

1 **What passes through the extinction filter? Historical and contemporary patterns of**
2 **vulnerability of the most extinction-prone bird family (Aves: Rallidae)**

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25

26 Abstract

27 Patterns of extinction risk can vary across taxa, with species of some groups being particularly
28 vulnerable to extinction. Rails (Aves: Rallidae) represent one of the most extreme yet well
29 documented cases of mass extinction within a modern vertebrate group. Between 54 and 92% of
30 rail species became extinct following waves of human contact during both the Holocene and the
31 Anthropocene eras, and a third of the extant species are currently threatened or near-threatened.
32 Here we (1) examine extinction filters through consecutive human contacts with rails, investigating
33 the role of intrinsic life-history traits; and (2) investigate drivers of contemporary vulnerability.
34 During the most-recent wave of extinction, we found that body size was the important correlate of
35 rail extinctions, with both smaller and larger bodied species more likely to become extinct. Island
36 endemism and small clutch size were the strongest predictors of contemporary vulnerability.
37 Overall, island endemic rails tend to take the same trajectory as extinct species, suffering mostly
38 from invasive predators and overhunting, but with different traits targeted contemporarily compared
39 to past extinctions. Moreover, modern anthropogenic threats have created the potential for new
40 intricate pathways – or a contemporary ‘field of bullets’ – making future vulnerability potentially
41 less predictable.

42

43 Impact statement

44 Vulnerability to extinction in rail bird species has shifted over time, from traits like flightlessness
45 and naivety to humans, to slow reproduction in the modern context. While past extinctions
46 primarily occurred on islands, contemporary threats have diversified, making future vulnerability
47 less predictable and highlighting the urgent need for tailored solutions to island conservation.

48

49 **Introduction**

50 In just over three centuries, the pace of extinction has accelerated far beyond natural background
51 rates (Pimm *et al.*, 1995; Crutzen, 2002; Ceballos *et al.*, 2015), leading experts to consider this sixth
52 major extinction event as a new geological epoch, termed the Anthropocene (Crutzen, 2002;
53 Zalasiewicz *et al.*, 2008). Understanding why and how species become extinct when facing
54 anthropogenic activities is a major question in extinction biology (Diamond, 1989). This provides
55 the potential to better predict future biodiversity loss with the ultimate goal of providing efficient
56 conservation efforts (Brook & Alroy, 2017). A particularly critical aspect is the need to determine
57 whether past extinction events are provoked randomly: the ‘field of bullets’ hypothesis (Raup,
58 1991), or linked to species’ life-history traits: the ‘extinction-filter effect’ hypothesis (Pimm *et al.*,
59 1995; Balmford, 1996; Turvey & Fritz, 2011).

60 During past extinction events, some taxa were over-represented in the assemblages of
61 extinct species. Within the avifauna, for example, island endemic birds were disproportionately
62 vulnerable during first human contact in the Holocene (Steadman, 1995) and at a subsequent
63 contact on islands (mostly with European settlers, starting in the 16th century; Pimm *et al.*, 2006;
64 Duncan *et al.*, 2013). Some bird families were found to be systematically more prone to extinction
65 during these events, with many hundreds or thousands of species going extinct due to vulnerabilities
66 induced by specific life-history traits such as island endemism, large body size and flightlessness
67 (Steadman, 2006; Boyer, 2010; Duncan *et al.*, 2013). This suggests that these island-bird
68 extinctions were driven by extinction filters.

69 Identifying potential shifts in vulnerability between past and contemporary patterns can be
70 crucial to provide reliable context and potential projections for the future. These shifts are expected,
71 as predominant threats have changed throughout time and may therefore target different traits or
72 species (Boyer, 2010; Bromham *et al.*, 2012). Identifying them would answer the question of ‘can
73 past avian extinctions help to forecast extinction risk in birds?’ Historically, overhunting,
74 introduced predators, and to a lesser extent habitat changes were the main anthropogenic threats to
75 birds (Johnson & Stattersfield, 1990; Steadman, 1995; Blackburn *et al.*, 2004; Duncan *et al.*, 2013),
76 while habitat loss created by accelerated land-use changes and climate change are more impactful to
77 species in contemporary times (Bennett *et al.*, 2001; Urban, 2015; Ducatez & Shine, 2017).
78 Contemporary anthropogenic activities also appear to be magnified by an increase in amplitude,
79 intensity, and diversity, relative to the past. For example, the IUCN Red List references 38 different
80 types of anthropogenic threats to wildlife (IUCN, 2019).

81 Most comparative studies on extinction risk investigate contemporary patterns globally and
82 across taxa to extract intrinsic reasons for vulnerability. However, human impacts are not spatially
83 or temporally consistent and species responses to threats can depend on their resistance to previous
84 extinction filters (Diamond, 1984; Steadman, 1999; Biber, 2002; Boyer, 2008; Bromham *et al.*,
85 2012). Therefore, analysing the evolution of vulnerability within extinction-prone families that went
86 through successive extinction waves is a way to break down patterns of extinction and resistance,
87 and to identify intrinsic causes.

88 Rails (Aves: Rallidae) are the most extinction-prone bird family, with 54 to 92% of all species
89 going extinct after their first contact with humans during the mid-Holocene (representing 200 to 2,000
90 estimated extinct species; Steadman, 1995; Curnutt & Pimm, 2001). They went through a second
91 wave of extinction from the 16th century when European settlers spread worldwide (hereafter ‘Era of
92 Colonialism’). Globally, a third of extant rails are currently threatened or near-threatened (47
93 species). Island endemic rails are the most threatened rails (Lévêque *et al.*, 2021) and have historically
94 been observed in diverse situations of human contact, resulting in either extinction or coexistence. In
95 the context of island rails, it is evident that their interactions with humans have varied substantially
96 over time, offering a compelling lens through which to explore biogeographical patterns and
97 processes. Some rail species have coexisted with humans since the Pleistocene/Holocene transition,
98 adapting to early human-induced changes, while others encountered humans much later, during the
99 mid- to late Holocene or even as recently as the Era of Colonialism (16th to 20th century), in locations
100 such as Saint Helena, Ascension, and Tristan da Cunha. This staggered timeline of human arrival and
101 colonisation across different islands has led to a diverse array of impacts on rail populations, from
102 minimal disturbance in some areas to complete extinction in others. By analysing these varied
103 interactions and their outcomes, we can dissect the roles of different extinction filters—such as habitat
104 destruction, introduced predators, and over-hunting—and their sequential impact as islands were
105 colonised over time. This biogeographical perspective can both shed light on the historical dynamics
106 that have shaped current rail distributions and yield insights into the broader principles governing
107 species survival and extinction on islands.

108 Here, we provide a thorough review of correlates to extinction risk and vulnerability
109 throughout different temporal (Era of Colonialism or current time) and spatial scales (globally or on
110 islands only), using the rail family as our exemplar (Fig. 1, Fig. 2, see detailed hypotheses and
111 references in Table S1). The scientific records for ancient rail extinctions (prior the 16th century)
112 and their life-history traits are largely incomplete from the many hundreds or thousands of species

113 estimated (Steadman, 1995; Curnutt & Pimm, 2001). Therefore, our study focuses on the
114 extinctions that happened from the Era of Colonialism onwards.

115 The study aims are to investigate how the traits of rail species (body size, habitat diversity,
116 migration behaviour, island endemism, island characteristics, flightlessness, naivety to humans and
117 predators, and socio-economic status of countries, Table 1) are associated with:

- 118 1) Extinction or persistence on islands (as all extinctions previously occurred on islands)
- 119 2) Contemporary IUCN status (threatened or not), globally and on islands
- 120 3) Major threat categories (habitat loss, overhunting, introduced predators), globally and on
121 islands.

122

123 **Methods**

124 **Database of rail traits and threats**

125 We compiled information on life-history traits, biogeographic, and socio-economic contexts that
126 have been hypothesised to increase extinction risk in birds using the comprehensive Guide to the
127 Rails, Crakes, Gallinules and Coots of the world (Taylor & van Perlo, 1998) and other external
128 sources for information (Table 1; see Table S1 for references and data sources). We constructed a
129 database for the 124 species of extant rails, including 33 island endemic species and 27 recently
130 extinct species (25 officially extinct and 2 considered as extinct in this analysis only, Table S2) and
131 we extracted their threatened status and impact from threats from the online 2019-version of the
132 International Union for Conservation of Nature (IUCN) Red List database (IUCN, 2019;
133 <http://iucnredlist.org>). Some variables could not be reliably obtained across species and were
134 excluded from the global analysis (in Part 2 [overall vulnerability with IUCN threatened status]:
135 diet, clutch size, and mating system). We considered island endemic species as those restricted to
136 one (single-island endemics) or a group of islands (multi-island endemics).

137

138 Focal taxa included Rallidae (Gruiformes) and followed IUCN classification. IUCN still includes
139 the Sarothruridae (flufftails) as members of this family. Species of both families have convergent
140 body plans leading to taxonomic confusion regarding their placement based on morphology alone
141 (e.g., Livezey, 1998). However, genetic data recovered the sister relationship of flufftails and
142 Heliornithidae (Hackett *et al.*, 2008) and continues to reveal species of “rail” e.g., *Rallicula forbesi*
143 as flufftails (Garcia-R *et al.*, 2020). Therefore, we excluded and included known flufftails from our
144 analyses herein (Appendix 1).

145 Species considered ‘data deficient’ or that have not been recognised by the IUCN (e.g., due
146 to a recent phylogenetic split) were excluded from the analyses (Table S2). The metrics for all
147 countries in which a species occurred were averaged. For human density, we used the density of the
148 land where present (i.e., countries, or if present on an island only, would use human density for that
149 island).

150 Herein we define ‘extinction risk’ as the likelihood of becoming extinct or not for a species,
151 and ‘vulnerability’ as the likelihood of being considered threatened, according to the IUCN Red
152 List (a threatened status being attributed for ‘vulnerable’, ‘endangered’, or ‘critically endangered’
153 status).

154

155 **Classification of extinct and extant rail species**

156 We determined different pathways for rail extinctions at either one of three critical time periods: (i)
157 as naïve species experiencing their first contact with humans in the Pleistocene/Holocene or (ii)
158 during the Era of Colonialism, or (iii) at second contact with humans after surviving their initial
159 contact during the Pleistocene/Holocene (‘savvy’, Fig. 2). We defined ‘contact’ as a period of
160 significant human impact (e.g., introduction of alien species) or settlement. Recent extinctions (e.g.,
161 1970s) resulting from the lasting impacts of the Era of Colonialism (e.g., introduced predators) were
162 analysed as part of the Era of Colonialism. Two species went extinct due to contemporary causes
163 (Fig. 2, ‘(iii) Extinct (ignored)’ and were therefore analysed retrospectively as ‘savvy’ during the
164 Era of Colonialism (Table S1). Too little information was available from ancient extinctions for a
165 robust classification of life-history traits or extinction drivers, thus extinctions from (i) were not
166 analysed. We compiled the causes to island rails’ extinctions since the 16th century. To the best of
167 our knowledge, no rail species has been described extinct nor fossil remains of extinct rails dating
168 younger than Pleistocene were found on continental landmasses. The Era of Colonialism concerned
169 mostly European settlers but some extinctions in New Zealand islands were linked to the impact of
170 Polynesian settlers.

171 *Gallirallus lafresnayanus* and *Pareudiastes pacificus* are two ‘critically endangered’ rail
172 species that have not been seen with certainty since the 19th century and are suspected to be already
173 extinct by some authors (IUCN, 2019); they were considered as extinct for the analyses (Table S2).
174 *Hypotaenidia owstoni* was considered as ‘extinct in the wild’ until 2019 (when its status changed
175 for ‘critically endangered’; IUCN, 2019) and therefore was considered extinct for the analysis.

176

177 **Statistical analysis**

178 We implemented all modelling in R (version 3.6.3; R Core Team, 2021). We used Boosted
179 Regression Trees (BRTs) to investigate correlates of extinction risk and vulnerability globally and
180 on islands. BRT is a powerful machine-learning approach recognised for its capacity to handle
181 high-dimensional data, capture non-linear relationships implicitly, and tolerate collinearity among
182 predictors. BRTs distinctively learn the structure of data, helping to adaptively uncover complex
183 patterns that can be overlooked by traditional methods. Simple linear models (GLM) were initially
184 run (see Appendix 2), however they fitted the data poorly, therefore BRTs were preferred. Different
185 results between the GLM and BRT analyses could be observed (Appendix 2).

186 Unlike traditional linear models, BRTs do not require predictors to be orthogonal. This is
187 due to their tree-based structure, where the algorithm selects variables for splitting based on their
188 individual contributions to reducing prediction error, rather than their interrelationships. This
189 process, combined with BRT's ability to model non-linear relationships and complex interactions
190 through an additive approach of combining multiple trees, substantially mitigates the impact of
191 collinear variables. Consequently, BRTs can effectively handle high-dimensional and correlated
192 data, ensuring the reliability of analyses in such cases. This robustness makes it particularly suitable
193 for classification tasks (like whether rails went extinct or not), when faced with a multifaceted array
194 of possible ecological, socio-economic, and biological predictor variables. We note that while BRTs
195 inherently accommodate hierarchical dependencies, they do not explicitly account for phylogenetic
196 autocorrelation; however, they are robust even in the presence of incompletely independent data
197 (Jones *et al.*, 2006; Boyer, 2010). Model coefficients are shown as mean \pm standard error. The
198 variables 'Island size', 'Human density', and 'GDP' were \log_{10} -transformed, and all continuous
199 variables (including the ones log-transformed) were standardised using z-scores. Information on
200 clutch size was scarce and the data was missing for 44% of the species in the extant island endemic
201 species, as well as for 93% of the extinct species. Therefore, we did not include the clutch size
202 variable in island models.

203

204 ***Part 1: Past extinction risk on islands***

205 We investigated the role of naivety to humans, island size, flightlessness, and body size as
206 correlates of historical extinction risk for island rails during the Era of Colonialism. The model for
207 past island extinctions took the form:

208 • ISLAND_Extinctions ~ body size + flightlessness + island size + naivety to humans

209

210 ***Part 2: Contemporary vulnerability (IUCN threatened status)***

211 For the correlates of contemporary vulnerability in rails, we tested how life-history traits (island
212 endemism, island characteristics, body size, habitat diversity, migration behaviour) and socio-
213 economic attributes of the countries where present (GDP, human population growth, human
214 density), were associated with the likelihood of a rail species being threatened or not (Table 1).

215 Models were run at two spatial scales: i) globally (all modern rail species) and ii) on islands (island
216 endemic rails).

217 • GLOBAL_Vulnerability-IUCN ~ migratory behaviour + body size + clutch size + habitat
218 diversity + island endemism + GDP + population growth + human density_{countries}

219 • ISLAND_Vulnerability-IUCN ~ body size + habitat diversity* + flightlessness* + island size +
220 island isolation* + human density_{islands}

221 Where * indicates predictor variables that were excluded from the island model after
222 preliminary results, to avoid overfitting with too many marginal predictors (their importance was
223 below 0.4 in initial models). Remaining parameters were island size, body size and human density.

224 We modelled vulnerability as a binomial dependent variable: ‘non-threatened’ species (category
225 including ‘least concern’ and ‘near-threatened’ IUCN Red List status) versus ‘threatened’ species
226 (‘vulnerable’, ‘endangered’, and ‘critically endangered’ status; IUCN, 2019). Four species that were
227 classified as ‘threatened’ by the IUCN were done so on the basis of *potential* future threats. As this
228 was outside the scope of this study, we attributed them with a (current) ‘non-threatened’ status for
229 the analysis (Table S2).

230

231 ***Part 3: Contemporary vulnerability (impact from threats: habitat loss, overhunting,
232 introduced sp.)***

233 We assessed how habitat loss, overhunting, and introduced species can disproportionately impact
234 species with particular life-history traits, at both global and island scales. We used the ‘Threat Impact
235 Scoring System (IUCN – CMP Unified Classification of Direct Threats, version 3.2)’ proposed by
236 the IUCN (2019) (<https://www.iucnredlist.org/resources/threat-classification-scheme>) to extract
237 whether a species was impacted by either habitat loss, overhunting, or introduced species. Current
238 and past impacts were included. Species suffering from habitat loss would be classified as such if
239 their habitats were impacted through ‘1. Residential & Commercial Development’, ‘2. Agriculture’,
240 ‘3. Energy Production & Mining’, or ‘7. Natural System Modifications’ under the IUCN categories

241 of threats, encompassing all types of habitat alteration (following Green (1996)). Species were
 242 classified as suffering from introduced species and overhunting if they were recognised by the IUCN
 243 as suffering from a threat of respectively ‘8.1 Invasive non-native/alien species/diseases’ and ‘5.1
 244 Hunting & collecting terrestrial animals’.

245 Models used for the threat of habitat loss, globally and on islands, respectively, took the forms:

- 246 • GLOBAL_Vulnerability-HABITAT LOSS ~ habitat diversity + artificial habitat + island endemic
- 247 • ISLAND_Vulnerability-HABITAT LOSS ~ habitat diversity + artificial habitat** + island size +
 248 flightlessness

249 Models used for the threat of overhunting, globally and on islands, respectively:

- 250 • GLOBAL_Vulnerability-OVERHUNTING ~ body size + clutch size + island endemism
- 251 • ISLAND_Vulnerability-OVERHUNTING ~ body size + island size + flightlessness

252 Models used for the threat of introduced species, globally and on islands, respectively:

- 253 • GLOBAL_Vulnerability-INTRODUCED SPECIES ~ body size + clutch size + island endemism
- 254 • ISLAND_Vulnerability-INTRODUCED SPECIES ~ body size + island size + flightlessness** +
 255 naivety to predators

256 Where ** indicates predictor variables that were excluded from the island models after
 257 preliminary analyses to avoid overfitting with too many marginal predictors (their importance was
 258 below 0.6 in initial models).

259

260 **Modelling process**

261 *Step 1: Selection of the optimum parameters for the boosted regression tree models*

262 For each of the aforementioned models we performed a grid search (Table 1) to estimate which
 263 boosted regression model’s parameters would maximise the out-of-bag true skill statistic (TSS)
 264 score (see results in Table 2). TSS evaluates how well a predicted outcome can distinguish between
 265 positive and negative instances, taking into account all components of the confusion matrix
 266 (Allouche *et al.*, 2006; Rahmati *et al.*, 2019). The TSS score was calculated using the `predict`
 267 function (package `caret`, thresholded at 0.5). We used the `gbm.step` function (package `dismo`),
 268 using deviance as the loss function to estimate the optimum number of trees in order to avoid over-
 269 fitting (Elith *et al.*, 2008). Models were run using cross-validation with five folds and a maximum
 270 of 10,000 trees. The minimum number of observations per node (`n.minobsinnode`) was kept at 10

271 during the creation of the model but could decrease to 5 for predictions because of small datasets
272 (Table 1).

273

274 ***Step 2: Variable importance and fluctuations in the models***

275 We used the `gbm` function (package `gbm`) with the optimum number of trees and parameters
276 identified in step 1 (Table 3). Relationships between the response variable and the predictors were
277 analysed by producing partial-dependence plots.

278

279 **Results**

280 **Part 1: Past extinction risk**

281 During the Era of Colonialism, there were 27% naïve species (18/67), and 73% savvy species (of
282 which, 37% (25/67) had met and survived earlier contact/settlement with arriving sailors, and 36%
283 (24/67) had coevolved with indigenous people since the Pleistocene/Holocene (Fig. 3). At least
284 62% of the rails were flightless (39 species), and of those, only 36% were naïve to humans. All
285 extinctions took place on islands.

286 Body size was the most influential predictor in the extinction risk model (explaining 90% of
287 the relative influence; TSS = 0.5, n=67, Table 3, Fig. 4), with smaller (≤ 24 cm) and larger body
288 sizes (≥ 35 cm) being the most extinction-prone. Flightless rails were more prone to extinction than
289 flying ones but the relative importance of flightlessness in the model was only 6% (Fig. 4). Small
290 island size and naivety had very little relative influence in the model (Fig. 4, 14 species naïve
291 species went extinct).

292

293 **Part 2: Contemporary vulnerability (IUCN status)**

294 Globally, 23% of all rails are currently considered as threatened. The body size of modern rails
295 ranges from 12 to 63 cm (mean 27.4 ± 10.1 SD) and on average, they live in 2.6 different habitats
296 (± 1.5 SD) globally (i.e., two to three habitats per species), and in 2.4 different habitats (± 1.2 SD)
297 on islands. 29% of all rail species are island endemic and of these, 51% are threatened. Of the island
298 endemic rails, 46% are flightless and of these, 47% are threatened. 50% of the island flying rails are
299 threatened.

300

301 ***Globally***

302 Human density (country or island) was the main predictor of contemporary global rail vulnerability,
303 with > 36% relative variable importance (Fig. 5). The relationship between rail vulnerability and
304 human density was complex, with little consistency in its direction of influence, although the
305 overall trend was lower impacts at higher human densities. This result is likely to be indicative of a
306 random effect arising from differences between countries (see Discussion). Small clutch size (≤ 3
307 eggs), being an island endemic, and having a smaller body size ($< 28\text{cm}$) were all also associated
308 with being more at risk of being threatened (Fig. 5).

309

310 *On islands*

311 Our island model had a lower predictive performance (TSS=0.28, Table 3), suggesting relationships
312 with predictor variables were weak. Human density was the only predictor to influence the model
313 (100% relative influence).

314

315 **Part 3: Contemporary vulnerability (impact from threats)**

316 *Globally*

317 We analysed the impact of the three main anthropogenic threats (habitat loss, overhunting, and
318 introduced species) to rail vulnerability. Habitat loss was the most common anthropogenic threat
319 associated with rail vulnerability (Table 4), but this was not predicted well by any life-history
320 (intrinsic) traits we examined (Table 3). We found that vulnerability to overhunting and the threat
321 of introduced species were both predicted by the island endemism life-history trait (Fig. 6, Fig. S2).
322 Overhunting was also predicted by clutch size (most strongly, accounting for over 40% of the
323 model influence, with rails with clutches smaller than 3 eggs or larger than 8 eggs being the most
324 vulnerable to overhunting), and increasing body size (Fig. 6). To the threat of introduced species,
325 large bodied-rails were also more vulnerable.

326

327 *On islands*

328 The proportion of species impacted by habitat loss, overhunting, and introduced species was higher
329 on islands than globally (Table 4). While there was no pattern found for habitat loss globally, the
330 signal on islands was much stronger (TSS=0.88; Table 3). Island size was the main factor leading to
331 increased vulnerability from habitat loss on islands, with species living on islands between 4,000

332 km² and 163,790 km² (approximately log₁₀ 3.6 to 5.2 area units) having up to 96% chance of being
333 impacted by habitat loss (Fig. S5; 33% of the island rails). Smaller habitat diversity also increases
334 the risk of habitat loss.

335 Island size was also the most important factor for predicting overhunting, with rails on
336 larger islands having more chance to being over hunted. Large rails and flightless rails were also
337 more likely to be over-hunted (Fig. S3).

338 Vulnerability to introduced predators was predominantly explained by the naivety to
339 mammal predators (i.e., absence of native mammals; Fig. S4). Island size and body size and had
340 little influence on the vulnerability to introduced species (Fig. S4).

341

342 **Discussion**

343 **Part 1. Extinction risk**

344 As hypothesised (Fig.1, Table S1), our study revealed that rail extinction events did not occur at
345 random, and that during the Era of Colonialism the extinction-filter targeted island-endemic rails
346 only. While we posited that naïve, flightless and large-bodied rails would be more likely to extinct,
347 we found that both smaller and larger rails were more likely to go extinct during human occupation.
348 Flightlessness or naivety were not found to play a role in these extinctions during this time. The
349 other predictors displayed complex or no clear relationships to extinction vulnerability, as explored
350 in detail below.

351

352 ***Holocene extinctions***

353 Holocene extinctions (not modelled explicitly herein) help in understanding the context of
354 extinctions happening during the Era of Colonialism (focus of this study). During the first human-
355 initiated extinction wave during the Holocene, all extinct island birds were naturally naïve to people
356 and most of them had no anti-predatory behaviour as the oceanic islands they evolved on had no
357 mammalian predators. Local studies on island-groups (e.g., Hawaii, New Zealand, Pacific islands)
358 found that flightlessness and body size were the main extinction drivers, both for rails (Steadman,
359 1995; Curnutt & Pimm, 2001; Duncan *et al.*, 2013; Alcover *et al.*, 2015) and other birds (Boyer,
360 2010; Sayol *et al.*, 2020) during this first extinction wave. Nevertheless, focusing on the case of
361 New Zealand's birds, Duncan *et al.* (2002) concluded that flightlessness was not an important factor

362 during the first bird extinction wave (whereas body size and naivety were), because naïve birds
363 were easy to hunt regardless of their flight ability, since they lacked anti-predator behaviour.

364

365 ***Recent extinctions***

366 Body size

367 In the rails' second extinction wave (during the Era of Colonialism, the focus of this study) we
368 found that body size was the key factor of extinction risk (with species <24 cm & >35 cm being
369 most prone to extinction). The observation that intermediate-sized rails were most resilient is
370 challenging to explain but might be an example of a 'critical weight range' that was large enough to
371 avoid predation by rodents (at small sizes) and small enough to avoid being targeted by people (at
372 large sizes), or having a sufficiently high reproductive rate (which allometrically, is correlated
373 negatively with body size) to compensate for increased depredation. Indeed, studies have previously
374 found that while the extinction-filter at first contact with humans drove large naïve birds extinct, the
375 effects of body size on the surviving birds were more complex during the next extinction wave:
376 studies mostly found either no effect (Bromham *et al.*, 2012) or non-linear and complex effects
377 (Boyer, 2008, 2010). In cases where body size played a role (e.g., Hawaii), two pathways to
378 extinction were proposed (Boyer, 2010): smaller species became extinct due to the predation of
379 their eggs or chicks by small introduced predators such as rodents (Holdaway, 1999), while larger
380 species went extinct due to the predation by larger introduced predators (e.g. dog, pig) and human
381 hunting who targeted mostly larger prey. Indeed, in support of this general hypothesis, 62% of the
382 recent rail extinctions were linked to overhunting, and to introduced predators for 69%, including
383 rats for 62% of them (Lévêque *et al.*, 2021).

384

385 Naivety to humans

386 Most studies working on modern extinctions (Era of Colonialism) compare small island groups
387 through the different waves of extinctions (e.g., Boyer, 2008, 2010; Bromham *et al.*, 2012), and
388 consequently do not account for the role of naivety to humans – excluding places with long-term
389 cohabitation with people (e.g., Indonesia, Madagascar) or remote human-free islands (e.g., Tristan
390 da Cunha, Galápagos Islands, Mascarene Islands). We found that rails that had survived initial
391 contact or coevolved with humans were not less vulnerable to the second wave of extinction than

392 naïve ones, indicating that previous human colonisation had not pre-selected resilient rail species
393 like some have suggested for birds (Biber, 2002).

394 One explanation is that the second wave of extinction might have operated via different
395 mechanisms to the first (Holocene), for which savvy rails did not have adequate defences. For
396 example, a new wave of introduced predators (e.g., dog, pig, cat) exerted different predatory
397 pressures to humans and rats, and the introduction of new competitor species (e.g., goat) and
398 diseases (Milberg & Tyrberg, 1993; Loehle & Eschenbach, 2012) that can contribute to the
399 accelerated demise of endemic species (Wood *et al.*, 2017; Kouvari & van der Geer, 2018).
400 Moreover, each island had different types of contact with people (varying in intensity, duration,
401 type of settlement, introduction of alien species, etc.) which could influence the species' responses
402 (Wood *et al.*, 2017), whose impacts could be buffered by the local biodiversity composition. More
403 research on identifying the intrinsic mechanisms that determine resistance at first contact for island
404 endemics would provide interesting insights on the mechanisms of extinctions.

405

406 **Parts 2 & 3: Contemporary pattern of vulnerability**

407 Our hypotheses were that sedentary, habitat specialist, island endemic, large-bodied, slow breeders,
408 and flightless species would be more threatened. Developing or human-dense countries and small,
409 isolated, and human-dense islands would support more threatened species (IUCN status). We found
410 that human density, small clutch size, island endemism, and small body size were the four main
411 predictors for contemporary global rail vulnerability. Human density was the main predictor
412 however the signal was complex and likely to play a random effect in the model. We did not find a
413 pattern of overall vulnerability for contemporary island endemic rails.

414 For the threats of habitat loss, overhunting and introduced predators, we hypothesised that
415 introduced predators and overhunting would have a greater impact on large, island endemic, and
416 flightless species, as well as species living on small islands, naïve to mammal predators, and with
417 smaller clutch size. Habitat loss was hypothesised to impact more habitat specialists, island endemic
418 and flightless species, as well as species living on small islands and unable to exploit disturbed
419 habitats. We found that vulnerability to overhunting and introduced species was predicted by island
420 endemism. Overhunting was also predicted by both smaller and larger clutch size, and larger body
421 size. As to the threat of introduced species, large bodied-rails were also more vulnerable. Habitat
422 loss was not predicted by any life-history we examined. On islands, large island size was a factor of
423 vulnerability to overhunting and habitat loss. Large and flightless rails were also more likely to be

424 over-hunted. Vulnerability to introduced predators was predominantly explained by the naivety to
425 mammal predators while island size and body size had little influence.

426 As most bird extinctions and all rail extinctions occurred on islands, our models found that
427 island-endemic rails comprised most of the threatened rail species. This also held true when
428 considering island endemism as a predictor of vulnerability to introduced predators and
429 overhunting. Island endemic birds are globally threatened, and this trend is increasing – they
430 represented 39% of all threatened birds in 1990 (Johnson & Stattersfield, 1990), and 47% 20 years
431 later (BirdLife International, 2017a). In Rallidae, 67% of threatened species are island endemic
432 (Lévêque *et al.*, 2021).

433 Owens and Bennett (2000) compared different bird lineages and found that rails had various
434 routes to vulnerability, from habitat loss, human persecution (overhunting) and introduced
435 predators, because they were typically more ecologically specialised, with larger bodies and slower
436 breeding rates compared with other families. Our analyses showed that some of these life-history
437 traits were indeed increasing rails' vulnerability to these external threats. Globally, clutch size and
438 body size had little influence on vulnerability to introduced species, but rail species with smaller
439 and larger clutch sizes and larger bodies were more vulnerable to overhunting. For island endemics,
440 large-bodied and flightless species, as well as the ones living on large islands, were more threatened
441 by overhunting, while naivety to predators was the main factor to the threat of introduced predators.
442 Interestingly, while smaller rails are at more risk to be threatened globally, we found that larger
443 rails are at more risk to the threat of overhunting (both globally and at the island scale), validating
444 our initial hypotheses. This pattern is also found overall in birds (Ripple *et al.*, 2017). This suggests
445 overall that body size is a complex driver of vulnerability that can also interact with other
446 ecological traits in ways that are not yet fully understood (Bennett & Owens, 1997; Boyer, 2010).

447 Similarly, Bennett *et al.* (2001) have suggested that smaller-sized birds, when specialised
448 and fast breeding like rails, would be more likely to be threatened due largely to habitat loss.
449 However, looking broadly within the rail family, we did not find any link between small body size
450 or any other intrinsic trait to the threat of habitat loss. Nevertheless, the main IUCN justification for
451 the threatened status of small-bodied rails in this study (nine species) was that they generally had a
452 very restricted range, often in wetlands that were fragmented and with ongoing loss. Most of these
453 species were continental, found in South America and Asia, and half were from the genus
454 *Laterallus*. While no traits were found to increase rails vulnerability to habitat loss globally, at the

455 island scale, rails living on large islands were found to be more at risk of becoming threatened due
456 to habitat loss, and for species with smaller habitat diversity.

457

458 *Clutch size and body size*

459 We also found that at the global scale, rails with small clutches (≤ 3 eggs) and smaller bodies (< 20
460 cm) were also the most likely to have a threatened IUCN status (i.e., “VU”, “EN”, or “CR”). Small
461 clutch size, a measure of slow reproductive rate, is known to increase vulnerability due to the slow
462 regeneration of population and validates our hypotheses at the global scale (Bennett & Owens,
463 1997; Lee & Jetz, 2011; Garcia-R & Di Marco, 2020). Interestingly, rail species with either larger
464 clutches (>8 eggs) or clutches with fewer eggs (<3 eggs) are the most vulnerable to the threat of
465 overhunting. This suggests that perhaps species that produce more eggs tend to be targeted by
466 overhunting because of the abundance of eggs they provide, while slow-breeding species would
467 struggle to recover from exploitation (Owens & Bennett, 2000).

468 The effect of small body size in the vulnerability of rails contradicts most studies on birds,
469 where threatened species were mostly large bodied (Gaston & Blackburn, 1995; Bennett & Owens,
470 1997; Lee & Jetz, 2011; Ripple *et al.*, 2017), while some studies report no relationship (Morrow &
471 Pitcher, 2003; Chichorro *et al.*, 2019). As the last extinction wave targeted large or small (but not
472 medium-sized) rails, we can suppose that all large-bodied vulnerable rails went extinct, while there
473 are still vulnerable smaller-bodied rails that are still facing the on-going threat of extinction. With
474 the new diversity of threats impacting rails (Lévêque *et al.*, 2021), different processes can now
475 affect rails. For example, Ripple *et al.* (2017) found that the lightest-bodied birds were mostly
476 impacted by agriculture, and agriculture is one of the three predominant threats to the rails globally
477 (Lévêque *et al.*, 2021).

478

479 *Socio-economic status of countries*

480 Human density was the main predictor of global vulnerability for rails, but the complex and
481 apparently counterintuitive relationship (overall lower vulnerability of rails with higher human
482 density) makes it challenging to interpret the exact role. Our interpretation is that human density is
483 acting like a random effect in the decision tree (i.e., it captures a variety of unmeasured tapering
484 effects associated with the idiosyncratic environment and history of any given island), rather being
485 an actual predictor. However, it could not be modelled formally as a random effect, because there
486 was almost always only one rail species per island.

487 High GDP of the countries where the species inhabit also played a role in increasing the
488 threatening processes, most likely through the encroachment of natural habitats and direct
489 exploitation due to economic development (Czech, 2000). This pattern has also been found in
490 parrots (Olah *et al.*, 2016). Human population growth was another socio-economic attribute that
491 was found as influencing vulnerability, but to a much lesser extent. The predictor's negative
492 relationship contradicted our original hypothesis that high human population growth would lead
493 species to be more vulnerable. We suspect this to be linked to some species' particular occurrence:
494 human population growth is particularly high for species occurring in African countries, where rails
495 have high habitat diversity and have long coevolved with high rates of human pressure.
496 Alternatively, the hunting or poaching of predators in those regions could also act to 'release' rail
497 populations from natural mortality pressures.

498 Results from the literature are variable, and while Davies *et al.* (2006) found a negative
499 effect of GDP on vulnerability of birds globally, indicating that areas of high economic
500 development support fewer threatened bird species, McKee *et al.* (2013) found that overall higher
501 human density and GDP is linked to an increase in the number of threatened species. Our
502 conflicting results with socio-economic predictors (GDP, human population growth, and human
503 density) suggest that the relationship between human development and threatening processes in
504 rails is complex and would require more research to disentangle.

505

506 ***Vulnerability on islands***

507 Interestingly, we did not find a pattern of overall vulnerability for contemporary island endemic
508 rails. To explain the randomness observed, we propose different pathways to vulnerability. Most
509 threatened rails, being island endemics, often take the same trajectory as extinct species, suffering
510 mostly from invasive predators (Lévêque *et al.*, 2021) and also overhunting. As extinction-filters
511 selected savvy rails throughout the different extinction waves, different island traits could
512 contribute to the elevated vulnerability such as small ranges and population sizes, low genetic
513 diversity, inbreeding, etc. (Frankham, 1998; Purvis *et al.*, 2000a; Frankham, 2005). Furthermore, as
514 the breadth of anthropogenic threats has intensified and became more complex, threatened island
515 rails are impacted by more threats than previously (four threat types on average and up to nine
516 different threats, e.g., mining, recreational activities, dam management, Lévêque *et al.*, 2021). The
517 consequence of this was to either create new and intricate pathways to vulnerability, or to result in a
518 contemporary 'field of bullets' (Raup, 1991) where intense and large-scale disturbances make

519 vulnerability unpredictable (largely stochastic or happenchance). Similar results have been found in
520 other taxa (Duncan & Lockwood, 2001). The increased diversity of impacts leading to habitat loss
521 on islands might also create extinction debts on islands (Triantis et al., 2010; Otto et al., 2017).

522

523 *On islands – flightlessness and predator naivety*

524 While flightlessness was strongly associated with ancient extinctions (during the first wave in the
525 mid-Holocene), it diminished in importance for the more recent extinction wave (Era of
526 Colonialism), and following this continuity, flightless rails are no more threatened than flying ones
527 in contemporary times. This highlights the role of humans in the selection of resilient species.
528 Vulnerable flightless rails were initially easy prey to the first human arrivals on their islands, with
529 those flightless species surviving that first wave being resilient in other ways (e.g., behaviourally
530 adaptive or preferring habitats like wetlands that were less accessible). A global study on the roles
531 of flightlessness and naivety for bird extinctions (beyond just Rallidae), via different extinction
532 waves at a global scale, would help shed light on the drivers of the more recent extinctions. With
533 only 19 flightless rails remaining from the many hundreds (or perhaps thousands) that existed in the
534 Holocene (Steadman, 1995; Curnutt & Pimm, 2001), there is a high conservation imperative to
535 protect these iconic birds.

536 While flightlessness was not a predictor of overall vulnerability on islands, we did find that
537 flightless rails were more vulnerable to overhunting specifically. Flightless bird species tend to be
538 more threatened than volant species, and this is generally associated with predator naivety (Duncan
539 *et al.*, 2002; Steadman, 2006; Boyer, 2008). This is consistent with our findings where we found
540 that rails, whether flying or flightless, were more acutely impacted by introduced predators when
541 naïve and lacking anti-predator behaviours. While this is not a surprising result and has been
542 suggested in the literature (Balmford, 1996), little empirical work has been done on this. The role of
543 naivety for island birds to withstand systematic threat from introduced predators and to other threats
544 (e.g., overhunting) is an area of research that deserves more attention.

545

546 *Island size*

547 Contrary to our expectations, large islands had more rails threatened by overhunting and habitat loss
548 than smaller islands. One explanation might be that large islands have the potential to be more
549 similar to continents in terms of threats, and some threat types would be absent from smaller islands
550 (Manne *et al.*, 1999). For example, rates of habitat loss and fragmentation could be far greater on

551 large islands (Didham *et al.*, 2005), and it might be that only larger islands have sufficient resources
552 to support introduced predators and competitors. However, this could also be simply a result of a
553 (pre)historical selection bias, wherein extinctions have already wiped-out rails from the majority of
554 small islands, due for instance to smaller maximum population sizes (see Green (1996) for similar
555 results with Anatidae).

556

557 **Conclusion**

558 Extinction events in rails were not random, with some life-history traits being selected through
559 human-driven extinction filters. However, the pattern of contemporary vulnerability differs from
560 past extinctions. Threatened species today are represented mostly by slow-reproducing and island
561 endemics, while the pattern of vulnerability is essentially random on islands. Returning to our
562 original question ‘can understanding past avian extinctions help to forecast extinction risk in
563 birds?’, it seems to be a quixotic goal to draw conclusions from past extinctions to predict future
564 extinctions, at least for rails. Contemporary species have survived intense extinction filters that
565 were driven by a few threats only, but the increase in the diversity and intensity of modern
566 anthropogenic threats is likely to be responsible for the change in pattern. Beyond endemism, there
567 is little commonality in which persisting rails are now vulnerable, although the roles of genetic
568 stochasticity (Evans & Sheldon, 2008; Sarre & Georges, 2009) and extinction debt due to past
569 habitat loss and modification, warrant further investigation. Overall, islands appear as the most
570 sensitive unit of conservation for rails, and preserving the remaining island endemic and flightless
571 species is clearly a high conservation priority, which would also greatly benefit most island wildlife
572 (Graham *et al.*, 2017), including the 69 subspecies of rails (47%) that are island endemic. Protecting
573 islands also opens the possibility for rails to naturally, or via human assistance, recolonise islands
574 on which they became extinct (Curnutt & Pimm, 2001; Morris *et al.*, 2021).

575

576 **References**

- 577 Alcover, J.A., Pieper, H., Pereira, F. & Rando, J.C. (2015) Five new extinct species of rails (Aves:
578 Gruiformes: Rallidae) from the Macaronesian Islands (North Atlantic Ocean). *Zootaxa*,
579 **4057**, 151-190.
- 580 Allouche, O., Tsoar, A. & Kadmon, R. (2006) Assessing the accuracy of species distribution
581 models: prevalence, kappa and the true skill statistic (TSS). *Journal of Applied Ecology*, **43**:
582 1223-1232. <https://doi.org/10.1111/j.1365-2664.2006.01214.x>
- 583 Balmford, A. (1996) Extinction filters and current resilience: the significance of past selection
584 pressures for conservation biology. *Trends in Ecology & Evolution*, **11**, 193-196.
- 585 Barshep, Y., Erni, B., Underhill, L.G. & Altwegg, R. (2017) Identifying ecological and life-history
586 drivers of population dynamics of wetland birds in South Africa. *Global Ecology and*
587 *Conservation*, **12**, 96-107. <https://doi.org/10.1016/j.gecco.2017.09.001>
- 588 Bennett, P.M. & Owens, I.P.F. (1997) Variation in extinction risk among birds: chance or
589 evolutionary predisposition? *Proceedings of the Royal Society of London. Series B:*
590 *Biological Sciences*, **264**, 401-408. 10.1098/rspb.1997.0057
- 591 Bennett, P.M., Owens, I.P.F. & Baillie, J.E.M. (2001) The History and Ecological Basis of
592 Extinction and Speciation in Birds. *Biotic Homogenization* (ed. by J.L. Lockwood and M.L.
593 Mckinney), pp. 201-222. Springer US, Boston, MA. [http://dx.doi.org/10.1007/978-1-4615-](http://dx.doi.org/10.1007/978-1-4615-1261-5_10)
594 [1261-5_10](http://dx.doi.org/10.1007/978-1-4615-1261-5_10)
- 595 Biber, E. (2002) Patterns of endemic extinctions among island bird species. *Ecography*, **25**, 661-
596 676. <https://doi.org/10.1034/j.1600-0587.2002.t01-1-250603.x>
- 597 BirdLife International (2017) Many threatened birds are restricted to small islands. Downloaded
598 from <http://www.birdlife.org> on 15/07/2019
- 599 Blackburn, T.M. (2004) Extinction in island endemic birds reconsidered. *Ecography*, **27**, 124-129.
600 10.1111/j.0906-7590.2004.03775.x
- 601 Blackburn, T.M., Cassey, P., Duncan, R.P., Evans, K.L. & Gaston, K.J. (2004) Avian Extinction
602 and Mammalian Introductions on Oceanic Islands. *Science*, **305**, 1955-1958.
603 10.1126/science.1101617
- 604 Blackburn, T.M., Cassey, P., Duncan, R.P., Evans, K.L. & Gaston, K.J. (2008) Threats to Avifauna
605 on Oceanic Islands Revisited. *Conservation Biology*, **22**, 492-494.
- 606 Blaikie, P. & Jeanrenaud, S. (1997) Biodiversity and human welfare. *Social change and*
607 *conservation. Environmental politics and impacts of national parks and protected areas*, 46-
608 70.
- 609 Boyer, A.G. (2008) Extinction patterns in the avifauna of the Hawaiian islands. *Diversity and*
610 *Distributions*, **14**, 509-517. <https://doi.org/10.1111/j.1472-4642.2007.00459.x>
- 611 Boyer, A.G. (2010) Consistent Ecological Selectivity through Time in Pacific Island Avian
612 Extinctions. *Conservation Biology*, **24**, 511-519. 10.1111/j.1523-1739.2009.01341.x
- 613 Bromham, L., Lanfear, R., Cassey, P., Gibb, G. & Cardillo, M. (2012) Reconstructing past species
614 assemblages reveals the changing patterns and drivers of extinction through time.
615 *Proceedings of the Royal Society B: Biological Sciences*, **279**, 4024-4032.
616 doi:10.1098/rspb.2012.1437
- 617 Brook, B.W. & Alroy, J. (2017) Pattern, process, inference and prediction in extinction biology.
618 *Biology Letters*, **13** 10.1098/rsbl.2016.0828
- 619 Ceballos, G., Ehrlich, P.R., Barnosky, A.D., García, A., Pringle, R.M. & Palmer, T.M. (2015)
620 Accelerated modern human-induced species losses: Entering the sixth mass extinction.
621 *Science Advances*, **1** 10.1126/sciadv.1400253
- 622 Chichorro, F., Juslén, A. & Cardoso, P. (2019) A review of the relation between species traits and
623 extinction risk. *bioRxiv*, 408096. 10.1101/408096

- 624 Cronk, Q.C.B. (1997) Islands: stability, diversity, conservation. *Biodiversity & Conservation*, **6**,
625 477-493. [10.1023/a:1018372910025](https://doi.org/10.1023/a:1018372910025)
- 626 Crutzen, P.J. (2002) Geology of mankind. *Nature*, **415**, 23-23.
- 627 Curnutt, J. & Pimm, S. (2001) How many bird species in Hawaii and the Central Pacific before first
628 contact? *Studies in Avian Biology*, **22**, 15-30.
- 629 Czech, B. (2000) Economic growth as the limiting factor for wildlife conservation. *Wildlife Society*
630 *Bulletin*, **28**, 4-14.
- 631 Davies, R.G., Orme, C.D.L., Olson, V., Thomas, G.H., Ross, S.G., Ding, T.-S., Rasmussen, P.C.,
632 Stattersfield, A.J., Bennett, P.M., Blackburn, T.M., Owens, I.P.F. & Gaston, K.J. (2006)
633 Human impacts and the global distribution of extinction risk. *Proceedings of the Royal*
634 *Society B: Biological Sciences*, **273**, 2127-2133. <https://doi.org/10.1098/rspb.2006.3551>
- 635 de Lima, R.F., Bird, J.P. & Barlow, J. (2011) Research effort allocation and the conservation of
636 restricted-range island bird species. *Biological Conservation*, **144**, 627-632.
637 <https://doi.org/10.1016/j.biocon.2010.10.021>
- 638 Diamond, J. (1984) Historic extinctions: a rosetta stone for understanding prehistoric extinctions. .
639 In: In: Martin, P. S. and Klein, R. G. (eds), Quaternary extinctions: a prehistoric revolution.
640 Univ. of Arizona Press, pp. 824–862.
- 641 Diamond, J.M. (1989) The Present, Past and Future of Human-Caused Extinctions. *Philosophical*
642 *Transactions of the Royal Society of London. B, Biological Sciences*, **325**, 469-477.
643 [10.1098/rstb.1989.0100](https://doi.org/10.1098/rstb.1989.0100)
- 644 Didham, R.K., Ewers, R.M. & Gemmell, N.J. (2005) Comment on Avian extinction and
645 mammalian introductions on oceanic islands. *Science*,
- 646 Ducatez, S. & Shine, R. (2017) Drivers of Extinction Risk in Terrestrial Vertebrates. *Conservation*
647 *Letters*, **10**, 186-194. [10.1111/conl.12258](https://doi.org/10.1111/conl.12258)
- 648 Duncan, J.R. & Lockwood, J.L. (2001) Extinction in a field of bullets: a search for causes in the
649 decline of the world's freshwater fishes. *Biological Conservation*, **102**, 97-105.
650 [https://doi.org/10.1016/S0006-3207\(01\)00077-5](https://doi.org/10.1016/S0006-3207(01)00077-5)
- 651 Duncan, R.P., Blackburn, T.M. & Worthy, T.H. (2002) Prehistoric bird extinctions and human
652 hunting. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, **269**,
653 517-521. <https://doi.org/10.1098/rspb.2001.1918>
- 654 Duncan, R.P., Boyer, A.G. & Blackburn, T.M. (2013) Magnitude and variation of prehistoric bird
655 extinctions in the Pacific. *Proceedings of the National Academy of Sciences*, **110**, 6436-
656 6441. [10.1073/pnas.1216511110](https://doi.org/10.1073/pnas.1216511110)
- 657 Elith, J., Leathwick, J.R. & Hastie, T. (2008) A working guide to boosted regression trees. *Journal*
658 *of Animal Ecology*, **77**, 802-813.
- 659 Evans, S.R. & Sheldon, B.C. (2008) Interspecific Patterns of Genetic Diversity in Birds:
660 Correlations with Extinction Risk. *Conservation Biology*, **22**, 1016-1025. [10.1111/j.1523-
661 1739.2008.00972.x](https://doi.org/10.1111/j.1523-1739.2008.00972.x)
- 662 Fischer, J. & Lindenmayer, D.B. (2007) Landscape modification and habitat fragmentation: a
663 synthesis. *Global Ecology and Biogeography*, **16**, 265-280. [10.1111/j.1466-
664 8238.2007.00287.x](https://doi.org/10.1111/j.1466-8238.2007.00287.x)
- 665 Frankham, R. (1998) Inbreeding and Extinction: Island Populations. *Conservation Biology*, **12**, 665-
666 675. [10.1111/j.1523-1739.1998.96456.x](https://doi.org/10.1111/j.1523-1739.1998.96456.x)
- 667 Frankham, R. (2005) Genetics and extinction. *Biological Conservation*, **126**, 131-140.
668 <https://doi.org/10.1016/j.biocon.2005.05.002>
- 669 Garcia-R, J.C. & Di Marco, M. (2020) Drivers and trends in the extinction risk of New Zealand's
670 endemic birds. *Biological Conservation*, **249**, 108730.
671 <https://doi.org/10.1016/j.biocon.2020.108730>

- 672 Garcia-R, J.C., Lemmon, E.M., Lemmon, A.R. & French, N. (2020) Phylogenomic Reconstruction
 673 Sheds Light on New Relationships and Timescale of Rails (Aves: Rallidae) Evolution.
 674 *Diversity*, **12**, 70. <https://doi.org/10.3390/d12020070>
- 675 Garcia-R., J.C., Gibb, G.C. & Trewick, S.A. (2014) Deep global evolutionary radiation in birds:
 676 diversification and trait evolution in the cosmopolitan bird family Rallidae. *Molecular*
 677 *Phylogenetics and Evolution*, **81**, 96-108. <https://doi.org/10.1016/j.ympev.2014.09.008>
- 678 Gaston, K.J. & Blackburn, T.M. (1995) Birds, Body Size and the Threat of Extinction.
 679 *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*,
 680 **347**, 205-212. 10.1098/rstb.1995.0022
- 681 Graham, N.R., Gruner, D.S., Lim, J.Y. & Gillespie, R.G. (2017) Island ecology and evolution:
 682 challenges in the Anthropocene. *Environmental Conservation*, **44**, 323-335.
 683 10.1017/S0376892917000315
- 684 Green, A.J. (1996) Analyses of Globally Threatened Anatidae in Relation to Threats, Distribution,
 685 Migration Patterns, and Habitat Use. *Conservation Biology*, **10**, 1435-1445.
 686 <https://doi.org/10.1046/j.1523-1739.1996.10051435.x>
- 687 Hackett, S.J., Kimball, R.T., Reddy, S., Bowie, R.C., Braun, E.L., Braun, M.J., Chojnowski, J.L.,
 688 Cox, W.A., Han, K.L., Harshman, J. and Huddleston, C.J. (2008). A phylogenomic study of
 689 birds reveals their evolutionary history. *Science*, **320**, 1763-1768.
- 690 Holdaway, R.N. (1999) Introduced predators and avifaunal extinction in New Zealand. *Extinctions*
 691 *in near time*, pp. 189-238. Springer.
- 692 IUCN (2019) *The IUCN Red List of Threatened Species. Version 2019-3*. Available at:
 693 <http://www.iucnredlist.org> (accessed 12 December 2019)
- 694 Johnson, T. & Stattersfield, A. (1990) A global review of island endemic birds. *Ibis*, **132**, 167-180.
- 695 Jones, M.J., Fielding, A. & Sullivan, M. (2006) Analysing Extinction Risk in Parrots using
 696 Decision Trees. *Biodiversity & Conservation*, **15**, 1993-2007. 10.1007/s10531-005-4316-1
- 697 Kerr, J.T. & Currie, D.J. (1995) Effects of Human Activity on Global Extinction Risk.
 698 *Conservation Biology*, **9**, 1528-1538. <https://doi.org/10.1046/j.1523-1739.1995.09061528.x>
- 699 Kouvari, M. & van der Geer, A.A.E. (2018) Biogeography of extinction: The demise of insular
 700 mammals from the Late Pleistocene till today. *Palaeogeography, Palaeoclimatology,*
 701 *Palaeoecology*, **505**, 295-304. <https://doi.org/10.1016/j.palaeo.2018.06.008>
- 702 Lee, T.M. & Jetz, W. (2011) Unravelling the structure of species extinction risk for predictive
 703 conservation science. *Proceedings of the Royal Society of London B: Biological Sciences*,
 704 **278**, 1329-1338.
- 705 Lévêque, L., Buettel, J.C., Carver, S. & Brook, B.W. (2021) Characterizing the spatio-temporal
 706 threats, conservation hotspots and conservation gaps for the most extinction-prone bird
 707 family (Aves: Rallidae). *Royal Society Open Science*, **8**, 210262. doi:10.1098/rsos.210262
- 708 Livezey, B. C. (1998). A phylogenetic analysis of the Gruiformes (Aves) based on morphological
 709 characters, with an emphasis on the rails (Rallidae). *Philosophical Transactions of the Royal*
 710 *Society of London. Series B: Biological Sciences*, **353**, 2077-2151.
- 711 Livezey, B.C. (2003) *Evolution of flightlessness in rails (Gruiformes, Rallidae)*. American
 712 Ornithologists' Union.
- 713 Loehle, C. & Eschenbach, W. (2012) Historical bird and terrestrial mammal extinction rates and
 714 causes. *Diversity and Distributions*, **18**, 84-91. 10.1111/j.1472-4642.2011.00856.x
- 715 Lomolino, M., Riddle, B. & Whittaker, R.J. (2017) *Biogeography: Biological Diversity Across*
 716 *Space and Time*, 5th edn. Sinauer Associates, Sunderland, Massachusetts.
- 717 MacArthur, R.H. & Wilson, E.O. (1967) *The Theory of Island Biogeography*. Princeton university
 718 press.

- 719 Manne, L.L., Brooks, T.M. & Pimm, S.L. (1999) Relative risk of extinction of passerine birds on
 720 continents and islands. *Nature*, **399**, 258. 10.1038/20436
 721 <https://www.nature.com/articles/20436#supplementary-information>
- 722 McKee, J., Chambers, E. & Guseman, J. (2013) Human Population Density and Growth Validated
 723 as Extinction Threats to Mammal and Bird Species. *Human Ecology*, **41**, 773-778.
 724 10.1007/s10745-013-9586-8
- 725 Milberg, P. & Tyrberg, T. (1993) Naïve birds and noble savages-a review of man-caused prehistoric
 726 extinctions of island birds. *Ecography*, **16**, 229-250.
- 727 Morris, S.D., Brook, B.W., Moseby, K.E. & Johnson, C.N. (2021) Factors affecting success of
 728 conservation translocations of terrestrial vertebrates: A global systematic review☆. *Global
 729 Ecology and Conservation*, **28**, e01630. <https://doi.org/10.1016/j.gecco.2021.e01630>
- 730 Morrow, E.H. & Pitcher, T.E. (2003) Sexual selection and the risk of extinction in birds.
 731 *Proceedings of the Royal Society of London. Series B: Biological Sciences*, **270**, 1793-1799.
 732 doi:10.1098/rspb.2003.2441
- 733 Newbold, T., Hudson, L.N., Contu, S., Hill, S.L.L., Beck, J., Liu, Y., Meyer, C., Phillips, H.R.P.,
 734 Scharlemann, J.P.W. & Purvis, A. (2018) Widespread winners and narrow-ranged losers:
 735 Land use homogenizes biodiversity in local assemblages worldwide. *PLOS Biology*, **16**,
 736 e2006841. 10.1371/journal.pbio.2006841
- 737 Newton, I. (2010) *The migration ecology of birds*. Elsevier.
- 738 Olah, G., Butchart, S.H.M., Symes, A., Guzmán, I.M., Cunningham, R., Brightsmith, D.J. &
 739 Heinsohn, R. (2016) Ecological and socio-economic factors affecting extinction risk in
 740 parrots. *Biodiversity and Conservation*, **25**, 205-223. [https://doi.org/10.1007/s10531-015-
 741 1036-z](https://doi.org/10.1007/s10531-015-1036-z)
- 742 Otto, R., Garzón-Machado, V., del Arco, M., Fernández-Lugo, S., de Nascimento, L., Oromí, P.,
 743 Báez, M., Ibáñez, M., Alonso, M.R. & Fernández-Palacios, J.M. (2017) Unpaid extinction
 744 debts for endemic plants and invertebrates as a legacy of habitat loss on oceanic islands.
 745 *Diversity and Distributions*, **23**, 1031-1041. 10.1111/ddi.12590
- 746 Owens, I.P.F. & Bennett, P.M. (2000) Ecological basis of extinction risk in birds: Habitat loss
 747 versus human persecution and introduced predators. *Proceedings of the National Academy
 748 of Sciences*, **97**, 12144-12148. <https://doi.org/10.1073/pnas.200223397>
- 749 Pimm, S., Raven, P., Peterson, A., Şekercioğlu, Ç.H. & Ehrlich, P.R. (2006) Human impacts on the
 750 rates of recent, present, and future bird extinctions. *Proceedings of the National Academy of
 751 Sciences*, **103**, 10941-10946. <https://doi.org/10.1073/pnas.0604181103>
- 752 Pimm, S.L., Jones, H.L. & Diamond, J. (1988) On the Risk of Extinction. *The American Naturalist*,
 753 **132**, 757-785. doi:10.1086/284889
- 754 Pimm, S.L., Russell, G.J., Gittleman, J.L. & Brooks, T.M. (1995) The future of biodiversity.
 755 *Science*, **269**, 347.
- 756 Purvis, A., Gittleman, J.L., Cowlishaw, G. & Mace, G.M. (2000) Predicting extinction risk in
 757 declining species. *Proceedings of the Royal Society of London. Series B: Biological
 758 Sciences*, **267**, 1947-1952. 10.1098/rspb.2000.1234
- 759 R Core Team (2021) R: A language and environment for statistical computing. R Foundation for
 760 Statistical Computing, Vienna, Austria. <<https://www.R-project.org/>>.
- 761 Rahmati, O., Kornejady, A., Samadi, M., Deo, R.C., Conoscenti, C., Lombardo, L., Dayal, K.,
 762 Taghizadeh-Mehrjardi, R., Pourghasemi, H.R., Kumar, S. & Tien Bui., D. (2019) PMT:
 763 New analytical framework for automated evaluation of geo-environmental modelling
 764 approaches. *Science of The Total Environment*, **664**: 296-311.
- 765 Raup, D.M. (1991) *Extinction: bad genes or bad luck?* WW Norton & Company.

- 766 Ripple, W.J., Wolf, C., Newsome, T.M., Hoffmann, M., Wirsing, A.J. & McCauley, D.J. (2017)
767 Extinction risk is most acute for the world's largest and smallest vertebrates. *Proceedings of*
768 *the National Academy of Sciences*, **114**, 10678-10683. 10.1073/pnas.1702078114
- 769 Sarre, S.D. & Georges, A. (2009) Genetics in conservation and wildlife management: a revolution
770 since Caughley. *Wildlife Research*, **36**, 70-80. <https://doi.org/10.1071/WR08066>
- 771 Sayol, F., Steinbauer, M.J., Blackburn, T.M., Antonelli, A. & Faurby, S. (2020) Anthropogenic
772 extinctions conceal widespread evolution of flightlessness in birds. *Science Advances*, **6**,
773 eabb6095. 10.1126/sciadv.abb6095
- 774 Sekercioglu, C.H. (2007) Conservation Ecology: Area Trumps Mobility in Fragment
775 Bird Extinctions. *Current Biology*, **17**, R283-R286.
776 <https://doi.org/10.1016/j.cub.2007.02.019>
- 777 Sodhi, N.S., Liow, L. & Bazzaz, F. (2004) Avian extinctions from tropical and subtropical forests.
778 *Annu. Rev. Ecol. Evol. Syst.*, **35**, 323-345.
- 779 Steadman, D.W. (1995) Prehistoric extinctions of Pacific island birds: Biodiversity meets
780 zooarchaeology. *Science (New York, N.Y.)*, **267**, 1123.
781 <https://doi.org/10.1126/science.267.5201.1123>
- 782 Steadman, D.W. (1999) The prehistoric extinction of south Pacific birds: catastrophe versus
783 attrition. *Pacific from 5000 to 2000 Bp*, 375-+.
- 784 Steadman, D.W. (2006) *Extinction and biogeography of tropical Pacific birds*. University of
785 Chicago Press.
- 786 Taylor, B. & van Perlo, B. (1998) *Rails: a guide to rails, crakes, gallinules and coots of the world*.
787 Pica Press, Mountfield, U.K.
- 788 Triantis, K.A., Borges, P.A.V., Ladle, R.J., Hortal, J., Cardoso, P., Gaspar, C., Dinis, F., Mendonça,
789 E., Silveira, L.M.A., Gabriel, R., Melo, C., Santos, A.M.C., Amorim, I.R., Ribeiro, S.P.,
790 Serrano, A.R.M., Quartau, J.A. & Whittaker, R.J. (2010) Extinction debt on oceanic islands.
791 *Ecography*, **33**, 285-294. <https://doi.org/10.1111/j.1600-0587.2010.06203.x>
- 792 Turvey, S.T. & Fritz, S.A. (2011) The ghosts of mammals past: biological and geographical
793 patterns of global mammalian extinction across the Holocene. *Philosophical Transactions of*
794 *the Royal Society B: Biological Sciences*, **366**, 2564-2576. 10.1098/rstb.2011.0020
- 795 Urban, M.C. (2015) Accelerating extinction risk from climate change. *Science*, **348**, 571-573.
796 10.1126/science.aaa4984
- 797 Wood, J.R., Alcover, J.A., Blackburn, T.M., Bover, P., Duncan, R.P., Hume, J.P., Louys, J., Meijer,
798 H.J.M., Rando, J.C. & Wilmshurst, J.M. (2017) Island extinctions: processes, patterns, and
799 potential for ecosystem restoration. *Environmental Conservation*, 1-11.
800 10.1017/S037689291700039X
- 801 Zalasiewicz, J., Williams, M., Smith, A., Barry, T.L., Coe, A.L., Bown, P.R., Brenchley, P.,
802 Cantrill, D., Gale, A. & Gibbard, P. (2008) Are we now living in the Anthropocene? *Gsa*
803 *Today*, **18**, 4.

804 **FIGURES LEGEND**

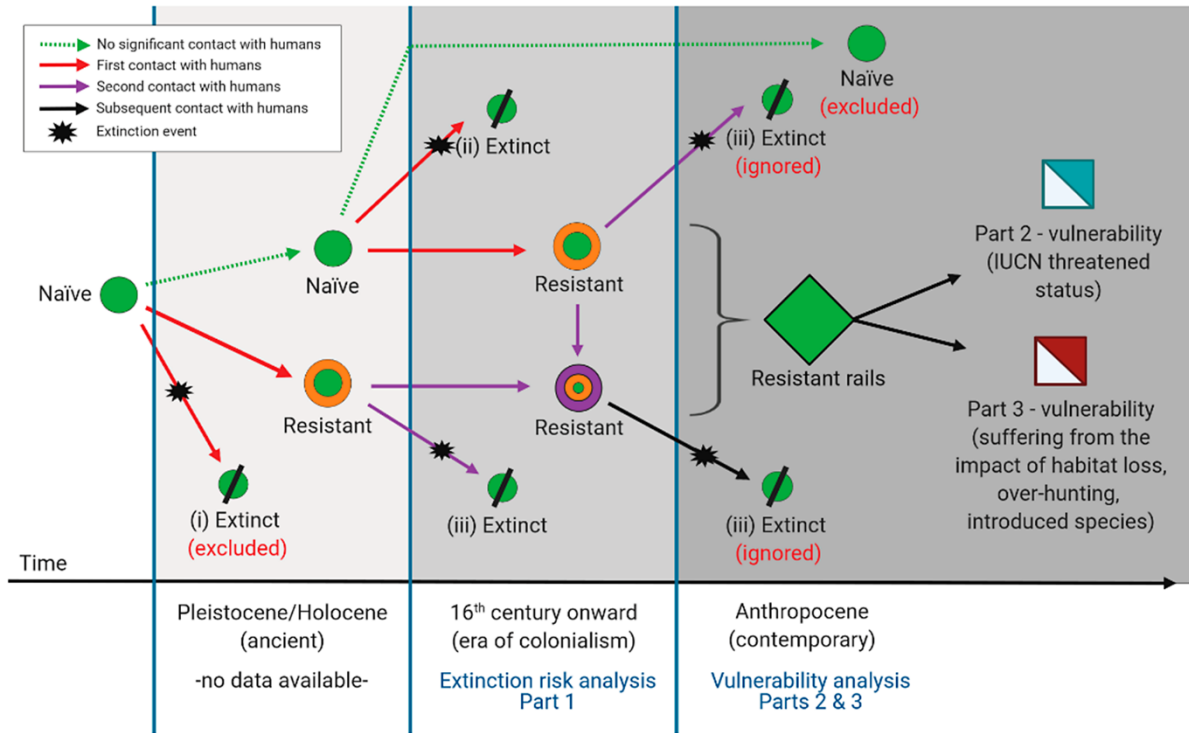
805 **Fig. 1.** Overview of analytical framework: this chart delineates the three distinct parts of our study—
 806 Past Extinction Risk, Contemporary Vulnerability (IUCN Status), and Contemporary Vulnerability
 807 (Impact from Threats). Each section outlines the response variables, the set of predictor variables
 808 used, the temporal and spatial scales of analysis, and the primary hypotheses tested herein. The
 809 analysis uses Boosted Regression Trees with sample sizes indicated for each part. Detailed
 810 justification for each hypothesis and trait selection, alongside associated references, can be found in
 811 Table S1.

<u>PART 1: Past extinction risk</u>
<p>Response variable: extinct/extant Predictor variables: naivety to humans, body size, flightlessness, island size Time scale: 16th-20th centuries Spatial scale: Islands Analysis: Boosted regression trees (n=67) Hypotheses:</p> <ul style="list-style-type: none"> -Rails naïve to humans are expected to be more extinction-prone than rails that evolved alongside humans since the Pleistocene/Holocene. -Flightless and large-bodied rails were more likely to go extinct. -Small islands facilitated rails extinctions.
<u>PART 2: Contemporary vulnerability (IUCN status)</u>
<p>Response variable: IUCN status (threatened/non-threatened) Predictor variables: migratory behaviour, body size, clutch size, habitat diversity, island endemism, socio-economic status of countries, flightlessness, island size Time scale: Contemporary Spatial scale: Globally & islands Analysis: Boosted regression trees (n=139) Hypotheses:</p> <ul style="list-style-type: none"> -Sedentary, habitat specialist, island endemic, large-bodied, slow breeders, and flightless species would be more threatened. -Developing or human-dense countries would support more threatened species. Small, isolated and human-dense islands would carry more threatened species.
<u>PART 3: Contemporary vulnerability (impact from threats)</u>
<p>Response variable: impacted/not impacted by i) overhunting, ii) habitat loss, iii) introduced species Predictor variables: body size, clutch size, habitat diversity, island endemism, flightlessness, island size, naivety to predators, ability to survive in artificial habitats Time scale: Contemporary Spatial scale: Globally & islands Analysis: Boosted regression trees (n=106-139) Hypotheses:</p> <ul style="list-style-type: none"> -Introduced predators and overhunting would impact more large, island endemic, and flightless species, as well as species living on small islands, naïve to predators, and with small clutch size. -Habitat loss would impact more habitat specialists, island endemic and flightless species, as well as species living on small islands and unable to exploit disturbed habitats.

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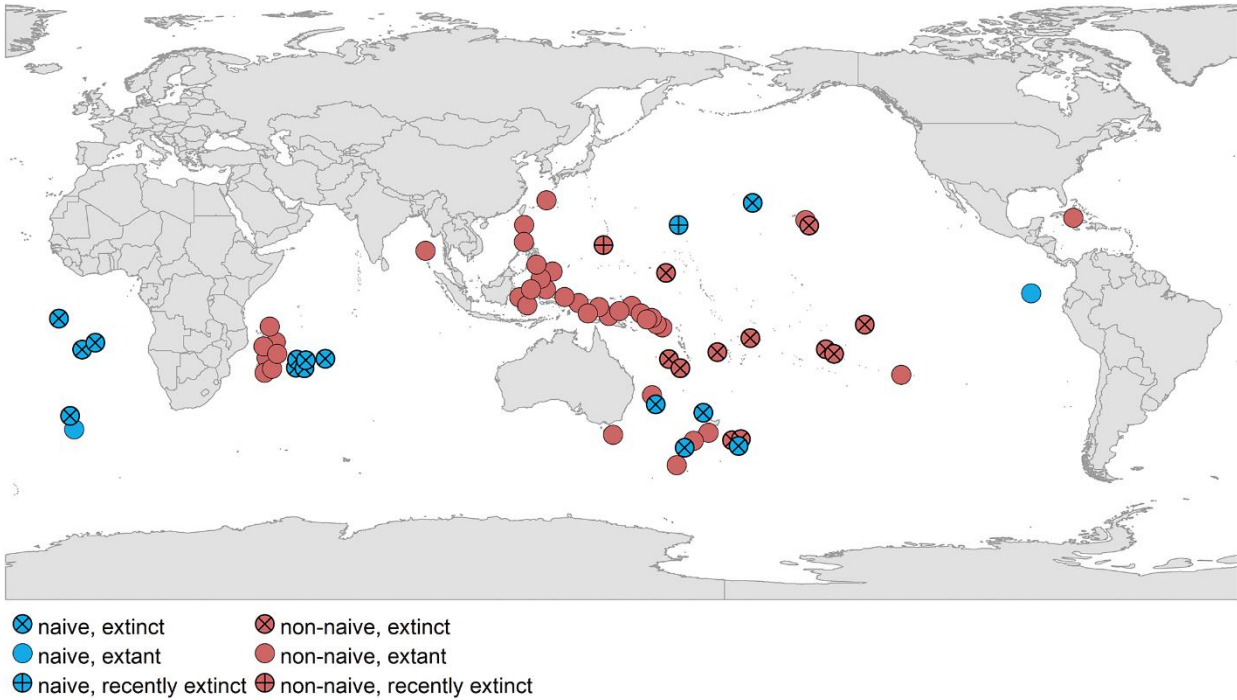
814 **Fig. 2.** Diagram of different rails' fate (extinction or persistence) over time and their use in the
 815 different parts of the analyses. We determined different pathways for rails extinctions: at first
 816 contact with humans during (i) the Pleistocene/Holocene or (ii) the Era of Colonialism, and (iii) at
 817 second or subsequent contact with humans. “(excluded)” means that the species have been excluded
 818 from the analysis and “(ignored)” that the species' previous state is considered for the analysis of
 819 extinction risk. Figure made with BioRender (<https://biorender.com/>).



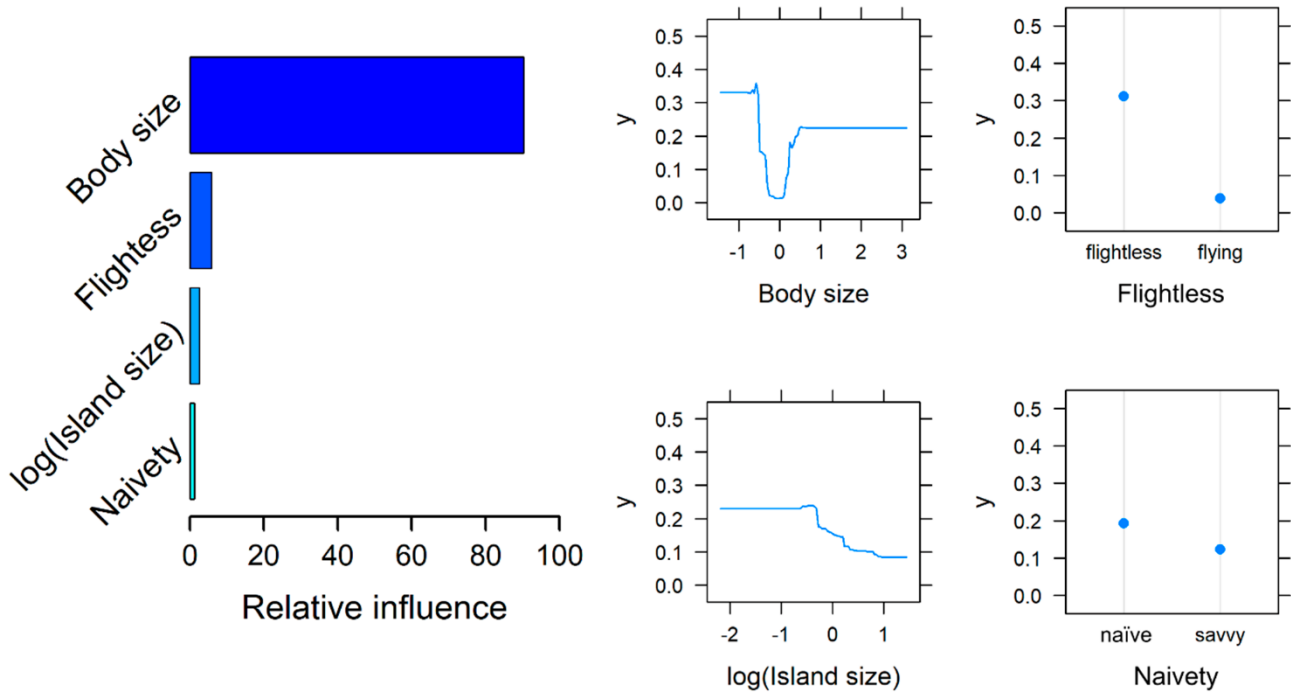
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822 **Fig. 3.** Global distribution of island rails since the Era of Colonialism (i.e., 16th century onwards).
 823 Symbols illustrate their fate of extinction (cross: extinct, vertical cross: extinct for contemporary
 824 reasons (i.e., extant in the analyses), plain: extant). Colours illustrate rails' state of naivety to
 825 humans at the time of contact (blue: naïve, pink: not naïve). The Inaccessible Rail (*Atlantisia*
 826 *rogersi*) was excluded since it did not have a substantial contact with humans. Projection
 827 information: WGS84, centred on 150°E.



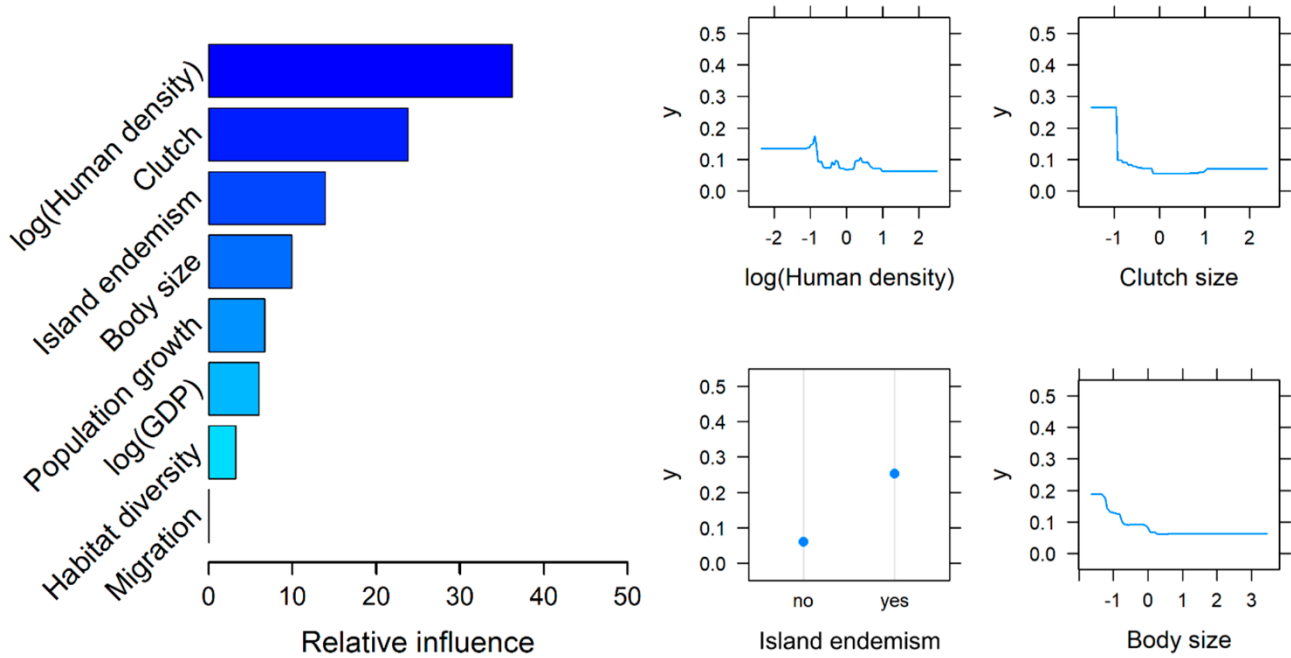
830 **Fig. 4.** Extinction risk in island rails: the relative influence (left) and partial dependence plots (right)
831 of predictor variables for the boosted regression tree model on extinction risk. Y is the probability
832 of becoming extinct. All continuous variables were standardised using z-scores.



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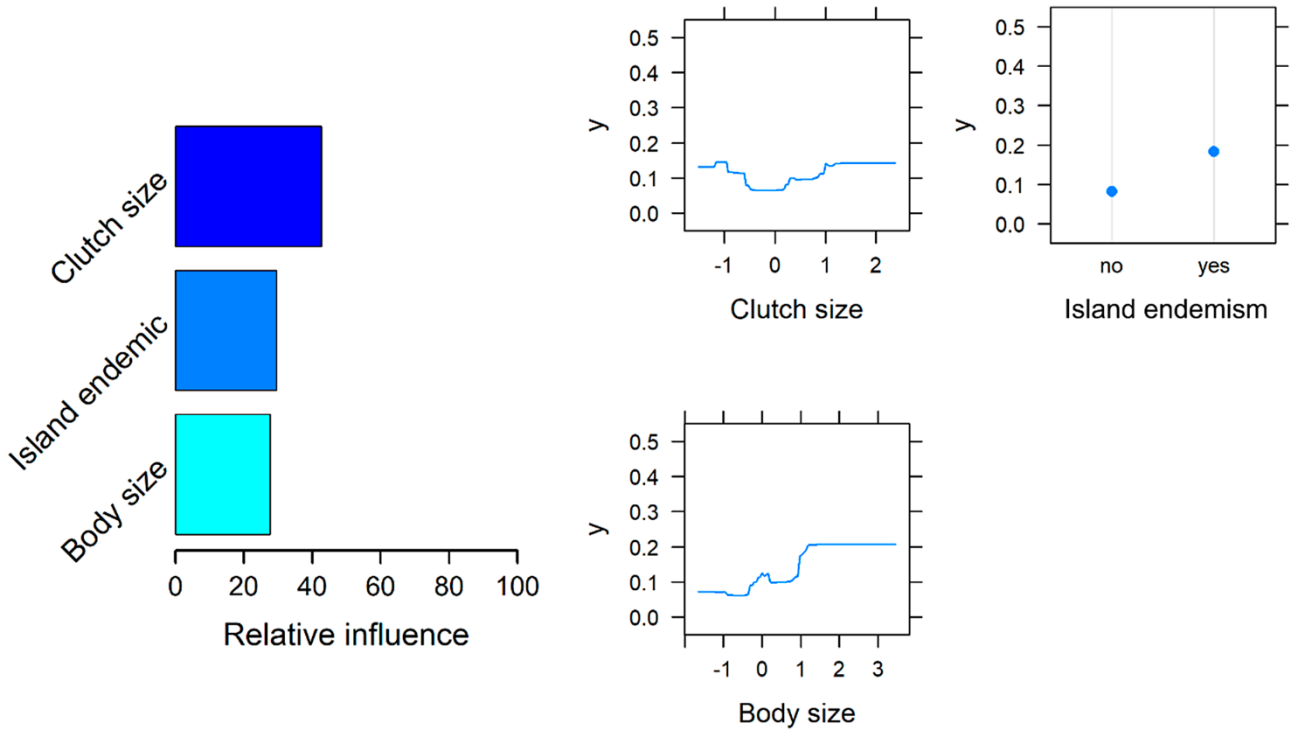
835 **Fig. 5.** Global vulnerability: the relative influence (left) and partial dependence plots for the four
 836 main predictor variables (right) of the boosted regression tree model on rails' global vulnerability.
 837 See Fig. S1 for partial dependence plots for all predictor variables. Y is the probability of being
 838 threatened. All continuous variables were standardised using z-scores.



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841 **Fig. 6.** Global vulnerability to overhunting: relative influence (left) and partial dependence plots
842 (right) of predictor variables for the boosted regression tree model on rails' vulnerability to
843 overhunting globally. Y is the probability of being threatened by overhunting. All continuous
844 variables were standardised using z-scores.



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847 **TABLES**

848 **Table 1.** Explanatory variables used in extinction risk and vulnerability models for rails. See Table
 849 S1 for references and data sources.

Variables	Description
Human naivety	Did not have a significant contact with humans in the past
Body size	Body length (cm)
Flightlessness	If the species is flightless or almost flightless
Island size	km ²
Isolation	Distance to the nearest continent (km)
Island endemic	Yes/No
Habitat diversity	Number of habitat types used
Migratory behaviour	Migrant/Sedentary
Socio-economic status of countries*	Human density (people/km ² of land area)
	GDP (\$US)
	Human population growth (%)
Predator naivety	Presence of native mammalian predators
Artificial	Known to exploit artificial man-modified habitats
Clutch size	Number of eggs produced per clutch (averaged)

850 *Human density: *Population density is midyear (2017) population divided by land area in square kilometers.*
 851 GDP: *GDP per capita (PPP) compares GDP on a purchasing power parity basis divided by population as of*
 852 *1 July for the same year.*

853 Human population growth: *Population growth rate compares the average annual percent change in*
 854 *populations, resulting from a surplus (or deficit) of births over deaths and the balance of migrants entering*
 855 *and leaving a country. The rate may be positive or negative.*

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858 **Table 2.** The combinations of the parameters and model settings used to derive the best model and
 859 the optimum number of boosted regression trees. N is the total number of species used in each
 860 analysis.

	N	Learning rate	Tree complexity	Bag fraction	Step size	n.minobsinnode in predictions
Part 1 – Extinction	67	0.001, 0.005, 0.01	1, 2, 3	.5, .6, .7, .8, .9	50	10
Part 2 – Vulnerability						
Global scale	124	0.001, 0.005, 0.01	1, 2, 3, 4, 5	.5, .6, .7, .8, .9	50	10
Island scale	33	0.0005, 0.001, 0.005, 0.01	1, 2, 3	.9	20	5
Part 3 – Habitat loss						
Global scale	124	0.0005, 0.001, 0.005, 0.01	1, 2, 3, 4, 5	.5, .6, .7, .8, .9	50	10
Island scale	33	0.0005, 0.001, 0.005, 0.01	1, 2, 3	.9	20	5
Part 3 – Overhunting						
Global scale	124	0.001, 0.005, 0.01	1, 2, 3, 4, 5	.5, .6, .7, .8, .9	50	10
Island scale	33	0.0005, 0.001, 0.005, 0.01	1, 2, 3	.9	20	5
Part 3 – Introduced species						
Global scale	124	0.001, 0.005, 0.01	1, 2, 3, 4, 5	.5, .6, .7, .8, .9	50	10
Island scale	33	0.0005, 0.001, 0.005, 0.01	1, 2, 3	.9	20	5

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863 **Table 3.** Optimum parameters and model performance for the boosted regression trees. Note that
 864 results presented for Part 2 (islands) have a reduced number of predictors after an initial model
 865 selection. TSS is the out-of-bag True Skill Statistic score.

Model	Learning rate	Tree complexity	Bag fraction	Optimal n.trees	Deviance	Sensitivity	Specificity	TSS	n
Part 1 – Extinction risk									
Island scale	0.01	2	0.5	1400	1.00	0.90	0.56	0.46	67
Part 2 – Vulnerability									
Global scale	0.001	2	0.6	6000	0.77	0.96	0.65	0.61	124
Island scale	0.005	3	0.9	210	1.37	0.53	0.75	0.28	33
Part 3 – Habitat loss									
Global scale	0.01	4	0.6	3300	1.25	0.87	0.33	0.21	124
Island scale	0.005	3	0.9	3090	1.18	1	0.89	0.88	33
Part 3 – Overhunting									
Global scale	0.01	3	0.7	200	0.76	0.98	0.45	0.43	124
Island scale	0.001	1	0.9	1750	1.33	1	0.57	0.57	33
Part 3 – Introduced sp.									
Global scale	0.01	4	0.7	200	0.63	0.93	0.8	0.73	124
Island scale	0.01	3	0.9	150	1.20	0.67	0.90	0.57	33

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869 **Table 4.** Proportion of rail species impacted by the three main threatening processes currently or in
870 the recent past.

	Habitat loss	Overhunting	Introduced species
Globally	36%	22%	20%
On islands	52%	55%	64%

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