Extinction debt on reservoir land-bridge islands

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ABSTRACT

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

1. INTRODUCTION

There are 58 402 large dams (dam height >15 m) operating globally, constructed predominantly for irrigation and hydropower generation (ICOLD, 2016). A growing human population is predicted to increase the demand for water by 2-3% per year, and the demand for energy by >56% globally, and by 90% in increasingly industrialised countries with emerging economies between 2010-2040 (EIA, 2013; WCD, 2000). Concurrently, changing climatic and precipitation patterns, including severe droughts, will likely further increase demand for water and reduce hydropower generation from large reservoirs (Oki and Kanae, 2006).

Hydropower is regarded as a renewable “green” energy source, and dams constructed in areas with steep topography and high rainfall produce the most energy per unit area (Finer and Jenkins, 2012). However dams are often constructed in low-lying high conservation value areas: for example 154 dams operate in the Amazon basin with a further 277 planned (Castello et al., 2013; Lees et al., 2016). The construction of dams directly impacts both terrestrial and freshwater ecosystems through inundation of habitat, compositional changes in aquatic communities, and the loss of structural and functional connectivity between upper and lower reaches of watersheds (Finer et al., 2008; Nilsson et al., 2005; Lees et al., 2016; Palmeirim et al., 2014; Sá-Oliveira et al., 2015).

Over 50% of the world’s large river systems and >60% of the combined habitat area of tropical, subtropical and boreal forests, tropical and subtropical grasslands, savannahs and shrublands have been estimated to be impacted by dams (Nilsson et al., 2005). Inundation of terrestrial habitats, and tropical forests in particular, can also result in significant carbon emissions from reservoirs in the form of CO_2 and CH_4, which can persist for many years after inundation and often over the lifetime of the reservoir (Abril et al., 2005; Demarty & Bastien, 2011; Fearnside, 2002; Fearnside & Pueyo, 2012). Direct social impacts arise from the loss of indigenous lands, displacement of communities, and disruption to local economies reliant on fisheries often concurrently affected by heavy metal accumulation (Boudou et al., 2005; Fearnside, 1999). Additionally, increased access to previously undisturbed habitat can elevate levels of hunting and deforestation in areas surrounding reservoirs (Kirby et al., 2006; Peres and Lake, 2003).

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

Fragmentation of habitat causes a number of impacts to species, such as population reductions and local extinctions; the strength of fragmentation impacts differ depending on the taxonomic group and life-history traits of species (Bender et al., 1998; Fahrig 2003; Forman, 1995). Previous studies of reservoir island archipelagos have shown that island taxa typically experience a novel hyper-disturbance regime, resulting in drastic shifts in species diversity and community composition through species turnover and altered carrying capacity of remaining habitat (Benchimol & Peres, 2015a; Cosson et al., 1999a; Ferreira et al., 2012; Hanski & Ovaskainen, 2000; Terborgh et al., 2001). Local species extinctions on reservoir islands have been observed for plants (Benchimol & Peres, 2015a; Yu et al., 2012), invertebrates (Emer et al., 2013; Feer & Hingrat, 2005), birds (Yu et al., 2012), bats (Cosson et al., 1999b), small-mammals (Gibson et al., 2013; Lambert et al., 2003), and midsized to large-bodied vertebrates (Benchimol & Peres, 2015b, 2015c). In contrast, populations of some species can become hyper-abundant on islands, further impacting other taxa (Chauvet & Forget, 2005; Feeley & Terborgh, 2006; Lopez & Terborgh, 2007), as can the establishment of invasive species (Gibson et al., 2013).

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

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

Here, we quantitatively review peer-reviewed research detailing responses of terrestrial taxa to habitat fragmentation, and subsequent isolation, on reservoir land-bridge islands. We then analyse species richness data from 249 islands and adjacent continuous habitats through time. In particular, we ask: (1) is there evidence of an extinction debt existing for reservoir island species; i.e. compared to continuous habitat, does island species richness decrease with increasing island isolation time? and (2) how does island size, distance to continuous habitat and distance to other islands relate to patterns of species richness and rates of species loss?

2. METHODS

2.1. Literature summary

2.1.1 Dataset collation

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

2.1.2 Data extraction

Data such as the number of islands surveyed and island area, taxonomic groups investigated, and time since island isolation were extracted from studies (see Database A). Each study was assigned a broad habitat type (wet tropical forest, tropical grassland e.g. *cerrado*, subtropical forest, Mediterranean forest, boreal forest). Taxa investigated were broadly grouped into mammals, birds, invertebrates, herptiles, plants, and fungi. If multiple taxa were included within a study, data were extracted for each group separately due to the potential for different responses. The precise isolation time of islands is seldom reported, thus we estimated island isolation time as the year of dam closure minus the year of field data collection. In six studies field data collection dates were not reported, thus, data collection date was conservatively estimated as two years prior to publication date.

2.1.3. Assigning study response directions

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

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

2.2 Species richness analysis

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

2.2.1. Data collection

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

2.2.2. Data analysis

For each study the ratio of island species richness to average control species richness (S_{RICH}) was calculated (see Database B . If a study contained data over multiple years, and thus, multiple isolation times, then species richness for control sites over the same isolation time period was averaged. If a study had multiple species richness values for the same island size, taxon, and isolation time, species richness values were averaged to avoid pseudo-replication.

To normalise data, all data were logged (natural logarithm) prior to analysis. S_{RICH} values were modelled using linear mixed effects models (lmer using lme4; Bates et al., 2014), as a function of island isolation time (T_{ISO}), island area (AREA), distance to mainland (D_{MAIN}) and distance to nearest island (D_{ISLAND}) as fixed effects, with taxonomic group (TAXA), dam identity (DAM; a surrogate for location), and study (STUDY; to account for differing survey methods and survey intensity between studies) as random effects (Bunnefeld and Phillimore, 2012; see Database B). Interaction terms were included between AREA, $T_{\mathrm{ISO},}$ D_{MAIN} and D_{ISLAND}, as well as between TAXA, DAM and STUDY; quadratic terms were also tested for.

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

3. RESULTS

3.1. Literature summary

The 100 dataset studies examined here were predominantly from Neotropical wet tropical forest habitats (Fig. 1; 2a). Mammals were the best-studied taxonomic group (Fig. 2b); responses of terrestrial taxa isolated on reservoir islands were most often expressed in terms of species richness and presence/absence, and rarely with regards to behaviour, genetic or functional diversity (Fig. 2c). An overall negative response of terrestrial taxa to dam creation was reported in >75% of studies, and these negative responses were seen across all habitat types, ecological metrics, and taxonomic groups investigated (Fig. 2a-c). Overall positive responses were confined to only two of the 100 studies (Fig. 2a), of which one reported increased and more stable population densities of small mammals (Adler, 1996), and the second, increased food resources for a raptor due to prey being ‘captive’ on isolated islands (Benchimol and Venticinque, 2010). Studies report results for islands isolated from <1 to 92 years, with the mean island isolation age of ~33 years (Fig. 2d).

3.2. Species richness analysis

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

For all taxonomic groups and dams, species richness declined with island isolation time, with larger islands retaining more species than smaller islands (Fig. 3): predicted S_{RICH} on the largest island (1690 ha, Balbina hydroelectric dam, Brazilian Amazon) is predicted to be 3.2 at the mean isolation time of islands in the analysis compared to a predicted S_{RICH} of 1.2 on the smallest island (0.17 ha, Cabra

Corral, Argentina). Even the largest island (1690 ha) exhibits reduced species richness compared to mainland continuous habitat in less than 30 years of isolation; Barro Colorado Island (~1500 ha, Gatun Lake, Panama) isolated for the longest period in our study (~92 years) similarly shows sustained species richness declines.

The estimates for the random effect of DAM (BLUPs) showed for the majority of dams (66%) lower species richness levels than the overall intercept estimated by the fixed effects; only islands in Gatun Lake, Balbina, and Thousand Island Lake maintain higher species richness than the modelled fixed effects intercept (Fig. 3; Table B3). Using our model we can predict S_{RICH} values for islands of mean area at a given isolation time, and islands of different areas at the mean isolation time for each reservoir. For example the S_{RICH} for mean island size within Gatun Lake reduces from 2.24 at five years of isolation to 1.49 after 90 years of isolation; in Lake Kenyir, which maintains the lowest expected species richness values, a small island of 5ha (at mean island isolation time) has a predicted S_{RICH} value of 1.35, with is increased to just 2.23 on an island of 1000 ha. There was no evidence that islands located nearer other terrestrial habitat or mainland continuous habitat had reduced levels of species loss.

4. DISCUSSION

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

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

4.1. Island species richness, area, and isolation time

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

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

In the case of reservoir islands, remnant terrestrial habitat fragments are surrounded by a high-contrast, inhospitable matrix, presenting a prohibitive dispersal barrier for certain taxa. Such an extreme dispersal barrier effectively renders all islands as too isolated for any “rescue effect” from wider species source pools to maintain island communities and species richness, and explains the lack of distance effects we find in our analysis (Watson, 2002). The evolutionary history and traits of species resident in continuous habitats make many incapable of dispersing through open habitats, across large distances, or through a high-contrast matrix such as land and water (see Fig. 2 in Ewers & Didham, 2006). The ability of tropical understorey bird species to disperse across a water matrix between islands was tested in Gatun Lake, Panama, where some species were limited to <100m of flight (Moore et al., 2008). Species reliant on continuous habitats can be averse to crossing even small clearings, such as logging roads, even when the forest canopy is closed (Develey & Stouffer, 2001; Laurance et al., 2004).

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

We find a reduction in species richness on all islands with increasing time since initial habitat loss. Such a pattern of sustained and delayed species loss is indicative of extinction debt (Tilman et al., 1994; Kitzes & Harte, 2015; Kuussaari et al., 2009). Extinction debts are especially high in areas subject to recent large-scale habitat loss, such as islands created by rapid flooding of terrestrial habitats (Hanski and Ovaskainen, 2002). Our analysis illustrates that reservoir islands are of limited long-term conservation value due to evidence of an extinction debt: species loss appears most rapid on smaller islands and even the largest islands studied (~1690 ha) exhibited lowered species richness in under 30 years of isolation. Ongoing species losses have been reported on another large island in our synthesis: Barro Colorado Island (BCI, ~1500 ha) has been isolated for 92 years since the formation of the Gatun Lake, Panama. In less than a century of island isolation, and despite strict environmental protection of BCI and surrounding peninsulas, 65 bird species (Robinson, 1999) and 23 butterfly species (Basset et al., 2015) have become locally extinct, alongside long-term degradation of the tree community (Leigh et al., 1993). In the Balbina hydroelectric megadam system in Amazonia, to conserve >80% of terrestrial and arboreal vertebrates on islands, a threshold island size of 475 ha was identified by Benchimol & Peres (2015b). However, only 25 out of 3546 islands in the Balbina archipelago meet this size criterion. Balbina is protected by the largest biological reserve in Brazil, and thus represents a best case scenario for biodiversity conservation within an artificial archipelago system. Species inhabiting other such systems, without protection, will therefore likely suffer not only from direct habitat loss through flooding and potential extinction debt, but additional human-mediated impacts such as deforestation, agriculture, hunting, and fire (Laurance, 2008; Peres, 2001).

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

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

Data for island taxa in artificial archipelagos come from snapshots of responses to isolation in <100 years of reservoir lifetime, across multiple taxa and habitat types. In addition, no studies monitored changes in insular community dynamics over a significant post-isolation time. Consequently, we cannot currently determine if the rates of local species loss are predictable beyond the relatively short time frame analysed here. Nor can we accurately quantify extinction debt to predict the eventual number of species able to persist in the artificial archipelago systems created due to the assumptions that would be required to do so. Further long-term monitoring of reservoir island biota is needed to allow these more detailed assessments to be made, since at present only Gatun Lake, Panama, provides data for a reservoir >90 years of age.

4.2. Conservation implications

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

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

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

4.3. Conclusions

We have shown that there is an overall negative response of terrestrial species and communities to isolation on reservoir land-bridge islands. These trends are seen across a broad spectrum of taxonomic groups and ecological metrics. Species isolated on reservoir islands will likely experience extinction debt, and the rate of local extinctions is driven by island size and island isolation time, independently of distance from potential source populations within the landscape. Our synthesis of current literature allows broad conclusions about the ecological impacts of reservoirs through time, and highlights the need for further research from a greater number of reservoirs over the duration of their lifetime. Building upon the findings that we present here, investigation of the many other direct and indirect ecological impacts of reservoirs such as loss of river habitats and connectivity, land tenure rights, and the impacts of wider infrastructure development on surrounding habitats, should be a priority for future research.

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FIGURES

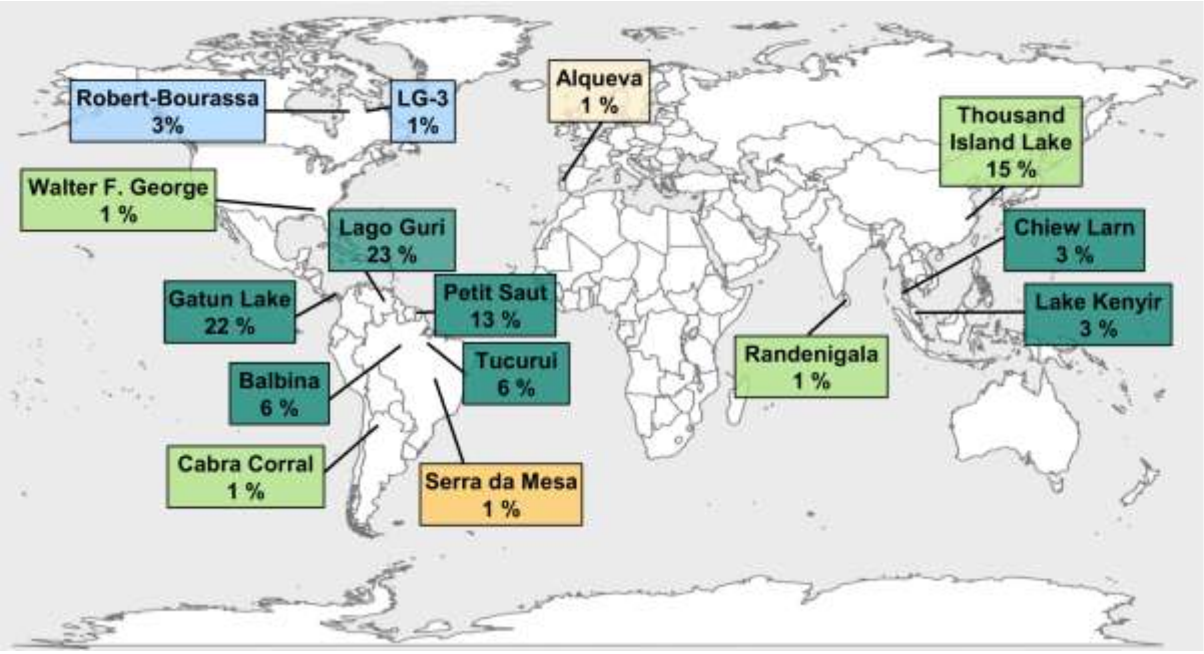

Figure 1: Geography of research detailing responses of terrestrial taxa to isolation on reservoir land-bridge islands. Dam names and the percentage of total dataset studies (n = 100) originating from each are presented. Broad habitat type is indicated by colour: dark green = wet tropical forest; light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

[2 column fitting]

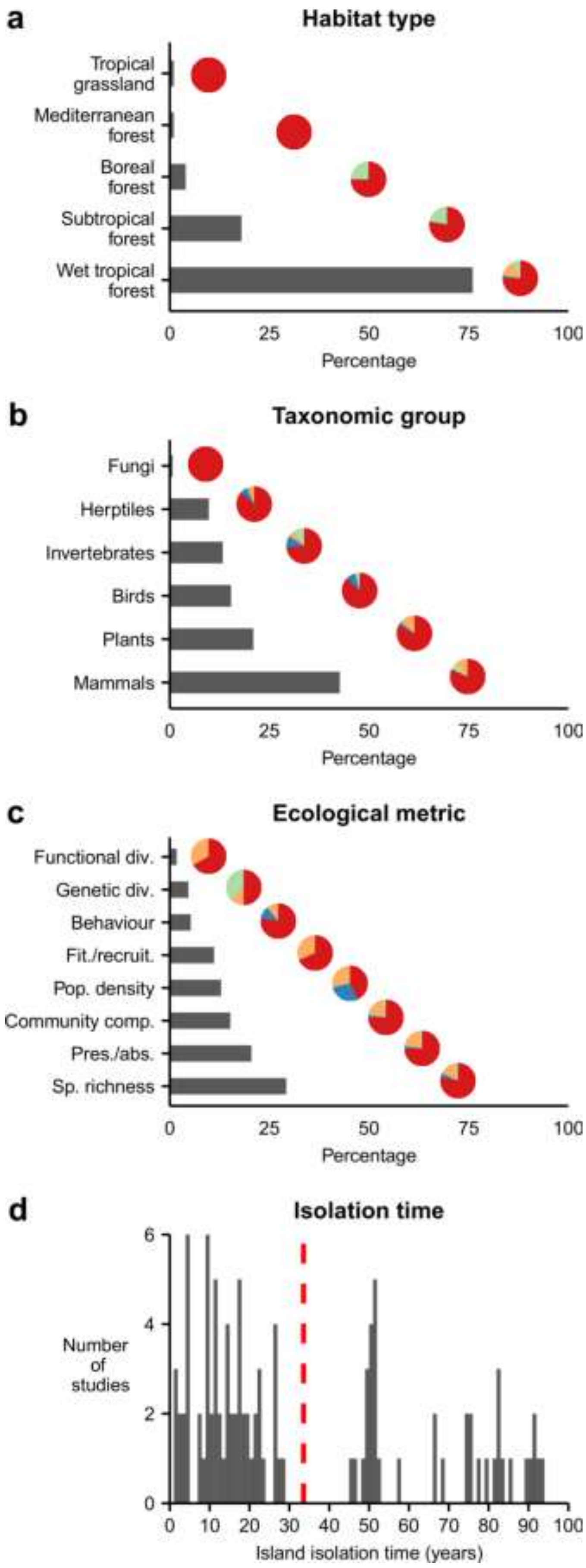
a
Habitat type
Tropical grassland
Mediterranean forest
Boreal forest
Subtropical forest
Wet tropical forest
0
25
50
75
100
Percentage
b
Taxonomic group
Fungi
Herptiles
Invertebrates
Birds
Plants
Mammals
0
25
50
75
100
Percentage
c
Ecological metric
Functional div.
Genetic div.
Behaviour
Fit./recruit.
Pop. density
Community comp.
Pres./abs.
Sp. richness
0
25
50
75
100
Percentage
d
Isolation time
Number of studies
0
2
4
6
0
10
20
30
40
50
60
70
80
90
100
Island isolation time (years)

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

[Single column fitting]

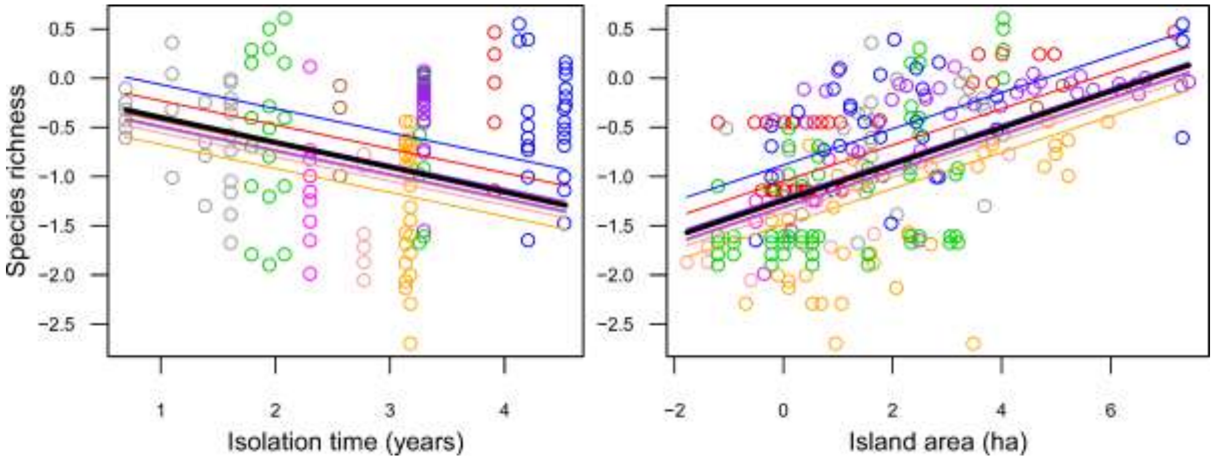

Figure 3: Analysis of species richness (S_{RICH}) data from 249 islands and 84 control sites available from nine dams in three broad habitat types (wet tropical forest, subtropical forest, and tropical grassland), modelled with time since island isolation (T_{ISO}) and island area (AREA). Bold black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

[2 column fitting]

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

[Single column fitting]

APPENDINX A

Full reference list for Database A

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APPENDIX B

Table B1

Summary of research articles used in the species richness analysis. For full references, see reference list below Table A1

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

Table B2

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

Fixed effects	Estimate	SE	t-value	df	x^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

Table B3

Intercepts for the best linear unbiased predictors (BLUPs) for each dam generated using the ‘ranef’ function in lme4 (Bates et al., 2014).

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