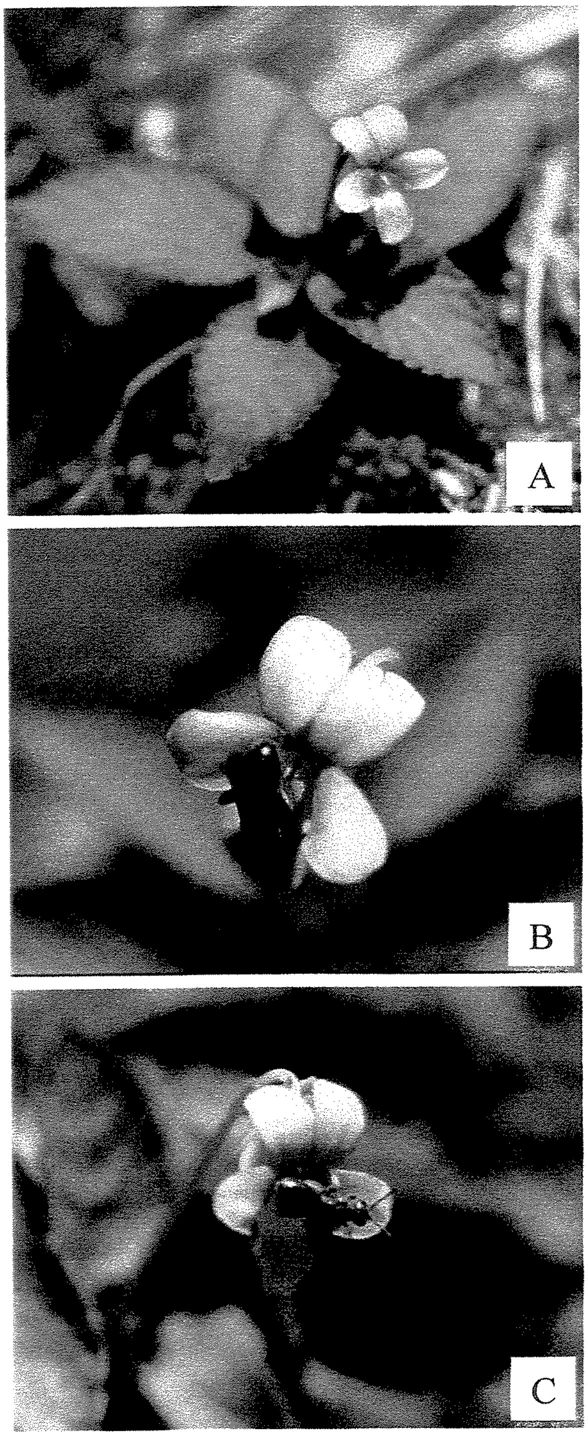

Fig. 1. Flower and pollinators of *Viola cerasifolia* in a high-altitude grassland in southeastern Brazil. A, Flower in front view; note the conspicuous yellow patch at the floral tube entrance. B, A female of *Anthrenoides* aff. *meridionalis* (Andrenidae) visiting a flower in the supine position. In this position the bee's body touches the stigma. Note the yellow pollen mass of *Viola* on the hind leg. C, A male of *Augochlorodes turrifaciens* (Halictidae) sitting on a flower after visiting it in search of nectar. This bee patrols the *Viola* cluster looking for females.

The three-aperturate pollen grains are spheroid and small (ca. 20 μm in diameter), with a smooth and non-reticulate exine. The pollen viability ranged from 66.1% to 79.6% (mean 72.5%, n = 5). We found a tangled mass of germinating pollen grains within the anther cone in one flower examined by electron microscopy (Fig. 3B).

The gynoecium is syncarpous, superior and three-carpelled, with one unilocular ovary and a mean of 26 ovules (SD = 2.67, n = 10). The 2-3 mm long style is tubular and soft without any constricted area of flexure, in contrast with other studied species (see Beattie, 1969*a, b*). It contains a lumen - filled by a mucilaginous substance - which is continuous with the cavity of the ovary. The stigma is simple and truncate, without lips (Fig 2A), and its border is moistened with the mucilage. After pollen grain deposition, the stigma closes (Fig. 3C). The time course of the stigma closing seems to be highly variable among flowers.

Flower visitors and pollinators

In our observations, *Viola cerasifolia* was pollinated only by small solitary bees, *Anthrenoides* aff. *meridionalis* (Schrottky, 1906) (Panurginae, Andrenidae), *Augochlorodes turrifaciens* Moure, 1958 (Augochlorini, Halictidae) and *Dialictus* sp. (Halictini, Halictidae). In all visits, bees adopted a supine feeding posture (Fig. 1B). To achieve that position, bees landed directly on the superior petals with their heads oriented to the inferior petal, or rotated their bodies 180° after landing on the inferior petal. The inferior petal has a curvature forming a chamber at the beginning of the corolla tube. In order to put their head into the tube chamber, bees aligned their bodies in a perpendicular position in relation to the main axis of the corolla tube (Fig. 1B). In such a position, the ventral parts of the bee's body touched the stigma just before the animals entered completely into the tube for pollen collection or probing for nectar. The contact with the stigma at the beginning of the visit by the bees could favor the deposition of outcrossed pollen on the stigma. Inside the tube, the bees used their forelegs to hold onto the stamen cuff. When a bee entered into the floral tube, its head pushed the hook forward in the direction of the corolla base. As the inferior projections are connected to the lateral ones, the hook displacement moved them down (Fig. 2A). As a result, a small amount of pollen - which was within the cone - was released over the bee's ventral parts.

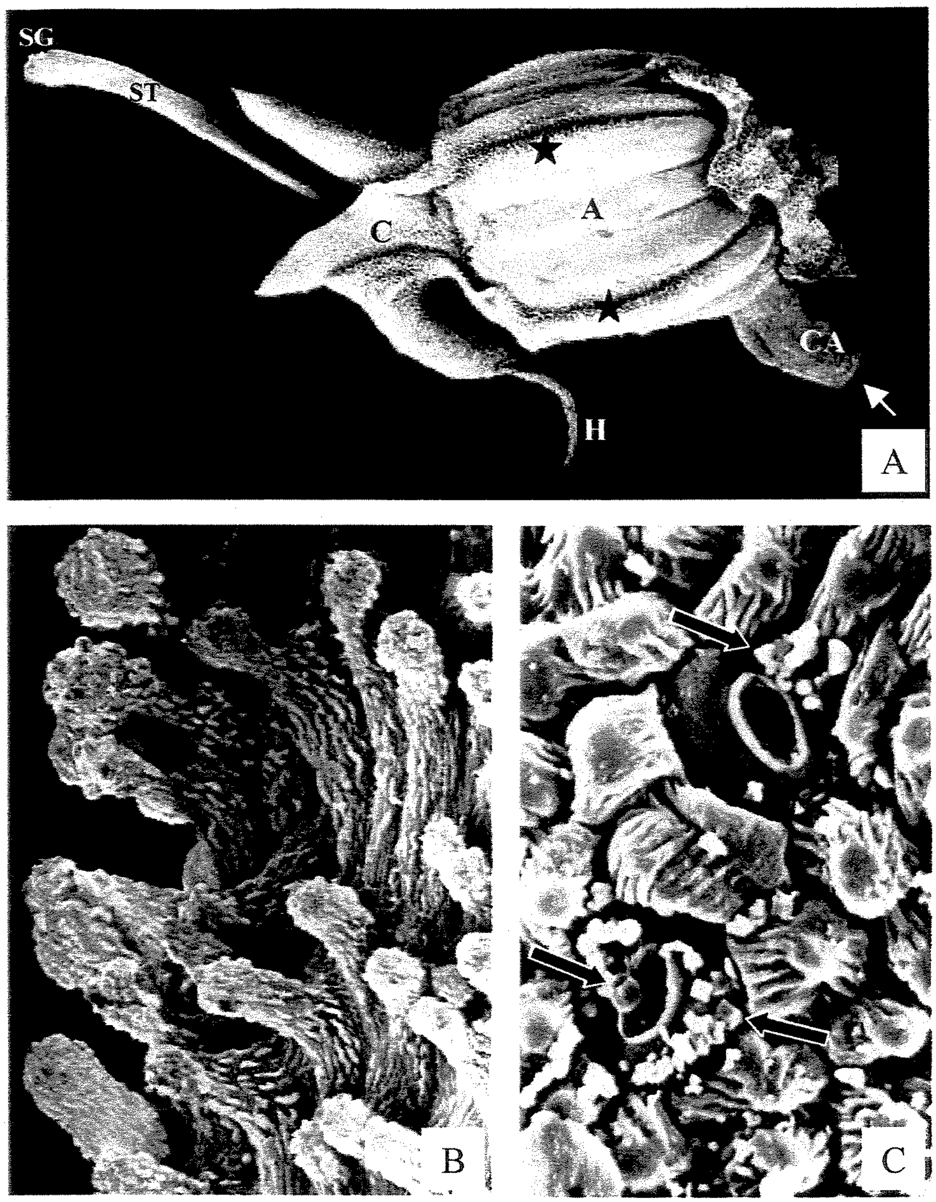

Fig. 2. Scanning electron micrograph (SEM) of *V. cerasifolia*. A, The gynoecium and the androecium in a longitudinal view. During preparation, the hook was moved in direction toward the connective appendages, and consequently, the cone around the style is opened. The same movement is carried out by the bees when they enter into the corolla tube to collect pollen, and this is the way by which pollen is released. Note the region of anthers joined by papillae (stars). Nectar is produced in the tip of connective appendage (arrow). 2 cm = 1 mm. B, Some papillae in the region of fusion between anthers. Note the elaborate ornamentation. 2 cm = 35 µm. C, Detail of the connective appendage tip showing modified stomata, by which nectar is exuded. Cubic crystals over stomata (arrows) seem to be sugar, but may be preparation artifacts. 2 cm = 17 µm. A – anther, C – cone, CA – connective appendage, H – hook, SG – stigma, ST – style.

Pollen is the chief resource offered by *V. cerasifolia*, and we observed female bees collecting pollen in all their visits. The movement of the hook when the bee enters into the floral tube is the primary mechanism of pollen gathering by bees. Bees exhibited two behaviors that improved pollen collection: 1. vibration (buzz-pollination), and 2. "backward-forward movements". The females of *A.* aff. *meridionalis* and *A. turrifaciens* harvested pollen by vibration while holding onto the anther cuff. Pollen within the thecae was released by vibration, in addition to pollen deposited on the cone. Further we observed *A.* aff. *meridionalis* bees collecting pollen by retracting their bodies from the corolla tube until only the head remained inside (Fig. 1B), and then moving forward to enter into the tube again. This backward-forward movement was repeated two to four times at each visited flower. As a result, the cone was opened several times and a larger amount of pollen was released. Once they had mostly withdrawn from the tube, bees groomed pollen from their heads and thoraxes and packed it into their scopae (pollen-carrying structures). A female individual of *Dialictus* sp. (Halictini) was once observed collecting pollen by backward-forward movements. The movement was repeated seven times in a single visit of this bee species.

Males of *A.* aff. *meridionalis* moved commonly around *V. cerasifolia* plants in search of females. They stayed on *Viola* leaves and flowers, or on surrounding plants of other species. They flew toward the flowers at some times, hovered very fast in front of them and moved around the *Viola* cluster. We observed one copulation after a female visited a flower. Visits of *A.* aff. *meridionalis* males to *Viola* flowers were uncommon and their behavior could not be followed in detail. A male of *A. turrifaciens* also patrolled the *Viola* cluster for two hours in February (Fig. 1C). During that time, it visited eleven flowers in four rounds. The bee entered the flower in a similar way as the females did (supine position), but with proboscis extended, indicating that it was in search of nectar. Pollen grains were deposited on the ventral surface of its body. The repeated visits indicated that the bee possibly found nectar in the flowers. Thus, nectar is a secondary floral resource, used by male bees and perhaps by female ones, although we do not know if females feed on nectar during their pollen collection.

We observed a single visit of a syrphid, *Toxomerus watsoni* (Curran, 1930). This hoverfly landed on the inferior petal and fed directly on some pollen grains deposited on this petal (remains of a previous bee's visit), but it did not touch the stigma nor enter into the corolla tube, thus, it did not act as a pollinator.

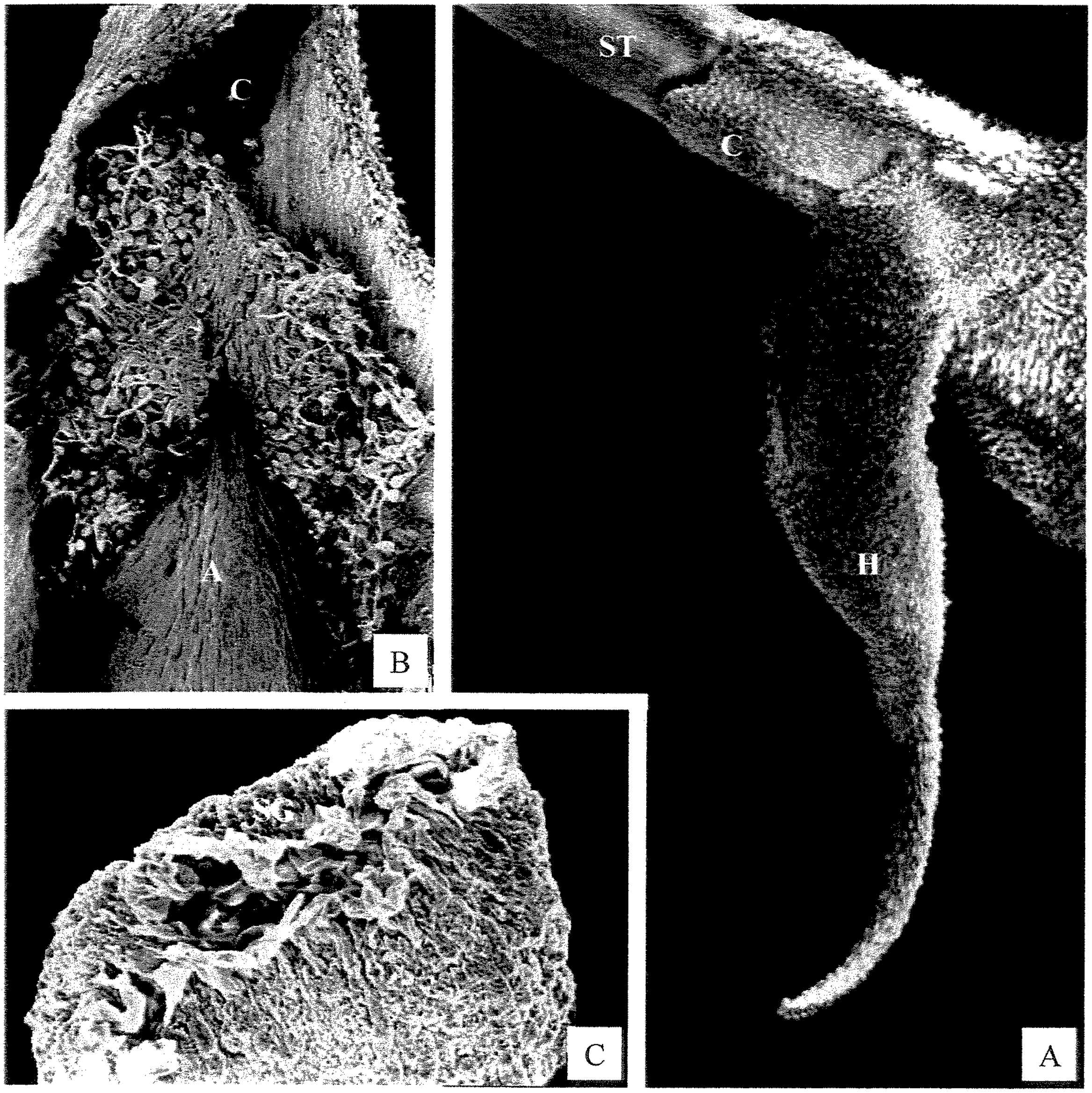

Fig. 3. Scanning electron micrograph (SEM) of parts of a *V. cerasifolia* flower. A, Detail of the hook. Note cone close to the style (rest position). 2 cm = 0.3 mm. B, A mass of germinating pollen within the cone. 0.5 cm = 55 μm. C, The stigmatic cavity closed after pollen deposition. 2 cm = 60 μm. A – anther, C – cone, H – hook, SG – stigma, ST – style.

DISCUSSION

The manifest zygomorphic and spurred flowers of *Viola* species support the classical view that they are "nectar flowers" pollinated by bees (Knuth 1904, Lovell 1918). Beattie (1971, 1972) showed that nectar is the main floral resource in three *Viola* species pollinated by hoverflies, beeflies and butterflies, in addition to large and small bees. However, some of these pollinators also utilized pollen as a food source, characterizing a more generalist pollination system in those *Viola* species (Beattie, 1971, 1972). In contrast to the other species in the genus, pollen is the almost exclusive floral resource of *V. cerasifolia*. This conclusion is supported by three observations: 1. the reduced size of both corolla spur and connective appendages, and the poor nectar production; 2. the shape and size of the inferior connective projections (hook), a structure apparently related to pollen collection by bees; and 3. the behavior of female bees collecting pollen in all visits either by vibration or by backward-forward movements. The degree of specialization in the pollination system of *V. cerasifolia* may be higher than in most of the North-temperate species of the genus (see Beattie, 1974) studied thus far. The scanty nectar production and the elaborated mechanism for pollen release could be related to this higher specificity.

We detected a somewhat low percentage of pollen viability in *V. cerasifolia*, but pollen stainability may be unsuitable to assess pollen viability (Heslop-Harrison *et al.*, 1984), in special in this case because pollen grains stain slowly in *Viola* species (see Beattie, 1969*a*). Germination of pollen within the anthers of chasmogamous (CH) flowers has been reported in wild and cultivated populations of several European *Viola* species, such as *V. sylvatica* and *V. biflora* (Sablon, 1900), *V. riviniana* (West, 1930) and *V. odorata* (Mayers and Lord, 1983). The capacity of CH pollen to germinate within the anthers could be a first stage in the evolution of CL flowers from the CH form (Goebel, 1905 apud Mayers and Lord, 1983). Although, we did not detect CL flowers on *Viola cerasifolia*, the presence of this flower type is probable in this species since most species of *Viola* sect. *Leptidium* in Mesoamerica and the northern Andes produce both CH and CL flowers (H. E. Ballard, pers. comm.).

The pollinators of *Viola cerasifolia* visit the flowers exclusively in the supine position (sternotriby). Beattie (1974) argued that sternotriby is the basal condition in the genus, and that species belonging to more derived sections in the genus would show a progressive decrease in sternotriby. However, the infrageneric classifications used by Beattie to propose this scenario (Clausen 1927, 1929; Gershoy, 1928) are not completely in accordance with a recent phylogenetic study based on internal transcribed spacer DNA sequences (Ballard *et. al.*, 1999). In *V. cerasifolia*, sternotriby seems to be related to floral structures adapted to pollen collection by bees, and these floral traits may be derived characters in the section *Leptidium* (St. Vogel, pers. comm.).

Vibratory pollination by bees (buzz-pollination) is typically observed in "pollen flowers" with poricidal anthers, such as in many Solanaceae and Melastomataceae species (Buchmann, 1983). Although anthers of *V. cerasifolia* dehisce longitudinally, they work as a single poricidal anther due the intimate contact of the anthers and the arrangement of the connective projections. This elaboration for pollen presentation is analogous to that described in other taxa with longitudinal anthers working as poricidal ones, as in *Chamaecrista* species (Gottsberger and Silberbauer-Gottsberger, 1988) and in some genera of Ochnaceae (Kubitzki and Amaral, 1991). The gynoecium/androecium arrangement in *V. cerasifolia* (Fig. 2A) resembles that of "*Solanum*-type" flowers, which are characteristic of buzz-pollination and usually are associated with small and dry pollen and absence of nectar (Buchmann, 1983). Similarities between *V. cerasifolia* and *Solanum*-type flowers apparently represent an example of morphological convergence, and in this sense, the floral traits of *V. cerasifolia* could be result of evolutionary pressures exerted by pollen-collecting bees, which are able of pollination by vibration (see also Kubitzki and Amaral, 1991).

Anthrenoides aff. *meridionalis* gathered pollen by the backward-forward movements, which is a hitherto unreported behavior for pollen collection. In addition, these bees were only observed in the flowers of *V. cerasifolia* among the 124 plant species surveyed as part of a study of pollination biology at the community level in the high altitude grasslands of Serra da Bocaina (chapter I of this volume). Oligolectic bees restrict pollen collection to a few related plants (Linsley, 1958) and frequently show behavioral, morphological or physiological traits associated with the gathering and transport of pollen of certain flowers (Gaglianone, 2000). In this sense, the record of *Anthrenoides* aff. *meridionalis* visiting only *Viola cerasifolia* flowers in the community, their behavior for pollen collection, and the presence of males patrolling *Viola* clusters indicate that these bees could be oligolectic foragers at Serra da Bocaina's grasslands. In addition, bees belonging to the genus *Anthrenoides* in search of pollen are the main pollinators of *Viola subdimidiata* flowers at Serra dos Órgãos, another Brazilian montane area (L. Freitas, pers. obs.). Several bee species belonging to Panurginae in South America have oligolectic foraging behavior, such as *Callonychium petuniae* (Wittmann *et al.*, 1990) and *Cephalurgus anomalus* (Gaglianone, 2000), and further studies may clarify the degree of specificity in the interaction between species of *Viola* and *Anthrenoides* in the southeastern Brazilian highlands.

Some of the floral traits of *Viola cerasifolia* seem to be plesiomorphic for the genus, such as the simple and truncate stigma and the absence of lateral hairs on the corolla. In contrast, the hook-shaped anther projection, the reduction of both spur and connective appendages and the scanty nectar secretion are apparently derived traits, which would reflect adaptations for pollen collection by bees. All species of *Viola* sect. *Leptidium* except for *V. arguta* - which has ornithophilous flowers - have highly reduced spurs in relation to the more basal *Viola* sect. *Rubellium* and other Latin American groups of the genus (H. E. Ballard, pers. comm.). Thus, the reduced spur in *V.* sect. *Leptidium* as a whole is probably apomorphic. We examined flowers of two other Brazilian species (*V. gracillima* and *V. subdimidiata*) and found a floral structure similar to that of *V. cerasifolia*, i.e., short spur and prolonged staminal projections (hook). Further, St. Vogel (pers. comm.) has failed to find nectar in other species of *V.* sect. *Leptidium*, such as *V. stipularis* from Colombia, *V. sumatrana* from Borneo and *V. hederacea* from Australia (the latter studied in cultivation). These observations indicate that "pollen flowers" may be widespread in this genus section, an idea first suggested by St. Vogel (pers. comm.). In this sense, the flowers of *V. cerasifolia*, as well of other species of *V.* sect. *Leptidium*, seem to have evolved toward “pollen flowers” from the primitive state in the genus of “nectar flowers”.

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CAPÍTULO III:

Daily blooming pattern and pollination by syrphids in *Sisyrinchium vaginatum* (Iridaceae) in southeastern Brazil[1]

Abstract. Most species of *Sisyrinchium* bear oil-secreting flowers, which are pollinated by certain bees. Here we report on the pollination by hoverflies in a species of this genus bearing pollen flowers. Data on floral biology, daily blooming pattern, and floral longevity of *S. vaginatum* are discussed in relation to the visitation pattern and behavior of the pollinators in a high-altitude grassland in southeastern Brazil. The yellow and dish-shaped flowers last 1 to 4 days. Flowers open and close each day, and may even stay closed for one day after the first day of anthesis, to then, re-open in the subsequent day. Anthesis starts between 10:00 and 16:30 h, but most flowers open in the middle of the day. The pattern of pollinator visits overlaps the blooming pattern. Dehiscence of the anthers is gradual along the anthesis, thus, just a portion of the produced pollen is available to pollinator at any moment. This mechanism may improve pollination, since syrphids usually feed on all available pollen at each visit. Flower longevity and blooming pattern in *S. vaginatum* are in accordance to that observed in other species of the genus, suggesting that phylogenetic constraints are important in their regulation. However, climatic conditions and pollinator activity also seem to exert influence on these variables. *S. vaginatum* fit on a group of species with nectarless flowers, which are pollinated mainly by syrphids, markedly during the winter, in the studied grasslands.

Key words: bees, blooming pattern, floral biology, hoverflies, pollen flowers, *Sisyrinchium*.

Introduction. *Sisyrinchium* is a mainly New World genus of Iridaceae with ca. 80 species (Goldblatt 1990). This genus is noticeable as the largest in the family producing oil - through glands named elaiophores - as a floral resource (Vogel 1974; Cocucci and Vogel 2001). The production of not volatile floral oil, which is collected by certain bees to provide their larvae or to apply as lining on the inner walls of the brood cells, is an outstanding phenomenon found in eight plant families of different geographic provenience (see Neff and Simpson 1981, Cane et al. 1983, Vogel 1988). The presence of pollen flowers - i.e., with pollen as the only floral resource -

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[1] Following the *Journal of the Torrey Botanical Society* format

among *Sisyrinchium* species was recently reported for the first time by Cocucci and Vogel (2001), in their extensive study on pollination biology of the oil-producing flowers of this genus. Pollen-collecting polylectic bees are the expected pollinators of the *Sisyrinchium* species bearing pollen flowers, but as far as we know, observation on pollinators was done only for *S. palmifolium* (Cocucci and Vogel 2001).

Sisyrinchium vaginatum - a highly polymorphic and widely distributed taxon in America, occurring from Mexico to Brazil and Uruguay (Chukr 1992) - is among species of the genus with pollen flowers. We studied aspects of the floral biology and pollination by syrphids in *S. vaginatum* in a high-altitude grassland area in southeastern Brazil, and here we report on (1) its floral longevity and daily blooming pattern; and (2) the pollinator behavior on flowers and their visitation pattern.

Study system. The study was carried out in areas of the Parque Nacional da Serra da Bocaina, between Rio de Janeiro and São Paulo States, southeastern Brazil. This montane area is covered mainly by high altitude grasslands, which are surrounded by mixed broadleaf and Araucarian forest (Eiten 1970). Annual rainfall is up to 2100 mm, with a rainy season mostly from October to March and monthly rain lower than 50 mm from June to August. Average annual temperature is approximately 15 ° C and temperatures may fall below 0 ° C during the dry season, with the presence of frost. The vegetation of the grassy fields is a mosaic of shrubs (mainly species of Asteraceae and Melastomataceae) set within a matrix of species of Poaceae and Cyperaceae (Safford 1999).

Sisyrinchium vaginatum Spreng. is a herb, 15-60 cm long, with sympodial branching and great variability in its vegetative traits (e.g., leaf form and size), but with a more constant floral pattern (Chukr 1992). Plants of this species grow in edges of the montane forests, well drained high-altitude grasslands and temporary swamps (i.e., only flood on summer months) at Serra da Bocaina. Plants generally were distributed alone or in small clusters (2-5 individuals). However - in a place called Santa Cruz, at the Fazenda Pinheirinho (22°43’43”S, 44°38’08”W, ca. 1400 m a.s.l.) - ca. 100 plants were growing crowded on a ca. 500 m^2 patch in a grassland area that is continuous to a temporary swamp. Most observations were carried out in this latter population. The flowering pattern of *S. vaginatum* was continuous at the populational level and subannual at the individual level in 1998 and 1999 (sensu Newstrom et al. 1994). Individuals growing in either well drained soils or swamps flowered mainly during the wet or the dry season, respectively. The population at Santa Cruz was in flowering peak from May to Aug. Voucher specimens (L. Freitas, 346, 365, 515, 696) are deposited in the Herbário da Universidade Estadual de Campinas (UEC).

Material and methods. Seventy flower buds - which were opening for the first time in the morning on May 19, 1999 - were tagged and numbered. The tagged flowers were followed for four days. We registered the time of both opening and closing in each flower, at intervals of 30 min. Flower opening is a slow process and the anthesis beginning is marked by the tepals expansion at ca. 60°. At this stage, one thecae at least is already opened, and pollinators are attracted to flowers. Additional data on floral longevity were obtained from 39 flowers along the years 1998 and 1999. For this, we tagged buds, and it was verified if the flowers were opened in the following days between 12:00 and 15:00 h.

Pollen viability was tested through its stainability using the technique of acetocarmine (Zeisler 1938). Color names of the floral parts follow Kornerup and Wanscher (1963). We registered the frequency of visitors to flowers in ten focal plants during two days at Santa Cruz population. Observations were carried out for 15 min each 30 min, between 10:00 and 18:00 h. Additional observations in the middle of the day were done along several days during the flowering peak months, totaling ca. 15 hours. We analyzed the pollinator behavior by direct observation and photographic records. The captured insects were sent for identification by specialists, and are deposited in the Museu de História Natural da Universidade Estadual de Campinas.

Results. Floral morphology is in accordance to Cocucci & Vogel (2001). The terminal and erect cymose inflorescence bears actinomorphic, hexamerous, dish-shaped flowers. Each plant presents one, or exceptionally two to four, opened flowers at a given moment. Flowers are erect, and the diameter ranges from 1.9 to 2.7 cm in completely opened flowers. The six sub-equal tepals are arranged in two whorls horizontally spread, and have acute apex (Fig. 1). Perigon is light to vivid yellow, and a white mark - outlined in brownish - is usually present at the base of the tepal (Fig. 1B), although some individuals have a completely yellow perigon (Fig. 1A). The three stamens are basally connate - along a half of the filament length - building a column, which supports their large extrorse anthers. The anthers are orange yellow (Fig. 1B), and pollen grains are orange. The three styles are united along their basal half and the free parts are alternated to the filaments. Each style finishes in a dry and globular stigma. Pollen viability was high, ranging from 88% to 96%. We did not detect differences in pollen viability between first- and second-day flowers. Flowers lack detectable odor. Oil glands or nectaries are absent, thus pollen is the only available floral resource for pollinators.

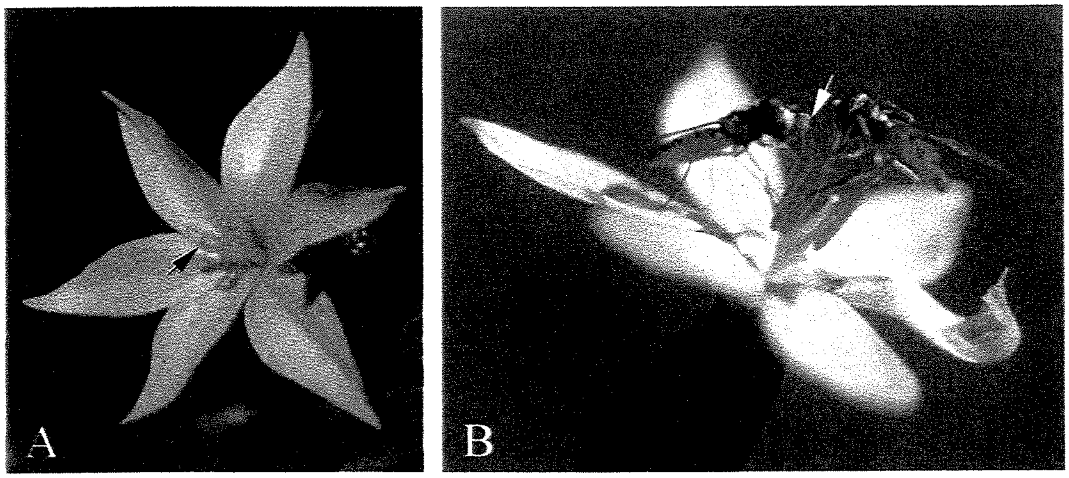

Fig. 1. A. Flower of *Sisyrinchium vaginatum* at the Serra da Bocaina grasslands. Note the anthers curled (arrow) after pollen removal. B. Two individuals of *Toxomerus watsoni* (Syrphidae) feeding on pollen of a *S. vaginatum* flower. Note the collapse on the distal part of the anthers (arrow).

Tepal opening was slow, and the time of anthesis beginning was variable. Flowers lasted one to four days, and those which lasted two or more days opened and closed each day. The flower closing occurred by upward movements of the tepals, which returned to the position they had in the bud. On May 19, anthesis started between 10:00 and 16:30 h, although most flowers opened between 13:00 and 15:00 h (Fig. 2A). All flowers were closed at sunset - an event that started at 16:00 h but became intense after 17:00 h (Fig. 2A). Hence, the day period in which more flowers were opened was between 15:00 and 17:00 h. In the following day (May 20) no flowers opened. Almost a half of the flowers re-opened and closed in the third day (May 21, Fig. 2B), and a few flowers opened again (and closed) on the following day (May 22, Fig. 2C). The end of anthesis is marked by perigon wilting. The daily blooming pattern was similar during the three days (Fig. 2). Data from additional observations confirmed the variability in flower longevity, since flowers lasted one to four days, but most of them lasted two days (mean 2.00, S.D. = 0.72, n = 39).

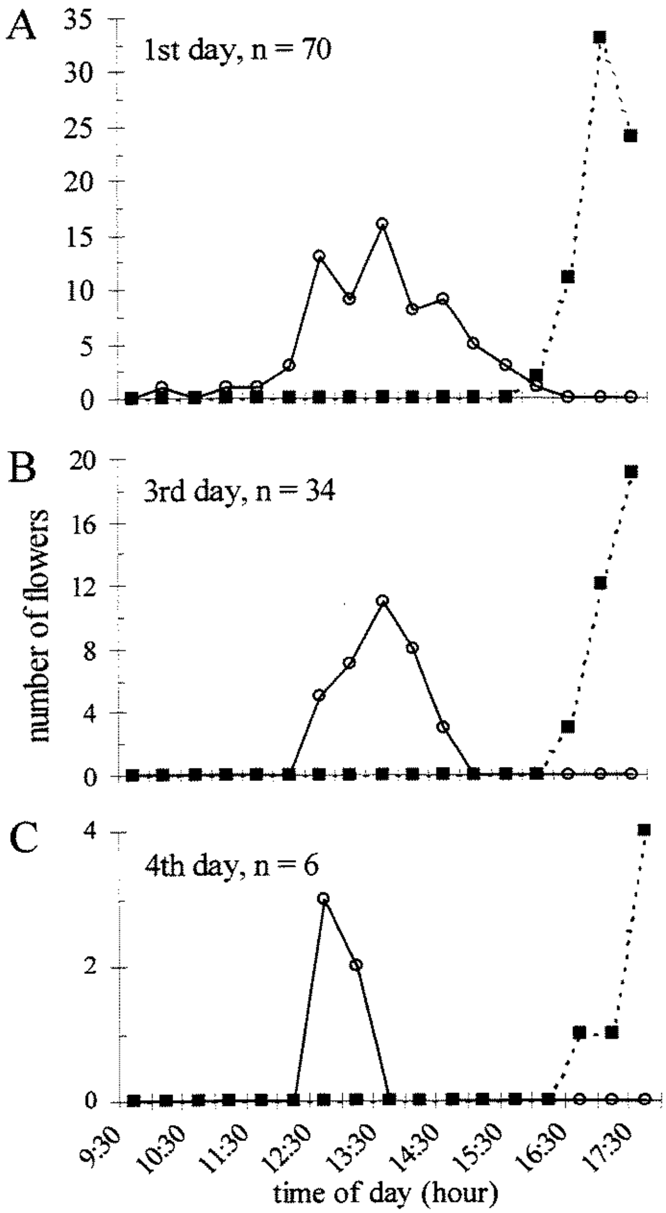

Fig. 2. Daily blooming pattern of 70 flowers of *Sisyrinchium vaginatum* between 19 and 22 May, 1999 at Serra da Bocaina grasslands. Lines show the number of flowers that opened (open circles) and closed (close squares) at each 30 min interval. Note that no flowers opened on the second day (May 20).

During the week of May 16, 1999, the daily minimum temperature at Santa Cruz was around 0° C with frost early in the morning, followed by low temperatures until noon (e.g., 3.5° to 7° C at 08:00 h), and the daily maximum temperature was between 14.5° and 17° C. The wind was weak almost all time, and the sky was clear from sunrise until mid-afternoon (ca. 15:00 h), when it became clouded very fast, but without rain. However, on May 20 - when no flower opened - there was no frost in the morning, and daily temperature oscillation was low (9.5° and 13° C of minimum and maximum temperature, respectively). The sky was clear all day long, but very strong winds blew unceasingly from the previous night to next dawn. During this day, very few flying-insects were seen in activity.

The anthers dehisce longitudinally from the distal end toward the base (Fig. 1B). In each flower, the dehiscence of the anthers was sequential, but this event was highly variable. Anthers may open some hours apart - hence the three anthers were open at any time (see the three anthers with collapsed distal portion in the Fig. 1B) - or alternatively, only after the first anther was empty, the second one started to open. Each anther commonly dehisced slowly, and in some cases, the dehiscence of a single theca was completed in two days. As a result the pollen was progressively available to the pollinators throughout the flower lifetime. The complete dehiscence of each anther seems to last more time on unvisited flowers than on visited ones. As pollen is removed from the thecae by the pollinators, their walls collapse and the anthers progressively curl down (Fig. 1A).

Sisyrinchium vaginatum was pollinated mainly by *Toxomerus watsoni* (Syrphidae). These hoverflies settled directly on the reproductive parts, but the perigon could occasionally be used as a support (Fig. 1B). During the landing, the hoverflies may touch stigma and anthers with their ventral parts, and probably, this was the occasion in which most pollination was effected. The visitor - landed on the anthers - fed directly on pollen (Fig. 1B). At this occasion, pollen grains could be deposited on the head and legs of the syrphids, but they used to lick the pollen from their forelegs. Syrphids could access, at any moment, only a part of the pollen grains of each anther, due to the gradual dehiscence of the thecae (Fig. 1B). After feeding all the available pollen from one anther, the visitor moved around the flower looking for another opened anther, and also at this occasion, pollen grains could adhere on its body. Visits may last few seconds to some minutes, in accordance to the pollen availability. Each anther was emptied usually after three or four syrphid visits along a day.

Visits by syrphids to the flowers started after 11:00 h and stopped before 15:00 h on May 19, 1999 (Fig. 3). Visits were intensified after noon, and peaked (more than one visit per flower) between 13:30 and 14:00 h. After the peak time, the number of visits fell down abruptly. The daily visiting pattern overlapped the daily blooming pattern (Fig. 3), i.e., as more flowers opened, more visits occurred. Patterns of visits on May 17 and 19 were similar, although visits were more frequent on the latter (Fig. 3).

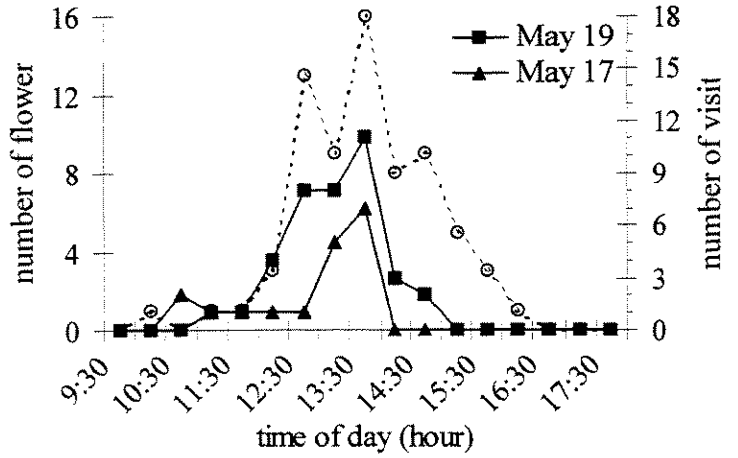

Fig. 3. Daily visit pattern by syrphids to *Sisyrinchium vaginatum* flowers (continuous lines). Visits were registered in ten focal flowers during two days on May, 1999. Compare the syrphid visit pattern to the blooming pattern on May 19, 1999 (open circles/dashed line).

Other species of hoverflies and small bees belonging to the family Halictidae visited rarely the flowers of *S. vaginatum*. *Toxomerus* sp. 1 and an uncollected species of Syrphidae visited the flowers in the same way as described above for *T. watsoni*. Two uncollected species of Augochlorini (Halictidae) landed directly on the column during the visits. One species brushed its abdomen directly on the anthers to collect the pollen. The other species introduced its glossa into the anther, and after this, it moved the head toward one of its hindlegs and brushed its glossa - with many adhered pollen grains - on the scopae. Honey-bees were observed collecting pollen one day in Aug, 1999. Both *Apis mellifera* (Apidae) and Halictidae bees may pollinate the flowers.

We planned to follow the studied population of *S. vaginatum* until the fruit formation, in order to assess possible differences in reproductive success related to the anthesis dynamics. However, Santa Cruz area was burned at the beginning of June, 1999.

Discussion. Fly pollination (myiophily) has been considered mostly accidental and highly unspecialized, since flies do not feed their young and may have other food sources than flowers (Faegri and van der Pijl 1979, Kearns 1992, Proctor et. al. 1996). Some traits, such as regular blossom, small size, and light - but dull - colors, easily accessible nectar, exposed sexual organs, and imperceptible odor, characterize the typical unspecialized myiophilous flower (Faegri and van der Pijl 1979, Proctor et al., 1996). In general, these flowers are polyphilic, and may be pollinated by several insects in addition to flies (Endress 1994, Arruda and Sazima 1996, Proctor et al. 1996). Specialized fly-pollination is basically related to sapromyophilous flowers pollinated by deceit, including trap and fungus gnat flowers (see Endress 1994). However, many other cases of specialized pollination have been reported (see Faegri and van der Pijl 1979, Kevan and Baker 1983), for example, the pollination by long-tongued flies among Iridaceae (Goldblatt et al. 1995, Goldblatt and Manning 1999). Despite the regular shape and the well-exposed sexual organs, the showy, nectarless flowers of *S. vaginatum* do not fit on the typical myiophilous flower, and further, they are not polyphilic. In fact, although pollinated mainly by hoverflies, floral traits of *S. vaginatum* are similar to those usually associated to pollination by small bees (see Proctor et al. 1996, Cocucci and Vogel 2001), which may be important pollinators in this species (see below).

Cocucci and Vogel (2001) related that most *Sisyrinchium* species bear oil-secreting flowers, which show a narrow association with some bees of the tribe Tapinotaspidini (Apidae) - a group predominantly distributed in southern South America. Pollen flowers were recently reported for the first time in *S. palmifolium* and *S. vaginatum* (Cocucci and Vogel 2001). In addition to the absence of elaiophores, the large anthers in these two species seem to be the most distinctive floral character in relation to the oil-producing species. Similarly, some Malpighiaceae species with eglandular flowers are known to have larger anthers than the species with oil-secreting flowers, and this trait was suggested to be an evolutionary response to pollen collecting visitors (Anderson 1979, see also Sazima and Sazima 1989).

Small pollen-collecting bees were minor pollinators of *Sisyrinchium vaginatum* at Serra da Bocaina. However, small pollen-collecting bees were the exclusive pollinators of *S. vaginatum* in a Brazilian "cerrado" area (Barbosa 1997). Further, species of Halictidae bees, followed by syrphids, were the most important pollinators of this species in high altitude grasslands at Serra dos Órgãos (pers. obs., Jan 2002). In central Argentina, flowers of *S. palmifolium* were exclusively pollinated by pollen-collecting bees of several groups (species of *Bombus*, Halictidae, and Megachilidae, and *Apis mellifera*) (Cocucci and Vogel 2001). Thus, the pollination of the *Sisyrinchium* species with pollen flowers is connected to both bees and syrphids, and the importance of each pollinator group seems to be variable. Syrphids could be more important during the winter, as we observed for *S. vaginatum* at Serra da Bocaina grasslands, since bees are more frequent during the summer in these grasslands (see Chapter I). Anyway, pollen consumption by hoverflies and pollen collection by bees seem to be common on elaiophore-bearing species of *Sisyrinchium* (see Arroyo et. al. 1982, Schlindwein 1998, Alves dos Santos 1999, Cocucci and Vogel 2001), including on *S. micranthum* at Serra da Bocaina (Chapter I). Pollen flowers seem to be a derived condition in *Sisyrinchium*, and the existence of these opportunistic visitors (pollen-collectors bees and pollen-consumers flies) in the oil-flowers may have been an important step in the shift from the pollination by oil-collecting bees to the pollination by syrphids and pollen-collecting bees within the genus.

Data on flower longevity in *Sisyrinchium* are restricted to four oil-secreting species - *S. azureum*, *S. chilense*, *S. laxum*, and *S. minutiflorum* - and to the pollen flowers of *S. palmifolium*. Flowers last two days and open and close each day in the these five species (Cocucci and Vogel 2001), approaching our data on *S. vaginatum*. Thereby, despite the differences in the offered resource, and consequently in the pollination ecology, flowers lasting two days seem to be common in the genus. Flowers that last several days, in which the perigon open and, partly or completely, close each day, are not restricted to *Sisyrinchium* among Iridaceae taxa. Similar mechanisms have been registered in other genera, such as *Lapeirousia* (Goldblatt et al. 1995), *Gladiolus* (Goldblatt and Manning 1999), and *Moraea* (Goldblatt and Bernhardt 1999) in southern Africa. Further, a similar pattern of blooming was detected in flowers of another iridaceous - *Calydorea campestris* - as well as in its probably mimetic pair - *Zygostigma australe* (Gentianaceae) - at the Serra da Bocaina grasslands (pers. obs.). There is great variation in floral morphology and pollination systems among these Iridaceae genera, suggesting that taxonomic constraints at the family level may be important determinants of flower longevity and the tepal open/close mechanism among these taxa. In fact, family membership may be the most important determinant of flower longevity among angiosperms (Stratton 1989). However, other Iridaceae taxa present one-day flowers, such as species of *Trimezia* (J. Semir, pers. comm.)

Further, flower longevity and the dynamics of flower opening in *S. vaginatum* varies at the individual and the space/temporal levels. Climatic conditions seem to influence these patterns. The peculiar phenomenon registered on May 20 - when all observed flowers remained closed to re-open in the following day - coincided with atypical climatic conditions, especially the incessant and strong winds. Similarly, flower opening in *S. vaginatum* seems to be refrained on cloudy conditions (pers. obs. for Serra da Bocaina and Serra dos Órgãos). Climatic condition also influences in several ways the flower longevity and anthesis dynamics in African species of Iridaceae (Goldblatt et al. 1995, Goldblatt and Manning 1999, Goldblatt and Bernhardt 1999).

Syrphids, and also Halictidae bees, restricted their activity in either windy or cloudy periods (or days) at the Serra da Bocaina grasslands. In fact, both light intensity and wind are among the most important factors affecting flying-insect activities (Kevan and Baker 1983, see Gilbert 1985 for syrphids). Thus, the same climatic factors seem to influence both the anthesis dynamics on *S. vaginatum* and the activity pattern of its pollinators. Furthermore, visiting pattern of *Toxomerus watsoni* to flowers of *S. vaginatum* overlapped its daily blooming pattern. The activity pattern of this syrphid species agreed with general trends among this family, i.e., activity peak around mid-morning, and also, activity strongly reduced in late afternoon (Gilbert 1985). The overlap between the syrphid activity and the blooming pattern may have some significance for the reproduction of *S. vaginatum*.

Pollinator activity can affect flower longevity, for example, petals (tepals) may wilt and abscise more rapidly after pollen deposition on stigma or pollen tube growth through the style (e.g., Gilissen 1977, Proctor and Harder 1995), or even after nectar removal (e.g., Galetto et al. 1997, Freitas and Sazima 2001). Syrphids feeding pollen on *S. vaginatum* flowers seems to exert a direct influence on the anthesis dynamics, accelerating the anther dehiscence. Similarly, pollen removal from the anthers affects significantly the staminate phase duration in *Lobelia cardinalis* (Lobeliaceae, Devlin and Stephenson 1984) and in several species of *Sinningia* and *Vanhouttea* (Gesneriaceae, I. San Martin-Gajardo, pers. comm.). Flower life cessation in *Sisyrinchium* is marked by the rapid perigon wilting to a partially liquefied rounded mass (Cocucci and Vogel 2001). Flower wilting in this genus - differing from most monocots - is ethylene-sensitive (van Doorn 2001), but as far as we know, there is no information relating the pollinator activity on flowers and the physiological and biochemical aspects of this phenomenon. In *S. vaginatum*, pollen removal on the distal portion of the anther could affect the environmental conditions (e.g., temperature and wetness) of the portions below, acting as a trigger to the slit dehiscence. More detailed studies may show in which extension the pollen removal by pollinators affects dynamics of the anther dehiscence, and also, the flower longevity in this species.

As a general trend, the importance of fly-pollination increases in high altitude environments (e.g., Arroyo et. al. 1982), since overall insect abundance decreases with increasing elevation, but fly densities are more constant across elevation gradients (Kearns 1992). Syrphids were the exclusive pollinators in three species and pollinators in association with other groups in other 31 among 107 species at the Serra da Bocaina grasslands (Chapter I). Furthermore, dipterans other than syrphids were among the pollinators of 29 species. In this high-altitude, tropical environment, fly-pollination - in special due to Syrphidae - is important specially during the cold and dry season, when diversity and abundance of small bees is reduced (Chapter I). At the community level, *Sisyrinchium vaginatum* fits on a floral group, in which species are pollinated exclusively or mainly by syrphids in search of pollen. This group is composed by eight species belonging to four families, such as *Drosera montana* (Droseraceae), *Deianira nervosa* (Gentianaceae), and *Xyris asperula* (Xyridaceae). These species present nectarless, dish-shaped and actinomorphic flowers, which are showy, and yellow- or pink-colored. Pollen is required mostly by hoverfly females during the stages of ovarial development (Haslett 1989). Thus, pollen flowers adapted to hoverfly-pollination are expected to evolve, since pollen is an important protein source for these flies.

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CAPÍTULO IV:

Nectar Features in *Esterhazya macrodonta*, a Hummingbird-Pollinated Scrophulariaceae in Southeastern Brazil [1]

We analyzed the nectar features in a hummingbird-pollinated Scrophulariaceae. Nectar production is constant during the first days of anthesis and ceases after this period. Removals carried during the first days may decrease sugar production. *Esterhazya macrodonta* is scarcely visited by hummingbirds, a fact that may be related to its low flower production and nectar features.

Key words: Brazilian Atlantic Forest - High-altitude grasslands - Hummingbird pollination - Nectar removal effect - Nectar secretion pattern - Nectar standing crop

The foraging behavior of hummingbirds exerts influence on the genetic structure of plant populations (Linhart 1973, Waser and Price 1983), and consequently on the evolution and ecology of plants (Feinsinger 1978, Fenster 1991). Hummingbirds are sensitive to nectar availability in plants and can change their foraging behavior in response to nectar supplies (Feinsinger 1976, Sazima *et al.* 1996). Thus, information about nectar features is critical to understand hummingbird-foraging behavior on plants.

Although there are few studies on the anthecology of their tropical representatives, the cosmopolitan Scrophulariaceae – with ca. 4,500 species - have great variation in floral structure and pollination systems (Endress 1994). In Brazil, the genus *Esterhazya* includes a few species commonly present in montane grasslands (Joly 1979). A study of the floral biology of the hummingbird-pollinated *E. splendida* (Ormond *et al.* 1998a, b) provides no data on nectar features.

We studied the pollination by hummingbirds and the nectar features of *E. macrodonta* (Cham.) Benth., a herb growing in high altitude areas in southeastern Brazil. Although its flowers are visually attractive, we observed that hummingbird visits were markedly scarce. Characteristics of its nectar secretion pattern could be among the factors explaining the scarcity of pollinator visits to this plant. We therefore addressed the following questions: i. How do nectar volume, concentration, and amount of sugar vary

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[1] Freitas L. & Sazima M. 2001. *Journal of Plant Research* **114**: 187-191.

throughout the flower lifetime? ii. How does *E. macrodonta* respond to nectar removal? iii. What is the nectar standing crop available to pollinators? Based on the data obtained, we discuss the significance of these nectar features in relation to the pollination biology of *E. macrodonta*.

The study was conducted in the montane area of the Parque Nacional da Serra da Bocaina, in the Serra do Mar range, southeastern Brazil (22°44'50"S, 44°36'57"W, about 1650 m a.s.l.). This area is covered mainly by Araucarian forest and high-altitude grasslands, a subtype of the Atlantic Forest ecosystem (Safford 1999). The vegetation of the grassy fields is a mosaic of shrubs (mainly Asteraceae and Melastomataceae) within a matrix of Cyperaceae and Poaceae. In addition to *E. macrodonta*, the locally rare *Agarista hispidula* (Ericaceae) was the only hummingbird-pollinated species flowering during Jul-Aug 1999 in the grasslands. A voucher of *E. macrodonta* has been deposited at the Universidade Estadual de Campinas (UEC 103.773, L. Freitas 244).

In 1999 *E. macrodonta* flowered between Jun and Oct, with a blooming peak (more than 50% of the individuals in flower) during Jul-Aug. This perennial herb bears tubular (ca. 2.5 cm long), odorless, reddish-orange flowers (Fig. 1). One to four flowers are open per plant at any time. Flowers have diurnal anthesis and last up to six days. The stigma is receptive as soon as the flower opens but the style is initially shorter than the already open anthers, characterizing a protandrous system. Spontaneous self-pollination may occur since small quantities of pollen are expelled by wind. Pollen viability inferred from cytoplasm stainability is close to 90% (aceto-carmine technique, Radford *et al*. 1974).

We recorded the foraging behavior of visitors on clusters of four to eight plants. We spent a total of 73 hours watching hummingbirds during morning and afternoon periods (6:00 h to 18:00 h) for 17 days during the flowering seasons of 1998 and 1999.

Nectar analysis were carried out between Aug 27-31, 1999. We observed 55 flowering individuals along a ± 1 Km transect on a south-facing slope. This hill had more individuals than adjacent grassland areas, which in general had fewer than ten flowering *Esterhazya* plants along 1 Km transect. We evaluated nectar secretion and effect of nectar removal in 10 sets of four or five flowers (total 46 flowers from 34 individuals). We tagged the flowers in bud stage for identification and covered them using paper bags to prevent pollinator visits. We extracted the nectar with a graduated microliter syringe (Hamilton, Nevada, USA) without removing the flowers from the plants.

Fig.1. The hummingbird-pollinated flower of *Esterhazya macrodonta*. Corolla length is about 2.5 cm.

We took extreme care to avoid any damage to nectaries and other floral parts. We removed the nectar from the same flower repeatedly twice a day at 7:00 h and 18:00 h, taking care to withdraw all the nectar present. We measured immediately two variables: nectar sugar concentration (% sucrose, wt / total wt) with a hand refractometer (Atago HSR 500, Japan) and nectar volume (in µL). The amount of sugar produced was expressed in mg and calculated after Bolten *et al.* (1979). We compared the total mean nectar volume produced, mean nectar sugar concentration, and total mean sugar produced in each flower set by one-way analysis of variance (ANOVA) at the 0.05 significance level.

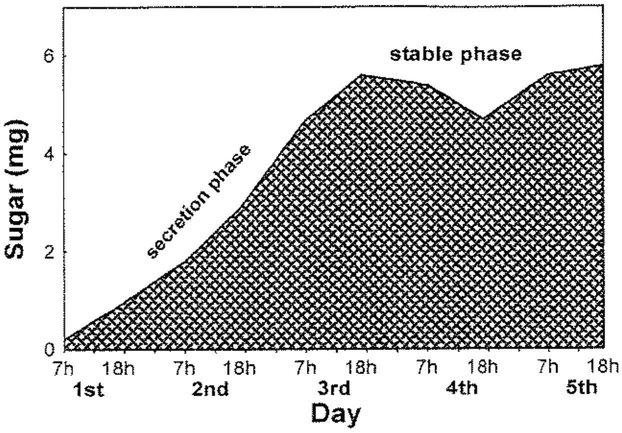

Fig.2. Nectar sugar production of *Esterhazya macrodonta* throughout anthesis.

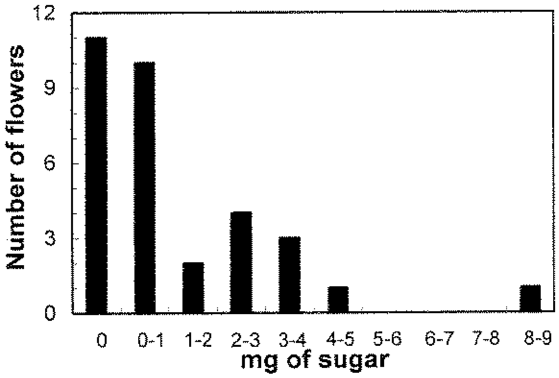

Fig.3. Histogram of nectar standing crop of *Esterhazya macrodonta*.

We assessed the amount of nectar present in a flower in a given moment (standing crop) by measuring nectar volume and concentration, and calculating mg of sugar, in 32 randomly chosen individual flowers exposed to pollinators (unbagged flowers). We collected these data on Aug 29, 1999 at 9:00 h. Standing crop was evaluated for the same plant population used for experiments on nectar removal (buds bagged on Aug 25 and 26). Thus, most two- to four-day-old flowers had been bagged in this population, and the standing crop data probably involved many one-day-old flowers.

The White-throated Hummingbird, *Leucochloris albicollis* was the only flower visitor for *E. macrodonta*. During its hovering visits, the bird touched the flower's reproductive organs with its crown. We registered only four visits of *L. albicollis*, three between 7:00 h and 8:00 h and one just before 17:00 h. The hummingbird probed only two to six flowers from two or three plants, flying to adjacent forest areas after the visits. Few visits and a similar visiting behavior were observed for *L. albicollis* and the Scale-throated Hermit *Phaethornis eurynome* to flowers of *E. campestris* in another montane area (Sazima *et al.* 1996, pers. obs.). We observed the Glittering-bellied Emerald, *Chlorostilbon aureoventris*, near *E. macrodonta* clusters twice but it did not visit the flowers. This hummingbird is the main pollinator of the sympatric *Agarista hispidula*, while *L. albicollis* is its secondary pollinator (pers. obs.).

The mean nectar sugar production per flower - not submitted to removals - was 3.6 ± 2.49 mg (13.4 μL, 26.0%, n = 46). Buds immediately before anthesis had no or only a small amount of nectar (less than 1 μL and 0.5 mg of sugar). The rate of sugar secretion increased continuously until the morning of the third day of anthesis (0.06, 0.07, 0.10 and 0.14 mg/h for continuous intervals among sets 1 to 5). Flowers reached a mean of 4.7 mg of sugar at the end of this phase (Fig. 2). In contrast, flowers alternated periods of nectar secretion (0.01 to 0.08 mg/h) and slight reabsorption (-0.01 to -0.06 mg/h) from the third day to the end of anthesis. Mean sugar level per flower during this phase did not differ statistically among sets (ANOVA, df = 4, $F = 0.15$, $p = 0.96$), ranging from 4.7 to 5.8 mg (Fig. 2). Hence, the pattern of nectar sugar production in *E. macrodonta* presents two phases, a secretion phase (sets 1 to 5), followed by a stable phase (from set 6 on) (Fig. 2). Similarly to the pattern of sugar secretion, nectar volume increased markedly during the first three days, becoming stable from the fourth day on (Table 1, data on diagonal). In contrast, nectar concentration values were more stable throughout the flower lifetime, ranging from 20% to 30% (Table 1). Variation in nectar volume as a function of flower age and constancy in nectar concentration throughout anthesis have been found in other plants (see references in Galetto

Table 1. Nectar removal in *Esterhazya macrodonta*

Nectar volume (μL)

SET	N	1st day		2nd day		3rd day		4th day		5th day		Total*		
		7h	18h	7h	18h	7h	18h	7h	18h	7h	18h			
Set 1	5	0.8±0.76	1.8±2.14	0.4±0.89	0.2±0.45	0	0	cd				3.2±3.90	a	e
Set 2	5		2.8±2.25	3.5±1.77	2.9±2.48	0.2±0.45	0	cd				9.4±5.19	ab	ef
Set 3	5			8.4±3.56	6.5±6.86	1.2±1.64	0.7±1.56	0	cd			16.8±9.52	bc	fgh
Set 4	5				10.3±4.45	2.2±2.28	1.7±2.64	0	cd			14.2±8.43	abc	fg
Set 5	5					18.6±4.26	4.8±1.82	0	0	cd		23.4±5.61	c	h
Set 6	5						17.2±3.40	2.2±1.6	0.6±0.89	0	cd	20.0±3.02	bc	gh
Set 7	4							16.9±9.17	1.0±1.41	0	cd	17.9±9.68	abc	fgh
Set 8	4								16.4±4.89	0.9±0.63	cd	17.2±5.39	abc	fgh
Set 9	4									17.6±1.03	0	17.6±1.03	abc	fgh
Control	4										24.9±4.33	24.9±4.33	c	h

Nectar concentration (% sucrose, w/w)

SET	N	1st day		2nd day		3rd day		4th day		5th day		Mean total sugar secreted (mg)*		
		7h	18h	7h	18h	7h	18h	7h	18h	7h	18h			
Set 1	5	24.5±8.26	17.0±3.61	19.0	17.0	0	0	cd				0.7±0.91	a	e
Set 2	5		25.1±11.25	21.6±3.74	21.9±4.09	38.9	0	cd				2.5±1.53	ab	ef
Set 3	5			20.0±6.16	21.2±4.21	18.4±2.71	16.6	0	cd			3.5±1.94	abc	fg
Set 4	5				28.6±7.95	14.3±2.53	14.2±1.63	0	cd			3.6±1.36	abc	fgh
Set 5	5					24.2±6.64	17.0±3.73	0	0	cd		5.5±1.56	bc	ghi
Set 6	5						29.7±4.82	20.3±4.96	30.0±14.14	0	cd	6.3±1.42	c	i
Set 7	4							29.9±6.67	25.5±2.12	0	cd	5.7±3.22	bc	ghi
Set 8	4								26.6±4.22	20.2±4.46	cd	4.9±1.70	bc	ghi
Set 9	4									28.8±6.87	0	5.6±1.35	bc	ghi
Control	4										22.0±4.22	5.8±2.25	bc	ghi

Data were measured in flower sets subjected to different removal schedules during the lifetime of the flower, values are mean ± S.D.

* Groups of flower sets that differed significantly ($p<0.05$) from each other in total of nectar production (volume and secreted sugar) during the lifetime of the flowers were identified by both "Tukey HSD test for unequal sample sizes" (a,b,c) and "Least significant difference (LSD) test" (e,f,g,h,i).

cd = Corolla dropped in all flowers of the set.

Note: Flower sets did not differ significantly from each other in mean nectar concentration per flower (ANOVA, df = 9, $F = 1.96$, $p = 0.07$). Data on diagonal (first measurements of each set) correspond to the nectar production pattern in this species.

and Bernardello 1993).

Nectar removal may affect nectar secretion. This fact is evident from differences in total secreted volume and total nectar sugar among the experimental sets of flowers (Table 1). After a removal performed on the first day (sets 1 and 2), there was a significant reduction in the total amount of nectar secreted. Nectar removal on the second day (sets 3 and 4) further reduced nectar production, and from the third day on nectar removal did not affect total production. Thus, the earlier the removal, the smaller the total amount of nectar secreted. In addition, nectar secretion ceased after one to four removals (Table 1). In short, nectar production may be reduced or cease after hummingbird visits. There are at least two reasons why this could benefit *E. macrodonta* plants, as previously postulated by Heinrich (1983) and Feinsinger (1978): i. reduction in nectar costs that could benefit seed production, and ii. pollen transfer maximization, since hummingbirds have to visit different plants in order to satisfy their metabolic requirements. Nectar removal also affected flower lifespan, which was reduced in sets subjected to several removals (Table 1). This has also been observed in flowers of, for example, *Stenorrhynchos orchioides* (Orchidaceae) (Galetto *et al.* 1997).

Mean standing crop was 1.3 ± 1.86 mg (4.0 μL, 28.2%, n = 32), almost three times less than mean nectar sugar production. Figure 3 shows that 34% of flowers had no nectar and 31% had less than 1 mg of nectar available for pollinators. Most of these flowers probably were one-day-old flowers, since three out of five recently opened flowers had no nectar (based on nectar production pattern, above). Nine flowers (28%) contained two to six times more nectar sugar than the average value of samples and represent "lucky hits", in the sense of Southwick (1982). This pattern of variable intrapopulation nectar availability is similar to that detected in other hummingbird-pollinated species, such as *Hamelia patens* (Rubiaceae) (Feinsinger 1978) and *Ipomopsis aggregata* (Polemoniaceae) (Pleasants 1983, Zimmerman 1988).

The total mean nectar volume produced by a flower of *E. macrodonta* (16.2 μL in flowers subjected to removals), as well as its nectar concentration (Table 1), is in accordance to the values recorded for four hummingbird-pollinated assemblages in the Neotropics (Snow and Snow 1980, 1986, Arizmendi and Ornelas 1990, Sazima *et al.* 1996). Therefore, nectar concentration and volume may not explain the low visitation rate of hummingbirds to *E. macrodonta* flowers, which may be related to other nectar features, as the reduction on nectar secretion after removals.

In contrast to the studied grassland, adjacent high-montane forests contained several *Leucochloris*-pollinated species, such as *Collaea speciosa* (Leguminosae), *Fuchsia regia* (Onagraceae), and Bromeliaceae (see Sazima *et al.* 1996). Grassland plants seem to be a complementary nectar source for hummingbirds at Serra da Bocaina, while the flowers of the adjacent forest plants represent its main resource (see Sazima *et al.* 1996). For example, flowers of *C. speciosa*, which are mainly pollinated by *L. albicollis* in that place, secrete a similar quantity of nectar that *E. macrodonta* flowers (one day production: 3.7 ± 0.87 mg, 14.1 µL, 24.9%, n = 5 - pers. obs.). However, *C. speciosa* presents around 30 open flowers per plant. A cluster of five plants of *Collaea* thus offers approximately the same amount of nectar as does the entire *Esterhazya* population.

Hummingbirds are expected to optimize foraging (Feinsinger 1978), and we conclude that the low abundance of *E. macrodonta* flowers and reduced nectar production after removals may thus negatively affect hummingbird foraging.

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CONSIDERAÇÕES FINAIS

Este estudo mostrou que os padrões gerais das interações planta-polinizador nos campos de altitude da Serra da Bocaina se assemelham ao observado em ecossistemas com afinidades biogeográficas, por exemplo, os campos rupestres, campos cerrados e as vegetações sub-alpinas andinas, tais como o "morichal" venezuelano. Entretanto, o grau de generalização dos sistemas de polinização - i.e., diversificação de grupos ecológicos/ taxonômicos atuando na polinização de cada espécie - nos campos da Serra da Bocaina parece ser maior que nestes outros ecossistemas, o que reflete as características florais predominantes nos campos de altitude - i.e., flores de néctar, simples e pequenas. Mais adiante, o grande número de espécies da família Asteraceae nos campos de altitude influencia marcadamente as características florais predominantes da comunidade.

Condições climáticas típicas das áreas de altitude do sul/sudeste do Brasil, tais como temperaturas médias baixas, amplitude térmica diária alta, chuvas concentradas no verão, geadas no inverno, neblina e ventos fortes, também são determinantes dos padrões detectados na comunidade. Por exemplo, as baixas taxas de visitação às flores pelos polinizadores, a redução da importância da polinização por abelhas no inverno, a longevidade floral extensa e os períodos de floração longos, que foram observados na comunidade, podem ser causados, entre outros fatores, pelas condições climáticas adversas. Em adição, a possibilidade de polinização por vários agentes pode ser vantajosa para plantas que crescem em hábitats com tais condições climáticas.

As partes mais altas das serras que abrigam os campos de altitude são formadas por uma série de formações distintas distribuídas em mosaico e, portanto, os campos de altitude deveriam ser entendidos como parte deste complexo de formações (q.v., Semir, 1991). Assim, estudos sobre a biologia da polinização em nível de comunidade que considerem todo este complexo são encorajados, uma vez que podem identificar padrões para os próprios campos de altitude que não foram detectados neste estudo. Além disto, pesquisas em nível de populações que quantifiquem a contribuição de diferentes grupos de polinizadores para a reprodução das espécies de plantas generalistas nos campos de altitude são muito promissoras e, portanto, também são encorajadas.

A maior parte das áreas que abrigam campos de altitude pertencem a unidades de conservação estaduais ou federais (e.g., Parques Nacionais do Itatiaia, Serra dos Órgãos, Serra do Caparaó e Parques Estaduais do Desengano, RJ, Campos do Jordão, SP e Serra do Brigadeiro, MG). Porém, apesar de seu status de proteção, estas áreas estão sob pressão antrópica, cuja intensidade varia entre as localidades. A frequência das queimadas e a intensidade de pastoreio são altos em várias áreas de altitude do Parque Nacional da Serra da Bocaina e de seu entorno. As conseqüências destas ações no meio físico (e.g., solos, micro-clima, nascentes) e na estrutura e dinâmica da flora e fauna das formações de altitude não foram até o momento estudadas em profundidade, mas impactos negativos são esperados. Assim sendo, maior atenção deve ser dada à preservação efetiva destas áreas, não somente por estas abrigarem vegetação ímpar no Brasil, mas por serem a fonte primária das bacias responsáveis pelo abastecimento de água de ca. 25% da população do país (q.v., Safford, 1999). Estudos comparativos sobre as interações planta-polinizador de campos de altitude em áreas com maior impacto (e.g., Serra da Bocaina) e áreas mais bem preservadas (e.g., Serra dos Órgãos) são indicados para a avaliação das conseqüências de ações antrópicas neste ecossistemas.

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