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Research

Biotic homogenization of oceanic islands depends on taxon, spatial scale and the quantification approach

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Biotic homogenization reduces the regional distinctiveness of biotas with significant ecological and evolutionary consequences. The outcome of this process may depend on the spatial scale of inquiry (both resolution and extent), the selected taxon and dissimilarity index as well as on the contribution of species extinctions and introductions. In the present research, we try to disentangle the effects of these factors on homogenization patterns comparing six taxonomic groups (pteridophytes, spermatophytes, breeding birds, mammals, reptiles and non-marine molluscs) within and between five Atlantic archipelagos of the Macaronesian Region. Taxonomic homogenization was analyzed by partitioning β-diversity into spatial turnover of species composition and nestedness. Total compositional change was divided into changes related to extinctions/extirpations of native and to introductions of alien species. Analyses were carried out at two different spatial resolutions (island versus archipelago unit) and geographic extents (within each archipelago and across the whole Macaronesian Region). Pteridophytes and reptiles tended to taxonomic differentiation, while mammals and molluscs showed homogenization regardless of scale and resolution. For spermatophytes, the most species-rich group, taxonomic heterogenization traded off with homogenization from the local to regional extent. Birds revealed heterogenization at the island, but not at the archipelago resolution. Extirpations of native species generally led to homogenization at the local extent, whereas the effect of alien introductions varied according to taxon and spatial scale. Furthermore, overall changes in species pool similarities were driven both by spatial turnover and nestedness. We demonstrate that biotic homogenization after human colonization within Macaronesia clearly depended on taxon, spatial scale and the dissimilarity measure. We suggest that homogenization of island biotas is first conditioned by initial dissimilarity related to taxon characteristics, such as dispersal capacity or endemicity, evolutionary processes, archipelago configurations and environmental variation along spatial scales. Thus, similarity change is the outcome of the impacts of number, proportion and distribution type of lost and gained species. Rare extirpated and common introduced species homogenize, while common extirpated and rare introduced species differentiate island biotas. Partitioning of beta diversity helps to improve our understanding of the homogenization process.

Introduction

As humans have spread across the globe, natural biogeographic barriers have been disrupted, and many plant and animal species have become established outside their natural distributional range (Dar and Reshi 2014). This human induced influx of species in conjunction with the loss and alteration of natural habitats is causing profound changes in the geographic distribution of organisms. These changes are characterized by the spread of cosmopolitan alien species and the extirpation or extinction of native and endemic ones (Olden and Poff 2003, Capinha et al. 2015). In general, such changes can increase the genetic, taxonomic or functional similarity between biotas of distant areas (McKinney and Lockwood 1999, Olden et al. 2011). This process, termed biotic homogenization, not only threatens the regional distinctiveness of biotas, but has significant ecological and evolutionary consequences (Olden et al. 2004) and is a growing conservation issue in the context of the current biodiversity crisis (Olden 2006).

Biotic homogenization has increased so rapidly over the recent historical period that some have considered it to be a new era 'The Homogecene' (Rosenzweig 2001, McKinney 2005a). According to Olden et al. (2004), biotic homogenization may be divided into three main components: taxonomic, genetic and functional homogenization. Homogenization at the taxonomic level can be expressed as the increase in the compositional similarity between communities (Olden et al. 2004, Olden and Rooney 2006). This is frequently quantified by comparing dissimilarity indices based on species presence or absence matrices in time or space (Olden and Rooney 2006, Dar and Reshi 2014). β-Diversity measures can be divided in two groups, those that represent only true compositional change implying replacement of some species by others (e.g. Simpson index) and the more commonly used ones that additionally incorporate changes in species richness (e.g. Jaccard index or Sørensen index, Baselga 2010).

Taxonomic homogenization has already been addressed in many studies, both at a continental (Qian and Ricklefs 2006) and island level (Cassey et al. 2007, Baiser et al. 2012), and for different taxonomic groups: amphibians, birds, fish, insects, mammals, plants, reptiles, snails, etc. (Olden et al. 2006, Shaw et al. 2010). Nevertheless, our knowledge about the processes driving homogenization and its real magnitude is limited (Dar and Reshi 2014). Consequently, studies focusing on this topic should be a priority in conservation biology.

The growing literature highlights that different patterns of taxonomic homogenization, or even differentiation (i.e. decrease in biota similarity: heterogenization) can be detected depending on the spatial scale of inquiry. These patterns are affected by both the spatial resolution (Olden et al. 2006, Castro et al. 2007, Spear and Chown 2008) and the

geographic extent of the study area (McKinney 2005b, Cassey et al. 2007, Shaw et al. 2010) and also by the taxon (Olden et al. 2006, Shaw et al. 2010, Florencio et al. 2015), the hemisphere (Castro and Jaksic 2008) or even the ecosystem (Dar and Reshi 2014).

An increase in the taxonomic similarity (homogenization) at a regional or global scale between distant areas is often observed, while taxonomic differentiation (heterogenization) is more common at the local scale between nearby communities (Rosenzweig 2001, Baiser et al. 2012). Species introduction to 'neighboring' areas that tend to show similar native assemblages frequently leads to reduced taxonomic similarity (Spear and Chown 2008). On the other hand, the introduction of the same pool of alien species in two distant and already differentiated communities increases the homogenization level (McKinney 2004, 2008). The initial taxonomic similarity of native assemblages in two regions depends on past and current environmental conditions as well as on historical (evolutionary) processes, and tends to decrease with geographic distance, this is known as distance decay (Soininen et al. 2007, La Sorte et al. 2008). Although influenced by climate, alien species pools are more determined by historical patterns of human activity and colonization (Cassey et al. 2007, Kueffer et al. 2010, Seipel et al. 2012).

Biotic homogenization is particularly relevant for island ecosystems, since they harbor some of the richest and most vulnerable biotas worldwide, hosting a high number of endemic species (Whittaker and Fernández-Palacios 2007, Kueffer et al. 2010). Features like small population size, restricted distribution, evolution in isolation and ecological release make island biotas much more fragile and invasible than their mainland counterparts (Sax et al. 2002, Shaw et al. 2010). In fact, the number of historical extinctions and introduced species are far more abundant in island than in continental systems (Rejmanek and Randall 1994, Whittaker and Fernández-Palacios 2007). However, within island systems, the introduction rate of alien species usually surpasses the extinction rate of native ones, although extinctions might be delayed due to extinction debts (Whittaker and Fernández-Palacios 2007, Triantis et al. 2010, Chiarucci et al. 2017, Otto et al. 2017). Additionally, islands are discrete units with clear natural biogeographic barriers, which make them convenient systems to analyze natural processes, such as biotic homogenization (Whittaker and Fernández-Palacios 2007). For instance, patterns of bird assemblage convergence (i.e. taxonomic homogenization) or divergence (i.e. taxonomic differentiation) among islands in four different oceans depend on the scale of examination, the evolutionary processes of the region, as well as its history of human colonization (Cassey et al. 2007).

Homogenization patterns might differ between taxonomic groups due to differences in the way and time species were introduced by humans and to species traits such as dispersal ability or vagility (Lockwood 2006). Species of vagile taxa like birds or ferns that are introduced to a single island may reach other islands within the same archipelago by their own movements, increasing the probability of homogenization at

a local scale. By contrast, species of less dispersive taxa depend more on human activity to colonize the whole archipelago, which might restrict these species to highly populated and disturbed islands. On the other hand, a high initial similarity of native assemblages as expected for vagile taxa, provided the same habitats are available, might increase the likelihood of differentiation of biotas following the introduction of alien species.

This research investigates the scale and taxonomic dependency of biotic homogenization caused by native species extirpations and alien species introductions in the Macaronesian Region by using some of the most accurate and updated sets of biotic check-lists available for six major taxonomic groups across five archipelagos and 36 islands. For each species group (pteridophytes, spermatophytes, non-marine molluscs, reptiles, birds and mammals), we tested for changes in the taxonomic similarity of island pairs after human induced species extirpations and introductions at two different spatial resolutions (island versus archipelago) and geographic extents (within an archipelago and across the whole Macaronesian Region). The hypotheses to be tested are: 1) taxonomic homogenization occurs at a regional scale and differentiation at a local scale (importance of spatial scale), 2) differences in taxon characteristics, such as dispersal capacity and endemicity, influence biotic homogenization (importance of taxon characteristics), and 3) the outcome of biotic homogenization also depends on the type of dissimilarity measure (importance of quantification approach).

Methods

Data sources

The Macaronesian Region includes five North Atlantic archipelagos: Azores, Madeira, Selvagens Islands, Canary Islands and Cape Verde. We examined a set of 36 islands, larger than $1\,km^2$, which differ in geographic, geological and anthropogenic parameters (Table 1): nine in Azores, four in Madeira (considering as a single island each of the two tiny Madeiran

archipelagos of Desertas and Selvagens Islands), 11 in the Canary Islands and 12 in Cape Verde.

The primary data for the analyses include presence–absence data for pteridophytes (ferns and allies), spermatophytes (vascular plants except ferns), non-marine molluscs, reptiles, breeding birds and mammals, groups for which the geographic distribution and taxonomy are well known in the region. Although the inclusion of species abundance data may be desirable (McKinney 2008), this is almost impossible at such biogeographic scales, which rely on datasets assembled from multiple sources and with variable data quality (Chiarucci et al. 2011a). Data of extant native and introduced species as well as the proportion of endemic species were obtained from the most recent versions of the Biota Checklists of the Macaronesian archipelagos and additional sources (Supplementary material Appendix 1). Human induced species extirpations and extinctions were extracted from a recent, still unpublished database (Fructuoso Alonso 2016). For each taxonomic group and archipelago, three species list were prepared with a) the initial native species (before human induced extinctions and extirpations, called simply extirpations from here on), b) the extant native species (after extirpations) and c) the total extant species (after extirpations and introductions by humans). A summary for the whole Macaronesian Region is shown in Table 2.

Data analyses

There are two types of pairwise dissimilarity indices to measure beta diversity, those that account for both spatial turnover and changes in species richness (e.g. Jaccard, Sørensen, Bray–Curtis) and those that reflect only spatial turnover but not changes in species richness (Simpson index, Baselga 2010; β_{-3} index, Caravalho et al. 2013). Richness change can be related to nestedness, meaning that the species assemblage of one site is a subset of that of the other site. Following the approach of Baselga (2010), we partitioned overall beta diversity (measured by Sørensen index, βsor) into the two additive components of pure spatial turnover (measured by Simpson index, βsim) and nestedness (difference between the two indices, βnest): βsor = βsim + βnest.

Table 1. Some geographical, geological and anthropogenic parameters of the Macaronesian Region. Source: Fernández-Palacios (2010).

Parameter	Azores	Madeira	Selvagens	Canaries	Cape Verde	Macaronesia
No. islands > $1\,km^2$	9	3	1	11	12	36
Area (km^2)	2764	815	4	7445	4033	15061
Maximum elevation (m)	2351 (Pico)	1862 (Madeira)	163 (S. Grande)	3718 (Tenerife)	2835 (Fogo)	3718
Continental isolation (km)	1369 (São Miguel)	630 (P. Santo)	388 (S. Grande)	97 (Fuerteventura)	571 (Boa Vista)	97
Mean intra-archipelago isolation (km)	220	32	20	196	141	–
Age of the oldest emerged island (My)	6 (St Maria)	14 (P. Santo)	27 (S. Grande)	20 (Fuerteventura)	25.6 (Sal)	27
Last volcanic eruption	1957 (Faial)	25 Ky BP (Madeira)	3.4 My BP (S. Grande)	2011 (El Hierro)	2015 (Fogo)	2015
Latitude (°)	37–40 N	33 N	30 N	27–29 N	15–17 N	40–15 N
Colonization date	1432 AD	1420 AD	–	ca 2500 BP	1456 AD	–
Human population 2010 (M)	0.25	0.35	–	2.2	0.45	3.2

Table 2. Number of initial native (nat i) and extant native (nat e) species, human induced species extinctions/extirpations (ext) and species introductions (int) as well as total extant species (total) for all taxonomic groups analyzed in Macaronesia. Mean initial dissimilarity (βsor = Sørensen index, βsim = Simpson index) of all within-archipelago island pairs and mean proportion of endemic species in the initial native archipelago species pool. Proportions (%) are related to the initial native species pools.

Taxonomic group	nat i	nat e	ext	% ext	int	% int	total	βsor	βsim	% end
Birds	142	112	30	21.1	12	8.5	124	0.37	0.21	19.3
Mammals	18	14	4	27.8	17	94.4	31	0.57	0.43	19.6
Reptiles	42	39	3	7.1	9	21.4	48	0.50	0.39	81.5
Non-marine molluscs	443	434	9	2	69	15.6	503	0.68	0.49	89.1
Pteridophytes	92	92	0	0	28	30.4	120	0.50	0.13	8.2
Spermatophytes	1938	1934	4	0.2	1141	58.9	3075	0.45	0.20	32.9

The Sørensen dissimilarity index (Sørensen 1948, βsor) is one of the most used indices of beta diversity and formulated as:

$$\beta sor = (b + c) / (2a + b + c)$$

where a is the number of species shared among both geographic units (islands or archipelagos), b is the number of species present only in the first unit but not in the second unit and c the number of species present only in second unit but not in the first unit. The Simpson dissimilarity index (Simpson 1943, βsim) is quantified as:

$$\beta sim = \min(b, c) / (a + \min(b, c))$$

where a, b and c are the same variables as defined for Sørensen dissimilarity. Finally, βnest is the difference between βsor and βsim.

To disentangle the effects of species extirpations and introductions on taxonomic homogenization in the Macaronesian Region, we calculated changes in pairwise dissimilarity by matrix subtraction, first comparing the matrices of initial and extant native species (effect of extirpations) and second the matrices of extant native and total extant species (effect of introductions). Finally, we subtracted the matrix of total extant species from the matrix of initial native species (total effect of both extirpations and introductions). Matrix subtractions, obtained by subtracting the corresponding elements (same row and column) of the two matrices, were performed for all three dissimilarity measures. Positive values within these dissimilarity change matrices imply a decrease in dissimilarity (homogenization) and negative values an increase in dissimilarity (heterogenization), and no change despite species exchange is known as biotic tracking (Castro and Jaksic 2008).

Given the importance of spatial scale (either resolution or extent) in controlling species diversity (Scheiner et al. 2011), analyses were carried out at two different spatial resolutions: island versus archipelago as the geographic unit, and two spatial extents: local (between islands within the same archipelago) versus regional (between islands or archipelagos across the whole Macaronesian Region). Furthermore, geographic distances between all island pairs were calculated and related to initial dissimilarity and dissimilarity change. Numbers of

pairwise combinations were: 36 for Azores, 6 for Madeira (and Selvagens), 55 for the Canary Islands, 66 for Cape Verde and 630 (using island resolution) and 6 (using archipelago resolution) for the whole Macaronesian Region.

To test the hypothesis that the mean value of a dissimilarity change matrix is different from 0, either positive indicating homogenization or negative showing heterogenization, we applied a bootstrap approach (Crawley 2007). We took 10 000 random samples with replacement from the total number of values of each dissimilarity change matrix. Then, we calculated 95, 99 and 99.9% confidence intervals with lower and upper bounds of the cumulative probability distribution of the 10 000 bootstrapped mean values of the random samples. If the confidence interval excludes the value 0, then we can accept the hypothesis. The test for significant difference between mean values of changes in βsor and βsim of corresponding matrices was carried out in the same way. The relationships between within-archipelago initial dissimilarity, proportion of endemic species and dissimilarity change of island biotas was tested by linear regression. The correlations between matrices of inter-island distance and initial dissimilarity or dissimilarity change were tested for each taxonomic group by mantel tests. Analyses were performed using the R (3.5.3) statistical software (R Development Core Team).

Results

By far the richest taxonomic group across the whole Macaronesia Region was represented by spermatophytes, followed by molluscs, pteridophytes and birds (Table 2, Supplementary material Appendix 2 Table A1). As expected for oceanic islands, the total number of native mammals and reptiles was extremely low. The group of birds suffered most from extirpations with 30 species, 21% of the initial species pool, while only 12 (8.5%) bird introductions have occurred, the lowest percentage of all groups. Mammals lost 28%, reptiles 7%, molluscs 2%, spermatophytes 0.2% and pteridophytes no species after human arrival. High proportions of introductions were recorded for mammals and spermatophytes (94% and 59%, respectively) and intermediate levels for reptiles, molluscs and pteridophytes (21, 16 and 30%, respectively). Initial dissimilarity for within-archipelago island pairs was high for mammals, non-marine molluscs and reptiles, low to intermediate for birds and spermatophytes,
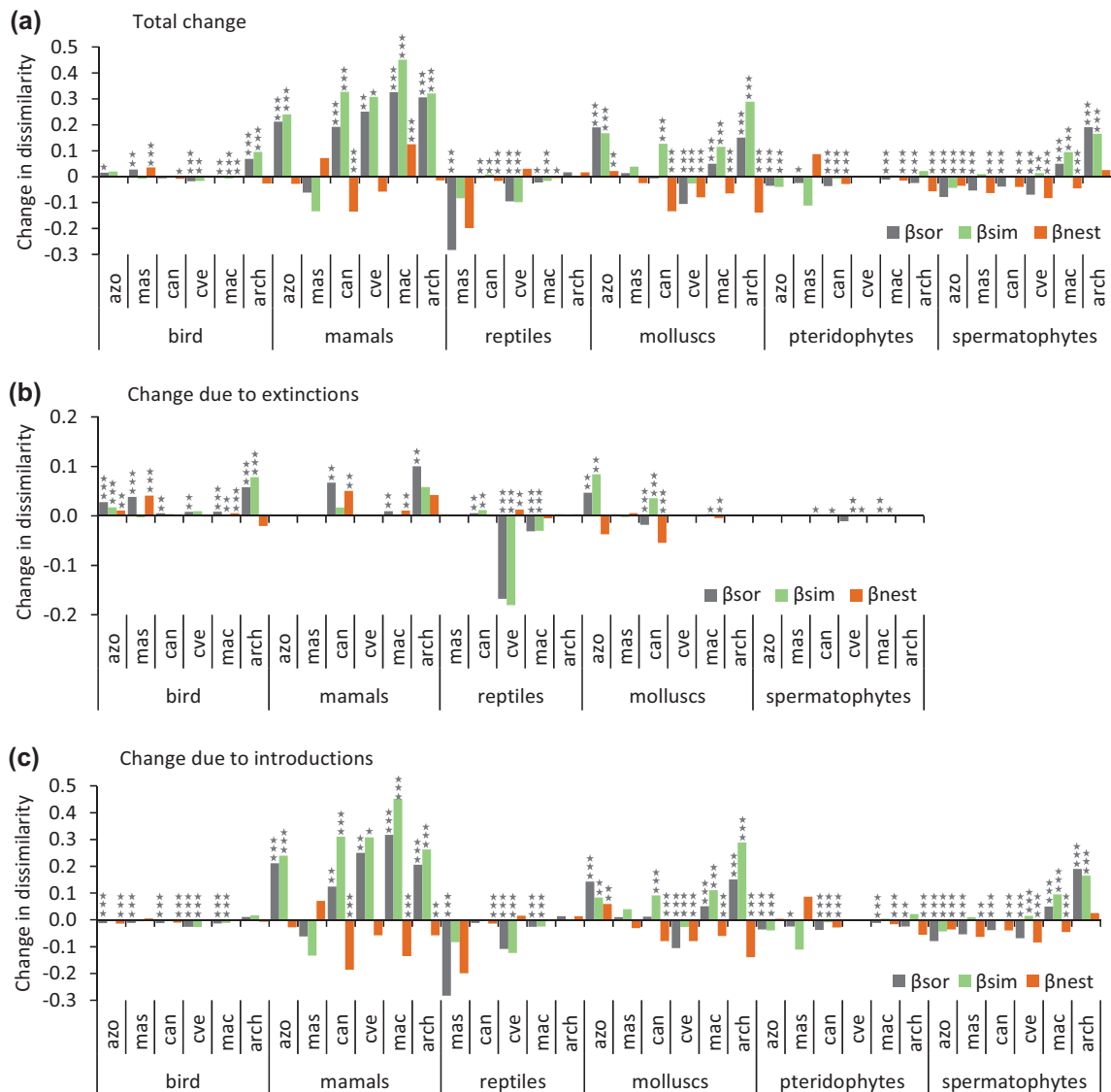
Figure 1. Mean values of dissimilarity change between island pairs measured by Sørensen index (βsor), Simpson index (βsim) and nestedness (βnest) for all taxonomic groups and spatial scales (geographic extents and spatial resolutions): local extent and island resolution: azo = Azores, mas = Madeira and Selvagens, can = Canary Islands, cve = Cape Verde, regional extent: mac = Macaronesian island resolution, arch = Macaronesian archipelago resolution. Positive values reflect homogenization, negative values heterogenization. Results of bootstrap tests for significant differences from 0 are shown by symbols: * p < 0.05, ** p < 0.01, *** p < 0.001.

and very low for pteridophytes. Averaged over all taxonomic groups, the Canary Islands showed the highest values of dissimilarity (βsim) between island biotas, followed by Cape Verde, Madeira and the Azores. Molluscs and reptiles showed a high proportion of endemic species (> 80%) in initial native archipelago species pools, while this proportion was lower for spermatophytes (34%), mammals (20%), birds (19%) and pteridophytes (8%).

Analyses of changes in pairwise dissimilarity showed that species extirpations generally led to homogenization with the exceptions of reptiles and spermatophyte in Cape Verde, regardless of spatial resolution or extent of the study (Fig. 1b, Table 3, Supplementary material Appendix 2 Table A2).

The effect of alien species introductions on dissimilarity of island biotas depended greatly on the taxa and the spatial scale studied (resolution and extent, Fig. 1c, Table 3). Generally, mammals and molluscs showed homogenization (exception for molluscs on Cape Verde) for both measures of resolution and extent. To the contrary, birds, reptiles, pteridophytes and spermatophytes tended to differentiate after the arrival of alien species at the local extent and island resolution. A clear shift from taxonomic heterogenization at local extent to homogenization at regional extent (comparing all island pairs within the entire Macaronesian Region) was only found for spermatophytes. Analyzing the effects of both extirpations and introductions, (Fig. 1a, Table 3) total change

Table 3. Summary of dissimilarity change of island pairs for each taxonomic group and for the different geographic extents and resolutions. Ext = change due to species extirpations, Int = change due to species introductions, Tot = total change, dark grey = homogenization, light grey = no clear trend, white = heterogenization, no = no data. The trend is based on the number of significant changes measured by Sørensen and Simpson index.

Extent	Archipelago local			Macaronesia regional			Macaronesia regional		
Resolution	island			island			archipelago		
Effect	Ext	Int	Tot	Ext	Int	Tot	Ext	Int	Tot
Birds									
Mammals									
Reptiles									
Non-marine molluscs									
Pteridophytes	no			no			no		
Spermatophytes									

in dissimilarity was very similar to the response caused by introductions, since the number of introduced species was much higher than the number of extirpated species except for birds, which showed more extirpations than introductions. For birds, total dissimilarity change depended on the stronger effect of either homogenization by extirpations or differentiation by introductions for each archipelago. Regarding species pools of entire archipelagos (archipelago resolution), species extirpations and introductions led to significant homogenization in all taxonomic groups but reptiles and pteridophytes.

When comparing dissimilarity change measures, we detected significant differences between the Sørensen and Simpson indices for the same dissimilarity matrix in 53% of the cases (Fig. 1, Supplementary material Appendix 2 Table A2), although both indices usually showed the same direction of change (heterogenization or homogenization). Only in two cases (pteridophytes at the Macaronesia extent and spermatophytes within Cape Verde), a switch from heterogenization to homogenization or vice versa between the two measures could be observed. In 62% of the cases, total changes in overall dissimilarity (βsor) were better explained by spatial turn over than by changes in richness related to nestedness (absolute values βsim > absolute values βnest). By contrast, in 38% of cases, nestedness contributed more to dissimilarity changes than turn over. In 26% of cases, βsim indicated significant homogenization, while βnest showed significant heterogenization or vice versa.

Initial dissimilarity of biotas was correlated with both within- and between-archipelago pairwise dissimilarity changes (Fig. 2a–b). This means that the higher the initial compositional dissimilarity (βsim) of two biotas, the higher the probability for homogenization of their biotas after species exchange (loss and gain); and the lower the initial dissimilarity, the higher the probability for heterogenization. Furthermore, mean initial pairwise dissimilarity within archipelagos was also related to the proportion of endemics in the initial species pool (Fig. 2c). Mantel test showed that the initial dissimilarity of islands pairs within the whole Macaronesian Region was strongly correlated with the geographic distance between the two islands (Fig. 3, Supplementary material Appendix 2
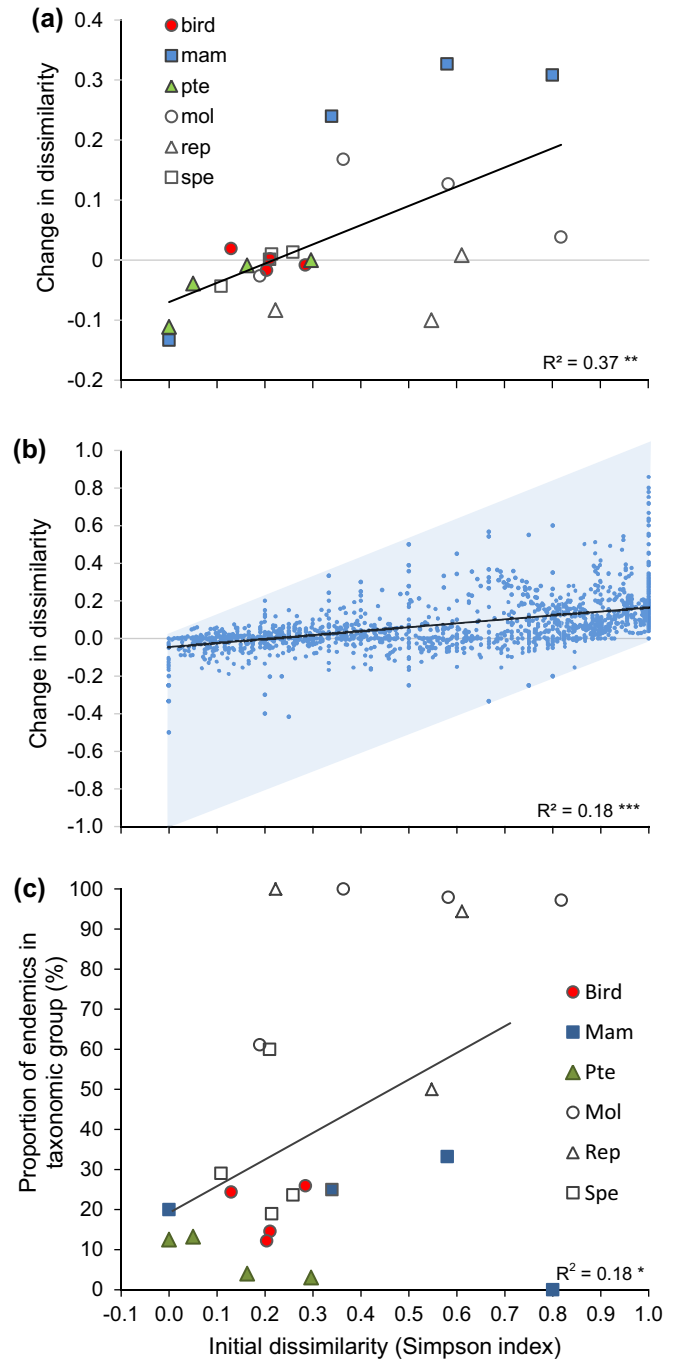

Figure 2. Relationship between initial dissimilarity (Simpson index), dissimilarity change (βsim, total change after extirpations and introductions) and proportion of endemic species, (a) and (c) indicate mean values of all island pairs within an archipelago for each taxonomic group (n = 23, spermatophytes, birds, non-marine molluscs, pteridophytes, reptiles, no native reptiles in the Azores, and mammals), (b) represents all combinations of island pairs within the whole Macaronesian Region (n = 3057, island pairs with species present), the shaded area shows the range of statistically possible values. Negative dissimilarity change values indicate heterogenization and positive values homogenization (R² = coefficient of determination, *** p < 0.001, ** p < 0.01, * p < 0.05).
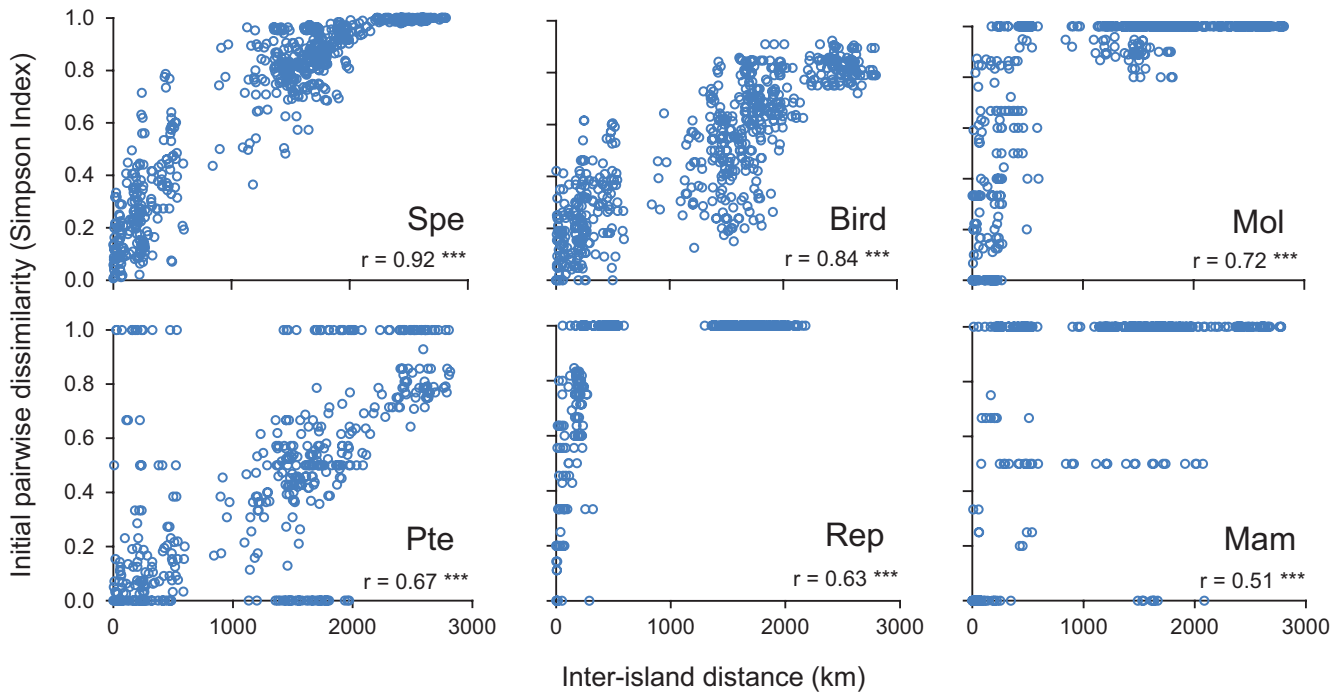
Figure 3. Relationship between inter-island geographic distance and initial pairwise dissimilarity measured by the Simpson index for each taxonomic group (spermatophytes, birds, non-marine molluscs, pteridophytes, reptiles and mammals) and all combinations of island pairs within the whole Macaronesian Region. There are no native reptiles in the Azores Islands, hence the maximum inter-island distance is between Porto Santo and Brava (r = mantel correlation coefficient, *** significance p < 0.001).

Table A3). Spermatophytes showed the strongest, mammals the weakest distance-decay. Before human arrival, island pairs that are more than 2000 km apart did not share any species of reptiles, molluscs and mammals, while birds and pteridophytes revealed spatial turnover in species composition up to the maximum inter-island distance. For all taxonomic groups but birds, mantel correlation coefficients revealed a significant positive relationship between inter-island distance and homogenization (Fig. 4, Supplementary material Appendix 2 Table A3). Negative values, meaning taxonomic differentiation, were only common at short distances, especially up to 600 km, the longest inter-island distance within an archipelago (Azores), while at longer distances almost exclusively positive values, meaning homogenization, or no change (tracking) occurred. Mammals showed an extremely high magnitude of homogenization, followed by molluscs and spermatophytes, with maximum values for dissimilarity change of 0.85, 0.78 and 0.4, respectively.

Discussion

Our results indicate that changes in species composition of island biotas after human arrival and colonization did not always lead to homogenization, meaning a loss of distinctiveness, as suggested in many earlier studies (Olden et al. 2004, Olden and Rooney 2006, Cassey et al. 2007, Baiser et al. 2012). The outcome of species exchange between island pairs in the Macaronesian Region depended on many factors, such

as taxon, spatial scale and related initial dissimilarity as well as on how beta diversity was measured. Furthermore, the processes of species loss and gain showed different contributions to changes in beta diversity, in some cases even opposite effects.

Species extirpations on the Macaronesian islands led to homogenization of their biotas. The case of reptiles on Cape Verde was an exception to this trend, where the common giant wall gecko *Tarentola gigas* was extirpated from all but Branco and Raso Island leading to differentiation in reptile composition. To the contrary, most species which became extinct in Macaronesia were rare species restricted to one (single-island endemics or SIE) or a few islands (multi-island endemics or MIE) causing a homogenization effect of their biotas (Fructuoso Alonso 2016). Although extirpations were included in many studies on taxonomic homogenization (Cassey et al. 2007, Winter et al. 2009, Baiser et al. 2012), only a few have attempted to disentangle the effects of species loss and gain (Olden and Poff 2004, Su et al. 2015, Rosenblad and Sax 2016). Our results support the idea that the spatial distribution of an extirpated species, i.e. the commonness or rarity within the archipelago, together with the initial dissimilarity of island pairs influences the change in species composition (Longman et al. 2017). The extirpation of a species previously only on one island in the island pair, typical for rare species, has a clear homogenizing impact for taxa with low to intermediate initial dissimilarity (Rosenblad and Sax 2016). In our study, this is the case for birds in all archipelagos, Canary Island mammals and molluscs in Azores
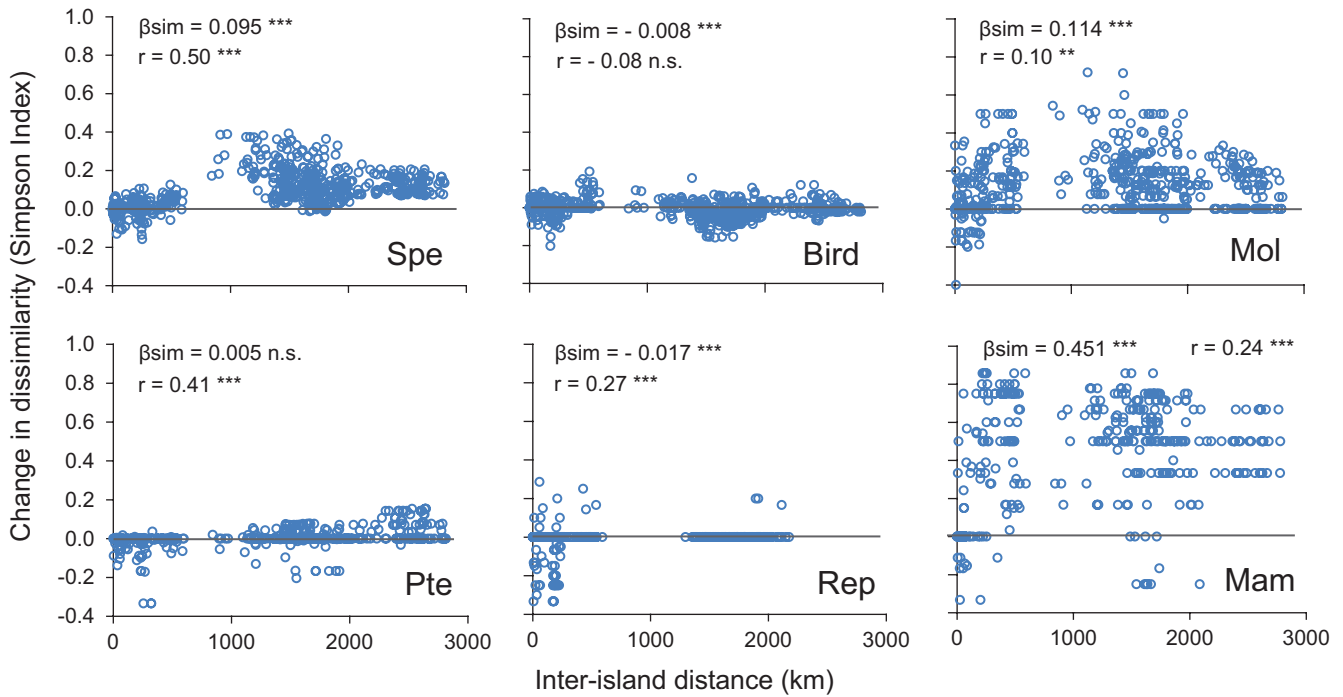
Figure 4. Relationship between inter-island geographic distance and change in dissimilarity (βsim, indicating species turnover, total change after extirpations and introductions) for each taxonomic group (Fig. 3) and all combinations of island pairs within the whole Macaronesian Region (βsim = mean value of all island pairs, *** significant difference of βsim from 0 in bootstrap tests, negative dissimilarity change values indicate heterogenization and positive values homogenization, r = mantel correlation coefficient, *** significance p < 0.001, ** significance p < 0.01).

and the Canary Islands, while the loss of a native species on both islands of the pair, typical for common species, has a strong differentiating effect for taxa with intermediate to high levels of initial dissimilarity, such as reptiles in Cape Verde.

On both islands and continents, the general effect of alien species introductions at the macro-regional scale is homogenization, while at local extents heterogenization between areas and biotas has often been detected (Qian and Ricklefs 2006, Cassey et al. 2007, Spear and Chown 2008, Winter et al. 2009, Castro et al. 2010, Baiser et al. 2012). This general trend could be confirmed only for spermatophytes, when mean values of dissimilarity change were considered. However, analyzing the relationship of geographic inter-island distance and compositional turnover, we noted a change from differentiation to homogenization with increasing geographic distance, also for reptiles, molluscs and pteridophytes. Only mammals showed overall high levels of homogenization along the whole spatial gradient, while differentiation was more common for birds.

At the local extent, changes in taxonomic similarity depended on taxon and archipelago characteristics. The dispersal capacity or vagility of a taxon may have a substantial influence on biogeographic patterns and should be taken into account in its interpretation (Greve et al. 2005). The higher the dispersal capacity of a given taxon, the higher the expected initial similarity and the lower the proportion of endemics in the species pool of the compared island biotas providing habitat availability is also similar within the

archipelago, thus increasing the likelihood of differentiation by alien species introduction. For instance, native ferns and birds in Macaronesia show a limited degree of endemicity (Vanderpoorten et al. 2011, Illera et al. 2012) and a high degree of homogeneity (Table 2). Due to the small size of spores (pteridophytes) and active dispersal (birds), these species are able to colonize the majority of the islands within an archipelago if their preferential habitat is available (Whittaker 2004, Chiarucci et al. 2011b). In this context, the introduction of a diverse array of species may result in reduced similarity between islands (Olden and Poff 2004). However, this tendency may be reversed over time as alien vagile species tend to invade all islands in the region rather than just one island, favoring homogenization. Even within a vagile species group such as birds, initial compositional dissimilarity of avian communities may differ between subgroups with different dispersal capacities (Pitta et al. 2014). On the other hand, low vagility taxa are expected to have highly differentiated native biotas with high levels of endemism, since their distribution is likely to be restricted by island isolation rather than by habitat availability (Sax et al. 2002, Olden and Rooney 2006), which may become more similar as new species are introduced (Dar and Reshi 2014).

In this study, taxa with a low or variable degree of vagility combined with high initial dissimilarity (molluscs and mammals) showed taxonomic homogenization regardless of geographic extent, whereas taxonomic groups with high dispersal power and low initial dissimilarity (pteridophytes and birds)

exhibited heterogenization within archipelagos after alien introductions confirming the expectations. The initial pool of native mammals in the Macaronesian Region included both non-vagile species (four Canary Island rodents) and species with high dispersal ability, such as bats and the monk seal (Silva et al. 2008, Masseti 2010). However, mammals displayed high levels of initial dissimilarity for the Canary and Cape Verde Islands due to uneven distribution of species. By contrast, reptiles showing low vagility and, hence, relative high levels of initial dissimilarity and endemicity, tended to differentiate after human colonization, which may be explained by the pattern of alien introductions. The introduction of a rare alien species to only one or few islands of an archipelago has a differentiating effect, while a common alien species present on many islands leads to homogenization (Su et al. 2015, Rosenblad and Sax 2016). Consequently, the proportion of these two types in the alien species pool influences the outcome of beta diversity change. In our case, most alien reptiles in Macaronesia with few exceptions were introduced, up to now, to only one or few islands within an archipelago, leading to differentiation, while most alien mammals, known invasive species such as rats, mice and rabbits, are present on all islands even the smallest ones, which had a strong homogenizing impact (Longman et al. 2017). Mammal introductions on specific islands, such as the mouflon *Ovis aries* in Tenerife and barbarian goat *Ammotragus lervia* in La Palma (Masseti 2010), which favor differentiation are exceptions. Overall, as for extirpations, not only the initial similarity of island biotas but also the number and the distribution type of introduced alien species influence changes in beta diversity (McKinney 2004, Chiarucci et al. 2010, Su et al. 2015, Rosenblad and Sax 2016).

Spermatophytes have an intermediate position following this scheme due to their intermediate levels of dispersal capacity and endemicity. Hence, the effect of alien plants varied between archipelagos. Regarding compositional change (βsim), we found heterogenization for the Azores, homogenization for Cape Verde and no significant change for the Madeira and the Canary Island archipelagos. However, all archipelagos showed significant differentiation due to nestedness, meaning that richness gradients between islands increased. These differences between archipelagos might be explained both by the environmental variability within each archipelago and by distinct levels of socio-economic development of each island, which determines the invasion process (Kueffer et al. 2010). Environmental filtering as well as human-induced dispersal pressure influence distribution of alien species within archipelagos and islands (Alexander et al. 2011). In the Azores, heterogenization by alien plants might be explained by the high initial similarity of the native flora, consequence of the almost complete absence of SIEs and the homogeneity of the environmental conditions, the few Azorean endemics are widespread across all the islands, thus being MIEs (the Azores enigma, sensu Carine and Schaefer 2010, Triantis et al. 2012). The introduction of almost 800 alien plants after human colonization, 80% of the current flora, made island floras more diverse in terms of species

turnover and richness. In the Canary Islands, the arrival of alien plants caused an increase in richness gradients but not in species turnover, meaning that alien species pools of smaller islands are mainly subsets of those of bigger islands. Alien species richness was, generally, positively correlated with the size of the human populations (Qian and Ricklefs 2006) and human development on islands (Kueffer et al. 2010). Finally, island floras in Cape Verde became more similar in composition but more diverse due to nestedness after alien introductions. Here, we can highlight the importance and usefulness of the partitioning of beta diversity that allows a more detailed interpretation of homogenization processes.

Some authors argued that biotic homogenization is a process that operates at larger spatial and temporal scales (Olden et al. 2004). Due to differences in environmental conditions and evolutionary processes, areas separated by large distances usually have highly distinctive biotas and, therefore, share few species. As a result, they are more likely to increase their similarity when alien species are introduced (Cassey et al. 2007, Shaw et al. 2010). To the contrary, communities separated by short distances share a higher component of their biotas and could become differentiated due to the unequal establishment of alien species (McKinney 2004, 2008).

Our results support this idea suggesting that the phenomenon of homogenization may be partly interpreted as a matter of geographic distance (La Sorte et al. 2008, Dar and Reshi 2014, Capinha et al. 2015). Despite the observed importance of taxon characteristics and archipelago configurations for changes in beta diversity at the local extent, we found a strong relationship between geographic distance and both initial dissimilarity and dissimilarity change of island pairs, a pattern consistent across taxa. Only in the case of birds, distance decay was not associated with dissimilarity change, observation that is supported by a global study of birds on islands (Cassey et al. 2007). In fact, only birds and pteridophytes, the most vagile taxa, shared species on distant islands (> 2000 km apart). Hence, if island pairs share only few or no species, showing high initial compositional dissimilarity (βsim), we can expect a high probability for homogenization or biotic tracking (no change). Consequently, if we increase the spatial scale of the study system, from the local to the global extent, in our case, including always more archipelagos and ocean basins, then the comparison or mean dissimilarity value of all island pairs will be based on increasingly fewer short-distance and more long-distance island pairs leading necessarily to a higher probability of homogenization, just for statistical reasoning.

However, both the global and local approach is needed to better understand processes of biotic homogenization (Olden et al. 2018). Local studies, i.e. the habitat or ecosystem approach, may give insights into species interactions with their physical environment and enable effective conservation measures to be planned (Bühler and Roth 2011). Studies at the community level have yielded interesting results in the Macaronesia, especially for vascular plants. For instance, Arévalo et al. (2010) found that taxonomic homogenization

due to alien plants increases with human disturbance in roadside communities, while Connor et al. (2012) observed that human colonization did not homogenize Azorean flora in highland ecosystems. Also, in the Azores, colonization of alien species did not trigger homogenization of arthropod assemblages in human-disturbed landscapes, since alien species revealed to be habitat specialists (Florencio et al. 2015).

Not only the spatial extent, but also the spatial resolution plays an important role when studying taxonomic homogenization (Olden et al. 2018). Consequently, coarse-grained scales of investigation should increase the likelihood of recording the introduction of a given species, increasing the number of shared species and therefore leading to a greater level of homogenization (McKinney 2008, Spear and Chown 2008). To the contrary, fine-grained scales (i.e. higher resolution) increase the likelihood of detecting the introduction of rare alien species, accentuating taxonomic differentiation (Olden and Poff 2004, Olden 2006). In our study, coarse grained analyses showed no significant changes or heterogenization for pteridophytes and reptiles but homogenization for the rest of taxa confirming the trend.

Taxonomic homogenization, per se, is not a threat to biodiversity or to the functioning of ecological communities, it is just the result of human-mediated dispersal of species and can lead to a reorganization of biogeographic boundaries (Capinha et al. 2015). More critical is how many of and in which ways these alien species interact with native species and communities (Kueffer et al. 2010). Although only a small percentage of introduced species ever become invasive and may alter ecosystem functions, biotic homogenization will increase the pressure on native biota and the risk for conservation problems. Climate change and the intensification of human disturbances will probably accelerate both extinctions of rare insular species, including those related to extinction debts (Triantis et al. 2010, Otto et al. 2017), and introductions of generalist alien species, which might increase biotic homogenization also at a local scale (Chiarucci et al. 2017).

Conclusions

Biotic homogenization has revealed to be scale and taxon dependent across the Macaronesian Region. Extirpations of native species led to homogenization while introductions of alien species showed different results. The effects of species exchange on beta diversity depended on initial dissimilarity, which can be associated with taxon characteristic such as dispersal capacity and proportion of endemicity, as well as with differences in environmental conditions over spatial scales. However, not only initial similarity influences the homogenization process but also the number and spatial distribution of extirpated and introduced species. The geographic extent of the study area has a stronger influence on the outcome of biotic homogenization than the spatial resolution, i.e. when comparing island versus archipelago species pools. Our results also indicate that the decrease in compositional similarity with geographic distance between compared biotas, termed distance decay, strongly drives homogenization, i.e. biotic homogenization is very likely a global phenomenon, but not necessarily a local one.

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