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Research

Non-random patterns of invasion and extinction reduce phylogenetic diversity in island bird assemblages

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Anthropogenically driven changes in bird communities on oceanic islands exemplify the biotic upheaval experienced by island floras and faunas. While the influence of invasions and extinctions on species richness and beta-diversity of island bird assemblages has been explored, little is known about the impact of these invasions and extinctions on phylogenetic diversity. Here we quantify phylogenetic diversity of island bird assemblages resulting from extinctions alone, invasions alone, and the combination of extinctions and invasions in the historic time period (1500 CE to the current), and compare it to the expected phylogenetic diversity that would result if these processes involved randomly selected island bird species. We assessed phylogenetic diversity and structure at the scale of the island ($n = 152$), the archipelago containing the islands ($n = 22$), and the four oceans containing the archipelagos using three measures. We found that extinction, invasion, and the combination of invasion and extinction generally resulted in lower phylogenetic diversity than expected, regardless of the spatial scale examined. We conclude that extinction and invasion of birds on islands are non-random with respect to phylogeny and that these processes generally leave bird assemblages with lower phylogenetic diversity than we would expect under random invasion or extinction.

Introduction

Oceanic islands provide the context for some of the best-known ecological and evolutionary phenomena. They have inspired foundational theories (Darwin 1859, MacArthur and Wilson 1967) housed spectacular examples of adaptive radiation (Losos et al. 1998, Lerner et al. 2011) and exemplified macroecological patterns (Van Valen 1973, Lomolino 1985). On the other hand, islands are among the most threatened ecosystems on Earth (Paulay 1994, Vitousek et al. 1995, Ricketts et al. 2005). Dating back to prehistory (i.e. before 1500 CE), human activities have dramatically altered island ecosystems (Olson and James 1982, James 1995, Steadman 1995), in some cases leading to complete ecological collapse (Flenley et al. 1991). Threats to island biodiversity continued through the colonization of islands by Europeans (Blackburn et al. 2004) and are still present today (Vitousek et al. 1995).



Changes in bird communities on oceanic islands exemplify the biotic upheaval experienced by island floras and faunas. For birds, islands are hotspots of both extinction (Biber 2002) and invasion (Lockwood 2006), with over 90% of extinctions in the historic time period (1500 CE to the current) and 70% of introductions occurring on oceanic islands (Blackburn and Duncan 2001). Extinction and extirpation of island bird species, along with the introduction and establishment of exotics in the historic time period, have generally resulted in little to no change in species richness, as invasions have matched extinctions in number at the island scale (Sax et al. 2002). However, many native island birds are threatened (Lee and Jetz 2011), and the extinction of such species may change this pattern. Despite the fact that species richness from the historic time to the current time period has remained relatively stable, beta-diversity has changed. For example, bird species composition on the Hawaiian Islands has homogenized (i.e. decreased in beta-diversity) as a result of the establishment of common exotics and extinctions of island endemics (Lockwood 2006, Cassey et al. 2007). In contrast, the bird community composition on Guam, which is well-known for biodiversity loss resulting from the invasion of the brown tree snake *Boiga irregularis* (Savidge 1987), has become more distinct (i.e. increased in beta-diversity) compared to other islands in the Marianas archipelago (Cassey et al. 2007). While species richness and beta-diversity of island bird assemblages have been explored, little is known about how phylogenetic diversity has changed as a result of invasion and extinction.

There is increasing interest in incorporating phylogenetic information into measures of biodiversity (Faith 1992, Mace et al. 2003, Winter et al. 2013, Bennett et al. 2014, Veron et al. 2017) as it provides additional information for assessing biodiversity and developing conservation targets beyond species richness (Davies and Buckley 2011). For example, phylogenetic diversity can be a proxy for functional trait diversity (Mouquet et al. 2012), which suggests that maintaining phylogenetic diversity will help maintain ecosystem functioning (Winter et al. 2013). Assemblages with high phylogenetic diversity also retain 'evolutionary potential', which may be important for adaptation to future conditions (Lavergne et al. 2010). Furthermore, rare taxa, which tend to be the focus of conservation efforts, are often evolutionary distinct (i.e. having no closely related taxa) (Mi et al. 2012) and thus can be prioritized based on measures of phylogenetic diversity (Winter et al. 2013). Apart from providing insight into novel patterns and processes, examining extinctions and invasions of island birds in a phylogenetic context provides a complementary measure to pair with species richness and beta-diversity for examining rapidly changing biodiversity patterns on islands.

Extensive research on birds shows that there is taxonomic selectivity for both extinction risk (Gaston and Blackburn 1995, Bennett and Owens 1997, Russell et al. 1998) and the probability of exotic establishment (Lockwood 1999,

Lockwood et al. 2000, Blackburn and Duncan 2001). Eight families – Psittacidae (parrots), Phasianidae (pheasants), Procellariidae (albatrosses), Rallidae (rails), Gruidae (cranes), Cracidae (cracids), Megapodidae (megapodes) and Columbidae (pigeons and doves) – have more species threatened with extinction than expected by chance (Bennett and Owens 1997). Furthermore, extinctions in the historical time period are non-randomly concentrated in species-poor genera (Russell et al. 1998, Szabo et al. 2012). Across all birds, non-random extinction has resulted in a greater loss of phylogenetic diversity than expected if extinctions were random (Purvis et al. 2000, Von Euler 2000). For exotic species, taxonomic analyses of island invaders have shown that the seven families – Anatidae (ducks and geese), Passeridae (sparrows and estrildid finches), Psittacidae, Phasianidae, Columbidae, Rheidae (rheas), and Odontophoridae (New World quails) – have a greater number of successfully established exotic species than expected by chance (Lockwood 1999).

How taxonomic selectivity in extinction and invasion across the avian phylogeny contributes to the change in phylogenetic diversity at the local scale (e.g. islands) is unknown. Changes in phylogenetic diversity will depend on the interacting effects of the evolutionary history of the island, extinctions, and invasions (Heard and Mooers 2000, Von Euler 2000, Jackson et al. 2015). For example, taxonomic selectivity in extinctions may not greatly reduce phylogenetic diversity on a given island if species that are closely related to the extinct species remain. On the other hand, extinctions targeting species poor groups (Russell et al. 1998) resulting in the loss of entire clades, can substantially reduce phylogenetic diversity. In terms of invasions, exotics that are distantly related to native island avifaunas may increase phylogenetic diversity markedly, while exotics that are closely related to natives will add less phylogenetic diversity. Interestingly, because several of the avian families that have experienced high extinction also contain high numbers of invaders (e.g. Psittacidae), invaders may simply replace the phylogenetic diversity lost to extinction, resulting in little to no change in phylogenetic diversity (Jackson et al. 2015, Sobral et al. 2016).

Here we quantify phylogenetic diversity of breeding island bird assemblages resulting from extinctions alone, invasions alone, and the combination of extinctions and invasions in the historic time period (1500 CE to the current time), and compare it to the expected phylogenetic diversity that would result if these processes involved randomly selected island bird species. We explore phylogenetic diversity at the scale of islands ($n = 152$), archipelagos containing the islands ($n = 22$), and the four oceans containing the archipelagos to better understand the influence of spatial scale of invasions and extinctions on phylogenetic diversity. By taking a phylogenetic perspective to understanding how invasions and extinctions have reshaped bird assemblages on oceanic islands, we hope to gain insight into the ecological and evolutionary fate of island bird communities.

Methods

Dataset

We extracted presence/absence data from a database of bird species on 152 oceanic islands compiled by Blackburn et al. (2004) and Cassey et al. (2007) from species lists, field guides, and literature. These data represent two time periods, historical and current. The species lists for the historical time period reflect species present when islands were discovered by European colonists (~1500 CE), and thus, they do not include species that went extinct in the pre-historic time period due to human activities (Steadman 1995, Duncan et al. 2013). The current time period lists reflect species that have gone extinct or been extirpated and exotics species that have established after the arrival of Europeans (i.e. the current composition). We also used these island lists to create presence/absence species lists for the archipelagos and oceans that the islands are embedded in for both the historical and current time periods (see Supplementary material for species lists).

We obtained island characteristics from the literature including: distance to mainland in km ('isolation'), island area in km² ('area'), time since first human arrival ('first human arrival'), island elevation in m ('elevation'), current human population size ('human population'), number of native bird species ('native richness'), number of exotic bird species that established ('exotic richness'), and number of native bird species that have gone extinct ('native extinctions').

Phylogenetic tree

Estimates of phylogenetic diversity and structure depend on a phylogenetic tree, usually with ultrametric branch lengths scaled to time (Faith 1992, 1994, 2002, Helmus et al. 2007). For all analyses, we first used the phylogenetic tree of Burleigh et al. (2015), which contains 6714 of the ~10 500 bird species and was built from a 29-locus supermatrix using maximum likelihood (ML), implemented in RAxML (Stamatakis 2006). The branch lengths were scaled to time (in millions of years) and made ultrametric using penalized likelihood implemented in r8s (Sanderson 2003). The penalized likelihood analysis used 20 carefully vetted fossil calibrations throughout the tree, and the root was constrained to a maximum age of 130 million yr ago. We used a smoothing parameter of 10, which was determined by a cross validation analysis using the fossil calibrations. To examine whether our results are robust to different estimates of the avian phylogeny, we also used an avian tree assembled by Jetz et al. (2012) that was built using molecular data from 6663 bird species based on the backbone higher-level topology from Hackett et al. (2008). The trees from Jetz et al. (2012) and Burleigh et al. (2015) share a similar overall topology; however, there are some differences in the ultrametric branch lengths; for example, the Jetz et al. (2012) tree indicates the origin of many major lineages before the Cretaceous-Paleogene extinction, while the Burleigh et al. (2015) tree indicates that most lineages arose afterwards.

The ML tree from Burleigh et al. (2015) uses species names from the Clements taxonomy ver. 6.6 (Clements et al. 2013). We first reconciled the island species lists with the Clements taxonomy, for example by checking taxonomic histories in AviBase (<<http://avibase.bsc-eoc.org/avibase.jsp>>). However, 648 of the total 1528 species, including the extinct taxa, were not found in the Burleigh et al. (2015) tree even after reconciling the names. To account for uncertainty in the phylogenetic placement of these missing species, we generated 100 'augmented trees' by randomly inserting the missing taxa into the ML tree in a position from the stem branch preceding the most recent common ancestor of the species from the same family in the tree to the tips descending from the stem. The branch length of the inserted branches extended to the present time, so the augmented tree remained ultrametric.

We similarly reconciled some of the names from the Jetz et al. (2012) tree to the Clements taxonomy (Clements et al. 2013). The Jetz et al. (2012) study augments the tree of species with molecular data with most extant birds without molecular data. Yet these augmented still do not include many species found on the island species lists, which include extinct species. We used the same approach described above to generate 100 augmented trees that include the 648 species that were in the island species lists but missing from the Jetz et al. (2012) tree of species with molecular data. A list of the inserted taxa for both Jetz et al. (2012) and Burleigh et al. (2015), the stem groups in which they were inserted, and the 100 augmented trees from each study are available in the Supplementary material.

Phylogenetic diversity analyses

For each set of assemblages (i.e. islands, archipelagos, or oceans), we performed analyses to look at the impact of extinction, invasion, and extinction and invasion together on three common measures of phylogenetic diversity. The first measure, phylogenetic diversity (PD) (Faith 1994), is the sum of all branch lengths present in an assemblage. Our second metric is mean pairwise distance (MPD), which is calculated by taking the mean pairwise phylogenetic distance of all species in a given assemblage. Finally, we calculated the mean nearest taxon distance (MNTD) which takes the mean nearest neighbor phylogenetic distance across all species in an assemblage. For each analysis, we estimated each measure of phylogenetic diversity or structure (PD, MPD, and MNTD) for each locale based on all 100 augmented ultrametric trees from the Jetz et al. (2012) and Burleigh et al. (2015) studies. That is, for each assemblage (island, archipelago, or ocean), we calculated the branch lengths of the subtree that includes all of its species. We then averaged the given metric (for simplicity, we will use PD as an example when we discuss our methods from here on) across the 100 augmented trees, and consider this the 'observed PD'. All metrics were calculated using phylocom ver. 4.2 (Webb et al. 2008).

Extinction analysis

In the extinction analysis, we first selected all assemblages that had at least one extinction or extirpation event after European colonization. Again, we conducted each analysis using PD, MPD, and, MNTD, but only use PD in the text for simplicity. For each of the 100 augmented trees from the Jetz et al. (2012) or Burleigh et al. (2015) studies, we measured the PD after the extinction event(s) and averaged them. This is the 'observed PD' after extinction. Then, on each augmented tree, we performed 100 replicates in which we randomly removed the same number of taxa from the assemblage as went extinct. For each augmented tree, we then calculated the standardized change in PD, which is the (observed PD – average PD from 100 random extinctions)/(standard deviation of the PD from 100 random extinctions). We report the average standardized change in PD from the 100 augmented trees, which we will refer to as 'stdPD'. A negative stdPD indicates that the observed extinction event resulted in lower PD than we would expect from a random extinction event involving the same number of species. On the other hand, a positive stdPD indicates that the observed extinction event resulted in greater PD than we would expect under random extinction of the same number of species.

Invasion analysis

In the invasion analyses, we first selected all assemblages that had at least one successful invasion event after European arrival. For each of the 100 augmented trees from the Jetz et al. (2012) or Burleigh et al. (2015) studies, we measured the PD after the invasion event(s) (i.e. including exotics in the tree), without removing the species that went extinct or were extirpated and then averaged these values. This is the 'observed PD' after invasion. Then, on each augmented tree, we performed 100 random invasion sequences in which we added to the historical species list (and tree) the observed number of exotics by randomly selecting them without replacement from a null pool of species. For island and archipelago assemblages, we used two different null pools of species: one consisting of all exotics that occur on any island in the data set (global invasion pool) and one consisting of all exotics that occur on any island in the ocean in which the island/archipelago is found (ocean invasion pool). For the ocean assemblages, we only used the global invasion pool. When selecting the random invasive species for an assemblage, we excluded any species that were in the historical species list of the focal assemblage.

For each augmented tree, we then calculated the stdPD, which is the (observed PD – average PD from 100 random invasions)/(standard deviation of the PD from 100 random invasions). We report the average stdPD from the 100 augmented trees. A negative stdPD indicates that the observed invasion resulted in lower PD than we would expect from a random invasion event involving the same number of species (without any extinctions), and a positive stdPD indicates that the observed invasion event

resulted in greater PD than we would expect from a random invasion event involving the same number of species, again, without extinctions.

Extinction + invasion analysis

The extinction + invasion analyses are a combination of the individual extinction and invasion analyses. We selected all assemblages that had at least one extinction/extirpation and at least one successful invasion event after European contact. For each of the 100 augmented trees from the Jetz et al. (2012) or Burleigh et al. (2015) studies, we measured the PD for the current species list, which accounts for all of the extinctions and invasions that occurred after European contact. The average of these values is the 'observed PD' after extinction and invasion. Then, on each augmented tree, we performed 100 replicates to randomly remove species from an assemblage as described in the Extinction analysis and then to randomly add species to an assemblage in accordance with the Invasion analysis. For each augmented tree, we then calculated the stdPD, which is the (observed PD – average PD from 100 random extinctions and invasions)/(standard deviation of the PD from 100 random extinctions and invasions). We report the average stdPD from the 100 augmented trees. A negative stdPD indicates that the observed change in species composition through extinction and invasion resulted in lower PD than we would expect from a random change in composition involving the same number of extinctions and invasions. A positive stdPD indicates that the observed change in species composition via extinction and invasion resulted in greater PD than randomly expected.

Drivers of island PD

We explored the relationship between each measure of standardized phylogenetic diversity or structure (i.e. stdPD, stdMPD, and stdMNTD) at the island scale and eight island attributes (Supplementary material Appendix 1). First, we screened the variables with univariate linear regression. We then built models with all subsets of variables that had p-values ≤ 0.10 in the univariate analyses and compared models using AIC.

Data deposition

Data available from the Dryad Digital Repository: <<http://dx.doi.org/10.5061/dryad.rs714>> (Baiser et al. 2017).

Results

Our results are qualitatively similar using the Jetz et al. (2012) and the Burleigh et al. (2015) trees, and the conclusions we draw based on each tree are the same. We present the results from the Burleigh et al. (2015) tree below and the results from the Jetz et al. (2012) tree in Supplementary material Appendix 2.

Extinction and extirpation

Island scale

Of the 152 islands on our dataset, 72 experienced the extinction or extirpation of one or more native species. For these 72 islands, the mean number of species lost per island was 3.95 (min = 1, max = 20, SD = 4.43). The average standardized phylogenetic diversity, mean pairwise distance, and mean nearest taxon distance values were all negative (Table 1), and over 74% of islands had lower phylogenetic diversity, mean pairwise distance, and mean nearest taxon distance (i.e. negative stdPD, stdMPD, and stdMNTD values) than expected under random species loss (Table 1, Fig. 1A) (Supplementary material Appendix 3 for stdMPD and stdMNTD figures).

Archipelago scale

At the archipelago scale, 14 of out 22 archipelagos experienced extirpation or extinction. The mean standardized PD, MPD, and MNTD across these 14 archipelagos were all negative (Table 1). Eleven archipelagos showed lower PD and MPD than expected under random extinction, while 10 archipelagos had lower than expected MNTD (Table 1, Fig. 1B) (Supplementary material Appendix 3 for stdMPD and stdMNTD figures).

Ocean scale

All four oceans in our study had lower PD, MPD, and MNTD than expected under random species loss (Table 1, Fig. 1C) (Supplementary material Appendix 3 for stdMPD and stdMNTD figures). The average standardized PD, MPD, and MNTD were negative for each ocean (Table 1).

Invasion

Island scale

We found a general trend that species' invasions left islands with lower phylogenetic diversity than expected from randomly adding species from the invasive species pool. Of the 94 islands that had one or more exotic species establish, the average number of exotic species was 6.77 (SD = 8.56). The mean standardized PD, MPD, and MNTD were all negative (Table 2). However, stdPD and stdMNTD were lower than stdMPD (Table 2). The establishment of exotic birds resulted in lower PD and MNTD than expected under random

introductions for 75 islands (80%), but only 54 islands (57%) has a lower than expected MPD under random introductions (Table 2, Fig. 2A) (Supplementary material Appendix 3 for stdMPD, and stdMNTD figures). Furthermore, we found similar results using the oceanic invasive species pool for the null model (Supplementary material Appendix 4).

Archipelago scale

The 15 archipelagos that experienced the establishment of one or more exotic species had negative stdPD and stdMNTD and a positive stdMPD (Table 2). Overall 14 (93%) and 10 (67%) archipelagos had a lower PD and MNTD, respectively, than expected under random invasion, while only six (40%) archipelagos had lower than expected MPD (Table 2, Fig. 2B) (Supplementary material Appendix 3 for stdMPD and stdMNTD figures). The same pattern was also observed when using the oceanic invasive species pool for the null model (Supplementary material Appendix 4).

Ocean scale

Exotic species introductions at the ocean scale, showed mixed results for the three measures of phylogenetic diversity. Of the four oceans, three, two, and one showed lower than expected PD, MPD, and MNTD, respectively (Table 2, Fig. 2C) (Supplementary material Appendix 3 for stdMPD and stdMNTD figures). Mean values were negative for stdPD and stdMPD and positive for stdMNTD (Table 2).

Combination of extinction/extirpation and invasion

Island scale

Fifty-five islands experienced both invasions and extinctions from the historical to the current time period. These islands had a negative mean standardized phylogenetic diversity with over 76% of the islands exhibiting lower PD, MPD, and MNTD than expected under random invasions and extinctions (Table 3, Fig. 3A) (Supplementary material Appendix 3 for stdMPD and stdMNTD figures). We observed the same pattern using the oceanic invasive species pool for the null model (Supplementary material Appendix 4).

Archipelago scale

Eleven archipelagos experienced both extinctions/extirpations and invasions. Across all 11 archipelagos, mean standardized phylogenetic diversity was negative for all metrics (Table 3).

Table 1. Standardized phylogenetic diversity (stdPD, stdMPD, and stdMNTD) resulting from extinctions/extirpations at the island, archipelago and ocean scales. Positive refers to the number of locales (i.e. islands, archipelagos, or oceans) in which the standardized phylogenetic metric was > 0 and thus showed greater phylogenetic diversity than expected under random extinctions. Negative refers to the number of locales in which the standardized phylogenetic metric was < 0 and thus showed lower phylogenetic diversity than expected under random extinctions. The mean and standard deviation for the set of locales is also reported.

Metric	Island			Archipelago			Ocean		
	PD	MPD	MNTD	PD	MPD	MNTD	PD	MPD	MNTD
Positive	19	18	17	3	3	4	0	0	0
Negative	53	54	55	11	11	10	4	4	4
Mean (SD)	-0.7 (0.93)	-0.74 (1.03)	-0.68 (0.91)	-0.67 (0.80)	-0.58 (1.08)	-0.55 (0.60)	-1.43 (0.47)	-1.58 (1.32)	-1.33 (0.56)

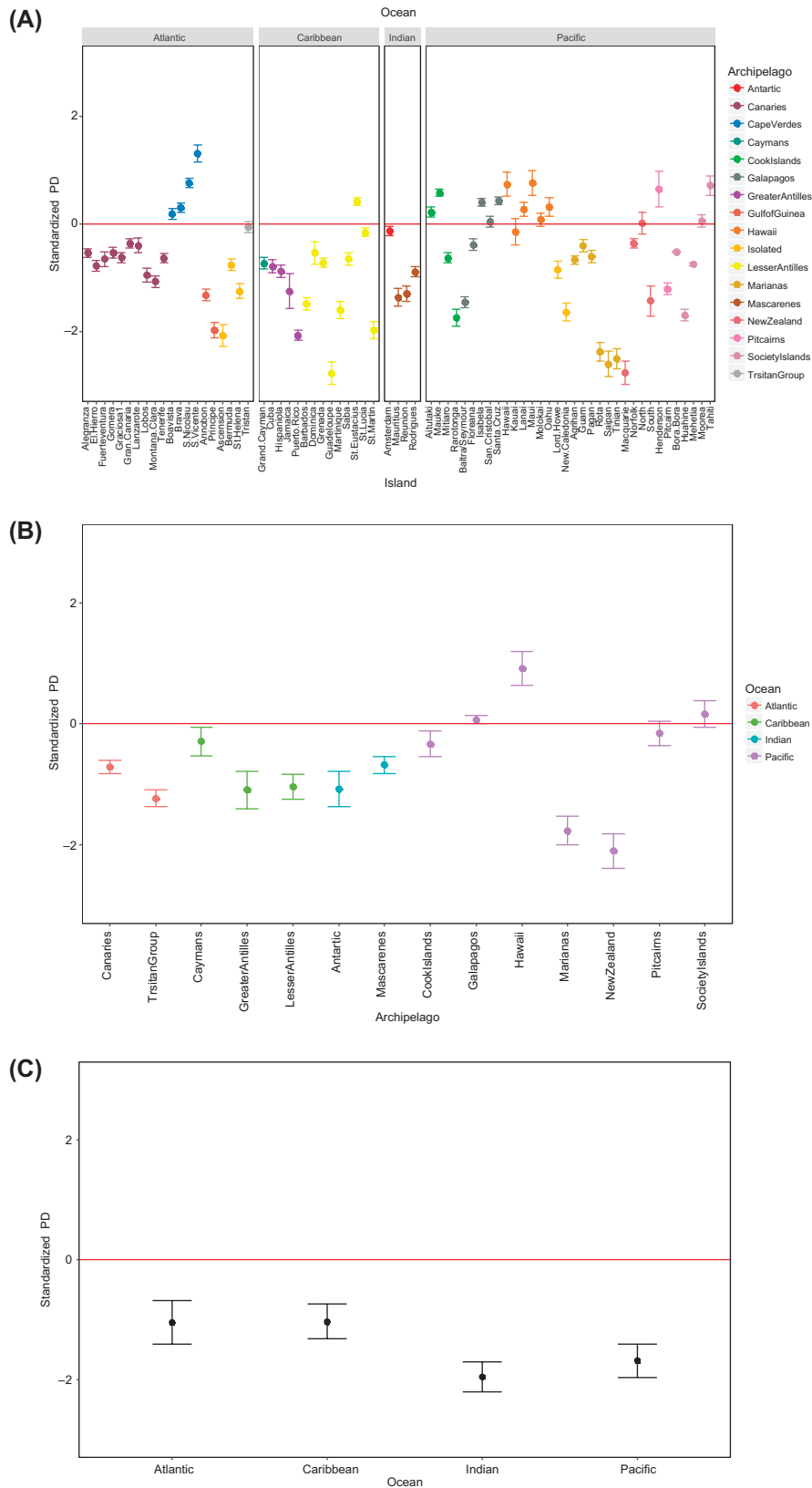


Figure 1. Standardized phylogenetic diversity (stdPD) as a result of extinctions/extirpations at the (A) island scale, (B) archipelago scale, and (C) ocean scale. Mean \pm one standard deviation from the 100 augmented trees for each island/archipelago/ocean are shown. The same figures for stdMPD and stdMNTD are in Supplementary material Appendix 3.

Table 2. Standardized phylogenetic diversity (stdPD, stdMPD, and stdMNTD) resulting from invasions at the island, archipelago and ocean scales. Positive refers to the number of locales (i.e. islands, archipelagos, or oceans) in which the standardized phylogenetic metric was >0 and thus showed greater phylogenetic diversity than expected under random invasions. Negative refers to the number of locales in which the standardized phylogenetic metric was <0 and thus showed lower phylogenetic diversity than expected under random invasions. The mean and standard deviation for the set of locales is also reported.

Metric	Island			Archipelago			Ocean		
	PD	MPD	MNTD	PD	MPD	MNTD	PD	MPD	MNTD
Positive	19	40	19	1	9	5	1	2	3
Negative	75	54	75	14	6	10	3	2	1
Mean (SD)	-0.84 (0.91)	-0.07 (1.17)	-0.85 (1.00)	-0.65 (0.80)	0.31 (1.26)	-0.41 (0.91)	-0.18 (0.90)	-0.14 (1.34)	0.48 (1.11)

Ten of the eleven archipelagos had lower PD, MPD, and MNTD than expected under a sequence of random invasions and extinctions (Table 3, Fig. 3B) (Supplementary material Appendix 3 for stdMPD and stdMNTD figures). Using the oceanic pool of exotic species, more archipelagos had greater stdMNTD and stdPD than expected and the mean stdMNTD and stdPD was positive (Supplementary material Appendix 4).

Ocean scale

At the ocean scale, extinctions and invasions rendered bird assemblages with negative stdPD, stdMPD, and stdMNTD (Table 3). All four oceans had lower MNTD and MPD than expected under random invasion and extinction, and three of the four oceans had a lower than expected PD (Table 3, Fig. 3C) (Supplementary material Appendix 3 for stdMPD and stdMNTD figures).

Drivers of island phylogenetic diversity

Extinction and extirpation

Of the eight explanatory variables (Supplementary material Appendix 1) we analyzed in relation to our phylogenetic diversity metrics under extinction, only three variables (first human arrival, island isolation, and exotic species richness) had p -values ≤ 0.10 in the univariate screening stage of our analysis. The model with stdMNTD as a response variable did not have any variables with p -values ≤ 0.10 . The best fit model for stdPD showed a trend that islands that were more isolated and had earlier human arrivals tended to have lower stdPD. (Supplementary material Appendix 4 Table D1). The top model for stdMPD showed a significant positive relationship with island isolation (Supplementary material Appendix 4 Table D2).

Invasion

Five explanatory variables (native richness, native extinctions, exotic richness, island isolation, and first human arrival) had univariate relationships with our phylogenetic diversity metrics under invasion with p -values ≤ 0.10 . The top ranked regression models ($\Delta AIC < 2$) for stdPD showed that only exotic bird richness and isolation were significant (p -values ≤ 0.05 ; Supplementary material Appendix 4 Table D3). stdPD had a negative relationship with exotic bird richness (Fig. 4A) and a positive relationship with isolation

(Fig. 4B). The top ranked models ($\Delta AIC < 2$) for stdMPD showed that islands with earlier human arrivals had significantly lower stdMPD (p -values ≤ 0.05 ; Supplementary material Appendix Table D4). There was also a trend that more isolated islands had higher stdMPD (Supplementary material Appendix 4 Table D4). The top ranked models for stdMNTD, showed a significant negative relationship with exotic bird species richness and a positive relationship with the time since first human arrival (Supplementary material Appendix 4 Table D5).

Combination of extinction/extirpation and invasion

Five explanatory variables (native richness, native extinctions, exotic richness, and island elevation) had univariate relationships with our phylogenetic diversity metrics under extinction and invasion with p -values ≤ 0.10 . For stdMNTD, we found no univariate relationships with p -values ≤ 0.10 . The top ranked regression models ($\Delta AIC < 2$) showed that only exotic richness was significantly related to stdPD (Supplementary material Appendix 4 Table D6). Islands with a greater number of exotic species had lower stdPD (Fig. 5). With stdMPD as the response variable, no variables were significant in the top ranked models (Supplementary material Appendix 4 Table D7).

Discussion

We found that species extinction, invasion, and the combination of both generally resulted in lower than expected phylogenetic diversity at the island, archipelago, and ocean scale in the historical time period. This first indicates that the extinction or extirpation of island birds targets evolutionary distinct species (i.e. longer phylogenetic branch lengths than expected by chance) and/or multiple species in a clade, resulting in the loss of entire clades. Secondly, exotic species tend to be relatively closely related to native species and/or closely related to other invaders that establish at the same locale, and thus, they represent the addition of shorter than expected phylogenetic branch lengths. Furthermore, the combination of species losses and gains has resulted in lower phylogenetic diversity than expected. Exploring specific cases of islands that had the highest and lowest phylogenetic diversity relative to random expectation can help elucidate how the invasion and extinction processes alter phylogenetic diversity.

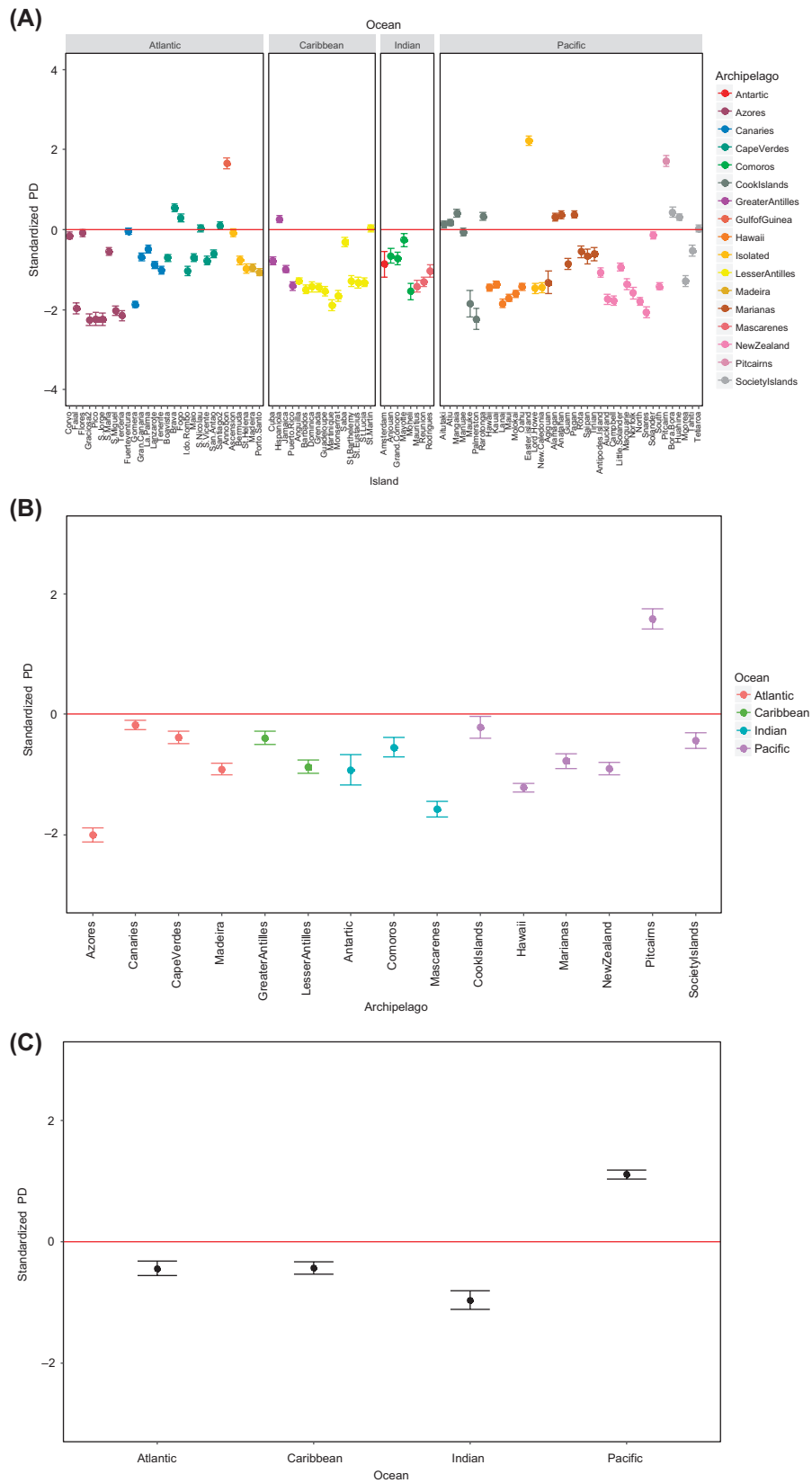


Figure 2. Standardized phylogenetic diversity (stdPD) as a result of invasions at the (A) island scale, (B) archipelago scale, and (C) ocean scale. Mean \pm one standard deviation from the 100 augmented trees for each island/archipelago/ocean are shown. The global invasive species pool was used for randomizations. The same figures for stdMPD and stdMNTD are in Supplementary material Appendix 3.

Table 3. Standardized phylogenetic diversity (stdPD, stdMPD, and stdMNTD) resulting from invasions and extinctions at the island, archipelago and ocean scales. Positive refers to the number of locales (i.e. islands, archipelagos, or oceans) in which the standardized phylogenetic metric was >0 and thus showed greater phylogenetic diversity than expected under a random sequence of invasions and extinctions. Negative refers to the number of locales in which the standardized phylogenetic metric was <0 and thus showed lower phylogenetic diversity than expected under random invasions and extinctions. The mean and standard deviation for the set of locales is also reported.

Metric	Island			Archipelago			Ocean		
	PD	MPD	MNTD	PD	MPD	MNTD	PD	MPD	MNTD
Positive	10	13	13	1	1	1	1	0	0
Negative	45	42	42	10	10	10	3	4	4
Mean (SD)	-1.02 (1.00)	-0.74 (1.04)	-0.69 (0.98)	-0.92 (1.14)	-0.77 (1.06)	-0.77 (0.52)	-1.29 (1.36)	-1.35 (0.97)	-1.38 (0.84)

One of the islands with the lowest phylogenetic diversity as a result of extinctions and extirpations is Macquarie Island (stdPD = -2.77, stdMNTD = -1.51, stdMPD = -1.00), located in the Pacific Ocean. The Macquarie Island rail *Gallirallus philippensis macquariensis* and the Macquarie Island parakeet *Cyanoramphus erythrotis* went extinct in the historical time period. These species were the only members of their respective orders on the island, and thus, their loss greatly reduced phylogenetic diversity. The loss of species that are the only representative of their order or family is a common occurrence among islands with low standardized phylogenetic diversity (e.g. the loss of the only Anseriform, *Anas platyrhynchos* on Tinian (stdPD = -2.51, stdMNTD = -1.20, stdMPD = -1.86) and Saipan (stdPD = -2.61, stdMNTD = -1.03, stdMPD = -1.98) in the Marianas). However, the island of Guadeloupe in the Lesser Antilles lost several species that were the only representatives of their respective families and additionally lost three closely related species that were the only representatives of the order Psittaciformes. These processes interact on Guadeloupe resulting in greater than expected loss of phylogenetic diversity (stdPD = -2.78, stdMNTD = -1.39, stdMPD = -0.65). On the other hand, the island of São Vicente in the Cape Verde Islands is among the islands with the highest standardized phylogenetic diversity (stdPD = 1.30, stdMNTD = 1.55, stdMPD = 1.17) as a result of species losses. Two of the species that were extirpated, *Sylvia atricapilla* and *Passer hispaniolensis*, left behind extant species in their genera (*Sylvia conspicillata* and *Passer iagoensis*, respectively) and the third extirpated species, *Milvus milvus*, has an extant species in the same order. Therefore, these extirpations reduced phylogenetic diversity by relatively little (i.e. the loss short phylogenetic branch lengths) because of the closely related extant species inhabiting São Vicente.

Several factors must be considered in understanding the influence of extinctions and extirpations on phylogenetic diversity. The loss of phylogenetic diversity depends on whether or not species losses are phylogenetically clustered (Nee and May 1997, Purvis et al. 2000, Veron et al. 2017), the underlying structure of the phylogenetic tree for the bird communities in our study (Purvis et al. 2000, Von Euler 2000, Veron et al. 2017), and whether or not extinctions and extirpations are concentrated in species poor clades (Russell et al. 1998, Szabo et al. 2012). The examples above demonstrate that clustered extinctions (e.g. Psittaciformes in Guadeloupe) and extinctions targeting species-poor clades

(e.g. Macquarie Island) all contribute to the greater than expected loss of phylogenetic diversity in oceanic island bird assemblages. The massive extinction that occurred due to pre-historic human colonization of oceanic islands (Olson and James 1982, Steadman 1995, Duncan et al. 2013) likely also influenced the structure of the phylogenetic tree for many locales in our study. It is estimated that thousands of oceanic island bird species went extinct in the Pacific Ocean alone before the arrival of Europeans. These extinctions were non-random and left certain clades with few representative species. For example, Steadman (1995) estimated that each Pacific island had one to four endemic rail species. Extinctions and extirpations in the prehistoric time period greatly reduced Rallidae diversity at the island, archipelago, and ocean scale compared to its prehistoric level (Steadman 1995). Many species that survived this extinction filter went extinct after European contact (e.g. *Gallirallus philippensis macquariensis* on Macquarie Island) or are endangered today (e.g. *Porzana atra* on Henderson Island). Columbidae and Psittacidae likely underwent similar prehistoric extinctions (Steadman 1995). Tree imbalance due to prehistoric extinctions and non-random extinction in the historical time period likely both contributed to greater than expected loss of phylogenetic diversity in island bird assemblages that we observed. This result is consistent with findings that the combination of tree imbalance and non-random extinctions were drivers of phylogenetic diversity loss across the global evolutionary tree of birds (i.e. islands and continents) in the historical time period (Von Euler 2000).

Turning our focus to invasions, Graciosa Island in the Azores was among the islands with the lowest standardized phylogenetic diversity (stdPD = -2.25, stdMNTD = -2.30, stdMPD = -1.47) as a result of exotic species establishment. Three exotic species successfully established on Graciosa. The rock dove *Columba livia* is in the same genus as the native *Columba palumbus azorica*, and the invaders *Serinus canaria* and *Carduelis* are in the same family (Fringillidae) as the native *Fringilla coelebs*. The close phylogenetic relationship between the exotics and extant natives, and the fact that two of the exotics are closely related to each other, resulted in the addition of less phylogenetic diversity than expected at random.

The question of whether successfully established exotics are more closely or distantly related to native species was first asked by Darwin (1859), who suggested that exotic plants

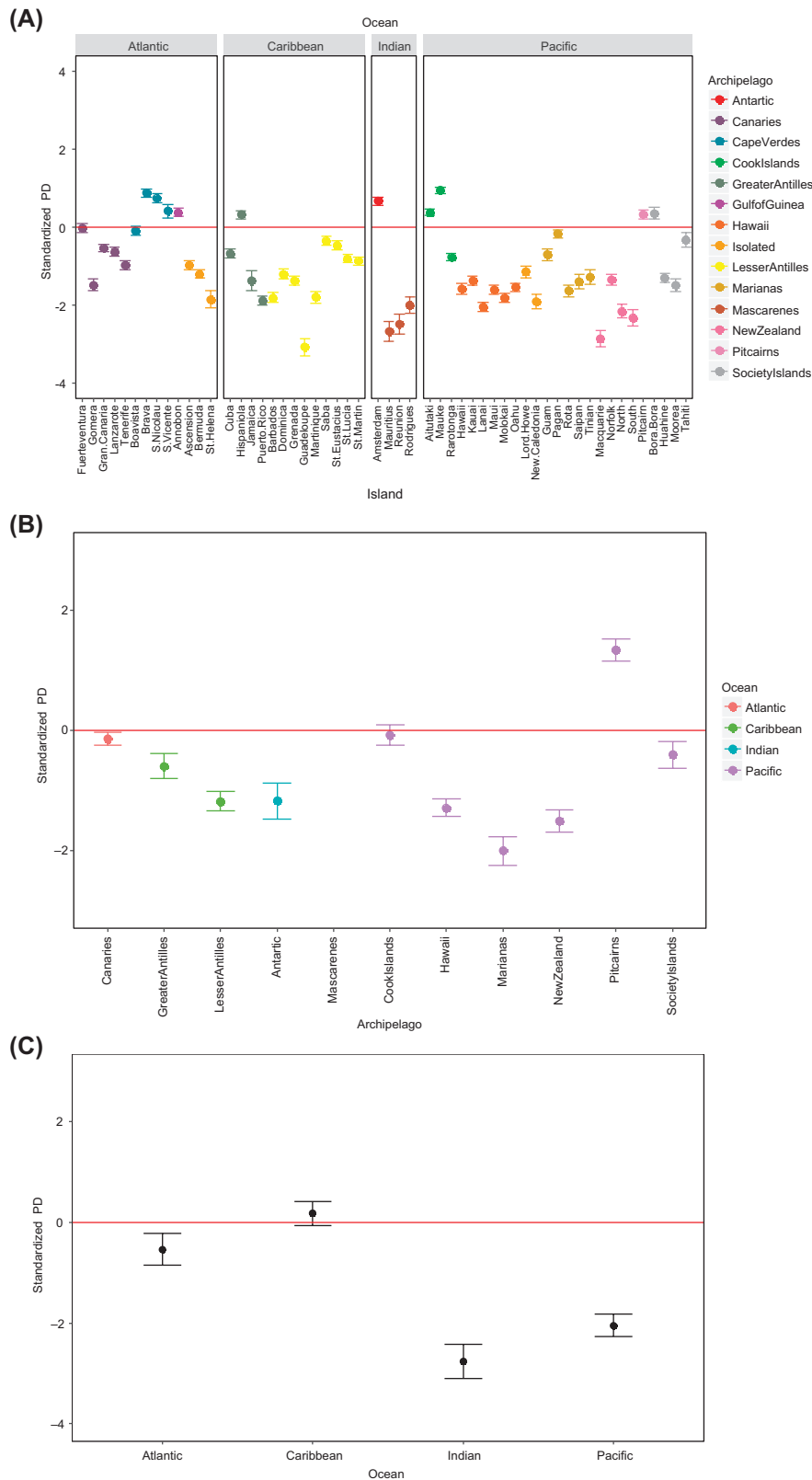


Figure 3. Standardized phylogenetic diversity (stdPD) as a result of extinctions/extirpations and invasions at the (A) island scale, (B) archipelago scale, and (C) ocean scale. Mean \pm one standard deviation from the 100 augmented trees for each island/archipelago/ocean are shown. The global invasive species pool was used for invasion randomizations. The same figures for stdMPD and stdMNTD are in Supplementary material Appendix 3.

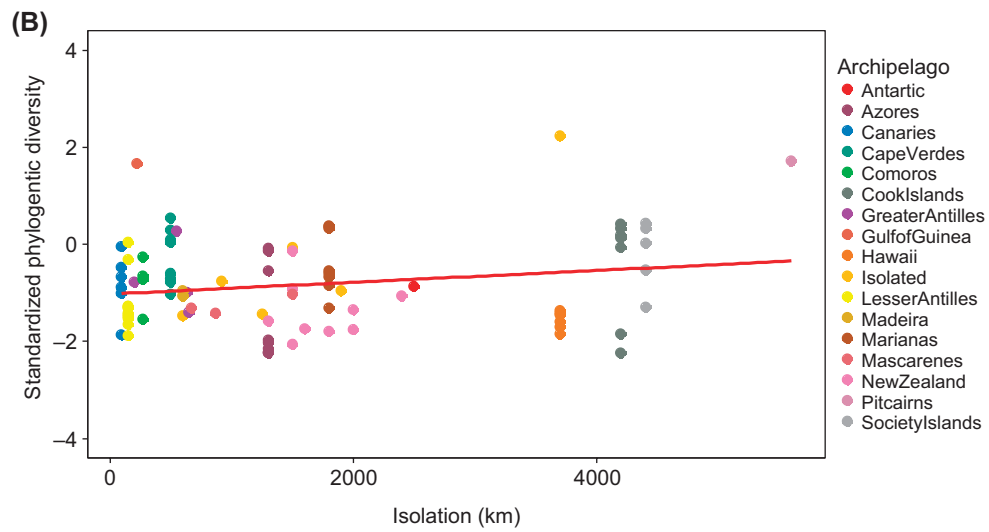
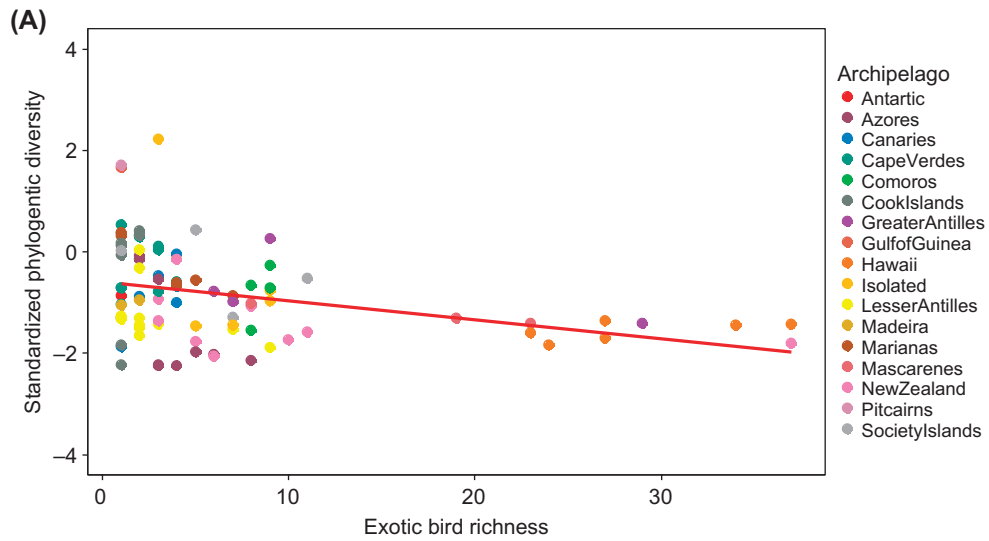


Figure 4. Univariate relationship between standardized phylogenetic diversity (stdPD) due to species invasion and (A) exotic species richness and (B) isolation.

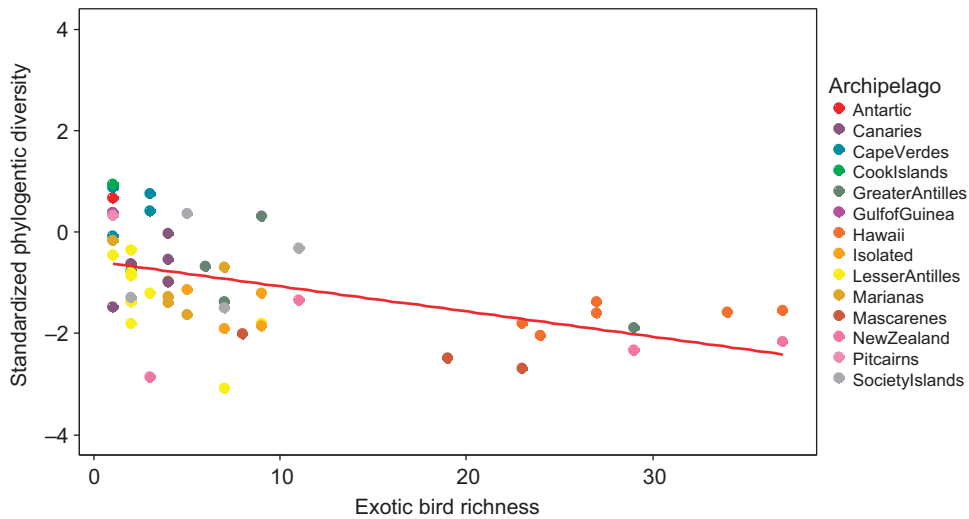


Figure 5. Univariate relationship between standardized phylogenetic diversity (stdPD) due to species invasion and extinctions and exotic species richness.

were less likely to establish in the presences of congeneric species. Our result of lower phylogenetic diversity than expected under random invasion from either the global or ocean invader pools for the majority of islands suggests the opposite of Darwin's naturalization hypothesis. As exemplified by species invasion on Graciosa, exotic species that establish are more closely related to native species or other exotics that have established. Supporting our conclusion, Maitner et al. (2012) showed that successfully established exotic birds are more closely related to extant native species than failed invaders in New Zealand and Hawaii (and Florida). However, the presences or absence of closely related species is likely not the only factor determining invasion success. For example, selectivity in the transport stage (Lockwood et al. 2013) and differences in propagule pressure (Lockwood et al. 2009, Cassey et al. 2014) may play a role in patterns of establishment and thus phylogenetic diversity on islands. In addition, not every species in the invader pool was introduced to each island, archipelago, or ocean.

Some islands receive evolutionarily distinct exotics. The island of Pitcairn in the Pitcairn archipelago was one of the islands that had greater phylogenetic diversity than expected (stdPD = 1.71, stdMNTD = 1.54, stdMPD = 2.66) due to invasion. This is due to the establishment of *Gallus gallus*, which is the only member of Galliformes on the island. Not only does this species represent a new order on the island, but Galliformes descend from a basal split within neoaves (i.e. they are associated with a long phylogenetic branch length). The introduction of *Gallus gallus* similarly drives the greater than expected phylogenetic diversity observed for the Pitcairn archipelago. It also appears that the Pacific Ocean received some evolutionary distinct species resulting in greater phylogenetic diversity than expected. Although this scenario occurs in a few cases, it appears to be uncommon in the islands, archipelagos, and oceans in our study.

While exploring how extinction and invasion independently alter phylogenetic diversity is important for understanding each processes, current patterns of phylogenetic diversity on islands, archipelagos, and oceans usually depend on both. Because many of the same orders of birds are non-randomly targeted for both extinction and invasions (Lockwood et al. 2000), it is possible that combined effect of invasions and extinctions could differ from that of extinctions and invasions separately. Considered in tandem, the extinction of a species may not represent a large loss of phylogenetic diversity if a closely related exotic species establishes in its place. On the other hand, an exotic species can represent the addition of a relatively large amount of phylogenetic diversity when it is replacing the extinct species as opposed to if it was simply added to the assemblage with no extinctions. While clearly some taxonomic replacement is taking place (e.g. Psittaciformes in the Mascarenes (Jackson et al. 2015)), this does not appear to be a common occurrence (Sobral et al. 2016) as our results show that the lower than expected phylogenetic diversity observed under extinctions and invasions

independently is also observed when they are considered at the same time.

A lower than expected PD, MPD, MNTD does not necessarily mean that the net values for these values has decreased. Comparing standardized measures of phylogenetic diversity with change in phylogenetic diversity (e.g. for PD, $\Delta PD = PD_{\text{current}} - PD_{\text{historical}}$) between the historical and current time periods allows us to explore this relationship (Appendix D). The majority of assemblages had negative standardized phylogenetic diversity (e.g. stdPD) and a positive change in raw phylogenetic diversity (e.g. ΔPD), indicating that even though these assemblages may have had a net increase in raw measures of phylogenetic diversity, the invasions and extinctions are phylogenetically less diverse than expected under random invasions and extinctions. Generally, islands, archipelagos (e.g. Hawaiian Islands, New Zealand) and oceans (e.g. Pacific) that had the greatest number of invaders also had the largest positive change in raw phylogenetic diversity (Supplementary material Appendix 4). Islands (e.g. Guam, Rodrigues), archipelagos (e.g. Mascarenes) and oceans that had both negative standardized phylogenetic diversity and negative change in raw phylogenetic diversity tended to have more extinctions than invasions (Supplementary material Appendix 4).

Correlations with island properties can lend insight into what may be driving patterns of phylogenetic diversity in bird assemblages. Overall, our explanatory variables explained little variation in our measures of standardized phylogenetic diversity. However, islands that were more isolated tended to lose less phylogenetic diversity from extinctions than expected. Focusing on invasions only, the significant negative relationship between stdPD and the number of exotic species on an island suggests that the more invaders an island receives the more likely the invaders will be closely related to one another and thus introduce shorter branch lengths than expected from random draws from the invader pool. This may be caused in part because nearly 40% of the islands with one or two invaders had a Galliform invader (i.e. *Gallus gallus*, *Numida meleagris*, or *Alectoris rufa*). As described with Pitcairn Island, this often results in greater than expected phylogenetic diversity because Galliformes taxa generally represent a new order on islands and a particularly long branch. As a result, there is often greater than expected phylogenetic diversity due to invasion when few invaders establish. Also, patterns of bird introduction are not only non-random with respect to taxonomic group (Lockwood 1999, Lockwood et al. 2000) but are also non-random in terms of the origin of the exotics and the location of introduction (Blackburn and Duncan 2001). Consequently, several native species in a given location are captured and then introduced to a given island. The species in this scenario may be closely related to each other (relative to a random draw of exotic birds from across the globe) because they are from the same region and because they likely have similar traits that make them ideal exotics. The non-random origin and introduction loca-

tion tends to apply to islands that have many invaders. For example, the Hawaiian Islands have over ten exotics from the family Estrildidae, which are native to the old world tropics and Australasia and likely escaped captivity to establish in the wild in Hawaii. Furthermore, New Zealand has received a majority of its exotics from Brittan (Blackburn and Duncan 2001). As a result, the islands of Hawaii and New Zealand have gained less phylogenetic diversity than expected under random invasion.

The number of native extinctions and exotic species are correlated with standardized phylogenetic diversity when considering invasions and extinctions at the same time. This likely depicts the influence of non-random extinctions and invasions observed at the global scale (Gaston and Blackburn 1995, Bennett and Owens 1997, Russell et al. 1998, Lockwood 1999) translating to the island scale. The negative relationship between standardized phylogenetic diversity and exotic species richness has the same explanation as the pattern due to invasions alone; the more invaders that establish, the more likely they are closely related to each other due to non-random origin and introduction locations (Blackburn and Duncan 2001), resulting in the addition of relatively short branch lengths. The negative relationship between stdPD and number of extinctions indicates that when extinctions/extirpations target certain clades, more extinctions increase the probability that an entire clade will be lost. Still, the predictor variables described little variation, and further studies may reveal other potential drivers of phylogenetic diversity in island bird assemblages.

Extinction and invasion in birds are non-random processes at the global scale (Gaston and Blackburn 1995, Bennett and Owens 1997, Russell et al. 1998, Lockwood 1999). Our results indicate that these processes are also phylogenetically non-random at the island, archipelago, and ocean scales. Any taxonomic group that is subject to non-random invasions and/or extinctions (e.g. mammals (Purvis et al. 2000)) may also show a lower phylogenetic diversity than expected regardless if they are on islands or not. Continental bird assemblages are subject to the same non-random processes of invasions and extinctions that island birds have experienced in the historical time period. However, due to the fact that fewer species have gone extinct and become invasive in continental ecosystems (Blackburn and Duncan 2001), it remains unclear how phylogenetic diversity has changed relative to random expectation.

While raw phylogenetic diversity generally increases with invasion only or when there is a net gain of species after invasions and extinctions (Supplementary material Appendix 5), lower than expected phylogenetic diversity (e.g. stdPD) has implications for the conservation, ecology, and evolution of ecological assemblages. Given the uncertain and rapid environmental change predicted due to human induced global change, the lack of phylogenetic diversity may imply the decreased ability of species to adapt on both ecological and evolutionary timescales. Since phylogenetic diversity can be considered a proxy for functional diversity,

lower than expected phylogenetic diversity driven by non-random extinctions and/or invasions may greatly alter ecosystem functioning. Finally, because drivers of extinction can vary through time (Bromham et al. 2012), constructing phylogenies that encompass prehistoric assemblages and tracking phylogenetic diversity from the pre-historic time period to the time of first European contact would help contextualize the patterns of phylogenetic change we observed on ocean islands and in ecosystems worldwide.

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Author contributions – BB conceived the study. JGB and ZZ conducted the phylogenetic analyses and BB conducted the statistical analyses. BB and JGB wrote the first draft of the manuscript and all authors edited the manuscript.

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References

- Baiser, B., Valle, D., Zelazny, Z. and Burleigh, J. G. 2017. Data from: Non-random patterns of invasion and extinction reduce phylogenetic diversity in island bird assemblages. – Dryad Digital Repository, <<http://dx.doi.org/10.5061/dryad.rs714>>.
- Bennett, J. R. et al. 2014. Balancing phylogenetic diversity and species numbers in conservation prioritization, using a case study of threatened species in New Zealand. – *Biol. Conserv.* 174: 47–54.
- Bennett, P. M. and Owens, I. P. 1997. Variation in extinction risk among birds: chance or evolutionary predisposition? – *Proc. R. Soc. B* 264: 401–408.
- Biber, E. 2002. Patterns of endemic extinctions among island bird species. – *Ecography* 25: 661–676.
- Blackburn, T. M. and Duncan, R. P. 2001. Establishment patterns of exotic birds are constrained by non-random patterns in introduction. – *J. Biogeogr.* 28: 927–939.
- Blackburn, T. M. et al. 2004. Avian extinction and mammalian introductions on oceanic islands. – *Science* 305: 1955–1958.
- Bromham, L. et al. 2012. Reconstructing past species assemblages reveals the changing patterns and drivers of extinction through time. – *Proc. R. Soc. B* 279: 4024–4032.
- Burleigh, J. G. et al. 2015. Building the avian tree of life using a large-scale, sparse supermatrix. – *Mol. Phylogenet. Evol.* 84: 53–63.
- Cassey, P. et al. 2007. Spatial scale and evolutionary history determine the degree of taxonomic homogenization across island bird assemblages. – *Divers. Distrib.* 13: 458–466.
- Cassey, P. et al. 2014. A population model for predicting the successful establishment of introduced bird species. – *Oecologia* 175: 417–428.
- Clements, J. F. et al. 2013. The eBird/Clements checklist of birds of the world. – Version 6.6.
- Darwin, C. 1859. *On the origin of species*. – Murray.
- Davies, T. J. and Buckley, L. B. 2011. Phylogenetic diversity as a window into the evolutionary and biogeographic histories of present-day richness gradients for mammals. – *Phil. Trans. R. Soc. B* 366: 2414–2425.

- Duncan, R. P. et al. 2013. Magnitude and variation of prehistoric bird extinctions in the Pacific. – *Proc. Natl Acad. Sci. USA* 110: 6436–6441.
- Faith, D. P. 1992. Conservation evaluation and phylogenetic diversity. – *Biol. Conserv.* 61: 1–10.
- Faith, D. P. 1994. Phylogenetic pattern and the quantification of organismal biodiversity. – *Phil. Trans. R. Soc. B* 345: 45–58.
- Faith, D. P. 2002. Quantifying biodiversity: a phylogenetic perspective. – *Conserv. Biol.* 16: 248–252.
- Flenley, J. R. et al. 1991. The Late Quaternary vegetational and climatic history of Easter Island. – *J. Quat. Sci.* 6: 85–115.
- Gaston, K. J. and Blackburn, T. M. 1995. Birds, body size and the threat of extinction. – *Phil. Trans. R. Soc. B* 347: 205–212.
- Hackett, S. J. et al. 2008. A phylogenomic study of birds reveals their evolutionary history. – *Science* 320: 1763–1768.
- Heard, S. B. and Mooers, A. Ö. 2000. Phylogenetically patterned speciation rates and extinction risks change the loss of evolutionary history during extinctions. – *Proc. R. Soc. B* 267: 613–620.
- Helmus, M. R. et al. 2007. Phylogenetic measures of biodiversity. – *Am. Nat.* 104: 1–24.
- Jackson, H. et al. 2015. Micro-evolutionary diversification among Indian Ocean parrots: temporal and spatial changes in phylogenetic diversity as a consequence of extinction and invasion. – *Ibis* 157: 496–510.
- James, H. F. 1995. Prehistoric extinctions and ecological changes on oceanic islands. – In: Vitousek, P. et al. (eds), *Islands: biological diversity and ecosystem function*. Springer, pp. 87–102.
- Jetz, W. et al. 2012. The global diversity of birds in space and time. – *Nature* 491: 444–448.
- Lavergne, S. et al. 2010. Biodiversity and climate change: integrating evolutionary and ecological responses of species and communities. – *Annu. Rev. Ecol. Evol. Syst.* 41: 321–350.
- Lee, T. M. and Jetz, W. 2011. Unravelling the structure of species extinction risk for predictive conservation science. – *Proc. R. Soc. B* 278: 1329–1338.
- Lerner, H. R. et al. 2011. Multilocus resolution of phylogeny and timescale in the extant adaptive radiation of Hawaiian honeycreepers. – *Curr. Biol.* 21: 1838–1844.
- Lockwood, J. L. 1999. Using taxonomy to predict success among introduced avifauna: relative importance of transport and establishment. – *Conserv. Biol.* 13: 560–567.
- Lockwood, J. L. 2006. Life in a double-hotspot: the transformation of Hawaiian passerine bird diversity following invasion and extinction. – *Biol. Invasions* 8: 449–457.
- Lockwood, J. L. et al. 2000. Taxonomic homogenization of the global avifauna. – *Anim. Conserv.* 3: 27–35.
- Lockwood, J. L. et al. 2009. The more you introduce the more you get: the role of colonization pressure and propagule pressure in invasion ecology. – *Divers. Distrib.* 15: 904–910.
- Lockwood, J. L. et al. 2013. *Invasion ecology*. – John Wiley and Sons.
- Lomolino, M. V. 1985. Body size of mammals on islands: the island rule reexamined. – *Am. Nat.* 125: 310–316.
- Losos, J. B. et al. 1998. Contingency and determinism in replicated adaptive radiations of island lizards. – *Science* 279: 2115–2118.
- MacArthur, R. H. and Wilson, E. O. 1967. *The theory of island biogeography*. – Princeton Univ. Press.
- Mace, G. M. et al. 2003. Preserving the tree of life. – *Science* 300: 1707–1709.
- Maitner, B. S. et al. 2012. Patterns of bird invasion are consistent with environmental filtering. – *Ecography* 35: 614–623.
- Mi, X. et al. 2012. The contribution of rare species to community phylogenetic diversity across a global network of forest plots. – *Am. Nat.* 180: 17–30.
- Mouquet, N. et al. 2012. Ecophylogenetics: advances and perspectives. – *Biol. Rev.* 87: 769–785.
- Nee, S. and May, R. M. 1997. Extinction and the loss of evolutionary history. – *Science* 278: 692–694.
- Olson, S. L. and James, H. F. 1982. Fossil birds from the Hawaiian Islands: evidence for wholesale extinction by man before western contact. – *Science* 217: 633–635.
- Paulay, G. 1994. Biodiversity on oceanic islands: its origin and extinction. – *Am. Zool.* 34: 134–144.
- Purvis, A. et al. 2000. Nonrandom extinction and the loss of evolutionary history. – *Science* 288: 328–330.
- Ricketts, T. H. et al. 2005. Pinpointing and preventing imminent extinctions. – *Proc. Natl Acad. Sci. USA* 102: 18497–18501.
- Russell, G. J. et al. 1998. Present and future taxonomic selectivity in bird and mammal extinctions. – *Conserv. Biol.* 12: 1365–1376.
- Sanderson, M. J. 2003. r8s: inferring absolute rates of molecular evolution and divergence times in the absence of a molecular clock. – *Bioinformatics* 19: 301–302.
- Savidge, J. A. 1987. Extinction of an island forest avifauna by an introduced snake. – *Ecology* 68: 660–668.
- Sax, D. F. et al. 2002. Species invasions exceed extinctions on islands worldwide: a comparative study of plants and birds. – *Am. Nat.* 160: 766–783.
- Sobral, F. L. et al. 2016. Introductions do not compensate for functional and phylogenetic losses following extinctions in insular bird assemblages. – *Ecol. Lett.* 19: 1091–1100.
- Stamatakis, A. 2006. RAxML-VI-HPC: maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. – *Bioinformatics* 22: 2688–2690.
- Steadman, D. W. 1995. Prehistoric extinctions of Pacific island birds: biodiversity meets zooarchaeology. – *Science* 267: 1123–1131.
- Szabo, J. K. et al. 2012. Global patterns and drivers of avian extinctions at the species and subspecies level. – *PLoS One* 7: e47080.
- Van Valen, L. 1973. Pattern and the balance of nature. – *Evol. Theory* 1: 31–49.
- Veron, S. et al. 2017. Predicting loss of evolutionary history: where are we? – *Biol. Rev.* 92: 271–291.
- Vitousek, P. et al. 1995. *Islands: biological diversity and ecosystem function* (vol. 115). – Springer.
- Von Euler, F. 2000. Selective extinction and rapid loss of evolutionary history in the bird fauna. – *Proc. R. Soc. B* 268: 127–130.
- Webb, C. O. et al. 2008. Phylocom: software for the analysis of phylogenetic community structure and trait evolution. – *Bioinformatics* 24: 2098–2100.
- Winter, M. et al. 2013. Phylogenetic diversity and nature conservation: where are we? – *Ecol. Evol.* 28: 199–204.

Supplementary material (Appendix ECOG-02738 at <www.ecography.org/appendix/ecog-02738>). Appendix 1–5.