A global comparison of plant invasions on oceanic islands

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Abstract

Oceanic islands have long been considered to be particularly vulnerable to biotic invasions, and much research has focused on invasive plants on oceanic islands. However, findings from individual islands have rarely been compared between islands within or between biogeographic regions. We present in this study the most comprehensive, standardized dataset to date on the global distribution of invasive plant species in natural areas of oceanic islands. We compiled lists of moderate (5–25% cover) and dominant ($>25\%$ cover) invasive plant species for 30 island groups from four oceanic regions (Atlantic, Caribbean, Pacific, and Western Indian Ocean). To assess consistency of plant behaviour across island groups, we also recorded present but not invasive species in each island group.

We tested the importance of different factors discussed in the literature in predicting the number of invasive plant species per island group, including island area and isolation, habitat diversity, native species diversity, and human development. Further we investigated whether particular invasive species are consistently and predictably invasive across island archipelagos or whether island-specific factors are more important than species traits in explaining the invasion success of particular species.

We found in total 383 non-native spermatophyte plants that were invasive in natural areas on at least one of the 30 studied island groups, with between 3 and 74 invaders per island group. Of these invaders about 50% (181 species) were dominants or co-dominants of a habitat in at least one island group. An extrapolation from species accumulation curves across the 30 island groups indicates that the total current flora of invasive plants on oceanic islands at latitudes between c. 35°N and 35°S may eventually consist of 500–800 spermatophyte species, with 250–350 of these being dominant invaders in at least one island group. The number of invaders per island group was well predicted by a combination of human development (measured by the gross domestic product (GDP) per capita), habitat diversity (number of habitat types), island age, and oceanic region (87% of variation explained). Island area, latitude, isolation from continents, number of present, non-native species with a known invasion history, and native species richness were not retained as significant factors in the multivariate models.

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Among 259 invaders present in at least five island groups, only 9 species were dominant invaders in at least 50% of island groups where they were present. Most species were invasive only in one to a few island groups although they were typically present in many more island groups. Consequently, similarity between island groups was low for invader floras but considerably higher for introduced (but not necessarily invasive) species – especially in pairs of island groups that are spatially close or similar in latitude. Hence, for invasive plants of natural areas, biotic homogenization among oceanic islands may be driven by the recurrent deliberate human introduction of the same species to different islands, while post-introduction processes during establishment and spread in natural areas tend to reduce similarity in invader composition between oceanic islands. We discuss a number of possible mechanisms, including time lags, propagule pressure, local biotic and abiotic factors, invader community assembly history, and genotypic differences that may explain the inconsistent performance of particular invasive species in different island groups.

Introduction

Biotic invasions are widely considered as one of the main threats to native biodiversity (Mack et al., 2000; Millennium Ecosystem Assessment, 2005), particularly on oceanic islands (Cronk and Fuller, 1995; Denslow, 2003; Tassin et al., 2006; Reaser et al., 2007). A number of explanations have been proposed to explain the invasiveness of non-native plants in new geographic areas (Mooney et al., 2005; Richardson and Pyšek, 2006). These include competitive advantages under particular environmental conditions (Daehler, 2003), the release from natural enemies (DeWalt et al., 2004), or the possession of novel traits such as nitrogen fixation compared with the flora in the introduction area (Vitousek, 1990). However, it has proven difficult to predict the outcome of particular invasions (National Academies of Sciences, 2002), especially over the long term (Strayer et al., 2006).

Oceanic islands provide a convenient study system to generalize about the outcome of biotic invasions (Whittaker and Fernández-Palacios, 2006; Denslow et al., 2009). They are isolated, replicated systems distributed globally that have experienced major biotic invasions over the past 200 years. They vary broadly in size, isolation, geology (volcanic vs. continental origin), and ecology (diversity of floras, faunas, microclimates, and habitats). Importantly, often the same non-native species have been introduced to many oceanic islands around the world. Comparing the presences and performance of invasive species among oceanic island groups therefore allows us to test the consistency of invasive plant behaviour. Because of their long history of large-scale anthropogenic disturbances and introduction of non-native species, oceanic islands can serve as early warning system for continental systems that have not yet experiences such a disturbance history.

In this study, we intend to quantitatively document patterns of plant invasions on oceanic islands on a global scale in order to identify patterns across island groups and oceanic regions and to provide a baseline for future comparative research in invasion biology. We compiled lists of common and dominant invasive plant species in natural areas for 30 island groups from four oceanic regions (Atlantic, Caribbean, Pacific, and Western Indian Ocean). In contrast to our study, previous analyses of non-native species richness on oceanic islands have not focused on species that were actually common or dominant in natural areas. Either all naturalized species were included in the analysis (Sax et al., 2002) or the occurrence of species from regional invasive plant lists was checked (Denslow et al., 2009). Knowledge on invasive plants on oceanic islands has been compiled in a number of regions including the Pacific (Meyer, 2000, 2004; Denslow et al., 2009), Macaronesia (Silva et al., 2008), the Caribbean (Kairo et al., 2003), the Western Indian Ocean (Kueffer et al., 2004), the UK Overseas Territories (Varnham, 2005), and the sub-antarctic islands (Frenot et al., 2005). However, data format, quality and completeness differ widely between studies. We have therefore compiled our own dataset based on a standardized methodology and drawn from a wide range of literature and expert opinion.

We quantitatively addressed the following research questions with our compiled dataset and discuss these based on a review of literature on plant invasions on oceanic islands:

1. How many plant species are threatening oceanic island ecosystems?
2. What predicts the number of invasive species on different island groups?
3. How similar are invader floras between oceanic island groups?
4. Which invasive plants are the most problematic ones on oceanic islands? How consistent and predictable is the performance of particular non-native plant species on different island groups?
5. What are the traits of common and dominant invasive plant species oceanic islands?

Methods

Species occurrences and abundances

We considered in this study only invaders of natural areas, whereby natural areas were defined as areas without frequent anthropogenic disturbance (Kueffer and Daehler, 2009). Ruderal sites, roadsides, agricultural land and urban areas were not considered. Invasive, non-native spermatophyte species on each of the 30 island groups were separated into two classes. Moderate invaders (M) are common but not dominant invaders of natural areas of a particular island group, i.e. they attain a maximal relative vegetation cover of c. 5–25% in natural areas. Dominant invaders (D) are habitat dominants or co-dominants in natural areas of a particular island group, i.e. they attain a maximal relative vegetation cover >25% in natural areas. The complete list of the species that were assessed as either an M or D invader on at least one of the 30 island groups represents the total species pool that was analysed in this study (383 species). To assess the extend of occurrence for these species across each island group, we further determined where these species were recorded as present but not as M or D invaders, while also noting if species were native in any of the island groups.

We separately analysed patterns for dominant invaders ('D invaders') and dominant and moderate invaders combined ('All invaders'). All invaders may be interpreted broadly as invasive species of natural areas *sensu* Richardson et al. (2000b), although no minimal cover value is discussed by the latter authors. D invaders may be interpreted as dominating invasive species with a high potential to have negative impacts, keeping in mind that an invasive species with a lower abundance may also have negative impacts. For comparisons among island groups, we further analysed patterns for Present invaders. For a given island group, Present species included all species present, among the global pool of 383 island invaders, irrespective of their local behaviour. Thus, the three sets of species used for island group comparisons were nested: D invaders are a subset of All invaders (D + M invaders) and All invaders are a subset of Present species (D + M invader, plus all present species that were recorded as D or M invaders for at least one island group).

Only invasion of terrestrial (i.e. not littoral, mangrove or wetland) habitats was considered because status (native, non-native) is often not clear in coastal habitats. Obligate aquatic species were not included in this study. Data on species occurrences, abundances and status (native, non-native) were derived from local literature and expert knowledge (see Appendix 1). For the Pacific, presences were also checked in the Pacific Islands Ecosystems at Risk (PIER) online database (http://www.hear.org/Pier/, last checked in January 2009). We followed the nomenclature of the USDA Germplasm Resources Information Network (GRIN) taxonomy database (http://www.ars-grin.gov/cgi-bin/npgs/html/index.pl, last checked in January 2009).

Species traits

For all species, the life form (annual, biennial, perennial) and growth form (graminoid, forb/herb, vine, shrub, tree) were derived from the USDA Plants database (http://plants.usda.gov/, last checked in September 2008). Taxonomic family, native range (on a country level) and use (agriculture/agroforestry/food, forestry, pasture, soil improvement/erosion control/re-vegetation, ornamental) were compiled from the USDA GRIN database. Some species were assigned to several use categories, while for some species no use was recorded. Native range was classified into five climatic zones (polar/alpine, temperate, continental, dry/Mediterranean, subtropical/tropical). Assignment to the five climatic zones was based on the updated Köppen–Geiger world climate map by Peel et al. (2007).

Island characteristics

Island characteristics are recorded in Table 1 and were derived from the CIA World Factbook (CIA, 2006), the UN Islands Directory (http://islands.unep.ch/, last checked in October 2008) and in a few cases local sources (see Appendix 1). For geographic isolation from the nearest continent the data in the UN Islands Directory was used. In each island group, only islands of a minimum elevation of 150 m above sea level were used for determining island area, i.e. low-lying coralline islands were excluded. Most of the island groups where true oceanic islands of volcanic origin, while six were continental fragments.

The gross domestic product (GDP) per capita is based on purchasing power parity (PPP). It had to be estimated for some of the island groups: Ascension (St. Helena value used), Galapagos (Ecuador), Hawaii (USA), Canary Islands (Spain), Madeira and Azores (Portugal), Juan Fernandez and Rapa Nui (Chile), Pitcairn (lowest value, i.e. Samoa).

Habitats were assigned to eight classes (lowland dry, lowland wet, mesic/humid mid-altitude, montane mist forest, subalpine heath, alpine herbaceous vegetation, young volcanic flows, and pastures/grasslands, compare e.g. Mueller-Dombois, 2002) based on local literature and expert judgement (see Appendix 1). For the Pacific, additionally Mueller-Dombois and Fosberg (1998) was used for habitat classification. Coastal, mangrove, and wetland habitats were not considered in the analysis. The number of habitats per island was calculated based on this classification.

Table 1a. Geographic characteristics of the 30 studied island groups.

Island name	Island type[a]	Region[b]	Latitude	Isolation[c] (km)	Area[d] (km^2)	Altitude[e] (m)	Age[f] (million years)
Ascension	oc	Atl	8°S	1700	97	859	1
Australs	oc	Pac	22°S	5600	108	650	12
Azores	oc	Atl	39°N	1300	2335	2351	5
Canary Islands	oc	Atl	28°N	96	7275	3717	21
Cape Verde	oc	Atl	16°N	620	4033	2829	180
Cook Islands	oc	Pac	20°S	4500	167	653	65
Dominican Rep.	cont	Car	19°N	570	48,380	3175	40
Galapagos	oc	Pac	1°S	850	7035	1707	5
Gambier	oc	Pac	22°S	5000	40	445	6
Hawaii	oc	Pac	22°N	3650	10,400	4205	5
Jamaica	cont	Car	18°N	625	10,831	2256	40
Juan Fernandez	oc	Pac	34°S	600	149	1320	6
Madeira	oc	Atl	32°N	560	749	1862	5
Marquesas	oc	Pac	8°S	6800	1050	1276	6
Mauritius	oc	WIO	20°S	1800	1874	828	8
Mayotte	oc	WIO	13°S	500	371	660	8
New Caledonia	cont	Pac	21°S	1200	16,750	1628	80
Palau	oc	Pac	7°N	756	458	245	20
Pitcairn	oc	Pac	26°S	4800	8	347	1
Puerto Rico	cont	Car	18°N	700	8870	1338	40
Rapa Nui	oc	Pac	27°S	3700	166	511	3
Réunion	oc	WIO	21°S	1200	2507	3069	3
Rodrigues	oc	WIO	20°S	2200	108	396	2
Saint Helena	oc	Atl	16°S	1960	122	823	14
Samoa	oc	Pac	14°S	3900	3143	1857	2
Seychelles	cont	WIO	4°S	1400	235	915	65[g]
Society	oc	Pac	17°S	6000	1598	2241	7
Tonga	oc	Pac	19°S	3200	348	1033	10
US Virgin Islands	cont	Car	18°N	780	346	475	40
Wallis and Futuna	oc	Pac	14°S	3900	255	765	22

[a]Island type: oc = oceanic, cont = continental fragment.
[b]Geographic region: Atl: Atlantic, Car: Caribbean, Pac: Pacific, WIO: Western Indian Ocean.
[c]Distance to the closest continent.
[d]Total area of all islands with elevation >150 m asl. in the island group.
[e]Maximum elevation in the island group.
[f]Age of oldest island in million years.
[g]Time since complete separation from Gondwana.

Statistical analyses

All statistical analyses were performed in R (V 2.8.1, R Development Core Team, 2008). The number of D invaders, All invaders and Present species per island group was modelled with generalized linear models (glm) with a Poisson error distribution to account for non-normality in residual distribution. The following predictors were used in the modelling (after either log- or square root-transformation if distribution of the predictor across island groups was skewed, see Table 1): Region, Latitude, sqrt(Isolation), log(Area), log(Altitude), log(Age), sqrt(Number of habitats), log(Number of native species), log(GDP), and sqrt(Population density). For the prediction of number of D or All

invaders, the number of present species minus the number of D invaders viz. All species (to exclude effect of autocorrelation) was also included in the model, but was not significant. Model selection was done both automatically based on Akaike's Information Criterion and by manual stepwise de-selection of non-significant terms.

Multivariate analyses, which were used to explore patterns among islands in presence/absence of D invaders, All invaders and Present species were based on Euclidean ecological distances and done with R package 'vegan' (V 1.15-1, Oksanen et al., 2008). The extrapolation of the total invasive flora on oceanic islands based on species accumulation curves was estimated with the function 'specpool' from R package 'vegan' (V 1.15-1, Oksanen et al., 2008). Geographic

Table 1b. Ecological and socioeconomic characteristics of the 30 studied island groups.

Island name	No. habitats[a]	Native species[b]	IAS (D)[c]	IAS (All)[d]	IAS (Present)[e]	GDP (US$)[f]	Population density[g]
Ascension	4	10	10	25	88	2500	11.3
Australs	4	180	7	21	90	17,500	58.4
Azores	6	160	30	57	128	17,900	104.1
Canary Islands	7	1198	22	64	184	23,300	274.3
Cape Verde	6	205	6	11	85	1400	103.7
Cook Islands	3	180	3	10	147	5000	128.1
Dominican Rep.	6	4612[h]	21	49	143	6300	185.0
Galapagos	6	447	6	18	108	3700	5.7
Gambier	2	61	3	13	52	17,500	27.1
Hawaii	8	956	47	74	306	40,100	127.0
Jamaica	6	2540	8	16	121	4100	252.2
Juan Fernandez	3	155	5	9	43	10,700	4.0
Madeira	5	1088	22	69	149	17,900	328.2
Marquesas	4	226	7	23	105	17,500	8.0
Mauritius	3	677	23	47	233	12,800	635.3
Mayotte	4	540	17	29	102	2600	521.9
New Caledonia	6	3000	7	31	169	15,000	12.9
Palau	2	802	2	9	107	9000	44.3
Pitcairn	2	35	4	6	44	2300	5.8
Puerto Rico	5	2221	17	43	154	17,700	441.6
Rapa Nui	2	30	3	12	65	10,700	13.9
Réunion	8	835	35	70	245	6000	309.9
Rodrigues	3	134	11	18	95	12,800	370.4
Saint Helena	4	55	8	34	89	2500	61.1
Samoa	4		7	16	114	6800	76.9
Seychelles	4	250	9	19	136	7800	345.5
Society	7	450	18	46	162	17,500	142.6
Tonga	3	450	0	3	102	2300	323.1
US Virgin Islands	3		6	9	86	17,200	314.2
Wallis and Futuna	3	310	4	9	82	3800	62.8

[a]Number of eight habitat types represented in island group.
[b]Number of native flowering plant species – data for some islands are best estimates based on probably incomplete data.
[c]Number of non-native invasive plants assessed as dominant invader (D).
[d]Total number of non-native invasive plants assessed as either moderate or D invader (All).
[e]Number of species from the total species pool present on the particular island in any habitat or abundance.
[f]Gross domestic product (GDP) at Purchasing Power Parity (PPP) per capita in US$.
[g]Inhabitants per km^2.
[h]For Hispaniola (Dominican Republic and Haiti).

distance between all island group pairs was calculated based on latitudes and longitudes with the function 'rdist.earth' from R package 'fields' (V 5.02, Furrer et al., 2009).

Results

The total species pool of moderate and dominant invaders

In total, 383 invasive spermatophyte species from 277 genera and 96 families were recorded ('All invaders') on at least one of the 30 island groups and represent the total species pool analysed in this study. 47% of All invaders were assessed as D invaders on at least one island group (181 species from 146 genera and 63 families). 25% of All invaders and 20% of D invaders are native on at least one island group. These species are mostly native to the less isolated Caribbean (60%) or Macaronesian (23%) regions and neighbouring continental regions; however, there are a few exceptions where island endemics have become invaders (e.g. the highly invasive tree *Morella [Myrica] faya* from Macaronesia, or *Juniperus bermudiana* that is critically endangered in its native range). An extrapolation from the species accumulation curves for D and All invaders across the 30 island groups indicates that the total
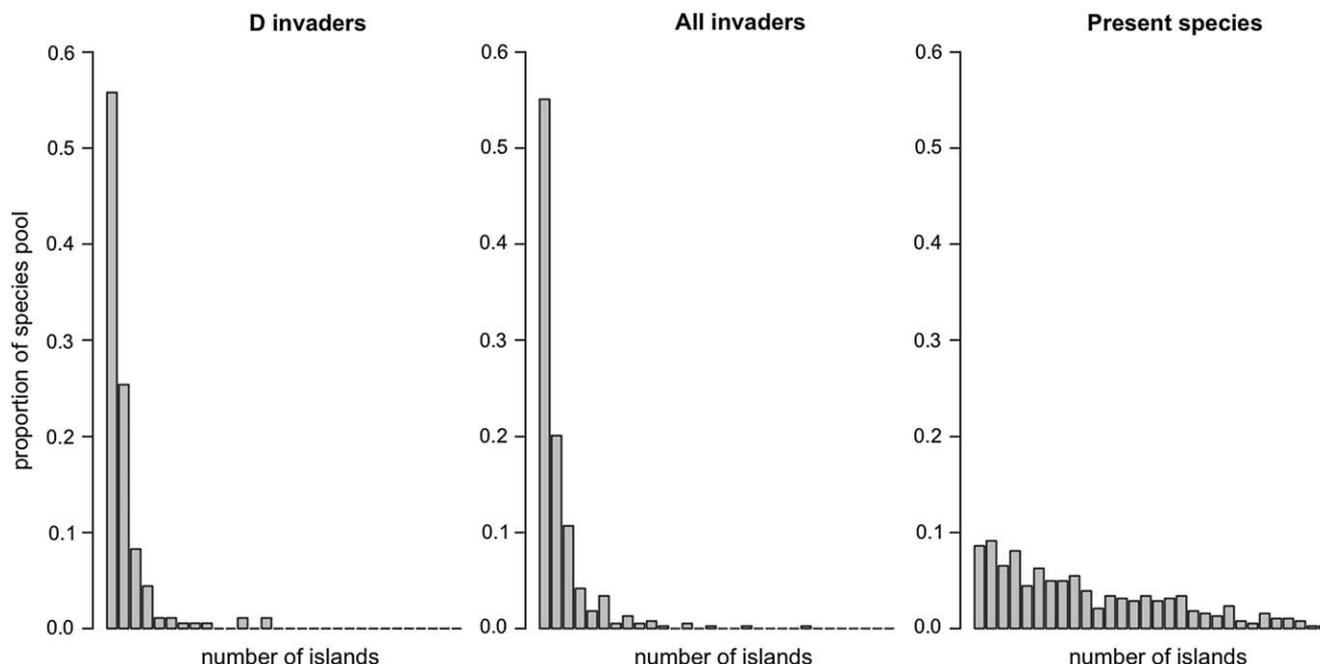
Fig. 1. Rank–abundance distribution of occurrences of the invaders of the total species pool across the 30 island groups. On the *y*-axis, the number of invaders (as a proportion of the respective total species number, i.e. 181 for D invaders, and 383 for All invaders and Present species) that occur on a particular number of island groups (*x*-axis) is indicated. Data are given for dominant invaders ('D invaders'), moderate or D invaders ('All invaders'), and presences in any habitat and abundance (anthropogenic areas, weeds, or invader of natural areas; 'Present species').

current flora of invasive plants on oceanic islands at latitudes between c. 35°N and 35°S may eventually consist of 500–800 spermatophyte species, with 250–350 of these being dominant invaders in at least one island group.

75% of the species in the total species pool consisted of moderate or dominant invaders only in 1 or 2 island groups (All invaders, Fig. 1). Even fewer, only 19% of the D invaders have become dominant in more than 2 island groups (D invaders, Fig. 1). In contrast, a majority of the species were present (without being invasive) on many island groups (Present species, Fig. 1).

Species present on five or more island groups

Species that are present on five or more islands (259 species, 68% of total species pool, Fig. 1) may be used to further assess the consistency of the performance of particular species in different island groups. Of these species 25 (24 genera, 19 families, 10% of the species present on 5 or more island groups) were assessed as D invader on at least 33% of the islands where present (Table 2). Considering All invaders (i.e. either moderate or D invader), 68 species (65 genera, 36 families, 26%; 10 Fabaceae, 6 Asteraceae, 5 Poaceae, 4 Myrtaceae) were recorded as invaders on at least 33% of the islands where present. Only 9 species were assessed as D on at least 50% of the islands where present (*Ardisia elliptica*,

Clidemia hirta, *Cytisus scoparius*, *Hiptage benghalensis*, *Lantana camara*, *Leucaena leucocephala*, *Litsea glutinosa*, *Melinis minutiflora*, and *Ulex europaeus*). Table 2 lists the 35 species that are either D invaders on at least 33% of the islands or All invaders (D or M) on at least 50% of the islands where present. These species are all from different genera. These 35 invader species may be considered consistently invasive species. The Fabaceae are represented by 7 species (20%) and are over-represented compared with the total species pool (11%, see below).

Among the species that are currently present in less than five island groups there are some that are very problematic (e.g. *Morella faya* in Hawaii or *Ligustrum robustum* subspec. *walkeri* in the Mascarenes), but the consistency of their invasive behaviour cannot be assessed with this dataset.

Traits of moderate and dominant invasive plant species

Taxonomy

Considering the total pool of invaders across all island groups, c. 1% are gymnosperms (3 Pinus, 1 Cryptomeria, and 1 Juniperus for All invaders), c. 20% are monocotyledons (55% Poaceae, 15 genera for All

Table 2. Species that are present on at least 5 island groups and were assessed as dominant (D) invader on at least 33% of the island groups where present or moderate or D (All) invader on at least 50% of the island groups.

Species	Family	Present	Regions	% All	% D
Clidemia hirta	Melastomataceae	9	3	89	78
Litsea glutinosa	Lauraceae	6	1	83	67
Leucaena leucocephala	Fabaceae	28	4	82	50
Delairea odorata	Asteraceae	5	2	80	40
Ardisia elliptica	Myrsinaceae	9	3	78	67
Lantana camara	Verbenaceae	26	3	69	54
Ageratina riparia	Asteraceae	6	2	67	33
Falcataria moluccana	Fabaceae	15	2	67	20
Melinis minutiflora	Poaceae	21	4	62	57
Ailanthus altissima	Simaroubaceae	5	1	60	20
Cytisus scoparius	Fabaceae	5	1	60	60
Erigeron karvinskianus	Asteraceae	10	3	60	30
Fuchsia magellanica	Onagraceae	5	3	60	20
Hiptage benghalensis	Malpighiaceae	5	1	60	60
Ulex europaeus	Fabaceae	10	3	60	50
Solanum mauritianum	Solanaceae	12	3	58	25
Holcus lanatus	Poaceae	7	3	57	29
Caesalpinia decapetala	Fabaceae	9	2	56	11
Syzygium jambos	Myrtaceae	27	3	56	44
Castilla elastica	Moraceae	11	3	55	18
Cinchona pubescens	Rubiaceae	6	1	50	33
Cryptostegia madagascariensis	Apocynaceae	8	2	50	38
Haematoxylum campechianum	Fabaceae	12	3	50	17
Paraserianthes lophantha	Fabaceae	6	2	50	33
Pennisetum setaceum	Poaceae	8	2	50	25
Hedychium gardnerianum	Zingiberaceae	13	4	46	46
Carpobrotus edulis	Aizoaceae	9	1	44	44
Merremia peltata	Convolvulaceae	9	2	44	33
Psidium cattleianum	Myrtaceae	24	3	42	38
Flacourtia indica	Salicaceae	10	1	40	40
Opuntia stricta	Cactaceae	5	1	40	40
Pittosporum undulatum	Pittosporaceae	8	2	38	38
Ardisia crenata	Myrsinaceae	6	1	33	33
Oxalis pes-caprae	Oxalidaceae	6	1	33	33
Phormium tenax	Agavaceae	9	2	33	33

Indicated are the number of island groups where the species is present, the number of regions (Atlantic, Caribbean, Pacific, Western Indian Ocean) where the species is an All invader on at least one island group, and the percentage of island groups where the species is an All viz. D invader (table sorted by % All).

invaders) and c. 80% are dicotyledons. The distribution of the number of D or All invaders per genus or family is highly skewed with only a few genera and families containing many species while most species are from genera or families with one or few invaders. The families with most invaders are as follows: Fabaceae (43 species, 11%), Poaceae (41 species, 11%), Asteraceae (28, 7%), Myrtaceae (14), Solanaceae (11), Rosaceae (10), Polygonaceae, Apocynaceae (both 8), and Meliaceae, Melastomataceae (both 7). The genera with most invaders are as follows: *Acacia* (13 species), *Rubus* (7), *Paspalum* (6), and *Fuchsia*, *Passiflora*, *Pennisetum* (all 5). Among these genera and families, the following contain more than 50% D invaders: Fabaceae (56%), Melastomataceae (86%), Myrtaceae, Poaceae (59%), Rosaceae, *Fuchsia*, *Rubus* (86%). The two most prominent families (Fabaceae, Poaceae) contain 27% of all D invaders and 22% of All invaders. D invaders are more evenly distributed among genera and families than All invaders (1.2 D vs. 1.4 All invaders per genus, 2.9 D vs. 4 All invaders per family in average), but the same ratios as those observed for D invaders were generated through random re-sampling of sets of 181 species from the total pool of All invaders. Thus, a random sampling effect may explain the observed patterns of species per genus and species per family. The same patterns were
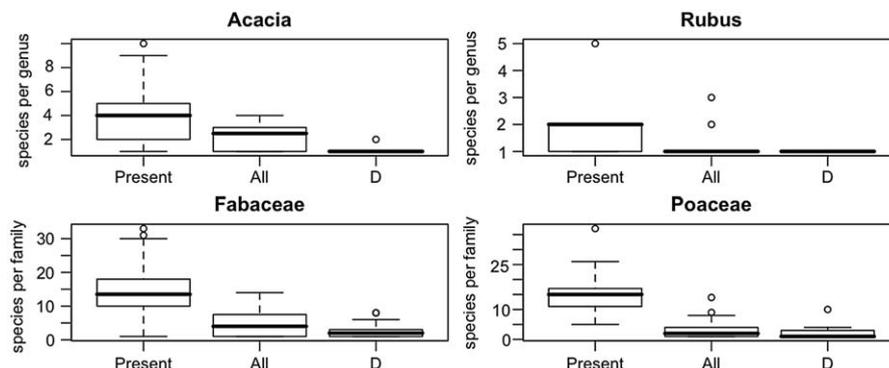
Fig. 2. Number of species per genus or family across the 30 different island groups for the two genera (Acacia, Rubus) and families (Fabaceae, Poaceae) with the most All species. The box-whisker-plots indicate the median (line), first and third quartiles (box), and the range of the data, with outliers indicated by open circles and defined as being more than 1.5 times the interquartile range above/below the first/third quartile.

also found on individual islands, where typically not more than one to a few invaders per genus or family were present even in the case of the most invader-rich taxonomic groups (Fig. 2).

Life forms and use

Among all recorded invaders, 57% are shrubs or trees; 28% are forbs, herbs or succulents; 10% are grasses; and 5% are obligate vines – with almost all of them being perennial species (93%). The most common use category was ornamentals (50%), while the invaders were relatively equally distributed among the other use categories: soil improvement, erosion control or re-vegetation (15%); agricultural or food related species (13%); forestry (12%), and pasture species (5%). The results only for D invaders do not differ generally from those for All invaders. The proportion of perennials (97%) and shrubs and trees (60%) tended to be higher among D than All invaders, but these differences were not significant ($p > 0.2$, χ^2 test). Among the consistently invasive species (Table 2), 100% of the species are perennials and 63% are shrubs or trees.

Climate

On the different island groups the proportion of (sub)tropical species decreased with increasing latitude, while the numbers of dry/Mediterranean and temperate species increased. On most subtropical and tropical islands over 95% of D invaders were (sub)tropical, while on the islands in higher latitudes (Macaronesian islands except Cape Verde, and Juan Fernandez) only 25–40% of the D invaders were (sub)tropical. There were four (sub)tropical islands (Réunion, St. Helena, US Virgin Islands, and Hawaii) that did not follow this pattern and had a lower proportion of (sub)tropical species (65–75%). The matching between the climate of the island group and the native climate range of the non-native species increased significantly from the pool of

present species ($82 \pm 1.3\%$ of species are (sub)tropical on (sub)tropical islands [Réunion, St. Helena, US Virgin Islands, and Hawaii excluded], average across islands $\pm$ standard error) to All ($96 \pm 1\%$) and D ($99 \pm 0.7\%$) invaders ($p < 0.001$, paired t-test between pairs of species groups).

Number of moderate and dominant invasive plant species per island group

Among All invaders between 3 and 74 species were recorded per island group (Table 1b). Pairwise correlations among all measures of non-native species richness (D invaders, All invaders, and present species) and island characteristics are listed in Appendix 2. There are linear relationships between the number of D invaders and moderate (M) invaders ($R^2 = 0.59$, $p < 0.001$) as well as present species (i.e. number of present species minus number of D invaders to exclude effect of autocorrelation) ($R^2 = 0.56$, $p < 0.001$). Consequently, the ratio of D per All (i.e. M or D) invaders per island group is relatively constant, with in average c. 40% (31–52%, first quartile to third quartile) of All invaders being D invaders. The relationship between All invaders and present species is less steep. On average 22% (14–28%) of the present species are invaders and 9% (6–12%) are D invaders. In other words, in average c. 80% of the species that are invasive on some island group(s) (Present species) were not recorded as invasive (M or D) on a particular island group even when present.

There is only a weak relation between the number of invaders and the number of native flowering plants per island group ($R^2 = 0.16$, $p = 0.03$), with in average 0.07 (median, 0.04–0.12, first to third quartile) All invaders per native flowering plant species. At the extremes, for Ascension there are 2.5 invaders per native species, while on island groups with over 2000 native plant species

(Dominican Republic, New Caledonia, Jamaica, and Puerto Rico) there are some 0.01 invaders per native plant species.

Further, pairwise correlations of the numbers of D or All species are significant with the following continuous predictors: area, altitude, number of habitats, gross domestic product, and population size and density (Appendix 2). Among the categorical predictors, neither island type (oceanic vs. continental, $p > 0.8$) nor region (Atlantic, Caribbean, Pacific, Western Indian Ocean, $p > 0.1$) had on its own a significant effect on presence of D or All invaders.

In multivariate generalized linear models to explain the number of D invaders per island group, the following predictors were retained after automatic stepwise model selection: region, island age, number of habitats, and gross domestic product (87% of variation explained). In the case of All invaders, isolation and number of native plants were also retained (89% of variation explained), but a model without these two additional predictors still explained 87% of the variation. In the case of number of Present invaders per island group, models are less clear and the following predictors were retained: region, isolation, area, altitude, number of habitats, GDP, and population density (85% of variation explained). In this case a model with region, island age, number of habitats, and GDP explains only 71% of the variation.

Overall, the number of invasive plant species per island group consistently increased with habitat diversity (number of habitats) and economic development (GDP) (Fig. 3). According to this model, island groups in the Pacific region tended to have in our dataset less invaders than expected, while the Azores and Madeira in the Atlantic and the Mascarenes and Mayotte in the Western Indian Ocean had more invaders than expected (Fig. 3). For the Pacific region separately, a model with number of habitats and GDP as predictors explained 92% (D invaders) and 93% (All invaders) of the variation across the 15 Pacific island groups.

Similarity of invasive floras among island groups

Multivariate analyses did not reveal strong patterns in the similarity of D invaders, All invaders or present species among island groups. In a PCA based on species composition, the first two axis explained c. 20% (All) and 30% (D, Present) of the variation and clustered three Macaronesian island groups – Canary Islands, Azores and Madeira, while separating Hawaii and Réunion from all other islands. For further analyses, we calculated differences in species composition and island characteristics (geographic distance, and the differences of latitude, altitude, area, number of habitats, GDP, and population density) for each of the
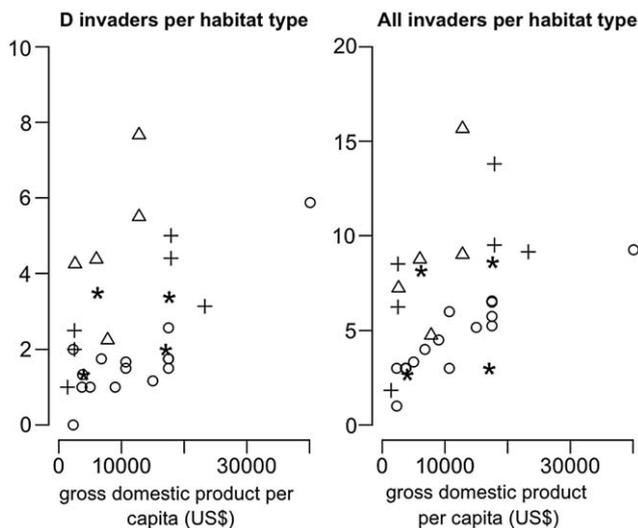

Fig. 3. Numbers of All and D invaders per island group were well predicted by just 3 factors (region, number of habitat types, and gross domestic product per capita (GDP), 82% and 81% of variation explained, respectively). The figure presents the number of D or All invaders per habitat type as a function of GDP, with regions indicated in different symbols (circle: Pacific, triangle: Western Indian Ocean, crosses: Atlantic, stars: Caribbean).
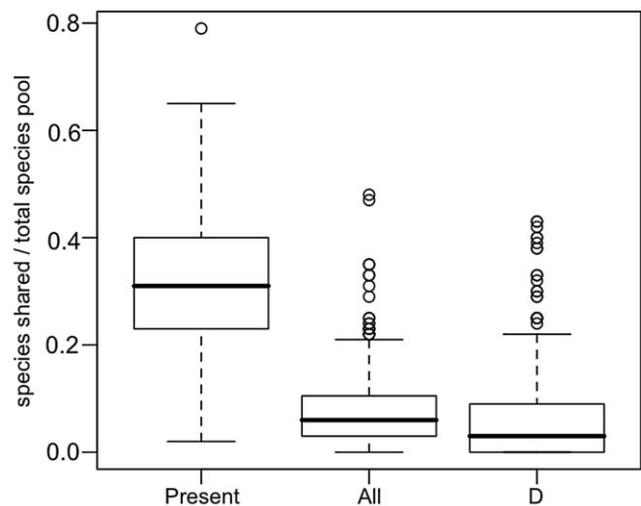

Fig. 4. Similarity of species composition among island groups measured as the ratio of the number of invaders shared between pairs of island groups to the total number of invaders that occurred on either of the two island groups (species shared/total species pool, Jaccard similarity index). Data are given for dominant (D) invaders, D and moderate invaders (All) and all species present (Present). The box-whisker-plots indicate the median (line), first and third quartiles (box), and the range of the data, with outliers indicated by open circles and defined as being more than 1.5 times the interquartile range above/below the first/third quartile. Differences in the means between all pairs of species groups were significant ($p < 0.001$, Wilcoxon-test).

435 pairs of island groups. As a measure of similarity of species composition among pairs of island groups we used the ratio of the number of species present on both island groups to the total number of species that occurred on either of the two island groups ('ratio of shared species', Jaccard similarity index). The ratio of shared species was higher for Present (0.31) than All (0.06) or D invaders (0.03) (Fig. 4, $p < 0.001$). With the exceptions of geographic distance ($r = -0.21$ [D], -0.33 [All], -0.22 [Present]) and latitude ($r = -0.16$ [D], -0.29 [All], -0.43 [Present]) none of the island characteristics was considerably correlated with the ratio of shared Present, All and D invaders ($r < 0.09$). Geographic distance and latitude were not correlated ($r = 0.01$). The relation between geographic distance and shared Present, All and D invaders was restricted to distances of less than c. 5000 km (Fig. 5). In this range,

the correlation was stronger for Present ($r = -0.55$) than All and D ($r = -0.45$) invaders.

Discussion

How many invasive plant species are threatening oceanic island ecosystems?

We found in total 383 non-native spermatophyte plants that were invasive in natural areas on at least one of the 30 studied island groups in the four oceanic regions – Atlantic, Caribbean, Pacific, and Western Indian Ocean. Thereby we counted a non-native plant as an invasive species if it reached a maximal relative vegetation cover of at least 5% on a scale larger than a single patch in a natural area ('moderate invader' in our
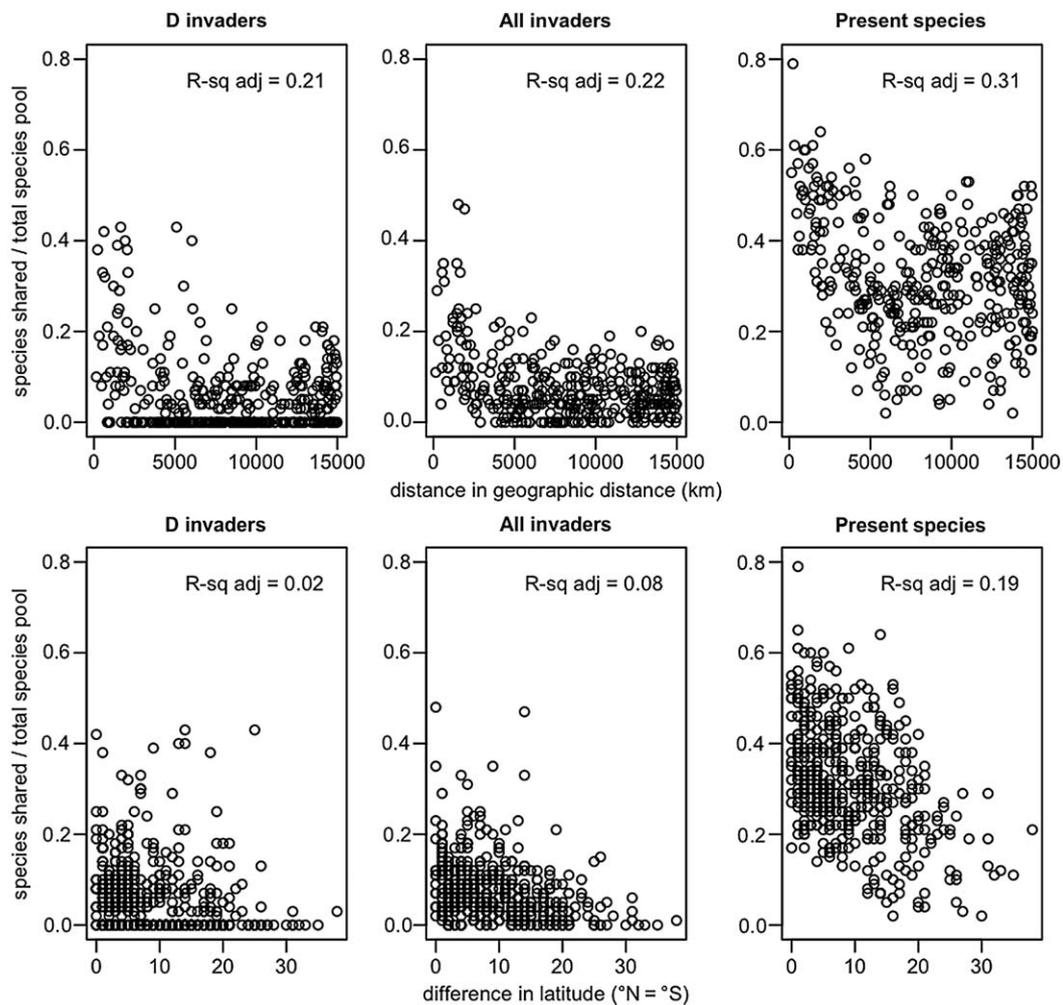

Fig. 5. The number of species shared by pairs of island groups as the ratio of the number of invaders shared between pairs of island groups to the total number of invaders that occurred on either of the two island groups (species shared/total species pool, Jaccard similarity index) plotted against the geographic distance between the island groups of the pair in km (upper panels) and difference in latitude (lower panel). Shown are the data for dominant invaders (D), dominant and moderate invaders (All), and all present species (Present). In upper panels, data are not shown for pairs separated by more than 15,000 km and adjusted R^2 is given for distances of less than 5000 km only.

terminology). Of these invasive species about 50% (181 species) were dominants or co-dominants of a habitat in at least one island group. These dominant invaders may be interpreted as invasive species that likely have a strong impact on invaded biotic communities and ecosystems – whether negative or positive. However, it has to be kept in mind that also rare non-native species may affect native biotas, e.g. through hybridization with a rare native species (Daehler and Carino, 2001; Reaser et al., 2007), or by occupying a specific microhabitat (cf. Kueffer and Daehler, 2009). Extrapolation based on species accumulation curves indicate that the total current flora of invasive plants on oceanic islands at latitudes between c. 35°N and 35°S may eventually consist of 500–800 spermatophytes, with 250–350 of these being a dominant invader in at least in one island group. Daehler (1998) and Weber (2003) reported similar numbers, i.e. 381 and 448 plant species, respectively, for the global natural areas invader flora of oceanic islands and continents combined. These numbers for natural area invaders alone are considerably lower than those of non-native floras that include weed species invading anthropogenic and ruderal areas. The Global Compendium of Weeds (Randall, 2002) for instance lists some 28,000 weed species globally.

In summary, once weed species of anthropogenic habitats are filtered out, a relatively small number of plant species seems currently invasive in natural areas on oceanic islands, given that for instance for the Hawaiian Islands alone over 10,000 introduced, non-native plant species have been recorded (Imada et al., 2006). However, new non-native plants are being continuously introduced to oceanic islands (e.g. Tye, 2006; Kueffer and Loope, 2009) – in particular ornamental plants (Meyer and Lavergne, 2004; Meyer et al., 2008), so the number of invaders will increase. In the Galapagos, for instance, the number of recorded introduced species increased in the past 20 years from c. 250 to some 800 (Tye, 2006; Jaramillo et al., 2008).

What predicts the number of invasive species on different island groups?

Our multivariate regression models indicate that the number of moderate or dominant invaders per island group is well predicted by a combination of human development (measured by the gross domestic product per capita) and habitat diversity (number of habitat types) (Fig. 3). Further, geographic region was retained as a significant factor in all models. This may be because of some unidentified regional differences (e.g. in anthropogenic disturbance history), and it can also not be ruled out that differences between regions partly reflect regional differences in the assessment of invaders. Although we identified clear criteria for M and D

invaders, we had partly to rely on subjective expert judgments for assessment of the abundance of invader species, as well as the frequency of anthropogenic disturbance where those species occurred.

The number of dominant (D) invaders decreased with increasing age of the island group. It could be argued that older islands have older floras and therefore less open niche opportunities for invaders, but plotting the residuals of the model (with GDP, habitat diversity and region) against island age indicates that the significance of this predictor may rather stem from some outlier groups. In particular, the young and small Ascension and Pitcairn islands have more D invaders than expected from the model, but these islands are composed of largely human-transformed landscapes, which are not reflected in their GDP. More interestingly, the two isolated, continental fragment islands, Seychelles and New Caledonia have less D invaders than predicted by the model. One may wonder if the floras of these island groups that were not assembled through long-distance dispersal but are remnants of former continental floras may be more resistant to invasions. It may also be argued that continental fragment islands tend to have extremely nutrient-poor soils, which may enhance the resistance to the invasion of those non-native species that are not specifically adapted to extreme soil conditions (Kueffer et al., 2008; Kueffer, 2009). But clearly more data are needed to test these ideas.

Human development and habitat diversity as key determinants of invasive plant species richness on oceanic islands

Our results correspond well with a recently published study on presence of known invasive and potentially invasive plants on 15 Pacific island groups (Denslow et al., 2009), whereby 30% of the Pacific island groups overlap between their and our study. Denslow et al. (2009) selected a model with area, GDP and population size (although as a non-significant predictor) that explained 88% of the variation in occurrence of species among island groups. With our data for 15 Pacific island groups, a model based on GDP and area explains a very similar 85% of the variation (data not shown), while a model with GDP and number of habitats explains 93% of the variation. This indicates that an explicit consideration of habitat diversity may improve our understand of invader numbers on oceanic islands, and evidences are accumulating that habitat diversity (in combination with area) is also relevant to explain native species richness patterns on oceanic islands (e.g. Triantis et al., 2003; Price, 2004; Duarte et al., 2008). Different habitats on oceanic islands differ strongly in their characteristics (e.g. Mueller-Dombois and Fosberg, 1998), and consequently different habitat types harbour

different invasive species assemblies (e.g. Dirnböck et al., 2003; Kueffer et al., 2004; Baret et al., 2006).

GDP may be an important predictor of invader numbers for a number of reasons. In particular, economic development may be correlated with the scale of non-native species introductions (propagule pressure) (Tye, 2006; Daehler, 2008) or anthropogenic disturbance of natural areas. Propagule pressure has recurrently been shown to be important in explaining the degree of invasion (e.g. Lonsdale, 1999; Lockwood et al., 2005). However, the number of present species (i.e. the species from the total species pool considered in this study that are present on a particular island) proved to be of lesser predictive power in this study. A direct comparison of number of invaders (according to this study) and total number of introduced plant species is possible for a few island groups with up-to-date surveys of non-native species and further corroborates that other factors besides number of introduced species are important in determining invasive species richness. Namely, these proportions differ considerably from c. 1% of introduced plant species being invasive for Hawaii (some 10,000 introduced plant species, Imada et al., 2006) to 2% for Galapagos (c. 800 introduced plant species, Tye, 2006; Jaramillo et al., 2008), 3% for the Juan Fernandez Archipelago (c. 330 introduced plant species, Castro and Jaksic, 2008), and 6% for Rapa Nui (c. 200 introduced plant species, Castro and Jaksic, 2008; Meyer, 2008). Nevertheless, it may still be that in island groups with more economic activity the magnitude of introduction and plantings of particular species (propagule pressure) is higher than in less developed islands (Woodcock, 2003; Daehler, 2008), which may enhance the probability of invasion by these species (Lockwood et al., 2005). A causal link between propagule pressure and human development may thus be more important than indicated by the number of introduced species *per se*.

Anthropogenic disturbance is a major driver of invasions on oceanic islands. For instance, lowland habitats have on most islands been heavily transformed and are nowadays almost exclusively composed of non-native species (e.g. Mueller-Dombois and Fosberg, 1998; Ashmole and Ashmole, 2000; Kueffer et al., 2004; Strasberg et al., 2005), while less disturbed habitats such as inselbergs (Kueffer and Vos, 2004), mountain mist forest (Kueffer and Vos, 2004; Strasberg et al., 2005), or subalpine and alpine vegetation (Daehler, 2005; Strasberg et al., 2005) are relatively resistant to plant invasions. However, the relationship between anthropogenic disturbance and economic development on islands is a complex one. The landscapes of islands that are today mostly uninhabited and without much economic activity, such as Ascension, St. Helena, or Pitcairn have been massively transformed in the past (Ashmole and Ashmole, 2000; Kingston and

Waldren, 2003), and anthropogenic disturbance is also high on economically poor islands such as Cape Verde (Lindskog and Delaite, 1996). Nevertheless, economically rich islands such as Hawaii, Canary Islands, or some Caribbean islands (CIA, 2006) are heavily disturbed and invaded.

In summary, economic development seems to be a foremost determinant of invasive plant richness on oceanic islands and there are a number of possible mechanisms, but the relative importance of these cannot be clarified by this study.

Is invasive species richness on oceanic islands correlated with native species richness, isolation from continents or latitude?

Native species richness and geographic isolation from the closest continent are two other factors that have been discussed in the literature as predictors of invasive species richness on oceanic islands but that were not identified as important factors in this study. A close match of native and non-native species richness of oceanic islands has been proposed (Sax et al., 2002) and discussed in the light of community assembly theory (Sax and Gaines, 2008). We found no strong correlation between these two measures of plant diversity. Rather, on islands with small native floras the number of invasive plants far exceeds those of native species, while on very species-rich islands the native flora is clearly larger than the invasive flora.

Further, it has been argued that more isolated oceanic islands should be less resistant to invasions than less isolated ones, either because endemic plants of isolated oceanic islands are weak competitors (Cronk and Fuller, 1995; Denslow, 2003) or because they harbour an ecologically less diverse species pool (i.e. a sampling effect, Herben, 2005; Daehler, 2006; Kueffer et al., 2009). However, we found no correlation between isolation and number of invaders. Other factors such as environmental degradation seem to be more relevant than the nature of oceanic island floras for the vulnerability of oceanic islands to plant invasions, but this result does not rule out the possibility that isolated oceanic floras are more strongly impacted by invaders, or that floras on oceanic islands are less resistant to plant invasions than continental floras. Regarding the weak competitor hypothesis, recent experimental results indicate that native and invasive plants do not generally differ in seedling growth performance under undisturbed conditions even on the very isolated Seychelles (Schumacher et al., 2008, 2009). Then again, about one quarter of all known vascular plant species are endemic to islands (cf. Kreft et al., 2008), but only very few of the invaders identified in this study are island endemics. This may be an indication that island endemics are less likely to become invasive, however, it may also be due to a bias in introduction rates of island vs. continental

plant species to novel areas. Regarding the sampling effect hypothesis, it has been recurrently shown that some functional traits tend to be missing on oceanic islands, which may provide empty niche opportunities for invasive plants – for instance N-fixation (Vitousek, 1990), fast-growing, early-successional species (Kueffer et al., 2008; Mueller-Dombois, 2008; Schumacher et al., 2009), fruits with particular high sugar or lipid content (Kueffer et al., 2009), or mast flowering and fruiting (Meyer, 1998).

Finally, our study confirms the results of previous analyses (Lonsdale, 1999; Pyšek and Richardson, 2006), which indicate that there is no difference in invasive species richness between tropical and temperate oceanic islands. Neither latitude nor the climate zones as a categorical variable (tropical [25°N to 25°S] vs. temperate) were significant predictors of invasive species richness on their own or in a multiple regression.

How consistent and predictable is the performance of particular non-native plant species on different island groups?

This study confirmed that only a relatively small sample of introduced species becomes invasive (see above). However, the invasive species identified in this study seem to be drawn from a wide range of ecologically and taxonomically contrasting species, and only few of these invasive species are consistently invasive across island groups where present (Fig. 1, Table 2).

Consistency of invader performance across island groups

We found only 35 species out of 383 that were relatively consistent invaders in different island groups (Table 2), while most species were invasive only in one to a few island groups (Fig. 1). Similar skewed distributions of occurrences across different regions were found previously for naturalized, non-native species in Europe (Weber, 1997), the Pacific (Denslow et al., 2009) and the Mediterranean islands (Lloret et al., 2004). However, in contrast to these studies our data goes further in two important aspects. First, we assessed for each island group if a particular species is abundant on a habitat scale (and not just present in any abundance), and, second, we recorded species that were introduced to each of the island groups, even when they were not invasive, allowing us to determine consistency of behaviour among the island groups where species were present. In average c. 80% of the species that are invasive on some island group(s) (present species) were not recorded as invasive (M or D) on a particular island group even when present. Hence, present species were more evenly distributed among islands than moderate or dominant invaders (Fig. 1), and consequently similarity

among island pairs was higher in present species than invaders (Fig. 4). In fact, in close-by island pairs c. 50% of present species are shared (Fig. 5), and even among far-apart islands some 20–40% of the present species are shared, while moderate and dominant invader floras were overall highly dissimilar among island groups (Fig. 5). Further, moderate and dominant invaders are distributed across a wider range of genera and families than present species (Fig. 2), which implies that homogenization between different island floras on higher taxonomic levels is more pronounced among present compared with invasive plant species. There have recently been a number of publications that discuss the role of non-native plants in increasing the biotic homogenization among oceanic islands floras (Castro et al., 2007; Castro and Jaksic, 2008). Our study indicates that similarity among dominant and moderate invaders of different oceanic islands is in fact lower than among the present non-native species from the total species pool analysed in this study (Fig. 4). Thus, studies that are based on present or introduced species may overestimate biotic homogenization. Castro and Jaksic (2008) also found that inclusion of non-established species (i.e. all introduced species in contrast to naturalized species only) tends to increase biotic homogenization between islands. This may be due to a common history of deliberate introductions among islands, possibly shaped by common colonial history (Woodcock, 2003; Kueffer et al., 2004; Daehler, 2008) or agricultural and forestry policies of international organizations (Richardson, 1998) in the past. In fact, the vast majority of the invader species in our study had at least one category of economic importance (such as forestry, agriculture or ornamental plant) assigned in the GRIN database (see the section 'Methods'). We do not know if these uses were the actual purpose of introduction, but in Hawaii (cf. Daehler, 2008) and the Western Indian Ocean (Kueffer et al., 2004), for instance, over 90% of invasive species in natural areas were intentionally introduced. In contrast, among naturalized species (including weeds) only 60% (Hawaii, Wester, 1992) or 45% (Azores, Silva and Smith, 2004) were deliberately introduced. Along the same lines, in Galapagos accidental introductions were much more likely to become naturalized than intentionally introduced species, but relatively more of the naturalized intentionally introduced species became invasive in natural areas (Mauchamp, 1997). Thus, in the case of naturalized or weed species a skewed distribution of occurrences across regions may be mainly driven by a random introduction process (i.e. accidental introductions), but in the case of invaders of natural areas on oceanic islands, introductions have been mostly deliberate and similar across islands, and a skewed occurrence distribution across island groups emerged only after the introduction stage, through community assembly

processes that occur during establishment and spread in natural areas.

In summary, only c. 10% of the identified invader species were relatively consistent invaders where present. Nevertheless, knowledge of a species' invasiveness in island natural areas elsewhere may still have useful predictive value. For instance in Hawaii, 24% of the species present from the total species pool of invaders on oceanic islands (according to this study) became invasive (i.e. a moderate or dominant invader), while if the same number of invaders is compared with all known naturalized plants in Hawaii (c. 800 well-naturalized species, Daehler, 2006) then this proportion is only c. 10%. Hence, a known invader may be more than twice as likely to become invasive on a particular island group than an arbitrary naturalized non-native plant.

Is there a common set of traits characterising invasive plants on oceanic islands?

We have identified in this study some traits that are common among most invasive plants of natural areas. In particular, invasive species are climatically pre-adapted and are perennials. Almost all invasive species in a particular island group were native to the corresponding climatic zone. Climatic pre-adaptation (or climate matching) is known to be an important factor in plant invasions – for instance on Southern Ocean Islands (Chown et al., 2005). In this study, the ratio of climatically pre-adapted species increased from present to All (moderate and dominant) and dominant invaders, which indicates that for predicting high abundance (or negative impacts) of an invasive species climate matching may be even more important than for predicting occurrence. Climate matching was less evident on subtropical, high-elevation islands (e.g. La Réunion and Hawaii), but these are, thanks to their topography, characterised by a wide range of climate zones including cool climates. In fact, a sorting of non-native species according to climate zones within oceanic islands has been recurrently observed and predicted through modelling studies (Dirnböck et al., 2003; Baret et al., 2006; Arteaga et al., 2009). Accordingly, U. europaeus is a problematic invader of subalpine heathlands in subtropical islands (Kueffer and Lavergne, 2004; Daehler, 2005), but of lowland barren land in the temperate Azores (Silva and Smith, 2006).

The very high proportion of perennials contrasts with studies that do not separate between naturalized species and dominant invaders (compare e.g. Silva and Smith, 2004). The two ecological groups of all naturalized species on the one hand and common to dominant invaders of natural areas on the other hand need to be separate to increase generalization in invasion biology (see Daehler, 1998). It has, however, to be kept in mind that our criteria based on abundance to assess the invasiveness of a species may underestimate the risk of

species that invade microhabitats (e.g. as epiphytes), which may more likely be non-woody and non-perennial species.

Otherwise, however, the identified invaders were ecologically and taxonomically very diverse. They represent a wide range of taxonomic groups as has been shown previously for the global invader flora (Daehler, 1998) and particular oceanic island groups (e.g. Silva and Smith, 2004). The Fabaceae and Poaceae were the two families with most invaders but they are also among the families with the most introduced non-native species (Daehler, 1998). However, the Fabaceae were also conspicuously overrepresented among the consistently invasive species (Table 2), and nitrogen-fixing species may in fact be particularly problematic on islands because they fill an empty niche (Vitousek, 1990). The number of invaders from the Poaceae depended on whether abandoned pastures were considered natural areas or not. We were in this study restrictive in considering grasslands as natural areas, which has lowered the number of Poaceae in the total species list.

We did not screen any other traits systematically in this study, but the 35 species that proved to be most consistently invasive across island groups (Table 2) illustrate the wide range of ecological specialisations among highly problematic invaders. The list includes light-demanding species (e.g. L. camara, L. leucocephala) as well as very shade-tolerant species (e.g. Ardisia crenata, Hedychium gardnerianum, Psidium cattleianum, Syzygium jambos). Life forms vary from vines (e.g. Delairea odorata, H. benghalensis, Merremia peltata), to mat-forming herbs (e.g. Erigeron karvinskianus), tall herbs (e.g. H. gardnerianum), succulents (e.g. Carpobrotus edulis, Opuntia stricta), grasses (Holcus lanatus, M. minutiflora, Pennisetum setaceum), ruderal (Ageratina riparia) and understory subshrubs (C. hirta), shrubs (e.g. C. scoparius, U. europaeus), small trees (e.g. Cinchona pubescens), and very tall trees (e.g. Falcataria moluccana). Similarly, habitat preferences, growth rates, and dispersal mode differ. The observed diversity of invaders is in line with the recent argument that a universal set of traits that characterise invasive species is unlikely (Thompson et al., 1995; Kueffer and Daehler, 2009; Kueffer et al., 2009). In fact, a wide spectrum of ecological specialisation has been documented for invader floras on particular oceanic islands (Lloret et al., 2005; Kueffer et al., 2008, 2009; Lambdon et al., 2008; Schumacher et al., 2008, 2009).

Why are invasive plant species on oceanic islands not consistently invasive where introduced?

A number of mechanisms may explain some of the variation in performance of the same invasive species across multiple introductions. A better understanding of

these factors may increase our ability to predict the outcome of plant invasions.

Time lags

There may be a time lag effect that explains why more recently introduced species are not yet invasive in some island groups, but we could not test this systematically. Indeed, many of the recorded invasive plants have been introduced in the early 1900s or before (compare e.g. Ashmole and Ashmole, 2000; Greimler et al., 2002; Woodcock, 2003; Kueffer and Lavergne, 2004; Kueffer and Mauremootoo, 2004; Kueffer and Vos, 2004; Daehler, 2008). However, it has recently also been shown that time from introduction to invasion has been very short in Hawaii if the invaders are planted near natural areas (Daehler, 2009). In general, for a species to reach the abundance levels we defined for invaders will require some time, but in some cases dominant invaders have established high population density within a few decades, e.g. *C. hirta* in Seychelles (Kueffer and Vos, 2004), *Rubus niveus* in Galapagos (Mauchamp, 1997), or *Senecio madagascariensis* in Hawaii (Kueffer and Loope, 2009). Most species we recorded as present but not invasive were introduced at least several decades ago, but we had no information on locations of plantings relative to appropriate natural areas, which could have restricted or slowed the spread of many potential invaders such that they did not yet have an opportunity to cross our abundance thresholds for invasive species.

Habitat factors

There are a number of abiotic and biotic habitat factors that may modulate invader performance on oceanic islands and only some are briefly discussed here. First, volcanic islands and continental fragments differ in their geology and soil chemistry. For instance, the impact of the nitrogen-fixing tree, *F. moluccana* on soil properties and seedling regeneration of non-native plants differs greatly between invasions on very nitrogen-poor soils on the volcanic islands of Hawaii (Hughes and Denslow, 2005) and on very phosphorus-poor soils on the granitic islands of the Seychelles (Kueffer et al., 2008; Kueffer, 2009). Second, disturbance by hurricanes facilitates invasions by early-successional species in natural areas; for instance, in the case of *Pittosporum undulatum* in the Blue Mountains of Jamaica (Bellingham et al., 2005). But only some oceanic islands are frequently visited by strong hurricanes, and depending on intensity and frequency of hurricanes and local species pool, the vegetation succession after hurricanes may differ among island groups (Thompson et al., 2007). Similarly, other natural disturbances such as fires (e.g. in montane habitat in the Dominican Republic, Martin et al., 2007) or stand-level forest dieback (Mueller-Dombois, 2008) provide particular opportunities for

invasions on some oceanic islands. Third, biotic interactions with the native or already established introduced flora and fauna may shape plant invasions. For instance, herbivores and pests may differentially affect a particular species in different island groups. Release from natural enemies is a major factor explaining the invasion of *C. hirta* in Hawaii (DeWalt et al., 2004). Herbivory levels differ considerably between non-native plants in a particular island group, e.g. in the Seychelles (Dietz et al., 2004; Hazell et al., 2008), and biological control agents have been specifically introduced to control invasive plants on oceanic islands – for instance against *L. camara* or Opuntia species (Cruttwell McFadyen, 1998; Fowler et al., 2000). Another major biotic factor differing between oceanic island groups is the presence or absence of non-native large herbivores such as cattle, goats, sheep, deer, or donkeys that can facilitate the invasion of grazing-adapted non-native species (Merlin and Juvik, 1992; Courchamp et al., 2003; Daehler, 2005; Wilkinson et al., 2005; Cuevas and Le Quesne, 2006). Besides negative interactions with herbivores and pests, mutualisms with pollinators or seed dispersers are also important in modulating invasion success (e.g. Richardson et al., 2000a; Kueffer et al., 2009).

Propagule pressure

The magnitude of introduction of a species (propagule pressure) increases the probability for a species to become invasive. For instance, many forestry species (Richardson, 1998; Kueffer et al., 2004), European pasture species such as *H. lanatus* in high-elevation ecosystems in Hawaii (Daehler, 2005), *Chrysobalanus icaco* in Seychelles for erosion control (Kueffer and Vos, 2004), or *Phormium tenax* on St. Helena for flax production (Cronk, 1989) have profited from large-scale introductions. Such former plantings may nowadays be situated in the middle of conservation areas, which may make even poorly dispersed non-native species problematic for conservation; e.g. *Pentadesma butyracea* in Seychelles that is only dispersed by gravity but former plantations now form dense stands in the middle of National Parks (Kueffer and Vos, 2004).

History of community assembly

Timing of introduction may have facilitated or aggravated invasion of some species. For instance, *Cinnamomum verum* in Seychelles seems to have profited from an early introduction in the late 18th century in a time when most of the native forest was cut down (Kueffer and Vos, 2004), and thanks to effective dispersal by birds (Kueffer et al., 2009) and an adaptation to eroded soils, it could colonize the barren land. In contrast, in the current forested landscape dominated by *C. verum* the seedling survival of the species seems to be rather poor and its continued dominance of the vegetation seems mainly to depend on

a very high abundance and seed production on the landscape scale (Kueffer et al., 2007). Similarly, the current abundance of invasive species such as, for instance, *P. tenax* on St. Helena (Cronk, 1989), *Ravenala madagascariensis* in Mauritius (Kueffer and Mauremootoo, 2004), *Acaena argentea* in the Juan Fernandez Archipelago (Greimler et al., 2002), or *S. jambos* on Pitcairn (Kingston and Waldren, 2003) may stem from such windows of opportunity in the past.

How such monotypic stands may develop in the future will again differ between species. An invader may enhance growth of other plant invaders through impacts on soil properties (Hughes and Denslow, 2005, but see Kueffer, 2009) or the frequency and intensity of fires (D'Antonio and Vitousek, 1992). While stands of early-successional invasive trees in Puerto Rico (Lugo, 2004) or *C. verum* in Seychelles (Kueffer et al., 2007) may partly be replaced by or intermixed with native species with time, in contrast *Miconia calvescens* stands in Tahiti (Meyer and Florence, 1996) or non-native secondary forests in Hawaii (Mascaro et al., 2008) seem to hinder native regeneration and may remain for longer time periods. Within an island group, native species from different habitat types may differ in their ability to regenerate under the influence of a non-native species (Jäger et al., 2007).

More generally, it has been suggested that invasive plants may profit from empty niche opportunities not filled by the native and established non-native flora (Meyer, 1998; Denslow, 2003; Mueller-Dombois, 2008; Kueffer et al., 2009); and these may differ in particular between small and isolated islands and larger and less isolated ones (Herben, 2005). The same idea has also been tested for taxonomic similarity. However, it could not be confirmed for Hawaii (Daehler, 2001) or the Mediterranean islands (Lambdon and Hulme, 2006) that species that are closely related to established native or non-native species are less likely to invade. In our dataset, moderate and dominant invaders were more evenly distributed across genera and families than present species (Fig. 2), but this could be explained by a null model based on random sampling of species from the total species pool.

Genotypic differences

Genetic differences on a sub-species level may be relevant, i.e. it may matter which genotype has been introduced to a particular island group, and only some genotypes may prove to be invasive. For instance, for *Cortaderia selloana*, that is recorded as an invader only in some island groups where present, it has been suggested that local adaptation may explain its first delayed but then fast spread in California (Lambrinos, 2001). In contrast, for a number of the consistently invasive plants (*C. hirta*, *M. calvescens*, *P. setaceum*, *Rubus alceifolius*), it has been shown that genetic diversity within and between island groups is very low

(Amsellem et al., 2000; DeWalt and Hamrick, 2004; Le Roux et al., 2007, 2008).

Conclusions

In this study, we present the most comprehensive, standardized dataset to date on the global distribution of invasive plant species on oceanic islands. Our dataset allowed testing the generality and consistency of patterns of plant invasions on oceanic islands. While we conclude that contingent factors play an important role in modulating the invasiveness of particular non-native species in different island groups, a number of consistent patterns emerged that are of relevance to future invasive species management and research.

First, human activity is an important factor determining invasive species patterns in natural areas on oceanic islands. Economic development (measured as gross domestic product) is one of the most important predictors of invasive species richness on islands (Fig. 3). Most plant invaders were deliberately introduced, and deliberate introduction led to a high similarity among island groups in the presence of non-native species with a history of invasion on oceanic islands (Figs. 2, 4 and 5). Hence, future research should have a stronger focus on the roles of human action (Daehler, 2008; Kueffer and Hirsch Hadorn, 2008), e.g. by studying how novel introduction pathways such as the ornamental trade shape floras of introduced species and their similarity between island groups, and by better understanding the links between economic development, frequency and magnitude of novel introductions and out-plantings of non-native plants, and habitat disturbance (compare Fig. 3). For management, it indicates the continued high relevance of preventing deliberate introductions of likely invasive species, and the need to avoid or reduce unnatural disturbance factors in natural areas such as grazing by non-native ungulates.

Second, on every island group many non-native species that are problematic on other island group(s) are already present. In Hawaii for instance some 80% of the total species pool of problematic species analysed in this study are already present (Table 1). Prevention can therefore not stop at borders but most include a continuous early detection monitoring program within the islands (Kueffer and Loope, 2009).

Third, non-native plants with a history of invasion in other oceanic islands have a higher probability to become invasive than an arbitrary naturalized non-native species. However, only c. 10% of invasive plant species become relatively consistently invasive while 90% do so only in some cases. To enhance predictive power, invasive species risk assessments should combine species traits with local factors such as habitat conditions, anthropogenic disturbance regimes, or levels of propagule pressure

(compare Kueffer and Daehler, 2009). Studying community assembly history (e.g. Daehler, 2001), filling of niche space (e.g. Lambdon et al., 2008; Kueffer et al., 2009), and the long-term dynamics of mixed native and non-native plant communities (e.g. Lugo, 2004; Kueffer et al., 2007) may help to better predict the vulnerability of particular island ecosystems to invasions by particular species. Comparing multivariate case studies (cf. Kueffer, 2006; Kueffer and Hirsch Hadorn, 2008) of invasion scenarios by particular species (see Table 2) or transitions between different habitat states (Wilkinson et al., 2005) across multiple oceanic islands may help to identify recurrent syndromes of invasions characterised by clusters of species traits, habitat factors and human action. Since nearby islands are not necessary those with the most similar invader floras, research opportunities, and management challenges (compare Fig. 5), comparative studies that include multiple oceanic regions may be important for understanding patterns and likely impacts.

Acknowledgements

Appendix 1. Overview of experts and literature

The listed sources were used to determine the presence and abundance of moderate and dominant invasive plant species in the different island groups. In some cases, local sources were also used to complement information on environmental and socioeconomic characteristics of the different island groups (see Table A1).

Appendix 2

Pairwise correlations among the different measures of alien species richness (D, All, present) and island characteristics (see Table 1 in article for abbreviations) (Table B1).

Table A1

Island	Experts	Literature
Ascension	Phil Lambdon	Ashmole and Ashmole (2000), Gray et al. (2005), Varnham (2005)
Australs	Jean-Yves Meyer	Florence et al. (2007), Fourdrigniez and Meyer (2008), Meyer (2004), Meyer (2000)
Azores	Luis Silva	Borges et al. (2005), Marler and Boatman (1952), Schäfer (2002), Silva et al. (2008), Silva and Smith (2004), Tutin (1953)
Canary Islands	Rüdiger Otto	Arévalo et al. (2005), Izquierdo et al. (2004), Kunkel (1993), Silva et al. (2008)
Cape Verde	Lazaro Sanchez Pinto	Arechavaleta et al. (2005), Lobin and Zizka (1987)
Cook Islands		Cook Islands Natural Heritage Trust (2007), Meyer (2004), Meyer (2000), Space and Flynn (2002a)
Dominican Republic	Brígido Peguero	Acevedo-Rodríguez and Strong (2007), García et al. (1994), Graham (2003), Hager and Zanoni (1993), Huggins et al. (2007), INBIDOM (2003), Iturralde-Vicent and MacPhee (1999), Kairo et al. (2003), Liogier (2000), Martin et al. (2004), Myers et al. (2004), Peguero (2006), Roth (1999), Salazar Lorenzo et al. (2000), Santiago-Valentín and Olmstead (2004)
Galapagos	Rachel Atkinson, Christopher Buddenhagen	Guézou et al. (2007), Itow (2003), Jaramillo et al. (2008), Tye et al. (2001), van Leeuwen et al. (2008), Wiggins and Porter (1971)
Gambier	Jean-Yves Meyer	Florence et al. (2007), Fourdrigniez and Meyer (2008), Meyer (2004), Meyer (2000)
Hawaii	Curt Daehler	Anon (2008a, b), Haselwood and Motter (1983), Motooka et al. (2003), Wagner et al. (2005-), Wagner et al. (1999)
Jamaica		Acevedo-Rodríguez and Strong (2007), Adams (1972, 1997), Camirand and Evelyn (2003), Goodland and Healey (1996), Graham (2003), Huggins et al. (2007), IABIN, Iturralde-Vicent and MacPhee (1999), Kairo et al. (2003), March et al. (2008), Santiago-Valentín and Olmstead (2004)
Juan Fernandez	Sergio Castro	Castro and Jaksic (2008), Castro et al. (2007), Cuevas et al. (2004), Greimler et al. (2002a,b)
Madeira	Luis Silva	Borges et al. (2008), Press et al. (1994), Silva et al. (2008)
Marquesas	Jean-Yves Meyer	Florence et al. (2007), Fourdrigniez and Meyer (2008), Meyer (2004), Meyer (2000),
Mauritius	Christoph Kueffer, Christophe Lavergne	Bosser et al. (1976-), CBNM (2007), Kueffer and Mauremootoo (2004), Rouillard and Guého (1999)
Mayotte	Fabien Barthelat	Rolland and Boullet (2005), Vos (2004)

Table A1. (*continued***)**

Island	Experts	Literature
New Caledonia	Jean-Yves Meyer	Gargominy et al. (1996), Meyer et al. (2006), Meyer (2000)
Palau	Curt Daehler, Joel Miles	Endress and Chinea (2001), Space et al. (2003)
Pitcairn		Florence et al. (1995), Kingston and Waldren (2003), Meyer (2004), Meyer (2000), Varnham (2005), Waldren et al. (1995)
Puerto Rico	Marcos Caraballo Ortiz, Christian Torres-Santana, Miguel Vives	Acevedo-Rodríguez (2005), Acevedo-Rodríguez and Strong (2005, 2007), Brandeis et al. (2007), Ewel and Whitmore (1973), Francis and Lowe (2000), Francis and Liogier (1991), Graham (2003), Huggins et al. (2007), Iturralde-Vicent and MacPhee (1999), Kairo et al. (2003), Liogier and Martorell (2000), Santiago-Valentín and Olmstead (2004)
Rapa Nui	Sergio Castro, Jean-Yves Meyer	Castro and Jaksic (2008), Castro et al. (2007), Meyer (2008), Meyer (2004), Meyer (2000), Zizka (1991)
Réunion	Christophe Lavergne	Baret et al. (2006), Bosser et al. (1976-), CBNM (2007), Kueffer and Lavergne (2004), Rouillard and Guého (1999), Tassin et al. (2006a, b)
Rodrigues	Christoph Kueffer, Christophe Lavergne	Bosser et al. (1976), CBNM (2007), Kueffer and Mauremootoo (2004), Rouillard and Guého (1999)
Saint Helena	Andrew Darlow	Ashmole and Ashmole (2000), Cronk (1989), Varnham (2005)
Samoa (incl. American S.)	Arthur Whistler	Meyer (2000), Space and Flynn (2002b), Space and Flynn (2000)
Seychelles	Christoph Kueffer	Fleischmann (1997), Friedmann (1986), Kueffer and Vos (2004), Robertson (1989)
Society	Jean-Yves Meyer	Florence et al. (2007), Fourdrigniez and Meyer (2008), Meyer (2004), Meyer (2000)
Tonga	Arthur Whistler	Franklin et al. (2006), Meyer (2000), Space and Flynn (2001)
US Virgin Islands	Daniel Clark, Rudy O'Reilly	Acevedo-Rodríguez (2005), Acevedo-Rodríguez and Strong (2005, 2007), Acevedo-Rodríguez et al. (1996), Anon (1994), Brandeis and Oswalt (2007), Ewel and Whitmore (1973), Graham (2003), Huggins et al. (2007), Iturralde-Vicent and MacPhee (1999), Kairo et al. (2003), NPSpecies (2003), Santiago-Valentín and Olmstead (2004)
Wallis and Futuna	Jean-Yves Meyer	Meyer (2007), Meyer (2000)

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Table A1. (*continued*)

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Table B1

	Number (D)	Number (All)	Number (present)	Latitude	Isolation	Area	Altitude	Age	Number habitats	GDP	Population	Population density
Number (D)	1.00	0.92***	0.82***	0.32	−0.20	0.27**	0.71***	−0.20	0.70***	0.58*	0.32***	0.36**
Number (All)	0.92***	1.00	0.79***	0.35	−0.24	0.30**	0.70***	−0.20	0.73***	0.56**	0.35***	0.33
Number (present)	0.82***	0.79***	1.00	0.06	−0.14	0.27***	0.65***	−0.02	0.68***	0.53*	0.27***	0.42**
Latitude	0.32	0.35	0.06	1.00	−0.06	0.01	0.23	−0.15	0.07	0.37**	0.06	0.02
Isolation	−0.20	−0.24	−0.14	−0.06	1.00	−0.29**	−0.25*	−0.28	−0.26	0.17	−0.32**	−0.40*
Area	0.27**	0.30**	0.27***	0.01	−0.29**	1.00	0.51***	0.21	0.42***	0.05	0.90***	0.00
Altitude	0.71***	0.70***	0.65***	0.23	−0.25*	0.51***	1.00	0.18	0.90***	0.40	0.46***	0.03
Age	−0.20	−0.20	−0.02	−0.15	−0.28	0.21	0.18	1.00	0.18	−0.21	0.13	−0.01
Number habitats	0.70***	0.73***	0.68***	0.07	−0.26	0.42***	0.90***	0.18	1.00	0.33	0.35***	0.06
GDP	0.58*	0.56**	0.53*	0.37**	0.17	0.05	0.40	−0.21	0.33	1.00	0.05	0.05
Population	0.32***	0.35***	0.27***	0.06	−0.32**	0.90***	0.46***	0.13	0.35***	0.05	1.00	0.24***
Population density	0.36**	0.33	0.42**	0.02	−0.40*	0.00	0.03	−0.01	0.06	0.05	0.24***	1.00

Significance of correlations was tested with two-sided Spearman's rank correlation ρ (*$p < 0.05$, **$p < 0.01$, ***$p < 0.001$).

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