Diversity, flower visitation frequency and generalism of pollinators in temperate rain forests of Chiloé Island, Chile

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Species richness and taxonomic composition of pollinator assemblages are documented for 26 plant species from temperate rain forests of northern Chiloé Island, southern Chile (42°30′S). We investigated the patterns of generalism and specialization among plants and animal pollinators by comparing the flower visit frequency by different pollen vectors during the spring and summer months of three consecutive years (2000–2002). Species studied exhibited a range of floral morphologies (radial vs. zygomorphic, open vs. tubular) and rewards (nectar and/or pollen). Overall, we recorded 172 pollinator species, with an average of 6.6 species of pollen vectors/plant species. Pollinators visited an average of 15.2 plant species/pollen vector. Pollinator assemblages were dominated by Coleoptera (75 species), Diptera (56 species) and Hymenoptera (30 species), but passerine birds and hummingbirds were also important. The most specialized plants were vines, including the bee-pollinated genus *Luzuriaga* (Philesiaceae) and two endemic species of hummingbird-pollinated Gesneriaceae. Hymenoptera contributed 41.2% of all visits, with the bumblebee *Bombus dalhbomii* accounting for 22.5% of these. Plants with unspecialized flower morphology supported a higher species richness of pollinators, but visiting rates did not differ from specialized flowers.

ADDITIONAL KEYWORDS: bees – birds – hummingbirds – Myrtaceae – plant–pollinator interactions – pollination systems – specialization.

INTRODUCTION

Studies of plant–animal mutualisms provide good models for understanding the underlying causes of ecological and evolutionary patterns (Bawa *et al*., 1985). Pollination studies have contributed useful information on the degree of mutual dependence between species within a community, the reproductive ecology of plant communities, and the effects of landscape change on pollen flows and resource supply for pollen vectors. Community studies of plant–pollinator interactions are the first step for defining pollinator and plant 'guilds', and for assessing specialization and generalization trends among plants and pollinators in Neotropical forests (e.g. Janzen, 1971; Stiles, 1978; Bawa *et al*., 1985; Endress, 1994; Kress & Beach, 1994; Proctor, Yeo & Lack, 1996), in Mediterranean shrublands (e.g. Herrera, 1988; Herrera, 1989; Petanidou & Vokou, 1990), in alpine plant communities (e.g. Arroyo, Primack & Armesto, 1982; Primack, 1983; Arroyo, Squeo & Lanfranco, 1987; Squeo, 1991) and in Malaysian dipterocarp forests (e.g. Kato, 1996, Momose *et al*., 1998).

Some patterns found in community-wide studies of pollination interactions are more general. Several floral characteristics, such as corolla shape and colour, flowering phenology, and type and quantity of nectar or pollen rewards, have been directly associated with the identity of pollinators (Barth, 1991; Proctor *et al.*, 1996; Devy & Davidar, 2003). Floral morphology is one of the aspects more frequently considered in studies of generalist vs. specialized plant–pollinator interactions

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(Nilsson, 1988; Stanton & Preston, 1988; Mitchell, 1994; Thompson, 1994). Depending on floral morphology, plant species differ in the type of reward offered to the pollinating agent, or in the accessibility of this reward to a particular pollinator. On the other hand, pollinators differ widely in their efficiency of deposition and pollen transfer. Plants with open dish (generalist) morphology are visited by many insect species, often including various orders and families (Primack, 1983; Motten, 1986; Arroyo *et al*., 1987; Herrera, 1987, 1989; Herrera, 1988; Eckhart, 1992; Waser *et al*., 1996; Sakai, Kato & Inouye, 1999; Johnson & Steiner, 2000; Thompson, 2000; Aizen, Vazquez & Smith-Ramírez, 2002). Evidence suggests that such species should face low selection on floral characters (Johnson & Steiner, 2000), thus allowing a greater number of flower visitors.

In the highly endemic temperate rain forests of southern Chile, we set out to: (i) assess the species richness and taxonomic composition of pollinator assemblages associated with a representative number of species of the local flora; (ii) determine the frequency of pollinator visits to each flower/plant studied; (iii) assess floral characteristics (morphology and resources) that may account for visiting patterns found among pollinators; (iv) identify potential keystone pollinators of the plant community; and (v) determine the plant species that are potential keystones for maintaining the diversity of forest pollinators. This study should contribute new information on plant–pollinator interactions and biodiversity in the highly endemic Chilean rain forests (Armesto *et al*., 1998; Smith-Ramírez, 2004). Previous studies, focused on regional patterns of pollination syndromes (Aizen & Ezcurra, 1998; Aizen *et al.*, 2002), have shown the relevance of biotic pollination and described pollen vectors at the order and family level for some plant species in Andean forests (Rivero, 1991). Other studies have documented visitation rates for plant species pollinated mainly by passerines and hummingbirds (Smith-Ramírez & Armesto, 1998, 2002). However, the patterns of interaction at the species level remain unexplored.

SITE AND METHODS

Vegetation and climate

We studied 26 species of trees, shrubs and vines (Table 1) occurring in a mosaic of old-growth and second-growth forest patches within a rural landscape in northern Chiloé Island, southern Chile (Fig. 1). Forest patches are generally surrounded by grazing pastures, wetlands and/or shrublands. Floristic composition of forest fragments is typical of Valdivian and North Patagonian rain forest types (Aravena *et al*., 2002), some

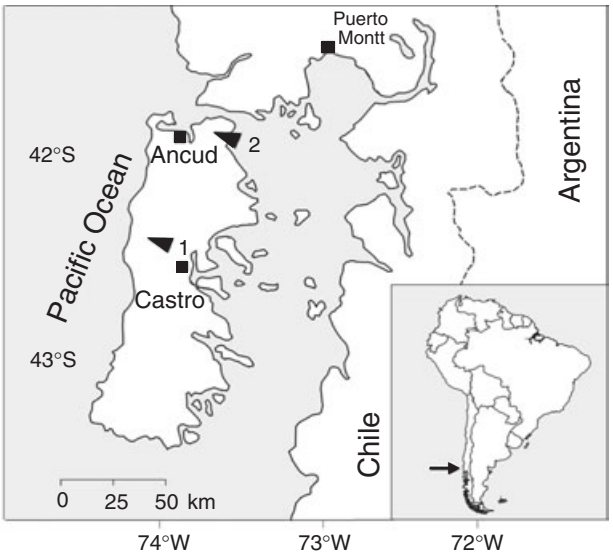

Figure 1. Arrow indicates the location of the study area in a rural landscape of northern Chiloé Island, southern Chile.

of the richest forest associations in the temperate region of Chile. Our observations were conducted mainly on plant species that occurred along a riparian forest corridor within Senda Darwin Biological Station (SD) (42°S, 73°35′W, 30 m above sea level). This riparian forest was connected to other larger forest fragments and has a floristic composition similar to old-growth forests in the same area (Aravena *et al*., 2002).

Monthly maximum precipitation, based on records from the meteorological station at SD over a period of three years, varied between 400 and 500 mm in April and July. The lowest values were recorded between October and February, with monthly precipitation between 150 and 35 mm. Total annual precipitation during the study period ranged from 2100 mm (1999) to 2258 mm (2000) and 2177 mm (2001). Monthly maximum temperatures recorded in SD during the period of study averaged 16–18 °C (December and January), and monthly minimum temperatures ranged from 2 to –1 °C (May and July).

Flowering periods of the 26 species studied are given in Smith-Ramírez & Armesto (1994). Table 1 summarizes available information on reproductive biology for the plant species included in this study.

Study species

The 26 plant species included in this study were selected to represent the diversity of floral resources available for animal pollinators (pollen and/or nectar) in southern temperate rain forests, and the entire

Table 1. General characteristics of flowers of 26 plant species in temperate rain forests of Chiloé Island, Chile

Species	Family	Life form	Corolla shape	Flower colour	Resource	Month of flowering peak	Reproductive system	Dependence on pollinator
Berberis buxifolia	Berberidaceae	Shrub	Bell	Yellow	Nectar, pollen	S	SI	High*
Berberis darwinii	Berberidaceae	Shrub	Bell	Yellow	Nectar, pollen	O	SC	High*
Caldcluvia paniculata	Cunoniaceae	Tree	Absent	White	Nectar, pollen	D	SC	Partial*
Gaultheria phillyreifolia	Ericaceae	Shrub	Bell	White	Nectar, pollen	N	D	Absolute*
Gaultheria mucronata	Ericaceae	Shrub	Bell	White	Nectar, pollen	D	–	–
Eucryphia cordifolia	Eucryphiaceae	Tree	Disc	White	Nectar, pollen	F	SI	High*
Asteranthera ovata	Gesneriaceae	Vine	Tubular	Red	Nectar, pollen	D–J	SI	High*
Mitraria coccinea	Gesneriaceae	Vine	Tubular	Orange	Nectar, pollen	D–J	SI	High*
Luzuriaga polyphylla	Philesiaceae	Vine	Bell	White	Nectar, pollen	N	SI	Absolute†
Luzuriaga radicans	Philesiaceae	Vine	Bell	White	Nectar, pollen	N	SI	Absolute*
Anagallis alternifolia	Primulaceae	Herb	Bell	White	Nectar, pollen	J	–	–
Embothrium coccineum	Proteaceae	Tree	Tubular	Red	Nectar, pollen	O–N	SI	Absolute*
Gevuina avellana	Proteaceae	Tree	Tubular	Yellow	Nectar, pollen	F	–	–
Rhaphithamnus spinosus	Verbenaceae	Shrub	Tubular	Violet	Nectar, pollen	O	SC	Partial*
Ovidia pillopillo	Thymeliaceae	Shrub	Disc	White	Pollen	O	D	Absolute*
Hydrangea serratifolia	Hydrangeaceae	Vine	Absent	White	Pollen	D	D	Absolute*
Myrteola nummularia	Myrtaceae	Dwarf shrub	Disc	White	Pollen	N	SC	Null*
Ugni candollei	Myrtaceae	Shrub	Bell	Pink	Pollen	D	–	–
Ugni molinae	Myrtaceae	Shrub	Bell	Pink	Pollen	D	SC	High‡
Amomyrtus luma	Myrtaceae	Tree	Disc	White	Pollen	O	SC	Partial*
Amomyrtus meli	Myrtaceae	Tree	Disc	White	Pollen	N	SC	Partial†
Luma apiculata	Myrtaceae	Tree	Disc	White	Pollen	F	SI	High*
Myrceugenia planipes	Myrtaceae	Tree	Disc	White	Pollen	J	SI	High*
Myrceugenia parvifolia	Myrtaceae	Shrub	Disc	White	Pollen	F	–	–
Myrceugenia ovata	Myrtaceae	Tree	Disc	White	Pollen	J	SC	High§
Tepualia stipularis	Myrtaceae	Shrub	Disc	White	Nectar, pollen	F	–	–

Reproductive system and dependence on pollinators from *Riveros (1991), †Arroyo & Humaña (1999), ‡Seguel (1986), §C. Smith-Ramírez, (unpubl. data).
SI, self-incompatible; SC, self-compatible; D, dioecious.
– No information available

range of life forms (eight tree species, 12 shrubs, five vines and one herb). These numbers of woody species represent 57.5% of all biotically pollinated trees, 63% of shrubs, 71% of vines and 25% of herbs occurring in the interior of lowland forests in northern Chiloé Island. Plant species are representative of the floristic spectrum that characterizes lowland rain forests, although not all the species were present in a single forest fragment. These species also encompass the variety of flowering periods in Valdivian rain forests (Table 1). Observations of pollinators were conducted during three consecutive reproductive seasons, from October 1999 to January 2000, from October 2000 to March 2001 and from October 2001 to February 2002.

To assess the identity, number and frequency of animal pollinators visiting the flowers, field observations were concentrated during the period (approximately 1 week) of maximum blooming of each plant species, approximated from previous phenological records in the same area (Smith-Ramírez & Armesto, 1994). Floral visitors to a given plant species were recorded during several 20 min observation periods (sample unit). Observations were made with the naked eye from the ground or from a short platform (2 m tall) and hence, records of visitors were limited to flowering branches located up to 4 m high in the case of trees. Observation periods were uniformly distributed between 10.00 and 18.00 each day. During each 20 min period, a single plant species was viewed from a fixed point by one observer, and each pollinator visit to a previously defined number of visible (exposed) open flowers was recorded. The number of 20 min periods in 1 day depended on the weather conditions of the day (rainy or windy conditions were avoided). The number of sampling periods per plant species was variable, but observations were maintained until the accumulation curve of the number of pollinator species vs. observation time approached an asymptote. For the 26 plant species, a total of 26 780 min, or 446 h of field observations, was accumulated over 3 years, with a total per species varying between 80 and 7260 min (average = 1030 min/plant species; Table 2).

Table 2. Species richness and visiting rates of pollinators for 26 plant species of temperate rain forests of Chiloé Island, Chile

Plant species	Number of pollinator species	Total number of visits	Average number of flowers observed	Accumulated observation time (min)	Visits/flower/min $\times 10^{-3}$
Asteranthera ovata	1	16	59.5	460	0.6
Myrteola nummularia	2	8	51.7	1160	0.1
Mitraria coccinea	2	251	60	2000	2.1
Ugni candollei	4	9	64	80	1.8
Luzuriaga radicans	4	6	22.5	460	0.6
Luzuriaga polyphylla	5	34	24	520	2.7
Embothrium coccineum	5	1647	600	7260	0.4
Anagallis alternifolia	6	130	123.5	280	0.4
Gaultheria mucronata	10	97	132.5	400	2.0
Ovidia pillo pillo	11	76	100	200	3.8
Hydrangea serratifolia	12	102	208.5	220	2.2
Rhaphithamnus spinosus	12	107	392	260	1.0
Myrceugenia parvifolia	15	32	65.1	780	0.6
Berberis microphylla	15	30	148	320	0.6
Gaultheria phillyreifolia	18	322	717	580	0.8
Ugni molinae	18	70	144.5	760	0.6
Berberis darwinii	19	103	99.7	440	2.3
Amomyrtus luma	24	126	333	1950	0.2
Luma apiculata	29	288	105.4	1180	2.3
Gevuina avellana	29	309	119	840	3.1
Caldcluvia paniculata	32	159	561.3	300	0.5
Myrceugenia planipes	39	600	146.4	1180	3.4
Amomyrtus meli	40	265	217	850	1.4
Eucryphia cordifolia	52	421	52	1440	5.6
Tepualia stipularis	54	249	100	1020	2.4
Myrceugenia ovata	60	437	155	1845	1.5

Before starting an observation period, the observer counted all the open flowers (or inflorescences) contained in an arbitrary volume of the plant canopy that could be easily observed from a short distance (usually <1 m) without disturbing the animal visitors; this was considered the 'target area'. The total number of flowers observed per plant varied with the plant species (Table 2) and depended on the size and abundance of flowers. Each individual insect or bird contacting the stigma or anthers of a flower within the target area of the plant was recorded as a flower visitor and considered a 'pollinator' for the purpose of this work. We calculated the frequency of each visitor (or class of pollinator) to the flowers of a given plant species as the number of times an individual was recorded contacting at least one flower within the target area for a unit time period (Kears & Inouye, 1984).

A major difficulty of this study was that the insect fauna of Chilean rain forests was almost completely unknown. To identify each pollinator to species, we captured a small number of specimens of each new 'type' of flower visitor using entomological nets. Samples were kept as references. Any suspected new types recorded during the observation periods were also collected. Each morphotype, suspected to be a different pollinator species, was given a code name for field identification, and this name was kept throughout the study until the scientific name became available. Specialists in the different insect groups identified specimens (see Acknowledgements). To date, a total of 172 pollinator species has been identified on the flowers of 26 plant species; 168 of these pollinators are insects and the remaining four are birds. Due to taxonomic identification problems, 130 insect species were classified only to genus. Complete scientific names were available for only 62 species (Appendices 1, 2).

Pollinator censuses were based on observations on a total of two to 14 individuals for each plant species, with a modal number of seven individuals per species. The types and quantities of pollen grains transported by insects and birds were not quantified in this study (for pollen carried by birds see Smith-Ramírez, 1993; Smith-Ramírez & Armesto, 1998). In two cases, for the species *Anagallis alternifolia* Cav. and *Asteranthera ovata* (Cav.) Hanst., we made nocturnal observations of possible pollinators on nights of full moon or using lamps with red light for a total of 600 and 480 min, respectively. These two species were observed after dark because their flowers produced abundant nectar but received almost no visits during the day.

Flower traits

The most distinctive floral characteristics of the species studied are summarized in Table 1. All of the species included in this study may be classified as having entomophilous and/or ornithophilous floral morphology (Faegri & van der Pijl, 1979). The main traits that distinguish entomophilous flowers from each other (Table 1) are the types of floral rewards (usually pollen and/or nectar) and floral shape. The most common floral shapes were cup or disc forms with open polypetalous corollas and many stamens, as seen in the Myrtaceae (e.g. species of *Myrceugenia* and *Amomyrtus*). Other species had short floral tubes (< 8 mm) that are totally or partially sympetalous (*Embothrium*, *Gevuina* and *Rhaphithamnus*). Finally, two species had long (> 15 mm), tubular, sympetalous corollas (Gesneriaceae). Our study also included species with apetalous corollas presented in panicles (*Caldcluvia* and *Hydrangea*). These groups of plant species based on floral morphology often also differed from each other in flowering phenology and reproductive systems (Table 1). For the purpose of comparing pollinator assemblages, we classified the flower types in two groups. We considered as specialized flowers all the flowers with tubular and bell-shaped corollas (independent of size) having nectar as a reward (Table 1). We considered as nonspecialized flowers all the flowers with a disc shape or without corollas (independent of size), without nectar and with white-coloured petals when present. We did not include in these two groups the flowers of *Eucryphia* and *Tepualia*, which have intermediate characteristics.

Data analyses

The species richness of the pollinator assemblage associated with one plant species was assumed to be equivalent to the value of the asymptote of the relationship between the accumulated number of pollinator species and accumulated observation time (all observation periods added) for that plant species. For interspecific comparisons of pollinator assemblages, Jaccard's similarity index (Magurran, 1988) was calculated for all plant species pairs and a dendrogram of affinities among plant species was constructed. Species were grouped based on their similarities in pollinator assemblages using presence/absence data in the matrix of plants and pollinator species. Jaccard's index was calculated as $2c/a + b$, where a and b are the numbers of pollinator species visiting two different plant species being compared, and c is the number of pollinator species shared by both plant species. Groups (clusters) of plant species in the dendrogram having similar pollinator assemblages were contrasted with qualitative grouping of species based on flower morphology (Table 1).

To test whether differences in floral morphology influenced pollinator species richness and flower visitation rates in this rain forest, we used a two-factor ANOVA. In the ANOVA, floral morphology had two

levels (specialized vs. nonspecialized flowers, see Table 1). The dependent variables were the number of animal species visiting each plant species and the overall visitation rate (all pollinators combined) for each plant species.

RESULTS

Pollination guilds

The 26 plant species were grouped in five qualitative categories or 'guilds' based on compositional similarity of pollinator assemblages (Fig. 2). The guilds were as follows. (1) Plants pollinated by both passerines and hummingbirds: one tree species, the red-flowered Proteaceae, *Embothrium coccineum*. Among the most frequent visitors to this species were the passerines *Elaenia albiceps*, *Carduelis barbatus* and *Phrygilus patagonicus*. (2) Plants pollinated mainly by hummingbirds and secondarily by the bumblebee *Bombus dalhbomii* (two vine species, *Mitraria coccinea* and *Astherantera ovata*). (3) Plants pollinated exclusively by the hymenopterans *Bombus dalhbomii* and *Diphaglossa gayi* (two vine species in the genus *Luzuriaga*). The flowers of both *Luzuriaga* species are flashy white and present both pollen and nectar as floral rewards (Table 1). (4) Plants pollinated by several species of Hymenoptera including *Bombus* among other equally important hymenopteran species (seven plant species, i.e. *Gevuina*, *Rhaphithamnus*, *Gaultheria*, *Hydrangea*, *Berberis darwini*, *B. buxifolia*, *Myrceugenia planipes*). (5) Broad generalist species, i.e. plants visited by many pollinator species in various insect orders including coleopterans, dipterans, hymenopterans and, less frequently, lepidopterans, and occasionally by hummingbirds (14 species, Appendices 1, 2). There were no plant species in Chiloé forests pollinated exclusively by butterflies, ants, coleopterans or dipterans.

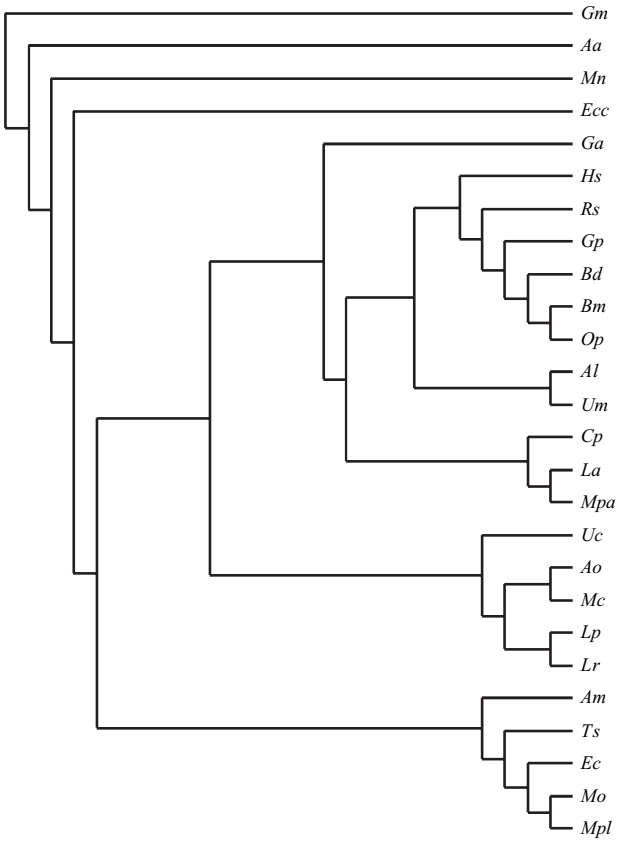

Figure 2. Dendrogram of similarities (Jaccard's index) of pollinator assemblages among plant species in rain forests of Chiloé. Similarities are based on presence/absence data. Species codes are given in Appendix 2.

The dendrogram, based on compositional similarity of pollinator assemblages (Fig. 2), was partly consistent with our initial classification of pollination guilds (see above). The analysis discriminated five forest species that did not group with the rest. These species had either very few flower visitors, those they had being predominantly flies [e.g. the shrubs *Myrteola nummularia* (Poir.) Berg, *Gaultheria mucronata* (L.f.) Gaud ex Spreng. and the herb *Anagallis alternifolia*], or a very unique pollinator assemblage, as in the case of *Embothrium coccineum* J. R. et G. Forster, which was the only tree species visited by nectarivorous passerines (guild 1 above). Among the species groups (or clusters) sharing similar pollinator assemblages (Fig. 2), we recognize two homogeneous groups. One group was formed by four Myrtaceae species [*Tepualia stipularis* (H. et A.) Griseb., *Amomyrtus meli* (Phil.) Legr. et Kaus., *Myrceugenia planipes* (H. et A.) Berg and *M. ovata* (H. et A.) Berg var. *ovata*] and *Eucryphia cordifolia* Cav. (Eucryphiaceae); all of them are canopy or subcanopy trees that are visited by many different pollinators including bees, flies and coleopterans (guild 5) and hence, considered broad generalists. The second group included the two vines in the genus *Luzuriaga*, which are pollinated by two bee species, one of them highly restricted, as well as the vines *Mitraria coccinea* Cav. and *Asteranthera ovata*, which are pollinated primarily by hummingbirds. These species can be considered the most specialized with regard to the richness of their pollination assemblages (guilds 2 and 3 above). This cluster also included *Ugni candollei* (Barn.) Berg, which has few bee pollinators, sharing one of them, *Bombus dahlbomi* Guér., with the other four species. Finally, there is one broad cluster comprising 12 species (Fig. 2), mostly species belonging to guild 5 but also including some species in the predominantly bee-pollinated guild 4. The shrubs and trees in the diverse family Myrtaceae appear dispersed in all of the clusters defined by the dendrogram.

According to these results, a high percentage (70%) of the 26 plant species monitored may be considered to be generalist species because they attracted a diverse array of pollinators. Within the guild of generalist plant species (Appendices 1, 2), the large emergent tree *Eucryphia cordifolia* (Eucryphiaceae) and the canopy tree *Myrceugenia ovata* were remarkable in having the largest species richness of pollinators (52 and 60 species, respectively).

Although, during this study, we recorded visits to the red flowers of the epiphyte *Astherantera* (Gesneriaceae, see Appendices 1, 2) only by the bumblebee *B. dalhbomi*, in plants observed outside the study area, we recorded visits by the hummingbird, *Sephanoides sephaniodes* (Molina) = *S. galeritus*. Nocturnal observations of flowers of *Astherantera* did not reveal additional pollinators. We also conducted nocturnal observations of the herb *Anagallis alternifolia* but found no evidence of nocturnal pollinators.

Pollinator species richness

Pollinator species accumulation curves for each plant species are shown in Figure 3. Data are not shown for eight plant species that were visited by fewer than six species of pollinators [these were *Luzuriaga polyphylla* (Hook.) Macbr., *L. radicans* R. et P., *Asteranthera ovata*, *Mitraria coccinea*, *Ugni candollei* and *M. nummularia*). For most plant species represented (Fig. 3), the number of morphospecies of pollinators identified approximated an asymptote after 100 (*Gevuina avellana* Mol.) to 800 (*E. cordifolia*) min of observation had accumulated. For those species that were observed for shorter time intervals, the number of species of pollinators continued to increase after 500 (*Berberis microphylla* Lam. = *B. buxifolia*) and 300 min [*Caldcluvia paniculata* (Cav.) D. (Don)] of observation (Fig. 3).

Floral visitation rates

The rate at which pollinators visited flowers of the rain forest species varied between a maximum of 5.6×10^{-3} visits/flower/ h in the large emergent tree *Eucryphia cordifolia*, followed by the trees *Ovidia pillopillo* (Gay) Meisn. and *Myrceugenia planipes* (H. et A.) Berg. with 3.8×10^{-3} and 3.4×10^{-3} visits/flower/ h, respectively (Table 2). The smallest visiting rate recorded was 0.1×10^{-3} visits/flower/ h in the dwarf shrub *Myrtreola* (Table 2).

Pollinators

The major orders of insect pollinators represented in the entomofauna of this forest were: Diptera with 43.9% ($N = 75$) of the total number of pollinator species recorded in this study, followed by Coleoptera 32.7% ($N = 56$) and Hymenoptera 17.4% ($N = 30$) (Appendices 1, 2). Birds represented < 5% of all species visiting flowers in this forest (Fig. 4).

Although Hymenoptera had lower species richness than other pollinator insect orders reported in this study, they accumulated the highest frequency of total visits (42%). Plant species most visited by Hymenoptera are those with flowers that offered both nectar and pollen as rewards. The plants that showed the strongest dependence on Hymenoptera for pollination were the two species of *Luzuriaga*, *Gevuina*, *Hydrangea serratifolia* (H. et A.) F. Phil. and *Tepualia*.

Only 10% of the floral visits in this forest were made by coleopterans. These insects visited, almost exclusively, flowers with an open corolla such as Myrtaceae species. Members of the Diptera (excluding Syrphidae) accumulated 16% of the total number of visits to flowers. Within dipteran pollinators are several families with a diversity of species, each occurring in low frequency, as in the case of 12 species of Sarcophagidae, 11 species of Muscidae and six species of Tachinidae. Plant species differed widely in the frequency of avian visitation. Birds accounted for 86% of the visits to *E. coccineum* but only 8% of the visits to *M. coccinea* and 1% of visits to *Rhaphithamnus spinosus* A.L. Juss. Mold.

The most frequent visitors by family were Halictidae (Hymenoptera) and Syrphidae (Diptera). Overall, several species of Halictidae presented the highest visitation rates (8.9%, Fig. 5), particularly five species of the genus *Corynura*, *Callochlora chloris* Spinola *and Cadeguala albopilosa* Spinola (Appendices 1, 2). However, three species of hymenopterans showed clear preferences for a limited number of plant species. This was the case for *Diphaglossa gayi* Spin. (Colletidae), which was the only insect pollinator of the flowers of *Embothrium* (Appendices 1, 2). However, this bee species also pollinated the flowers of *Amomyrtus* (Phil.) Legr. Et Kaus., with a very low frequency (1.2%), and the two *Luzuriaga* species. The second species of Hymenoptera that was relatively specialized was *Cadeguala occidentalis* Spin. (Colletidae), which was recorded only at flowers of *Tepualia*. Individuals of the halictid bee *Caenohalictus movilicornis*, which measured 8–14 mm in length, were found only in the medium-sized (4–15 mm, Table 1) flowers of *Gevuina* and larger flowers of *Eucryphia*.

The pollinator assemblage of the Syrphidae family (Diptera) was represented by 22 species and nine genera. The relative proportion of total flower visits made by Syrphidae was 17% (Fig. 5). Syrphids varied in size from 7 to 22 mm and visited flowers from a wide spectrum of types and sizes. However, syrphids did not visit large tubular flowers (> 20 mm in length, e.g.

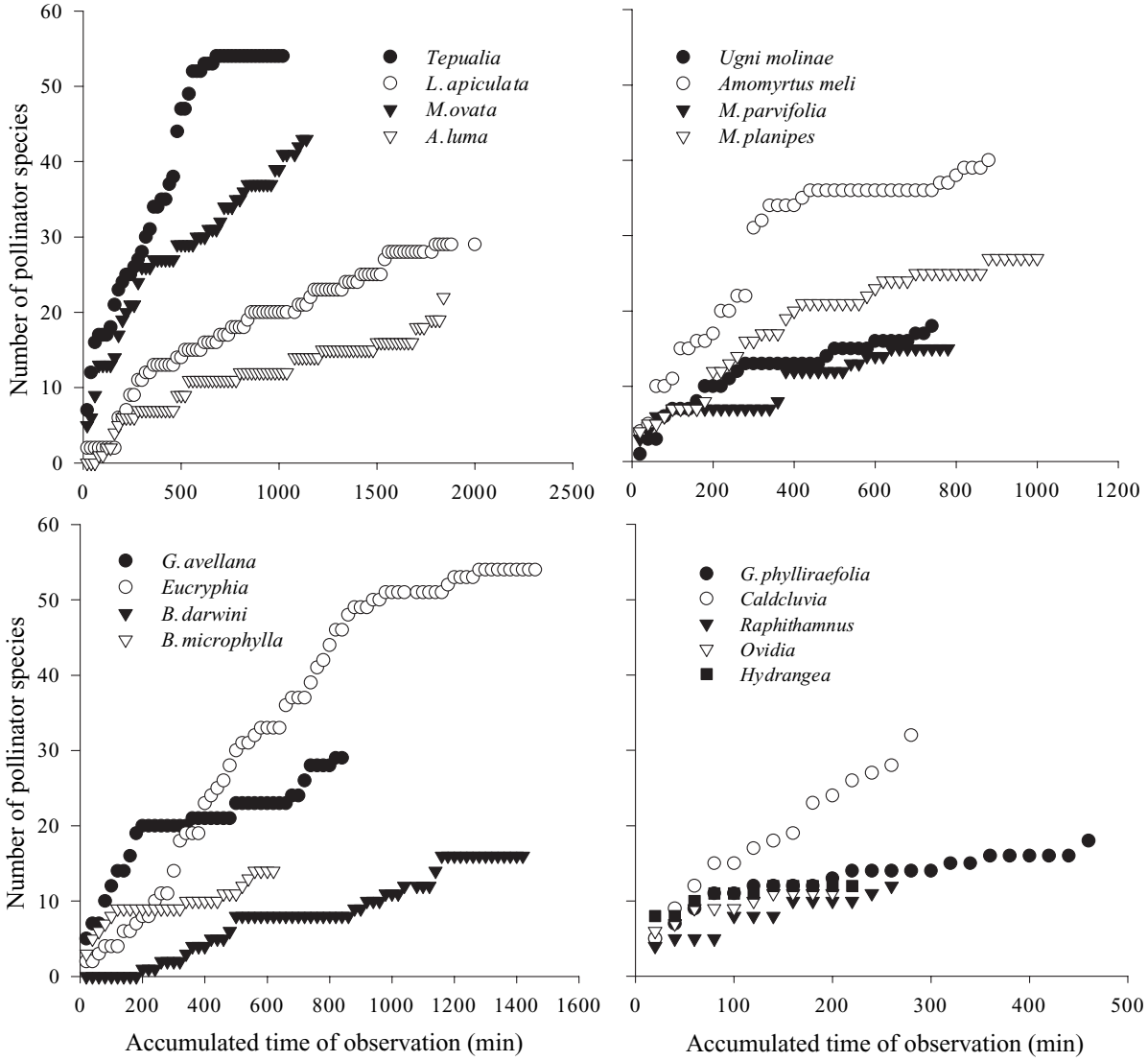

Figure 3. Cumulative number of pollinator species vs. accumulated time of observation for selected plant species studied in temperate rain forests of Chiloé Island, Chile.

Mitraria and *Astherantera*) and the bell-shaped flowers of the genus *Luzuriaga* (Appendix 2).

The pollinator responsible for the greatest frequency of visits, considering all 26 plant species together, was *Bombus dalhbomi* (Apidae), with 18.7% of the floral visits (Fig. 5). *Bombus* was the largest species of insect pollinator, with body lengths of 20 mm (worker) and 50 mm (queen). This proportion of visits to flowers may be divided between *Bombus* workers (66% of the total) and queen bees (34%; C. Smith-Ramírez, unpubl. data). *Bombus* pollinated the flowers of 21 plant species (81% overall, Appendix 2). The few flowers that were not visited by *Bombus* had morphological characteristics that restricted the access of large bees, such as narrow tubular corollas, e.g. *Embothrium* and *Gevuina*. Other species not visited by *Bombus* were several small creeping shrubs of undergrowth and herbs, such as *Myrteola*, *Gevuina* and *Anagallis*, all of them having small flowers (Table 1). Some plant species were pollinated mainly by bumblebee workers (species of the genus *Myrceugenia*), and others were pollinated by both types of individuals, such as myrtaceous species of *Ugni*, as well as *Eucryphia* and *Rhaphithamnus*.

The pollinator species that came second and third with regard to the relative number of visits to flowers in this forest were two Hymenoptera. One of them was an introduced species, the European bee *Apis mellifera* Linn. (Apidae), which accounted for 9.6% of all visits to flowers, while the other was the endemic

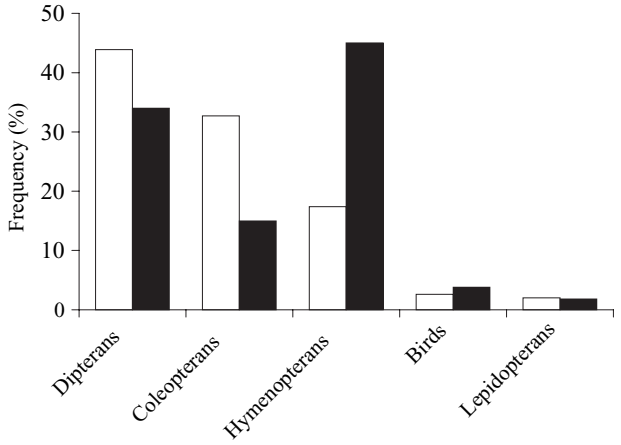

Figure 4. Relative importance (percentage of all species, open bars) of the main insect orders and bird pollinators of 26 plant species in the rain forest of Chiloé, and their relative frequency of visits to flowers (percentage of all visits, filled bars).

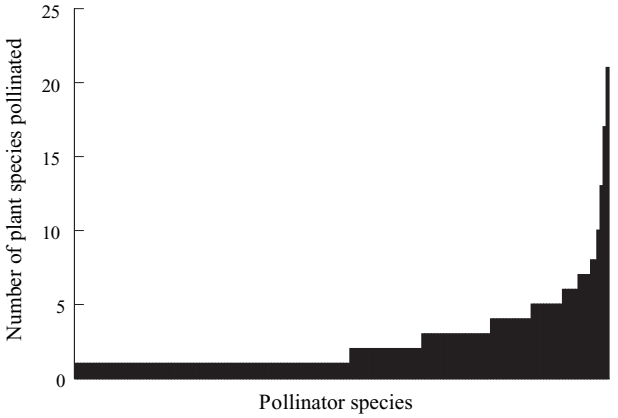

Figure 6. Number of pollinator species per plant species. Plant species ranked along the *x*-axis from the most specialized to the most generalist regarding pollinator visits. Scientific names of plants are given in Appendix 2.

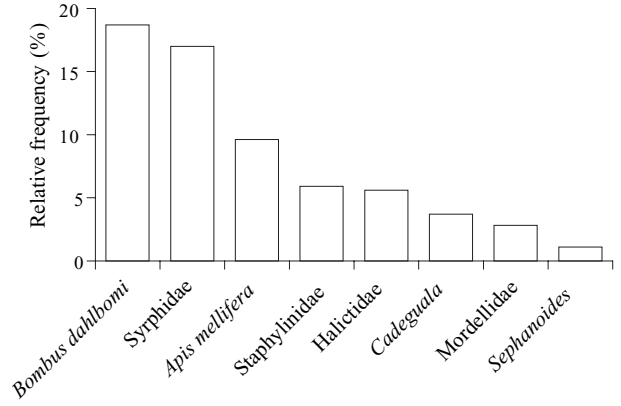

Figure 5. Relative frequency (%) of visits to flowers by the main species, genera and families of pollinators of 26 plant species in the temperate rain forests of Chiloé. Syrphidae (21 species) are flies, Staphylinidae (seven species) and Mordellidae (nine species) are small beetles, Halictidae (seven species) are bees, excluding two species of *Cadeguala* shown separately, *Sephanoides* refers to the only species of hummingbird.

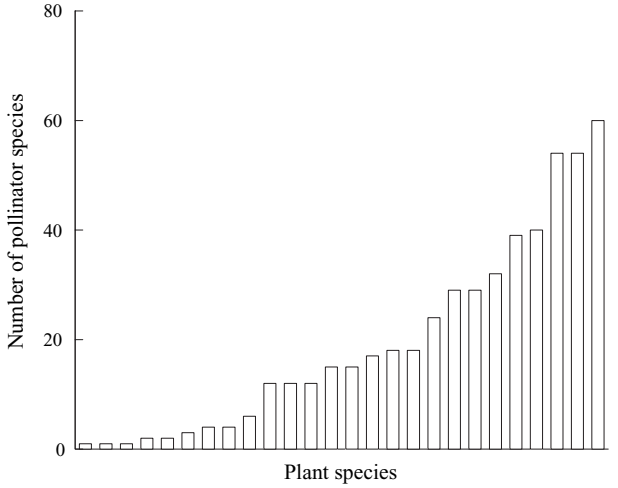

Figure 7. Number of plant species visited by each species of pollinator. Pollinator species are arranged along the *x*-axis from the most specialized to the most generalist. Scientific names of pollinators are given in Appendix 1.

bee *Cadeguala albopilosa* (Halictidae), which accounted for 3.7% of total visits. A high proportion of the visits by *Apis* was to individuals of *Myrceugenia planipes* that grew in a section of forest near a local apicultural facility. *Cadeguala*, a solitary bee the size of *Bombus* workers (15 mm body length), visited medium-sized flowers (Table 1). The plant species most visited by *Cadeguala* were *Amomyrtus luma*, *A. meli*, *Berberis darwinii*, *Gaultheria*, *Myrceugenia ovata*, *Ovidia*, *Ugni* sp., *Rhaphithamnus* and the panicles of *Hydrangea*.

Generalization and specialization in plants and pollinators

The number of pollinators per plant species was highly variable (Figs 6, 7), ranging from one species in *Asteranthera* to 60 species of pollinators (*Myrceugenia*

ovata) (Table 2). There was a tendency among pollinator species towards a generalized foraging behaviour. However, there were many insect pollinators (Appendices 1, 2) and three species of birds that visited only one plant species. The 56 species of floral-visiting coleopterans found in this study pollinated between one and six plant species (average = 2.4 plant species per coleopteran). Dipterans showed a similar pattern, pollinating between one and eight plant species (average = 2.3 plant species). One exception to this rule was the dipteran *Melanostoma* sp. (Syrphidae) that visited 13 plant species (Appendix 2). Each species of Hymenoptera visited between one and 21 plant species (average = 3.7 plant species per hymenopteran).

Plant species with a specialized floral morphology (Table 1) had significantly lower species richness of flower visitors than did species with less specialized morphology ($F = 4.61$, d.f. = 1, 24, $P = 0.03$). However, visitation rates did not differ between these two groups of flowers.

DISCUSSION

Overall, we found that pollinator assemblages of lowland rain forest tree, shrub and vine species in Chiloé were considerably rich. We found an average of 6.5 pollen vector species/plant species, a similar value to that reported by Vazquez & Simberloff (2002) who surveyed pollinators of rain forest trees at a similar latitude in Andean forests of Argentina. Argentinean forests are located in the steppe–forest transition, which may contribute to the enhancement of species richness of insect pollinators in the eastern side of the Andes because of steppe immigrants (see below). In the Mediterranean climate region of central Chile (33°S), Arroyo & Uslar (1993) reported a notably low proportion of 1.2 pollinator species per plant species in a montane sclerophyllous scrubland. In this case, each plant species was sampled for a shorter time than in our study. In the high Andean vegetation of central Chile, Arroyo *et al.* (1982) reported an average of 1.1 species of pollinators per plant species. All of these community level studies in central Chile suggest strong specialization among pollinators. Community level studies of pollinator assemblages in other regions of the world (Ramírez, 1989; Devy & Davidar, 2003) have frequently found similarly low ratios of pollinator species per plant species, with the exception of Barrett & Helenurm (1987) who found 13.9 insect pollinator species per plant in an assemblage of 12 herbaceous species in a boreal forest.

We report here an elevated species richness of pollinators, particularly in the case of tree and shrub species of the family Myrtaceae in Chiloé forests, with an average of 31.2 pollinator species per plant species. This high number of pollinator species resembles the number of pollinators found by Primack (1983) in an intensive survey of the myrtaceous shrub *Leptospermum scoparium* from New Zealand, whose flowers were visited by 45 insect species. The diversity of pollinators in *Leptospermum* is in the middle range of values reported here for all the species of Myrtaceae in Chiloé forests, which ranged from two to 60 pollinator species.

Along with the elevated pollinator species richness in temperate forest species documented in this study, many plant species were visited by a broad spectrum of insect pollinators, often representing several orders. However, in terms of effective pollination, as measured by parameters such as amount of pollen transferred between conspecifics, it is likely that the number of effective pollinators associated with each plant species would be less (Vázquez & Simberloff, 2002). For example, various studies have shown that coleopterans are poor pollinators, more often behaving as pollen predators and occasionally as accidental pollinators (Proctor *et al.*, 1996). In contrast, hymenopterans are frequently the most effective pollinator group (Proctor *et al.*, 1996). Among the Hymenoptera found in Chiloé forests, there are several species which are endemic to Chilean–Argentinean temperate forests. Examples of these endemic taxa are species of the genera *Cadeguala*, *Corynura*, *Diphaglossa* and *Manuelia* (Michener, 1979), which are members of the Anthophoridae (the first genus) and Halictidae families. Other bee species, such as species in the genus *Callochlora* (Moldenke, 1976), show an even more restricted endemism, occurring only in southern Chilean forests. We did not find representatives of *Colletes*, *Chilicola* and *Evylaeus*, genera that have been recorded across the Andes in Andean temperate forests of Argentina (Vázquez & Simberloff, 2002). These taxa may represent incursions of Patagonian steppe species into forest habitats in these transitional locations.

The remarkable specialization documented for the hymenopteran, *Diphaglossa gayi*, which visited almost exclusively one genus of plant species (*Luzuriaga*), is also known for other Colletidae bees in the central Chilean Andes (Arroyo *et al.*, 1987). On the other hand, three parasitoid hymenopteran species of the family Braconidae were found in low frequency in trees of *Eucryphia* and *Myrceugenia*, which presented some of the richer insect pollinator assemblages. The Braconidae pollinators were also reported in temperate forests across the Andes (Aizen *et al.*, 2002).

Some of the dipteran pollinators recorded in Chiloé forests are also common in mountain habitats of central Chile, Argentina and New Zealand (Arroyo *et al.*, 1982; Primack, 1983), and other regions of the world (Arroyo *et al.*, 1982; Primack, 1983; Barth, 1991;

Vázquez & Simberloff, 2002). This is the case for the commonly recorded families Syrphidae and Tachinidae (Primack, 1983). Tachinidae and other dipterans are important pollinators because, in addition to their hairy bodies, they forage for pollen on cold and rainy days when other pollinators are rare, or not present (Primack, 1983).

Overall, we found a notably low species richness and frequency of visits by lepidopterans in this lowland temperate forest, as reported earlier for forests on the eastern side of the Andes (Aizen *et al.*, 2002). However, this poor butterfly pollinator fauna contrasts notably with the composition of pollinator assemblages in high mountain flora of the central and Patagonian Andes (Arroyo *et al.*, 1987). Southern rain forests apparently represent poor habitats for pollen-feeding butterflies.

A large proportion of pollinator species in this temperate forest are generalists, with some notable exceptions already cited. Among bird-pollinated plants, *Embothrium* congregated an exceptionally large assemblage of nine bird species (Smith-Ramírez & Armesto, 2002), although only four species are likely to be effective pollinators (Smith-Ramírez & Armesto, 1998). Other red-flowered species that produce nectar in volumes and sugar concentrations similar to the nectar of *Embothrium*, for example the vines *Astherantera* and *Mitraria*, have fewer pollinators and are not visited by passerines. The only previous mention of nectarivory by passerines in southern South America is the consumption of flower nectar of the shrub *Fuchsia magellanica* Lam. by *Phrygilus patagonicus* Lowe in Tierra del Fuego, although in this case the bird is a nectar robber rather than a pollinator (Traveset, Willson & Sabag, 1998).

The most distinctive pollination guild in Chilean–Argentinean temperate forests comprises the plants pollinated almost exclusively by the hummingbird *Sephanoides* (Smith-Ramírez, 1993). All of these plants have bright red, tubular corollas and/or flowers with red dots in their petals and petioles, or red leaves surrounding the flowers, and secrete abundant but dilute nectar (Faegri & van der Pijl, 1979; Smith-Ramírez, 1993). Two vine species studied here, *Mitraria* and *Astherantera*, belong to the guild of ornithophilous species in southern temperate forest, along with *Crinodendron hookerianum* Gay., *Desfontainia spinosa* R. et P., *Fuchsia magellanica*, *Latua pubiflora* (Griseb.) Phil., *Campsidium valdivianum* (Phil.) Skottsb., *Lapageria rosea* R. et P., *Sarmienta scandens* R. et P., *Tristerix verticillatus* (R. et P.) Barlow et Wiens, *Tristerix corymbosus* (R. et P.) Mart. and *Fascicularia bicolor* (R. et P.) Mez. (Smith-Ramírez, 1993). The specialized floral morphology of these plants excludes many nectar- and pollen-feeding insects and therefore, their reproduction is strongly dependent on the local abundance of hummingbirds.

We found that nonspecialized flowers received visits from a larger number of species (and orders) of pollinators than species with a more specialized floral morphology, but this difference was not expressed in a higher frequency of visits, a result which is consistent with that reported by Johnson & Steiner (2000).

Finally, we propose that *Eucryphia* and the species of Myrtaceae, particularly *Tepualia*, *Myrceugenia* and *Amomyrtus*, should be considered pivotal species for this temperate forest community, since they maintain the richest assemblage of insect pollinators, including 89% of the 172 species found in this study. Likewise, the hymenopteran *Bombus* should also be considered a pivotal pollinator species, since it is the most frequent flower visitor in this community, visiting 21 of 26 plant species studied. More detailed studies, at the specific level, are necessary to assess the relative importance of wide ranging pollinators in terms of pollen transfer. For example, we need to assess whether *Bombus* is a better pollinator than the hummingbird *Sephanoides* for the ornithophyllous plants *Mitraria*, *Asteranthera* and other red-flowered species with tubular corollas, such as *Sarmienta* and *Fuchsia*.

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APPENDIX 1

SPECIFIC NAMES AND FAMILIES OF ALL THE POLLINATORS RECORDED AND IDENTIFIED IN 26 PLANT SPECIES IN THE RAIN FORESTS OF SOUTHERN CHILE

Some pollinators could not be identified to species and they are separated as morpho-species with different numbers, indicating their current assignment within a genus or family.

Order Coleoptera	
Family	
1. Cantharidae	*Chauliognathus* sp.
2. Cantharidae	*Dysmorphocellus* sp.
3. Cantharidae	*Hyponotum kraussei*
4. Cerambycidae	*Callideriphus laetus*
5. Cerambycidae	*Chenoderus testaceus*
6. Cerambycidae	*Platynocera gracilipes*
7. Cerambycidae	*Platynocera gracilis*
8. Chrysomelidae	*Clamirius apicarius*
9. Cleridae	*Eurymetopun obscurum*
10. Cleridae	*Eurymetopun prasinum*
11. Cleridae	*Eurymetopun proteus*
12. Coccinelidae	*Adalia deficiens*
13. Curculionidae	*Dasydema hirtella*
14. Curculionidae	*Rhopalomerus tenuirostris*
15. Chrysomelidae	*Chlamysus* sp.
16. Lathididae	*Melanophthalma* aff. *seminigra*
17. Melyridae	*Hylodanacea binotus*
18. Melyridae	*Hylodanacea elegans*
19. Mordellidae	*Mordella erythrura*
20. Mordellidae	*Mordella luctuosa*
21. Mordellidae	Species 1
22. Mordellidae	Species 2
23. Mordellidae	Species 4
24. Mordellidae	Species 5
25. Mordellidae	Species 6
26. Mordellidae	Species 7
27. Mordellidae	Species 8
28. Oedemeridae	*Mecopselaphus maculicollis*
29. Scarabaidae	*Schizochelus serratus*
30. Scirtidae	Species 1
31. Scirtidae	Species 2
32. Scirtidae	Species 4
33. Scirtidae	Species 7
Order Coleoptera	
Family	
34. Scirtidae	Species 10
35. Scirtidae	Species 11
36. Scirtidae	Species 12
37. Scirtidae	Species 13
38. Scirtidae	Species 15
39. Scirtidae	Species 16
40. Scirtidae	Species 17
41. Staphylinidae	Aleocharinae (subf.) Species 1
42. Staphylinidae	Aleocharinae (subf.) Species 2
43. Staphylinidae	Aleocharinae (subf.) Species 3
44. Staphylinidae	Aleocharinae (subf.) Species 4
45. Staphylinidae	Aleocharinae (subf.) Species 5
46. Staphylinidae	Aleocharinae (subf.) Species 6
47. Staphylinidae	Aleocharinae (subf.) Species 7
Order Diptera	
Family	
48. Acroceridae	*Megalybus crassus*
49. Bombylidae	Species 1
50. Calliphoridae	Species 1

APPENDIX 1 *Continued*

51. Calliphoridae	Species 2
52. Calliphoridae	Species 4
53. Calliphoridae	Species 5
54. Dolichopodidae	*Thrypticus* sp. 1
55. Empididae	Species 1
56. Lauxaniidae	Species 1
57. Lauxaniidae	Species 4
58. Muscidae	*Craspedochaeta linbinervis*
59. Muscidae	*Fannia* Species 1
60. Muscidae	*Fannia* Species 2
61. Muscidae	*Fannia* Species 3
62. Muscidae	*Fannia* Species 4
63. Muscidae	*Fannia* Species 5
64. Muscidae	*Fannia* Species 6
65. Muscidae	*Fannia* Species 8
66. Nemestrinidae	*Trichophthalma commutata*
67. Nemestrinidae	*Trichophthalma herbsti*
68. Sarcophagidae	Species 1
69. Sarcophagidae	Species 3
70. Sarcophagidae	Species 4
71. Sarcophagidae	Species 5
72. Sarcophagidae	Species 6
73. Syrphidae	*Allograpta hortensis*
74. Syrphidae	*Allograpta pulchra*
75. Syrphidae	*Cheilosia nitescens*
76. Syrphidae	*Dolichogyna chilensis*
77. Syrphidae	*Dolichogyna nigripes*
78. Syrphidae	*Eristalis assimilis*
79. Syrphidae	*Eristalis elegans*
80. Syrphidae	*Eristalis tenax*
81. Syrphidae	*Fazia bullaephora*
82. Syrphidae	*Fazia macquarti*
83. Syrphidae	*Macrometopia atra*
84. Syrphidae	*Melanostoma chalconotus*
85. Syrphidae	*Melanostoma fenestratus*
86. Syrphidae	*Melanostoma lundbladi*
87. Syrphidae	*Melanostoma* sp.
88. Syrphidae	*Mesograpta calceolatus*
89. Syrphidae	*Mesograpta philippi*
90. Syrphidae	*Stilbosona cyanea*
91. Syrphidae	*Syrphus octomaculatus*
92. Syrphidae	*Tropidia* sp.
93. Syrphidae	New species
94. Tabanidae	*Scaptia* (pseudomelpia) *horrens*
95. Tachinidae	*Lypha erigonopsidis*
96. Tachinidae	*Morphodexia* sp.
97. Tachinidae	*Peleteria filipalpis*:
98. Tachinidae	Tachininae (subf.) Species 2
99. Tachinidae	Tachininae (subf.) Species 3
Order Hymenoptera	
Family	
100. Apidae	*Apis mellifera*
101. Apidae	*Bombus dahlbomii*
102. Braconidae	Species 2
103. Colletidae	*Diphaglossa gayi*
104. Halictidae	*Cadeguala albopilosa*
105. Halictidae	*Cadeguala occipitalis*
106. Halictidae	*Corynura corynogastra*
107. Halictidae	*Corynura patagonica*
108. Halictidae	*Corynura rubella*
109. Halictidae	*Corynura* aff. *lepida*
110. Halictidae	*Corynura* aff. *atrovirens*
111. Halictidae	*Caenohalictus movilicornis*
112. Halictidae	*Callochlora chloris*
113. Ichneumonidae	Species 1
114. Ichneumonidae	Species 2
115. Mirmecophagidae	Species 1
116. Pompilidae	Species 1
117. Pompilidae	Species 2
118. Vespidae	*Hypodynerus* sp.
119. Vespidae	*Vespula germanica*
120. Vespidae	Euneminae (subf.) Species 1
121. Vespidae	Species 2
122. Microhymenoptera	Species 1
Order Lepidoptera	
Family	
123. Papilionidae	*Vanessa* sp.
124. Pieridae	*Eroessa chilensis*
Order Hemiptera	
Family	
125. Miridae	Species 1
Order Megaloptera	
Family	
126. Sialidae	*Protosialis chilensis*
Birds	
Family	
127. Fringillidae	*Carduelis barbatus*
128. Fringillidae	*Phrygilus patagonicus*
129. Tirannidae	*Elaenia albiceps*
130. Trochilidae	*Sephanoides sephaniodes*

APPENDIX 2

MATRIX OF POLLINATORS AND PLANT SPECIES IN RAIN FORESTS OF CHILOÉ ISLAND, CHILE

A 'one' indicates that the pollinator species was recorded visiting the flowers of the respective plant species. Pollinator species are identified by numbers given in Appendix 1. Orders are: C = Coleoptera; D = Diptera; H = Hymenoptera; L = Lepidoptera; HE = Hemiptera; ME = Megaloptera; B = birds. Plant species are: Aa = *Anagallis alternifolia*; Al = *Amomyrtus luma*; Am = *Amomyrtus meli*; As = *Asteranthera ovata*; Bb = *Berberis buxifolia*; Bd = *Berberis darwinii*; Cp = *Caldcluvia paniculata*; Ecc = *Embothrium coccineum*; Ec = *Eucryphia cordifolia*; Ga = *Gevuina avellana*; Gp = *Gaultheria phillyreifolia*; Gm = *Gaultheria mucronata*; Hs = *Hydrangea serratifolia*; La = *Luma apiculata*; Lr = *Luzuriaga radicans*; Lp = *Luzuriaga polyphylla*; Mc = *Mitraria coccinea*; Mn = *Myrteola nummularia*; Mo = *Myrceugenia ovata* var. *ovata*; Mp = *Myrceugenia planipes*; Mpv = *Myrceugenia parvifolia*; Op = *Ovidia pillo pillo*; Rs = *Rhaphithamnus spinosus*; Ts = *Tepualia stipularis*; Uc = *Ugni candollei*; Um = *Ugni molinae*.

Order	Pollinator	Al	Am	Aa	Ao	Bd	Bb	Cp	Ec	Ecc	Gm	Gp	Ga	Hs	La	Lp	Lr	Mc	Mn	Mo	Mp	Mpv	Op	Rs	Ts	Uc	Um
C	1								1						1					1	1				1		
C	2			1																	1						
C	3		1						1						1					1	1						
C	4		1																					1			
C	5		1																								
C	6		1																								
C	7	1																		1							
C	8	1																									
C	9		1																								
C	10	1																									
C	11	1																									
C	12		1																		1						
C	13	1													1												
C	14		1						1																1		
C	15																				1						
C	16																								1		
C	17		1																								
C	18	1																									
C	19		1					1	1						1					1					1		
C	20																								1		
C	21																								1		
C	22							1																			
C	23			1																1							
C	24		1					1	1						1					1		1					
C	25																								1		
C	26																								1		
C	27								1																		
C	28								1																1		

APPENDIX 2 *Continued*

Order	Pollinator	Al	Am	Aa	Ao	Bd	Bb	Cp	Ec	Ecc	Gm	Gp	Ga	Hs	La	Lp	Lr	Mc	Mn	Mo	Mp	Mpv	Op	Rs	Ts	Uc	Um
C	29	1																									
C	30																			1	1						
C	31	1	1																								
C	32																								1		
C	33		1																								
C	34		1																						1		
C	35																								1		
C	36																				1				1		
C	37																								1		
C	38												1		1							1					
C	39								1																1		
C	40								1				1							1		1					
C	41																								1		
C	42														1						1				1		
C	43			1				1												1					1		
C	44												1		1										1		
C	45																								1		
C	46																								1		
C	47																								1		
D	48								1						1												
D	49																			1							
D	50								1																		
D	51												1														
D	52								1																		
D	53								1																		
D	54														1						1	1			1		
D	55							1																			
D	56	1	1					1	1						1					1		1					
D	57		1						1																		
D	58		1																	1							
D	59		1																								
D	60								1																		
D	61																			1					1		
D	62								1				1														

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APPENDIX 2 *Continued*

Order	Pollinator	Al	Am	Aa	Ao	Bd	Bb	Cp	Ec	Ecc	Gm	Gp	Ga	Hs	La	Lp	Lr	Mc	Mn	Mo	Mp	Mpv	Op	Rs	Ts	Uc	Um
D	97							1																			
D	98										1																
D	99																								1		
H	100	1	1			1	1	1	1	1		1	1	1	1					1	1	1	1	1	1		1
H	101	1	1		1	1	1	1	1			1		1	1	1	1	1		1	1	1	1	1	1	1	1
H	102									1												1					
H	103		1							1						1	1										
H	104	1	1			1	1					1	1										1	1			
H	104																								1		
H	105	1											1							1							
H	106		1																		1						
H	107	1	1			1						1		1	1					1	1	1		1			
H	108													1	1					1							
H	109																			1							
H	110												1														
H	111					1							1							1	1		1				
H	112																										
H	113									1																	
H	114								1																		
H	115																										
H	116							1																	1		
H	117								1																		
H	118								1																		
H	119																								1		
H	120		1						1																1		
H	121							1	1					1											1		
H	122																								1		
L	123																							1			
L	124								1																		
HE	125								1																1		
ME	126		1																								
A	127									1																	
A	128									1																	
A	129									1																	
A	130				1	1			1	1								1						1			