

The angiosperm flora of the Archipelago Juan Fernandez (Chile): origin and dispersal

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Abstract: We review the hypothesized origin and the methods of arrival of the angiosperm colonists to the Juan Fernandez Islands. We also summarize the dispersal capabilities of the current flora, including data on fruit type, fruit length, and dispersal unit length, correlating these features with dispersal and establishment. Most species originated from South America, followed by Pantropical, Australian, New Zealand, and Pacific colonizers. Sea and land birds were the most important initial long-distance dispersal agents. Most colonizing species are hermaphroditic flowered, and thus all dispersal methods are represented among them. Monoecious, andromonoecious and gynomonoecious, dioecious, and polygamous species were mainly carried by birds. Most wind- and bird-pollinated colonizing genera arrived with birds as did most annual herbs and species with bright-colored flowers. In the current flora, the majority of the species have dry fruits. In monoecious, andromonoecious and gynomonoecious, and dioecious species, achenes predominate. Fleshy fruits are limited to perennials. Most species have medium to small dispersal units, and generally, the larger the flower, the larger the fruit. Large- and medium-sized dispersal units are common in shrubs and trees. Abiotic dispersal is common in the current flora, which may reflect the ancestral dispersal capability of the colonizers, or adaptation to the absence of a fauna to disperse seeds and fruits. Anemochorous and autochorous species are mainly perennial and have medium to large, unisexual flowers. Anemochorous species have small dispersal units and dull-colored flowers, whereas large dispersal units and brightly colored flowers are frequent in autochorous species. Medium-sized dispersal units are represented in autochorous or ornithochorous species. The establishment and evolution of this flora was previously discussed to have occurred with very few pollination and (or) reproductive options. This study suggests that elements associated with dispersal are also analogously limited.

Key words: Juan Fernandez Islands, anemochory, autochory, ornithochory, long-distance dispersal, loss of dispersibility.

Résumé : Les auteurs réévaluent l'origine et les méthodes hypothétiques de l'arrivée des angiospermes colonisatrices des îles Juan Fernandez. Ils résument également les capacités de dispersion de la flore actuelle, incluant des données sur le type de fruit, la longueur du fruit ainsi que la longueur des unités de dispersion, tout en corrélant ces caractéristiques avec la dispersion et l'établissement. Pour la plupart, ces espèces proviennent de l'Amérique du Sud, suivies de colonisatrices pan-tropicales, australiennes, néo-zélandaises ou du Pacifique. Des oiseaux marins et terrestres ont été responsables des principales dispersions originales sur longues distances. La plupart des espèces colonisatrices sont hermaphrodites, et on y retrouve ainsi toutes les méthodes de dispersion. Des espèces monoïques, andromonoïques et gynomonoïques, dioïques et polygames ont été transportées surtout par des oiseaux. La plupart des genres colonisateurs pollinisés par le vent ou les oiseaux, sont arrivés avec les oiseaux, tout comme la plupart des herbacées et des espèces possédant des fleurs fortement colorées. Dans la flore actuelle, la majorité des espèces ont des fruits secs. Chez les espèces monoïques, andromonoïques et gynomonoïques, et dioïques, les achènes prédominent. Les fruits charnus se limitent aux espèces pérennes. La plupart des espèces possèdent de petites ou moyennes unités de dispersion et, généralement, plus les fleurs sont grandes, plus les fruits sont gros. On retrouve souvent de grosses et moyennes unités de dispersion chez les arbustes et les arbres. Dans la flore actuelle, la dispersion abiotique est fréquente, ce qui pourrait refléter la capacité ancestrale de dispersion des colonisateurs, ou une adaptation à l'absence d'une faune pour disperser les graines et les fruits. Les espèces anémochores et autochores sont surtout pérennes et possèdent des fleurs unisexuées de grandes ou moyennes dimensions. Les espèces anémochores ont de petites unités de dispersion et des fleurs peu colorées, alors que les grosses unités de dispersion et les fleurs fortement colorées sont fréquentes chez les espèces autochores. On retrouve des unités de dispersion de moyenne dimension chez les espèces autochores ou ornithochores. On a déjà discuté que l'établissement et l'évolution de cette flore seraient survenues avec très peu d'options de pollinisation et de reproduction. Cette étude suggère que les éléments associés à la dispersion, sont aussi analogiquement limités.

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Mots clés : îles Juan Fernandez, anémochorie, autochorie, ornitochorie, dispersion à longue distance, perte de capacité de dispersion.

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Introduction

The biota of oceanic islands frequently bear a different assemblage of plant families than equivalent mainland areas (Carlquist 1965, 1974; Adersen 1995; Grant 1998). As islands are difficult to reach and continental species possess a wide array of dispersal capabilities, islands will possess a nonrepresentative sample of the species from the adjacent continents. This disharmony in composition of an insular biota with its continental source flora is considered prime evidence for the filter effect of long-distance dispersal (Carlquist 1974). Long-distance dispersal capability is related to size of disseminule, desiccation resistance, cold resistance, and other features that can vary within a taxonomic group, and, of course, ultimately depends on the existence of appropriate vectors as well (Carlquist 1974).

Clearly, chance also plays an important role in determining which species arrive, when, and in what numbers (Carlquist 1981). In addition, difficulties of both establishment and reproduction (Stebbins 1957; Baker 1967; Whittaker 1998) will further influence the composition of island communities by favoring some types of colonists over others. Thus, it is not simply dispersal of propagules to islands that limits their occurrence, but also the availability of an open niche in which they can establish a viable population, before events that might lead to their extinction are experienced (Kingston et al. 2003).

Understanding evolution on oceanic islands must be based on sound principles of dispersal and biogeography, and there is still much to be learned on these subjects for these waif biotas (Darlington 1957; Thorne 1963; Carlquist 1974; Adersen 1995; Crawford and Stuessy 1997; Cronk 1997). Increasingly, and sadly, the distribution of even continental species becomes more insular, with scattered small patches of native biota in a sea of human-altered landscapes and noxious invasive species (Saunders et al. 1991; Hobbs and Yates 2003).

We chose the angiosperm flora of the Juan Fernandez archipelago for a comprehensive study of this kind, because it has a manageable size, it is particularly interesting because of its high rate of endemism, and, unfortunately, it is considered highly vulnerable and threatened (Stuessy 1995). In addition, we have done extensive fieldwork there (e.g., Stuessy et al. 1998a, 1998b, 1998c; Anderson et al. 2001; Crawford et al. 2001; Bernardello et al. 2002). Although the Juan Fernandez Islands were discovered in 1574 by the homonymous Spanish navigator, they did not attract the attention of naturalists for some time. The absence of signature animals (other than the only endemic island hummingbird; Colwell 1989), in contrast with the biota of archipelagos like the Galapagos, may have played an important role in this lack of interest. However, after some study, the zoocentrism was overcome, and this archipelago was regarded as a “botanical paradise”, with many noteworthy endemic plants including

the monotypic, endemic, family Lactoridaceae of the basal angiosperms (Stuessy et al. 1998a).

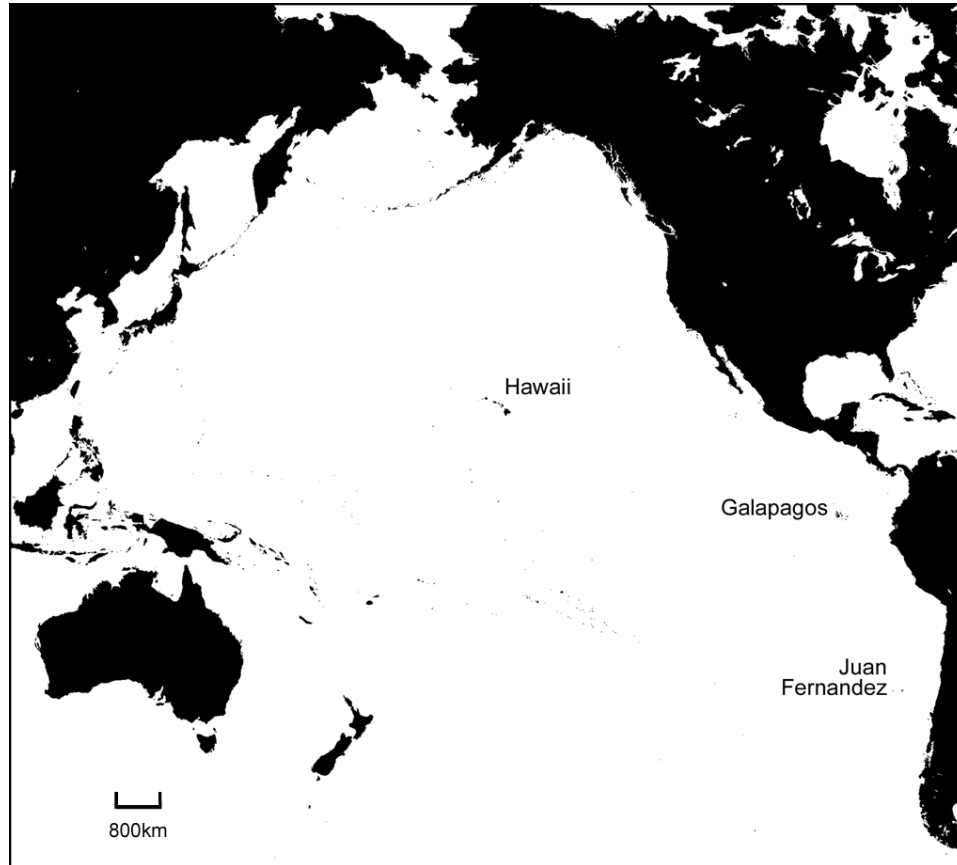
Systematic exploration of the archipelago only goes back as far as the third decade of the 19th century (Johow 1896). Colla (1834–1837), Hooker and Arnott (1833), Gay (1845–1854), and Philippi (1856) are among the most influential botanists to study and recognize the enormous value of the Juan Fernandez flora. Later, Hemsley (1884), Johow (1896), and Skottsberg (1921, 1925, 1928, 1951), produced the most significant and comprehensive studies of this highly unusual vegetation.

The archipelago, located at a latitude of 33°S (Fig. 1), consists of three small oceanic islands (total 100 km²; Stuessy 1995): Isla Robinson Crusoe (= Masatierra), Isla Santa Clara (both 667 km W of continental Chile), and Isla Alejandro Selkirk (= Masafuera; 181 km further west). Isla Robinson Crusoe has been dated at ca. 4 million years old, Isla Alejandro Selkirk at 1–2 million years old, and Isla Santa Clara at 5.8 million years old (Stuessy et al. 1984). The archipelago had no permanent human settlements before the 16th century (Woodward 1969).

Isla Alejandro Selkirk is dominated by a dome-shaped high-altitude plateau that attains an elevation of 1380 m above sea level (a.s.l.) (Mount Los Inocentes) and is surrounded by deep ravines and cliffs near the shore. Isla Robinson Crusoe is more eroded, with the high peaks (915 m a.s.l., Mount Yunque) surrounded by broad valleys, whereas Isla Santa Clara attains only 350 m a.s.l. The climate is influenced by fluctuations in the flow of the Humboldt current and the southeast trade winds. The annual mean temperature is 15.18 °C, and total precipitation is 922.10 mm (Novoa and Villaseca 1989).

The angiosperm flora of the archipelago is small and reasonably well known (156 taxa, 152 species; Marticorena et al. 1998), and its origin has been the subject of considerable study and debate (i.e., Skottsberg 1925, 1934, 1956; van Balgooy 1960, 1971). The high level of endemism of this remarkable flora (about 63%; 2.1 native species/km² and ca. 1 endemic/km²) is regrettably among the most threatened in the world (Davis et al. 1995; Mittermeier et al. 1999). An analysis of the vegetation change in the past 80 years indicates that the native forest has decreased by approximately a third and that several introduced species, such as *Acaena argentea*, *Aristotelia chilensis*, *Rubus ulmifolius*, and *Ugni molinae*, have increased their area from about 5% to 14% depending on the species (Dirnböck et al. 2003). In addition, the historical and continued foraging by feral goats and rabbits have posed another significant threat to these unique plants (Wester 1991; Bourne et al. 1992; Stuessy et al. 1998b), including the recent discovery of the highly invasive Argentine ant on the three main islands (Ingram et al. 2006). There is also a greater urgency for studies of this flora, because insular species are being lost at a higher rate than are

Fig. 1. Map of the Pacific Ocean showing the archipelagos of Hawaii, Galapagos, and Juan Fernandez.



their continental relatives (Reid and Miller 1989; Smith et al. 1993).

Though the flora is small, the terrestrial fauna of the islands is far less impressive than the flora. There are no native mammals, amphibians, or reptiles, and the insect fauna is small (Kuschel 1952; Wilson 1973). The total (land and sea) bird diversity of the Juan Fernandez is (very) small. The last comprehensive survey of birds (Lönnerberg 1921) lists fewer than 30 species in total. That includes 8 native breeding land birds and 6 breeding sea birds (the rest of Lönnerberg's list includes the following: 3 species accidental visitors, 5 species South American "visitors", 5 species "roving" sea birds, and 2 species introduced). Presuming this extant fauna to represent that available to serve as original dispersal agents, the opportunities for dispersal are relatively few. The endemic land bird species notably include the Juan Fernández firecrown, *Sephanoides fernandensis* (the only endemic hummingbird known on oceanic islands; Colwell 1989; Roy et al. 1998) and among the native birds a second sister hummingbird species, these, of course, important for pollination, not dispersal (Bernardello et al. 2002). The other endemic land birds are the rayadito from Isla Alejandro Selkirk, *Aphrastura masafuerae*, and the Juan Fernandez tit-tyrant, *Arlairetes fernandezianus*, whereas native bird species shared with continental Chile include the short-eared owl, *Asio flammeus*, the green-backed firecrown, *Sephanoides sephanioides*, the austral thrush, *Turdus falcklandii*, and the austral blackbird, *Guracus curaeus* (Hahn 1996).

Floral visitors are absent or rare in these island forests (Skottsberg 1928; Anderson et al. 2001; Bernardello et al. 2002), other than the two hummingbird species. Approximately 9% of the extant flora is hummingbird pollinated. The diet of the hummingbirds includes nectar from 14 autochthonous plant species (Bernardello et al. 2000; Anderson et al. 2001). It is estimated that around 47% is wind pollinated, whereas the pollination of the remaining 44% of the flora is unknown (Bernardello et al. 2002).

Upon this background, here we review the probable places of origin and the methods of arrival of the first angiosperm colonists to the Juan Fernandez Islands. In addition, we summarize the dispersal capabilities of the present angiosperm flora, including data on fruit type, fruit length, and dispersal unit size, and we correlate species characteristics with dispersal and establishment. Thus, we intend to synthesize data to help understand the origin and evolution of this distinctive island flora and provide a broader foundation for insular floras in general.

Materials and methods

The angiosperm species (Table 1) reported for the islands were used to assess the natural processes of plant migration to the Juan Fernandez archipelago and dispersal within it. The recent catalogue of the vascular flora by Marticorena et al. (1998) was used for the list of species and their habit, whereas the "conservation status" of the species was taken

Table 1. Autochthonous flora checklist of the Juan Fernandez islands indicating conservation status, habit, probable place of origin, method of arrival of the first colonizers, fruit type, fruit length, dispersal unit length, and current dispersal.

Family, genus	No. of species	Species		Status	Habit	Place of origin	Method of arrival	Fruit type	Fruit length (mm)	Dispersal unit length (mm)	Dispersal
		Native	Endemic								
Apiaceae											
<i>Apium</i>	2	<i>A. australe</i>	<i>A. fernandezianum</i>	Rare	Perennial herb	S. America	Bird internal	Schizocarp	2	2	Anemochory
<i>Centella</i>	1	<i>C. asiatica</i>			Perennial herb	S. America	Bird internal/ bird external	Schizocarp	2.5	2.5	Endozoochory
<i>Eryngium</i>	3		<i>E. bupleuroides</i> <i>E. inaccessum</i> <i>E. sarcophyllum</i>	Endangered/ rare	Shrub/tree	S. America	Bird external	Schizocarp	2	2	Epizoochory
Arecaceae											
<i>Juania*</i>	1		<i>J. australis</i>	Endangered	Tree	Neotropics	Bird internal	Drupe	15	15	Autochory
Asteraceae											
<i>Abrotanella</i>	1	<i>A. linearifolia</i>		Vulnerable	Perennial herb	S. America	Bird external	Achene	1.5	1.5	Autochory
<i>Centaurodendron*</i>	2		<i>C. dracaenoides</i> <i>C. palmiforme</i>	Endangered	Tree	Neotropics	Bird external	Achene	5	5	Autochory
<i>Dendroseris*</i>	11		<i>D. berteriana</i> <i>D. gigantea</i> <i>D. litoralis</i> <i>D. macrantha</i> <i>D. macrophylla</i> <i>D. marginata</i> <i>D. micrantha</i> <i>D. neriifolia</i> <i>D. pinnata</i> <i>D. pruinata</i> <i>D. regia</i>	Endangered	Shrub/tree	S. America	Bird external	Achene	4	4	Autochory
<i>Erigeron</i>	4		<i>E. fernandezianus</i> <i>E. ingae</i> <i>E. luteoviridis</i> <i>E. rupicola</i>	Rare	Shrub	Neotropics	Bird external/ wind	Achene	2	2	Anemochory
<i>Gamochaeta</i>	1		<i>G. fernandeziana</i>	Vulnerable	Perennial herb	Pantropics	Bird external	Achene	1	1	Anemochory
<i>Lagenophora</i>	1	<i>L. hariotii</i>		Vulnerable	Perennial herb	Neotropics	Bird external	Achene	2.5	2.5	Autochory
<i>Robinsonia*</i>	7		<i>R. berteroi</i> <i>R. evenia</i> <i>R. gayana</i> <i>R. gracilis</i> <i>R. macrocephala</i> <i>R. masafueriae</i> <i>R. thurifera</i>	Endangered	Shrub	S. America	Bird external	Achene	3.5	3.5	Autochory
<i>Taraxacum</i>	2	<i>T. fernandezianum</i>		Vulnerable	Perennial herb	S. America	Bird external/ wind	Achene	3	3	Anemochory

Table 1 (continued).

Family, genus	No. of species	Species				Place of origin	Method of arrival	Fruit type	Fruit length (mm)	Dispersal unit length (mm)	Dispersal
		Native	Endemic	Status	Habit						
		<i>T. subspatulatum</i>									
<i>Yunquea*</i> Berberidaceae	1		<i>Y. tenzii</i>	Endangered	Tree	S. America	Bird external	Achene	6	6	Autochory
<i>Berberis</i>	2		<i>B. corymbosa</i>	Endangered	Shrub	S. America	Bird internal	Berry	8	8	Endozoochory
Boraginaceae <i>Selkirkia*</i>	1		<i>B. masafuerana</i> <i>S. berteroi</i>	Endangered	Shrub	S. America	Bird internal	Nutlet	25	25	Epizoochory
Brassicaceae <i>Cardamine</i>	3		<i>C. chenopodioides</i> <i>C. flaccida</i>	Endangered (end.)	Annual/perennial herb	S. America	Bird internal	Siliqua	35	2	Autochory
Bromeliaceae <i>Greigia</i>	1		<i>G. berteroi</i>	Endangered	Shrub	S. America	Bird external	Dry berry	17	17	Autochory
<i>Ochagavia</i>	1		<i>O. elegans</i>	Rare	Shrub	S. America	Bird external	Dry berry	10	10	Autochory
Campanulaceae <i>Lobelia</i>	1	<i>L. alata</i>			Annual herb	S. America	Bird external	Capsule	7	0.7	Autochory
<i>Wahlenbergia</i>	5		<i>W. berteroi</i> <i>W. fernandeziana</i> <i>W. grahamiae</i> <i>W. masafuerae</i> <i>W. tuberosa</i>	Endangered	Shrub	Australia	Bird external	Capsule	4	0.5	Anemochory
Caryophyllaceae <i>Spergularia</i>	2		<i>S. confertifolia</i>	Vulnerable	Perennial herb	Chile	Bird internal/bird external	Capsule	4	1.5	Autochory
Chenopodiaceae <i>Chenopodium</i>	3		<i>S. masafuerana</i> <i>Ch. cruseoanum</i> <i>Ch. nesodendron</i> <i>Ch. sanctae-clarae</i>	Endangered	Shrub	S. America	Bird external	Utricle	2	2	Anemochory
<i>Sarcocornia</i> Convolvulaceae	1	<i>S. fruticosa</i>			Perennial herb	Pantropics	Bird external	Utricle	2	2	Hydrochory
<i>Calystegia</i>	1	<i>C. tuguriorum</i>			Shrub	New Zealand	Bird internal	Capsule	8	2	Autochory
<i>Dichondra</i> Cyperaceae	1	<i>D. sericea</i>			Perennial herb	Pantropics	Bird internal	Capsule	3	2	Autochory
<i>Carex</i> , <i>Cyperus</i> , <i>Eleocharis</i> , <i>Macherina</i> , <i>Oreobolus</i> , <i>Scirpus</i> , <i>Uncinia</i>	13	9 species	4 species	Endangered	Perennial herb	Pantropics	1 bird internal, 4 bird external, 2 bird internal/bird external	Achene	2	2	Anemochory, endozoochory
Empetraceae											

Table 1 (continued).

Family, genus	No. of species	Species		Status	Habit	Place of origin	Method of arrival	Fruit type	Fruit length (mm)	Dispersal unit length (mm)	Dispersal
		Native	Endemic								
Ericaceae <i>Empetrum</i>	1	<i>E. rubrum</i>			Shrub	S. America	Bird internal	Drupe	9	9	Endozoochory
Euphorbiaceae <i>Pernettya</i>	1		<i>P. rigida</i>	Vulnerable	Shrub	Chile	Bird internal	Berry	8	8	Endozoochory
Fabaceae <i>Dysopsis</i>	1		<i>D. hirsuta</i>	Vulnerable	Perennial herb	S. America	Bird internal	Schizocarp	1	1	Active ballistic
Flacourtiaceae <i>Sophora</i>	2		<i>S. fernandeziana</i> <i>S. masafuerana</i>	Endangered	Tree	Pacific area	Water	Legume	60	8	Autochory
Gunneraceae <i>Azara</i>	1		<i>A. serrata</i> var. <i>fernandeziana</i>	Endangered	Tree	S. America	Bird internal	Berry	8	8	Endozoochory
Haloragaceae <i>Gunnera</i>	4		<i>G. bracteata</i> <i>G. glabra</i> <i>G. masafuerae</i> <i>G. peltata</i>	Vulnerable	Perennial herb	Chile	Bird internal	Drupe	3	3	Autochory
Iridaceae <i>Haloragis</i>	2		<i>H. masafuerana</i> <i>H. masatierrana</i>	Endangered	Perennial herb	New Zealand	Bird internal	Nutlet	3	3	Autochory
Juncaceae <i>Libertia</i>	1	<i>L. chilensis</i>			Perennial herb	Chile	Bird internal	Capsule	10	2	Autochory
Lamiaceae <i>Juncus</i>	5	<i>J. capillaceus</i> <i>J. imbricatus</i> <i>J. pallescens</i> <i>J. planifolius</i> <i>J. procerus</i>			Perennial herb	Pantropics	Bird external/ wind	Capsule	4	0.8	Anemochory
Lactoridaceae <i>Luzula</i>	1		<i>L. masafuerana</i>	Vulnerable	Perennial herb	N. America	Bird external	Capsule	3	1.5	Anemochory
Lamiaceae <i>Cuminia</i> *	1		<i>C. eriantha</i>	Endangered	Shrub	Pantropics	Bird internal	Nutlet	12	12	Autochory
Lactoridaceae <i>Lactoris</i> *	1		<i>L. fernandeziana</i>	Endangered	Shrub	Gondwana relict	Wind	Follicle	3	0.7	Anemochory
Loranthaceae <i>Notanthera</i>	1	<i>N. heterophylla</i>			Shrub	S. America	Bird external	Drupaceous	6	6	Epizoochory, endozoochory
Myrtaceae <i>Myrceugenia</i>	2		<i>M. fernandeziana</i> <i>M. schulzei</i>	Vulnerable	Tree	S. America	Bird internal	Berry	9	9	Endozoochory
Myrtaceae <i>Myrteola</i>	1	<i>M. nummularia</i>		Endangered	Shrub	S. America	Bird internal	Berry	8	8	Endozoochory
Orchidaceae <i>Ugni</i>	1		<i>U. selkirkii</i>	Endangered	Shrub	Neotropics	Bird external	Berry	8	8	Endozoochory

Table 1 (continued).

Family, genus	No. of species	Species			Habit	Place of origin	Method of arrival	Fruit type	Fruit length (mm)	Dispersal unit length (mm)	Dispersal
		Native	Endemic	Status							
Piperaceae <i>Gavilea</i>	1		<i>G. insularis</i>	Rare	Perennial herb	S. America	Wind	Capsule		0.05	Anemochory
<i>Peperomia</i>	4		<i>P. berteriana</i> <i>P. fernandeziana</i> <i>P. margaritifera</i> <i>P. skottsbergii</i>	Endangered, rare	Perennial herb	Chile	Bird external	Drupe	1	1	Epizoochory
Plantaginaceae <i>Plantago</i>	3	<i>P. australis</i> <i>P. firma</i>	<i>P. fernandezia</i>	Endangered (end.)	Perennial herb/tree	Neotropics	Bird external	Capsule	3	1.5	Cnemochory
Poaceae <i>Agrostis, Bromus, Chaetotropis, Chusquea, Danthonia, Leptophyllochloa, Megalachne, *Nassella, Piptochaetium, Podophorus,* Trisetum</i>	15	10 species	5 species	Endangered, 1 extinct	Annual/ perennial herb	S. America	2 bird internal, 9 bird external	Caryopsis	4	4	Anemochory, endozoochory
Ranunculaceae <i>Ranunculus</i>	1		<i>R. caprarum</i>	Endangered	Perennial herb	Pacific area	Bird internal/bird external	Achene	7	7	Autochory
Rhamnaceae <i>Colletia</i>	1		<i>C. spartioides</i>	Vulnerable	Shrub	S. America	Water	Drupe	10	10	Autochory
Rosaceae <i>Acaena</i>	1		<i>A. masafuerana</i>	Endangered	Perennial herb	S. America	Bird external	Achene	1	1	Epizoochory
<i>Margyraciaena</i>	1		<i>M. skottsbergii</i>	Vulnerable	Perennial herb	S. America	Bird external	Drupe	6	6	Autochory
<i>Margyricarpus</i>	1		<i>M. digynus</i>	Vulnerable	Perennial herb	S. America	Bird external	Drupe	6	6	Autochory
<i>Rubus</i>	1	<i>R. geoides</i>			Perennial herb	N. America	Bird internal	Aggregate	4	18	Endozoochory
Rubiaceae <i>Coprosma</i>	2		<i>C. oliveri</i> <i>C. pyrifolia</i>	Vulnerable	Tree	New Zealand	Bird internal/bird external	Drupaceous	20	20	Autochory
<i>Galium</i>	1		<i>G. masafueranum</i>	Vulnerable	Perennial herb	S. America	Bird internal	Schizocarp	2	2	Endozoochory
<i>Hedyotis</i>	1	<i>H. salzmannii</i>			Perennial herb	Pacific area	Bird internal/bird external	Capsule			Endozoochory
<i>Nertera</i>	1	<i>N. granadensis</i>			Perennial herb	Pantropics	Bird internal	Drupe	5	5	Endozoochory
Rutaceae <i>Fagara</i>	2		<i>F. externa</i> <i>F. mayu</i>	Vulnerable	Tree	S. America	Bird internal	Follicle	3	3	Endozoochory
Santalaceae											

Table 1 (concluded).

Family, genus	No. of species	Species		Status	Habit	Place of origin	Method of arrival	Fruit type	Fruit length (mm)	Dispersal unit length (mm)	Dispersal
		Native	Endemic								
<i>Santalum</i>	1		<i>S. fernandezianum</i>	Extinct	Tree	Indo-pacific area	Bird internal	Drupe	4	4	Endozoochory
Saxifragaceae											
<i>Escallonia</i>	1		<i>E. callcottiae</i>	Vulnerable	Shrub/tree	S. America	Bird external	Capsule	4	1	Anemochory
Scrophulariaceae											
<i>Euphrasia</i>	1		<i>E. formosissima</i>	Vulnerable	Shrub	Pantropics	Bird external	Capsule	3	0.8	Anemochory
<i>Mimulus</i>	1	<i>M. glabratus</i>		Vulnerable	Annual herb	Chile	Bird external	Capsule	4	0.5	Anemochory
Solanaceae											
<i>Nicotiana</i>	1		<i>N. cordifolia</i>	Endangered	Shrub	S. America	Bird external/ wind	Capsule	10	0.3	Anemochory
<i>Solanum</i>	2	<i>S. pentlandii</i> subsp. <i>interandinum</i>	<i>S. fernandezianum</i>	Endangered (end.)	Perennial herb	S. America	Bird internal	Berry	6	6	Endozoochory
Urticaceae											
<i>Boehmeria</i>	1		<i>B. excelsa</i>	Vulnerable	Tree	Pantropics	Bird internal/ bird external	Achene	1.5	1.5	Anemochory
<i>Parietaria</i>	1	<i>P. debilis</i>		Vulnerable	Annual herb	Pantropics	Bird internal	Achene	1	1	Anemochory
<i>Urtica</i>	3	<i>U. berter- oana</i>	<i>U. glomeruliflora</i>	Vulnerable (end.)	Annual/ per- ennial herb	S. America	Bird external	Achene	1	1	Anemochory
			<i>U. masafuerae</i>								
Verbenaceae											
<i>Rhaphithamnus</i>	1		<i>R. venustus</i>	Vulnerable	Tree	S. America	Bird internal	Drupe	15	15	Autochory
Winteraceae											
<i>Drimys</i>	1		<i>D. confertifolia</i>	Vulnerable	Tree	Chile	Bird internal	Follicle	7	2	Autochory

Note: Characteristics were generally considered at the genus level. Empty cells indicate that information is missing. Where there is more than one species per genus, the general character state or average (e.g., size), is given; if some species are very different, the individual character states are given. For species, varieties are only included when the variety is the only representative of the species occurring in the archipelago. Where appropriate, the species to which the status corresponds is given in parentheses. The place of origin, methods of arrival, and dispersal are all presumed. For habit, slashes indicate the genus or the species has two habits.

*Endemic genus.

mainly from Stuessy et al. (1998b, 1998c) and Baeza et al. (2002).

Species were assigned to one of seven classes according to their place of origin: 1, Chile; 2, Neotropics (lowland tropical zones); 3, remaining parts of South America; 4, North America; 5, Pan tropics; 6, Australia; 7, New Zealand; 8, Pacific or Indo-Pacific area. The works by Skottsberg (1956) on the Juan Fernández Islands, van Balgooy (1960, 1971) on plant geography of the Pacific, Carlquist (1974) on islands in general, Porter (1983) on the Galápagos, and Wagner et al. (1990) on Hawaii were used as guidelines to make determinations on the possible origins and methods of arrival of the Fernandezian species. When available, phylogenies were used as well (e.g., Sang et al. 1995; Mitchell and Heenan 2002; Ruiz et al. 2004).

Dispersal methods for arrival were tabulated into four categories, the most common in studies of this type: 1, bird internal (seeds or fruits eaten and carried internally); 2, bird external (either mechanically attached to feathers or embedded in mud on feet); 3, wind (air flotation); and 4, water (oceanic drift).

Information on fruit features was taken mainly from Hemsley (1884), Johow (1896), and Skottsberg (1921, 1951), supplemented with personal observations in several expeditions to the archipelago (cf. Bernardello et al. 2002); the works by Gay (1845–1854), Reiche (1896–1911), and Moore (1983) were also consulted. The variables measured or scored included: fruit length, dispersal unit size length, and fruit type (as schizocarpic fruit, achene, berry, nutlet, silique, capsule, drupe or drupaceous, legume, follicle, aggregate, or caryopsis). Measurements were taken of the dispersal units (whole fruit or only the seeds). The fruit size categories were defined as small when they fell in the interval 0–2.0 mm, medium in the interval 2.5–10 mm, large in the interval 11–30 mm, and very large for 40 mm and above. We selected the categories by using the data for all fruit sizes, and by nonoverlapping intervals.

Categories of dispersal of the current flora basically follow van der Pijl (1982), and are based on our own observations of the species of the archipelago. Species were assigned to one of the following six classes, according to the characteristics of their fruits and seeds: 1, endozoochory (dispersed by fruit-eating birds); 2, epizoochory (dispersed passively by birds that carry fruits or seeds attached to feathers); 3, hydrochory (water dispersal); 4, anemochory (wind dispersal); 5, autochory (autonomous passive dispersal); and 6, active ballistic (by tension in dead, hydroscopic tissues).

To compare these traits with other features, such as flower sex, flower color, pollination of the colonizers, and current pollination system (either observed or inferred from morphology), data were taken from Bernardello et al. (2002).

Results

Native and endemic angiosperm species on the archipelago were scored for their area of origin, method of arrival, fruit type and length, dispersal unit length, dispersal type, as well as conservation status and habit (Table 1). Seventy-seven percent of the species are suggested to have come

from South America (e.g., species of *Colletia*, *Chenopodium*, *Nicotiana*), as judged from the closest relatives distribution and the respective areas of the families. Nine percent of them are supposed to be specifically indigenous to Chile (e.g., species of *Drimys*, *Gunnera*, *Mimulus*, *Peperomia*, *Pernettya*, and *Spergularia*), where they are well represented with analogous species, and 19% to the Neotropics (e.g., species of Asteraceae, *Juania*, and *Ugni*). Pan tropical elements are next in abundance (11%, e.g., species of Cyperaceae, *Dichondra*, *Nertera*, and *Sarcocornia*), all taxa widely distributed and represented in different Pacific Islands. North American colonists are rare, only *Rubus* and *Luzula* are supposed to come from this region, as well as Australian (e.g., *Wahlenbergia*), New Zealand (e.g., *Haloragis*), Pacific (e.g., *Ranunculus*), and Indo-Pacific colonizers (e.g., the extinct *Santalum fernandezianum*) that are all found in smaller proportions.

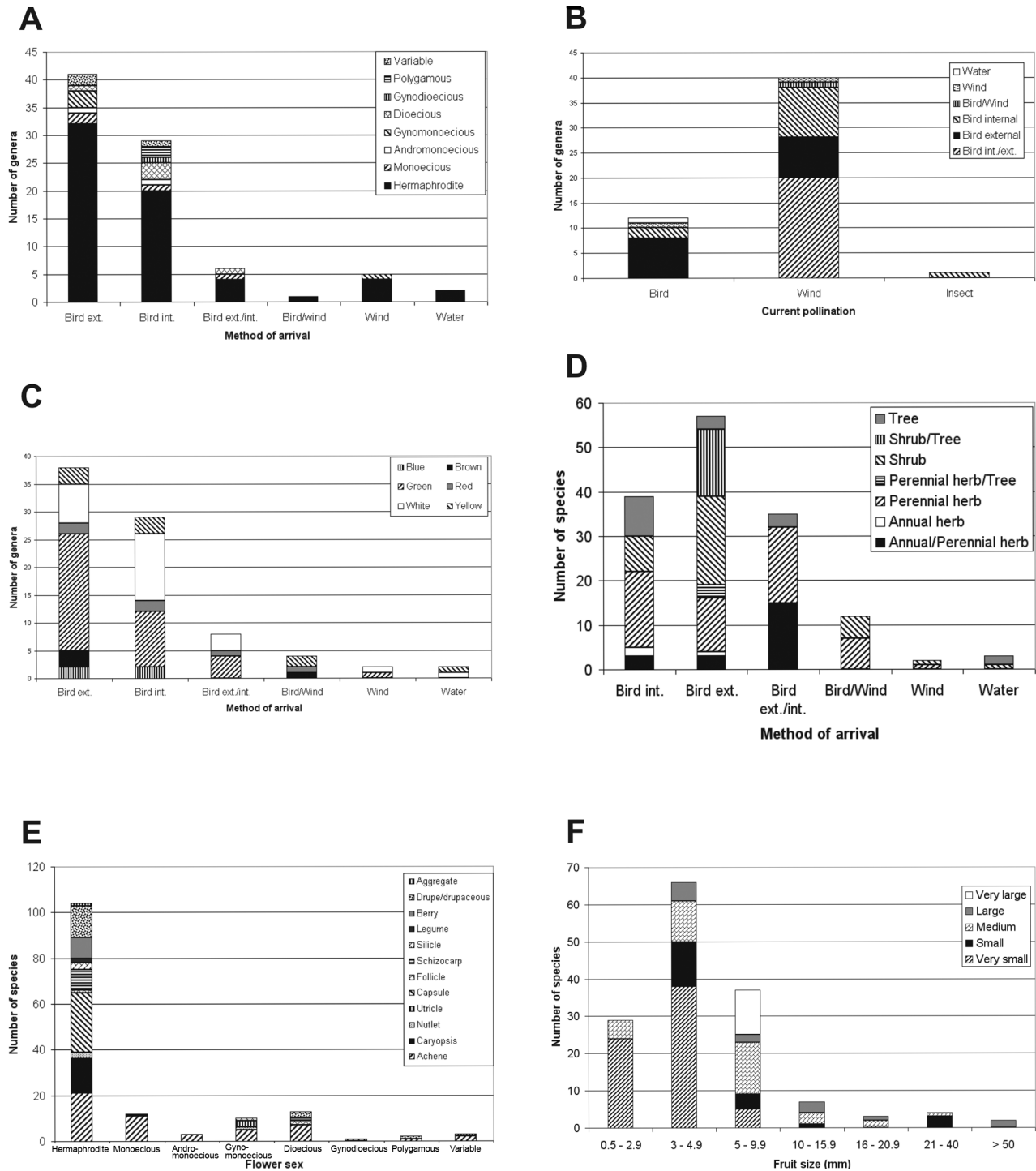
Among the families that have numerous endemic genera, Asteraceae (4 genera and 26 species) and Poaceae (2 genera and 5 species) stand out, and all six genera are derived from South American colonists. Genera with several endemic species are *Gunnera* and *Peperomia* (4 species each) with their ancestral colonists from Chile, *Chenopodium* and *Eryngium* (3 species each) from South America, and *Wahlenbergia* (5 species) from Australia. A number of genera have 2 endemic species each: *Berberis*, *Fagara*, and *Myrceugenia* and are all derived from South America, *Urtica* and *Spergularia* from Chile, *Haloragis* and *Coprosma* from New Zealand, and *Sophora* is from the Pacific area derived from Eurasian ancestors.

Comparisons of the Juan Fernandez genera to Chile indicate that 77% of the 84 genera are shared. The exceptions are *Boehmeria*, *Coprosma*, *Fagara*, *Haloragis*, *Margyrcacaena*, *Santalum*, and *Sarcocornia* together with 8 Fernandezian endemic genera. At the species level, almost all native, nonendemic species (47 out of 50) are shared with Chile.

Birds seem, by far, to have been the most important dispersal agents of colonizers to the archipelago (ca. 90%). Close to half (46%) of the bird-dispersed species would have reached the islands carried externally: with seeds or fruits mechanically attached to feathers by barbs and awns (e.g., Poaceae, *Acaena*), by viscid appendages (e.g., *Peperomia*), or simply embedded in mud on feet. The other significant portion of species (35%) likely were carried internally as bird-ingested seeds or fruits. The method of bird dispersal for the remaining 10% of species is uncertain. The two other long-distance dispersal agents are: (i) wind (2%), for species with small seeds (e.g., Orchidaceae, *Nicotiana*) or fruits with appendages that promote flying (e.g., some Asteraceae), or (ii) oceanic drift (2%; only *Colletia* and *Sophora*). Finally, 10% of the species were carried either by wind or birds.

Given that hermaphroditic-flowered species are the most frequent on the archipelago, few telling correlations of the method of arrival with the sexual systems were expected: Fig. 2A shows that all the dispersal methods are represented among the hermaphroditic-flowered species. Similarly, no notable associations could be drawn between the presumed pollination type of the colonizers and the method of arrival. Additionally, comparisons of the current pollination system (known for 56% of the flora; Bernardello et al. 2002) with the presumed method of arrival (Fig. 2B) shows little associ-

Fig. 2. Histograms comparing the frequency of (A) method of arrival with sexual system, (B) method of arrival with current pollination system, (C) method of arrival with flower color, (D) method of arrival with habit, (E) fruit type with flower sex, and (F) fruit size with flower size in the Juan Fernandez angiosperm flora.

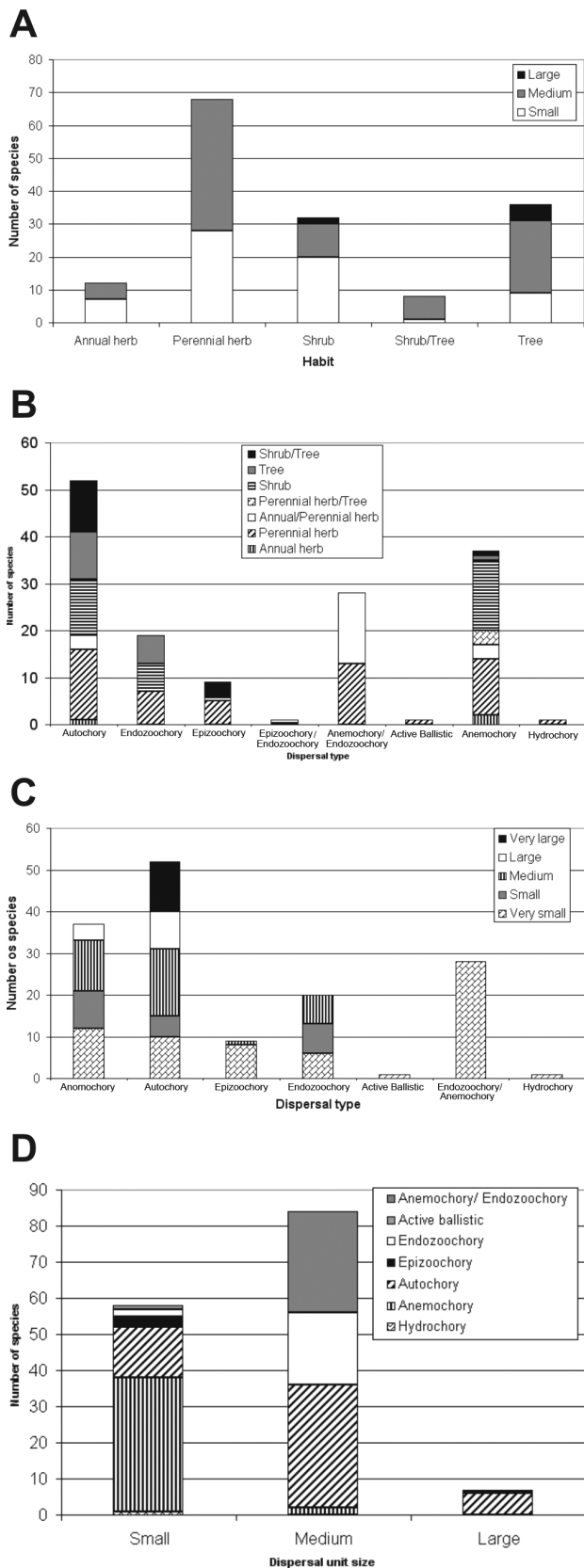


ation. Association with bird arrival is so pervasive that it would be surprising if most of the bird-pollinated species had not also arrived by bird dispersal. Similarly, species currently considered wind pollinated mostly arrived carried by birds. Given that there is no logical reason to associate dispersal and pollination syndromes, there is no association between method of arrival and pollination system. A comparison supports this contention: most wind- and bird-

pollinated genera arrived by birds, rarely by wind (Fig. 2B). Thus, the method of dispersal is independent of the method of pollination.

Most species with bright-colored flowers (Fig. 2C), (i.e., yellow, white, and blue), as well as the species that are annual herbs (Fig. 2D), seem to have arrived through avian transport to the archipelago. However, because 90% of the species are presumed to be originally bird dispersed, there

Fig. 3. Histograms comparing the frequency of (A) habit with dispersal unit size, (B) dispersal types with habit, (C) dispersal types with flower size, and (D) dispersal types with dispersal unit sizes in the Juan Fernandez angiosperm flora.



is not much variability to parse among types. As with the hermaphroditic condition above, the type that is most common, species with green flowers, do include the dispersants that also arrived by wind or water.

There are various features of fruits that provide some insight into the dispersal of the present flora. Most species (80%) have dry fruits, achenes are the most common (33%, chiefly Asteraceae and Cyperaceae), followed by capsules (18%, e.g., Campanulaceae, Convolvulaceae, Juncaceae), caryopses (10%, Poaceae), and schizocarpic fruits (7%, e.g., Apiaceae, Euphorbiaceae, Rubiaceae). The most common reproductive class, hermaphroditic-flowered species, have all fruit types (Fig. 2E), but in the group with more unusual sexual systems, monoecious, andro- and gynodioecious, and dioecious species, achenes predominate.

Fleshy fruits are comparatively uncommon, and are represented by two types: drupe or drupaceous (13%, e.g., Flacourtiaceae, Gunneraceae, Piperaceae,) and berry (7%, e.g., Ericaceae, Myrtaceae, *Solanum*). Fleshy fruits are present exclusively in perennial species, whereas achenes and caryopses are also found in annual herbs.

An analysis of the size of the dispersal units shows that the vast majority of the species have medium (57%) or small (38%) units, and only 5% have large units (e.g., *Juania*, *Rhaphithamnus*, *Coprosma*). In general, the larger the flower, the larger the fruit (Fig. 2F), that is, very small and small flowers produce fruits that mainly range from 0.5 to 5 mm, whereas larger flowers tend to be associated with average- or medium-sized fruits. In terms of dispersal unit size compared with the habit of the species (Fig. 3A), large and medium units are mainly present in shrubs and trees.

Four classes of dispersal typify most of the current flora. A substantial proportion of species (34%) have autochorous dispersal, with anemochory (25%) and ornithochory (20%, including epizoochory and endozoochory) following in magnitude. Cyperaceae and Poaceae, considered wind- or bird-dispersed, account for 19% of the flora. Active ballistic and hydrochorous species are unusual; only *Dysopsis hirsuta* and *Sarcocornia fruticosa*, respectively, are dispersed in these ways. Given that species with different dispersal modes are very diverse in their fruit types, no correlations can be drawn, except for the aggregate fruits and berries that are, as expected, among the endozoochorous species.

Both anemochorous and autochorous species are mainly perennial (Fig. 3B) and they have medium to large (Fig. 3C), unisexual flowers. Anemochorous species, as expected, generally have small dispersal units (Fig. 3D). On the other hand, species with large dispersal units are mainly autochorous, and medium-sized ones, either autochorous or ornithochorous. Most autochorous species have predominantly brightly colored flowers, whereas those that are anemochorous bear dull-colored flowers.

Interestingly, the four endemic genera of Asteraceae possess achenes with reduced dispersal ability, which is in contrast with most of the members of the family. Effectively, *Centaurodendron*, *Dendroseris*, *Robinsonia*, and *Yunquea* species have bristles that are reduced or break easily. In addition, in *Centaurodendron* and some *Robinsonia* species, the involucre bracts tend to retain the achenes within the capitula, whereas the achenes of *Yunquea* and several *Den-*

droseris species have irregular shapes and rugose surfaces, features that would reduce their dispersibility even further.

Correlating the geographic origin of the species with current means of dispersal, South American, Neotropical, and Panropical species are mainly dispersed by wind and birds or have autochorous dispersal. Anemochorous species are mostly South American, Panropical, or Neotropical.

Discussion

Biogeographically, the Juan Fernandez Islands have been considered as a separate floristic region, generally placed within the Neotropical kingdom (e.g., Engler 1882; Turrill 1959; Thorne 1963; Mattick 1964; Takhtajan 1969; Good 1974). Later, Takhtajan (1986) took a different view, considering the flora most similar to that of the Chile-Patagonian region, thus including the Fernandezian region within his Holoantarctic kingdom. Our analysis of the various publications positing origins of the Fernandezian species clearly suggests that the overall affinities of the Juan Fernandez flora are with the South American continent as a whole (Skottsberg 1934, 1956; van Balgooy 1960, 1971; Takhtajan 1986). The Asteraceae, a worldwide family with its cradle in South America (Bremer 1994; Stuessy et al. 1996), is a particularly notable family with several genera and species endemic to the archipelago. The recent work of Sang et al. (1995) confirms the hypothesis that the species of Asteraceae are indeed most closely linked with those on the South American continent.

According to Carlquist (1974), relicts in the strictest sense are scarce on oceanic islands (i.e., if primitive forms have migrated to islands and the mainland remnants have become extinguished recently, the insular representatives appear as relicts). The Juan Fernandez archipelago is outstanding because it has two relicts: *Lactoris fernandeziana* and *Thyrsopteris elegans*, regrettably both considered endangered (Stuessy et al. 1998b, 1998c). *Lactoris fernandeziana* is a so-called paleoherb that constitutes a monotypic dicotyledonous family; it is now exclusively confined to Isla Robinson Crusoe, but around 70–90 million years ago it was more widely distributed in the Southern hemisphere (Stuessy et al. 1998a; Macphail et al. 1999). Today, there are only a few populations isolated in the highest reaches of the island, but fortunately each contains dozens of plants (Bernardello et al. 2002). The second relict, *T. elegans*, is a monotypic genus of ferns in the Dicksoniaceae that was distributed in Mesozoic forests 80–170 million years ago in both hemispheres (Moran 1993), but now lives solely on the two large Juan Fernandez islands (Robinson Crusoe and Alejandro Selkirk), where it is an important component of the upper montane forest communities (Greimler et al. 2002).

Two species are likely extinct: the Fernandezian endemic sandalwood, *Santalum fernandezianum*, the last tree photographed in 1908 (Skottsberg 1910; Stuessy et al. 1998b, 1998c), and the monotypic endemic grass genus *Podophorus bromoides* (Baeza et al. 2002).

Migration to islands is chiefly governed by chance (Carlquist 1981), although habitat availability is a significant factor determining the composition and size of a flora (Kingston et al. 2003). After arrival, selection must have operated, selecting propagules, and their attributes for success-

ful establishment. The disproportionate occurrence of certain attributes in the flora (for instance, dry fruits, small to medium dispersal units, as reported here) may be evidence for dispersal-mediated species selection.

Among the several agents of long-distance initial dispersal, land or sea birds seem to have been the most important vector in bringing plant colonizers to this archipelago (around 90% of the species). Long-distance bird transport of fruits and seeds, either externally or internally, is generally regarded as the most common long-distance dispersal mechanism (cf. Carlquist 1974; Cox and Moore 1993). In particular, for the high islands of the Pacific, migratory birds are generally suggested as the primary method of arrival for most groups of angiosperms (Ridley 1930; Carlquist 1974; Porter 1976; Ono 1991). Carlquist (1974) supported the primacy of bird dispersal for the Juan Fernandez, though as indicated in the introduction, there are few bird species associated with these small and isolated islands.

The other primary initial dispersal agent emerging from our analysis is air flotation. Carlquist's (1974) general estimates for islands of the eastern Pacific and Polynesia, as well as those for the Juan Fernandez, attribute less importance than we do to anemochorous dispersal. Finally, oceanic drift would have been negligible, although it was proposed as significant for several Indian Ocean and other Pacific Ocean islands (Guppy 1890; Carlquist 1974; Murray 1986; Green 1999).

Carlquist's comprehensive work (1974) allows us to make comparisons with other archipelagos, in particular, the Galapagos Islands. The proportions for different arrival modes are analogous percentages, except for drift and air flotation, where Carlquist (1974) proposes higher percentages for the Galapagos than we think evident on Juan Fernandez. The Juan Fernandez Islands are closer to the South American continent than the Galapagos, on which basis we might expect passive mechanisms like drift to account for more dispersal. However the patterns of ocean currents (the Humboldt current flows north from the Antarctic along the west coast of South America to southern Ecuador, then west; Akin 1991) and the prevailing winds (trade winds circulate counter-clockwise around a high-pressure center located at about the Juan Fernandez Islands, turning west near the equator; Akin 1991) may be responsible explanations for the differences found.

Fleshy fruits are adapted for vertebrate dispersal (van der Pijl 1982), are very common in most tropical and subtropical rain forests, and are moderately common in some north temperate forests and some south temperate moist forests (Willson et al. 1989). Given that internal dispersal by birds is the most common long-distance dispersal mechanism for oceanic islands (Ridley 1930; Carlquist 1974; Burrows 1994; Lord 1999), it might be expected that the Juan Fernandez flora contains a high proportion of species possessing fleshy fruits. However, our data show that fleshy fruited forms account for only 20% of the flora. The explanation does not seem to lie in the nature of the primary source flora, in that data from the flora for mainland temperate forest species of Chile and Argentina show that ca. 42% bear fleshy fruits (Donoso Zegers 1993).

It is obvious that chance is also essential in determining what disseminules arrive, although hydrochory and endozo-

chory are mechanisms in which there is greater likelihood of more than one propagule arriving together. For hermaphroditic, self-compatible species, a single individual may be sufficient for establishment (Baker 1967). But for dioecious or self-incompatible species, more than one disseminule or dispersal event is needed. In this context, perennial plants have been alleged to possess an advantage over annuals, because their longevity increases the likelihood of "finding" a mate, achieving successful outcrossing, and securing sufficient pollination to produce seeds to establish and maintain a species (Wallace 1895; Böhle et al. 1996). Data available on the Juan Fernandez flora (Bernardello et al. 2002) support these trends: the flora is typically composed of perennials, most species are hermaphroditic, and most of the species for which data are available are self-compatible.

Current levels of endemism in oceanic islands are the result of the ease with which certain highly dispersible groups can cross ocean gaps (McGlone et al. 2001). In addition, the presence of certain taxa in island systems from a given area may indicate an ancestral capability for long-distance dispersal. For instance, the Asteraceae, mainly wind dispersed, have four endemic genera in the Juan Fernandez and the Galapagos Islands, and seven in Hawaii (Wiggins and Porter 1971; Wagner et al. 1990). Also the wind- and bird-dispersed Cyperaceae and Poaceae have several endemic species in these three archipelagos. However, many of these genera may be the result of a single introduction, therefore in addition to the propensity to disperse, the ability of colonizers to establish and then radiate and speciate is significant.

The following nonendemic genera, shared by the Juan Fernandez and Galapagos Islands, suggest that they are highly dispersible: *Callitriche* (Callitrichaceae), *Centella* (Apiaceae), *Dichondra* (Convolvulaceae), *Nicotiana* (Solanaceae), *Parietaria* (Urticaceae), *Pernettya* (Ericaceae), and *Sarcocornia* (Chenopodiaceae). In addition, *Fagara* (Rutaceae), *Lobelia* (Campanulaceae), *Peperomia* (Piperaceae), *Plantago* (Plantaginaceae), *Ranunculus* (Ranunculaceae), and *Solanum* (Solanaceae) are shared by these two archipelagos and the remote Hawaiian archipelago as well. In addition to the families cited above, the Brassicaceae, Boraginaceae, Caryophyllaceae, Euphorbiaceae, Fabaceae, Iridaceae, Juncaceae, Lamiaceae, Myrtaceae, Portulacaceae, Rhamnaceae, Rubiaceae, Scrophulariaceae, and Verbenaceae are common to the three island systems, suggesting capacity for long-distance dispersal and establishment.

Interestingly, the highly dispersible Orchidaceae (with exceedingly small seeds, apparently dispersed as easily as the spores of often ubiquitous ferns) is rare in the Juan Fernandez, with only one species endemic (on the more distant and younger Isla Alejandro Selkirk). The absence of insect pollinators or the fact that the symbiotic fungus needed for their germination is missing may provide explanations for the virtual absence of orchids on the Juan Fernandez.

Curiously, the Amaranthaceae, Cucurbitaceae, Cuscutaceae, and Apocynaceae that are families widespread in the South American flora, are not present on the Juan Fernandez, though there are representatives in the Galapagos and Hawaii. In addition, Boraginaceae, Convolvulaceae, and Euphorbiaceae, are under-represented in the Juan Fernandez

based on comparisons with the other two archipelagos and with the source flora.

An assessment of the current dispersal mechanisms in operation for the Fernandezian flora shows that the majority of the species have abiotic dispersal, chiefly autochory and anemochory. This fact may reflect either the ancestral dispersal capability of the colonizers, or the absence of a conspicuous fauna to disperse seeds and fruits. The few land and sea bird species associated with these islands (Lönnerberg 1921; Brooke 1987) disperse 20% of the plant species in two ways: actively by carrying seeds and fruits in their digestive tracts (endozoic) or passively by adhesion to their external body surfaces (ectozoic). Unfortunately, the birds also disperse the most aggressive noxious introduced invasives, such as *Rubus ulmifolius*, *Aristotelia chilensis*, and *Ugni molinae*. The invasives have severely affected the native vegetation leading to a significant decrease of endemic plants in the montane forests and native shrublands (Dirnböck et al. 2003). Unfortunately, the newly arrived and potentially dangerous alien species *Lantana camara* and *Lonicera japonica* (Swenson et al. 1997) are also bird dispersed. In addition to the damage that these aggressive invasives cause in terms of displacing the autochthonous species, there is a perhaps even more pernicious aspect of their presence. That is, the fruits of these invasives are often preferred by the native bird dispersers. This preference leads to decreased native plant dispersal, and simultaneous enhancement of the dispersal of the introduced invasives, spreading the latter further and faster, and at the expense of the natives. A notable feature of many island colonizers, both animals and plants, that have become adapted to oceanic islands is the postestablishment loss of dispersal ability (Darwin 1855; Zimmerman 1948; Carlquist 1965, 1974; Roff 1990; Eliasson 1995). Obviously, dispersal mechanisms and dispersal ability are likely to be selected against, because those that retain good dispersal mechanisms are more likely to have more propagules lost to the surrounding sea than those with poor dispersal.

Although most Fernandezian species seem to have retained the dispersal mode of their ancestral immigrants, the four endemic genera of Asteraceae (see above) are a noteworthy exception. This family is known for having lost dispersibility in other archipelagos (Carlquist 1966, 1974; Cody and Overton 1996). The primary dispersal mode of its members is anemochory, but there is a trend towards diaspores with lower dispersibility in oceanic island species (Carlquist 1966, 1974; Cody and Overton 1996). In the particular case of the Juan Fernandez Islands, Carlquist (1966, 1974) suggested that the first Asteraceae colonizers adapted to the wet forest and lost dispersibility chiefly because of this ecological shift.

In many ways the diversity of the flora is impressive given how young the islands are, how remote they are, and the small bird fauna associated with them. In previous work, we discussed the establishment and evolution of the flora in the context of very few pollination and (or) reproductive options (e.g., Anderson et al. 2001; Bernardello et al. 2002). This present study makes it clear that elements associated with dispersal are also analogously limited. The biota of the Juan Fernandez is interesting from many vantage points in-

cluding as a paradigm for establishment and persistence in the face of strong distance, size, and age “filters”.

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