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1 **TITLE:**

2 **Extinction debt on reservoir land-bridge islands**

3 **AUTHORS:**

4 Isabel L. Jones<sup>a\*</sup>, Nils Bunnefeld<sup>a</sup>, Alistair S. Jump<sup>a</sup>, Carlos A. Peres<sup>b</sup>, Daisy H. Dent<sup>a,c</sup>

5 <sup>a</sup>Biological and Environmental Sciences, University of Stirling, Stirling, FK9 4LA, UK.

6 \*Corresponding author. Phone +44 (0)7738 009612, email <i.l.jones@stir.ac.uk>

7 <sup>b</sup>School of Environmental Sciences, University of East Anglia, Norwich, NR4 7TJ, UK.

8 <sup>c</sup>Smithsonian Tropical Research Institute, Apartado 0843–03092, Balboa, Panama.

9

10 **KEYWORDS:**

11 Conservation policy; dams; hydropower; fragmentation; isolation; species richness

12

13 **ABSTRACT**

14

15 Large dams cause extensive inundation of habitats, with remaining terrestrial habitat confined to  
16 highly fragmented archipelagos of land-bridge islands comprised of former hilltops. Isolation of  
17 biological communities on reservoir islands induces local extinctions and degradation of remnant  
18 communities. “Good practice” dam development guidelines propose using reservoir islands for  
19 species conservation, mitigating some of the detrimental impacts associated with flooding terrestrial  
20 habitats. The degree of species retention on islands in the long-term, and hence, whether they are  
21 effective for conservation is currently unknown. Here, we quantitatively review species’ responses to  
22 isolation on reservoir islands. We specifically investigate island species richness in comparison with  
23 neighbouring continuous habitat, and relationships between island species richness and island area,  
24 isolation time, and distance to mainland and to other islands. Species’ responses to isolation on  
25 reservoir islands have been investigated in only 15 of the >58 000 large-dam reservoirs (dam height  
26 >15 m) operating globally. Research predominantly originates from wet tropical forest habitats and  
27 focuses on mammals, with species richness being the most widely-reported ecological metric.  
28 Terrestrial taxa are, overall, negatively impacted by isolation on reservoir islands. Reservoir island  
29 species richness declines with isolation time, and although the rate of loss is slower on larger islands,  
30 all islands exhibit depauperate species richness <100 years after isolation, compared to continuous  
31 mainland habitats. Such a pattern of sustained and delayed species loss following large-scale habitat  
32 disturbance is indicative of an extinction debt existing for reservoir island species: this pattern is  
33 evident across all taxonomic groups and dams studied. Thus, reservoir islands cannot reliably be used  
34 for species conservation as part of impact mitigation measures, and should instead be included in area  
35 calculations for land impacted by dam creation. Environmental licensing assessments as a  
36 precondition for future dam development should explicitly consider the long-term fate of island  
37 communities when assessing biodiversity loss vs energy output.

38

39 **1. INTRODUCTION**

40

41 There are 58 402 large dams (dam height >15 m) operating globally, constructed predominantly for  
42 irrigation and hydropower generation (ICOLD, 2016). A growing human population is predicted to  
43 increase the demand for water by 2-3% per year, and the demand for energy by >56% globally  
44 between 2010-2040. Energy demand is estimated to rise by 90% in increasingly industrialised  
45 countries with emerging economies over the same period (EIA, 2013; WCD, 2000). Concurrently,  
46 changing climatic and precipitation patterns, including severe droughts, will likely further increase  
47 demand for water and reduce hydropower generation from large reservoirs (Oki and Kanae, 2006).  
48  
49 Hydropower is regarded as a renewable “green” energy source, and dams constructed in areas with  
50 steep topography and high rainfall produce the most energy per unit area (Finer and Jenkins, 2012).  
51 However dams are often constructed in low-lying areas with high conservation value: for example  
52 154 dams operate in the Amazon basin with a further 277 planned (Castello et al., 2013; Lees et al.,  
53 2016). The construction of dams directly impacts both terrestrial and freshwater ecosystems through  
54 inundation of habitat, compositional changes in biological communities, and the loss of structural and  
55 functional connectivity between upper and lower reaches of watersheds (Finer et al., 2008; Lees et al.,  
56 2016; Nilsson et al., 2005; Palmeirim et al., 2014; Sá-Oliveira et al., 2015).  
57  
58 Over 50% of the world’s large river systems and >60% of the combined habitat area of tropical,  
59 subtropical and boreal forests, tropical and subtropical grasslands, savannahs and shrublands have  
60 been estimated to be impacted by dams (Nilsson et al., 2005). Inundation of terrestrial habitats, and  
61 tropical forests in particular, can result in significant carbon emissions from reservoirs in the form of  
62 CO<sub>2</sub> and CH<sub>4</sub>, which can persist for many years after inundation and often over the lifetime of the  
63 reservoir (Abril et al., 2005; Demarty & Bastien, 2011; Fearnside, 2002; Fearnside & Pueyo, 2012).  
64 Direct social impacts arise from the loss of indigenous lands, displacement of communities, and  
65 disruption to local economies reliant on fisheries often concurrently affected by heavy metal  
66 accumulation (Boudou et al., 2005; Fearnside, 1999). Additionally, increased access to previously  
67 undisturbed habitat can elevate levels of hunting and deforestation in areas surrounding reservoirs  
68 (Kirby et al., 2006; Peres and Lake, 2003).

69

70 When dams are built, habitat is lost through inundation, with remnants of previously continuous  
71 terrestrial habitat confined to highly fragmented land-bridge island archipelagos comprised of former  
72 hilltops. “Good practice” guidelines (International Energy Agency, 2006) for dam developers to  
73 mitigate ecological impacts from dam construction, include implementing protected areas covering  
74 land-bridge islands and habitat surrounding reservoirs. For example, the REBIO Uatumã (the largest  
75 Biological Reserve in Brazil) encompasses approximately half of the Balbina hydroelectric reservoir,  
76 including all islands east of the former left bank of the Uatumã river and mainland areas extending  
77 away from the eastern edge of the reservoir. Strictly-protected area status has largely deterred small-  
78 scale slash-and-burn agriculture and extraction of resources within the REBIO Uatumã, on both  
79 islands and within surrounding continuous forest (Benchimol & Peres, 2015a, 2015b). However, we  
80 do not know whether protecting reservoir islands is effective for biodiversity conservation, due to a  
81 lack of long-term monitoring. The International Energy Agency highlights the dearth of systematic  
82 evaluation of any mitigation, enhancement, and compensation measures currently being  
83 recommended to large dam developers (International Energy Agency, 2000; Trussart et al., 2002).

84

85 Fragmentation of habitat causes a number of impacts to species, such as population reductions and  
86 local extinctions; the strength of fragmentation impacts differ depending on the taxonomic group and  
87 life-history traits of species (Bender et al., 1998; Fahrig 2003; Forman, 1995; Turner, 1996). Previous  
88 studies of reservoir island archipelagos have shown that island taxa typically experience a novel  
89 hyper-disturbance regime, resulting in drastic shifts in species diversity and community composition  
90 through species turnover, and altered carrying capacity of the remaining habitat (Benchimol & Peres,  
91 2015a; Cosson et al., 1999b; Ferreira et al., 2012; Hanski & Ovaskainen, 2000; Terborgh et al., 2001).  
92 Local species extinctions on reservoir islands have been observed for plants (Benchimol & Peres,  
93 2015a; Yu et al., 2012), invertebrates (Emer et al., 2013; Feer & Hingrat, 2005), birds (Yu et al.,  
94 2012), bats (Cosson et al., 1999a), small-mammals (Gibson et al., 2013; Lambert et al., 2003), and  
95 mid-sized to large-bodied vertebrates (Benchimol & Peres, 2015b, 2015c). Populations of some  
96 species can become hyper-abundant on islands, and invasive species can establish, further impacting

97 other taxa (Chauvet & Forget, 2005; Feeley & Terborgh, 2006; Gibson et al., 2013; Lopez &  
98 Terborgh, 2007).

99

100 Changes in island communities may not occur immediately after inundation; instead, species may be  
101 subject to an “extinction debt” whereby a portion of species are initially lost, followed, potentially  
102 multiple generations later, by further species extinctions (Halley et al., 2014; Kitzes and Harte, 2015;  
103 Kuussaari et al., 2009; Tilman et. al., 1994). Thus, the effects of fragmentation and isolation can  
104 persist for years after initial habitat loss, as communities undergo “relaxation” towards a new  
105 equilibrium community (Diamond, 1972; Diamond, 2001; Ewers and Didham, 2006; Feeley et al.,  
106 2007; Terborgh et al., 1997; Wang et al., 2009). The “relaxation” process is likely mediated by island  
107 area, with species losses faster on smaller islands, and a greater time-lag for species loss on larger  
108 islands (Diamond, 1972; Gonzalez, 2000). There are a number of empirical methods for calculating  
109 extinction debt (Kitzes and Harte, 2015; Wearn et al., 2012), and here we consider a decline in species  
110 richness on islands over time, compared to mainland continuous habitat, as evidence of extinction  
111 debt. In the absence of extinction debt, we assume that all species extinctions would happen  
112 immediately, with no evidence of further degradation of insular biological communities through time  
113 (Kitzes and Harte, 2015).

114

115 In the long-term it is unknown how reservoir island communities will continue change with increasing  
116 isolation time, as the creation of artificial archipelagos from dam construction has only occurred over  
117 the past century. Our present knowledge of ecological communities within artificial archipelagos  
118 comes from multiple snapshot studies from different countries, dams, habitats and taxa, at different  
119 time points since the originally continuous habitat was fragmented. Bringing these snapshots together  
120 enables identification of general trends across disparate studies, aiding development of policy-relevant  
121 recommendations in terms of the conservation value of reservoir islands.

122

123 Here, we quantitatively review peer-reviewed research detailing responses of terrestrial taxa to habitat  
124 fragmentation and subsequent isolation on reservoir land-bridge islands. We then analyse species

125 richness data from 249 islands and adjacent continuous habitats through time. In particular, we ask:  
126 (1) is there evidence of an extinction debt existing for reservoir island species; i.e. compared to  
127 continuous habitat, does island species richness decrease with increasing island isolation time? and (2)  
128 how does island size, distance to continuous habitat and distance to other islands relate to patterns of  
129 species richness and rates of species loss?

130

## 131 **2. METHODS**

132

### 133 **2.1. Literature summary**

134

#### 135 *2.1.1 Dataset collation*

136 We conducted a literature search using Web of Knowledge and Google Scholar search engines  
137 between January 2014 and June 2015 using the key words: hydropower or hydroelectric, reservoir or  
138 dam, island or land-bridge, and forest islands or fragments. Only full-text, peer-reviewed articles in  
139 English were retained; unpublished or grey literature was not included. Studies researching terrestrial  
140 species, guilds, taxonomic groups or communities on reservoir islands, attributing ecological  
141 responses observed to reservoir creation were retained. Experimental studies or those not explicitly  
142 stating an aspect of reservoir creation as a causal factor for the response observed were excluded.  
143 Studies which met the inclusion criteria were entered into a dataset (henceforth referred to as “dataset  
144 studies”). Literature cited in the dataset studies was also screened for inclusion, and searches for  
145 names of dams in dataset studies were performed. A total of 129 studies were assessed for inclusion in  
146 our study, 100 of which met the criteria to be retained.

147

#### 148 *2.1.2 Data extraction*

149 Data such as the number of islands surveyed, island area, taxonomic groups investigated, and time  
150 since island isolation were extracted from studies (see Appendix A). Each study was assigned a broad  
151 habitat type (wet tropical forest, tropical grassland e.g. *cerrado*, subtropical forest, Mediterranean  
152 forest, boreal forest). Taxa investigated were broadly grouped into mammals, birds, invertebrates,

153 herptiles, plants, and fungi. If multiple taxa were included within a study, data were extracted for  
154 each group separately due to the potential for different responses. The precise isolation time of islands  
155 is seldom reported, thus we estimated island isolation time as the year of dam closure minus the year  
156 of field data collection. In six studies field data collection dates were not reported, thus, data  
157 collection date was conservatively estimated as two years prior to publication date.

158

### 159 *2.1.3. Assigning study response directions*

160 For each study the authors' key results and conclusions were used to assign an overall response of the  
161 study taxa to isolation on islands (response: positive, negative, variable, or neutral; see Appendix A,  
162 column 'L'). For example, a study reporting declining species richness on islands would be assigned  
163 an overall negative response. An overall positive response would be assigned if, for example,  
164 recorded sightings (e.g. presence/absence data) were higher on islands. Overall variable responses  
165 could result from research involving different species within the same taxon, e.g. two species of bat  
166 exhibiting divergent responses to isolation. Neutral responses would result if no differences or  
167 alterations in taxa on islands compared to mainland sites were reported. If authors did not draw a  
168 conclusion as to the response directions observed, we examined the data reported and assigned a  
169 response direction accordingly. If multiple response directions for the same taxa were observed over  
170 time, the predominant response direction (i.e. over most years) was used as the overall direction.

171

172 To account for within-study complexity i.e. inclusion of multiple taxonomic groups and/or ecological  
173 metrics, response directions were derived for each taxonomic group and ecological metric  
174 investigated (see Appendix B, columns 'M-P'). Ecological metrics included species richness,  
175 population density, behaviour (e.g. foraging behaviour), community composition, presence/absence,  
176 fitness/recruitment (e.g. breeding output), genetic diversity, and functional diversity.

177

## 178 **2.2 Species richness analysis**

179



180 Estimates of species richness were the most widely-reported and accessible data available in the  
181 collated studies, and therefore we selected this ecological metric for in-depth analysis.

182

### 183 *2.2.1. Data collection*

184 Dataset studies presenting species richness data for islands and nearby continuous (control) habitat, as  
185 well as island areas and isolation time, were used to assess variation in species richness on reservoir  
186 islands compared to control habitat (Table B1). These data also allowed investigation of the  
187 relationships between species richness and island area, isolation time, distance to mainland and  
188 distance to nearest island. Of the 100 dataset studies, 17 presented species richness data for islands ( $n$   
189 = 249; size range <1-1690 ha; isolation time <1-92 years) and control sites ( $n = 84$ ), and were used for  
190 the in-depth analysis of species richness data (Table B1; Appendix B). If data for the distance to  
191 mainland or nearest island were not presented, then if possible these data were calculated from  
192 satellite imagery using Google Earth Pro (Google, 2015). Geographically, the 17 studies suitable for  
193 species richness analysis originated from nine dams, located on three continents in three broad habitat  
194 types (wet tropical forest, subtropical forest, and tropical grassland; Table B1).

195

### 196 *2.2.2. Data analysis*

197 For each study the average species richness for control sites was calculated. The ratio of island species  
198 richness to average control species richness ( $S_{\text{RICH}}$ ) was then calculated for each site and used for  
199 analysis (see Appendix B). If a study contained data over multiple years, and thus, multiple isolation  
200 times, then species richness for control sites over the same isolation time period was averaged. If a  
201 study had multiple species richness values for the same island size, taxon, and isolation time, species  
202 richness values were averaged to avoid pseudo-replication.

203

204 To normalise data, all data were logged (natural logarithm) prior to analysis.  $S_{\text{RICH}}$  values were  
205 modelled using linear mixed effects models (lmer using lme4; Bates et al., 2014), as a function of  
206 island isolation time ( $T_{\text{ISO}}$ ), island area (AREA), distance to mainland ( $D_{\text{MAIN}}$ ) and distance to nearest  
207 island ( $D_{\text{ISLAND}}$ ) as fixed effects, with taxonomic group (TAXA), dam identity (DAM; a surrogate for

208 location), and study (STUDY; to account for differing survey methods and survey intensity among  
209 studies) as random effects (Bunnefeld and Phillimore, 2012; see Appendix B). Interaction terms were  
210 included between AREA,  $T_{ISO}$ ,  $D_{MAIN}$  and  $D_{ISLAND}$ , as well as between TAXA, DAM and STUDY;  
211 quadratic terms were also tested for.

212

213 Due to missing values for  $D_{MAIN}$  and  $D_{ISLAND}$  we reduced the dataset to only those data rows  
214 containing values for all variables being tested (n islands = 178) and used this dataset for linear  
215 regression and model selection in R (R Core Team, 2015). Models were simplified following stepwise  
216 deletion of non-significant terms i.e. those with a t-value <2 and models compared using Chi-square  
217 tests in ANOVA (Crawley, 2005; Table B2). Following model simplification, the final model did not  
218 include variables with missing values, thus, the final model was fitted to the whole dataset (n islands  
219 = 249). The best linear unbiased predictors (BLUPs) for each dam were extracted using the ‘ranef’  
220 function within the lme4 R package (Pinheiro and Bates, 2000). Each dam has a different intercept,  
221 which can fall above or below that of the overall model: positive BLUPs indicate that the dam has  
222 higher than expected levels of species richness estimated from the fixed effects, and those falling  
223 below the model average indicate that species richness is lower than expected. A variance components  
224 analysis was carried out for the random effects (Crawley, 2005).

225

### 226 **3. RESULTS**

227

#### 228 **3.1. Literature summary**

229

230 The 100 dataset studies examined here were predominantly from Neotropical forest habitats (Fig. 1;  
231 2a). Mammals were the best-studied taxonomic group (Fig. 2b); responses of terrestrial taxa isolated  
232 on reservoir islands were most often expressed in terms of species richness and presence/absence, and  
233 rarely with regards to behaviour, genetic or functional diversity (Fig. 2c). An overall negative  
234 response of terrestrial taxa to dam creation was reported in >75% of studies, and these negative  
235 responses were seen across all habitat types, ecological metrics, and taxonomic groups investigated

236 (Fig. 2a-c). Overall positive responses were confined to only two of the 100 studies (Fig. 2a), of  
237 which one reported increased and more stable population densities of small mammals (Adler, 1996),  
238 and the second, increased food resources for a raptor due to prey being ‘captive’ on isolated islands  
239 (Benchimol and Venticinque, 2010). Studies report results for islands isolated from <1 to 92 years,  
240 with the mean island isolation age of ~33 years (Fig. 2d).

241

### 242 **3.2. Species richness analysis**

243

244 The final model for analysis of  $S_{RICH}$  included  $T_{ISO}$  and AREA as fixed effects, and TAXA, DAM and  
245 STUDY as random effects (Table 1);  $D_{MAIN}$  and  $D_{ISLAND}$  had no significant effect on  $S_{RICH}$ , and no  
246 interaction terms were significant (Table B2). Of the random effects, 36% of variation was explained  
247 by STUDY, 17% explained by DAM, with 47% residual variance; TAXA did not explain any variance.

248

249 For all taxonomic groups and dams, species richness declined with island isolation time, but this  
250 effect was mediated by island size with larger islands retaining more species than smaller islands (Fig.  
251 3). For example, predicted  $S_{RICH}$  on the largest island (1690 ha, within the Balbina hydroelectric dam,  
252 Brazilian Amazon) is predicted to be 3.2 at the mean isolation time of islands in the analysis,  
253 compared to a predicted  $S_{RICH}$  of 1.2 on the smallest island (0.17 ha, Cabra Corral, Argentina). In  
254 terms of island isolation time, even the largest island studied (1690 ha) exhibits reduced  $S_{RICH}$  in <30  
255 years of isolation, and Barro Colorado Island (~1500 ha, Gatun Lake, Panama), which has been  
256 isolated for the longest period in our study (~92 years), similarly shows sustained species richness  
257 declines (Fig. 3).

258

259 The estimates for the random effect of DAM (BLUPs) show that the majority of dams (66%) maintain  
260 lower than expected levels of species richness i.e. species richness values fall below those predicted  
261 by the overall model (Fig. 3; Table B3). Only islands in Gatun Lake, Balbina, and Thousand Island  
262 Lake maintain higher species richness than predicted. Using our model we can predict  $S_{RICH}$  values for  
263 islands of mean area at a given isolation time, and islands of different areas at the mean isolation time,

264 for each reservoir. For example, the  $S_{RICH}$  for mean island size within Gatun Lake reduces from 2.24  
265 at five years of isolation to 1.49 after 90 years of isolation. In contrast, in Lake Kenyir which  
266 maintains the lowest expected species richness values, a small island of 5 ha (at mean island isolation  
267 time) has a predicted  $S_{RICH}$  value of 1.35, which is increased to just 2.23 on an island of 1000 ha.  
268 There was no evidence that islands located nearer other terrestrial habitat or mainland continuous  
269 habitat had reduced levels of species loss.

270

#### 271 **4. DISCUSSION**

272

273 Our study finds that terrestrial taxa isolated on reservoir islands experience significant reductions in  
274 species richness in less than a century of isolation. Such sustained local species losses after the initial  
275 loss of habitat indicates that reservoir island species are subject to an extinction debt, which is evident  
276 across all dams, habitats, and taxa. All islands showed depauperate levels of species richness  
277 compared to continuous habitats, with smaller islands maintaining lower species richness than larger  
278 islands. Island isolation time and area, but not distance from other terrestrial habitat or the mainland,  
279 were the drivers of species richness patterns observed.

280

281 More broadly, we show that the majority of taxa are negatively impacted by reservoir creation across  
282 a range of other ecological metrics including behaviour and genetic diversity. Our current knowledge  
283 of the impacts of reservoir creation is disproportionately focussed on mammals, and originates  
284 predominantly from evergreen Neotropical forest habitats. While not all dams create archipelagic  
285 landscapes, research within our synthesis covers just 15 of the >58 000 large dams operating globally,  
286 representing a small and potentially biased sample of possible island systems. However, even with  
287 such limited data we clearly demonstrate the negative impact of dam creation on island species  
288 richness. Furthermore, we highlight the shortfalls in current conservation and impact mitigation  
289 strategies for dam development, particularly in terms of long-term biological costs, in addition to the  
290 immediate direct loss of lowland habitat during flooding.

291

292 **4.1. Island species richness, area, and isolation time**

293

294 Classic island biogeography theory (IBT, MacArthur & Wilson, 1967) explains variation in island  
295 species richness through a balance of species immigration and distance from species source pools. In  
296 the artificial archipelagic systems we investigate in our analysis, rather than a process of species  
297 accumulation on islands, remnant communities of formerly continuous habitat undergo species loss  
298 (“relaxation”) until a new equilibrium community is reached (Diamond, 1972; Gonzalez, 2000;  
299 Lomolino, 2000).

300

301 Area was a significant predictor of species richness on islands within our analysis, as expected from  
302 the species-area relationship and IBT (Connor & McCoy, 1979; MacArthur & Wilson, 1967; Triantis  
303 et al., 2012). However distance, both to the mainland and other islands, was not a significant predictor  
304 of island species richness: this represents a departure from the IBT, and suggests the reduced  
305 importance of metapopulation dynamics (Hanski and Gilpin, 1991; With and King, 2001) and the  
306 “rescue effect” (Brown and Kodric-Brown, 1977) for maintaining insular populations in artificial  
307 archipelagic systems.

308

309 In the case of reservoir islands, remnant terrestrial habitat fragments are surrounded by a high-  
310 contrast, inhospitable water matrix, presenting a prohibitive dispersal barrier for certain taxa. Such an  
311 extreme dispersal barrier effectively renders all islands as too isolated for any “rescue effect” from  
312 wider species source pools to maintain island communities and species richness, and explains the lack  
313 of distance effects we find in our analysis (Watson, 2002). The evolutionary history and traits of  
314 species resident in continuous habitats make many incapable of dispersing through open habitats,  
315 across large distances, or through a high-contrast matrix such as open water (see Fig. 2 in Ewers &  
316 Didham, 2006). For example, the ability of tropical understorey bird species to disperse across a  
317 water matrix between islands was tested in Gatun Lake, Panama, where some species were limited to  
318 <100m of flight (Moore et al., 2008); species reliant on continuous habitats can be averse to crossing

319 even small clearings, such as logging roads, even when the forest canopy is closed (Develey &  
320 Stouffer, 2001; Laurance et al., 2004).

321

322 Habitat fragments surrounded by water therefore represent a worse-case scenario in terms of  
323 fragmentation effects; aside from the dispersal barrier preventing species migration, islands are  
324 subject to extreme edge effects from e.g. increased UV and wind damage, often penetrating deep into  
325 islands leading to further degradation of island biota (Benchimol & Peres, 2015b; Laurance, 2008;  
326 Murcia, 1995). Habitat fragments embedded within a more similar and potentially hospitable, but  
327 low-quality, terrestrial habitat matrix (e.g. forest fragments within an agricultural landscape) can  
328 retain higher levels of species diversity, with reduced local extinction rates (Mendenhall et al., 2011),  
329 when compared to reservoir islands of a similar size (Mendenhall et al., 2014).

330

331 We find a reduction in species richness on all islands with increasing time since initial habitat loss.  
332 Such a pattern of sustained and delayed species loss is indicative of extinction debt (Tilman et al.,  
333 1994; Kitzes & Harte, 2015; Kuussaari et al., 2009). Extinction debts are especially high in areas  
334 subject to recent large-scale habitat loss, such as islands created by rapid flooding of terrestrial  
335 habitats (Hanski and Ovaskainen, 2002). Our analysis illustrates that reservoir islands are of limited  
336 long-term conservation value, due to evidence of an extinction debt: species loss appears most rapid  
337 on smaller islands, but even the largest islands studied (~1690 ha) exhibited lowered species richness  
338 in under 30 years of isolation. Ongoing species losses have been reported on another large island in  
339 our synthesis: Barro Colorado Island (BCI, ~1500 ha) has been isolated for 92 years since the  
340 formation of the Gatun Lake, Panama. In less than a century of island isolation, and despite strict  
341 environmental protection of BCI and surrounding peninsulas, 65 bird species (Robinson, 1999) and 23  
342 butterfly species (Basset et al., 2015) have become locally extinct, alongside long-term degradation of  
343 the tree community (Leigh et al., 1993). In the Balbina hydroelectric mega-dam system in Amazonia,  
344 Benchimol and Peres (2015b) calculated that a threshold island size of 475 ha was needed to conserve  
345 >80% of terrestrial and arboreal vertebrates on islands. However, only 25 out of 3546 islands in the  
346 Balbina archipelago meet this size criterion. Balbina is protected by the largest biological reserve in

347 Brazil, and thus represents a best case scenario for biodiversity conservation within an artificial  
348 archipelago system. Species inhabiting other such systems, without protection, will therefore likely  
349 suffer not only from direct habitat loss through flooding and potential extinction debt, but additional  
350 human-mediated impacts such as deforestation, agriculture, hunting, and fire (Laurance, 2008; Peres,  
351 2001).

352

353 The data we use for analysis of species richness on reservoir land-bridge islands originate from 249  
354 islands within 9 of the 15 dams presented in Fig. 1 and allow us to show patterns applicable to all  
355 dams and taxonomic groups, although we acknowledge that publication bias towards negative impacts  
356 of reservoir creation could influence the response patterns presented. While the data do not allow us to  
357 disentangle species richness patterns for individual taxonomic groups, dams and habitat types, we  
358 have addressed this shortcoming by using random effects in linear mixed effects models (Bunnefeld  
359 and Phillimore, 2012). Similarly we cannot calculate the magnitude of extinction debts for individual  
360 taxonomic groups and/or habitat types, and instead highlight evidence that all reservoir islands are  
361 subject to an extinction debt, and therefore cannot be relied upon for long-term species conservation.

362

363 It is possible that the observed patterns of depauperate island species richness could be shaped by  
364 landscape attributes prior to inundation and non-random loss of more species-rich lowland habitat  
365 during flooding (Seabloom et al., 2002). Mainland species richness levels may have been elevated  
366 through surveying lowland habitats; such a potential sampling effect should be accounted for during  
367 survey site selection (e.g. Benchimol and Peres, 2015a). In continuous habitats the greater availability  
368 of resources allows more species to inhabit a given area, compared to the same area of isolated habitat  
369 (Ewers and Didham, 2006). Thus, sampling islands can inherently give lower species richness values  
370 than an equal area of continuous habitat (Crawley & Harral, 2001; Gonzalez, 2000; Halley et al.,  
371 2014; MacArthur & Wilson, 1963).

372

373 Data for island taxa in artificial archipelagos come from snapshots of responses to isolation in <100  
374 years of reservoir lifetime, across multiple taxa and habitat types. In addition, no studies monitored

375 changes in insular community dynamics over a significant post-isolation time. Consequently, we  
376 cannot currently determine if the rates of local species loss are predictable beyond the relatively short  
377 time frame analysed here. Nor can we accurately quantify extinction debt to predict the eventual  
378 number of species able to persist in the artificial archipelago systems created due to the assumptions  
379 that would be required to do so. Further long-term monitoring of reservoir island biota is needed to  
380 allow these more detailed assessments to be made, since at present only Gatun Lake, Panama,  
381 provides data for a reservoir >90 years of age.

382

#### 383 **4.2. Conservation implications**

384

385 Our study strongly suggests that islands within reservoir systems do not sustain full complements of  
386 flora and fauna in the long term; larger islands retain species for longer than smaller islands, but all  
387 island communities likely face an extinction debt. Given that degradation of island communities can  
388 be predicted to occur in all artificial archipelagic systems created by dam development, we emphasise  
389 that reservoir islands cannot be used for species conservation as part of impact mitigation strategies.  
390 The combined area of reservoir islands should be explicitly included in environmental impact  
391 assessments, in addition to the area of habitat directly lost through inundation.

392

393 Current policy to mitigate the negative impacts of dam creation on terrestrial environments consists of  
394 “good practice” guidelines with no statutory legislation requiring specific actions by developers  
395 (International Energy Agency, 2006). Environmental legislation is highly variable among countries,  
396 and there is no signatory international agreement on how to forecast, prevent or mitigate the effects of  
397 large dams. Mitigation measures can take a multitude of forms, ranging from conducting wildlife  
398 inventories and environmental impact assessments before reservoir filling, creating new habitats such  
399 as wetland zones within the reservoir system, and conservation offsets such as strictly protecting land  
400 both within and surrounding reservoirs. There is however no long-term monitoring of such practices  
401 to assess whether these mitigation measures are effective (International Energy Agency, 2000).

402



403 In light of the many dams that are planned to meet future water and electricity needs, especially in  
404 developing countries, we call for better trade-off calculations (Kareiva, 2012) to be made for future  
405 dams, accounting for long-term species loss on islands created by flooding. In addition, enhanced  
406 protection of larger islands and surrounding non-fragmented habitats is essential to avoid biological  
407 collapse in artificial archipelagic systems. We highlight the potential for additional impacts from  
408 long-term degradation of high carbon-storing habitats such as tropical forests, where erosion of island  
409 tree communities (Benchimol and Peres, 2015a) could lead to future carbon loss from tropical dams,  
410 exacerbating the greenhouse gas emissions already documented from this “green” energy source  
411 (Demarty and Bastien, 2011; Fearnside, 2009).

412

### 413 **4.3. Conclusions**

414

415 We have shown that there is an overall negative response of terrestrial species and communities to  
416 isolation on reservoir land-bridge islands. These trends are seen across a broad spectrum of taxonomic  
417 groups and ecological metrics. Species isolated on reservoir islands will likely experience extinction  
418 debt, and the rate of local extinctions is driven by island size and island isolation time, independently  
419 of distance from potential source populations within the landscape. Our synthesis of current literature  
420 allows broad conclusions about the ecological impacts of reservoirs through time, and highlights the  
421 need for further research from a greater number of reservoirs over the duration of their lifetime.

422 Building upon the findings that we present here, investigation of the many other direct and indirect  
423 ecological impacts of reservoirs, such as loss of river habitats and connectivity, land tenure rights, and  
424 the impacts of wider infrastructure development on surrounding habitats, should be a priority for  
425 future research.

426

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433

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435

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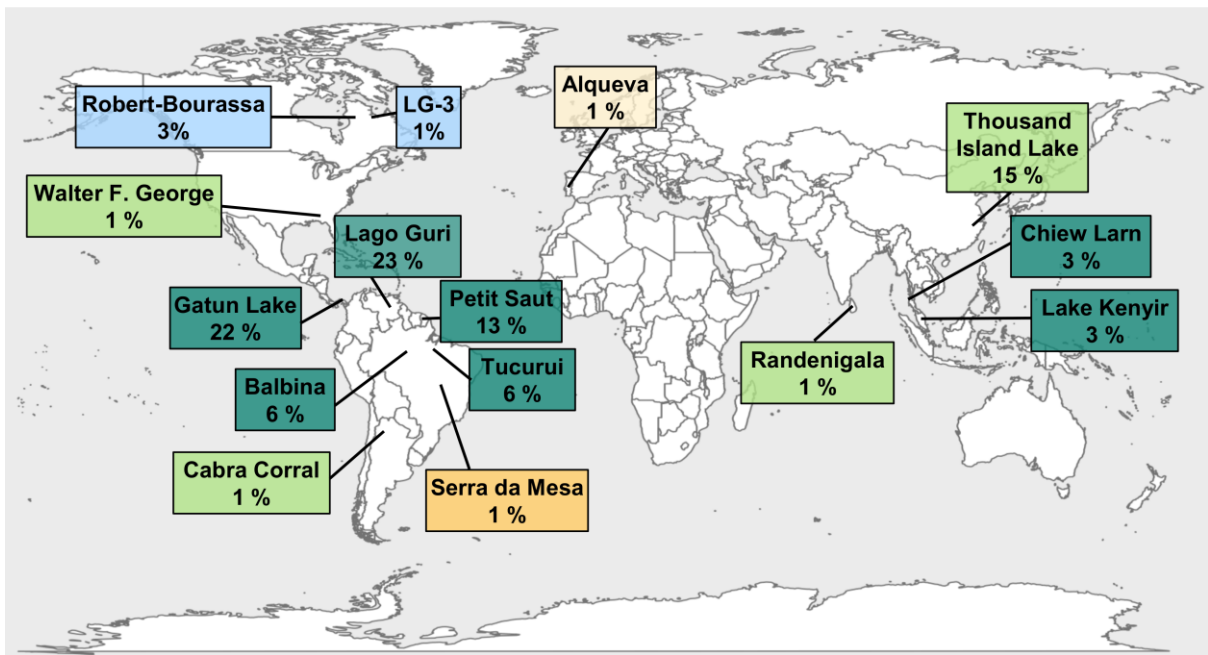
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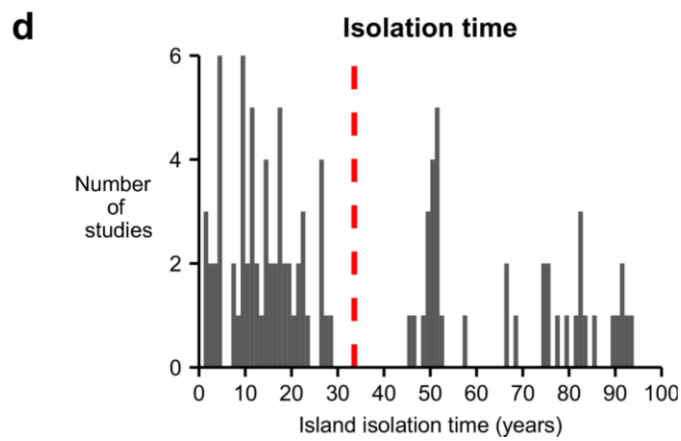
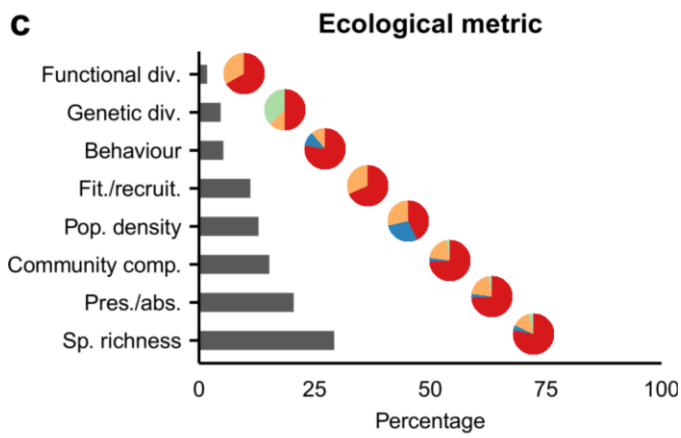
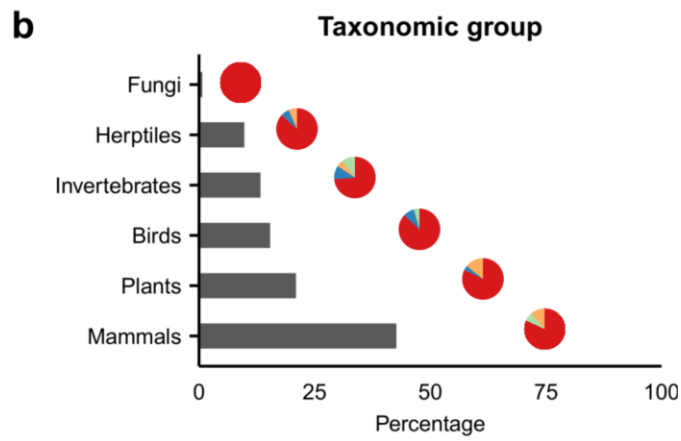
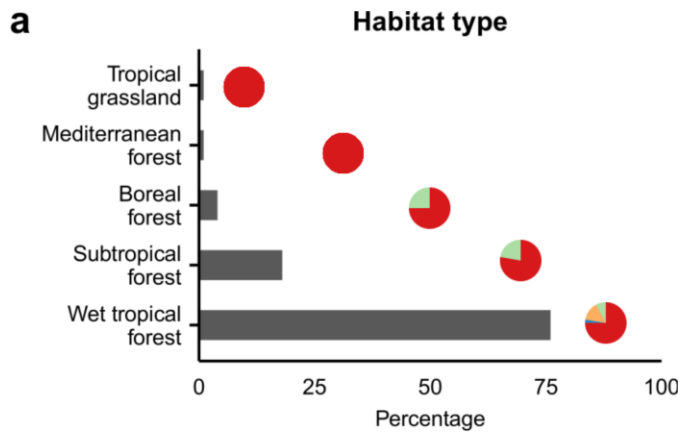


655

656 **Figure 1:** Geography of research detailing responses of terrestrial taxa to isolation on  
 657 reservoir land-bridge islands. Dam names and the percentage of total dataset studies (n = 100)  
 658 originating from each are presented. Broad habitat type is indicated by colour: dark green =  
 659 wet tropical forest; light green = subtropical forest; yellow = tropical grassland (e.g. *cerrado*);  
 660 cream = Mediterranean forest; blue = boreal forest.

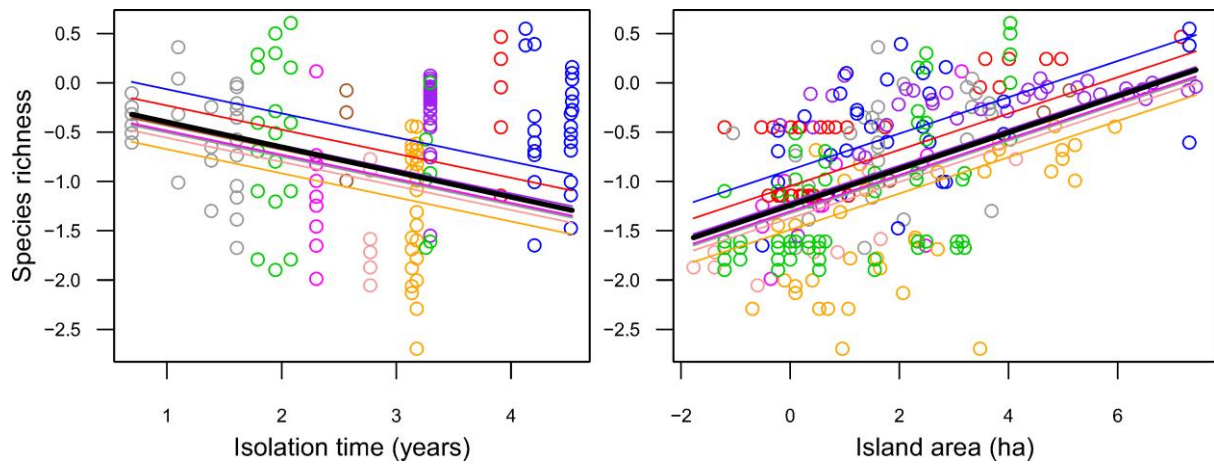
661 [2 column fitting]

662



664 **Figure 2:** Overview of research presented within dataset studies (n=100). 2a-c) present the  
665 proportion of total studies (black bars) for habitat type, ecological metric and taxonomic  
666 group investigated respectively; pie charts represent overall response directions (red =  
667 negative; blue = positive; green = neutral; yellow = variable). 2d) presents the distribution of  
668 studies through island isolation time (red dashed line represents mean island isolation time,  
669 ~33 years).

670 **[Single column fitting]**



671

672 **Figure 3:** Analysis of species richness ( $S_{RICH}$ ) data from 249 islands and 84 control sites available  
 673 from nine dams in three broad habitat types (wet tropical forest, subtropical forest, and tropical  
 674 grassland), modelled with time since island isolation ( $T_{ISO}$ ) and island area ( $AREA$ ). Bold black lines  
 675 represent the slope for the overall model, with individual lines for each dam fitted using the BLUPs  
 676 extracted from random effects. Colour indicates dam identity: grey = Petit Saut; green = Chiew Larn;  
 677 magenta = Lago Guri; brown = Randenigala; light pink = Cabra Corral; orange = Lake Kenyir; purple  
 678 = Balbina; red = Thousand Island Lake; blue = Gatun Lake. Axes are on a natural log scale.

679 [2 column fitting]

680 **Table 1:** Coefficient estimates for fixed effects in the most parsimonious model used for  
 681 species richness analysis, with TAXA, DAM and STUDY as random effects; t-values >2 were  
 682 treated as significant.

|           | Estimate | Standard Error | t-value |
|-----------|----------|----------------|---------|
| Intercept | -0.514   | 0.237          | -2.168  |
| AREA      | 0.185    | 0.015          | 11.944  |
| $T_{ISO}$ | -0.244   | 0.067          | -3.641  |

686

687 **[Single column fitting]**

688 **APPENDIX A1**

689 **Full reference list for Appendix A**

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963 **APPENDIX B1**964 **Table B1**

965 Summary of research articles used in the species richness analysis. For full references, see  
 966 Appendix A1. For data used in the analysis, see Appendix B.

| Reference                      | Habitat type        | Region          | Country       | Dam                  | Isolation time (years) | Number of islands studied | Number of control sites | Island areas (ha) |
|--------------------------------|---------------------|-----------------|---------------|----------------------|------------------------|---------------------------|-------------------------|-------------------|
| Badano et al. (2005)           | Subtropical forest  | South America   | Argentina     | Cabra Corral         | 15                     | 9                         | 1                       | 0.16-62.5         |
| Benchimol & Peres (2015)       | Wet tropical forest | South America   | Brazil        | Balbina              | 26                     | 34                        | 12                      | <1-1690           |
| Cosson et al. (1999)b          | Wet tropical forest | South America   | French Guiana | Petit Saut           | 1                      | 6                         | 3                       | 2-40              |
| Estrada-Villegas et al. (2010) | Wet tropical forest | Central America | Panama        | Gatun Lake           | 92                     | 8                         | 6                       | 2.5-50            |
| Feer & Hingrat (2005)          | Wet tropical forest | South America   | French Guiana | Petit Saut           | 4                      | 7                         | 3                       | 1.1-25.5          |
| Gibson et al. (2013)           | Wet tropical forest | Asia            | Thailand      | Chiew Larn           | 26                     | 16                        | 1                       | 0.3-56.3          |
| Granjon et al. (1996)          | Wet tropical forest | South America   | French Guiana | Petit Saut           | 1                      | 10                        | 1                       | 0.35-30           |
| Karr (1982)b                   | Wet tropical forest | Central America | Panama        | Gatun Lake           | 66                     | 1                         | 2                       | 1500              |
| Leigh et al. (1993)            | Wet tropical forest | Central America | Panama        | Gatun Lake           | 66                     | 7                         | 4                       | 0.6-1500          |
| Meyer & Kalko (2008)a          | Wet tropical forest | Central America | Panama        | Gatun Lake           | 91                     | 11                        | 6                       | 2.5-50            |
| Pons & Cosson (2002)           | Wet tropical forest | South America   | French Guiana | Petit Saut           | 2                      | 16                        | 1                       | <6-28             |
| Qui et al. (2011)              | Wet tropical forest | Asia            | Malaysia      | Lake Kenyir          | 23                     | 24                        | 3                       | <1-383.3          |
| Terborgh et al. (1997)         | Wet tropical forest | South America   | Venezuela     | Lago Guri            | 9                      | 12                        | 1                       | 1-350             |
| Wang et al. (2009)             | Subtropical forest  | Asia            | China         | Thousand Island Lake | 49                     | 42                        | 7                       | 0.67-1289.23      |
| Weerakoon (2009)               | Subtropical forest  | Asia            | Sri Lanka     | Randenigala          | 12                     | 6                         | 5                       | 2-167             |
| Yong et al. (2010)             | Wet tropical forest | Asia            | Malaysia      | Lake Kenyir          | 22                     | 6                         | 2                       | <20- >100         |
| Yong et al. (2012)             | Wet tropical forest | Asia            | Malaysia      | Lake Kenyir          | 22                     | 6                         | 2                       | <20- >100         |

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968

969 **Table B2**

970 Coefficients for the fixed effects of models that treat study identity, dam, and taxonomic  
 971 group as random effects. The Chi-square ( $\chi^2$ ) value and p-value from model comparison by  
 972 ANOVA is given. The final model used in analysis only included significant fixed effects:  
 973 AREA and  $T_{ISO}$ . Values presented in this table are from model comparisons using a reduced dataset (n  
 974 islands = 148) to account for missing values. Following model comparison, the final model was used  
 975 on the full dataset (n islands = 249) which did not have missing values for the variables included in  
 976 the model.

| Fixed effects | Estimate | SE    | t-value | df | $\chi^2$ | p-value |
|---------------|----------|-------|---------|----|----------|---------|
| Intercept     | -0.514   | 0.237 | -2.168  |    |          |         |
| AREA          | 0.237    | 0.02  | 11.958  | 1  | 94.744   | <0.001  |
| $T_{ISO}$     | -0.328   | 0.069 | -4.720  | 1  | 16.136   | <0.001  |
| $D_{MAIN}$    | -0.037   | 0.039 | -0.951  | 1  | 0.894    | 0.344   |
| $D_{ISLAND}$  | -0.062   | 0.043 | -1.434  | 1  | 1.991    | 0.158   |

977

978 **Table B3**

979 Intercepts for the best unbiased linear predictors (BLUPs) for each dam generated using the  
 980 ‘ranef’ function in lme4 (Bates et al., 2014). Negative BLUPs indicate lower species richness  
 981 values than predicted by the model; positive BLUPs indicate higher species richness values  
 982 than predicted.

| Dam                  | Intercept (Dam) |
|----------------------|-----------------|
| Balbina              | 0.0367          |
| Cabra Corral         | -0.131          |
| Chiew Larn           | -0.071          |
| Gatun Lake           | 0.361           |
| Lago Guri            | -0.059          |
| Lake Kenyir          | -0.247          |
| Petit Saut           | -0.079          |
| Randenigala          | -0.007          |
| Thousand Island Lake | 0.196           |

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