

Spatial scale and evolutionary history determine the degree of taxonomic homogenization across island bird assemblages

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ABSTRACT

It is widely documented that human activities have elevated the extirpation of natural populations as well as the successful introduction to new areas of non-native species. These dual processes of introduction and extirpation can change the similarity of communities, but the direction and magnitude these changes take are likely to depend on the manner in which introductions and extirpations occur, the spatial scale at which the changes are measured, and the initial similarity of the communities before the human-induced drivers occurred. Here, we explore patterns of extirpation and introduction and their influence on the similarity of global oceanic island bird assemblages from four different Oceans (Atlantic, Caribbean, Indian, Pacific). We show that different historical patterns of introduction and extirpation have produced varying trends in compositional similarity both between islands within archipelagos and between islands across different archipelagos within the same ocean. Patterns of bird assemblage convergence (i.e. taxonomic homogenization) or divergence (i.e. taxonomic differentiation) among islands depended on the scale of examination, the evolutionary associations among species of the region, and the cultural history of human colonization. These factors are all likely to be leading to a series of multiple interacting processes that are shaping the complex compositional changes observed among global island bird faunas over time.

Keywords

Beta-diversity, biodiversity, community similarity, homogenization, introduction and extirpation, oceanic birds, species turnover.

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INTRODUCTION

It is well known that human colonization is typically accompanied by changes in the number of species through the dual processes of human-mediated extirpation of native species and the introduction of non-native species (Sax & Gaines, 2003). Less widely appreciated is that extirpation and introduction may change not only the species richness of a biota, but also its composition relative to other biotas. In general, the widespread introduction of a limited number of cosmopolitan species across a range of biotically distinct locations, and the extirpation of unique native populations, may decrease the distinctiveness of the communities at those locations. This process has been termed biotic homogenization (McKinney & Lockwood, 1999), which we call taxonomic homogenization to distinguish it from genetic and functional homogenization (Olden & Rooney, 2006). The converse is also possible, as the establishment of different non-native species at different localities, combined with

the extirpation of local populations of ubiquitous species, can increase the distinctiveness of communities at these locations, termed taxonomic differentiation. The magnitude and direction in which the similarity of different communities change following extirpation and introduction events depend on the frequency of these events, on the identity of the species being lost and gained in the communities, the initial species richness of communities, and on the historical or initial similarity among the communities (Olden & Poff, 2003). It is essential to recognize that by tracking the composition of an assemblage, through the changing identity of its residents, the resulting change in similarity is not merely correlated with species turnover. This has been shown to be particularly true for examples of insular systems where the species membership by way of extirpation and introduction are well defined (Olden & Poff, 2003; Cassey *et al.*, 2006).

Although interest in the extent to which compositional similarity is being altered by human-mediated extirpation and introduction is growing, taxonomic homogenization/differentiation

has still been quantified in only a few cases (e.g. La Sorte & Boecklen, 2005a,b; Lockwood, 2006; Marchetti *et al.*, 2006) (reviewed in Olden, 2006). Moreover, knowledge of how similarity increases or decreases, and by what process(es) is still limited (cf. La Sorte & McKinney, 2006). Building on the study of McKinney & Lockwood (1999), Olden & Poff (2003) proposed a conceptual model detailing how the number and manner in which species introductions and extirpations occur may lead to different levels of homogenization or differentiation. They presented 14 different scenarios for the effects of introduction and extirpation on the similarity of simple model assemblages, which differed in whether the same or different (or no) species invade or go extinct in different assemblages. For example, in the absence of any extirpation, the introduction of the same non-native species at two separate localities will lead to increases in the similarity of the communities holding them. Conversely, the introduction of a different non-native species at each locality will decrease similarity. However, the extent of the change in similarity is inversely proportional to the initial similarity of the communities in each case (Olden & Poff, 2004): the more similar the communities initially, the less the homogenizing effect of common invaders, and the greater the differentiating effect of unique invaders. This model provides a preliminary understanding of taxonomic homogenization for different taxonomic groups (Olden *et al.*, 2006).

Olden & Poff (2004) used their mechanistic model to examine the drivers of homogenization/differentiation in freshwater fish assemblages at three nested spatial scales in the continental USA. The relationship between initial similarity and change in similarity between two communities differs between different introduction and extirpation scenarios, allowing the likely mechanism driving change in similarity to be assessed. The authors showed that the fish faunas of the 48 coterminous states of the USA, which had generally increased in similarity following European colonization (Rahel, 2000), had most likely done so through the combination of widespread, shared introductions, and the differential extirpation of native species that were initially shared by states. For fish faunas of different zoogeographical provinces within the state of California, consistent increases in similarity (Marchetti *et al.*, 2001) most closely matched a scenario of shared introduction across provinces but no province-wide extirpation. The fish faunas of different watersheds within four of these Californian provinces had mainly differentiated, except where initial similarity was low (Marchetti *et al.*, 2001, 2006). This pattern most closely matches a model of the establishment of different non-native species in different watersheds, and either no extirpation, or the differential extirpation of native species that the watersheds did not initially share (Olden & Poff, 2004).

The scale dependency of the homogenization process suggests that changes in compositional similarity may be influenced by characteristics of the taxon concerned. Lockwood (2006) showed a pattern of 'hub and spoke' dispersal for bird species introduced to the Hawaiian Islands, whereby many species released on the main island of Oahu subsequently reached other islands in the archipelago under their own power. Together with a major extinction event among the native bird species, this has resulted in substantial homogenization of the avifaunas across islands in

the Hawaiian chain. Thus, homogenization patterns for vagile taxa like birds may differ from those for less dispersive groups such as freshwater fish. However, in the absence of more investigations like those of Olden & Poff (2004), no general statements can be drawn about the patterns for change in compositional similarity, especially when considering the effects of spatial scale on similarity change.

Here, we address this shortcoming by exploring patterns in the change in similarity of assemblages of birds on 152 oceanic islands from the Atlantic, Pacific, Indian and Caribbean Oceans. Oceanic islands have experienced very high rates of species extirpations and introduction. Johnson & Stattersfield (1990) estimate that 90% of bird extinctions that occurred during historical times have occurred on islands even though less than a fifth of the world's bird fauna are restricted to islands. On the other side of the diversity ledger, 70% of avian introduction events (i.e. occasions when individuals of a non-native bird species were released) were to islands even though islands represent less than 3% of the Earth's ice-free surface (Blackburn & Duncan, 2001). Taken together, these statistics suggest that oceanic islands are extremely valuable repositories of the Earth's biodiversity while at the same time these are the places that have experienced the most profound changes in species composition during historical times. Using data compiled by Blackburn *et al.* (2004b), we explicitly examine the historical period of human colonization, and assess how the accompanying human-mediated extirpations of native species and introductions of non-native species influence the similarity of the bird assemblages of oceanic islands.

METHODS

Species assemblages

The data set follows Blackburn *et al.* (2004b) and is summarized in Appendices S1 and S2 in Supplementary Material. We assembled species lists for 152 oceanic islands (i.e. those without known land bridge connections to continents in the past) using published literature and recent field guides. We also used these information sources to derive a list of avian species that became extirpated from each island since European colonization, and a list of non-native species that have successfully established self-sustaining populations on these islands. Our data set includes a total of 1491 species representing 82 families. We included all species that regularly breed on the islands, however, we did not include species that only appear as migrants or overwinter on the islands. The distribution of introductions and extirpations across families closely matches previous research showing taxonomic selectivity in these processes at the global level (e.g. Lockwood *et al.*, 2000). Some families have many population extirpations and no introduced populations (e.g. rails), some families have many introduced populations and no extirpations (e.g. starlings and mynahs), and some families have several of both types of populations (e.g. parrots; see Appendix S1 in Supplementary Material). Note that the list of island extirpations does not necessarily imply that these species have become globally extinct (i.e. our list of islands does not include all known islands), and if one non-native bird established on more than one island it was

counted as ‘present’ on each of these. Note also that we had consistent information across all islands only on extirpations back to European colonization and thus we could not evaluate the effects of prehistorical extirpations on changes in similarity. In this way, we constructed species lists for each island and derived from these lists historical species richness, number of historical extirpations, and number of non-native species established.

The 152 islands represent 24 archipelagos that are located within one of four ocean basins: Caribbean, Atlantic, Indian, and Pacific. For many of the islands within these archipelagos, published information on historical extirpations, or non-native bird introductions, was not available. Thus the set of islands we include here does not necessarily represent all islands in each archipelago, and indeed the set of archipelagos does not represent all archipelagos in an ocean. The mean number of islands within an archipelago in our data set is greater than seven and ranges from two to 15 (see Appendix S2 in Supplementary Material).

Statistical analyses

We used the Sørensen index as our measure of across-assemblage similarity. The index (S_{jk}) represents the compositional similarity between two sampling units and ranges from 0, in the case where no species are in common between localities j and k , to 100, in the case where two localities are identical in composition (Legendre & Legendre, 1998). The Sørensen index is simply the complement of the Bray–Curtis dissimilarity index when the data are presence/absence.

Using the historical species lists for each island, we calculated the initial average compositional similarity (CS_i) among islands at two spatial scales (Fig. 1). The first scale measures how similar each island is, on average, to all other islands within its archipelago, and the second measures the average similarity of each island to all other islands outside the archipelago but within the same ocean basin. The end result is two measures of average assemblage similarity, across nested spatial scales, which can be directly compared. We then recalculated these two similarity measures for the current avian assemblages on these islands (CS_c), which may have changed from the initial assemblages through either, both, or neither of the processes of native extirpation and non-

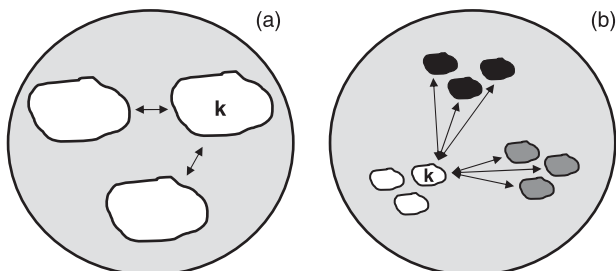


Figure 1 Conceptual diagram of the two scales at which we calculated similarity values for a single island within an ocean; (a) between island ‘k’ and all other islands within its archipelago, and (b) between island ‘k’ and all other islands within different archipelagos.

native introduction following human colonization of the islands. We use ΔCS to examine how similarity has changed at the two different scales, and to compare the direction of change in the different components within these scales. If ΔCS is positive, the locale has (on average) become more similar to the other locales after introduction and extirpation, i.e. taxonomic homogenization. If the ΔCS is negative, the locale has (on average) become less similar to the other locales, i.e. taxonomic differentiation.

We followed Olden & Poff (2004) in testing the relationship between initial similarity (CS_i) and change in similarity (ΔCS) to assess the relative influence of extirpations and introductions on the change in bird assemblage similarity on islands around the world, at the two spatial scales. This assessment enables us to explore scale dependency in the patterns of homogenization/differentiation for a second taxon, and one with very different evolutionary and life-history characteristics to freshwater fish. In a subsequent paper, we will consider how these different components of change in assemblage similarity relate to various aspects of the biogeography and colonization history of the islands.

Comparisons across spatial scales

We initially plotted the frequency distribution of CS_i and ΔCS scores by ocean to examine differences in the distribution of values between ocean basins. This allows us to determine if there is a difference in CS_i and ΔCS scores between the two spatial extents of investigation and test whether the ΔCS scores are significantly different from zero.

To understand better how ΔCS values are related across spatial scales, we created bivariate scattergrams where ΔCS of islands within archipelagos was plotted against ΔCS of islands between archipelagos. Despite using the same focal population, the ΔCS scores for the two scales are considered independent since all of the average pairwise Sørensen similarity scores were computed using completely separate sets of islands (i.e. those within an island’s archipelago vs. those outside of an island’s archipelago). A positive relationship observed in these plots indicates that an increase in ΔCS at one scale equates to increases at the other scale. In contrast, a negative relationship indicates that ΔCS at one scale corresponds with the opposite pattern in ΔCS at the other scale (i.e. islands have opposing similarity responses to introductions and extirpations across scales). The scatter of points within these same bivariate plots also indicates the direction of ΔCS (homogenizing or differentiating) and how this compares across spatial scales. If most points in the scatter plots have positive ΔCS values then the islands are homogenizing at both spatial scales. If most points have negative ΔCS values, then the islands are differentiating at both spatial scales. Finally, a mix of ΔCS values indicates that the islands are homogenizing at one scale and differentiating at another, and the distribution of points tells us at what scale each process is occurring.

We followed Olden & Poff (2004) and related ΔCS to CS_i for islands within archipelagos and for archipelagos within oceans. We evaluated the significance of these relationships using simple linear regression. The results of Rahel (2000), Taylor (2004) and Marchetti *et al.* (2001) suggest that our relationships should

Table 1 Average numbers of avian species extirpations and introductions per island [\pm SE] calculated across all islands for a given ocean. Average number of historical species extirpations does not correspond to the number of global extinction events within each island because the loss of a species from one (or more) island(s) does not imply global extinction. Similarly, the average number of non-native species introductions includes some species established on multiple islands within the same ocean. Also included here is the average historical species richness (i.e. excluding extirpations and introductions) per island, the mean change in richness per island, and the number of islands within each ocean used to calculate these averages. The average difference across islands in these traits was tested among oceans with a generalized linear model in SAS version 8.0.

Ocean (no. of islands)	Historical species richness	Historical extirpations	Non-native species introductions	Change in richness
Atlantic ($n = 45$)	22.7 [1.9]	1.1 [0.3]	2.2 [0.4]	+1.1 [0.4]
Caribbean ($n = 21$)	51.5 [7.3]	1.4 [0.4]	4.0 [1.4]	+2.7 [1.3]
Indian ($n = 11$)	31.5 [2.1]	5.2 [2.3]	7.7 [2.3]	+2.5 [1.8]
Pacific ($n = 75$)	18.1 [1.9]	2.0 [0.4]	4.8 [1.1]	+2.8 [0.8]
<i>F</i> -test ($F_{4,148}$)	18.07***	3.97**	2.12†	0.87

*** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$, † $P < 0.1$.

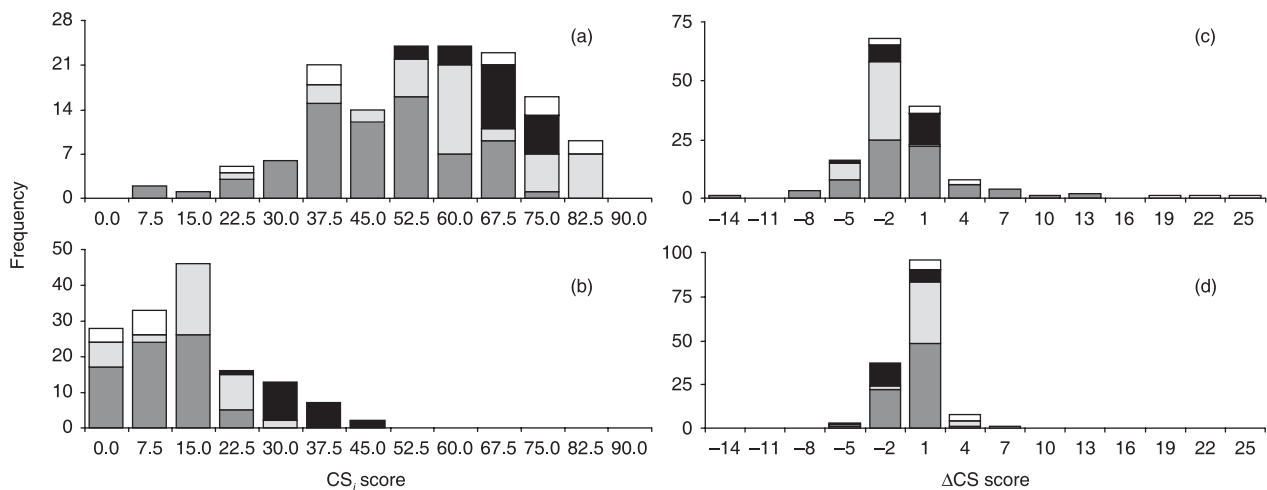


Figure 2 Frequency histograms of the initial assemblage similarity values (CS_i) and changes in similarity (ΔCS) between islands within an archipelago (a and c, respectively) and for islands between different archipelagos (b and d, respectively) within the Pacific (dark grey), Atlantic (light grey), Caribbean (black), and Indian (hollow) oceans.

most likely be negative, indicating that low values of CS_i will translate into high ΔCS , and vice versa.

RESULTS

The average number of native species per island varied according to ocean basin, such that islands in the Caribbean Ocean held, on average, twice as many species as were found in the Pacific or Atlantic, and islands in the Indian Ocean contained numbers in between these extremes (Table 1). There were also differences in the average number of historical extirpations and introductions across the four ocean basins. On average, the islands in the Indian Ocean lost significantly greater numbers of bird species to extirpation in historical times (nearly five species), whereas islands in the other ocean basins lost one to two species. Similarly, on average, islands in the Indian Ocean are home to more non-native avian invaders (*c.* eight species) than islands in the

other oceans, which received between two to five non-native species. Despite these differences in average losses and gains in species across islands, the average change in species richness was not significantly different between oceans (Table 1).

Initial assemblage similarity (CS_i) varies between spatial scales such that islands within the same archipelago are much more similar on average than are islands between archipelagos (Fig. 2). Also, CS_i only takes values less than 0.50 (50% similarity) when it is calculated between islands within different archipelagos (Fig. 2b), whereas CS_i spans nearly the full range of potential values (0–100) for comparisons of islands within archipelagos (Fig. 2a). CS_i scores tended to be larger for islands within archipelagos than between archipelagos holds regardless of the ocean basin in which the islands are found [average $CS_{iw} - CS_{ib}$ (\pm SE); Atlantic = 47.0 (1.9), Caribbean = 33.6 (1.2), Indian = 54.1 (6.4), Pacific = 36.3 (1.8)]. However, we found a difference in CS_i scores between ocean basins within each spatial scale. Initial

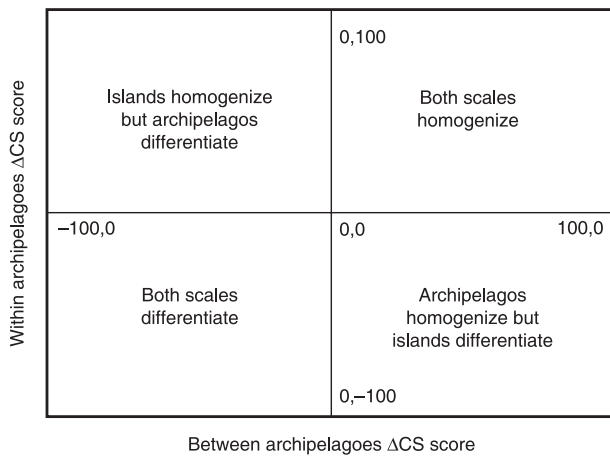


Figure 3 Conceptual diagram of the relationship between changes in similarity (Δ CS) among islands within an archipelago and Δ CS of islands between different archipelagos.

assemblage similarity is higher at both spatial scales for islands in the Caribbean Ocean and Atlantic Ocean, and lower at both spatial scales for islands within the Indian Ocean and Pacific Ocean (within archipelagos Fig. 2a, $F_{3,141} = 18.01, P < 0.001$; between archipelagos Fig. 2b, $F_{3,141} = 82.90, P < 0.001$).

Comparisons of Δ CS values at each spatial scale showed that approximately half (50% Fig. 2c and 52% Fig. 2d) of the island values are individually significantly different from zero (t -test, $\alpha = 0.05$), where a zero value indicates no change in assemblage similarity through time. Similar to the results for CS_i , Δ CS values differ between spatial scales. When Δ CS is computed for islands within archipelagos (Fig. 2c), we found that most islands within the Indian Ocean have become slightly more similar to one another through time (mean = 6.8, SE = 2.9), with a maximum positive Δ CS of 24% (Rodrigues Is.), although there are still instances of differentiation. In contrast, Δ CS values for islands within archipelagos in the Atlantic have all differentiated, whereas in the other oceans, they range from clearly negative (differentiation) to strongly positive (homogenization). The maximum negative value Δ CS is -13% for the island of Guam.

The pattern in Δ CS between islands within different archipelagos also varies across ocean basins (Fig. 2d). Islands in the Atlantic and Indian Oceans have tended to homogenize when compared to other islands within the ocean, whereas islands within the Caribbean and Pacific Oceans have tended to differentiate ($F_{3,141} = 20.10, P < 0.001$).

Comparisons of Δ CS across scales (Fig. 3) showed that for islands in the Indian Ocean ($r = 0.64, n = 11, P = 0.033$) changes in Δ CS at one scale are positively related to changes in Δ CS at the other (Fig. 3b). In contrast, for islands in the Atlantic ($r = 0.12, n = 41, P = 0.439$) and Caribbean ($r < 0.01, n = 20, P = 0.985$; not including the highly influential point for Puerto Rico — otherwise $r = 0.60, n = 21, P = 0.004$) oceans, changes in Δ CS at one spatial scale are unrelated to changes at the other spatial scale (Fig. 3a,c). There is a significant negative relationship of Δ CS for islands in the Pacific Ocean ($r = -0.30, n = 72, P = 0.011$) (Fig. 3d).

If we view the panels in Fig. 3 in the context of whether islands are homogenizing or differentiating across scales (as depicted in Fig. 4), it is clear that islands within each ocean are behaving in a unique manner. Islands in the Mascarene and Comoros groups in the Indian Ocean are homogenizing regardless of spatial scale at which changes are measured (i.e. all data points are located in the upper right quadrant of Fig. 3b), whereas the similarity of islands in the Antarctic group has not changed (i.e. all data points are located at the origin). In the Caribbean (with the obvious exception of Puerto Rico), some islands have differentiated and others have homogenized with a slight tendency to becoming more differentiated between archipelagos (Fig. 3c). A more even scatter of Δ CS values can also be seen among the islands within the Pacific Ocean (Fig. 3d). When Δ CS is calculated within the Atlantic, islands within their archipelago have all clearly differentiated. In contrast, when these same islands are compared to others outside their archipelago they have become, on average, more homogenous (Fig. 3a).

Most islands show minimal concordance in patterns of change in compositional similarity across scales (Fig. 5a,b). However, Indian Ocean islands that are compared to others within their own archipelago show a clear negative relationship between Δ CS and CS_i (slope = -0.33, $t = -2.88, P = 0.018$). Caribbean (slope = -0.13, $t = -2.77, P = 0.012$) and Pacific (slope = -0.04, $t = -2.70, P = 0.008$) islands compared to others outside of their archipelago show significant negative relationships, whereas Indian Ocean islands, in contrast to all other comparisons, show a positive association between Δ CS and CS_i (slope = 0.26, $t = 2.52, P = 0.033$).

DISCUSSION

Oceanic islands tend to be hotspots of avian extirpation and introduction (Olson & James, 1982; Steadman, 1995; Case, 1996; Blackburn & Duncan, 2001; Curnutt & Pimm, 2001; Cassey, 2003; Blackburn & Gaston, 2005), and for this reason we may suspect that these assemblages have a high tendency to exhibit taxonomic homogenization through time (e.g. Lockwood, 2006). Recent evidence suggests that patterns of homogenization or differentiation may vary according to the spatial scale of inquiry (Olden & Poff, 2004; Marchetti *et al.*, 2006) and the manner in which species are gained and lost across the landscape (Olden & Poff, 2003; Cassey *et al.*, 2006). For global oceanic island bird assemblages, our study shows that the spatial extent of investigation and evolutionary history influences patterns of taxonomic homogenization and differentiation within and across what appear to be equivalent spatial units (i.e. ocean basins). Our finding that patterns of taxonomic homogenization differ between and among archipelagos suggests that this process is both complex and particular to the spatial scale of investigation.

Despite large differences in average losses and gains in species across islands, the ratio of introductions to extirpations (2 : 1) and the average change in species richness (+ 1–3 species) were remarkably similar across all islands regardless of their ocean membership (Table 1). Moving from averages to consideration of individual islands, we found that many islands have become much more similar to other islands within their own archipelago

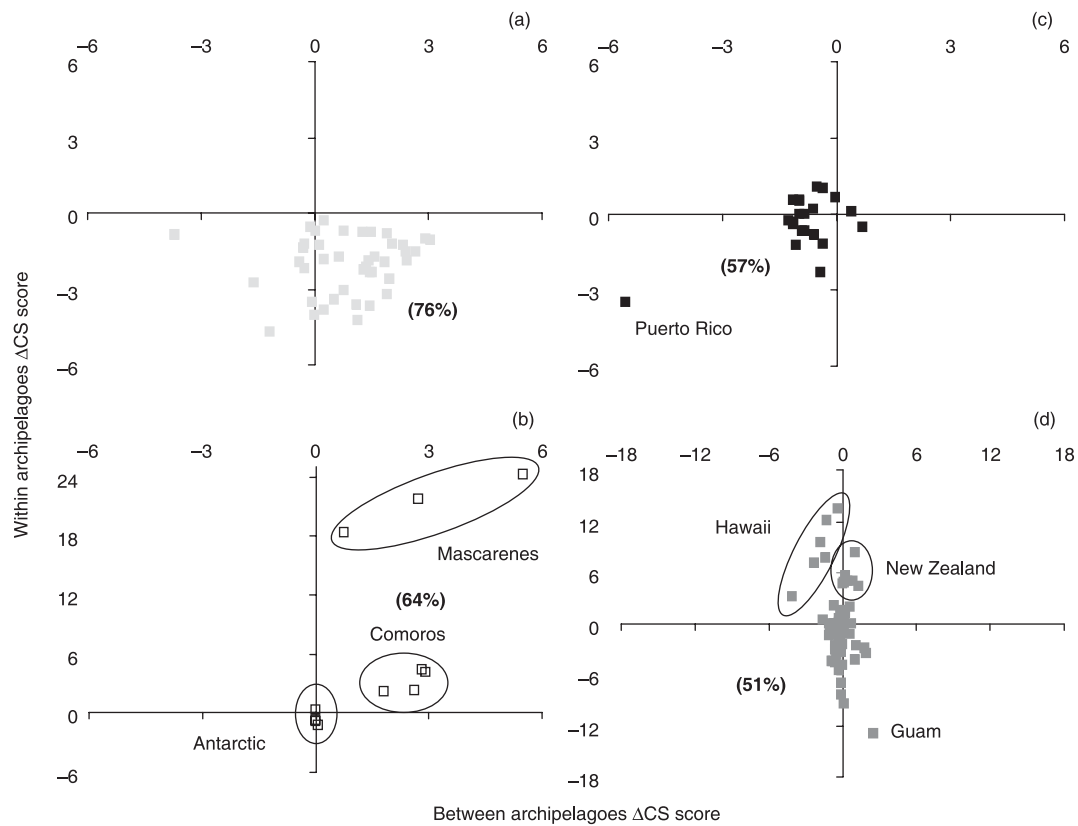


Figure 4 Bivariate scatterplots of the relationship between changes in similarity (Δ CS) among islands within an archipelago and Δ CS of islands between different archipelagos within the Atlantic (light grey), Caribbean (black), Indian (hollow), and Pacific (dark grey) oceans. Percentages relate to the quadrat (see Fig. 4) with the greatest number of member islands. Islands and archipelagos that are explicitly discussed in the main text are indicated for reference.

than between different archipelagos (Figs 2 & 3). However, these changes are not consistent across oceanic basins or spatial scales (Fig. 3). Interestingly, the pattern for Δ CS in oceanic island birds is not consistently associated with underlying differences in initial similarity (Fig. 5), unlike for freshwater fishes (Olden & Poff, 2004).

Avian assemblages of oceanic islands tend to be more similar to other islands within their archipelago (small spatial extent) than to islands outside their archipelago (larger spatial extent). The reasons for this pattern are fairly obvious if we consider the evolutionary history of oceanic birds. Many archipelagos harbour unique assemblages of bird species because they evolved *in situ*, and these species are more likely to be shared between islands within this archipelago but not across archipelagos, as islands and island groups emerged from the sea at very different rates through geological time. Similarly, non-endemic avian species tend to occupy all islands in the group, rather than just one, because of their inherent vagility. This vagility, however, only goes so far. Most native avian species are not likely to occupy many archipelagos within a single ocean, as these tend to be separated by distances that many species in even a vagile group like birds cannot cross. It is noteworthy that we still detect a clear signature of this evolutionary history in our analyses even though we know that there were many avian extinction events due to first human contact that we were not able to incorporate (i.e. our data set reflects a

prehistorical extinction filter). This (remaining) evolutionary history is then overlain by human cultural history that drives the numbers of invasions and extirpations per island, what these species are, and thus the resulting changes in overall assemblage similarity.

For example, islands in the Indian Ocean have become much more similar to each other whether or not this is assessed within or between archipelagos (Fig. 4). Although homogenization seems to be the rule for these islands, the relationship of this change to initial similarity is scale dependent (Fig. 3). At smaller spatial scales (islands within archipelagos), we see the expected pattern of low initial similarity leading to greater homogenization (Fig. 5a). However, this relationship reverses at the larger spatial scale of islands between archipelagos (Fig. 5b). There is no precedent in the model of Olden & Poff (2003) for a pattern of increasing homogenization as initial similarity increases. It remains to be shown whether this result is a spurious consequence of the small number of islands compared in the Indian Ocean ($n = 11$), or genuine evidence that when multiple introduction and extirpation processes occur, they can encompass multiple scenarios (as described by Olden & Poff, 2004). Interestingly, recent evidence suggests that the latter may similarly be the case for other taxonomic groups (Olden *et al.*, 2006).

Moreover, it is likely that the spatial distribution of the Indian Ocean archipelagos in our data set influences both the suite of

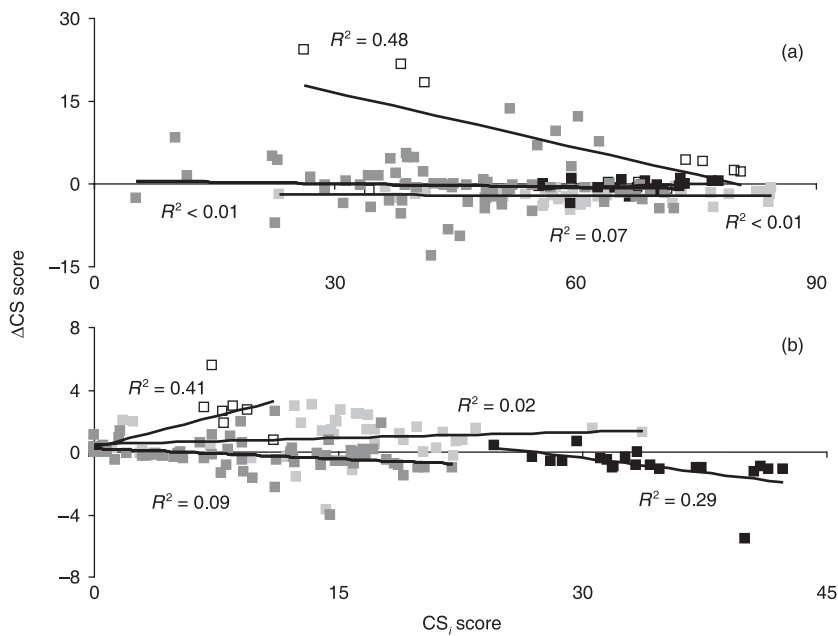


Figure 5 Bivariate scatterplots of the relationship between changes in similarity (ΔCS) and the initial similarity (CS_i) between (a) islands within an archipelago, and (b) ΔCS and CS_i between islands among different archipelagos, within the Indian (hollow), Caribbean (black), Atlantic (light grey), and Pacific (dark grey) oceans.

non-native species introduced and the homogenization patterns observed. Low initial similarity can lead to greater homogenization if the same suite of invaders is introduced to different islands within an archipelago. Similarly, if archipelagos that are in close proximity have higher initial similarities and also tend to get similar sets of non-native species then overall we would expect the pattern of homogenization to increase with increasing initial similarity. While not a direct test of this, Blackburn & Duncan (2001) and Cassey (2003) showed that a relatively high proportion of non-native bird species tend to derive from the biogeographical region in which the recipient location is sited. This proportion was particularly high for the Malagasy region, where many of the islands in the Indian Ocean basin are found. This suggests that the biogeographical factors that determine the similarity of native faunas, such as isolation or distance to a source pool, may also influence the similarity of non-native faunas, at least in the Indian Ocean.

Islands in the Atlantic Ocean tend to differentiate in relation to other islands within their own archipelago, but homogenize when compared to islands outside their archipelago. None of these islands have experienced relatively high extirpation or introduction histories, and thus changes in across-island similarity are correspondingly minor. The changes in similarity suggest that a pattern of the introduction of common non-natives and/or extirpation of endemic natives is driving an increase in similarity between archipelagos, while the introduction of different sets of non-natives (and perhaps the extirpation of widespread native species) is increasing differentiation within archipelagos. While these changes would be expected to produce detectable negative relationships at each scale between change in similarity and initial similarity, this is clearly not necessarily so (Fig. 5).

The islands in the Caribbean and Pacific oceans show no clear pattern either towards being predominantly homogenized or differentiated at either spatial scale. Similarly, highly variable

patterns of homogenization and differentiation have been observed for freshwater fishes (e.g. Rahel, 2000; Taylor, 2004; Marchetti *et al.*, 2006), plants (e.g. McKinney, 2004; Rooney *et al.*, 2004), and reptiles and amphibians (e.g. Smith, 2006). Instead, some islands seem to have been drastically altered by introductions and extirpations and others left largely unchanged (Fig. 3). For example, in the Pacific Ocean, the Hawaiian Islands have had a plethora of avian introductions and extirpations that have increased between-island similarity (see also Lockwood, 2006), while at the same time these changes have made the islands much more distinct from the other islands in the Pacific. The same is true for the islands of New Zealand, although to a lesser extent. On Guam the large number of very well-known extirpations (Savidge, 1987) has strongly differentiated the island from others in the Marianas archipelago. In the Caribbean ocean, only Puerto Rico has seen equivalent numbers of introductions as New Zealand and Hawaii (although only half or fewer extirpations). Because Puerto Rico has had similar numbers of extirpations as the other islands within, and outside, its own archipelago while hosting such large numbers of invaders has greatly differentiated in composition at both spatial scales. Most other islands in the Pacific and Caribbean oceans have had many fewer introductions and extirpations, and the identity of these species appears somewhat idiosyncratic such that there is no clear overall pattern in either homogenization or differentiation. Whether this lack of pattern reflects truth, or is perhaps a function of an extinction filter applied to these islands by their earlier colonization by humans (Biber, 2002; Blackburn *et al.*, 2004a) relative to those in the Indian and Atlantic Oceans, remains to be seen.

The search for general rules and laws in ecology is greatly hampered by a high degree of context-specific contingency. Progress towards such principles will be best served by testing potentially important discoveries across different ecological systems (Osenberg *et al.*, 1999; Gurevitch *et al.*, 2001; Cassey & Blackburn,

2006) and different temporal and spatial scales, and hence identifying which elements vary, and which do not. Our analyses of changes in across-assemblage diversity reveal that oceanic island birds show both similarities and differences in patterns of homogenization and differentiation when compared with previous studies of North American freshwater fish assemblages (Rahel, 2000; Marchetti *et al.*, 2001; Olden & Poff, 2004). In part, these differences may reflect how increases in spatial scale are measured between the fish and bird studies. In the fish studies, increases in spatial extent are also accompanied by increases in spatial grain. Thus, Olden & Poff (2004) examined homogenization across watersheds (grain) within provinces (extent), across provinces (grain) within California (extent), and across States (grain) within the USA (extent). In our study, the grain size remains constant (the island) as extent (either the archipelago or the ocean) changes.

Nevertheless, in contrast to the fish assemblages, patterns of avian homogenization in oceanic islands do not universally conform to mechanistic models for the changes proposed by Olden & Poff (2004). This suggests that single introduction–extirpation processes are playing a dominant role in shaping assemblage change in fish faunas, whereas multiple, interacting processes are operating on oceanic islands. This may result in homogenization/differentiation patterns that are more complex, and more difficult to predict. These differences, and the differences we have observed in the changes in island avifaunas across ocean basins, suggest that a general theory of homogenization will need to incorporate additional key elements. Our results, as discussed above, highlight what we think will be three likely such elements.

First, taxa will differ in important aspects of their life histories that will influence initial similarity and how it changes. For example, freshwater fish have restricted dispersal ability relative to birds, which may cause different patterns of initial variation in similarity with spatial grain, and so lead to different patterns of homogenization following human colonization. Second, locations differ in their biogeographical histories, and in the influence of different biogeographical variables on these histories, that will again influence initial similarity and how it changes. Vagility may again be an important driver of these histories, albeit that it is likely to interact with isolation and geology in driving spatial patterns of colonization and extirpation in the different taxa. Third, assemblages will differ in their cultural histories. The timing of initial (or European) human colonization, the history of isolation of the faunas, the geographical distributions of native species, and the manner in which human colonists have modified the environment through habitat destruction, hunting, and the introduction of non-native predators and competitors, will all interact to influence how assemblage similarity changes. Clearly then, there is still much to explore in terms of what ecological mechanisms are driving the changes in diversity, especially since these changes are so variable.

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SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article:

Appendix S1 Taxonomic composition of the 1491 island species used in our analyses.

Appendix S2 List of islands used in analyses and the archipelagos and oceans to which they belong.

This material is available as part of the online article from: <http://www.blackwell-synergy.com/doi/abs/10.1111/j.1472-4642.2007.00366.x>

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