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Forest patch isolation drives local extinctions of Amazonian orchid bees in a 26 years old archipelago

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A B S T R A C T

Major hydroelectric dams are among key emergent agents of habitat loss and fragmentation in lowland tropical forests. Orchid bees (Apidae, Euglossini) are one of the most important groups of specialized pollinators of flowering plants in Neotropical forests. Here, we investigate how an entire assemblage of orchid bees responded to the effects of forest habitat loss, isolation and forest canopy degradation induced by a hydroelectric reservoir of Central Brazilian Amazonia. Built in 1986, the Balbina Dam resulted in a vast archipelagic landscape containing 3546 primary forest islands of varying sizes and isolation, surrounded by 3129 km^2 of freshwater. Using scent traps, we sampled 34 islands, 14 open-water matrix sites, and three mainland continuous forests, yielding 2870 male orchid bees representing 25 species. Local orchid bee species richness was affected by forest patch area but particularly by site isolation. Distance to forest edges, either within forest areas or into the open-water matrix, was the most important predictor of species richness and composition. Variation in matrix dispersal of individual species to increasingly isolated sites was a key determinant of community structure. Given the patterns of patch persistence and matrix movements of orchid bees in increasingly fragmented forest landscapes, we outline how forest bees respond to the landscape alteration induced by major hydroelectric dams. These results should be considered in environmental impact studies prior to the approval of new dams.

1. Introduction

Hydroelectric dams are among the new leading drivers of tropical forest fragmentation and biodiversity loss (Lees et al. 2016). Hydropower reservoirs often inundate vast areas of once continuous lowland primary forest that become subdivided into upland forest patches of different sizes, shapes and degrees of isolation (Nilson et al., 2005; Finer and Jenkins, 2012). Major hydropower infrastructure projects are expected to proliferate in the future given renewed ‘clean-energy’ subsidies, with some 277 additional dams expected to be constructed in the next two decades across the Amazon Basin, 30 of which > 20 MW in installed capacity (Fearnside, 2014; Lees et al., 2016).

Forest habitat fragmentation is a key threat to tropical biodiversity and one of the main drivers of native pollinator declines (Potts et al., 2010; Viana et al., 2012). Changes in landscape structure and configuration of habitat patches affect the movements of wide-ranging pollinators across hostile matrix habitats (Lennartsson, 2011). Bees are considered the most important group of directional pollen vectors in tropical forests (Bawa, 1990), and often decline in numbers and species diversity in fragmented landscapes created by varying degrees of deforestation and matrix permeability (Brosi, 2009; Steffan-Dewenter et al., 2002).

Patterns of local habitat occupancy and colonization-extinction dynamics are often driven by patch isolation, the structure of the intervening matrix, and edge effects, all of which affect how species express their inherent dispersal capacity (Ewers and Didham, 2006). Dispersal movements between patches are critical for long-term species persistence in newly fragmented landscape (Bommarco et al., 2010). However, species vary widely in their intrinsic susceptibility to habitat isolation according to their dispersal capacity, perception of habitat boundaries, and tolerance of edge effects. Species are typically most affected by edge effects in patches where the structural contrast of the patch-matrix interface is greatest (Perfecto and Vandermeer, 2002; Didham et al., 2012). Some species, however, can easily move between habitat patches and are thus largely unaffected by isolation (Hanski and Ovaskainen, 2000). On the other hand, species unable to traverse an

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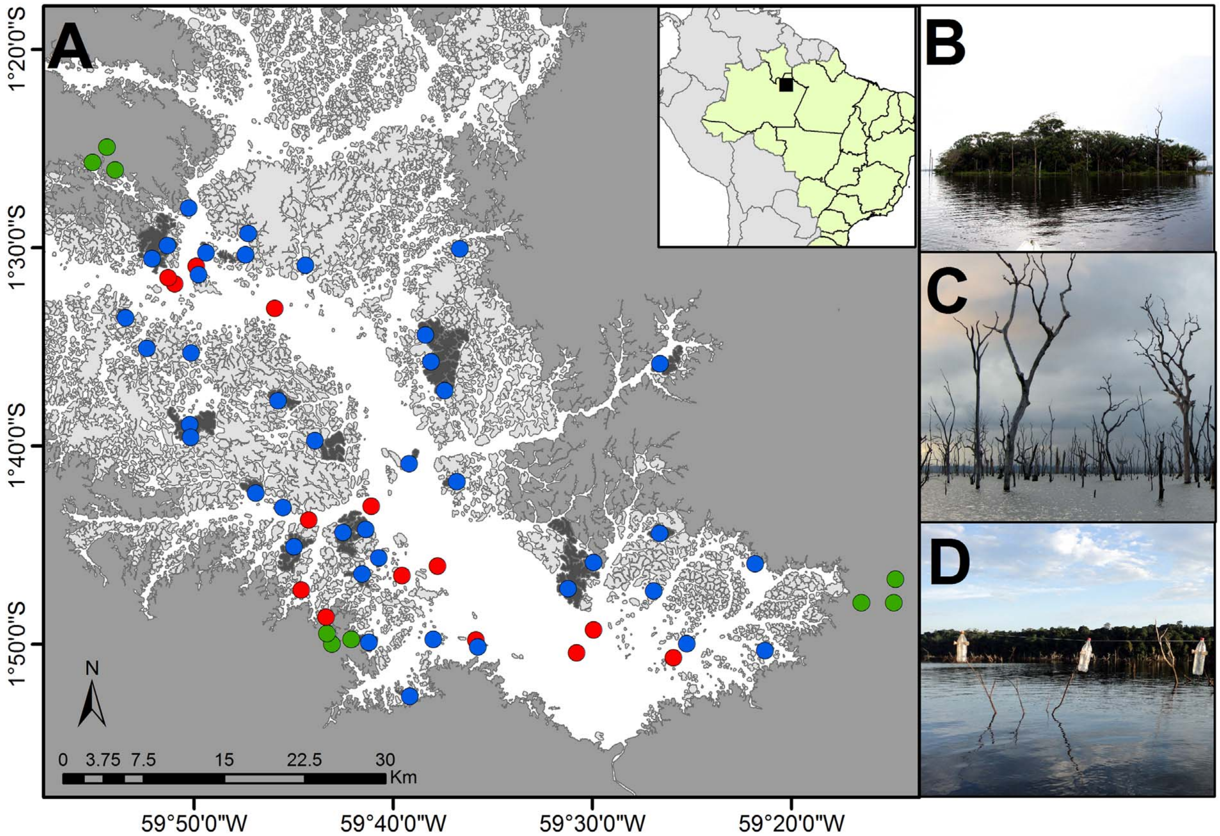

Fig. 1. (A) Study area showing the spatial distribution of the trapping sites (solid circles) throughout the Balbina Hydroelectric Reservoir Landscape (BHRL) of Central Brazilian Amazonia. Three mainland sites (green circles), 14 open-water matrix sites (red circles), and 34 [of the 3546] islands (blue circles) across the reservoir archipelago were sampled. Surveyed islands, unsurveyed islands, and the surrounding matrix of undisturbed continuous forest are shown in dark grey, light grey and intermediate grey, respectively; (B) small isolated islands within the reservoir; (C) typical open-water matrix, showing a large number of standing dead trees representing the decomposing necromass across vast areas of open water; and (D) trap-array in the open-water matrix, showing an Euglossine bee scent trap. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

inhospitable matrix may continue to persist as isolated populations in suitable patches, but cannot rescue local extinction events in less suitable patches (e.g. Lees and Peres, 2009). Dispersal capacity also modulates the shape of species-area relationships, which are expected to be weakest when matrix movements are frequent, but steepest when matrix movements are prohibitive (Benchimol and Peres, 2013; Öckinger and Smith, 2006).

Euglossine or orchid bees (Apidae, Euglossini) represent one of the most specialized groups of tropical forest pollinators (Dressler, 1982; Roubik and Hanson, 2004). The ecology of euglossines remains poorly investigated but both males and females visit flowers of several plant families, particularly the Orchidaceae, from which males collect odoriferous substances. Although the biological functions of those compounds remain unclear, they are apparently used as sexual attractants in chemical communication prior to mating (Roubik and Hanson, 2004). Over 200 euglossine bee species are distributed from northern Argentina to the southern United States, but are most diverse in lowland Amazonia (Dressler, 1982; Roubik and Hanson, 2004), the world's largest tropical forest stronghold. Some species can fly across wide gaps between habitat patches in fragmented landscapes (Janzen, 1971; Wikelski et al., 2010), which may reflect the patchy spatial distribution of their floral resources in continuous forests. Evidence of genetic differentiation in *Euglossa cordata* at three Atlantic Forest islands and a mainland forest site indicates that gene flow across open-water is undeterred by distances of ~2 km, but gaps of 7–11 km represents a significant dispersal barrier (Boff et al., 2014). However, species-specific patterns of forest patch occupancy and dispersal across a non-forest matrix remains poorly understood, particularly for entire local assemblages.

Several studies have examined the effects of forest habitat loss and fragmentation on euglossine bees (Aguiar and Gaglianone, 2012; Becker et al., 1991; Brosi, 2009; Gonçalves et al., 2014; Morato, 1994; Nemésio and Silveira, 2010; Sofia and Suzuki, 2004; Storck-tonon et al., 2013). Although these studies have shown that some orchid bee species can persist in small, degraded forest patches and use non-forest areas, most species are restricted to large areas of mature forest habitats (Roubik and Hanson, 2004, p.154). However, the effects of forest habitat fragmentation on bee assemblages remain inconclusive because all fragmentation ecology studies to date addressing tropical bees have been conducted in terrestrial landscapes where forest fragments are surrounded by a structurally heterogeneous vegetation matrix of pastures, scrub, and young second-growth, where forest patch isolation is not as effective as in true islands (MacArthur and Wilson, 1967). In contrast, archipelagos created by major hydroelectric dams present a unique opportunity to investigate forest fragmentation effects on tropical biotas because habitat patches in these landscapes were isolated simultaneously by a uniform open-water matrix following dam closure. Indeed, these land-bridge island systems have a number of experimental advantages over terrestrial fragmented landscapes, with significant consequences to residual faunas of volant, arboreal and strictly terrestrial organisms (Mendenhall et al., 2014).

Here, we examine the community-wide responses of euglossine bees to forest insularization induced by a mega hydroelectric dam to assess changes in community structure of this emblematic group of pollinators. We conducted standardized quantitative inventories of orchid bees in a large set of continuous forest, water matrix, and island sites, following 26 years of isolation. We also examine the effects of patch and landscape metrics on orchid bee species occupancy and assemblage