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SPATIOTEMPORAL PATTERNS OF SPECIES TURNOVER IN GROUND-DWELLING ANT ASSEMBLAGES (HYMENOPTERA: FORMICIDAE) IN AN AMAZON BASIN HYDROELECTRIC POWER PLANT

PADRÕES ESPAÇO-TEMPORAIS DE SUBSTITUIÇÃO DE ESPÉCIES EM ASSEMBLEIAS DE FORMIGAS DE SOLO (HYMENOPTERA: FORMICIDAE) EM UMA HIDRELÉTRICA NA BACIA AMAZÔNICA

ALANA FERREIRA LOPES

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Orientadora: Dra. Elizabeth Franklin Chilson
Coorientadores: Dr. Jorge Luiz Pereira de Souza
Dr. José Wellington de Morais

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Sinopse:

Estudou-se qual o efeito das fases de enchimento da Usina Hidrelétrica Santo Antônio na substituição de espécies de formigas presentes na área. Análises temporais, espaciais e de direcionalidade das assembleias foram levadas em consideração de forma a determinar de que modo o enchimento afeta a dinâmica de substituição de espécies nessas assembleias.

Palavras-chave: Formigas, Ecologia de Comunidades, Substituição de espécies, Direcionalidade, Hidrelétricas.

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RESUMO

Assembleias e comunidades variam naturalmente ao longo do tempo e espaço. Entretanto, a construção de hidrelétricas e sua supervalorização na produção de energia são uma grande ameaça para comunidades de animais nestas áreas e em áreas que sofrem a influência destas construções. Dessa forma, é essencial monitorar comunidades de animais e plantas nessas áreas. Formigas constituem um dos grupos mais abundantes de insetos e são sensíveis às mudanças ambientais, sendo assim excelentes modelos ecológicos em estudos de diversidade. Neste estudo foi analisada a influência do enchimento do reservatório da Usina Hidrelétrica de Santo Antônio no padrão espaço-temporal da taxa de substituição de espécies e direcionalidade das assembleias de formigas de solo ao longo de 10 campanhas, entre os anos de 2011 e 2014. As coletas foram realizadas utilizando um Extrator de Winkler em 24 parcelas de 250 m de comprimento instaladas em quatro módulos de 4km localizados a diferentes distâncias do Rio Madeira. Foram coletadas 37.969 formigas distribuídas em 47 gêneros e 206 espécies e morfoespécies. A taxa de substituição de espécies foi dinâmica ao longo do tempo. Antes, durante e após do enchimento do reservatório, a média de substituição foi 50,3%, 44,8% e 49,3%, respectivamente. Durante o enchimento ocorreu uma redução na substituição de espécies, chegando a 38,2%, homogeneizando as assembleias. Entretanto, este processo foi revertido no início da fase de pós enchimento, voltando a valores semelhantes à antes do enchimento. Juntamente com a mudança na substituição de espécies, também ocorreu mudança direcional significativa nas assembleias de formigas da área. Uma vez que as variáveis ambientais (e.g. altitude, inclinação do terreno e teor de argila do solo) são consideravelmente estáveis, o processo de enchimento do reservatório foi o fator que influenciou mais fortemente na substituição de espécies em todos os módulos. Além disso, não houve diferença significativa entre as taxas de substituição em diferentes distâncias da margem do rio , fortalecendo a importância do processo de enchimento na substituição de espécies. A resiliência das assembleias de formigas permitiu uma recuperação da taxa de substituição de espécies assim que o processo de enchimento foi encerrado. Desta forma é importante frisar a importância de se inserir análises de mudança de direcionalidade de comunidades em estudos que levem em consideração a substituição de espécies em áreas que sofrem influências de perturbações, como em áreas de hidrelétricas. Além disso, a combinação destas análises com o padrão espaço-temporal de substituição de espécies dentro dessas comunidades permite uma melhor visão de como corre a dinâmica e quais os efeitos na substituição de espécies nestas condições.

ABSTRACT

Assemblages and communities vary naturally throughout time and space. However, hydroelectric power plant constructions and the fact that they are still seen as the best way to the growing energy demand are a big threat to animals' communities within and on the areas that are influenced by those constructions. Therefore, it is important to monitor animals' and plants' communities within those areas. Ants are one of the most abundant insects' groups and are sensitive to environmental changes, being excellent ecological models. In this study, we analyzed the influence of the Santo Antônio hydroelectric plant reservoir filling on the spatiotemporal patterns of species turnover and directionality of ant assemblages over 10 monitoring campaigns from 2011 to 2014. To sample the ant fauna, Winkler extractor were used in 24 250m plots, located in four 4km modules installed at different distances from the Madeira River. During the monitoring, 37,969 ants were sampled, divided in 47 genera and 206 species and morphospecies. The species turnover was dynamic throughout time. Before the reservoir filling, an average of 50,3% of ants were substituted, while during the filling, 44,8% and post-filling, 49,3%. During the reservoir filling, an expressive decay in the species substitution happened, reaching 38,2%, homogenizing the assemblages. However, this process was rapidly reverted on the beginning of the post-filling phase, when turnover values returned to ones observed before. Along with the species substitution decay, there was a significant directional change in assemblages' composition throughout the monitoring. As environmental variables (e.g. altitude, clay content and terrain slope) are considerably stable in the area, the filling process was the strongest factor influencing on the species turnover on ants' assemblages also over space, in all different modules. In addition, there was not significant difference on the species substitution at different distances from the margin, strengthen the importance of the filling process on the species substitution. The high ant's assemblages' resilience allowed a recover in the rate of species' substitution to happen. Thus, it is important to emphasize the importance of analyzing the communities' directionality throughout time in studies that take into account the substitution of species in areas that are influenced by disturbances, such as in hydroelectric areas. In addition, the combination of these analyses with the spatiotemporal pattern of species substitution within these communities allows a better understanding of the dynamics and what are the effects on the substitution of species in these conditions.

SUMMARY

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1. Introduction

Hydroelectric dam constructions have an expressive social, monetary and environmental impact, although decisions on building new hydroelectric dams are usually made over underestimating these aspects and extrapolating the benefits (Fearnside, 2016). By 2015, the Brazilian Amazon had 15 large dams and additional 37 dams planned or under construction (Fearnside, 2016). Those constructions are not only an increasing threat to tropical forests (Emer *et al*., 2013), but also induce habitats fragmentation, creating barriers to the fauna (Lees *et al.*, 2016). Those barriers can lead to changes in local fish migrations (Barthem *et al.*, 1991), possibly induce extinction of turtles, primates and birds' species (Benchimol & Peres, 2015) and affect ants assemblages composition, richness and functional diversity (Gomes, 2017). Environmental damages caused by dams' implementations are largely known (e.g. Emer *et al*., 2013; Fearnside, 2016, Lees *et al*., 2016), and since the constructions of dams for power generation are taking an increasing portion of the Amazon forest (Fearnside, 2015), the assessment of its impacts on animals and plants populations and communities is crucial to the biological conservation of the area where the dam is being constructed.

Although there is a wide range of studies assessing changes in the spatial patterns of species, there are still a reduced number of studies assessing temporal changes and even less assessing both aspects. It is important to measure changes throughout time, as species and communities frequently are substituted not only spatially, but also temporally (Brown, 1998). Studies that incorporate space and time can ben extensively costly and time consuming (Wolfe *et al.*, 1987; Margules, *et al.* 2002; Whittaker *et al.*, 2005), which frequently leads to an analysis of only one of these parameters. However, changes in the turnover throughout time can be a result of population expansion or shrinkage, as much as processes like extinction or immigration, leading to changes in the community's dynamics (Shimadzu *et al.*, 2015). In addition, the use of both spatial and temporal analyses is crucial not only to determine changes in biodiversity (Magurran *et al.*, 2010), but also to describe evolutionary diversity of species communities (Pavoine *et al*., 2009). It is important to emphasize, however, that space and time are different parameters, as space is non-directional and time can only be directional and one dimensional (White, 2007), which allows studies to address these aspects separately. Therefore all these difficulties lead to a limited knowledge about communities combining temporal and spatial changes (Donoso, 2017).

During natural flooding processes, the called “flooding pulses”, common in tropical flooded forests, the invertebrates establish throughout the flooded gradient, developing different surviving strategies (Adis & Junk, 2002). Those flooding pulses are a natural and cyclic disturbance, which in the Amazon can occur in areas with very nutrient water, named “Várzea”, or areas with poor-nutrient water, named “Igapó” (Walker, 1990). However, during dam constructions, the filling of the reservoir frequently results in artificial flooding (Fearnside, 2014), not related with natural flooding pulses. The fauna’s feedback to either natural or artificial flooding processes can be divided between migrants and non-immigrants. Migrant animals can move both along the water line, characterized as horizontal migration or along the trunks, toward the top of the trees, characterized as vertical immigration (Adis, 1997). In Addition, after flooding events, there is a tendency of more generalist species establishing in the area (Baccaro *et al*., 2013). Thus, horizontal distance from the flooding area might determine which species can be established in the area, changing the assemblages’ composition and therefore species substitution (Oliveira, 2013). However, during artificial flooding events, as in hydroelectric reservoir flooding, the natural landscape modification may negatively affect local fauna due fragmentation, as in order to survive in those habitats the species must have specific survival strategies (Adis, 1997), which may not be achieved in such short time period.

Despite the obstacles to assess biodiversity changes throughout time and space simultaneously, there is a substantial amount of researches assessing directionality of the communities (Magurran *et al*., 2010), which determines the degree of temporal variability (Collins *et al.*, 2010). Temporal turnover occurs both by natural and external factors, such as anthropogenic disturbance, which can lead to challenges in determining the causes of changes within the communities (Magurran *et al*., 2010). Although communities tend to be highly resilient to environmental modifications (Chapin III *et al.*, 2006), depending on the level of disturbance, they can have their structure and functions modified (Walker *et al*., 2004). The relation between the positive and the negative community feedbacks to these disturbances is the main key influencing the entire community structure (Chapin III *et al*., 2006). In addition, even though there is a consistent number of studies’ assessing the vulnerability of the communities due to anthropogenic disturbance, the resilience of those communities and their threshold has just begun to be investigated (Walker *et al*., 2004), it is highly likely that allying spatiotemporal analyses and the rate of community directionality within researches that assess naturally changing or anthropic modified landscapes provide a more reliable source for future predictions in similar areas (Collins *et al.*, 2000). Successive assessments based on those sources will be essential to the conservation of the biodiversity in the area.

Insects can act as bio indicators of environmental disturbances (Agosti *et al*., 2000; Ré, 2007; Ribas, 2012; Rocha *et al.* 2015) due to their high diversity, abundance (Rocha *et al*., 2015), high capacity of nutrient cycling (Hughes & Westoby, 1990), acting as predators, seeds dispersers, decomposers and pollinators (Borror, 2011). Within this group, ants are one of the most abundant, representing a large proportion of the terrestrial animal biomass in the Amazon Forest (Fittkau & Klinge, 1973; Ellwood & Foster, 2004). They are highly sensitive to environmental changes and their taxonomy is widely known (Agosti *et al.*, 2000), having a rapid response to driving environmental variables and also being excellent ecological models in studies with diversity approaches (Holldobler & Wilson, 1990). Several studies have been made to measure the influence of ecological stressors upon ants' assemblages and their response (e.g. Lutinski *et al.*, 2014; da Conceição *et al.*, 2015). However, very few studies address temporal (e.g. York, 2000; Donoso, 2017) and spatial variance of ants' assemblages (e.g. Baccaro *et al.*, 2013; Bishop *et al.*, 2014; Bestelmeyer & Wiens, 2016) and no studies combining spatial and directionality of ants assemblages influenced by an hydroelectric dam have been made.

The present study aims to survey the spatiotemporal variance and assess the directionality of ants' assemblages within an Amazon Basin hydroelectric, located in the Rondônia State, prior, during and after the reservoir filling, between 2011 and 2014. The goal is to determine the effects of this anthropogenic disturbance in the ants' assemblages' turnover throughout 10 monitoring campaigns and different spatial locations and to evaluate if these effects resulted in changes in the direcionality of the assemblages' composition throughout the monitoring period.

Therefore, the three questions of this study are: 1) Does the UHE Santo Antônio reservoir filling affects the ants' assemblages turnover overtime? 2) Does the distance to the river margin affects the ants' species turnover in the modules' plots?

and 3) Was there a change in directionality of the assemblages' composition throughout this time?.

2. Material and methods

2.1 Study area

The ant sampling occurred in the influenced area of the Santo Antônio hydroelectric power plant area (UHE Santo Antônio), 8° 48′ 4″ S, 63° 56′ 59.8″ W, located in the Madeira River, distant 7 kilometers from Porto Velho, the capital of the Rondônia State, North of Brazil (Fig. 1). The Madeira River has an extended area of 1,420,000 km encompassing Brazil, Bolivia and Peru (Ribeiro Neto, 2006), being the biggest affluent of the Amazonas River. The vegetation varies, being mainly characterized by Open Ombrophilous Forest. The soil is predominantly red-yellow latosol, but gleisoil and latosol can also be found in the area (Cavalcante, 2012).

2.2 Sampling Design

The sampling is part of the Subprogram "Monitoramento da Entomofauna nas Áreas de Influência da UHE Santo Antônio, Porto Velho, Rondônia", which integrates the "Fauna Conservation Program", following the PBA (Environmental Basic Plan), from the UHE Santo Antônio. This material comes from the 10 campaigns monitoring that were carried out between 2011 and 2014 in four sampling 4km modules (Ilha do Búfalo, Ilha da Pedra, Teotônio and Jaci Paraná; Fig. 1), installed in the hydroelectric area. The period corresponds to the pre-filling, filling and post-filling events of the UHE Santo Antônio. During the landscape deforestation, due the flooding that occurred in the module, the Teotônio's plots were not sampled, on the first campaign. Throughout the reservoir filling process, none of the modules sampled on this study was flooded.

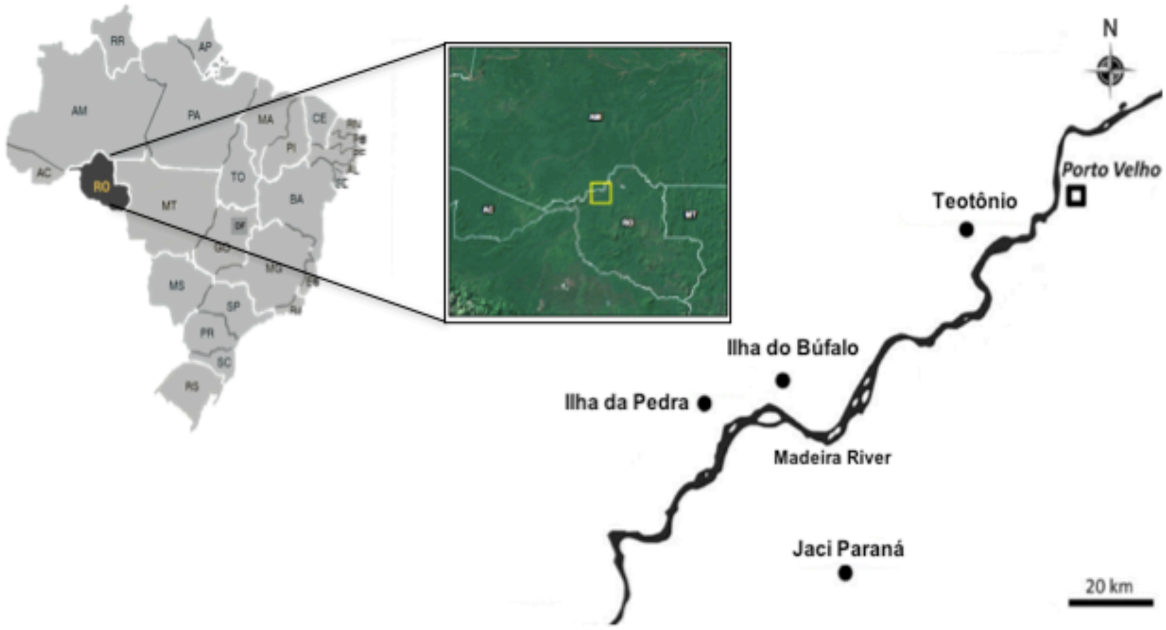

Figure 1. Location of the UHE Santo Antônio and the four modules installed in its area, in Rondônia State, north of Brazil. Modified image from: Fauna Conservation Program, SAE, 2014 and Dias-Terceiro *et al*. (2015).

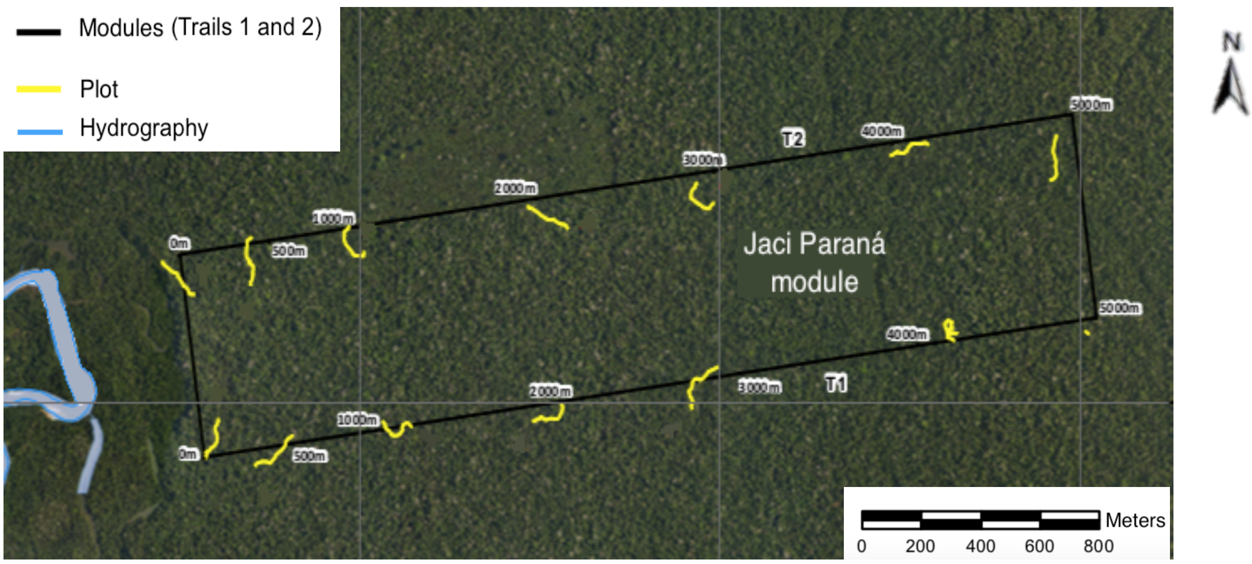

Figure 2. Trails 1 and 2 from the Module Jaci-Paraná installed in the UHE Santo Antônio. Picture shows the area after the post-filling phase of the UHE Santo Antônio. Image source: Fauna Conservation Program, SAE, 2014.

Each one of the modules has a 4 km extent trail containing six 250m plots (Fig. 2). These plots were installed in a 0, 0.5, 1, 2, 3 and 4 km distance from the river margin (horizontal distance). Five sampling spots were taken at distances of 50, 100, 150, 200 and 250 m along the plot (Fig. 3).

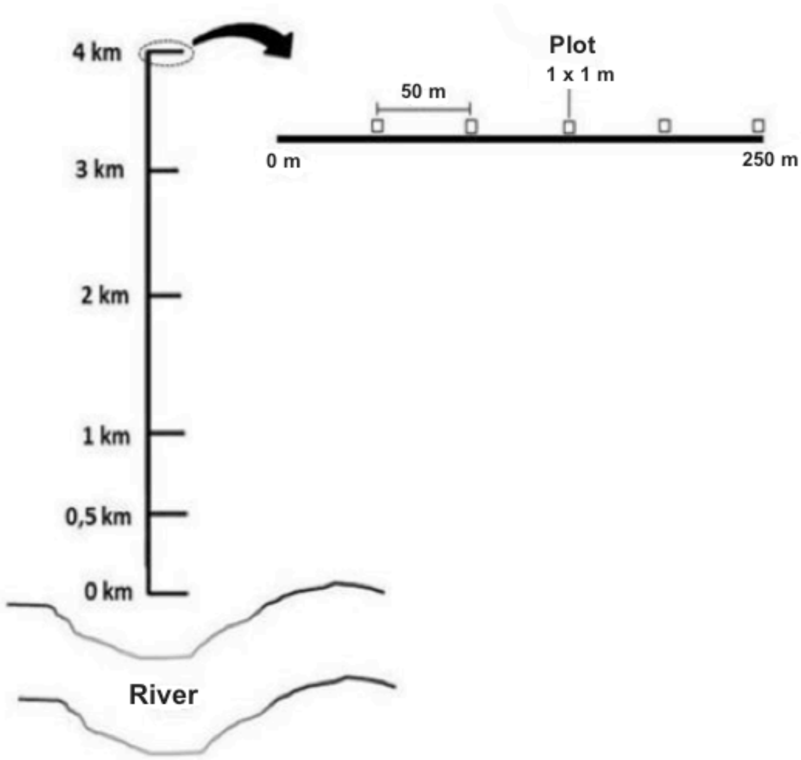

Figure 3. Schematic drawing of the trails installed in the modules located in the UHE Santo Antônio, in Porto Velho, Rondônia State. Image source: Fauna Conservation Program, SAE, 2014.

2.3 Ant Sampling

We used the previously sampled database in the hydroelectric power plant (Fernandes & Souza, 2018). The ants were sampled with a Winkler extractor (Agosti *et al.*, 2000) (Fig. 6). In each of the plots, five samples of $1m^2$ of litter were taken every 50 m. All the material was then placed inside a $1cm^2$ fabric knitted sieve (Fig. 5). The sieved litter was placed inside the Winkler sac, consisted of a rectangular metal support hang by a cotton mesh. In the inferior part of the support, a ribbon is placed to hang the plastic cup that retains the invertebrates. Alcohol 90% was placed inside the cup to the invertebrate’s conservation.

Figure 4. Demarcation of a $1m^2$ litter sampled in the plots installed at the UHE Santo Antônio, Porto Velho, Rondônia State. Source: Fauna Conservation Program – SAE, 2014.

Due to logistic reasons, the sample stayed in the extractor for a 24-hour period, in which the ants tend to migrate towards the bottom recipient that is filled with alcohol. Five sub-sets of sample per plot were collected, resulting in 30 sub-sets per module in each campaign. The Teotônio module was not sampled during the first campaign due deforestation occurring in the area, totalizing 270 sub-sets in all the campaign events.

2.4 Statistical analyses

A total of 62 singletons, 45 doubletons and additional six species of Army ants (*Eciton burchelli*, 02 species of *Labidus,* and 03 species of *Neivamyrmex*) were removed from the analyses, as the exclusion of both singletons and doubletons removes the influence of rare species on the assemblages' analyses. In addition, army ants do not permanently establish nests in specific areas, moving frequently and consequently biasing the analyses, as one single colony can be registered more than once (Donoso, 2017). For the analyses, the packages Codyn (Hallett *et al.,* 2016) and Vegan (Jari *et al*., 2016) were used. All the analyses were made using “The R foundation for Statistical Computing” software, version 3.5.0. (R Core Team, 2016)

Effects of the UHE Santo Antônio reservoir filling phases on the temporal and spatial ants’ species turnover

The sampling unit for this objective was all the modules together per campaign, representing the total area. A data set containing the campaigns, the species’ names and the species’ abundance was used for this analysis. Temporal changes in the assemblages’ turnover were calculated using the function “turnover” from the R library package Codyn (Hallet *et al*., 2016). Turnover function calculates the proportion of species either gained or lost compared to the total number of species from both time periods. In this analysis, the turnover is calculated from one campaign to another (campaigns’ comparisons), evidencing if there are major or minor turnover changes throughout time. Therefore the results return one turnover value for each comparison (campaign 1 vs. campaign 2; campaign 2 vs. campaign 3 and so on). The values can range from 0 (no species were gained or lost) and 1 (all (100%) species were substituted in the assemblages).

The influence of the distance to the river margin (horizontal distance) on the ants’ species turnover

To assess the influence of the distance from the river, the species turnover was calculated using all plots in the area (0, 0.5, 1, 2, 3 and 4 km), not distinguishing the modules. A dataset containing the campaigns, the plots, the species and the species abundance was used, returning turnover values for all plots over campaign comparisons. These values were calculated using the function “turnover” from the R library package Codyn (Hallet *et al.*, 2016). To test if there were significant ($p < 0.05$) differences between the species turnover for every horizontal distance (plots) an Analysis of variance - ANOVA (Chambers & Heiberger, 1992) was calculated.

The influence of the UHE Santo Antônio reservoir filling phases on the directionality of the ants' assemblages

The sampling unit for this objective was all the modules together, representing the total area. To calculate if there was a change in directionality of the assemblages throughout time, (Collins *et al*., 2000) the Bray Curtis distances at increasing time intervals was used. Using the function “vegdist”, a dissimilarity matrix was calculated for every campaign, representing all species sampled in that moment. To determine if there were changes in the assemblages' direction during the monitoring time, those distance matrix were compared through increasing time interval, using the function “mantel”, which compares two distance matrixes. As there were 10 monitoring campaigns, the function returns 9 values for one campaign time lags (campaign 1 vs. campaign 2, campaign 2 vs. campaign 3…), 8 values for two campaigns time lags (campaign 1 vs. campaign 3, campaign 2 vs. campaign 4…), 7 values for three campaigns time lag (campaign 1 vs. campaign 4…) and there forth.

When the r square values found for all these comparisons are regressed over time it is possible to visualize if there were changes in the direction of the assemblages. The slope in the plot represents the rate. A slope of 0 indicates no structural changes in the assemblage overtime, while a linear positive slope indicates unstable assemblages, going through significant directional change. On the opposite, a linear negative slope indicates unstable assemblages with a converging directional structure. The higher slope inclination represents a stronger directionality change over time.

3. Results

3.1 Ant Sampling

A Total of 37,969 ants were recorded during the monitoring years (2011, 2012, 2013, 2014), over 10 censuses in the selected plots in the UHE Santo Antônio. These specimens were classified in 47 genera and 206 species and morphospecies. The specimens in the final dataset were divided in 8 subfamilies (Agroecomyrcinae, Cerachyinae, Dolichoderinae, Ectatominae, Formicinae, Myrmicinae, Ponerinae, Proceratiinae). Species in Myrmicinae were the most frequent, representing 75.4%

frequency of all species sampled (Appendix A). The most abundant genera were *Pheidole* (39 spp.), *Strumigenys* (18 spp.), *Trachymyrmex* (11 spp.), *Hypoponera* (9 spp.) and *Solenopsis* (9 spp.). In addition, the five most frequent species (core species) were *Pheidole* sp. 02, *Solenopsis* cf. *castor, Strumigenys denticulata*, *Hypoponera* sp. 04 and *Octostruma balzani* (Table 1). These species represented about 28% of the total absolute species frequency found in this study.

Table 1. Absolute frequency of the five core ant species during the monitoring of the UHE Santo Antônio, over the filling phases of the hydroelectric power plant in Amazon basin.

Subfamily	**Species**	**Filling phases**			
		Pre-filling	Filling	Post-filling	Total
Myrmicinae	*Solenopsis* c.f. *castor*	177	305	347	829
	Pheidole sp. 2	149	182	164	495
	Strumigenys denticulata	2	224	265	491
	Octostruma balzani	31	75	158	264
Ponerinae	*Hypoponera* sp. 4	73	123	141	337

3.2 Temporal and Spatial species turnover

Over the 10 monitoring campaigns, there was a high level of species turnover (> 38%) during all phases of the reservoir filling. During the pre-filling phase, on average, 50.3% of the species present were replaced over the first four campaigns. Between campaigns five and seven, during the filling phase, there was a reduction of the turnover percentage average; 44,8%, which was similar to the post-filling phase average, between campaigns 8 and 10; 49.3%. The highest turnover rate occurred during the pre-filling period, between the second and the third campaigns. The lowest rate was found between campaigns seven and eight, corresponding to the transition between the filling and the post-filling phases, between the years 2013 and 2014, when 38.2% of the species were substituted (Table 2).

Table 2. Rates and percentages of species turnover from 2011 to 2014 in the UHE Santo Antônio, over the nine pairwise campaign comparisons. The phases (pre-filling, filling and post-filling) are also shown.

Pairwise campaign comparison	Year	Filling phase	% (Turnover percentage)
1 - 2	2011	Pre-filling	46.2
2 - 3	2011/2012	Pre-filling	54
3 - 4	2012	Pre-filling	50.9
4 - 5	2013	Filling	48.5
5 - 6	2013	Filling	48.6
6 - 7	2013	Filling	44.2
7 - 8	2013	Filling	38.2
8 - 9	2014	Post-filling	48.4
9 - 10	2014	Post-filling	50.3

In general, turnover values tended to decay after the pre-filling phase, between campaigns four and five, reaching its' lowest value in phase transitions, between campaigns seven and eight, during the late reservoir filling. In contrast, as the post-filling phase started, the rate of species being substituted tended to become higher again, reaching similar values to the ones registered in the pre-filling and filling phases. In addition, the last campaign had a turnover rate equal to the average turnover value of campaigns in the pre-filling phase, therefore the proportion of species being substituted in the last campaign was the same as during the pre-filling of the reservoir (Fig. 6)

Species turnovers within the sampled modules were, on average, very similar over the different filling phases, ranging from 56.2% to 68% (Table 3). It means that regardless from which module the sampling was occurring and besides its' spatial location, the species were being substituted at similar rates.

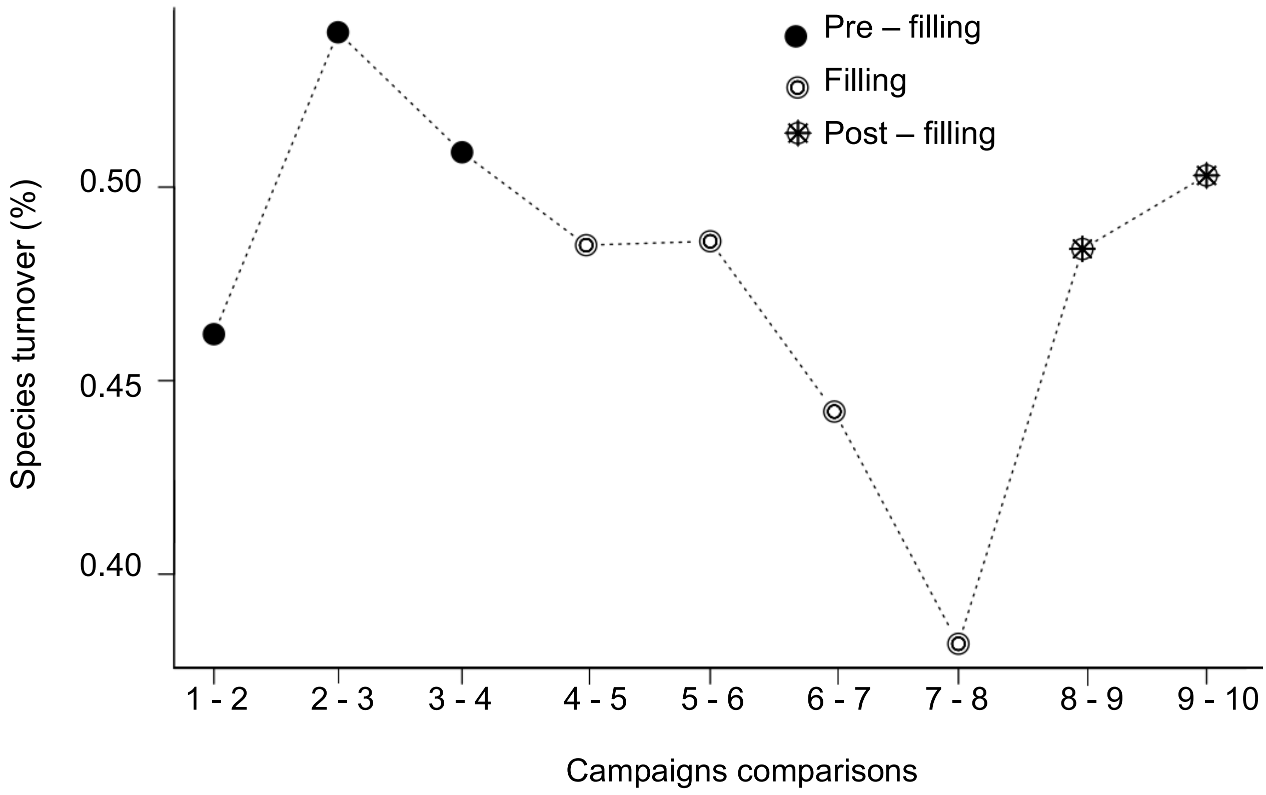

Figure 5. Ground-dwelling ants' species turnover within the UHE Santo Antônio over nine pairwise monitoring campaigns comparisons.

Accordingly, the species turnover average for the modules was also very similar. The highest species turnover occurred in Jaci Paraná, during the pre-filling phase. On the opposite, the lowest turnover occurred in the Ilha do Búfalo, during the post-filling phase. Overall, the values tended to be similar as they correspond to the campaigns turnover averages per phase (Table 3), carried out in the monitoring period. However, turnover values tended to be higher when analyzed per campaign comparison in each module in the area (Table 4).

There were turnover similarities (e.g. the highest turnover occurred in the same moment in the Ilha do Búfalo and Ilha da Pedra modules) and it tended to stay high in most of the modules during the entire monitoring. The lowest turnover of all monitoring process was 49.3% and occurred in the Teotônio module, between the eighth and the ninth campaigns, during the post-filling phase. In this same module, the highest rate of species being substituted occurred between the fifth and the sixth campaigns. The peak of turnover for the entire monitoring occurred in the Jaci Paraná module, between the second and the third campaigns, when 75.2% of the species in the area were substituted (Table 4).

Table 3. Turnover percentage average per flooding phase by monitored module in the UHE Santo Antônio, in Rondônia State.

Module	Average turnover (%)/Filling phases			
	Pre-filling	Filling	Post-Filling	Average
Ilha do Búfalo	65.2	63.5	56.2	62.3
Ilha da Pedra	63.6	60.8	64.7	62.6
Jaci Paraná	68	62.6	65.6	61.5
Teotônio	64.3	63.4	57.4	56.4

Range differences in the total turnover were more noticeable in the Jaci Paraná module. At that location, there was a 24% turnover difference between the moment in which less species and the moment the most species were substituted. Even though the modules tended to follow the same pattern over time, ranges in turnover values were higher in this furthest module from the hydroelectric plant base. On the other hand, there was a less evident species substitution in Teotônio module. In this module, the turnover rates were lower, meaning the ants' species tended to remain the same throughout the monitoring. Furthermore, during the post-filling phase, in the comparison of the eight and nine campaigns, turnover tended to happen differently in all four modules and then with species being substituted more equally in the last comparison.

In the modules Ilha do Búfalo, Jaci Paraná and Teotônio, the last turnover value (%) registered for each (58.2, 64.3 and 65.5, respectively) was very similar to the first turnover value registered (58.9, 69.4 and 66.2, respectively). In these modules, approximately the same amount of species was being substituted in the first and the last comparisons, evidencing a tendency of the assemblages to absorb the disturbance and return to its' original state, in which over 55% of the species were being substituted (Fig. 7).

Table 4. Turnover percentage per module during the filling phases/monitoring campaigns of the UHE Santo Antônio, in Rondônia State. Teotônio module was not sampled in the first campaign. Bolded values show the lowest and the highest turnover value for each module. The time intervals correspond to a comparison of the following campaign to the previous.

Filling Phases	Campaigns comparisons	Modules/Turnover (%)			
		Ilha do Búfalo	Ilha da Pedra	Jaci Paraná	Teotônio
Pre-filling	1 - 2	58.9	59.4	69.4	-
Pre-filling	2 - 3	**74.3**	**73.6**	**75.2**	66.2
Pre-filling	3 - 4	62.7	**57.8**	60.0	62.1
Filling	4 - 5	62.9	59.6	63.1	64.8
Filling	5 - 6	63.4	62.0	72.4	**67.9**
Filling	6 - 7	65.2	61.0	64.4	56.7
Filling	7 - 8	61.4	60.8	**50.5**	60.4
Post-filling	8 - 9	**54.3**	61.3	66.9	**49.3**
Post-filling	9 - 10	58.2	68.2	64.3	65.5

3.3 Influence of the distance to the river margin (horizontal distance) on the ants' species turnover.

The species' turnover at 6 different distances within the modules (0, 0.5, 1, 2, 3 and 4 km) is not directly/significantly being influenced by their spatial location in the UHE Santo Antônio (ANOVA, $F = 2.18$, $p = 0.07$). Hence, the assemblages' distances from the river are not the factor influencing on how the species are being substituted on the modules throughout time.

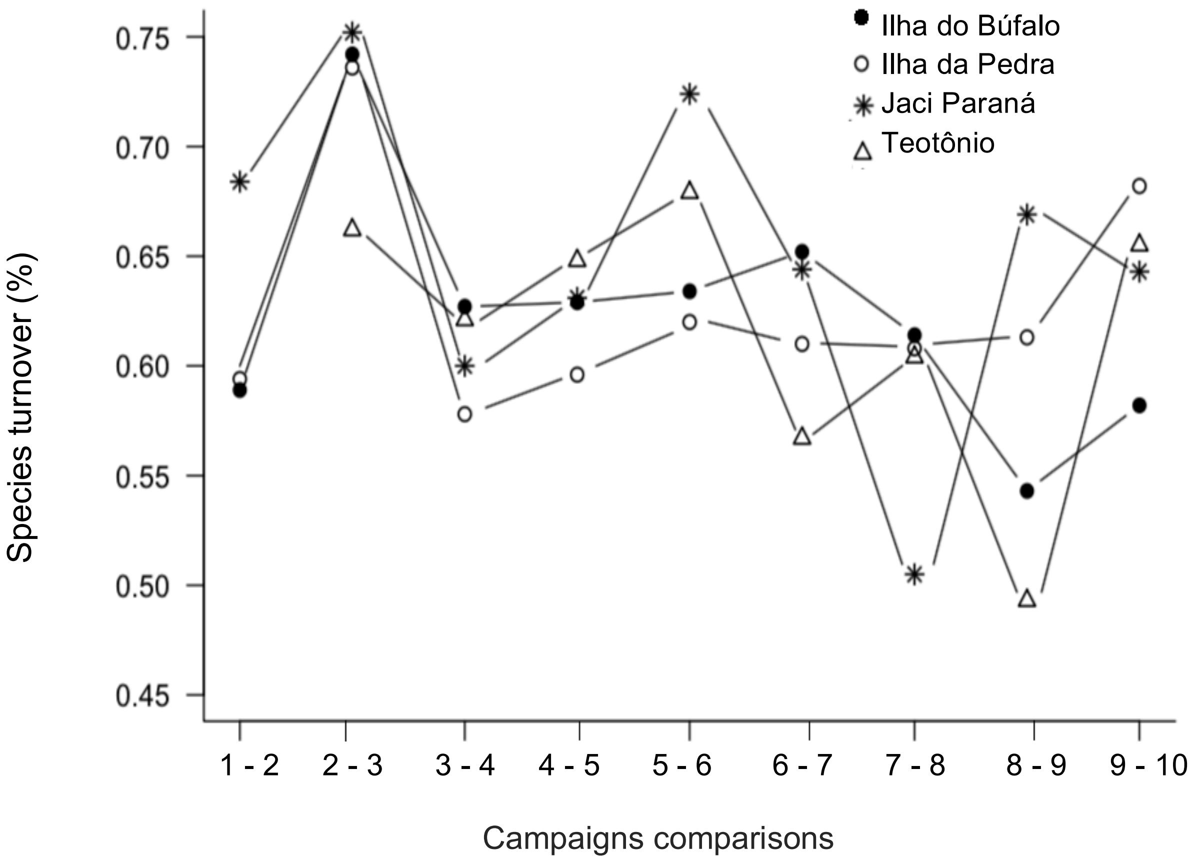

Figure 6. Ground-dwelling ants' species turnover over time in the four modules sampled within the UHE Santo Antônio. No sampling occurred in Teotônio module in the first campaign.

3.4 Changes in directionality of ants' assemblages

Over the 10 monitoring campaigns a significant shift in directionality was found on ground-dwelling ants assemblages' composition. The comparison between assemblages' distances matrixed over increasing time intervals was positive and explained 9% of the variation. ($p= 0.03$, $R^2= 0.09$) (Fig 8.), meaning that the ground-dwelling ant's assemblages in the area went through directional change throughout the monitoring.

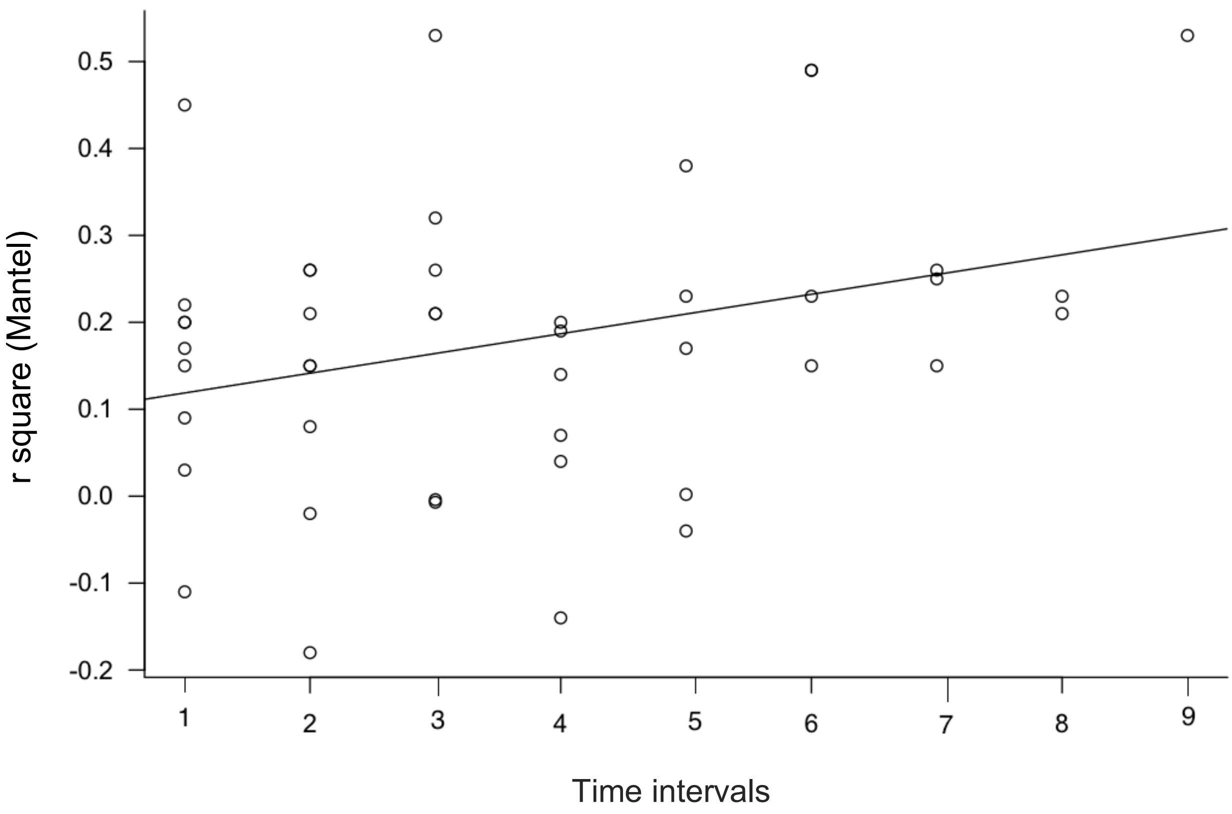

Figure 7. Mantel r square values of assemblages' matrixes over increasing time intervals the UHE Santo Antônio, in Rondônia State. Each dot represents communities' similarity at different time intervals, totalizing 45 dots.

4. Discussion

In the present study, the noticeable percentage decay of species being substituted during the UHE Santo Antônio reservoir filling affected the directionality of the assemblages, meaning there were structural changes on ant's assemblages in the area. In addition, the physical distance of the assemblages to the river margin (where the level of perturbation was higher) did not significantly affect how the species were being substituted, which means the species tended to be homogenized equally in all areas during the filling process. In contrast, in the same area, the horizontal distance to the margin is correlated to the species richness' variation and functional diversity (Gomes, 2017). Studies measuring changes in the diversity have been growing in the last decades. Many have debated about how alpha, beta and gamma diversities change over time (e.g. Donoso, 2017; Gosper *et al.*, 2012; Lafleur *et al*., 2006) but most have analyzed it across space (e.g. Baselga, 2010; Bishop *et al.*, 2015; Koleff *et al*., 2003; Vasconcelos & Vilhena, 2006; Whittaker, 1972). Moreover, there is a lack of studies investigating how the changes in the species substitution is affecting/affected the directionality of the communities and to what degree the changes can be taken as permanent or temporary.

4.1 Effects of the filling phases on the temporal and spatial ant's species turnover.

The ground-dwelling ants' assemblages in the UHE Santo Antônio were dynamic throughout the 10 monitoring campaigns and the filling of the reservoir, as a high rate of species substitution was detected in these areas. However, a very abrupt difference in the species turnover was detected when the filling of the reservoir begun, suggesting this process interfered on how the species were being substituted in the area previously. Ants' communities tend to have a very stable and high turnover rate in undisturbed areas, neither permanently gaining nor losing species over time (Donoso, 2017). Accordingly, it is expected that only half of the species registered in one census, can also be registered in the next one, as these assemblages tend to be highly dynamic (Donoso, 2017). This explains the patterns found before the filling of the reservoir and also right after this process ended, when the assemblages were more likely to be shown as they are when there is no disturbance. The abrupt reduction of the turnover rate during the filling of the reservoir suggests a rapid and high homogenization of the assemblages, with these sharing more species during the process of the reservoir filling. Moreover, disturbed areas usually have fewer feeding resources in general, narrowing the number of ants' species adapted to the conditions and therefore able to remain in the space (Gibb & Parr, 2010).

Additionally, the rate of species substitution is usually lower in disturbed habitats, where generalist species gain bigger proportion due to their adaptation to a wider range of feeding resources and niche settlement, which reduces the environmental filtering (Marsh *et al.*, 2018). Ants' assemblages within the areas influenced by the filling process of the UHE Santo Antônio had their richness, composition and functional diversity affected (Gomes, 2017). Even though the richness is higher after the filling, as occasional flooding tend to increase number of ants' species (Baccaro *et al*., 2013), the composition changed, homogenizing the species and therefore affecting the functional diversity, interfering the development of larger ants species in the area (Gomes*,* 2017). Thus, during the filling of the reservoir, the assemblages were not only more similar to each other's composition but the species probably also shared the same guild.

Evidences of spatial distance strongly influencing on communities' composition can be seen in either vertebrates such as birds and amphibians (Buckley & Jetz, 2008) and invertebrates, as ground-dwelling ants (Vasconcelos *et al.*, 2003). As turnover reflects the difference between two or more communities over a spatial or temporal gradient (White *et al*., 2010), turnover rates similarities between the sampling sites throughout the monitoring campaigns found in this study are associated with the geographic proximity of the samples. Even though multiple studies evidence the close relation between environment variables (e.g. topography, clay content, elevation, inclination, etc.) and species' composition (e.g. Vasconcelos *et al.*, 2003; Oliveira *et al.*, 2009; de Moraes *et al.*, 2011; Pansonato *et al.*, 2013; Bishop *et al.*, 2015), in disturbed areas, variance in ants' species within assemblages seem to be influenced by either the disturbance itself (Gomes, 2017) or variation in space (e.g. congruence of species among closer sites) (Landeiro *et al*., 2012).

Accordingly, Gomes *et al*., (2017), during a study in the same modules sampled on the present study, verified that differences in the species' composition between the modules were mainly explained by the campaign filling phases, with no significant influence of environment variables, such as clay content and slope of terrain. Gomes (2017) tested the spatial autocorrelation of the modules in order to determine if the proportion of species similarities/differences within the assemblages is mostly influenced by their physical distance in the area or by other factors. The correlogram (Bjornstad & Falk, 2001) was made using the package "ncf" in the Statistical Software R. The autocorrelation values varied between (+0.5 and -0.5) (Appendix B.). The spatial autocorrelation of the modules sampled found in the same study is likely to have influenced not only in the similarity of the assemblages' species composition, but also on how the turnover is happening across space and time, as closer sites tend to be more similar. Thus, the higher turnover variation found in Jaci Paraná compared to the other modules is likely to be explained by its' geographic distance from the other sites.

4.2 Influence of the distance to the river margin (horizontal distance) in the ants' species turnover in the reservoir.

Even though the horizontal distance from the margin to the plots seemed to significantly influence in the ants' species richness and assemblages' composition (Gomes, 2017), the analysis of variance result found on this study indicates that this parameter does not influence on the species turnover during the filling of the reservoir. This result strengthens the fact that the phases of the reservoir are more likely the factor influencing the species substitution throughout that specific time in the area. It shows that parameters directly influencing on assemblages' composition does not necessarily are also influencing on how the species are being substituted spatially and temporally. Therefore, it is highly recommended that studies assessing different parameters' influence on species composition and richness also assess the turnover rates in the area, as both aspects are not necessarily directly related. Moreover, the present study suggests that all turnover variation detected throughout the monitoring was influenced by the different filling phases of the reservoir, as environmental variables in the area tend to be stable and not significantly influent on species' composition.

4.3 Influence of the UHE Santo Antônio reservoir filling phases on the directionality of the ants' assemblages in the area.

The abrupt change in the species turnover during the disturbance in the area might lead to question either or not there was a change in directionality of the assemblages' composition. As evidenced by the comparison of the assemblages' distance matrixes over time intervals, it is noticeable that the assemblages went through a directional change during the monitoring campaigns. It means that although there was a rapid homogenization of the assemblages' composition when the filling of the reservoir occurred, their composition at the post-filling phase was significantly different compared to pre-filling monitoring campaigns. However

However, ants' assemblages within non-disturbed areas seem to not go through directional change, remaining stable over time (Donoso, 2017), reinforcing the influence of the reservoir filling on the shift of ants' assemblages' composition during the UHE Santo Antônio monitoring.

Even though changes in soil resources are usually the trigger to reach communities' threshold, disturbance events, acting on both soil resources and communities' composition together, pushes communities towards its threshold (Chapin III *et al*., 2006). Although communities tend to be highly resilient to environmental changes (Holling, 1973), those disturbance events might catalyze changes in assemblages' composition, rapidly leading them to a new state, resulting in directional change (Chapin III *et al*., 2006), which seems to be the case for ants' assemblages within the UHE Santo Antônio area. The period right after a disturbance event can be crucial to determine if communities will return to its original state (Holling and Gunderson, 2002). However, as only the interaction of communities' composition and continuous disturbance determines in which state the community will stabilize (Chapin III *et al*., 2006), the ten monitoring campaigns made at UHE Santo Antônio might not be enough to evidence if ants' assemblages will either remain in a new structure state or not. Moreover, predictions cannot be strongly made for communities undergoing rapid changes, as it is more difficult to determine stable patterns for those communities (Walker *et al*., 2004).

In this study, the reservoir filling seems to act as a catalyzer, exerting strong influence on species composition within assemblages. Those structural changes evidence that even though resilient communities are capable of absorbing the disturbance without having its structure and feedbacks modified (Walker *et al*., 2004), ants' assemblages within UHE Santo Antônio area seem to have reached its threshold on the time scale analyzed.

5. Conclusion

Effects of the UHE Santo Antônio on the temporal and spatial ant's species turnover

The limited knowledge of hydroelectric constructions' impacts on invertebrates' community dynamics and the increasing demand of energy generation leads to an unbalanced scenario in which conservational predictions and approaches cannot be strongly made. However, the role of ants as ecological models can be used as predictors to a wide range of other invertebrates. As surveyed in this study, the ant's species turnover within assemblages tends to decay once the reservoir filling starts and recover as soon as the post-filling phase begins. Their response to environmental modifications proved to be useful in this study, evidencing what might also have happened to other animals' assemblages and communities' dynamics within the area during the reservoir filling phases.

Influence of the distance to the river margin (horizontal distance) on the ant's species turnover

The non-influence of the distance to the margin on the ant's species turnover reinforces the strong relation between he reservoir filling to the species being substituted in lower or higher rate overtime. It is likely that not only ant's species but also other invertebrates' species are being substituted equally, no matter the distance from the disturbance in those modules and plots. Therefore, investigating the relation between assemblage's composition and richness with environmental variables (e.g. terrain slope, clay content and altitude) in those disturbed areas might not show the entire picture of how assemblages and communities are affected by the hydroelectric dam constructions.

Influence of the UHE Santo Antônio reservoir filling phases on the directionality of the ants' assemblages in the area

The narrowed relation between reservoir filling events and significant directional change in ants' assemblages evidences how strongly those processes can affect communities within disturbed areas. These events can also act as catalyzer for other similar invertebrate groups. Additional post-disturbance monitoring is recommended to determine if assemblages permanently change to a new state or if there is a tendency of returning to their original state.

Within areas that have been under environmental disturbances caused by hydroelectric constructions it is highly recommended to analyze how species were being substituted during the filling process, but also to asses if there were changes in the communities direction. Communities with low resilience might go under substantial structure and functional modifications. In addition, high resilient communities also must be constantly assessed, as their threshold are usually unknown.

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7. Appendices

Appendix A. Absolute frequency of the ground-dwelling ants' species sampled within the 1,200 sub-plots (240 plots) in the four modules (Ilha do Búfalo, Ilha da Pedra, Jaci Paraná, Teotônio) located in the UHE Santo Antônio between 2011 and 2014 in Rondônia state.

Subfamily	Species	Pre Filling	Filling	Post Filling	Total
Agroecomyrmecinae	*Tatuidris tatusia*	0	0	4	4
Cerapachyinae	*Cerapachys augustae*	1	0	3	4
	Cerapachys splendens	0	0	3	3
Dolichoderinae	*Azteca* sp. 1	5	10	1	16
	Azteca sp. 2	5	5	1	11
	Azteca sp. 5	0	2	1	3
	Dolichoderus bispinosus	24	5	14	43
	Dolichoderus decollatus	3	2	0	5
	Dolichoderus imitator	0	1	6	7
	Tapinoma melanocephalum	0	0	4	4
	Tapinoma sp. 1	0	0	4	4
Ectatomminae	*Ectatomma brunneum*	5	8	5	18
	Ectatomma edentatum	6	8	13	27
	Ectatomma lugens	7	1	1	9
	Gnamptogenys ericae	0	0	3	3
	Gnamptogenys haenschi	1	0	2	3
	Gnamptogenys horni	26	42	64	132
	Gnamptogenys moelleri	4	12	19	35
	Gnamptogenys pleurodon	0	1	2	3
	Gnamptogenys relicta	9	3	2	14
	Gnamptogenys sp. 5	4	0	0	4

	Gnamptogenys tortuolosa	2	0	1	3
Formicinae	*Nylanderia guatemalensis*	48	59	83	190
	Brachymyrmex sp. 1	39	42	38	119
	Nylanderia c.f. *caeciliae*	27	30	47	104
	Nylanderia sp. 3	13	22	51	86
	Camponotus fastigatus	12	10	6	28
	Nylanderia c.f. *fulva*	3	5	12	20
	Brachymyrmex sp. 2	3	6	5	14
	Nylanderia sp. 5	6	4	0	10
	Camponotus crassus	5	3	0	8
	Camponotus rectangularis	4	3	1	8
	Acropyga sp. 1	2	0	5	7
	Camponotus blandus	3	1	1	5
	Camponotus femoratus	0	3	1	4
	Brachymyrmex sp. 3	0	2	1	3
	Camponotus novogranadensis	1	2	0	3
	Camponotus rapax	3	0	0	3
	Gigantiops destructor	2	0	1	3
Myrmicinae	*Allomerus octoarticulatus*	0	4	0	4
	Apterostigma auriculatum	1	2	2	5
	Apterostigma pilosum	3	18	33	54
	Atta sexdens	11	2	4	17
	Basiceros militaris	0	1	2	3
	Blepharidatta brasiliensis	21	26	3	50
	Carebara lignata	0	3	0	3
	Carebara sp. 1	8	1	10	19
	Carebara urichi	2	8	27	37
	Cephalotes pusillus	2	1	1	4
	Crematogaster acuta	1	2	0	3

Crematogaster brasiliensis	3	45	64	112
Crematogaster flavosensitiva	8	14	10	32
Crematogaster limata	33	51	23	107
Crematogaster sotobosque	5	8	13	26
Crematogaster sp. 2	5	0	0	5
Crematogaster stollii	2	1	0	3
Crematogaster tenuicula	71	55	42	168
Cyphomyrmex laevigatus	11	15	32	58
Cyphomyrmex c.f. *lectus*	0	3	20	23
Cyphomyrmex minutus	0	14	43	57
Cyphomyrmex peltatus	17	15	36	68
Cyphomyrmex rimosus	36	30	74	140
Cyphomyrmex sp. 12	0	4	1	5
Cyphomyrmex sp. 3	0	3	0	3
Cyphomyrmex sp. 4	0	2	5	5
Hylomyrma dentiloba	0	0	9	9
Hylomyrma c.f. *dolochops*	30	3	18	51
Hylomyrma longiscapa	0	2	11	13
Megalomyrmex balzani	0	2	3	5
Megalomyrmex cuatiara	7	2	19	28
Megalomyrmex goeldii	0	0	28	28
Megalomyrmex leoninus	22	1	10	33
Megalomyrmex sp. 2	5	0	0	5
Megalomyrmex sp. 5	6	0	1	7
Megalomyrmex sp. 8	0	1	2	3
Megalomyrmex wallacei	1	19	6	26
Mycetarotes sp. 1	0	5	0	5
Mycocepurus sp. 1	1	4	4	9
Mycocepurus sp. 2	0	2	1	3

Mycocepurus sp. 3	0	1	4	5
Myrmicocrypta sp. 1	6	2	22	30
Myrmicocrypta sp. 2	19	20	66	105
Ochetomyrmex semipolitus	14	61	112	187
Octostruma balzani	31	75	158	264
Octostruma iheringi	2	2	6	10
Octostruma sp. 2	6	0	0	6
Oxyepoecus ephippiatus	3	12	6	21
Pheidole biconstricta	19	66	23	108
Pheidole flavens	14	12	88	114
Pheidole sp. 1	30	27	32	89
Pheidole sp. 10	15	20	17	52
Pheidole sp. 12	9	3	5	17
Pheidole sp. 14	6	1	0	7
Pheidole sp. 15	15	26	17	58
Pheidole sp. 16	5	8	21	34
Pheidole sp. 17	1	3	2	6
Pheidole sp. 18	34	50	0	54
Pheidole sp. 19	10	22	11	43
Pheidole sp. 2	149	182	164	495
Pheidole sp. 20	1	3	0	4
Pheidole sp. 21	20	24	17	61
Pheidole sp. 22	4	1	12	17
Pheidole sp. 23	3	4	8	15
Pheidole sp. 24	3	4	2	9
Pheidole sp. 26	4	3	7	14
Pheidole sp. 28	2	4	3	9
Pheidole sp. 29	1	4	3	8
Pheidole sp. 3	25	0	0	25
Pheidole sp. 30	4	64	81	149

Pheidole sp. 32	2	11	11	24
Pheidole sp. 40	0	15	10	25
Pheidole sp. 41	0	4	5	9
Pheidole sp. 42	0	7	8	15
Pheidole sp. 43	0	19	1	20
Pheidole sp. 44	0	1	2	3
Pheidole sp. 45	0	3	7	10
Pheidole sp. 47	0	4	1	5
Pheidole sp. 48	0	5	3	8
Pheidole sp. 49	0	3	14	17
Pheidole sp. 51	0	0	4	4
Pheidole sp. 53	0	0	4	4
Pheidole sp. 55	0	0	3	3
Pheidole sp. 7	8	11	2	21
Pheidole vorax	0	4	4	7
Pseudomyrmex sp. 3	0	1	1	2
Pseudomyrmex tenuis	9	1	7	17
Pseudomyrmex termitarius	5	3	5	13
Rogeria alzatei	29	30	103	162
Rogeria c.f. *belti*	1	1	1	3
Rogeria c.f. *cornuta*	0	3	16	19
Rogeria cuneola	2	2	15	19
Rogeria leptonana	5	32	59	96
Rogeria sp. 1	19	0	0	19
Rogeria sp. 2	18	0	0	18
Sericomyrmex sp. 1	10	14	16	40
Sericomyrmex sp. 2	6	2	5	11
Solenopsis c.f. *castor*	177	305	347	829
Solenopsis clytemnestra	12	57	76	145
Solenopsis geminata	1	12	6	19

Solenopsis c.f. *loretana*	0	9	6	15
Solenopsis c.f. *saevissima*	92	93	63	248
Solenopsis sp. 3	36	20	0	56
Solenopsis sp. 5	0	6	1	7
Solenopsis sp. 7	3	6	7	16
Solenopsis substituta	2	14	28	44
Strumigenys beebei	1	7	16	24
Strumigenys denticulata	2	224	265	491
Strumigenys elongata	3	15	35	53
Strumigenys inusitata	1	2	4	7
Strumigenys perparva	34	20	32	86
Strumigenys smithii	3	0	20	23
Strumigenys sp. 1	3	0	0	3
Strumigenys sp. 10	0	0	6	6
Strumigenys sp. 13	0	11	6	17
Strumigenys sp. 3	9	0	0	9
Strumigenys sp. 4	0	0	10	10
Strumigenys sp. 5	5	1	1	7
Strumigenys sp. 6	7	2	4	13
Strumigenys sp. 7	11	11	19	41
Strumigenys sp. 8	0	4	27	31
Strumigenys sp. 9	0	3	0	3
Strumigenys trudifera	5	16	31	52
Strumigenys zeteki	43	32	43	118
Tetramorium sp. 2	1	4	1	6
Trachymyrmex bugnioni	7	11	16	34
Trachymyrmex cornetzi	0	2	3	5
Trachymyrmex diversus	12	1	2	15
Trachymyrmex farinosus	0	0	3	3
Trachymyrmex mandibulares	2	4	6	12

	Trachymyrmex opulentus	3	1	8	12
	Trachymyrmex c.f. *ruthae*	2	4	3	9
	Trachymyrmex sp. 10	0	2	3	5
	Trachymyrmex sp. 7	4	0	5	9
	Trachymyrmex sp. 9	5	2	0	7
	Wasmannia auropunctata	57	48	43	148
Ponerinae	*Anochetus diegensis*	18	37	3	58
	Anochetus horridus	0	6	5	11
	Anochetus sp. 1	0	11	11	22
	Hypoponera sp. 1	49	39	60	148
	Hypoponera sp. 2	20	4	9	33
	Hypoponera sp. 3	13	19	29	61
	Hypoponera sp. 4	73	123	141	337
	Hypoponera sp. 5	2	8	14	24
	Hypoponera sp. 6	8	1	0	9
	Hypoponera sp. 7	4	8	36	48
	Hypoponera sp. 8	7	13	5	25
	Hypoponera sp. 9	0	3	14	17
	Mayaponera constricta	27	44	39	110
	Neoponera verenae	0	2	2	4
	Odontomachus bauri	0	3	3	6
	Odontomachus chelifer	5	0	2	7
	Odontomachus haematodus	10	14	22	46
	Odontomachus meinerti	4	0	1	5
	Odontomachus sp. 1	4	4	1	9
	Odontomachus sp. 2	0	1	2	3
	Pachycondyla harpax	6	11	29	46
	Pachycondyla impressa	8	2	2	12
	Pachycondyla sp. 1	0	0	3	3
	Pachycondyla striata	9	28	20	57

	Pseudoponera stigma	7	1	4	12
	Rasopone arhuaca	2	7	5	14
Proceratiinae	*Discothyrea denticulata*	2	1	2	5
	Discothyrea humilis	4	1	3	7
	Discothyrea sexarticulata	1	0	3	4

Appendix B. Spatial autocorrelation of distances between the sampling UHE Santo Antônio modules (Gomes, 2017).

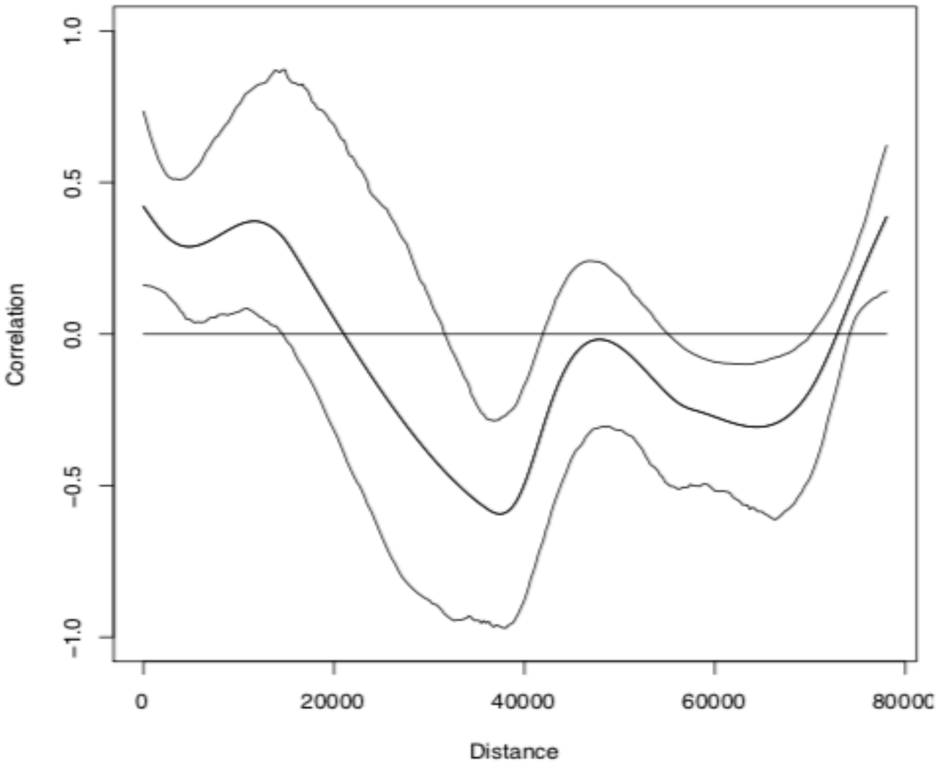

Figure. Spatial autocorrelation correlogram between the modules located in the UHE Santo Antônio (Gomes, 2017).