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Environmental determinants of social wasp diversity and assemblage structure in an Amazonian archipelagic landscape

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ABSTRACT

Hydropower development has become an important driver of habitat loss and fragmentation across lowland tropical forests. Despite ample evidence on the detrimental effects of insular habitat fragmentation on biodiversity, invertebrate taxa, that may be critical to ecosystem functioning, have been overlooked. We assessed the assemblage-level responses of social wasps to forest insularization induced by the Balbina Hydroelectric Dam in Central Brazilian Amazonia. Employing Malaise trapping, we captured wasps on 27 forest islands and three continuous forests. We constructed Generalized Linear Models and employed a model selection approach to examine the impact of local variables (fire severity (*FIRE*) and basal area of pioneer tree species (*PIONEER*)) and landscape-scale variables (amount of habitat (*COVER*)) on patterns of species richness, composition, and body size of wasps. A total of 374 individuals (29 species) were collected across all sampling sites. *COVER* was the main predictor of species richness, while *PIONEER* was the only variable that explained variation in community composition, with a negative effect on body size. Our results add evidence to the pervasive impacts of large hydroelectric dams on tropical forest biodiversity, and suggest that social wasps, among other invertebrates, can be used as bioindicators in infrastructure development projects.

Keywords: Habitat amount hypothesis; Habitat fragmentation; Habitat loss; Hydroelectric dams; Invertebrates

INTRODUCTION

Mega hydropower projects have been rapidly expanding across the globe to provide energy for human populations (Chen et al., 2016), especially in emerging economies such as China and Brazil (Da Silva Soito & Freitas, 2011; Flecker et al., 2022). However, even recently built hydroelectric dams continue to cause major detrimental effects, including social and economic impacts on local communities (Richter et al., 2010) and several environmental impacts (Gibson et al., 2017), despite the limited economic benefits obtained in the Global South (Fan et al., 2022). Researchers have shown that aquatic biodiversity is rapidly affected due to river impoundment (de Brito Ribeiro et al., 1995), but terrestrial biotas are also pervasively affected due to habitat loss, fragmentation and degradation (Lees et al., 2016). Indeed, the flooding of lowland areas leads to drastic changes in the original environments, often resulting in insular landscapes where terrestrial species become stranded on islands, most of which succumbing to local extinctions (Jones et al., 2016). Understanding how terrestrial species cope with habitat insularization caused by dams becomes crucial to determine

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the ecological impacts of dams and propose mitigation actions.

From Asia to South America, several studies have shown the pervasive impacts of large dams on biodiversity retention on forest islands created after the river flooding (Jones et al., 2016). At the landscape-scale, total habitat cover, rather than island size and isolation, may be a better predictor of species richness on forest islands (the so-called "habitat amount hypothesis"; Fahrig, 2013). At the local-scale, habitat quality is typically related to the degree of additional human-induced disturbances, such as that imposed by previous fire events (Barlow et al., 2016). For instance, in the Chiew Larn reservoir in Thailand, native small mammals experienced high extinction rates and virtually disappeared from all surveyed islands during the 33 years of post-isolation history, which was aggravated by a hyperdominant rat species (Moore et al., 2022). In the Guri reservoir in Venezuela, a failure in top-down control mechanisms induced by the extirpation of apex predators led to a substantial increase of herbivores on islands, severely impacting tree regeneration (Terborgh et al., 2001). In two major Amazonian reservoirs, avifaunal assemblages have become impoverished, especially on small islands where forest-specialists experienced high rates of species loss (Aurélio-Silva et al., 2016; Bueno et al., 2018). Thus, local extinctions on reservoir forest islands are ubiquitous across hydropower projects worldwide, especially driven by habitat area effects. However, most studies have focused on charismatic vertebrates (Jones et al., 2016), overlooking other taxa that are key in tropical forest ecosystem functioning.

Insects comprise by far the dominant class of animals in terms of overall numbers and species diversity, controlling much of the food web in tropical forests (Greenwood, 1987). In addition, insects deliver key ecosystem services including pollination, nutrient cycling, pest control, and detritus removal (Didham et al., 1996; Schowalter, 2013). Although the importance of insects in ensuring ecosystem functioning in tropical ecosystems is undeniable, their role has often been neglected when designing management strategies favouring biodiversity maintenance. Indeed, insects are rarely considered in ecological impact assessments (Rosenberg et al., 1986). However, several anthropogenic activities are known to severely depress the diversity of insects, triggering cascade effects that may culminate in the disruption of ecological interactions and consequent extirpation of both plants and animals (Greenwood, 1987). For instance, forest loss leads to greater abundance of herbivorous arthropods in tropical forest patches, resulting in increased leaf damage that likely affects plant recruitment and regeneration (Faria et al., 2023). In the Central Brazilian Amazon, forest fragments harboured both fewer species and smaller beetles compared to neighbouring continuous forests, potentially altering faecal decomposition and other key ecological processes (Klein, 1989). Regarding hydroelectric landscapes, assemblages of dung beetles (Qie et al., 2011; Storck-Tonon et al., 2020), orchid bees (Storck-Tonon & Peres, 2017) and harvestmen (Tourinho et al., 2020) are substantially affected due to habitat insularization, mostly due to either island area or isolation. Nevertheless, invertebrates comprise a mega diverse group, with most insect orders lacking any assessment of their responses to habitat loss and fragmentation to enhance our understanding of their vulnerability in human-modified landscapes.

Among flying insects, social wasps are of extreme importance in the trophic balance of ecosystems (Prezoto et al., 2016), playing critical roles as predators of insect pests (Prezoto & Machado, 1999) and pollinators (Sühs et al., 2009). Linked to their eusocial colonies, social wasps are remarkably abundant, widely distributed (Carpenter & Marques, 2001), and thus comprise important components of local food webs. Polistinae wasps are well known from a taxonomic standpoint, and the literature on their evolution and behaviour is vast (Carpenter & Marques, 2001; Silveira et al., 2021, Somavilla & Carpenter, 2021). In south-eastern Australia, small and highly disturbed fragments harbour completely distinct wasp assemblages compared to larger and less-disturbed fragments (Gibb & Hochuli, 2002). Likewise, forest fragmentation poses a major threat to social wasps in Central Amazonia, as marked differences in species richness, abundance and composition can be found between fragmented and continuous forest sites (Ferreira et al., 2020; Graça & Somavilla, 2019). Given that forest insularization induced by hydropower dams has been considered more detrimental to biodiversity compared to forest patches embedded within a terrestrial vegetation matrix (Benchimol & Peres, 2015a), we expect the structure of social wasp assemblages to be greatly altered on reservoir islands.

Here, we assessed how forest insularization induced by a mega Amazonian dam has affected patterns of species richness and composition of social wasps after nearly ~35 years post-isolation. To do so, we surveyed social wasps using Malaise traps on 27 forest islands distributed across a gradient of landscape forest cover, and three nearby mainland continuous forest sites, at the Balbina Hydroelectric Reservoir landscape, located in Central Brazilian Amazonia. We then related both the overall number of social wasp species, species composition and mean body size to a set of environmental variables measured at both the local (i.e., basal area of pioneer trees and fire severity) and the landscape-scale (i.e., amount of forest cover). Considering that the basal area of pioneer tree species can be a proxy for habitat quality (Benchimol & Peres, 2015b) and that fire incidence likely affects social wasps mainly through the destruction of nests, we hypothesised that both variables would exert a negative effect on species richness, also leading to greater dissimilarities in patterns of wasp species composition. Moreover, in light of the habitat amount hypothesis (Fahrig, 2013), we expect that overall forest cover at the landscape-scale would also contribute to explaining patterns of species richness and composition. Finally, we hypothesised that islands exhibiting higher basal area of pioneer tree species, subjected to greater fire incidence and embedded within lower amounts of surrounding forest will retain wasp assemblages predominantly comprised by large-bodied species, since small-bodied species are presumably more affected by the decay in habitat quality and are unable to fly over longer distances, thereby presenting lower colonisation capacity.

MATERIALS AND METHODS

Study area

Social wasps were surveyed in the Balbina Hydroelectric Reservoir landscape and its immediate surroundings, in Central Amazonia (S1°48′, W59°29′; Figure 1). This vast hydropower reservoir was created in 1986, following the completion of a major dam on the Uatumã River, a left-bank

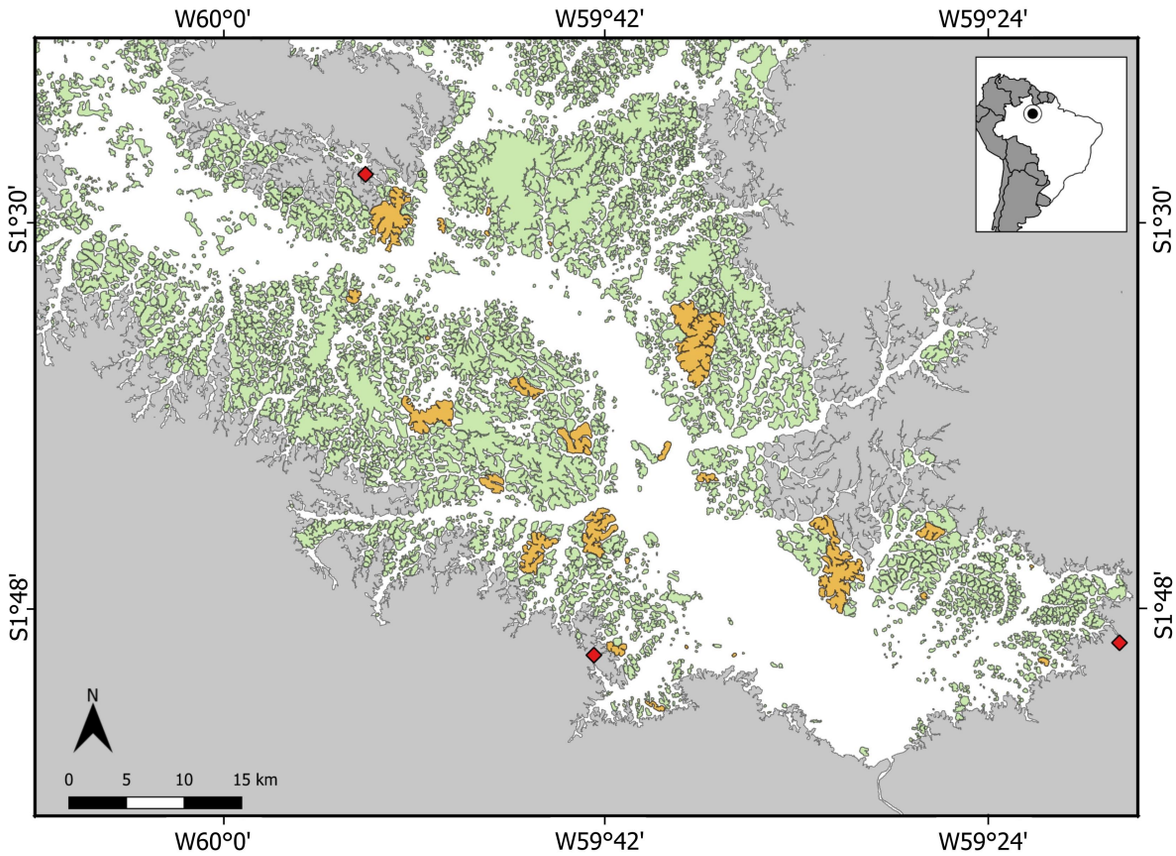

Figure 1 Study area showing the spatial distribution of the sampled sites distributed throughout the Balbina Hydroelectric Reservoir, in the Brazilian Amazonia

Survey sites included 27 forest islands (orange polygons) and three mainland forest sites (red diamonds). Grey areas indicate large tracts of continuous forest around the reservoir. Unsurveyed islands are shown in light green.

tributary of the Amazon River. Balbina currently comprises one of the largest reservoirs in South America, occupying 443 772 ha. A total of 312 900 ha of pristine forest areas was flooded, creating 3 546 forest islands (Jones et al., 2021). Most islands consist of dense closed-canopy *terra firme* (i.e., non-flooded) forests. The mean annual temperature and rainfall in this region is 28°C and 2 376 mm, respectively (IBAMA, 1997). As a compensatory policy, part of the reservoir and a large continuous forest area on the left bank of the Uatumã River were legally protected since 1990 by the creation of the 942 786 ha Uatumã Biological Reserve, which is Brazil's largest protected area in this category. As such, the islands surveyed in this study were not subject to logging nor hunting, but experienced a variable intensity of understorey fires during the El Niño drought of late 1997 to early 1998 (Benchimol & Peres, 2015a).

We performed wasp surveys on a set of islands and adjacent mainland forest sites previously surveyed for other vertebrate, invertebrate and plant taxa, including medium to large-sized mammals and trees (Benchimol & Peres, 2015a). Initially, a previous study (Benchimol & Peres, 2015b) carefully selected 37 islands, based on their size and degree of isolation, which also covered a wide range of landscape forest amount. In particular, we selected a subset of 27 islands, which ranged in their landscape forest amount, within a radius of 1 000 m (forest cover: 49.5%±2.12 (mean±standard deviation); min=3.9; max=84.2), and distribution across the reservoir, while ensuring they were at least 1 km apart. In addition, three continuous forest sites were also sampled.

Sampling of social wasps

Social wasps were sampled in September 2012 and, at each sampling site, we deployed a standardised Malaise trapping protocol (including cups containing a 95% alcohol preservation solution) to survey social wasps over a 48 h period. To reduce sampling bias of the sampled area, the number of Malaise traps deployed varied proportionally with island sizes: one trap on islands <750 ha, two traps on islands between 750 and 1 500 ha, and three traps on islands >1 500 ha and mainland forest sites (Figure 1). Therefore, the trap density (i.e., the number of Malaise per ha) was higher on smaller islands**.** All captured wasps were subsequently identified at the lowest possible taxonomic level by specialists and deposited in the Entomological Collection of the Instituto Nacional de Pesquisas da Amazônia (INPA), Manaus, Brazil.

Ethical approval

All relevant international, national, and/or institutional guidelines for the care and use of animals were strictly followed and social wasps collection was approved by the Brazilian Instituto Chico Mendes de Conservação da Biodiversidade (SISBIO License No. 35211–1).

Body size

To measure the body size of individual species, we randomly selected, among all specimens collected in this study, five individuals of each species (or all individuals in case of species collected ≤5 individuals). For each individual, we measured total wing length and intertegular distance. We performed these measurements using a Leica M205A

stereomicroscope coupled with a Leica DMC4500 digital camera, using the LAS v.4.10 software. Total wing length and intertegular distance were highly correlated (r=0.89, n=83), so we used the latter as a proxy for body size, which has been shown to be an excellent proxy for flight capacity in other hymenopterans (e.g. bees; Greenleaf et al., 2007).

Habitat quality and landscape-scale variables

We considered a set of local and landscape-scale metrics as indicators of the degree of forest degradation and habitat loss at each surveyed site. At the local-scale, data on pioneer trees (*PIONEER*) were obtained on each island and continuous forest site by inventorying one to four 0.25 ha forest plots according to island size. Vegetation plots on islands were always spaced by ≥50 m from the nearest forest edge to minimise edge effects. All live trees ≥10 cm in diameter at breast height (DBH) within each plot were measured, tagged, and identified to species level by an expert botanist (for details on floristic surveys, see Benchimol & Peres, 2015b). Based on 118 tree species classified as either short-lived or long-lived pioneers, we considered the basal area density (m^2/ha) of pioneer species in each plot, or the mean value among plots if more than one plot had been surveyed at the same site. Density of pioneers is a strong predictor of the degree of floristic turnover of the relict old-growth stands on islands in the aftermath of isolation. Also at the local-scale, we obtained a metric of fire severity (*FIRE*), estimated as an ordinal score (0–3) of burn intensity (based on charred trees and eight of char marks on each tree) (for details on floristic surveys and fire, see Benchimol & Peres, 2015b).

We also extracted the landscape forest amount for each of our sampling sites (*COVER*). For this, we used high-resolution multi-spectral RapidEye© imagery (5-band colour imagery at 5-m resolution) of the entire study landscape and calculated the percentage of land mass area within multiple buffers (within a radius of 250 500 and 1 000 m) using ArcMap 10.1 (ESRI, 2012). We thus calculated the "scale of effect", i.e., the spatial scale at which the investigated responses (i.e., richness and composition against *COVER*) is maximised, using the "multifit" package and function (Huais, 2018). We identified that 1 000 m was the most appropriate scale in explaining the variation in our response variables.

Data analysis

We constructed species richness extrapolation curves using the "iNEXT" function and package to standardise the sampling effort between the islands and mainland, based on the total number of Malaise traps used across all islands (n=34). Both rarefaction curves tended to asymptote, suggesting that sampling effort employed on surveyed sites (islands and mainland) was adequate (Supplementary Figure S1).

We thus investigated the effects of all predictors on patterns of social wasp species richness, composition and body size using Generalized Linear Models (GLMs). In this study, we did not use abundance data because social wasps are, by definition, colonial so the presence of an individual in a trap is equivalent to the presence of a nest in the sampled site, which may shelter hundreds of conspecific wasps. Therefore, all analyses were performed using binary (presence/absence) data. The multidimensionality of social wasp species composition across all sites was reduced using Principal Coordinates Analysis (PCoA) ordination based on binary data and the Jaccard similarity index. The first axis of PCoA was used in models as a descriptor of species composition. We constructed models with all three predictors (*PIONEER*, *FIRE*, and *COVER*) and all possible combinations of subsets of them. We assumed a negative binomial distribution error structure for species richness and Gaussian for species composition and body size. Since some sites were sampled by more than one trap, the number of traps was included in the models as an offset. We controlled for high levels of multicollinearity among variables by performing Variation Inflation Factors (VIF) (Dormann et al., 2013) using the "HH" package (Heiberger, 2020) and excluded the collinear variables (VIF<3). However, all variables presented a VIF<3 and, therefore, were retained in our models. We used the dredge function in the "MuMIn" package (Barton, 2018) to build models containing all possible variable combinations. For that, we selected only those models that presented a ΔAICc<2 (Burnham et al, 2011). We then build model averages from the selected models using the model.avg function. All analyses were performed within the R 4.3.1 environment (R Core Team, 2018).

RESULTS

In total, we collected 374 individuals representing 29 species of social wasps (Supplementary Table S1). The most widespread species was *Angiopolybia pallens*, recorded on 18 islands (66%) and all mainland sites, followed by *Agelaia fulvofasciata* and *A. pallipes*, both of which recorded on nine islands and two mainland sites. From the remaining 18 species, 15 were recorded at a single site. In total, we recorded 23 species on the islands and 14 species on the continuous forest. However, mainland sites had a higher mean species richness (8.33±2.08 (mean±standard deviation); min=6; max=10) than the islands (2.66±1.27 (mean±standard deviation); min=1; max=5). Six species occurred exclusively on continuous forest, 15 on island and eight species occurred on both island and continuous forest (Supplementary Table S1).

When all variables were included in the GLMs, *COVER* was the strongest predictor of species richness and was included in the three selected models (Table 1). *FIRE* and *PIONEER* were also selected in models with ΔAICc<2, each being present in one of the three selected models, yet only *COVER* was significant (Figure 2A), with a positive impact on the species richness of social wasps (Figure 2B). For species composition, two models exhibited ΔAICc<2. The first model included only *PIONEER* and the second model included *PIONEER* and COVER as predictors, but only *PIONEER* was significant (Figure 3A; Table 1). Finally, for the average body size of the species found at each site, only one credible model was obtained ΔAICc<2, which included only *PIONEER* (Figure 4A; Table 1), with a negative effect (Figure 4B).

DISCUSSION

To our knowledge, this is the first study to investigate the effect of habitat modification at local and landscape-scales on the diversity of social wasps in insular landscapes induced by a hydroelectric powerplant in Amazon forests. As predicted by the habitat amount hypothesis (Fahrig, 2013), islands embedded within larger amounts of landscape-scale forest cover exhibited higher species richness. Yet, forest quality mediated by the basal area of pioneer tree species best explained patterns of species composition and average wasp body size.

Table 1 Results of the Generalized Linear Models (GLMs) explaining the effects of PIONEER trees, FIRE severity and forest COVER on the species richness, composition, and size structure of social wasps on the islands of the Balbina hydroelectric reservoir

	Intercept	*PIONEER*	*FIRE*	*COVER*	Degrees of freedom	AICc	ΔAICc	Weight
Species richness	1.069	–	–	0.465	3	110.58	0	0.444
	1.066	–	−0.179	0.337	4	110.851 3	0.271 307	0.388
	1.064	−0.108	–	0.434	4	112.523	1.942 631	0.168
Species composition	−4.6E-18	0.111	–	–	3	3.740	0	0.719
	1.06E-17	0.097	–	-0.040	4	5.617	1.877 686	0.281
Body size	1.815	−0.077	–	–	3	−11.631	0	1

Only the best models are shown (ΔAICc<2).
–: Not included.

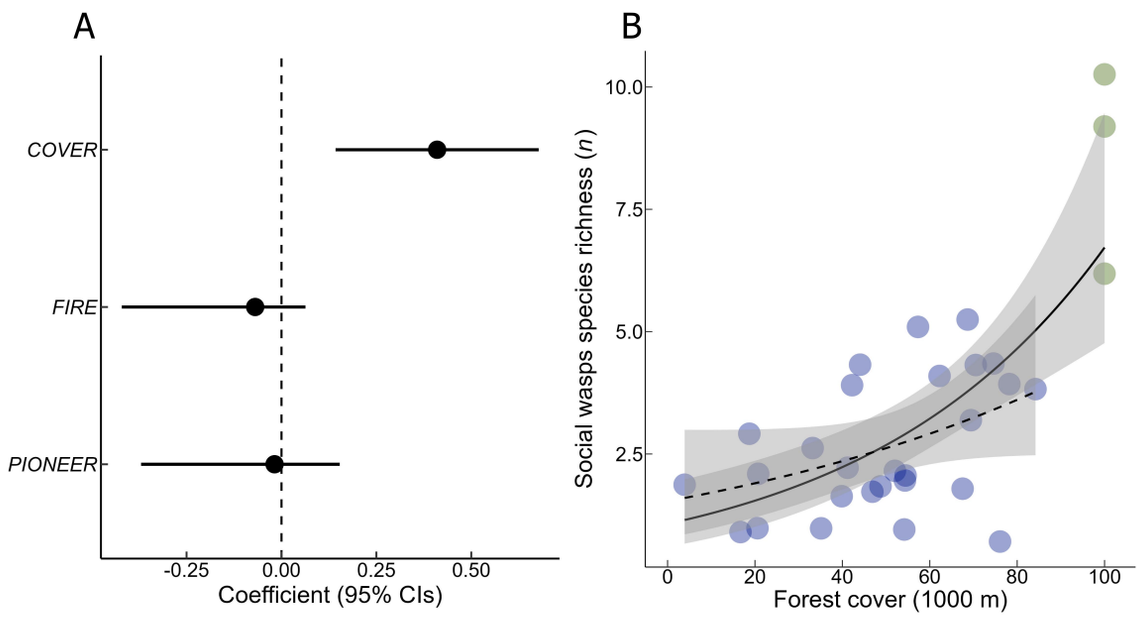

Figure 2 Effects of predictor variables on the species richness of social wasps in the Balbina Hydroelectric Reservoir, in the Brazilian Amazonia

A: Predictors of social wasp species richness at 27 islands and three continuous forests of the Balbina hydroelectric reservoir, Brazilian Amazonia. Model averaging results of candidate models within AICc<2, explaining the variation in species richness. B: Relationship between social wasp species richness and forest *COVER* (within a 1 000 m buffer). Blue and green symbols represent islands and mainland sites, respectively. CIs: Confidence intervals.

We also demonstrate that social wasp species richness observed on islands was higher than that in the continuous forest. However, we highlight that the overall sampling effort allocated to the islands was almost twice as high (816 hours of sampling on islands vs. 432 hours at mainland sites), which may explain the higher absolute species richness observed on the islands. Even so, with about half of the sampling effort, continuous forests showed a higher mean species richness, hosting about 50% of the species richness at all sites including 20% of unique species. It is also important to emphasise that the probability of an individual being captured by any flight interception trap is greater in smaller areas and, therefore, trap efficiency must have been higher on islands than in vast areas of continuous forest. These results reinforce the fact that islands had a low capacity to retain the diversity of social wasps found in continuous forests. On the other hand, the higher average richness of social wasps observed in the mainland can be explained by the greater structural complexity of these environments compared to the islands (Benchimol & Peres, 2015b). Continuous forests often span a wide habitat diversity, including treefall clearings, lowlands, streams, slopes, plateaus, all of which retain amarked variation in vegetation structure and diversity (August, 1983). This allows for the establishment and survival of more species of social wasps, providing greater protection from predators (Dejean et al., 1998; Diniz & Kitayama, 1994), creating distinct microhabitats for organisms (de M Santos et al., 2007; Graça & Somavilla, 2019), and increasing the availability and diversity of food resources and nesting substrates (Graça & Somavilla, 2019; Somavilla et al., 2014; Wenzel, 1991).

Surprisingly, we note that our islands had a greater number of unique species than continuous forest sites. However, about a third of those species belong to the Mischocyttarini tribe, a group comprised exclusively of species that typically occur at low densities and whose nests also contain few individuals (Prezoto et al., 2021). For these reasons, species in this group experience a low capture success particularly over extensive areas such as mainland sites, where species movements are not restricted in space. On the other hand, the smaller habitat area that generally characterises the islands surveyed in this study may increase the probability of interception of Mischocyttarini species. A similar explanation was proposed for the higher capture rates of small mammals on small islands (Palmeirim et al., 2021). This could also

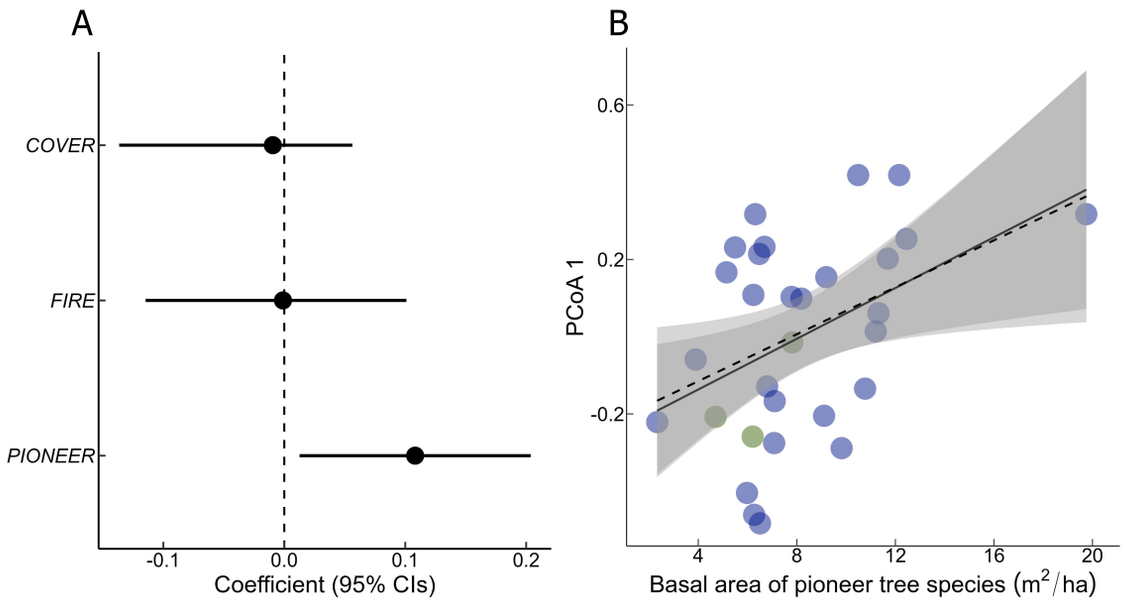

Figure 3 Effects of predictor variables on the species composition of social wasps in the Balbina Hydroelectric Reservoir, in the Brazilian Amazonia

A: Predictors of social wasp species composition at 27 islands and three continuous forests of Balbina hydroelectric reservoir, Brazilian Amazonia. Model averaging results of candidate models within AICc<2, explaining the variation in species composition, expressed as the first PCoA axis. B: Relationship between social wasp species composition and PIONEER tree abundance (basal area of pioneer tree species (m^2/ha)). Blue and green symbols represent islands and mainland, respectively. CIs: Confidence intervals.

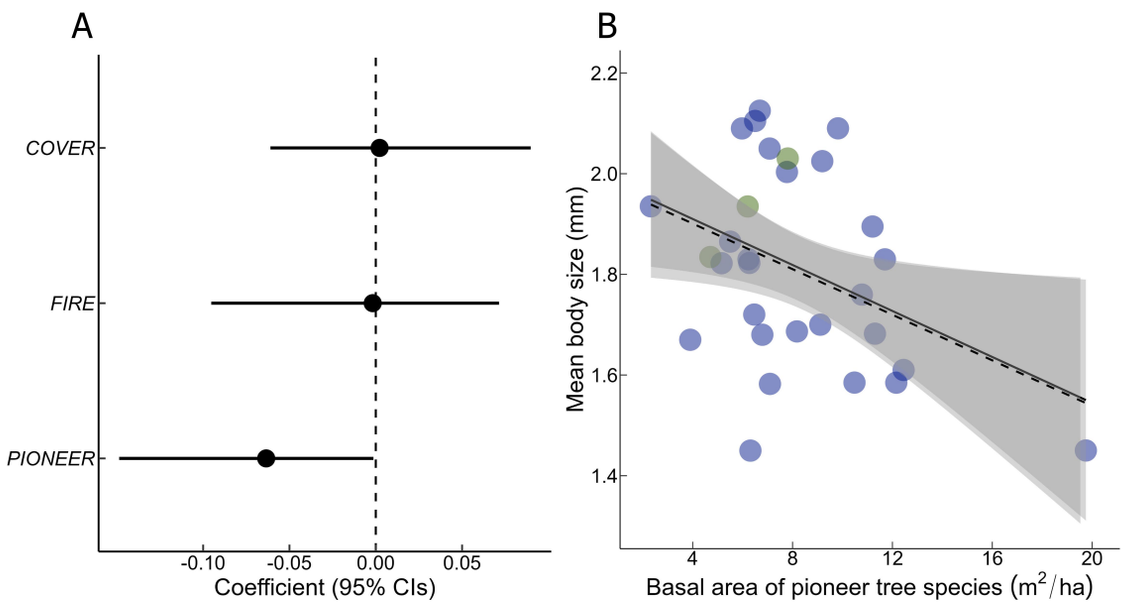

Figure 4 Effects of predictor variables on the mean body size of social wasps in the Balbina Hydroelectric Reservoir, in the Brazilian Amazonia

A: Predictors of the size structure of social wasps at 27 forest islands and three continuous forests of Balbina hydroelectric reservoir, Brazilian Amazonia. Model averaging results of candidate models within AICc<2, explaining the variation in mean body size of social wasp species per site. B: Relationship between mean body size of social wasp species and PIONEER trees (basal area of pioneer tree species (m^2/ha)). Blue and green symbols represent islands and mainland, respectively. CIs: Confidence intervals.

explain the non-occurrence of any individual from the Polistini tribe, which is unusual especially in the Amazon. The Polistini tribe is also characterised by species occurring at relatively low densities (de Oliveira et al., 2010), which may similarly explain the unusual fact that we did not record any species in this group, which is both frequent and extremely diverse in tropical regions (Carpenter, 1996; Somavilla et al., 2021a), especially in the Amazon (Somavilla et al., 2020, 2021b).

Our results also demonstrate that, among the variables included in our models, landscape-scale forest amount was the only predictor explaining patterns of social wasp species richness. According to our hypothesis, social wasp species richness was positively affected by the amount of habitat at the landscape-scale. Ecological studies that investigate the

effects of landscape modification on the diversity patterns of social wasps are still scarce and restricted to agricultural landscapes (but see Bueno et al., 2019; Ferreira et al., 2020; and Perillo et al., 2020). However, studies conducted in agricultural landscapes have shown that both the amount of native habitat at the landscape-scale (Ferreira et al., 2020) and fragment size (Bueno et al., 2019) positively affect the species richness of social wasps. Our results show that the amount of habitat available to these insects is an important predictor of species richness, even for social wasps that are, in general, opportunistic predators (Michelutti et al., 2017) and apparently well adapted to anthropogenic landscapes (Graça & Somavilla, 2019; Somavilla et al., 2016).

Overall habitat amount around each patch reflects not only the amount of habitat available to social wasps, but also the isolation of each island from neighbouring islands, so that a lower amount of landscape-scale habitat results in greater isolation. Isolation severely impacts species with specific habitat and resource requirements (Devictor et al., 2008; Nordén et al., 2013), thereby limiting their spatial occurrence and causing the native assemblage structure to break down. Isolation effects are often associated with the ability of species to disperse across the wider landscape. Unfortunately, we do not have information quantifying actual flight distance of social wasp workers or queens; i.e., the distance they are able to fly to either forage or start new colonies. This would help us elucidate and better understand the patterns of movement and colonisation of these wasps. Body size is, however, positively associated with flight capacity and distance (Greenleaf et al., 2007), so that large-bodied species likely travel over a larger foraging area and, consequently, access resources unavailable to smaller species, as demonstrated for bees (Mayes et al., 2019). However, we show that mean body size of local wasp assemblages was unaffected by the amount of surrounding habitat. This suggests that lower levels of habitat amount negatively affects key properties of social wasp assemblages, regardless of species-specific dispersal capacity.

Contrary to our expectations, *FIRE* and *PIONEER* did not show any effect on species richness, and *PIONEER* was the only predictor of social wasp species composition. Pioneer tree species are fast growing and benefit from disturbances in forest fragments, especially mediated by fire and edge effects. Therefore, in the most disturbed islands, pioneer trees dominate adult tree communities and can be used as a proxy for environmental quality (Benchimol & Peres, 2015b). In terms of species composition, over one-third (28%) of all species collected in this study were singletons, which constrains our inferences on the effects of local habitat quality, since the absence of several taxa at specific sites could be attributed to the low detectability of rare species. However, it is noteworthy that only seven of a total of 29 species were recorded on islands with high relative abundance of pioneer tree species (>47% of trees), and six of these species (*A. fulvofasciata*, *A. pallipes*, *A. pallens*, *Polybia liliacea*, and *P. rejecta*) are known to be widely tolerant and abundant in disturbed environments, such as forest edges, agricultural areas, and urban forest fragments (Graça & Somavilla, 2019; Somavilla et al., 2016). Environmental disturbances, such as fire incidence, likely altered the tree species composition, resulting in a process of “secondarization”, whereby primary forest tree species are replaced by pioneers associated with early secondary forests (Barlow & Peres, 2008). Here, we show that local disturbance events leading to wholesale changes in tree species composition may also result in alterations in the composition of social wasp species, especially through the dominance of more common and smaller-bodied species.

Local disturbances and changes in habitat quality can exert different effects on social wasp assemblage. For example, the great abundance of pioneer tree species can benefit wasps by favouring the abundance of herbivorous insects, especially Lepidoptera larvae (De Carvalho Guimarães et al., 2014), which are the main source of protein for social wasps (Detoni & Prezoto, 2021). However, the increased supply of resources only favours species with greater environmental plasticity and capable of persisting in these altered environments, as seems to be the case with *A. pallens*. In fact, this was the only species that occurred on the island with the highest basal area density of pioneer tree species, also showing the highest abundance of individuals on this island. The basal area of pioneers was also the only predictor of the body size, and negatively affected the average body size of social wasps. This result suggests that larger species tend to be disproportionately affected by local-scale habitat modification in ways that benefit smaller species. In fact, when we consider the five most abundant species that presented wide occurrence, our results indicate that small species, such as *A. pallens*, *A. fulvofasciata*, and *A. pallipes* (both with mean intertegular distance <1.9 mm), had high occurrence and abundance even on more distant islands.

Fire severity was the only variable in our models that did not have a significant effect on species richness, composition or mean body size of social wasps. In fact, fire can negatively affect insect assemblages by destroying their nests and causing mortality due to excessive temperature rise and smoke (Moretti et al., 2006). However, fire occurred more than 20 years from our field surveys, and given the rapid life cycle of the wasps, assemblages have had enough time to recover. Studies that investigated the effects of fire occurrence on the diversity of social wasps are scarce and we consequently lack robust information to support our discussion. Yet, Clemente et al. (2019) investigated such effects and, contrary to the results found in our study, the authors demonstrated that the occurrence of fire in an area of the Cerrado reduced the species richness by one third and affected the species composition of social wasps. However, in that study, wasp surveys were carried out immediately after the occurrence of the fire event. The fact that we did not find a significant effect of fire intensity on species richness may be associated with the time of occurrence of burning events on the Balbina Islands (~25 years ago), which could be sufficient for recolonization and reestablishment of the species.

CONCLUSION

Typical patterns of insularization generated by major hydroelectric dams, including Balbina, affected the local species richness and composition of social wasps after ~30 years of isolation. Our results show that the number of co-existing social wasp species was affected by landscape-level processes, with habitat amount serving as an important predictor in explaining richness patterns. Conversely, species composition was more heavily affected by changes at the local level, in which the basal area abundance of pioneer trees (used as a proxy of local habitat quality) affected species composition, exerting a negative impact on large-bodied

species. Finally, our results add mounting evidence to how terrestrial biodiversity is affected by large hydropower reservoirs in the Amazon, especially those forming shallow areas where a large number of small islands are created but subsequently harbour limited species diversity. Therefore, we suggest that environmental assessments of large hydroelectric plants should include efficiently sampled insect taxa in their protocols, since these organisms often comprise good indicators of habitat degradation in these systems.

SUPPLEMENTARY DATA

Supplementary data to this article can be found online.

COMPETING INTEREST

The authors declare that they have no known competing interests.

AUTHORS' CONTRIBUTIONS

D.S., A.S., M.B. and C.A.P. conceived the ideas and designed methodology; D.S. and A.S. collected the data; A.S. identified the species; D.S. and M.B. performed all geoprocessing analysis; J.V.A.F and D.S. analysed the data; J.V.A.F., D.S., A.S., M.B., A.F.P. and C.A.P. led the writing of the manuscript. All authors read and approved the final version of the manuscript.

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