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A new framework for investigating biotic homogenization and exploring future trajectories: oceanic island plant and bird assemblages as a case study

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Studies of biotic homogenization have focused primarily on characterizing changes that have occurred between some past baseline and the present day. In order to understand how homogenization may change in the future, it is important to contextualize the processes driving these changes. Here, we examine empirical patterns of change in taxonomic similarity among oceanic island plant and bird assemblages. We use these empirical cases to unpack dynamic properties of biotic homogenization, thereby elucidating two important factors that have received little attention: 1) initial similarity and 2) the influence of six classes of introduction and extinction events. We use Jaccard's Index to explore the interplay among these factors in determining the changes in similarity that have occurred between human settlement and the present. Specifically, we develop general formulas for changes in similarity resulting from each of the six types of introductions and extinctions, so that the effect of each event type is formulated in terms of initial similarity and species richness. We then apply these insights to project how similarity levels would change in the future if the present patterns of introductions and extinctions continue. We show that the six event types, along with initial similarity, can show dramatically different behavior in different systems, leading to widely variable influences on similarity. Plant and bird biotas have homogenized only slightly to date, but their trajectories of change are highly divergent. Although existing patterns of colonization and extinction might not continue unchanged, if they were to do so then plant assemblages would show little additional change, whereas bird assemblages would become much more strongly homogenized. Our results suggest that moderate changes in similarity observed to date mask the potential for more dramatic changes in the future, and that the interaction among initial similarity and differential introduction and extinction regimes drives these dynamics.

Biotic homogenization is often listed as a conservation concern in the context of ongoing global change because it can have profound impacts on taxonomic makeup (through the loss of unique endemic species), ecological functioning (through the loss in buffering capacity that variation in biotic assemblages can provide to environmental perturbations), and evolutionary potential (through a loss of adaptive capacity) (Olden et al. 2004, Olden 2006, Rooney et al. 2007, Clavel et al. 2011). In spite of these concerns, however almost no effort has thus far been devoted to quantitatively projecting how patterns of similarity might change in the future. So, for instance, although a wealth of studies have demonstrated why rates of extinction are expected to accelerate dramatically by the end of this century, no such literature exists for the topic of biotic homogenization. Indeed, although the entire topic of homogenization is predicated on concerns for the future (McKinney and Lockwood 1999), exactly how much change in similarity we might expect or how this might vary among taxonomic groups has not been explored. Biotas could become more similar, leading to biotic homogenization, or less similar, leading to biotic differentiation, but the magnitude of such changes and how they might vary by spatial scale, geographic context and taxonomic group are not well understood. The bulk of attention in studying changes in similarity has focused on characterizing past changes and in understanding the processes that have driven these changes. This attention has led to important advances in documenting typical changes to date across taxonomic groups (Baiser et al. 2012) and to improving our understanding of how changes in certain patterns found among assemblages, such as species turnover and nestedness, relate to changes in similarity (Leprieur et al. 2011, Baiser et al. 2012, Carvalheiro et al. 2013). There is also a rich literature examining the interplay among spatial scale, species richness and species turnover (Lennon et al. 2001, Cassey et al. 2006, Gambi et al. 2013). Collectively, this work has led some to suggest that changes in similarity are best studied with multi-site indices instead of traditional pairwise approaches (Diserud and Odegaard 2007, Baselga 2013). While the utility of such multi-site approaches are undeniable, in the context of projecting future changes in similarity, there is likely still some utility in advancing methods with pairwise similarity indices.

To investigate future similarity trajectories, it is necessary to unpack two aspects of the internal dynamics of changes in similarity that have yet to receive much attention. First, while it is understood that the effects of introduction and extinction events on similarity depend on the 'types' of events occurring, i.e. whether the species added and lost are the same or different across assemblages (Olden and Poff 2003, 2004, Smith et al. 2009), the relative importance of alternative event types has not been well characterized. For instance, while we know that the introduction of a novel species to just one assemblage in a pair would generally have a differentiating impact, whereas its introduction to both assemblages in a pair would generally have a homogenizing impact, we do not know whether the magnitude of differentiation caused by the first type of event (introduction to just one assemblage in a pair) would equal the magnitude of homogenization caused by the second type of event (introduction to both assemblages in a pair). Second, while it is understood that initial similarity among assemblages can influence subsequent similarity dynamics (Olden and Poff 2003, 2004, Cassey et al. 2007, Shaw et al. 2010), the relative importance of initial similarity in dictating these dynamics is not well understood. For example, we know that differences in initial similarity among assemblage pairs can allow exactly the same set of turnover events (i.e. introductions and extinctions) to lead to qualitatively different outcomes in one assemblage pair than another, i.e. to homogenization or differentiation (Fig. 1). However, we do not know how sensitive changes in similarity are to differences in initial similarity among actual biotic assemblages and whether qualitatively different sensitivities might exist in different systems. Further, interactions among turnover event types, their frequencies, and initial similarity are fully unexplored. Finally, while there is utility in exploring similarity dynamics in idealized systems, there are also likely to be insights gained by studying such dynamics in actual biotic assemblages.

The biotas of oceanic islands are an ideal system in which to study biotic change. These biotas have been heavily impacted by human activity and have experienced many anthropogenic introductions and extinctions (Sax et al. 2002, Steadman 2006, Loehle and Eschenbach 2012); consequently, they have been a particular focus of homogenization studies to date (Cassey et al. 2007, Castro et al. 2010, Shaw et al. 2010). Islands are advantageous for studying species turnover due to their clear borders, which facilitate documentation of species addition and loss, and also because they have good historical and sometimes fossil records of biotic change since human colonization (Olson and James 1982, Flenley et al. 1991, Steadman 2006, Sax and Gaines 2008). Islands also offer a means to investigate how differential introduction and extinction frequencies influence similarity dynamics. For example, on oceanic islands, plants have experienced few extinctions, but many introductions, whereas birds have experienced many extinctions and introductions (Sax et al. 2002). Furthermore, island communities contain both widespread and range-restricted exotics (Lever 1987), which present an opportunity to explore the outcomes of a broad spectrum of introduction event types. Additionally, given the high endemism rates on many islands, they offer the potential to examine similarity dynamics in systems that begin with very low compositional similarity. Consequently, islands are a useful study system for determining how turnover event types and initial similarity have driven changes in similarity and, thus, how these same factors may drive similarity dynamics in the future.

In this study, we assess changes in similarity among vascular plant and land bird assemblages on oceanic islands worldwide since human settlement. We then examine these changes with respect to metrics often used to characterize patterns of homogenization, such as distance between assemblage pairs. Next, we introduce and apply a novel, quantitative framework for the study of changes in similarity, based on turnover event types, event frequencies, initial similarity, and the interactions among these factors. We use this framework to unpack the dynamics that have occurred to date. Finally, we extend this framework and apply it to a 'thought experiment' to develop projections of how similarity levels would change in the future if the present patterns of introductions and extinctions continue.

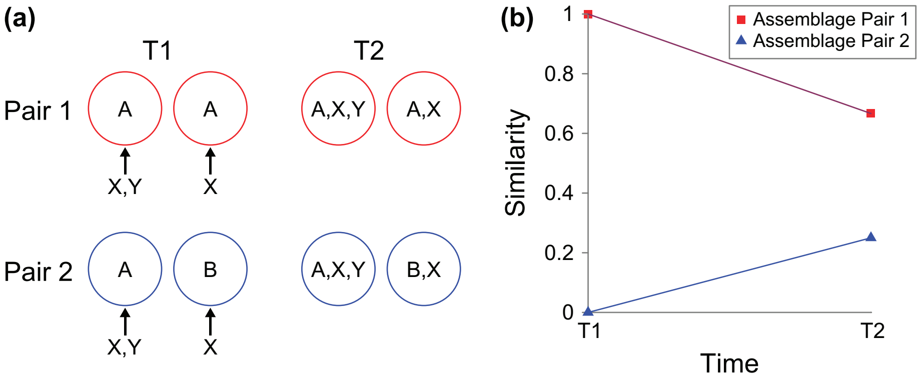

Figure 1. Changes in Jaccard's index of similarity depend on initial similarity. (a) At the first time point (T1), assemblage Pair 1 (red circles) has one species, which is present in both assemblages, while Pair 2 (blue circles) has two species, with a different species in each assemblage. T2 shows the resulting species composition if species X and Y are added in exactly the same way to each assemblage pair. (b) Similarity changes from T1 to T2 in both assemblage pairs, but the direction of change (increasing or decreasing similarity) depends on initial similarity, even though exactly the same introduction events occurred in both assemblage pairs.

Material and methods

Plant and bird assemblages

We examined oceanic islands and archipelagos with data on land birds and vascular plants. Specifically, we considered species using terrestrial and freshwater resources but excluded those dependent solely on marine resources. Following Sax et al. (2002), we treated oceanic archipelagos and lone islands as equivalent, examining each as a single unit (referred to as 'islands' henceforth). We focused on islands where we could assemble full lists of both currently extant species and species present at the time of first human occupation (European or otherwise – see Sax et al. (2002) for information on each island's human history, including whether an island was colonized by humans prior to European discovery, whether such populations were still present when Europeans arrived, etc.). To assemble these lists, we updated Sax et al.'s (2002) data by surveying the literature for new information on each island's species assemblages published since 2000 (Supplementary material Appendix A1), when data collection was completed for Sax et al. (2002). We excluded some islands examined by Sax et al. (2002) because information regarding the species present at first human occupation was incomplete. One island (Wake Island) was excluded because it holds no extant land bird species. We examined a total of 11 islands with plant data and 20 islands with bird data (Supplementary material Appendix A2). For plants, the islands ranged in area from 15 sq. km (Pitcairn Island) to 270 692 sq. km (New Zealand) with a mean of 26 216 sq. km and a standard error of 24 494 sq. km. For birds, the islands ranged in area from 17 sq. km (Lord Howe Island) to 270 692 sq. km (New Zealand) with a mean of 16 349 sq. km and a standard error of 13 439 sq. km. In sum, the initial and current species lists contained 6520 plant and 622 bird species. The plants experienced 4135 introductions and 120 extinctions, whereas the birds experienced 268 introductions and 271 extinctions. Supplementary material Appendix A3 shows initial and current species lists by island.

Assessing changes in similarity

For each possible pairing of two plant or bird assemblages in our data set (55 plant and 190 bird pairs), we calculated Jaccard's Index of Similarity (J) for the species present at human settlement ($J_{initial}$) and for the current assemblages ($J_{current}$). We quantified the change in similarity for each assemblage pair as follows: $\Delta J = J_{current} - J_{initial}$. The statistical significance of the observed changes in similarity was assessed using the Wilcoxon signed ranks test. We used the Mann–Whitney–Wilcoxon test to determine whether changes in similarity were significantly different between plants and birds.

We used Mantel tests to determine whether ΔJ correlates significantly with the following variables: inter-island geographic distance, area difference, and initial similarity. Due to recent concerns regarding misapplication of the Mantel test (Guillot and Rousset 2013), we used the R package memgene (Galpern et al. 2014, Peres-Neto and Galpern 2014) to confirm that there was no spatial clustering of ΔJ values.

All statistical analyses were conducted with R software (R Core Team). In addition to the aforementioned R packages, we used vegan (Oksanen et al. 2013) and sp (Pebesma and Bivand 2005).

Quantifying initial similarity's influence

To determine how initial similarity modulates the homogenizing or differentiating effects of introduction and extinction events, we first outlined the six fundamental ways in which an introduction or extinction can affect a pair of species assemblages – i.e. the six types of biotic turnover events (see Fig. 3 for a list of these event types). To quantify the effect of each biotic turnover event type on similarity at a given initial similarity level, we developed formulas for a generic pair of assemblages containing a total of T species, S of which are present in both assemblages – i.e. 'shared'. For this hypothetical assemblage pair, Jaccard's index of similarity before a biotic turnover event is calculated as $J = S/T$. Similarity following any event is calculated according to how S and/or T change. For example, Event I01 leaves S unchanged and increases T by one, so similarity following Event I01 is calculated as: $J_{I01} = S/(T + 1)$. The change in similarity due to the event is then calculated by subtracting initial similarity from post-event similarity, e.g. $\Delta J_{I01} = J_{I01} - J = S/(T + 1) - S/T$. Since S is the product of T and J, we can substitute TJ for S so that ΔJ due to any event is then defined in terms of initial similarity and total species number, e.g. $\Delta J_{I01} = TJ/(T + 1) - TJ/T = -J/(T + 1)$. When T is large, the formulas for the six event types can be simplified by an approximation that makes all six effects scale proportionally with species richness. Thus, the relative effects on similarity of the six event types, when T is large, can be approximated well by simple ratios for any assemblage pair at any given initial similarity level. Both the exact and approximate formulas for each event type are provided in Supplementary material Appendix A4.

In order to examine how initial similarity influenced similarity dynamics in our systems given the observed event frequencies, we estimated what changes in similarity would have resulted if the same biotic turnover events had occurred in systems with the same species richness, but different initial similarity levels. To characterize the biotic turnover events observed in our systems, we calculated the mean number of events of each type that occurred across all assemblage pairs. These means represent the average set of events experienced by assemblage pairs in our system. Similarly, to characterize the pairwise species richness patterns in our systems, we calculated the mean initial species number across all assemblage pairs. These parameters represent the 'average island pair'. Finally, we calculated the changes in Jaccard's index of similarity that would have resulted if the average set of events had occurred in the average island pair, starting from a range of alternative initial similarity levels.

Projecting biotic change

To determine what similarity trajectories the current biotic turnover regimes would lead to if they persist in the future, we identified the similarity end-points that will be reached or approached asymptotically by each assemblage pair if the observed biotic turnover events continue occurring at the same absolute rates. Since Jaccard's index of similarity is calculated as the ratio of shared to total species (i.e. $J = S/T$), any set of biotic turnover events fundamentally influences similarity by changing S and/or T, as discussed above. Consequently, if the biotic turnover events observed in an assemblage pair continue occurring at the same absolute rates over time, then the observed trends in S and T will persist as well, leading to a determined end level of similarity that will be reached or approached asymptotically. For example, consider an island pair that originally had two species, one of which was shared. The S and T values at human settlement would have been 1 and 2, respectively. If one new species has been introduced to both islands since human settlement (i.e. one I02 event has occurred), then there are currently three species, two of which are shared. Thus, S and T have each increased by 1 between human settlement and the present, so S is 2, T is 3, the observed change in S (ΔS) is 1, and $\Delta T = 1$. If the same introduction regime continues, in this case with one I02 event per time period, then S and T will each continue to increase by 1 at regular intervals. Consequently, similarity (S/T) for this island pair will eventually reach 3/4, then 4/5, then 5/6, etc. To find the similarity level that this island pair is ultimately approaching, we can take the limit as X approaches infinity of $(S + \Delta S \times X)/(T + \Delta T \times X)$, where X represents time. In this example, we take the limit as X approaches infinity of $(2 + 1X)/(3 + 1X)$, which simplifies to 1. Thus, projected similarity for this assemblage pair is 1. Supplementary material Appendix A5 shows the projected similarity level for any assemblage pair under any combination of changes in S and/or T, provided S and T continue changing at the same absolute rates over time. Supplementary material Appendix A5's legend provides explanations of mathematical details for all possible projection scenarios. Note that the projected similarity values for six of the nine possible scenarios in Supplementary material Appendix A5 are unrelated to initial similarity. We applied this framework in our system to identify the projected similarity value for each plant and bird assemblage pair.

Comparing pairwise and multi-site indices

Since recent work has indicated that use of multiple-site dissimilarity metrics in biotic change studies can lead to different results than pairwise similarity measures, and that studying compositional turnover rather than aggregate dissimilarity can also affect results (Baselga 2010, 2013), we computed multi-site Simpson dissimilarity ('Beta-SIM', also known as the turnover component of Sorensen dissimilarity) for past, present, and projected future time points in our study using the R package betapart (Baselga et al. 2013). Past and present value calculations were straightforward, but some input values required by the Beta-SIM formula (Baselga 2010) cannot be determined for the projected end-points of similarity we investigated in our pairwise procedure. Consequently, the multi-site index, unlike a pairwise approach, cannot currently be used to examine projected end-points of similarity. Instead, to facilitate a direct comparison of future similarity projections between our approach and the Beta-SIM approach, we calculated the similarity levels that will be reached two time steps in the future under present biotic turnover regimes. We defined a time step as the length of our study interval from prior to human disturbance to the present day. To calculate Beta-SIM and pairwise Jaccard similarity two time steps in the future, we needed three values for each island pair: shared species number (S), total species number (T), and the number of unique species found on the island with fewer unique species ($\min[b_{ij},b_{ji}]$, sensu Baselga 2010). We also needed two values for the full system: the sum of the species richness values of all individual islands, and overall system species richness. We generated each of these needed input values for the future by calculating the change observed between past and present and then applying that change to the present value two more times. This approach is the same one we used in projecting future shared and total species numbers for island pairs (see I02 event example in 'Projecting biotic change' above), except the same logic is now applied to system-wide parameters. For example, if system species richness at human settlement had been 100, and current system richness were 90, the observed change in system richness would be –10. We would then add –10 (the observed change) to 90 (the current value) twice, resulting in a projected future system richness of 70.

Data available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.c9s61> (Rosenblad and Sax 2016).

Results

Island plant and bird assemblages have both homogenized since human occupation. For plants, all 55 assemblage pairs increased in similarity (Fig. 2, Supplementary material Appendix A6). Of 190 bird assemblage pairs, 154 increased in similarity, 31 maintained their initial similarity levels, and 5 decreased in similarity (Fig. 2). The mean increase in Jaccard's index of similarity was 0.029 for plants (from an initial 0.045), and the mean increase was 0.044 for birds (from an initial 0.021). Median increases in similarity for both plants and birds were statistically significant (Wilcoxon

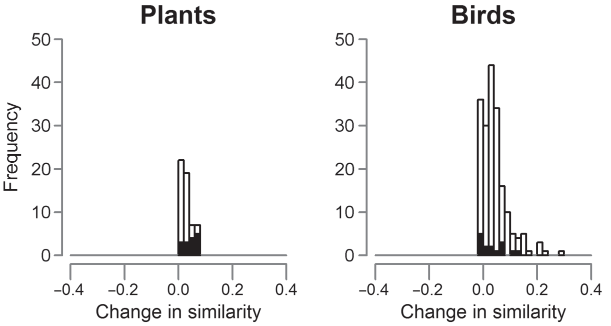

Figure 2. Changes in Jaccard's index of similarity for each island pair between human settlement and the present. Median changes in similarity for the full data set (white bars) are significantly greater than zero for plants and birds, indicating homogenization, and are not significantly different from each other, indicating comparable changes in similarity of plant and bird assemblages. Qualitatively identical results were observed for the subset of six islands (black bars) for which both plant and bird data were available.

signed ranks test, $p < 0.001$ for both tests). Changes in similarity were not significantly different between plants and birds (Mann–Whitney–Wilcoxon test, $p = 0.21$). The six islands for which both bird and plant data were available (black bars, Fig. 2) show similar results, such that the median increase in similarity was significant for plants (Wilcoxon signed ranks, $p < 0.001$) and birds (Wilcoxon signed ranks test, $p < 0.01$), whereas changes in similarity were not significantly different between plants and birds (Mann–Whitney–Wilcoxon test, $p = 0.30$). Finally, changes in similarity were not related to geographic distance or to differences in the area of island pairs (Supplementary material Appendix A7 and A8).

Our novel analytical exploration of pairwise similarity dynamics showed that different biotic turnover event types can vary in their relative influence on changes in similarity depending on initial similarity. Two of the event types (I12 and E21) are insensitive to differences in initial similarity, and their influence, relative to each other, does not vary with initial similarity (Fig. 3, Supplementary material Appendix A9). In contrast, the other four event types vary in the relative magnitudes of their effects based on initial similarity, and these differences can become larger as initial similarity becomes more extreme (Fig. 3, Supplementary material Appendix A4, A9). For example, when initial similarity is at 0.05, the homogenizing effect of an I02 introduction is 20 times stronger than the differentiating effect of an I01 introduction, whereas their effects are of equal magnitude when initial similarity is 0.5 (Fig. 3, Supplementary material Appendix A9). The values in Fig. 3 are based on the 'approximate' formulas shown in Supplementary material Appendix A4, which are applicable whenever the species richness of an assemblage pair (T) is large. When T is small, however, the 'exact' formulas in Supplementary material Appendix A4 are more accurate, as they account for the influence of differences in species richness on changes in similarity, producing values with slightly different relationships among the six event types.

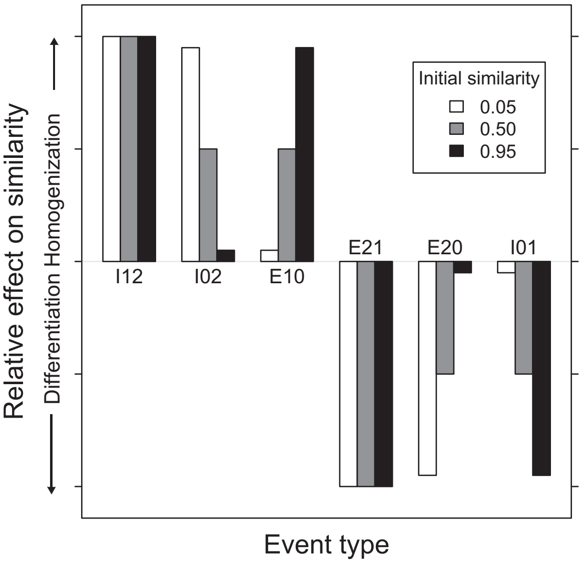

Figure 3. The magnitude of effects of introductions and extinctions on changes in Jaccard's index of similarity for assemblage pairs vary by event type and initial similarity. We consider six possible event types, i.e. types of introductions and extinctions. An introduction can increase the number of assemblages occupied by a species from one to two (Event I12), zero to two (I02), or zero to one (I01), whereas an extinction (or extirpation) can decrease the number of assemblages occupied from two to one (E21), two to zero (E20), or one to zero (E10). The white, gray, and black bars for each event type show the strength and direction of that event's effect on similarity when initial similarity is 0.05, 0.5, or 0.95, respectively. There is no numeric scale on the y axis because the relative heights of the bars simply indicate the relative strengths of effects. For example, when initial similarity is at 0.05, the homogenizing effect of an I02 introduction will always be 20 times stronger than the differentiating effect of an I01 introduction, regardless of how strong or weak the two effects are in absolute terms. See Material and methods and Supplementary material Appendix A4 for a discussion of when the values shown here are sensitive to differences in species richness among assemblage pairs.

Our plant and bird assemblages varied strongly in their frequencies of the six event types we have defined, which appear to be related to differences in initial similarity in some cases. The only frequent event type for plant assemblage pairs was I01 (Fig. 4). In contrast, bird assemblage pairs experienced many I01 events, but also experienced many E10 Events (Fig. 4). Both I01 and E10 events are only frequent in pairs with low initial similarity (Supplementary material Appendix A10). Finally, initial similarity shows a weak positive correlation with changes in similarity for both plant and bird assemblages (Supplementary material Appendix A11).

Using our data set to examine average island pairs through our new framework, we found that initial similarity influenced the direction and magnitude of change in similarity we observed for plants, but not birds. If plant assemblages were only slightly more similar on average initially, e.g. 0.1 instead of 0.05, then the same turnover events observed would have differentiated, rather than homogenized, the average island pair (Fig. 5, Supplementary material Appendix A12). Furthermore, differences in initial similarity of plant assemblages would have strong influences on the magnitude of observed changes (Fig. 5). In contrast,

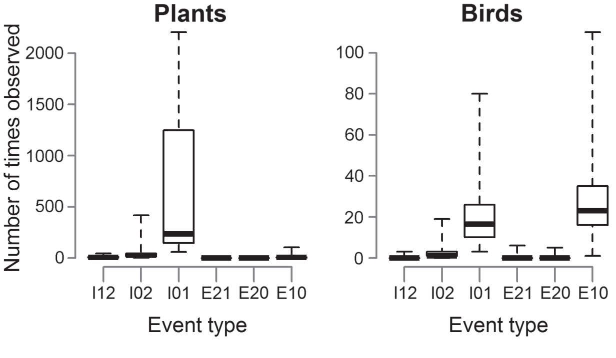

Figure 4. Number of times each of the six types of biotic turnover events has occurred across assemblage pairs. See Fig. 3 for event type definitions. The ends of the whiskers for each box represent the minimum and maximum number of times each event type occurred in any assemblage pair, the ends of each box represent the first and third quartiles, and the middle bar represents the median. Event I01 was common among both plant and bird assemblages, whereas Event E10 was only common among bird assemblages. These two event types have opposing effects on similarity, which are modulated differently by changing initial similarity (Fig. 3, Supplementary material Appendix A4, A9). This discrepancy indicates that plant and bird assemblages have experienced fundamentally different biotic turnover regimes.

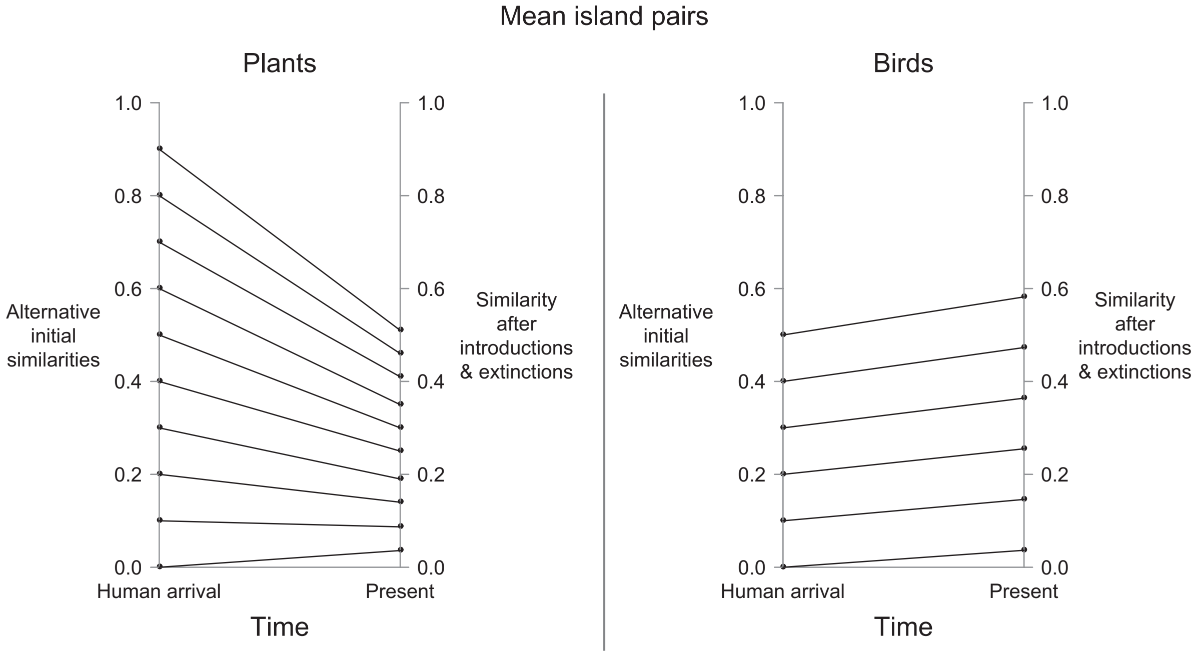

Figure 5. Changes in Jaccard's index of similarity that would have occurred between human settlement and the present if the same observed introductions and extinctions had occurred in systems with alternative initial levels of similarity. The similarity trajectories depicted are based on applying the mean observed number of each of the six biotic turnover events to island pairs with mean initial species richness. For example, if a plant assemblage pair initially had species richness identical to the system-wide average, but an initial similarity level of 0.9, then the average observed set of introduction and extinction events would have driven strong differentiation, decreasing similarity to approximately 0.5. In contrast, an initial similarity of 0 would have led to homogenization, as shown by the positive slope of the line segment originating at this point, whereas all of the greater initial similarity levels shown would have led to differentiation, as shown by the negative slopes on all other line segments for plants. Thus, there is a critical 'pivot point' of initial similarity between 0 and 0.1 that determines the direction of change in similarity. Additionally, once initial similarity surpasses the pivot point, the magnitude of differentiation grows stronger with higher initial similarity, as shown by the much steeper slopes of line segments that begin higher on the y axis. In contrast, for birds, all possible levels of initial similarity lead to homogenization, as shown by the positive slopes on all line segments. For both plants and birds, some initial similarity levels were not considered – e.g. 0.6 and higher for birds – because there would not be enough shared or unshared species for the required introductions and extinctions to occur.

the biotic turnover events observed in bird faunas would have driven homogenization at any initial similarity level, and the magnitude of this homogenization is not as strongly influenced by initial similarity (Fig. 5, Supplementary material Appendix A12). Consequently, the plant assemblages show a pivot point with initial similarity, whereas the bird assemblages do not.

Projections of future end-points of similarity, based on an assumption of the continuation of current biotic turnover regimes, indicate large differences between plant and bird assemblages. Although both plant and bird assemblages have experienced comparable, and relatively small, changes in similarity to date, the projected future trajectory shows relatively little additional change for plant assemblages, but dramatic increases for bird assemblages (Fig. 6). Average island pairs have dynamics driven by the differences in the relative effects of events at different levels of initial similarity (Fig. 3) and event frequencies (Fig. 4). Consequently, the average island pair for birds has an accelerating trend toward complete homogenization (Fig. 6a) because, as the baseline similarity level for new introductions and extinctions keeps increasing, the homogenizing effects of these introductions and extinctions grow increasingly strong (Fig. 5, Supplementary material Appendix A12), whereas the average island pair for plants stabilizes over time (Fig. 6a) because it is homogenizing toward its pivot point of approximately 0.1 similarity (Fig. 5, Supplementary material Appendix A12). Projections for actual pairs of islands show the same qualitative trend of dramatically increasing similarity for birds (Fig. 6b), but much smaller increases in similarity for plants (Fig. 6c). While the changes projected for both groups are significantly greater than zero (both groups: Wilcoxon signed ranks test, $p < 10^{-9}$), the median change in similarity for birds, 0.887, is significantly greater than the median change for plants, 0.0256 (Mann–Whitney–Wilcoxon test, $p < 10^{-11}$). These median differences, however, do not capture the significant variation projected among island pairs, with a clustered unimodal distribution of projected change for plant assemblages, but a highly variable and bimodal distribution for bird assemblages (Fig. 6b, c).

Pairwise metrics analyzed with the Jaccard Index (reported above) and Baselga's (2010) multi-site index, 'Beta-SIM' produced results that were qualitatively similar in most cases. Both indices showed moderate levels of homogenization to date for both plant and bird assemblages, although the magnitude of change between the two groups varied slightly (Supplementary material Appendix A13). Projections with both methods at two time steps into the future (see Material and methods) showed larger changes in similarity for birds than for plant assemblages, i.e. the additional projected

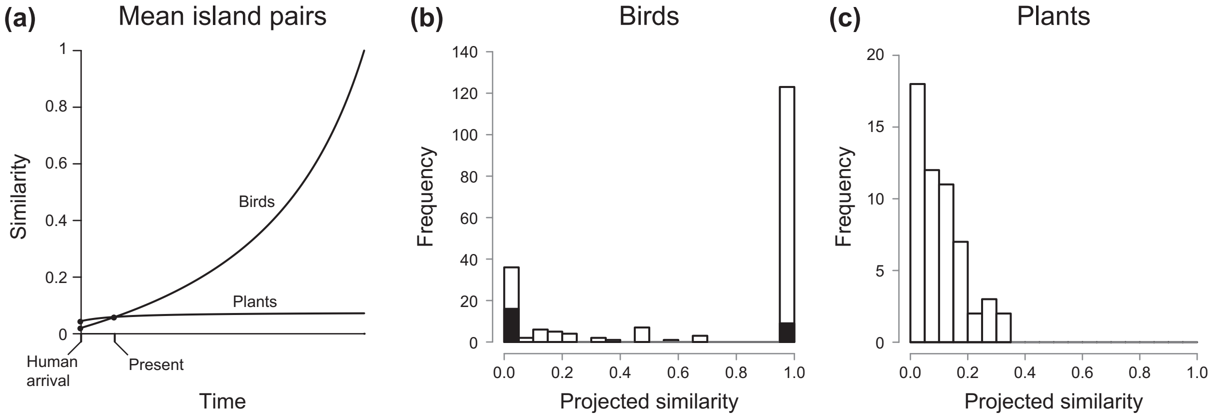

Figure 6. Past, present, and projected future values of Jaccard's index of similarity for plant and bird assemblages. (a) Changes in similarity over time for the 'average island pair' of both bird and plant assemblages. An average island pair has the mean initial similarity and species richness for that taxonomic assemblage type, and it experiences the mean observed number of each event type between human settlement and the present; this same frequency of events is repeated at regular intervals going forward to project future changes in similarity (see Material and methods for additional details). For the average plant island pair, change in similarity is never steep, and it levels off at a relatively low level. In contrast, for birds, the average island pair homogenizes at an accelerating rate until reaching total similarity. (b, c) Projected future levels of similarity for actual assemblage pairs for birds and plants, respectively. The black bars represent island pairs for which the future projection was influenced by initial similarity. Projections for all other island pairs were determined solely by observed biotic turnover events. Although projected median changes for bird assemblage pairs are much higher than those for plants (see text), projected similarity for bird pairs is highly bimodal, with the majority projected to homogenize totally, but a sizeable minority projected to differentiate totally.

change in similarity from currently calculated levels is expected to be larger for birds than for plants with both methods (Supplementary material Appendix A13).

Discussion

Plant and bird assemblages on oceanic islands have experienced comparable, relatively low levels of homogenization to date, despite large differences in numbers of introductions and extinctions between these two groups. However, these similar historical patterns of change in similarity mask the potential for starkly different future trajectories. If current introduction and extinction regimes continue unchecked, then plant assemblages will experience additional homogenization, but only to a very limited extent – of less than 50% above their current level on average. In contrast, if bird assemblages continue on their current trajectory, they will dramatically increase in homogenization, by an average of more than 500%. On a scale from 0–1 (Jaccard's index of similarity), this would result in an average similarity of about 0.1 for plant and 0.7 for bird assemblages. This difference is remarkable considering that both assemblages currently have average similarity levels below 0.1. This key insight, namely that vastly different trajectories of change in similarity are possible, despite similar levels of change observed to date, only becomes apparent after unpacking how alternative turnover event types drive these dynamics.

Our framework shows how event types can vary in their relative effects, how this variation relates to initial similarity, and how these dynamics have shaped the changes in similarity that have been observed to date in oceanic island plant and bird assemblages. Plant assemblages have most frequently experienced I01 events (Fig. 4), which have a differentiating effect. Nevertheless, these assemblages have become homogenized on average because I02 events, which were much less frequent (Fig. 4), each have a homogenizing effect that is approximately 20 times more impactful when initial similarity is as low as 0.05 (Fig. 3, Supplementary material Appendix A4), as was observed in these plant assemblages. If, however, initial similarity had been even slightly higher, e.g. 0.1, the relative effects of these events would have been shifted enough to produce net differentiation (Fig. 5). Thus, oceanic island plant assemblages as a whole are near a 'pivot point' of similarity, in which precisely the same frequency of turnover events could produce either homogenization or differentiation depending on small differences in initial similarity. It is because of this pivot point that the current trajectory of change in similarity allows for only a subtle increase in homogenization. In contrast to plant assemblages, bird assemblages have most frequently experienced E10 events, which have a homogenizing effect, followed by slightly less frequent I01 events, which have a differentiating effect (Fig. 3, Fig. 4, Supplementary material Appendix A4). These two event types have effects equal to each other in magnitude across all initial similarity levels, such that the most frequent one determines the direction of change (Fig. 3, Supplementary material Appendix A4). Consequently, the observed set of introductions and extinctions leads to increasing homogenization on average, regardless of initial similarity level, because of differences in event frequencies (Fig. 5). However, because individual island pairs have not all experienced the average event frequencies, the future trajectory of each pair is somewhat different, with the majority on a trajectory towards total homogenization, another set leveling out at intermediate similarity levels, and a third set differentiating to total dissimilarity (Fig. 6b). Finally, it is worth noting that given sufficient time, the trajectory of change in similarity for all plant assemblage pairs, and most bird assemblage pairs, becomes independent of initial similarity (see white and black bars, Fig 6b, c). Regardless of these long-term dynamics, however, current short-term dynamics are strongly influenced by initial similarity.

To better understand how these communities might actually change going forward, it is important to understand the assumptions of our projections and how breaking those assumptions would change future levels of similarity. There are two key assumptions: first, that turnover events will continue to occur, and second, that they will occur in the same relative frequencies, e.g. that I01 events will continue to occur more frequently than I02 events. Although changes in similarity observed to date are generally analyzed as if they were discrete events, i.e. before and after human arrival to islands, in reality the process of biotic turnover is ongoing and dynamic. Plants and birds are continuing to be introduced (Sax and Gaines 2008, Blackburn et al. 2015) and birds are continuing to go extinct (Pimm et al. 2006). Indeed, species invasions, despite active management, are continuing to occur and show no indication of slowing in frequency. Plant invasions on islands have showed a nearly linear increase over the past couple of centuries, including the past few decades (Sax and Gaines 2008), and birds have shown a strong linear increase in numbers since the mid-1800s (Blackburn et al. 2015). Extinctions of plants have been few, and there is no evidence of a recent increase in frequency (Sax and Gaines 2008). Bird extinctions are also ongoing, with many in the past few decades, although an analysis of the impact of conservation efforts suggests that they have succeeded in reducing these rates by approximately two-thirds (Pimm et al. 2006). However, because more than 10% of all birds globally are threatened with extinction (Pimm et al. 2014) and the majority of those birds occur on islands (Manne et al. 1999), a sizeable portion of island birds are currently at risk of extinction. Therefore, bird extinctions are likely to continue, albeit at a somewhat slower pace. This evidence suggests that the assumption that the relative frequency of extinction events observed to date for birds could change in the future, whereas patterns of introduction for birds and both rates for plants might continue unchanged.

Any changes in the relative rates of introductions or extinctions would have impacts on the projections we generated. For plant assemblages, it is conceivable that extinction rates will increase dramatically in the future, particularly if extinction debt manifests strongly in these systems (Sax and Gaines 2008, Jackson and Sax 2010). If such extinctions strongly impact endemic species, then the frequency of homogenizing E10 extinctions would increase, yielding greater homogenization. Further, although plant extinction rates are currently unrelated to the taxonomic richness of communities (Sax et al. 2002), if future extinctions became positively related to assemblage richness (as they are with birds) then this would likely push the assemblages toward increased homogenization. Such extinctions might be prevented, however, if future conservation efforts are successful. For bird assemblages, it is conceivable that current efforts to conserve endangered island species could fail, particularly in the context of additional threats posed by changes in climate (Jetz et al. 2007). If this failure occurs, then rates of homogenizing E10 events are likely to increase, which would further increase homogenization. In contrast, if future conservation efforts are so successful that no or few additional bird extinctions occur, then projected changes in similarity would become dependent on species introductions. Somewhat counterintuitively, reducing species introductions would not necessarily be helpful in reducing homogenization of bird assemblages, since the most frequent introduction events to date have been I01 events, which actually serve to differentiate these systems.

Characteristics of island pairs that are correlated with changes in similarity could influence the projections we calculated. While geographic distance has been a strong predictor of change in some studies (Leprieur et al. 2008, Castro et al. 2010), and differences in area between island pairs could also influence similarity dynamics, these factors were not strong predictors here. Had we examined less isolated islands, such as islands within an archipelago or single ocean basin, we might have found different results, namely such islands might have had higher initial similarity and different event frequencies, both of which could result in different observed or projected changes. The positive relationships we observed between initial similarity and change in similarity were marginally significant for plants and significant for birds, but were weak enough relationships that they did not appear to be driving the dynamics in these systems; instead, it appears to be the interaction between initial similarity and event frequencies that primarily drives the dynamics we observed. However, the observation that only island pairs with low initial similarity had frequent I01 events (Supplementary material Appendix A10) appears to have some importance in understanding the similarity dynamics for plant assemblages. This is because the low frequency of this differentiating event type for island pairs with high initial similarity, which otherwise might have been expected to differentiate, were instead pushed towards homogenization by the constellation of other event types. This tendency likely explains why all plant assemblage pairs have homogenized (Fig. 2) even though a small minority began with initial similarity levels above the average island pair's 'pivot point' of approximately 0.1 (Supplementary material Appendix A6).

In designing our study approach, we made several decisions worth highlighting. First, we calculated average assemblage pairs (as shown in Fig. 5 and Supplementary material Appendix A12) by holding the species richness of assemblage pairs constant across a range of initial similarities. The alternative would have been to hold the richness of individual assemblages constant. If we had chosen the latter option, the results would have differed quantitatively, but not qualitatively, because initial species richness never influences the direction of change in similarity – only the magnitude (Supplementary material Appendix A4). Second, in extrapolating projected similarity, we repeated the same number of introductions and extinctions for each island pair in each future time period. For example, if an island pair is observed to have experienced two E10 events in the past, then our projection method would involve simulating two more E10 events for each time period in the future, rather than re-scaling the number of events with each simulated time step as the species richness of the island pair changes. The alternative approach of re-scaling event rates proportionally to species richness could be valid and merits further exploration. Third, we did not use a multi-site index of dissimilarity as our primary method, nor did we attempt to decompose similarity into discrete turnover and nestedness components. Multi-site methods are advantageous for characterizing patterns of species occurrence across more than two sites (Diserud and Odegaard 2007, Baselga 2013). Likewise, examinations of change in nestedness vs turnover provide additional clarity in understanding changes in similarity that have occurred to date (Harrison et al. 1992, Jost 2007, Baselga 2010). In our study, however, we were most interested in exploring how future trajectories of similarity could differ, and for that purpose, the traditional pairwise indices provide distinct advantages. The pairwise Jaccard index is amenable to extrapolation of observed trends to project future biotic change, and also to simple algebraic rearrangements that demonstrate the role of initial similarity and the effects of the six event types. Nevertheless, comparison of our primary results with those calculated with Balselga's (2010) multi-site index, Beta-SIM, produced results that were qualitatively consistent with our key findings: 1) plant and bird assemblages have both homogenized since human occupation of islands, 2) additional homogenization is projected for both assemblage types, and 3) projections show greater change from present similarity for bird than for plant assemblages.

Our new approach to exploring the interaction between initial similarity and the six types of biotic turnover events offers a framework for understanding similarity dynamics observed in other studies. Specifically, this framework could help explain why, as others suggest, the direction and magnitude of changes in similarity observed are influenced by the taxonomic group, region, and spatial scale of examination (Olden 2006, Cassey et al. 2007, Castro et al. 2010, Shaw et al. 2010), since each of these factors should impact both initial similarity and event frequencies. For instance, the differences found in the direction of change in similarity for California fish faunas across spatial scales – homogenization at largest and smallest, but differentiation at intermediate scales (Marchetti et al. 2001, 2006) could be explained by differences in initial similarity and event frequencies. At the largest spatial scale, the zoogeographic province, the probability that any introduced species will occur in a given sampling area is high (Olden 2006), which would tend to elevate the number of assemblage pairs that share introduced species, thereby increasing the frequency of homogenizing I02 events. Furthermore, since initial similarity is low for most province pairs in this system (i.e. similarity < 0.5; Marchetti et al. [2001], Fig. 2), the homogenizing effects of I02 events are strong (Fig. 3, Supplementary material Appendix A4, A9). In contrast, at the intermediate spatial scale, most non-native fish species have been introduced to only one or a few watersheds with minimal subsequent dispersal (Marchetti et al. 2006), which would result in a high frequency of differentiating I01 events. Finally, at the smallest spatial scale examined by Marchetti et al. (2006), it is much easier for introduced fishes to spread among sampling areas. This would lead to many homogenizing I02 events, which would contribute to the observed homogenization. Beyond these insights for California fishes, our framework could also explain why, across taxa and spatial scales, introductions from nearby sources tend to be more homogenizing than introductions from distant sources (McKinney 2005, Leprieur et al. 2008). Since species from nearby sources tend to be introduced more often within the study system (McKinney 2005) and are more likely to already be present in some sampling areas, they are most likely to cause homogenizing I02 and I12 events, whereas species introduced from distant sources are more likely to cause differentiating I01 events. Ultimately, these examples underscore the utility of considering the influence of initial similarity levels and the frequencies of event types in studying changes in similarity.

Given the broad and often cited interest in understanding homogenization in the context of conservation (Olden 2006, Rooney et al. 2007, Clavel et al. 2011) it seems worthwhile to develop efforts to elucidate future trajectories. Whether we should expect extreme 'Homogecene' scenarios (McKinney and Lockwood 1999, Rosenzweig 2001) is worth investigating. It would be particularly valuable to extend this framework to regions within continental systems, where differences in the levels of historic isolation among different taxonomic groups (and hence differences in initial similarity) could contribute to qualitatively different trajectories of change over the medium term. It is also worth considering the specific management interventions that can most efficiently prevent unwanted outcomes, as our framework shows that individual event types can have dramatically different influences on changes in similarity. Finally, it would also be worthwhile to explore more rigorously the time horizon of past and potentially future changes. Although some islands in our data set were colonized millennia ago and others in the just the last few hundred years, most show relatively similar trends and trajectories, which suggests that relatively recent human actions might be dominating the changes observed to date. If that is true, then future 'time steps' of change might manifest much more rapidly than might otherwise be expected, raising the possibility that some of the more extreme projections we've provided here might be possible in the not too distant future.

Additional references to the data sources may be found in Supplementary material Appendix A1.

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Supplementary material (Appendix ECOG-02652 at <www.ecography.org/appendix/ecog-02652>). Appendix 1–13.