Magnitude and variation of prehistoric bird extinctions in the Pacific

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The largest extinction event in the Holocene occurred on Pacific islands, where Late Quaternary fossils reveal the loss of thousands of bird populations following human colonization of the region. However, gaps in the fossil record mean that considerable uncertainty surrounds the magnitude and pattern of these extinctions. We use a Bayesian mark-recapture approach to model gaps in the fossil record and to quantify losses of nonpasserine landbirds on 41 Pacific islands. Two-thirds of the populations on these islands went extinct in the period between first human arrival and European contact, with extinction rates linked to island and species characteristics that increased susceptibility to hunting and habitat destruction. We calculate that human colonization of remote Pacific islands caused the global extinction of close to 1,000 species of nonpasserine landbird alone; nonpasserine seabird and passerine extinctions will add to this total.

endemism | human impact | island biogeography | zooarchaeology | avifauna

The remote islands of the eastern Pacific were the last habitable region on Earth to be colonized by humans. People had moved east into the Pacific as far as the islands of Samoa and Tonga (including settlement of the islands of Vanuatu, New Caledonia, Fiji, and the Marianas) by ~3,500 y ago (1, 2) and then colonized the more remote islands, including Hawaii, New Zealand, and Rapa Nui, only 900–700 y ago during a phase of rapid expansion (3). Human impact on the biota of Pacific islands has been preserved in Late Quaternary fossil bone deposits that reveal widespread and catastrophic extinctions of birds (4–7). Estimates of extinction in the relatively short period between first human arrival and subsequent European contact (depending on location, a period of hundreds to a few thousand years), based on this fossil record, are subject to considerable and largely unquantified uncertainty, but range from ~800 to >2,000 species, and up to 8,000 island populations (6–9).

Overhunting by humans, exacerbated by forest clearance, was a major cause of prehistoric bird extinctions reflected in particularly high rates of loss among large-bodied flightless species on islands across the Pacific (4–7, 10–14). Though this pattern of selective extinction is evident in the fossil record, we lack a more complete understanding of the nature and extent of species losses caused by human arrival for two reasons. First, fossil bone collections from most Pacific islands are incomplete because relatively few fossils have been collected from most islands that have been studied (7). Consequently, many extinct bird species remain to be discovered, confounding attempts to quantify more precisely the number and type of species lost across the region (6–9, 15). Second, the rate of species loss will have varied from island to island due to wide differences in features such as area, topographic diversity, and rainfall, which would have influenced the extent of prehistoric forest clearance (16) and hunting efficiency (7). Rates of extinction would have varied further depending on the diversity of bird species present—particularly characteristics such as body mass and flying ability (10), and hence species' desirability and ease of hunting (14)—and the ability of populations to sustain

harvest (17). The magnitude of such island- and species-level variation is unknown, but large variation would imply substantial differences in the susceptibility of avifauna to human impacts as a consequence of biotic (species-level) and abiotic (island-level) factors. Such variation is central to understanding the pattern and extent of prehistoric extinctions across these remote islands that vary widely in environmental features and biogeographic history (7, 9).

Here, we address these issues by applying analytical techniques that use all of the available data to estimate prehistoric extinction rates for birds across the Pacific while accounting for uncertainties associated with incomplete detection in the fossil record, at the same time quantifying variation in extinction rates among species and islands. To do this we treat the issue of incomplete detection as a mark-recapture problem (8) in which the species recorded following European arrival are "marked" species that are available for "recapture" in the fossil record. From this we can estimate probabilities of detecting species in the fossil record and use these to calculate the number of extinct species that remain undiscovered and associated extinction rates. We capitalize on recent advances in the analysis of mark-recapture data using Bayesian hierarchical methods (18, 19) to incorporate the uncertainties associated with incomplete detection when fossil sample sizes on some islands are small, and to simultaneously model variation in detection and extinction probabilities among species and islands. Failing to incorporate the variation in detection probability, both among species, due to factors such as body size that affects rates of bone preservation (20), and among islands, due to factors such as variable fossil collection effort (7), has the potential to substantially bias estimates of extinction rates (19). The outcome is an estimate of the magnitude of prehistoric bird extinctions across the Pacific that accounts for known gaps in the fossil record and provides insight into how and why human impacts varied across the region.

Results and Discussion

We used data from 41 Pacific islands on which fossil bones have been collected (Table S1), confining our analysis to the remote islands most recently colonized by humans (approximately the past 3,500 y) during recent expansion across the region. We excluded New Zealand from our primary analysis because extinction rates here are not subject to the same uncertainties associated with incomplete detection elsewhere (21). We further restricted our analysis to nonpasserine landbirds because these are relatively well documented in the fossil record, whereas the record for passerine birds and seabirds is patchy and reliable data are available from few islands (7). Nonpasserine species were selectively hunted by
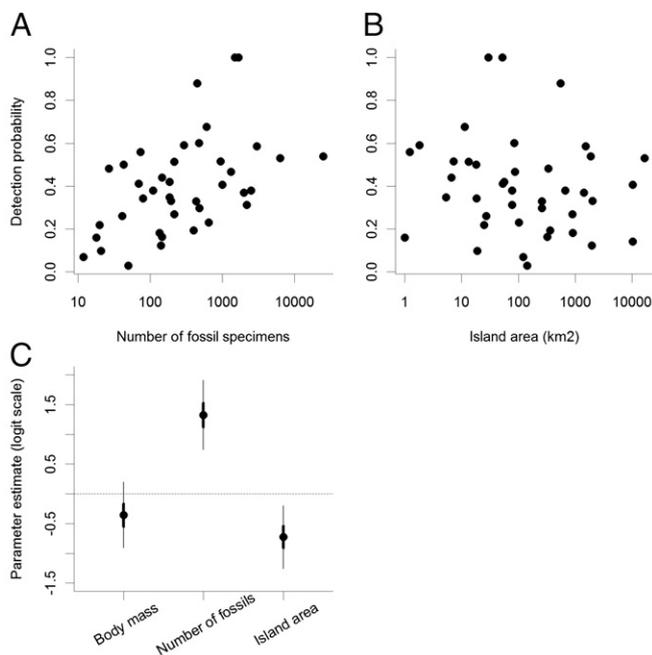
Fig. 1. Scatter plots of island-level probabilities of detection for a species of average body mass as a function of (*A*) the number of fossil specimens identified on an island and (*B*) island area. (*C*) Parameter estimates for the relationship between a species-level trait (body mass), island-level characteristics (number of fossil specimens identified and island area), and probability of detection (on the logit scale). Circles show the median; thick lines the 50% credible intervals; and thin lines the 95% credible intervals of the parameter posterior distributions.

humans due to their larger body size (14). Larger body size also meant that nonpasserine populations would have been less impacted by predation from the widely introduced Pacific rat, relative to passerines and ground- or burrow-nesting seabirds (13, 22), although introduced dogs and pigs would have been predators. For each of the 41 islands, we estimated the prehistoric rate of extinction based on the estimated number of species in the prehuman avifauna that were lost before European arrival (*Materials and Methods*). The loss of a species from an island equates to a global extinction event if the species was endemic to the island or disappeared from all other islands on which it occurred.

Across the 41 Pacific islands the median probability of detecting a nonpasserine landbird species in the fossil record was 0.37, but detection probability varied widely among islands ([Fig. S1](#)). Medians of the posterior distributions ranged from 1 (Henderson Island, which has been well studied) down to 0.03 (Tutuila), albeit often with wide uncertainty around these estimates reflecting sometimes small fossil collections. Though larger-bodied species are more likely to be preserved as fossils (14, 20), our results showed a tendency toward a negative relationship between body mass and detection probability, although the 95% credible intervals (CI) of the posterior distribution do not rule out a positive effect (Fig. 1C). Because our analysis excluded smaller-bodied passerine birds, this may have weakened any relationship between body mass and preservation rates seen in previous studies. In addition, larger-bodied species would have less chance of being detected if they occurred on islands at lower density than smaller-bodied birds.

We related estimates of detection probability on individual islands to two island-level features: the number of fossil specimens identified and island area, ensuring that the uncertainty in detection probability for each island was propagated through the analysis. Detection probability was strongly linked to collection

effort: the more fossil specimens identified on an island, the greater the probability of detecting a species that was present (Fig. 1 *A* and *C*). Moreover, for a given collection effort, detection probability declined with island area (Fig. 1 *B* and *C*). Because larger islands support more species, for any given collection effort a greater proportion of species will be sampled on smaller islands.

A total of 618 populations of 193 species of nonpasserine landbirds have been identified on the 41 islands, comprising 371 populations present at the time of European contact and 247 populations known only as fossils (7, 10). Taking into account the detection probabilities for each island, and the likely taxonomic and trait composition of the avifauna given the biogeographic region, we estimated the total number of species by island populations of nonpasserine landbirds present at the time of human arrival: Fig. 2*A* shows the posterior distribution, which has a median of 1,113 (95% CI: 683–2,363); this implies that approximately one-third of prehistorically extinct populations have been detected in the fossil record, and that two-thirds (0.67, 95% CI: 0.46–0.84) of nonpasserine landbird populations on these 41 islands went extinct in the period between first human arrival and European contact (Fig. 2*B*).

The islands vary greatly in extinction rates (Fig. 3), and the posterior distributions have medians ranging from 0.25 (Tegua in Vanuatu, where no prehistorically extinct nonpasserine landbird species have been identified, although the number of fossils collected and detection probability is low) to 0.93 (Ua Huka in the Marquesas, where 12 extinct species have been identified from fossils, and three species occur in the modern record). In addition, extinction probability varied among species and was strongly linked to species' traits (Fig. 4*C*). As previously observed (10, 11, 13), flightless species and those with larger body mass suffered higher rates of extinction, whereas widespread species, species endemic to archipelagos, and species endemic to single islands had progressively higher extinction probabilities (Fig. 4*C*). These
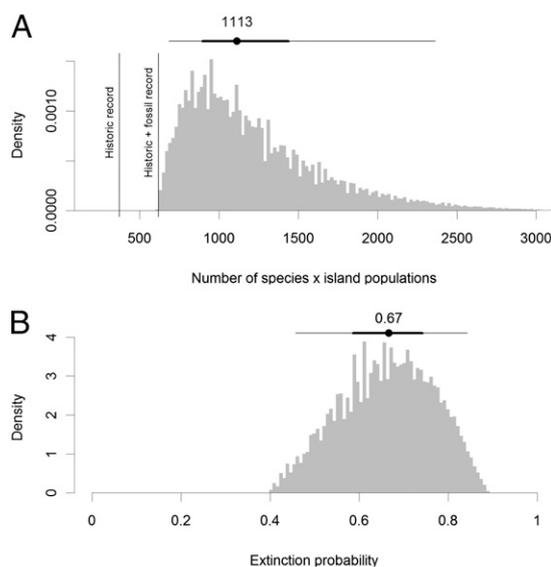

Fig. 2. (*A*) Posterior probability distribution (gray shaded bars) of the number of species by island populations of nonpasserine landbirds in the prehuman avifauna of 41 Pacific islands, taking account of uncertainties associated with incomplete detection in the fossil record. Vertical lines show the number of species known from the historic record (post-European arrival) and from the historic plus fossil record. (*B*) Posterior probability distribution of the overall probability of a species becoming extinct on an island in the period between first human contact and European arrival. In both *A* and *B*, the median of the posterior distribution is shown as a filled circle (with the value given above), along with the 50% (thick horizontal lines) and 95% (thin horizontal lines) credible intervals.
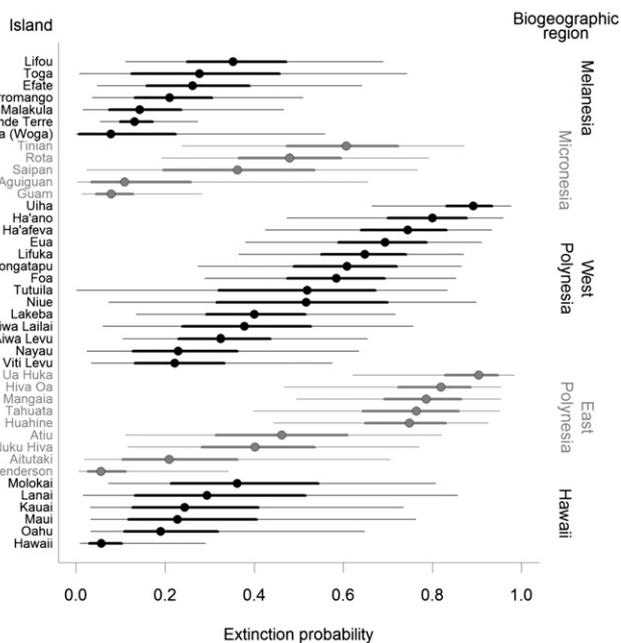
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Fig. 3. The probability that a species of nonpasserine landbird went extinct on each of 41 Pacific islands grouped by biogeographic region, with shading to differentiate regions. The median of the posterior distribution for each island is shown as a filled circle, along with the 50% (thick horizontal lines) and 95% (thin horizontal lines) credible intervals.

effects were strong: expressing the parameter estimates as odds ratios reveals that flightless species were 33 times more likely to go extinct than species able to fly, whereas single-island endemics were 24 times more likely to go extinct than widespread species. These outcomes are consistent with the selective extinction of species having traits that increase their susceptibility to human hunting and habitat loss. Large-bodied flightless species were easier and more profitable to hunt (14), and their lower rates of population growth inhibited recovery from overhunting or habitat loss (17). The selective extinction of island-endemic species independent of body mass and flying ability has been linked to predator naivety (12, 13), because species endemic to isolated islands often lose behavioral responses to mainland predators, making them tame and easy to hunt when humans arrive. Such species may also be in the later stages of the taxon cycle, and therefore characterized by relatively small population sizes and specialized habitat requirements (23).

Bird species in different taxonomic groups are not distributed uniformly across the Pacific. Pigeons and doves (order Columbiformes), for example, are widespread but notably absent from the Hawaiian Islands, whereas waterfowl (order Anseriformes) have greater diversity in Hawaii than elsewhere. Because extinction probability is linked to species traits (Fig. 4C), some of the variation in overall rates of extinction among islands (Fig. 3) could be due to differences in trait composition resulting from the over- or underrepresentation of certain taxonomic groups. To control for this we compared extinction probabilities across islands for a given trait set (a widespread nonpasserine landbird species of average body mass that could fly), ensuring that the uncertainty in extinction probability for each island was propagated through the analysis. Variation among islands in the probability of extinction was strongly associated with two island-level features: smaller islands and those with lower rainfall had higher rates of extinction (Fig. 4 A and C; there was no evidence of an interaction between these variables). Islands with lower annual rainfall were more extensively deforested in the period

between first human and European arrival (16), suggesting that higher rates of extinction were associated with greater loss of forest habitat in lower-rainfall areas. For a given rainfall, larger islands had lower rates of extinction, most likely for two reasons. First, larger islands would have supported larger bird populations, providing some buffering from extinction. Second, and probably more importantly, larger islands are more topographically diverse (there was a strong positive correlation between island area and maximum elevation: $r = 0.69$, df = 39, $P < 0.001$), with forest likely to persist at higher elevations and in areas of more rugged topography that would have been less accessible to human hunters.

Human colonization of the remote Pacific occurred in a phase of rapid expansion (3), and even small human populations appear to have rapidly devastated the native avifauna on islands, resulting in the extinction of susceptible species within a few hundred years of colonization (24). Though human impacts were widespread and rapid, our results show they were nonetheless mediated by geographical features associated with island size and rainfall. Extinction rates for the well-studied New Zealand archipelago are less subject to uncertainties associated with incomplete detection, providing an opportunity independently to validate the outcomes observed for other islands. New Zealand's North and South Islands have large area, mountainous topography, and high rainfall. Using the modeled relationships among extinction rate, island area, and rainfall from other Pacific islands, the extinction rate predicted for the North Island is 0.23 (95% CI: 0.10–0.47) and for the South Island is 0.22 (0.08–0.49). These predictions are close to the actual values, providing independent support for our results: for the North Island, 18 of 68 (0.26), and for the South Island, 21 of 75 (0.28) nonpasserine landbird species went extinct before European arrival (21). Though New Zealand provides the best-documented example of
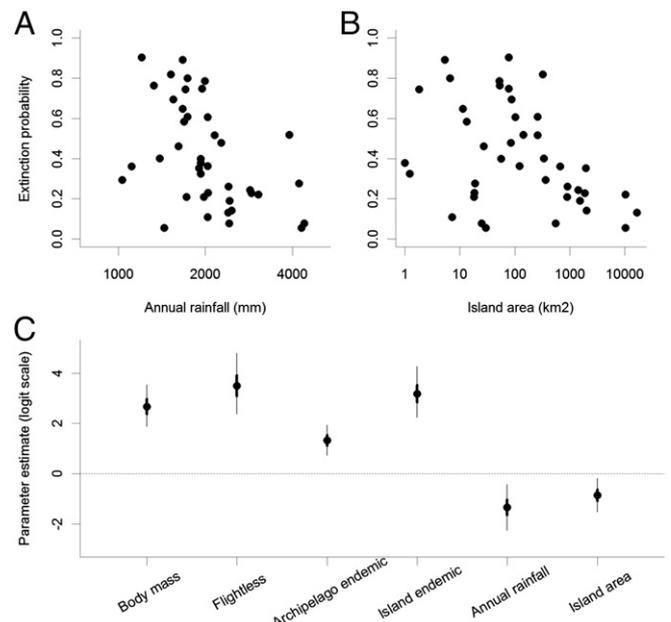

Fig. 4. Scatter plots of island-level probabilities of extinction for a species with fixed traits (a widespread species of average body mass that is able to fly) as a function of (A) maximum annual rainfall and (B) island area. (C) Parameter estimates for the relationship between species-level traits (body mass, ability to fly, and level of endemism), island-level characteristics (maximum annual rainfall and island area), and probability of extinction (on the logit scale). Circles show the median; thick lines the 50% credible intervals; and thin lines the 95% credible intervals of the parameter posterior distributions.

how human colonization and overhunting devastated an island avifauna (4, 13, 14, 17, 22), its extinction rate is relatively low by Pacific island standards. New Zealand's large size, rugged topography, and high rainfall sets it apart from other remote Pacific islands, and these features appear to have allowed species to persist until European arrival that would otherwise have been lost, including currently threatened, large-bodied, flightless birds such as kiwi, takahe, and kakapo.

Estimating the number of species that became globally extinct on Pacific islands is problematic (9). The mark-recapture approach we used models explicitly the characteristics of undetected species on each island, taking into account the manner in which detection and extinction probabilities are influenced by taxonomic composition and traits, including level of endemism. This approach provides estimates of the number of undiscovered island-endemic species on each island, each of which represents an unrecorded global extinction event. Sixty-three extinct island-endemic species are known from fossils on the 41 islands, though the median value of the posterior distribution of the number that remain to be discovered (Fig. 5A) implies the global extinction of 160 island-endemic species (95% CI: 68–430) on these islands. To extend these results, we identified 269 Pacific islands within the study region (excluding New Zealand) that were large enough (≥ 5 km^2) and sufficiently isolated (>10 km apart) to have supported at least one island-endemic species. We estimated the total number of extinct island-endemic species on these 269 islands by sampling with replacement from the distribution of the number of extinct island endemics on the 41 study islands, accounting for variation in island area and incorporating the uncertainties in the number of undiscovered species (*Materials and Methods*). The results imply that human colonization of remote Pacific islands caused the global extinction of at least 983 nonpasserine landbird species (Fig. 5B; 95% CI: 731–1,332). This minimum estimate will increase with the addition of global extinctions of nonisland endemics that were driven extinct on all of the islands they occupied.
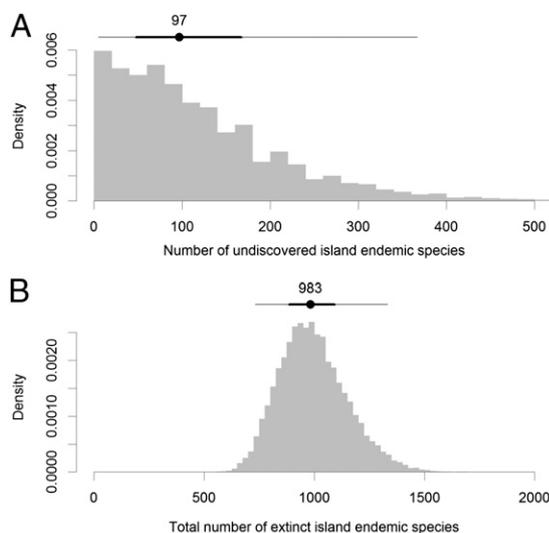

Fig. 5. (A) Posterior probability distribution (gray shaded bars) of the number of undiscovered island-endemic species on 41 Pacific islands. (B) Posterior probability distribution (gray shaded bars) of the total number of extinct island-endemic species on the 269 Pacific islands in the study region (excluding New Zealand) that were ≥5 km^2 in area and >10 km distant from each other. In A and B, the median of the posterior distribution is shown as a filled circle (with the value given above), along with the 50% (thick horizontal lines) and 95% (thin horizontal lines) credible intervals.

Additional extinctions also occurred among nonpasserine seabirds and passerines, which make up an unknown percentage of the prehuman avifauna on most Pacific islands, but comprised ~45% of the well-documented New Zealand avifauna, and ~25% of pre-European species extinctions there (4). These New Zealand figures suggest a total number for pre-European bird species extinctions across the Pacific (~1,300) that falls within the midrange of previous estimates (6–8), agreeing closely with ref. 9, and that more than 10% of total global bird biodiversity (currently ~10,000 extant species) was lost in this extinction event. European arrival initiated a second wave of extinctions among Pacific island birds. Previous studies have shown that the traits predisposing species to prehistoric extinction (flightless, highly endemic species with large body mass) were also associated with a higher probability of extinction post-European arrival (11, 13). Our results show that consistent selectivity through time also occurred across islands: the prehistoric rate of extinction for nonpasserine landbird species (Fig. 3) was positively correlated with the proportion of all bird species that became extinct post-European arrival ($r = 0.55, n = 28$ islands, $P = 0.003$, using historical extinction data in ref. 25). Despite suffering high rates of loss prehistorically, bird species on small, low-rainfall islands remained especially vulnerable to the additional impacts that accompanied European arrival (25).

Materials and Methods

We built a database of all known indigenous nonpasserine landbirds found on 41 Pacific islands primarily using the data in ref. 7. Details of database construction are given in refs. 10 and 11, with the addition that we updated the record for the island of Guam using data in ref. 26. We included all Pacific islands in the study area where nonpasserine landbirds have been identified in the fossil record. For each species in the database, we gathered data on body mass (in grams), ability to fly (yes or no), and level of endemism [widespread, species range limited to one archipelago (archipelago endemic), or species range limited to one island (island endemic)]. Each species was known either from observations of living birds recorded following European arrival or as fossils. Trait data for living species were gathered from the literature, whereas data for extinct species known only from fossils were based on osteological descriptions and the ecology of living relatives. For extinct species, body mass was estimated from allometry of hind-limb skeletal measurements (10, 11).

For each island, we gathered data on the total number of identified specimens of fossil birds (a measure of fossil collection effort), island area, and maximum elevation (10, 11). Island area and elevation were strongly positively correlated (Pearson $r = 0.69$, df = 39, $P < 0.0001$), and so we included only island area in regression models (see below) but interpreted the results in light of their covariation. We estimated maximum annual rainfall on each island using WorldClim annual precipitation data (version 1.4) with a 2.5-min resolution grid (27) by identifying the grid overlapping each island that had the highest annual rainfall. We used this measure of rainfall (as opposed to taking an average across all grids) to better capture the likelihood that forest would have persisted on islands. The extent of deforestation following first human arrival is strongly correlated with mean annual rainfall across islands but also varies within islands, with higher rainfall areas more likely to retain forest (16). Table S1 shows the 41 islands included in the analysis and their characteristics.

Modified Bayesian Mark-Recapture Model. The species recorded on each island are known either from observations of living birds recorded following European arrival, as fossils, or both. This situation is analogous to a mark-recapture problem in that the species recorded following European arrival can be thought of as marked species that are available for recapture in the fossil record. The proportion of marked species that are recaptured provides an estimate of detection probability in the fossil record, which can be used to estimate the number of undetected species and the probability of extinction. This approach has been previously applied to estimate the magnitude of Pacific island bird extinctions (8), but our analysis explicitly models the heterogeneity in detection and extinction probabilities among islands and species, and biogeographic variation in the distribution of taxonomic groups across the region, fully accounting for the uncertainty in parameter estimates by implementing this in a Bayesian framework.

We assumed that all species recorded on an island were present before first human arrival and then either went extinct in the period between first

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human contact and European arrival (prehistorically extinct birds known only from fossils) or survived first human contact to be observed by Europeans; this excludes the possibility that species colonized islands post-human arrival, and we therefore removed from the data five highly dispersive species likely to have done this (7): *Tyto alba*, *Asio flammeus*, *Gallirallus philippensis*, *Porphyrio porphyrio*, and *Porzana tabuensis*.

Coding presence in the fossil record and presence in the post-European record as 1 (yes) or 0 (no), observations of the ith species on the kth island will fall into one of three outcome categories, y_{ik}, with the following interpretations, shown as [(fossil, post-European)]: $y_{ik} = (0, 1)$, the species survived on the island until European arrival but has not been discovered in the fossil record; $y_{ik} = (1, 0)$, the species went extinct before European arrival and is known only from the fossil record; and $y_{ik} = (1, 1)$, the species survived until European arrival and has also been discovered in the fossil record.

In addition, an island may have species that went extinct before European arrival that have not been discovered in the fossil record, which is the unobserved outcome $y_{ik} = (0, 0)$. If n_k species have been recorded on the kth island, our aim is to estimate the total number of species on that island before human arrival, which is the n_k species in the three observed outcome categories plus the unknown number of species in the unobserved outcome category.

The probability, μ_{iky}, that the ith species on the kth island occurs in outcome category y can be defined in terms of the probability that the species has been detected in the fossil record on that island, pf_{ik}, and the probability that it went extinct on that island before European arrival, pe_{ik}. The four outcome categories have probabilities

$$\mu_{ik(0,1)} = (1\text{-}pf_{ik})(1\text{-}pe_{ik})$$

$$\mu_{ik(1,0)} = pf_{ik}pe_{ik}$$

$$\mu_{ik(1,1)} = pf_{ik}(1\text{-}pe_{ik})$$

$$\mu_{ik(0,0)} = (1\text{-}pf_{ik})pe_{ik}.$$

A feature of the data are that the n_k species recorded on an island will be a biased subset of all species present before human arrival, tending to be species less likely to have gone extinct (low pe_{ik}) and/or species more likely to be detected in the fossil record (high pf_{ik}). Consequently, probabilities of detection or extinction estimated using only the data for observed species are likely to be biased. To accommodate this, we used the method in Royle (19) and augmented the n_k species recorded on the kth island with M_k species having $y_{ik} = (0, 0)$. We then used a latent variable, z_{ik}, to indicate whether the ith species was actually present on the kth island ($z_{ik} = 1$) or not ($z_{ik} = 0$). For those species recorded on the island ($i = 1, 2, \ldots, n_k$), this outcome is known and $z_{ik} = 1$. For the augmented species ($i = n_k + 1, \ldots, M_k$), this outcome is unknown but was modeled as a draw from a Bernoulli distribution: $z_{ik} \sim$ Bernoulli (ψ_k), where ψ_k is the probability that a species in the augmented list was actually present on the kth island. This latent variable model is linked to the data by modeling the outcome categories, y_{ik}, as drawn from a multinomial distribution:

$$y_{ik} \sim \text{Multinomial}(\mu_{ik(0,1)}, \ \mu_{ik(1,0)}, \ \mu_{ik(1,1)}, \ \mu_{ik(0,0)})$$

$$\mu_{ik(0,1)} = z_{ik}(1\text{-}pf_{ik})(1\text{-}pe_{ik})$$

$$\mu_{ik(101)} = z_{ik}pf_{ik}pe_{ik}$$

$$\mu_{ik(1,1)} = z_{ik}pf_{ik}(1\text{-}pe_{ik})$$

$$\mu_{ik(0,0)} = z_{ik}(1\text{-}pf_{ik})pe_{ik} + (1\text{-}z_{ik})$$

$$z_{ik} \sim \text{Bernoulli}(\psi_k).$$

In addition to specifying the probabilities of detection and extinction on each island, the above model provides an estimate of the total number of species on the kth island before human arrival as $N_k = \sum_{i=1}^{M_k} z_{ik}$. Furthermore, we can incorporate heterogeneity among species in their detection and extinction probabilities by including covariates thought to influence these processes (19). Large-bodied species, for example, are more likely to be preserved and detected in the fossil record (14, 20), potentially biasing our perception of extinction patterns. We allowed for this by including body mass [log$_{10}$ transformed, centered, and standardized by dividing by 2× the SD to allow comparability with the binary covariates below (28)] as a covariate for fossil detection probability, using a logit function to constrain probabilities to

lie between 0 and 1: logit$(pf_{ik}) = \alpha_k + \beta_1 \log_{10}(\text{body mass}_i)$, where α_k is the baseline probability (on the logit scale) of detecting a species of average body mass on the kth island, and β_1 is the parameter describing the change in detection probability associated with a change in body mass, which is assumed to be the same across all islands. Similarly, we included body mass, ability to fly, and level of endemism as covariates for extinction probability: logit$(pe_{ik}) = \varepsilon_k + \beta_2 \log_{10}(\text{body mass}_i) + \beta_3 \text{ flightless}_i + \beta_4 \text{ archipelago}_i + \beta_5 \text{ island}_i$, where ε_k is the baseline probability of extinction on the kth island for a widespread species of average body mass that can fly, β_2 is the parameter describing the effect of a change in body mass on extinction probability, β_3 is the parameter describing the change in extinction probability associated with the shift from being able to fly to being flightless (with flightless or not coded as 1 or 0 for each species), and β_4 and β_5 are parameters describing the change in extinction probability associated with the shift from being a widespread species to being endemic to an archipelago or to an island, respectively (with these variables coded as 1 or 0 for each species).

For each of the M_k species in the augmented list that were present on an island, the covariate values for body mass, and the flight and endemism categories are missing; however, they can be estimated from the data conditional on the traits of species that were recorded and how traits influence detection and extinction probabilities. To ensure that the trait values of undetected species were representative of those likely to occur on an island, we first modeled the taxonomic order that each undetected species belonged to by drawing from a multinomial distribution where the probability of belonging to a particular order depended on the biogeographic region in which the island was located (Melanesia, Micronesia, West Polynesia, East Polynesia, or Hawaii). We did this because of biogeographic differences among regions that lead to differences in representation at the order level, which could translate to differences in trait distributions. Pigeons and doves (order Columbiformes), for example, are widely distributed across the Pacific but absent from the Hawaiian islands, whereas waterfowl (order Anseriformes) are a particularly diverse group in Hawaii. Consequently, traits associated with pigeons and doves will be absent, and those associated with waterfowl will be overrepresented, on Hawaiian Islands relative to other regions. Missing trait values were modeled conditional on the order to which species were assigned: for log-transformed body mass we drew values from a normal distribution specifying a different mean for each order, and for the flight and endemism categories we drew from multinomial distributions with probability of occurrence in each category differing among orders, which is consistent with the observation that most of the variation in avian body mass resides at the order level (29), and that there is substantial variation among orders in the proportion of species able to fly and in level of island endemism (7).

We fitted this model in a Bayesian framework using Markov Chain Monte Carlo (MCMC) methods, using OpenBUGS v. 3.2.1 (30) called from R v. 2.14.1 (31). Being a Bayesian model, all parameters had to be given prior distributions, and we specified noninformative or weakly informative priors to allow the data to drive estimation. Specifically, for each island, we augmented the species list with 5× the number of species recorded on an island, up to a maximum of 200 species, to make the augmented list sufficiently large that it specified a noninformative uniform prior distribution for the value of N_k (19). Following ref. 32, we specified weakly informative priors for the parameters involved in logit regressions to avoid problems with separation that can arise when the data imply probabilities of 0 or 1 (often because of small sample sizes), causing parameter estimates on the logit scale to tend to minus or plus infinity. To avoid this, we specified a Cauchy density function with scale 10 for baseline probabilities of extinction and detection, and a Cauchy density function with scale 2.5 for the remaining parameters in logit regressions. For modeling the missing values of extinct species, multinomial variables (avian order and level of endemism) were given Dirichlet prior distributions on the category probabilities; the binary variable flying ability was given a uniform prior on the probability; the mean of body mass was a given a normal prior with mean 0 and variance 10,000; and the SD of body mass a uniform prior in the range 0–100 (33). We ran three MCMC chains, each with a burn-in of 10,000 iterations. The posterior distributions were then sampled from a further 10,000 iterations of each chain, which were checked for convergence by visually inspecting the chain histories.

Across-Island Comparisons. From the model above, we obtained posterior distributions of the baseline detection and extinction probabilities on each island. Keeping these on the logit scale, we used the median of each distribution as a best estimate of detection or extinction probability, and the variance as a measure of the uncertainty around that estimate. We then examined whether variation in the detection or extinction probabilities across islands could be explained by island-level characteristics taking into

account the uncertainties around each probability. To do this, we modeled detection or extinction probability on the kth island, p_k, as

$$\text{logit}(p_k) \sim \text{Normal}\left(\mu_k, \sqrt{(\sigma^2 + s_k^2)}\right),$$

where μ_k is the median extinction or detection probability on the kth island modeled as a function of explanatory variables (see below), σ^2 is the between-island variation in extinction or detection probability estimated from the data, and s_k^2 is the uncertainty in the estimate of detection or extinction probability on the kth island (the variance of the posterior distribution).

For extinction probability we included island area and maximum annual rainfall as explanatory variables (both log-transformed and then centered to mean 0 and standardized by dividing by 2× the SD) (28):

$$\mu_k = \beta_0 + \beta_1 \text{ area} + \beta_2 \text{ rainfall}.$$

For detection probability we included the number of fossil specimens identified on an island and island area (both log-transformed and then centered to mean 0 and standardized by dividing by 2× the SD):

$$\mu_k = \beta_0 + \beta_1 \text{ number of fossil specimens} + \beta_2 \text{ area}.$$

These models were also fitted in a Bayesian framework, with the inclusion of the s_k^2 terms ensuring that the uncertainties associated with incomplete detection of species in the fossil record were propagated through the analysis. Models were fitted using MCMC methods as implemented in OpenBUGS v. 3.2.1 (30) called from R v. 2.14.1 (31). Regression parameters (β_0–β_2) were given noninformative normal prior distributions with mean 0 and variance 10,000, and the between-island variation term was given a uniform prior in the range 0–100 on the SD (33). We ran three MCMC chains each with a burn-in of 10,000 iterations. The posterior distributions were then sampled from a further 10,000 iterations of each chain, which were checked for convergence by visually inspecting the chain histories.

Estimating the Number of Global Extinctions. To estimate the total number of extinct island-endemic species across the study region we needed to (*i*) estimate the number of Pacific islands that could have supported at least one island-endemic species, and (*ii*) estimate how many island-endemic species went extinct on each of those islands. We obtained data on the latitude, longitude, and area (km^2) of 3,041 Pacific islands >0.1 km^2 in our study region (Vanuatu, New Caledonia, Fiji, the Marianas, and islands to the east of these, excluding New Zealand) from the Global, Self-Consistent, Hierarchical,

High-Resolution Shoreline Database (34). Most of these islands were too small or too close to neighboring islands to have supported endemic species. Curnutt and Pimm (9) showed that only Pacific islands greater than ~5 km^2 in area would support an endemic rail species, and suggested that islands less than ~10 km apart would not be sufficiently isolated to produce endemic species. Grouping islands less than 10 km apart and including only those ≥5 km^2 in area yields 269 islands that could have supported endemic species in the study region. The 41 islands in our study are not a representative sample of these 269 islands, tending to be those of larger area (median island areas = 87 and 21 km^2, respectively); this is important because, although overall rates of extinction were negatively correlated with island area (Fig. 4C), the number of island-endemic species estimated to have gone extinct on each of the 41 islands increased with area ($r = 0.62$, df = 39, $P < 0.0001$), meaning that estimates of total endemic losses based on data from these 41 islands would likely overestimate the actual number of island-endemic extinctions on all 269 islands. We also tested whether the 41 islands in our study were a biased subset with regard to degree of isolation, because more isolated islands are likely to have lower rates of colonization, leading to fewer species overall, but higher rates of endemism. For each island we calculated an index of isolation as the sum of the square roots of distance to the nearest island, distance to the nearest island group, and distance to mainland New Guinea. The mean island isolation index for the 41 islands in our study (115.5) was similar to that for the remaining islands (114.5), suggesting no bias.

To allow for the bias in island size, we classified each of the 269 islands into one of five size categories (≥5–10, >10–100, >100–1,000, >1,000–10,000, and >10,000 km^2). We then estimated the number of extinct endemic species on islands in each size category by sampling with replacement from the distribution of the total number of extinct island-endemic species (the number known from fossils on each island plus the number of undiscovered island-endemic species on each island estimated from the model) using the subset of the 41 islands in the same size category. We incorporated the uncertainty associated with estimating the number of undiscovered species by repeating this process 30,000 times, each time using the number of undiscovered species obtained from one iteration of each chain of the MCMC sampler (three chains × 10,000 iterations).

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