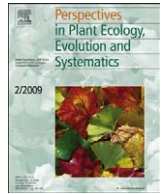




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Review

Conservation of oceanic island floras: Present and future global challenges

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ABSTRACT

Current threats to the planet's biodiversity are unprecedented, and they particularly imperil insular floras. In this investigation, we use the threat factors identified by the Millennium Ecosystem Assessment as the main drivers of biodiversity loss on islands to define and rank 13 current, continuing threats to the plant diversity of nine focal archipelagos where volcanic origin (or in the Seychelles a prolonged isolation after a continental origin) has produced a high degree of endemism and fragility in the face of habitat alteration. We also conduct a global endangerment assessment based on the numbers of insular endemic plants in the endangered (EN) and critically endangered (CR) IUCN categories for 53 island groups with an estimated 9951 endemic plant species, providing a representative sample of the world's insular systems and their floristic richness. Our analyses indicate that isolation does not significantly influence endangerment, but plant endemics from very small islands are more often critically endangered. We estimate that between 3500 and 6800 of the estimated 70,000 insular endemic plant species worldwide might be highly threatened (CR+EN) and between ca. 2000 and 2800 of them in critical danger of extinction (CR). Based on these analyses, and on a worldwide literature review of the biological threat factors considered, we identify challenging questions for conservation research, asking (i) what are the most urgent priorities for the conservation of insular species and floras, and (ii) with the knowledge and assets available, how can we improve the impact of conservation science and practice on the preservation of island biodiversity? Our analysis indicates that the synergistic action of many threat factors can induce major ecological disturbances, leading to multiple extinctions. We review weaknesses and strengths in conservation research and management in the nine focal archipelagos, and highlight the urgent need for conservation scientists to share knowledge and expertise, identify and discuss common challenges, and formulate multi-disciplinary conservation objectives for insular plant endemics worldwide. To our knowledge, this is the most up-to-date and comprehensive survey yet to review the threat factors to native plants on oceanic islands and define priority research questions.

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Islands are an enormously important source of information and an unparalleled testing ground for various scientific theories. But this very importance imposes an obligation on us. Their biota is vulnerable and precious. We must protect it. We have an obligation to hand over these unique faunas and floras with a minimum of loss from generation to generation.

Ernst Mayr (1967)

Introduction

Islands are of particular importance for the conservation of global plant diversity. Although they make up only some 5% of the Earth's land surface, about one quarter of all known extant vascular plant species are endemic to islands (Kreft et al., 2008). Indices of vascular plant diversity are markedly higher for islands than for continental areas (Kier et al., 2009), and 20 of the 34 biodiversity hotspots defined by Conservation International (Myers et al., 2000, and updates in <http://www.biodiversityhotspots.org>) are islands, or have an important insular component. In addition to this legacy of a unique evolutionary history, insular ecosystems are also key to the livelihood, economy, well-being and cultural identity of 600 million islanders, roughly one-tenth of today's world population (Lutchman et al., 2005).

Humans have heavily affected island ecosystems (Millennium Ecosystem Assessment [MEA], 2005; Whittaker and Fernández-Palacios, 2007; Kingsford et al., 2009). For instance, of some 80 documented plant extinctions in the last 400 years, about 50 were island species (Sax and Gaines, 2008). In the near future, human pressure on ecosystems will likely increase more markedly on islands than on continents (Brooks et al., 2002; Millennium Ecosystem Assessment [MEA], 2005; Kier et al., 2009). The small population sizes and ranges of island organisms, and their unique characteristics resulting from prolonged evolutionary isolation, make them particularly sensitive to anthropogenic change (Frankham, 1998). All of these features make islands invaluable but fragile and vulnerable arks of biodiversity.

Island plant conservationists are thus faced with a huge global conservation challenge. Nevertheless, contact among researchers and managers of threatened plants on different archipelagos has been limited (for example in Macaronesia, Caujapé-Castells et al.,

2006, 2007a, b), although some local or regional surveys of endangerment patterns on different oceanic archipelagos have been carried out (Médail and Quezel, 1997; Jaffre et al., 1998; Broughton and McAdam, 2002; Sakai et al., 2002; Kingston and Waldren, 2005; Strasberg et al., 2005; Danton and Perrier, 2006; Maunder et al., 2008; Reyes-Betancort et al., 2008). Wider discussions of conservation issues common to different island systems have happened sporadically, but researchers in different regions have rarely synthesized their conclusions, and global comparisons are lacking.

We present here what we believe is the first comprehensive synthesis of plant conservation issues across major oceanic archipelagos. For nine focal island groups (Azores, Madeira, Canary Islands, Cape Verde, Hawaii, Galápagos, Juan Fernández, Mascarenes, Seychelles) we review the threats to native floras and the present state of conservation research and practice. The nine archipelagos belong to eight countries and three oceans: Atlantic, Pacific and Indian. We complement this with a literature review and an analysis of patterns of endangerment covering 62 additional island groups, providing quantitative estimates of threats to island floras worldwide. We compare across archipelagos the patterns of endangerment, threat factors, and research results that have been successfully incorporated into management practices. We review the present resources and weaknesses in particular archipelagos, identify individual and shared knowledge gaps, and use these to suggest priorities for future research. We suggest how existing scientific knowledge may be used to identify additional knowledge gaps, launch priority studies to generate the necessary information, and develop strategies to preserve island floras. We also discuss results and experiences that extend beyond the local context. We believe that, beyond its local relevance, plant conservation research on oceanic islands can also serve as a model for continents and shed light on general topics in ecology (Kueffer et al., 2010; Kaiser-Bunbury et al., 2010).

In particular, we address the following questions:

- What is the level of endangerment of oceanic island vascular plants, and how does it differ between island groups?
- What are the main threats to endemic vascular plants on oceanic islands, and how does the relevance of these factors vary among island groups?

- What is known about the underlying mechanisms through which the different threat factors affect island plant diversity?
- What future research and management are needed to conserve island plant diversity?

Methods

Focal study system

A sample of nine tropical and sub-tropical oceanic archipelagos was selected for analysis: Galápagos, Hawaii and Juan Fernández

in the Pacific Ocean, the Mascarenes and the granitic islands of the inner Seychelles in the Western Indian Ocean, and Madeira (plus the Selvagens), Azores, Canary Islands, and Cape Verde in Macaronesia (Atlantic Ocean). This represents a broad geographic sample (Fig. 1), encompassing 59 main islands and ca. 268 minor islands, and ranging widely in physical, geographic, floristic, and socioeconomic characteristics (Tables 1 and 2). The main islands of the Seychelles are formed of granitic bedrock of continental origin, while all other focal islands are true oceanic islands of volcanic origin. Total endemic vascular plant species richness can be divided into three size classes: fewer than 100 species (Azores, Cape Verde, Seychelles), 100–200 species (Galápagos, Juan

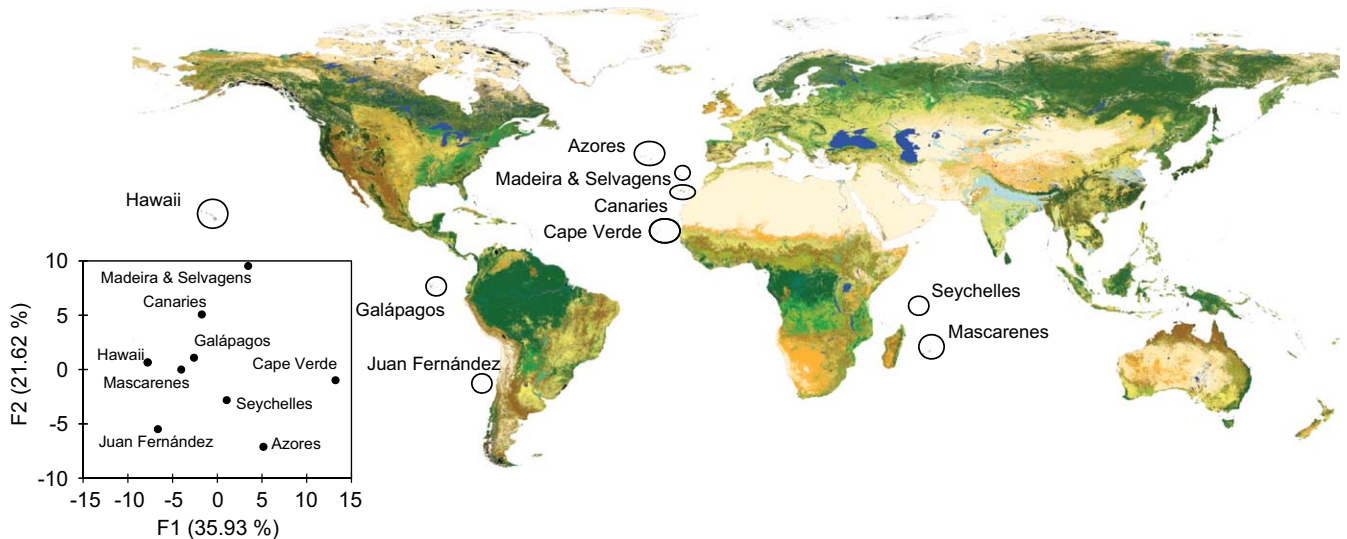


Fig. 1. Geographical location of the nine focal archipelagos, and their position in the multivariate space defined by the two first axes of the PCA analysis (see section “Methods”). This representation explains 57.55% of the detected inter-archipelago variability in the impact of the 13 threat factors considered on the decline of insular endemic plant diversity.

Table 1

Physico-geographical features of the island systems considered, and indicators of protection of the endemic flora.

Archipelago	NI	dm	di	Di	A	nat	pro	Ma	ma	h	C	δ	T	\$
Azores	9	1343	6	615	2332	ca. 22 ^a	ca. 20	8	0.25	2531	243,018 (2006)	ca. 105	858,832 ^b	T,I,A
Canaries	7	95	5	485	7545	ca. 15	ca. 40	20.6	1.12	3718	2,025,951 (2008)	ca. 269	9,326,116	T,I,A
Cape Verde	9	576	ca. 15	279	4033	2	0.2 ^c	7.6 ^d	3.2 ^d	2829	426,998 (2008)	ca. 102	312,880	T,A
Galápagos	14	1000	4	141	7900	2 ^e	96	4	0.07	1700	ca. 25,000 (2006)	ca. 3	ca.150,000	T,C,A
Hawaii	8 ^f	3900	ca. 11	128	16,636	ca. 27	ca. 5 ^g	5.1 ^h	0.43	4205	1,283,388 (2007)	ca. 77	7,627,819	T,A,Mi
Juan Fernández	3	590	1	150	100	1	ca. 90	5.8	1.0	1320	600 (2005)	ca. 6	ca. 3000	A,T,G
Madeira & Selvagens	2	630	57	57	794	5	ca. 67	18	5	1861	246,689 (2007)	ca. 307	988,692	T,I,A
Mascarenes	3	665 ⁱ	164	740	4528	21	25 ^j	10	3	3070	2,061,546 (2008)	ca. 455	1,342,839	T,S,M
Seychelles	4	⁹ 930 ⁱ	4.5	50	235	7	16	65 ^k	60 ^l	915	81,000 (2002)	ca. 345	ca. 161,000	T,A

An island is defined as any land mass isolated by sea from other land masses at all stages of the annual tidal cycle, and able to support at least one species of terrestrial plant (i.e., other than mangroves, etc.). NI: number of main islands; dm: minimum distance to the mainland (in Km); di: minimum distance between two main islands (in km); Di: maximum distance between two main islands (in Km); A: total land area (in km²); nat: number of nature reserves and national parks; pro: percentage of the land area that is protected by law; Ma: maximum estimated island age of the present main islands (upper estimate, in my); ma: minimum estimated island age of the present main islands (upper estimate, in my); h: maximum height (in m); C: number of censused inhabitants (census year); δ: population density; T: number of tourists that visited the archipelago in 2007. \$: main economic activities of the islands, in order of importance [codes are A: agriculture, livestock and fishery, C: conservation, G: government employment, I: industry (including construction and wine industry), M: manufactures, Mi: military, S: sugar production, T: tourism and services].

^a Apart of the 13 existing Nature preserves, each of the 9 islands will have a single natural park encompassing the areas of relevancy for conservation.

^b This figure corresponds to stays in traditional hotels.

^c World resources institute, <http://earthtrends.wri.org/text/biodiversity-protected/country-profile-34.html>.

^d Data communicated by J. Richard Wilson (jrw@geo.au.dk); the island of Maio has geological formations from the Jurassic (ca. 160 mya).

^e These occupy 96% of the land area (Galápagos National Park) and the entire sea area around the archipelago (Galápagos Marine Reserve).

^f 10 smaller land masses, included in the total of 124 small islands, reefs, and shoals (see http://www.soest.hawaii.edu/GG/HCV/haw_volc.html).

^g This is the estimate of the area really protected and managed for biodiversity (other areas are protected in the state natural reserve area, but with no enforcement, some are protected because they are on military land so access is limited, some are managed by The Nature Conservancy).

^h There are islands no longer above sea level that date back to about 64.7 Ma (see http://www.soest.hawaii.edu/GG/HCV/haw_formation.html).

ⁱ To Madagascar.

^j The exact area of the national park in Réunion may change as an area may be excised from it to enable geothermal prospecting.

^k This is the probable date of separation of Seychelles and India, i.e. complete isolation of the Seychelles islands. The bedrock granite of the islands is up to 750 Ma old.

^l Age of youngest main island Silhouette.

Fernández and Madeira-Selvagens), and more than 600 species (Hawaii, the Mascarenes and the Canaries). If we consider number of endemic species per km², Juan Fernández (1.33) is by far the most diverse system, followed by Seychelles (0.29), Madeira-Selvagens (0.17), the Mascarenes (0.15), Canaries (0.08), Hawaii (0.06), Azores (0.03), Galápagos (0.022) and Cape Verde (0.020).

From the vast area of Oceania, we included only Hawaii among our focal archipelagos, as the information available for other archipelagos from this region is scarce, at best. Conservation International identified plants from Polynesia-Micronesia as a key information gap for red listing (http://www.conservation.org/explore/priority_areas/hotspots/asia-pacific/Polynesia-Micronesia/Pages/conservation.aspx), and a recent red-list review for Oceania (Pippard, 2009) shows that only ca. 5% of Dicots and 1% of Monocots have been assessed for the IUCN red list. However,

many of the Oceania archipelagos are included among our broader sample of 62 island groups. Our focal archipelagos also do not include the Caribbean, but plant conservation in that region is well covered in a recent review by Maunder et al. (2008), and many Caribbean islands are included in our broader sample.

Expert survey

A questionnaire on floristic, geographic, and socioeconomic aspects of the nine focal archipelagos was completed by the participating authors, with help from others knowledgeable about their archipelagos (see Acknowledgements), and the responses were used to construct Tables 1 and 2. The contributing experts then developed a conceptual framework of 13 threat factors on

Table 2
Indicators of botanical richness of the nine focal archipelagos, and main geographical links of their floras (in order of importance).

Archipelago	G	sp	lsp	%end	%red	Ext	Major geographical links of the present endemic flora
Azores	1 (1)	72 ^a	5	ca. 7	^b	1	Western Europe, Canaries-Madeira, N-A
Canaries	23 (49)	ca. 607 ^c	ca.399	ca. 45	ca. 30	2	MED, Saharan W-A, E-A, Arabian peninsula, S-A, NW
Cape Verde	1 (7)	82 ^d	30	34	ca. 43	3	MED, Canaries-Madeira, NW-A
Galápagos	7 (35)	180 ^e	40	ca. 35	ca. 60	3	S-Am coast, Andes, Caribbean, SW-North America
Hawaii	32 (288)	929 ^f	624	90 ^{g,h}	ca. 53 ^{g,h}	ca. 100 ^g	Pacific, widespread, neotropical, N-temperate, Austro-Malaysia
Juan Fernández	12 (33)	133 ⁱ	101	ca. 94	ca. 75	< 6	S-Am, Pantropical, New Zealand
Madeira & Selvagens	5 (11)	136 ^j	94	ca. 13	49	1	MED
Mascarenes	35(81)	ca. 688 ^{g,k}	547	72	ca. 50	ca. 40	Africa/Madagascar, Indo-Malaysia
Seychelles	12 (13) ^g	ca. 70 ^l	ca. 14 ^g	ca. 40	71	2 < Ext < 5	Africa/Madagascar, Indo-Malaysia
Total	129 (518)	ca. 2897	ca. 1854	ca. 48	ca. 54	ca. 160	

G: number of endemic genera (species); sp: total endemic species; lsp: number of endemic species exclusive from a single island; %end: proportion of plant endemism; %red: proportion of endemic taxa that are in the red list under some kind of threat (CR/EN/VU); Ext: reported historical extinctions of plants; Geographical links' abbreviations are A: Africa, Am: America, MED: Mediterranean, NW: new world.

^a Silva et al. (2005a) and Mónica Moura (unpubl. data).

^b Although the Azores currently lack a Red List, information on anthropogenic threats, natural risks, biological limitations, conservation actions proposed and research needs for the 90 most endangered plants in this archipelago will be available with the impending publication of the book "Açorean Vascular Flora: Priorities in Conservation".

^c Aceves-Ginové et al. (2004) and Arnaldo Santos-Guerra (unpubl. data).

^d Sánchez-Pinto et al. (2005) and Wolfram Lobin (unpubl. data).

^e Wiggins and Porter (1971) and Alan Tye (unpubl. data).

^f Wagner et al. (2005) and Ann Sakai (unpubl. data).

^g Data for flowering plants only.

^h See Sakai et al. (2002).

ⁱ Marticorena et al., (1998) and Daniel J. Crawford (unpubl. data).

^j Jardim and Sequeira (2008).

^k <http://www.plantmasc.org/>.

^l Kueffer et al. (2007a) and Katy Beaver (unpubl. data).

Table 3
Ranks (numbered in decreasing order of importance, ties allowed) and relevances (A: not present, or of low relevance; B: relevant factor, but not considered a priority threat; C: priority threat factor, a potential major driver of plant diversity loss; D: data deficient) of the 13 threats to the endemic plant biodiversity assessed in the nine focal archipelagos.

Threats	AZO	CAN	CAP	GAL	HAW	JUA	MAD	MAS	SEY
Biological									
Small population sizes and fragmentation	1C	6B	4C	9B	5C	4C	9B	6C	1C
Lost mutualisms	11A	12D	5A	12D	10B	6B	11D	11A	10D
Habitat alteration and destruction	1C	4C	1C	3B	4C	3C	4C	3C	4B
Invasive alien plant species	1C	2C	8C	2C	1C	2C	3C	1C	2B
Invasive alien invertebrates and pathogens	12A	7B	12B	7C	1C	10D	6B	10A	3B
Invasive alien vertebrates	10B	1C	13A	1C	1C	1C	5C	2C	9A,D ^a
Climate change and pollution	13A	13D	7A	12D	6C	12A	8D	12A	11D
Socio-economic									
Demographic and economic growth	5C	3C	2B	3C	11C	13A	1C	7C	5B
Tourism	9B	5C	6B	11B	11B	7B	2C	4C	7B
Lack of laws or enforcement	6C	10A	11B	3B	7C	5B	13A	8B	6B
Poor education and awareness	8B	9B	9B	10C	9C	9B	12A	9B	9B
Overexploitation	4C	8C	3C	3B	8C	11B	7B	13A	8B
Lack of natural resource management capacity	6C	11C	10C	8C	11C	8B	10B	5C	6B

Shadowed cells signal priority threat factors, irrespective of their ranked importance. Abbreviations are the first three letters of each focal archipelago's name.

^a A: grazers, D: rodents.

the nine archipelagos (Table 3), based on the five threats identified by the Millennium Ecosystem Assessment [MEA] (2005) as the main drivers of biodiversity decline on islands, namely habitat change, climate change, invasive alien species, over-exploitation, and pollution. For more detailed analysis of the threats considered important on many of these archipelagos, 'habitat change' and 'over-exploitation' were represented in this assessment by Tourism impact, Habitat alteration and destruction (including land use change), Demographic and economic growth, Overexploitation, and Small population sizes and fragmentation. Similarly, 'invasive alien species' was split into Invasive alien plants, Invasive alien vertebrates, and Invasive alien invertebrates and pathogens (see Table 3). Climate change and pollution were assessed jointly, as their predicted effects on plant biodiversity do not lend themselves to easy quantification. We also considered threats related to socio-economic factors not highlighted by the MEA. The ranks of the 13 resulting threat factors (Table 3) were standardized and used to carry out a principal component analysis (PCA, Fig. 1) based on the matrix of pairwise variances-covariances among them.

Though the MEA assesses both past and future threats, our rankings were based only on the current, continuing impacts of the 13 factors considered, not on their influence in the past, when their relative importance often differed from what it is today. We also considered only their direct impacts on plant biodiversity, rather than indirect impacts via other threat factors. So for

example, tourism is ranked in terms of its direct impacts on plant communities or populations of rare plants, such as visitor pressure or the construction of tourist installations, and demographic growth is ranked on the direct impacts of increasing numbers of residents and their required infrastructure. The experts then assessed the current or short-term relevance of each threat factor based on four categories (see Table 3), and a conceptual representation of the most important interactions among the threat factors (Fig. 2) was drawn to complement the PCA. The main weaknesses and strengths of conservation research on each focal archipelago were summarized (Appendix 1) to help identify future priorities for local conservation action and global collaboration.

Endangerment analysis of the world's insular plant endemics

To provide quantitative information on patterns of endangerment in insular systems of the world, the IUCN red list database (www.redlist.org) was searched for endangered (EN) and critically endangered (CR) island plant species and subspecies. After sifting the records for 62 island groups, assigning each taxon to its islands of distribution and eliminating nine outliers, we remained with 53 island groups (see Appendix 2). Of the nine outliers, Antigua and Barbuda, Barbados, Montserrat, Saint Kitts and Nevis, and the Virgin Islands were excluded because of their very low number of endemic species, and/or of inconsistencies between the

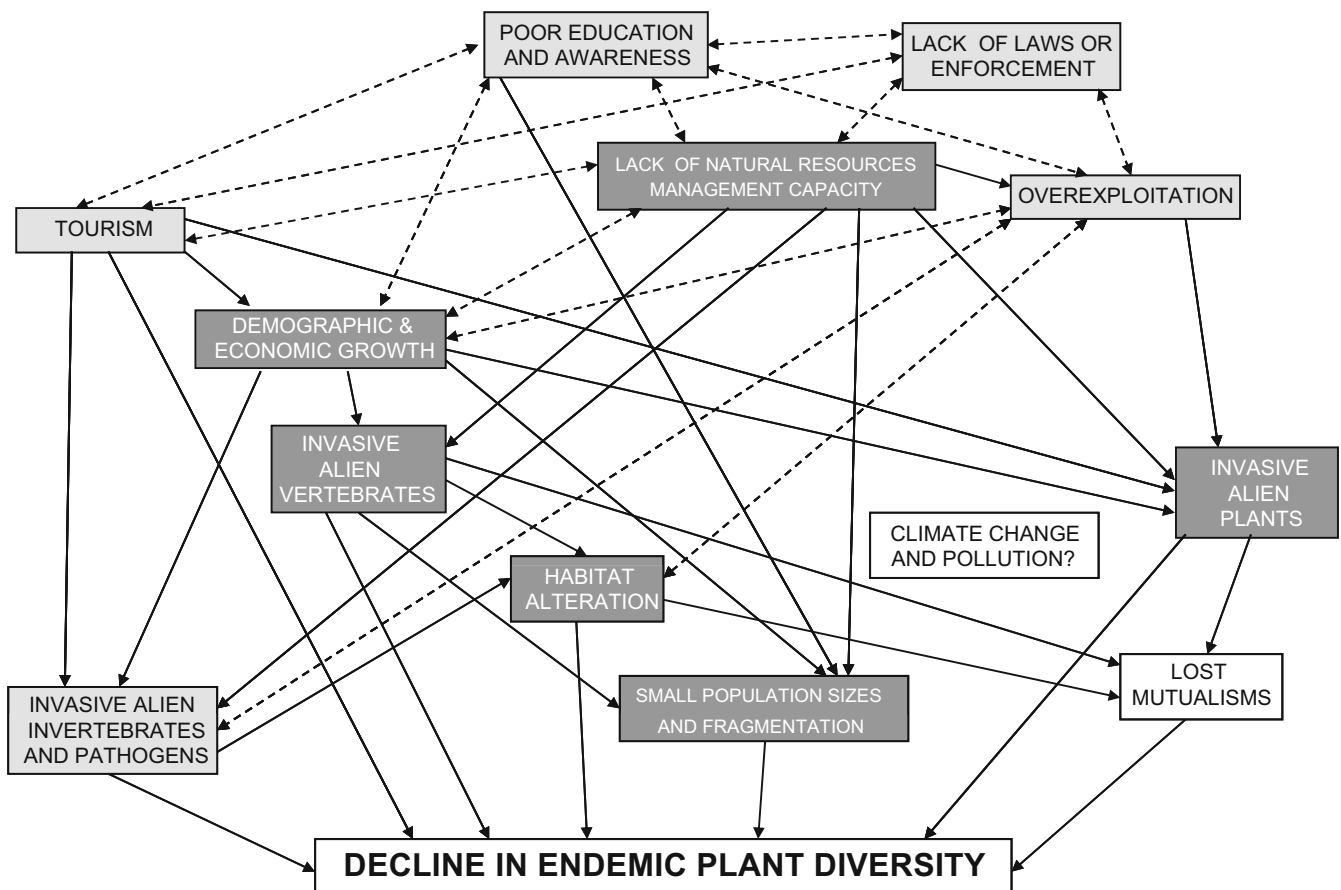


Fig. 2. Conceptual representation of some of the major interactions among the 13 threat factors considered in this paper, and of their impact on the decline of plant endemic diversity. For clarity, not all possible relationships, feedbacks or multiple level interactions among factors are shown. Arrows indicate only the predominant direction(s) of relationships that exacerbate related factors; for instance, poor education could result in a decrease of the effectiveness of laws to protect biodiversity or enforcement thereof, and could also lead to an increase in demographic growth. Two-headed arrows are connected by dashed lines. We refrained from linking arrows to 'Climate change and pollution' because the interactions between this factor and the others are probably manifold, but not yet well known and thus difficult to quantify (see text). Box fillings indicate factors that were identified as major drivers of plant diversity loss in 5 or more of the focal archipelagos (dark gray filling), in between 2 and four of them (light gray filling), and in one or none of them (no filling).

data in the red list and the estimated number of endemic species (i.e. more CR or EN species than endemics described in the corresponding literature source); Madagascar, Borneo, Papua New Guinea, and New Caledonia were excluded because the extremely high numbers of endemics on these islands of continental origin fall clearly outside the overall pattern of distribution. Correlation analyses were run between the proportions of EN and CR taxa in the total endemic flora in each of the remaining 53 archipelagos

and the \log_{10} of the archipelago's land area in km^2 (Appendix 2, Fig. 3). We calculated the proportions of “highly threatened” (CR+EN) and critically endangered (CR) taxa in our sample by (i) dividing the total number of species and subspecies in the (CR+EN) and CR IUCN categories by the total 9951 endemic species, and (ii) calculating the proportion of (CR+EN) and CR taxa in each archipelago relative to the estimated number of endemic species in that archipelago, and then averaging these proportions

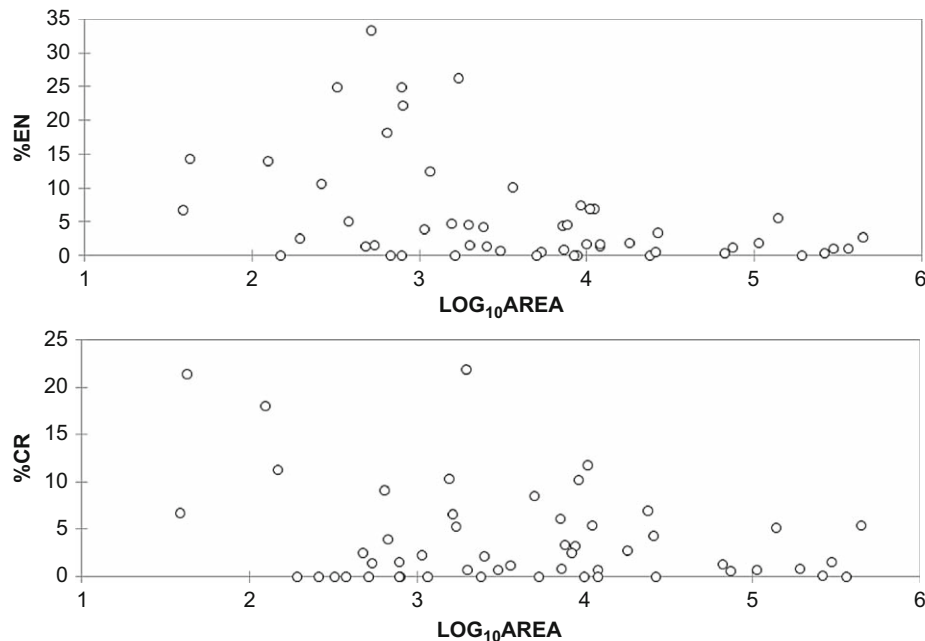


Fig. 3. Proportions of EN and CR taxa with respect to total endemic species in the 53 archipelagos included in the global statistical analysis, plotted against \log_{10} of archipelago land area (in km^2).

Table 4

Averages and Kruskal–Wallis test significances in five factors tested for the number of endemic vascular plant species per unit area, proportion of critically endangered species (CR) and proportion of endangered species (EN) in the 53 islands/island groups analyzed.

Categories tested	Endemics/area	%CR	%EN	%CR+EN
Island size				
Very small [16]	0.181	4.741	11.212	15.953
Small [23]	0.056	4.778	4.452	9.230
Large [14]	0.011	1.660	1.593	3.254
	(< 0.0001)***	(0.181)	(0.044)*	(0.002)**
Isolation Index				
5 < II < 80 [40]	0.052	2.828	5.326	8.155
II > 80 [13]	0.173	7.374	7.003	14.377
	(< 0.0001)***	(0.063)	(0.263)	(0.102)
Geographic region				
Pacific Ocean [17]	0.123	4.135	4.392	8.527
Atlantic Ocean [21]	0.081	2.772	9.240	12.012
Indian Ocean [10]	0.049	5.507	3.486	8.993
Mediterranean Sea [5]	0.013	5.083	0.106	5.189
	(0.278)	(0.044)*	(0.002)**	(0.831)
Atlantic Ocean				
East Atlantic [6]	0.150	3.382	3.826	7.244
Caribbean [15]	0.053	2.528	11.392	13.919
	(0.062)	(0.866)	(0.062)	(0.161)
Pacific Ocean				
Asia & Oceania [13]	0.058	1.732	3.773	5.505
Eastern Pacific Ocean islands [4]	0.334	11.943	6.405	18.348
	(0.089)	(0.006)**	(0.212)	(0.009)**

Island size designations are: “very small”: area < 1000 km^2 ; “small”: 1000 km^2 < area < 15,000 km^2 ; and “large”: area > 15,000 km^2 . Higher values of the isolation index (II) correspond to more remote islands (see Appendix 2 for explanation). Numbers in brackets after the sub-category names are the numbers of island groups included in each test. Numbers in parentheses under the averages indicate the respective *P* values for each variable and category tested.

***: *P* < 0.001; **: *P* < 0.01; *: *P* < 0.05.

for the 53 archipelagos. Subsequently, these proportions were used to estimate how many of the 70,000 plant species thought to be endemic to the world's islands (Kreft et al., 2008) could be highly threatened (CR+EN), or critically endangered (CR). Finally, we tested the influence of five factors related to island size, isolation and geographic location on the numbers of endemic taxa per unit area and of the numbers of taxa in the EN and CR IUCN categories using Kruskal–Wallis tests (Table 4). All statistical analyses were carried out with XLSTAT 2009.1.01 (Addinsoft, 2009).

Results and discussion

We first discuss the limitations of plant diversity data on oceanic islands, then present the global endangerment analysis, followed by the threat analysis of the nine focal archipelagos. Our threat analysis is based on taxa assessed as threatened by the IUCN red-list process, so species not assessed by red-list criteria are not included. However, focal archipelagos were chosen on the basis that they have a high proportion of their endemic vascular plant taxa assessed, so the main gap is consideration of widely distributed threatened plant taxa. Although some of these may be globally threatened and should be part of conservation strategies, they cannot be readily included in this type of analysis. However, we consider that an archipelago comparison based on endemics reveals adequately patterns of threat, endangerment and conservation requirements.

Because the threat factors assessed may act differently in archipelagos not included in the focal group, a literature review of the impacts of the biological threat factors across archipelagos worldwide complements the above-detailed analysis, allowing us to generalize findings to a global scale. Finally, we highlight some major implications of our assessments. Important socioeconomic and cultural factors such as differences among archipelagos in the per capita incomes or in education and awareness are not comprehensively treated, as we focus our analyses on the biological factors. However, underlying socioeconomic factors are included among the threat factors considered, and some of them are highlighted as priorities to be addressed in many of the focal archipelagos (Appendix 1), as well as for others included in our broader sample.

Documentation of plant diversity on oceanic islands: status and future prospects

Because successful conservation requires reliable identification and population estimates, understanding the state of our knowledge of these two factors is critical.

Taxonomic knowledge varies sharply between archipelagos. Published floras or checklists exist for most oceanic islands, including most of our nine focal archipelagos (e.g. Wiggins and Porter, 1971; Lawesson et al., 1987; Acebes-Ginovés et al., 2004; Silva et al., 2005a; Sánchez-Pinto et al., 2005; Jardim and Sequeira, 2008). Some are accessible on the Web (e.g. Hawaii [<http://botany.si.edu/pacificislandbiodiversity/hawaiianflora/>], the Marquesas [<http://botany.si.edu/pacificislandbiodiversity/marquesasflora/index.htm>], the Cook Islands [<http://cookislands.bishopmuseum.org/search.asp>], French Polynesia [<http://www.herbier-tahiti.pf>], La Réunion [<http://flore.cbnm.org/>], the West Indies [<http://persoon.si.edu/antilles/westindies/index.htm>], the Greater Antilles [<http://www.nybg.org/bsci/fga/>]). However, for very few islands have all taxonomic groups been treated thoroughly.

DNA sequence data and other non-morphological traits may be critical for producing more objective classifications. This is especially important for endangered populations, whose taxo-

nomous rank may affect their legal conservation status. Molecular population genetic or phylogenetic investigations are contributing to more refined insights into the population biology and systematics of endemics in several archipelagos (e.g. Crawford et al., 1987; Baldwin et al., 1991; Francisco-Ortega et al., 1996; Carine et al., 2004; Nuez et al., 2004; Ruiz et al., 2004; Moore et al., 2006; Archibald et al., 2006; Oliva-Tejera et al., 2006; Díaz-Pérez et al., 2008; Maunder et al., 2008; Andrus et al., 2009; González-Pérez et al., 2009). Currently, a sample of the endemic flora of Garajonay National Park (La Gomera, Canaries) is being used to test the potential usefulness of cpDNA sequences in complementing morphological variables for the identification of the whole Canarian Flora (Caujapé-Castells et al., 2007a, b).

Resolution of taxonomic and floristic uncertainties could lead to reductions in the number of endemics on some archipelagos, whereas increased exploration could reveal more. Many archipelagos have highly dissected or unstable terrain that generates the distinctive evolutionary patterns seen in their plant endemics, but which is also a powerful impediment to botanical exploration. Consequently, large gaps in knowledge of the status and distribution of endemic plants remain in most archipelagos (Maunder et al., 2008; this study). Species thought to be extinct, or new populations of rare species, continue to be discovered on oceanic islands. For example, in Galápagos, populations of *Linum cratericola* (Linaceae) and of both varieties of *Scalesia atractyloides* (Asteraceae) were rediscovered after they had been presumed extinct (Mauchamp, 1996; Mauchamp et al., 1998; Tye, 1997, 2002). In Cape Verde, three botanical expeditions organised in 2006 and 2007 by the Jardín Botánico Canario “Viera y Clavijo” (JBCVC) to the islands of Santo Antão, São Nicolau, Fogo and Santiago found many previously undocumented populations of the dragon tree *Dracaena draco* (Dracaenaceae), which had been considered scarce [Marrero-Rodríguez and Almeida, unpubl. data]. Since 2000, the botanic garden in La Réunion has implemented a specific method to facilitate the rediscovery of species, including the production of information leaflets on the prioritized species (Boullet et al., 2006; Baret et al., 2007). So far, seven plant species have been rediscovered in the wild thanks to this approach, including *Nesogenes orerensis* (Orobanchaceae) rediscovered after 150 years (Baret et al., 2006) and the only known wild population of an endemic palm discovered next to habitation in a coastal site (Lavergne et al., 2004).

Other than endemics, the status (alien or native) of many plants on oceanic islands is often unclear (e.g. Tye, 2006a) although palaeobotanical research may be able to clarify status. An illustrative example is the recent use of pollen records to confirm as native in the Galápagos six plant species that were formerly believed or suspected to be alien species there (Van Leeuwen et al., 2008).

Among the nine focal archipelagos, there are large differences between the numbers of known recent extinctions documented. In the Galápagos and Juan Fernández there is reasonable certainty that not many anthropogenic extinctions have occurred, while Hawaii and the Mascarenes have experienced far more than the others (Table 2). Further, in Hawaii, the Canaries, Madeira-Selvagens, and the Seychelles there may have been many anthropogenic extinctions before scientific study began, as on most oceanic islands that were settled by humans in early prehistory (e.g. Whittaker and Fernández-Palacios, 2007). For instance, pollen records show that the legume shrub *Kanaloa kahoolawensis* was a dominant species of lowland habitats in Hawaii before ca. 1550 A.D., but it was unknown to science until its discovery in 1992 (Lorence and Wood, 1994).

The inception of DNA sequencing has enabled a wealth of studies on the origins and post-colonisation history of island plant groups (e.g., Baldwin, 1992; Moore et al., 2006; Dillon et al., 2007;

Andrus et al., 2009; Jaén-Molina et al., 2009). DNA sequences are useful in detecting phylogenetic patterns important in biodiversity conservation planning, e.g. speciose clades such as radiating crown groups, or species-depauperate sister groups that may be isolated and in danger of extinction. DNA sequences also may be used to estimate phylogenetic diversity, a quantitative measure of biodiversity based on phylogeny (Faith, 1992; Faith et al., 2004; Forest et al., 2007).

The magnitude of plant diversity endangerment on the world's islands

Data were retrieved from the IUCN red list on 657 endangered (EN) and 739 critically endangered (CR) species and subspecies, respectively representing 94 and 107 vascular plant families in the 62 islands and island groups listed in Appendix 2. After the removal of nine outliers as described above, a sample of 53 island groups contained an estimated 9951 endemic species and subspecies. There are several reasons to exercise caution in the interpretation of these data. First, the IUCN database may underestimate the numbers of taxa in the two categories considered: roughly 82% of the EN and 74% of the CR taxa included in the global analysis correspond to assessments made in 1998, and need updating. Further, the red-list criteria may not readily detect changes from naturally small sizes and ranges to critical states (Martín, 2009). For instance, the proportion of CR+EN endemics is higher on the focal archipelagos that have red lists (30–75%, Table 2) than on the 53 island groups included in the global analysis (average 28%). Second, red-list peer review is not yet implemented for many archipelagos (see http://www.iucnredlist.org/static/info_sources_quality), so the comparisons are between assessments that may not be as standardized as they should be. Finally, there might be a bias towards higher proportions of threatened taxa for insular regions where conservation research has been more intense.

With these considerations in mind, our analysis showed that the proportions of EN and CR taxa were negatively correlated with island area (Fig. 3), with stronger correlations for EN ($r = -0.426$, $P = 0.001$) than for CR ($r = -0.289$, $P = 0.036$). Both “very small” and “small” islands have significantly higher numbers of endemics per unit area and higher proportions of EN and (EN+CR) endemics than “large” islands (Table 4), although the differences among the three island size groups for CR taxa alone were not significant. In our sample, ca. 25% of the endemic taxa from very small and small islands are highly threatened (either CR or EN), whereas this proportion is much lower in large islands (ca. 3%). This indicates higher threats to endemic plant diversity on smaller islands.

Although isolated island groups (isolation index > 80: see Table 4) have more than three times as many endemics per unit area than islands closer to continents or to other island groups (0.173 vs. 0.052, $P < 0.0001$), isolation did not influence endangerment significantly (Table 4).

The islands in the Indian Ocean and the Mediterranean Sea had significantly higher average proportions of CR taxa than those in the Pacific and the Atlantic (Table 4); however, the average proportion of EN taxa is significantly higher in the Atlantic Ocean than in the remaining regions, with the lowest value in the Mediterranean. Whereas there are no significant differences at any level examined between islands in the Caribbean and the East Atlantic, both endemics per unit area and the proportion of CR taxa are significantly lower in the islands of Asia/Oceania than in the islands of the eastern Pacific.

In our survey, species and subspecies in the (CR+EN) and CR categories account for 5.07% and 2.87%, respectively of the total endemic species, and the average proportions

of (CR+EN) and (CR) taxa among the total endemic species per archipelago are, respectively 9.68% and 3.94%. Thus, of the estimated 70,000 plant species endemic to the world's islands (Kreft et al. 2008), between ca. 3500 and 6800 insular endemic plant species worldwide might be highly threatened (EN+CR), of which between ca. 2000 and 2800 could be in critical danger of extinction (CR).

A network of threat factors affecting island plants

The PCA representation in Fig. 1 describes the relationships among the focal archipelagos in the multivariate space defined by the 13 threat factor rankings (Table 3), and shows a conspicuous lack of correspondence with the geographical position of these archipelagos. The threat factors that were most commonly regarded as major drivers of plant diversity loss (category “C” in Table 3) were ‘Habitat alteration and destruction’ and ‘Invasive alien plant species’ in eight archipelagos. ‘Small population sizes and fragmentation’, ‘Demographic and economic growth’, ‘Lack of natural resource management capacity’, and ‘Invasive alien vertebrates’ were regarded as major drivers in six archipelagos. ‘Lost mutualisms’ and ‘Climate change and pollution’ were mostly assessed as either data deficient or of low relevance (categories ‘D’ and ‘A’, respectively, in Table 3). The literature review, however, indicated that these factors might already be or could soon become major threat factors, highlighting either important knowledge gaps or the emergence of new threat factors.

Some of the threat factors have both direct and indirect effects, while some act primarily as ultimate causes that work through other more proximate factors. The most important interactions between threat factors reveal a semi-hierarchical arrangement (Fig. 2). As an example from Galápagos, threat factor 3 (tourism) is the main driver of the economy, and thereby the main cause of threat 4 (human demographic growth), which in turn is the underlying cause behind the increasing number of invasive plants (threat 1) and invertebrate pests (7), while threat 9 (poor education about the gravity of threats to biodiversity), may be seen as a root cause contributing to the poorly planned development of the economy, including tourism. Since tourism works primarily through other factors and its direct impacts are relatively limited, it is ranked fairly low in importance on most of the nine focal archipelagos. However, this does not reflect its underlying importance in contributing to overall loss of biodiversity by working through the other factors considered here.

Small population sizes and fragmentation

Many plants on oceanic islands have naturally small populations, restricted to small geographic areas, while others may have been brought to this state through prehistoric (e.g. palms on many oceanic islands, Prebble and Dowe, 2008) or more recent anthropogenic impact. As highlighted for Hawaii (Sakai et al., 2002), extinction risk is strongly associated with limited geographic distribution at several scales. Taxa endemic to only one archipelago are at greater risk than taxa with extra-archipelago ranges, and single-island endemics are more at risk than multi-island endemics, with the smallest islands having the highest proportions of endemic taxa at risk. Our analyses (Table 4) show that these patterns are valid globally.

In the three focal archipelagos with the highest endemism (Table 2), more than 60% of the endemics are single-island endemics (67.2% in Hawaii, 79.5% in the Mascarenes, and 65.7% in the Canaries), and the proportions are similar in Juan Fernández

and Madeira-Selvagens (75.9% and 69.1%, respectively). The Seychelles (20.0%), the Galápagos (22.2%), Cape Verde (36.6%), and Azores (6.9%) have lower proportions of single island endemics. Overall, these data show that most plant endemics in the focal archipelagos with the richest plant biodiversity have limited distributions, and are likely at higher risk than those where most endemics are more widespread (e.g., the Azores Carine and Schaefer, 2009).

Rarity may make species vulnerable to extinction for three main reasons: environmental stochasticity, demographic stochasticity, and low genetic variability (Soulé and Wilcox, 1980; Frankel and Soulé, 1981). Plants restricted to very small areas may be at higher risk of extinction due to natural catastrophes such as fires, hurricanes or diseases (e.g. Kingston and Waldren, 2005). Little is known about the demography of oceanic island plants relative to continental species, but many are slow growing (e.g. Pattison et al., 1998; Schumacher et al., 2008, 2009) and long lived (e.g. Carlquist, 1974; Hart, 2008). For instance, many large individuals of the dominant tree *Metrosideros polymorpha* in a Hawaiian wet forest were estimated to be 400 years or more of age, with the oldest ones dated at approximately 600 years (Hart, 2008). Similarly, it takes 6–7 years for a fruit of the Seychelles Coco-de-Mer (*Lodoicea maldivica*) to develop (cf. Edwards et al., 2003). Such species may be less vulnerable to short-term demographic stochasticity, and their longevity and naturally low regeneration over long periods may result in underestimates of population viability where only adult tree counts are used for population estimates (e.g. Fleischmann et al., 2005). However, life history and demography vary considerably among oceanic island plants: not all are slow-growing and long-lived (e.g. Hamann, 2001; Schumacher et al., 2008, 2009).

Detecting populations with reduced genetic variation and increased inbreeding is particularly important for determining extinction risk, especially in the small, isolated populations characteristic of many island endemic plants (Barrett and Kohn, 1991; Frankham and Ralls, 1998; Frankham, 1998; Cole, 2003). Because deleterious genetic consequences related to small population size can impede population responses to sudden environmental shifts including competition from alien invasives (Courchamp et al., 2003), the influence of population size on the genetics and reproduction of insular endemics is of major concern to conservation.

Numerous conservation plans for rare and fragmented populations exist, but minimum viable population sizes (MVP) are generally not known. The estimation of MVP for plants is still unreliable, in part because it is heavily influenced by models adapted from animal biology (see e.g. Menges 1991), which are inconsistent with many of the population dynamic parameters of plants. Thus, even though the MVP concept may assist conservation planning, the only real consensus, that thousands to tens of thousands of individuals are required for an MVP, is debatably realistic, even without entering into the difficult issue of the definition and timescale of “viable”. MVPs and extinction probabilities are likely to vary over different populations, in different environments and with different demographic and genetic parameters, and many of these factors cannot be measured precisely (Menges 1991). Much research is still needed to develop a realistic MVP model for plants.

Although traits associated with rarity may make some species more prone to extinction, in other cases rarity can be related to evolutionary persistence (Fiedler and Ahouse, 1992; Kunin and Gaston, 1997). While species that have been rare for millennia may have developed adaptations to counter the genetic disadvantages associated with small population sizes and fragmentation, historically widespread species that have recently become rare may be more susceptible to such genetic stresses (e.g. Millar

and Libby, 1991). Because it is often difficult to determine the past history of populations, the interpretation of the effects of rarity on the risk of endangerment may be complicated.

Molecular techniques may detect trait states that imperil population survival (e.g. inbreeding), help predict the relationship between population size and probability of extinction (Shaffer, 1981), or estimate the population sizes necessary to maintain the genetic diversity of a species. However, these predictions can be especially difficult in plants, where they are complicated by the plethora of breeding systems, effective population sizes, and methods of pollination and dispersal, all of which influence the transmission of genetic variation between generations (Cole, 2003).

Francisco-Ortega et al. (2000) and Crawford et al. (2001) reviewed allozyme diversity in endemic plant species from the Canaries and the Juan Fernández, respectively, and concluded that the level of genetic cohesion of these insular floras (as measured by the parameter G_{ST} , Nei, 1973) is much lower than in Hawaii (Helenurm and Ganders, 1985) or other insular or mainland areas. Consequently, both studies called for more intensive conservation measures on the grounds that alterations of genetic connectivity could cause genetic homogenization, severe reductions in genetic diversity among populations, or hybridization (Francisco-Ortega et al., 2000). Nonetheless, estimates of high differentiation among natural populations in many published studies could be a spurious consequence of biased intra-population sampling, rather than a true representation of the biological characteristics of these insular floras (Caujapé-Castells, 2009a).

Although the number of papers describing genetic variation in island populations has mushroomed in the last 10 years, very few of them include mainland congeners in comparisons. Hence, we lack robust measurements of the genetic depauperation of island taxa. In one exception, Frankham (1997) showed reduced variation in island populations for a few plant species studied. It is also unclear to what extent the effects of genetic bottlenecks differ between island species that are naturally plastic and widespread (e.g. *Metrosideros polymorpha* in Hawaii) and species with a narrow natural niche (e.g. some species of *Lobelia* in Hawaii and *Linum* species in Galápagos).

Lost mutualisms

Plants depend on pollination and seed dispersal mutualisms for successful reproduction. There is increasing evidence that island plants suffer from the extinction or decline of seed dispersers (e.g. Hansen and Galetti, 2009; Hansen et al., 2008; Whittaker and Fernández-Palacios, 2007; McConkey and Drake, 2006; Cox et al., 1991), and pollinators (e.g. Mortensen et al., 2008; Cox and Elmqvist, 2000). Further, invasive plants and animals may interfere with plant–animal mutualisms, in both positive and negative ways (see below and Kaiser-Bunbury et al., 2010).

Plants also depend on other mutualisms, especially mycorrhizae. Soils on oceanic islands are often nutrient-poor, especially in phosphorus, and many plants depend on mycorrhizal mutualisms (Tedersoo et al., 2007; Koske et al., 2002). It is not known to what extent mycorrhizal associations have been or will be disrupted through anthropogenic change, but such an effect has been suggested for some endemic trees in the Seychelles (Tedersoo et al., 2007).

Finally, it is important to conserve “keystone” or “umbrella” species, many of which are not red-listed because they are not endemic or endangered. These species are however essential to the structure and functioning of island ecosystems, and protection of their habitats can also benefit species that are more vulnerable.

Habitat alteration and destruction

Habitat destruction on oceanic islands has been substantial, and overall has perhaps been the most important factor in causing declines of island plants in the past (e.g. Rolett and Diamond, 2004; Kirch and Hunt, 1997). Today, only a small fraction of primary vegetation remains on many oceanic islands (e.g. Brooks et al., 2002; Kueffer et al., 2004; Kingston and Waldren, 2005; Whittaker and Fernández-Palacios, 2007; Kingsford et al., 2009); however, the higher elevations on some high islands have higher proportions of less-disturbed vegetation compared to most insular areas (e.g. Hawaii, La Réunion, Mueller-Dombois and Fosberg, 1998; Strasberg et al., 2005). In general, past habitat destruction has most heavily impacted species in lowland dry to mesic habitats (e.g. Strasberg et al., 2005; Sakai et al., 2002; Kirch and Hunt, 1997), although Galapagos is an exception, with impacts having been greater in the mesic highlands than the dry lowlands (Snell et al., 2002).

Low rainfall and soil fertility appear to be especially important predictors of prehistoric deforestation rates, at least on Pacific Islands (Rolett and Diamond, 2004). In present times, deforestation has stopped or reversed on many islands with a strong tourism sector and a service-based economy, or alternatively, that are now mostly uninhabited (e.g. Kueffer et al., 2004; Lugo, 2004; Wilkinson, 2004), while on others, habitat transformation continues or accelerates in coastal areas (Whittaker and Fernández-Palacios, 2007). Wildfires and soil erosion may lead to further habitat loss (e.g. Kingston and Waldren, 2005; D'Antonio and Vitousek, 1992).

On some islands that have been heavily deforested, secondary forest has regrown (e.g. in Ascension, Puerto Rico, or Seychelles; Kueffer and Vos, 2004; Lugo, 2004; Wilkinson, 2004), while on others deforestation rates remain among the highest in the world (e.g., some islands in the Caribbean and the Philippines, Brooks et al., 2002). Oceanic islands thus vary widely in their relative composition of anthropogenic land, degraded secondary vegetation, secondary vegetation of conservation value, and relatively undisturbed habitat (compare Kueffer and Daehler, 2009).

Models based on species–area relationships predict that the extinction risk of species on islands is very sensitive to habitat loss (Brooks et al., 2002). Consequently, rare and endemic plant species are more common in undisturbed than in secondary vegetation (e.g. Mueller-Dombois and Fosberg, 1998; Perry and Morton, 1999; Endress, 2002; Strasberg et al., 2005), and are often concentrated in small, isolated habitat patches (e.g. Cronk, 1980; Mueller-Dombois and Fosberg, 1998; Wiser et al., 2002; Kueffer et al., 2004; Kingston and Waldren, 2005; Seamon et al., 2006). It is not clear, however, which species can survive in such restricted habitats in the long term (e.g. Wiser et al., 2002). Small habitat fragments may be more vulnerable to disturbances such as fires, hurricanes or invasions, and edge effects may reduce the effective size of fragments of value for plant conservation (e.g. Mueller-Dombois and Fosberg, 1998; Wiser et al., 2002; Seamon et al., 2006). For instance, reproduction was negatively correlated with size of habitat fragments for a species of *Dombeya* in La Réunion (Gigord et al., 1999). Besides the complete transformation of habitats, more subtle alterations such as disturbance of the forest canopy or changes in soil stability or fertility may directly or indirectly (e.g. through the facilitation of invasions), reduce the quality of a habitat for particular native plant species.

Invasive alien plant species

Plant invasions on oceanic islands have long been considered dramatic examples of the success of alien plants in colonizing

natural areas (Elton, 1958; Cronk and Fuller, 1995; Tye et al., 2002; Tye, 2003; Denslow, 2003; Kueffer et al., 2010). Nowadays, alien plants are an important component of many habitats on most oceanic islands. However, the extent to which alien plant invasions have brought about the decline and extinction of native plants on islands is still debated (Simberloff, 1995; Sax et al., 2002; Denslow, 2003; Gurevitch and Padilla, 2004; Sax and Gaines, 2008). The assumption that invasive plants cause extinctions has been countered by observations that native and alien plant species richness on different oceanic islands are positively rather than negatively correlated (Sax et al., 2002; Sax and Gaines, 2008), and negative impacts of alien plants on native plants had rarely (until recently) been rigorously demonstrated (Simberloff, 1995; Gurevitch and Padilla, 2004). Suggestions that invasive plant species drive declines in native plant richness are confounded by plant invasions and native species declines both coinciding with some other environmental change such as habitat destruction (e.g. Gurevitch and Padilla, 2004). Alien species richness is indeed strongly correlated with indices of economic development across oceanic islands (Denslow et al., 2009; Kueffer et al., 2010), possibly in part because anthropogenic habitat alteration is a strong driver of plant invasions (cf. Kueffer et al., 2010) or because economic development favours the deliberate introduction of a wider range of alien species (Tye, 2006a).

The past role of plant invasions versus habitat destruction in the decline of island plant diversity may thus be difficult to disentangle. However, it should be of high priority to understand how invasive plants currently affect endemic plants, especially where habitats are heavily disturbed and invaded, and population sizes of many native species are small, and studies are now beginning to reveal cases in which invasive plants are clearly the direct cause of declines in native plants on islands.

The mechanisms by which invasive plants may affect native plants include direct competition, interference with plant–animal interactions, alteration of habitats, and hybridization.

Competition—It has been argued that oceanic island plants are less competitive than plants of continental origin (cf. Denslow, 2003). In Hawaii, many invasive species have higher growth rates and physiological traits adapted to more extreme conditions than native species (studies reviewed in Denslow, 2003). However, in Seychelles, growth rates vary considerably within the groups of native and invasive woody plants (Fleischmann, 1999; Schumacher et al., 2008, 2009). Nevertheless, even under low light, some invasive plants show higher growth rates and lower mortality than many native species, e.g. *Psidium cattleianum* (Schumacher et al., 2008, 2009).

Examples clearly demonstrating that an invasive plant is competitively replacing a native plant without other major anthropogenic disturbances are rare. Meyer et al. (2003) showed that successful reproduction of two rare species of *Psychotria* is negatively correlated with the density of the invasive *Miconia calvescens*. Baider and Florens (2006) showed that fruit production of *Sideroxylon grandiflorum* in Mauritius was markedly lower in weed-infested areas. Denslow (2003) reported that the introduced *Rubus ellipticus* is competitively superior to the Hawaiian native *R. hawaiiensis*. Invasion by the understory herb *Hedychium gardnerianum* can affect overstorey native trees, probably through competition for nutrients (Asner and Vitousek, 2005). Similarly, alien grasses negatively affect water uptake by native trees in dry habitats (Cabin et al. 2002; Cordell and Sandquist, 2008). Trees invading naturally treeless environments can have particularly severe competitive effects on native vegetation through shading, as well as via other environmental changes such as fog-drip generation (Jäger et al., 2007, 2009).

Further, some alien plants can invade relatively undisturbed vegetation rich in rare native species, and form dense understory

or canopy stands, including for instance *Clidemia hirta*, *Hedychium gardnerianum*, *Psidium cattleianum* or *Miconia calvenscens* (Meyer and Florence, 1996; Meyer, 2004; Tassin et al., 2006; Asner et al., 2008; Kueffer et al., 2010). In such cases, experimental removal of the invasives generally increases native regrowth, which strengthens the evidence that the invasive species displace native species. For instance, removal of *Hedychium gardnerianum* from forests in La Réunion led to an increase in the regrowth of native plants (Lavergne, 2005), and the release of a biological control agent against *Miconia calvenscens* in Tahiti has increased the regeneration of the critically endangered tree *Myrsine longifolia* (Meyer et al., 2007). However, there are also cases where regeneration of at least some native species is good in alien-dominated forests (e.g. in Palau [Endress, 2002], Puerto Rico [Lugo, 2004], or Seychelles [Kueffer et al., 2007b]). In some cases, established alien plants may facilitate native regeneration by hindering invasion by other alien species (cf. Kueffer et al., 2007b). In fact, invasion by new alien species is often one result of removal of invasive plants (e.g. Lavergne, 2005). However, where the remaining populations of a highly threatened native species are being invaded by introduced plants, management of the invasive species is clearly important, as in the cases of the critically endangered *Impatiens gordonii* in the Seychelles invaded by *Clidemia hirta* (Huber and Ismail, 2006) and *Linum cratericola* invaded by *Lantana camara* in Galápagos (Simbaña and Tye, 2009).

Invasive species may displace native species in habitats with relatively minor anthropogenic disturbance through natural disturbance processes such as hurricanes. Although the native flora on many oceanic islands, especially atolls, and dry islands such as Galápagos, is of a pioneer, fast-growing character (e.g. Hamann, 1979, 1993), the native floras of some others lack light-demanding, fast-growing species (Mueller-Dombois, 2008), and gaps create an opportunity for fast-growing invasive species to establish and gain high abundance. Examples of invasive species profiting from natural gap formation are *Pittosporum undulatum* in the Caribbean (Bellingham et al., 2005), or various vines on many oceanic islands (e.g. Kueffer et al., 2004; Meyer, 2004). Invasive species may sometimes even accelerate gap formation, e.g. in montane cloud forests in Seychelles (Kueffer, 2006). Even minor anthropogenic impacts such as trails (Baret and Strasberg, 2005) may enable light-demanding invasives to establish in natural areas.

In summary, invasive species tend to be competitively superior to native species especially in disturbed and open environments, although alien invasives may occasionally have positive impacts on the viability of some native plant species. A few invasive plant species can successfully invade undisturbed vegetation patches, where they may become dominant; unfortunately, these species are difficult to identify and predict (Tye, 2006a; Kueffer et al., 2010).

Interference with plant–animal interactions—Invasive alien plants may produce flowers or fruits of different quality than native species (e.g. Kueffer et al., 2009), thus competing with native species for pollinators or seed dispersers. In some cases alien plants may support higher densities of pollinators or seed dispersers in a habitat. Alien plants may also facilitate the spread of pests in natural areas, as may be the case with the spread of the polyphagous insect *Aleurodicus dispersus* into natural areas in Seychelles (Hazell et al., 2008). Kaiser et al. (2007) report how coffee plantations increased pest load on endemic plants in nearby natural areas. Kaiser-Bunbury et al. (2010) review the role of invasive plants in plant–animal mutualisms.

Alteration of habitat—Invasive alien plants can strongly alter habitat conditions and thus inhibit native species recovery and habitat rehabilitation. In particular, alien grasses in dry habitats often accelerate fire cycles, thereby hindering the establishment

of native plants, or increasing their mortality (e.g. D'Antonio and Vitousek, 1992; D'Antonio et al., 2000). Invasive nitrogen-fixing trees may increase soil N availability and thereby favour invasive species over native ones (e.g. Hughes and Denslow, 2005), but even non-N-fixers may change litter and nutrient cycles, with generally unknown impacts on the balance between native and introduced species (Jäger et al. 2009). The impacts and roles of invasive species in a habitat and ecosystem context have been widely reviewed, drawing extensively on oceanic island examples (e.g. Zavaleta et al., 2001; Levine et al., 2003; Ewel and Putz, 2004; Mooney et al., 2005), or specifically focusing on islands (e.g. D'Antonio and Dudley, 1995; Tassin et al., 2006; Reaser et al., 2007; Kueffer and Daehler, 2009). A general conclusion important for conservation is that in highly degraded island ecosystems alien species can play both positive and negative roles, so impacts have to be assessed specifically for every habitat (Kueffer and Daehler, 2009).

Hybridization—The risk of hybridization between a native species and a closely related alien species may be particularly problematic on islands (Francisco-Ortega and Santos-Guerra, 2001; Levin et al., 1996). In the Juan Fernández, cultivation of several species of *Dendroseris* (Asteraceae) in the Corporación Nacional Forestal (CONAF) garden resulted in the production of inter-specific hybrids, which could endanger the integrity of the species. Daehler and Carino (2001) have recently reviewed hybridization between native and alien plants with a special focus on Hawaii.

Invasive alien invertebrates and pathogens

New alien pests have been and still are introduced at a very rapid rate in oceanic islands, but there is relatively little information on their effects on native plants. Krushelnycky et al. (2005) report that inspection of cargo in one Hawaiian airport during only 20 weeks in 2000–2001 detected 125 alien insect species and 16 plant pathogens not known to be established in Hawaii. Today, at least some 2700 alien insect species are present in Hawaii (Juvik and Juvik, 1998). Similarly, in Galápagos, 463 alien insect species had been recorded by 2006, an increase of 186 introductions since an inventory in 1998 (Causton et al., 2006), almost all of them brought accidentally to the islands.

Some alien invertebrates constitute direct threats for the endemic flora. The Cottony Cushion Scale Insect *Icerya purchasi* caused severe damage to mangroves and a range of endemic plant species when introduced accidentally to Galápagos, to the point that some populations of threatened species were almost completely lost. This damage was successfully controlled by the introduction of the ladybird *Rodolia cardinalis* as a biological control agent (Causton et al., 2006). Invertebrates can also act as disease vectors; in the Seychelles, the common coastal Takamaka tree (*Calophyllum inophyllum*) was strongly affected by an introduced wilt disease transmitted by an alien species of bark beetle (Wainhouse et al., 1998). This outbreak was partly controlled by increasing attention to hygienic forestry practices, and the tree species is still not threatened (Hill et al., 2003); however, additional measures are required, such as the removal of dead and dying trees combined with under-planting of other native trees.

Due to the small area of many islands, pests may very rapidly spread and affect endemic species. Alien diseases affect endemic plants on many islands (e.g. Brooks, 2002), and several dramatic examples have been reported where most individuals of a species have been affected by a new pest within less than a year (e.g. the *Erythrina* Gall Wasp in Hawaii, Heu et al., 2006; Yalamar et al., 2009). The coffee berry moth *Prophantis smaragdina* severely and

rapidly reduced the reproductive success of threatened endemic plant species on Mauritius (Kaiser et al., 2007). On the other hand, the separation of islands by ocean can be an opportunity for containing the spread of a disease or pest across an archipelago (e.g. Wainhouse et al., 1998).

Beyond a few dramatic examples, there is relatively little information on pest impacts on oceanic island plants. However, based on extensive survey, Messing et al. (2007) found alien aphids feeding and reproducing on 64 native Hawaiian plants (16 indigenous species and 48 endemic species) in 32 families. Messing and Wright (2006) report that a single recent invader (a leafhopper from China) attacks some 70 endemic plants in Hawaii, including 14 rare and endangered species. Indirect effects on native plants through interference with pollinators are reviewed by Kaiser-Bunbury et al. (2010).

Invasive alien vertebrates

Perhaps the best-documented ecological disturbance resulting from biological invasions is the invasion of island ecosystems by vertebrate herbivores (Holdgate, 1967; Atkinson, 2001; Courchamp et al., 2003). Besides habitat loss, invasive mammals are viewed as one of the most important drivers of past (Drake and Hunt, 2009) and present (this study) biodiversity loss on islands.

Aside from the often dramatically obvious impacts of large herbivorous ungulates, there is also compelling evidence from many oceanic islands that predation on fruits or seeds of native plants by rodents and other invasive animals can strongly limit recruitment (Meyer and Butaud, 2009; Traveset et al., 2009). For instance, Meyer and Butaud (2009) estimated that > 99% of the seeds of a species of sandalwood were eaten by rats before ripening, and they suggested that some plant families in Polynesia, e.g. Arecaceae, Elaeocarpaceae, Rubiaceae, Santalaceae, and Sapotaceae, are particularly vulnerable to seed predation. Especially during the dry season, rodents may also prey on seedlings e.g. of palms (Kueffer, 2006), and on the stem and bark of adult trees (Meyer and Butaud, 2009). Baider and Florens (2006) showed that predation by invasive monkeys on unripe fruits had a major impact on the regeneration of the very rare tree *Sideroxylon grandiflorum* in Mauritius. Monkeys may also virtually defoliate whole adult trees (Cheke and Hume, 2008). Invasive pigs uproot native plants (e.g. Culliney, 2006 in Hawaii), and feed on fruits and seedlings (e.g. in Guam, Wiles et al., 1996). Invasive animals may also interfere with pollination and/or seed dispersal mutualisms (Campbell and Atkinson, 2002; Traveset and Richardson, 2006; Meyer and Butaud, 2009; Traveset et al., 2009).

Endemic island plants can have high levels of compounds such as polyphenols or anthocyanins (Hansen et al., 2004; Kueffer et al., 2008), which provide defence against generalist herbivores. Nonetheless, many insular species have not evolved effective defences against vertebrate grazing, as a consequence of their prolonged evolution in the absence of vertebrate herbivores (Carlquist, 1974; Atkinson, 1989; Bowen and Van Buren, 1997; Courchamp et al., 2003; but see Hansen et al., 2004; Hansen and Galetti, 2009). Consequently, grazing and trampling by introduced cattle, goats, sheep, donkeys, horses or deer has greatly affected vegetation on many oceanic islands (e.g. Loope et al., 1988; Courchamp et al., 2003; Reaser et al., 2007).

Eradication of invasive vertebrate herbivores has been successful on many small islands (Campbell and Donlan, 2005; Smith et al., 2006; Howald et al., 2007; Cheke and Hume, 2008), and has led to rapid recovery of native vegetation on many oceanic islands. In the Galápagos, feral goats, donkeys, pigs, and cattle have been eradicated or controlled on many islands, including some of the largest eradication projects for these animals in the

world (Campbell et al., 2004; Campbell and Donlan, 2005; Cruz et al., 2005; Carrión et al., 2007). Recovery of Galapagos vegetation after eradication has often been rapid (Hamann, 1979, 1993; Tye, 2006b) and post-eradication research has focused on the lack of recuperation of certain species. For example, the failure of recovery of *Opuntia megasperma* (Cactaceae) after the eradication of goats from Española Island led to an experimental recovery programme and a reassessment of giant tortoise re-introduction to the island (Tye, 2006b).

Cessation of free grazing by goats and sheep on the mountains of Porto Santo and Madeira in 1995 and 2003 allowed the regeneration of natural vegetation and the expansion of endemic species that had been confined to the higher peaks until then (Silva et al., 2005b). Similarly, the eradication of rabbits on Deserta Grande and Selvagem Grande made possible the remarkable recovery of the vegetation of these islands. In Mauritius, goats and rabbits have been eradicated from Round Island, following which native vegetation has recovered greatly; rabbits and rats were also eradicated from Gunner's Quoin, with similar success (Baider and Florens, 2005; Cheke and Hume, 2008). In the Canaries, cessation of traditional grazing after more than two millennia on the summits of La Palma and Tenerife triggered rapid recovery of the flora in these areas, including several extremely endangered species (A. Santos-Guerra, personal observation). In the Hawaiian Islands, large fencing projects in the national parks led to remarkable recovery of several native plant species (Loope and Medeiros, 1994).

Invasive animals seem to be the key threat factor for many plants in the Canaries, Hawaii, Galápagos and Juan Fernández, while for others they may be one among several factors involved in the decline (Meyer and Butaud, 2009; Perry and Morton, 1999). In rare cases, some native plants may profit from the presence of alien animals (e.g. Traveset et al., 2009), and introduced animals can also reduce the abundance of some plant invaders (e.g. Campbell and Donlan, 2005; Kueffer, 2006).

Climate change and pollution

The impacts of climate change on island plant biodiversity are likely to be substantial (Millennium Ecosystem Assessment [MEA], 2005; Mimura et al., 2007). Changes in precipitation patterns are difficult to predict, because most oceanic island climates are influenced by large-scale weather systems such as the position of the inter-tropical convergence zone, the Asian monsoon or the El Niño Southern Oscillation, and it is not clear how these systems will shift in a changing climate (Mimura et al., 2007; Sachs et al., 2009). However, an overall trend towards less rainfall has been suggested for tropical and subtropical oceanic islands (Giambelluca et al., 2008). Climate change may also lead to shifts in the trade wind inversion layer, thereby affecting rainfall generated by local orographic effects (Mimura et al., 2007; Loope and Giambelluca, 1998; Sachs et al., 2009). Climate change could also increase inter-annual variability in precipitation, which might disrupt the highly specific conditions necessary to sustain cloud forests and dryland vegetation in subtropical and tropical oceanic islands (Mimura et al., 2007; Kueffer et al., 2007a; Loope and Giambelluca, 1998). An increased incidence of extreme events such as hurricanes, floods or droughts can be expected on many islands (Mimura et al., 2007), promoting enhanced habitat disturbances, which could lead to increased mortality of native species, or facilitate invasion by non-native species. Sea level rise will reduce the area for coastal vegetation in some places; for instance, a 50% loss of mangrove area is predicted for American Samoa (Mimura et al.,

2007). Increased dry periods may also increase the risk of fires (Martín, 2009; James, 2008).

With changing climate, oceanic island plants have fewer options than mainland plants to migrate to suitable habitat. On high islands, some altitudinal movement may be possible (Gillespie et al., 2008) but on small and low-lying islands it may not. Habitat fragmentation or competition from non-native species may impede migration of many species (James, 2008), and oceanic island plant endemics often demonstrate low dispersability (e.g. Carlquist, 1974).

Some island plants may have sufficient phenotypic plasticity to adapt to novel climatic conditions. Some oceanic island plants tolerate environmental stress (e.g. drought) through a resource-conserving, slow growth strategy (Castillo et al., 2007; Schumacher et al., 2008) that probably makes them resilient to some degree of climate change. On high islands, there are typically some species that are common across broad climatic gradients, e.g. *Metrosideros polymorpha* or *Acacia koa* in Hawaii, which may be able to adapt to climate changes through genetic adaptation (Ares et al., 2000) or phenotypic plasticity. However, most *in situ* speciation on islands occurred within particular habitats and climate zones (e.g. Gillespie et al., 2008), as revealed by the many endemic plants that have narrow distributions in limited habitats, and are particularly vulnerable to extinction (e.g. Sakai et al., 2002 for Hawaii). Thus, vulnerability to climate change may be particularly high for rare island species (James, 2008).

Some of the characteristics that constitute the “island syndrome” (Carlquist, 1974) may also make insular endemics more vulnerable to shifts in environmental conditions. In particular, woodiness, which allows longer generation times when climatic conditions are stable, could represent a serious hindrance to survival in a changing environment (David Bramwell, pers. commun.). Increasing temperatures and aridity are contrary to the conditions supposed by Carlquist (1974) to favour the development of woodiness (i.e., a moderate, humid climate with long growing seasons). The percentage of woody endemics with respect to the total endemic flora in our nine studied archipelagos is high: 76% for the Seychelles (Huber and Ismail, 2006), ca. 73% for Hawaii (Sakai et al., 2002), 72% for the Canaries (Aldridge, 1979), 63% for Cape Verde (W. Lobin, unpubl. data), or 52% in Madeira (R. Jardim, unpubl. data). In Juan Fernández, the percentage of trees, sub-trees and shrubs in the flora is smaller (47%), but 85% of the native and endemic taxa are perennials (Bernardello et al., 2001). The Azores show the lowest percentage of woody endemics (19%) but, similarly to Juan Fernández, ca. 86% of the plant endemics are long-lived perennial hemicryptophytes (M. Moura, unpubl. data).

While oceanic islands are often remote and may be less affected by pollution, air pollution is globally transported and deposited. Increase of CO₂ may favour some non-native life forms over native ones (Weltzin et al., 2004). Given the very low soil nutrient availabilities and correspondingly finely tuned limitation of biotic processes by several nutrients typical for many oceanic islands (Vitousek, 2004; Kueffer, 2009), oceanic island vegetation may be especially sensitive to even relatively small nutrient changes, as illustrated by the well-known fertilization-driven vegetation changes on islands (Ostertag and Verville, 2002; Hughes and Denslow, 2005).

Need for a better knowledge base

Knowledge of the taxonomy, distribution and threat status of plants on oceanic islands is insufficient. Our estimation that between 3500 and 6800 insular plant endemics are endangered worldwide might be a severe underestimate. Urgent efforts are

needed in all archipelagos to train the next generation of plant taxonomists to address these limitations. New technologies such as DNA “barcoding” projects (Faith and Williams, 2005) and other DNA databanks such as those initiated in some insular regions (e.g., Macaronesia, Hawaii) may contribute many new insights, including the design of nature reserves through estimates of phylogenetic diversity per unit area. The “Moorea Biocode Project” is an initiative to barcode all living organisms including vascular and non-vascular plants (Check, 2006; see also <http://moorea.berkeley.edu/biocode> and <http://www.mooreabiocode.org/>). Greater DNA banking of insular endemics is needed to complement research on systematics, and permit conservation initiatives based on the new taxonomic information generated.

Knowledge of the basic reproductive biology of endemic plants varies greatly between the focal archipelagos assessed in this study. In Hawaii, little is known for all but a very few species (e.g. Carr et al., 1986; Sakai et al., 1989, 1995a, b; Drake and Morden, 2008). In Juan Fernández, Anderson et al. (2001) and Bernardello et al. (2001) surveyed floral traits, breeding systems, floral visitors and pollination systems, and presented an extensive discussion of the conservation implications of their results. In the Mascarenes, there have been numerous studies on breeding systems and pollinators of the flowering plants (e.g. Humeau and Thompson, 2001; Litrico et al., 2005a, b; Micheneau et al., 2006, 2008). In Galápagos, studies have centred on the population dynamics of some large species (e.g. Hamann, 2001), pollination biology (e.g. McMullen, 1994, 2007) and, more recently, on breeding systems (e.g. Nielsen et al., 2007). Although data are accumulating on aspects of the reproductive biology of various Azorean (Pereira, 2008) and Canarian endemics (e.g. Calero and Santos-Guerra, 1993; Anderson et al., 2006; Dupont and Olesen, 2006; Crawford et al., 2008; Rodríguez-Rodríguez and Valido, 2008), a broad knowledge of this aspect of the flora in all Macaronesian archipelagos is lacking, which impedes understanding of the biological implications of most population genetic studies (e.g. Caujapé-Castells et al., 2008a, b).

Greater knowledge of breeding systems may help to identify where reductions in gene flow may lead to increased inbreeding depression and lowered fitness that may undermine the ability of endemics to compete with introduced species, or limit adaptations to habitat/climatic changes (Frankham, 1998; Francisco-Ortega et al., 2000). Flow charts incorporating biological information (e.g. breeding system), plant life history traits, rarity and distribution may help to prioritise research on the reproductive biology of endangered oceanic island plants (Kueffer et al., 2007; Drake and Morden, 2008). Established protocols could be adapted for archipelagos lacking plant reproductive studies, in order to promote efficient data collection and its application to conservation. In self-incompatible plants, molecular techniques can estimate where stochastic loss of S-alleles has removed cross-compatible genotypes (see Raspé and Kohn, 2002), thereby providing another tool for prioritizing *in situ* action.

First aid measures

Establishment of protected areas and community-based management areas for *in situ* conservation is essential to mitigate threats to plant biodiversity. In the nine focal archipelagos, the proportion of land area devoted to *in situ* conservation averages 40% (Table 1), but ranges from only about 0.2 in Cape Verde and 5% in Hawaii to almost total protection in Juan Fernández and Galápagos (ca. 90% and 96%, respectively). Clearly, the land area protected should be increased in most archipelagos.

However, many of the biological threats can undermine the intrinsic survival capabilities of many endangered insular plants,

even if their habitats are protected and managed, and the generally higher sensitivity of insular plant endemics to environmental shifts and natural catastrophes makes it advisable to back up *in situ* conservation measures by preserving them out of their natural areas of occurrence. Major investment in *ex situ* conservation (i.e. the propagation and conservation of plants and seeds in Botanic Gardens and other similar facilities) is thus an urgent complementary measure. One example of how *in situ* and *ex situ* strategies can be successfully combined is provided by *Lotus eremiticus* and *L. pyranthus*, two Canarian endemic Fabaceae from La Palma island that consist of fewer than 10 and 20 individuals, respectively (Mesa-Coello 2007a, b). The 'Cabildo de La Palma' decreed a conservation plan (Boletín Oficial de Canarias, 2006) that comprises the protection and management of their habitats, the maintenance of clones of most individuals in the Cabildo's plant nursery to complement the *in situ* protection measures (Félix Manuel Medina, pers. commun.), and the genetic characterisation of all the individuals (Jaén-Molina et al., unpubl. data).

Within the focal group, Hawaii, the five Macaronesian archipelagos, and the Mascarenes all have seed banks with specialized staff and facilities devoted to collecting and properly storing germplasm. Starting in 1973, project Artemis of the Universidad Politécnica de Madrid (Gómez-Campo, 1986) has also conserved seeds from Macaronesia, distributing duplicates from Canaries and Madeira to other seed banks. In Juan Fernández, the seed bank consists of CONAF personnel simply placing seeds in labelled plastic bags containing silica gel in a refrigerator. Galápagos and Cape Verde do not have seed banks for endemic plant populations, although one is planned for Galápagos. The ca. 154 seed accessions collected in Cape Verde by staff of the JBCVC are kept as a trust fund in the seed bank of this institution, with a small number of accessions kept at the Berlin Botanical Garden.

Despite its importance, implementing seed banking in or for some of the archipelagos presently lacking seed banks could be difficult, for reasons ranging from poor finance or inadequate staff capacity to legal restrictions on export of live material (see Appendix 1). However, given the political will, it seems feasible that seeds could be collected by trained local staff and sent to established seed banks in other archipelagos or mainland areas (see Table 2), either temporarily until the corresponding archipelago can build and maintain its own facility, or under a permanent agreement. Although seed collections of all endemics may not be possible, it should be a priority to collect critically endangered species and those suffering rapid declines in range or abundance. The use of molecular genetic information to select population targets for seed collection and to maximize the amount of genetic diversity captured in these species is not yet a common practice, though it is being initiated in the JBCVC (Vilches et al., 2004; Caujapé-Castells, 2009b). The seed bank in Mauritius addresses indirectly such intra-species genetic variation by collecting seeds of a given species from several distinct populations when possible.

Although molecular studies can be carried out on live-collected plant material and herbarium specimens, seed banks would increase the possibilities for identifying priority populations where inbreeding is more severe, or for selecting the most suitable seed sources for reinforcement of ailing populations (through estimates of evolutionary closeness). Seed bank samples are frequently used in population reintroduction or enhancement, and estimates of the genetic representativeness of collections would improve the conservation value and success of these initiatives, while facilitating monitoring. In Madeira, a LIFE project, carried out by the Jardim Botânico da Madeira between 1999 and 2003, implemented various conservation measures and studies of eight priority rare endemic species. These involved

reintroduction and reinforcement of natural populations, seed banking, and restoration of natural habitats in Pico Branco (Porto Santo Island).

In the Azores, the Biology Department of the Universidade dos Açores has carried out *ex situ* conservation of endemics since the early 1990's (Maciel, 1995, 1996, 2004; Moura, 1995, 1998, 2006; Toste, 1995), whereas in Juan Fernández, understanding seed germination requirements is a priority for many endemics. In Galápagos, the stated conservation goal of the Galápagos National Park is complete *in situ* conservation and restoration. It has therefore been a lesser priority to establish seed banks and other *ex situ* collections. However, extinct populations of the single-island endemic *Scalesia atractyloides* may be re-established in the future using material from living collections from these populations in Copenhagen Botanic Garden, while experiments towards using cultivated seedlings to reinforce and re-establish populations of the Critically Endangered *Linum cratericola* on Floreana Island and *Calandrinia galapagosa* on San Cristóbal, and of the locally endangered *Scalesia affinis* on Santa Cruz (Atkinson et al., 2009) have been undertaken. In the Canaries, the government has increased funding to prioritise *in situ* recovery plans of threatened species, that occasionally promotes seed banking or use the existing seed collections in the reinforcement of natural populations.

Conclusions

This review offers the most comprehensive analysis of the threats to insular endemic plants to date. Remote islands have more endemics per unit area, but isolation does not influence extinction risk significantly, whereas island size is a more important predictor of endangerment. Critically, many threat factors act synergistically, producing impacts that reverberate across entire ecosystems (Fig. 2). Therefore, species decline can also lead to cascading extinctions (Koh et al., 2004; Fordham and Brook, 2009), and our calculation of between 2000 and 2800 endemic insular plant species on the verge of extinction worldwide might be a severe underestimate.

The role of specific threat factors depends on the particular endemic and its ecological context. Nevertheless, we see potential for pattern generalisation beyond single cases. More data are needed for assessing the relationships among threats, testing their impacts, and developing ways to prioritise action and strategically guide plant conservation. Appendix 1 summarises the present assets and weaknesses for plant conservation in each focal archipelago, and identifies research and political guidelines that could help improve local action in the future. In addition, urgent coordinated action seems necessary to tackle all the relevant factors of threat through a holistic conservation approach.

The impacts of major threat factors on the endemic plant biodiversity of the nine focal archipelagos appear to be unrelated to their geographical proximity (Fig. 1), emphasizing the need for enhanced contact among island conservation scientists throughout the world. Better communication and coordination of research efforts among archipelagos with different levels of expertise in each priority problem would provide opportunities for mutual assistance, synergistic action and perhaps common political approaches to plant conservation. An island plant conservation network with appropriate communication tools, such as a website, could be instrumental in coordinating knowledge sharing and comparative research among archipelagos. While there are examples of regional plant conservation networks (e.g. for the Mascarenes at <http://www.plantmasc.org/>, or for the Hawaii and the Pacific at <http://www.hear.org/>), there is no global network to date, although one existing network which might be developed with these objectives is the network of plant

specialist groups of the IUCN Species Survival Commission. Many ecological, socioeconomic, institutional, and methodological challenges specific to islands can only be addressed by sharing experiences across island groups and oceanic regions. The proposed network would also facilitate exchange of information on new methods, threats and management techniques, and stimulate common initiatives between research groups in different countries. Its web site should contain historical and current information, research materials such as otherwise inaccessible literature, hyperlinks to the web pages of research groups, lists of plant materials available, and other information relevant for research such as permit conditions for collecting and fieldwork. These resources would help researchers to overcome the diverse hurdles encountered in different archipelagos, while promoting enhanced collaboration among scientists working on conservation of island floras.

We hope that the present paper will promote the development of such a coordinated global research effort to help share knowledge and expertise, to discuss common challenges, and to formulate multi-disciplinary conservation objectives for insular plant endemics on a worldwide basis.

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Appendix 1

See Table A1

Appendix 2

See Table A2

Table A1

Indicators of present and future scientific-political conservation needs in the nine featured archipelagos, according to the priorities identified by the participating scientists.

Archipelago	Conservation research assets at present			Foresight of urgent future needs in conservation	
	Weaknesses	Strengths	Suggested improvements	Scientific	Political
Azores	<ul style="list-style-type: none"> • Lack of man power. • Lack of consistent financial support. • Dispersal of resources among competing institutions/teams. 	<ul style="list-style-type: none"> • Material easily reachable. 	<ul style="list-style-type: none"> • Increase collaboration with renowned foreign investigation institutions, to benefit from already developed infrastructure assets and knowledge base. • Greatly increase cooperation and coordination of research at regional level. 	<ul style="list-style-type: none"> • Medium-term monitoring data to determine population trends (probability of extinction) and to clarify the impact of different threats. • Exhaustive molecular work for taxonomic re-evaluations and population genetic analysis, development of plant propagation techniques. 	<ul style="list-style-type: none"> • Revise and enforce legislation. • Develop and approve species specific recovery plans, based on scientific data, with very precise goals and with a legal nature. • Consistent financial support, with the development of a line of grants exclusively dedicated to support Azorean flora and vegetation studies
Canaries	<ul style="list-style-type: none"> • Poor funding. • Some staff needs updated training in modern research methods. • Poor English communication skills of most specialised staff. 	<ul style="list-style-type: none"> • Dedication and knowledge of biologists in staff. • Good facilities for research. • Good connections among local plant conservation centres and researchers, and with other Macaronesian archipelagos. • The network of nature reserves and national parks provides excellent support for research. 	<ul style="list-style-type: none"> • Review the checklist of wild plants to publish a Flora. • Open access of researchers to all existing databases. • Create a virtual herbarium. • Better coordination of efforts among centres of research. • Set up a virtual pdf-library with all specialised literature. 	<ul style="list-style-type: none"> • Increase the offer of jobs as field botanists/taxonomists. • Stabilise staff who can support research through their skills. • Carry out and publish basic reproductive biology studies for most endemic plants. • Train more young local botanists in modern scientific research methods. • Increase institutional collaboration at the regional and international levels. • Glean information on historical collections out of the archipelago, including typification of the endemic Flora. 	<ul style="list-style-type: none"> • Improve funding schemes • Enforce the application of the existing laws • Improve administrative control of grazing and invasive alien species. • Relax the bureaucracy needed at present for local botanists to sample wild specimens, maybe through a general “researcher ID”. • Recognize the population as the minimum biological conservation unit deserving legal protection. • Implement institutional support for the facilities devoted to the <i>ex-situ</i> preservation of the flora (herbaria, seed and DNA banks), and to store information relevant to biodiversity research. • Increase interaction between the administration and researchers.

Table A1 (continued)

Archipelago	Conservation research assets at present			Foresight of urgent future needs in conservation	
	Weaknesses	Strengths	Suggested improvements	Scientific	Political
Cape Verde	<ul style="list-style-type: none"> Lack of funding by government and thus of institutional stability to carry out basic research. Lack of training in modern research methods. 	<ul style="list-style-type: none"> Openness toward collaboration with foreign institutions. 	<ul style="list-style-type: none"> Training programs addressed to local biologists. 	<ul style="list-style-type: none"> Basic research activities on populations of threatened species. Increase capacity of staff through higher level training. 	<ul style="list-style-type: none"> Consistent financial support.
Galápagos	<ul style="list-style-type: none"> Not highly valued by responsible institutions. Under-funded. Programme not strategically designed. 	<ul style="list-style-type: none"> Dedication of local biologists. 	<ul style="list-style-type: none"> Improvements in policy, planning and capacity at local research and management institutions. 	<ul style="list-style-type: none"> Survey, monitoring, population dynamics studies, population management. 	<ul style="list-style-type: none"> Enforcement of existing laws and protocols. More funding.
Hawaii	<ul style="list-style-type: none"> Lack of funds Conflicts of interests with other stakeholders. 	<ul style="list-style-type: none"> Dedication of local conservation staffs. 	<ul style="list-style-type: none"> Increase funding. More interactions of local groups, national, and international conservation biologists. 	<ul style="list-style-type: none"> Alien species control (both for invasive diseases/ insect pests that are affecting endangered plants, and for invasive plants). Protection of habitat. Studies of endemic species (reproductive biology, anticipated responses to global change ...). 	<ul style="list-style-type: none"> Will to control feral mammals like pigs, goats, and deer. Will to set up an effective biosecurity programme that keeps new disease, pests, and weeds out of Hawaii and has a rapid response to those that get through the barriers. Will for funding to effectively protect conservation zones.
Juan Fernández	<ul style="list-style-type: none"> No well curated seed bank and no DNA bank Lack of one central herbarium. Lack of trained conservation advisors for CONAF staff. Poor success in limiting areas where cattle can graze. 	<ul style="list-style-type: none"> Awareness of the uniqueness and fragility of the endemic flora. Concerted effort to educate the local human population on the importance of the flora. Programme to assist locals in identifying new invasives and in reporting them to CONAF personnel. Success in the cultivation of most endangered species. 	<ul style="list-style-type: none"> Need to document occurrence of new populations in the herbarium. Deposit duplicates in herbarium on mainland Chile Require that applications for permission to work in the islands include agreement to deposit with CONAF in Chile publications resulting from work. Use CONAF personnel to attempt to limit the introduction of invasives. 	<ul style="list-style-type: none"> Reduce further the goats and rabbits. Prevent the continued encroachment of several aggressive invasives into native forest. Restoration of the extensive eroded areas. Studies of the basic biology of endemics (demography, reproductive biology, and population genetics). 	<ul style="list-style-type: none"> Enforce the rule of no animal husbandry in the park. Requirement to give vouchers to CONAF before anyone working on the flora can leave the islands. Concerted efforts to prevent introduction of exotic plant species. Continued development of ecotourism that enhances economy but has minimal environmental impact. Plan to minimize the conflict between the local human population and CONAF on issues such as cattle grazing and land use in the national park lands. Support for professional conservation biologist in residence in the islands to interact with CONAF personnel. Obtain support from private foundations, foreign governments, etc., for basic research on the flora.
Madeira & Selvagens	<ul style="list-style-type: none"> Lack of funds. Lack of human resources. 	<ul style="list-style-type: none"> Large protected areas. Easily accessible plant populations. 	<ul style="list-style-type: none"> Coordination of efforts with the different Madeiran institutions working on plant studies and conservation. Increase funding for continuing conservation projects. 	<ul style="list-style-type: none"> Increase studies on endemic species (molecular, reproductive biology, ...). Increase monitoring. Measures to control invasive alien species. 	<ul style="list-style-type: none"> A effective control programme for the invasive alien species. Regional legislation to conserve Madeiran species.
Mascarenes	<ul style="list-style-type: none"> Low government commitment (except Réunion). Most staff poorly 	<ul style="list-style-type: none"> Well curated Herbaria. Floral diversity and endangerment status well known. 	<ul style="list-style-type: none"> Increase collaboration (local - island scale-, regional - Mascarene scale-, and beyond). Increase capacity of staff 	<ul style="list-style-type: none"> Improve understanding of alien species impacts on native plants and communities. 	<ul style="list-style-type: none"> Proper enforcement of existing legislation (Mauritius and Rodrigues mainly).

Table A1 (continued)

Archipelago	Conservation research assets at present			Foresight of urgent future needs in conservation	
	Weaknesses	Strengths	Suggested improvements	Scientific	Political
	<ul style="list-style-type: none"> trained in ecology and conservation (except Réunion). Lack of good research facilities (except Réunion). 	<ul style="list-style-type: none"> Dedicated staff. Openness to collaboration with external institutions. Biological invasions strategies published for Mauritius (2008) and Réunion (2009) 	<ul style="list-style-type: none"> through higher level training. (mostly Mauritius, Rodrigues) Mainstream conservation. 	<ul style="list-style-type: none"> Improve the effectiveness and lower the cost of invasive alien species control. Develop more cost effective methods of ecosystem restoration. 	<ul style="list-style-type: none"> Improvement of legislation particularly regarding non introduction of potentially invasive alien species. Commitment to a meaningful ecosystem approach to conservation as defined for e.g. in the National Biodiversity Strategy and Action Plan of Mauritius and Rodrigues. Proper use of the existing line of funds dedicated to conservation (Mauritius and Rodrigues).
Seychelles	<ul style="list-style-type: none"> Lack of local trained botanists. Although government sees the need for plant conservation activities and research, an NGO (PCA) with little human resources and time capacity struggles to be effective. 	<ul style="list-style-type: none"> Plant Conservation Research Agenda published in 2007. Established links with several overseas research institutions. Increasing awareness of the need for conservation research. Success in propagating many endemic species. New UNDP-GEF project on management of invasive alien species and biosecurity measures. 	<ul style="list-style-type: none"> Widen the network of research institutions. Actively access local, regional & international finance. Increase human and financial capacity for research Improve curation of the national herbarium and create seed collection. 	<ul style="list-style-type: none"> Improve the plant diversity information base, including genetic studies. Improve <i>ex-situ</i> conservation techniques and protocols. Prioritise species and habitats for conservation action. Research in plant-environment inter-relationships and biotic interactions. Prioritise species and methodologies for <i>in situ</i> conservation work. Identify potential climate change impacts on habitats and species. 	<ul style="list-style-type: none"> Better enforcement of existing laws. Collaboration with local and overseas organisations to find new ways of funding training, research and conservation efforts. Ensure research projects include capacity building element, inputs to local data bases, etc. Improve media and educational awareness of plant conservation issues and successes. Encourage the development of participatory methods of resolving stakeholder conflicts over land use, resource use, etc.

Table A2

Summary of data from 62 archipelagos, of which 53 were used for the endangerment level analyses. Island/island group areas were taken from the data available at the UNEP islands website (<http://islands.unep.ch/>).

Islands	Region	II	Area (km ²)	Plant endemics		
				Total	EN	CR
Andaman and Nicobar	Indian	38.6	7193.2	¹ 227	10	14
Antigua and Barbuda ^{ε,ο}	Caribbean		277.0	¹ 0	2	0
Azores	East Atlantic	75.7	2434.5	² 72	3	0
Bahamas	Caribbean	36.2	12,092.2	¹ 117	2	0
Baleares	Mediterranean	31.7	5021.0	¹ 94	0	8
Barbados ^ο	Caribbean	46.0	462.4	¹ 2	1	0
Bermuda	Caribbean	91.0	39.3	¹ 15	1	1
Borneo ^{ς,ο}	Indian		733,099.0	¹ 6750	101	213
Canaries	East Atlantic	30.4	7,349.9	³ 607	5	5
Cayman Is.	Caribbean	44.7	262.3	² 19	2	0
Comoros	Indian	48.5	2021.3	¹ 136	2	1
Corse	Mediterranean	23.0	8741.4	¹ 126	0	4
Crete	Mediterranean	28.0	8349.7	¹ 159	0	4
Cuba	Caribbean	28.5	105,805.5	¹ 3,193	59	22
Dominica	Caribbean	41.0	787.3	¹ 12	3	0
Fiji	Asia/Oceania	86.5	18,070.6	¹ 812	14	22
Galápagos	East Pacific	63.8	7,610.2	⁴ 180	8	6
Grenada	Caribbean	34.0	322.7	¹ 4	1	0
Guadeloupe	Caribbean	33.0	1726.2	¹ 19	5	1
Guam	Asia/Oceania	86.0	541.0	¹ 69	1	1
Hawaii	East Pacific	120.0	10,434.0	⁵ 929	64	109

Table A2 (continued)

Islands	Region	II	Area (km ²)	Plant endemics		
				Total	EN	CR
Hispaniola	Caribbean	43.0	73,929.0	¹ 1,400	15	8
Jamaica	Caribbean	48.0	11,189.9	¹ 852	59	46
Japan	Asia/Oceania	38.0	363,931.5	¹ 222	2	0
Java	Indian	39.3	138,794	¹ 250	14	13
Juan Fernández	East Pacific	58.5	148.5	⁶ 133	0	15
Madagascar ^o	Indian		587,713.3	¹ 7569	110	66
Madeira & Selvagens	East Atlantic	66.0	793.3	¹ 36	0	2
Mariana	Asia/Oceania	80.0	477.3	¹ 81	1	2
Marquesas	Asia/Oceania	115.9	1081.2	¹ 132	5	3
Martinique	Caribbean	42.0	1166.6	¹ 24	3	0
Mauritius	Indian	91.0	1984.6	¹ 311	14	68
Moluccas	Indian	49.7	66,347.1	¹ 300	1	4
Montserrat ^o	Caribbean	39.0	124.1	¹ 2	1	0
New Caledonia ^o	Asia/Oceania		16,648.4	¹ 2,551	66	28
New Zealand	Asia/Oceania	78.6	261,079.9	¹ 1942	7	2
Palau	Asia/Oceania	81.5	516.1	¹ 3	1	0
Papua New Guinea ^o	Asia/Oceania		785,753.0	¹ 13,250	6	1
Philippines	Asia/Oceania	49.6	295,995.5	¹ 3471	32	55
Pitcairn	East Pacific	106.3	42.9	¹ 14	2	3
Puerto Rico	Caribbean	59.0	9249.9	¹ 215	16	22
Reunión	Indian	73.0	2535.2	¹ 234	3	5
Saint Helena	East Atlantic	113.0	125.5	¹ 50	7	9
St. Kitts and Nevis ^o	Caribbean		263.1	¹ 1	1	0
St. Lucia	Caribbean	41.0	639.8	¹ 11	2	1
St. Vincent and Grenadines	Caribbean	37.0	381.0	¹ 20	1	0
Samoa	Asia/Oceania	91.8	3048.9	¹ 149	1	1
Sao Tomé and Príncipe	Caribbean	39.0	10,033.3	¹ 119	2	0
Sardegna	Mediterranean	22.7	23,949.0	¹ 115	0	8
Seychelles	Indian	72.8	1564.2	⁷ 70	4	9
Sicily	Mediterranean	5.0	25,662.4	¹ 188	1	8
Society Is.	Asia/Oceania	102.5	1627.7	¹ 273	0	18
Socotra	Indian		3606.7	¹ 260	26	3
Solomon Islands	Asia/Oceania	69.9	26,556.5	¹ 30	1	0
Sulawesi	Indian	38.8	193,640.5	¹ 500	0	4
Sumatera	Indian	17.0	443,065.8	¹ 1200	32	64
Tonga	Asia/Oceania	78.5	672.5	¹ 25	0	1
Trinidad and Tobago	Caribbean	21.0	5317.5	¹ 215	1	0
Tristan Da Cunha	East Atlantic	106.5	192.8	¹ 40	1	0
Turks and Caicos	Caribbean	42	797.2	¹ 9	2	0
Vanuatu	Asia/Oceania	56.4	12,105.8	¹ 150	2	1
Virgin Islands* ^o	Caribbean		452.5	¹ 5	5	7

The Isolation Index (II) given in the UNEP islands website for a particular island is the sum of the square roots of the distances to the nearest equivalent or larger island, the nearest island group or archipelago, and the nearest continent. For archipelagos and island groups, II was estimated by averaging the IIs of the islands where such data were available at the cited UNEP website. The total data for the EN and CR endemics retrieved from the IUCN Red-List Database (<http://www.iucnredlist.org/>) are available through the permalinks <http://www.iucnredlist.org/search/link/4a4b66e1-ae0a8ae7> (EN), and <http://www.iucnredlist.org/search/link/4a4b672b-0d3a83e0> (CR). The total numbers of endemic plants per island were obtained from the references indicated by numerical superscripts.

¹ Data unavailable for Barbuda; ² Only Kalimantan, Sabah, and Sarawak; ³ Data unavailable for St. John, St. Thomas and St. Croix; ⁴ Outlier islands, excluded from the statistical analyses (see section "Methods"); ⁵ Davis et al. (1997); ⁶ Silva et al. (2005a), and Mónica Moura (unpubl. data); ⁷ Acebes-Ginóvès et al. (2004) and Arnoldo Santos-Guerra (unpubl. data); ⁸ Wiggins and Porter (1971) Flora of the Galápagos Islands, and Alan Tye (unpubl. data); ⁹ Wagner et al. (2005) and Ann Sakai (unpubl. data); ¹⁰ Marticorena et al. (1998), and Daniel J. Crawford (unpubl. data); ¹¹ Kueffer et al. (2007a) and Katy Beaver (unpubl. data).

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