Biological Conservation 214 (2017) 55–65

Contents lists available at ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/biocon

Non-random lizard extinctions in land-bridge Amazonian forest islands after 28 years of isolation

Ana Filipa Palmeirim[a,b,*], Marcus Vinícius Vieira[a], Carlos A. Peres[b]

[a] *Laboratório de Vertebrados, Departamento de Ecologia, Universidade Federal do Rio de Janeiro, CP 68020, Rio de Janeiro, RJ CEP 21941–590, Brazil*
[b] *Centre for Ecology, Evolution and Conservation, School of Environmental Sciences, University of East Anglia, Norwich Research Park, Norwich NR4 7TJ, UK*

ARTICLE INFO

Keywords:
Habitat fragmentation
Hydroelectric dams
Island biogeography
Reptiles
Species-area relationship
Thermoregulation
Trait-environment relationship

ABSTRACT

Major hydropower infrastructure has become a leading driver of biodiversity loss in the lowland tropics. Terrestrial species typically become stranded in post-isolation land-bridge islands within hydroelectric reservoirs. Understanding the resulting extinction dynamics of insular communities is critical to inform, if not to avert, the ongoing blitzkrieg of dam development. Here we assess the effects of forest patch and landscape metrics on diurnal lizard species richness and composition within the Balbina Hydroelectric Dam and surrounding areas in the Central Brazilian Amazon. This 28-yr-old dam created a reservoir of ~4438 km^2, comprising 3546 islands. We sampled 25 of these islands (0.83–1466 ha) and five mainland continuous forest sites, one of which placed along stream banks. We further related morpho-ecological traits and the geographic distribution of lizard species to the spatial metrics of islands where they occurred. Using 100 L-pitfall traps operated over 5447 trap-days, we recorded 1123 lizards from 17 taxa, two of which exclusively found along stream banks within continuous forest. Island area was the best predictor of species richness and composition. Small islands ($\leq$ 2 ha) harboured fewer than a third of all species typically observed in larger islands and continuous forest ($\geq$ 8 species), and only islands $\geq$ 100 ha retained nearly complete lizard faunas. Lizard assemblages inhabiting small, isolated islands consisted almost exclusively of an oversimplified set of widely distributed, large-bodied, habitat generalist, heliophile species associated with open areas and forest edges, and that feed on a wide spectrum of prey sizes. These wholesale changes in lizard community structure were characterized by severe losses in functional traits, and may profoundly affect ecosystem functioning.

1. Introduction

Hydropower development is currently one of the primary means of habitat loss and fragmentation in lowland tropical forests, hence a key threat to biodiversity (World Commission on Dams, 2000; Lees et al., 2016; Winemiller et al., 2016). River damming inundates low elevation areas while previous ridgetops in undulating terrain often become land-bridge islands, creating complex archipelagic landscapes within reservoirs. Currently, this is the case of at least 14 M hydroelectric dams worldwide (Jones et al., 2016). In lowland Amazonia, due to the typically flat relief, damming further creates proportionally shallow lakes that are prone to siltation, flooding vast areas and high levels of greenhouse gas emissions (Fearnside and Pueyo, 2012). Nevertheless, Amazonia is now one of the main target regions for ambitious hydropower development plans (Zarfl et al., 2014). To date, 191 dams have already been built and another 246 are planned or under construction (Lees et al., 2016).

In the aftermath of damming, the aquatic realm becomes widely degraded (Palmeirim et al., 2014; Castello and Macedo, 2015), while terrestrial habitats become extremely reduced and highly fragmented. Species diversity in newly created land-bridge islands are likely to be affected by both the remaining area, which constrains species population sizes and limits habitat diversity (Hutchinson, 1957; MacArthur and Wilson, 1967), and degree of isolation from other islands and the mainland, which affects species colonization rates (MacArthur and Wilson, 1967). Also, given increased wind damage, edge effects penetrate deeply into the islands, modifying its vegetation structure and precluding changes in the availability of trophic and structural resources (Laurance et al., 1998; Benchimol and Peres, 2015a). Species responses to habitat fragmentation largely depend on the intrinsic ecological traits of different species (Cabrera-Guzmán and Reynoso, 2012; Lion et al., 2016). For example, it is expected that forest-dependent animal species tend to disappear from structurally degraded islands (Benchimol and Venticinque, 2014). Identifying those traits that predispose species to extinction following fragmentation has important implications for proactive conservation management (Wang et al.,

---

[*] Corresponding author at: Laboratório de Vertebrados, Departamento de Ecologia, Universidade Federal do Rio de Janeiro, CP 68020, Rio de Janeiro, RJ, CEP 21941-590, Brazil.
E-mail address: anafilipapalmeirim@gmail.com (A.F. Palmeirim).

http://dx.doi.org/10.1016/j.biocon.2017.08.002
Received 18 May 2017; Received in revised form 20 July 2017; Accepted 1 August 2017

2009; Carvajal-Cogollo and Urbina-Cardona, 2015).

Our knowledge to date on the ecological impacts of reservoir creation is disproportionately focussed on mammals and birds, while lizards have been considered in only one-tenth of all impact studies (Jones et al., 2016). Yet lizards, and reptiles in general, include the most threatened and least studied terrestrial vertebrate taxa (IUCN, 2015) and their global scale declines have been mainly attributed to habitat loss and degradation, including habitat fragmentation (Gardner et al., 2007a; Todd et al., 2010; Böhm et al., 2013). Lizards are ectothermic, often specialized on a substrate type, and typically exhibit low dispersal capacity (Garda et al., 2013), all of which render them dependent on specific microhabitats and climatic conditions. They play important roles in natural ecosystems as predators, prey, grazers, seed dispersers and commensal species. Also, due to their specific microhabitat associations, lizards are thought to be good ecological indicators of habitat quality (Silva, 2005; Todd et al., 2010).

Amazonian lizard communities are usually rich and structurally complex (Martins, 1991). Individual species are separated on the basis of food and microhabitat types, which are closely linked to their metabolism (Vitt et al., 1999). Two thermoregulation modes or strategies to maintain their body temperature can be recognized for diurnal forest lizards: heliophile species that expose themselves to direct sun-flecks, and heliophobe species that, instead, avoid direct exposure to sun light (Martins, 1991; Vitt et al., 1998). Warm-adapted lizards also tend to be larger-bodied and feed on a variety of arthropods and smaller vertebrates (Vitt et al., 1998), usually corresponding to generalist species.

Here we assess the influence of forest patch and landscape metrics on the species richness and composition of insular lizard assemblages within the Balbina Hydroelectric Dam of Central Brazilian Amazonia. The Balbina reservoir comprises an area of 443,772-ha, including 3546 land-bridge forest islands. This study was carried out following a 28-year island post-isolation history and uncovers processes that could occur in similar artificial archipelagic landscapes that are currently proliferating throughout the Amazon (Lees et al., 2016). Along the island size gradient, we further examined (1) species abundance and biomass, considering species with contrasting thermoregulation modes separately; (2) the corresponding rank-abundance distribution curves; and (3) the relationships between morpho-ecological traits and the geographic distribution of lizard species and the spatial metrics of sites where they occurred. Overall, we predicted that ‘sun-loving’, widely distributed, large-bodied species with generalist habits were likely to dominate highly disturbed small forest islands, whereas the diversity of all functional groups should only accumulate in considerably larger islands and continuous forest sites, because those will also include shade-tolerant, narrow range, small-bodied specialists.

2. Methods

2.1. Study landscape

This study was carried out in the archipelagic landscape of the Balbina Hydroelectric Reservoir and its surrounding mainland areas in the Central Brazilian Amazon (1°48′S, 59°29′W; Fig. 1). The Balbina Dam was built in 1987 on the Uatumã River, a left-bank tributary of Amazon River. Given the typically undulating topography of the inundated area, this dam flooded a vast area, with its reservoir comprising 443,772-ha (FUNCATE/INPE/ANEEL, 2000). In the aftermath of damming, the former hilltops of the pre-inundation forest area were converted into 3546 land-bridge islands widely distributed throughout the reservoir lake. Although some islands are large (e.g. 4860 and 4878 ha), most of them are relatively small, with 94.7% smaller than 100 ha (Fig. 1). Within the wider open-water matrix, dead relics of large canopy trees still remain standing, as the vegetation of the submerged area was never cleared, except for the area immediately adjacent to the dam. As the inundated landscape matches lower elevation areas, most of which corresponded to riparian areas prior to damming, this habitat type virtually vanished from entire archipelago. The mean annual temperature in this region is 28 °C and the mean annual rainfall is 2376 mm (IBAMA, 1997). The area within and around the former left bank of the Uatumã river was legally protected since the dam was built by the 942,786-ha Uatumã Biological Reserve, the largest reserve in its category in Brazil. This reserve largely explains the reasonably low levels of post-damming anthropogenic disturbance throughout the study landscape.

Terrestrial diurnal lizard assemblages were sampled at 25 islands previously selected according to its size, isolation and spatial distribution, so a wide range of island configurations within the reservoir could be accomplished. Sampled islands ranged in island area from 0.83 to 1466 ha (Table A.1) and distances to continuous forest (CF) from 10 to 11,885 m. We further sampled five sites (i.e. blocks of trapping-arrays) within four mainland CF regions that were widely distributed in the adjacent mainland (Fig. 1). Three of the sites were placed within 1500 m from reservoir margin (CF_1, CF_3 and CF_4) and two farther than 2000 m (CF_2 and $CF_{2\text{-riparian}}$). These two additional sites were located in the same region, but one was positioned alongside riparian forest habitat along a ~7 m-wide perennial stream. Due to logistic constraints, riparian habitat could not be sampled at other CF regions, so that our CF samples consist of four upland sites that matched the topography of island samples (CF_1–CF_4) and one riparian site ($CF_{2\text{-riparian}}$).

2.2. Lizard sampling

At each sampling site, trapping plots were 60-m long in total length, composed of three pitfall traps (buried 100 L buckets) spaced 20-m, but connected by a 50-cm high plastic fence. An additional 10-cm of plastic fencing was buried underground, thereby deterring leaf-litter lizards from crossing the pitfall-trap-line. The number of trapping plots placed at each site was proportional to its area. This allowed us to obtain a significantly larger number of individuals at larger forest sites, where trap density, and consequently the probability of an individual passing near a trap, was much lower (Table A. 1). Due to spatial restrictions in small islands, alternative smaller plots were established therein. Thus, all islands smaller than 2 ha and those between 2 and 10 ha were sampled by trapping plots of only one and two pitfall arrays, respectively. Larger islands were sampled by as many as four trapping plots, according to their size categories: 10 to 50 ha, 50 to 200 ha, 200 to 500 ha and > 500 ha, respectively; CF sites were sampled by either four ($n = 3$) or six trapping plots ($n = 2$; for further details on sampling effort per site, see Table A.1).

We sampled a total 5447 trap-days across 71 trapping plots which were sampled twice during 16 consecutive days at each site, from April to November in 2014 and the same season in 2015, except for four CF sites (CF_1, CF_2, $CF_{2\text{-riparian}}$ and CF_4). Due to logistic restrictions, those CF four sites were only sampled during either the first (2014) or second (2015) field season (Table A.1). All traps were checked daily and four voucher specimens of each species were deposited at the herpetofaunal collection of the National Institute of Research of the Amazon (Instituto Nacional de Pesquisas da Amazônia – INPA), Manaus, Brazil. In addition, during the second field season we collected tissue samples for genetic analyses by carefully removing the tail tip of every individual. This further allowed us to distinguish individuals that had been previously captured. As observed during the second field season, recaptures corresponded to a small fraction of the total number of records (< 2%), with only three species being recaptured – *Ameiva ameiva* (recapture rate = 6.1%), *Arthrosaura reticulata* (0.8%) and *Kentropyx* spp. (2.7%). For this reason, all individuals recorded during the first field season were assumed to have been captured only once. Furthermore, captures representing the genera *Leposoma* spp. (*L. percarinatum* and *L. guianense*), *Norops* spp. (*N. planiceps* and *N. chrysolepis*), and *Kentropyx* spp. (*K. calcarata* and *K. altamazonica*) could not be identified to species level at all sampled sites. As congeners within those genera are ecologically very similar (Ávila-Pires, 1995), we hereafter