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

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ABSTRACT

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 3,546 primary forest islands of varying sizes and isolation, surrounded by 3,129-km^2 of freshwater. Using scent traps, we sampled 34 islands, 14 open-water matrix sites, and three mainland continuous forests, yielding 2,870 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.

Keywords: habitat fragmentation; hydroelectric dams; landscape ecology; island biogeography; Euglossini

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 >20MW 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 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 & 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 structure, and consider the degree to which forest patch quality can further explain bee community structure.

2. Methods

2.1 Study Area

The Balbina Hydroeletric Reservoir Landscape (BHRL) is located along the Uatumã River, some 180km northeast of Manaus, Amazonas, Brazil (1°48’S, 59°29’W; Fig. 1). The dam was closed in October 1986, subsequently isolating 3,546 upriver forest islands within one of the largest lowland tropical forest hydroelectric reservoirs, spanning an area of 3,129 km^2 of open-water and 1,308 km^2 encompassing all islands. Over 95% of the lowland primary forest within the submerged area was not cleared prior to dam closure, resulting in a residual necromass consisting of millions of dead canopy trees, many of which are still standing throughout the reservoir (see Appendix A). Our study landscape therefore consists of thousands of islands of varying sizes, shapes and degrees of isolation, a vast surrounding matrix of open-water, and extensive areas of undisturbed continuous primary forests in the adjacent mainland, all of which protected by the Uatumã Biological Reserve (Fig. A.1).

2.2 Orchid bee sampling

Orchid bees were sampled at 34 forest islands (size range = 0.83 –1690 ha) that were spaced by at least 1 km from one another; nine mainland sites distributed across three widely spaced continuous forest areas adjacent to the reservoir; and 14 widely distributed ‘nonpatch’ open-water matrix sites (Table A.1). Sites were sampled sequentially along subregions within the reservoir, with sites near one another sampled simultaneously. Trap-arrays on islands and matrix sites were isolated from the nearest island by a mean distance of 389.9 ± 658.1m SD (range = 10 – 3,900m, *N* = 54). The number of trapping sites allocated to each forest and matrix site was proportional to their sizes: (i) matrix sites and islands <750 ha, (ii) islands between 750 and 1500 ha, and (iii) islands >1500 ha and continuous forest areas were sampled using one, two, and three trap-arrays, respectively. This amounted to a total of 63 trap-arrays distributed throughout the entire study landscape (Fig. 1).

All sites were sampled during the dry season (September 2012) and the subsequent wet season (April 2013). Male orchid bees were collected using a standardized scent trap-array, whereby a cluster of four scent-traps. Each of the four scent traps at each trap-array were baited with one of four complementary chemical lures: cineole , methyl salicylate, methyl cinnamate and vanillin. Scent traps within an array were spaced by 2 m from one another, and placed along a straight line, 1.5 m above ground at all sampling sites. The trap model was hand-made using a 2L plastic bottle that contained three entrance holes with a landing platform attached to each entrance with a mixture of glue and sand (see Sydney and Gonçalves, 2014). Open-water matrix sites used the same design, but traps were installed on dead tree branches 1.5 m above water (see Fig. A.1). During each trapping session, traps were exposed at each site for 3 consecutive days prior to collecting. All bees captured therein were deposited at the Entomological Collection of the Instituto Nacional de Pesquisas da Amazônia (INPA), Manaus, Brazil.

2.3 Landscape and patch metrics

We measured a set of environmental covariates related to our trap-arrays within forest patches, matrix sites and mainland areas. Using ArcGIS (v. 10.1), these patch and landscape metrics were extracted from a 6,980-km^2 RapidEye$^®$ mosaic (5-m resolution) of georeferenced satellite imagery overlapping the entire BHRL, including 28 juxtaposed tiles obtained from March 2011 to September 2012. Following a semi-supervised classification, we were able to classify four clearly distinguishable land-cover classes: closed-canopy forest, open-canopy forest, bare ground and open water. At the patch scale, we quantified total island area; island forest area; and the proportional area (%) comprised of closed-canopy forest pixels (30m x 30m) on the basis of preprocessed satellite images (see Benchimol and Peres 2015). In terms of landscape metrics, we quantified the straight-line edge-to-edge distance between each trap-array and the nearest continuous forest area in the mainland; the nearest neighbour distance (hereafter, NND) to any mainland area or island larger than 10ha; and the percentage of both closed-canopy and open-canopy forest cover within external buffer radii of 250m, 500m, 1000m and 2000m. These landscape buffer sizes were highly correlated ($r > 0.9$), so we used a 500-m buffer, which provided the best explanatory power across all models. We also calculated a modified proximity index (*sensu* McGarigal et al., 2002), but considered the total forest area of any land mass included within those buffers, rather than excluding any land area outside the buffer for patches contained within the buffer. We then calculated either the negative or positive straight-line distance between each trap-array and the nearest forest edge. Sampling sites within forest patches were assigned negative edge-distance values, whereas open-water matrix sites were assigned positive values. In addition, on the basis of 87 quarter-hectare (0.25 ha) permanent forest plots (sampled by Benchimol and Peres, 2015) across all forest sites, we quantified the richness and Simpson diversity of tree species, and the percentage of pre-damming old-growth canopy trees persisting at each 0.25-ha plot.

2.4 Data analysis

We initially used species-area relationships (SARs), abundance-area relationships (AARs) and linear regression models to examine how orchid bee species richness and abundance are affected by forest patch size, which was then repeated for NND and edge distance as measures of patch (or trap-array) isolation. Second, we ran three types of regression models both including and excluding matrix sites to determine to what extent forest patch area (here defined as zero for matrix sites) and isolation of trap-arrays predicted species richness and composition: (i) patch area only, (ii) site isolation only, and (iii) the interaction between area and isolation. Patch area (ha) and NND (m) were log-transformed prior to analyses to ensure direct comparison of regression coefficients; this was repeated for untransformed data, but results were similar. Due to the wide variation in the total number of bees collected at different trap-arrays and sites, we derived rarefied species richness (S_{rar}) estimates using a standardized sample size of 30 individuals per trap-array using the *vegan* package within R. We also used linear regression to examine the relationship between numbers of individuals captured and species richness, and the effects of old-growth trees on SARs, considering only islands.

We investigated abundance-based multivariate patterns of species composition (individuals captured per trap-array) using non-metric multidimensional scaling (NMDS). To assess differences in bee assemblage structure among the three types of landscape units (islands, mainland, and matrix) we used permutational multivariate analysis of variance (PERMANOVA) using the *adonis* and *betadisper* functions within the *vegan* package in R (Anderson and Braak, 2003; Oksanen et al., 2012). Permutational analysis of multivariate dispersion (PERMDISP: Anderson, 2006) was also used to investigate whether separations between landscape unit groupings indicated by PERMANOVA were affected by between-group differences in dispersions. SIMPER analysis was also used to identify those species that most contributed to compositional differences between landscape units (Oksanen et al., 2012). Prior to analysis, data were Hellinger-transformed to downweight the influence of rare species (Legendre & Gallagher, 2001).

We further performed Generalized Linear Models (GLMs) to investigate the effects of patch and landscape metrics on species richness and species composition, using a Gaussian error structure and the *MumIn* package within R (Barton, 2016), both including and excluding the matrix sites, to examine the strength of forest patch, landscape metrics, and forest habitat quality predictors of orchid bee species richness and composition. We tested for multicollinearity among variables using the Variation Inflation Factor (VIF) and excluded those variables that were excessively collinear (VIF ≥ 5). We selected the most parsimonious "best" models ($\Delta AIC_c < 2.0$) based on a multimodel approach and the Akaike Information Criterion for small sample sizes (AIC_c). We also integrated geographic coordinates of trap-arrays (UTM_x, UTM_y) as isotropic smooth terms into Generalized Additive Models (GAMs) to account for structural spatial gradients (Wood, 2006). However, examination of semi-variograms of model residuals confirmed that no spatial structure remained in the residuals after the smoothing of coordinates, and that explicitly incorporating the spatial data did not improve model performance. A Mantel test implemented with the *vegan* package (Oksanen et al., 2011) was also used to examine the strength of spatial autocorrelation across trap-arrays using a Bray-Curtis similarity matrix (of the abundance-based species composition) and the Euclidian distance matrix, using 1,000 permutations (Fortin and Gurevitch, 1993). This further confirmed that bee species presence/absence and abundance-based similarity across all trap sites were not affected by geographic distance (Mantel $r < 0.012$, $p > 0.39$).

To investigate the relative contributions of environmental and spatial variables to patterns of bee assemblage structure we used partial redundancy analysis (pRDA), for which the species data were Hellinger-transformed. Spatial variables were obtained by eigenfunction analysis using Principal Coordinates of Neighbourhood Matrices (PCNM: Borcard & Legendre 2002). We ran RDA models for either spatial or environmental variables separately and, if significant, we used a forward selection procedure to retain only those variables most related to local assemblages to be used in the pRDA (Blanchet et al., 2008). Using pRDA and variance partitioning, we then obtained the variance components explained by (1) environmental variables, (2) environmental variables that are spatially structured, and (3) spatial variables alone. These analyses were conducted using the *vegan* (Oksanen et al., 2011) and *packfor* packages (Dray et al., 2009).

3. Results

A total of 2,870 male orchid bees representing 25 species and four genera were captured across all trap-arrays throughout the BHRL. In terms of the overall occupancy records, 27.8% of all traps deployed at forest patches (N = 1,225 records) were occupied, but this was reduced to only 8.0% (N = 350 records) of traps at open-water matrix sites. Of all species sampled, 24 were detected at island sites, 18 at mainland sites, and only five were ever present at any of the matrix sites: *Eulaema meriana*, *Eulaema bombiformis*, *Eulaema mocsaryi*, *Eulaema cingulata* and *Euglossa avicula* (Fig. A.2). *E. meriana* and *E. bombiformis* were by far the most abundant species (N = 1,150 and N = 1,086 individuals, respectively), were both recorded at 61 of the 63 trapping sites, and represented a combined total of 77.8% of all bees sampled. The number of individuals captured at each trap-array was a good predictor of species richness detected across all islands (R^2= 0.50, $p < 0.001$), but this relationship was not significant for mainland and water-matrix sites (Fig. A.3). Orchid bee species richness was positively related to tree species diversity (R^2= 0.48; $p < 0.001$), although cause-effect relationships may be indirect and mediated by other area-dependent habitat variables.

Considering only islands, insular forest area explained only 10% of the overall variation in species richness and 6% of the variation in the first NMDS axis scores describing species composition (Fig. 2). Considering all mainland continuous forest, island and matrix sites, however, species-area relationships (SARs) were strongly mediated by isolation effects expressed in terms of NND (the nearest distance to forest patches larger than 10 ha). These relationships were highly positive in highly isolated matrix and island sites (R^2= 0.53, β = 0.73), moderately positive in islands under intermediate contexts of isolation (R^2= 0.15, β= 0.38), and weakly negative in poorly isolated forest islands and mainland sites (R^2= 0.08, β = –0.28; Fig. A.4). This reflects trivariate regression models in which only the interaction between area and isolation effects, rather than either area or isolation alone, were significant terms explaining either species richness (R^2= 0.53, p = 0.002) or species composition (R^2= 0.54, p = 0.003). In particular, both species richness and species composition were strongly affected by the magnitude and direction of trap isolation distances to the nearest forest-matrix interface, with edge-distance having a positive effect on the rarefied species richness at trap sites within land-masses, but a negative effect at trap sites scattered throughout the vast open-water matrix (Fig. 2D, A.5). This is consistent with the fact that species richness was positively related with the total amount of surrounding forest cover within radial buffers of 250m: (R^2= 0.69, p<0.001), 500m (R^2= 0.45, p<0.001), and 1000m (R^2= 0.54, p<0.001), and the forest proximity index (PROX) at these distance thresholds (250m: R^2= 0.36, p<0.001; 500m: R^2= 0.38, p<0.001; 1000m: R^2= 0.37, p<0.001). When all explanatory variables were incorporated, GLMs also consistently indicated that edge distance was the most important predictor of either species richness (β = –1.20, p < 0.001; Fig.3A) or the abundance-weighed species composition as described by the first NMDS axis (β = 0.46, p < 0.01; Fig. 3B). However, the best models (ΔAICc <2.00) included edge distance, NND and forest patch area as the main predictors of species richness and species composition (Table A.2).

Forest island, water matrix, and continuous forest sites were significantly different in their bee species composition (PERMANOVA: F= 6.59, P < 0.002), and these patterns were not significantly affected by the spatial variation of trap-arrays within each landscape context (PERMDISP: F = 2.71, P = 0.11). NMDS ordination further indicated that area and landscape context were moderately good predictors of bee species similarity across sites (Fig. 4). As expected, the two most abundant species (*E. bombiformis* and *E. meriana*) contributed most to compositional differences among landscape contexts (SIMPER: 23% and 21%, Table A.3). Variation partitioning based on pRDA analysis showed that both the full environmental and full spatial model were significant for the overall assemblage structure. Forward selection retained two environmental variables (patch area and edge-distance) and three derived spatial variables (PCNM 2, 3, 5) as significant predictors of the variation in bee assemblage structure in reduced models. Further partitioning the environmental and spatial variance showed that predictor variables explained 16% of the overall variance. The variance component that can be attributed to pure environmental effects had a significant influence on bee species composition (R^2= 0.11, F = 3.91, P = 0.005), whereas the spatial contribution was not significant.

4. Discussion

Consistent with the general principles of island biogeography, we provide a resounding endorsement of how the interaction between habitat area and isolation affects local habitat occupancy of organisms equipped with varying degrees of matrix dispersal capacity given species differences in body size, flight autonomy, and matrix tolerance. Our analysis of euglossine bee assemblages in a *de facto* fragmented aquatic/terrestrial landscape shows that patch area in itself was a poor predictor of aggregate species occupancy, explaining only ~10% of the variance in trap-scale rarified species richness. Only the interaction between area and isolation was significant in predicting species richness, with the strength of SARs gradually increasing in more isolated subsets of islands, confirming long-held expectations from oceanic archipelagos (e.g. Diamond, 1972).

Our study provides several advantages over other fragmentation ecology studies in entirely terrestrial landscapes in which the structure of the matrix, separating the often arbitrarily defined as *habitat patches*, is a decisive determinant of species sensitivity to both patch area and isolation effects (Fahrig, 2001; Prugh et al., 2008). The Balbina reservoir aquatic matrix is structurally uniform, except for the sparse dead snags in shallow areas of the lake, which do not provide trophic or nesting resources for orchid bees. In contrast, the typically high heterogeneity of terrestrial matrix habitats will effectively reduce isolation effects, often serving as stepping stones or foraging habitat for many volant and nonvolant organisms (e.g. Lees & Peres, 2009). Moreover, all Balbina islands were isolated simultaneously, with hardly any changes in landscape configuration since the reservoir floodwaters rose in 1986-87. This suddenly forced euglossine bees and all other forest organisms to readjust to a new metapopulation scenario, in which the number of landscape-scale subpopulations will be inversely related to the maximum matrix dispersal distances exhibited by different species (Vandermeer and Carvajal, 2001). For example, matrix-vagrant, large-bodied bees exhibiting high flight capacity such as the two highly abundant, widely distributed species (*E. bombiformis* and *E. meriana*, both >24mm) reached even the most isolated island and matrix sites. Both of these species visited traps in 12 out of our 14 matrix sites that were surrounded by >1km of water in all directions and isolated from the mainland by up to 14.4 km; and *E. meriana* was captured in our most isolated matrix site (3,900 m from any island >10 ha). Each of these species therefore effectively represented a single population across the entire fragmented landscape. In contrast, several other species, were unable to overcome even narrow matrix gap distances of ~50m, thereby likely forming many metapopulations across spatially cohesive island clusters.

The overall number of species documented in this study is similar or lower than that in the BDFFP (Biological Dynamics of Forest Fragments Project), located north of Manaus, ~70 km from our study landscape (Morato, 1994; Oliveira and Campos 1995). However, we found only five euglossine species at trap sites placed on the water matrix, whereas 20 species were recorded at matrix sites dominated by abandoned cattle pastures at BDFPP (Morato, 1994). This difference is almost certainly related to the high structural contrast between the matrices at these two landscapes. The intervening matrix at BDFFP consists of poorly-managed pastures, scrub and secondary forest, which represent a relatively benign habitat compared to vast areas of open-water at a true archipelagic landscape. When the matrix is not sufficiently hostile, species exhibiting high dispersal capacity across open habitats, such as exotic Africanized honey bees (*Apis* spp.), are able to compensate for forest habitat loss by making use of matrix resources (Ewers and Didham, 2006). Among the five species collected across the BHRL water-matrix, four are large-bodied bees in the genus *Eulaema* that appear to be adept at long commuting flights across wide open-habitat gaps. These large-bodied bees were able to fly distances of at least 370 – 3,878 m across the BHRL open-water matrix. Large orchid bees were recorded flying ~5 km over open water (Janzen 1971), but flight distances of 7 – 11 km can be a significant barrier to orchid bee dispersal (Boff et al., 2014). Rocha-Filho et al. (2013) found no significant genetic differences between populations of four euglossine species in an Atlantic forest island and a mainland forest separated by 30 km. Indeed, considering all species sampled at Balbina, the overall filling of the species-by-site matrix was relatively low (31.7% of a possible 1,116 cells), and likely related to severe dispersal limitation for most species throughout the matrix and many small forest islands (Svenning and Skov, 2004). Most of these species were small-bodied (16 of all 25 species <15mm). These results are in sharp contrast with a genetic study of Costa Rican populations of a large- and a small-bodied euglossine bee (*E. bombiformis* and *E. championi*), which found that the larger species showed higher genetic differentiation than the smaller species and concluded that other factors such as male territoriality can be better predictors of dispersal ability that body size (Suni and Brosi 2012). The large-bodied *E. meriana* and *E. bombiformis*, which were hyperabundant in this study, are also highly abundant and widespread in all Amazonian human-modified landscapes studied to date (Morato, 1994; Oliveira and Campos, 1995; Storck-Tonon et al., 2009).

Considering the high structural contrast between our main landscape units, we expected to record a larger number of species at mainland sites compared to most islands. However, this is likely a function of (1) the greater spectrum and higher availability of floral resources competing with artificial scents at continuous forest sites, due to their higher habitat heterogeneity; (2) islands being more exposed to wind currents, so scents in baited traps are easily dispersed omnidirectionally than in primary forest where the potential attractability of scents may be more efficient; and (3) trap density (trap-arrays/ha) being higher in smaller islands, thereby elevating the capture probability per site. Determining an adequate sampling effort required to sample an entire bee assemblage at a vast landscape is a difficult task, yet 72% of all species sampled at all island sites were also recorded at mainland sites. The proportion of species that were unique to any given landscape unit was low, and only one species was unique to the mainland. Orchid bee species composition was also not significantly different between primary and secondary forests in eastern Amazonia, likely due to their high landscape vagility (Barlow et al. 2007).

Orchid bee abundance and species richness were positively correlated at both the site and trap-array scales, which is consistent with studies in forest fragments surrounded by pastures and regrowth (Becker et al., 1991; Morato, 1994; Storck-Tonon et al., 2013). However, this relationship was not significant for either matrix sites or mainland continuous forests. This is likely a function of community-wide dispersal limitation, except for a few widely vagrant species that were able to traverse the nonforest matrix, so cumulative numbers of species failed to track the number of individuals captured. The opposite pattern was true in mainland continuous forests, where numbers of species per individual sampled had the highest increase.

Orchid bee species richness was also positively related to plant diversity, a pattern consistent with other hymenopteran studies (Fründ et al., 2010; Steffan-Dewenter and Tscharntke, 2001; Tscharntke et al.,1998). Male and female Euglossine bees visit at least 60 plant families and hundreds of orchid species across Neotropical forests, so that the higher resource spectrum associated with high plant diversity can sustain larger numbers of individuals and/or species (Dressler, 1982; Roubik and Hanson, 2004). However, the strength of pollinator-plant diversity relationships remains unclear, and both plant and bee diversity may respond to other area-dependent variables (Fründ et al., 2010).

Although species-area relationships amount to one of the few ironclad rules in ecology, euglossine species richness only marginally covaried with island size. Similar results were found in forest fragments of southeastern Costa Rica (Brosi, 2009), and other neotropical studies (Nemésio and Silveira, 2010; Peruquetti et al., 1999; Storck-tonon et al., 2013; Tonhasca et al., 2002). Given the high flight capacity of some orchid bees

(Janzen, 1971; Wikelski et al., 2010), matrix movements can be facilitated by stepping-stones and other benign matrix features, which typically comprise most terrestrial landscape mosaics (Ricketts, 2001). However, the strength of SARs should become more evident as patch isolation increases by either greater distances or a more uniformly hostile matrix structure as shown for ants, birds and mammals at BHRL (Emer et al., 2013; Aurélio-Silva et al., 2016; Benchimol and Peres, 2015). When only matrix and mainland sites were considered, SARs were strongly influenced by patch isolation with their slopes gradually increasing from the least to the most isolate sites. This is consistent with the equilibrium theory of island biogeography, and plant, bird and mammal communities on islands under varying degrees of isolation (Sólymos and Lele, 2012).

Small, isolated patches are expected to have low species richness, including native pollinators (Potts et al., 2010; Winfree et al., 2009). In agricultural landscapes, other bee abundance and diversity typically declines with increasing distance to forest areas (Bailey et al., 2014). At Balbina, distance from edges was a strong predictor of directional transitions in tree species composition (Benchimol and Peres, 2015), and both species richness and composition of orchid bees were strongly affected by isolation metrics, such as edge distance and the total amount of surrounding forest cover. We found a positive effect of edge distance at island and mainland sites presumably as habitat quality increased towards core forest areas that were less exposed to hostile microclimates and boundary effects (Ries and Sisk, 2010). Conversely, this effect became negative at matrix sites as increasing isolation from forest areas filtered out bee species of decreasing vagility in open areas. Orchid bee species richness in southwestern Amazonia was also negatively related to forest edges (Storck-Tonon et al. 2013). However, other studies have shown that overall orchid bee species richness is unaffected by edge effects (Morato, 1994; Nemésio and Silveira, 2006). We surmise that these apparent discrepancies in edge responses are due to differences in matrix habitat quality between true islands and old-growth forest patches embedded within successional matrices.

Conclusions

We showed that the interaction between insular forest patch area and patch isolation explained a higher proportion of the variance in both the species richness and composition of orchid bees than either one of these variables alone. However, when all predictors were considered simultaneously, only level of forest patch isolation was the most important driver of orchid bee species richness, composition and community structure of one of the world's largest man-made archipelagos, 26 years after it was created. Habitat area effects, although significant, were a comparatively poor predictor of bee species occupancy. Only large-bodied, widely vagile 'supertramp' species were able to traverse long distances across the wider aquatic matrix to visit the most isolated traps. We assume that these patterns were largely a function of a homogeneously hostile open-water matrix, compared to most other fragmentation ecology studies, which are deployed in entirely terrestrial landscapes.

Given renewed investments in a large number of mega hydropower infrastructure projects in the Amazon basin (Castello et al 2013; Lees et al. 2016), many pollinator and plant taxa are likely to be affected by habitat loss and isolation, fueling growing concerns over pollinator declines and consequent losses in plant diversity (Potts et al., 2010). We therefore call for a greater understanding of the long-term impacts of major dams on terrestrial biodiversity, and strategies that can mitigate these impacts. Orchid bees comprise an important group of neotropical pollinators, so understanding how habitat loss and fragmentation affect their diversity and community structure is a research priority. We suggest that pollinator taxa should be monitored in the aftermath of habitat isolation induced by infrastructure projects, and that this should be considered in environmental impact assessment of new dams.

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Figure legends

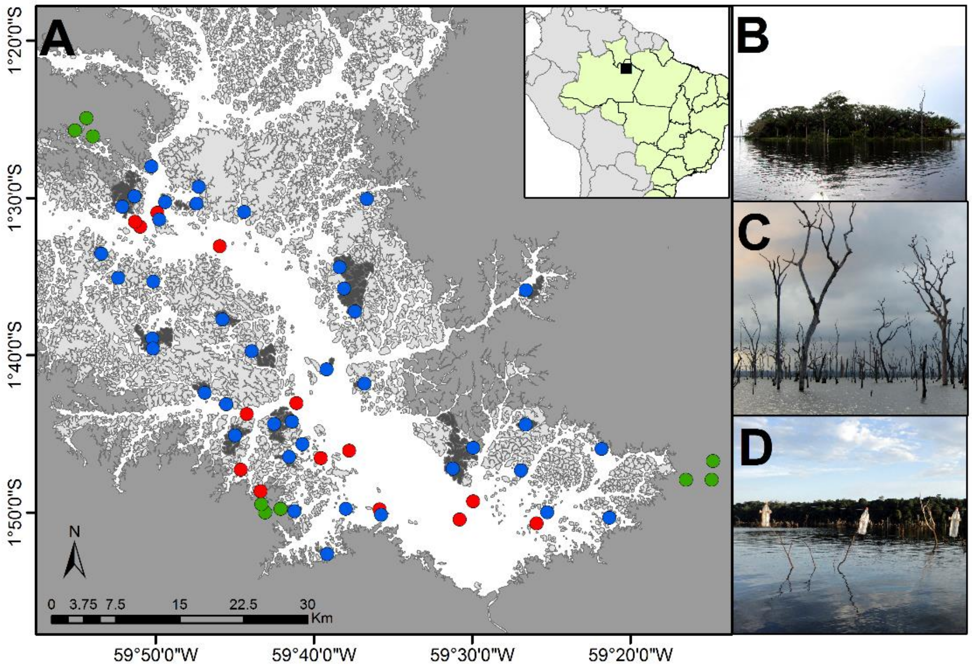
Fig. 1. (A) Study area showing the spatial distribution of the trapping sites (solid circles) throughout the Balbina Hydroelectric Reservoir Landscape (BHRL) of Central Brazilian Amazonia. Three mainland sites (green circles), 14 open-water matrix sites (red circles), and 34 [of the 3,546] islands (blue 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.

Fig. 2. Relationship between forest area and rarefied species richness (A-C) and edge distance and rarefied species richness (D-F) in the open-water matrix, forest island and continuous forest sites in the mainland sampled throughout the BHRL.

Fig. 3. Mean ± 95% confidence intervals of regression coefficients obtained from GLMs showing the effect size of key habitat patch, landscape metrics and forest habitat quality variables explaining (a) the sample-rarefied orchid bee species richness and (b) the first NMDS axis describing the species composition at the scale of 63 trapping sites. NND = $\log_{10}$ distance to nearest neighbouring land mass >10 ha; Area = $\log_{10}$ forest patch area; % Forest = percentage of closed-canopy forest within each patch; Tree D = Simpson's diversity of live old-growth trees ≥10 cm DBH within each patch; Edge.Dist = Distance to the nearest forest edge within a patch >10 ha.

Fig. 4. Nonmetric multidimensional scaling (NMDS) ordination using a Bray-Curtis similarity matrix of orchid bee species composition in islands (blue circles), mainland forest (green circles) and water matrix sites (red circles) sampled across the Balbina archipelago. Circles are sized in proportion to the area of sampled sites, except for matrix sites. Lines connecting circles indicate subsets of trap-arrays sampled within the same site.

Figure 1


A
B
C
D
1°20'0"S
1°30'0"S
1°40'0"S
1°50'0"S
59°50'0"W
59°40'0"W
59°30'0"W
59°20'0"W
N
0 3.75 7.5 15 22.5 30
Km

730

Figure 2

735

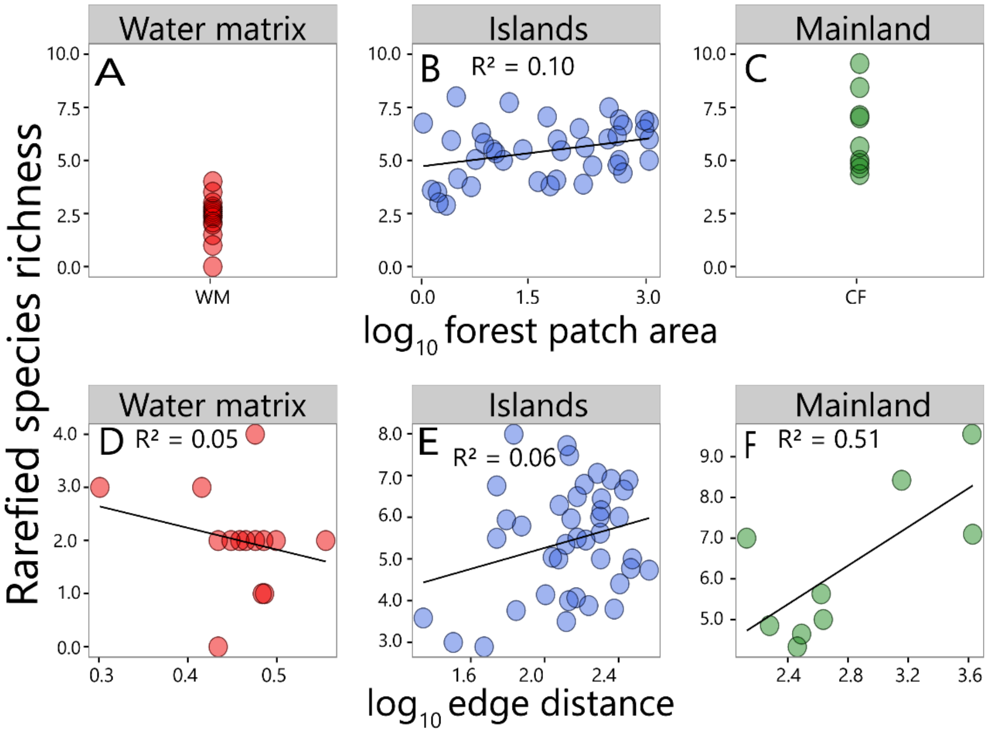

Water matrix
Islands
Mainland
A
B
R² = 0.10
C
Rarefied species richness
10.0
7.5
5.0
2.5
0.0
WM
0.0
1.5
3.0
CF
log10 forest patch area
Water matrix
Islands
Mainland
D
R² = 0.05
E
R² = 0.06
F
R² = 0.51
4.0
3.0
2.0
1.0
0.0
0.3
0.4
0.5
8.0
7.0
6.0
5.0
4.0
3.0
1.6
2.0
2.4
9.0
8.0
7.0
6.0
5.0
2.4
2.8
3.2
3.6
log10 edge distance

Figure 3

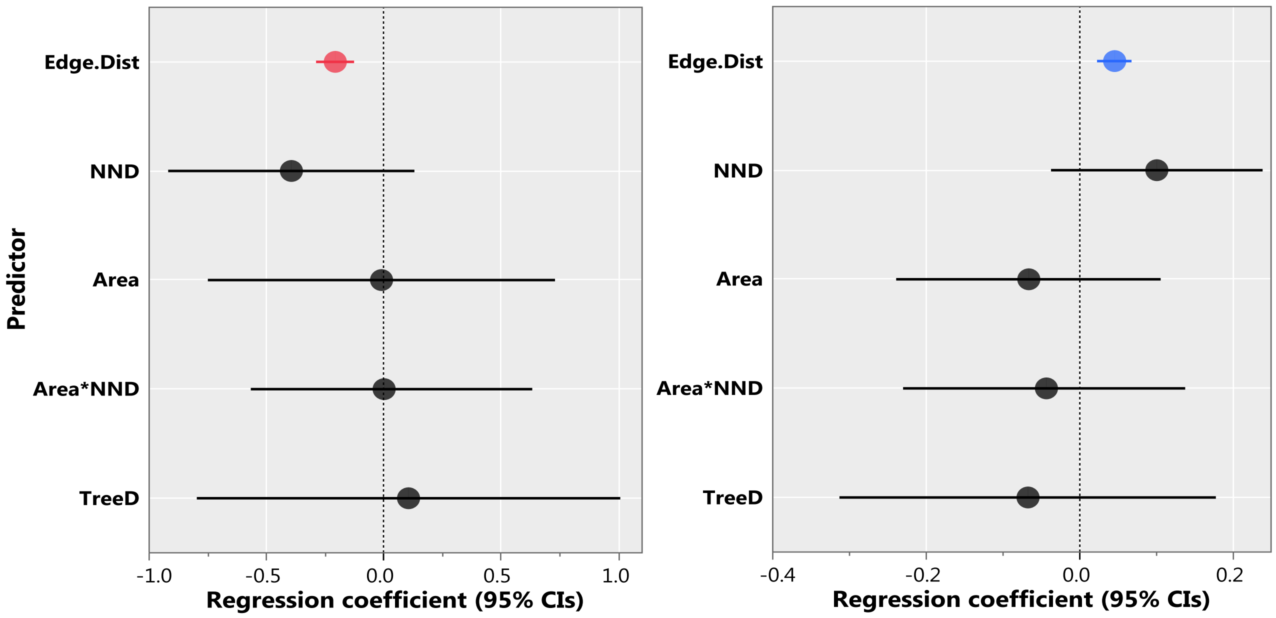
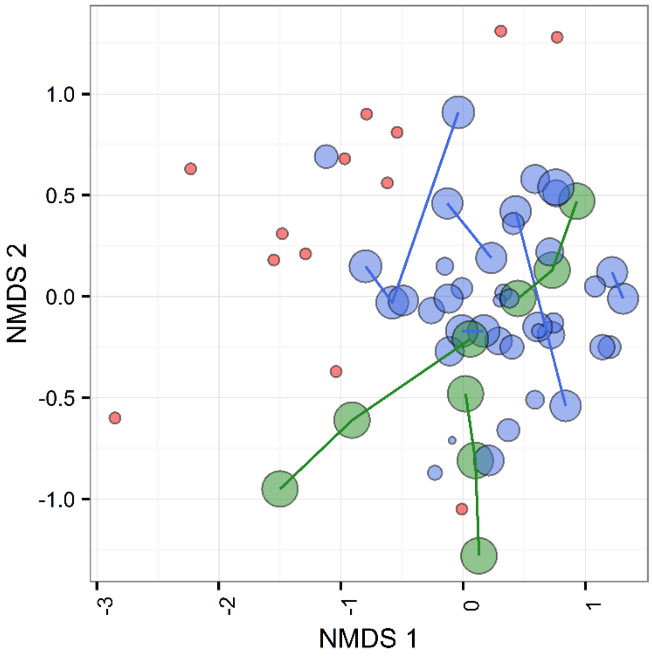

Predictor
Edge.Dist
NND
Area
Area*NND
TreeD
-1.0
-0.5
0.0
0.5
1.0
Regression coefficient (95% CIs)
Edge.Dist
NND
Area
Area*NND
TreeD
-0.4
-0.2
0.0
0.2
Regression coefficient (95% CIs)

Figure 4



750

755

760

Appendix A. Supplementary Information

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

Danielle Storck-Tonon and Carlos A. Peres

Table A.1. Geographic location, forest area and isolation of island, open-water matrix, and mainland continuous forest sites sampled throughout the Balbina Hydroelectric Reservoir Landscape (BHRL).

Site	**Site class**	**Distance to mainland**	**Area (ha)**	**UTM (X)**	**UTM (Y)**
Toquinho	Island	5013	0.83	193046	9809792
Joaninha	Island	6125	1.15	185184	9831524
Xibe	Island	345	1.45	184359	9837426
Formiga	Island	5017	1.52	230702	9797149
Andre	Island	10679	2.17	180451	9824638
Cafundo	Island	2000	2.70	209613	9833955
Panema	Island	2960	3.53	200419	9803597
Torem	Island	2017	3.94	207096	9797589
Pe Torto	Island	146	5.85	237118	9804515
Jiquitaia	Island	800	7.28	211331	9796843
Arrepiado	Island	12675	8.35	195111	9832440
Garrafa	Island	11872	9.54	184620	9824267
Abusado	Island	4862	13.41	201895	9804887
Piquia	Island	7484	13.59	189588	9833341
Coata	Island	6646	17.45	189721	9834874
Palhal	Island	5803	21.21	227620	9802094
Neto	Island	581	32.92	238378	9796254
Bacaba	Island	3714	53.30	185791	9834066
Relogio	Island	8089	72.10	205429	9815025
Sapupara	Island	4278	78.44	209362	9812209
Adeus	Island	54	97.62	205064	9792225
Moita	Island	7528	98.84	177596	9827596
Pontal	Island	66	110.43	200258	9797872
Furo	Island	912	193.00	228359	9808020
Cipoal	Island	5580	218.74	190502	9811122
Jabuti	Island	11668	231.39	192651	9820569
Tucumari	Island	90	292.41	229622	9824006
Martelo	Island	13217	471.00	196973	9814617
Tristeza	Island	792	487.50	194478	9805095
Beco do Catitu A	Island	5556	637.49	198737	9806219
Beco do Catitu B	Island	5556	637.49	200791	9807783
Mascote A	Island	4625	673.35	182883	9818284
Mascote B	Island	4625	673.35	184490	9816342
Fuzaca A	Island	65	761.02	182475	9834117
Fuzaca B	Island	65	761.02	180888	9832973
Porto Seguro A	Island	44	1466.00	220417	9800867
Porto Seguro B	Island	44	1466.00	222037	9804708
Gaviao Real A	Island	3822	1690.04	208080	9820719

Gaviao Real B	Island	3822	1690.04	206889	9823390
Gaviao Real C	Island	3822	1690.04	206385	9825864
Mainland 1	Mainland	0	∞	194892	9795365
Mainland 2	Mainland	0	∞	249932	9801631
Mainland 3	Mainland	0	∞	179365	9844218
Mainland 1	Mainland	0	∞	247000	9800940
Mainland 2	Mainland	0	∞	249026	9800938
Mainland 3	Mainland	0	∞	251062	9799963
Mainland 1	Mainland	0	∞	175363	9841937
Mainland 2	Mainland	0	∞	176542	9842108
Mainland 3	Mainland	0	∞	177467	9841242
Water matrix 1	Water matrix	123	0	197120	9799615
Water matrix 2	Water matrix	1550	0	211072	9797484
Water matrix 3	Water matrix	6900	0	195512	9808650
Water matrix 4	Water matrix	5700	0	222036	9798426
Water matrix 5	Water matrix	5600	0	183006	9830607
Water matrix 6	Water matrix	14400	0	192311	9828354
Water matrix 7	Water matrix	9100	0	201316	9809958
Water matrix 8	Water matrix	3700	0	229474	9795829
Water matrix 9	Water matrix	5200	0	220448	9796308
Water matrix 10	Water matrix	4800	0	182382	9831199
Water matrix 11	Water matrix	5700	0	185010	9832279
Water matrix 12	Water matrix	1100	0	194806	9802132
Water matrix 13	Water matrix	5300	0	204180	9803449
Water matrix 14	Water matrix	8400	0	207515	9804354

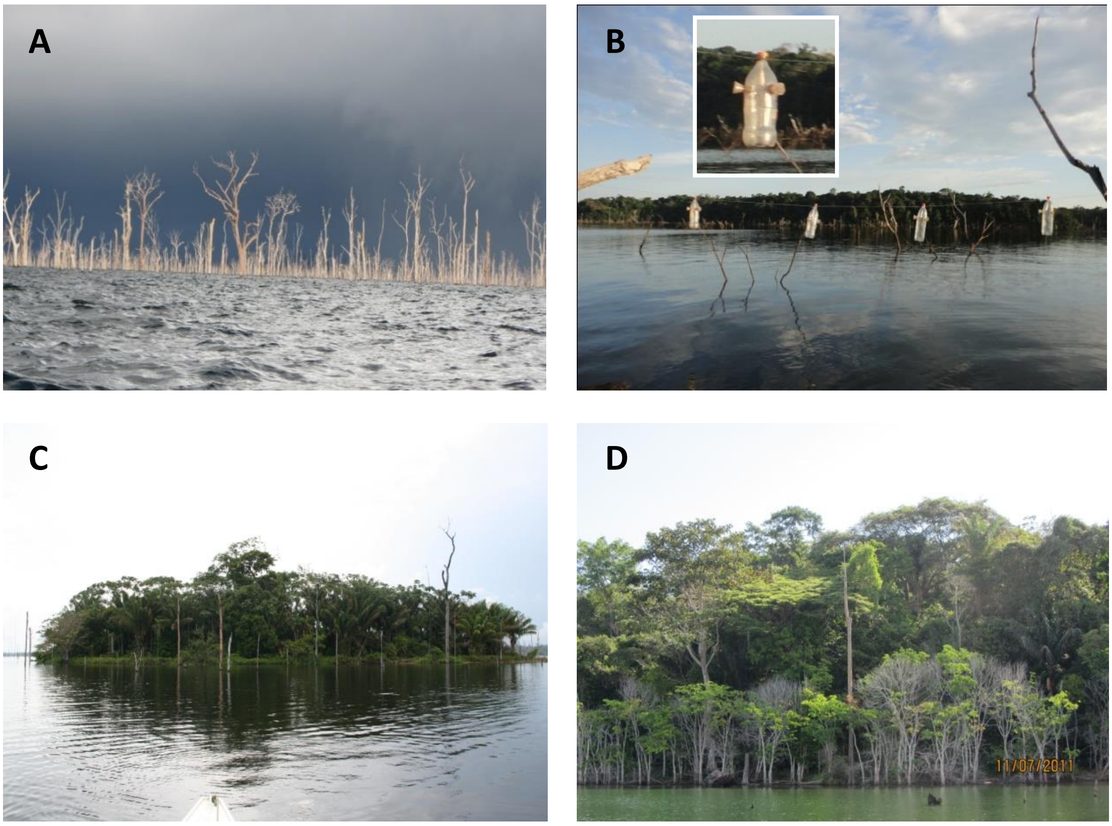


Fig. A.1. (A) Typical open-water matrix within the Balbina Hydroelectric Reservoir of Central Brazilian Amazonia, showing a large number of standing dead trees representing the decomposing necromass across vast areas of open water; (B) example of trap-array set in the open-water matrix, showing Euglossine bee scent traps (see detail in inset photo); (C) small isolated island within the reservoir; and (D) forest edge of a large island.

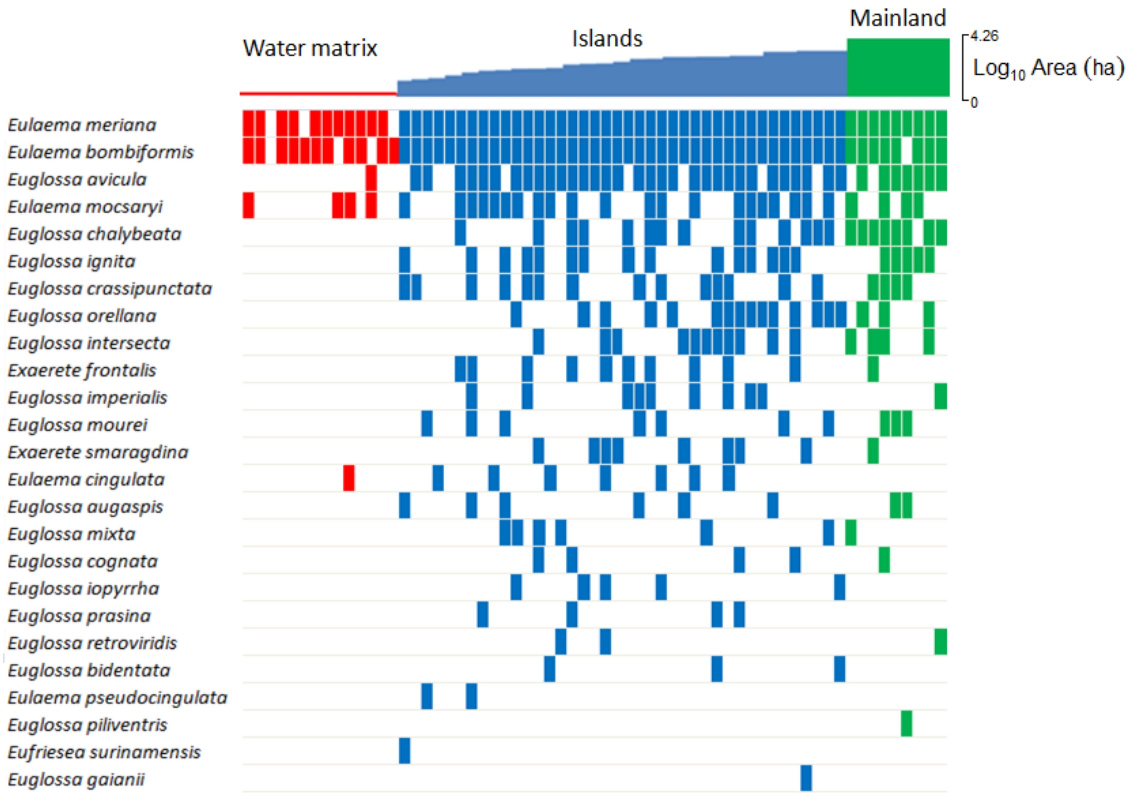


Fig. A.2. Checklist and site records of 25 orchid bee species sampled across 63 trapping sites distributed throughout the Balbina Hydroelectric Reservoir of Central Brazilian Amazonia. Species occupancies within water matrix, island, and continuous forest sites are represented by red, blue and green rectangles, respectively.

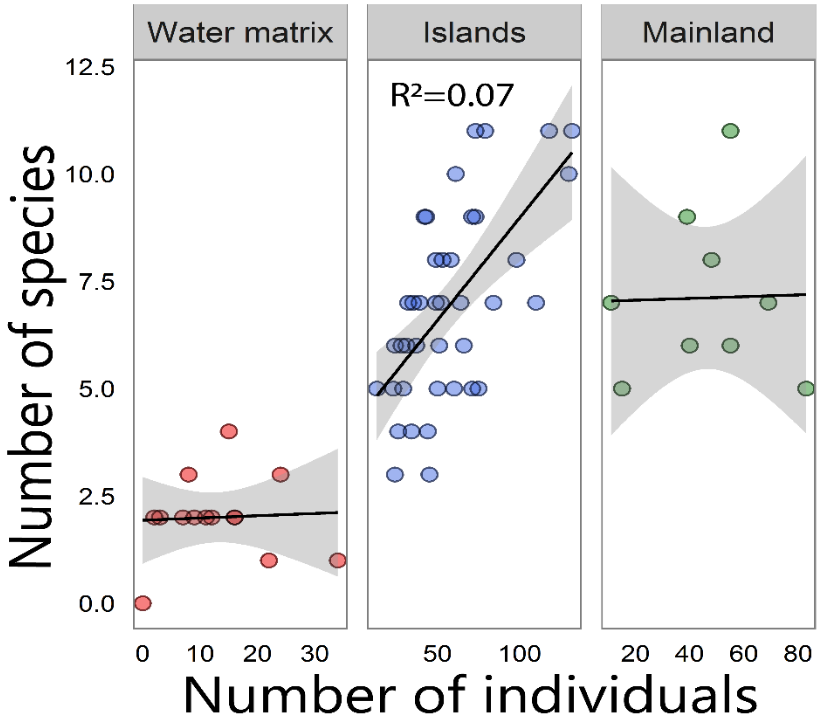


Fig. A.3. Relationship between the number of individuals and species richness of orchid bees sampled across the water matrix, island and mainland continuous forest sites in the Balbina Hydroelectric Reservoir.

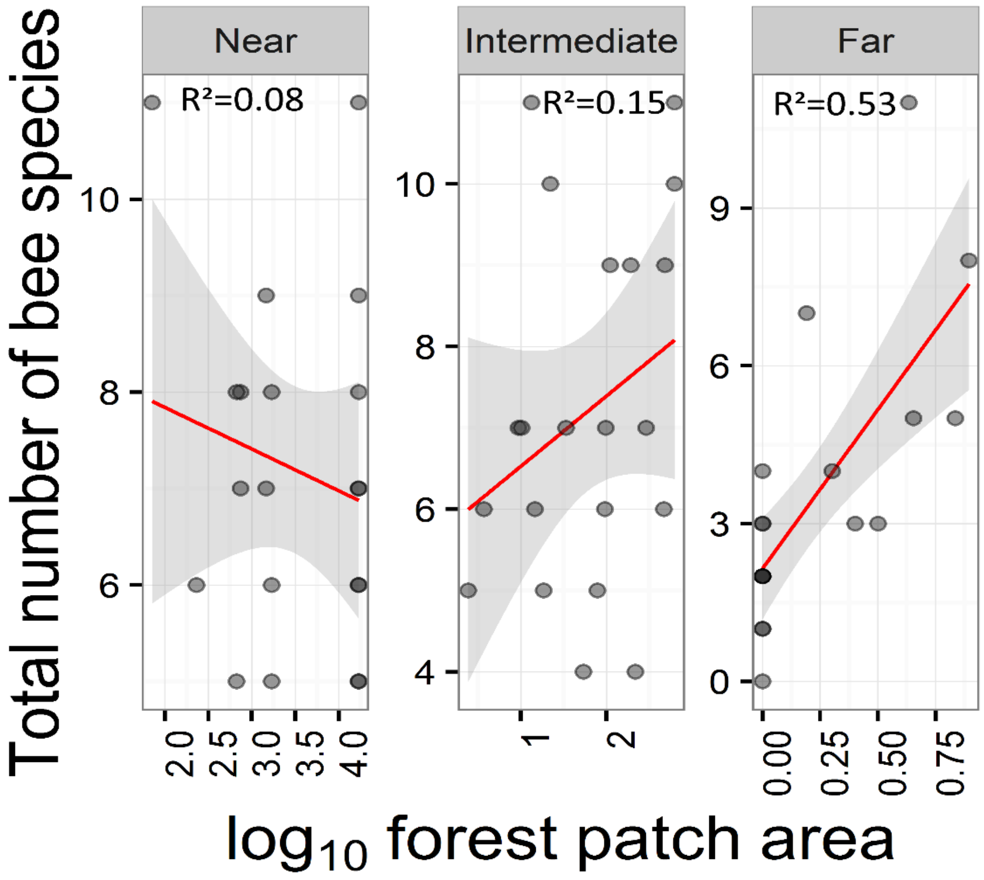


Fig. A.4. Relationship between forest area and orchid bee species richness at the Balbina archipelagic landscape, considering three levels of isolation from forest patches. R^2-values are shown for each panel.

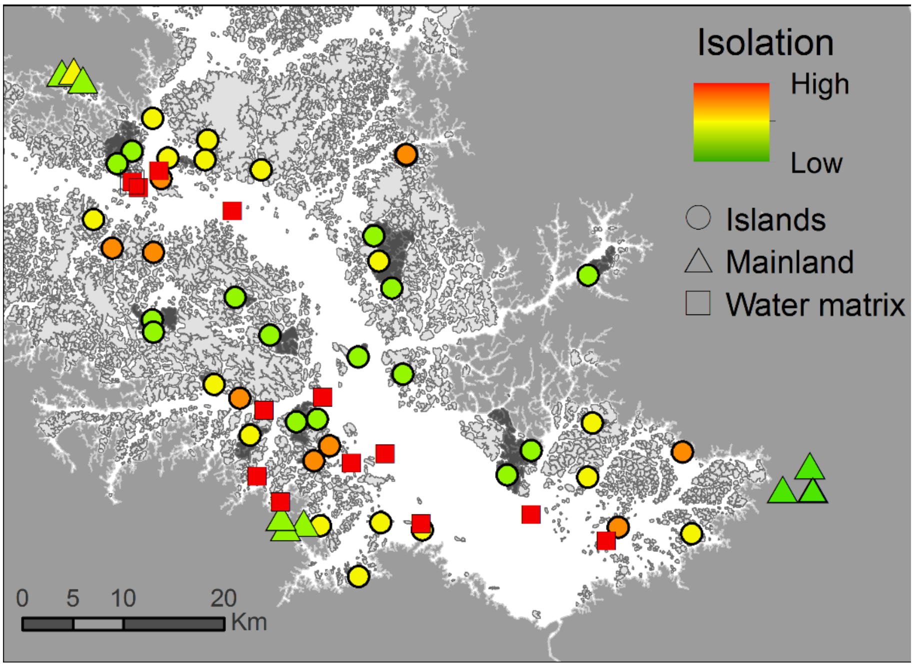


Fig. A.5. Study landscape showing the spatial distribution of trapping sites and edge distances at 34 forest islands (circles), 14 open-water matrix sites (squares) and nine continuous forest sites (triangles) throughout the Balbina Hydroelectric Reservoir. Isolation ranged from lowest in dark green sites to highest in dark red sites. A total of 3,546 islands across the lake reservoir and surrounding areas of undisturbed continuous forest in the mainland are shown in light and dark grey, respectively. Surveyed islands and the wider open-water matrix are shown in very dark grey and white, respectively.

Table A.2. GLM model results showing the effects of forest habitat patch, landscape metrics and forest habitat quality variables on the rarefied species richness, species composition and overall abundance of orchid bees. NND = log10 distance to nearest neighbouring land mass >10 ha; Area = log10 forest patch area; % Forest = remotely-sensed percentage of closed-canopy forest within each patch; Tree D = Simpson's diversity of live old-growth trees ≥10 cm DBH within each patch; Edge.Dist = straight-line distance between each trap-array and the nearest forest edge; Area × Edge.Dist = Interaction between area and NND. Best models = Most parsimonious models (ΔAICc <2).

	Best models	**AICc**	**ΔAICc**	**Akaike weights**
Rarefied species richness	Edge.Dist + NND	209.2	0.00	0.283
	Edge.Dist	209.6	0.45	0.226
	Edge.Dist + NND + Area	211.2	1.99	0.105
Species composition	Edge.Dist + NND	45.9	0.00	0.264
	Edge.Dist	46.7	0.80	0.177
	Edge.Dist + NND + Area	1.04	1.04	0.157

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Table A.3. SIMPER (similarity percentage) analysis showing the contribution of different orchid bee species at three levels of patch isolation in terms of major types of landscape units within the Balbina Hydroelectric Reservoir of Central Brazilian Amazonia.

	Islands			**Mainland**			**Water matrix**		
Species	Average abundance	Contribution (%)	Cumulative (%)	Average abundance	Contribution (%)	Cumulative (%)	Average Av. abundance	Contribution (%)	Cumulative (%)
Eulaema meriana (Olivier)	23.73	49.88	49.88	16.11	54.86	54.86	8.77	60.59	60.59
Eulaema bombiformis (Packard)	20.63	39.8	89.68	16.33	21.26	76.12	4.31	37.6	98.19
Euglossa avicula Dressler	5.1	5.97	95.64	3.22	8.47	84.6	0.46	1.81	100
Eulaema mocsaryi (Friese)	1.13	1.21	96.86	3	7.47	92.07	0.15	0	100
Euglossa chalybeata Friese	0.9	0.57	97.43	1.22	2.53	94.6	0	0	100
Euglossa crassipunctata Moure	0.83	0.56	97.99	2	2.06	96.66	0	0	100
Euglossa orellana Roubik	0.58	0.5	98.49	0.67	0.98	97.64	0	0	100
Euglossa ignita Smith	0.88	0.46	98.95	0.56	0.91	98.55	0	0	100
Exaerete frontalis (Guérin)	0.4	0.23	99.18	0.67	0.75	99.3	0	0	100
Euglossa intersecta Latreille	0.43	0.17	99.35	1	0.56	99.86	0	0	100
Euglossa imperialis Cockerell	0.33	0.14	99.49	0.44	0.14	100	0	0	100
Exaerete smaragdina (Guérin)	0.3	0.1	99.59	0.11	0	100	0	0	100
Euglossa augaspis Dressler	0.3	0.08	99.67	0.11	0	100	0	0	100
Euglossa sp.	0.15	0.08	99.75	0.11	0	100	0	0	100
Euglossa mourei Dressler	0.23	0.07	99.82	0.11	0	100	0	0	100
Eulaema cingulata (Fabricius)	0.2	0.07	99.9	0.22	0	100	0.08	0	100
Euglossa iopyrrha Dressler	0.35	0.04	99.94	0	0	100	0	0	100
Euglossa prasina Dressler	0.1	0.02	99.96	0	0	100	0	0	100
Euglossa bidentata Dressler	0.1	0.02	99.97	0.11	0	100	0	0	100
Euglossa cognata Moure	0.13	0.02	99.99	0	0	100	0	0	100

Euglossa retroviridis Dressler	0.05	0.01	100	0.11	0	100	0	0	100
Eulaema pseudocingulata Oliveira	0.05	0	100	0	0	100	0	0	100
Euglossa piliventris Guérin	0	0	100	0	0	100	0	0	100
Eufriesea surinamensis (Linnaeus)	0.03	0	100	0	0	100	0	0	100
Euglossa gaianii Dressler	0.03	0	100	0	0	100	0	0	100