

1 **Modelling habitat suitability for the Critically Endangered Manumea**
2 **or Tooth-Billed Pigeon (*Didunculus strigirostris*) using past and**
3 **present baselines**

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

33

34 **Keywords:** environmental archives, historical baselines, island extinctions, MaxEnt,
35 museum records, species distribution models

36 **Introduction**

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

45 It is therefore important to assess the information-content of alternative data types
46 with relevance for establishing management baselines. One such data source is the
47 historical record, which has potential to provide unique insights into past species
48 distributions and ecosystem composition, dynamics and drivers of declines, and
49 vulnerability and resilience to environmental change (McClenachan et al. 2012; Turvey
50 and Saupe 2019). For example, historical data can be used to generate predictive
51 species distribution models (SDMs) for threatened taxa, based upon the statistical
52 relationship between occurrence records and environmental variables (Elith et al.
53 2011). Historical baselines are particularly important for generating SDMs for species
54 that now survive only as tiny remnant populations, because understanding the
55 ecological parameters associated with past distributions can indicate whether known
56 populations persist in optimal environments or ecologically marginal refugia, and can
57 identify priority areas to search for possible undetected populations (Lees et al. 2021;
58 Lentini et al. 2018). However, historical archives are limited and incomplete, for
59 example in terms of resolution and accuracy of past records, due to huge variation in
60 rigour, standardisation and scope of pre-modern recording effort (Newbold 2010). For

61 example, historical data typically represent presence-only data, with reliable absences
62 difficult to determine due to non-systematic recording effort (Graham et al. 2004). The
63 usefulness of historical data to establish conservation baselines, provide predictive
64 insights and resolve questions for particular threatened species is therefore uncertain.

65 The Manumea or Tooth-Billed Pigeon (*Didunculus strigirostris*) is an evolutionarily
66 distinct species endemic to the Samoan archipelago. It is historically recorded from the
67 islands of Savai'i (1820km²), Upolu (1110km²), Nu'utele (1.2km²) and Nu'ulua (0.2km²)
68 in the Independent State of Samoa (Collar 2015), and is also known from a prehistoric
69 archaeological assemblage on Ofu Island, American Samoa (Weisler et al. 2016). It is the
70 only living representative of the genus *Didunculus* following prehistoric extinction of the
71 Tongan species *D. placopedetes* (Steadman 2006b) and an unnamed species from
72 Vanuatu (Worthy et al. 2015). Although historical abundance is uncertain, the Manumea
73 is thought to have declined by over 90% since the 1980s due to invasive rats and cats,
74 hunting, and habitat loss from human activities and cyclones; it is listed as Critically
75 Endangered by IUCN, with only a tiny remnant population likely to survive (Beichle
76 1987; BirdLife International 2024; Collar 2015; Serra et al. 2017, 2018). A series of
77 recovery actions have been proposed within two consecutive recovery plans, including
78 habitat conservation and management, reduction of hunting, invasive species
79 eradication, establishment of translocated populations and/or an ex situ breeding
80 programme, and increasing public awareness and local conservation capacity (BirdLife
81 International 2024; MNRE 2006; MNRE and SCS 2020).

82 A first step for practical implementation of field-based conservation actions is to
83 locate any surviving populations or individuals. Several 'Manumea Key Rainforest
84 Areas' (MKRAs) have been identified based upon locations of relatively recent sightings
85 or field call detections, including the Falealupo and Central Savai'i KBAs (Key

86 Biodiversity Areas) and the Tafua & Salelologa rainforest on Savai'i, and the Apia
87 catchments and Uafato-Tiavea KBAs on Upolu (MNRE and SCS 2020) (Figure 1A).
88 However, recent records generally derive from opportunistic encounters or one-off
89 surveys of specific sites, making it unclear whether MKRAs represent optimal regions to
90 locate surviving birds.

91 Incomplete knowledge of Manumea ecology also hinders assessing the distribution
92 of suitable habitat. Past observations indicate that Manumea occur in both primary and
93 secondary tropical forest across a relatively wide elevational range, and are closely
94 associated with *Dysoxylum* trees for feeding, especially *D. maota* and *D. samoense*
95 (Beichle 1982, 1987; Collar 2015; DuPont 1972). Samoa's three native *Dysoxylum*
96 species have distinct elevational ranges, with the two preferred food species more
97 widely distributed in lower elevations and replaced by the little-used *D. huntii* at higher
98 elevations (Whistler 1978, 1980, 1992). However, it is unclear whether Manumea are
99 therefore ecologically excluded from Samoa's extensive upland areas above 1000m
100 elevation (Collar 2015); this region includes much of the largest MKRA, the Central
101 Savai'i KBA (MNRE and SCS 2020). Acoustic surveys have also been used in recent
102 efforts to detect Manumea, with the species' inferred occurrence in some localities
103 based upon interpretation of acoustic data (Baumann and Beichle 2020; Serra et al.
104 2021). However, the Manumea's call is similar to that of the more common sympatric
105 Pacific Imperial-Pigeon (*Ducula pacifica*) and is hard to differentiate in the field even by
106 knowledgeable local hunters, leading to suggestions that at least some purported
107 acoustic records may be misidentifications (Atherton and Jefferies 2012; Baumann and
108 Beichle 2020; Pratt and Mittermeier 2016; Serra et al. 2018).

109 Numerous historical Manumea records are available from field observations and
110 specimen-collecting trips from the nineteenth century onwards (Beichle 1982; Collar

111 2015), but have not been investigated within a quantitative spatial framework to
112 understand the species' ecology and distribution. To strengthen the Manumea
113 conservation evidence-base, we use historical and modern records to generate a series
114 of SDMs to predict areas of suitable habitat across Samoa. Our findings provide a new
115 baseline to support conservation planning, identify environmental variables that
116 influence Manumea distribution, and assess previous assumptions about its ecology and
117 the potential accuracy of acoustic records reported for the species.

118

119 **Methods**

120

121 *Presence data*

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

130 Many locality records lacked coordinate data, so coordinates for these records were
131 calculated by georeferencing locality descriptions using Google Earth
132 (earth.google.com), using consistent rules to reduce spatial bias (Appendix S1).
133 Reported localities that were too vague or general (e.g., "Samoa", "Savai'i") were
134 excluded. If multiple records were reported within the same protected area or KBA
135 without further spatial information, records were spaced evenly across the area.

136

137 *Environmental and land cover variables*

138 Nineteen bioclimatic variables were obtained from WorldClim v.2.1 (worldclim.org) at
139 30 arc-second resolution. Collinearity and associated potential for model overfitting
140 were minimised by excluding variables displaying high correlation ($r > 0.8$; Elith et al.
141 2006), preferentially removing variables that showed collinearity with > 1 other
142 variable, and leaving seven independent variables for inclusion. Digital elevation data
143 were obtained from CGIAR-CSI GeoPortal v.4 (Jarvis et al. 2008) at 90m resolution. A
144 separate slope raster was generated from the elevation data with raster analysis slope
145 tool GDAL v.3.3.0, using default parameters (Lundbäck et al. 2021). A surface soil
146 classification layer was obtained from PacGeo (2017) at 9 arc-second resolution,
147 classified following Allen and Wald (2009), with high values representing hard rock and
148 low values representing soft soils (Castellaro et al. 2008). Four land cover layers (forest,
149 thicket, surface soil, cropland) dating from March 2015 ($1^\circ \times 1^\circ$ cells, scale 1:50,000)
150 were obtained from GEOINT (2015).

151

152 *Species distribution modelling*

153 Maximum entropy modelling was conducted in MaxEnt v.3.4.4 (Phillips et al. 2016).
154 This approach can use presence-only data and has superior accuracy compared to other
155 SDM methods when datasets contain < 100 unique values, and is the primary method for
156 modelling habitat suitability for species with limited occurrence data (van Proosdij et al.
157 2016; Wisz et al. 2008). Analyses were conducted in R v.1.4.1106 (R Core Team 2020).

158 To reduce potential for spatial autocorrelation and accommodate possible minor
159 inaccuracies in estimating locations from historical descriptions, data were analysed at
160 the pixel resolution of a proxy for Manumea home range. No direct estimates are

161 available for Manumea home range or local/seasonal movements, and home range
162 inference from closely related taxa is not possible because the species is
163 phylogenetically distant from other extant pigeons (Jetz et al. 2014). As home range
164 data are largely unavailable for other tropical Pacific pigeons, an estimate of 4km²
165 (2×2km grid cell) was used from the New Zealand kererū (*Hemiphaga novaeseelandiae*),
166 another large-bodied Pacific pigeon (Baranyovits 2017). Presence records were
167 spatially thinned in QGIS v.3.20.0 (QGIS Development Team 2021) using the ‘random
168 selection within subsets’ tool to randomly select one record within each pixel; this
169 method has little effect on model performance (Verbruggen et al. 2013). Home range
170 diameter (2.257km) was not used, as distance-based thinning can discard important
171 data from regions with densely-concentrated records (Verbruggen et al. 2013).
172 Environmental layers were resampled to this pixel size in QGIS using median
173 resampling, to allow inclusion of records from coastal regions that are excluded using
174 nearest-neighbour resampling.

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

180 Four SDMs were generated to investigate whether different subsets of locality data
181 provided differing habitat suitability predictions, and to enable comparison between
182 data types: (1) ‘visual reduced’, fitted with all spatially-resolved visual/physical
183 presence records (historical and recent) and with environmental layers only
184 (bioclimatic, elevation, slope, soil layers); (2) ‘visual combined’, fitted with
185 visual/physical presence records from 2000 onwards and with both environmental and

186 modern land cover layers; (3) 'acoustic reduced', fitted with acoustic presence records
187 and environmental layers; (4) 'acoustic combined', fitted with acoustic presence records
188 and with both environmental and modern land cover layers. All acoustic records are
189 recent, so a model containing only recent visual data (visual combined model) was
190 therefore included to allow comparison; these models were fitted with land cover layers
191 as well as environmental layers, as they can be assessed against modern land cover
192 conditions. Conversely, the visual reduced model contained all visual/physical
193 Manumea presence records, which include both historical and recent records and so
194 cannot be assessed against modern land cover conditions; the acoustic reduced model
195 was therefore also included to allow comparison with the visual reduced model and
196 investigate the effect of reduced explanatory variables on model performance. An
197 alternate version of the visual reduced model was also generated using only records
198 where accurate Manumea identification was supported by museum specimens,
199 observations in peer-reviewed scientific papers, or eBird reports by experienced
200 birders.

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

208 To fit models and evaluate model predictions in the thinned variable set after
209 exclusion of low-contributing variables, 80% of presence records were allocated as
210 training data and 20% as test data (Merow et al. 2013). Use of 20% as test data was

211 selected because it provided the highest training AUC with only a small reduction in TSS
212 compared to alternative 85:15% or 90:10% data-splits (after exclusion of low-
213 contributing variables: (1) 80:20%, training & test AUC = 0.681 & 0.529, TSS = 0.155;
214 (2) 85:15%, training & test AUC = 0.650 & 0.688, TSS = 0.185; (3) 90:10%, training &
215 test AUC = 0.669 & 0.649, TSS = 0.185).

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

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

230 Between-model differences in habitat suitability projections were evaluated
231 through pairwise comparisons in ENMTools (Warren et al. 2010), using two similarity
232 measures: Schoener's index (D; Schoener 1970) and Hellinger distance (I; Warren et al.
233 2008). Both metrics range from 0 (poor similarity) to 1 (high similarity) (Warren et al.
234 2010).

235

236 **Results**

237 Our initial dataset contained 282 Manumea presence records (143 museum records,
238 139 literature records) from 1872 to 2018. After excluding records without precise
239 locality details, we retained 131 records (28 museum records, 103 literature records)
240 from 1924 to 2018. The final dataset included 98 physical/visual-only records, 31
241 acoustic-only records, and two combined visual+acoustic records (Figure 1B-D;
242 Appendix S2). After data-thinning, the visual reduced model included 74 records
243 (Savai'i: 31, Upolu: 42, Nu'utele: 1), the visual combined model included 62 records
244 (Savai'i: 22, Upolu: 39, Nu'utele: 1), acoustic models included 28 records (Savai'i: 18,
245 Upolu: 7, Nu'utele: 3).

246 Using the default regularisation multiplier value, our four main models all had
247 average (>0.7), good (>0.8) or excellent (>0.9) AUC values, but lower TSS values (<0.45).
248 The acoustic combined model had highest model fitness after removing seven variables
249 (mean $AUC_{\text{training}}=0.910$, $TSS=0.442$). Similar model fitness was shown by the acoustic
250 reduced model after removing five variables (mean $AUC_{\text{training}}=0.832$, $TSS=0.359$), and
251 the visual reduced model after removing four variables (mean $AUC_{\text{training}}=0.881$,
252 $TSS=0.354$). The visual combined model had lowest model fitness after removing four
253 variables (mean $AUC_{\text{training}}=0.718$, $TSS=0.193$). Variable contribution that explained
254 $>70\%$ of variation differed across the four final models, with different variables
255 associated with probability of Manumea presence (*visual combined*: BIO12, BIO17,
256 slope, elevation; *visual reduced*: forest, slope, elevation, soil hardness, BIO12; *acoustic*
257 *combined*: forest, BIO2, soil hardness, cropland; *acoustic reduced*: soil hardness, BIO12,
258 BIO17, BIO2). Elevation explained $\geq 10\%$ of variation in three of the four final models
259 (visual combined, visual reduced, acoustic reduced). Probability of Manumea presence
260 had ≥ 0.5 probability close to sea level in both visual models and declined in probability

261 with increasing elevation, dropping to almost 0 probability around 1000m asl in the
262 visual combined model, but with a second peak of almost 0.5 probability at 1770m asl in
263 the visual reduced model. Conversely, probability of presence had a fairly constant
264 relationship with elevation (<0.5 probability) across Samoa's elevational profile in the
265 acoustic reduced model, with slight probability peaks at lowest and highest elevations
266 (Table 1; Appendix S3).

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

284 The best-performing alternate visual reduced model based upon better-confirmed
285 records included only 25 records after data-thinning (Savai'i: 9, Upolu: 15, Nu'utele: 1),

286 and performed less well than the full visual reduced model (mean $AUC_{\text{training}}=0.786$,
287 $TSS=0.302$). This model mainly predicted low-elevation coastal areas as having high
288 habitat suitability, along with central Upolu (Appendix S4). Models generated with the
289 increased regularisation multiplier (value=2) also performed less well, with lower AUC
290 values that were only average (>0.7) or good (>0.8), and lower (<0.4) TSS values. The
291 acoustic combined model had highest fitness after removing eight variables (mean
292 $AUC_{\text{training}}=0.823$, $TSS=0.377$), closely followed by the visual combined model after
293 removing eight variables (mean $AUC_{\text{training}}=0.810$, $TSS=0.221$). The two reduced models
294 showed lower fitness (*acoustic reduced*: mean $AUC_{\text{training}}=0.765$, $TSS=0.153$; *visual*
295 *reduced*: mean $AUC_{\text{training}}=0.726$, $TSS=0.122$). Final model outputs contained differing
296 variables that together explained $>70\%$ of variation (*acoustic combined*: BIO6, BIO17,
297 slope, cropland, soil surface, woodland; *acoustic reduced*: BIO2, BIO6, BIO17, slope, soil
298 hardness; *visual combined*: BIO6, BIO17, slope, elevation, cropland, woodland; *visual*
299 *reduced*: BIO12, BIO14, BIO17, slope, soil hardness). Slope and BIO17 were retained in
300 all four final models, explaining $\geq 8\%$ and $\geq 7\%$ of variation respectively, whereas
301 elevation remained in only one of the final models (visual combined), explaining $>19\%$
302 of variation (Appendix S5).

303

304 **Discussion**

305 In this study, we explore the potential for pre-modern records of the Critically
306 Endangered Manumea to provide new insights into the ecology and possible current
307 distribution of this extremely threatened bird, and compare spatial and habitat
308 predictions and information-content of different available record types. As is
309 unfortunately the case with many long-term baselines for threatened species (Newbold
310 2010), many older records lack sufficiently detailed or precise locality information and

311 could not be incorporated into SDMs. We had to exclude 116 of 136 available museum
312 records and could only utilise records from four out of 27 museums that contained
313 *Manumea* specimens (Appendix S2), and an alternate visual reduced model that only
314 used better-supported data was limited to 25 records and had lower support. Similar
315 data limitations may also exist with museum specimens for other insular taxa, for which
316 older accession records may only report their island of origin rather than specific
317 geographic information needed for environmental analysis (Collar et al. 2004).
318 However, we were still able to utilise spatially well-resolved records spanning much of
319 the twentieth century, representing a unique data source that can test and challenge
320 assumptions about *Manumea* ecology and distribution, and with important implications
321 for conservation.

322 MaxEnt performed relatively well in predicting habitat suitability for all models
323 based on AUC values (all >0.7), but the relative contributions made by different
324 explanatory variables varied between models. Here we only discuss outputs from
325 models generated with the default regularisation multiplier value, as these models
326 performed better than those generated using a higher value, although we note the
327 additional differences in explanatory variable contribution between these model sets.

328 Forest cover provided a high percentage contribution (>30%) in models within
329 which recent land cover data could be included (visual combined and acoustic
330 combined), as expected for a species known to be associated with forest, with this
331 strong relationship thus reducing the relative contribution made by other variables.
332 Correlation with cropland and surface soil (inverse relationships in response curves)
333 provided a further >20% percentage contribution in the acoustic combined model and
334 >10% in the visual combined model, providing additional support for the importance of
335 forest cover in predicting *Manumea* distribution compared to other variables. The

336 higher contribution of bioclimatic variables within both reduced models, notably annual
337 precipitation and precipitation of driest quarter, also likely represents a proxy for forest
338 cover, since these variables are associated with regulating tropical rainforest
339 distribution (Corlett and Primack 2011).

340 A positive relationship with increasing soil hardness provided a high percentage
341 contribution (33.4%) within the acoustic reduced model. Soil conditions might
342 represent a further proxy for forest cover, explaining the high contribution of the
343 variable to this reduced model where land cover is not included. Alternatively, this
344 correlation might indicate a more specific *Manumea* habitat preference. Harder soils
345 within tropical forests can be associated with higher-elevation sloped regions (Hattori
346 et al. 2005). Conversely, a negative relationship is seen between elevation and
347 likelihood of occurrence in both visual models, consistent with the suggestion that
348 *Manumea* are less likely to occur at higher elevations where preferred *Dysoxylum* food
349 species are replaced by *D. huntii*. However, soil hardness, elevation and slope provide
350 relatively low percentage contributions in most models (<15%), indicating they are
351 generally poor predictors of *Manumea* distribution, and thus not excluding the
352 possibility that *Manumea* might occur at high elevations across Savai'i and Upolu.
353 Indeed, elevation remained in only one of the final models generated with the higher
354 regularisation multiplier value, although slope was retained in all these models.

355 Our SDMs predict different spatial patterns of habitat suitability across Samoa, with
356 practical implications for understanding *Manumea* ecology and where to focus spatial
357 search effort for surviving individuals. Threatened species often become restricted to
358 ecologically marginal high-elevation refugia as populations decline (Fisher 2011;
359 Turvey et al. 2015), raising the possibility that models which only include recent
360 *Manumea* records might show more restricted niche predictions compared to models

361 also containing older records. Indeed, Steadman (2006b) suggested that *Didunculus*
362 survived on Samoa but died out on Tonga because Savai'i and Upolu are larger, higher
363 and steeper islands. However, this possibility is contradicted by the relatively high
364 spatial congruence between our visual reduced model (historical and recent visual
365 records) and our visual combined model (recent-only visual records), and the negative
366 correlation and low percentage contribution of elevation across our models, providing
367 little evidence for elevational change in Manumea records over the past century. If
368 Manumea were already rare by the nineteenth century, as suggested by several
369 contemporary observers (Collar 2015; Layard 1876; Ramsay 1864; Stair 1897), it is
370 possible that niche contraction caused by anthropogenic pressures might have already
371 occurred before the period represented by our historical dataset. However, although
372 there has not been extensive recent search effort in remote high-elevation landscapes,
373 some of the few recent verified Manumea sightings are from very low elevations (MNRE
374 and SCS 2020), and these areas are highlighted as suitable in the alternate visual
375 reduced model based only upon better-supported records. A similar pattern of minimal
376 range change as populations decline toward extinction is also observed in some other
377 extremely rare species, possibly associated with across-landscape movements tracking
378 spatially fluctuating resource availability (Turvey et al. 2010). If Manumea do persist
379 across broadly the same environmental range, this might be associated with
380 unpredictable fruiting periodicity and spatiotemporal resource patchiness in *Dysoxylum*
381 (e.g., mast fruiting), with birds potentially exhibiting nomadic behaviour in following
382 food resources. This spatial behaviour is seen widely in nectarivorous and frugivorous
383 tropical Pacific birds (Brown and Hopkins 1996; Smetzer et al. 2021).

384 Conversely, our visual and acoustic models exhibit reduced congruence in pairwise
385 comparisons, with distinct spatial differences in predicted habitat suitability across

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

407 Given these considerations about model congruence and potential data accuracy,
408 we suggest that initial field-based searches for Manumea should target areas that
409 represent high habitat suitability across all models. This approach would prioritise
410 surveys across the forested central axis of Upolu (also highlighted by the alternate

411 visual reduced model), and including the Uafato-Tiavea KBA to the east, which together
412 constitute the largest continuous or semi-continuous region of predicted suitable
413 habitat in all models. We also recommend surveys in discrete low-elevation coastal
414 forest regions identified as suitable habitat. These regions include the Falealupo KBA
415 and the Tafua & Salelologa rainforest on Savai'i, and Nu'utele island, which may all
416 represent more accessible survey sites compared to the high-elevation interior of both
417 main islands. We do not exclude the importance of also surveying the Central Savai'i
418 KBA, but varying SDM evidence for extensive suitable habitat in this remote region
419 suggests that limited conservation resources should possibly be prioritised elsewhere
420 to begin with. We note that these areas of high predicted habitat suitability derived
421 from our models are spatially congruent with some MKRAs that are based upon recent
422 Manumea detections, but also highlight other landscapes not currently prioritised as
423 MKRAs (MNRE and SCS 2020). It is also important to recognise that SDMs are only able
424 to generate predictions about distribution of inferred habitat suitability based upon
425 available environmental parameters (Franklin 2009). This does not necessarily indicate
426 continued survival of target species (Loiselle et al. 2003), and it is unfortunately likely
427 that Manumea have been extirpated from most areas of good-quality habitat, reflecting
428 an example of 'empty forest' syndrome (Wilkie et al. 2011).

429 Due to limited availability of high-resolution environmental layers for Samoa, our
430 spatial analyses could only include a single forest layer for investigating land cover. We
431 encourage additional research into the relationship between Manumea records and
432 variation in forest structure and quality to further determine habitat factors that might
433 regulate the species' distribution, to help address the recognised need to understand its
434 ecology (MNRE and SCS 2020). In particular, we recommend quantitative mapping of
435 cyclone damage to Samoa's forests (BirdLife International 2024; Collar 2015), and more

436 detailed analysis of Manumea occurrence in relation to different primary/secondary
437 and lowland/upland forest types across Samoa (Whistler 1978, 1980, 1992).
438 Specifically, such analysis should assess Manumea occurrence in relation to the
439 elevational ranges, distributions, and specific ecological requirements of preferred food
440 trees (*Dysoxylum maota* and *D. samoense*). Such investigations would provide a better
441 understanding of whether Manumea distribution is regulated by specific local-scale
442 environmental factors that could not be incorporated within our region-wide models.
443 Further insights into Manumea ecological tolerances could also potentially be obtained
444 through assessment of past environmental parameters associated with prehistoric
445 *Didunculus* remains.

446 However, the habitat suitability projections established in this study represent a
447 new baseline to support existing conservation planning for Samoa's national bird. They
448 can contribute toward the priority objectives defined in the 2020-2029 Manumea
449 recovery plan, notably by helping to define proposed MKRA boundaries (objective 2.1),
450 and to understand relevant aspects of Manumea ecology (objective 5.5) (MNRE and SCS
451 2020). Although the development of effective standardised methods for detecting
452 Manumea in the field is recognised as a top priority, our model outputs can be used to
453 help guide searches for surviving birds once appropriate survey methods are identified,
454 notably through highlighting new landscapes as potential priority areas alongside
455 recognised MKRAs. We hope that our research can thus contribute toward efforts to
456 prevent the possible imminent extinction of this remarkable species. We also
457 recommend further use of ecological data associated with past records to inform
458 decision-making for other poorly-known threatened species in urgent need of evidence-
459 based conservation.

460

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465

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467

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

686

Variables	VR	VC	AR	AC
Bioclimatic:				
<i>Mean diurnal range (BIO2)</i>	—	—	16.4	15
<i>Isothermality (BIO3)</i>	<i>10.8</i>	<i>6.1</i>	—	—
<i>Min 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	<i>17.4</i>	<i>7.2</i>
<i>Precipitation of driest month (BIO14)</i>	6.0	—	—	—
<i>Precipitation of driest quarter (BIO17)</i>	21.6	—	<i>16.9</i>	<i>6.8</i>
Elevation	<i>14.5</i>	<i>10</i>	<i>15.9</i>	—
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>		<i>6.2</i>		—
<i>Surface soil</i>		<i>3.2</i>		<i>9.9</i>
<i>Cropland</i>		<i>7</i>		<i>11.1</i>

687

688 **Table 2.** Pairwise comparisons of models, compared using Schoener's index (D) and
689 Hellinger distance (I). VR, visual reduced model; VC, visual combined model; AR,
690 acoustic reduced model; AC, acoustic combined model.

691

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

692

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

698

699 **Figure 2.** Manumea species distribution models: **A**, visual reduced model (threshold:
700 37.894); **B**, visual combined model (threshold: 53.459); **C**, acoustic reduced model
701 (threshold: 48.671); **D**, acoustic combined model (threshold: 34.258). See main text for
702 method used to determine occupancy likelihood thresholds.

703

704 **Figure 3.** Pairwise comparisons between models: **A**, visual reduced–visual combined; **B**,
705 visual combined–acoustic combined; **C**, visual reduced–acoustic combined; **D**, visual
706 combined–acoustic reduced; **E**, visual reduced–acoustic reduced; **F**, acoustic reduced–
707 acoustic combined.