1

2

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

5

Cassandra E Benkwitt[1]*, Rachel L Gunn[1], Matthieu Le Corre[2], Peter Carr[3,4], Nicholas AJ Graham[1]

8

[1] Lancaster Environment Centre, Lancaster University, Lancaster UK LA1 4YQ.

[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, United Kingdom.

[4] Environment and Sustainability Institute, University of Exeter, Penryn Campus, Cornwall TR10 9EZ, United Kingdom.

*Lead contact and corresponding author: Cassandra Benkwitt (c.benkwitt@lancaster.ac.uk)

Twitter handle: @cbenkwitt

18

Summary

    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[4–6]. 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.

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

Results and Discussion

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

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

Rat eradication enhances seabird biomass

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

3

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 data[26] 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 surveys[27], 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 palms[28] 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 δ^{15}N), in part because they feed at high trophic levels in

103   the open ocean[5,34]. Thus, high δ^{15}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 δ^{15}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 δ^{15}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

5

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 spiders[20]. 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.

6

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 time[38].

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 δ^{15}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   δ^{15}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 δ^{15}N still decreased by

7

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 δ^{15}N was variable around rat-infested islands

171   (Table S5). Because δ^{15}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 δ^{15}N with increasing

178   distance to seabird colonies[36,39], then the δ^{15}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 δ^{15}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

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

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

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

In contrast, herbivorous damselfish have enhanced growth around islands that never had rats compared to rat-infested islands in the Chagos Archipelago[6]. There are several plausible, non-mutually exclusive, explanations for this discrepancy. Demographic rates of fishes vary due to a variety of biotic and abiotic factors, including temperature, habitat, food availability, competition, and predation[42–44]. Across the Scattered Islands, which cover a larger geographic area than the Chagos Archipelago, such factors may have a stronger influence on growth than rat invasion status. Moreover, nutrient isotopic signatures incorporate information over several months, but there is likely a longer lag time between rat eradication and demographic responses. The

9

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 fishes[42], 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 nutrients[46]. 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 management[24], and integrated land-sea

247 conservation[37]. 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 removal[49]. 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

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.

Figure 2. **$\delta^{15}N$ values for terrestrial and marine samples collected on and around islands**

that never had invasive rats, islands with rats eradicated, and islands with rats still present.

(A-E, F-J) Raw data for $\delta^{15}N$ values across the Scattered Islands and Chagos Archipelago,

respectively. Each point represents one sample, box limits represent first and third quantiles (25%

and 75% percentiles), middle line represents the median (50% percentile), and whiskers represent

smallest and largest observations less than or equal to 1.5x inter-quartile range. (K) Estimated

difference in $\delta^{15}N$ values for *a priori* comparisons among islands with different rat invasion

statuses. Points represent median estimates, thin lines represent 95% HPDI, thick lines represent

75% HPDI for each comparison. Any points above the dashed zero line indicate support for the

following hypotheses: $\delta^{15}N$ is higher on/around islands where rats are absent than where rats are

present (green), $\delta^{15}N$ is higher on/around islands where rats were eradicated than where rats are

present (orange), or $\delta^{15}N$ is higher on/around islands where rats are absent than where rats were

eradicated (purple). See also Table S3 and S4.

Figure 3. **Estimated effect of distance to shore on $\delta^{15}N$ values for marine samples collected**

around rat-eradicated versus rat-infested islands. Points represent raw data, shapes represent

islands where they were collected and fill represents rat invasion status. Colored lines are best-fit

from Bayesian models, with shading indicating 95%, 80%, and 50% confidence regions. See also

Table S5.

Figure 4. **Age-at-length plots for damselfish collected across the Scattered Islands.** Blue

coloration indicates islands that had rats eradicated, red coloration indicates islands with rats

present. Points show raw data, curves represent VBGF growth curves from non-linear Bayesian

models, with shading indicating 95%, 80%, and 50% confidence regions. Inset shows median

(points), 95% (thin lines), and 75% (thick lines) HPDIs for each VBGF parameter. See also Table

S6 and S7.

13

STAR Methods

RESOURCE AVAILABILITY

Lead contact

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

Materials availability

This study did not generate new unique reagents.

Data and code availability

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

EXPERIMENTAL MODEL AND SUBJECT DETAILS

Study sites

We conducted this study across 20 remote islands in the central and western Indian Ocean with varying rat invasion and eradication histories (Figure 1, Table S1). All islands were part of the Chagos Archipelago or the Scattered Islands, which are protected from local human influences and considered ecological benchmarks for the region[50,51]. The Chagos Archipelago is located in the central Indian Ocean, and is encompassed by a large (640,000 km^2) marine protected area[50,52]. We investigated 15 islands in the northern atolls of the archipelago, chosen to be similar in size, location, and environment, with the exception of rat invasion status. All of the islands have been uninhabited since the 1970s. Black rats (*Rattus rattus*) were introduced to nine of these islands at least several hundred years ago, while six of these islands have never had rats. A failed rat eradication campaign occurred on one island in 2006 (Eagle Island), but in recent years renewed efforts have been successful on several smaller islands, with rats eradicated from two of our study islands in 2014 (Île Vache Marine and Île Jacobin). There are no other invasive predatory mammals on any of the study islands, but native flora was cleared for coconut plantations on many of the islands.

14

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 basis[51]. 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   1900s[53]. Rats were eradicated from Île du Lys in 2003 and Tromelin in 2005, but are still present

353   on the other islands[53]. 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 Europoa, 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 $\delta^{15}N$ of

368   terrestrial samples were higher in the Scattered Islands compared to the Chagos Archipelago, but

369    $\delta^{15}N$ 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 Archipelago[29], 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 from[27] based on censuses conducted between 2008 – 2019. Seabird data for the Scattered

16

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 island[6]. 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 equator[27]. 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 defacation 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 foraging[6].

17

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

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

Immediately following collection, we dried all samples at 60˚C for 48 hours in preparation for stable isotope analysis. Samples collected in the Chagos Archipelago in 2015 were analyzed at the University of Windsor (Canada) using a Finnigan MAT Deltaplus mass spectrometer with B2153 and USGS 40 standards. These isotopic results have been published previously[6]. All other samples were analyzed at Lancaster University (UK), where they were combusted using an Elementar Vario MICRO cube Elementer Analyser and analyzed using an Isoprime 100 Isotope 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 seabirds[6]. 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.

QUANTIFICATION AND STATISTICAL ANALYSIS

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

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

Rat eradication is easier on smaller islands, so eradication efforts have generally focused on small islands and are only now expanding to larger islands[61]. As a result, many of the islands where rats were eradicated were also some of the smallest islands studied. Despite this constraint, we were able to survey islands across a reasonably similar range of sizes within each rat invasion status, especially with regard to minimum island size (rat-free: 8 − 81 ha, rat-eradicated: 2 − 97 ha, rat-infested: 2 − 2223 ha) (Table S1). Still, because islands encompassed a range of sizes, and

20

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 δ^{15}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) δ^{15}N decreases with increasing distance to shore (i.e., slope < 0) and (2)

511   δ^{15}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    $$L_t = L_\infty - (L_\infty - L_0)e^{-kt}$$

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

21

curve. We then calculated HPDIs for each parameter around each island, and conducted pairwise

comparisons of the growth parameters between islands. If rat eradication enhances damselfish

growth, we expect L_∞ and/or k to be consistently higher around rat-eradicated islands compared

to rat-infested islands, but similar among islands with the same rat invasion status.

For all models, we used weakly informative priors and ran the model for four chains, each

with at least 3,000 iterations including a warm-up of 1,000 iterations. Convergence and model fits

were checked using graphical posterior predictive checks, traceplots, and the Gelman-Ruban

convergence diagnostic (R-hat). We used Pareto smoothed importance-sampling leave-one-out

cross-validation (PSIS-LOO) to check for highly influential datapoints. The only time pareto-k

values were greater than the generally-accepted threshold (0.7)[62] was for the island Grande

Glorieuse in the seabird biomass and nitrogen input models. In these cases, we compared the

posterior distributions with and without Grande Glorieuse, and found that our interpretations were

similar regardless. All analyses were conducted in R (version 3.6.1) and implemented in STAN

using the package brms with additional packages bayesplot, loo, tidybayes, and tidyverse[63–70].

Supplemental Information Supplemental information contains Tables S1-S7.

References

1. Bellard, C., Cassey, P., and Blackburn, T.M. (2016). Alien species as a driver of recent extinctions. Biology Letters *12*, 20150623.

2. Early, R., Bradley, B.A., Dukes, J.S., Lawler, J.J., Olden, J.D., Blumenthal, D.M., Gonzalez, P., Grosholz, E.D., Ibañez, I., Miller, L.P., et al. (2016). Global threats from invasive alien species in the twenty-first century and national response capacities. Nat Commun *7*, 12485.

3. Jones, H.P., Holmes, N.D., Butchart, S.H.M., Tershy, B.R., Kappes, P.J., Corkery, I., Aguirre-Muñoz, A., Armstrong, D.P., Bonnaud, E., Burbidge, A.A., et al. (2016). Invasive mammal eradication on islands results in substantial conservation gains. PNAS *113*, 4033–4038.

4. Polis, G.A., Anderson, W.B., and Holt, R.D. (1997). Toward an integration of landscape and food web ecology: the dynamics of spatially subsidized food webs. Annual Review of Ecology and Systematics *28*, 289–316.

5. Croll, D.A., Maron, J.L., Estes, J.A., Danner, E.M., and Byrd, G.V. (2005). Introduced predators transform subarctic islands from grassland to tundra. Science *307*, 1959–1961.

550   6.   Graham, N.A.J., Wilson, S.K., Carr, P., Hoey, A.S., Jennings, S., and MacNeil, M.A. (2018). Seabirds enhance
551   coral reef productivity and functioning in the absence of invasive rats. Nature *559*, 250–253.

552   7.   Doughty, C.E., Roman, J., Faurby, S., Wolf, A., Haque, A., Bakker, E.S., Malhi, Y., Dunning, J.B., and
553   Svenning, J.-C. (2016). Global nutrient transport in a world of giants. PNAS *113*, 868–873.

554   8.   Doherty, T.S., Glen, A.S., Nimmo, D.G., Ritchie, E.G., and Dickman, C.R. (2016). Invasive predators and global
555   biodiversity loss. PNAS *113*, 11261–11265.

556   9.   Russell, J.C., and Kueffer, C. (2019). Island biodiversity in the anthropocene. Annual Review of Environment
557   and Resources *44*, 31–60.

558   10.   Tershy, B.R., Shen, K.-W., Newton, K.M., Holmes, N.D., and Croll, D.A. (2015). The importance of islands for
559   the protection of biological and linguistic diversity. BioScience *65*, 592–597.

560   11.   O'Dowd, D.J., Green, P.T., and Lake, P.S. (2003). Invasional 'meltdown' on an oceanic island. Ecology Letters
561   *6*, 812–817.

562   12.   Jones, H.P., Tershy, B.R., Zavaleta, E.S., Croll, D.A., Keitt, B.S., Finkelstein, M.E., and Howald, G.R. (2008).
563   Severity of the effects of invasive rats on seabirds: a global review. Conservation Biology *22*, 16–26.

564   13.   Towns, D.R., Atkinson, I.A.E., and Daugherty, C.H. (2006). Have the harmful effects of introduced rats on
565   islands been exaggerated? Biol Invasions *8*, 863–891.

566   14.   DISE (2018). The Database of Island Invasive Species Eradications.

567   15.   Pyšek, P., Richardson, D.M., Pergl, J., Jarošík, V., Sixtová, Z., and Weber, E. (2008). Geographical and
568   taxonomic biases in invasion ecology. Trends in Ecology & Evolution *23*, 237–244.

569   16.   Russell, J.C., and Holmes, N.D. (2015). Tropical island conservation: Rat eradication for species recovery.
570   Biological Conservation *185*, 1–7.

571   17.   Prior, K.M., Adams, D.C., Klepzig, K.D., and Hulcr, J. (2018). When does invasive species removal lead to
572   ecological recovery? Implications for management success. Biol Invasions *20*, 267–283.

573   18.   Zavaleta, E.S., Hobbs, R.J., and Mooney, H.A. (2001). Viewing invasive species removal in a whole-ecosystem
574   context. Trends in Ecology & Evolution *16*, 454–459.

575   19.   Jones, H.P. (2010). Seabird islands take mere decades to recover following rat eradication. Ecological
576   Applications *20*, 2075–2080.

577   20.   Jones, H.P. (2010). Prognosis for ecosystem recovery following rodent eradication and seabird restoration in an
578   island archipelago. Ecological Applications *20*, 1204–1216.

579   21.   Mulder, C.P.H., Grant-Hoffman, M.N., Towns, D.R., Bellingham, P.J., Wardle, D.A., Durrett, M.S., Fukami, T.,
580   and Bonner, K.I. (2009). Direct and indirect effects of rats: does rat eradication restore ecosystem functioning of
581   New Zealand seabird islands? Biol Invasions *11*, 1671–1688.

582   22.   Buckner, E.V., Hernández, D.L., and Samhouri, J.F. (2018). Conserving connectivity: Human influence on
583   subsidy transfer and relevant restoration efforts. Ambio *47*, 493–503.

584   23.   Álvarez-Romero, J.G., Pressey, R.L., Ban, N.C., Vance-Borland, K., Willer, C., Klein, C.J., and Gaines, S.D.
585   (2011). Integrated Land-Sea Conservation Planning: The Missing Links. Annual Review of Ecology, Evolution,
586   and Systematics *42*, 381–409.

587   24.   Loreau, M., Mouquet, N., and Holt, R.D. (2003). Meta-ecosystems: a theoretical framework for a spatial
588   ecosystem ecology. Ecology Letters *6*, 673–679.

589   25. Brooke, M. de L., Bonnaud, E., Dilley, B.J., Flint, E.N., Holmes, N.D., Jones, H.P., Provost, P., Rocamora, G.,
590   Ryan, P.G., Surman, C., et al. (2017). Seabird population changes following mammal eradications on islands.
591   Animal Conservation *21*, 3–12.

592   26. Le Corre, M., Danckwerts, D.K., Ringler, D., Bastien, M., Orlowski, S., Morey Rubio, C., Pinaud, D., and
593   Micol, T. (2015). Seabird recovery and vegetation dynamics after Norway rat eradication at Tromelin Island,
594   western Indian Ocean. Biological Conservation *185*, 85–94.

595   27. Carr, P., Votier, S., Koldewey, H., Godley, B., Wood, H., and Nicoll, M.A.C. (2020). Status and phenology of
596   breeding seabirds and a review of Important Bird and Biodiversity Areas in the British Indian Ocean Territory.
597   Bird Conservation International, 1–21.

598   28. Carr, P., Trevail, A., Bárrios, S., Clubbe, C., Freeman, R., Koldewey, H.J., Votier, S.C., Wilkinson, T., and
599   Nicoll, M.A.C. (In review). Potential biodiversity benefits of rewilding abandoned coconut plantations on
600   degraded tropical seabird islands. Restoration Ecology.

601   29. Perez- Correa, J., Carr, P., Meeuwig, J.J., Koldewey, H.J., and Letessier, T.B. (2020). Climate oscillation and
602   the invasion of alien species influence the oceanic distribution of seabirds. Ecology and Evolution *10*, 9339–
603   9357.

604   30. McCauley, D.J., DeSalles, P.A., Young, H.S., Dunbar, R.B., Dirzo, R., Mills, M.M., and Micheli, F. (2012).
605   From wing to wing: the persistence of long ecological interaction chains in less-disturbed ecosystems. Scientific
606   Reports *2*, 409.

607   31. Jones, H.P., and Kress, S.W. (2012). A review of the world's active seabird restoration projects. The Journal of
608   Wildlife Management *76*, 2–9.

609   32. Kappes, P.J., and Jones, H.P. (2014). Integrating seabird restoration and mammal eradication programs on
610   islands to maximize conservation gains. Biodivers Conserv *23*, 503–509.

611   33. Smith, J.L., Mulder, C.P.H., and Ellis, J.C. (2011). Seabirds as Ecosystem Engineers: Nutrient Inputs and
612   Physical Disturbance. In Seabird Islands: Ecology, Invasion, and Restoration, C. P. H. Mulder, W. B. Anderson,
613   D. R. Towns, and P. J. Bellingham, eds. (Oxford University Press).

614   34. Lorrain, A., Houlbrèque, F., Benzoni, F., Barjon, L., Tremblay-Boyer, L., Menkes, C., Gillikin, D.P., Payri, C.,
615   Jourdan, H., Boussarie, G., et al. (2017). Seabirds supply nitrogen to reef-building corals on remote Pacific
616   islets. Scientific Reports *7*, 3721.

617   35. Fukami, T., Wardle, D.A., Bellingham, P.J., Mulder, C.P.H., Towns, D.R., Yeates, G.W., Bonner, K.I., Durrett,
618   M.S., Grant-Hoffman, M.N., and Williamson, W.M. (2006). Above- and below-ground impacts of introduced
619   predators in seabird-dominated island ecosystems. Ecology Letters *9*, 1299–1307.

620   36. Savage, C. (2019). Seabird nutrients are assimilated by corals and enhance coral growth rates. Scientific Reports
621   *9*, 4284.

622   37. Mulder, C.P., Anderson, W.B., Towns, D.R., and Bellingham, P.J. eds. (2011). Seabird islands: ecology,
623   invasion, and restoration (Oxford University Press).

624   38. Moreno-Mateos, D., Barbier, E.B., Jones, P.C., Jones, H.P., Aronson, J., López-López, J.A., McCrackin, M.L.,
625   Meli, P., Montoya, D., and Rey Benayas, J.M. (2017). Anthropogenic ecosystem disturbance and the recovery
626   debt. Nature Communications *8*, 14163.

627   39. Bokhorst, S., Convey, P., and Aerts, R. (2019). Nitrogen inputs by marine vertebrates drive abundance and
628   richness in antarctic terrestrial ecosystems. Current Biology *29*, 1721-1727.e3.

629   40. Vidal, E., Jouventin, P., and Frenot, Y. (2003). Contribution of alien and indigenous species to plant-community
630   assemblages near penguin rookeries at Crozet archipelago. Polar Biology *26*, 432–437.

631   41. Benkwitt, C.E., Taylor, B.M., Meekan, M.G., and Graham, N.A. (in review). Natural nutrient subsidies alter
632   demographic rates in coral-reef fish. Scientific Reports.

633   42. Wootton, R.J. (2012). Ecology of teleost fishes (Springer Science & Business Media).

634   43. Figueira, W.F., Lyman, S.J., Crowder, L.B., and Rilov, G. (2008). Small-scale demographic variability of the
635   biocolor damselfish, Stegastes partitus, in the Florida Keys USA. Environmental Biology of Fishes *81*, 297–311.

636   44. Ruttenberg, B.I., Haupt, A.J., Chiriboga, A.I., and Warner, R.R. (2005). Patterns, causes and consequences of
637   regional variation in the ecology and life history of a reef fish. Oecologia *145*, 394–403.

638   45. Rankin, L., and Jones, H. (2021). Nearshore ecosystems on seabird islands are potentially influenced by invasive
639   predator eradications and environmental conditions: a case study at the Mercury Islands, New Zealand. Marine
640   Ecology Progress Series *661*, 83–96.

641   46. Kurle, C.M., Zilliacus, K.M., Sparks, J., Curl, J., Bock, M., Buckelew, S., Williams, J.C., Wolf, C.A., Holmes,
642   N.D., Plissner, J., et al. (2021). Indirect effects of invasive rat removal result in recovery of island rocky
643   intertidal community structure. Scientific Reports *11*, 5395.

644   47. Benkwitt, C.E., Wilson, S.K., and Graham, N.A.J. (2019). Seabird nutrient subsidies alter patterns of algal
645   abundance and fish biomass on coral reefs following a bleaching event. Global Change Biology *25*, 2619–2632.

646   48. Benkwitt, C.E., Wilson, S.K., and Graham, N.A.J. (2020). Biodiversity increases ecosystem functions despite
647   multiple stressors on coral reefs. Nature Ecology & Evolution *4*, 919–926.

648   49. Jones, H.P., and Schmitz, O.J. (2009). Rapid recovery of damaged ecosystems. PLOS ONE *4*, e5653.

649   50. Hays, G.C., Koldewey, H.J., Andrzejaczek, S., Attrill, M.J., Barley, S., Bayley, D.T.I., Benkwitt, C.E., Block,
650   B., Schallert, R.J., Carlisle, A.B., et al. (2020). A review of a decade of lessons from one of the world's largest
651   MPAs: conservation gains and key challenges. Mar Biol *167*, 159.

652   51. Quétel, C., Marinesque, S., Ringler, D., Fillinger, L., Changeux, T., Marteau, C., and Troussellier, M. (2016).
653   Iles Eparses (SW Indian Ocean) as reference ecosystems for environmental research. Acta Oecologica *72*, 1–8.

654   52. Sheppard, C.R.C., Ateweberhan, M., Bowen, B.W., Carr, P., Chen, C.A., Clubbe C., Craig M. T., Ebinghaus R.,
655   Eble J., Fitzsimmons N., et al. (2012). Reefs and islands of the Chagos Archipelago, Indian Ocean: why it is the
656   world's largest no- take marine protected area. Aquatic Conservation: Marine and Freshwater Ecosystems *22*,
657   232–261.

658   53. Russell, J.C., and Le Corre, M. (2009). Introduced mammal impacts on seabirds in the Îles Éparses, Western
659   Indian Ocean. Marine Ornithology *37*, 121–128.

660   54. Russell, J.C., Cole, N.C., Zuël, N., and Rocamora, G. (2016). Introduced mammals on Western Indian Ocean
661   islands. Global Ecology and Conservation *6*, 132–144.

662   55. Jaquemet, S., Le Corre, M., and Quartly, G.D. (2007). Ocean control of the breeding regime of the sooty tern in
663   the southwest Indian Ocean. Deep Sea Research Part I: Oceanographic Research Papers *54*, 130–142.

664   56. Le Corre, M. (2001). Breeding seasons of seabirds at Europa Island (southern Mozambique Channel) in relation
665   to seasonal changes in the marine environment. Journal of Zoology *254*, 239–249.

666   57. Le Corre, M., and Jaquemet, S. (2005). Assessment of the seabird community of the Mozambique Channel and
667   its potential use as an indicator of tuna abundance. Estuarine, Coastal and Shelf Science *63*, 421–428.

668   58. Le Corre, M. (1996). The Breeding Seabirds of Tromelin Island (western Indian Ocean): Population Sizes,
669   Trends and Breeding Phenology. Ostrich *67*, 155–159.

670   59. Young, H.S., McCauley, D.J., Dunbar, R.B., and Dirzo, R. (2010). Plants cause ecosystem nutrient depletion via
671   the interruption of bird-derived spatial subsidies. Proceedings of the National Academy of Sciences *107*, 2072–
672   2077.

673   60. Froese, R., and Pauly, D. (2018). FishBase. World Wide Web electronic publication.

674   61. Howald, G., Donlan, C.J., Galván, J.P., Russell, J.C., Parkes, J., Samaniego, A., Wang, Y., Veitch, D., Genovesi,
675   P., Pascal, M., et al. (2007). Invasive rodent eradication on islands. Conservation Biology *21*, 1258–1268.

676   62. McElreath, R. (2020). Statistical rethinking: A Bayesian course with examples in R and Stan (CRC press).

677   63. R Core Team (2019). R: a language and environment for statistical computing (R Foundation for Statistical
678   Computing).

679   64. Carpenter, B., Gelman, A., Hoffman, M.D., Lee, D., Goodrich, B., Betancourt, M., Brubaker, M., Guo, J., Li, P.,
680   and Riddell, A. (2017). *STAN*: a probabilistic programming language. Journal of Statistical Software *76*.

681   65. Bürkner, P.C. (2017). brms: An R package for Bayesian multilevel models using Stan. Journal of Statistical
682   Software *80*, 1–28.

683   66. Bürkner, P.C. (2018). Advanced Bayesian multilevel modeling with the R package brms. The R Journal *10*, 395–
684   411.

685   67. Gabry, J., and Mahr, T. (2019). bayesplot: plotting for bayesian models. R package version 1.7.0. mc-
686   stan.org/bayesplot.

687   68. Vehtari, A., Gabry, J., Magnusson, M., Yao, Y., Bürkner, P., Paananen, T., and Gelman, A. (2020). loo: Efficient
688   leave-one-out cross-validation and WAIC for Bayesian models. R package version 2.3.1. https://mc-stan.org/loo.

689   69. Kay, M. (2020). tidybayes: tidy data and geoms for bayesian models. R package version 2.0.3.
690   http://mjskay.github.io/tidybayes/.

691   70. Wickham, H. (2017). tidyverse: easily install and load the "tidyverse". R package version 1.2.1.
692   https://CRAN.R-project.org/package=tidyverse.

693

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Biological samples		
Soil	This study, [6]	Table S2
Leaves (*Heliotropium forthiarum, Suriana maritima, Scaveola taccada*)	This study, [6]	Table S2
Macroalgae (*Halimeda spp, Turbinaria spp*)	This study, [6]	Table S2
Turf algae	This study, [6]	Table S2
Damselfish (*Plectroglyphidodon lacrymatus, Stegastes fasciolatus*)	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
$\delta^{15}N$ 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 *brms*	[65], [66]	cran.rstudio.com/web/packages/brms/
R package *bayesplot*	[67]	mc-stan.org/bayesplot
R package *loo*	[68]	mc-stan.org/loo
R package *tidybayes*	[69]	mjskay.github.io/tidybayes/
R package *tidyverse*	[70]	CRAN.R-project.org/package=tidyverse
Custom code to complete all statistical analyses	This study	github.com/cbenkwitt/derat-islands-reefs
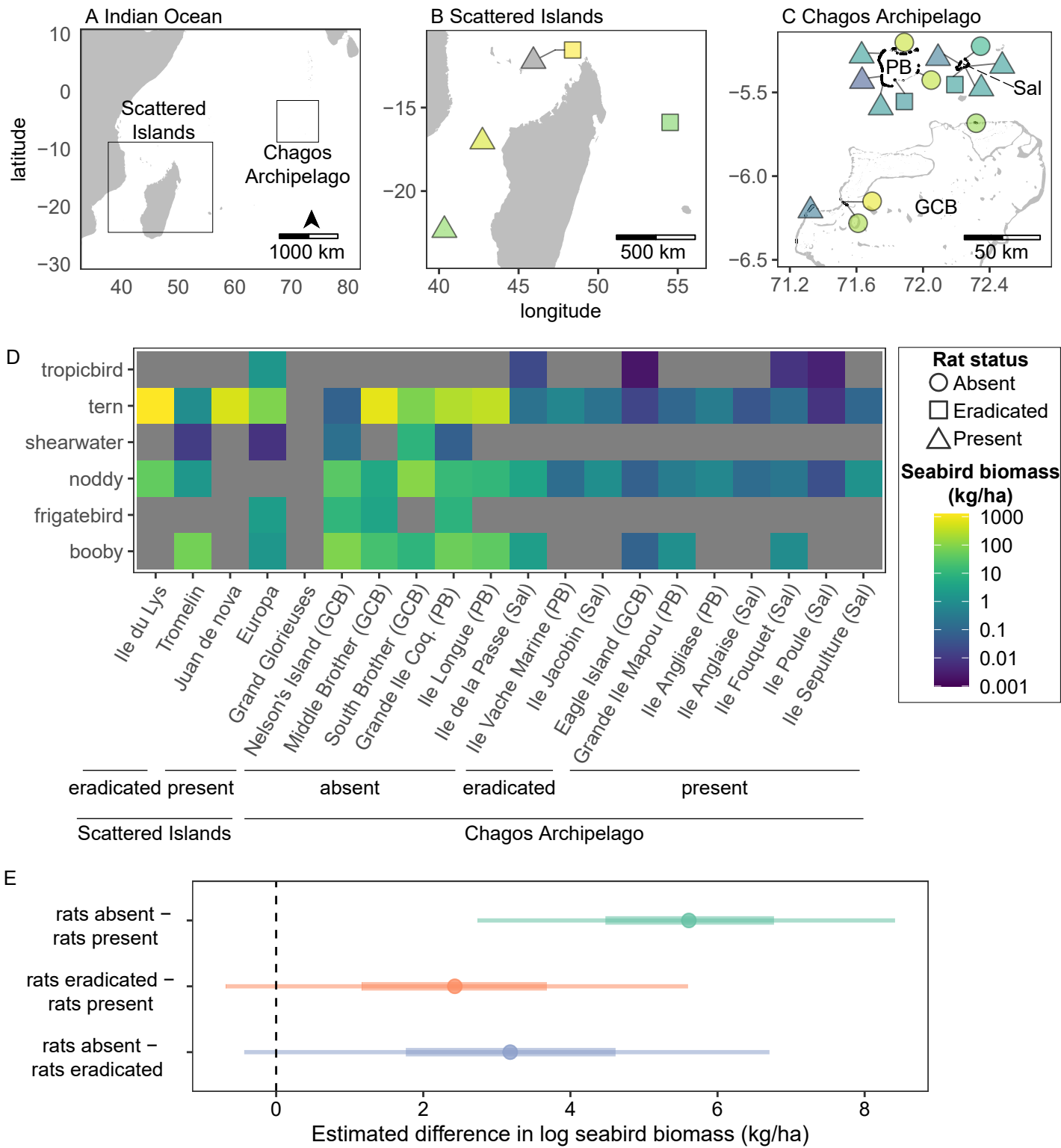
Figure 1

Scattered Islands

A soil B leaves C macroalgae D turf E fish

δN^{15}

eradicated present

Chagos Archipelago

F soil G leaves H macroalgae I turf J fish

δN^{15}

absent eradicated present

K all samples

Estimated difference in δN^{15}

rats absent − rats present
rats eradicated − rats present
rats absent − rats eradicated

soil leaves macroalgae turf algae fish

Figure 2

A macroalgae

rats eradicated
rats present

Europa
Grand Glorieuse
Ile du Lys
Juan de Nova
Tromelin

δN¹⁵

Distance to shore (m)

B turf algae

δN¹⁵

Distance to shore (m)

C fish

δN¹⁵

Distance to shore (m)

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 (*R. rattus*)	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 (*R. rattus*)	none	1	0	0.35	0	0.1	0	1.45
	Ile Anglaise (PB)	12	rats present (*R. rattus*)	none	0	0	0.66	0	0.33	0	0.99
	Ile Anglaise (Sal)	76	rats present (*R. rattus*)	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 (*R. rattus*)	none	0.85	0	0.25	0	0.14	0.01	1.25
	Ile Jacobin (Sal)	2	rats eradicated in 2014 (*R. rattus*)	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 (*R. rattus*)	none	0	0	0.03	0	0.01	0	0.04
	Ile Sepulture (Sal)	2	rats present (*R. rattus*)	none	0	0	1.18	0	0.1	0	1.28
	Ile Vache Marine (PB)	14	rats eradicated in 2014 (*R. rattus*)	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 (*R. rattus*)	goat	1.57	2.36	0	0.01	82.05	1.57	87.56
	Grande Glorieuse	470	rats present (*R. norvegicus*)	cat, mouse	0	0	0	0	0	0	0
	Ile du Lys	12	rats eradicated in 2003 (*R. rattus*)	none	0	0	41.63	0	1200.07	0	1241.71
	Juan de Nova	561	rats present (*R. rattus*)	mouse[2]	0	0	0	0	534.89	0	534.89
	Tromelin	97	rats eradicated in 2005 (*R. norvegicus*)	mouse	62.14	0	1.63	0.01	0.89	0	64.67

[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]Cats 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	Pl - 10	-
	Grande Ile Coquillage (PB)	2015	10	St - 10	H - 10	10	Pl - 10	-
	Grande Ile Mapou (PB)	2015	10	St - 10	H - 10	10	Pl - 10	-
	Ile Anglaise (PB)	2015	10	St - 10	H - 10	10	Pl - 10	-
	Ile Anglaise (Sal)	2015	10	St - 10	H - 10	10	Pl - 10	-
	Ile de la Passe (Sal)	2015	10	St - 10	H - 10	10	Pl - 10	-
	Ile Fouquet (Sal)	2015	10	St - 10	H - 10	10	Pl - 10	-
	Ile Jacobin (Sal)	2018	10	St - 10	-	-	-	-
	Ile Longue (PB)	2015	10	St - 10	H - 9	10	Pl - 10	-
	Ile Poule (PB)	2015	10	St - 10	H - 10	10	Pl - 10	-
	Ile Sepulture (Sal)	2018	10	St - 10	-	-	-	-
	Ile Vache Marine (PB)	2018	10	St - 10	H - 10	10	Pl - 5	-
	Middle Brother (GCB)	2015	9	St - 10	H - 10	10	Pl - 10	-
	Nelson's Island (GCB)	2015	10	St - 10	H - 10	10	Pl - 10	-
	South Brother (GCB)	2015	10	St - 10	H - 10	10	Pl - 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	Pl - 10, Sf - 1	Pl - 10
	Juan de Nova	2019	5	Hf - 10, Sm - 5	H - 10	9	Pl - 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: Pl = *Plectroglyphidodon lacrymatus*, Sf = *Stegastes fasciolatus.*

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

Sample type	Estimated δ^{15}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 δ^{15}N values for samples collected from islands with different rat-invasion statuses. Related to Figure 2. Estimated median δ^{15}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 $\delta^{15}N$ 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) $\delta^{15}N$ values are higher on/around islands where rats are absent (and were never present) than on islands where rats are present, (2) $\delta^{15}N$ values are higher on/around islands where rats were eradicated than on islands where rats are still present, and (3) $\delta^{15}N$ 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
Damselfish	(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 δ^{15}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 δ^{15}N values around rat-eradicated islands, (2) effect of distance to shore on δ^{15}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., δ^{15}N decreases with increasing distance to shore around rat-eradicated islands), (2) slope for distance to shore around rat-infested islands < 0 (i.e., δ^{15}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 δ^{15}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).