

Floristic homogenization as a teleconnected trend in oceanic islands

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ABSTRACT

Aim We searched for evidence of floristic homogenization in widespread oceanic archipelagos.

Location Twelve oceanic archipelagos in the Atlantic and Pacific oceans: Ascension, Azores, Canary, Cape Verde, Desventuradas, Easter, Galápagos, Hawaii, Juan Fernández, Madeira, Puerto Rico and Savage.

Methods By using Jaccard's index, we established the floristic similarity between pairs of archipelagos at two stages: original (pre-European; J_o) and current flora (J_c). Then, we calculated $\Delta J = J_c - J_o$, where positive differences imply that similarity has increased floristic homogenization.

Results We found that floristic similarity increased fourfold on average, from 1.6% to 6.3% for original and current floras, respectively. In fact, we recorded 64 cases in which floristic similarity increased and only two in which it decreased. The importance of invasions exceeds that of extirpations as a driver of biotic change by more than an order of magnitude (2679 versus 142 species, respectively).

Main conclusions The vascular floras of these 12 insular oceanic systems have increased in compositional similarity, a phenomenon consistent with the trend towards biotic homogenization. It can be characterized as a teleconnected process that operates across vast geographical distances, driven by the unprecedented capacity of humans for translocation. Trends in biotic homogenization differ depending on the geographical location (i.e. Pacific < Atlantic archipelagos) and phylogenetic groups (island vascular plants > island birds reported in a previous study), emphasizing the complexity of biotic change.

Keywords

Alien plants, biological invasions, biotic change, extinction, extirpation, native plants, naturalized plants.

INTRODUCTION

Diverse human activities are modifying the global distribution of biodiversity (Sala *et al.*, 2000; Chapin *et al.*, 2001). Underlying this phenomenon are two main processes that determine species richness, extinctions and biological invasions (Vitousek *et al.*, 1996), the rates of which are thought to be increasing (Vermeij, 1991; Chapin *et al.*, 2001). Because extinctions usually occur among native and often endemic species, while invasions involve the spread of widely distributed species, the balance of these processes potentially drives an increase in local species richness (i.e. when extinctions < invasions), accompa-

nied by a decrease in global species richness (Vitousek *et al.*, 1996; Sax & Gaines, 2003).

Considering that invasions and extinctions constitute geographically ubiquitous processes, the loss of global biodiversity may result in a collateral process called biotic homogenization (McKinney & Lockwood, 1999). Biotic homogenization can be defined as an increase in the compositional similarity among initially more dissimilar areas, as a consequence of invasions and extinctions (McKinney & Lockwood, 1999; Olden & Poff, 2003). Unlike the expected decrease in global biodiversity, biotic homogenization is a less perceptible process because it can only be noted by comparing the species composition

between different areas. Although studies of biotic homogenization have increased in the past few years (see Olden & Rooney, 2006), they still do not demonstrate the extent of this phenomenon at a global scale (but see Cassey *et al.*, 2007; Spear & Chown, 2008).

Most studies of biotic homogenization involve areas of limited geographical extent, the results of which are difficult to extrapolate to larger scales. Furthermore, rates and trends of biotic change seem to be heterogeneous, depending on the geographical location (e.g. Castro & Jaksic, 2008a), spatial scale (e.g. Olden *et al.*, 2008) and phylogenetic group (e.g. Olden, 2006). Nevertheless, a lack of quantitative evidence for biotic homogenization at a global scale has not prevented the development of concepts such as the 'Homogocene' or the 'New Pangaea' (McKinney, 2005) to describe a supposedly global phenomenon.

Oceanic islands are home to biological communities that are highly vulnerable to human impacts (Drake *et al.*, 2002; Blackburn *et al.*, 2004; Kreft *et al.*, 2007), which is why they are used as sensitive indicators of biotic change (Vitousek, 2002). Many of them have only been inhabited since European colonization and their biotas have experienced severe modifications since European occupation (Carlquist, 1974; Vitousek, 2002). In general terms, the biotas of oceanic islands are characterized by small numbers of species, disharmonic representation of phylogenetic groups according to their dispersal abilities and high endemism (MacArthur & Wilson, 1967; Whittaker, 1998). Because human impact has strongly modified their biotic composition (Denslow, 2001), and because islands are widely distributed across the globe, insular systems constitute a model to evaluate whether biotic homogenization has occurred in a similar way among these distant communities.

In this study, we compare the floristic composition of 12 widespread oceanic archipelagos located in two oceans (Pacific and Atlantic) and in both Northern and Southern Hemispheres, testing the hypothesis that islands have undergone biotic homogenization since the arrival of Europeans and that homogenization constitutes a consistent phenomenon in widely separate islands. We also examined the relative importance of extinctions and invasions in the homogenization process.

METHODS

The islands

We studied the floristic composition of 12 oceanic archipelagos, each encompassing from one to 14 main islands: Ascension, Azores, Canary, Cape Verde, Desventuradas, Easter, Galápagos, Hawaii, Juan Fernández, Madeira, Puerto Rico and Savage. Eight of them were uninhabited by the time of European discovery, whereas four were initially colonized by aborigines (Canary, Easter, Hawaii and Puerto Rico). All of these archipelagos are of volcanic origin or are continental fragments (e.g. Puerto Rico), with a geological age ranging from 2.9 to 180 million years; other geographical, geological and population descriptors are given in Table 1. Five of the archipelagos are located in the Pacific Ocean and seven are in the Atlantic Ocean, in both Northern and Southern Hemispheres (Fig. 1).

Vascular flora

For each island, we recorded the best-known composition of vascular plants before and after European colonization, based on local herbaria and recently published floras (see following

Table 1 Geographical, geological and historical characteristics of the 12 archipelagos studied: Ascension (AS), Azores (AZ), Canary (CA), Cape Verde (CV), Desventuradas (DE), Easter (EA), Galápagos (GA), Hawaii (HA), Juan Fernández (JF), Madeira (MA), Puerto Rico (PR) and Savage (SA). Variables are the following: Size of current human resident population (HumPop), total geographical area (TArea; adding up all islands in the respective archipelagos), number of islands (NoIsl), human density (HumDen), geological age (GeoAge), maximum elevation (MaxEle), distance to nearest continental mass (DistCon) and year of European discovery (YrDisc).

Archipelagos	HumPop (No.)	TArea (Km ²)	NoIsl (<i>n</i>)	HumDen (No. × Km ⁻²)	GeoAge (my)	MaxEle (m)	DistCon (km)	YrDisc (yr)
AS	1100	91	1	12	5	859	1600	1501
AZ	241,350	2333	9	103	7	2352	1200	1431
CA	2,070,465	7447	7	278	30	3718	95	1312
CV	434,263	4033	10	108	25.6	2829	570	1460
DE	0	3.9	2	0	2.9	479	972	1521
EA	3800	163	1	23	3	560	3500	1722
GA	40,000	7900	14	5	4.5	1494	960	1535
HA	1,211,537	28,311	8	43	40	4205	3850	1778
JF	630	183	3	3	4	1650	667	1574
MA	246,689	799	5	309	20	1818	630	1418
PR	3,971,000	8870	5	448	40	1338	112*	1493
SA	0	3	3	0	22	151	374	1438

*To Dominican Republic.

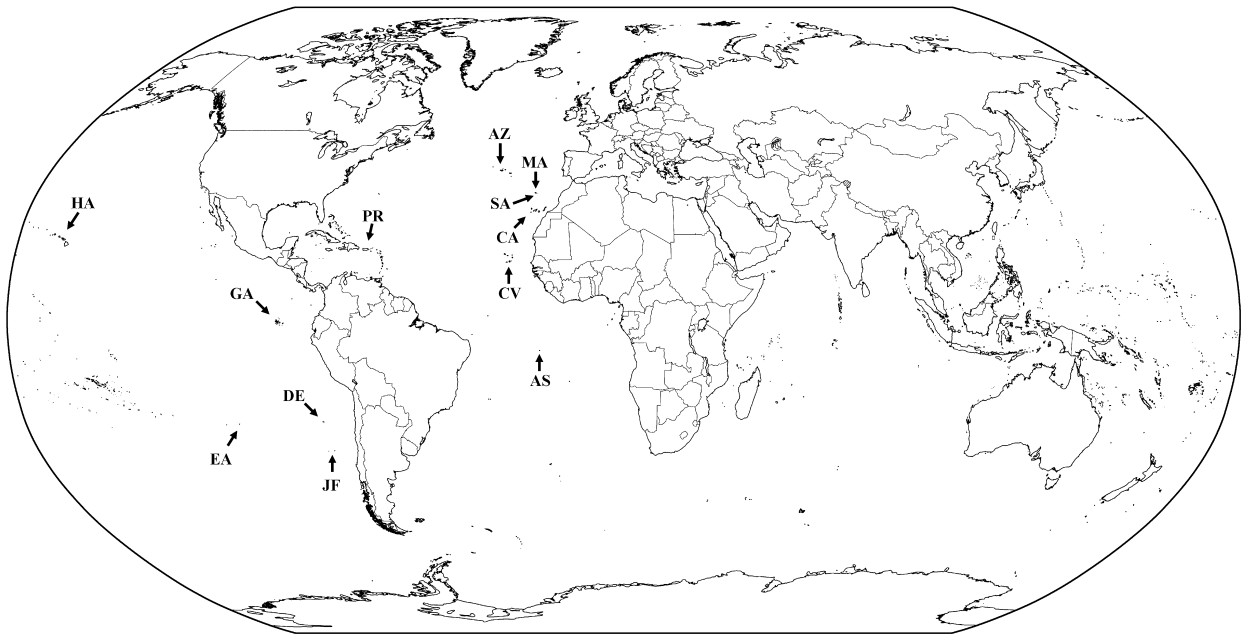


Figure 1 Location of the 12 archipelagos studied: Ascension (AS), Azores (AZ), Canary (CA), Cape Verde (CV), Desventuradas (DE), Easter (EA), Galápagos (GA), Hawaii (HA), Juan Fernández (JF), Madeira (MA), Puerto Rico (PR) and Savage (SA).

paragraph). We defined the original flora as those native or presumed native species documented as extant by or slightly after the time of European colonization. This set included species that became extinct or extirpated from islands after European colonization. Here, we use the term 'extirpated' because not all species lost from islands are island endemics; those species may still occur elsewhere. Then, we defined the current flora by including all naturalized plants (*sensu* Richardson *et al.*, 2000) on the islands (according to botanical records after European colonization) while excluding the extirpations of native species. Because the naturalized plants were species alien to the islands and islands consist of relatively small physical areas, in this study naturalized species are considered to be successful invaders of islands. Because of limitations of the floristic records, it was not possible to obtain species distributions by island, thus analyses were made at the archipelago level.

Floristic and taxonomic information was obtained from collections, herbaria and publications as follows: Ascension (Gray *et al.*, 2005), Azores (Silva *et al.*, 2005), Canary (Acebes-Ginovés *et al.*, 2004), Cape Verde (ORT-Jardín de Aclimatación de la Orotava, TFC-Universidad de La Laguna; Sánchez-Pinto *et al.*, 2005), Desventuradas (Herbarium CONC, STGO; Castro *et al.*, 2007), Easter (Herbarium CONC, STGO; Zizka, 1991; Castro *et al.*, 2007), Galápagos (CDF Herbarium Database, Charles Darwin Foundation, Galapagos, Ecuador), Hawaii (Wagner *et al.*, 1999, 2005), Juan Fernández (Herbarium CONC, STGO; Castro *et al.*, 2007), Madeira (ORT-Jardín de Aclimatación de la Orotava, TFC-Universidad de La Laguna; Hansen & Sunding, 1993; Press & Short, 1994; Jardim & Francisco, 2000; Costa *et al.*, 2004; Jardim &

Sequeira, 2008), Puerto Rico (Liogier, 1989; Proctor, 1989; Francis & Liogier, 1991; Ackerman, 1995; Figueroa-Colón, 1996; Molina & Alemañ, 1997; Acevedo-Rodríguez, 2005; Acevedo-Rodríguez & Strong, 2005, 2007; Gann & Bradley, 2007–2008; Liogier & Martorell, 2000) and Savage (ORT-Jardín de Aclimatación de la Orotava, TFC-Universidad de La Laguna; Perez de Paz & Acebes, 1978; Monod, 1990; Press & Short, 1994; Hansen & Sunding, 1993; Jardim & Sequeira, 2008).

These floristic records included vascular plants, both monilophytes (i.e. ferns) and spermatophytes (Judd *et al.*, 2002), the latter constituting the gymnosperms and angiosperms. We did not include taxa with doubtful or uncertain naturalization status, nor did we include taxa that were not determined to the specific level or documented only by vernacular name. The synonymy was standardized according to taxonomic information available in the literature as well as in herbaria consulted. For these purposes, a list of synonyms was generated and compared one by one with the taxa recorded across the sampled archipelagos. Then, we considered as valid taxa those more recently described or re-described. Finally, the nomenclature of all taxa was standardized using The International Plant Name Index (<http://www.ipni.org>).

Analyses

By using Jaccard's index, we established the floristic similarity between pairs of archipelagos at two stages: original (pre-European) and current flora. This analysis yielded two matrices of archipelago \times archipelago similarity, for original (J_o) and current (J_c) floras, that were then compared by calculating

$\Delta J = J_c - J_o$. Positive differences imply that similarity has increased (floristic homogenization); negative differences indicate that similarity has decreased (floristic differentiation). To determine the statistical significance of the values of ΔJ , we carried out two procedures. First, we conducted a nonparametric signed-ranks test (Wilcoxon test) between J_c and J_o matrices, looking for a significant difference between the medians of the two related samples, while using a nonparametric Wilcoxon–Mann–Whitney test (U) to compare ΔJ between different oceans. Second, we resampled 10,000 times the distribution matrices of species \times archipelago, thus obtaining a frequency distribution of random pseudovalues of similarity against which we compared the observed values of ΔJ . Differences beyond the 0.05 or 0.95 percentile were considered significant trends of floristic change, towards either homogenization or differentiation.

Because archipelagos closer to one another may be more similar than those farther apart, we also determined the effect of geographical distance between archipelagos by analysing the spatial autocorrelation of similarity values. This analysis was conducted separately for archipelagos located in the Pacific and Atlantic oceans. For this, J_c and J_o matrices and similarity differentials (ΔJ) were subjected to a Mantel's test against the matrix of geographical distance among archipelagos.

Multivariate regression was used to examine the relationship between geographical, geological and human attributes of archipelagos versus changes in floristic similarity. Specifically, we used the human population density (size of current human resident population/total geographical area), number of islands, geological age, maximum elevation, distance to nearest continental mass and year of European discovery; all these variables were log transformed and correlated with mean value for ΔJ and $\Delta J/J_o$ ratio on each island. All statistical analyses were performed using R software (R Development Core Team 2005; <http://cran.r-project.org/manuals.html>).

RESULTS

Insular flora, richness, invasions and extirpations

The pre-European flora of all archipelagos totalled 5958 species: 703 monilophytes, 11 gymnosperms and 5244 angiosperms (Table 2). Although floristic richness varied among archipelagos (21–2333 species), most species were distributed only in one archipelago (5207; 87.4%; Fig. 2). The remaining species (751; 12.6%) were distributed over two to seven archipelagos; a cumulative percentage of 0.08% included species distributed in six and seven archipelagos (see Fig. 2). The most widespread species was *Ruppia maritima* (seven archipelagos), while four species occurred in six archipelagos (*Adiantum capillus-veneris*, *Cyperus laevigatus*, *Psilotum nudum* and *Pteridium aquilinum*). The composition of the current flora totalled 7749 species (Table 2), a net increase of 1791 species, represented mainly by angiosperms (1750 species), followed by gymnosperms (18) and monilophytes (23). About 75% of the species were present on a single archipelago (Fig. 2), while ca.

Table 2 Floristic composition of the archipelagos of Ascension (AS), Azores (AZ), Canary (CA), Cape Verde (CV), Desventuradas (DE), Easter (EA), Galápagos (GA), Hawaii (HA), Juan Fernández (JF), Madeira (MA), Puerto Rico (PR) and Savage (SA).

Archipelagos	Original Flora				Current Flora			
	Mon.	Gym.	Ang.	Total	Mon.	Gym.	Ang.	Total
AS	10	0	13	23	20	7	261	288
AZ	43	2	200	245	64	4	836	904
CA	49	6	1311	1366	61	11	1956	2028
CV	32	0	277	309	32	1	721	754
DE	0	0	21	21	0	0	27	27
EA	17	0	29	46	17	0	91	108
GA	102	0	390	492	102	0	653	755
HA	146	0	1000	1146	174	5	1733	1912
JF	51	0	145	196	51	4	406	461
MA	52	3	591	646	68	8	1147	1223
PR	358	4	1971	2333	353	8	2550	2910
SA	1	0	79	80	3	0	99	102
Total	703	11	5244	5958	726	29	6994	7749

Mon., Monilophytes; Gym., Gymnosperms; Ang., Angiosperms.

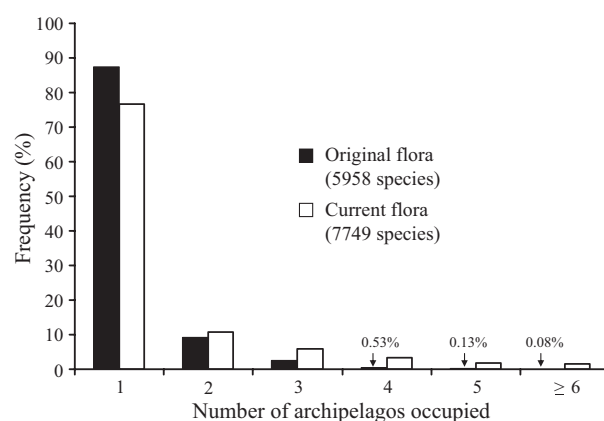


Figure 2 Frequency distribution of shared species in the original and current floras of 12 archipelagos.

25% were distributed between two and 11 archipelagos (Fig. 2); among these, only three species (0.03%) were present in 11 archipelagos (*Bidens pilosa*, *Nicotiana tabacum* and *Sonchus oleraceus*); five species (0.06%) were present in 10 archipelagos (*Chenopodium murale*, *Portulaca oleracea*, *Chenopodium ambrosioides*, *Lantana camara* and *Ricinus communis*). The cumulative percentage of species distributed between six and 11 archipelagos was 1.59% (see Fig. 2). The frequency distribution of archipelago occupation by original and current floras showed a significant difference ($\chi^2 = 18.6$; d.f. = 2; $P < 0.05$), indicating that more species are currently shared among the archipelagos.

Changes in floristic composition and richness were chiefly determined by the number of species invasions (2679 species), which greatly exceeded the number of recorded extirpations (142; Table 3). Angiosperms (2599 species) exceeded

Table 3 Floristic composition of invasions and extirpations in Ascension (AS), Azores (AZ), Canary (CA), Cape Verde (CV), Desventuradas (DE), Easter (EA), Galápagos (GA), Hawaii (HA), Juan Fernández (JF), Madeira (MA), Puerto Rico (PR) and Savage (SA).

Archipelagos	Invasions				Extirpations			
	Mon.	Gym.	Ang.	Total	Mon.	Gym.	Ang.	Total
AS	10	7	249	266	0	0	1	1
AZ	21	2	637	660	0	0	1	1
CA	12	5	645	662	0	0	0	0
CV	1	0	444	445	0	0	0	0
DE	0	0	6	6	0	0	0	0
EA	0	0	64	64	0	0	2	2
GA	0	0	266	266	0	0	3	3
HA	31	5	805	841	3	0	72	75
JF	0	4	262	266	0	0	1	1
MA	16	5	558	579	0	0	2	2
PR	9	4	620	633	14	0	41	55
SA	2	0	22	24	0	0	2	2
Total	61	19	2599	2679	17	0	124	142

Mon., Monilophytes; Gym., Gymnosperms; Ang., Angiosperms.

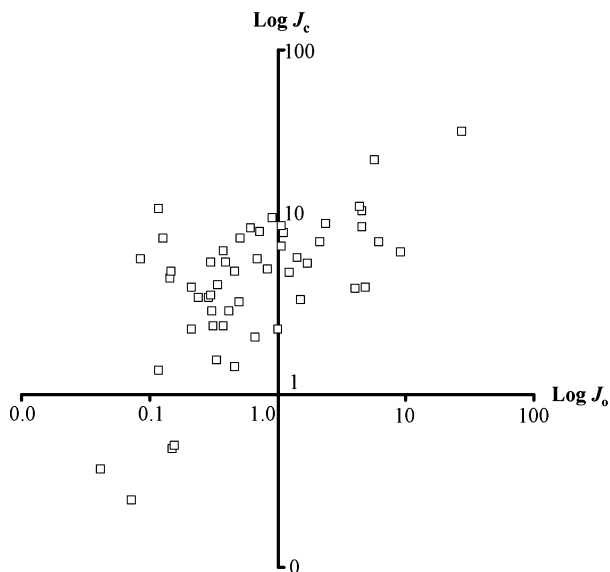


Figure 3 Jaccard's similarity between original (J_o) and current (J_c) flora among 12 archipelagos.

monilophytes and gymnosperms, which together totalled 80 species (Table 3).

Changes in floristic similarity

In the original flora, similarity ranged from 0 to 28% (Fig. 3), whereas in the current flora, similarity ranged from 0 to 37% (Fig. 3). In 12 of 66 comparisons, similarity was originally zero, involving archipelagos located in different oceans (Table 4).

Differentials of similarity (ΔJ) between current and original floras spanned from -2 to 23% (Fig. 4). In 64 of 66 comparisons, there was an increase, while in only two cases was ΔJ negative (Fig. 4; Savage versus Canary Islands and Savage versus Madeira; see Table 4). The frequency distribution of ΔJ values showed a median value that was significantly different from zero (Signed-ranks test; $\chi^2 = 15.3$; d.f. = 1; $P < 0.05$), indicating that similarity in current floras is greater than among original floras, which is consistent with the process of biotic homogenization. Re-sampling procedures allowed identifying those archipelagos whose floristic similarity differed significantly (see Table 4). There were 40 cases in which current similarity changed significantly with respect to the original flora; 38 of them corresponded to increases and only two to decreases in floristic similarity.

Atlantic archipelagos had larger ΔJ than those in the Pacific (7.6 versus 2.4 , respectively; $U = 208$; $P < 0.05$). However, when the $\Delta J/J_o$ rates were considered, the differences between oceans were not significant ($U = 9.5$; $P > 0.74$), indicating that larger ΔJ values for Atlantic archipelagos may be linked to larger J_o values in the Atlantic. The effects of geographical distance on similarity (J_o , J_c and ΔJ) showed different trends between oceans. In Pacific archipelagos, there was no significant spatial correlation between original ($r = -0.104$), current ($r = 0.246$) and change in floristic similarity ($r = 0.316$) (Mantel's test, all $P > 0.63$), whereas in Atlantic archipelagos, both original ($r = -0.678$) and current similarity ($r = -0.574$) showed a negative and significant relationship with geographical distance (Mantel's test, $P < 0.05$), but not with change in similarity ($r = -0.215$) (Mantel's test, $P > 0.45$). Multivariate regressions testing for relationships between ΔJ and geographical and historical attributes of islands were not significant.

DISCUSSION

In climatology, the term teleconnection has been used to describe linked patterns that span vast geographical areas (e.g. Norman & Taylor, 2003) and we propose that floristic homogenization can be usefully conceptualized as a teleconnected process. Understanding a teleconnection pattern requires analysis of the pattern and linkages at a global scale. In the case of biotic homogenization, translocation by humans is clearly among the most important drivers of the pattern, but quantitative studies of human movements and their relationship to biotic homogenization, especially at a global scale, remain in their infancy (Ruiz & Carlton, 2003).

In the archipelagos studied, change in floristic similarity was 4.7% on average, the highest quantitative trend towards biotic homogenization documented for widely separate areas of the world. For example, Spear & Chown (2008) documented that homogenization in ungulate mammals increased 2% on average among a sample of 41 countries globally. Cassey *et al.* (2007) documented 0% – 3% increased similarity for bird assemblages on oceanic islands, while Castro *et al.* (2007) found a 2% average increase in vascular floras of oceanic islands in the south-eastern Pacific. Only when biotic

Table 4 Floristic similarity for current and original flora determined by Jaccard's index ($100 \times J$) for the archipelagos of Ascension (AS), Azores (AZ), Canary (CA), Cape Verde (CV), Desventuradas (DE), Easter (EA), Galápagos (GA), Hawaii (HA), Juan Fernández (JF), Madeira (MA), Puerto Rico (PR) and Savage (SA). Values for J_o are above the diagonal and those of J_c are below.

	AS	AZ	CA	CV	DE	EA	GA	HA	JF	MA	PR	SA
AS	–	0.4	0.1	0.9	0.0	4.6	0.7	<0.1	0.5	0.3	0.2	0.0
AZ	6.8*	–	5.7	2.4	0.0	0.3	0.4	0.7	0.0	13.6	0.3	1.2
CA	4.8*	22.9*	–	4.6	<0.1	0.2	0.3	0.5	0.1	27.5	0.2	4.9
CV	10.5*	9.9*	11.6*	–	0.0	1.7	2.1	1.1	0.4	4.4	1.1	4.0
DE	1.3	0.5	0.2	0.4	–	0.0	0.0	0.0	0.5	0.2	0.0	1.0
EA	9.4*	4.3*	2.4	5.8*	1.5	–	1.5	0.5	0.8	0.3	0.3	0.0
GA	7.1*	4.0	3.6	10.6*	0.4	4.4	–	1.4	0.7	0.4	6.3	0.2
HA	6.1*	8.8*	8.0*	8.7*	0.3	3.4	8.7*	–	0.1	0.6	1.1	0.0
JF	5.2*	14.6*	8.1*	5.8*	1.5	5.4*	3.2	5.2*	–	0.1	0.1	0.0
MA	5.9*	37.3*	33.5*	12.4*	0.5	3.7*	4.9	9.3*	12.0*	–	0.3	9.2
PR	4.2*	3.1*	3.6*	7.2*	0.1	1.6	10.3	9.5*	1.4	3.8*	–	<0.1
SA	4.6*	5.1*	4.2¶	4.1	2.4	2.9	1.1	1.3	4.6*	6.7¶	0.4	–

Significant increases or decreases in similarity are indicated by (*) and (¶), respectively.

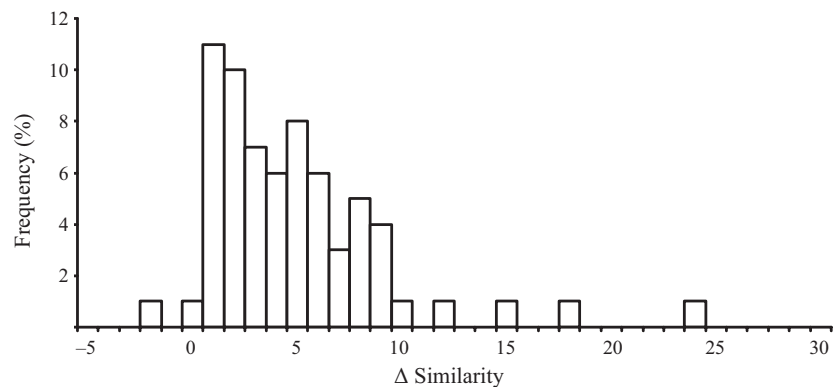


Figure 4 Frequency distribution of similarity differentials ($\Delta J = J_c - J_o$) among 12 archipelagos.

homogenization has been measured at smaller geographical scales are differences in similarity larger: 17% for freshwater fishes in the Iberian Peninsula (Clavero & García-Berthou, 2006), 7% for freshwater fishes in the United States (Rahel, 2000) and 3% for freshwater fishes in Australia (Olden *et al.*, 2008).

Considering the evidence of biotic homogenization on oceanic islands to date, differences among taxonomic groups can be noted by comparing our study on plants with that of Cassey *et al.* (2007) on birds, who found that the avifauna in Pacific archipelagos differentiated while those in Atlantic archipelagos homogenized. In contrast, the vascular flora in both Pacific and Atlantic oceans homogenized, but with a threefold difference among Atlantic ($\Delta J = 7.6$) compared to Pacific archipelagos ($\Delta J = 2.3$). Probably, these differences between the two oceans arise because of an earlier and extensive European colonization of Atlantic islands. Additionally, archipelagos located in different oceans also exhibited differing patterns of floristic similarity with distance. This situation probably results from a broader geographical separation among the sampled archipelagos in the Pacific (Fig. 1), reducing the potential for spatial correlation. In a global survey

of abundant invasive plants on islands, Kueffer *et al.* (2010) found decreasing similarity with increasing geographical distance up to around 5000 km, but no pattern was observed at larger distances.

The increased similarity in our study was principally caused by 2544 naturalized alien species introduced to the islands. Extirpations (142 species) contributed weakly to changes in similarity. This ratio (18:1) differs ninefold from that reported for birds in oceanic islands (2:1; Cassey *et al.*, 2007), but the greater importance of invasions over extinctions has been highlighted by other researchers (Rahel, 2000; Sax *et al.*, 2002; Cassey *et al.*, 2007; Castro *et al.*, 2007; Sax & Gaines, 2008; Spear & Chown, 2008). Current floristic richness of the insular flora totalled 7749 taxa, 1791 more than the original condition. Because the islands share a high proportion of introduced species, richness has increased by 180% on average, i.e. nearly twofold the original richness (see Sax *et al.*, 2002 for a similar finding), but at the expense of increased similarity. Our study focused on measuring homogenization contributed by all naturalized plants. In contrast, Kueffer *et al.* (2010) examined only dominant plant invaders of natural areas on islands around the world and found 3% similarity between island

groups, whereas 6% similarity was observed when moderate and dominant invaders were pooled. These findings show that the degree of homogenization observed depends on the categorization of introduced plants (see also Castro & Jaksic, 2008b). Geographical studies of biotic homogenization have so far focused on species presence and absence, but further insights may be revealed by future studies that also incorporate measures or categories of abundance.

Biological invasions constitute the chief mechanism (*sensu* Olden *et al.*, 2004) of floristic change and the principal driver of diversity on islands (see Castro *et al.*, 2007). It must be emphasized that extinctions or extirpations may be underestimated because they are harder to record (Sax & Gaines, 2008). According to the IUCN Red List criteria, a taxon is Extinct (or extirpated in our islands) when there is no reasonable doubt that the last individual has died, or presumed Extinct (or extirpated in our islands) when exhaustive surveys in known and/or expected habitat, at appropriate times, throughout its historic range have failed to record an individual. Nevertheless, the imbalance between invasions and extirpations documented in these islands seems to be real. Furthermore, many native plants have distributions that include other islands or neighbouring continents; therefore, local extirpations do not necessarily signify extinction, as for 48 species considered extirpated from Puerto Rico. Multivariate regression showed no significant effect of number of islands, human density, geological age, maximum elevation, distance to nearest continental mass or year of European discovery on changes in similarity (both ΔJ and $\Delta J/J_0$ ratio). These results indicate that human, geographical and historical attributes of these archipelagos are not associated with similarity increases. The lack of effect of human density is particularly intriguing because several authors have identified human population and urbanization as principal drivers of biotic homogenization (Chown *et al.*, 1998), especially in continental communities (Duncan & Lockwood, 2001; La Sorte & McKinney, 2006; McKinney, 2006; Olden *et al.*, 2008). Thus, our results highlight a qualitative difference in biotic change between oceanic islands and continental ecosystems. One explanation for the lack of correlation between human factors and ΔJ is that the effect of shared naturalized species on ΔJ is smaller for islands that have larger native floras, and humans may more intensively colonize larger or less remote islands, both of which tend to have larger native floras. Thus, although islands that are more heavily affected by humans may have a larger absolute number of invasive plant species (Kueffer *et al.*, 2010), a corresponding larger number of native species can moderate the effects of naturalizations on ΔJ for these islands, resulting in no expected relationship between intensity of human activity and ΔJ .

Overall, our results demonstrate that the vascular floras of 12 insular oceanic systems of two oceans in both hemispheres have increased in compositional similarity, a phenomenon consistent with the trend towards biotic homogenization as a globally teleconnected process. Also, our results demonstrate the much higher importance of invasions over extirpations as the chief

driver of biotic change. Our evidence reveals different trends in biotic homogenization depending on geographical location (Pacific versus Atlantic oceans) and phylogenetic group (vascular plants versus birds), emphasizing the complexity of biotic change at a global scale. Currently, the phenomenon of biotic homogenization is considered a central concern in the agenda of global biodiversity conservation (Olden *et al.*, 2004). Efforts to reduce the introduction of alien plants are being implemented in several of these archipelagos, but we think that these initiatives need some coordination to stop or revert the process of floristic homogenization here documented.

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REFERENCES

- Acebes-Ginovés, J.R., Del Arco-Aguilar, M., García-Gallo, A., León-Arencibia, M.C., Pérez de Paz, P.L., Rodríguez-Delgado, O., Wildpret, W., Martín-Osorio, V.E., Marrero-Gómez, M.C. & Rodríguez-Navarro, M.L. (2004) Pteridophyta, Spermatophyta. *Lista de especies silvestres de Canarias (hongos, plantas y animales terrestres)* (ed. by J.L. Martín, N. Zurita and M. Arechavaleta), pp. 99–143. Consejería de Medio Ambiente y Ordenación Territorial, Gobierno de Canarias, España.
- Acevedo-Rodríguez, P. (2005) Vines and climbing plants of Puerto Rico and the Virgin Islands. *Contributions from the United States National Herbarium*, **51**, 1–483.
- Acevedo-Rodríguez, P. & Strong, M.T. (eds) (2005) Monocotyledons and gymnosperms of Puerto Rico and the Virgin Islands. *Contributions from the United States National Herbarium*, **52**, 1–415.
- Acevedo-Rodríguez, P. & Strong, M.T. (2007) *Catalogue of the seed plants of the West Indies Website*. National Museum of Natural History, The Smithsonian Institution, Washington, DC.
- Ackerman, J.D. (1995) An Orchid Flora of Puerto Rico and the Virgin Islands. *Memoirs of the New York Botanical Garden*, **73**, 1–203.
- Blackburn, T.M., Cassey, P., Duncan, R.P., Evans, K.L. & Gaston, K.J. (2004) Avian extinction risk and mammalian introductions on oceanic islands. *Science*, **305**, 1955–1958.
- Carlquist, S. (1974) *Island biology*. Columbia University Press, New York.
- Cassey, P., Lockwood, J.L., Blackburn, T.M. & Olden, J.D. (2007) Spatial scale and evolutionary history determine the degree of taxonomic homogenization across island bird assemblages. *Diversity and Distributions*, **13**, 458–466.

- Castro, S.A. & Jaksic, F.M. (2008a) How general are global trends in biotic homogenization? floristic tracking in Chile, South America. *Global Ecology and Biogeography*, **17**, 524–531.
- Castro, S.A. & Jaksic, F.M. (2008b) Role of non-established plants in determining biotic homogenization patterns in Pacific Oceanic Islands. *Biological Invasions*, **10**, 1299–1309.
- Castro, S.A., Muñoz, M. & Jaksic, F.M. (2007) Transit towards floristic homogenization on oceanic islands in the south-eastern Pacific: comparing pre-European and current floras. *Journal of Biogeography*, **34**, 213–222.
- Chapin, S. III, Sala, O.E., Huber-Sannwald, E. & Leemans, R. (2001) The future of biodiversity in a changing world. *Global biodiversity in a changing environment: Scenario for the 21st century* (ed. by F.S. Chapin III, O.E. Sala and E. Huber-Sannwald), pp. 1–4. Springer Verlag, New York.
- Chown, S.L., Gremmen, N.J.M. & Gaston, K.J. (1998) Ecological biogeography of southern ocean islands: specie-area relationships, human impacts, and conservation. *The American Naturalist*, **152**, 562–575.
- Clavero, M. & García-Berthou, E. (2006) Homogenization dynamics and introduction routes of invasive freshwater fish in the Iberian Peninsula. *Ecological Applications*, **16**, 2313–2324.
- Costa, J.C., Capelo, J., Jardim, R. & Sequeiro, M. (2004) Catálogo florístico do Arquipélago da Madeira. *Quercetea*, **6**, 187–200.
- Denslow, J.S. (2001) The ecology of insular biotas. *Trends in Ecology and Evolution*, **16**, 423–424.
- Drake, D.R., Mulder, C.P.H., Towns, D.R. & Daugherty, C.H. (2002) The biology of insularity: an introduction. *Journal of Biogeography*, **29**, 563–569.
- Duncan, J.R. & Lockwood, J.L. (2001) Spatial homogenization of aquatic fauna of Tennessee: extinction and invasion following land use change and habitat alteration. *Biotic Homogenization* (ed. by J.L. Lockwood and M.L. McKinney), pp. 245–258, Kluwer Academic/Plenum Publishers, London.
- Figueroa-Colón, J.C. (1996) Phytogeographical trends, center of high species richness and endemism, and the question of extinctions in the native flora of Puerto Rico. *Annals of the New York Academy of Science*, **776**, 89–102.
- Francis, J.K. & Liogier, H.A. (1991) *Naturalized Exotic Tree Species in Puerto Rico. General Technical Report SO-82*. USDA-Forest Service, Southern Forest Experimental Station, New Orleans, Louisiana.
- Gann, G.D. & Bradley, K.A. (2007–2008) *The Floristic Inventory and Assessment of Puerto Rico Database Online (Beta)*. The Institute for Regional Conservation in collaboration with the International Institute of Tropical Forestry, Miami, Florida.
- Gray, A., Pelembe, T. & Stroud, S. (2005) The conservation of the endemic vascular flora of Ascension Island and threats from alien species. *Oryx*, **39**, 1–6.
- Hansen, A. & Sunding, P. (1993) Flora of Macaronesia. Checklist of vascular plants. *Sommerfeltia*, **17**, 1–295.
- Jardim, R. & Francisco, D. (2000) *Flora Endêmica da Madeira*. Múchia Publicações, Funchal.
- Jardim, R. & Sequeira, M. (2008) Lista das plantas vasculares (Pteridophyta e Spermatophyta). *A list of the terrestrial fungi, flora and fauna of Madeira and Selvagens archipelagos* (ed. by P.A.V. Borges, C. Abreu, A.M.F. Aguiar, P. Carvalho, R. Jardim, I. Melo, P. Oliveira, C. Sérgio, A.R.M. Serrano and P. Vieira), pp. 179–207, Direcção Regional do Ambiente da Madeira and Universidade dos Açores, Funchal and Angra do Heroísmo.
- Judd, W.S., Campbell, C.S., Kellogg, E.A. & Stevens, P.F. (2002) *Plant Systematics: A phylogenetic approach*. Sinauer Associates, Sunderland, MA.
- Kreft, H., Jetz, W., Mutke, J., Kier, G. & Barthlott, W. (2007) Global diversity of island floras from a macroecological perspective. *Ecology Letters*, **11**, 116–127.
- Kueffer, C., Daehler, C.C., Torres-Santana, C.W., Lavergne, C., Meyer, J.-Y., Otto, R. & Silva, L. (2010) A global comparison of plant invasions on oceanic islands. *Perspectives in Plant Ecology Evolution and Systematics*, **12**, 145–161.
- La Sorte, F.A. & McKinney, M.L. (2006) Compositional similarity and the distribution of geographical range size for assemblages of native and non-native species in urban floras. *Diversity and Distributions*, **12**, 679–686.
- Liogier, H.A. (1989) *Las plantas introducidas en las Antillas después del descubrimiento y su impacto en la ecología*. Boletín de la Comisión Puertorriqueña para la Celebración del Quinto Centenario del Descubrimiento de América y Puerto Rico, San Juan, Puerto Rico.
- Liogier, H.A. & Martorell, L.F. (2000) *Flora of Puerto Rico and adjacent islands: A systematic synopsis*, 2nd edn. Editorial de la Universidad de Puerto Rico, San Juan.
- MacArthur, R.H. & Wilson, O.E. (1967) *The Theory of Island Biogeography*. Princeton University Press, Princeton, NJ.
- McKinney, M.L. (2005) New Pangea: homogenizing the future biosphere. *Proceedings of the California Academy of Sciences, USA*, **56**, 119–129.
- McKinney, M.L. (2006) Urbanization as a major cause of biotic homogenization. *Biological Conservation*, **127**, 247–260.
- McKinney, M.L. & Lockwood, J.L. (1999) Biotic homogenization: a few winners replacing many losers in the next mass extinction. *Trends in Ecology and Evolution*, **14**, 450–453.
- Molina, S. & Alemañy, S. (1997) *Species Code for the Trees of Puerto Rico and the U.S. Virgin Islands. General Technical Report SO-122* USDA Forest Service, Southern Research Station, Asheville, NC.
- Monod, T. (1990) Conspectus florae Salvagicae. *Bolletín Museu Municipal do Funchal, Supplement*, **1**, 1–79.
- Norman, S.P. & Taylor, A.H. (2003) Tropical and north Pacific teleconnections influence fire regimes in pine-dominated forests of north-eastern California, USA. *Journal of Biogeography*, **30**, 1081–1092.
- Olden, J.D. (2006) Biotic homogenization: a new research agenda for conservation biogeography. *Journal of Biogeography*, **33**, 2027–2039.

- Olden, J.D. & Poff, N.L. (2003) Toward a mechanistic understanding and prediction of biotic homogenization. *The American Naturalist*, **162**, 442–460.
- Olden, J.D. & Rooney, T.P. (2006) On defining and quantifying biotic homogenization. *Global Ecology and Biogeography*, **15**, 113–120.
- Olden, J.D., Poff, N.L., Douglas, M., Douglas, M.E. & Fausch, K.D. (2004) Ecological and evolutionary consequences of biotic homogenization. *Trends in Ecology and Evolution*, **19**, 18–24.
- Olden, J.D., Kennard, M.J. & Pusey, M.J. (2008) Species invasions and the changing biogeography of Australian freshwater fishes. *Global Ecology and Biogeography*, **17**, 25–37.
- Perez de Paz, P.L. & Acebes, J.R. (1978) Las Islas Salvajes: contribución al conocimiento de su flora y vegetación. *Contribución al estudio de la Historia Natural de las Islas Salvajes* (ed. by F. García-Talavera), pp. 77–105, Cabildo Insular de Tenerife, Museo de Ciencias Naturales, Santa Cruz de Tenerife.
- Press, J.R. & Short, M.J. (1994) *Flora of Madeira*. The Natural History Museum, London.
- Proctor, G.R. (1989) Ferns of Puerto Rico and the Virgin Islands. *Memoirs of the New York Botanical Garden*, **53**, 1–389.
- Rahel, F.J. (2000) Homogenization of fish faunas across the United States. *Science*, **288**, 854–856.
- Richardson, D.M., Pyšek, P., Rejmánek, M., Barbour, M.G., Panetta, F.D. & West, C.J. (2000) Naturalization and invasion of alien plants: concepts and definitions. *Diversity and Distributions*, **6**, 93–107.
- Ruiz, G.M. & Carlton, J.T. (eds) (2003) *Invasive species: Vectors and management strategies*. Island Press, Washington, DC.
- Sala, O.E., Chapín, F.S., Armesto III, J.J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L., Jackson, R.B., Kinzing, A., Leemans, R., Lodge, D.M., Mooney, H.A., Oesterheld, M., Poff, N., Sykes, M.T., Walter, B.H., Walker, M. & Wall, D.W. (2000) Global biodiversity scenarios for the year 2100. *Science*, **287**, 1770–1774.
- Sánchez-Pinto, L., Rodríguez, M.L. & Rodríguez, S. (2005) Pteridophyta, spermatophyta. *Lista preliminar de especies silvestres de Cabo Verde* (ed. by M. Arechavaleta, N. Zurita, M.C. Marrero and J.L. Martín) pp. 38–57. Consejería de Medio Ambiente y Ordenación territorial, Gobierno de Canarias, España.
- Sax, D.F. & Gaines, S.D. (2003) Species diversity: from global decreases to local increases. *Trends in Ecology and Evolution*, **18**, 561–566.
- Sax, D.F. & Gaines, S.D. (2008) Species invasions and extinction: the future of native biodiversity on islands. *Proceedings of the National Academy of Sciences USA*, **105**, 11490–11497.
- Sax, D.F., Gaines, S.D. & Brown, J.H. (2002) Species invasions exceed extinctions on island worldwide: a comparative study of plants and birds. *The American Naturalist*, **160**, 766–783.
- Silva, L., Pinto, N., Press, B., Rumsay, F., Carine, M., Henderson, S. & Sjögren, E. (2005) Lista das plantas vasculares (Pteridophyta e Spermatophyta). *A list of the terrestrial fauna (Mollusca and Arthropoda) and flora (Bryophyta, Pteridophyta and Spermatophyta) from the Azores* (ed. by P.A. Borges, R. Cuhna, R. Gabriel and *et al.*), pp. 131–156. Direcção Regional do Ambiente and Universidade do Açores, Horta, Angra do Heroísmo and Ponta Delgada.
- Spear, D. & Chown, S.L. (2008) Taxonomic homogenization in ungulates: patterns and mechanisms at local and global scales. *Journal of Biogeography*, **35**, 1962–1975.
- Vermeij, G.J. (1991) When biotas meet: understanding biotic exchange. *Science*, **253**, 1099–1104.
- Vitousek, P.M. (2002) Ocean islands as model systems for ecological studies. *Journal of Biogeography*, **29**, 573–582.
- Vitousek, P.M., D'Antonio, C.M., Loope, L.L. & Westbrooks, R. (1996) Biological invasions as global environmental change. *The American Scientist*, **84**, 468–478.
- Wagner, W.L., Herbst, D.R. & Sohmer, S.H. (1999) *Manual of the flowering plants of Hawaii*. Revised edition. Bernice P. Bishop Museum Special Publication. University of Hawai'i Press/Bishop Museum Press, Honolulu.
- Wagner, W.L., Herbst, D.R. & Lorence, D.H. (2005) Flora of the Hawaiian Islands website. Available at: <http://botany.si.edu/pacificislandbiodiversity/hawaiianflora/> (accessed 19 March 2009).
- Whittaker, R.J. (1998) *Island biogeography: ecology, evolution, and conservation*. Oxford University Press, Oxford.
- Zizka, G. (1991) Flowering plants of Easter Island. *Palmen-garten*, **3**, 1–108.

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