Biological Conservation 187 (2015) 61–72

Contents lists available at ScienceDirect

Biological Conservation

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

Predicting local extinctions of Amazonian vertebrates in forest islands created by a mega dam

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ARTICLE INFO

Article history:
Received 18 December 2014
Received in revised form 30 March 2015
Accepted 9 April 2015

Keywords:
Biodiversity
Habitat fragmentation
Landscape structure
Life-history traits
Mammals
Occupancy

ABSTRACT

Hydropower projects are rapidly expanding across lowland Amazonia, driving the conversion of large tracts of once-continuous forests into archipelagos embedded within a vast open-water matrix. Forest vertebrate populations thus become stranded in habitat islands, with their persistence governed by a combination of species life-history traits, habitat patch, and landscape context. We investigate the patterns of species extinction of 34 arboreal and terrestrial vertebrate species within three continuous forest sites and 37 land-bridge islands within one of the largest South American hydroelectric reservoirs, based on a combination of camera trapping, line-transect censuses, sign surveys, and armadillo burrow counts. Forest area was the best predictor of species persistence, so we classified all species into three levels of vulnerability to habitat insularization, with most species defined as 'area-sensitive'. However, island occupancy was decisively determined by individual species traits, with wide-ranging species and poor dispersers showing high local extinction rates. We detected higher island occupancy rates of large vertebrate species compared to other Neotropical fragmented forest landscapes, suggesting that this is critically attributed to the absence of hunting pressure at Balbina. Nevertheless, most terrestrial and arboreal species have been driven to local extinction within the vast majority of islands, which have been largely defaunated. We predicted species composition across all 3546 islands within the reservoir, indicating that only ⩽2% of all islands continue to harbour at least 75% of all species. To minimise loss of vertebrate diversity, future hydroelectric dam projects in lowland tropical forests, if unavoidable, should consider their geographic location and landscape structure to maximise both island size and landscape connectivity, and set aside strictly protected reserves within reservoir areas.

1. Introduction

Mega hydroelectric dams have become a major driver of forest habitat loss and fragmentation across several Amazonian river basins, with dozens of new major hydropower projects either planned or currently under construction (Finer and Jenkins, 2012; Fearnside, 2014). In Brazilian Amazonia, a total of 1,105,400 ha of pristine forests have already been inundated by eleven major hydroelectric dams (ECOA, 2012), but over 10 million ha of forests are expected to become permanently inundated following the planned construction of new dams (Fearnside, 2006). Assessments of the social and environmental impacts of large dams worldwide have so far primarily focused on flooding of indigenous territories and displacements of local communities (Esselman and Opperman, 2010), alterations in fluvial hydrology (Nilsson et al., 2005), augmented emissions of greenhouse gases (Almeida et al., 2013), and losses in fisheries and aquatic biodiversity (Barthem et al., 1991; Alho, 2011; Liermann et al., 2012; Palmeirim et al., 2014). In contrast, the performance of terrestrial vertebrate populations in tropical ecosystems affected by dams has received comparatively little attention (but see Terborgh et al., 1997; Cosson et al., 1999; Gibson et al., 2013; Benchimol and Venticinque, 2014). Given hugely escalating investments in hydropower infrastructure worldwide, impact assessments of mega-dams on terrestrial biodiversity in many terrestrial systems, including the Amazonian basin, are conspicuously missing.

As mega-consumers and apex predators, large-bodied vertebrates are often considered as good bioindicators of intact tropical forests, as they provide key ecological services for ecosystem dynamics and are sensitive to forest disturbance and hunting

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http://dx.doi.org/10.1016/j.biocon.2015.04.005

(Dirzo et al., 2014). Local extinctions from forest patches can induce a series of trophic cascades, promoting unexpected shifts in forest composition and function. For instance, predator-free land-bridge islands in Venezuela are typically denuded by hyperabundant herbivores, decimating seedling recruitment of canopy trees (Terborgh et al., 2001). Also, rising floodwaters drastically reduced vertebrate species diversity in newly formed islands compared to continuous forest areas only four years after French Guiana's Petiti Saut Dam was built (Cosson et al., 1999), suggesting that isolation effects in true islands are more severe than in habitat patches surrounded by a non-water matrix.

Newly isolated vertebrate assemblages could undergo nonrandom drifts in species composition within tropical land-bridge islands following a long relaxation time, but this is a function of species-specific responses to patch- and landscape-scale variables and life-history traits. Vertebrate persistence in Neotropical fragmented landscapes is likely to be affected by landscape structure and the history of human disturbance (Michalski and Peres, 2005; Canale et al., 2012), with a range of species responses to habitat fragmentation. Rare, matrix-intolerant species unable to disperse amongst remnant patches are usually considered more extinction-prone in fragmented landscapes (Davies et al., 2000; Henle et al., 2004). Hence, some life-history traits can be excellent predictors of forest patch occupancy, and coupled with patch and landscape-scale site attributes, can help predict species survival within forest remnants and inform species-specific conservation guidelines.

Here, we assess how 34 terrestrial and arboreal vertebrate species responded to the insularization process induced by a major hydroelectric dam in lowland Central Amazonia, based on intensive, well-replicated field surveys in a large number of islands and neighbouring continuous forests. Specifically, we examine (1) the observed and estimated forest patch occupancy of each species (accounting for imperfect detection), assessing minimum critical area required to ensure their persistence; (2) how different patch, landscape and habitat quality metrics affect patterns of occupancy for individual species; and (3) the relative importance of landscape context and species traits in explaining pattern of local extinction across all islands. Based on these results, we predict the aggregate vertebrate species richness and composition across >3500 islands within the reservoir, pinpointing priority sites for conservation, and dissect how large hydroelectric dams affect terrestrial vertebrate diversity in lowland Amazonia.

2. Material and methods

2.1. Study area

This study was conducted within the Balbina Hydroelectric Reservoir (BHR), a man-made reservoir within the Uatumã River basin of central Brazilian Amazonia (1°48″S; 59°29′W). The Balbina Dam was completed in 1986 to supply hydropower to Manaus, the state of Amazonas capital city. The rising floodwaters inundated an area of 312,900 ha, resulting in the formation of 3546 land-bridge islands ranging in size from <1 to 4878 ha. In 1990, the lake became protected by the creation of the ~940,000-ha Uatumã Biological Reserve, the largest protected area of this type in Brazil. Most islands consist of dense closed-canopy *terra firme* forest. There is no history of logging nor hunting in the study area within the reservoir (Benchimol and Venticinque, 2014), but many islands experienced ephemeral understorey fires during the El Niño drought of late-1997 to early-1998 (Benchimol and Peres, 2015).

We conducted intensive vertebrate surveys within a subset of 37 islands and three widely spaced neighbouring continuous forest sites adjacent to the lake, which were spaced by at least 1 km from one another, spanning a study area of 396,400 ha (Fig. 1). Islands were selected on the basis of their size, isolation and spatial distribution, to represent a wide range of island configurations within the reservoir. We assigned arbitrary area values of one order of magnitude greater than our largest island for mainland continuous forest sites. Surveyed islands ranged in forest area from 0.55 to 1685.38 ha, and isolation distances from each focal island to the nearest mainland continuous forest ranged from 40 m to 17.73 km (Table 1).

2.2. Vertebrate sampling

We used a combination of four different sampling techniques to determine occupancy of the midsized to large-bodied vertebrate fauna at each island and mainland site between June 2011 and December 2012: camera trapping, line-transect censuses, sign surveys, and armadillo burrow counts. These methods were selected considering the wide range of ecological and behavioural characteristics of target species, with different activity times (diurnal, nocturnal and cathemeral), and use of vertical space (terrestrial, arboreal and scansorial). Indeed, all of these methods have been widely used for quantitative surveys (see Silveira et al., 2003; Michalski and Peres, 2007; Munari et al., 2011; Thornton et al., 2011a, 2012). Although nocturnal line transect censuses have been used as a complementary wildlife survey technique in tropical forests, this provided little additional information for most nocturnal species in a pristine Amazonian landscape (Munari et al., 2011) so we opted not to conduct night surveys on foot. We restricted surveys to non-flying medium- and large-bodied terrestrial and arboreal mammals (except sloths), terrestrial birds and tortoises, which were widely distributed across the study landscape. Only tortoise congeners (*Chelonoidis carbonaria* and *Chelonoidis denticulata*) were pooled under a single genus, given that they could not usually be identified to species and their strong ecological similarities. To facilitate surveys, we cut linear transects of 0.5–3 km in length at each island, according to island size and shape, so that a representative island area could be covered (see Table A1). On each continuous forest site, three parallel 4-km linear transects were established, separated from each other by 1 km (Fig. 1).

We deployed two to ten *Reconyx Hyperfire* camera traps (hereafter, CTs) at each island according to its size, and 15 CTs at continuous forest sites (five along each transect) to maximise the heterogeneity of environments sampled in each survey site and minimise variation in density of CT stations (Table A1; Michalski and Peres, 2007). In all sites, CTs were deployed for two continuous periods of 30 days each. We placed unbaited CTs 30 cm above ground along transects, spaced by at least 500 m (except for small islands). We configured each CT to obtain a sequence of five photographs for each animal or animal cluster recorded, using 15-s intervals between records. Additionally, we conducted eight visits including line-transect surveys per island, each of which at different times either in the morning (06:15 h to 10:30 h) or afternoon (14:00 h to 17:30 h), following standardised guidelines proposed by Peres (1999). Two trained observers walked quietly at a constant speed (~1 km/h) on all transects established on each site. We recorded all visual or acoustic encounters of individuals or groups of any target species. On return walks along each transect, we conducted sign surveys, intensively searching for any indirect evidence of any target terrestrial species, including tracks, superficial digging, burrows, fecal material, hair, and partly consumed fruits/seeds. Finally, we searched for armadillo burrows to enhance our detection and identification of the four armadillo species occurring in the study area. In doing so, we searched all burrows ⩾50 cm depth within a 5-m strip either side of each transect and measured them following Michalski and Peres (2007). This was done during return census walks, but only once per transect per survey session, during the first day of censuses. In total,