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Replacement or nestedness: what drives short-scale temporal variation in Amazonian macroinvertebrate assemblage structure?

Substituição ou aninhamento: o que determina a variação temporal de curta escala na estrutura da assembleia de macroinvertebrados amazônicos?

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Abstract: Aim: Short-term variations in macroinvertebrate assemblage structure are often unusual due to the complexity of detecting comprehensive patterns at a fine temporal scale, leading to uncertainties in the dynamics of species composition. Here, we used artificial substrates to test whether five days of exposure is sufficient to reveal significant changes in macroinvertebrate composition in a floodplain lake in Central Amazonia. **Methods:** Differences in macroinvertebrate composition among treatments were assessed through a multivariate generalized linear model, taxa replacement and nestedness magnitude were assessed through abundance-based additive partitioning of beta diversity. **Results:** Our results showed that taxa composition significantly differed among times of exposure. Replacement contributed relatively more than nestedness to taxa dissimilarity along the exposure time gradient. **Conclusions:** Here, we provide evidence of day-scale macroinvertebrate turnover in artificial substrates, adding information on the distribution of aquatic assemblages in Amazonian systems.

Keywords: temporal scale; artificial substrate; macroinvertebrate colonization; exposure time; turnover.

Resumo: Objetivo: Variações de curta escala na estrutura da assembleia de macroinvertebrados são geralmente incomuns devido à complexidade de detectar padrões abrangentes em uma escala temporal refinada. Aqui, usamos substratos artificiais para testar se cinco dias de exposição são suficientes para revelar mudanças importantes na composição de macroinvertebrados em um lago de várzea na Amazônia Central. **Métodos:** Diferenças na composição de macroinvertebrados entre os tratamentos foram acessadas através de um modelo linear generalizado multivariado e a magnitude de substituição de táxons e de aninhamento foi acessada através de partição aditiva da beta diversidade baseada em abundância. **Resultados:** Nossos resultados mostraram que a composição dos táxons diferiu significativamente entre os tempos de exposição. Substituição contribuiu mais

que aninhamento para a dissimilaridade dos táxons ao longo do gradiente de tempo de exposição. **Conclusões:** Aqui, fornecemos evidências de substituição de táxons de macroinvertebrados em uma escala diária usando substratos artificiais para adicionar informações sobre a distribuição de assembleias aquáticas em sistemas amazônicos.

Palavras-chave: escala temporal; substrato artificial; colonização de macroinvertebrados; tempo de exposição; substituição de táxons.

1. Introduction

Temporal variability affects the structure of aquatic assemblage dynamics, determining the rate of colonization by organisms (Hepp et al., 2021; Castro et al., 2025). This variation is scale dependent and may be manifested in a matter of days, weeks, months, seasons and years (Melo & Froehlich, 2001; Monk et al., 2008; Korhonen et al., 2010). Therefore, the sufficient time to visualize significant patterns in macroinvertebrates composition is still uncertain. For example, in seasonal-temporal scales, variations in assemblage demographic aspects can be influenced by hydrological pulses throughout the year, as proposed by the Flood Pulse Concept (Junk et al., 1989; Bispo et al., 2006). During the dry season, the relative abundance and richness of species are higher than in the rainy season (Leung & Dudgeon, 2011) due to the absence of flood events, which reduces taxa mortality (Grimm & Fisher, 1989) and drift effects (Peralta & Martin, 2015). However, on a daily-temporal scale, variations in assemblage structure and colonization rates are unpredictable and not well investigated (Heino et al., 2015a), especially in tropical systems.

Freshwater invertebrates are considered good models in short-temporal studies since they present a relatively short life cycle, respond rapidly to environmental variations, and have generally restricted mobility (Petrucio & Esteves, 2000; Lopes et al., 2011). They also represent a highly diverse group, occurring in different types of habitats, where variations among these habitats result in different invertebrate assemblage structures, colonization patterns, and trophic functional group composition (Milesi et al., 2008; Arimoro, 2013).

Frequently, invertebrates' assemblage structure depends mainly on substrate complexity, even for artificial substrates (Milesi et al., 2016; Wolters et al., 2019). Complexity, in this case, means how many substrate elements and coverage are available for colonization. If the substrate is relatively heterogeneous and/or available in sufficient amounts, species' composition may increase linearly (Hepp et al., 2012; Magossi et al., 2023). Although, what is sufficient to sustain a high species composition is uncertain and depends greatly on the environment. Conversely, species richness and abundance may depend more on colonization time than substrate complexity. The balance between spatial and temporal aspects is crucial for a great species composition (Williams, 1964). Therefore, the time interval that an area is sampled could define diversity patterns.

Species composition does not increase linearly over time (Fisher et al., 1943; Preston, 1960). For example, variations in species compositional patterns among one, four, and ten years of sampling are significantly different and may result in higher diversity in intermediate time periods (e.g., four years in this case) (Fisher et al., 1943). Thus, at short timescales (e.g., days, weeks), sampling methods, as well as stochasticity in species richness and abundance distributions, possibly affect species composition more than other major biological processes (e.g., niche selection, evolution) (Korhonen et al., 2010). Furthermore, differences in species composition within a region (i.e., beta diversity) are related to many factors (e.g., environmental conditions, dispersion, and stochasticity) that may affect species replacement and/or nestedness (i.e., species loss/gain) rates (Mittelbach, 2012). Understanding the mechanisms behind diversity patterns (e.g., spatial or temporal) are crucial to fill the gaps on what may be the causes of species distribution among habitats. For example, strong replacement is mostly common among sites/periods that experience great environmental variation, where environmental filtering or species sorting prevents some species combinations (Leibold et al., 2004). Conversely, nestedness is more common due to non-deterministic drivers (e.g., dispersal capacity, historical factors) that homogenize composition across space and time (Heino et al., 2015b). Moreover, both replacement and nestedness contribute to total assemblage dissimilarity, although their relative importance varies with the processes that affect species distribution (Tonkin et al., 2016). Therefore, it is pivotal to decompose beta diversity components in order to comprehend the processes generating diversity patterns along the landscapes.

Studies related to short-temporal colonization of aquatic invertebrates, especially related to unpredictable daily taxa variability in artificial substrates, are lacking in Central Amazonia, where fish assemblage colonization has been recently investigated (Pires et al., 2023; Rocha et al., 2024). Amazonian aquatic systems are highly diverse (Ribas et al., 2025), encompassing from small streams to large rivers. Due to different origins, streams and rivers have different water types (e.g., black, white, and clear) (Wallace, 1853; Sioli, 1950) and, therefore, variations in the physical-chemical aspects of water are common (e.g., turbidity, electrical conductivity, pH) (Leenheer, 1980). In Central Amazonia, the confluence of the Negro and Solimões rivers creates a highly diverse system, with potential exchange of taxa along the floodplain. Here, we investigated, using artificial substrates, whether a five-day exposure period is sufficient to accumulate significant differences in macroinvertebrate taxa composition in a floodplain lake, and whether those differences are more related to replacement or nestedness components.

2. Material and Methods

2.1. Study system

This study was conducted in Catalão Lake (3°10'04"S; 59°54'45"W), located on the floodplain near the confluence between Negro and Solimões rivers, ~10-km from Manaus city (Amazon, Brazil) (Figure 1). Catalão Lake presents an average depth of 10-m, with a variation range of 7-m depending on the season. Aquatic plants are common in the Catalão Lake limits, mostly represented by *Lemna valdiviana* (Araceae), *Paspalum repens* (Poaceae), *Pistia stratiotes* (Araceae) and *Salvinia auriculata* (Salviniaceae) (Junk & Piedade, 1993; Bleich et al., 2014).

2.2. Sampling design

The experiment was performed over five days in July 2017 during the receding water level of both rivers, the transition period between the high and low waters. Here, our aim was to conduct the experiment for a week and use this as a proxy for a short timescale. However, due to logistical issues we end up sampling for only five days (six if we count

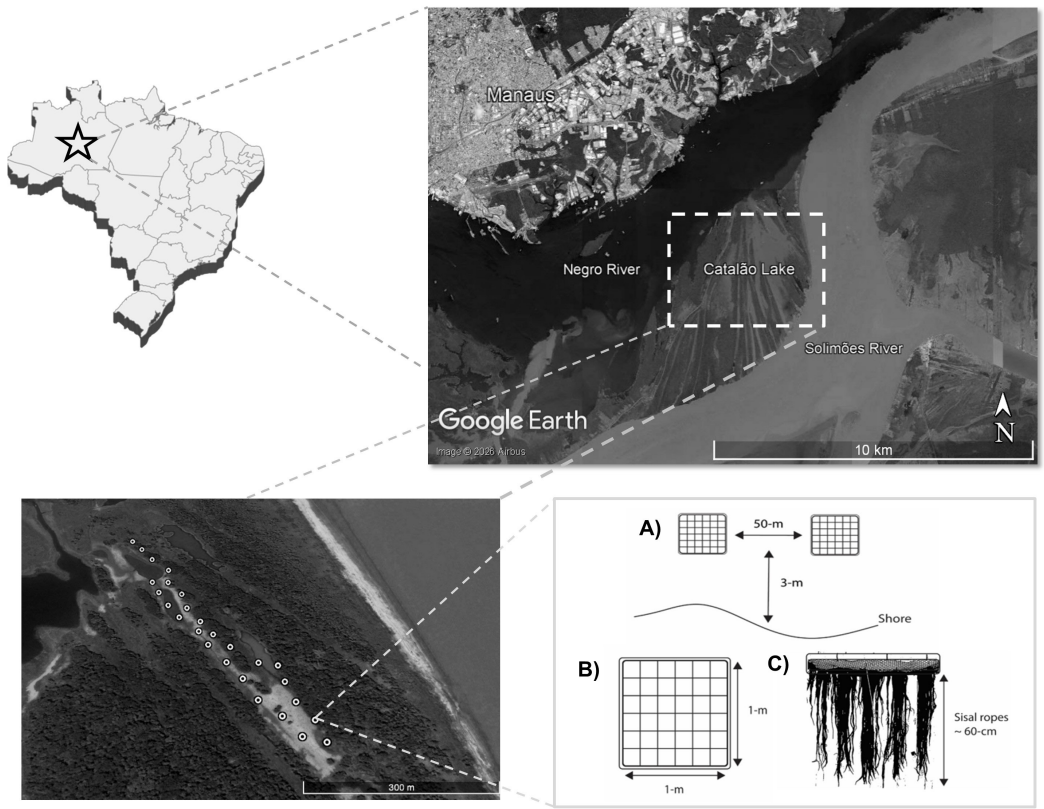

Figure 1. Catalão Lake location showing the distribution of 25 floating artificial islands. (A) The islands were positioned away from the lake shore and spaced apart from each other within the same area; (B) Each island was constructed using PVC pipes and connectors to form a 1-m² square; (C) 60-cm natural sisal ropes were used to simulate aquatic herbaceous roots.

the installation day). Twenty-five artificial "islands" (i.e., floating substrates) were used as substrates to simulate aquatic herbaceous roots (Figure 1). Artificial islands were constructed using four 40-mm diameter PVC pipes and four PVC connectors to form a 1-m^2 floating square and coated with a plastic polyethylene screen. To mimic aquatic plants roots, we used 60-cm long sisal ropes (i.e., natural ropes made of *Agave sisalana*) distributed along the floating square. These same islands were used in a previous study focusing on fish assemblages structure (Rocha et al., 2024) and were initially inspired by the design of Santos et al. (2011).

Artificial islands were placed 3-m from the shore and 50-m from one another to minimize pseudoreplication, and were anchored with heavy rocks. Five experimental treatments were conducted (24, 48, 72, 96, and 120 hours of exposure), with five islands removed per day. Islands were removed randomly using hand nets (1.2-m side; 0.6-m deep; 1-mm mesh). The collected material was washed in a 0.5-mm mesh sieve net and individuals were identified to the family level (mostly) using stereomicroscopes and specialized guides (Hamada et al., 2014). Family-level approaches for studies regarding aquatic insects have been shown to effectively capture multiscale spatial and ecological signals on assemblages, as well as providing similar evidence to genus-level studies (Godoy et al., 2019; Simião-Ferreira et al., 2026).

2.3. Statistical analysis

To test for differences in macroinvertebrate composition among treatments, we performed a multivariate generalized linear model using the *manyglm* function from the *mvabund* package (Wang et al., 2012), assuming residuals with *negative-binomial* distribution. This model approach captures specific effects of location and dispersion without jeopardizing the mean–variance relationship (Warton et al., 2012). To assess the significance of the tests, we used the *anova.manyglm* function based on Wald's statistic, adjusted PIT-trap method, and p-values from 999 bootstraps (Warton et al., 2017). To visualize possible patterns in macroinvertebrate composition among treatments, we constructed a Non-Metric Multidimensional Scaling (NMDS) ordination plot in the *vegan* package (Oksanen et al., 2026) through the *metaMDS* function using a Bray-Curtis distance matrix and 999 permutations. Specific taxa variation along the exposure-time gradient was assessed visually from a direct ordination using the *generico* function.

To assess if the variation in macroinvertebrate composition among treatments was more related to replacement or nestedness, we performed an extension of Baselga's incidence-based (presence/absence) dissimilarity (Baselga, 2010) to encompass variations in species composition based on abundance differences using the function *beta.multi.abund* with Bray-Curtis dissimilarity (Baselga, 2017) from *betapart* package (Baselga & Orme, 2012). This method is useful for assessing variation in dissimilarity among taxonomic groups, in sets of multiple units (spatial or temporal) (Gómez-Rodríguez, Freijeiro & Baselga 2015; Baselga 2017), and for analyses where occurrence data are redundant. Abundance-based dissimilarity produces two analogous components to incidence-based dissimilarity: balanced variation ($\beta_{BC.BAL}$; replacement) and abundance gradients ($\beta_{BC.GRA}$; nestedness). Overall dissimilarity is represented by β_{BC} (i.e., $\beta_{BC} = \beta_{BC.BAL} + \beta_{BC.GRA}$). Component values range from 0, indicating no differentiation, to 1, indicating complete differentiation. We also performed an incidence-based dissimilarity analysis; however, our occurrence data was very redundant and did not capture variation as well as the abundance data. Although the interpretation of the methods was the same. All statistical analyses were performed in the R software version 4.6.0 (R Core Team, 2026).

3. Results

A total of 10,196 macroinvertebrates belonging to 30 taxa were collected (Table 1). Corixidae was the most representative taxon (62.1%), followed by Conchostraca (15.55%) and Planorbidae (10.3%). Macroinvertebrate composition differed significantly among treatments (*Wald* = 14.21; $p = 0.003$). Pairwise comparisons indicated that macroinvertebrate composition significantly differed only between the 24h-treatment with treatments 96h and 120h (Table S1, available at data availability). Overall, there was conspicuous overlap in macroinvertebrate composition among treatments, although dissimilarity was particularly observed between the 24h-treatment and the others (Figure 2), which caused most of the variation. Direct ordination of macroinvertebrate composition showed evident taxa variation across the exposure-time gradient, evidenced by a pattern of taxa replacement over time (Figure 3).

Table 1. Taxa abundance of macroinvertebrates in different hours of exposure in artificial islands in Catalão Lake (Amazonas, Brazil) during July 2017.

	Treatments					
Taxa (Class/Order/Family)	**24h**	**48h**	**72h**	**96h**	**120h**	**Total**
Gastropoda						
Physidae	0	14	17	9	10	50
Planorbidae	133	200	246	197	273	1049
Bivalvia	2	2	3	0	3	10
Conchostraca	142	261	293	394	495	1585
Acari	3	2	16	19	12	52
Insecta						
Ephemeroptera						
Baetidae	9	18	34	62	71	194
Caenidae	1	3	6	21	66	97
Euthyplociidae	2	4	8	9	20	43
Hemiptera						
Belostomatidae	6	7	4	3	3	23
Corixidae	1207	1375	1365	1554	831	6332
Gerridae	2	9	16	11	11	49
Hebridae	21	17	8	5	4	55
Mesoveliidae	17	4	14	27	20	82
Naucoridae	0	0	1	0	1	2
Nepidae	0	0	0	1	0	1
Notonectidae	21	6	2	16	2	47
Pleidae	1	2	1	0	2	6
Veliidae	1	0	0	0	0	1
Odonata						
Aeshnidae	0	0	0	0	1	1
Calopterygidae	0	2	1	1	3	7
Coenagrionidae	0	0	0	0	1	1
Libellulidae	28	45	40	68	83	264
Coleoptera						
Dytiscidae larvae	6	3	4	3	2	18
Dytiscidae adult	6	3	10	5	7	31
Gyrinidae larvae	4	5	6	3	1	19
Gyrinidae adult	1	0	0	0	0	1
Hydrophilidae	1	4	1	4	3	13
Diptera						
Chironomidae	1	20	14	33	50	118
Culicidae	4	5	7	1	5	22
Stratiomyidae	2	2	4	0	7	15
Trichoptera						
Hydroptilidae	0	0	0	4	4	8

Values for dissimilarity components from balanced variation ($\beta_{BC.BAL}$) and abundance gradients ($\beta_{BC.GRA}$) were marginally different ($\beta_{BC.BAL}$ = 0.21; $\beta_{BC.GRA}$ = 0.12), indicating that taxa replacement, even subtle, contributed more than nestedness to explain macroinvertebrate variation among the treatments, with the differences between the first and the last two days of exposure accumulating most of the variation (Figure 4; Table S2, available at data availability). Although nestedness also had a low relative contribution to taxon variation (Figure 4; Table S3, available at data availability).

4. Discussion

We demonstrated significant variations in macroinvertebrate composition on artificial substrates over only five days of exposure. The abundance of organisms in a location is mainly dependent on habitat quality (e.g., food availability, predation rates), which influences the likelihood that organisms survive and reproduce in a particular environment (Fonseca & Hart, 2001). Macroinvertebrates rapidly occupied the artificial islands, and changes in the assemblage structure

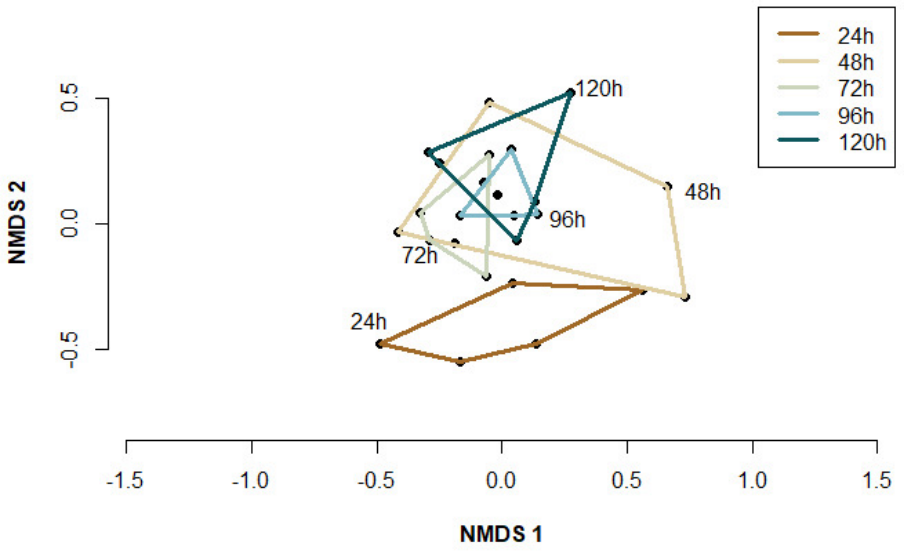

Figure 2. NMDS plot illustrating dissimilarity in macroinvertebrate composition among different exposure times (hours) for macroinvertebrate assemblage of Catalão Lake (Amazonas, Brazil).

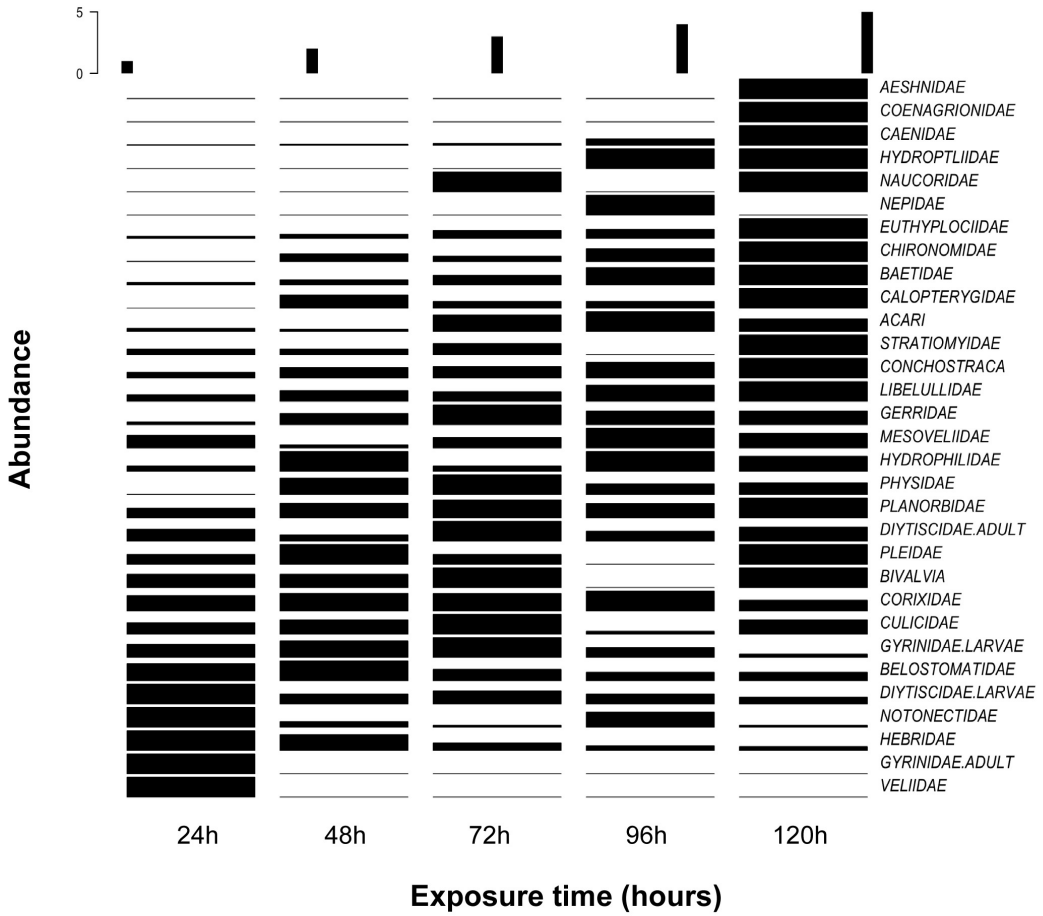

Figure 3. Direct ordination of macroinvertebrate taxa along the exposure-time gradient (hours). Exposure time is presented in ascending order (24h to 120h).

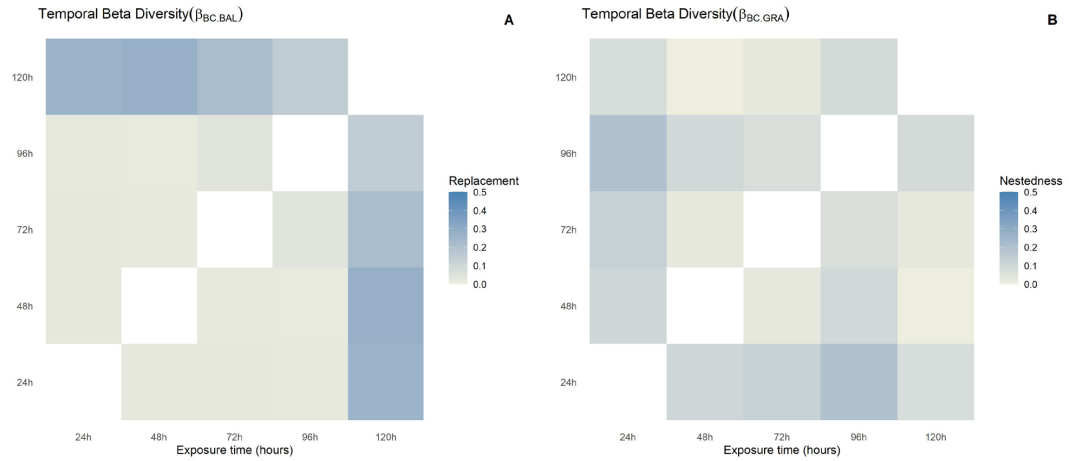

Figure 4. Pairwise comparison for balanced variation component/replacement – $\beta_{BC.BAL}$ (A) and abundance gradients/nestedness – $\beta_{BC.GRA}$ (B) between the exposure time periods. Light blue squares indicate low dissimilarity, and dark blue squares indicate high dissimilarity due to taxa replacement or nestedness.

between the first and the last day likely indicate abrupt ecological succession. Moreover, some taxa, such as Corixidae, Planorbidae, and Libellulidae remained present throughout the whole study period. Corixidae encompassed more than 60% of all individuals, and that may be related to its feeding strategies. Unlike most Nepomorpha (i.e., predators), Corixidae species are omnivorous and may feed on algae and plant debris (Hädicke et al., 2017; Schuh & Weirauch, 2020), which our substrate was composed of. On the other hand, Lopes et al. (2011), in their study at the Catalão Lake limits, found dominance of Oligochaeta, Chironomidae, and Hydrophilidae among living aquatic macrophytes, showing that substrate type could influence taxon dominance.

Taxa variation was initiated by individuals from Gyrinidae, Chironomidae, and Corixidae families, which colonized the artificial substrates since the first day, demonstrating that they were pioneers in the colonization process. Chironomidae and Corixidae maintained high dominance throughout the study period, suggesting high tolerance, efficient dispersal, and short life cycles that facilitate rapid colonization (Flory & Milner, 2000; Magossi et al., 2023). Taxa such as Veliidae and Gyrinidae (adult) were present only on the first day, which may be due to their occasional occurrence. By the fifth day of exposure, other taxa, especially predators such as Aeshnidae, Coenagrionidae, and Hidroptilidae, began to colonize, contributing to the gradual change in taxon composition. These taxa would probably not be able to colonize these new substrates before previous organisms arrived (Brower & Zar, 1984; Carvalho & Uieda, 2004), especially as predators, necessitating the presence of prey to establish. It was noticeable that Corixidae and Gyrinidae (larvae) abundance significantly dropped with the arrival of predators, probably in order to avoid predation by them. In the present study, however, the macroinvertebrate assemblage probably had not yet reached equilibrium by the end of the experiment, as its composition was still changing on the last day.

Here, differences in macroinvertebrate composition among days of exposure were more related to taxa replacement than nestedness. This pattern may indicate that habitat heterogeneity (through environmental filtering or species-sorting dynamics) may play a fundamental role in taxa dissimilarity (Leibold et al., 2004; Mittelbach, 2012). However, islands were exposed to similar habitat-resource availability, and taxa replacement may also result from stochasticity (Mateo-Tomás et al., 2019), which may be the case. Moreover, nestedness presented a low relative contribution to taxa dissimilarity, which may be associated with species differential dispersal capacity (Mouquet & Loreau, 2003; Ulrich et al., 2009); although that depends greatly on the scale (e.g., biogeographic, metacommunity) (Gianuca et al., 2017).

Since Catalão Lake did not experience significant environmental variation throughout the experiment and artificial substrates were subject to similar habitat availability, taxa variation was probably caused by sampling and/or random effects, where the method type and period may exert a direct effect on results, as well as stochasticity on species

richness and abundance distributions. However, it is difficult to differentiate colonizers exploiting resources from those merely passing by (Benzie, 1984), which could explain the high heterogeneity in the composition of some of the experimental treatments. Nonetheless, the observed variation in taxa composition fits a replacement-biased pattern, showing conspicuous turnover along the time gradient. Although our ecological knowledge at the species level is still lacking, recognizing new patterns for macroinvertebrate fauna at different taxonomic levels can provide crucial information for invertebrate distribution at fine temporal scales for the Amazonia region.

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Data availability

All data analyzed in the present research is available in the SciELO Dataverse Repository. Access is available in https://doi.org/10.48331/SCIELODATA.0CWCKD.

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