
Rat eradication restores nutrient subsidies from seabirds across terrestrial and marine ecosystems

Benkwitt Cassandra E. ^{1,*}, Gunn Rachel L. ¹, Le Corre Mathieu ², Carr Peter ^{3,4},
Graham Nicholas A.J. ¹

¹ Lancaster Environment Centre, Lancaster University, Lancaster LA1 4YQ, UK

² UMR ENTROPIE, Université de La Réunion, IRD, CNRS, IFREMER, Université de Nouvelle-Calédonie, Avenue René Cassin, 97490 Sainte Clotilde, La Réunion

³ Institute of Zoology, Zoological Society of London, Regent's Park, London NW1 4RY, UK

⁴ Environment and Sustainability Institute, University of Exeter, Penryn Campus, Cornwall TR10 9EZ, UK

* Corresponding author : Cassandra E. Benkwitt, email address : c.benkwitt@lancaster.ac.uk

Abstract :

Biological invasions pose a threat to nearly every ecosystem worldwide.^{1,2} Although eradication programs can successfully eliminate invasive species and enhance native biodiversity, especially on islands,³ the effects of eradication on cross-ecosystem processes are unknown. On islands where rats were never introduced, seabirds transfer nutrients from pelagic to terrestrial and nearshore marine habitats, which in turn enhance the productivity, biomass, and functioning of recipient ecosystems.^{4, 5, 6} Here, we test whether rat eradication restores seabird populations, their nutrient subsidies, and some of their associated benefits for ecosystem function to tropical islands and adjacent coral reefs. By comparing islands with different rat invasion histories, we found a clear hierarchy whereby seabird biomass, seabird-driven nitrogen inputs, and the incorporation of seabird-derived nutrients into terrestrial and marine food chains were highest on islands where rats were never introduced, intermediate on islands where rats were eradicated 4–16 years earlier, and lowest on islands with invasive rats still present. Seabird-derived nutrients diminished from land to sea and with increasing distance to rat-eradicated islands, but extended at least 300 m from shore. Although rat eradication enhanced seabird-derived nutrients in soil, leaves, marine algae, and herbivorous reef fish, reef fish growth was similar around rat-eradicated and rat-infested islands. Given that the loss of nutrient subsidies is of global concern,⁷ that removal of invasive species restores previously lost nutrient pathways over relatively short timescales is promising. However, the full return of cross-ecosystem nutrient subsidies and all of their associated demographic benefits may take multiple decades.

Highlights

► Removing invasive rats boosts seabird biomass on tropical islands ► Seabird nutrients return to islands and coral reefs within 16 years of rat removal ► Nutrients from seabirds extend >300 m from shore around rat-eradicated islands ► Full recovery of nutrient subsidies and associated benefits had not yet occurred

Keywords : coral reef ; cross-ecosystem nutrients ; eradication ; invasive species ; island ; nutrient subsidy ; rat ; ecosystem recovery ; seabird ; tropics

44 **Results and Discussion**

45 Invasive mammals are a major threat to island ecosystems, where they drive declines in
46 native species and transform entire food webs and ecosystems^{1,5,8-11}. Rats are one of the most
47 common and damaging invasive species^{12,13}, and consequently rat eradication is gaining
48 momentum as an effective conservation intervention^{8-10,14}. Although the majority of rat
49 eradications and associated research have focused on temperate islands^{12,15,16}, eradication
50 programs are now increasing on tropical islands, where the benefits may extend to nearshore coral
51 reefs. However, the effectiveness of rat eradication for restoring these cross-ecosystem nutrient
52 pathways, and their associated benefits, is not currently known. Such information is important
53 because removing invasive species can lead to variable responses and recovery dynamics^{17,18}, yet
54 knowledge of broader ecological responses to rat eradication is limited and restricted to terrestrial
55 systems¹⁷⁻²¹.

56 Here, we test for multi-ecosystem recovery following rat eradication by comparing remote
57 islands across the Indian Ocean with varying invasion and eradication histories: islands that never
58 had rats, islands with rats eradicated, and islands with rats still present. By measuring seabird
59 populations, nutrient signatures of terrestrial and marine organisms, and growth rates of an
60 herbivorous reef fish, we provide the first estimates of the magnitude, timing, and spatial extent
61 over which rat eradication affects cross-ecosystem processes on tropical islands and coral reefs.
62 These findings, in turn, can help evaluate and guide management actions, including the removal
63 of invasive species^{17,18}, the restoration of natural nutrient pathways^{7,22}, and the integration of land
64 and sea conservation planning^{23,24}.

65 66 *Rat eradication enhances seabird biomass*

67 The biomass of breeding seabirds ranged from zero to >1200 kg/ha among the twenty
68 islands with different rat invasion statuses (Figure 1, Table S1). Despite high variation in seabird

69 biomass even among islands with similar rat invasion statuses, there was a clear hierarchy
70 whereby biomass was greatest on islands that never had rats, intermediate on islands that had rats
71 eradicated, and lowest on islands with rats present (Figure 1, evidence ratios and posterior
72 probabilities: rat absent > rat present = 641.38, 1.00; rat absent > rat eradicated = 12.75, 0.93; rat
73 eradicated > rat present = 9.83, 0.91). Higher seabird biomass on rat-free and rat-eradicated
74 islands compared to rat-infested islands is consistent with previous studies demonstrating strong
75 negative effects of invasive rats on island-breeding seabirds via their consumption of eggs and
76 chicks^{12,13}, and that removing invasive predators from islands benefits native biodiversity,
77 including seabirds^{3,25}.

78 That seabird biomass on rat-eradicated islands was still lower than on islands which never
79 had rats is likely due to the timescales over which increases in seabird populations occur.
80 Combining previously-published data²⁶ with updated surveys revealed that populations of
81 breeding seabirds have been steadily increasing following rat eradication on two islands in the
82 Scattered Islands (Île du Lys and Tromelin, rats eradicated in 2003 and 2005, respectively). There
83 has been an 8-fold increase in seabirds on Tromelin and a 10-fold increase in brown noddy
84 (*Anous stolidus*) on Île du Lys 15 years after rat eradication. There has not yet been any noticeable
85 change in populations of breeding seabirds on two islands in the Chagos Archipelago (Île Vache
86 Marine and Île Jacobin, rats eradicated in 2014), likely because rats were only eradicated 5 years
87 prior to these surveys²⁷, but frigatebirds and boobies roost on Île Vache Marine. In addition to
88 time since eradication, factors including oceanic prey productivity, native vegetation, and
89 characteristics of remnant seabird populations (e.g., size, isolation) likely contribute to variation
90 in the pace of seabird recovery^{25,28-30}. To quicken the recovery of seabird populations, rat
91 eradication can be paired with additional local management interventions such as promoting
92 native vegetation over coconut palms²⁸ and actively restoring seabird populations by translocating
93 chicks or attracting prospecting adults with sounds and decoys^{31,32}. None of these techniques were

94 employed on our study islands, so our estimated timescales to recovery are based on invasive rat
95 eradication alone, and are likely longer than would be possible by combining multiple
96 management interventions.

97

98 *Rat eradication enhances nutrients from seabirds on islands and coral reefs*

99 When seabirds return from their pelagic feeding grounds to islands where they roost and
100 breed, they transport nitrogen and phosphorous to terrestrial systems in the form of guano, some
101 of which then runs-off into nearshore marine systems^{4,33}. Seabird guano has elevated ratios of the
102 nitrogen isotope N15:N14 (expressed as $\delta^{15}\text{N}$), in part because they feed at high trophic levels in
103 the open ocean^{5,34}. Thus, high $\delta^{15}\text{N}$ values provide a reliable indicator of the incorporation of
104 seabird-derived nutrients into terrestrial and nearshore marine food chains^{5,6,30,34-36}. We tested
105 whether rat eradication can facilitate the return of this natural nutrient pathway by modelling
106 nitrogen input by seabirds to islands of varying rat statuses and comparing $\delta^{15}\text{N}$ values in
107 terrestrial (soil and leaves) and marine (coral-reef associated algae and herbivorous fish) samples.

108 Similar to seabird biomass, seabird-derived nitrogen inputs were highly variable, but still
109 greatest to islands that never had rats (median estimate: 274 kg ha⁻¹ year⁻¹), intermediate to islands
110 that had rats eradicated (13 kg ha⁻¹ year⁻¹), and lowest to islands with rats present (1 kg ha⁻¹ year⁻¹)
111 (evidence ratios and posterior probabilities: rat absent > rat present = 614.38, 1.00; rat absent > rat
112 eradicated = 13.39, 0.93; rat eradicated > rat present = 11.72, 0.92). As a result of these increased
113 nitrogen inputs, a higher proportion of seabird-derived nutrients was incorporated into terrestrial
114 and marine food chains on islands where rats were absent (both because they were never
115 introduced or recently eradicated) compared to islands where invasive rats were present (Figure 2,
116 Table S3). Specifically comparing islands where rats were recently eradicated to those where rats
117 were still present, the probability that $\delta^{15}\text{N}$ from rat-eradicated islands were higher than those
118 from rat-infested islands was $\geq 82\%$ for all samples (Figure 2, Table S4). The effect sizes were

119 greatest for terrestrial samples, with an estimated 1.49 times more seabird-derived nutrients in soil
120 and 1.82 times more seabird-derived nutrients in leaves on rat-eradicated islands than on rat-
121 infested islands. For marine organisms, the proportion of seabird-derived nutrients around rat-
122 eradicated islands was an estimated 1.33 times greater in macroalgae, 1.34 times greater in turf
123 algae, and 1.15 times greater in damselfish (Tables S3,S4).

124 These results represent the first evidence that rat eradication can restore seabird-derived
125 nutrient subsidies to tropical islands, and that these benefits extend to coral reefs. These findings
126 are consistent with a large body of evidence that seabird-derived nutrients are lower on and
127 around rat-infested versus rat-free islands^{6,35,37}, but represent a significant advance by
128 concurrently comparing terrestrial and marine systems across rat-infested, rat-free, and rat-
129 eradicated islands. Three previous studies from temperate islands in New Zealand similarly
130 demonstrated enhanced terrestrial nutrient signals on rat-eradicated versus rat-infested islands^{19–}
131 ²¹. Indeed, that we measured enhanced seabird-derived nutrient subsidies to soil and leaves within
132 16 years of rat eradication is remarkably consistent with Jones (2010)'s estimate that 15 years is
133 necessary to observe changes to nitrogen signatures in soil, leaves, and spiders²⁰. Although based
134 on only two studies, such consistency across tropical and temperate systems, islands with
135 different species of seabirds, and islands where different species of invasive rats were eradicated
136 is noteworthy. Additional work should be conducted to confirm whether this timeframe is
137 generalizable and can be broadly used as a basis for monitoring the return of nutrient pathways
138 following eradications. Moreover, we observed a temporal matching in the return of seabird-
139 derived nutrients to terrestrial and marine environments, with a return of subsidies to coral reefs
140 also occurring within 16 years of rat eradication. These results support increasing calls to
141 incorporate spatial links among ecosystems into conservation plans and to integrate land and sea
142 management^{23,24}, as island management can influence both terrestrial and adjacent marine systems
143 over similar time scales.

144 Although seabird-derived nitrogen signatures were greater on and around islands that were
145 rat-eradicated compared to rat-infested islands, for soil, leaves, and macroalgae they were still
146 lower than those from rat-free islands (Figure 2, Tables S3, S4). Seabird biomass and estimated
147 nitrogen input were also intermediate on rat-eradicated islands, and thus are likely drivers of this
148 hierarchical pattern of nitrogen signatures. These intermediate levels of recovery align with the
149 expectation of a ‘recovery debt’, whereby even when species and ecosystem-level processes
150 benefit from the removal of human-caused disturbances, full restoration relative to baselines is
151 not achieved for extended periods of time³⁸.

152 153 *Nutrients from seabirds extend at least 300 m from rat-eradicated islands*

154 After establishing that seabird-derived nutrients enter the marine environment around rat-
155 eradicated islands, we further quantified the spatial footprint of rat eradication by comparing $\delta^{15}\text{N}$
156 signatures of marine algae and fish at various distances to shore around rat-eradicated versus rat-
157 infested islands, which were the two island types for which we had replicate samples of the same
158 organisms at a range of distances to shore.

159 For marine organisms, the effect of distance to shore on the proportion of seabird-derived
160 nutrients varied between rat-eradicated and rat-infested islands (Figure 3, Table S5). In general,
161 the proportion of seabird-derived nutrients decreased with increasing distance from shore around
162 rat-eradicated islands, but there was little change with distance to shore around islands with
163 invasive rats. There was the strongest statistical support for this pattern in macroalgae (Table S5),
164 which was also the organism for which our sampling covered the widest range of distances to
165 shore from the most islands. For each additional 10 m from shore around rat-eradicated islands,
166 $\delta^{15}\text{N}$ in macroalgae decreased by 0.02 (95% HPDI = -.03 to -.01). Similarly, nutrient signatures in
167 damselfish decreased by 0.08 for each additional 10 m from shore around rat-eradicated islands
168 (95% HPDI = -.17 to .01). For turf algae, the pattern was less clear, but $\delta^{15}\text{N}$ still decreased by

169 0.005 for each additional 10 m from shore around rat-eradicated islands (95% HPDI = -.01 to
170 .09). By contrast, the effect of distance to shore on $\delta^{15}\text{N}$ was variable around rat-infested islands
171 (Table S5). Because $\delta^{15}\text{N}$ decreases with increasing distance from seabird colonies^{20,30,34,36,39,40},
172 these results provide additional evidence for increased seabird-derived nutrient subsidies around
173 islands on which rats were eradicated.

174 Based on the range of distances for which we have the most data across all sample types,
175 the effects of rat eradication on nutrient signatures of coral-reef organisms are evident to at least
176 300 m from shore. If we project the intersection of best-fit lines assuming the trends remain
177 linear, which is reasonable given previously-documented linear declines in $\delta^{15}\text{N}$ with increasing
178 distance to seabird colonies^{36,39}, then the $\delta^{15}\text{N}$ signatures of organisms around rat-eradicated
179 islands became equivalent to those around rat-infested islands at 509 m from shore for damselfish,
180 800 m from shore for macroalgae, and 1,280 m from shore for turf algae. These values represent
181 the first estimates of the spatial footprint of rat eradication into the marine environment, with
182 many coral reefs located within several hundred meters of shore and thus likely to be influenced
183 by rat eradication. Similarly, on reefs in the Pacific Ocean around rat-free islands, the effects of
184 seabirds on $\delta^{15}\text{N}$ of coral and their symbionts were evident to 400 m of shore^{34,36}. That we
185 observed a similar spatial footprint around rat-eradicated islands compared to these islands that
186 never had rats suggests the spatial extent of seabird nutrients extends rapidly following rat
187 eradication. In other words, despite only a partial return of seabird biomass, nitrogen input, and
188 incorporation of seabird-derived nutrients into terrestrial and marine food chains around rat-
189 eradicated compared to rat-free baseline islands (Figures 1-2), there was a return of the spatial
190 extent of seabird-driven nutrient pathways (Figure 3). Thus, with increasing time since
191 eradication and additional gains in seabird populations, we expect an increase in the magnitude,
192 but not necessarily spatial footprint, of nutrient subsidies.

193

194 *Fish growth is similar around rat-eradicated and rat-infested islands*

195 The presence and restoration of seabird-derived nutrient subsidies is important in part
196 because by providing limiting nutrients, they can boost demographic rates of recipient consumers,
197 which in turn alters key properties of recipient ecosystems^{4,5}. Specifically on tropical coral reefs,
198 abundant seabird populations enhance $\delta^{15}\text{N}$ in algae, corals, and herbivorous fishes, leading to
199 faster growth rates^{6,34,36,41}. Therefore, we provide the first test of whether the restoration of
200 seabird populations and their associated nutrient subsidies leads to demographic benefits in
201 nearshore marine ecosystems by comparing growth of a common herbivorous damselfish around
202 islands that had rats eradicated to nearby islands that still have invasive rats.

203 Despite strong evidence for the restoration of seabird-derived nutrient subsidies following
204 rat eradication (Figures 2-3), we found no evidence that these nutrients translate to demographic
205 benefits in a coral-reef fish (Figure 4, Table S6). There was a high degree of overlap in estimates
206 of the growth parameter k among rat-eradicated and rat-infested islands (Figure 4, Table S8,
207 median estimates ranged from 0.54 to 0.89). There was slightly more separation in maximum
208 asymptotic length (L_{∞}) among islands (median estimates ranged from 9.15 to 11.02), although
209 again there was no evidence that L_{∞} differed consistently between rat-eradicated and rat-infested
210 islands (Figure 4, Table S8).

211 In contrast, herbivorous damselfish have enhanced growth around islands that never had
212 rats compared to rat-infested islands in the Chagos Archipelago⁶. There are several plausible, non-
213 mutually exclusive, explanations for this discrepancy. Demographic rates of fishes vary due to a
214 variety of biotic and abiotic factors, including temperature, habitat, food availability, competition,
215 and predation⁴²⁻⁴⁴. Across the Scattered Islands, which cover a larger geographic area than the
216 Chagos Archipelago, such factors may have a stronger influence on growth than rat invasion
217 status. Moreover, nutrient isotopic signatures incorporate information over several months, but
218 there is likely a longer lag time between rat eradication and demographic responses. The

219 damselfish captured in this study were between 1-15 years old, which means the oldest fish were
220 born around the time that rats were eradicated. Because early growth can be a strong determinant
221 of future growth trajectories of fishes⁴², we may see a stronger growth response in the coming
222 years. Alternatively, enhanced demographic rates in consumers may only occur when islands
223 support high seabird populations and nutrient inputs, such as the levels observed on islands that
224 never had rats (Figures 1-2). Similarly, on temperate islands terrestrial arthropod abundance and
225 diversity had not recovered within 8-13 years of rat eradication, and macroalgal diversity had not
226 recovered within 30 years, despite a partial return of seabird-derived nutrients following rat
227 eradication^{20,45}. By contrast, changes to community structure in the rocky intertidal following rat
228 eradication can occur within 11 years, but the mechanism for these shifts are top-down effects of
229 seabirds as predators, rather than bottom-up effects of seabird-derived nutrients⁴⁶. Thus, the
230 partial return of seabird populations and natural nutrient pathways does not guarantee a return of
231 concomitant benefits for ecosystem functions of consumers in either terrestrial or marine systems.
232 Consequently, other cross-ecosystem benefits provided by seabird-derived nutrients, including
233 enhanced biomass, diversity, and ecosystem function of fishes on coral reefs, may also display a
234 prolonged time-lagged return following rat eradication^{6,47,48}.

235

236 *Conclusions*

237 Combined, these results clarify the magnitude, timing, and spatial extent of island
238 management actions across multiple systems. By systematically sampling across both terrestrial
239 and adjacent marine systems, we demonstrate that rat eradication is effective at restoring nutrient
240 pathways provided by seabirds across multiple ecosystem boundaries, with the effects extending
241 at least several hundred meters from shore. Furthermore, the timescales to recovery were not
242 system-specific, with a return of seabird-derived nutrient subsidies to terrestrial and marine
243 systems both occurring within 16 years of rat eradication. That the removal of invasive species,

244 even after hundreds of years of infestation, can restore ecosystem and cross-ecosystem benefits
245 over relatively short timescales is promising for numerous conservation initiatives, including
246 restoring lost nutrient pathways^{7,22}, meta-ecosystem management²⁴, and integrated land-sea
247 conservation³⁷. However, seabird biomass, nitrogen input, and the magnitude of seabird-derived
248 nutrients into terrestrial and marine food chains were still lower on rat-eradicated islands
249 compared to baseline islands that never had rats, and the benefits of rat eradication did not extend
250 to all ecosystem functions (namely, coral-reef fish productivity). Conversely, full recovery of
251 communities and ecosystems in a range of other systems is possible within 10 years of invasive
252 species removal⁴⁹. Thus, pairing rat eradications with active restoration strategies may be
253 necessary to speed the recovery of seabird populations and their associated benefits^{31,32}, and
254 should be considered as part of management plans when the goal is rapid recovery of the full
255 magnitude and spectrum of cross-ecosystem benefits provided by seabirds. Prioritizing
256 monitoring efforts before, during, and after the many planned eradications on islands will further
257 our understanding of the contexts and timescales over which ecological restoration is achieved,
258 and thus further bolster the success of these management actions.

259

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272

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274 RLG, MLC, PC, NAJG collected data; CEB analyzed the data and led the writing of the
275 manuscript. All authors contributed to critically revising manuscript drafts.

276

277 **Declaration of Interests** The authors declare no competing interests.

278

279 **Figure Legends**

280 **Figure 1. Map of study sites and seabird biomass on islands that never had invasive rats,**

281 **islands with rats eradicated, and islands with rats still present.** (A) Location of islands within
282 the Indian Ocean and close-up of the (B) Scattered Islands and (C) Chagos Archipelago. (D)

283 Annual biomass of seabirds by seabird family and island. Symbols in (A-C) indicate whether each
284 island has never had rats (rats absent, circle), had rats eradicated (square), or still has rats present
285 (triangle). Colors for (A-D) represent seabird biomass (kg/ha) on a log-transformed scale, with

286 gray indicating no seabirds in that family/island. (E) Estimated difference in seabird biomass for *a*
287 *priori* comparisons among islands with different rat invasion statuses. Points represent median
288 estimates, thin lines represent 95% HPDI, thick lines represent 75% HPDI for each comparison.

289 Any points above the dashed zero line indicate support for the following hypotheses: seabird
290 biomass is greater on islands where rats are absent than where rats are present (green), seabird

291 biomass is greater on islands where rats were eradicated than where rats are present (orange), or
292 seabird biomass is greater on islands where rats are absent than where rats were eradicated

293 (purple). See also Table S1.

294 **Figure 2. $\delta^{15}\text{N}$ values for terrestrial and marine samples collected on and around islands**
295 **that never had invasive rats, islands with rats eradicated, and islands with rats still present.**

296 (A-E, F-J) Raw data for $\delta^{15}\text{N}$ values across the Scattered Islands and Chagos Archipelago,
297 respectively. Each point represents one sample, box limits represent first and third quartiles (25%
298 and 75% percentiles), middle line represents the median (50% percentile), and whiskers represent
299 smallest and largest observations less than or equal to 1.5x inter-quartile range. (K) Estimated
300 difference in $\delta^{15}\text{N}$ values for *a priori* comparisons among islands with different rat invasion
301 statuses. Points represent median estimates, thin lines represent 95% HPDI, thick lines represent
302 75% HPDI for each comparison. Any points above the dashed zero line indicate support for the
303 following hypotheses: $\delta^{15}\text{N}$ is higher on/around islands where rats are absent than where rats are
304 present (green), $\delta^{15}\text{N}$ is higher on/around islands where rats were eradicated than where rats are
305 present (orange), or $\delta^{15}\text{N}$ is higher on/around islands where rats are absent than where rats were
306 eradicated (purple). See also Table S3 and S4.

307 **Figure 3. Estimated effect of distance to shore on $\delta^{15}\text{N}$ values for marine samples collected**
308 **around rat-eradicated versus rat-infested islands.** Points represent raw data, shapes represent
309 islands where they were collected and fill represents rat invasion status. Colored lines are best-fit
310 from Bayesian models, with shading indicating 95%, 80%, and 50% confidence regions. See also
311 Table S5.

312 **Figure 4. Age-at-length plots for damselfish collected across the Scattered Islands.** Blue
313 coloration indicates islands that had rats eradicated, red coloration indicates islands with rats
314 present. Points show raw data, curves represent VBGF growth curves from non-linear Bayesian
315 models, with shading indicating 95%, 80%, and 50% confidence regions. Inset shows median
316 (points), 95% (thin lines), and 75% (thick lines) HPDIs for each VBGF parameter. See also Table
317 S6 and S7.

318

319 **STAR Methods**

320 **RESOURCE AVAILABILITY**

321 *Lead contact*

322 Further information and requests for resources and reagents should be directed to and will
323 be fulfilled by the lead contact, Cassandra Benkwitt (c.benkwitt@lancaster.ac.uk).

324 *Materials availability*

325 This study did not generate new unique reagents.

326 *Data and code availability*

327 All data and code supporting the findings in this paper are publically available on GitHub
328 (github.com/cbenkwitt/derat-islands-reefs).

329 **EXPERIMENTAL MODEL AND SUBJECT DETAILS**

330 *Study sites*

331 We conducted this study across 20 remote islands in the central and western Indian Ocean
332 with varying rat invasion and eradication histories (Figure 1, Table S1). All islands were part of
333 the Chagos Archipelago or the Scattered Islands, which are protected from local human influences
334 and considered ecological benchmarks for the region^{50,51}. The Chagos Archipelago is located in
335 the central Indian Ocean, and is encompassed by a large (640,000 km²) marine protected area^{50,52}.
336 We investigated 15 islands in the northern atolls of the archipelago, chosen to be similar in size,
337 location, and environment, with the exception of rat invasion status. All of the islands have been
338 uninhabited since the 1970s. Black rats (*Rattus rattus*) were introduced to nine of these islands at
339 least several hundred years ago, while six of these islands have never had rats. A failed rat
340 eradication campaign occurred on one island in 2006 (Eagle Island), but in recent years renewed
341 efforts have been successful on several smaller islands, with rats eradicated from two of our study
342 islands in 2014 (Île Vache Marine and Île Jacobin). There are no other invasive predatory
343 mammals on any of the study islands, but native flora was cleared for coconut plantations on
344 many of the islands.

345 We surveyed all five of the Scattered Islands (Les Îles Éparses), which are located in the
346 western Indian Ocean and are managed by the French Southern and Antarctic Lands (Terres
347 Australes et Antarctiques Françaises, TAAF)⁵¹. The islands have no permanent human
348 populations, although four of the islands are occupied by small numbers of military/TAAF
349 personnel on a rotating basis⁵¹. Black rats (*R. rattus*) were introduced to Europa and Île du Lys in
350 the 1800s and to Juan de Nova in the 1900s, while brown/Norway rats (*R. norvegicus*) were
351 introduced to Grande Glorieuse in the 1800s and Tromelin between the mid-1800s and mid-
352 1900s⁵³. Rats were eradicated from Île du Lys in 2003 and Tromelin in 2005, but are still present
353 on the other islands⁵³. In addition to rats, goats are present on Europa, mice are present on Juan de
354 Nova and Grande Glorieuse, and cats are present on Grande Glorieuse (and were eradicated from
355 Juan de Nova in 2015)^{53,54} (Table S1). Although free from rats, Tromelin still has mice, while Île
356 du Lys is the only island with no invasive mammals present^{53,54} (Table S1). Native vegetation has
357 mostly remained intact on Europa, Tromelin, and Île du Lys, but has been replaced by casuarina
358 plantations on Juan de Nova and coconut plantations on Grande Glorieuse.

359 In addition to encompassing a range of rat invasion and eradication histories, our studied
360 islands span a wide latitudinal range encompassing various climates (Figure 1). Within the
361 Scattered Islands, rainfall increases as one moves from the south to the north such that Europa is
362 dry most of the year, Juan de Nova has intermediate levels of rainfall, and Grande Glorieuses, Île
363 du Lys and Tromelin have high rainfall. The islands of the Chagos Archipelago are all closer to
364 the equator and experience more rainfall. These climatic differences are relevant to cross-
365 ecosystem nutrient subsidies because heavy rains may more readily wash seabird-derived
366 nutrients into the marine environment, whereas more nutrients may remain on the islands in more
367 arid regions. Indeed, after controlling for sample type and rat invasion category, median $\delta^{15}\text{N}$ of
368 terrestrial samples were higher in the Scattered Islands compared to the Chagos Archipelago, but
369 $\delta^{15}\text{N}$ of marine samples were higher in the Chagos Archipelago (Figure 2). Regional climatic

370 conditions can also affect seabird populations, and thus their cross-ecosystem nutrient subsidies,
371 by influencing oceanic prey productivity. Specifically, the Indian Ocean Dipole influences prey
372 availability and seabird distributions at-sea within the Chagos Archipelago²⁹, while the Southern
373 Equatorial Current affects breeding seabirds in the Scattered Islands^{55,56}. Including region and
374 island in our statistical models enabled us to account for these climatic differences and focus on
375 our hypotheses regarding rat invasion status (see *Statistical analyses* below).

376 We followed institutional and local regulations for all fieldwork and collections (permit
377 numbers 0005SE15, 0001SE18, 0004SE18, 0007SE18, 000SE19). Ethical approval for
378 damselfish collections was obtained from James Cook University (approval number A2166, for
379 sampling in 2015) and the Lancaster University Animal Welfare and Ethical Review Body
380 (AWERB permit number A100143, for sampling in 2018-2019). Data on sex of damselfish was
381 not collected, as males and females are not visually distinguishable.

382

383 **METHOD DETAILS**

384 To test for the restoration of seabird-derived nutrient pathways across terrestrial and
385 marine environments following rat eradication, we used a space-for-time substitution design. The
386 study consisted of three main parts: (1) seabird censuses to test for an effect of rat invasion status
387 on seabird populations (conducted 2005 – 2020), (2) nutrient sampling to test for an effect of rat
388 invasion status on nutrient signatures in terrestrial and marine samples (conducted 2015 and 2018-
389 2019), and (3) demographic sampling to test for an effect of rat invasion status on the growth
390 rates of a coral-reef fish (conducted 2019).

391 ***Seabirds***

392 To test the hypothesis that rat eradication restores seabird populations, censuses of
393 breeding seabirds were conducted at each island. Seabird data for the Chagos Archipelago were
394 obtained from²⁷ based on censuses conducted between 2008 – 2019. Seabird data for the Scattered

395 Islands were obtained from^{26,57}, combined with additional surveys conducted at all islands
396 between 2005 and 2020.

397 Because it is more directly related to the quantity of nutrients that seabirds provide to
398 islands, we converted the number of breeding pairs per island to total annual biomass per hectare
399 using species-specific average body weight multiplied by the number of breeding birds, island
400 area, and the period of year that each seabird species breeds on each island⁶. Even within a
401 species, breeding phenology varies across islands and regions. Therefore, we used island-specific
402 data for breeding phenology in the Scattered Islands from^{56,58} and additional surveys, which span
403 a wide range of latitudes. We used archipelago-specific information for the Chagos Archipelago,
404 which has little inter-island variation in breeding season due to its narrow range of latitudes and
405 proximity to the equator²⁷. Although some seabirds roost on islands outside of their breeding
406 season, we lacked such detailed information for many of the species and islands. For consistency
407 and simplicity, we therefore restricted our analysis to breeding pairs. This simplification means
408 that our estimates of breeding seabird biomass is likely lower than the total biomass of seabirds
409 that use the islands.

410 *Nutrients*

411 We estimated the yearly nitrogen input to each island from breeding seabirds using
412 previously-established scaling relationships^{5,6,59}. Specifically, we estimated species-specific daily
413 nitrogen input by scaling the known guano defecation rate of *Sula sula* by species-specific
414 average body weights and by the known nitrogen content of guano (18.1%)^{6,59}. We then
415 calculated yearly nitrogen input to each island by multiplying the species-specific nitrogen inputs
416 by annual biomass per hectare on each island (see *Seabirds* above) while accounting for the
417 proportion of time each species spends on the island during their breeding season relative to the
418 time spent off-island foraging⁶.

419 To trace seabird-derived nutrients through the food chains, we sampled terrestrial and
420 marine organisms for nitrogen stable isotope analysis in March 2015, May 2018, and April 2019.
421 We collected soil and leaves from islands, and macroalgae, turf algae, and fish from adjacent
422 marine environments (n = 5-15 per sample type, per island; Supplemental Table 2). We aimed to
423 collect the same species from all islands, although when this was not possible we substituted
424 ecologically and/or taxonomically similar species. The species/genera collected were: *Scaveola*
425 *taccada*, *Suriana maritima*, and *Heliotropium forthiarum* (leaves); *Halimeda spp* and *Turbinaria*
426 *spp* (macroalgae); and *Plectroglyphidodon lacrymatus* and *Stegastes fasciolatus* (herbivorous,
427 territorial damselfish) (Table S2).

428 On all islands, topsoil was collected inland of the coastal vegetation boundary, and leaves
429 were collected as close to shore as possible. In the Chagos Archipelago, all marine samples were
430 taken from the lagoonal side of each island. Macroalgae was sampled at approximately 1 m depth
431 and 100 m from shore and turf algae and damselfish were collected at approximately 3 m depth
432 and 230 m from shore. The Scattered Islands do not form atolls with distinct lagoons, but all
433 marine samples were still taken from the more wave-sheltered side (north/west) of each island.
434 We collected all marine organisms from a range of distances to shore in the Scattered Islands to
435 further test the spatial extent of seabird-derived nutrients (range = 87 – 1000 m from shore, 1 - 6
436 m depth).

437 Immediately following collection, we dried all samples at 60°C for 48 hours in preparation
438 for stable isotope analysis. Samples collected in the Chagos Archipelago in 2015 were analyzed at
439 the University of Windsor (Canada) using a Finnigan MAT Deltaplus mass spectrometer with
440 B2153 and USGS 40 standards. These isotopic results have been published previously⁶. All other
441 samples were analyzed at Lancaster University (UK), where they were combusted using an
442 Elementar Vario MICRO cube Elementer Analyser and analyzed using an Isoprime 100 Isotope
443 Ratio Mass Spectrometer, with international standards IAEA 600 and USGS 41. Accuracy based

444 on internal standards was within 0.3 permil standard deviation in both Windsor and Lancaster,
445 and selected samples were run in duplicate or triplicate to further ensure accuracy of readings.

446 ***Fish demography***

447 We tested for demographic benefits of rat eradication using territorial damselfish, which
448 are highly site-attached and have previously been shown to grow faster near islands with
449 abundant seabirds compared to those with few seabirds⁶. Focusing on damselfish also enabled us
450 to test for a clear pathway from seabird-derived nutrients to consumer demographic rates via
451 enrichment of turf algae, which damselfish feed on within their territories and which was also
452 collected as part of the nutrient analyses. To determine age-at-length of damselfish, we analyzed
453 otoliths (ear bones) from 133 individuals from across the Scattered Islands, which included fish
454 used in the isotope analyses combined with additional individuals to increase sample size (n = 10
455 – 34 individuals per island, Table S2). Because growth rates and maximum lengths vary among
456 fish species (e.g., maximum length is 10 cm for *P. lacrymatus* and 16 cm for *S. fasciolatus*⁶⁰), we
457 restricted our analysis to only include individuals within each island from the same species. This
458 criteria resulted in the exclusion of three individual *P. lacrymatus* from Juan de Nova and one *S.*
459 *fasciolatus* from Île du Lys (Table S2).

460 We measured total length (to the nearest mm) and removed the pair of sagittal otoliths
461 from each damselfish. One randomly selected otolith from each pair was mounted to the edge of a
462 glass slide using thermoplastic glue with the otolith core situated directly inside the slide edge.
463 The otolith material was sanded away to the slide edge using a 1200-grit diamond lap on a
464 lapping machine with constant water flow. The slide was heated and remounted with the newly
465 sanded surface placed flat against the slide, and the remaining bulk of otolith material was sanded
466 away until a thin transverse cross-section (150 µm) remained. Annuli, denoted by alternating
467 opaque and translucent growth bands, were counted independently three times using a stereo-
468 microscope, and fish age (in years) was assigned when two or more counts agreed.

469 QUANTIFICATION AND STATISTICAL ANALYSIS

470 We compared annual breeding seabird biomass and seabird-derived nitrogen input among
471 islands with different rat invasion statuses using Bayesian models with rat status (absent,
472 eradicated, or present) as an explanatory variable and a random intercept for Region (Scattered
473 Islands or Chagos Archipelago). We log-transformed seabird biomass and nitrogen input to help
474 with model fit and convergence. We performed non-linear hypothesis tests to calculate evidence
475 ratios and posterior probabilities for each of the following *a priori* hypotheses: (1) seabird
476 biomass/nitrogen input is higher on islands where rats were eradicated compared to rat-infested
477 islands, (2) seabird biomass/nitrogen input is higher on islands where rats were never present
478 compared to rat-infested islands, and (3) seabird biomass/nitrogen input is higher on islands
479 where rats were never present compared to islands where rats were eradicated.

480 To test the effect of rat invasion status on $\delta^{15}\text{N}$ of each sample type (soil, leaves,
481 macroalgae, turf algae, and damselfish, which is a reliable proxy for the uptake of seabird-
482 derived nutrients^{5,6,30,34–36}, we ran Bayesian models with rat status as an explanatory variable as
483 above. We included random intercepts for Region (Scattered Islands or Chagos Archipelago) and
484 Island ($n = 20$) to account for spatial non-independence among samples. An additional random
485 intercept for Species was included in models for sample types when multiple species were
486 collected (leaves, macroalgae, and damselfish). We calculated highest posterior density intervals
487 (HPDIs) of $\delta^{15}\text{N}$ for each rat invasion status and performed non-linear hypothesis tests as for
488 seabird biomass above.

489 Rat eradication is easier on smaller islands, so eradication efforts have generally focused
490 on small islands and are only now expanding to larger islands⁶¹. As a result, many of the islands
491 where rats were eradicated were also some of the smallest islands studied. Despite this constraint,
492 we were able to survey islands across a reasonably similar range of sizes within each rat invasion
493 status, especially with regard to minimum island size (rat-free: 8 – 81 ha, rat-eradicated: 2 – 97
494 ha, rat-infested: 2 – 2223 ha) (Table S1). Still, because islands encompassed a range of sizes, and

495 it is reasonable that island size could influence the amount of nutrient subsidies reaching the
496 ocean, we ran additional models with island size as a co-variate. We found it had little or no
497 influence on nitrogen signatures, with rat invasion status always emerging as a much stronger
498 predictor than island size. In addition, the model results were nearly identical regardless of
499 whether island size was included, so we only present the simpler models excluding size.

500 To test whether $\delta^{15}\text{N}$ varied as a function of distance from shore and rat invasion status,
501 we ran Bayesian models for marine samples collected from the Scattered Islands. We restricted
502 this analysis to the Scattered Islands because we collected the same sample type from multiple
503 distances to shore within each island, whereas in the Chagos Archipelago we only sampled one
504 distance from shore per sample type per island. Because the effects of distance from shore may
505 vary by rat invasion status, we included an interaction term between these two explanatory
506 variables. As above, we included a random intercept for Island in all models, so the effects of
507 distance to shore were estimated while accounting for differences among islands. We estimated
508 HPDIs of the slope for distance from shore for each rat invasion status and of the interaction
509 between distance x rat invasion status. For each of these estimates, we tested the following *a*
510 *priori* hypotheses: (1) $\delta^{15}\text{N}$ decreases with increasing distance to shore (i.e., slope < 0) and (2)
511 $\delta^{15}\text{N}$ decreases more rapidly around rat-eradicated islands than rat-infested islands (i.e., distance x
512 rat invasion status interaction > 0).

513 We modelled damselfish growth following the von Bertalanffy growth function (VBGF):

$$514 \quad L_t = L_\infty - (L_\infty - L_0)e^{-kt}$$

515 where L_t is the observed length at age t , L_∞ is the estimated asymptotic length, L_0 is the
516 theoretical length at age 0, and k is the estimated growth coefficient towards L_∞ . Using a non-
517 linear Bayesian model of the VBGF, we allowed both L_∞ and k to vary by island, and thus
518 estimated these parameters for each island. We modelled damselfish growth by island rather than
519 by rat invasion status in part to avoid pooling two different fish species into a single growth

520 curve. We then calculated HPDIs for each parameter around each island, and conducted pairwise
521 comparisons of the growth parameters between islands. If rat eradication enhances damselfish
522 growth, we expect L_{∞} and/or k to be consistently higher around rat-eradicated islands compared
523 to rat-infested islands, but similar among islands with the same rat invasion status.

524 For all models, we used weakly informative priors and ran the model for four chains, each
525 with at least 3,000 iterations including a warm-up of 1,000 iterations. Convergence and model fits
526 were checked using graphical posterior predictive checks, traceplots, and the Gelman-Ruban
527 convergence diagnostic (R-hat). We used Pareto smoothed importance-sampling leave-one-out
528 cross-validation (PSIS-LOO) to check for highly influential datapoints. The only time pareto-k
529 values were greater than the generally-accepted threshold (0.7)⁶² was for the island Grande
530 Glorieuse in the seabird biomass and nitrogen input models. In these cases, we compared the
531 posterior distributions with and without Grande Glorieuse, and found that our interpretations were
532 similar regardless. All analyses were conducted in R (version 3.6.1) and implemented in STAN
533 using the package brms with additional packages bayesplot, loo, tidybayes, and tidyverse^{63–70}.

534

535 **Supplemental Information** Supplemental information contains Tables S1-S7.

536

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693

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Biological samples		
Soil	This study, [6]	Table S2
Leaves (<i>Heliotropium forthiarum</i> , <i>Suriana maritima</i> , <i>Scaveola taccada</i>)	This study, [6]	Table S2
Macroalgae (<i>Halimeda spp</i> , <i>Turbinaria spp</i>)	This study, [6]	Table S2
Turf algae	This study, [6]	Table S2
Damselfish (<i>Plectroglyphidodon lacrymatus</i> , <i>Stegastes fasciolatus</i>)	This study, [6]	Table S2
Deposited data		
Biomass of breeding seabirds	This study, [26], [27], [57]	Table S1, github.com/cbenkwitt/derat-islands-reefs
Estimated nitrogen input from seabirds	This study	github.com/cbenkwitt/derat-islands-reefs
$\delta^{15}\text{N}$ of soil, leaves, macroalgae, turf algae, damselfish	This study, [6]	github.com/cbenkwitt/derat-islands-reefs
Age and length of damselfish	This study	github.com/cbenkwitt/derat-islands-reefs
Software and algorithms		
R software	[63]	r-project.org/
STAN software	[64]	mc-stan.org/
R package <i>brms</i>	[65], [66]	cran.rstudio.com/web/packages/brms/
R package <i>bayesplot</i>	[67]	mc-stan.org/bayesplot
R package <i>loo</i>	[68]	mc-stan.org/loo
R package <i>tidybayes</i>	[69]	mjskay.github.io/tidybayes/
R package <i>tidyverse</i>	[70]	CRAN.R-project.org/package=tidyverse
Custom code to complete all statistical analyses	This study	github.com/cbenkwitt/derat-islands-reefs

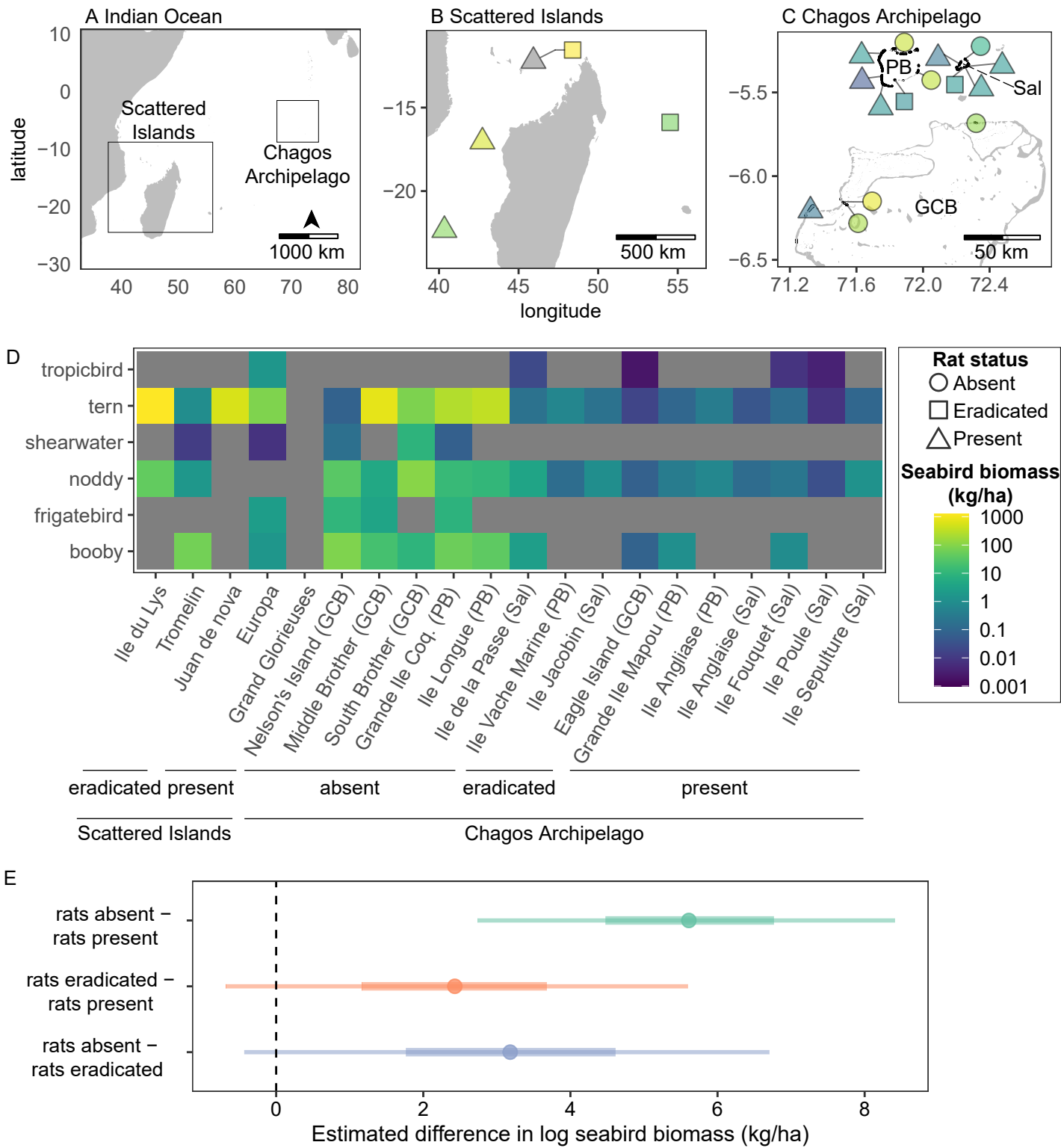
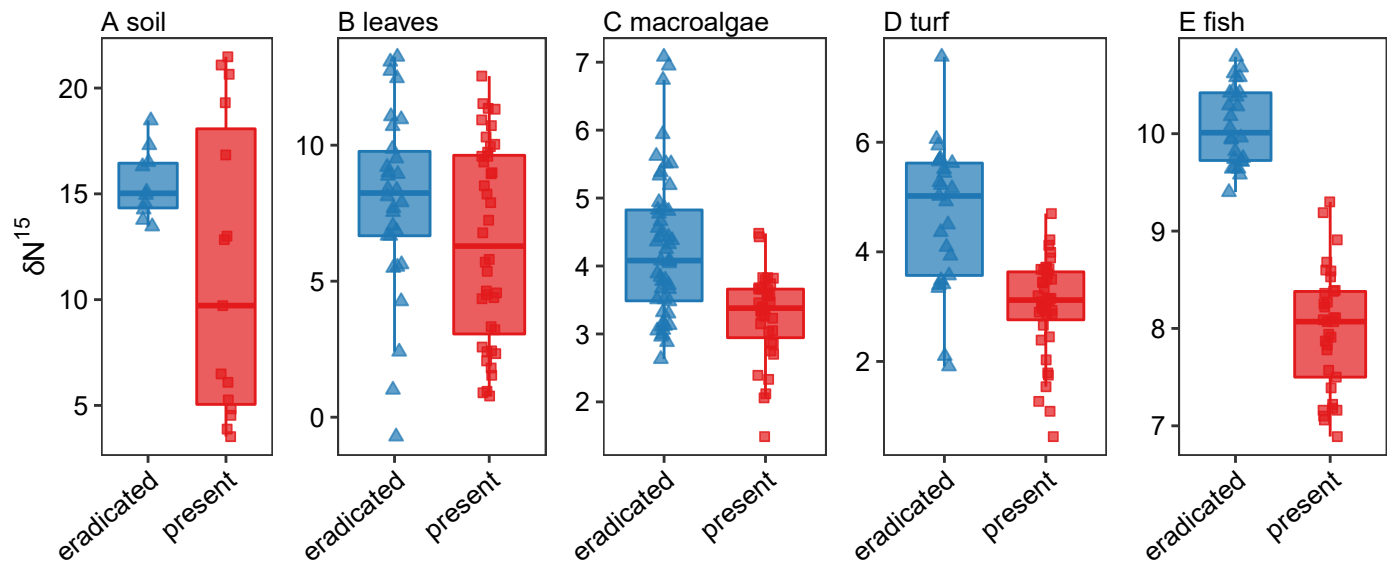
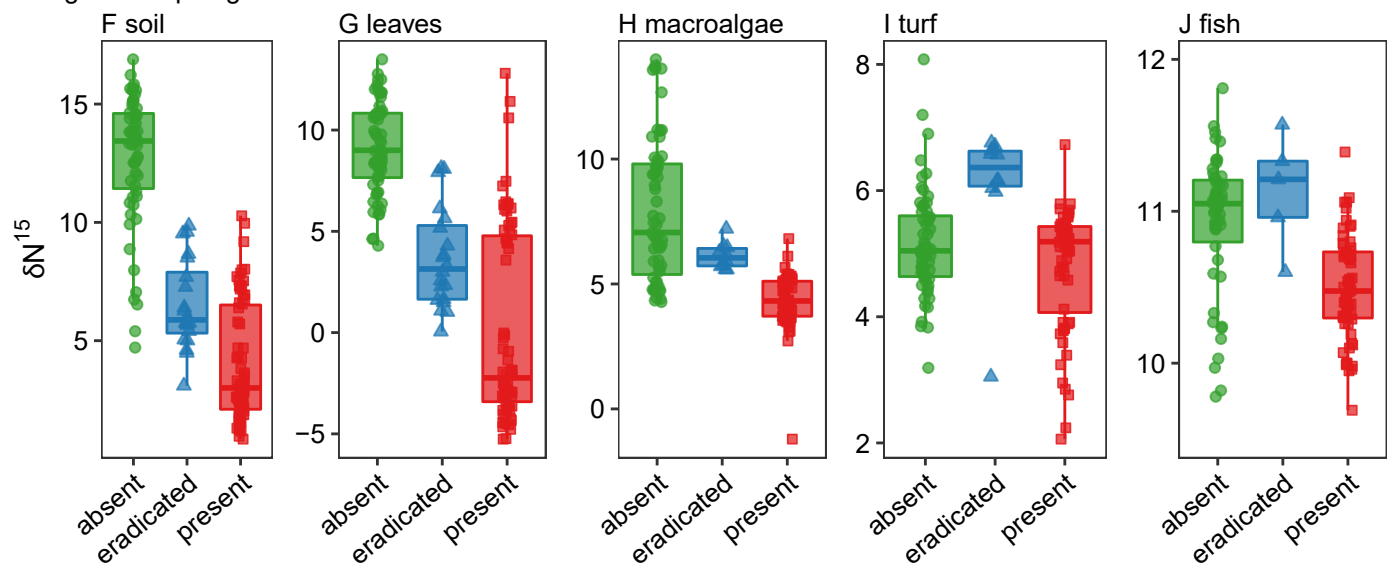


Figure 1

Scattered Islands



Chagos Archipelago



K all samples

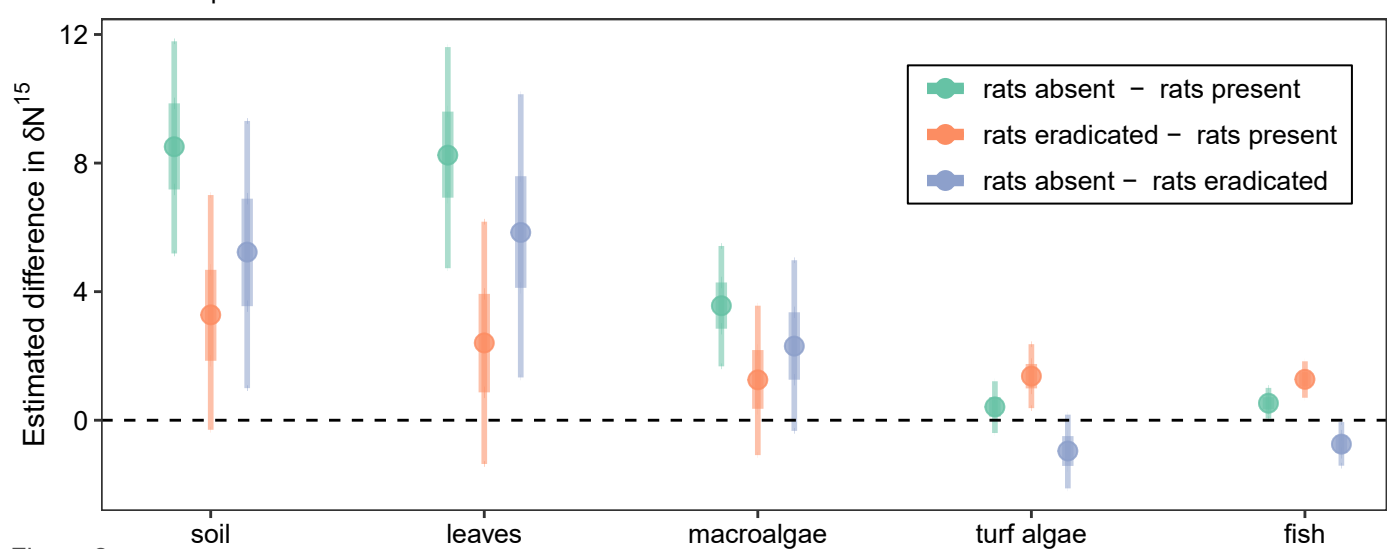
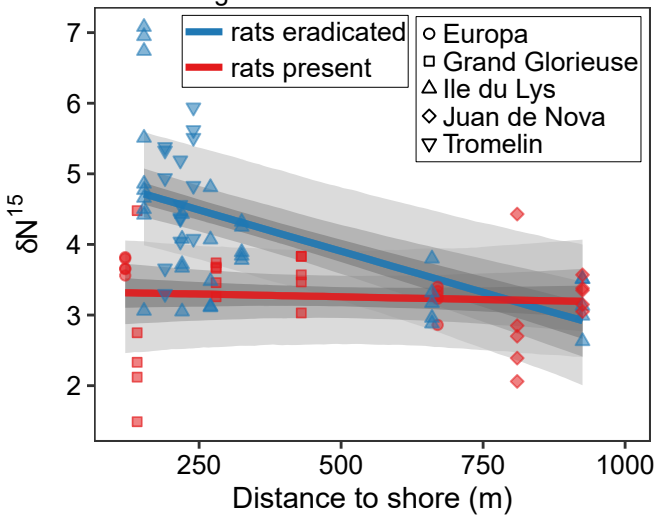
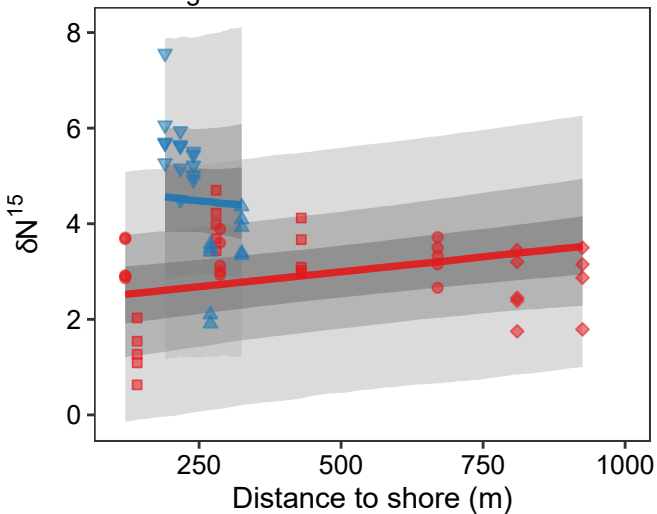


Figure 2

A macroalgae



B turf algae



C fish

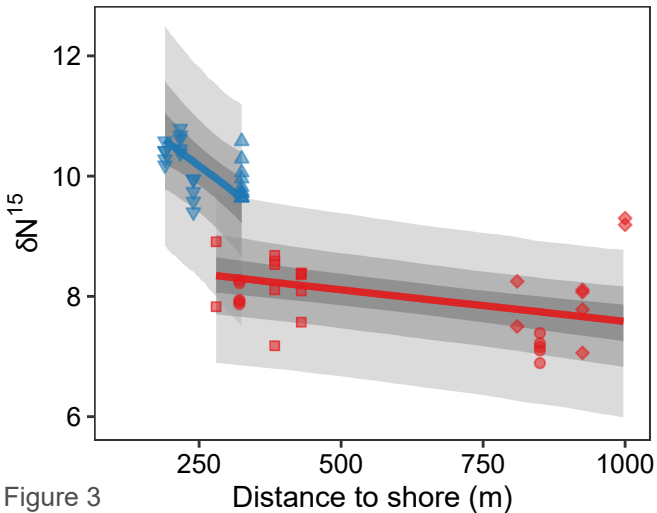


Figure 3

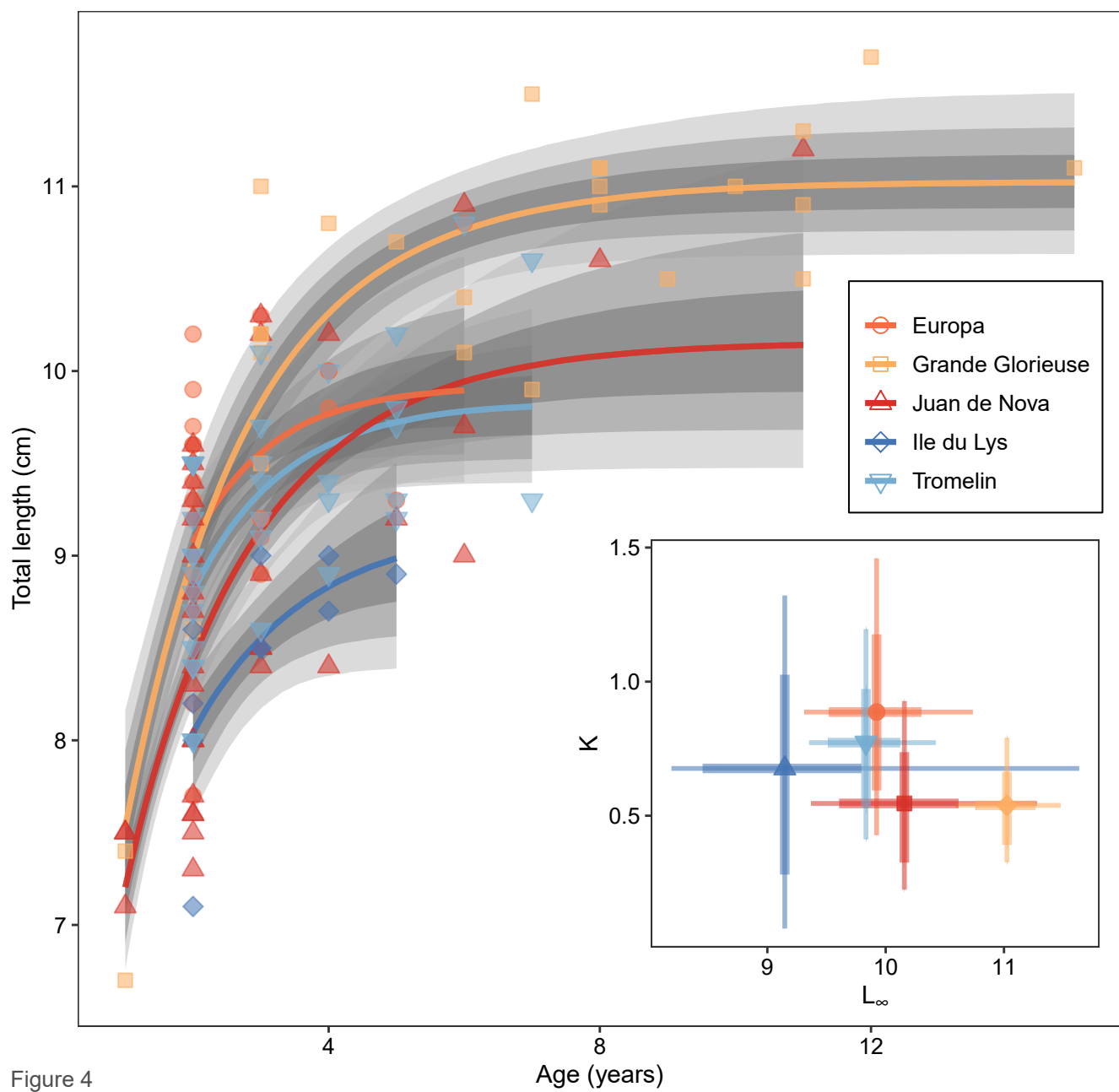


Figure 4

Region	Island ¹	Island area (hectares)	Invasive mammals		Breeding seabirds (annual biomass/ha)						
			Rat status	Other invasive mammals present	Booby	Frigate bird	Noddy	Shear water	Tern	Tropic bird	Total
Chagos Archipelago	Eagle Island (GCB)	244	rats present (<i>R. rattus</i>)	none	0.08	0	0.07	0	0.02	0	0.17
	Grande Ile Coquillage (PB)	28	rats absent	none	53.57	8.32	12.47	0.07	244.74	0	319.18
	Grande Ile Mapou (PB)	20	rats present (<i>R. rattus</i>)	none	1	0	0.35	0	0.1	0	1.45
	Ile Anglaise (PB)	12	rats present (<i>R. rattus</i>)	none	0	0	0.66	0	0.33	0	0.99
	Ile Anglaise (Sal)	76	rats present (<i>R. rattus</i>)	none	0	0	0.13	0	0.04	0	0.17
	Ile de la Passe (Sal)	26	rats absent	none	2.43	0	3.68	0	0.19	0.02	6.32
	Ile Fouquet (Sal)	40	rats present (<i>R. rattus</i>)	none	0.85	0	0.25	0	0.14	0.01	1.25
	Ile Jacobin (Sal)	2	rats eradicated in 2014 (<i>R. rattus</i>)	none	0	0	0.99	0	0.2	0	1.19
	Ile Longue (PB)	26	rats absent	none	37.95	0	10.58	0	332.5	0	381.04
	Ile Poule (PB)	108	rats present (<i>R. rattus</i>)	none	0	0	0.03	0	0.01	0	0.04
	Ile Sepulture (Sal)	2	rats present (<i>R. rattus</i>)	none	0	0	1.18	0	0.1	0	1.28
	Ile Vache Marine (PB)	14	rats eradicated in 2014 (<i>R. rattus</i>)	none	0	0	0.14	0	0.61	0	0.75
	Middle Brother (GCB)	8	rats absent	none	19.25	3.5	4.57	0	722.36	0	749.67
	Nelson's Island (GCB)	81	rats absent	none	82.18	9.75	32.79	0.17	0.08	0	124.97
	South Brother (GCB)	23	rats absent	none	9.13	0	100.94	8.47	79.03	0	197.57
Scattered Islands	Europa	2223	rats present (<i>R. rattus</i>)	goat	1.57	2.36	0	0.01	82.05	1.57	87.56
	Grande Glorieuse	470	rats present (<i>R. norvegicus</i>)	cat, mouse	0	0	0	0	0	0	0
	Ile du Lys	12	rats eradicated in 2003 (<i>R. rattus</i>)	none	0	0	41.63	0	1200.07	0	1241.71
	Juan de Nova	561	rats present (<i>R. rattus</i>)	mouse ²	0	0	0	0	534.89	0	534.89
	Tromelin	97	rats eradicated in 2005 (<i>R. norvegicus</i>)	mouse	62.14	0	1.63	0.01	0.89	0	64.67

¹For the Chagos Archipelago, the specific atoll in which each island is located is provided in parentheses: GCB = Great Chagos Bank, PB = Peros Banhos, Sal = Salomon.

²Cats were eradicated from Juan de Nova in 2015.

Table S1. Characteristics of the islands used in this study. Related to STAR Methods and Figure 1.

Region	Island ¹	Sampling year	Sample size per type					
			Soil (isotopes)	Leaves ² (isotopes)	Macroalgae ³ (isotopes)	Turf algae (isotopes)	Damselfish ⁴ (isotopes)	Damselfish ⁴ (growth)
Chagos Archipelago	Eagle Island (GCB)	2015	10	St - 10	H - 9	10	PI - 10	-
	Grande Ile Coquillage (PB)	2015	10	St - 10	H - 10	10	PI - 10	-
	Grande Ile Mapou (PB)	2015	10	St - 10	H - 10	10	PI - 10	-
	Ile Anglaise (PB)	2015	10	St - 10	H - 10	10	PI - 10	-
	Ile Anglaise (Sal)	2015	10	St - 10	H - 10	10	PI - 10	-
	Ile de la Passe (Sal)	2015	10	St - 10	H - 10	10	PI - 10	-
	Ile Fouquet (Sal)	2015	10	St - 10	H - 10	10	PI - 10	-
	Ile Jacobin (Sal)	2018	10	St - 10	-	-	-	-
	Ile Longue (PB)	2015	10	St - 10	H - 9	10	PI - 10	-
	Ile Poule (PB)	2015	10	St - 10	H - 10	10	PI - 10	-
	Ile Sepulture (Sal)	2018	10	St - 10	-	-	-	-
	Ile Vache Marine (PB)	2018	10	St - 10	H - 10	10	PI - 5	-
	Middle Brother (GCB)	2015	9	St - 10	H - 10	10	PI - 10	-
	Nelson's Island (GCB)	2015	10	St - 10	H - 10	10	PI - 10	-
	South Brother (GCB)	2015	10	St - 10	H - 10	10	PI - 10	-
Scattered Islands	Europa	2019	5	Sm -10	T - 10	15	Sf - 10	Sf - 31
	Grande Glorieuse	2019	5	Ht - 10, St - 5, Sm - 5	H - 15	15	Sf - 12	Sf - 25
	Ile du Lys	2019	5	Hf - 10, St - 5, Sm - 5	H - 25, T - 10	10	PI - 10, Sf - 1	PI - 10
	Juan de Nova	2019	5	Hf - 10, Sm - 5	H - 10	9	PI - 2, Sf - 9	Sf - 34
	Tromelin	2019	5	Hf - 10	H - 15	15	Sf - 15	Sf - 33

¹ For the Chagos Archipelago, the specific atoll in which each island is located is provided in parentheses: GCB = Great Chagos Bank, PB = Peros Banhos, Sal = Salomon.

² Leaves were sampled from three species: Ht = *Heliotropium forthiarum*, Sm = *Suriana maritima*, St = *Scaveola taccada*.

³ Two genera of macroalgae were sampled: H = *Halimeda spp*, T = *Turbinaria spp*.

⁴ Two species of damselfish were sampled: PI = *Plectroglyphidodon lacrymatus*, Sf = *Stegastes fasciolatus*.

Table S2. Information about samples used in this study. Related to STAR Methods.

Sample type	Estimated $\delta^{15}\text{N}$ (95% HPDI)		
	Rats absent	Rats eradicated	Rats present
Soil	14.79 (5.85, 22.03)	9.58 (0.99, 17.11)	6.42 (-1.97, 13.72)
Leaves	11.1 (2.46, 18.28)	5.3 (-3.07, 12.87)	2.91 (-4.98, 10.39)
Macroalgae	7.28 (0.82, 13.33)	4.89 (-1.78, 11.07)	3.67 (-2.84, 9.63)
Turf algae	4.42 (-1.46, 10.36)	5.32 (-0.43, 11.02)	3.98 (-2.15, 9.73)
Damselfish	8.94 (0.4, 14.95)	9.68 (1.28, 15.91)	8.43 (-0.25, 14.3)

Table S3. Estimated $\delta^{15}\text{N}$ values for samples collected from islands with different rat-invasion statuses. Related to Figure 2. Estimated median $\delta^{15}\text{N}$ and 95% highest posterior density intervals (HPDI) from Bayesian models.

Sample type	Comparison	Estimated difference	Evidence ratio	Posterior probability difference > 0
Soil	(1) rats absent - rats present	8.51	1999	1
	(2) rats eradicated - rats present	3.28	13.9	0.93
	(3) rats absent - rats eradicated	5.23	41.33	0.98
Leaves	(1) rats absent - rats present	8.25	887.89	1
	(2) rats eradicated - rats present	2.41	6.08	0.86
	(3) rats absent - rats eradicated	5.84	48.08	0.98
Macroalgae	(1) rats absent - rats present	3.56	499	1
	(2) rats eradicated - rats present	1.26	4.63	0.82
	(3) rats absent - rats eradicated	2.31	12.56	0.93
Turf algae	(1) rats absent - rats present	0.41	4.51	0.82
	(2) rats eradicated - rats present	1.37	67.97	0.99
	(3) rats absent - rats eradicated	-0.96	0.09	0.08
Damselfish	(1) rats absent - rats present	0.53	26.78	0.96
	(2) rats eradicated - rats present	1.27	1332.33	1
	(3) rats absent - rats eradicated	-0.74	0.04	0.04

Table S4. Estimated difference in $\delta^{15}\text{N}$ values for terrestrial and marine samples collected from islands with different rat-invasion statuses. Results are also depicted in Figure 2.

Evidence ratio and posterior probabilities indicate the likelihood that each difference is greater than zero. These comparisons test the following hypotheses: (1) $\delta^{15}\text{N}$ values are higher on/around islands where rats are absent (and were never present) than on islands where rats are present, (2) $\delta^{15}\text{N}$ values are higher on/around islands where rats were eradicated than on islands where rats are still present, and (3) $\delta^{15}\text{N}$ values are higher on/around islands where rats are absent (and were never present) than on islands where rats were eradicated.

Sample type	Parameter	Estimate (95% HPDI)	Evidence ratio	Posterior probability
Macroalgae	(1) distance (rat-eradicated)	-2.32 (-3.24, -1.33)	> 1000	1.00
	(2) distance (rat-infested)	-0.14 (-1.32, 1.05)	1.46	0.59
	(3) distance*rat status interaction	2.19 (0.65, 3.66)	443.44	1.00
Turf algae	(1) distance (rat-eradicated)	-0.53 (-10.39, 9.2)	1.18	0.54
	(2) distance (rat-infested)	1.3 (-0.2, 2.94)	0.05	0.05
	(3) distance*rat status interaction	1.89 (-8.06, 11.37)	1.81	0.64
Damsel fish	(1) distance (rat-eradicated)	-7.70 (-17.27, 1.15)	24.89	0.96
	(2) distance (rat-infested)	-1.14 (-2.15, -0.11)	74.47	0.99
	(3) distance*rat status interaction	6.60 (-2.04, 16.33)	14.38	0.94

Table S5. Estimated effect of distance to shore on $\delta^{15}\text{N}$ values for samples collected from rat-eradicated and rat-infested islands. Related to Figure 3. Bayesian model estimates (median and 95% HPDI) for the (1) effect of distance to shore on $\delta^{15}\text{N}$ values around rat-eradicated islands, (2) effect of distance to shore on $\delta^{15}\text{N}$ values around rat-infested island, and (3) interaction between distance to shore*rat status. Evidence ratio and posterior probability are for the following hypotheses: (1) slope for distance to shore around rat-eradicated islands < 0 (i.e., $\delta^{15}\text{N}$ decreases with increasing distance to shore around rat-eradicated islands), (2) slope for distance to shore around rat-infested islands < 0 (i.e., $\delta^{15}\text{N}$ decreases with increasing distance to shore around rat-infested islands), and (3) interaction between distance to shore*rat status > 0 (i.e., effect of distance to shore is different around rat-eradicated versus rat-infested islands, with $\delta^{15}\text{N}$ decreasing more around rat-eradicated islands).

Island	Rat status	k (95% HPDI)	L_{∞} (95% HPDI)
Europa	rats present	0.89 (0.43, 1.46)	9.92 (9.31, 10.73)
Grande Glorieuse	rats present	0.54 (0.33, 0.80)	11.02 (10.6, 11.48)
Ile du Lys	rats eradicated	0.68 (0.08, 1.32)	9.15 (8.19, 11.63)
Juan de Nova	rats present	0.55 (0.22, 0.93)	10.16 (9.37, 11.27)
Tromelin	rats eradicated	0.77 (0.41, 1.20)	9.83 (9.35, 10.42)

Table S6. Estimated growth parameters for damselfish from the Scattered Islands. Results are also depicted in Figure 4. Estimated medians and 95% highest posterior density intervals (HPDI) from Bayesian models.

Parameter	Comparison (rats eradicated - rats present)	Estimated difference	Evidence ratio	Posterior probability difference > 0
K	Ile du Lys - Grand Glorieuses	0.16	2.10	0.68
	Ile du Lys - Juan de Nova	0.15	1.92	0.66
	Ile du Lys - Europa	-0.21	0.34	0.26
	Tromelin - Grand Glorieuses	0.24	15.56	0.94
	Tromelin - Juan de Nova	0.23	11.29	0.92
	Tromelin - Europa	-0.12	0.50	0.33
Linf	Ile du Lys - Grand Glorieuses	-1.56	0.07	0.07
	Ile du Lys - Juan de Nova	-0.76	0.16	0.14
	Ile du Lys - Europa	-0.50	0.22	0.18
	Tromelin - Grand Glorieuses	-1.18	0.00	0.00
	Tromelin - Juan de Nova	-0.38	0.31	0.24
	Tromelin - Europa	-0.12	0.68	0.40

Parameter	Comparison (rats eradicated = rats eradicated, rats present = rats present)	Estimated difference	Evidence ratio	Posterior probability difference = 0
K	Ile du Lys = Tromelin	-0.08	2.04	0.67
	Grand Glorieuses = Juan de Nova	-0.01	5.69	0.85
	Grand Glorieuses = Europa	-0.37	0.94	0.49
	Juan de Nova = Europa	-0.35	1.02	0.50
Linf	Ile du Lys = Tromelin	-0.38	4.72	0.83
	Grand Glorieuses = Juan de Nova	0.80	2.76	0.73
	Grand Glorieuses = Europa	1.06	1.11	0.53
	Juan de Nova = Europa	0.26	12.81	0.93

Table S7. Estimated difference in growth parameters for damselfish from the Scattered Islands with different rat invasion statuses. Related to Figure 4. Ile du Lys and Tromelin = rats eradicated, Grand Glorieuses, Juan de Nova, and Europa = rats present. Evidence ratios and posterior probabilities indicate the likelihood that each difference is greater than zero when comparing growth parameters from an island where rats were eradicated to an island where rats are present (top portion of table). Evidence ratios and posterior probabilities indicate the likelihood that each difference is equal to zero when comparing growth parameters from islands with the same rat-invasion status (rat-eradicated island to rat-eradicated or rat present to rat present) (bottom portion of table). If growth parameters vary by rat invasion status, estimated differences in the top portion of the table should be positive, estimated difference in the bottom portion of the table should be close to zero, and all posterior probabilities should be high (close to 1).