

Research Article

Cite this article: Gough WB, Hudson MA, Young HG, Wood J, Whitehead H, Turvey ST (2024). Modelling habitat suitability for the Critically Endangered Manumea or Tooth-billed Pigeon *Didunculus strigirostris* using past and present baselines. *Bird Conservation International*, **34**, e20, 1–9
<https://doi.org/10.1017/S0959270924000133>

Received: 13 March 2023

Revised: 04 April 2024

Accepted: 13 April 2024


Keywords:

Environmental archives; Historical baselines; Island extinctions; MaxEnt; Museum records; Species distribution models

Corresponding author:

Samuel T. Turvey;
Email: samuel.turvey@ioz.ac.uk

Modelling habitat suitability for the Critically Endangered Manumea or Tooth-billed Pigeon *Didunculus strigirostris* using past and present baselines

William B. Gough¹, Michael A. Hudson^{2,3}, H. Glyn Young², Joe Wood^{4,5},
Hester Whitehead² and Samuel T. Turvey³ 

¹Imperial College London, Silwood Park Campus, Ascot, Berkshire, UK; ²Durrell Wildlife Conservation Trust, Trinity, Jersey, Channel Islands; ³Institute of Zoology, Zoological Society of London, London, UK; ⁴Toledo Zoo, Toledo, Ohio, USA and ⁵IUCN Species Survival Commission Pigeon and Dove Specialist Group, Gland, Switzerland

Summary

Evidence-based conservation can be hindered by limited field data, but historical archives have the potential to provide unique insights into conservation-relevant parameters, such as identification of suitable habitat for threatened species. The Manumea or Tooth-billed Pigeon *Didunculus strigirostris* has declined on Samoa and only a tiny remnant population still persists, and a key first step for conservation is to locate surviving birds. Numerous Manumea records are available from the nineteenth century onwards, and we used historical and modern records to generate a series of species distribution models to predict the distribution of suitable habitat across Samoa to guide new field searches. Manumea distribution is closely associated with forest cover or its proxies. Preferred Manumea food plants are suggested to be low-elevation trees, but elevation provides relatively low percentage contribution in most models, thus not excluding the possibility that Manumea might occur at high elevations. There is also little evidence for elevational change in records over the past century. Models based on visual versus acoustic records exhibit differences in predicted habitat suitability, suggesting that some purported acoustic records might not actually represent Manumea calls. Field searches should target areas representing high habitat suitability across all models, notably the forested central axis of Upolu.

Introduction

Evidence-based conservation planning can be hindered by a lack of robust data on key ecological parameters, including species distributions and environmental requirements (Christie et al. 2021). Such data-gaps may constitute a particular problem for tropical island birds, which have experienced extensive extinctions and exhibit high current-day risk (Spatz et al. 2017; Steadman 2006a), but are often the focus of limited conservation research (de Lima et al. 2011). Worryingly, island taxa often represent global conservation priorities on the basis of evolutionary history, reflecting their geographical isolation and adaptation to novel environments (Jetz et al. 2014).

It is therefore important to assess the information-content of alternative data types with relevance for establishing management baselines. One such data source is the historical record, which has the potential to provide unique insights into past species distributions and ecosystem composition, dynamics and drivers of declines, and vulnerability and resilience to environmental change (McClenachan et al. 2012; Turvey and Saupe 2019). For example, historical data can be used to generate predictive species distribution models (SDMs) for threatened taxa, based upon the statistical relationship between occurrence records and environmental variables (Elith et al. 2011). Historical baselines are particularly important for generating SDMs for species that now survive only as tiny remnant populations, because understanding the ecological parameters associated with past distributions can indicate whether known populations persist in optimal environments or ecologically marginal refugia, and can identify priority areas to search for possible undetected populations (Lees et al. 2021; Lentini et al. 2018). However, historical archives are limited and incomplete, for example in terms of resolution and accuracy of past records, due to huge variation in rigour, standardisation and scope of pre-modern recording effort (Newbold 2010). For example, historical data typically represent presence-only data, with reliable absences difficult to determine due to non-systematic recording effort (Graham et al. 2004). The usefulness of historical data to establish conservation baselines, provide predictive insights, and resolve questions for particular threatened species is therefore uncertain.

The Manumea or Tooth-billed Pigeon *Didunculus strigirostris* is an evolutionarily distinct species endemic to the Samoan archipelago. It is historically recorded from the islands of Savai'i (1,820 km²), Upolu (1,110 km²), Nu'utele (1.2 km²), and Nu'ulua (0.2 km²) in the Independent State of Samoa (Collar 2015), and is also known from a prehistoric archaeological assemblage on Ofu Island, American Samoa (Weisler *et al.* 2016). It is the only living representative of the genus *Didunculus* following prehistoric extinction of the Tongan species *D. placopedetes* (Steadman 2006b) and an unnamed species from Vanuatu (Worthy *et al.* 2015). Although historical abundance is uncertain, the Manumea is thought to have declined by over 90% since the 1980s due to invasive rats and cats, hunting, and habitat loss from human activities and cyclones; it is listed as Critically Endangered by the International Union for Conservation of Nature (IUCN), with only a tiny remnant population likely to survive (Beichle 1987; BirdLife International 2024; Collar 2015; Serra 2017; Serra *et al.* 2018). A series of recovery actions has been proposed within two consecutive recovery plans, including habitat conservation and management, reduction of hunting, invasive species eradication, establishment of translocated populations and/or an ex situ breeding programme, and increasing public awareness and local conservation capacity (BirdLife International 2024; MNRE 2006; MNRE and SCS 2020).

A first step for practical implementation of field-based conservation actions is to locate any surviving populations or individuals. Several "Manumea Key Rainforest Areas" (MKRAs) have been identified based upon locations of relatively recent sightings or field call detections, including the Falealupo and Central Savai'i Key Biodiversity Areas (KBAs) and the Tafua and Salelologa rainforest on Savai'i, and the Apia catchments and Uafato-Tiavea KBAs on Upolu (MNRE and SCS 2020) (Figure 1A). However, recent records generally derive from opportunistic encounters or one-off surveys of specific sites, making it unclear whether MKRAs represent optimal regions to locate surviving birds.

Incomplete knowledge of Manumea ecology also hinders assessing the distribution of suitable habitat. Past observations indicate that Manumea occur in both primary and secondary tropical forest across a relatively wide elevational range, and are closely associated with *Dysoxylum* trees for feeding, especially *D. maota* and *D. samoense* (Beichle 1982, 1987; Collar 2015; DuPont 1972). Samoa's three native *Dysoxylum* species have distinct elevational ranges, with the two preferred food species more widely distributed in lower elevations and replaced by the little-used *D. huntii* at higher elevations (Whistler 1978, 1980, 1992). However, it is unclear whether Manumea are therefore ecologically excluded from Samoa's extensive upland areas above 1,000 m elevation (Collar 2015); this region includes much of the largest MKRA, the Central Savai'i KBA (MNRE and SCS 2020). Acoustic surveys have also been used in recent efforts to detect Manumea, with the species' inferred occurrence in some localities based upon interpretation of acoustic data (Baumann and Beichle 2020; Serra *et al.* 2021). However, the Manumea's call is similar to that of the more common sympatric Pacific Imperial-Pigeon *Ducula pacifica* and is hard to differentiate in the field even by knowledgeable local hunters, leading to suggestions that at least some purported acoustic records may be misidentifications (Atherton and Jefferies 2012; Baumann and Beichle 2020; Pratt and Mittermeier 2016; Serra *et al.* 2018).

Numerous historical Manumea records are available from field observations and specimen-collecting trips from the nineteenth century onwards (Beichle 1982; Collar 2015), but have not been investigated within a quantitative spatial framework to understand the species' ecology and distribution. To strengthen the Manumea conservation evidence-base, we used historical and modern records to generate a series of SDMs to predict areas of suitable habitat across Samoa. Our findings provide a new baseline to support conservation planning, identify environmental variables that influence Manumea distribution, and assess previous assumptions about its ecology and the potential accuracy of acoustic records reported for the species.

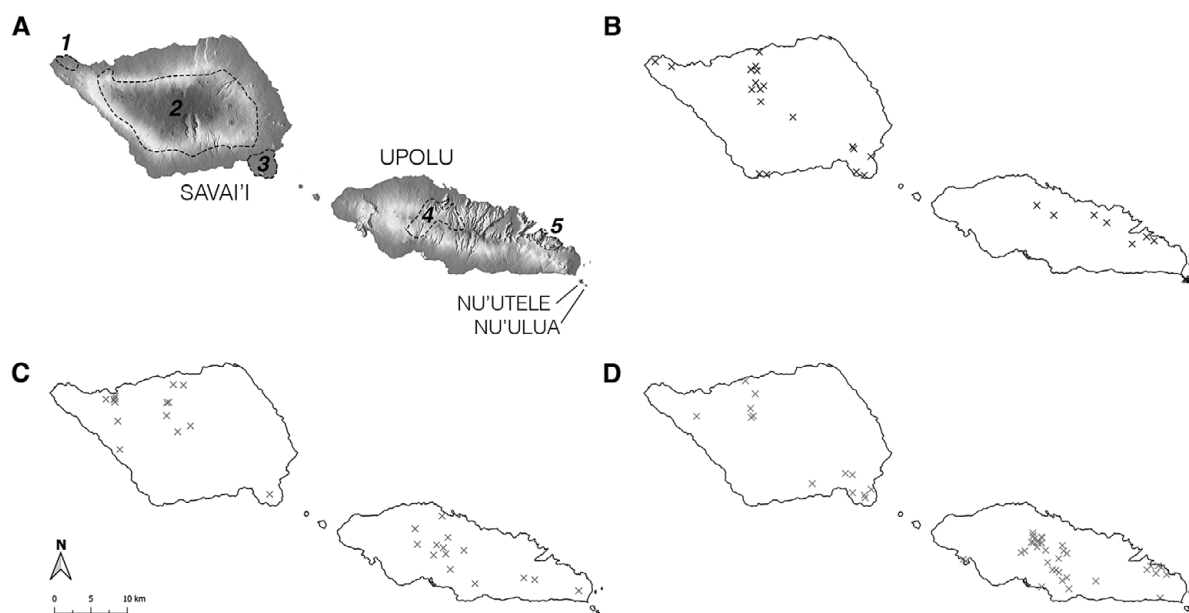


Figure 1. (A) Map of Samoa, showing the four islands on which Manumea are recorded and locations of Manumea Key Rainforest Areas: 1. Falealupo KBA; 2. Central Savai'i KBA; 3. Tafua and Salelologa rainforest; 4. Apia catchments KBA; 5. Uafato-Tiavea KBA. (B) Distribution of reported acoustic records. (C), Distribution of pre-2000 sightings or historical specimen collection localities. (D) Distribution of post-2000 sightings. KBA = Key Biodiversity Area.

Methods

Presence data

Manumea records were obtained by conducting a thorough survey of the published literature, unpublished grey literature (e.g. conservation plans, survey reports), museum accession records, and online birding trip reports (ebird.org). Museum specimens were identified through the literature, the Global Biodiversity Information Facility (gbif.org), and requests through the Natural Sciences Collections Association (NatSCA) network, with associated locality data accessed from online museum databases and email requests to curators. Presence records were divided into visual/physical observations and recent acoustic-only detections for analysis.

Many locality records lacked coordinate data, so coordinates for these records were calculated by georeferencing locality descriptions using Google Earth (earth.google.com), using consistent rules to reduce spatial bias (Supplementary material [Appendix S1](#)). Reported localities that were too vague or general (e.g. “Samoa”, “Savai’i”) were excluded. If multiple records were reported within the same protected area or KBA without further spatial information, records were spaced evenly across the area.

Environmental and land cover variables

Nineteen bioclimatic variables were obtained from WorldClim v.2.1 (worldclim.org) at 30 arc-second resolution. Collinearity and associated potential for model overfitting were minimised by excluding variables displaying high correlation ($r > 0.8$; Elith et al. 2006), preferentially removing variables that showed collinearity with > 1 other variable, and leaving seven independent variables for inclusion. Digital elevation data were obtained from CGIAR-CSI GeoPortal v.4 (Jarvis et al. 2008) at 90-m resolution. A separate slope raster was generated from the elevation data with raster analysis slope tool GDAL v.3.3.0, using default parameters (Lundbäck et al. 2021). A surface soil classification layer was obtained from PacGeo (2017) at 9 arc-second resolution, classified following Allen and Wald (2009), with high values representing hard rock and low values representing soft soils (Castellaro et al. 2008). Four land cover layers (forest, thicket, surface soil, cropland) dating from March 2015 (1×1 cells, scale 1:50,000) were obtained from GEOINT (2015).

Species distribution modelling

Maximum entropy modelling was conducted in MaxEnt v.3.4.4 (Phillips et al. 2016). This approach can use presence-only data and has superior accuracy compared with other SDM methods when data sets contain < 100 unique values, and is the primary method for modelling habitat suitability for species with limited occurrence data (van Proosdij et al. 2016; Wisz et al. 2008). Analyses were conducted in R v.1.4.1106 (R Core Team 2020).

To reduce potential for spatial autocorrelation and accommodate possible minor inaccuracies in estimating locations from historical descriptions, data were analysed at the pixel resolution of a proxy for Manumea home range. No direct estimates are available for Manumea home range or local/seasonal movements, and home range inference from closely related taxa is not possible because the species is phylogenetically distant from other extant pigeons (Jetz et al. 2014). As home range data are largely unavailable for other tropical Pacific pigeons, an estimate of 4 km^2 (2×2 km grid cell) was used from the New Zealand Kererū *Hemiphaga novaeseelandiae*, another large-bodied Pacific pigeon

(Baranyovits 2017). Presence records were spatially thinned in QGIS v.3.20.0 (QGIS Development Team 2021) using the “random selection within subsets” tool to randomly select one record within each pixel; this method has little effect on model performance (Verbruggen et al. 2013). Home range diameter (2.257 km) was not used, as distance-based thinning can discard important data from regions with densely concentrated records (Verbruggen et al. 2013). Environmental layers were resampled to this pixel size in QGIS using median resampling, to allow inclusion of records from coastal regions that are excluded using nearest-neighbour resampling.

Coastal pixels that contain $< 100\%$ land had reduced likelihood of containing Manumea records, and were effectively sampled with lower effort than non-coastal pixels. A bias file was incorporated that specified the reduced survey effort (due to reduced land availability) within each coastal pixel, expressed as the proportion of the pixel containing land.

Four SDMs were generated to investigate whether different subsets of locality data provided differing habitat suitability predictions, and to enable comparison between data types: (1) “visual reduced”, fitted with all spatially resolved visual/physical presence records (historical and recent) and with environmental layers only (bioclimatic, elevation, slope, soil layers); (2) “visual combined”, fitted with visual/physical presence records from 2000 onwards and with both environmental and modern land cover layers; (3) “acoustic reduced”, fitted with acoustic presence records and environmental layers; (4) “acoustic combined”, fitted with acoustic presence records and with both environmental and modern land cover layers. All acoustic records are recent, so a model containing only recent visual data (visual combined model) was therefore included to allow comparison; these models were fitted with land cover layers as well as environmental layers, as they can be assessed against modern land cover conditions. Conversely, the visual reduced model contained all visual/physical Manumea presence records, which included both historical and recent records and so cannot be assessed against modern land cover conditions; the acoustic reduced model was therefore also included to allow comparison with the visual reduced model and investigate the effect of reduced explanatory variables on model performance. An alternate version of the visual reduced model was also generated using only records where accurate Manumea identification was supported by museum specimens, observations in peer-reviewed scientific papers, or eBird reports by experienced birders.

Two assessments of model fitness were investigated: the area under the receiver operating characteristic curve (AUC) (Fielding and Bell 1997), and the True Skill Statistic (TSS) (Allouche et al. 2006), with the 10th percentile presence threshold used as the TSS threshold suitability value (Escalante et al. 2013). Variables with lowest percentage contribution were removed in a stepwise fashion until the greatest TSS and AUC values were achieved. The best-performing model was selected from the final variable set, and 20 bootstrap replications were run with random seed.

To fit models and evaluate model predictions in the thinned variable set after exclusion of low-contributing variables, 80% of presence records were allocated as training data and 20% as test data (Merow et al. 2013). Use of 20% as test data was selected because it provided the highest training AUC with only a small reduction in TSS compared with alternative 85:15% or 90:10% data-splits (after exclusion of low-contributing variables: (1) 80:20%, training and test AUC = 0.681 and 0.529, TSS = 0.155; (2) 85:15%, training and test AUC = 0.650 and 0.688, TSS = 0.185; (3) 90:10%, training and test AUC = 0.669 and 0.649, TSS = 0.185).

Projections used to represent final model outputs were based upon average maps generated from 10 replicates, which were then used to generate average training AUC values. This approach was followed to reduce bias that would result from selecting only the best map projections for each model. Thresholds for occupancy likelihood in each model output were calculated from the sum of maximum training sensitivity and specificity (Liu et al. 2013), with cumulative thresholds chosen from the first replication of each output.

Spatial autocorrelation in final thinned model residuals was assessed using Moran's I statistic with the R-package *spdep* (Bivand et al. 2023). As residuals showed autocorrelation (Moran I statistic standard deviate = -0.00769, $P = 0.038$), overfitting was addressed by running models twice, using differing regularisation multiplier values of 1 (default) and 2 (Radosavljevic and Anderson 2014). Performance of different model outputs was assessed by comparing mean AUC_{training} and TSS values from best-performing models.

Between-model differences in habitat suitability projections were evaluated through pairwise comparisons in ENMTools (Warren et al. 2010), using two similarity measures: Schoener's index (D; Schoener 1970) and Hellinger distance (I; Warren et al. 2008). Both metrics range from 0 (poor similarity) to 1 (high similarity) (Warren et al. 2010).

Results

Our initial data set contained 282 *Manumea* presence records (143 museum records, 139 literature records) from 1872 to 2018. After excluding records without precise locality details, we retained 131 records (28 museum records, 103 literature records) from 1924 to 2018. The final data set included 98 physical/visual-only records, 31 acoustic-only records, and two combined visual+acoustic records (Figure 1B–D, Appendix S2). After data-thinning, the visual reduced model included 74 records (Savai'i: 31, Upolu: 42, Nu'u-tele: 1), the visual combined model included 62 records (Savai'i: 22, Upolu: 39, Nu'u-tele: 1), and the acoustic models included 28 records (Savai'i: 18, Upolu: 7, Nu'u-tele: 3).

Using the default regularisation multiplier value, our four main models all had average (>0.7), good (>0.8) or excellent (>0.9) AUC values, but lower TSS values (<0.45). The acoustic combined model had the highest model fitness after removing seven variables (mean $AUC_{\text{training}} = 0.910$, TSS = 0.442). Similar model fitness was shown by the acoustic reduced model after removing five variables (mean $AUC_{\text{training}} = 0.832$, TSS = 0.359), and the visual reduced model after removing four variables (mean $AUC_{\text{training}} = 0.881$, TSS = 0.354). The visual combined model had the lowest model fitness after removing four variables (mean $AUC_{\text{training}} = 0.718$, TSS = 0.193). Variable contribution that explained >70% of variation differed across the four final models, with different variables associated with probability of *Manumea* presence (*visual combined*: BIO12, BIO17, slope, elevation; *visual reduced*: forest, slope, elevation, soil hardness, BIO12; *acoustic combined*: forest, BIO2, soil hardness, cropland; *acoustic reduced*: soil hardness, BIO12, BIO17, BIO2). Elevation explained $\geq 10\%$ of variation in three of the four final models (visual combined, visual reduced, acoustic reduced). Probability of *Manumea* presence had ≥ 0.5 probability close to sea level in both visual models and declined in probability with increasing elevation, dropping to almost 0 probability around 1,000 m a.s.l. in the visual combined model, but with a second peak of almost 0.5 probability at 1,770 m a.s.l. in the visual reduced model. Conversely, probability of presence had a fairly constant relationship with

Table 1. Percentage contribution of variables to final models. Variables removed from final models indicated by dashes. Positive correlations shown in bold, negative correlations shown in italics. VR = visual reduced model; VC = visual combined model; AR = acoustic reduced model; AC = acoustic combined model

Variables	VR	VC	AR	AC
Bioclimatic:				
<i>Mean diurnal range (BIO2)</i>	–	–	16.4	15
<i>Isothermality (BIO3)</i>	10.8	6.1	–	–
<i>Minimum temperature of coldest month (BIO6)</i>	–	5.4	–	3.5
<i>Mean temperature of wettest quarter (BIO8)</i>	–	–	–	–
<i>Annual precipitation (BIO12)</i>	25.1	7.2	17.4	7.2
<i>Precipitation of driest month (BIO14)</i>	6.0	–	–	–
<i>Precipitation of driest quarter (BIO17)</i>	21.6	–	16.9	6.8
Elevation	14.5	10	15.9	–
Slope	11.3	10.2	–	–
Soil hardness	10.7	8.9	33.4	14.7
Land cover:				
<i>Forest</i>	–	35.8	–	31.8
<i>Thicket</i>	–	6.2	–	–
<i>Surface soil</i>	–	3.2	–	9.9
<i>Cropland</i>	–	7	–	11.1

elevation (<0.5 probability) across Samoa's elevational profile in the acoustic reduced model, with slight probability peaks at lowest and highest elevations (Table 1, Appendix S3).

The two visual models predict similar areas of habitat suitability on Upolu, with much of the island's raised and forested east–west axis (including the Apia catchments and Uafato-Tiavea KBAs) identified as having high habitat suitability, as well as several small low-elevation regions along the southern coast. These models predict little suitable habitat in Savai'i, with only the Falealupo KBA, the Tafua and Salelologa rainforest, and other small discrete northern and southern low-elevation coastal areas identified as suitable by the visual combined model, and far fewer areas identified by the visual reduced model. The two acoustic models similarly predict that parts of the central axis of Upolu represent suitable habitat, but also predict higher habitat suitability for the northern low-elevation areas of Upolu, and some additional northern and western low-elevation coastal regions of Savai'i. The acoustic reduced model also predicts that a large area of the Central Savai'i KBA, including the highest-elevation central region of this island, represents good-quality habitat; the acoustic combined model predicts some good-quality habitat in this region, although across a smaller area. All models predict high suitability for Nu'u-tele (Figure 2). Spatial congruence was highest between both acoustic models, and lowest between the visual reduced and acoustic combined models (Table 2, Figure 3).

The best-performing alternate visual reduced model based upon better-confirmed records included only 25 records after data-thinning (Savai'i: 9, Upolu: 15, Nu'u-tele: 1), and performed less well than the full visual reduced model (mean $AUC_{\text{training}} = 0.786$, TSS = 0.302). This model mainly predicted low-elevation coastal areas as having high habitat suitability, along with central Upolu (Appendix

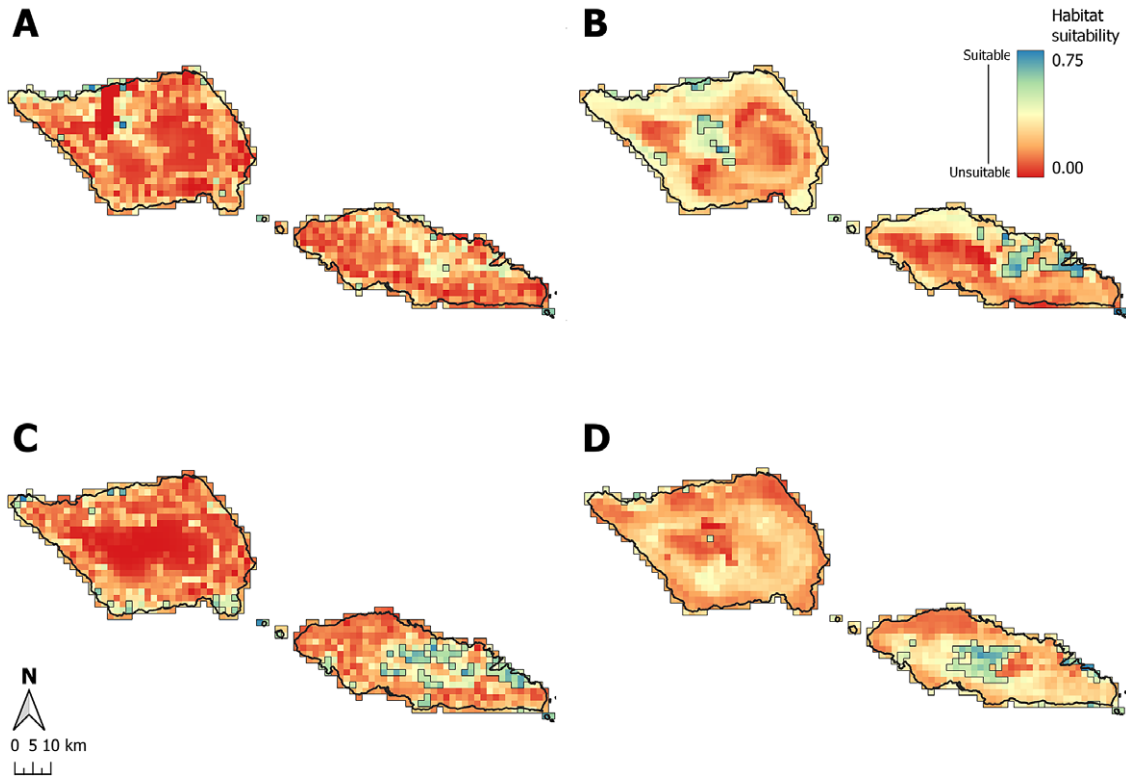


Figure 2. Manumea species distribution models: (A) visual reduced model (threshold: 37.894); (B) visual combined model (threshold: 53.459); (C) acoustic reduced model (threshold: 48.671); (D) acoustic combined model (threshold: 34.258). See main text for method used to determine occupancy likelihood thresholds.

Table 2. Pairwise comparisons of models compared using Schoener’s index (D) and Hellinger distance (I). VR = visual reduced model; VC = visual combined model; AR = acoustic reduced model; AC = acoustic combined model

Model pairwise comparison	D	I
VR – VC	0.712	0.925
VR – AR	0.724	0.941
VR – AC	0.663	0.906
VC – AR	0.699	0.915
VC – AC	0.717	0.922
AR – AC	0.763	0.943

S4). Models generated with the increased regularisation multiplier (value = 2) also performed less well, with lower AUC values that were only average (>0.7) or good (>0.8), and lower (<0.4) TSS values. The acoustic combined model had highest fitness after removing eight variables (mean $AUC_{training} = 0.823$, $TSS = 0.377$), closely followed by the visual combined model after removing eight variables (mean $AUC_{training} = 0.810$, $TSS = 0.221$). The two reduced models showed lower fitness (*acoustic reduced*: mean $AUC_{training} = 0.765$, $TSS = 0.153$; *visual reduced*: mean $AUC_{training} = 0.726$, $TSS = 0.122$). Final model outputs contained differing variables that together explained >70% of variation (*acoustic combined*: BIO6, BIO17, slope, cropland, soil surface, woodland; *acoustic reduced*: BIO2, BIO6, BIO17, slope, soil hardness; *visual combined*: BIO6, BIO17, slope, elevation, cropland, woodland; *visual reduced*: BIO12, BIO14, BIO17, slope, soil hardness). Slope and BIO17 were retained in all four final models, explaining $\geq 8\%$ and $\geq 7\%$ of variation respectively, whereas elevation remained in

only one of the final models (visual combined), explaining >19% of variation (Appendix S5).

Discussion

In this study, we explored the potential for pre-modern records of the Critically Endangered Manumea to provide new insights into the ecology and possible current distribution of this extremely threatened bird, and compare spatial and habitat predictions and information-content of different available record types. As is unfortunately the case with many long-term baselines for threatened species (Newbold 2010), many older records lack sufficiently detailed or precise locality information and could not be incorporated into SDMs. We had to exclude 116 of 136 available museum records and could only utilise records from four out of 27 museums that contained Manumea specimens (Appendix S2), and an alternate visual reduced model that only used better-supported data was limited to 25 records and had lower support. Similar data limitations may also exist with museum specimens for other insular taxa, for which older accession records may only report their island of origin rather than specific geographical information needed for environmental analysis (Collar et al. 2004). However, we were still able to utilise spatially well-resolved records spanning much of the twentieth century, representing a unique data source that can test and challenge assumptions about Manumea ecology and distribution, and with important implications for conservation.

MaxEnt performed relatively well in predicting habitat suitability for all models based on AUC values (all >0.7), but the relative contributions made by different explanatory variables varied between models. Here we only discuss outputs from models generated with the default regularisation multiplier value, as these

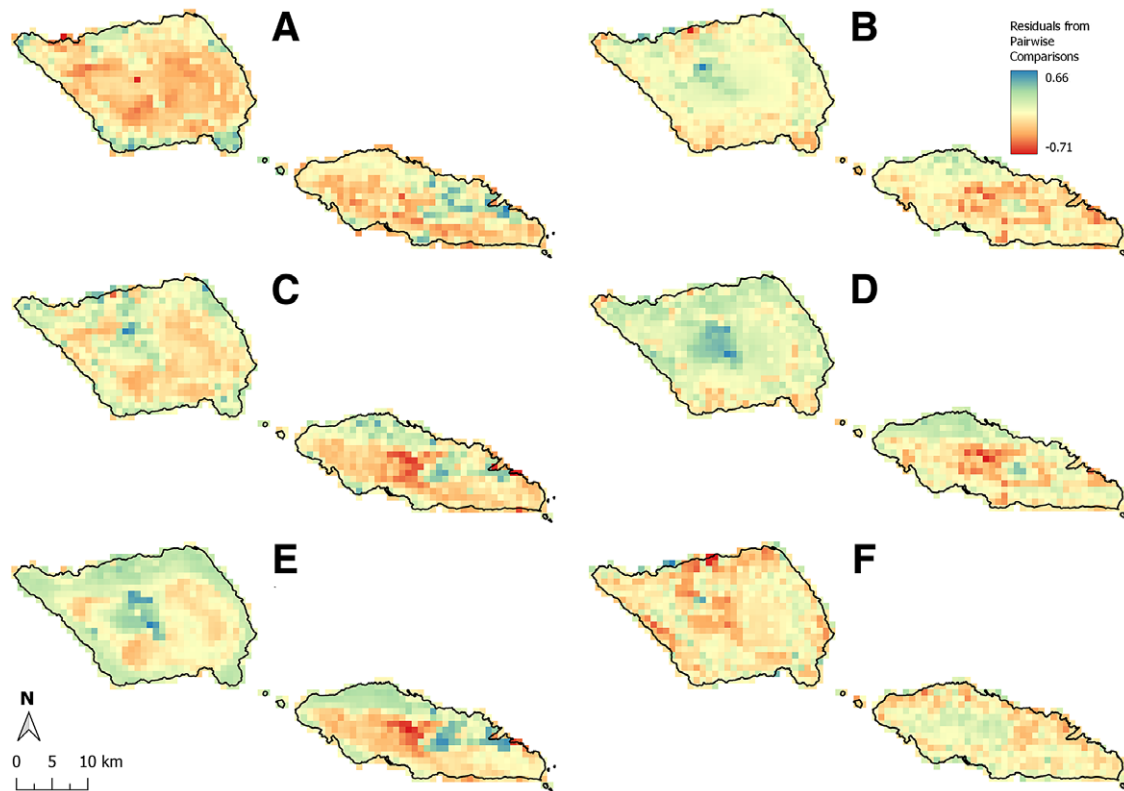


Figure 3. Pairwise comparisons between models: (A) visual reduced–visual combined; (B) visual combined–acoustic combined; (C) visual reduced–acoustic combined; (D) visual combined–acoustic reduced; (E) visual reduced–acoustic reduced; (F) acoustic reduced–acoustic combined.

models performed better than those generated using a higher value, although we note the additional differences in explanatory variable contribution between these model sets.

Forest cover provided a high percentage contribution (>30%) in models within which recent land cover data could be included (visual combined and acoustic combined), as expected for a species known to be associated with forest, with this strong relationship thus reducing the relative contribution made by other variables. Correlation with cropland and surface soil (inverse relationships in response curves) provided a further >20% percentage contribution in the acoustic combined model and >10% in the visual combined model, giving additional support for the importance of forest cover in predicting *Manumea* distribution compared with other variables. The higher contribution of bioclimatic variables within both reduced models, notably annual precipitation and precipitation of the driest quarter, also likely represents a proxy for forest cover, since these variables are associated with regulating tropical rain-forest distribution (Corlett and Primack 2011).

A positive relationship with increasing soil hardness provided a high percentage contribution (33.4%) within the acoustic reduced model. Soil conditions might represent a further proxy for forest cover, explaining the high contribution of the variable to this reduced model where land cover is not included. Alternatively, this correlation might indicate a more specific *Manumea* habitat preference. Harder soils within tropical forests can be associated with higher-elevation sloped regions (Hattori *et al.* 2005). Conversely, a negative relationship is seen between elevation and likelihood of occurrence in both visual models, consistent with the suggestion that *Manumea* are less likely to occur at higher elevations where preferred *Dysoxylum* food species are replaced by *D. huntii*. However, soil hardness, elevation and slope provide relatively low

percentage contributions in most models (<15%), indicating they are generally poor predictors of *Manumea* distribution, and thus not excluding the possibility that *Manumea* might occur at high elevations across Savai'i and Upolu. Indeed, elevation remained in only one of the final models generated with the higher regularisation multiplier value, although slope was retained in all of these models.

Our SDMs predict different spatial patterns of habitat suitability across Samoa, with practical implications for understanding *Manumea* ecology and where to focus spatial search effort for surviving individuals. Threatened species often become restricted to ecologically marginal high-elevation refugia as populations decline (Fisher 2011; Turvey *et al.* 2015), raising the possibility that models which only include recent *Manumea* records might show more restricted niche predictions compared with models also containing older records. Indeed, Steadman (2006b) suggested that *Manumea* survived on Samoa but died out on Tonga because Savai'i and Upolu are larger, higher and steeper islands. However, this possibility is contradicted by the relatively high spatial congruence between our visual reduced model (historical and recent visual records) and our visual combined model (recent-only visual records), and the negative correlation and low percentage contribution of elevation across our models, providing little evidence for elevational change in *Manumea* records over the past century. If *Manumea* were already rare by the nineteenth century, as suggested by several contemporary observers (Collar 2015; Layard 1876; Ramsay 1864; Stair 1897), it is possible that niche contraction caused by anthropogenic pressures might have already occurred before the period represented by our historical data set. However, although there has not been extensive recent search effort in remote high-elevation landscapes, some of

the few recent verified Manumea sightings are from very low elevations (MNRE and SCS 2020), and these areas are highlighted as suitable in the alternate visual reduced model based only upon better-supported records. A similar pattern of minimal range change as populations decline toward extinction is also observed in some other extremely rare species, possibly associated with across-landscape movements tracking spatially fluctuating resource availability (Turvey et al. 2010). If Manumea do persist across broadly the same environmental range, this might be associated with unpredictable fruiting periodicity and spatiotemporal resource patchiness in *Dysoxylum* (e.g. mast fruiting), with birds potentially exhibiting nomadic behaviour in following food resources. This spatial behaviour is seen widely in nectarivorous and frugivorous tropical Pacific birds (Brown and Hopkins 1996; Smetzer et al. 2021).

Conversely, our visual and acoustic models exhibit reduced congruence in pairwise comparisons, with distinct spatial differences in predicted habitat suitability across Samoa. This variation might reflect differences in the distribution of valid Manumea source data used for each pair of models. Non-congruent model predictions can result from spatial unevenness and bias between data sets, typically when data represent opportunistic detections rather than systematic region-wide survey effort. This can lead to variation in statistical associations between records from different landscapes and locally specific environmental parameters (Turvey et al. 2020). For example, visual records may be spatially skewed toward sites where observations can be made across wide areas (e.g. forest sites with viewing platforms). Conversely, predicted habitat suitability at higher elevations of central Savai'i shown by the acoustic models likely reflects the recent focus of acoustic survey effort and associated clustering of acoustic detections within this region (MNRE and SCS 2020). In contrast, a three-week survey of this region in 2012 produced only one uncorroborated visual record (Atherton and Jefferies 2012). However, this partial mismatch between predictions from visual versus acoustic models is also consistent with the suggestion that at least some acoustic records might not actually represent Manumea calls, and we cannot discount this concerning possibility. Indeed, the Pacific Imperial-Pigeon is distributed widely across upland regions of Savai'i (Atherton and Jefferies 2012; Reed 1980), consistent with the suggestion that this species is an alternative candidate for this region's acoustic records. Further investigation of all purported acoustic records using spectrographic analysis is therefore essential before using them for further planning (Baumann and Beichle 2020; Serra et al. 2021).

Given these considerations about model congruence and potential data accuracy, we suggest that initial field-based searches for Manumea should target areas that represent high habitat suitability across all models. This approach would prioritise surveys across the forested central axis of Upolu (also highlighted by the alternate visual reduced model), and including the Uafato-Tiavea KBA to the east, which together constitute the largest continuous or semi-continuous region of predicted suitable habitat in all models. We also recommend surveys in discrete low-elevation coastal forest regions identified as suitable habitat. These regions include the Falealupo KBA and the Tafua and Salelologa rainforest on Savai'i, and Nu'utele island, which may all represent more accessible survey sites compared with the high-elevation interior of both main islands. We do not exclude the importance of also surveying the Central Savai'i KBA, but varying SDM evidence for extensive suitable habitat in this remote region suggests that limited conservation resources should possibly be prioritised elsewhere to begin

with. We note that these areas of high predicted habitat suitability derived from our models are spatially congruent with some MKRAs that are based upon recent Manumea detections, but also highlight other landscapes not currently prioritised as MKRAs (MNRE and SCS 2020). It is also important to recognise that SDMs are only able to generate predictions about distribution of inferred habitat suitability based upon available environmental parameters (Franklin 2009). This does not necessarily indicate continued survival of target species (Loiselle et al. 2003), and it is unfortunately likely that Manumea have been extirpated from most areas of good-quality habitat, reflecting an example of "empty forest" syndrome (Wilkie et al. 2011).

Due to limited availability of high-resolution environmental layers for Samoa, our spatial analyses could only include a single forest layer for investigating land cover. We encourage additional research into the relationship between Manumea records and variation in forest structure and quality to further determine habitat factors that might regulate the species' distribution, to help address the recognised need to understand its ecology (MNRE and SCS 2020). In particular, we recommend quantitative mapping of cyclone damage to Samoa's forests (BirdLife International 2024; Collar 2015), and more detailed analysis of Manumea occurrence in relation to different primary/secondary and lowland/upland forest types across Samoa (Whistler 1978, 1980, 1992). Specifically, such analysis should assess Manumea occurrence in relation to the elevational ranges, distributions, and specific ecological requirements of preferred food trees (*Dysoxylum maota* and *D. samoense*). Such investigations would provide a better understanding of whether Manumea distribution is regulated by specific local-scale environmental factors that could not be incorporated within our region-wide models. Further insights into Manumea ecological tolerances could also potentially be obtained through assessment of past environmental parameters associated with prehistoric *Didunculus* remains.

However, the habitat suitability projections established in this study represent a new baseline to support existing conservation planning for Samoa's national bird. They can contribute toward the priority objectives defined in the 2020–2029 Manumea recovery plan, notably by helping to define proposed MKRA boundaries (objective 2.1), and to understand relevant aspects of Manumea ecology (objective 5.5) (MNRE and SCS 2020). Although the development of effective standardised methods for detecting Manumea in the field is recognised as a top priority, our model outputs can be used to help guide searches for surviving birds once appropriate survey methods are identified, notably through highlighting new landscapes as potential priority areas alongside recognised MKRAs. We hope that our research can thus contribute toward efforts to prevent the possible imminent extinction of this remarkable species. We also recommend further use of ecological data associated with past records to inform decision-making for other poorly known threatened species in urgent need of evidence-based conservation.

Supplementary material. The supplementary material for this article can be found at <http://doi.org/10.1017/S0959270924000133>.

Acknowledgements. We thank Imperial College London and Research England for financial support. We thank Nigel Collar for access to literature, and Rhian Rowson (Bristol Museum & Art Gallery) and the Natural Sciences Collections Association network for providing information on museum collections.

References

- Allen T.I. and Wald D.J. (2009). On the use of high-resolution topographic data as a proxy for seismic site conditions (VS30). *Bulletin of the Seismological Society of America* **99**, 935–943. <https://doi.org/10.1785/0120080255>
- Allouche O., Tsoar A. and Kadmon R. (2006). Assessing the accuracy of species distribution models: prevalence, kappa and the true skill statistic (TSS). *Journal of Applied Ecology* **43**, 1223–1232. <https://doi.org/10.1111/j.1365-2664.2006.01214.x>
- Atherton J. and Jefferies B. (eds) (2012). *Rapid Biodiversity Assessment of Upland Savai'i, Samoa*. Apia: Secretariat of the Pacific Regional Environment Programme.
- Baranyovits A.E. (2017). *Urban Ecology of an Endemic Pigeon, the Kererū*. PhD dissertation, School of Biological Sciences, University of Auckland.
- Baumann S. and Beichle U. (2020). Acoustical identification of *Didunculus strigirostris*, critically endangered tooth-billed pigeon of Samoa. *Journal of Ornithology* **161**, 439–446. <https://doi.org/10.1007/s10336-019-01742-y>
- Beichle U. (1982). *Untersuchungen zur Biologie und Systematik der Zahntaube, Didunculus strigirostris (Jardine, 1845)*. PhD dissertation, Faculty of Mathematics and Natural Sciences, University of Kiel.
- Beichle U. (1987). Habitat, population and feeding habits of the tooth-billed pigeon, *Didunculus strigirostris*. *Journal of Ornithology* **128**, 75–89. <https://doi.org/10.1007/BF01644791>
- BirdLife International (2024). Species factsheet: *Didunculus strigirostris*. Available at <https://datazone.birdlife.org/species/factsheet/tooth-billed-pigeon-didunculus-strigirostris> (accessed 14 April 2024).
- Bivand R., Altman M., Anselin L., Assunção R., Berke O., Blanchet F.G. et al. (2023). spdep: Spatial Dependence: Weighting Schemes, Statistics (1.3-1). Available at <https://cran.r-project.org/web/packages/spdep/index.html> (accessed 14 April 2024).
- Brown E.D. and Hopkins M.J.G. (1996). How New Guinea rainforest flower resources vary in time and space: implications for nectarivorous birds. *Australian Journal of Ecology* **21**, 363–378. <https://doi.org/10.1111/j.1442-9993.1996.tb00623.x>
- Castellaro S., Mulargia F. and Rossi P.L. (2008). VS30: proxy for seismic amplification? *Seismological Research Letters* **79**, 540–543. <https://doi.org/10.1785/gssrl.79.4.540>
- Christie A.P., Amano T., Martin P.A., Petrovan S.O., Shackelford G.E., Simmons B.I. et al. (2021). The challenge of biased evidence in conservation. *Conservation Biology* **35**, 249–262. <https://doi.org/10.1111/cobi.13577>
- Collar N.J. (2015). Natural history and conservation biology of the tooth-billed pigeon (*Didunculus strigirostris*): a review. *Pacific Conservation Biology* **21**, 186–199. <https://doi.org/10.1071/PC14923>
- Collar N.J., Fisher C.T. and Feare C.J. (eds) (2004). Why museums matter: avian archives in an age of extinction. *Bulletin of the British Ornithologists' Club* **123A** (Suppl.), 1–360.
- Corlett R. and Primack R. (2011). *Tropical Rain Forests: An Ecological and Biogeographical Comparison*, 2nd Edn. Oxford: Wiley-Blackwell.
- de Lima R.F., Bird J.P. and Barlow J. (2011). Research effort allocation and the conservation of restricted-range island bird species. *Biological Conservation* **144**, 627–632. <https://doi.org/10.1016/j.biocon.2010.10.021>
- duPont J.E. (1972). Notes from Western Samoa, including the description of a new parrot-finch (*Erythrura*). *The Wilson Bulletin* **84**, 375–376.
- Elith J., Graham C.H., Anderson R.P., Dudík M., Ferrier S., Guisan A. et al. (2006). Novel methods improve prediction of species' distributions from occurrence data. *Ecography* **29**, 129–151. <https://doi.org/10.1111/j.2006.0906-7590.04596.x>
- Elith J., Phillips S.J., Hastie T., Dudík M., Chee Y.E. and Yates C.J. (2011). A statistical explanation of MaxEnt for ecologists. *Diversity and Distributions* **17**, 43–57. <https://doi.org/10.1111/j.1472-4642.2010.00725.x>
- Escalante T., Rodríguez-Tapia G., Linaje M., Illoldi-Rangel P. and González-López R. (2013). Identification of areas of endemism from species distribution models: threshold selection and Nearctic mammals. *TIP Revista Especializada en Ciencias Químico-Biológicas* **16**, 5–17. [https://doi.org/10.1016/S1405-888X\(13\)72073-4](https://doi.org/10.1016/S1405-888X(13)72073-4)
- Fielding A.H. and Bell J.F. (1997). A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environmental Conservation* **24**, 38–49. <https://doi.org/10.1017/S0376892997000088>
- Fisher D.O. (2011). Trajectories from extinction: where are missing mammals rediscovered? *Global Ecology and Biogeography* **20**, 415–425. <https://doi.org/10.1111/j.1466-8238.2010.00624.x>
- Franklin J. (2009). *Mapping Species Distributions: Spatial Inference and Predictions*. New York: Cambridge University Press.
- GEOINT (2015). GEOINT New Zealand Data Service (GDS). Available at <https://geodata.nzdf.mil.nz/> (accessed 14 April 2024).
- Graham C.H., Ferrier S., Huettman F., Moritz C. and Peterson A.T. (2004). New developments in museum-based informatics and applications in biodiversity analysis. *Trends in Ecology and Evolution* **19**, 497–503. <https://doi.org/10.1016/j.tree.2004.07.006>
- Hattori D., Sabang J., Tanaka S., Kendawang J.J., Ninomiya I. and Sakurai K. (2005). Soil characteristics under three vegetation types associated with shifting cultivation in a mixed dipterocarp forest in Sarawak, Malaysia. *Soil Science and Plant Nutrition* **51**, 231–241. <https://doi.org/10.1111/j.1747-0765.2005.tb00027.x>
- Jarvis A., Reuter H.I., Nelson A. and Guevara E. (2008). Hole-filled Seamless SRTM Data. Version 4. Palmira: International Centre for Tropical Agriculture. Available at <https://srtm.csi.cgiar.org> (accessed 14 April 2024).
- Jetz W., Thomas G.H., Joy J.B., Redding D.W., Hartmann K. and Mooers A.O. (2014). Global distribution and conservation of evolutionary distinctness in birds. *Current Biology* **24**, 919–930. <https://doi.org/10.1016/j.cub.2014.03.011>
- Layard E.L. (1876). Notes on the birds of the Navigators' and Friendly Islands. *Proceedings of the Zoological Society of London* **44**, 490–506. <https://doi.org/10.1111/j.1096-3642.1876.tb02591.x>
- Lees A.C., Devenish C., Areta J.I., de Araújo C.B., Keller C., Phalan B. et al. (2021). Assessing the extinction probability of the purple-winged ground dove, an enigmatic bamboo specialist. *Frontiers in Ecology and Evolution* **9**, 624959. <https://doi.org/10.3389/fevo.2021.624959>
- Lentini P.E., Stirnemann I.A., Stojanovic D., Worthy T.H. and Stein J.A. (2018). Using fossil records to inform reintroduction of the kakapo as a refugee species. *Biological Conservation* **217**, 157–165. <https://doi.org/10.1016/j.biocon.2017.10.027>
- Liu C., White M. and Newell G. (2013). Selecting thresholds for the prediction of species occurrence with presence-only data. *Journal of Biogeography* **40**, 778–789. <https://doi.org/10.1111/jbi.12058>
- Loiselle B.A., Howell C.A., Graham C.H., Goerck J.M., Brooks T., Smith K.G. et al. (2003). Avoiding pitfalls of using species distribution models in conservation planning. *Conservation Biology* **17**, 1591–1600. <https://doi.org/10.1111/j.1523-1739.2003.00233.x>
- Lundbäck M., Persson H., Häggström C. and Nordfjell T. (2021). Global analysis of the slope of forest land. *Forestry* **94**, 54–69. <https://doi.org/10.1093/forestry/cpaa021>
- McClenachan L., Ferretti F. and Baum J.K. (2012). From archives to conservation: why historical data are needed to set baselines for marine animals and ecosystems. *Conservation Letters* **5**, 349–359. <https://doi.org/10.1111/j.1755-263X.2012.00253.x>
- Merow C., Smith M.J. and Silander J.A. (2013). A practical guide to MaxEnt for modelling species' distributions: what it does, and why inputs and settings matter. *Ecography* **36**, 1058–1069. <https://doi.org/10.1111/j.1600-0587.2013.07872.x>
- MNRE (2006). *Recovery Plan for the Manumea or Tooth-Billed Pigeon (Didunculus strigirostris) 2006–2016*. Apia: Ministry of Natural Resources & Environment, Government of Samoa.
- MNRE and SCS (2020). *Recovery Plan for the Manumea or Tooth-Billed Pigeon (Didunculus strigirostris) 2020–2029*. Apia: Ministry of Natural Resources & Environment, Government of Samoa/Samoa Conservation Society.
- Newbold T. (2010). Applications and limitations of museum data for conservation and ecology, with particular attention to species distribution models. *Progress in Physical Geography* **34**, 3–22. <https://doi.org/10.1177/0309133309355630>
- PacGeo (2017). Surface soil classification data. Available at http://www.pacgeo.org/layers/geonode:ws_soils_vs30 (accessed 14 April 2024).
- Phillips S.J., Dudík M. and Schapire R.E. (2016). Maxent Software for Modeling Species Niches and Distributions. Version 3.4.4. Available at http://biodiversityinformatics.amnh.org/open_source/maxent/ (accessed 14 April 2024).
- Pratt H.D. and Mittermeier J.C. (2016). Notes on the natural history, taxonomy, and conservation of the endemic avifauna of the Samoan archipelago. *The*

- Wilson *Journal of Ornithology* **128**, 217–241. <https://doi.org/10.1676/wils-128-02-217-241.1>
- QGIS Development Team (2021). QGIS Geographic Information System, Open Source Geospatial Foundation Project. Version 3.20.0. Available at www.qgis.org (accessed 14 April 2024).
- R Core Team (2020). *R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing. Available at <https://www.r-project.org/>.
- Radosavljevic A. and Anderson R.P. (2014). Making better Maxent models of species distributions: complexity, overfitting and evaluation. *Journal of Biogeography* **41**, 629–643. <https://doi.org/10.1111/jbi.12227>
- Ramsay E.P. (1864). On the *Didunculus strigirostris*, or tooth-billed pigeon from Upolu. *Ibis* **6**, 98–100.
- Reed S. (1980). The birds of Savai'i, Western Samoa. *Notornis* **27**, 151–159.
- Schoener T.W. (1970). Nonsynchronous spatial overlap of lizards in patchy habitats. *Ecology* **51**, 408–418. <https://doi.org/10.2307/1935376>
- Serra G. (2017). *Review of Implementation of Manumea Recovery Plan 2006–2016*. Apia: Ministry of Natural Resources and Environment of Samoa.
- Serra G., Sherley G., Failagi S.A., Foliga S.T., Uili M., Enoka F. et al. (2018). Traditional ecological knowledge of the critically endangered tooth-billed pigeon *Didunculus strigirostris*, endemic to Samoa. *Bird Conservation International* **28**, 620–642. <https://doi.org/10.1017/S0959270917000259>
- Serra G., Wood G.R., Failagi S.A., Foliga S.T., Uili M. and Enoka F. (2021). Using Samoan traditional ecological knowledge to identify calls of the critically endangered endemic tooth-billed pigeon (*Didunculus strigirostris*). *Pacific Conservation Biology* **27**, 275–283. <https://doi.org/10.1071/PC20052>
- Smetzer J.R., Paxton K.L. and Paxton E.H. (2021). Individual and seasonal variation in the movement behavior of two tropical nectarivorous birds. *Movement Ecology* **9**, 36. <https://doi.org/10.1186/s40462-021-00275-5>
- Spatz D.A., Zilliacus K.M., Holmes N.D., Butchart S.H.M., Genovesi P., Ceballos G. et al. (2017). Globally threatened vertebrates on islands with invasive species. *Science Advances* **3**, e1603080. <https://doi.org/10.1126/sciadv.1603080>
- Stair J.B. (1897). A romance of Samoan natural history; or records relating to the manu mea, or red bird of Samoa, now nearly, if not quite, extinct. *Transactions and Proceedings of the New Zealand Institute* **30**, 293–303.
- Steadman D.W. (2006a). *Extinction and Biogeography of Tropical Pacific Birds*. Chicago: University of Chicago Press.
- Steadman D.W. (2006b). An extinct species of tooth-billed pigeon (*Didunculus*) from the Kingdom of Tonga, and the concept of endemism in insular land-birds. *Journal of Zoology* **268**, 233–241. <https://doi.org/10.1111/j.1469-7998.2005.00010.x>
- Turvey S.T., Barrett L.A., Hart T., Collen B., Hao Y., Zhang L. et al. (2010). Spatial and temporal extinction dynamics in a freshwater cetacean. *Proceedings of the Royal Society B: Biological Sciences* **277**, 3139–3147. <https://doi.org/10.1098/rspb.2010.0584>
- Turvey S.T., Crees J.J. and Di Fonzo M.M.I. (2015). Historical data as a baseline for conservation: reconstructing long-term faunal extinction dynamics in Late Imperial–modern China. *Proceedings of the Royal Society B: Biological Sciences* **282**, 20151299. <https://doi.org/10.1098/rspb.2015.1299>
- Turvey S.T., Kennerley R.J., Hudson M.A., Nuñez-Miño J.M. and Young R.P. (2020). Assessing congruence of opportunistic records and systematic surveys for predicting Hispaniolan mammal species distributions. *Ecology and Evolution* **10**, 5056–5068. <https://doi.org/10.1002/ece3.6258>
- Turvey S.T. and Saupe E.E. (2019). Insights from the past: unique opportunity or foreign country? *Philosophical Transactions of the Royal Society B: Biological Sciences* **374**, 20190208. <https://doi.org/10.1098/rstb.2019.0208>
- van Proosdij A.S.J., Sosef M.S.M., Wieringa J.J. and Raes N. (2016). Minimum required number of specimen records to develop accurate species distribution models. *Ecography* **39**, 542–552. <https://doi.org/10.1111/ecog.01509>
- Verbruggen H., Tyberghein L., Belton G.S., Mineur F., Jueterbock A., Hoarau G. et al. (2013). Improving transferability of introduced species' distribution models: new tools to forecast the spread of a highly invasive seaweed. *PLOS ONE* **8**, e68337. <https://doi.org/10.1371/journal.pone.0068337>
- Warren D.L., Glor R.E. and Turelli M. (2008). Environmental niche equivalency versus conservatism: quantitative approaches to niche evolution. *Evolution* **62**, 2868–2883. <https://doi.org/10.1111/j.1558-5646.2008.00482.x>
- Warren D.L., Glor R.E. and Turelli M. (2010). ENMTools: a toolbox for comparative studies of environmental niche models. *Ecography* **33**, 607–611. <https://doi.org/10.1111/j.1600-0587.2009.06142.x>
- Weisler M.I., Lambrides A.B.J., Quintus S., Clark J. and Worthy T.H. (2016). Colonisation and Late Period faunal assemblages from Ofu Island, American Samoa. *Journal of Pacific Archaeology* **7**, 1–19.
- Whistler W.A. (1978). Vegetation of the montane region of Savai'i, Western Samoa. *Pacific Science* **32**, 79–94.
- Whistler W.A. (1980). The vegetation of eastern Samoa. *Allertonia* **2**, 45–190.
- Whistler W.A. (1992). Vegetation of Samoa and Tonga. *Pacific Science* **46**, 159–178.
- Wilkie D.S., Bennett E.L., Peres C.A. and Cunningham A.A. (2011). The empty forest revisited. *Annals of the New York Academy of Sciences* **1223**, 120–128. <https://doi.org/10.1111/j.1749-6632.2010.05908.x>
- Wisn M.S., Hijmans R.J., Li J., Peterson A.T., Graham C.H. and Guisan A. (2008). Effects of sample size on the performance of species distribution models. *Diversity and Distributions* **14**, 763–773. <https://doi.org/10.1111/j.1472-4642.2008.00482.x>
- Worthy T.H., Hawkins S., Bedford S. and Spriggs M. (2015). Avifauna from the Teouma Lapita Site, Efate Island, Vanuatu, including a new genus and species of megapode. *Pacific Science* **69**, 205–254. <https://doi.org/10.2984/69.2.6>