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Quantifying the unrecorded loss of avian phylogenetic diversity

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Humans have drastically reduced avian diversity, with the majority of extinctions occurring on islands. Previous studies have quantified various aspects of this decline, including both taxonomic and phylogenetic diversity loss due to recorded extinctions. Other studies have estimated that unrecorded island bird extinctions – those that left no known fossil evidence – may represent hundreds of additional losses. However, these analyses have only focused on species diversity. In this paper, we bridge these two research efforts by estimating the phylogenetic diversity lost due to unrecorded island bird extinctions. Our findings suggest that the loss of phylogenetic diversity may be substantially smaller than expected, given the number of extinctions. Our results suggest that while unrecorded extinctions probably represented around 60% of all species extinctions, the majority of the phylogenetic diversity loss was likely caused by the recorded extinctions. The reason for this is that while extant island endemics are on average slightly more phylogenetically distinct than expected by chance, a disproportionate number of unrecorded extinctions are predicted to have been from islands in the eastern Pacific. Extant birds from this region generally have lower phylogenetic distinctiveness than other birds and the extinct species therefore likely did as well.

Keywords: birds, biodiversity loss, extinctions, anthropogenic impacts, unknown diversity

Islands have suffered a disproportionate recorded loss of avian biodiversity, encompassing taxonomic, phylogenetic and functional diversity (Whittaker et al. 2023, Matthews et al. 2024). While increasing attention has been directed toward estimating the number of unrecorded bird extinctions, including earlier studies focusing solely

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on Pacific island birds (Duncan et al. 2013) and a recent global study (Cooke et al. 2023), these efforts have primarily focused on quantifying species diversity loss, leaving the estimation of the unrecorded loss of other dimensions of biodiversity largely unexplored. One such dimension is phylogenetic diversity (sensu Faith 1992, hereafter PD), which is particularly important for biodiversity conservation for several reasons. First, it is closely related to feature/trait diversity: distantly related species are more likely to exhibit functional differences (Rosindell et al. 2024). Consequently, the extinction of distantly related species is expected to have larger impacts for ecosystem functioning on average, although this relationship can vary (Matthews et al. 2024). Second, phylogenetic diversity itself may be a conservation priority. The longer evolutionary isolation of a given species can be argued to be a reason for its importance in conservation, as the loss of such species represents a greater loss of evolutionary history (Faith 1992).

In this study, we estimated the loss of phylogenetic diversity from unrecorded extinctions of island birds using extrapolations based on the approximately linear relationship between log(species number) and log(PD). We built four different models where PD loss from unrecorded extinctions was estimated based on the PD of either all island endemic birds or only based on extinct island endemic birds, and either based on a single global regression for island endemic birds or with separate regressions for different island regions. We then compared these estimates with a respective null model where the PD loss was estimated based on all birds rather than only island endemic species. When we estimated the PD loss without incorporating regional variation (i.e. the global regression), we found that PD loss was marginally higher than expected based on the null model, but when we allowed for regional variation in the slope of the relationship between PD and species richness, we instead found that PD losses were substantially lower than expected by chance. Irrespective of whether regional variation was included or not, we also found that the PD loss was substantially smaller if it was estimated only based on extinct island endemic species than if it was estimated based on both extinct and extant island species.

In general, incorporating data heterogeneity into analyses is desirable when it can be done without introducing bias. There is no inherent reason why accounting for geographic variation in the calculation of phylogenetic distinctiveness should produce biased results. Accordingly, the low PD loss observed in models that include regional variation appears to be the most plausible result. This low PD loss is likely because the majority of the estimated unrecorded extinctions are from the Eastern and Central Pacific (Cooke et al. 2023) and the avifauna of these regions have (on average) very low phylogenetic distinctiveness (Supporting information). These results match well with previous studies that found that some archipelagos outside the Eastern and Central Pacific, such as New Zealand, have relatively few species but high phylogenetic diversity (Valente et al. 2019), while the Pacific archipelago of Hawaii has high species richness but low phylogenetic diversity (Fleischer and McIntosh 2001).

It is harder to know if the results based on all island species or the ones based only on extinct island species are the more reliable. However, we tend to place greater confidence in the results derived from the analysis of extinct species alone. Known avian extinctions exhibit trait specificity (Sayol et al. 2020), which could influence phylogenetic distinctiveness and make models based on both extinct and extant species less reliable. However, extinct forms are generally only recognized if they are clearly morphologically distinct, and such distinctiveness tends to increase with phylogenetic distance (Phillips et al. 2018). As a result, models based on extinct species might overestimate the phylogenetic diversity of the unrecorded extinctions. Interestingly, our findings show the opposite pattern – lower PD loss relative to models based on all island species. This is unlikely to be driven by data biases, and it suggests that models based on extinct species may provide a more accurate estimate of the true PD loss from unrecorded extinctions.

Overall, our results suggest a surprisingly low PD loss from unrecorded extinctions. Recent estimates of PD loss as a consequence of recorded extinctions indicate that around ~ 2900 million years of unique evolutionary history have been lost from 610 extinctions, averaging ~ 4.8 million years per extinction (Matthews et al. 2024). In contrast, our estimate, based on the preferred model (i.e. incorporating regional variation and based on extinct species), suggests a median loss of ~ 2600 million years from a median of 881 unrecorded extinctions, averaging ~ 3.3 million years per extinction. Our results suggest that the current avifauna contains around 94% of the PD of the avifauna we would have without any anthropogenic extinctions, with the recorded and unrecorded extinctions contributing approximately equally to the loss (Fig. 1b). The estimated PD loss is surprisingly close to the estimate for mammals, where the combined historic and prehistoric anthropogenic PD loss was also estimated to be 6% (Davis et al 2018). The estimate in mammals was only based on known extinctions but the number of unrecorded mammal extinctions is likely relatively low since prehistoric mammal extinctions mostly involved large and widespread species, and both large body size and range size make species more likely to leave fossils (Plotnick et al. 2016).

Substantial land-use change on islands soon after human arrival (Nogué et al 2021, Whittaker et al. 2023) represents one of the most important early anthropogenic effects on biodiversity and likely led to vast, though largely unrecorded, numbers of extinctions for many organism groups. This raises the question of how much PD was lost during that time. However, prehistoric (pre-1500 CE) anthropogenic PD loss has only been estimated in two groups. For mammals, prehistorical extinctions resulted in a higher PD loss than would be expected from random extinctions (Davis et al. 2018). In contrast, our study on birds suggests that the PD loss was lower than random. Given this discrepancy, the question remains difficult to answer at present. We hope this study will inspire further research into early anthropogenic losses across other organism groups. Such efforts could help build a better understanding of humanity's early impacts on

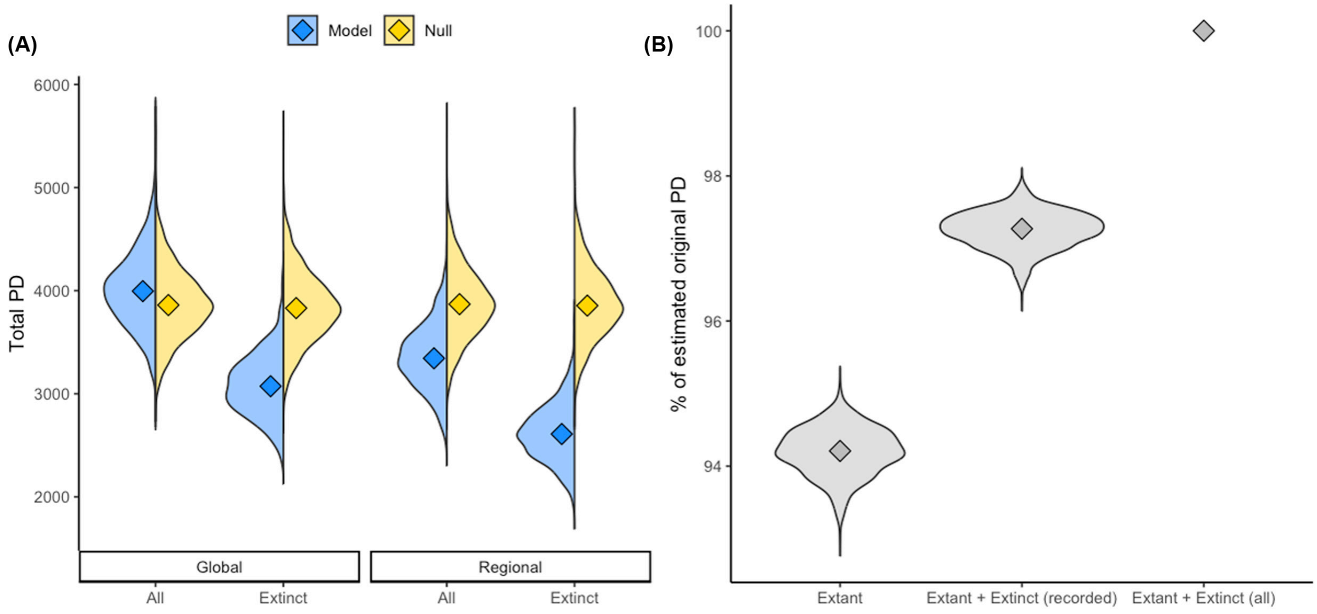

Figure 1. Distributions of phylogenetic diversity (PD) loss estimated across 1000 trees. (A) Estimated PD loss compared to null models. PD loss was estimated using four separate models based on either all island or only extinct island species, and either incorporating regional variation or not. (B) Percent changes in PD compared to the original values, i.e. showing the PD loss due to recorded and unrecorded extinctions. These percentages are calculated using the model based on extinct island species and including regional variation. The diamonds show the median values of each distribution.

ecosystems, and a clearer grasp of what has already been lost might strengthen the motivation to preserve what we still have.

Material and methods

Input data and data setup

Our analyses were based on combining data from multiple existing sources. We combined distribution data for extant bird species from BirdLife (BirdLife 2022) with distribution data on extinct species from Matthews et al. (2024). We retrieved information on the estimated number of unrecorded extinct bird species and their potential distributions from Cooke et al. (2023). We generated a phylogeny of all living birds and all known extinct birds from the Late Pleistocene or Holocene using the 'avotrex' R package ver. 1.2.0 (www.r-project.org; Matthews et al. 2024). We followed the approach outlined in Matthews et al. (2024), which involved grafting the known extinct species on to the BirdTree phylogenies for all living species from Jetz et al. (2012). We manually matched the taxonomies of Jetz et al. (2012) and BirdLife (2022), following Jetz et al. (2012) when the two sources disagreed.

Our analysis mainly focused on island endemic birds, which were defined as species not occurring on continents or any island connected to continents during the most recent ice age (n = 1934). We identified such islands as those where the depth of the shallowest sea between them and a continent is less than 140 meters, based on sea level maps from Weatherall et al. (2015). Some of our models involved further dividing the islands of the world into eight separate regions. These eight regions were based on the marine ecoregions from Spalding et al. (2007) but were modified to create relatively homogeneous regions with a large number of non-continental bird species. The eight regions are shown in the Supporting information. Four regions (1) Western Indo Pacific, 2) Eastern Indo Pacific, 3) Southern Ocean and 4) Temperate Australasia) were identical to the realms defined by Spalding et al. (2007). Two regions (5) Temperate Northern Atlantic provinces Lusitanian and Mediterranean Sea and 6) Tropical Atlantic province Tropical North-western Atlantic) were based on parts of predefined realms. Both regions include islands on both sides of the Atlantic in their definition in Spalding et al. (2007), but since all predicted unrecorded extinctions are from islands on one side, we restricted these regions to increase homogeneity. The seventh region included the entire realm of the Central Indo Pacific as well as the Cold Temperate Northwest Pacific province, which contains several islands near Japan. Because the Cold Temperate Northwest Pacific is species-poor, we combined it with the adjacent species-rich Central Indo Pacific region. The eighth region comprised several species-poor islands close to the Americas, including the realms of Tropical Eastern Pacific and Temperate South America, and the provinces Cold Temperate Northeast Pacific and Warm Temperate Northeast Pacific.

Analyses

We estimated the phylogenetic diversity (PD) lost from unrecorded island bird extinctions. The PD losses of unrecorded extinctions were estimated based on imputations derived from the nearly linear relationship between log-transformed species number and log-transformed PD; a relationship that was previously used for similar purposes by Sayol et al. (2020). We created four different models to estimate the lost PD represented by unrecorded extinctions, 1) modelling all island regions together, including both extant and extinct species; 2) modelling all island regions together, including only extinct species; 3) modelling island regions separately including both extant and extinct species; and 4) modelling island regions separately including only extinct species.

Our approach to estimating the PD lost from unrecorded extinctions can be described most easily by looking at the simplest regression model not incorporating regional variation. This simplest model was based on all extant or known extinct island endemic birds (n = 1934). For this, we randomly removed between 0 and 1934 island endemic birds from the phylogenetic tree of all birds 1000 times and fitted a linear regression between log(species number) and log(PD), with species number and PD being the values based on the species remaining in the trees after some species were removed. We then extrapolated this relationship to estimate what the PD would be without the unrecorded extinctions. Another model was based on known extinct island endemic birds (n = 487). For this, we removed between 0 and 487 species 1000 times and fitted a linear regression between the log(species number) and log(PD), and again extrapolated to what the PD is predicted to have been without extinctions. Our tree (which includes extant and known extinct birds and includes island endemic and non-endemic species) has 10 588 species and in the first replicate we assumed a total of 881 unrecorded extinctions (based on calculations in Cooke et al. 2023). This means that the PD loss for the simplest analyses with just one model was calculated as the difference between the PD for 10 588 species and predicted PD for 11 469 (10 588 + 881) species. For the last two models, we fitted multiple separate regressions for each island region. In these models we initially estimated the PD-loss of smaller subsets of species and then summed these to get the total PD-loss.

In order to assess if PD losses were larger than expected if species were lost at random, the resulting losses were compared to those calculated using null models, where instead of removing a random number of island endemic birds we removed the same number of species across all bird species (i.e. island endemics as well as species also or only occurring in continental regions). These null models show a near-perfect linear relationship between log(PD) and log(species number), with an R^2 of around 0.99 (Supporting information). However, the relationship is marginally non-linear, with a slight decrease in slope in the shallower parts of the phylogenetic tree. This non-linearity aligns with the well-known 'pull of the present' bias in lineage through time (LTT) plots, where extinctions cause an apparent increase in diversification rate near the present (Ricklefs 2007). To account for this potential influence on our conclusions, we ran separate null models for each of the four models discussed above. Each null model estimated the PD based on random removal of the same number of species as in the relevant model.

We assume that all unrecorded extinctions within the last 130 000 years are from islands, an assumption that has also been made in other recent analyses (Cooke et al. 2023). This is very unlikely to be completely true since extinct species from continents are continuously being described (Emslie and Mead 2023). However, it seems likely that the vast majority of unrecorded Late Pleistocene or Holocene avian extinctions were island endemics. Of the recorded 610 avian extinctions in this time period, 487 (80%) were island endemics (Matthews et al. 2024). Furthermore, it is well-established that the probability of species leaving fossil evidence is strongly influenced by its range size (Plotnick et al. 2016). Since island endemics typically have smaller range sizes, it is highly probable that most unrecorded species were also island species. The overall conclusion from this paper (i.e. that PD losses for extinct birds are lower than expected) is therefore unlikely to be influenced by this assumption.

All analyses were conducted across 1000 trees, and 1000 replicates from Cooke et al. (2023). Each of these replicates are derived from a distribution of the estimated number of unrecorded avian extinctions for each archipelago of the world. Each tree was analyzed with one of the extinction replicates.

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Author contributions

Søren Faurby: Conceptualization (lead); Data curation (lead); Formal analysis (lead); Funding acquisition (equal); Investigation (lead); Methodology (lead); Project administration (lead); Resources (equal); Visualization (supporting); Writing – original draft (lead); Writing – review and editing (lead). **Tom J. Matthews**: Conceptualization (supporting); Investigation (supporting); Methodology (supporting); Writing – review and editing (supporting). **Kostas A. Triantis**: Conceptualization (supporting); Investigation (supporting); Methodology (supporting); Writing – review and editing (supporting). **Ferran Sayol**: Conceptualization (supporting); Investigation (supporting); Methodology (supporting); Writing – review and editing (supporting); Visualization (leading).

Transparent peer review

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Data availability statement

All analyses are based on previously gathered data and are available from the sources provided in the references.

Supporting information

The Supporting information associated with this article is available with the online version.

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