

Diversity partitioning and distance-decay relationship of saprophytic flies (Insecta: Diptera) in the western Brazilian Amazon

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ABSTRACT

Studying beta-diversity patterns of biological communities and how species are organized in space is central to understanding the processes that maintain species diversity. Furthermore, knowledge on beta-diversity patterns is key for the protection and conservation planning of regional diversity. Insects represent the terrestrial animal group with the largest global biomass and a great body of information about spatial diversity patterns of megadiverse orders such as hymenopterans, lepidopterans, and coleopterans is available. However, studies dedicated to understanding these patterns in dipterans are scarce. Here, we aim to characterize the spatial variation of the assemblage of phytosaprophytic flies in the Amazon forest by investigating its distribution across hierarchies of spatial scales and the effect of geographical distance. The study site is located in the Direct Influence Area of the Belo Monte hydroelectric dam, Pará state, Brazil. Sampling followed the Rapid Assessments for Long Term Ecological Research experimental design. Fly assemblages were not uniform across most of the spatial scales investigated. The larger scale (from 10 to 100 km) contributed more to the gamma diversity of the region than the smaller ones (approximately 1 km). The beta diversity with a Shannon index of over 60 % of γ taxonomic diversity was influenced by the diversity within transects (α -diversity). Pairwise dissimilarity showed no significant relationship between geographical distance and Sorensen dissimilarity, turnover, nestedness, balanced variation in species abundances, or abundance gradient components. The absence of stochastic processes in the formation of the assemblages of phytosaprophytic flies indicates that environmental filters are more important to its structuring than neutral processes. Thus, studies on larger scales can provide more robust evidence on the assemblages distribution, both in preserved and highly impacted environments. Our study considered this wide-scale and our finding revealed some patterns in the assembly rules of the flies community Amazon.

1. Introduction

Diptera is one of the most diverse insect orders, with around 160,000 species described worldwide (Zhang, 2011). They show several distinct habits (Marshall, 2012), and function as pollinators (Orford et al., 2015) and decomposers of organic matter (Castelli et al., 2020). Some flies feed on rotting vegetal matter, such as Mesembrinellidae, Neriidae, and Ropalomeridae (Brown et al., 2010), representing phytosaprophytic families. Others like Sarcophagidae feed on decaying animal matter, including some species that can be of sanitary and forensic importance

(Xavier et al., 2015), displaying an important role in recycling organic matter on ecosystems (Castelli et al., 2020). Thus, many studies show how different factors in different ecosystems affect the spatial distribution and abundance of the communities of saprophytic flies. Indeed, several studies evaluated how these flies' composition, richness, and abundance are arranged according to land use (Carmo and Vasconcelos, 2016; Chust et al., 2004; Dufek et al., 2016; Vasconcelos and Salgado, 2014), resources abundance (Dufek et al., 2019, 2021), or different types of ecosystems (Sousa et al., 2010, 2011a, 2011b, 2016). However, studies evaluating the diversity additive partitioning on hierarchically nested

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scales in tropical areas are scarce, with only one study for the temperate region (Lévesque-Beaudin and Wheeler, 2011). Understanding the underlying causes of community composition and its spatial variation (β -diversity) remains a major goal in community ecology (Gallardo-Cruz et al., 2010; Sutherland et al., 2013).

Beta diversity can be defined as changes in the composition, richness, and abundance in a certain region, comparing diversity in different scales (Whittaker, 1960). Briefly, is expressed as the ratio (Whittaker, 1972) or the difference (Lande, 1996) between the local and the regional pool of species. Within the current beta diversity approach, community spatial variation can be analyzed in two ways: i) diversity partitioning, and ii) the distance-decay relationship (Barton et al., 2013). In the former, diversity can be partitioned into three components: within a community (alpha, α), within a region (gamma, γ), and the difference between several communities within a region (beta, β) (Whittaker, 1960). The latter aims to understand whether processes conducted by environmental restrictions (deterministic or niche) or processes based on dispersion limitations (stochastic or neutral) are more important to the species spatial distribution patterns (Chase, 2014).

Regardless, two processes are linked to the patterns of beta diversity: i) turnover ii) and nestedness. Turnover represents the substitution of species between sampling locations, while nestedness is related to changes in species richness (sampling locations with lower richness are a subset of the species from higher-richness sampling locations) (Antão et al., 2019; Baselga, 2010). Both processes are important to the formation of beta diversity patterns. While turnover can reflect environmental or spatial filters, historical restrictions (Qian et al., 2004) or dispersion processes, nestedness is frequently related to the number of available niches (da Silva et al., 2018), or to the extinction-colonization dynamics (Si et al., 2016). Analyzing patterns of beta-diversity and its response to the distance-decay relationship may reveal how Diptera diversity is spatially structured and assembled (Lévesque-Beaudin and Wheeler, 2011; Morlon et al., 2008). Thus, incorporating a spatial perspective into the β -diversity analysis has proven to be a powerful tool to elucidate, understand, and explain the underlying causes of complex biodiversity patterns and species turnover across space (Gallardo-Cruz et al., 2010).

In the Amazon rainforest, most of studies on saprophytic flies community ecology investigate aspects of cattle ranching (de Sousa et al., 2020); distribution, checklists (Amat, 2010; Carvalho-Filho and Esposito, 2008; Sousa et al., 2011a, 2015; Valverde Castro et al., 2017), vegetation types (Esposito et al., 2010; Sousa et al., 2010, 2016), urbanization (Barbosa et al., 2017), and conservation and bioindication (Sousa et al., 2011a, 2014). Thus, we aim to characterize the spatial variation of the assemblage of phytosaprophytic flies in different scales in the world's largest rainforest. Additionally, we investigate how this community is distributed across hierarchies of spatial scales and the effect of geographical distance on the dissimilarity. We expect that phytosaprophytic fly assemblages will not be uniform across all studied spatial scales (different than expected by chance), and that greater scales (between 10 and 100 km) will contribute more to the regional gamma diversity than smaller ones (approximately 1 km). Furthermore, we expect that processes associated with limiting dispersion will create nonrandom patterns of diversity partitioning, that is, geographical distance (stochastic process) acts as a factor that increases beta-diversity. If random patterns are found associated with geographical distance, we can infer that deterministic processes are more relevant to this community than stochastic ones, since stochastic process are processes associated with exclusively spatial factors (neutral-structured communities, Hubbell, 2001).

2. Material and methods

2.1. Study area

The study site is in the Direct Influence Area (DIA) of the Belo Monte

hydroelectric dam in a region known as Volta Grande, Xingu River, in Pará state, northern Brazil (03°26'S and 51°56'W, Fig. 1a). The area is located within the Amazon biome, with an original vegetation classified as dense ombrophilous non-flooded forest ("terra firme" forest), as well as floodplain forests on river banks ("várzeas" and "igapós") (Salomão et al., 2007). Sampling trips were carried out in five field campaigns between 2014 and 2016, with the first taking place in July 2014; the second in January and February 2015; the third in July and August 2015; the fourth in February and March 2016, and the fifth in July 2016.

2.2. Sampling methods, preparation of samples, and taxonomy

Sampling design followed RAPELD (Rapid Assessments for Long Term Ecological Research, in Portuguese), which merges rapid assessments with long-term studies (Magnusson et al., 2005). The RAPELD design consists of eight modules inserted in the study area, where each module is composed of two 5-km long parallel transects separated by 1 km (Lemos et al., 2015; Vaz-Silva et al., 2015). Each transect consisted of six perpendicular 250 m parcels on opposite sides, distant 1 km from each other. Each parcel was sampled with four traps for the collection of phytosaprophytic flies (Fig. 1b and c), and each trap was placed within parcels at distances of 10, 90, 150 and 250 m. Traps were manufactured based on those designed for fruit flies (Medeiros and Klaczko, 1999), consisting of 2-L plastic bottles, which insects can access through four openings ranging from 0.5 to 2.5 cm. A mixture of mashed banana and dry-bread yeast (*Saccharomyces cerevisiae*) fermented for 36 h was used as bait. Traps were exposed in the field for 48 h, with insects being removed every 24 h, to avoid the loss of the specimens once the Amazonian environments are hot and humid and easily breaks specimens (Fig. S1). Also, the bait was replaced every 24 h with a recently fermented banana (Fig. 1d). The specimens were transferred alive to plastic bags and posteriorly were freezing until the triage process. After that, the specimens were stored in 90 % alcohol and taken to the entomology laboratory of the Museu Paraense Emílio Goeldi (MPEG) for processing, mounting, and identification. Samples were collected under the IBAMA/SISBio license number 251/2013. These specimens are deposited in the Entomological Collection of MPEG.

Fly specimens were identified to species level with identification keys and by comparison with identified specimens in the MPEG collection. For the identification of Mesembrinellidae, keys were used from Guimarães (1977), Bonatto (2001), and Kosmann et al. (2013); for Neriidae the keys were by Carvalho-Filho and Esposito (2008) and Sepúlveda et al. (2013a, b); for Ropalomeridae the keys were by Prado (1966), Marques and Ale-Rocha (2005), Marques-Costa and Ale-Rocha (2005), Ale-Rocha and Alves (2006), and Kirst and Ale-Rocha (2012); and for Sarcophagidae the keys and other taxonomic tools were by Lopes (1939, 1946, 1958, 1975), Lopes and Tibana (1987), Lopes and Leite (1991), Tibana and Xerez (1985), Carvalho and Mello-Patiu (2008), Carvalho-Filho and Esposito (2012), and Buenaventura and Pape (2013). Only male specimens of Sarcophagidae were identified at specific level since identification is based mainly on features of male genitalia.

2.3. Data analysis

2.3.1. Description of the assemblage of phytosaprophytic flies

First, individual size- and coverage-based rarefaction and extrapolation (doubling to reference sizes) curves were built to describe the collected diversity profile using Hill numbers of $q = 0$ (species richness), $q = 1$ (Shannon diversity), and $q = 2$ (Simpson diversity) (Chao et al., 2014). The diversity profile by Hill number is interesting since it enables the observation of the effective number of species based on assemblages with different abundance equitabilities. For example, in assemblages where all collected species have equal abundances, all Hill numbers will be equal (i.e., the species richness value). On the other hand, in assemblages with uneven abundance, Hill numbers will reflect the

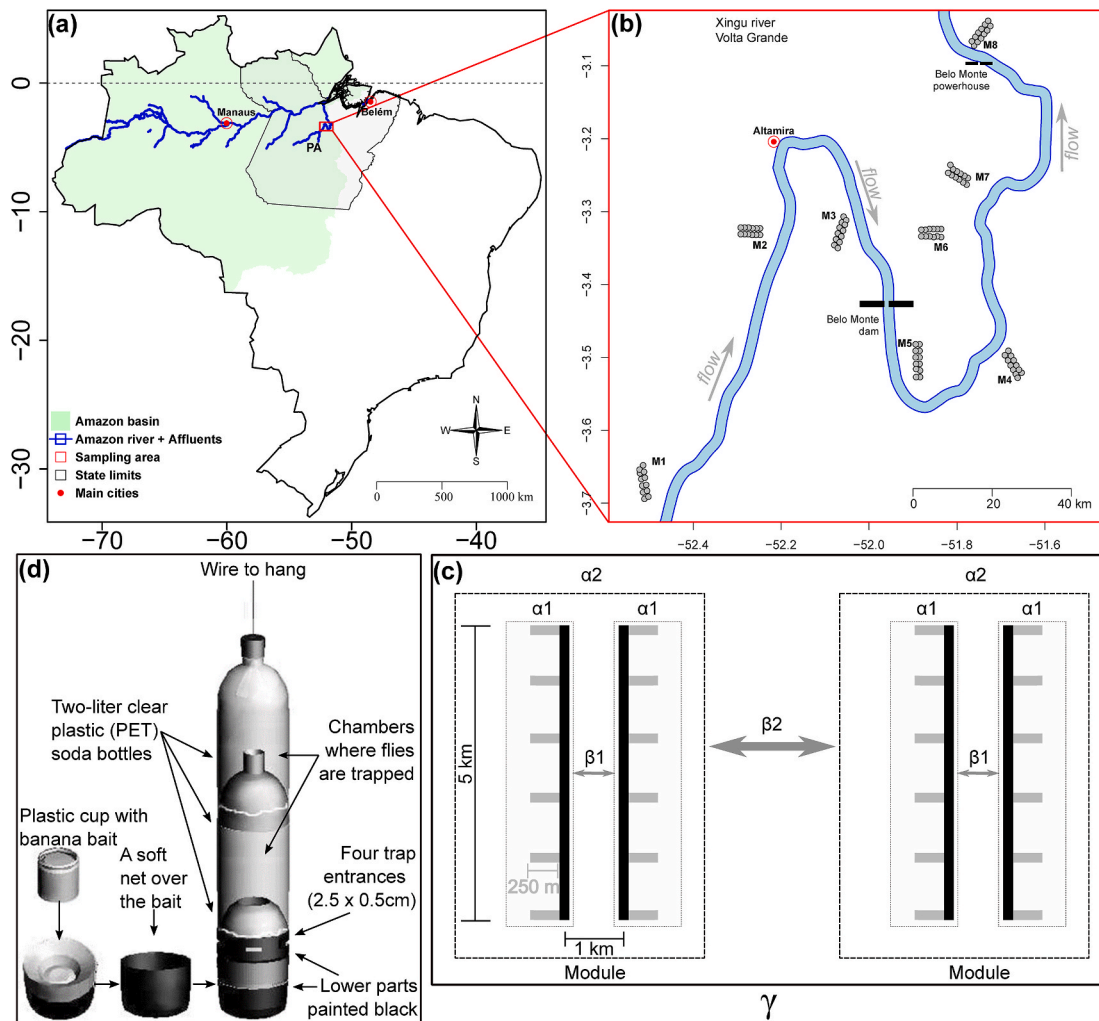


Fig. 1. Location of RAPELD sampling modules (M1 – M8; 1 to 8) on Volta Grande, Xingu River, Pará state, Brazil. (a) Detail of the geographic position in relation to the main river of the Amazon basin, and (b) highlight of the sampling modules distributions within the Belo Monte hydroelectric plant's area of influence. (c) Schematic drawing of the hierarchical model for the additive partitioning of phytosaprophytic flies diversity at spatial dimension. Diversity within transects (dotted box) is α_1 diversity; diversity among transects is β_1 diversity; diversity within a module (dashed boxes) is α_2 diversity; diversity among modules is β_2 diversity; and total diversity (solid box) is γ diversity. (d) General design of the trap used for collecting flies in the present study (for more details, see [Medeiros and Klaczko 1999](#)).

unevenness of species relative abundances ([Chao et al., 2014](#)). Therefore, the more uneven the distribution of relative abundances, the higher the differences across orders q ($0; 1; 2; \infty$) will be. For assemblages with closer relative abundances, the values of the orders $q \geq 1$ will be close to species richness ($q = 0$). Regardless, confidence intervals were determined by using 999 bootstraps for all rarefaction and extrapolation curves.

2.3.2. Additive partitioning of diversity

To understand the patterns of beta-diversity (diversity partitioning and distance-decay relationship) of the assemblage of phytosaprophytic flies, we removed 15 singletons (species with only one specimen collected; [Table 1](#)) from the data matrix to minimize possible errors caused by sampling failures ([Brasil et al., 2020; Poos and Jackson, 2012](#)), and also because beta-diversity metrics are strongly affected by rare species ([Barwell et al., 2015; Beck et al., 2013](#)). For our first prediction, we partitioned the spatial structure of phytosaprophytic flies diversity, grouping temporal data, and analyzing it at the level of 16 transects and eight modules. Thus, we used additive diversity partitioning ([Gering et al., 2003; Lande, 1996](#)) expressed by the species richness and the Shannon information index, in which γ -diversity is the sum of the α - and β -diversity values ($\gamma = \alpha + \beta$). The calculation of the

spatial hierarchy of the fly species' β -diversity was: 1) α -diversity: average richness or Shannon index within transects; 2) β_1 -diversity: the mean difference of assemblages between transects within a module; and 3) β_2 -diversity: the mean difference of the assemblages between modules in the Volta Grande region ([Fig. 1c](#)).

Given that alpha and beta diversities are average values and are thus expressed in the same units, we can evaluate the contribution of each nested spatial level for the total γ -diversity and the significance of each spatial component ([Veech et al., 2002](#)). Our null hypothesis is that phytosaprophytic fly diversity is uniform across all spatial scales. Hence, to assign some ecological process for beta-diversities, we first need to verify whether the observed values are higher or lower than the values expected from random variation due to the sampling design ([Crist et al., 2003; Gotelli and Graves, 1996](#)). For that, we used 9999 randomizations, with a 95 % confidence interval.

2.3.3. Distance-decay relationship

In our second prediction, we used matrices of composition incidence and abundance in relation to a spatial distance matrix to calculate the pairwise dissimilarity between modules and verify the distance-decay relationship pattern for the assemblage of phytosaprophytic flies ([Appendix A Table S1](#)). For incidence data, total dissimilarity was calculated

Table 1

Species list and abundances of phytosaprophytic flies by eight modules in the middle Xingu River, in the Belo Monte direct impact area, Pará state, Brazil. Species highlighted in bold are singletons removed from the spatial hierarchical partitioning analysis and distance-decay relationships.

Family	Species		Modules								Abundance	Proportion (%)
			M1	M2	M3	M4	M5	M6	M7	M8		
Calliphoridae	<i>Chloroprocta idioidea</i>	(Robineau-Desvoidy, 1830)	1	0	0	0	0	0	0	0	1	0.001
	<i>Chrysomya albiceps</i>	(Wiedemann, 1819)	0	1	0	0	0	0	0	0	1	0.001
	<i>Chrysomya megacephala</i>	(Fabricius, 1805)	1	0	0	0	0	0	0	0	1	0.001
	<i>Cochliomyia macellaria</i>	(Fabricius, 1775)	0	0	0	0	0	0	0	1	1	0.001
Mesembrinellidae	<i>Eumesebrinella quadrilineata</i>	(Fabricius, 1775)	0	1	0	2	3	2	11	0	19	0.015
	<i>Eumesebrinella randa</i>	(Walker, 1849)	0	0	0	1	0	0	2	0	3	0.002
	<i>Lanella perisi</i>	(Mariluis, 1987)	0	0	0	0	2	4	3	3	12	0.010
	<i>Mesembrinella batesi</i>	(Mariluis, 1987)	0	0	0	1	1	1	1	0	4	0.003
	<i>Mesembrinella bellardiana</i>	(Aldrich, 1922)	0	0	0	0	0	0	2	0	2	0.002
	<i>Mesembrinella bicolor</i>	(Fabricius, 1805)	3	4	9	8	13	11	60	6	114	0.092
Neriidae	<i>Cerantichir peruana</i>	(Hennig, 1937)	0	0	0	0	0	2	2	0	4	0.003
	<i>Glyphidops etele</i>	Aczél, 1961	0	0	1	0	0	2	2	0	5	0.004
	<i>Glyphidops filosus</i>	(Fabricius, 1805)	6	1	9	64	14	22	11	22	149	0.120
	<i>Glyphidops flavifrons</i>	(Bigot, 1886)	0	0	0	0	0	0	0	1	1	0.001
	<i>Glyphidops vittatus</i>	(Cresson, 1912)	0	0	0	1	0	0	0	0	1	0.001
	<i>Nerius pilifer</i>	Fabricius, 1805	1	2	5	1	6	1	7	2	25	0.020
Ropalomeridae	<i>Nerius plurivittatus</i>	Bigot, 1886	0	0	0	0	3	0	4	0	7	0.006
	<i>Apophorhynchus amazonensis</i>	Prado (1966)	0	0	0	0	1	0	1	0	2	0.002
	<i>Rhopalomera clavipes</i>	(Fabricius, 1805)	1	0	1	0	1	0	0	0	3	0.002
	<i>Rhopalomera stictica</i>	(Wiedemann, 1828)	0	0	2	0	1	0	0	0	3	0.002
	<i>Rhopalomera tessellata</i>	Prado (1966)	0	0	0	0	0	1	0	0	1	0.001
	<i>Rhopalomera tibialis</i>	Walker, 1852	0	0	1	0	0	0	0	0	1	0.001
Sarcophagidae	<i>Willistonella pleuropunctata</i>	(Wiedemann, 1824)	86	15	21	15	28	5	45	50	265	0.213
	<i>Argoraviniya rufiventris</i>	(Wiedemann, 1830)	0	0	0	0	0	0	0	1	1	0.001
	<i>Dexosarcophaga carvalhoi</i>	(Lopes, 1980)	0	0	0	0	0	0	0	1	1	0.001
	<i>Helicobia borgmeieri</i>	Lopes (1939)	0	0	0	0	0	1	0	0	1	0.001
	<i>Helicobia morionella</i>	(Aldrich, 1930)	0	0	0	0	0	0	0	1	1	0.001
	<i>Helicobia pilifera</i>	Lopes (1939)	0	0	0	0	0	0	0	18	18	0.015
	<i>Helicobia</i> sp.		0	0	0	0	0	0	0	2	2	0.002
	<i>Lepidodexia latifrons</i>	Kano & Lopes, 1969	0	0	0	0	1	0	0	0	1	0.001
	<i>Lepidodexia</i> sp.		0	0	0	1	0	1	1	1	4	0.003
	<i>Oxysarcodexia amorosa</i>	(Schiner, 1868)	0	0	0	0	1	0	0	1	2	0.002
	<i>Oxysarcodexia avincula</i>	(Lopes, 1933)	1	0	0	0	0	0	0	3	4	0.003
	<i>Oxysarcodexia bakeri</i>	(Aldrich, 1916)	1	1	0	0	0	0	0	14	16	0.013
	<i>Oxysarcodexia fringidea</i>	(Curran & Walley, 1934)	0	0	0	0	0	0	0	3	3	0.002
	<i>Oxysarcodexia intona</i>	(Curran & Walley, 1934)	0	0	0	0	0	0	0	1	1	0.001
	<i>Oxysarcodexia thornax</i>	(Wiedemann, 1830)	4	3	1	0	0	1	0	86	95	0.076
	<i>Peckia chrysostoma</i>	(Wiedemann, 1830)	2	2	12	1	1	0	0	5	23	0.019
	<i>Peckia collusor</i>	(Curran & Walley, 1934)	0	0	0	0	1	0	0	0	1	0.001
<i>Peckia lambens</i>	(Wiedemann, 1830)	1	0	3	0	0	0	0	11	15	0.012	
<i>Ravinia belforti</i>	(Wiedemann, 1830)	14	0	0	0	2	0	0	2	18	0.015	
<i>Ravinia effrenata</i>	(Prado & Fonseca, 1932)	17	0	4	0	1	0	0	120	142	0.114	
<i>Retrocitomyia retrocita</i>	(Hall, 1933)	2	0	0	0	0	0	0	0	2	0.002	
<i>Titanogrypa luculenta</i>	(Lopes, 1938)	3	0	1	0	0	0	0	17	21	0.017	
<i>Tricharaea occidua</i>	(Fabricius, 1794)	16	1	2	1	0	4	1	223	248	0.199	
Total abundance			160	31	72	96	80	58	153	595	1245	
Total richness			17	10	14	11	17	14	15	25	45	

using the Sorensen index (Baselga, 2010). Furthermore, to evaluate which process contributes the most to the total dissimilarity decrease, we separated dissimilarity into turnover and nestedness (Baselga, 2007; Harrison et al., 1992). We then calculated three matrices: (i) β_{SOR} , which represents the total compositional variation between all pairs of modules; (ii) β_{SIM} , which represents the change in composition due to turnover; and (iii) β_{SNE} , which is the dissimilarity resulting from nestedness, calculated as the difference between β_{SOR} and β_{SIM} (Baselga, 2010, 2012). As for the abundance matrix, we calculated total dissimilarity using the Bray-Curtis index (Baselga, 2013) and applied the same separation approach into two processes: balanced changes and abundance gradients (Baselga, 2013). Therefore, we calculated three matrices: (i) β_{BRAY} , an extension of the Sorensen index based on abundance; (ii) β_{BAL} , balanced variation in species abundance, which is analogous to species replacement in incidence-based patterns, as the abundance of some species declines from site 1 to site 2 in the same magnitude in which the abundance of other species increases from site 1 to site 2; and (iii) β_{GRA} , abundance gradients equivalent to species nestedness in incidence-based patterns, as the abundance of all species equally declines (or increases) from site 1 to site 2 (Baselga, 2013). To test the

significance of the relationship between geographical distance and dissimilarity distance matrices we fitted negative exponential functions, which are recognized as better descriptors for distance-decay patterns at large spatial scales (Nekola and McGill, 2014; Nekola and White, 1999).

We performed all analyses in the R environment version 4.0.3 (R Core Team, 2021). Additionally, we used the *iNEXT* (Hsieh et al., 2016) and *betapart* packages (Baselga and Orme, 2012) for computing: i) asymptotic diversity estimate curves, ii) additive partitioning - *adipart* function, iii) incidence dissimilarity matrices - *beta.pair* function, iv) abundance dissimilarity matrices - *beta.pair.abund* function, and vi) negative exponential model for the distance-decay relationship - *decay.model* function (Appendix A).

3. Results

We collected 1245 specimens from 45 species, distributed among 22 genera and five families, with an average \pm standard deviation of 15.37 \pm 4.62 species and 101.25 \pm 50.31 individuals per module (Table 1). Family richness and abundance followed an almost symmetrical distribution, with Sarcophagidae as the most representative one (22 species –

48 %; 620 individuals – 49.7 %), followed by Neriidae (7–15 %; 192–15.5 %), Ropalomeridae (6–13 %; 275–22.0 %), Mesembrinellidae (6–13 %; 154–12.3 %), and Calliphoridae (4–8.8 %; 4–0.3 %).

Asymptotic diversity estimates by size-based rarefaction and extrapolation curves showed that there was no stabilization for $q = 0$, implying that the asymptote was far from being reached (Fig. 2a), except for $q = 1$ (Shannon diversity, i.e. common taxa richness) and $q = 2$ (Simpson diversity, i.e. dominant taxa richness). However, the coverage-based rarefaction and extrapolation curves suggested that diversity at the studied region was well represented with a sample coverage percentage above 95 % for all diversities (Fig. 2b).

The spatially hierarchical partitioning of phytosaprophytic fly diversities based on species richness showed that β -diversity contributed with approximately 70 % of the diversity within the community (Fig. 3). Additionally, α -diversity (average richness inside the transect – $\alpha 1$) represented around 30 % of the sampled community (Fig. 3). The β -diversity between transects within the module ($\beta 1$) represented about 14 %, while the β -diversity between modules in the Belo Monte region ($\beta 2$) represented 55 % (Fig. 3). When analyzing the significance between the observed and the expected species richness results, we showed that the α -diversity is lower than the diversity expected at random ($S_{OBS} = 9.18$, $S_{EXP} = 12.68$, $P < 0.001$), while $\beta 2$ is higher than the expected at random ($S_{OBS} = 16.50$, $S_{EXP} = 13.00$, $P < 0.001$). On the other hand, $\beta 1$ does not differ significantly from the null hypothesis ($S_{OBS} = 4.31$, $S_{EXP} = 4.37$, $P = 0.95$; Table 2). Moreover, the partitioning expressed by the Shannon index showed that approximately 64 % is represented by the average diversity inside the transect ($\alpha 1$; Fig. 3) and is lower than the expected at random ($H'_{OBS} = 1.51$, $H'_{EXP} = 2.10$, $P < 0.001$). $\beta 1$ and $\beta 2$ represent around 35 % of the β -diversity calculated with the Shannon index, and both are higher than the expected at random ($\beta 1H'_{OBS} = 0.25$, $\beta 1H'_{EXP} = 0.12$, $P < 0.001$; $\beta 2H'_{OBS} = 0.60$, $\beta 2H'_{EXP} = 0.14$, $P < 0.001$; Table 2).

Patterns of pairwise dissimilarity with geographical distance for the assemblage of phytosaprophytic dipterans are only significant when we observe the abundance-based dissimilarity (Fig. 4d). Incidence-based dissimilarity yields no significant relationship with geographical distance, whether for general dissimilarity (Sorensen index, Fig. 4a), species substitution (turnover, Fig. 4b), or nestedness (Fig. 4c). The same pattern was verified when we separated pairwise dissimilarity based on the Bray-Curtis index into its components of balanced variation in species abundances and abundance gradients as neither showed any significant relationships (Fig. 4e and f).

4. Discussion

Many studies have been relevant to understanding the distribution

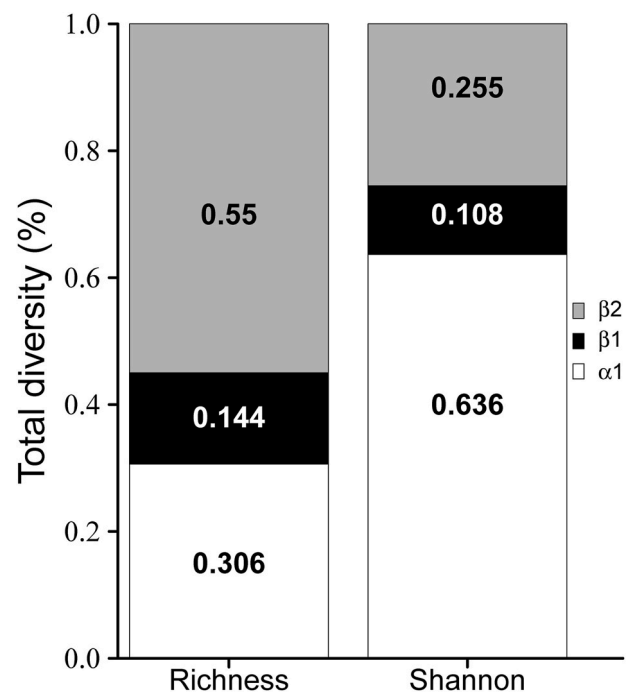
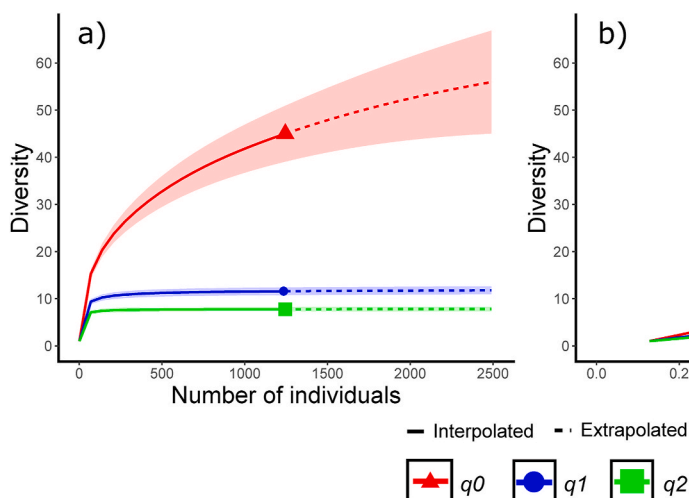


Fig. 3. Contribution (%) of alpha (a) and beta (b) components to the total gamma diversity, both species richness (left) and Shannon diversity (right) (additive partitioning) for phytosaprophytic flies in different spatial scales. For observed and expected values of alpha and beta components, see Table 2.

pattern and diversity of saprophytic flies in the Amazon biome (Esposito et al., 2010; Sousa et al., 2010, 2010, 2016, 2010) and other tropical Brazilian ecosystems (tropical rainforest: Cabrini et al. (2013); Vasconcelos et al. (2015); tropical seasonally dry forest: Oliveira and Vasconcelos (2018); Valverde Castro et al. (2017); savanna-like vegetation (cerrado): Rosa et al. (2011)). However, the present study is the first to highlight the beta-diversity pattern of phytosaprophytic flies in a tropical ecosystem in hierarchically-nested spatial scales. Here, we show that the community of phytosaprophytic flies is differently affected by the scales, i.e., larger scales have a higher contribution to the composition, whereas diversity is higher in smaller scales (Fig. 3). Second, the community is not randomly generated at nearly all spatial scales, thus indicating that ecological processes modulate the formation of phytosaprophytic fly communities (Table 2). Finally, spatial distance is an important factor only for the abundance dissimilarity and not for the

Fig. 2. Asymptotic diversity curve of phytosaprophytic flies for the Belo Monte's dam region, Amazon forest, Pará state, Brazil. (a) Size-based rarefaction (solid lines) and extrapolation (dashed lines) curves, and (b) coverage-based rarefaction (solid lines) and extrapolation (dashed lines) curves up to the corresponding coverage value. The 95 % confidence intervals (shaded areas) were obtained by a bootstrap method based on 999 permutations. (Color figure can be viewed in the online version.) (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

Table 2

Spatial partitioning of the assemblage of phytosaprophytic flies in Volta Grande region, Xingu River, Pará state, northern Brazil. Results highlighted in bold indicate that the observed diversity is significantly different from that expected in a random distribution. For all diversity indexes, the expected value is the mean of the null distribution by 999 randomizations (for more details, see Data analysis section). CI = 95 % confidence intervals.

Index	Scales	Observed	(%)	Expected	CI	P-value	
Richness	α	Within transect	9.18	0.30	12.68	12.06–13.31	0.001
	β_1	Among transects	4.31	0.14	4.37	3.68–5.06	0.959
	β_2	Between modules	16.50	0.55	13.00	12.00–13.87	0.001
	γ	Total	30.00	1.00			
Shannon	α	Within transect	1.51	0.63	2.10	2.04–2.15	0.001
	β_1	Among transects	0.25	0.10	0.12	0.09–0.16	0.001
	β_2	Between modules	0.60	0.25	0.14	0.09–0.20	0.001
	γ	Total	2.38	1.00			

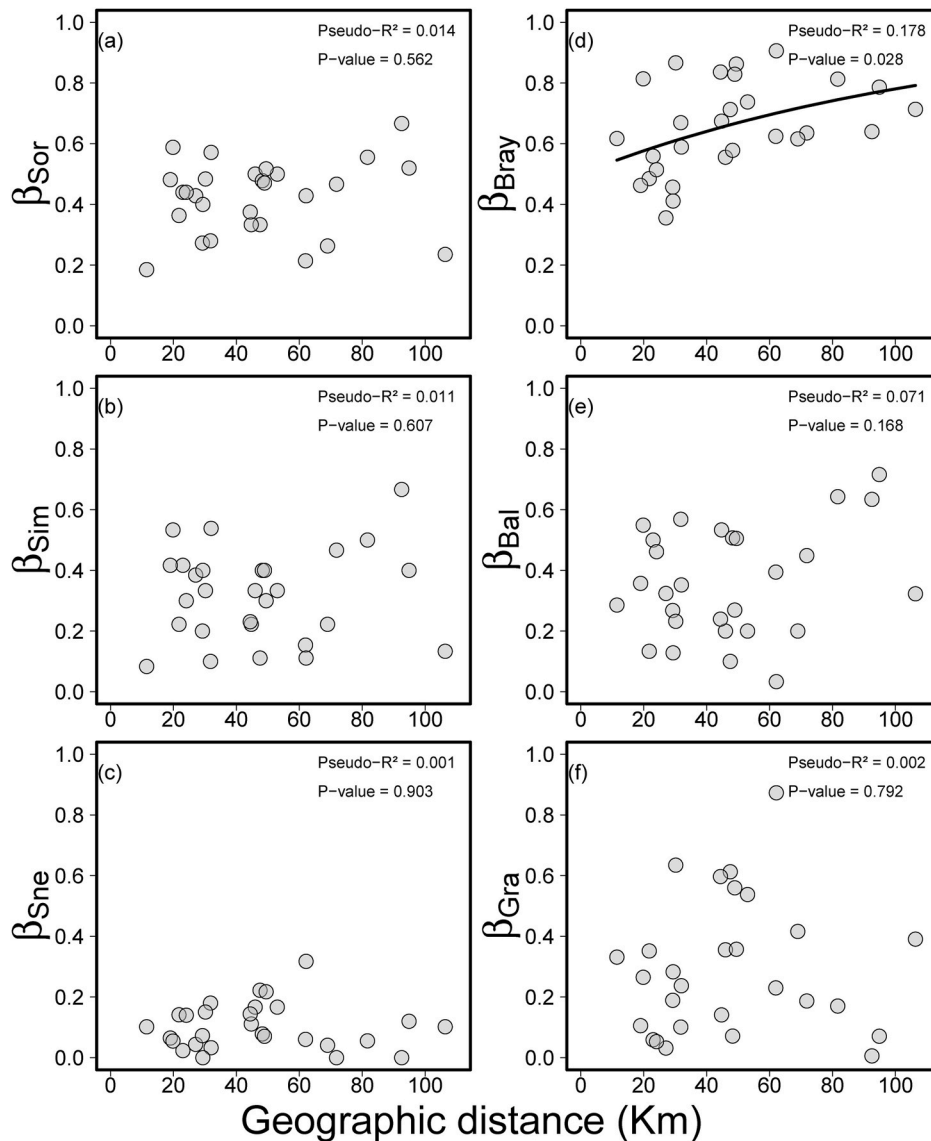


Fig. 4. Relationship between biotic dissimilarity and geographic distances using incidence (a–c) and abundance (d–f) data. Total dissimilarity (β_{SOR} and β_{BRAY}) and its components (β_{SIM} – turnover, β_{SNE} – nestedness, β_{BAL} – balanced variation, β_{GRA} – abundance gradients). Both determination coefficients (Pseudo- R^2) and significance (p , computed using *decay.model* function) for each relationship are shown.

incidence dissimilarity, which reinforces the idea that deterministic processes (niche) are more important than stochastic ones (neutral) for this assemblage (Fig. 4).

We encounter a species richness within transect (α -diversity) minor

those expected by the null model (Table 2), and a contribution higher than expected at this scale to the regional species pool than the diversity among transects. These results can be explained by three factors. First, can be an indicator of a sampling method bias in to be selective in collecting certain groups,

once we believe exist an underrepresentation of the Calliphoridae family. Second, an effect of the aggregate distribution of resources on a local scale, since the spatial aggregation is a common pattern from different communities (Veech 2005; Ribeiro et al., 2008). Lastly, due to the dispersal capacity of these flies at the 1-km scale (Amat, 2010; Chust et al., 2004; Finch and Collier, 2004; Meats and Smallridge, 2007), thus increasing species sharing between transects within the same module. We do not have environmental data on the local scale to affirmative how aggregate factors can drive diversity. These results establish open avenues for further research on how environmental local factors affect the α -diversity of phytosaprophytic flies in Amazon. The beta diversity among transects (β_1) was not significantly different from the expected value, indicating that all phytosaprophytic flies assemblages of transects are subsamples of the same species pool. The differences observed in the Shannon index, in these same scales, suggest that structural differences among transects affect the dominance patterns in these communities since the Shannon index gives more weight for common species than metrics that use species richness (Ribeiro et al., 2008).

The high contribution of beta-diversity for the composition of phytosaprophytic flies (>70 %) shows how environmental and spatial factors at local and regional scales are determinant to the formation of this community (Cottenie, 2005). However, this contribution is low at the scale of approximately 1 km (β_1), thus making the largest β_2 scale contribution (between 10 and 100 km). This high contribution of β_2 can be associated with the landscape attributes of Belo Monte, where local environmental conditions (β_1) are more similar when compared to the region (β_2). In other words, a possible explanation for the more contribution of β_2 is we have one heterogeneous mosaic of favorable and unfavorable habitats for the entire community in this scale (Lemos et al., 2015).

The pattern found for tropical phytosaprophytic flies is distinct from patterns found for the same group in temperate environments, this is not a novelty. Lévesque-Beaudin and Wheeler (2011) analyzed the β -diversity pattern of saprophytic flies in hierarchically nested spatial scales in Canada and found an opposite pattern to that of the present study. In the temperate region, the smaller scale (difference in fly communities between trees from the same locality) contributed more than the scale of approximately 1 km (β_2 in Lévesque-Beaudin and Wheeler (2011), which was similar to our β_1) and <5 % for the scale of approximately 10 km (β_3 in Lévesque-Beaudin and Wheeler (2011) and similar to our β_2). According to Lévesque-Beaudin and Wheeler (2011), this low β -diversity at the 10-km scale can result from recent fragmentation processes of a continuous forest, which separated the community into distinct sites, maintaining the diversity in these areas. In our case, the high contribution from β_2 can be explained by the dispersion limitation at this scale, since the flies' movement capacity is limited to distances shorter than 2 km (Finch and Collier, 2004; Meats and Smallridge, 2007).

This opposite β -diversity pattern between tropical and temperate regions appears to be a feature of the latitudinal diversity gradient (Brown, 2014). This phenomenon of the latitudinal diversity gradient is explained primarily by increasing temperature, wherein tropics the species occupy smaller geographical ranges and a narrower range of abiotic environmental conditions (Rapoport's rule). These patterns of beta diversity are consistent with the effect of temperature on ecological interactions and coevolutionary processes (Brown 2014). So, is probable that the differences in productivity and niche relationships between tropical and temperate be the factors that affect local (alpha) diversity, the spatial turnover (beta diversity), and finally to geographical scale species dynamics (gamma diversity) (Brown, 2014). This comparison may even seem biased, but it opens up perspectives demonstrating the need for further studies for assemblages of saprophytic flies that evaluate the beta diversity pattern in different spatial scales.

The β -diversity expressed by the Shannon index shows that certain fly species are dominant within transects. The Shannon index considers the species relative abundance and expresses the results according to the dominance and rarity of species inside communities (Crist et al., 2003).

In our results, both the local dominance and uniformity of several fly species in the transects are due to a higher contribution of the α scale relative to the β . In this case, the dominant species within the community is *Willistonella pleuropunctata* (Wiedemann, 1824) (Diptera: Ropalomeridae). This is the most sampled genus of Ropalomeridae, comprising about 50 % of specimens found in collections of this family, and is widely distributed across Central and South America (Marques and Ale-Rocha, 2005). However, the observed value was significantly different from the value expected at random for all scales of the Shannon index (α and β). Therefore, we can infer that the dominant species in each scale are different. These results follow similar patterns to those of other insect groups such as butterflies (Ribeiro et al., 2008), moths (Braga and Diniz, 2015), beetles (Gering et al., 2003), herbivorous, and parasitoids (Maia et al., 2019) (Fig. S2).

To the results on the distance-decay relationship, we argue that the increase in community dissimilarity with geographical distance is one of the most well-known and analyzed ecological patterns (Condit, 2002; Nekola and White, 1999; Tuomisto, 2003). However, depending on the scale, geographical distance is auto-correlated with environmental dissimilarity (i.e., the bigger the spatial distance, the bigger the environmental heterogeneity) (Chase, 2014; Jimenez-Valverde et al., 2010; Legendre, 1993). At the scale between 10 and ~100 km, only the abundance-based dissimilarity was significant with spatial distance (Fig. 4d). The lack of relationship between diversity and its components (turnover, nestedness, balanced variation, and abundance gradients) with spatial distance highlights the lack of stochastic processes (Hubbell, 2001) in the structuring of phytosaprophytic fly assemblages. In meta-community theory, neutral dynamics are associated with stochastic processes, while species sorting is more associated with deterministic processes, where both processes are not mutually exclusive and are scale-dependent (Ovaskainen et al., 2019). This result, together with the high contribution of β_2 (largest scale, Fig. 3) shows us that the Volta Grande region is heterogeneous regardless of spatial distances (i.e., the pairs of the most distant modules are not necessarily the most environmentally different ones). However, the abundance-based dissimilarity was significant in relation to spatial distance, thus showing that distance matters in this community profile (species dominance and rarity). Thus, examining communities' spatial structure can provide a strong approach to understand their dynamics, how they are structured, and help explain species diversity patterns (Kneitel and Chase, 2004).

In summary, it appears that in the western Brazilian Amazon, environmental processes are more important in structuring phytosaprophytic fly communities than spatial ones. Other studies demonstrate that the diversity of saprophytic flies can be affected by ecological factors such as anthropic activities (Carmo and Vasconcelos, 2016; Dufek et al., 2016), urbanization (Barbosa et al., 2017; Valverde Castro et al., 2017), food resources (Oliveira and Vasconcelos, 2018), and habitat type (Esposito et al., 2010; Sousa et al., 2010, 2011a, 2016). In the current scenario of biodiversity crisis and declining insect richness in the Anthropocene (McGill et al., 2015; van Klink et al., 2020), understanding the beta-diversity pattern of communities is important before they disappear. For conservation efforts, it is important to consider beta diversity studies to propose mitigation actions (Socolar et al., 2016). Within the Volta Grande region, the surrounding ecological impacts can be both local and synergistic, possibly leading to extinctions, changes in diversity and abundance and, consequently, to faunal homogenization (Akama, 2017).

5. Conclusion

Since purely spatial aspects do not help to explain the structure of the fly communities, we suggest that environmental filters (e.g.: configuration and composition of the landscape, anthropogenic aspects, seasonality, among others) are more important for the structure of fly communities in the Volta Grande region of the Amazon. It is important to maintain constant monitoring of areas influenced by the Belo Monte

dam, since some of the flies sampled in this study are considered synanthropic (associated with anthropic environments) and of medical-sanitary interest (Cadavid-Sanchez et al., 2015; de Souza and Von Zuben, 2016; Xavier et al., 2015), which can directly affect riverine populations. The species *Cochliomyia macellaria* are of medical interest because they cause secondary myiasis and nosocomial myiasis (Smith, 1986), while the species *Chrysomya albiceps*, *Chrysomya megacephala*, and Sarcophagidae family have forensic interest and are transmitters of pathogens (Buenaventura et al., 2009; Ferraz et al., 2010; Junqueira et al., 2017; Vairo et al., 2011). Another relevant aspect of this study is that beta-diversity patterns for phytosaprophytic flies are uncertain and poorly studied, and the environmental factors which explain their communities' distribution and composition need further elucidation (Lévesque-Beaudin and Wheeler, 2011). Thus, testing the effect of habitat heterogeneity in fly dispersion within these landscapes can be relevant to understanding the mechanisms underlying fly assemblages. Finally, studies on larger scales can provide more robust evidence on community distribution, both in preserved and highly impacted environments.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.actao.2021.103768>.

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