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RESEARCH PAPER

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# Extreme homogenization: The past, present and future of mammal assemblages on islands

Emily K. Longman[1] | Kyle Rosenblad[2] | Dov F. Sax[2]

[1]Department of Evolution and Ecology, University of California, Davis, Davis, California

[2]Department of Ecology and Evolutionary Biology, Brown University, Providence, Rhode Island

**Correspondence**
Department of Evolution & Ecology, University of California Davis, 2320 Storer Hall, One Shields Avenue, Davis, CA, 95616.
Email: eklongman@ucdavis.edu

**Funding information**
Brown University

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## Abstract

**Aim:** We documented how the similarity of mammal assemblages on continental and oceanic islands has changed since initial human colonization, since European arrival and overall. We investigated how levels of similarity might change in the future.

**Location:** Continental and oceanic islands worldwide.

**Time period:** Human settlement of islands to the present, as well as projections for the future.

**Major taxa studied:** Mammals.

**Methods:** We used mammal occurrence data on islands to calculate the change in similarity using a pairwise approach based on Jaccard's index and a multisite approach based on Jaccard's and Sørensen's measures. We divided the mammal assemblages into two time periods, before and after island colonization or trade began with Europeans. We unpacked the mechanisms driving changes in similarity, exploring how initial similarity interacts with seven types of species turnover events to determine overall change. Finally, we calculated how future similarity levels will change if past trends in introductions and extinctions continue.

**Results:** Mammals, on both continental and oceanic islands, show one of the most pronounced cases of homogenization ever observed, and on oceanic islands mammals show the largest increase in homogenization ever observed for a terrestrial group. Most of the homogenization observed to date has been driven by recent historical changes, not by changes that occurred before European arrival. If current patterns of species introductions and extinctions continue, then oceanic islands will experience little additional homogenization, whereas continental islands will homogenize greatly beyond current levels.

**Main conclusions:** Mammal assemblages on oceanic islands show nearly an order of magnitude greater change in similarity than plant and bird assemblages. Projections of future similarity indicate that continental and oceanic islands are on different trajectories of change. These trajectories could be altered by management actions, but in some cases those actions that would be impactful run counter to current conservation norms.

KEYWORDS
biodiversity, extinction, fossil, introduced species, invasion, Jaccard's index, similarity

## 1 | INTRODUCTION

The erosion of biotic distinctiveness of communities and regions, generally referred to as 'biotic homogenization', is a pressing concern for conservation biologists (McKinney & Lockwood, 1999; Olden, Lockwood, & Parr, 2011; Rooney, Olden, Leach, & Rogers, 2007). One source of concern is that stable numbers of species at regional scales might correspond to global biodiversity losses, for instance, if individual regions experience the loss of endemic species and the gain of cosmopolitan ones (McGill, Dornelas, Gotelli, & Magurran, 2015; McKinney & Lockwood, 1999; Sax & Gaines, 2003). There are also concerns that homogenization could reduce the long-term evolutionary potential of species assemblages or reduce the services that impacted ecosystems can provide (Clavel, Julliard, & Devictor, 2011; Olden, Poff, Douglas, Douglas, & Fausch, 2004). In spite of these concerns, however, most studies of biotic homogenization conducted to date have found relatively minor changes in similarity. A recent review by Baiser, Olden, Record, Lockwood, and McKinney (2012), which examined homogenization studies of a wide variety of taxonomic groups across a large range of spatial scales, found that the mean shift along a scale of change in similarity, which ranges from zero (no species in common) to one (all species in common), was just .03. That mean shift, however, belies the substantial variation observed among compared assemblages. Some assemblages have shown relatively dramatic increases in similarity, with the largest changes found for freshwater fishes, which have experienced increases in similarity as high as .2 (Olden et al., 2011). Some other assemblages have become more different from each other than they were historically (Baiser et al., 2012; Olden et al., 2011), that is, they have experienced 'biotic differentiation' (Olden & Poff, 2003). However, the low values of homogenization on average that have been found to date indicate the complexity of the homogenization process, particularly as there is often a disconnect between levels of change in similarity and levels of native species loss. For example, while most oceanic islands have lost *c*. 50% of their native bird species (Sax, Gaines, & Brown, 2002), the mean change in similarity observed across islands is only .04 (Rosenblad & Sax, 2017). Understanding this discrepancy requires unpacking the dynamics driving changes in similarity, but it also requires an understanding of how similarity might shift in the future with continued species turnover events.

Homogenization of mammal assemblages has received little investigation to date, with one study focusing on ungulates (Spear & Chown, 2008) and another that used scenarios to evaluate how much homogenization might have occurred among regions within North America (Olden, Poff, & McKinney, 2006). Mammals on islands, both continental and oceanic, have the potential to show changes in similarity as great as those observed in studies of freshwater fishes. Just as freshwater fishes experience extreme barriers to dispersal across land, mammals experience extreme barriers to dispersal across open expanses of ocean (Simpson, 1940). These barriers help to create highly differentiated assemblages that are ripe for disruption once these barriers are removed by human agency, both through actions that contribute to species extinction and, in particular, through actions that lead to species introduction. One might expect, however, that changes in similarity might vary considerably between continental and oceanic islands. Continental islands often have relatively rich mammal assemblages, whereas oceanic islands typically have few native mammal species; often only a few species of bats (Whittaker & Fernández-Palacios, 2007). Furthermore, the scale of species introductions is often staggering. For example, New Zealand has only three native mammal species (all bats), but has > 40 additional mammal species that have become naturalized (King, 2005; Tennyson, 2010), which represents more than an order of magnitude increase in richness of mammal species. Consequently, mammals have the potential to show strong patterns of homogenization.

Studying homogenization in mammals, particularly on well-studied islands that vary in levels of species loss and gain, could provide several advantages for understanding changes in similarity more generally. First, the potential differences among continental and oceanic islands allow for a comparison of the impacts of different types of species turnover events. Rosenblad and Sax (2017) describe six types of introduction and extinction events that can occur among island pairs: introduction of a species new to both, new to one and absent from the other, or new to one but already present on the other, and extinctions from both, from one and remaining on the other, or from one but not present on the other. These different turnover events vary in their relative magnitude of impact on change in similarity; for instance, the homogenizing impact of one type of event can be > 20 times the strength of another event type, and the relative importance of individual events can vary such that a given set of events might drive a net increase in similarity for one island pair and a net decrease for another island pair, depending on the initial similarity level of the island pair (Rosenblad & Sax, 2017). Oceanic and continental islands appear likely to vary in their number of extinction events because oceanic islands have relatively few native mammal species that could go extinct. If this supposition is correct and event frequencies do vary categorically between island types, then comparisons could be made within categories and between them to understand how these event frequencies shape changes in similarity observed to date.

A second advantageous feature of island mammal assemblages is that, because the total impact on change in similarity of insular mammal faunas is expected to be large and because there are relatively good fossil records of mammals on islands, as well as good historical records, it should be possible to differentiate between changes driven by humans before historical records from those that occurred after historical records began to be compiled. Although not widely appreciated until the 1980s (e.g., Olson & James, 1982), the scale of human transformation of insular faunas by Polynesians, as well as other groups that reached islands before European arrival, has been large and profound with respect to both species introductions and extinctions (Faurby & Svenning, 2015; Sax et al., 2002; Steadman, 1995). Differentiating between 'prehistoric' and 'historical' changes could provide insights into the relative influence of these two periods on changes observed to date.

Third, a strong signal of change in similarity together with information on the changes driven by prehistoric and historical periods could help to provide a context for how these faunas might continue to change in the future. If prehistoric changes caused the largest shifts in similarity then we might expect future shifts to be moderate, whereas if recent changes have driven the largest shifts in similarity then we might expect future changes to be stronger. Rosenblad and Sax (2017) showed that comparable changes in similarity observed to date between groups (plants and birds) can mask the possibility that they are on different trajectories, such that if current trends continue, one group might show little additional homogenization, but another might change dramatically. Consequently, studying mammal faunas provides the opportunity to explore how similarity might change in the future and whether we might expect patterns on continental and oceanic islands to differ. Ultimately, understanding how mammal faunas have changed to date, what the mechanisms of those changes have been and how these assemblages might change in the future provides a strong context for managing the conservation of these communities.

In this study, we collate records of species introductions and extinctions of mammals on continental and oceanic islands worldwide, using both fossil and historical records. We use Jaccard's pairwise index of similarity to determine how similarity changed between initial human arrival and the historical period, how it changed during the historical period and how it changed overall between initial human arrival and the present. We examine the influence of different species turnover event frequencies on changes during these periods and among island types (continental, oceanic and both). We then use this context for a thought experiment to project how mammal faunas might continue to change in the future if observed introduction and extinction regimes persist. Finally, we consider the conservation and management implications of this work.

## 2 | MATERIALS AND METHODS

### 2.1 | Mammal assemblages

We examined islands and archipelagos with data on the occurrence of mammals. Specifically, we considered species using terrestrial and freshwater resources but excluded those dependent solely on marine resources. Following Sax et al. (2002), we treated archipelagos and lone islands as equivalent, examining each as a single unit (referred to as 'islands' henceforth). We also followed Sax et al. (2002) in classifying islands as continental or oceanic based not only on their underlying geology, but also with respect to their biotas, such that two islands, New Zealand and Chatham, were treated as oceanic islands; see Supporting Information Table S1 for additional details. In total, we compiled data on 50 islands: 20 continental, 27 oceanic, and three with both oceanic and continental features (Figure 1; Supporting Information Table S1). We selected these islands because we could assemble information on species' native and naturalized status, the period in which individual species were introduced and the period in which individual species became extinct. Our dataset includes occurrences for 504 species, with a total of 97 extinction and 432 introduction events (Supporting Information Appendix S1).

Species were classified for each island with respect to their native status, time of establishment and time of extirpation. Specifically, we considered two time periods. We defined the first period as 'prehistoric', spanning from first human settlement of a given island to the island's first contact with Europeans, and the second period as 'historical', spanning from European colonization (or initiation of trade for previously inhabited islands) to the present; the split made between time periods for each island is shown in Supporting Information Table S1. Extirpated species were classified as corresponding to the prehistoric or historical periods using references cited in the Appendix. Extirpations determined to have occurred before human occupation of an island were not included in this dataset. There were a relatively small number of species (Supporting Information Appendix S1) with poorly constrained dates of extinction, for which it is uncertain whether they went extinct before or after human colonization of an island; these species were excluded from the analyses presented in this manuscript, but an alternative set of homogenization analyses were performed with these species included, and the qualitative results observed were unchanged. Introduced species were also classified as having been introduced during the prehistoric or historical period using references cited in the Appendix. We only considered introduced species that are currently naturalized (i.e., those that have self-sustaining populations). This means that we excluded domesticated species, unless they had feral populations, and that we excluded species that might have been naturalized in the past but have not maintained a population to the present; this latter category includes species that were actively eradicated by human management. We also created a category for those few cases of species that have recently colonized islands without human assistance; they were included in the analyses for the changes in similarity, but were excluded from the event type analyses. Finally, the native status of mammals on some continental islands is uncertain; we deferred to expert judgement whenever possible, but in its absence we considered a species with unspecified status on a continental island as being native whenever it was native to the adjacent mainland and had been observed to breed on the island or was observed there on three or more occasions.

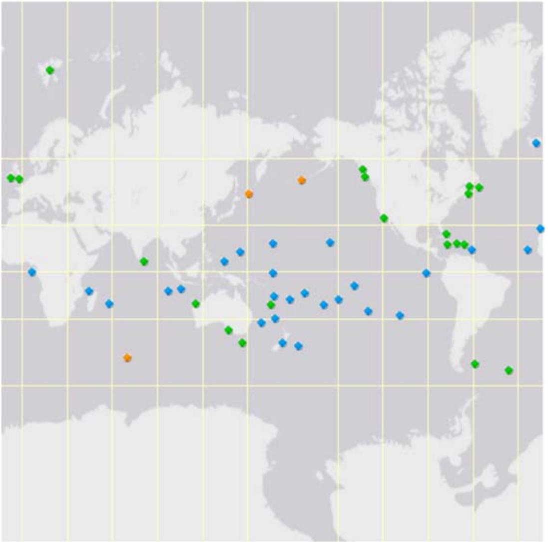


FIGURE 1 Map of the 50 islands used in the study (continental islands are represented in green, oceanic islands in blue, and islands with both continental and oceanic characteristics are represented in orange). The map projection is Web Mercator

The taxonomy of some species in the dataset is disputed. Whenever possible, we followed the taxonomic classification of the Integrated Taxonomic Information System (ITIS; http://www.itis.gov). However, extinct species known only by fossils are not treated by this resource, in which cases we deferred to the literature describing the extinct species (Appendix). Furthermore, we depended on the identification of species made in the literature describing species present on islands (Appendix).

## 2.2 | Changes in similarity

Changes in similarity of assemblages were made with a pairwise comparison method using Jaccard's index. Jaccard's index was selected because it can be calculated using occurrence data, for ease of comparison with previously published work on homogenization (as this is the most commonly reported measure of change in similarity; see Olden et al., 2011), and because it is readily amenable to producing forecasts of future change in similarity (Rosenblad & Sax, 2017). Pairwise comparisons were made across all possible pairs of islands, but also across only the pairs of oceanic islands and across only the pairs of continental islands. Three islands that have features of both oceanic and continental islands (Supporting Information Table S1) were included in the all-island pairwise comparisons, but excluded from the analyses of only oceanic or only continental islands. Islands that were uninhabited before contact with Europeans were removed from the prehistoric analyses. In total, 1,225 island pairs were analysed, with 351 solely oceanic pairs and 190 solely continental pairs. The change in similarity for a time period of interest was measured as the difference between the final similarity ($J_{\mathrm{final}}$) and the initial similarity ($J_{\mathrm{initial}}$). The statistical significance of the observed median changes in similarity was measured with the Wilcoxon signed rank test. Differences between island types and time periods were calculated using Mann–Whitney–Wilcoxon tests.

In addition to pairwise comparisons with Jaccard's index, we also measured changes observed to date with multisite measures. Such measures provide an alternative to traditional pairwise approaches and have been argued to provide a more appropriate measure of beta diversity (Baselga, 2010, 2013). Multisite measures suffer, however, from a lack of comparability across studies, as values calculated are sensitive to the number of biotas compared (Baselga, 2010), and it is debatable whether they have conceptual primacy over pairwise measures for studies of homogenization. Nevertheless, multisite measures have become a mainstay of recent work and are provided here as a point of comparison. Specifically, we measure Jaccard's and Sørensen's multisite measures as a whole, but also with respect to their 'turnover' and 'nestedness' components (Baselga, 2012). Calculations were made using the R package betapart (Baselga & Orme, 2012). We follow Baselga's (2010) example and control for the sensitivity of calculated values to differences in the number of samples (20 continental, 27 oceanic and 50 total islands) by calculating similarity values for oceanic and total islands using a resampling procedure. Specifically, we took 1,000 random samples of 20 inventories of oceanic islands and computed the average and then repeated this procedure for the all island comparisons; note that we followed this procedure for each of the time periods examined, adjusting the sampling to represent the number of inhabited islands during the prehistoric period. Additional R packages used were vegan (Oksanen et al., 2013) and sp (Pebesma & Bivand, 2005). All analyses were carried out using R software (Supporting Information Appendix S2; R Core Team, 2014).

## 2.3 | Predictors of changes in similarity

A variety of island characteristics were compiled and examined as possible correlates of observed changes in similarity. These characteristics included island surface area, elevation and isolation, as measured by the distance to the nearest mainland (Supporting Information Table S1). The distance between island pairs was also examined. Area, elevation and isolation data were obtained from the United Nations Environment Programme (UNEP) Island database (http://islands.unep.ch), and all other characteristics were compiled from the literature (Appendix). Analyses of area, elevation and isolation were evaluated by comparing the difference for a given island pair with its corresponding change in similarity. Mantel tests were used to determine the statistical significance of correlations, and the R package memgene was used to confirm that there was no spatial clustering of the changes in similarity (Galpern, Peres-Neto, Polfus, & Manseau, 2014; Peres-Neto & Galpern, 2014). In cases where spatial clustering in change in similarity occurred, a Mantel test was not performed, and scatter plots of these relationships were included instead.

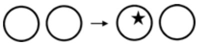
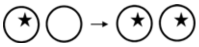
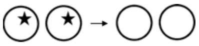
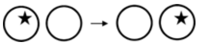
## 2.4 | Event types

We collated the number of seven types of species turnover events among island pairs, with respect to both island type and time period (Table 1). One of these species turnover event types (E1/I1), which refers to the extinction of a species from one island and the introduction of the same species to the other island in a pair, has no impact on similarity, because both before and after the event the species in question is still present on only one island in the pair. However, Rosenblad and Sax (2017) showed that the remaining six types of species turnover events have different impacts on the direction of change in similarity (increase or decrease) and on the relative magnitude of those impacts (e.g., with some event types, at some initial levels of similarity, having $>$ 20-fold difference in the resulting magnitude of change in similarity than some other event types). Three of these event types cause an increase in similarity (I12, I02 and E10) and three cause a decrease in similarity (E21, E20 and I01). The initial letter (I or E) differentiates between an introduction or extinction event, while the first number (0–2) represents the presence of the species on neither, one or both islands in the pair before the event and the second number represents the presence of the species after the event (Table 1).

## 2.5 | Projecting future changes in similarity

We projected future changes in similarity across all island pairs, for the oceanic only pairs and for the continental only pairs. To do this, we followed the method of Rosenblad and Sax (2017), which uses the turnover event frequencies observed to date to examine what similarity levels would be reached or approached asymptotically by each island pair if the previously observed frequency of turnover events continued into the future. These analyses of all, oceanic and continental pairs used the entire history of human-associated changes to date (i.e., changes observed cumulatively over the prehistoric and historical periods). However, we also examined what future changes in similarity would be across all island pairs based on the relative frequency of species turnover events from soley the prehistoric and soley the historical periods.

**TABLE 1** Description of the seven turnover event types, with a corresponding diagram

| Event type | Definition | Diagram |
|---|---|---|
| I01 | Introduction of a species to one island in the pair |  |
| I02 | Introduction of a species to both islands in the pair |  |
| I12 | Introduction of a species present on one island to the other island in the pair |  |
| E10 | Extinction of a species present on only one island in the pair |  |
| E20 | Extinction of a species present on both islands in the pair |  |
| E21 | Extinction of a species present on both islands from one island in the pair |  |
| E1/I1 | Extinction of a species from one island and the introduction of the same species to the other island |  |

*Note*. The diagram shows pairs of islands (illustrated as circles), before and after an event type involving the introduction or extinction of a mammal species (illustrated as a star) has occurred.

## 3 | RESULTS

### 3.1 | Change in similarity

Prior to human occupation, mammal faunas on islands worldwide had low initial similarity (mean .01, *SD* .05), as did oceanic islands (mean .01, *SD* .05) and continental islands (mean .03, *SD* .09). Mammal faunas have become more similar to each other since human occupation occurred (Wilcoxon signed rank test *p*-value < .001). Using Jaccard's index, the mean increase in similarity across all island pairs has been .12 (Table 2). The changes on oceanic islands have been significantly more pronounced, with a mean increase of .20, than those on continental islands, with a mean increase of .06 (Table 2; Mann–Whitney–Wilcoxon test *p*-value < .001). Increases in mean similarity across all islands over the prehistoric and historical periods were significantly different (Mann–Whitney–Wilcoxon test *p*-value < .001), with the level of change being roughly three times stronger over the historical period (Table 2). Continental islands were largely unchanged during the prehistoric period but strongly changed during the historical period, whereas oceanic islands showed pronounced changes in both the prehistoric and historical periods, with mean increases in similarity of .14 and .12, respectively (Table 2). These changes correspond to somewhat right-skewed frequency distributions across all pairs, oceanic pairs and continental island pairs, as well as across the entire, prehistoric and historical time periods (Figure 2; Supporting Information Table S2). Although some individual island pairs showed decreases in similarity (i.e., biotic differentiation), such outcomes were infrequent for each of the

**TABLE 2** Changes in similarity by island type (all islands, continental islands and oceanic islands) and time period (entire time period, prehistoric and historical) calculated with Jaccard's pairwise index and Baselga's (2012) multisite measures - Jaccard dissimilarity (Beta-JAC), turnover component of Jaccard dissimilarity (Beta-JTU) and nestedness-resultant component of Jaccard dissimilarity (Beta-JNE)

| | | Jaccard's pairwise index | | Baselga's multisite indices based on Jaccard's index | | |
|---|---|---|---|---|---|---|
| Time period | Island type | Mean | *SD* | Beta-JAC (aggregate) | Beta-JTU (turnover) | Beta-JNE (nestedness) |
| Entire period | All islands | .1202, | .1158 | .0183 | .0334 | −.0151 |
| Entire period | Continental | .0592, | .0628 | .0116 | .0177 | −.0061 |
| Entire period | Oceanic | .2030, | .1465 | .0335 | .0695 | −.0360 |
| Prehistoric | All islands | .0380, | .1158 | .0041 | .0049 | −.0008 |
| Prehistoric | Continental | −.0006, | .0136 | .0007 | .0014 | −.0007 |
| Prehistoric | Oceanic | .1414, | .2003 | .0197 | .0379 | −.0182 |
| Historical | All islands | .0937, | .1135 | .0154 | .0299 | −.0145 |
| Historical | Continental | .0588, | .0583 | .0107 | .0157 | −.0049 |
| Historical | Oceanic | .1183, | .1712 | .0227 | .0518 | −.0290 |

*Note*. Baselga's multisite measures are shown here with respect to change in similarity, such that positive values indicate an increase in similarity. Pairwise and multiple-site measures show qualitatively similar patterns of change, such that oceanic islands have homogenized more than continental ones and that these changes have been larger in the historical than prehistoric period. These aggregate changes qualitatively match the turnover component, but differ from the nestedness component of the multisite measures. Note that the quantitative values of pairwise and multisite measures are not directly comparable; see main text for details.

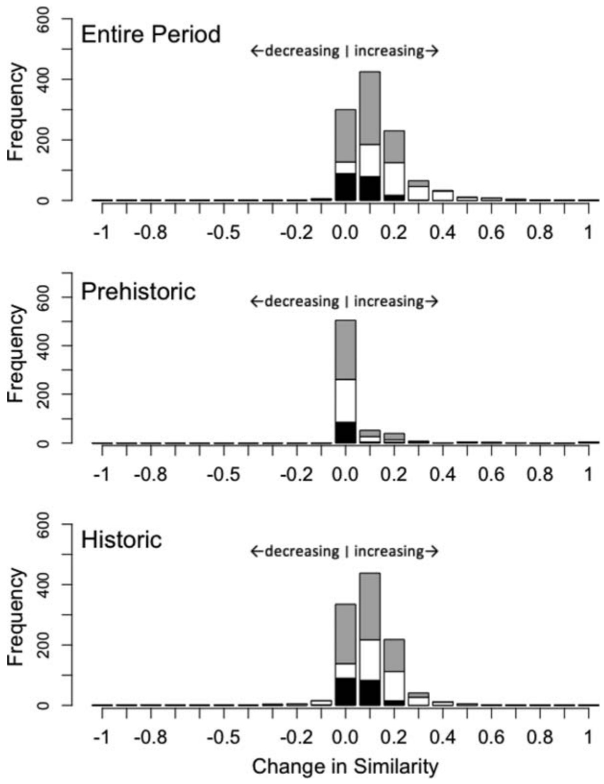


**FIGURE 2** Changes in Jaccard's index of similarity for each island pair across the entire time period since human settlement, during only the prehistoric period (spanning from first human settlement of a given island to the island's first contact with Europeans) and during only the historical period (the start of European influence to the present). The changes in similarity are shown relative to island type (continental island pairs are represented in black, oceanic island pairs in white, and continental–oceanic pairs in grey)

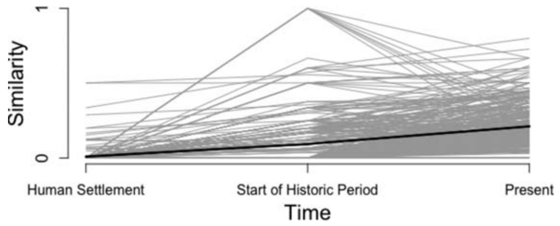


**FIGURE 3** Changes in Jaccard's index of similarity of mammal faunas on oceanic islands during the prehistoric and historical periods. Changes in individual island pairs (or sets of pairs with the same level of change) are shown as grey lines, whereas the mean trends over the two time periods are shown as continuous black lines. Note two key features: (a) that the mean trend lines belie the substantial variation among island pairs, and (b) that some island pairs 'flip-flopped' between periods (e.g., ones that became strongly homogenized during the prehistoric period subsequently became strongly differentiated in the historical period)

categories of comparisons (Supporting Information Table S2). Multisite measures, both Baselga's multisite measures based on Jaccard's Index (Table 2) and Baselga's multisite measures based on *Sørensen's* index (Supporting Information Table S3), showed qualitatively similar categorical changes to pairwise measures, such that similarity changed more over the historical than prehistoric periods and more on oceanic than continental islands. The turnover component of these multisite measures showed strong increases in similarity, whereas the nestedness component did not (Table 2; Supporting Information Table S3).

## 3.2 | Predictors of change in similarity

Changes in similarity across island pairs are related to characteristics of the islands examined. However, none of the characteristics (initial similarity, area, elevation, isolation or inter-island distance) had strong universal correlations with the change in similarity across both island types and time periods. Instead, the strength and statistical significance of these characteristics with changes in similarity varied with island type and time period (Supporting Information Table S4 and Figure S1). Most relationships examined were not significant (Supporting Information Table S4). Increased isolation was associated with higher levels homogenization, whereas differences in island area and elevational extent were associated with lower levels of homogenization (Supporting Information Table S4). Initial similarity was significantly related to the change in similarity only in the historical period (Supporting Information Table S4). Change in similarity on oceanic islands showed spatial clustering, so Mantel tests were not performed, but scatter plots of these relationships (Supporting Information Figure S2) did not show strong relationships.

Changes in similarity that occurred in the prehistoric period could influence changes in similarity that occurred in the historical period. This is particularly true on oceanic islands, where there is a strong negative relationship between change in similarity between the prehistoric and historical periods (slope $= -.4836$, adjusted $r^2 = .230$, $p < 10^{-9}$). Some oceanic island pairs showed a pronounced 'flip-flop', in which they became completely (or nearly completely) homogenized during the prehistoric period, but then were pushed back and strongly differentiated by species turnover events during the historical period (Figure 3). Most oceanic island pairs, however, showed relatively little change in the prehistoric period, followed by an increase in similarity in the historical period (Figure 3). Unlike oceanic islands, 'flip-flops' in similarity between periods were not common for continental islands, perhaps because the magnitude of change in similarity during the prehistoric period was so low.

## 3.3 | Event types

The frequency of the seven turnover events varied between island type and time period (Figure 4; Supporting Information Table S5). The most frequent were I01 events, which are cases where a species had been present on neither island and is introduced to one of them. I01 events occurred at least once on every island pair in the entire dataset and accounted for 59% of all turnover events. Oceanic islands had many I02 events (24% of all oceanic island pair events), whereas continental islands had many E10 events (32% of all continental island pair events). Continental islands, with a mean native species richness of 21.9, had greater potential for extinction events than oceanic islands (which had a mean native richness of 3.5). Indeed, after correcting for

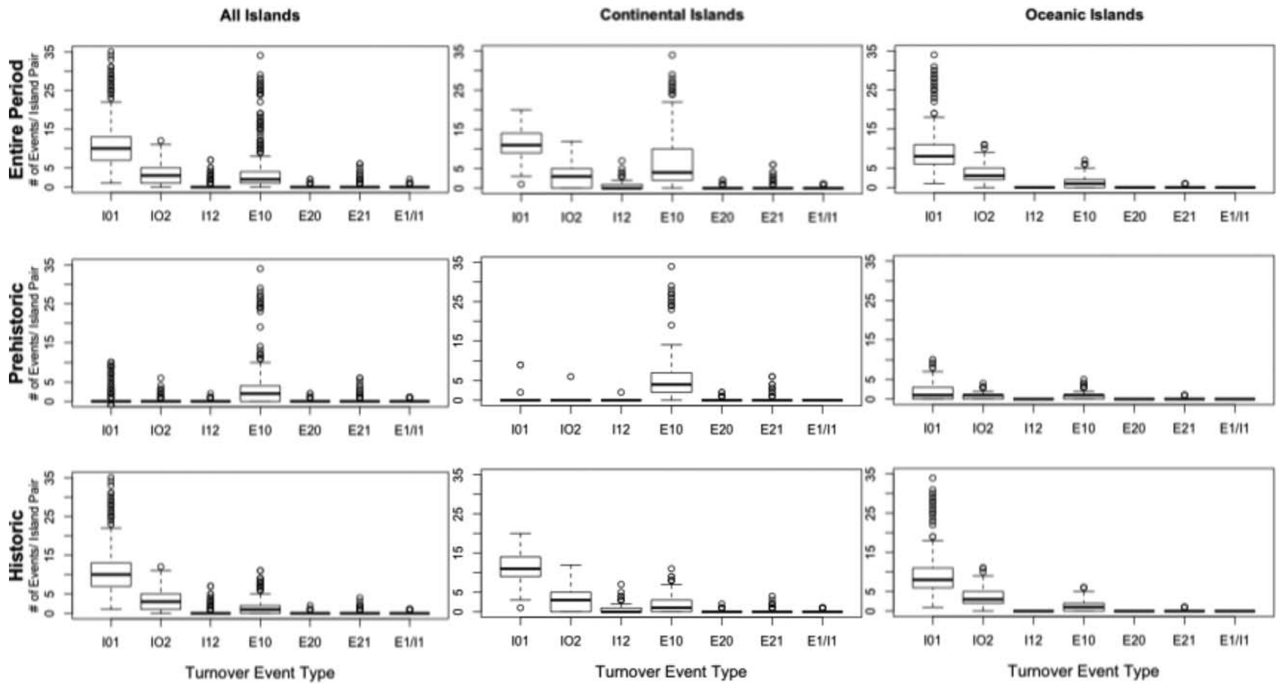


**FIGURE 4** Frequency of the seven types of turnover events per island pair with respect to island type and time period. The black bars represent the median, the ends of the boxes represent the first and third quartile, and the ends of the whiskers represent the maximal and minimal counts. Some event types (I01) vary strongly by time period, whereas others (E10) vary strongly by island type. Note that the most frequent event type (I01) reduces similarity, but that net similarity has increased because of the larger impact of less frequent event types; see main text

differences in the total number of pairs, continental islands had roughly six times more extinction events (summed across all extinction events: E10, E20, E21 and E1/I1) than oceanic island pairs. The prehistoric and historical periods also differed with respect to event frequencies, with the total number of events being more than five times greater during the historical period. This difference, however, was largely attributable to more frequent introduction events in the historical period, particularly I01 events (Figure 4). In contrast, the absolute numbers of extinction events were similar between time periods (Supporting Information Table S5).

### 3.4 | Projected similarity

Similarity is expected to continue to increase among islands if turnover events observed to date continue to occur at the same relative frequency in the future. If the frequency of events observed across the entire period on all islands continues unchanged, then island pairs will reach a mean similarity of .35 (Supporting Information Figure S2 and Table S6). This mean response would correspond with a much broader distribution of similarity values among island pairs (Figure 5; Supporting Information Table S6). Continental islands, which have a mode in similarity values that is currently only slightly displaced from initial values (i.e., before human occupation), are projected to be more spread out, including a second mode of island pairs that reach complete or nearly complete levels of homogenization (Figure 5). In contrast, oceanic islands are projected to maintain a single mode; one that will be only subtly shifted towards increased homogenization (Figure 5). Projected shifts in similarity are driven more strongly by changes during the historical period than during the prehistoric period. If we used only the relative frequency of turnover events that occurred during the prehistoric period to build our projections, then we would anticipate a less pronounced shift in the mode of similarity values than if we based our projections only on the relative frequency of events that occurred over the historical period (Figure 6).

## 4 | DISCUSSION

Mammal assemblages on islands have become strongly homogenized since human occupation. The overall change observed to date for mammals across all island types is more extreme than the values observed in a recent review by Olden et al. (2011) for any other group of animals or plants, except for freshwater fishes, which in some regions and at some spatial scales have shown stronger levels of homogenization. However, the increase in similarity shown by mammals on oceanic islands (mean of .20) is as large as those recorded for even the most extreme case of homogenization with freshwater fishes, as reported by Olden et al. (2011). Indeed, a recent meta-analysis of homogenization studies found that the mean increase in similarity across all groups studied was .03, with an *SD* of .08 (Baiser et al., 2012). This puts the change in similarity observed for mammals on oceanic islands at more than two standard deviations from the observed mean changes to date. Although one might imagine that changes on oceanic islands will necessarily be higher than changes observed in other regions, such a supposition is not correct. A recent study of plant and bird assemblages

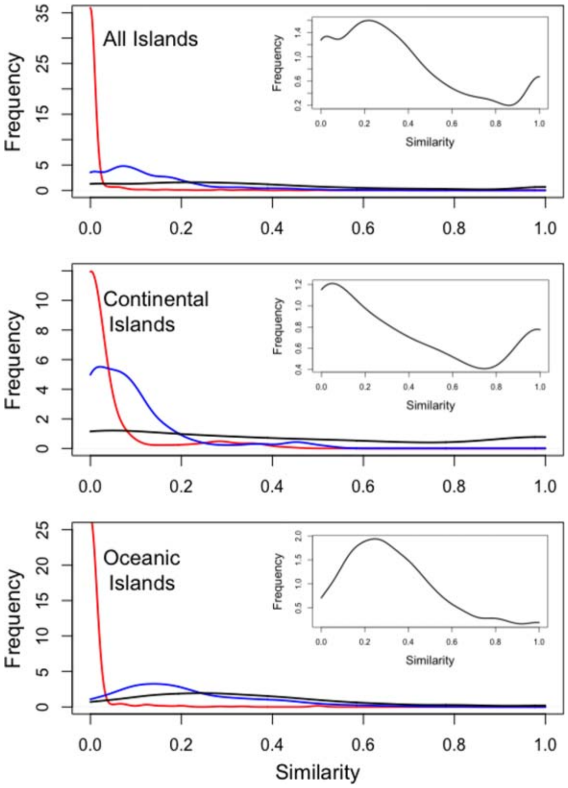


**FIGURE 5** Frequency distribution for initial similarity (red), current similarity (blue) and projected similarity (black) for all island, continental island and oceanic island pairs. The inset in each figure shows a close-up of the projected similarity. Although all projections show strong shifts in similarity, note that oceanic island pairs are projected to have a single mode in similarity, whereas continental island pairs are projected to have two modes, the latter of which shows nearly complete homogenization

on oceanic islands worldwide found mean changes in similarity of .03 and .04, respectively (Rosenblad & Sax, 2017), and a study of southern ocean islands found a small increase in similarity of insects, but a decrease in similarity of plants (Shaw, Spear, Greve, & Chown, 2010). The fact that only freshwater fishes have shown changes in similarity that are as high as mammals is intriguing because both groups experience strong dispersal limitation, as fish are often limited in their dispersal among watersheds on land, just as mammals are often limited in their dispersal among islands in the ocean.

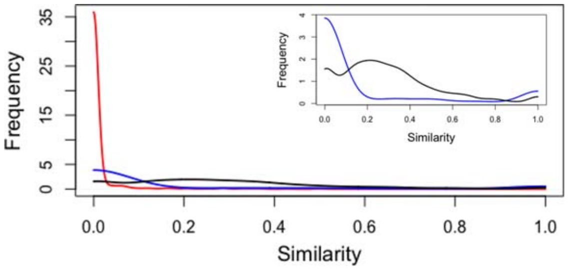


**FIGURE 6** Frequency curves of the projected similarity across all island pairs based on prehistoric changes (blue) and historical changes (black) relative to the initial similarity (red). The inset shows a close-up of the projected similarities. Note that projections based on historical changes show a much stronger shift in similarity than those based on prehistoric changes

The increases in similarity observed for mammals on islands can be understood by considering the relative frequency of species turnover events. By far the most frequent event type, I01, in which a species previously on neither island is introduced to one island in the pair, has a differentiating, not a homogenizing, impact on biotas. In spite of this influence, the assemblages have become homogenized. This apparent discrepancy can be explained by the fairly weak magnitude of impact that an I01 event has on similarity when initial similarity levels are low (Rosenblad & Sax, 2017), as was the case with insular mammal faunas. In contrast, the second most frequent event type, I02, the introduction of a species to both islands in the pair, has a relatively strong magnitude of impact when initial similarity levels are low. For example, if initial similarity is .05, then each I02 event will have an impact on change in similarity that is 20 times as strong as each I01 event, such that the differentiating impact of 20 I01 events is cancelled by the homogenizing impact of a single I02 event (Rosenblad & Sax, 2017). Given that I01 events were only roughly three times as frequent as I02 events, we observed a strong signal of homogenization. Of course, the other less frequent events also had an impact, most notably the third most frequent event type, E10, the extinction of a species previously on one island in the pair, which also has a homogenizing impact.

Differences observed in the change in similarity between island types and between time periods can also be understood by differences in turnover event frequencies. After I01 events, the next most common event types on both continental and oceanic islands are I02 and E10 events, both of which are homogenizing. However, when initial similarity is low, the strength of I02 events is much stronger, which helps to explain why oceanic islands have homogenized more than continental ones, because the former had more I02 events and the latter more E10 events. These differences in frequency of events between island types are likely to be constrained by their different introduction histories and the different contexts of their native mammalian faunas; for instance, as oceanic islands have few native species, it is impossible for them to have experienced many extinction events. The same differences in event frequencies between island types help to explain the differences in similarity observed between time periods, as the prehistoric time period was dominated by relatively weak E01 events and the historical more frequently had I02 events.

Multisite measures of change in similarity corroborated the qualitative differences shown with pairwise measures among time periods and island types. Although the magnitude of these changes in similarity was reduced for the multisite measures, it is difficult to interpret this difference from the pairwise results for two reasons. First, the multisite measures were recently proposed (e.g., Baselga, 2013), thus few empirical measures are available for comparison. Second, any such comparisons would be difficult because multisite indices are sensitive to the number of units analysed (Baselga, 2010), such that the values calculated for a study of birds on 20 islands would not be comparable to a study of plants on 40 islands. The ‘turnover’ and ‘nestedness’ components of these multisite measures made with our data suggest that changes in similarity observed were driven more strongly by changes in species composition than by changes in the total number of species on islands.

Some of the island pair characteristics we examined showed relationships with changes in similarity for certain island types or time periods, but none of these characteristics showed general relationships with changes in similarity across all island types or time periods. For example, the initial similarity of island pairs showed a significant negative correlation with change in similarity, but only over the historical period. Several characteristics examined, such as differences in area, showed no significant relationships with changes in similarity. One characteristic that appears informative for oceanic island pairs in the prehistoric but not the historical period was inter-island distance, which showed in the prehistoric period that only islands relatively close together became strongly homogenized. This sort of result points to the reduced importance of factors such as isolation in understanding changes in similarity as we move into the modern era (Helmus, Mahler, & Losos, 2014).

The projections presented in this study are not forecasts, but a thought experiment (sensu Rosenblad & Sax, 2017), which illustrates the future trajectory of change in similarity our system will follow if the observed types of species turnover events continue to occur at the same frequencies. Few previous studies have made projections of how similarity could change in the future. Lockwood (2006) found that if all currently endangered species went extinct, the future similarity of bird biotas among islands in Hawaii would be roughly comparable to current similarity levels. Rosenblad and Sax (2017) found, in spite of comparable and moderate levels of change in similarity to date, that bird and plant assemblages on islands were projected to diverge strongly in future levels of similarity. In the present study, we found a qualitatively similar result, namely that changes in the levels of similarity are projected to be different for mammals on oceanic versus continental islands. Continental islands are projected to homogenize more drastically than oceanic ones, largely because of the difference in their respective ratios of E10 to I01 events. Although I02, E10 and I01 events are all frequent in the dataset, the last two gain increasing impact on change in similarity as similarity levels increase (Rosenblad & Sax, 2017), such that the relative balance of their homogenizing (E10) and differentiating (I01) impacts become the dominant determinants of projected future change in similarity. Given that continental islands have a higher ratio of E10 to I01 events, the homogenizing effects of E10 events will play out most strongly among continental islands. Beyond differences in projected means, the differences in the projected number of modes are also intriguing. Given that the event frequencies of each individual island pair are used to make the projections, the variation in these frequencies among pairs determines the distributions (e.g., shown in Figure 5). The second projected mode on the continental islands is driven by two specific islands (Hispaniola and Kangaroo Island) that have a particularly high number of E10 events, which have a strong homogenizing effect.

It is important to emphasize that event frequencies might not continue unchanged and that any changes in those frequencies would impact projected changes in similarity. Introduction rates of some well-studied groups, such as plants, are expected to increase with increasing trade in the coming decades (Seebens et al., 2015). It is possible that the extinctions and introductions that have already occurred are the most vulnerable species and the most invasive species, respectively. In that case, the species remaining might be more resilient to human impacts, and the likelihood that the trends continue might be minimized. However, introduction rates of mammals remain high and currently are at rates roughly equivalent to those seen at the end of the 19th and beginning of the 20th centuries, after peaking globally in the 1950s (Seebens, Tim, & Blackburn, 2017). Consequently, continued introduction events for mammals seem likely. Unfortunately, extinctions of mammal species, particularly on islands, continue to the present day. In only the past 7 years, two insular endemic mammal species have gone extinct (Watson, 2016), and available work suggests that the status of endangered mammals has not improved over the past couple of decades, with $>$ 20% of mammals globally at some level of endangerment (Hoffmann et al., 2011). Consequently, continued extinction events also seem likely. Of course, even if extinctions and introductions continue at high rates, this does not necessarily mean that the frequency of specific event types will continue unchanged. E21 and E20 events have been rare historically and will probably remain that way, because there are not many shared native species across different islands at the scale we examined (i.e., at the scale of whole island archipelagos). This means that among extinction events, E10 events are likely to remain the most frequent. Among introduction events, we might expect I12 and I02 events to become more frequent if a common set of species is increasingly introduced. This could occur as an outcome of changing human introduction pressures and an increase in the global scale of those pressures. For example, the scale and commercial pressure of the wildlife trade has become vast, with an almost incomprehensible scope; for instance, billions of individual organisms, including hundreds of millions of mammals, were transported to the U.S.A. alone during a 7-year period (Smith et al., 2009). To the extent that these pressures lead to more I12 and I02 events, we would expect increased levels of homogenization.

Changes in similarity that have occurred to date, projections for the future and an unpacking of the event frequencies, as well as their relative importance, can help to inform management options for achieving conservation objectives, namely reducing additional homogenization or potentially even restoring similarity to levels seen before human occupation of islands. The most obvious actions to take fall within current management practice, namely preventing native extinctions and reducing additional introductions of non-native species, particularly of species that are already commonly introduced and for which the continued introduction to additional islands will lead to homogenizing I02 and I12 events. Other management options for reducing homogenization could include the somewhat unintuitive steps of protecting certain non-native populations and even introducing new ones, as I01 events are differentiating and can reduce homogenization. Few, perhaps no, managers would argue that combating homogenization is so important as to warrant such actions, but combating homogenization might be one ameliorating consideration when such non-traditional actions as protecting non-native populations would provide other conservation benefits (Schlaepfer, Sax, & Olden, 2011, 2012).

Gibson and Yong (2017) provide many examples of non-native populations that belong to species that are endangered in their own native range. In such cases, protecting some non-native populations could provide a type of insurance that could reduce the risk of global extinction events. For example, although the mongoose lemur (*Eulemur mongoz*) is not native to the Comoros Islands, it is critically endangered in its native range and potentially worth protecting in its exotic range (Schwitzer et al., 2014). Intentional introductions of non-native populations to meet conservation goals are currently rare, but such controversial actions could receive increased support if scientists take into account their impacts on homogenization, which would have a differentiating impact whenever they lead in aggregate to I01 events. So, for example, the Guam rail, which has been introduced to the island of Rota in order to reduce the species probability of extinction (Fontenot, Terrell, Malakooti, & Medina, 2006), in addition to this conservation benefit, also reduces biotic homogenization. Finally, it would also be conceivable to consider coordinated eradication programmes for commonly introduced species, thereby reversing the number of I02 and I12 events that have previously occurred. Ongoing efforts around the world to eradicate introduced rodents from islands are not conducted with the goal of reducing homogenization, but nevertheless could help to achieve this outcome (e.g., Lord Howe Island Board, 2009). Ultimately, the flip-flops from homogenization towards differentiation observed for a small number of islands between the prehistoric and historical periods emphasize that human actions can change levels of homogenization and not always in a way that are directly opposed to our conservation objectives. Although such interventions would be most effective on smaller islands with fewer species, because each turnover event that occurs there has a larger relative influence on similarity across island pairs, coordinated efforts could make an impact on all islands. It is also worth noting that most of the changes in similarity observed to date are a product of relatively recent changes during the historical period; this suggests that a lack of active management could lead to continued rapid increases in homogenization throughout the remainder of this century. Ultimately, more work is needed to determine how important considerations of homogenization should be in guiding conservation relative to a host of other conservation and societal objectives.

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## DATA ACCESSABILITY

The mammal occurrence data are accessible via the supporting information.

## ORCID

*Emily K. Longman* http://orcid.org/0000-0003-0237-8907
*Kyle Rosenblad* http://orcid.org/0000-0001-8778-7413

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## APPENDIX : DATA SOURCES USED TO DETERMINE ISLAND MAMMAL ASSEMBLAGES

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## BIOSKETCH

**Emily K. Longman** is interested in biogeography, marine community ecology and conservation biology.

**Kyle Rosenblad** is interested in conservation biogeography, particularly exotic species, habitat loss and modification, and extinction.

**Dov F. Sax** is interested in conservation and biogeography, with a focus on non-native species and species' responses to climate change.

## SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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