Contributed Paper

Consistent Ecological Selectivity through Time in Pacific Island Avian Extinctions

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Abstract: *Understanding the ecological mechanisms that lead to extinction is a central goal of conservation. Can understanding ancient avian extinctions help to predict extinction risk in modern birds? I used classification trees trained on both paleoecological and historical data from islands across the Pacific to determine the ecological traits associated with extinction risk. Intrinsic traits, including endemism, large body size, and certain feeding guilds, were tightly linked with avian extinction over the past 3500 years. Species ecology and phylogeny were better predictors of extinction risk through time than extrinsic or abiotic factors. Although human impacts on birds and their habitats have changed over time, modern endangered birds share many of the same ecological characteristics as victims of previous extinction waves. My use of detailed predictions of extinction risk to identify species potentially in need of conservation attention demonstrates the utility of paleoecological knowledge for modern conservation biology.*

Keywords: body size, conservation paleobiology, decision tree, extinction risk, fossil birds, Red List

Selección Ecológica Consistente a lo Largo del Tiempo en Extinciones de Aves en Islas del Pacífico

Resumen: *El entendimiento de los mecanismos que conducen a la extinción es una meta central para la conservación. ¿Podrá el entendimiento de las extinciones aviares antiguas ayudar a predecir el riesgo de extinción en las aves modernas? Utilicé árboles de decisión concentrados en datos paleoecológicos e históricos de islas en el Pacífico para determinar los atributos ecológicos asociados con el riesgo de extinción. Los atributos intrínsecos, incluyendo endemismo, tamaño corporal grande y ciertos gremios alimenticios, se relacionaron estrechamente con la extinción aviar en los últimos 3500 años. La ecología y filogenia de la especie fueron mejores predictores del riesgo de extinción que los factores extrínsecos o abióticos. Aunque los impactos humanos sobre las aves y sus hábitats han cambiado con el tiempo, las aves modernas en peligro comparten muchas de las características ecológicas con las víctimas de previas oleadas de extinción. Mi utilización de predicciones detalladas del riesgo de extinción para identificar especies que potencialmente requieren de acciones de conservación demuestra la utilidad del conocimiento paleoecológico para la biología de la conservación moderna.*

Palabras Clave: árbol de decisiones, aves fósiles, lista roja, paleobiología de la conservación, riesgo de extinción, tamaño corporal

Introduction

Human colonization of landmasses has coincided broadly with a marked increase in the extinction rate of native biota (Steadman 2006). Human presence is associated with three primary processes that have the po-

tential to cause extinctions: overexploitation of populations for food, habitat destruction and fragmentation, and introduction or facilitation of colonization by exotic species. Exotic species may detrimentally affect native birds through habitat destruction, competition, predation, and disease (Blackburn et al. 2004). Recent

research on oceanic island avifaunas implicates all three processes in ancient extinctions following human colonization (e.g., Milberg & Tyrberg 1993; Duncan et al. 2002; Roff & Roff 2003; Boyer 2008).

Knowledge of island birdlife has been revolutionized within the last 25 years by fossil discoveries on islands across the Pacific. In the Hawaiian islands, for example, the arrival of Polynesian colonists led to the extinction of about 50% of indigenous species of land birds (Olson & James 1982*a*). The extinction of birds in Oceania is considered one of the best substantiated rapid-extinction episodes in the vertebrate fossil record (Steadman & Martin 2003). Fossil discoveries allow reconstruction of the avifauna of the Pacific through the course of human history and may aid in understanding of both past and contemporary extinction episodes (Lyman 2006).

Pacific island birds remain severely threatened today. The region is home to 289 species of globally threatened birds (about one-quarter of all threatened birds) (BirdLife International 2008*a*). Understanding human-mediated extinction is a major goal of conservation biology (Jones et al. 2006), and efforts toward this goal have followed two separate research strands: understanding the extinction process in a general sense and predicting extinction risk in individual species. Both efforts have been hampered by a lack of available data to validate and date actual extinctions. The unusually complete fossil record of Pacific island birds offers a unique opportunity to overcome these limitations. Unlike data on extant endangered species, fossil data provide direct information on the extinction process and are an independent data set of extinction-related variables on which to build models of extinction risk. Nevertheless, the predictive power of such models is based on the assumption that similar biological factors, perhaps acting through different mechanisms, affect extinction risk through time.

The avian fossil record allows identification of ecological correlates of extinction risk through time comparison of historic risk factors with current threats to island birds. I aimed to determine the ecological and environmental correlates of extinction risk in ancient and modern Pacific island birds. I tested the consistency of factors associated with extinctions through time and evaluated the relative importance of intrinsic, ecological traits versus extrinsic factors in determining extinction risk.

Methods

Data Set

Integrating fossil and modern avian species occurrence data, I built a database of all known indigenous land birds found on 42 tropical Pacific islands (1256 populations of 497 species). A wide taxonomic breadth was represented with species from 13 avian orders and 44 families. I focused on land birds, but many breeding colonies of seabirds were also lost (Steadman 2006). The data set spanned the tropical Pacific from Melanesia (eight islands), western Polynesia (13 islands), and eastern Polynesia (10 islands) to the Marianas (five islands) and the Hawaiian islands (six islands) and represented a comprehensive picture of tropical Pacific island birdlife.

Species lists for each island were primarily gathered from Steadman (2006), but were supplemented by the information from a variety of published sources. Ecological data for each species included body mass, flight ability, endemism, nest location, dietary guild, and IUCN (International Union for Conservation of Nature) Red List status. Data on extant species were gathered from the literature, whereas information for fossil species was based on osteological descriptions and ecology of living relatives. For extinct species, body mass was estimated from allometry of hind limb skeletal measurements following the methods of Campbell and Marcus (1992).

For each island, data on land area, maximum elevation, isolation from the nearest similarly sized island, and isolation from the nearest Archipelago or continent were obtained from the United Nations Environment Programme (UNEP) islands directory (UNEP 1998). Relative degree of pre-European deforestation and secondary forest replacement for 22 islands in the data set were taken from Rolett and Diamond (2004). Information on the number of historically introduced birds and predatory mammal species was gathered from Blackburn et al. (2004) for the 27 islands common to the two datasets.

Timing of pre-European extinction closely matches the timing of human colonization on each island. Although Near Oceania was colonized >30,000 years ago, people of the Lapita cultural complex first spread from the Bismarck Archipelago eastward into Remote Oceania beginning about 3500 years ago (Kirch 2000). Most radiometrically dated fossil deposits included here are Holocene in age, with a few sites dating to the late Pleistocene (Olson & James 1982*b*; Steadman 2006); thus, the fossil data represent the ancient avifauna of each island immediately prior to human contact. Bird populations known only from pre-European fossil remains were classified as ancient extinctions, whereas populations observed after European contact (approximately 1800 AD on most Pacific islands) that later went extinct were classified as historic extinctions.

Underlying this analysis is the assumption that extant species were also present at initial human colonization. Archaeological evidence shows that most species predate the arrival of humans, but the Barn Owl (*Tyto alba*) and Short-eared Owl (*Asio flammeus*) appear to have colonized only after small mammals were introduced (Steadman 2006). There are no precultural records of the widespread, volant rails *Porzana tabuensis*, *Gallirallus philippensis*, and *Porphyrio porphyrio*, which suggests a recent (posthuman) arrival in remote islands of Oceania

(Steadman 2006). These five species were excluded from ancient extinctions but included in the historic analysis.

I chose populations as the unit of analysis because island-level extirpations were an important component of the extinction wave associated with human arrival. Of 188 species that occurred on more than one island before human impacts, almost one-third (53/188) suffered extirpation from one or more islands in their range. Examining extinctions at this level of biological detail allowed me to evaluate the importance of intrinsic traits (assessed at the species level) and extrinsic factors (assessed at the island level) independently. Throughout the paper, the term *extinction* refers to the loss of a species from an island and does not necessarily equate to global extinction.

Analyses

Paleontological data have inherent taphonomic biases and do not represent the entire prehistoric avifauna of any island. To estimate the number of extinct fossil species that remain undiscovered, I used a simple mark–recapture method (Pimm et al. 1994) derived from the relative proportions of birds observed alive and as fossils. This calculation yielded a conservative estimate of 169 undetected fossil species on the islands studied. I minimized potentially confounding preservation biases by including fossils from different preservational settings, including archaeological middens, lake bed and sand dune deposits, lava tubes, and sinkholes. Nevertheless, I examined preservation biases directly with a logistic regression of intrinsic traits on fossil preservation. For all species in the data set, fossil preservation was scored as 1 if the species was observed as a (sub) fossil and as 0 if no fossils were observed.

I found significant biases toward preservation in large-bodied species, endemics, ground nesters, and frugivores (Supporting Information). Because extinction patterns derived from these traits could reflect biases in the fossil record, I controlled for observed preservation biases and potentially undiscovered species. For each potentially confounding trait, the preservation bias was quantified with logistic regression; the inverse of this bias was used to assign trait values to undiscovered species. I quantified extinction patterns both including and excluding these undiscovered species (methods described in Boyer 2008, Appendix C).

Fossil sampling effort on each island could also affect extinction risk predictions; extensively studied islands are likely to record more prehistoric extinctions. As a lower bound on sampling effort, I limited the data set to islands where at least 10 fossil bones have been recovered and identified. In addition, the total number of identified specimens (NISP) of fossil birds from each island was included as a potential correlate of extinction in the analysis.

I used classification trees to relate extinction susceptibility to a variety of ecological and extrinsic predictors. Although classification trees have been used previously in ecology (Fielding 1999) and conservation biology (Jones et al. 2006), their application to paleoextinction data has been limited (but see Roff & Roff 2003; Boyer 2008). Classification trees represent a major advance over traditional and correlative approaches to conservation modeling because they identify nonlinear interactions and context dependency within a suite of predictor variables without making unnecessary assumptions about the data (Duda et al. 2001). Moreover, both continuous and categorical predictors can be used simultaneously and the graphical output provides clear conservation interpretations.

I built classification-tree models with the rpart package in the R statistical environment (R Foundation 2008). Predictor variables were included in the classification trees on the basis of existing knowledge from other studies (Duncan et al. 2002; Duncan & Blackburn 2004; Trevino et al. 2007) and data availability for fossil species.

Intrinsic ecological traits of each species considered were: body mass; diet (C, carnivore; I, insectivore; O, omnivore; N, nectarivore; F, frugivore; G, granivore; H, herbivore); endemism (W, widespread; A, species range limited to one archipelago; S, species range limited to one island; G, genus endemic to one island); flight ability (volant or flightless); nest location (elevated or ground nesting); and taxonomic order. Extrinsic variables associated with each island were: island area; maximum elevation; island isolation (distance from nearest island of equal or greater area); archipelago isolation (distance from nearest continent or major island group); biogeographic region (M, Melanesia; WP, western Polynesia; EP, eastern Polynesia; MR, Marianas; H, Hawaii); forest replacement (relative degree of pre-European secondary forest replacement); deforestation (relative degree of pre-European deforestation); introduced birds (number of introduced species); introduced mammals (number of predatory introduced species); and NISP, a measure of fossil sampling effort.

Model fit was quantified with the percentage of deviance explained (%DE), a measure analogous to the coefficient of determination (R^2) in linear modeling frameworks. To compare the factors associated with extinction in both the ancient and historic time periods, I constructed independent classification trees for each period. I compared the %DE of the full model to a model with only intrinsic traits to compare the relative effects of extrinsic and intrinsic variables. The full model was assessed at the population level, whereas classification trees for intrinsic traits were conducted at the species level.

Although classification trees perform well in comparison with other classification methods, the structure of the trees can be sensitive to small changes in the data set (Tong et al. 2003). Although final classifications may

not be affected, interpreting the importance of individual predictor variables can be problematic. I used a random forest of 500 classification trees (R package randomForest) to determine the relative importance of extinction predictors. Random forests improve predictive accuracy by generating a large number of bootstrapped trees (from random subsamples of the data), classifying each case on the basis of each tree in this "forest," and deciding a final predicted outcome by combining the results across all of the trees (Witten & Frank 2005). A robust measure of the importance of each predictor across the entire forest can then be obtained. Here, the importance of each predictor was measured by the decrease in classification accuracy observed after a random permutation of the focal predictor. Pairwise Z tests on mean decrease across all 500 trees were used to rank predictors.

To test the consistency of ecological risk factors facing birds in the past and today, I constructed a classification tree and random forest reflecting cumulative population-level extinctions over the past 3500 years. I compared extinction risk predictions from the cumulative random forest to current Red List status for 296 extant species in the region. Red List status, which is determined independently for each species on the basis of population decline, geographic range collapse, and other factors (IUCN 2007), was used as a proxy for current extinction risk. Species in the Red List category "least concern" are not generally considered at risk, whereas the categories "near threatened, vulnerable, endangered, and critically endangered" represent increasing levels of extinction risk (IUCN 2007). Because my goal was to describe past and predict current risk rather than to uncover its evolutionary basis, and classification trees require no assumptions of data independence, I did not consider the phylogenetic nonindependence between species (see also Westoby et al. 1995; Roff & Roff 2003; Jones et al. 2006). To gauge the importance of taxonomy (as a crude proxy for phylogeny) in extinction risk, however, I included taxonomic order as a predictor in the model.

Results

About one-third (448/1256) of the tropical Pacific island bird populations I considered here have been lost since human colonization. In the ancient extinction wave, 28% of populations (350/1217) were lost and 10% of the survivors (98/906) have disappeared in the past two centuries. In terms of species losses, 154 species disappeared before European contact and 28 more have gone extinct since then, leaving 296 extant species. Recorded extinctions represent a conservative estimate of the overall extinction severity because many extinct species may remain undetected.

Although fossil sampling on islands in the data set was far from complete, simple relationships between intrinsic
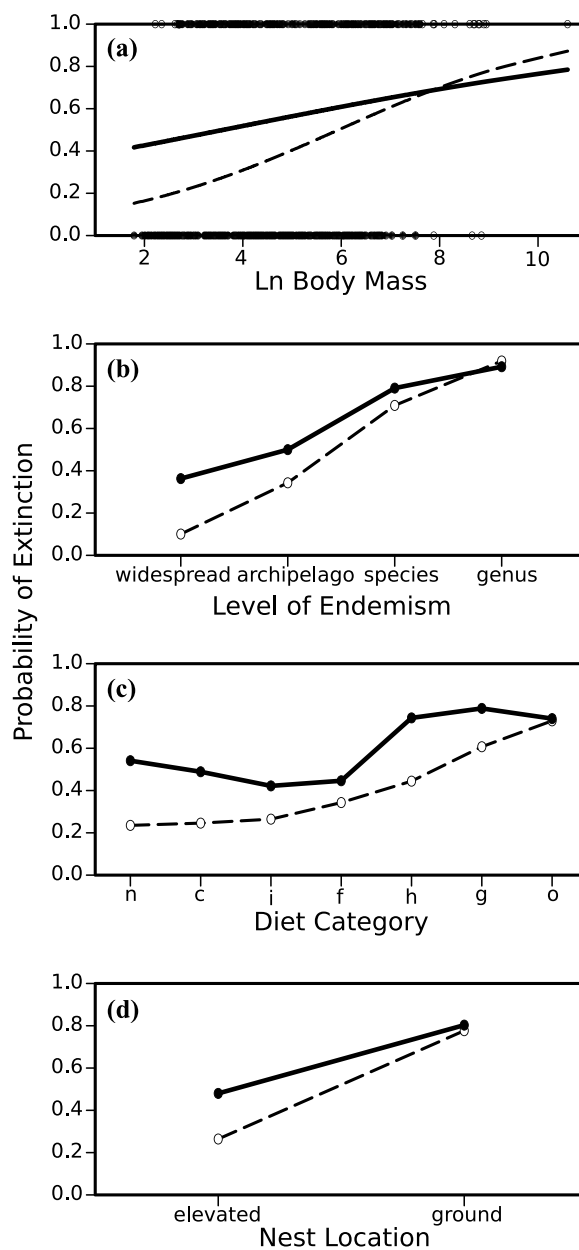

Figure 1. Relationships between intrinsic traits of birds and ancient extinction risk before (open circles & dashed lines) and after (filled circles & solid lines) accounting for observed preservation bias. In (a) species data points are shown as open circles, whereas they are omitted from (b–d) for graphical clarity.

traits and ancient extinction were robust to preservation biases (Fig. 1). After accounting for the observed biases, large body size remained significantly associated with extinction risk (logistic regression, $n = 637$, $\beta = 0.184$, $p < 0.001$; Fig. 1a). Endemic species and genera showed elevated extinction rates (logistic regression, $n = 637$, $\beta = 0.907$, $p < 0.001$; Fig. 1b). Herbivores, granivores, and omnivores were more likely to go extinct than other dietary guilds (logistic regression, $n = 637$, $\beta = 1.10$,
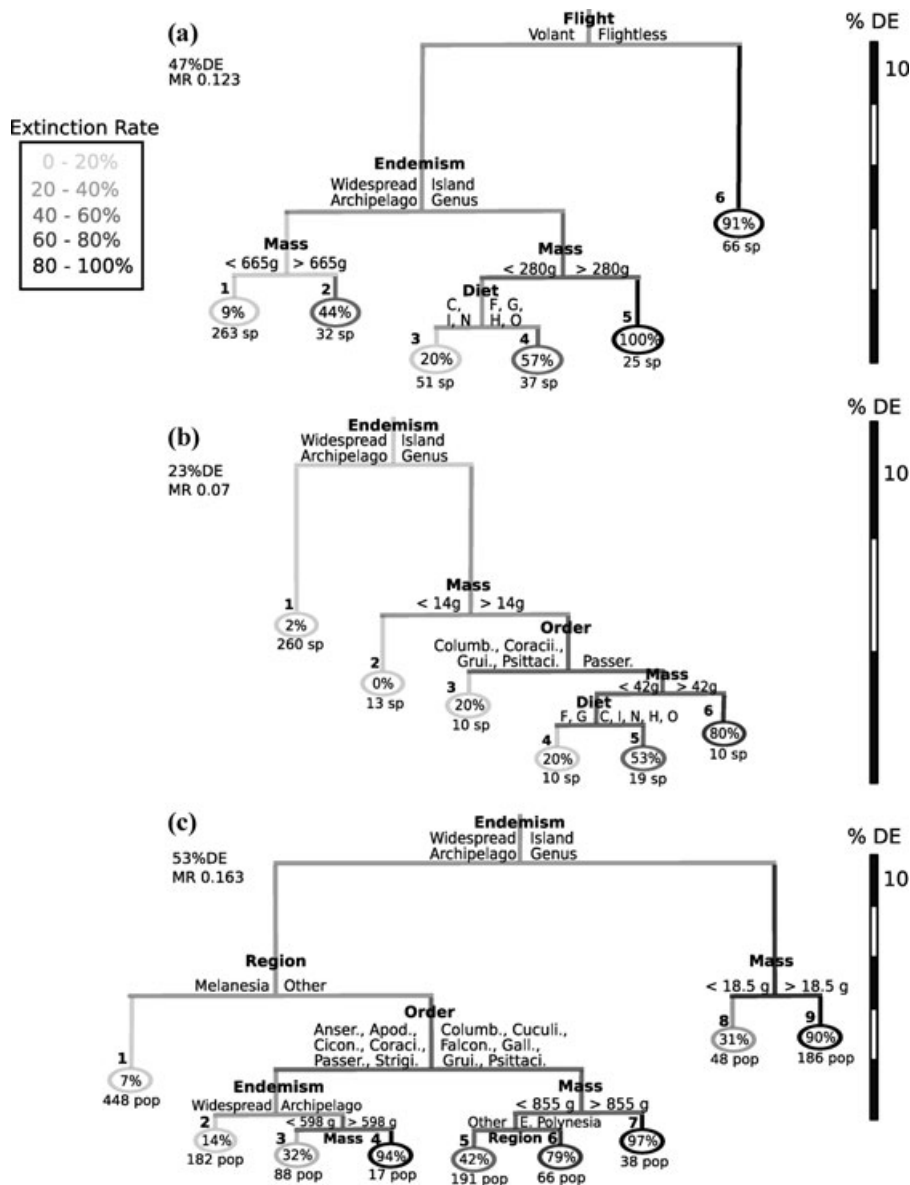
Figure 2. Classification-tree models for (a) intrinsic traits in ancient extinctions (3500–200 ybp), (b) intrinsic traits in historic extinctions (200 ybp—present), and (c) full model for cumulative extinctions. Percent deviance explained (%DE) and misclassification rate (MR) are given for each tree. Extinction probability increases to the right of each branch point, branches are shaded to reflect extinction risk, and vertical branch lengths are proportional to the amount of variance explained at each split. Terminal nodes show probability of extinction, sample size, and are numbered for reference.

1.36, and 1.09, respectively, $p < 0.01$ for each; Fig. 1c), and ground nesting remained a significant predictor of extinction (logistic regression, $n = 637$, $\beta = 1.48$, $p < 0.001$; Fig. 1d).

Intrinsic traits accounted for 47% of the variation (%DE) in ancient extinctions at the species level (3500–200 ybp; Fig. 2a). Four traits were particularly important in predicting ancient extinction. Flight ability was the most important, with 91% of flightless birds disappearing. Endemism was a secondary factor, with extinction of 50% of species or genera endemic to a single island, and large body size was also consistently associated with elevated extinction risk. Dietary categories frugivory, granivory, herbivory, and omnivory were associated with high extinction risk in small-bodied endemics. A full classification-tree model incorporating intrinsic and extrinsic predictors at the

population level accounted for 56%DE. Nevertheless, intrinsic traits remained the top extinction predictors.

Pacific island birds in the historic period (200 ybp–present) were necessarily survivors of the first extinction wave. Many of the most susceptible species were already extinct, and historic extinctions may have resulted from different and novel underlying causes (Boyer 2008). Nevertheless, ecology explained 23% of the variation (%DE) in historic extinction risk at the species level on the basis of the same characteristics (e.g., endemism, body size, and diet) that were key factors in the ancient extinctions (Fig. 2b). Because of the small number (six) of flightless species that survived into the historic period, flight ability was not identified as important in historic times. Here, differences in endemism accounted for the majority of explained variance, with relatively minor
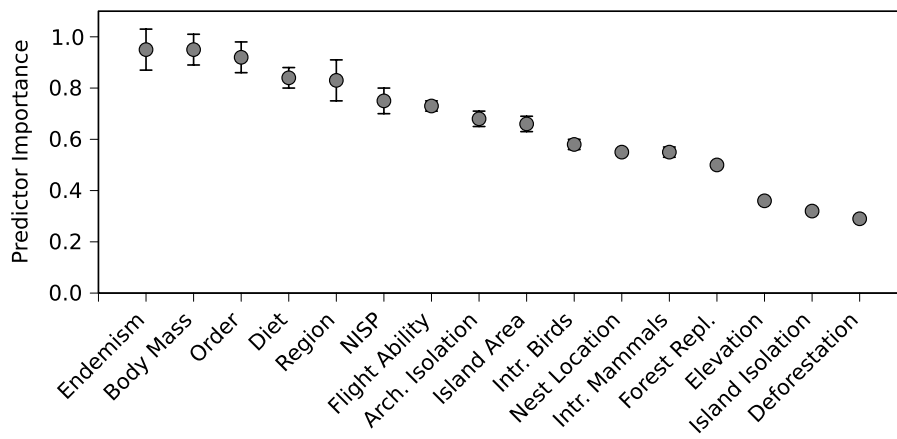
Figure 3. Relative importance (SD) of predictor variables over a random forest for cumulative extinction risk (arch., archipelago; intr., introduced; repl., replacement). Importance score reflects the impact of predictor removal on overall classification accuracy.

contributions from mass, taxonomy, and diet. A population-level tree incorporating extrinsic predictors showed no improvement in model fit, with only 22%DE for historic extinctions.

For cumulative extinctions (ancient and historic), intrinsic traits explained 48% of variation (%DE) in extinction risk over the past 3500 years, and the addition of extrinsic predictors improved model fit to 53%DE (Fig. 2c). Again, endemism and body mass were important extinction correlates, with the largest share of variation explained by endemism. Nonendemic populations on Melanesian islands showed lower extinction risk, and taxonomic order was identified as a strong predictor of extinction. This taxonomic bias in extinction rate, coupled with loss of endemics, resulted in a dramatic decrease in phylogenetic diversity across the Pacific. In the random-forest analysis, four intrinsic traits—endemism, body mass, taxonomic order, and diet—were the most important predictors of cumulative extinction (Fig. 3). Biogeographic region, NISP, flight ability, and archipelago isolation made up a second tier of predictors. Numbers of introduced birds and mammals and measures of deforestation and forest replacement did not provide much predictive power.

Extinction-risk predictions for populations of extant species from the cumulative random-forest model showed a strong correspondence with species-level red-list status (Fig. 4; logistic model, $n = 806$, $\beta = 5.79$, $p < 0.0001$). Species of least concern had significantly lower predicted risk; near threatened, vulnerable, and endangered species were at intermediate risk, and critically endangered species showed significantly higher risk (Tukey HSD test, $p < 0.05$). Thus, despite possible differences in human impacts, the ecological selectivity of contemporary extinctions appears to mirror the past.

Discussion

The historic extinction of birds in Oceania is often cited as a prominent example of anthropogenic extinction (Pimm

et al. 2006). Nevertheless, extinctions over the past few hundred years are only the most recent manifestations of anthropogenic impacts that began with initial human colonization over 3000 years ago. The extensive paleo-record of these islands provides evidence that species ecology, rather than extrinsic biotic or abiotic factors, is a powerful predictor of extinction risk through time. Because of the consistent ecological selectivity of extinction risk through time, past extinctions provide a valuable model of the extinction process in general for island birds.

Intrinsic traits of bird species were strongly associated with ancient extinction risk. Extinctions were ecologically selective and the observed patterns were consistent with previous work on the prehistoric extinction of New Zealand birds, islands not covered here. In the New Zealand extinction, Roff and Roff (2003) found that body size, flightlessness, and ground nesting were leading predictors of extinction risk. Endemism was also strongly associated with the extinction risk in New Zealand (Duncan & Blackburn 2004). Many of these patterns point to the importance of anthropogenic mechanisms in the extinction. High incidence of extinction in large flightless birds is consistent with a hypothesis of direct exploitation by people because human foragers tend to target large, profitable prey (Martin 1984; Duncan et al. 2002). Classic macroecological relationships show that large body size constrains reproductive rate and population density and, hence, total population size on an island (Brown 1995), which makes large species more vulnerable to extinction. Endemism broadly reflects range size, habitat specialization, and naïvete to predators, and endemics often fall victim to anthropogenic extinctions (Biber 2002). Human activities placed severe ecological constraints on island avifaunas such that large, endemic species with high metabolic and habitat requirements were more extinction prone. In the Polynesian period, introduced mammalian predators had an impact on small, ground-nesting, and flightless birds (Blackburn et al. 2004), but extinction rates remained lower for small birds than large-bodied species.
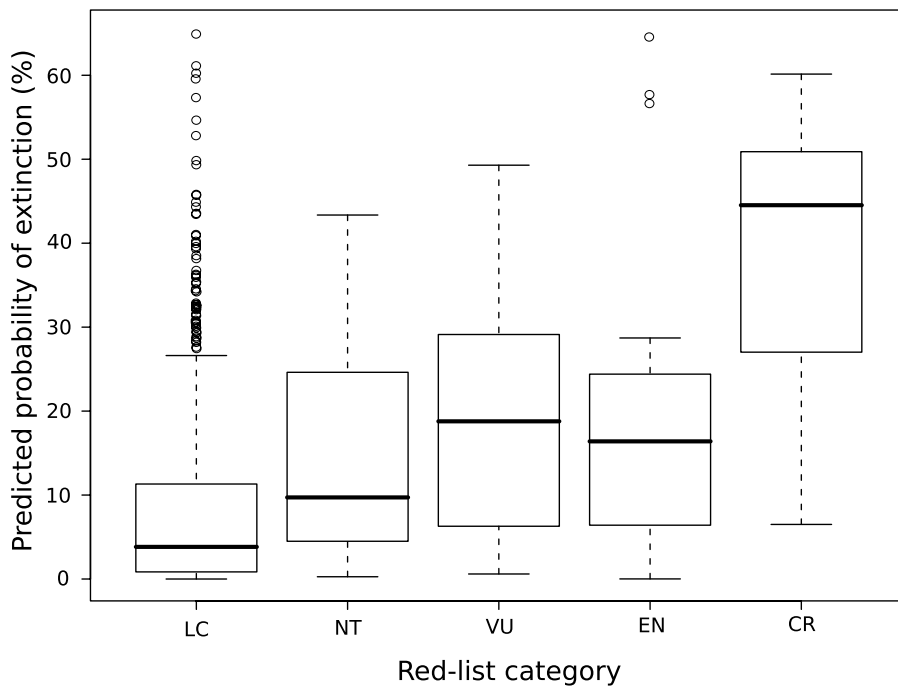
Figure 4. Correspondence between extinction-risk predictions and current Red List category for extant Pacific island bird populations. Boxplots show the distribution of predicted risk for each Red List category (median, interquartile range [IQR], and whiskers extending to ± 1.5 IQR). Statistical outliers are shown with circles. Sample size for each Red List category is as follows: LC (least concern), 692 populations; NT (near threatened), 27; VU (vulnerable), 33; EN (endangered), 39; CR (critically endangered), 16.

Over the past 200 years, human impacts on islands have intensified as habitat conversion and introduction of additional predators, avian competitors, and diseases have increased. In the historic period, species endemism alone accounted for more than one-third of explained variance in extinction risk, likely reflecting the impacts of a diverse suite of introduced predators and widespread habitat loss. For endemics, phylogeny, diet, and mass showed strong interactions, with larger passerines at highest risk and small frugivores or granivores at lower risk (Fig. 2b, nodes 4–6). The branch points for body mass in the historic tree occur at much smaller masses than in the ancient tree; within endemics a mass of just 14 g (about the size of many North American warblers) was enough to reach a 45% chance of extinction (Fig. 2b, nodes 3–6). In fact, in the historic period small to medium-sized birds were just as likely to go extinct as larger species (logistic regression, $n = 321$, $\beta = -0.12$, $p = 0.39$). This reversal of the prevalent body-size pattern reflects the impact of introduced mammalian predators on island birds, and exotic predators appear to have been more of a threat to birds in the historic period than in pre-European extinctions.

Although models built on intrinsic, ecological characteristics of species appear to fit the data well, many other variables are relevant to extinction risk and conservation. Recent studies (Karels et al. 2007; Trevino et al. 2007) indicate that island area and isolation are strongly associated with historic and modern extinction risk in island birds. Nevertheless, after incorporating these extrinsic predictors into the cumulative classification tree, endemism, diet, mass, and order remained the primary explanatory variables (Fig. 3). Island area and two measures of iso-

lation had significantly less explanatory power (*Z* test; $p < 0.01$) than the three main ecological variables. Biogeographic region, flight ability, and archipelago isolation made up a second tier of predictors. In general, Melanesian islands had lower extinction rates, possibly because they tend to be larger and less isolated, with native rodents on some islands, and they have a much longer history of human occupation (Steadman et al. 1999). More isolated island groups showed higher rates of extinction, which is at least partially linked to the endemism of their avifaunas (Pearson correlation coefficient, $r = 0.465$). Elsewhere, extinction risk in contemporary birds is associated with intrinsic traits, including body size, habitat specialization, and life-history characteristics (Owens & Bennett 2000). Extinction-risk predictions were moderately improved by including extrinsic predictors; however, no extrinsic predictor was more important than endemism, diet, or body size.

The ecological selectivity of avian extinctions on Pacific islands was quite consistent throughout human history, making the division of the past into two time intervals appear somewhat artificial. The classification tree describing cumulative extinction risk accurately predicted modern extinction risk in approximately 84% of birds in the region. The correspondence between past and present risk factors was particularly striking given that human impacts on islands have intensified through time and include changes in human populations, land-use patterns (Kirch 2000), and the rate of exotic species introductions (Blackburn et al. 2004). Extinction risk was not a simple function of diet, body size, or endemism; instead, there were complex interactions between traits. For example, within certain orders, birds endemic to one archipelago

Table 1. False-positive species and populations with high predicted extinction risk that are currently listed as vulnerable or lower.

Scientific name[a]	Common name	Red-list status[b]	Location
Outlier populations			
Aplonis opaca	Micronesian Starling	LC	northern Marianas: Guam
Ducula pacifica	Pacific Imperial Pigeon	LC	four islands in Tonga & Cook
Lalage maculosa	Polynesian Triller	LC	four islands in Tonga
Ptilinopus dupetithouarsii	White-capped Fruit Dove	LC	four islands in Marquesas
False-positive species			
Coracina analis	New Caledonian Cuckooshrike	LC	New Caledonia
Drepanoptila holosericea	Cloven-feathered Dove	NT	New Caledonia
Myadestes obscurus	'Öma'o	VU	Hawaiian Islands: Hawaii
Porzana atra	Henderson Crake	VU	Pitcairn group: Henderson
Ptilinopus insularis	Henderson Fruit Dove	VU	Pitcairn group: Henderson
Telespiza cantans	Laysan Finch	VU	Hawaiian islands: Laysan
Todiramphus ruficollaris	Mangaia Kingfisher	VU	Cook islands: Mangaia
Vini stepheni	Henderson Lorikeet	VU	Pitcairn group: Henderson

[a]*Outlier populations were identified on the basis of intrinsic and extrinsic factors (from Fig. 4), and false-positive species were identified on the basis of intrinsic traits alone.*
[b]*Abbreviations: LC, least concern; NT, near threatened; VU, vulnerable.*

were at relatively low risk overall (Fig. 2c), and this was especially true for species under approximately 600 g. Species in high-risk taxonomic groups (Fig. 2c, nodes 5–7), however, had a higher chance of extinction than small-bodied species endemic to a single island (Fig. 2c, node 8). The ability to visualize interactions between variables and to produce extinction-risk predictions for individual species and populations is an advantage of classification trees over linear-modeling frameworks. This type of general model for extinction risk in Pacific island birds may be particularly useful for rapid assessment and prioritization of poorly known species.

Although past extinctions predicted contemporary extinction risk for the majority of birds in the region, examination of the misclassifications can be informative. Of particular interest to conservation are false positives, species that share the characteristics of extinct species but are currently classified as unthreatened (Jones et al. 2006). I identified 13 populations of four species from the full cumulative model (statistical outliers from Fig. 4) and eight species from the intrinsic-only cumulative model with high (>50%) predicted extinction risk (Table 1). In some cases false positives may reflect the success of current conservation measures, or they may represent unusually resilient survivor species. Nevertheless, many species flagged as false positives may be in need of further study to determine whether additional conservation measures are necessary. For example, although all other extant species in node 9 of Fig. 2c are red-listed as vulnerable or higher, the Cloven-feathered Dove (*Drepanoptila holosericea*) and the New Caledonian Cuckooshrike (*Coracina analis*) are listed as near threatened and least concern, respectively. Although the Cloven-feathered Dove population is declining only very slowly, predictions suggest that it could easily become threatened in the future (BirdLife International 2008b). Three false-positive species are endemic

to tiny Henderson Island, an uninhabited karst island in the Pitcairn group (United Kingdom), which highlights the unique island as a priority for continued conservation attention.

Classification-tree models are no substitute for detailed studies of abundance, population declines, habitat loss, and other measures of conservation importance in island birds. To the contrary, however, quantitative predictions of extinction risk for identified false-positive species may help conservationists focus attention on the species that need it most. The correspondence between extinctions of birds over the past few thousand years of human impact in the Pacific with threats today is surprisingly strong. The overarching pattern underscores the importance of endemism, body size, and diet for extinction risk in living species and demonstrates the utility of paleoecological knowledge for conservation.

Acknowledgments

Supporting Information

An analysis of preservation bias in Pacific island birds is available as part of the on-line article (Appendix S1). The author is responsible for the content and functionality of

these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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