Title: The global loss of avian functional and phylogenetic diversity from anthropogenic extinctions

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Abstract: Humans have been driving a global erosion of species richness for millennia, but the consequences of past extinctions for other dimensions of biodiversity – functional and phylogenetic diversity – are poorly known. Here, we show that, since the Late Pleistocene, the extinction of 610 bird species has caused a disproportionate loss of the global avian functional space along with ~3 billion years of unique evolutionary history. For island endemics, proportional losses have been even greater. Projected future extinctions of more than 1000 species over the next two centuries will incur further substantial reductions in functional and phylogenetic diversity. These results highlight the severe consequences of the ongoing biodiversity crisis and the urgent need to identify the ecological functions being lost through extinction.

One-Sentence Summary: Anthropogenic bird extinctions caused major losses of global functional and phylogenetic diversity.

Main Text

The last 130,000 years have been characterised by substantial global environmental change due to natural climatic fluctuations and, increasingly, human actions, through drivers including habitat loss, hunting, introduced species, intensive agriculture and climate change (*1*,*2*). Anthropogenic drivers are known to have increased species extinction rates by orders of magnitude compared to the background extinction rate (*1*,*3*,*4*). Species losses have been especially severe on islands, with insular species representing c.75% of IUCN documented post-1500 CE extinctions despite islands comprising only c.7% of Earth's land area (*2*,*5*).

Birds have been particularly impacted, with hundreds of known extinctions (*6*–*10*). However, biodiversity is multidimensional and the ecological and evolutionary consequences of this species loss are still not fully understood (*11*,*12*). Birds contribute a range of important ecological functions, including pollination, predator–prey interactions, and seed dispersal (*13*–*17*). The ecological role of particular species is dictated by their functional traits: the morphological and ecological characteristics determining an organism's fitness or performance (*17*–*19*). Thus, estimates of functional diversity (FD) – the range of functional traits of all species in an assemblage – can provide a more mechanistic understanding of the effects of extinctions on ecosystem function than the traditional focus on species richness (*17*,*19*,*20*). In addition, phylogenetic diversity (PD) – the breadth of evolutionary history represented by a set of species – provides a complementary metric of ecological structure, offering insight into both the evolutionary processes shaping biodiversity and unmeasured niche dimensions that may not be captured in a given trait dataset (*21*–*25*). A combination of FD and PD therefore provides a vital window onto the ecological implications of extinction and the uniqueness of the species that have been lost.

Bird extinctions during the Late Pleistocene and Holocene, which on some archipelagos represent most of the native avifauna (*26*), are thought to have reduced avian FD and PD (*8*), but to what extent is unclear. Given the apparent high functional overlap among bird species at global scales, a null expectation would be that anthropogenic extinctions have resulted in relatively small reductions in global FD and PD (*16*,*27*). However, species traits are known to have influenced the susceptibility of island birds to extinction drivers (*2*,*10*,*28*). Hence, we may expect the loss of FD over this period to have exceeded that predicted by a null model that assumes no association between traits and extinction. If these traits are non-randomly associated with phylogenetic uniqueness, we may also expect PD loss to have been greater than expected. To date, these combined hypotheses remain untested at the global scale.

Here, we provide complete global estimates of the avian FD and PD lost through anthropogenic extinctions over the last 130,000 years, as well as estimates of the magnitude of expected future loss. As a first step, we compiled the most comprehensive dataset to date of all known bird extinctions during the Late Pleistocene and Holocene, distinguishing between anthropogenic extinctions and extinction events of unknown cause (*29*). For each extinct species, we measured eight functional traits (including beak, tarsus, and wing length) from museum skins and skeletal specimens (fig. S1). All are continuous traits previously shown to provide accurate and fine-grained information on the functional, behavioural and trophic niches of birds (*16*,*27*). To augment these measurements, we obtained published trait values from the literature where possible (including body mass) and filled remaining data gaps using Bayesian Hierarchical Probabilistic Matrix Factorization (*29*,*30*). This dataset was combined with a dataset of traits measured using the same methods from all the world's 11,003 extant bird species (*17*).

Using these global datasets, we calculated the amount of avian FD that has been lost through extinctions using kernel density hypervolumes built with the one-class support vector machine (SVM) method (*31,32*). FD was measured as the total volume of the hypervolume (functional richness), a measure of the amount of trait space occupied by an assemblage (*32*). To assess the robustness of our conclusions, we also calculated FD (i) as the dispersion of points within the hypervolume (functional dispersion; *32*), (ii) using body mass corrected traits, and (iii) with alternative approaches, including neighbour joining trees and convex hulls. We also examined specific traits or trait combinations known to be important indicators of bird function: body mass (correlated with a range of key functional attributes; *16*), hand-wing index (HWI; a measure of wing shape predicting dispersal ability; *33*), and beak morphology (linked to trophic niche and resource competition; *16,17*). Finally, we developed a null model to test whether the observed losses of FD were greater than expected based on the number of extinct species (*10*).

Using published data and expert taxonomic knowledge, we built a global bird phylogeny (fig. S2) including all known Late Pleistocene and Holocene extinct species by grafting the extinct species onto trees from the posterior distribution provided by (*25*). Using multiple phylogenetic tree topologies to account for phylogenetic uncertainty, alongside the same null model architecture as for FD, we then estimated the amount of avian PD that has been lost through extinction. PD was measured using Faith's PD metric (*23*) and the phylogenetic dispersion metric of (*34*).

We split our dataset into four subsets relating to different time periods: (i) species that were extant 130,000 years ago ('All'), including all extant and known extinct species, (ii) species recognised by the IUCN Red List as being extant in 1500 CE ('IUCN'), (iii) species that are currently extant (Current ['Cur'] avifauna), and (iv) hypothetical simulated Future ['Fut'] scenarios (the avifauna predicted to be present in 200 years' time) where a number of currently extant species have gone extinct (*29*). In the latter case, a species' extinction likelihood was weighted by their current IUCN Red List classification and generation length. We then assessed FD and PD loss across three time periods (see Fig. 1) by comparing: (i) the species known to be present 130K BP and the current global avifauna (All→Cur), (ii) the species considered extant in 1500 CE by the IUCN and the current avifauna (IUCN→Cur), and (iii) the current and simulated future avifaunas (Cur→Fut). The All→Cur comparison represents the total loss of FD and PD from known extinctions, while the IUCN→Cur comparison corresponds to the IUCN-documented loss since 1500 CE. The IUCN→Cur comparison offers a useful perspective given that previous analyses of bird extinctions (e.g., *35,36*) have generally focused on this more-recent subset of extinction events, allowing us to determine how far such studies underestimate the true loss of diversity from anthropogenic extinctions. We first ran the analyses considering all the world's bird species (the 'global avifauna'). Then, given that most known bird extinctions involve island endemics (*2,8,10*), we (i) reran the analyses focusing only on this subset of species and (ii) assessed the contribution of island endemics to overall FD and PD loss (*29*).

Global loss of avian functional and phylogenetic diversity from extinction

Over the last 130,000 years, we found records of 610 avian extinctions globally (Fig. 1), representing 5.3% of the known avifauna occurring within the period (based on the BirdLife taxonomy for extant species; *17*). Of these global extinctions, 165 occurred post-1500 CE and are documented by IUCN. We found evidence (see SI[29]) that humans have contributed to most of these 610 extinctions (at least 562 species; 92%). Focusing exclusively on these 562 species suggests an anthropogenic extinction rate over the 130,000-year period of at least 0.37

extinctions per million species per year (E/MSY), a value that increases to ~28 E/MSY when considering only IUCN-documented extinctions since 1500 CE. Both these values are likely higher than the background extinction rate (*1*). All these estimates are limited to known extinctions, and it is likely that there are many as-yet-undiscovered extinct bird species, particularly those that disappeared before 1500 CE (*3*,*6*,*37*,*38*). Indeed, a recent study (*37*) that combined known extinctions with models utilising data on fossil-record completeness estimated 1,430 bird extinctions over the same 130,000-year time-period, suggesting an accelerated anthropogenic extinction rate over this period of 0.88 E/MSY.

The known bird extinctions since the Late Pleistocene (All→Cur) have resulted in a loss of ~7% of avian functional diversity (FD), quantified as the total volume of the functional hypervolume (*31*,*32*). This FD loss was significantly larger than expected under random extinction ($P < 0.01$; Fig. 3; tables S1-S2). Given the extensive functional overlap exhibited by birds at a global scale (*16*,*19*,*27*), random extinction would be expected to result in much smaller percentage losses of FD (a median 1.6% decrease estimated from 1000 null model runs, well below the percentage loss of species [5.3%]; see also Fig. 3). The loss of FD (3%; volume of the functional hypervolume) was also greater than expected for the IUCN→Cur comparison (P = 0.047). Our estimates therefore suggest that avian extinction has been non-random with respect to traits, with certain types of species (e.g. large-bodied, flightless, ground-nesting; *10*,*28*,*39*) more likely to have been lost. These patterns of FD loss also indicate that extinct species contributed disproportionately in terms of unique ecological functions.

When considering all avian extinctions (All→Cur), there has also been a ~3% loss of phylogenetic diversity (PD), measured using Faith's PD metric (median value across 50 phylogenies = 3.3%; range = 3.0–3.5%; Fig. 2). Overall, approximately 3 billion years of unique evolutionary history have been lost (median value across 50 phylogenies = 2.91; range = 2.51–3.31 billion years). However, in contrast to functional traits, PD loss was not significantly greater than expected for any of the 50 analysed phylogenies for the All→Cur comparison or the IUCN→Cur comparison (Fig. 3; tables S3 and S4). These findings are likely related to the fact that, while three entire avian Orders (Aepyornithiformes [elephant birds], Dinornithiformes [moas] and Gastornithiformes: Dromornithidae [demon ducks]; *7*) have been lost, known extinctions have also involved the loss of multiple species within groups of numerous relatively young and closely-related species (e.g., Macaronesian quails and Pacific Island rails).

Island endemics have suffered disproportionate losses: 489 extinct species were island endemics (22% of the total known island endemic avifauna at 130K BP). These extinctions resulted in a significantly greater than expected loss (All→Cur) of 31% of the FD of island endemic birds ($P < 0.01$), and an average of 17% loss of PD, again similar to that predicted by null models in the majority of cases (47 out of 50 phylogenies) (Fig. 3). For the IUCN→Cur comparison, the loss of FD (13%) was also greater than expected ($P < 0.01$), while the loss of PD (average of 5%) was not significantly different than expected. The extinction of island endemic species accounts for 78% of the total loss of FD over the last 130K years, and a median of 70% of estimated PD losses (66%–73% across 50 phylogenies).

The sensitivity of island endemics to extinction is well known, arising from their small geographical ranges and population sizes, coupled with the evolution of trait combinations associated with increased extinction risk (e.g., flightlessness; *28*). The preponderance of island extinctions and the morphological uniqueness of island fauna (*2*) may help to explain why we find that anthropogenic extinctions have resulted in greater than expected losses of FD, but not PD. Specifically, many island taxa have undergone divergent trait evolution (e.g., as a result of the island rule or rapid adaptive radiation; *2,5*), and extinction clusters on archipelagos can wipe out multiple relatively young yet morphologically distinctive species (e.g., extinct Hawaiian honeycreepers). Overall, patterns of lost FD and PD support the view that anthropogenic extinctions are not targeted towards evolutionary uniqueness, but instead tend to remove species with high morphological and ecological uniqueness (*19*). Irrespective of the underlying mechanisms, our results highlight how FD and PD can show distinct patterns of loss, and caution against the widespread use of PD as a proxy for FD (*21,22*).

To further explore the impact of extinctions on FD and PD, we estimated the contribution of each species to overall FD (measured using a dendrogram) and PD (see the 'Functional and phylogenetic contributions' section in *29*). Overall, extinct species and threatened extant species (together comprising ~20% of total FD) represent significantly larger contributions to the total FD than expected based on the number of species involved, whereas lower-risk species contributed significantly less (Fig. 4 and tables S12–S13). The results were similar for island endemics, although here, extinct and threatened extant species represent 50% of the total FD of island endemics (Fig. 4). The summed contribution values across groups (extinct, threatened, lower-risk) were similar for PD, and were consistent across the 50 phylogenies (table S14). However, there was more variation in the significance of contribution values across phylogenies for each of the three groups, although there were no cases where extinct species contributed significantly more to total PD than expected (table S15). Anthropogenic extinctions contributed a much larger proportion (~5% in both cases) of total FD and PD (i.e., the FD and PD present 130,000 years ago) compared to the extinctions of unknown cause (<1% of both total FD and PD) (Fig. 4).

Results were broadly consistent when using alternative FD approaches and metrics, with only minor differences (figs. S3-S6 & S10, tables S5-S11). For example, functional and phylogenetic dispersion both decreased significantly, by 2% and 1% respectively (and 7% and 5% respectively for island endemics), in the All→Cur comparison. In the All→Cur and IUCN→Cur comparisons, FD loss was significantly greater than the null expectation across all three primary FD metrics tested (hypervolumes, convex hulls and trees). FD loss for the All→Cur comparison was slightly larger than in our main analyses when using body mass corrected traits (e.g., FD loss of 10% for the global avifauna) and convex hulls, but slightly lower when using trees, Gaussian hypervolumes and hypervolumes fitted using only body shape axes.

Predicted future loss of avian functional and phylogenetic diversity

Our simulations predict that c.1,305 bird species could go extinct over the next 200 years (based on the BirdLife taxonomy; the equivalent number for the BirdTree taxonomy is 1,141). These simulated future extinctions (Cur→Fut; Fig. 3) generate decreases of an average of 6% of FD and 7% of PD relative to current assemblage values (no. simulations = 100; details in tables S1-S8). Similar patterns were obtained for island endemics (Fig. 3), although the forecasted average reductions in FD (17%) and PD (15%) are even more severe. These scenarios indicate that, without effective conservation actions to avert further losses of avian biodiversity, future extinctions may have severe consequences on ecosystem functioning and resilience (*19,20,40-43*).

Interestingly, while the loss of FD (measured using a hypervolume) under our future extinction scenarios (global avifauna) was significantly larger than expected given random species loss ($Z = -1.75$ & $P = 0.04$; Table S2), the loss of PD was not (Table S4). The latter finding matches our analysis of extinct species, as well as previous studies of both mammals and birds (*24,43*). Further analysis indicated that the apparently random future loss of PD was not simply an artefact of our simulations, but instead indicates that threatened bird species are not, collectively, more phylogenetically unique than expected (see the 'Additional analyses' section in *29*). Also noteworthy is that future FD loss was not significantly higher than expected when measured using convex hulls, indicating that the species selected to go extinct in our simulations are located at various points within morphospace rather than being focused exclusively around the periphery (but see *19*).

Extinction-driven changes in the distributions of individual traits

As well as overall FD, we observed (sometimes substantial) changes in the distributions of individual traits due to extinctions (full results presented in tables S16-S17). Median body mass and body mass standard deviation (SD) decreased significantly more than expected across both time frames (All→Cur, IUCN→Cur), for both the global avifauna and island endemics, with the exception of body mass SD for the global avifauna IUCN→Cur comparison (fig. S7). These decreases were relatively large (e.g. All→Cur: 7% and 27% decreases in median body mass and 77% and 98% decreases in the SD of body mass, for the global avifauna and island endemics, respectively). There were significant decreases in median hand-wing index (HWI; higher HWI ≈ greater dispersal ability) for both comparisons (e.g. All→Cur comparison: 2% and 5% decreases for the global avifauna and island endemics, respectively) (fig. S8). The volume of avian beak morphospace did not significantly decrease across either comparison when focusing on the global avifauna, but there were significant decreases in the All→Cur comparison for island endemics (15% decrease; fig. S9). In the Cur→Fut global avifauna comparison, simulated future bird species extinctions would cause a significant further 3% decrease in median body mass (fig. S7), and a non-significant 3% decrease in the volume of beak morphospace (fig. S9).

While the changes in median and SD of body mass following extinction match *a priori* expectations (*10,39*), the decrease in median HWI (lower HWI generally representing poorer dispersal ability) may seem counter-intuitive. However, this may be because while flightless bird species (whose extinction would increase median HWI, all else being equal) are known to have been disproportionately affected by extinction (*28, 39*), many groups of species with relatively high dispersal ability, such as Procellariiformes and Charadriiformes, have also been heavily impacted (*2,10,40,44*).

Implications of avian extinctions for ecosystem function

Previous work based on genomic data found evidence that avian FD remained relatively stable for a million years before the global spread of humans, albeit with some changes in particular areas of functional space (*45*). Our results reveal that this situation has changed substantially over the last 130,000 years: the global avifauna has undergone substantial recent declines in functional diversity, coupled with large losses of evolutionary history. This is particularly concerning for islands, where approximately 50% of the FD and PD of island endemic birds has been lost or is threatened with future loss (Fig. 4). Some have already lost almost all of their native bird species (*6,26*). Similar processes of functional decline may be underway on continents, where species losses are increasing as extinction debts related to habitat loss start to be paid (*46*).

Given the wide range of important ecological roles performed by birds, the loss of avian FD has far-reaching implications for overall ecosystem functionality. It is likely that particular ecosystem services beneficial to humans have been impaired (*41*), although the specific impacts in a given ecosystem will depend on the type and magnitude of local losses. Removal of avian functional diversity can have various negative consequences, including disrupted mutualistic (*47*) and antagonistic interaction networks (*13*), resulting in reduced flower pollination (*15*, *48*), reduced seed dispersal (*12*, *14*), the breakdown of top-down control of insect populations, including many pests and disease vectors (*41*), as well as increased disease outbreaks due to reduced consumption of carrion (*40*). In addition, the downsizing of the global avifauna that we have documented here will likely affect the ability of many plant species to track present and future climate change (*49*).

Overall, these results are a timely reminder that the current extinction crisis is not just about species numbers. By identifying declines in avian functional and phylogenetic diversity driven by human actions, our findings highlight the urgent need to understand and predict the impacts of past and future anthropogenic extinctions on ecosystem function (*41*). This information is vital for setting effective targets for global conservation strategies, as well as ecosystem restoration and rewilding efforts (*50*).

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Supplementary Materials

Materials and Methods

Figs. S1 to S10

Tables S1 to S19

References (*53–91*)

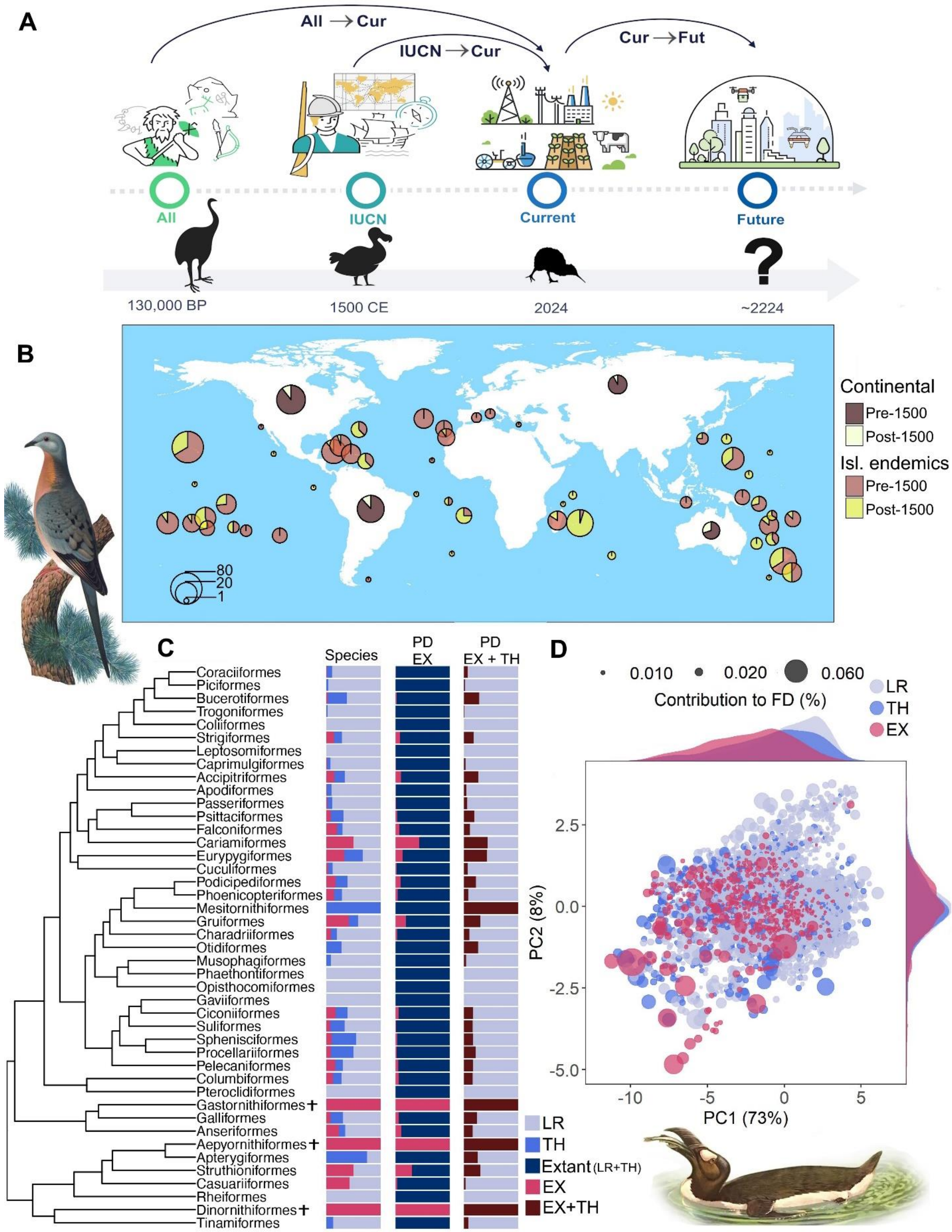

Fig. 1. Overview of the study design and a summary of the functional (FD) and phylogenetic (PD) diversity of extinct birds. (A) Diagram of our classification of species groups (130K BP [All], 1500 CE [IUCN], Current [Cur], and Future [Fut]) and the different time period comparisons used for assessing FD and PD loss. (B) Distribution of extinct bird species, separated into island endemics and continental species. In each case, the proportion of pre-1500

CE and post-1500 CE extinctions are shown; note that there are 19 post-1500 CE extinctions not currently recognised by IUCN. Some islands were grouped into archipelagos (e.g., Hawaii). Continental species are organised by realm: Nearctic, Palearctic, Australasia and Neotropics. In a small number of cases, species were endemic to multiple island groups or realms. The number of extinctions has been logged (with 1 added to each value) for visual clarity. (C) An illustrative phylogeny of avian orders showing the proportion of (i) species known to be present 130Kya that are extinct (EX), and classified as threatened (TH; species classified as CR, EN and VU) and lower-risk (LR) on the IUCN Red List; (ii) PD lost to extinction; and (iii) PD lost after removing both extinct and threatened extant species. PD proportions are averaged over 50 trees. † indicates extinct orders. (D) The 2-dimensional global avian functional space, where each point in the space represents an individual species. Point colour distinguishes EX, TH and LR species. Point size shows each species' functional contribution, calculated using a global functional dendrogram (*29*). The density curves along the top and right show the distribution of points along each axis, for each species category. Illustrations show, left, a passenger pigeon (*Ectopistes migratorius*) (drawing by K. Hayashi and in the public domain) and, bottom right, a great auk (*Pinguinus impennis*) (drawing by Julian Hume), two species driven to extinction by humans.

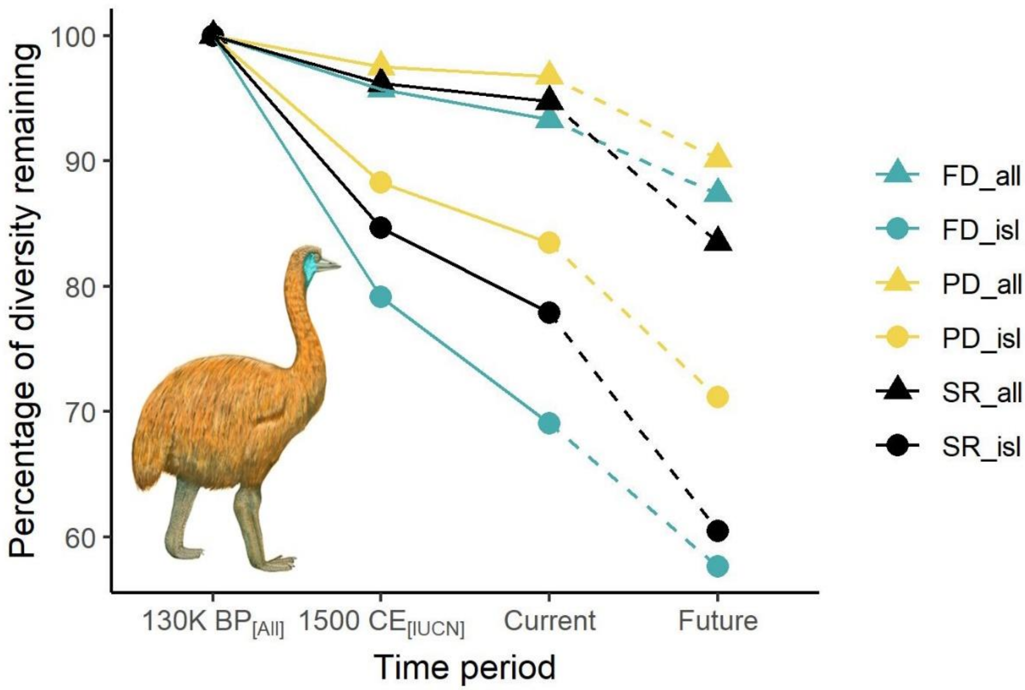

Fig. 2. The change in species richness (SR), functional diversity (FD) and phylogenetic diversity (PD) through time. Presented as the percentage of each metric remaining in each of three time period datasets (1500 CE$_{[IUCN]}$, Current and Future datasets; see Materials and Methods for details) relative to that known to be present 130,000 years ago (130K BP$_{[All]}$ dataset). Values are presented for the global avifauna ('all'; triangles) and for just island endemics ('isl'; circles). The PD values represent median percentage change values across 50 phylogenies. The Future FD and PD values are based on the percentage change between FD and PD in the 130K BP$_{[All]}$ dataset and the median FD and PD value of the Future datasets (i.e. the median of the 100 simulated Future datasets; see Materials and Methods). The uncertainty inherent within the future values is represented by the dashed lines. SR values are based on analyses using the BirdLife taxonomy. Illustration shows an elephant bird (*Aepyornis maximus*), representative of an extinct order native to Madagascar and one of the largest birds ever to exist, reaching three metres in height (drawing by Julian Hume).

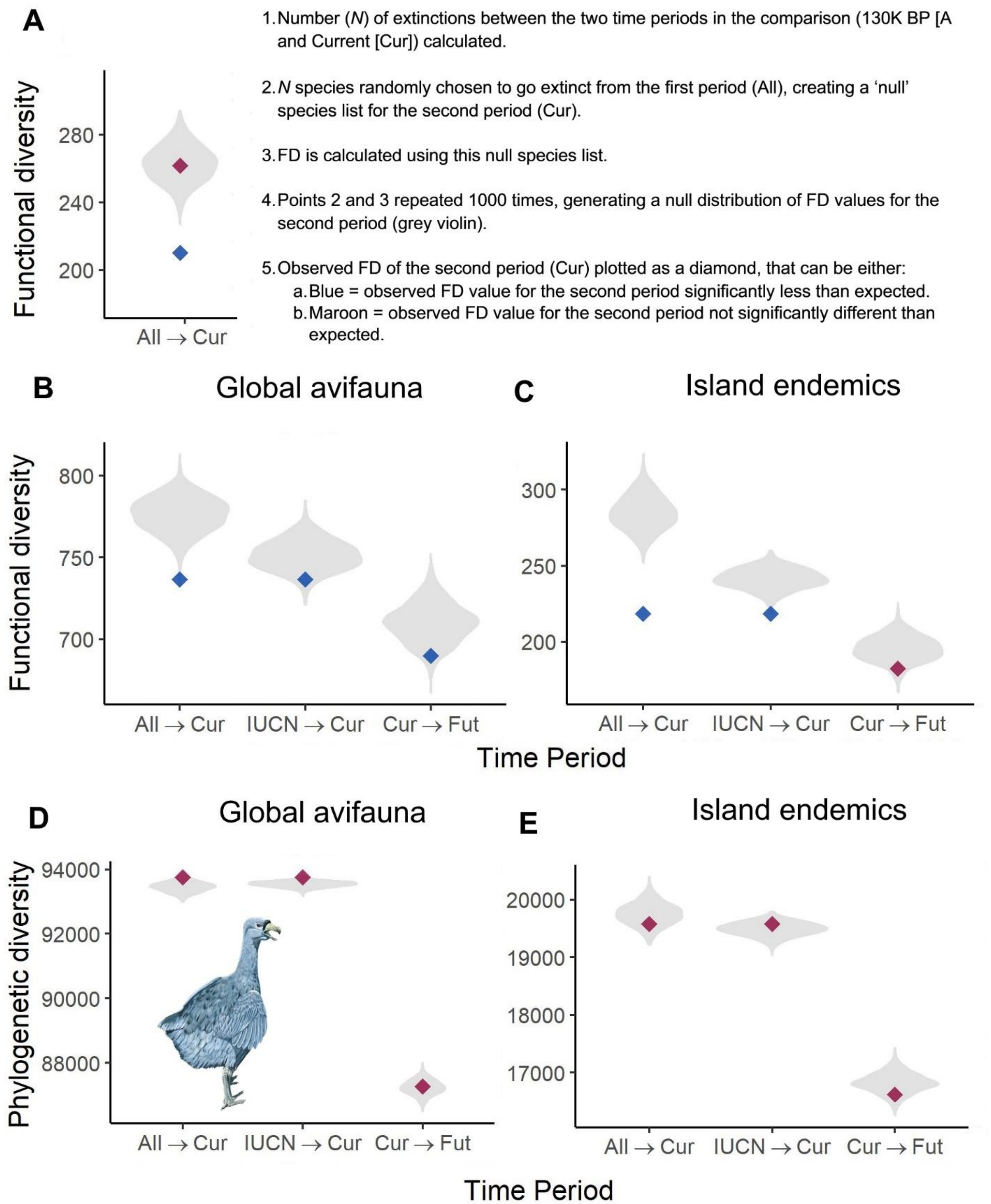

Fig. 3. The results of the null model analyses of functional (FD) and phylogenetic (PD) diversity change. Analyses undertaken across four time periods (three comparisons: All→Cur, IUCN→Cur, and Cur→Fut). Panel A provides information on how to interpret the null model plots, for a hypothetical pairwise comparison. FD (B and C) measured using kernel-density hypervolume diversity (the volume of the hypervolume) and PD (D and E) measured using Faith's PD metric. The PD null distributions and observed values were taken from the analysis of a randomly selected phylogeny. Statistical significance was based on a majority rule across 50 phylogenies (maroon = significant in <=25 of phylogenies). All tests were one-tailed. Diamond size is constant and does not convey information. Analyses were run twice, using the global avifauna (11,613 species in [B][BirdLife taxonomy] and

10,591 in [D][BirdTree taxonomy]), and only the island endemics (2,213 in [C] and 1,890 in [E]). Illustration shows a Rodrigues solitaire (*Pezophaps solitaria*), a flightless species endemic to the island of Rodrigues, driven extinct by humans in the 18th century (drawing by Julian Hume).

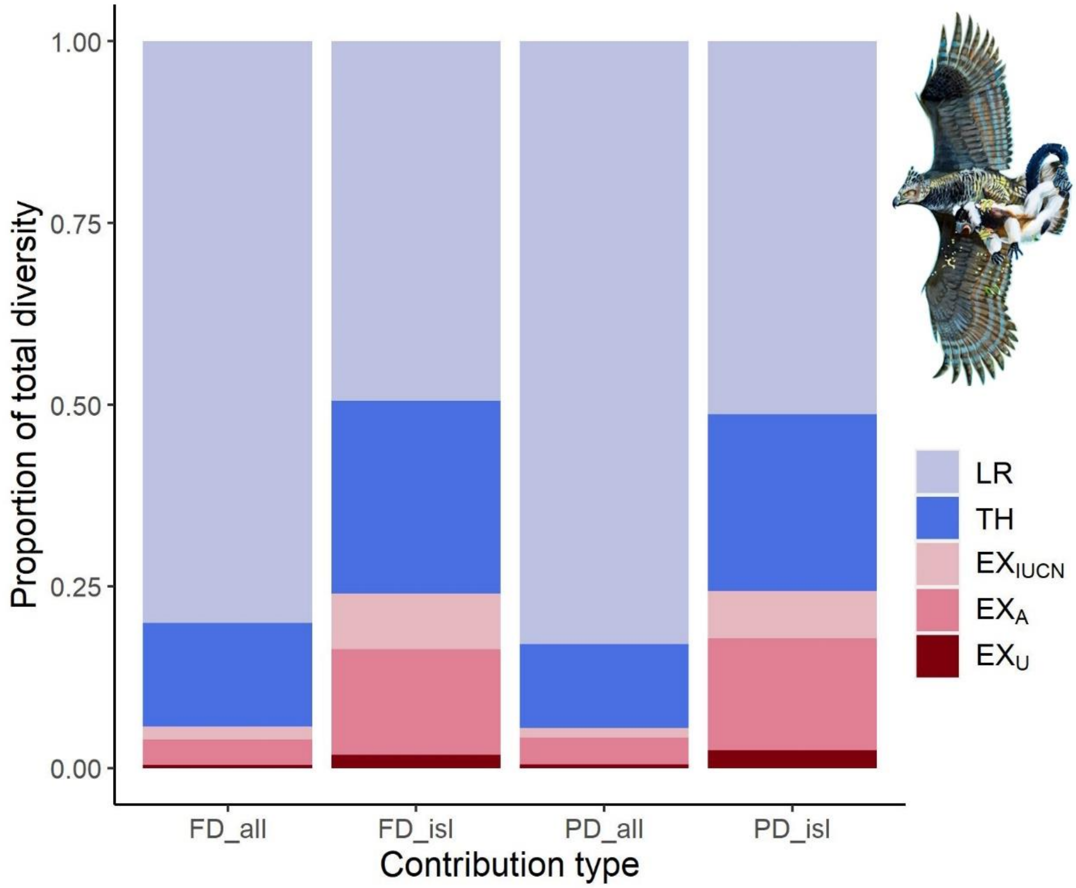

Fig. 4. The contribution of different species groups to total functional (FD) and phylogenetic (PD) diversity. FD and PD were measured using a dendrogram and a randomly selected phylogeny, respectively. Results are presented for the global avifauna (all) and island endemics (isl). EX = extinct species: EX_U = pre-1500 CE extinctions of unknown cause; EX_A = anthropogenic pre-1500 CE extinctions, and post-1500 CE extinctions not documented by the IUCN (all of which are considered anthropogenic); EX_{IUCN} = post-1500 CE extinctions documented by the IUCN (all of which are classed as anthropogenic); TH = threatened extant species; and LR = lower-risk extant species. Illustration shows an extinct Malagasy crowned eagle (*Stephanoaetus mahery*) (drawing by Julian Hume).