

BREEDING SYSTEM AND POLLINATION OF SELECTED PLANTS ENDEMIC TO JUAN FERNÁNDEZ ISLANDS¹

GREGORY J. ANDERSON,^{2,3} GABRIEL BERNARDELLO,⁴ TOD F. STUESSY,⁵
AND DANIEL J. CRAWFORD⁶

²Department of Ecology and Evolutionary Biology, Storrs, Connecticut 06269-3043 USA; ⁴Instituto Multidisciplinario de Biología Vegetal (CONICET-UNC), C. C. 495, 5000 Córdoba, Argentina; ⁵Department of Higher Plant Systematics and Evolution, Institute of Botany, University of Vienna, Rennweg 14, Vienna A-1030, Austria; ⁶Department of Evolution, Ecology and Organismal Biology, Ohio State University, Columbus, Ohio 43210 USA

We conducted field studies on the Juan Fernández Islands flora on the breeding system of 25 endemic species from 17 families. We recorded data on flower features, pollen and ovule number, pollen/ovule ratio, pollen size, self-compatibility, floral visitors, and pollination. Flowers are mostly hermaphrodite, inconspicuous, small, and green. Six species are dioecious. Over 80% of the cosexual species are self compatible. However, many species are dichogamous (mostly protandrous); thus, even the self-compatible species may require pollen transfer. Selfing through geitonogamy seems to be the most common system, and several species express mixed breeding systems. Floral visitors are uncommon to rare, except for two hummingbird species (one native and one endemic) that visit five species we studied. In more than 300 h of observation of flowers over three field seasons, we detected only 23 native insect visits representing ten species (Diptera, Lepidoptera, and Coleoptera). One species each of an introduced ant and an introduced bee were also observed on some flowers, all near the single human settlement of San Juan Bautista. Wind directly moving pollen, or indirectly via shaking the flowers, is the most important pollen distribution mechanism. The majority of the wind-pollinated species bear some typical anemophilous features, but also others not characteristic of wind pollination, that presumably represent the condition of their biotically pollinated ancestors. Floral features often reflect ancestral reproductive systems, so floral biology studies of oceanic islands in particular must be done with cognizance of presumed ancestral forms, because the observed characters can be misleading.

Key words: angiosperms; breeding system; floral biology; floral visitors; hummingbird pollination; island biology; self-compatibility; wind pollination.

Oceanic islands provide special natural laboratories for studying the processes of evolution because there are many endemic and unusual organisms (Carlquist, 1974). In addition, because they are separated from the sources of their biota by water, there is the additional feature of being able to date times of first colonization much more precisely (often fairly specific dates marking the emergence of the islands) than on continental areas. When the arrival of a biota can be dated, the divergence from nearest relatives can be assessed with much greater accuracy (e.g., Carlquist, 1974; Barrett, 1998; Anderson et al., 2000a). Furthermore, a detailed analysis of much of an entire island flora allows tests of prevailing hypotheses about such things as the extent of dioecy on islands vs. continents, compatibility studies of island species and the utility of floral feature syndromes as indicators of likely pollination.

Most of the work on island plants has focused on systematics, speciation, and biogeography (e.g., MacArthur and Wilson, 1967; Thornton, 1971; Carlquist, 1974; Adersen, 1995). Reproductive biology, although fundamental for systematic, evolutionary, and conservation studies (Ornduff, 1969; Holsinger, 1991; Anderson, 1995), with exceptions (Carlquist, 1974) has not been intensively analyzed on island plants (Eh-

rendorfer, 1979; Barrett, 1998). Significant impediments to the acquisition of reproductive information include the natural isolation of the islands and often inaccessible habitats. Both factors contribute to the difficulty in reaching the plants at the right stage to perform in situ observations and experimental work. As a consequence, there has not been much advancement of our understanding of island reproductive biology in the 25 yr since Carlquist's (1974) comprehensive book.

The Juan Fernández Archipelago or Robinson Crusoe Islands, in the southeastern Pacific Ocean at 33° latitude S, are a case in point. The Swedish botanist Carl Skottsberg (1928) was the first to study the pollination biology of endemic plants of this archipelago. There have been a few additions based on the study of single species (Sun et al., 1996; Bernardello et al., 1999; Anderson et al., 2000a) or brief comments as part of some broader study (Crawford et al., 1990; Ricci and Eaton, 1994). But, overall there has been little added in the seven decades since Skottsberg's work. These islands are one of the few regions in the world where humans did not settle prior to European maritime expansion during the 16th century (Woodward, 1969; Wester, 1991). The archipelago comprises three islands, all of volcanic origin: Isla Robinson Crusoe (= Masatierra) and tiny, mostly insignificant Isla Santa Clara to the east, 667 km west of continental Chile, and Isla Alejandro Selkirk (= Masafuera), 181 km farther west. Isla Robinson Crusoe has been dated at ~4 million yr old, Isla Alejandro Selkirk at 1–2.4 million yr old, and Santa Clara at 5.8 million yr old (Stuessy et al., 1984).

The native flora of the archipelago is, like the area of the islands (100.2 km²; Stuessy, 1995), small in number (156 flowering plant species; Marticorena, Stuessy, and Baeza, 1998). However, the archipelago contains a high level of endemic

¹ Manuscript received 3 January 2000; revision accepted 2 May 2000.

The authors thank the National Science Foundation, University of Connecticut Research Foundation, CONICET, SECYT-UNC, and CONICOR (Argentina) for support; the CONAF (Corporación Nacional Forestal, Chile) for help, especially CONAF Jefe on the Juan Fernández, I. Leiva; E. O. Wilson, C. Michener, M. Engel, H. Toro, and J. O'Donnell for insect identifications; M. Schlehofer and J. Hill for helping in many ways; and the Servicio Meteorológico from San Juan Bautista (Isla Robinson Crusoe). Valuable suggestions for improvement of the manuscript came from an anonymous reviewer, and the Nestor of island biology studies, Dr. Sherwin Carlquist.

³ Author for reprint requests.

vascular plants (~63%) including 11 genera and one family: Lactoridaceae (Stuessy et al., 1992, 1998a, b; Marticorena, Stuessy, and Baeza, 1998; Bernardello et al., 1999). In addition, the endemic species density is higher than any other oceanic island: 2.08 species/km². These species are of considerable importance because several species may provide basic elements in understanding evolution in certain groups (Stuessy et al., 1998a).

Many of these unique species have very few populations and, in several cases, even few individuals, surviving (Stuessy et al., 1998b). Furthermore, >50% of the endemics are threatened by human disturbance of the habitat, the historical and continued foraging by goats and rabbits, as well as the losses of habitat to aggressive introduced exotic weeds (Perry, 1984; Wester, 1991; Bourne et al., 1992; Stuessy et al., 1997). The native flora is also characterized by low fire tolerance and poor adaptation to herbivore resistance (Skottsberg, 1953), factors that taken together make many species especially vulnerable to human-induced disturbance. As a result, at least one of the endemic species has gone extinct during historical times (the native sandalwood, *Santalum fernandezianum*; Stuessy et al., 1997), and several others, with very few individuals, some not collected since the beginning of the century, are on the verge of disappearing. The importance of this flora and its level of endangerment are manifest by the Chilean government's designation of this archipelago as a National Park in 1935 and by the International Union for the Conservation of Nature in 1977 designating it as a World Biosphere Reserve, listed in their "most threatened" category (Wester, 1991).

The study of the reproductive biology of these plants, together with the analysis of their genetic variation (e.g., Crawford and Stuessy, 1987; Crawford, Stuessy and Silva, 1988; Crawford et al., 1990, 1992, 1993, 1994), provides data critical to their conservation. Both data sets are fundamental to the design of conservation programs that preserve the genetic potential of these endemic and endangered species (Hamrick et al., 1991; Holsinger, 1991; Holsinger and Gottlieb, 1991).

In the course of recent expeditions to Isla Robinson Crusoe, we conducted intensive field work on the reproductive biology of 25 endemic species of its flora, including *Robinsonia masafuerana* and *Nicotiana cordifolia* endemic to Isla Alejandro Selkirk. We recorded data on several aspects related to their breeding system: pollen and ovule number, pollen/ovule ratio, pollen size, compatibility, and pollination.

MATERIALS AND METHODS

Live specimens were studied and used for detailed analyzes of flowers and for experimental crosses in three field trips to Isla Robinson Crusoe (January 1991 and 1996, and December 1996/January 1997). In addition, alcohol-preserved buds and flowers were collected and vouchers were prepared and deposited at CONN (Anderson's specimens) or OS. Included in the Appendix is the complete list of material analyzed.

Flower shape—The structural flower classes of Faegri and van der Pijl (1979) were followed.

Pollen/ovule (P/O) ratio and pollen size—Buds and flowers were fixed in 70% ethanol. Buds examined for P/O ratios were near anthesis, so pollen was mature, but anthers had not dehisced. Pollen quantity was estimated using Anderson and Symon's (1989) modification of Lloyd's (1965) technique. A minimum of three buds per specimen were examined. With the aid of a dissecting microscope, all ovules were counted. Fifty pollen grains were measured to determine size, using the same slides prepared for pollen counts.

Experimental crosses—We carried out crosses during 1996 and 1997, either on naturally occurring populations or on plants grown in the experimental gardens of CONAF (Corporación Nacional Forestal, Chile) at San Juan Bautista, Isla Robinson Crusoe, the only permanent settlement in the archipelago. Given the relatively inaccessible habitat of many species, it was difficult to get to the plants, so some manipulations were limited. For these, we concentrated on experiments to test self-compatibility. Branches with buds were bagged with nylon net bags with 0.3 × 0.3 mm openings. Buds inside the bags were tagged and carefully emasculated. One or two days later, the field sites were revisited and self crosses were performed by applying pollen directly from recently opened anthers (using the anthers themselves as pollen applicators, except in *Wahlenbergia* spp. where we used the upper part of the styles covered with fresh pollen) onto stigmata of the same flower when possible, or onto receptive stigmata on other flowers of the same plant, in species determined to be dichogamous or monoecious. After 48 h, the field sites were visited a third time, and manipulated flowers were collected and fixed in 70% ethanol (for pollen tube assays). For other plants, flowers were left untouched until fruits were formed to determine seed production and to assess levels of self-compatibility.

Pollen tube growth—Gynoecia were softened with 8 mol/L NaOH for 1 h at 60°C in a water bath, rinsed, and stained in aniline blue-0.1 mol/L K₃PO₄ for 2 h (Martin, 1959). The gynoecia were dissected and flattened in glycerine on glass slides. Pollen tubes were examined with an epifluorescence microscope.

Floral visitors—A total of 17 populations were observed in the field for >300 h, during 1991, 1996, and 1997 in the sites given in the Appendix. Periods of observation ranged from 10 min to 1 h, all during daylight hours (from 0900 to 1600). We also observed flowers for 4 h, either at night or in the pre-dawn hours in the CONAF gardens in 1996 and 1997.

Seed germination—Seeds were placed in clean petri dishes lined with moistened Whatman number 1 filter paper and kept at 4°C for 14 d. They were regularly watered and their germination was recorded within a month after the experiment.

RESULTS

Flower form and color—The most common flower colors in the sampled species were white, green, and yellow, followed by red/pink and violet/purple (Table 1). Forty-four percent of the species had flowers >14 mm (either length or width), 32% ranged from 6 to 11 mm, and the remaining percentage (24%) had small flowers (<5 mm). The most frequent flower shape was dish (48%) followed by tube (24%), bell and inconspicuous flowers (12% each), and head (4%).

Gender distribution—Most species are hermaphroditic (56%), many are dioecious (24%), and fewer are monoecious, gynodioecious, or gynodioecious.

Pollen, ovules, and P/O ratio—In all species (Table 1), pollen size was comparatively small, falling within the range of anemophilous pollen (i.e., 20–60 μm). Only three species (*Rhaphithamnus venustus*, *Dendroseris nerifolia*, and *D. pruinata*) approached the upper size limit for the anemophilous category.

Pollen and ovule average numbers per flower are included in Table 1. Ovule numbers ranged from one (in all the Asteraceae and *Boehmeria excelsa*) to 447 in the *Wahlenbergia* hybrid (*W. fernandeziana* × *W. grahamiae*). Pollen quantity was determined from 2667 in *Robinsonia gracilis* to 144 300 in *Drimys confertifolia*.

In a now classic study, Cruden (1977) used pollen/ovule

TABLE 1. Floral features, experimental crosses, floral visitors, and likely pollination of selected Juan Fernández endemic plant species. Flower size is given as average length \times width of ten flowers; for the Asteraceae, the size is of the capitula. Pollen size is given as average of 50 grains measured. P/O = pollen/ovule ratio calculated from a minimum of three buds (assumes a total flower ratio of 1:1 for dioecious and monoecious species unless noted). In "Self crosses" column "%", indicates percentage of successful crosses as measured by either fruit set or pollen tubes reaching ovules, "n" the number of flowers used in each case; if no data are given, the tests were not performed. "Control flowers" = open pollinated flowers tested for natural pollen deposition and pollen tube growth ($n = 5$ flowers analyzed for each species), + = positive results, 0 = negative results. In the "Floral visitors" column, introduced insects are given within parentheses. Abbreviations for floral traits: D = dioecious, GM = gynomonoeocious, H = hermaphroditic, M = monoecious, PA = protandrous, PG = protogynous.

Species	Floral traits	Flower color	Flower size (mm)	Flower shape	Nectar	Pollen no. per flower	Ovule no. per flower	P/O	Pollen size (μm)	Self crosses		Con- trol flowers	Floral visitors	Likely pollination
										Fruit set	Pollen tubes			
Asteraceae														
<i>Dendroseris litoralis</i>	H, PA	orange	35 \times 40	dish	yes	8214	1	8214	40	55% ($n = 1574$)	80% ($n = 10$)	+	hummingbird	bird, selfer
<i>D. nerifolia</i>	H, PA	white	20 \times 25	dish	yes	4571	1	4571	52	0% ($n = 3478$)	0% ($n = 38$)	0	flies, moth	?
<i>D. pruinata</i>	H, PA	white	14 \times 14	dish	yes	7071	1	7071	52	0% ($n = 2639$)	0% ($n = 7$)	+	none	?
<i>Robinsonia evenia</i>	D	yellow	11 \times 7	dish	yes	3167	1	3167	22				none	wind
<i>R. guyana</i>	D	green/ yellow	4.5 \times 3	dish	yes	5500	1	5500	25				none	wind
<i>R. gracilis</i>	D	yellow	8 \times 5	dish	yes	2667	1	2667	21				none	wind
<i>R. masafuerae</i>	D	green	11 \times 9	dish	yes	4000	1	4000	21				none	wind
Berberidaceae														
<i>Berberis corymbosa</i>	H	yellow	6 \times 8	dish	yes	13500	4	3375	46	0% ($n = 6$)	0% ($n = 8$)	+	none	?
Campanulaceae														
<i>Wahlenbergia berteroi</i>	H, PA	pink	15 \times 7	bell	yes	33609	363	92	34	100% ($n = 5$)		+	fly (ant)	selfer, wind
<i>W. fernandeziana</i>	H, PA	carmine white	14 \times 11	dish	yes	31786	342	93	27	100% ($n = 5$)		+	moths (ant)	selfer
<i>W. fernandeziana</i> \times <i>W. grahamiae</i>	H, PA	white purple	14 \times 11	dish	yes	42889	447	96	27	100% ($n = 5$)		+	moth (ant, bee)	selfer
Ericaceae														
<i>Pernettya rigida</i>	D	white	8 \times 4	bell	yes	133429	109	1224 ^a	29			+	flies, beetle	wind
Euphorbiaceae														
<i>Dysoxys hirsuta</i>	M	green	2 \times 2	incons.	no	62492	3	2450 ^b	15			+	none	wind
Flacourtiaceae														
<i>Azara serrata</i> var. <i>fernandeziana</i>	H	yellow	4.3 \times 6	head	no	105850	137	769	11		70% ($n = 5$)		none	wind
Haloragaceae														
<i>Haloragis masaterrana</i>	H, PA	green	4.5 \times 7	dish	no	10333	4	2583	29		80% ($n = 10$)	+	none	wind
Lactoridaceae														
<i>Lactoris fernandeziana</i>	GM, PG	green	3.5 \times 3	incons.	no	11500	17.7	1339 ^c	37		♀ : 91% ($n = 90$), herm: 86% ($n = 33$)	+	none	wind

TABLE 1. Continued.

Species	Flower traits	Flower color	Flower size (mm)	Flower shape	Nectar	Pollen no. per flower	Ovule no. per flower	P/O	Pollen size (μm)	Self crosses		Control flowers	Floral visitors	Likely pollination
										Fruit set	Pollen tubes			
Lamiaceae														
<i>Cunila eriantha</i>	GM	violet	15 × 5	tube	yes	9833	4	1229 ^d	39				hummingbird	bird
Myrtaceae														
<i>Ugni selkirkii</i>	H	white	8 × 8	bell	yes	118033	72.3	1633	18		0	none	none	wind
Plantaginaceae														
<i>Plantago fernandezia</i>	H, PG	yellow-brown	5 × 2	tube	no	43500	2.5	17400	24	100% (n = 18)	+	none	none	wind
Rubiaceae														
<i>Coprosma oliveri</i>	D	green-brown	7 × 6	tube	no	43944	2	21972	31		+	none	none	wind
Saxifragaceae														
<i>Escallonia callcotiae</i>	H	red	15 × 5	tube	yes	122667	45	2726	18	60% (n = 70)	+	hummingbird, flies, moth	hummingbird, selfer, bird	
Solanaceae														
<i>Nicotiana cordifolia</i>	H, PA	dark red	24 × 4	tube	yes	85000	116	733	28	70% (n = 27)	+	hummingbird	hummingbird	bird
Urticaceae														
<i>Boehmeria excelsa</i>	M	green	1 × 1	incons.	no	116694	1	116694	27	100% (n = 10)	+	none	none	wind
Verbenaceae														
<i>Rhaphithamnus venustus</i>	GD, PA	purple	29 × 6	tube	yes	15500	4	3875	56	70% (n = 7)	+	hummingbird	hummingbird	bird
Winteraceae														
<i>Drimys confertifolia</i>	H, PG	white-yellow	4 × 23	dish	no	144300	114	1269	38	100% (n = 8)	0	none	none	wind

^a See Anderson et al. (2000a) for calculations.

^b Based on a 8.5:1 ratio of female:male flowers (see text).

^c See Bernardello et al. (1999); the calculations are complicated by gynodioecy.

^d For this gynodioecious species we assumed a 1:1 ratio for hermaphrodite:female flowers and calculated the P/O as P/2O.

TABLE 2. Insect visitors to Isla Robinson Crusoe plants. Collection numbers are those of G. J. Anderson. In each case only one individual insect was observed, except for the ants. The number in parentheses following the plant name indicates the number of individual plants observed. * = indicates the insect known to be introduced, ? = family not determined, NC = not collected, CONAF = Corporación Nacional Forestal gardens, San Juan Bautista.

Collection no.	Order	Family	Plant species	Site	Date	Pollen present on insect
96-6	Diptera	?	<i>Dendroseris neriifolia</i> (1)	CONAF	12 Jan 1996	little
96-7	idem	?	<i>D. neriifolia</i> (1)	CONAF	12 Jan 1996	little
96-8	idem	?	<i>Escallonia callcotiae</i> (4)	CONAF	12 Jan 1996	very little
91-1	idem	Syrphidae #1	<i>Libertia chilensis</i> (3)	Salsipuedes	15 Jan 1991	no
96-2	idem	Syrphidae #2	<i>Dendroseris neriifolia</i> (1)	CONAF	12 Jan 1996	yes
96-3	idem	idem	<i>D. neriifolia</i> (1)	CONAF	12 Jan 1996	little
96-4	idem	idem	<i>D. neriifolia</i> (1)	CONAF	12 Jan 1996	little
96-5	idem	idem	<i>D. neriifolia</i> (1)	CONAF	12 Jan 1996	little
96-13	idem	idem	<i>Pernettya rigida</i> (10)	Damajuana	12 Jan 1996	no
96-9	idem	Syrphidae #3	<i>P. rigida</i> (12)	Damajuana	12 Jan 1996	no
96-10	idem	idem	<i>P. rigida</i> (10)	Damajuana	12 Jan 1996	no
96-11	idem	idem	<i>P. rigida</i> (12)	Damajuana	12 Jan 1996	no
96-18	idem	idem	<i>Escallonia callcotiae</i> (4)	CONAF	20 Jan 1996	yes
96-12	Coleoptera	Cerambycidae	<i>Pernettya rigida</i> (11)	Damajuana	12 Jan 1996	no
96-15	Lepidoptera	Pyralidae, Phycitinae	<i>Wahlenbergia fernandeziana</i> (2)	Lighthouse	17 Jan 1996	no
96-16	Hymenoptera*	Formicidae ^a	<i>W. fernandeziana</i> (2)	Lighthouse	17 Jan 1996	no
96-17	idem	idem	<i>W. berteroi</i> (3)	Lighthouse	17 Jan 1996	no
96-7	Hymenoptera*	Halictidae ^b	<i>Wahlenbergia</i> hybrid (1)	CONAF	12 Jan 1996	no
96-20	idem	idem	<i>Wahlenbergia</i> hybrid (1)	CONAF	23 Jan 1996	very little
96-19	idem	idem	<i>Wahlenbergia</i> hybrid (1)	CONAF	20 Jan 1996	yes
NC	Diptera	?	<i>W. bertoi</i> (7)	Landing strip	31 Dec 1996	
NC	Lepidoptera	? (moth)	<i>W. fernandeziana</i> (2)	Lighthouse	17 Jan 1996	
NC	idem	idem	<i>Wahlenbergia</i> hybrid (1)	CONAF	24 Jan 1996	
NC	idem	idem	<i>Escallonia callcotiae</i> (4)	CONAF	24 Jan 1996	
NC	idem	idem	<i>Dendroseris neriifolia</i> (1)	CONAF	24 Jan 1996	
NC	Hymenoptera*	Formicidae	<i>Wahlenbergia</i> hybrid (1)	CONAF	10 Jan 1997	

^a *Linepithema humile* (Mayr).

^b *Lasioglossum* subgenus *Dialictus*.

ratios to make general estimates regarding breeding systems. It is clear from many subsequent analyses that these P/Os work best for comparisons within lineages. Nonetheless, P/Os are still useful first approximations. Thus, based on Cruden's P/O categories, most species in our study would be obligately (52%) or facultatively (36%) xenogamous, and a few facultatively autogamous (12%, the three *Wahlenbergia* taxa).

Floral visitors—Although some 68% of the species we studied had flowers that offer nectar as reward (Table 1), there are few floral visitors overall. And, in spite of records of a number of species, the total insect activity on flowers was very, very low (Table 2). Native insect pollinators are virtually absent. Both the ant and bee species are recent introductions and were observed in or near the single human settlement on the island, San Juan Bautista (Table 2). In >300 h of observation in three field trips, we detected a total of only 23 visits by apparently native insects (Table 2). They included about ten species of Diptera, Lepidoptera, and Coleoptera to seven plant species, which were mostly species with white flowers. Flies were the most common (4–5 spp., 13 visits), followed by moths and beetles. In addition to their rarity, the behavior displayed by the insect visitors was not characteristic of typical effective pollinators. The insects spent the majority of time on the leaves and stems, and most of the visits to flowers and within individual flowers seemed random, visiting other plant parts and inanimate objects with interest equivalent to that of flowers. This conclusion was supported by the general lack of pollen on the bodies of the insects (Table 2).

Hummingbirds, on the other hand, are essential, effective pollinators. Both sexes of two hummingbirds species, one native (*Sephanoides sephanioides*) and one endemic (*S. fernandezensis*), were observed actively taking nectar from five species (Table 3), and also protecting a feeding territory. The plant species from which they extract nectar have long tubular flowers with red, orange, violet, or purple corollas and are self-compatible (Table 1), except for *Cuminia eriantha* whose compatibility is unknown.

Breeding system and pollination—Sixteen taxa were tested for self-compatibility via pollen tube growth and/or seed set tests. Six others are dioecious, and for three others we were unable to obtain data (rare species or technical difficulties).

Self-incompatibility (SI)—Only three of the cosexual (hermaphroditic or monoecious) species were SI (19%; Table 1). Their P/O ratio (Table 1) implies they would be obligately xenogamous. In *Berberis corymbosa* pollen grains germinate on the stigmata, but pollen tubes do not grow beyond the stigmatic level. As is common in this genus, there is a mechanism through which the stamens automatically snap towards the stigma when touched or shaken by strong wind gusts. We never observed floral visitors on three cultivated specimens and in a natural population of ~20 plants. Thus, presumably, for this species where we observed no floral visitors, the "trip" mechanism contributes to stigmata clogging. In spite of this, we observed some naturally distributed pollen grains germinating in control flowers and seed set in the field.

TABLE 3. Hummingbird-visited plants on Isla Robinson Crusoe, arranged in alphabetical order by genus. The number(s) before the observation site indicate(s) the date of the observation and the number in parenthesis following indicates the number of plants observed. Observation time in each population was 10 min, except in the CONAF gardens, where observation time was 30 min.

Species	January 1991			January 1996			January 1997		
	15: Salsipuedes (3), 19: Vaquería (4)	3, 15: Corrales de Molina (3)	4, 12: Corrales de Molina (3); 11: Villagra (2); 16: El Camote (3)	2, 4, 6, 8, 14, 17, 19, 20, 21, 22, 25: CONAF gardens (5)	7: Pirámide (2); 24: Cerdón Central (2); 27: Pangal (3); 2, 4, 6, 8, 14, 17, 19, 20, 21, 22, 25: CONAF gardens (4)	1, 3, 5, 7, 9, 13, 17, 18: CONAF gardens (5)	1, 3, 5, 7, 9, 13, 17, 18: CONAF gardens (4); 7: Pirámide (3)	1, 3, 5, 7, 9, 13, 17, 18: CONAF gardens (8)	6: Mirador A. Selkirk (5); 11: Damajuana (3); 10: El Camote (3); 16: Corrales de Molina (4)
<i>Cumina eriantha</i> (Lamiaceae)									
<i>Dendroseris litoralis</i> (Asteraceae)	14, 16, 18, 20: CONAF gardens (5)								
<i>Escallonia callcottiae</i> (Saxifragaceae)	14, 16, 18, 20: CONAF gardens (4)								
<i>Nicotiana cordifolia</i> (Solanaceae)	14, 16, 18, 20: CONAF gardens (8)								
<i>Rhaphithamnus venustus</i> (Verbenaceae)	17: Mirador A. Selkirk (7); 14, 16, 18, 20: CONAF gardens (4)								

Two *Dendroseris* species (*D. pruinata*, *D. neriifolia*) also proved to be SI (Table 1). In these species, pollen germinates but tubes do not reach the ovules. In addition, seeds were not set in selfed flowers. Control flowers showed no pollen naturally distributed in *D. neriifolia*. Although we observed some insects visiting the flowers (Table 2), none behaved like effective pollinators. Quite the opposite was true for *D. pruinata*; we observed germinating pollen grains on stigmata, but recorded no visitors. However, studies of the natural seed set in *D. pruinata* showed that 79% of the 60 capitula scored had fruits with no seeds. The remaining 21% of the heads had very few full fruits, i.e., only 1–4 full fruits among 69–102 empty fruits per capitulum (total number of full fruits = 25 out of 5080 flowers, i.e., 0.5%). Germination tests of the few seeds set were positive, with a success rate of 65%.

Self-compatibility (SC)—The 13 (81%) remaining nondioecious species studied are SC (Table 1). Among the hermaphrodites (the most frequent category with ten spp.), two are homogamous, six protandrous, and two protogynous (Table 1).

Five taxa (three *Wahlenbergia*, *E. callcottiae*, and *D. litoralis*) are facultative selfers, all producing nectar as reward. In these, automatic self-pollination occurs in addition to the eventual cross-pollination. Two *Wahlenbergia* species (*W. berteroi* and *W. fernandeziana*) and one hybrid (*W. fernandeziana* × *W. grahamiae*) are facultatively autogamous according to Cruden's (1977) P/O categories. They are protandrous and have a system of secondary pollen presentation. As soon as the flower opens, in male phase, pollen is deposited onto a dense brush of collecting hairs located on the upper third of the style. After 2 d, the female phase begins when the three stigmatic branches unfold and reflex exposing their receptive papillate surfaces. As pollen continues to be present on the style (either held among pollen-collecting hairs or within the hair's basal cavities if they retract), male and female functions overlap at this stage. In *W. fernandeziana* and the hybrid, spontaneous selfing may occur late in the lifetime of a flower because the stigma branches recurve almost 360°, closely approaching or even touching the style and, thus, allowing autogamous pollen deposition. This is possible because at this stage pollen remains viable, as shown in bagging experiments (Anderson et al., 2000b). However, in *W. berteroi*, the degree of stigmatic recurvature is only ~ 200°–250°, which does not allow this type of autogamy. In this species there is a wind-aided mechanism of autogamy. Pollen grains deposited on the inner surface of the corolla throat by the pollen brush, while the corolla grows after flower opening, are gathered by the stigmatic lobes when shaken by the ever-present wind buffeting the exposed sea cliffs where *W. berteroi* grows. Visitation by insects is very rare for all taxa (Table 2). In addition to recently introduced bees and ants, we detected a few moths on the flowers of the hybrid and in *W. fernandeziana*. In all the *Wahlenbergia* taxa, seed set is variable, ranging from 21 to 188 seeds per flower. This circumstance may indicate that the level of autogamy is variable or it may simply be a manifestation of inbreeding depression.

The two other facultative selfers, *E. callcottiae* and *D. litoralis*, have a P/O ratio indicating obligate xenogamy. In contrast to *Wahlenbergia*, both species are frequently visited by hummingbirds (Table 3), which likely transfer the pollen. In addition, a few fly and moth visits were also recorded for *Escallonia* specimens planted at the CONAF gardens, but no visitors other than hummingbirds were ever observed on the

flowers of plants in situ (Table 3). The position of the globular stigma (very close to the anthers), its large size, and the fact that it is very humid and sticky, promote self-pollen deposition as soon as the flower opens. This system is apparently effective as we observed 100% fruit production from bagged flowers ($N = 20$ flowers). *Dendroseris litoralis*, as do many composites, may accomplish self-pollination when the stigmatic branches recurve back and touch residual pollen, if not removed in previous visits by hummingbirds, at the top of the anther tube. The natural seed set was relatively low: 53% ($N = 6$ capitula; mean seed number per capitulum = 262 ± 30 , range 208–293). Thus, both species have a mixed breeding system with different degrees of xenogamy and autogamy—including geitonogamy promoted by hummingbirds that we observed visiting several flowers of the same plant before going to the next plant.

The remaining SC species that are not facultative selfers can be divided into two groups: bird or wind pollinated. In the first group are *Nicotiana cordifolia* and *Rhaphithamnus venustus*. Both are frequently visited by hummingbirds seeking the abundant nectar in the flowers. Although SC, both species are herkogamous, and thus require pollen transfer because stigmata are normally located above the anthers. In addition, *R. venustus* is gynodioecious. The P/O ratio indicates facultative xenogamy for *Nicotiana* and obligate xenogamy for *Rhaphithamnus* (Cruden, 1977).

The anemophilous group is composed of six species. With the exception of the homogamous *Azara serrata* var. *fernandeziana*, the rest of the species displayed either temporal (dichogamy) or spatial (monoecy) separation of the sexes. Thus, they all require at least geitonogamous pollen transfer. We never recorded floral visitors for any of these species, and we thus conclude that they likely depend on the force of wind for pollen transfer. As expected, most of the species have inconspicuous green or brownish flowers with no floral reward and manifest several other characters suited for anemophily. For instance, *Plantago fernandezia*, hermaphroditic but strongly protogynous, has flowers with a small membranaceous corolla, large versatile anthers borne on long filaments, and pistils with feathery stigmas. The flowers of the monoecious *Boehmeria excelsa* have a short perianth, and the anthers dehisce explosively and simultaneously—releasing a puff of dry pollen. The large and feathery stigmas are appropriate for capture of wind-blown pollen. The P/O ratio is huge for this species, an order of magnitude larger than any of the others we studied. *Haloragis masatierrana* has small hermaphroditic protandrous flowers with large mobile anthers and feathery stigmata.

The protogynous and herkogamous “paleoherb” *Lactoris fernandeziana* is not a typical wind-pollinated species. Although it has several anemophilous features (e.g., reduced green perianth, relatively large stigmatic surface, dry pollen), other traits are less typical (e.g., low P/O, included anthers, stigma not feathery). However, bagging experiments demonstrated wind dispersal of pollen, but the protogyny, the inflorescence arrangement, and the pendant flower position combine to yield a geitonogamous system, with an opportunity for allogamy (Bernardello et al., 1999).

Azara serrata var. *fernandeziana* and *Drimys confertifolia* produce larger and more showy flowers. Careful observations failed to reveal any nectar or oil reward in either genus. We never observed insects or birds on any flowers of these species. Consequently, we postulate wind pollination (or apomixis) for both. In *Azara*, the stigmata are mostly located at the

same level as the anthers. This fact, together with the umbellate flower arrangement, suggests that selfing might take place when the branches are shaken by the wind. In the protogynous *Drimys*, the anthers open outward and liberate pollen tetrads onto the petals and even the leaves adjacent to inflorescences—as evidenced by large, obvious quantities of yellow pollen tetrads around inflorescences. In this way, pollen may reach the receptive stigmata of adjacent flowers in the many-flowered inflorescences.

Dioecy—Six species are dioecious. *Pernettya rigida* and *C. oliveri* are wind pollinated, and facultatively and obligately xenogamous, respectively, according to Cruden's P/O categories (1977). *Pernettya rigida* is cryptically dioecious, and recognition of the sex required careful flower analysis (Anderson et al., 2000a). It has several features facilitating wind pollen dispersal: the clustering of flowers at the end of branches, the nodding flower position, the poricidally dehiscent anthers, the small dry pollen tetrads with smooth exine, and dioecy itself. The longer and more curved pedicels of the male flowers seem to dispose flowers to agitation. Female flowers have traits like straighter pedicels, more exposed larger stigmata with longer papillae, that facilitate collection of airborne pollen. Furthermore, the 1:1 sex ratio (Anderson et al., 2000a) and the fact that individuals also reproduce vegetatively and grow in almost pure stands promotes pollen distribution by reducing the dispersal distance. *Coprosma oliveri* has clear characteristics implying wind pollination: small, green, inconspicuous flowers; long filaments; exposed anthers; dry, small pollen grains of the male flowers; and long, feathery, and exposed stigmata of the female flowers. The pollen quantity per flower is high. The very high P/O (assuming a 1:1 plant sex ratio, and equal number of flowers per plant) is also a strong indication of wind pollination.

As is typical, all the *Robinsonia* are dioecious. Their P/Os suggest obligate xenogamy (after Cruden, 1977). How pollination is accomplished in these species is not well understood. Their capitula are yellow or green and flowers seem to have nectar, but in many seasons of study (our data; Stuessy and Crawford, personal observation) no floral visitors have ever been recorded. Thus, we postulate wind pollination.

Unknown compatibility: For three species, we could not obtain sufficient data on their breeding system. The rare gynodioecious *Cuminia eriantha* has tubular pink flowers that produce abundant nectar, and their P/O ratio suggests facultative xenogamy (Cruden, 1977). Flowers are frequently visited by hummingbirds (Table 3), likely the pollinators, transferring pollen from hermaphroditic to female flowers and perhaps within the same flower if the species is SC.

In *Dysopsis hirsuta* and *Ugni selkirkii* (both facultatively xenogamous based on P/Os), wind seems to be the pollen distributor. The common, and apparently clonal, monoecious *D. hirsuta* grows in the shady understory of the forests carpeting many square metres. We found that there are more female flowers open on a plant at any given time than male flowers (8.5:1, in 426 plants scored from 17 populations). Male flowers with long mobile filaments are raised above the leaves and have anthers with explosive dehiscence and dry pollen, thus yielding airborne pollen. Female flowers are usually held below the leaves and have comparatively long stigmata suitable to collect pollen. We attempted many crosses on plants of this species, but all failed—presumably because of the apparently delicate nature of these small, tender, woodland herbs.

Although flowers on the very rare *U. selkirkii* are white and near 1 cm long, they have no nectar and we observed no visitors. However, we detected abundant pollen on petals and on leaves surrounding the flowers. This fact suggests that pollen can be wind dispersed at least over small distances, as is the case, we believe, for the widespread, introduced congener, *U. molinae*, that releases clouds of pollen when the branches are disturbed. The individuals of *U. selkirkii* are rare in the field, but grow in close groups of 4–5 plants, so wind can disperse pollen at least within the very small populations left of this species.

Overall, 52% of the taxa we studied are SC, 12% SI, and 24% dioecious. Regarding the pollination systems observed or presumed, most of the species are wind pollinated (60%) or hummingbird pollinated (20%), even if they are SC. A smaller number are purely autogamous (8%). The remaining percentages are still unknown, but probably wind pollinated.

DISCUSSION

Flower features—The general paradigm is that island angiosperms are characterized by small inconspicuous flowers that have a low percentage of showy, bright colors (Wallace, 1895; Carlquist, 1974). This trend is particularly remarkable in the flora of New Zealand (Lloyd, 1985; Webb and Kelly, 1993). In the sample of the Juan Fernández flora we have studied in detail, the most frequent flower colors are comparatively dull, and flowers are mostly small or medium-sized. And, as Carlquist (1974) pointed out for islands in general, simple bowl-shaped corollas are an accurate characterization for the Juan Fernández as well. Thus, the general color, size, and shape trends for island floras hold for the Juan Fernández archipelago.

As is typical for angiosperms, as well as for islands (Carlquist, 1974), hermaphroditic flowers are the most prevalent in this Juan Fernández sample. However, many of the hermaphrodites are characterized by temporal separation of the sexes (dichogamy; mostly protandry). Less frequent is the spatial separation of the sexes by herkogamy. The high percentage of dioecy (24%) in the species we studied here is not representative of the flora as a whole, which includes ~ 9% dioecy (Anderson et al., 2000a).

The P/O ratios, in general, agree with conclusions about the breeding systems implied from other floral features and from our field observations. For instance, a dioecious species like *P. rigida* should be xenogamous (though facultatively xenogamous based on Cruden's [1977] generalizations). However, there are some noteworthy exceptions. For instance, two facultative selfers (*E. callcottiae* and *D. litoralis*) would be considered obligately xenogamous based on Cruden's (1977) categories. Both of these species are bird pollinated, but that would not offer an explanation for the high P/Os. Likely the self-compatibility is the "anomaly" representing the retention of the kind of breeding system often necessary for the establishment of island colonizers (see more below). The P/Os of several other SC species are high (also facultative xenogamous), but these species on the archipelago are wind pollinated, so the higher P/O may be associated with that less efficient mode of pollen transfer. Alternatively, the P/O and other elements of the reproductive system for that matter, may not be congruent with extant pollination or reproductive system because there has not been sufficiently intense pressure, or time, to select new states; thus, the ancestral conditions, per-

haps "vestigial" features, might be retained. A particularly good example of this are the several nectar-producing species that are wind pollinated (Bernardello, Galeto, and Anderson, 2000).

Breeding system—"Baker's law" (Baker, 1955, 1967; Stebbins, 1957) suggests that the species most likely to become established after long-distance dispersal are self-compatible. Although comprehensive surveys of the compatibility status of island plants are, at present, rudimentary (Barrett, 1998), there are ample data to support this hypothesis (cf. Rick, 1966; Carlquist, 1974; Pandey, 1979; McMullen, 1987, 1990; Webb and Kelly, 1993). Our results show that this trend is also supported for the Juan Fernández; more than 80% are SC.

In addition, three SI species were detected, and several are dioecious. S. Carlquist has suggested (personal communication) that these exceptions to the general tendency might actually be the more interesting to study. The ancestors of the endemic genus *Dendroseris* are proposed to have been SI, based on the common condition among its extant closest relatives (Crawford et al., 1998). Two of the three species we tested were SI. The third, *D. litoralis*, is SC. The only other SI species is in *Berberis*, a genus for which some South American species are SI and others SC (Riveros, 1991).

Several dioecious species were also included. The sexual status of *Pernettya rigida* was a surprise and required careful anatomical, morphological, and experimental studies to clarify. That is because all the flowers are complete on all plants, but the species is functionally dioecious (Anderson et al., 2000a). The first colonists of *Pernettya* are suspected to have been cryptically dioecious (as are some closely related species; Anderson et al., 2000a). The dioecy in *Robinsonia* also seems to have arisen in situ, perhaps from SI ancestors, as suggested by Crawford et al. (1998). In contrast, almost all the species of *Coprosma* known are dioecious (Oliver, 1935). Thus, we presume that the original colonists that eventually led to *C. oliveri* were also dioecious. Skottsberg (1921) pointed out that although *C. oliveri* (as *C. triflorum*) is generally dioecious, a number of bisexual flowers on a branch of one female tree were found; as a consequence, this tree species was cited by Baker and Cox (1984) as a case of leaky dioecy. However, subsequently neither Fosberg (1968) nor we have detected any hermaphroditic flowers. Thus, the observation by Skottsberg (1921) seems to be exceptional for the species.

Visitors and pollination—Even though SC is very common, autogamy is not; pollen transfer is still required for several species (e.g., dichogamous or herkogamous species, as well as dioecious and monoecious species). In general, islands bear proportionately fewer animal species than their source continents (MacArthur and Wilson, 1967). Similarly, the pollinator faunas on islands are often smaller as well, with many continental groups of pollinators completely absent (Carlquist, 1974; McMullen, 1990; Howarth and Mull, 1992). The Fernandezian insect fauna is small in general (cf. Kuschel, 1952; Wilson, 1973) and is notably lacking species dedicated to floral visits (Skottsberg, 1928; Bernardello et al., 1999; Anderson et al., 2000a). In addition to their scarcity, the few insect floral visitors we recorded showed a lack of floral acumen (visiting corollas, even leaves and other plant parts with equal interest to stamens and nectaries), and very low or no fidelity to flowers in general (our data; Anderson et al., 2000a).

The Juan Fernández archipelago is particularly rich in bird

pollination. This little, isolated archipelago possess the only two known hummingbirds on oceanic islands (Colwell, 1989)—and one of them is an endemic. The plant species on which we observed hummingbirds were well known previously (Brooke, 1987; Meza, 1988; Colwell, 1989), all have abundant nectar, and a floral structure suited to hummingbird pollination. For example, *R. venustus* is a major source of nectar both because of its extensive flowering period and the large amount of nectar it produces.

Thornton (1971) and Carlquist (1974) have suggested that there is a higher frequency of anemophily on islands. Six of the 25 species we studied are clearly wind-pollinated (*Boehmeria excelsa*, *Coprosma oliveri*, *Dysopsis hirsuta*, *Haloragis masatierrana*, *Lactoris fernandeziana*, and *Plantago fernandezia*). Furthermore, we conclude, based on the absence of native insect pollinating groups (e.g., bees, wasps, lepidopterans), and on the lack of observation of insects visiting flowers in hundreds of person-hours in the field, that wind pollination is a significant feature in the reproductive biology of this flora. This is anemophily by default in a sense. Anemophily for a portion of the flora is expected given the ancestors; for many other species, the lack of alternatives has led to wind-activated pollen dispersal. Similar arguments have been made for elements of the continental flora isolated to habitats with little insect pollinator service (e.g., Berry and Calvo, 1989). Hagerup (1932, 1951) has reported instances where the rarity and inactivity of insects seemed to result in selfing, anemophily, or even rain pollination. Ehrendorfer (1979) proposed that the higher frequency of anemophily comes as a consequence of preadaptation of anemophilous species to island establishment.

On the other hand, McMullen (1987, 1990) indicated that floral morphology conducive to wind pollination is rarely encountered in the Galápagos Islands (also see Barrett, 1998). A subsequent study (McMullen and Close, 1993) analyzing the amount of airborne pollen produced by six species suggested that it was not of a magnitude sufficient for wind pollination. However, detailed study of the reproductive biology of the Galápagos has only included ~10–15% of the native flora to date.

Our data on the Juan Fernández plants show that a number of the anemophilous species lack the full suite of characters (Regal, 1982; Whitehead, 1983) that are typically associated with wind pollination. Thus, the floral morphology does not always give a precise indication of the pollination mode. Instead, the floral features many times may reflect retention of elements of the reproductive system of the progenitor of the island species. These features are expressed (as cited above for P/Os) perhaps because there has been relatively little time for evolution to modify the ancestral characters, or because there has been relatively little selection against ancestral traits. Relatively few species colonize islands, so that successful colonizers may move into new niches, both ecologically and evolutionarily. And, with fewer competitors (*vis-à-vis* continents), unusual forms (e.g., the habit of *Dendroseris* on the Juan Fernández) may be expressed (e.g., Carlquist, 1974), or ancestral conditions may persist because of lack of selection against them. Thus, the wind pollination of species may not be as obvious. More extensive studies of the pollination biology of floras, like the Galápagos, may reveal anemophily for species where the morphology would not have precluded it.

Diocely, in particular, has been associated with wind pollination in several floras (e.g., Conn, Wentworth, and Blum, 1980; Freeman, Harper, and Ostler, 1980; Muenchow, 1987;

Steiner, 1988), including the Hawaiian flora (Sakai et al., 1995). We studied six dioecious species, all of which are likely wind pollinated. However, only *Coprosma oliveri* has floral characters obviously and fully suited to anemophily. *Pernettya rigida*, although wind pollinated is intermediate in some ways. It combines a number of features facilitating wind pollination and vestigial features of a former entomophilous system (Anderson et al., 2000a). There is evidence of a similar combination of derived and ancestral characters in a continental species (*P. mucronata*; Arroyo and Squeo, 1987). *Robinsonia* species seem to be wind pollinated, although they express entomophilous (presumably vestigial) features as well. Additional studies are required in this composite genus to be certain of the current pollination of its species.

Self-crossing also is expected to be favored in situations where pollinators are scarce (Baker, 1955; Jain, 1976; Inoue, 1990; Jarne and Charlesworth, 1993), as is often the case on islands (e.g., Strid, 1970; Barrett, 1988, 1998). Some 26 of the 29 native and endemic species studied on the Galápagos by McMullen (1987, 1990) showed some degree of automatic self-pollination. But in the Juan Fernández, our data revealed few autogamous species. Even though a very large percentage of the species are SC, 48% have herkogamous or dichogamous mechanisms to promote outcrossing. Nevertheless, geitonogamy and, thus, selfing would be the most frequent mechanism of pollen transfer among the Fernandezian species. Geitonogamy is probably the most widespread mode of self-pollination, virtually inevitable in SC plants that produce a number of flowers at anthesis at the same time (Lloyd and Schoen, 1992). In another archipelago, the Faroes Islands, Hagerup (1951) pointed out that species with large inflorescences tended to be geitonogamous. However, Lloyd (1992) pointed out that most cosexual SC species may be unable to avoid mixed mating—as would most likely occur in all the SC hummingbird-pollinated species on the Juan Fernández Islands.

Conservation biology—Proportionally, there are many more recorded extinctions of vascular plants from islands vs. those from continental areas (Reid and Miller, 1989). Thus, it is not unreasonable to invest extra effort in protecting island species. Conservation or restoration programs cannot be effective without an understanding of breeding systems and pollination (Hamrick et al., 1991; Karron, 1991; Weller, 1994). Without it, the programs may well fail. In addition, these data are fundamental to achieving the most accurate interpretation of the molecular data on genetic diversity. Conservation comments on the different species studied follow, with the exception of *Lactoris*, *Pernettya*, and *Wahlenbergia*, taxa already discussed elsewhere (Bernardello et al., 1999; Anderson et al., 2000a, b).

Even though insect pollinators are virtually absent, wind pollination serves for most of the species and, pollen transfer, at some level, seems not to be a problem. Nevertheless, the majority of the anemophilous species lack some features that would make wind pollination most effective (Regal, 1982; Whitehead, 1983). Among these, one is very important for conservation purposes: close proximity of conspecifics, i.e., relatively close spacing of compatible plants. The current status of the invasives and the continuous foraging by goats and rabbits (Stuessy et al., 1997, 1998b) are significantly reducing and separating the already small populations of many species. As Weller (1994) pointed out, wholesale destruction of natural areas may have contributed far more to rarity than have evo-

lutionary inadequacies of plant breeding systems or pollination biology. The intrusion of invasives also exacerbates this situation. The pollination systems of island plants are fragile, and habitat changes may yield reduced rates of the already insufficient pollination, obviously with negative consequences for maintenance of populations and species.

There is special concern for the SI and dioecious species. For instance, in SI *Dendroseris neriifolia* (only three individuals in the wild in Quebrada Lápez [Stuessy et al., 1998b] plus a few individuals cultivated at CONAF), examination of open-pollinated flowers on cultivated individuals showed no pollen grains on stigmata or pollen tubes in styles, i.e., no natural pollination. And the natural seed set of the small cultivated (at CONAF) population of the SI *D. pruinata* was extremely low. Thus, in both instances, at least in part because of the reproductive system (coupled with rarity), the species are at severe risk of extinction in the near future if the existing very few individuals are not carefully protected and the pollination/reproduction not enhanced. A number of individuals of SI plants must be maintained for the species to reproduce sexually.

The ultimate fate of many species may depend on preserving their mutualistic relationships with pollinators and with the web of organisms that affect both plant and pollinator (Kearns, Inouye, and Waser, 1998). In the Juan Fernández Islands, that means that the plant-hummingbird relationship has to be preserved. In this instance as well, the density of conspecifics is very important to favor higher levels of interplant pollen transfer. This is another place where invasives can pose a serious risk. The recent population growth of some invasives on Isla Robinson Crusoe that produce nectar and that are visited by hummingbirds (Brooke, 1987; Colwell, 1989) may lead to a reduced visitation rate to the rare endemic species and, subsequently, to reduced pollination. The hummingbird-pollinated *Nicotiana cordiflora* is endemic to Isla Alejandro Selkirk where the endemic hummingbird (*S. fernandensis*) is considered now extinct, although inaccessible parts of this island may still be refuge for some individuals (Brooke, 1987; Colwell, 1989). Fortunately for the ornithophilous plant species, the native hummingbird (*S. sephaniodes*) has become established on Isla Alejandro Selkirk since about 1981, although it is not clear if they are a breeding population or only adventives from Isla Robinson Crusoe (Brooke, 1987; Colwell, 1989). Thus, either species of hummingbird is important for the reproduction of *N. cordifolia*. Unfortunately, the goat-maintained grassland of the island's lower slopes, largely composed of introduced species, and the native fern forest of the uplands combine to render Isla Alejandro Selkirk most unpromising hummingbird habitat (Brooke, 1987). So, in order to maintain this plant-animal interaction, the introduced goats should be eliminated and the native habitats restored. The interaction of hummingbirds with *Dendroseris litoralis* is also crucial to be maintained. This species is known presently only from several plants on Morro Spartan and the adjacent Santa Clara and hence is nearly extinct in the wild; fortunately it is extensively cultivated on Isla Robinson Crusoe (Stuessy et al., 1998b).

A recently introduced small halictid bee (Engel, unpublished data) is considered irrelevant in the evolution of the reproductive systems (Anderson et al., unpublished data). However, it may be important in the future conservation or restoration programs on the island. The bees, scarce at present, were observed collecting pollen only on the *Wahlenbergia* hybrid (Anderson et al., 2000b). Although introduced, they could become beneficial for promotion of allogamy for these and

other species as well, if present in sufficient numbers. Given the lack of significant native insect fauna, these bees would not seem to pose a competitive danger; they will displace no native pollinator fauna. However, just as the more common continental species of hummingbird may be responsible for the decline of the endemic species (Colwell, 1989), the introduced bees might outcompete the hummingbirds for floral nectar and have a negative effect on the vigor of this important class of vertebrate pollinators—and the sentinel animal species of the famous Juan Fernández/Robinson Crusoe Islands.

LITERATURE CITED

- ADSRSEN, H. 1995. Research on islands; classic, recent, and prospective approaches. In P. M. Vitousek, L. L. Loope, and H. Adersen [eds.], Islands: biological diversity and ecosystem function. *Ecological Studies* 115: 7–22.
- ANDERSON, G. J. 1995. Systematics and reproductive biology. In P. C. Hoch and A. G. Stephenson [eds.], Experimental and molecular approaches to plant biosystematics. *Monographs in Systematic Botany* 53: 263–272.
- , G. BERNARDELLO, P. LOPEZ S., T. F. STUESSY, AND D. J. CRAWFORD. 2000a. Dioecy and wind pollination in *Pernettya rigida* (Ericaceae) of the Juan Fernández Islands. *Botanical Journal of the Linnean Society* 132: 121–141.
- , D. J. CRAWFORD, AND T. F. STUESSY. 2000b. Reproductive biology of *Wahlenbergia* (Campanulaceae) endemic to Robinson Crusoe Island (Chile). *Plant Systematics and Evolution* 223: 109–123.
- , AND D. E. SYMON. 1989. Functional dioecy and andromonoecy in *Solanum*. *Evolution* 43: 204–219.
- ARROYO, M. T. K., AND F. A. SQUEO. 1987. Experimental detection of anemophily in *Pernettya mucronata* (Ericaceae) in western Patagonia, Chile. *Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie* 108: 537–546.
- BAKER, H. G. 1955. Self-compatibility and establishment after “long-distance” dispersal. *Evolution* 9: 347–349.
- . 1967. Support for Baker's law—as a rule. *Evolution* 21: 853–856.
- , AND P. A. COX. 1984. Further thoughts on dioecism and islands. *Annals of the Missouri Botanical Garden* 71: 244–253.
- BARRETT, S. C. H. 1988. The evolution, maintenance, and loss of self-incompatibility systems. In J. L. Doust and L. L. Doust [eds.], Plant reproductive ecology, 98–124. Oxford University Press, New York, New York, USA.
- . 1998. The reproductive biology and genetics of island plants. In P. R. Grant [ed.], Evolution on islands, 18–34. Oxford University Press, Oxford, UK.
- BERNARDELLO, G., G. J. ANDERSON, P. LOPEZ S., M. A. CLELAND, T. F. STUESSY, AND D. J. CRAWFORD. 1999. Reproductive biology of *Lactoris fernandeziana* (Lactoridaceae). *American Journal of Botany* 86: 829–840.
- , L. GALETTO, AND G. J. ANDERSON. 2000. Floral nectary structure and nectar chemical composition of some species from Robinson Crusoe Island (Chile). *Canadian Journal of Botany* 78: 862–872.
- BERRY, P. E., AND R. N. CALVO. 1989. Wind pollination, self-incompatibility, and altitudinal shifts in pollination systems in the high Andean genus *Espeletia* (Asteraceae). *American Journal of Botany* 76: 1602–1614.
- BOURNE, W. R. P., M. DE L. BROOKE, G. S. CLARKE, AND T. STONE. 1992. Wildlife conservation problems in the Juan Fernandez Archipelago, Chile. *Oryx* 26: 43–51.
- BROOKE, M. DE L. 1987. The Birds of the Juan Fernandez Islands, Chile in International Council for Bird Preservation Fauna and Flora Preservation Society World Wildlife Fund. Cambridge, UK.
- CARLQUIST, S. 1974. Island biology. Columbia University Press, New York, New York, USA.
- COLWELL, R. K. 1989. Hummingbirds of the Juan Fernández Islands: natural history, evolution and population status. *Ibis* 131: 548–566.
- CONN, J. S., T. R. WENTWORTH, AND U. BLUM. 1980. Patterns of dioecism in the flora of the Carolinas. *American Midland Naturalist* 103: 310–315.
- CRAWFORD, D. J., T. SANG, T. F. STUESSY, S.-C. KIM, AND M. SILVA O. 1998. *Dendroseris* (Asteraceae: Lactuceae) and *Robinsonia* (Asteraceae: Senecioneae) on the Juan Fernandez Islands: similarities and differences

- in biology and phylogeny. In T. F. Stuessy and M. Ono [eds.], *Evolution and speciation of island plants*, 97–119. Cambridge University Press, Cambridge, UK.
- , AND T. F. STUESSY. 1987. Allozyme divergence and the evolution of *Dendroseris* (Compositae:Lactuceae) on the Juan Fernandez Islands. *Systematic Botany* 12: 435–443.
- , ———, M. B. COSNER, D. HAINES, D. WEINS, AND P. PEÑAILLO. 1994. *Lactoris fernandeziana* (Lactoridaceae) on the Juan Fernandez Islands: allozyme uniformity and field observations. *Conservation Biology* 8: 277–280.
- , ———, D. W. HAINES, M. B. COSNER, M. SILVA O., AND P. LOPEZ. 1992. Allozyme diversity within and divergence among four species of *Robinsonia* (Asteraceae: Senecioneae), a genus endemic to the Juan Fernandez Islands, Chile. *American Journal of Botany* 79: 962–966.
- , ———, T. G. LAMMERS, M. SILVA O., AND P. PACHECO. 1990. Allozyme variation and evolutionary relationships among three species of *Wahlenbergia* (Campanulaceae) in the Juan Fernandez Islands. *Botanical Gazette* 151: 119–124.
- , ———, R. RODRIGUEZ, AND M. RONDINELLI. 1993. Genetic diversity in *Rhaphithamnus venustus* (Verbenaceae), a species endemic to the Juan Fernandez Islands. *Bulletin of the Torrey Botanical Club* 120: 23–28.
- , ———, AND M. SILVA O. 1988. Allozyme variation in *Chenopodium sanctae-clarae*, an endemic species of the Juan Fernandez Islands, Chile. *Biochemical Systematics and Ecology* 16: 279–284.
- CRUDEN, R. W. 1977. Pollen ovule ratios: a conservative indicator of breeding systems in flowering plants. *Evolution* 31: 32–46.
- EHRENDORFER, F. 1979. Reproductive biology in island plants. In D. Bramwell [ed.], *Plants and islands*, 293–306. Academic Press, London, UK.
- FAEGRI, K., AND L. VAN DER PIJL. 1979. *The principles of pollination ecology*, 3rd revised ed. Pergamon Press, Oxford, UK.
- FOSBERG, F. R. 1968. Studies in pacific Rubiaceae: VI–VIII. *Brittonia* 20: 287–294.
- FREEMAN, D. C., K. T. HARPER, AND W. K. OSTLER. 1980. Ecology of plant dioecy in the intermountain region of Western North America and California. *Oecologia* 44: 410–417.
- HAGERUP, O. 1932. On pollination in the extremely hot air in Timbuctu. *Dansk Botanisk Arkiv* 8: 1–20.
- . 1951. Pollination in the Faroes in spite of rain and poverty in insects. *Danske Biologiske Meddelelser* 18: 1–48.
- HAMRICK, J. L., M. J. W. GODT, D. A. MURRAWSKI, AND M. D. LOVELESS. 1991. Correlations between species traits and allozyme diversity: implications for conservation biology. In D. A. Falk and K. E. Holsinger [eds.], *Genetics and conservation of rare plants*, 75–86. Oxford University Press, New York, NY.
- HOLSINGER, K. E. 1991. Conservation of genetic diversity in rare and endangered plants. In E. C. Dudley [ed.], *The unity of evolutionary biology*, 626–633. Dioscorides Press, Portland, Oregon, USA.
- , AND L. D. GOTTLIEB. 1991. Genetics and conservation of rare plants. In D. A. Falk and K. E. Holsinger [eds.], *Genetics and conservation of rare plants*, 195–208. Oxford University Press, New York, New York, USA.
- HOWARTH, F. G., AND W. P. MULL. 1992. *Hawaiian insects and their kin*. University of Hawaii Press, Honolulu, Hawaii, USA.
- INOUE, K. 1990. Evolution of mating systems in islands populations of *Campanula microdonta*: pollinator availability hypothesis. *Plant Species Biology* 5: 57–64.
- JAIN, S. K. 1976. The evolution of inbreeding in plants. *Annual Review of Ecology and Systematics* 7: 469–495.
- JARNE, P., AND D. CHARLESWORTH. 1993. The evolution of the selfing rate in functionally hermaphrodite plants and animals. *Annual Review of Ecology and Systematics* 24: 441–466.
- KARRON, J. D. 1991. Patterns of genetic variation and breeding systems in rare plant species. In D. A. Falk and K. E. Holsinger [eds.], *Genetics and conservation of rare plants*, 87–98. Oxford University Press, New York, New York, USA.
- KEARNS, C. A., D. W. INOUE, AND N. WASER. 1998. Endangered mutualisms: the conservation of plant pollinator interactions. *Annual Review of Ecology and Systematics* 29: 83–112.
- KUSCHEL, G. 1952. Los insectos de las islas Juan Fernández. *Introducción. Revista Chilena de Entomología* 2: 3–6.
- LLOYD, D. G. 1965. Evolution of self-compatibility and racial differentiation in *Leavenworthia* (Cruciferae). *Contributions of the Gray Herbarium, Harvard University* 195: 1–134.
- . 1985. Progress in understanding the natural history of New Zealand plants. *New Zealand Journal of Botany* 23: 707–722.
- . 1992. Self- and cross-fertilization in plants. II. The selection of self-fertilization. *International Journal of Plant Science* 153: 370–380.
- , AND D. J. SCHOEN. 1992. Self- and cross-fertilization in plants. I. Functional dimensions. *International Journal of Plant Science* 153: 358–369.
- MACARTHUR, R. H., AND E. O. WILSON. 1967. *The theory of island biogeography*. Monographs of population biology. Princeton University Press, Princeton, New Jersey, USA.
- MARTICORENA, C., T. F. STUESSY, AND C. M. BAEZA. 1998. Catalogue of the vascular flora of the Robinson Crusoe or Juan Fernández Islands, Chile. *Gayana Botanica* 55: 187–211.
- MARTIN, F. W. 1959. Staining and observing pollen tubes in the style by means of fluorescence. *Stain Technology* 34: 125–128.
- MC MULLEN, C. K. 1987. Breeding systems of selected Galapagos Islands angiosperms. *American Journal of Botany* 74: 1694–1705.
- . 1990. Reproductive biology of Galapagos Islands angiosperms. *Monographs in Systematic Botany* 32: 35–45.
- , AND D. D. CLOSE. 1993. Wind pollination in the Galapagos Islands. *Noticias de Galápagos* 52: 12–17.
- MEZA H. J. 1988. Conservación del picaflor de Juan Fernández, Informe anual. CONAF, V Región, Chile.
- MUENCHOW, G. E. 1987. Is dioecy associated with fleshy fruit? *American Journal of Botany* 74: 287–293.
- OLIVER, W. R. 1935. The genus *Coprosma*. *Bernice P. Bishop Museum Bulletin* 132: 1–207.
- ORNDUFF, R. 1969. Reproductive biology in relation to systematics. *Taxon* 18: 121–133.
- PANDEY, K. K. 1979. Long-distance dispersal and self-incompatibility. *New Zealand Journal of Botany* 17: 225–226.
- PERRY, R. 1984. Juan Fernandez Islands: a unique botanical heritage. *Environmental Conservation* 11: 72–76.
- REGAL, P. J. 1982. Pollination by wind and animals: ecology of geographic patterns. *Annual Review of Ecology and Systematics* 13: 497–524.
- REID, W. V., AND K. R. MILLER. 1989. Extinction: how serious a threat? In W. V. Reid and K. R. Miller [eds.], *Keeping options alive: the scientific basis for conserving biodiversity*, 31–56. World Resources Institute, Washington, D.C., USA.
- RICCI, M., AND L. EATON. 1994. The rescue of *Wahlenbergia larrainii* in Robinson Crusoe Island, Chile. *Biological Conservation* 68: 89–93.
- RICK, C. M. 1966. Some plant-animal relations on the Galápagos Islands. In R. I. Bowman [ed.], *The Galápagos*, 215–224. University of California Press, Berkeley, California, USA.
- RIVEROS, M. 1991. *Biología reproductiva en especies vegetales de dos comunidades de la zona templada del sur de Chile*. Ph.D. thesis, Facultad de Ciencias, Santiago, Chile.
- SAKAI, A. K., W. L. WAGNER, D. M. FERGUSON, AND D. R. HERBST. 1995. Biogeographical and ecological correlates of dioecy in the Hawaiian flora. *Ecology* 76: 2530–2543.
- SKOTTSBERG, C. 1921. The Phanerogams of the Juan Fernandez Islands. In C. Skottsberg [ed.], *The natural history of the Juan Fernandez and Easter Islands*, vol. 2, Botany, 95–240. Almqvist & Wiksell, Uppsala, Sweden.
- . 1928. *Pollinationsbiologie und Samenverbreitung auf den Juan Fernandez Inseln*. In C. Skottsberg [ed.], *The natural history of the Juan Fernandez and Easter Islands*, vol. 2, Botany, 503–547. Almqvist & Wiksell, Uppsala, Sweden.
- . 1953. A supplement to the pteridophytes and phanerogams of Juan Fernandez and Easter Island. In C. Skottsberg [ed.], *The natural history of the Juan Fernandez and Easter Islands*, vol. 2, Botany, 763–792. Almqvist & Wiksell, Uppsala, Sweden.
- STEBBINS, G. L. 1957. Self-fertilization and population variability in the higher plants. *American Naturalist* 41: 337–354.
- STEINER, K. E. 1988. Dioecism and its correlates in the Cape flora of South Africa. *American Journal of Botany* 75: 1742–1754.
- STRID, A. 1970. Studies in the Aegean flora. XVI. Biosystematics of the *Nigella arvensis* complex. *Opera Botanica* 28: 1–169.
- STUESSY, T. F. 1995. Juan Fernandez Islands, Chile. In S. D. Davis, V. H. Heywood, and A. C. Hamilton [eds.], *Centres of plant diversity: a guide*

- and strategy for their conservation, vol. 2, 565–568. World Wide Fund for Nature and IUCN—the World Conservation Union, Cambridge, UK.
- , D. J. CRAWFORD, C. MARTICORENA, AND M. SILVA O. 1998a. Isolating mechanisms and modes of speciation in endemic angiosperms of the Juan Fernandez Islands. *In* T. F. Stuessy and M. Ono [eds.], *Evolution and speciation of island plants*, 79–96. Cambridge University Press, Cambridge, UK.
- , K. A. FOLAND, J. F. SUTTER, R. W. SANDERS, AND M. SILVA O. 1984. Botanical and geological significance of Potassium-Argon dates from the Juan Fernandez Islands. *Science* 225: 49–51.
- , C. MARTICORENA, R. RODRÍGUEZ R., D. J. CRAWFORD, AND M. SILVA O. 1992. Endemism in the vascular flora of the Juan Fernandez Islands. *Aliso* 13: 297–307.
- , U. SWENSON, D. J. CRAWFORD, G. J. ANDERSON, AND M. SILVA O. 1997. Plant conservation in the Juan Fernandez Islands. *Aliso* 16: 89–102.
- , C. MARTICORENA, U. MATTHEI, AND D. J. CRAWFORD. 1998b. Loss of plant diversity and extinction on Robinson Crusoe Islands, Chile. *In* C.-I. Peng and P. P. Lowry II [eds.], *Rare, threatened, and endangered floras of Asia and the Pacific Rim*, 243–257. Institute of Botany, Academia Sinica Monograph Series 16, Taipei, China.
- SUN, B. Y., T. F. STUESSY, A. M. HUMAÑA, M. RIVEROS G., AND D. J. CRAWFORD. 1996. Evolution of *Raphithamnus venustus* (Verbenaceae), a gynodioecious hummingbird-pollinated endemic of the Juan Fernandez Islands, Chile. *Pacific Science* 50: 55–65.
- THORNTON, I. 1971. Darwin's islands: a natural history of the Galápagos. Natural History Press, New York, New York, USA.
- WALLACE, A. R. 1895. Natural selection and tropical nature. Macmillan, London, UK.
- WEBB, C. J., AND D. KELLY. 1993. The reproductive biology of the New Zealand flora. *Trends in Ecology and Evolution* 8: 442–447.
- WELLER, S. G. 1994. The relationship of rarity to plant reproductive biology. *In* M. L. Bowles and C. J. Whelan [eds.], *Restoration of endangered species*, 90–117. Cambridge University Press, Cambridge, UK.
- WESTER, L. 1991. Invasions and extinctions on Masatierra (Juan Fernandez Islands): a review of early historical evidence. *Journal of Historical Geography* 17: 18–34.
- WHITEHEAD, D. R. 1983. Wind pollination: some ecological and evolutionary perspectives. *In* L. Real [ed.], *Pollination biology*, 97–108. Academic Press, Orlando, Florida, USA.
- WILSON, E. O. 1973. The ants of Easter Island and Juan Fernández. *Pacific Insects* 15: 285–287.
- WOODWARD, R. L. 1969. Robinson Crusoe Island: a history of the Juan Fernandez Islands. University of North Carolina Press, Chapel Hill, North Carolina, USA.

APPENDIX. Endemic species studied on Isla Robinson Crusoe (= Masatierra), Chile, except for *Robinsonia masafuerae* from Isla Alejandro Selkirk (= Masafuera) and *Nicotiana cordifolia*, native to Isla A. Selkirk and cultivated in the CONAF gardens in Isla R. Crusoe. Species are listed alphabetically. P/O = pollen/ovule ratio or pollen ovule counts for dioecious species, PT = pollen tube study for self pollen germination, C = control open pollination, SS = seed set of selfed flowers, V = observations made for floral visitors. Accession numbers are those of G. J. Anderson, except when noted. CONAF = planted specimens at the CONAF experimental gardens in San Juan Bautista, derived from seeds from natural populations on the island.

Species	Site	Accession no.	Study
<i>Azara serrata</i> var. <i>fernandeziana</i> (Gay) Reiche	Villagra	3014	P/O, V
	Villagra	4031	PT, P/O
<i>Berberis corymbosa</i> Hook. & Arn.	CONAF	2003	PT, P/O, V
	CONAF	2086	SS
	CONAF	4015	PT
	CONAF	4016	PT
	El Camote	not collected	V
<i>Boehmeria excelsa</i> (Bertero ex Steud.) Wedd.	CONAF	2004	PT, P/O, V
	Mirador trail	4024	C, V
	Villagra	4035	C, V
	Near landing strip	4079	C, V
	El Camote	4161	C, V
<i>Coprosma oliveri</i> Fosberg (♀)	Dama Juana	2014	C, V
	CONAF	3098	C, P/O, V
<i>Corposma oliveri</i> (♂)	Dama Juana	2017	P/O, V
	Dama Juana	4122	P/O
<i>Cuminia eriantha</i> (Benth.) Benth.	Salsipuedes	1582	V
	Cerro Agudo	4168	P/O, V
	Vaquería	not collected	V
	El Camote	4151	V
	Villagra	4113	V
	Corrales de Molina	4009	V
	CONAF	2006	SS, P/O
<i>Dendroseris litoralis</i> Skottsb. <i>Dendroseris neriifolia</i> (Decne.) Hook. & Arn.	CONAF	2005	P/O
	CONAF	2056	PT
	CONAF	4074	SS, PT
	CONAF	4157	C, PT, P/O
<i>Dendroseris pruinata</i> (Johow) Skottsb.	CONAF	2057	SS, PT, V
	CONAF	2021	P/O
	CONAF	3034	P/O
	CONAF	4000	C, PT
	CONAF	4078	C, PT
<i>Drimys confertifolia</i> Phil.	Puerto Francés	2040	P/O, V
	Plazoleta	4317	C, V
	El Yunque Mirador	3037	PT

APPENDIX. Continued.

Species	Site	Accession no.	Study
<i>Dysopsis hirsuta</i> (Müll. Arg.) Skottsbo.	Mirador trail	2024	P/O, V
	Dama Juana	4119	C, V
	Plazoleta	4127	C, V
	El Yunque		
	Plazoleta	4128	C
	El Yunque		
	Plazoleta	4138	C
	El Yunque		
	El Camote	4155	C, V
	El Camote	4158	C
<i>Escallonia callcottiae</i> Hook. & Arn.	CONAF	2010	PT, V
	CONAF	2071	SS
	CONAF	2072	C, SS
	Cordón Central	3023	P/O, V
	Mirador trail	4028	PT, V
	CONAF	4053	PT
	CONAF	4054	PT
	Pirámide	4056	PT, V
	Pirámide	4058	PT
	Pirámide	4060	PT
	Pangal	not collected	V
	CONAF	4082	PT, V
	CONAF	4083	PT
CONAF	4084	PT	
CONAF	4085	PT	
<i>Haloragis masatierrana</i> Skottsbo.	El Camote	4142	C, V
	Corrales de Molina	2053	P/O, V
	Corrales de Molina	4010	C, PT, V
	Corrales de Molina	4011	PT, V
	Corrales de Molina	4012	C, PT, P/O
	Corrales de Molina	4013	C, PT
<i>Libertia chilensis</i> (Molina) Gunckel	Salsipuedes	not collected	V
<i>Nicotiana cordifolia</i> Phil.	CONAF	2007	SS, P/O, V
	CONAF	4017	SS, PT
	CONAF	4018	C, PT
	CONAF	4019	PT
	CONAF	4020	PT
	CONAF	4021	PT
	CONAF	4022	PT
	Mirador trail	2022 ^a	P/O, V
	Mirador trail	4038	C
	Mirador trail	4042	P/O
<i>Pernettya rigida</i> (Bertero ex Colla) DC. (♂)	Mirador trail	4043	P/O
	Mirador trail	4044	P/O
	Mirador trail	4045	P/O
	Mirador trail	4046	P/O
	Dama Juana	2044 ^a	V
	Centinela/Pangal	3039 ^a , 3040 ^a	V
	Mirador trail	2022 ^a	P/O, V
	Mirador trail	4039	C, P/O
	Mirador trail	4047	P/O
	Mirador trail	4048	P/O
	Mirador trail	4049	P/O
	Mirador trail	4050	P/O
	Mirador trail	4051	P/O
El Camote	4164	C, V	
Dama Juana	2044 ^a	V	
Centinela/Pangal	3039 ^a , 3040 ^a	V	
<i>Plantago fernandezia</i> Bertero ex Barnéoud	CONAF	2013	PT, V
	CONAF	3049	C, PT, P/O
<i>Rhaphithamnus venustus</i> (Phil.) B. L. Rob.	CONAF	3004, 3007	P/O, V, PT
	CONAF	3057	SS
	CONAF	3059	SS
	CONAF	3060	SS
	CONAF	3061	SS
	Mirador	2027, 3004	V
	Dama Juana	2045–48	V
	Puerto Francés	2038–39	V
	Villagra	3008-11	V

APPENDIX. Continued.

Species	Site	Accession no.	Study
	Pangal	3043	V
	Centinela	3047	V
	El Camote	not collected	V
	Corrales de Molina	2050	V
<i>Robinsonia evenia</i> Phil.	Quebrada of Piedra Agujereada	Stuessy et al. 5393	P/O
<i>Robinsonia gayana</i> Decne.	S of Dama Juana	Stuessy et al. 5352	P/O
<i>Robinsonia gracilis</i> Decne.	Above Pangal and Piedra Agujereada	Stuessy et al. 5273	P/O
<i>Robinsonia masafuerae</i> Skottsbo.	Cuchillo del Imán	Landero & Gaete 9158A	P/O
<i>Ugni slekirkii</i> (Hook. & Arn.) O. Berg	Corrales de Molina	2055	P/O, V
	Mirador trail	4088	C, P/O, V
	Plazoleta	4139	C, V
	El Yunque		
	El Camote	4143	C, V
	El Camote	4144	C
<i>Wahlenbergia berteroi</i> Hook. & Arn.	Lighthouse	2018	PT, V
	Lighthouse	3069	SS, P/O
	Near landing strip	3095	C, V
	Lighthouse	3096	C
	Lighthouse	4006	C, PT
	Lighthouse	4007	C
<i>Wahlenbergia fernandeziana</i> A. DC.	Villagra	2026	P/O, V
	Lighthouse	4005	SS, C, V
	Corrales de Molina	4014	C, PT, V
	Villagra	4026	PT
	Villagra	4033	PT
	Villagra	4034	PT
<i>Wahlenbergia fernandeziana</i> × <i>W. grahamiae</i> Hemsl.	CONAF	2008	P/O, V
	CONAF	3097	SS, C
	CONAF	4002	PT
	CONAF	4003	PT

^a Population collection number.