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RESEARCH ARTICLE

Diversity and community structure of *Drosophila* (Hexapoda, Diptera) in post-mining sites under different forest restoration techniques in the Brazilian Amazon

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To mitigate the impacts of deforestation, Brazilian legislation requires the implementation of a Degraded Area Recovery Plan (PRAD). One way to assess the recovery of these areas is using bioindicators. This research tested the use of the drosophilid community structure as an indicator to evaluate post-mining area restoration. We compared two regeneration techniques within the same chronological sequence and as reference used the forest remnants within the exploration area. The study was conducted in the municipality of Paragominas—Pará, in areas managed by Hydro mining company. Five sites of forest remnants were selected, five in natural regeneration and five in the nucleation technique, the latter two making up the PRADs. A total of 5,919 male drosophilids were collected belonging to 10 genera, and 32 species. Rarefaction showed the curves of the PRADs to be more asymptotic, than forested areas. Forest areas are potentially richer and, on average, have lower abundances and lower diversity. Beta diversity components in the forest present greater turnover and less nestedness processes when compared to PRADs areas. The PRADs showed no differences between them for any of the analyzed patterns. *D. nasuta* and *D. sturtevanti* behaved as generalists in relation to habitats, *D. paulistorum* and *D. willistoni* as forest specialists. *D. malerkotliana*, *D. simulans*, *Scaptodrosophila latifasciaeformis*, and *Zaprionus indianus* behaved as specialists in PRADs areas. The structure of the drosophilid community varied according to the environment, proving to be a good indicator for forest and regenerating environments, but it did not detect differences between the PRADs environments in early regeneration (6 years).

Key words: beta diversity, bioindicator, exotic species, mining

Implications for Practice

- The analysis of entomofaunal communities can provide indicators for evaluating restoration of forest processes as well as providing a deeper understanding of the factors driving biotic homogenization.
- For this region of the Amazon rainforest, 5 years does not reflect an effect on fruit fly community structure between natural regeneration and nucleation techniques. Thus, in the short term, the natural regeneration technique is more economically feasible for forest restoration, but it is important to emphasize monitoring the fauna in the medium and long term to measure the performance of different restoration techniques.

Introduction

Tropical forests have been extensively exploited over the years, causing losses in biodiversity and significantly damaging their ecosystem functions (Laurance et al. 2014; Cole et al. 2016). Among the activities that generate impacts, bauxite mining, which removes forest cover to extract underground minerals, causes significant damage to ecosystems, such as fragmentation of forested areas, changes in the hydrological cycles, all of which can lead to loss of species (Mechi & Sanches 2010), making it necessary to apply measures to mitigate the impacts caused by this activity.

Forest restoration has been a viable means to compensate for losses and to minimize impacts caused by human activities (Cole et al. 2016). Restoration is founded on the theory of ecological succession, which relates to how a community of organisms can change over recovery time and become important for biodiversity recovery (Chang & Turner 2019). Forests planted in degraded environments can help in ecological succession, as well as promoting the recovery of biodiversity (Thompson et al. 2011). In this way, several techniques can be applied to improve the performance of forest succession and reduce the

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Author contributions: ROB performed the experiments; ABVJ analyzed data and reviewed the methodology; CLBP performed data curation; MBM supervised, designed the research, and reviewed the methodology.

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negative impacts caused by human actions (Khan et al. 2019). In addition to planting, other techniques have also been proposed to promote restoration; among the techniques that are frequently used are nucleation and natural regeneration (Corbin & Holl 2012). Monitoring the restoration of biodiversity by means of environmental indicators throughout the stages of forest recovery becomes necessary to assess restoration success (Palmer 2009; Borges et al. 2021). Many studies use vegetation parameters as indicators; however, these do not capture all the relevant relationships that lead to increased diversity (Siddig et al. 2016).

Indicators that only consider vegetation recovery aspects provide little information about the real probability of success in restoring biodiversity as a whole, which essentially results from interactive processes between animals and plants (Onésimo et al. 2021). Monitoring the success of forest restoration lacks fauna indicators that assess the trajectory of biodiversity recovery. Many taxa are used as ecological indicators, among them invertebrates are commonly used because they are easy to collect, can produce several generations in a short period of time, and actively participate in ecosystem processes relevant to regeneration (de Oliveira et al. 2014; Borges et al. 2021). According to Siddig et al. (2016), bioindicators have been widely used to monitor community responses to environmental changes, especially of anthropogenic origin. Species richness, abundance, and diversity measures are common ecological metrics to assess restoration success at the community or population level (Borges et al. 2021).

As the forest restoration process is long, taking from 30 to 50 years (Casimiro et al. 2019), it is essential to obtain parameters that assess the succession trajectory, so that adjustments can be made in a preventive manner. Thus, the search for indicators that estimate the dynamics of fauna in regeneration areas becomes crucial. The community structure of insects enhances information about the degree of recovery of these environments. Among invertebrates, flies of the Drosophilidae family are a good alternative for bioindication (Martins 1987; Parsons 1991; Ferreira & Tidon 2005; da Mata et al. 2008). Drosophilids are reasonably well known in terms of their biology and population dynamics; they are easily collected and can respond quickly to environmental changes through alteration in their abundance, species diversity, or species composition within their guilds (Monteiro et al. 2016).

These organisms can respond to variations in temperature and humidity (Parsons 1975; Tidon 2006); their composition can vary in a gradient of degradation, through changes in species (Gottschalk et al. 2007; da Mata et al. 2008); and the abundance varies with the type of environment (Martins 1987; Penariol & Madi-Ravazzi 2013; Furtado & Martins 2018). Thus, drosophilids are good tools to improve the understanding of patterns and processes related to the recovery of biodiversity, as well as the understanding of how human activities affect it (da Mata et al. 2010). This study tests the use of drosophilids to assess the success of forest restoration in terms of restoring local biodiversity. It uses the initial stage of restoration in post-mining areas to evaluate two restoration techniques with the same chronology and compare them with the surrounding forest remnants. The hypothesis investigated is that the structure of the drosophilid community (composition, richness, diversity, and abundance) changes according to the study environment, due to the differential capacity of species to inhabit different environments, thus highlighting the recovery trajectory.

Methods

Study Area

We conducted the study in a bauxite mining area owned by Hydro Mining Paragominas company, located in the municipality of Paragominas, State of Pará, Brazil, in the northeastern region of the Brazilian Amazon (03°15′02″ S, 47°44′03″ W) (Fig. 1). According to Köppen's classification, the region's climate is characterized as hot and wet (Aw) with well-defined rainy and dry seasons. Hydro, is located 70 km from the city center of Paragominas; its bauxite production is 11.4 million tons per year. The company has 18,763.98 ha of area, of which 3,246.9 ha are destined to the legal reserve and 2,486.4 ha correspond to the exploited areas that are in the recovery phase (Cerqueira et al. 2021; Hydro 2021). Hydro Mining Paragominas uses three different techniques to recover degraded areas after bauxite extraction: direct planting, natural regeneration, and nucleation technique. For this study, natural regeneration and nucleation techniques were used, both of which make up the Degraded Area Recovery Plans (PRADs) whose recovery was started 6 years before collections, in 2014.

The bauxite extraction process takes place at depths between 8 and 12 m of soil depth, where the topsoil is removed with the sterile layer, until reaching the ore; the removed soil is stored in open air. Natural regeneration is a low-cost technique in which the removed soil (both sterile and organic) is replaced. The areas are adjusted in a contour line to avoid erosion, and firstly, the sterile layer is spread through a topographic reshaping of the ground and afterward adding an organic soil layer (the previously removed topsoil) containing nontimber residues such as leaves and litter. After these procedures, there were no more interventions in the area and no chemical or biological treatment was applied (da Cruz et al. 2020). Forest regeneration occurs from the seed bank present in the topsoil and by successional events from the dispersal of propagules (de Araujo et al. 2021). Nucleation of the study area was made forming "topsoil" nuclei of residues and antlers (leaves, branches, stumps, etc.) from the suppressed vegetation in areas of approximately 10 m^3 in a "chessboard" layout. This technique started in 2013 on 9.16 ha and was later extended in 2014, 2015, and 2016, up to a total of 81.63 ha (da Cruz et al. 2020). This regeneration method aimed to provide a favorable microenvironment for the recolonization of the environment by a greater number of species, accelerating the process of forest regeneration (Corbin & Holl 2012; de Araujo et al. 2021).

Vegetation Description

The original vegetation is characterized by dense rainforest, with a predominance of soil classified as Latosol (Martins et al. 2018; de Araujo et al. 2021). The plant species commonly

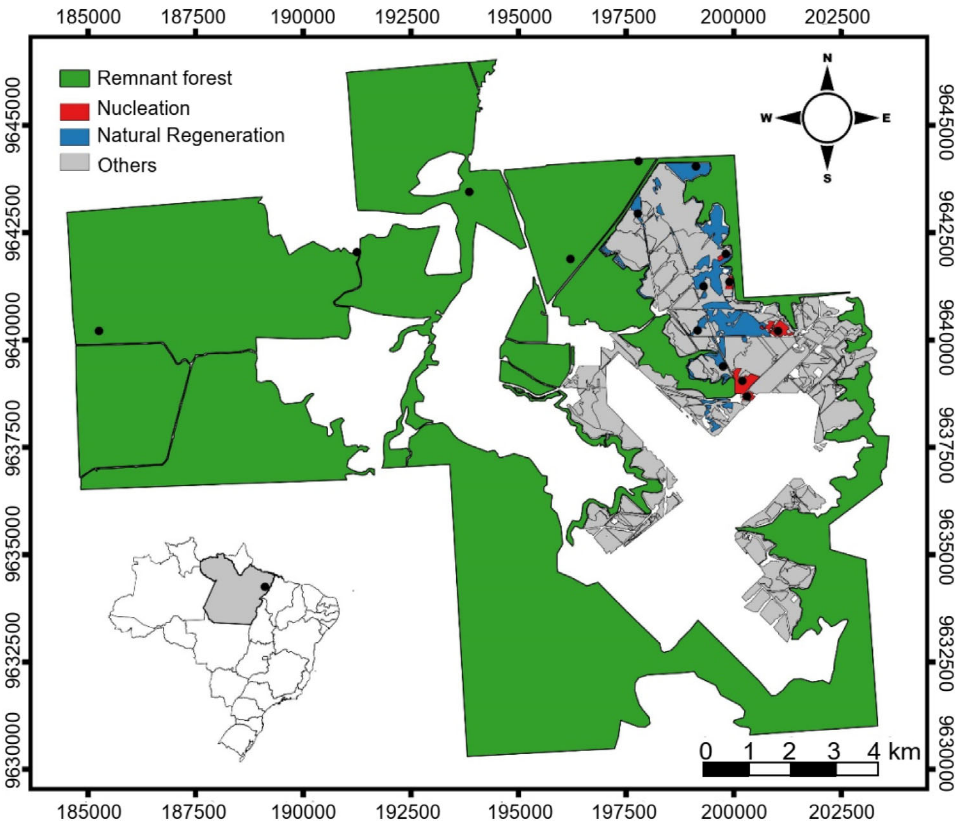

Figure 1. Location of the Hydro mining company in Paragominas, PA. Areas in the mining process are identified in white, forest remnants in green, and areas under recovery (PRAD) in gray. In blue, the recovery areas in natural regeneration since 2014 stand out, and in red, areas where nucleation techniques are being applied in the same period. Black dots identify the location of the 15 transects established in this study.

found in the forest remnants of the study area are mostly represented by the families Fabaceae, Lecythidaceae, and Sapotaceae (Martins et al. 2018; Cerqueira et al. 2021). In these forest remnants, a large part of the vegetation is altered due to fire or selective logging, that is, they have some degree of degradation (de Araujo et al. 2021). The landscape on Hydro's property until 2007, when mining activities began, was characterized by a mix of forest remnants, areas of secondary vegetation, and pastures. In naturally regenerating PRADs environments, the Euphorbiaceae, Urticaceae, and Fabaceae families are the most common (Martins et al. 2018). The formation of the arboreal stratum is due to the predominance of pioneer species, which are later replaced by secondary initial species (Brasil Neto et al. 2021). It is observed that the Fabaceae family has an ecological plasticity, which allows it to live in forest areas and environments undergoing restoration. The Solanaceae and Urticaceae families are the most common in nucleation areas. As this technique consists of forming a nucleus of plant galls and leaf litter, which provide greater coverage and fertility to the soil; it becomes a favorable environment for species such as those of the Urticaceae family, which are usually found in areas in early stages of forest succession, as well as in forest glades (Cerqueira et al. 2021).

Sample Design

Field activities took place in February 2020, the beginning of the rainy season in the region (Figueiredo et al. 2010; Padilha et al. 2018). We selected 15 study sites, comprising five forest remnant sites, five sites undergoing natural regeneration, and five sites undergoing regeneration by the nucleation method. These two methods are part of the PRAD.

We captured drosophilids with two complementary techniques: (1) Malaise-type trap and (2) bait trap (Fig. 2A & 2B). The Malaise-type trap captures several groups of flying insects by interception (Skvarla et al. 2021). We set up a Malaise trap at each sample site, totaling 15 traps that were exposed for 9 days. The insects in this trap were captured directly in containers with absolute alcohol. After these containers were removed, they were taken to the laboratory, where we proceeded with the screening of the family of the insects. In these same sites, we installed 5 traps with attractive bait, one placed in the center, with the Malaise trap as a reference, and another 4 distributed in relation to the four cardinal points 50 m away from the center, totaling 75 traps. Traps with attractive bait contained banana fermented for 48 hours in 100 g portions and the traps were exposed for 48 hours in order to capture frugivorous drosophilids (Martins et al. 2008). This exposure time is in agreement with other studies for surveying drosophilids

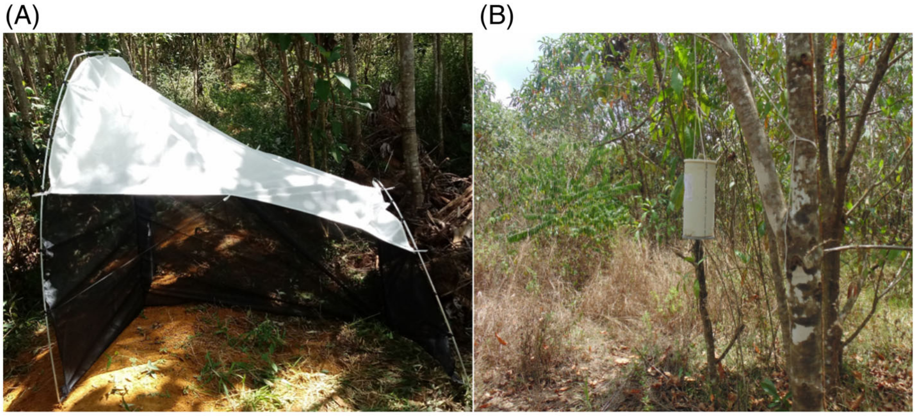

Figure 2. Traps used (A) Malaise trap installed in the forest, in (B) banana bait trap placed in restoration environment (PRAD) in the Hydro Mineração study area in Paragominas, Pará, Brazil.

(Martins 1987; de Medeiros & Klaczko 2004; Penariol et al. 2008; Coutinho-Silva et al. 2017; Mendes et al. 2017, 2021; Duarte et al. 2018), as well as effects of the loss of bait attractiveness after 48 hours (Nascimento et al. 2014). After this period, the collected drosophilids were removed from the traps with a mechanical sucker and stored in 96% alcohol and individualized by traps. All material was sent to the laboratory where it underwent a screening process, with the selection of all drosophilids. Drosophilidae were counted and separated into males and females. For identification at a specific taxonomic level, we analyzed the terminals (male sexual apparatus), using the available literature, such as Malogolowkin (1952), Magalhães and Bjornberg (1957), Vilela (1983), Vilela et al. (2002), Bächli et al. (2004) and the morphological comparison with material deposited in the collection of the Museu Paraense Emílio Goeldi (MPEG) and with image records stored in the image bank of the MPEG invertebrate ecology laboratory. When necessary, we removed the *aedeagus* for detailed morphological analysis, using the methodology proposed by Bächli et al. (2004). Only male individuals were counted in the analyses.

Climate Measures

To assess the abiotic environmental conditions, we measured local climatic variables at the sampling points. We installed a HOBBO Onset datalog at each site to take measurements of air temperature and humidity. Climatic data were measured at 12 sites, four in each environment. The equipment was in operation during the 9 days that Malaise traps remained exposed.

Data Analysis

All analyses were performed using R software (Rstudio Team 2021). First, we grouped the data from the two types of traps to generate a sample universe with 15 independent units. We then generated rarefaction and extrapolation curves based on the number of individuals for each environment. Each curve was extrapolated by up to 2× the number of individuals, recognizing that extrapolations beyond these values may be unreliable (Colwell et al. 2012; Chao et al. 2014). Extrapolations were made with 1,000 randomizations to compare richness between sampled habitats, using the iNEXT package (Hsieh et al. 2016).

To test the effect of the three environments on the richness, abundance, and diversity of drosophilids, we used generalized linear models (GLM). The species richness model was built using the Poisson family as the error distribution for count data and the adequacy of the distribution was verified through a residual analysis. Due to the presence of outliers in the abundance of collected drosophilids, this variable was log-transformed and together with the diversity variable (Hill number, $q = 1$), the models followed a Gaussian distribution (Ives 2015). Through an analysis of variance/deviance, the significance of the model was verified. We performed a contrast analysis for the models that showed a significant effect, in order to verify the difference between the three environments.

As the number of climate data samples was smaller ($n = 12$), we performed the climate models independently. As there is a multicollinearity between the measured climate variables (Fig. S1), we conducted a principal component analysis to reduce the dimensions and obtain a variable that represents most of the explained variance (Harrison et al. 2018). We selected four climatic measures: (1) average temperature, (2) average humidity, (3) temperature range (highest temperature minus lowest temperature of the period we sampled), and (4) humidity range (highest humidity minus lowest humidity of the period we sampled). These variables represent local climatic characteristics and aspects of environmental stress that are determinant for the response of the drosophilid community (Mendes et al. 2017; Lue et al. 2018). The first principal component generated scores that represented 97.64% of the explained variance (Fig. S2), and was used as an explanatory variable in climate models. We also use GLMs to test the relationship between the diversity attributes (species richness, ln[abundance] and Hill diversity) and the local climate profile of the sampled sites, following the same process of error distribution adequacy and residue analysis described above.

We evaluated the species composition of Drosophilidae using nonmetric multidimensional analysis (NMDS; metaMDS function).

To verify the significant effect of the composition of the drosophilid community, we applied a permutation multivariate analysis of variance (PERMANOVA; Anderson 2001), using the adonis function, followed by a pairwise comparison test using the pairwise adonis function (Arbizu 2020). All the analyses aforementioned were performed by inserting an incidence matrix and using the Jaccard distance as an index of dissimilarity. To complement our understanding of the processes that shape the structure of the *Drosophila* community, we calculated the beta diversity within sites, and examined whether the components responsible for species replacement (turnover) and species loss or gain (nesting) differed between the environments studied. For this, we calculated the beta diversity with Jaccard coefficient for presence and absence data, through the betapart package (Baselga & Orme 2012).

Finally, we use the species classification method (CLAM), proposed by Chazdon et al. (2011), which uses a multinomial model based on estimating the relative abundance of species in two habitats. This method minimizes bias due to differences in sampling intensities between the two habitat types, as well as insufficient sampling within each habitat. To this end, we organized the samples into two groups: samples from forest remnants and samples from recovery areas (PRAD). The latter encompasses both Natural Regeneration and Nucleation sites. Finally, the model classifies species into one of four groups: (1) generalists; (2) specialists in forest remnants, (3) specialists in PRAD, and (4) very rare to reliably classify via clamtest function of the Vegan package (Oksanen et al. 2020).

Results

The total collection corresponded to 5,919 male drosophilids distributed in two subfamilies (Drosophilinae and Steganinae), 10 genera, and 32 species. In forest environments, there were 327 males of 18 species (5 unnamed), in the nucleation 3,743 males of 22 species (7 unnamed) were captured and for natural regeneration, 1,849 specimens of 19 species (6 unnamed) were collected. In this survey, six exotic species were recognized, all from the Afro-Asian continents and some with a recent history of invasion in the Neotropics (Table 1). The three environments shared 10 species, natural regeneration and nucleation shared 15 species, the forest had two species shared only with nucleation and no species shared exclusively with natural regeneration. Six unique species were registered for forest environments, five for nucleation environments and four unique species for natural regeneration environments. Of the total species collected, 9 were common for both traps, the banana-baited trap contributed with 9 exclusive species and the Malaise trap with 14 species. The most abundant species were *Scaptodrosophila latifasciaeformis* and *Zaprionus indianus*, both exotic species, which corresponded to almost half of the individuals collected in this study.

It was observed through the rarefaction curves, based on the number of individuals, that the curves extrapolated from environments under restoration (nucleation and natural regeneration)—PRADs, were more asymptotic when compared to forest remnants (Fig. 3A), indicating that for forest remnants, greater sampling efforts may be necessary for greater completeness of the inventory. In the standardized sampling based on the environment with the lowest number of individuals collected, it was observed that the forest remnants have significantly higher species richness (95% non-overlapping confidence intervals) than areas undergoing regeneration (Fig. 3B).

The average species richness among the three studied environments did not show any significant difference ($F_{[2,12]} = 1.86$, $p = 0.1971$) (Fig. 4A). Both the abundance (Fig. 4B) and the diversity (Fig. 4C) were different between the environments, with the same response patterns: the forest environment showed, on average, lower abundance and lower diversity, when compared to areas in the process of regeneration (Fig. 4B, $F_{[2,12]} = 9.08$, $p = 0.003$; mean ± standard error [SE], forest $= 4.11 \pm 0.19$, regeneration $= 5.68 \pm 0.38$, nucleation $= 6.18 \pm 0.45$, Fig. 4C; $F_{[2,12]} = 5.24$, $p = 0.02$, mean ± SE, forest $= 2.94 \pm 0.30$, regeneration $= 3.86 \pm 0.49$, nucleation $= 4.55 \pm 0.20$).

The effect of the local climate profile on the diversity attributes showed weak evidence for richness ($F_{[1,10]} = 3.14$; $p = 0.07$; Fig. 5A) and abundance ($F_{[1,10]} = 3.89$; $p = 0.07$; Fig. 5B), while diversity was not related to the climate of the sites ($F_{[1,10]} = 1.15$; $p = 0.30$).

A clear distinction in the species composition between the studied environments was observed through the NMDS analysis. The forest remnants formed a distinct group of the restoration areas (natural regeneration and nucleation) (Fig. 6A), PERMANOVA showed a significant effect ($F_{[2,14]} = 3.10$; $r^2 = 0.34$; $p < 0.01$) with differences between the forest remnants and the natural regeneration ($p = 0.007$) and nucleation ($p = 0.011$) environments (Table S1). The processes of substitution (turnover) and loss/gain of species (nesting) show similar and opposite patterns. The areas under restoration do not differ from each other, but they are distinct from the forest remnants. Beta diversity components show that forest areas have a higher level of turnover and lower nestedness processes (Fig. 6B, $F_{[2,27]} = 19.148$, $p = 6.645^{-06}$, mean ± SE $= 0.335 \pm 0.034$; Fig. 6C, mean ± SE $= 0.073 \pm 0.018$) when compared to areas under restoration (natural regeneration: Fig. 6B, mean ± SE $= 0.067 \pm 0.029$, Fig. 6C, mean ± SE $= 0.206 \pm 0.043$; nucleation: Fig. 6B, mean ± SE $= 0.141 \pm 0.031$, Fig. 6C, mean ± SE $= 0.174 \pm 0.036$).

The species classification method (CLAM) showed two species as generalists, *Drosophila nasuta* and *Drosophila sturtevanti* (Fig. 7). For the dataset between forest remnant and restoration environments (natural regeneration and nucleation), it showed that *Drosophila paulistorum* and *Drosophila willistoni* were classified as specialists in forest remnants, while *Drosophila malerkotliana*, *Drosophila simulans*, *Scaptodrosophila latifasciaeformis*, and *Zaprionus indianus*, all exotic species, were classified as typical of environments undergoing restoration.

Discussion

Assessing different aspects of the structure of biological communities, we observed that both restoration techniques have not yet been able to demonstrate differences in their effectiveness from the point of view of the *Drosophila* assemblage

Table 1. List of species and abundance of Drosophilidae collected at Hydro Mineração Paragominas, state of Pará, Brazil. Code denominations* are recognized species (morphotypes) with no specific epithet identified and that may represent new species to science. ***Exotic species.* FL corresponds to Remnant Forest areas; NU are recovery areas through the nucleation method and RN are recovery areas through the natural regeneration method.

Species	*FL*	*NU*	*RN*	*Total abundance*	*%*	*Banana bait*	*Malaise trap*
Drosophila B21012	0	1	0	1	0.017	No	Yes
Drosophila cardini Sturtevant, 1916	0	0	4	4	0.067	Yes	Yes
Drosophila equinoxialis Dobzhansky, 1946	2	4	0	3	0.050	Yes	Yes
Drosophila fulvimacula Patterson & Mainland, 1944	0	2	0	2	0.034	Yes	No
***Drosophila malerkotliana* Parshad & Paika, 1964	18	1,271	358	1,643	27.637	Yes	Yes
***Drosophila melanogaster* Meigen, 1830	0	12	14	69	1.161	Yes	No
Drosophila moju Pavan, 1950	0	1	0	1	0.017	Yes	No
***Drosophila nasuta* Lamb, 1914	10	12	1	24	0.404	Yes	No
Drosophila nebulosa Sturtevant, 1916	1	21	35	57	0.959	Yes	Yes
Drosophila paulistorum Dobzhansky & Pavan in Burla et al., 1949	23	27	6	44	0.740	Yes	No
Drosophila prosaltans Duda, 1927	0	2	3	5	0.084	Yes	No
Drosophila saltans Sturtevant, 1916	1	0	0	1	0.017	Yes	No
***Drosophila simulans* Sturtevant, 1919	13	658	184	816	13.726	Yes	No
Drosophila sturtevanti Duda, 1927	8	32	14	54	0.908	Yes	Yes
Drosophila tropicalis Burla et al., 1949	1	36	1	79	1.329	Yes	No
Drosophila willistoni Sturtevant, 1916	238	341	64	642	10.799	Yes	Yes
**Hirtodrosophila* B21007	3	0	0	3	0.050	No	Yes
**Hirtodrosophila* B21010	0	1	0	1	0.017	No	Yes
Hirtodrosophila thoracis Williston, 1896	1	0	0	1	0.017	No	Yes
**Paramycodrosophila* C20009	0	1	0	1	0.017	No	Yes
**Paramycodrosophila* C20010	0	0	2	2	0.034	No	Yes
***Scaptodrosophila latifasciaeformis* Duda 1940	2	130	134	266	4.474	Yes	Yes
***Zaprionus indianus* Gupta, 1970	2	1,174	1,019	2,195	36.922	Yes	Yes
**Zygothrica* B21009	0	0	1	1	0.017	No	Yes
**Amiota* C20006	1	6	0	7	0.118	No	Yes
**Amiota* C20007	0	0	1	1	0.017	No	Yes
**Leucophenga* C20004	0	2	3	5	0.084	No	Yes
**Rhinoleucophenga* B21003	1	0	0	1	0.017	No	Yes
**Rhinoleucophenga* B21004	0	1	1	2	0.034	No	Yes
**Rhinoleucophenga* B21006	0	8	4	12	0.202	Yes	Yes
**Stegana* B21002	1	0	0	1	0.017	No	Yes
**Stegana* C20003	1	0	0	1	0.017	No	Yes
Total	327	3,743	1849	5,919			

recompositing. Some studies indicate that nucleation is an attractive option for forest recovery (Holl et al. 2020). This technique, through the formation of nuclei, antlers and topsoil, helps in the recolonization of plants and allows the creation of microenvironments that can be favorable to the colonization of organisms and facilitates seed dispersal (Corbin & Holl 2012; Piaia et al. 2020). Another relevant aspect of the results is the understanding of beta diversity patterns for the structuring of the fruit fly community in regeneration areas in the northeastern Amazon. Beta diversity patterns for several organisms are crucial for understanding the succession and restoration process of habitats, such as ants (Bishop et al. 2015), beetles (da Silva et al. 2018), bees (Perillo et al. 2021), saprophytic flies (Viana-Junior et al. 2021) and—here we highlight for the first time—drosophilids.

Restoration techniques can promote site heterogeneity, with the aim of improving environmental recovery (Mounsey et al. 2022), creating biotic and abiotic conditions favorable to forest species. Nucleation techniques are proposed as capable of accelerating natural restoration processes (Ramírez-Soto et al. 2018). Although some indicators point to the greater efficiency of the method, it is not yet proven that the improvements in soil conditions resulting from nucleation are reflected in the faster restoration of biodiversity. This work showed that 6 years of recovery are still not enough to identify differences between regeneration techniques in terms of biodiversity restoration regarding the composition of species in the focal group. This is probably due to the floristic and structural similarity that the sites of natural regeneration and nucleation have (da Cruz et al. 2020).

For this time of management, when observing the effect of restoration on the metrics of diversity, faunal composition and beta diversity pattern of drosophilids, the restoration environments present a homogeneous set of species more tolerant to open areas, with higher solar incidence, which may be contributing to diversity metrics. Despite not differing in

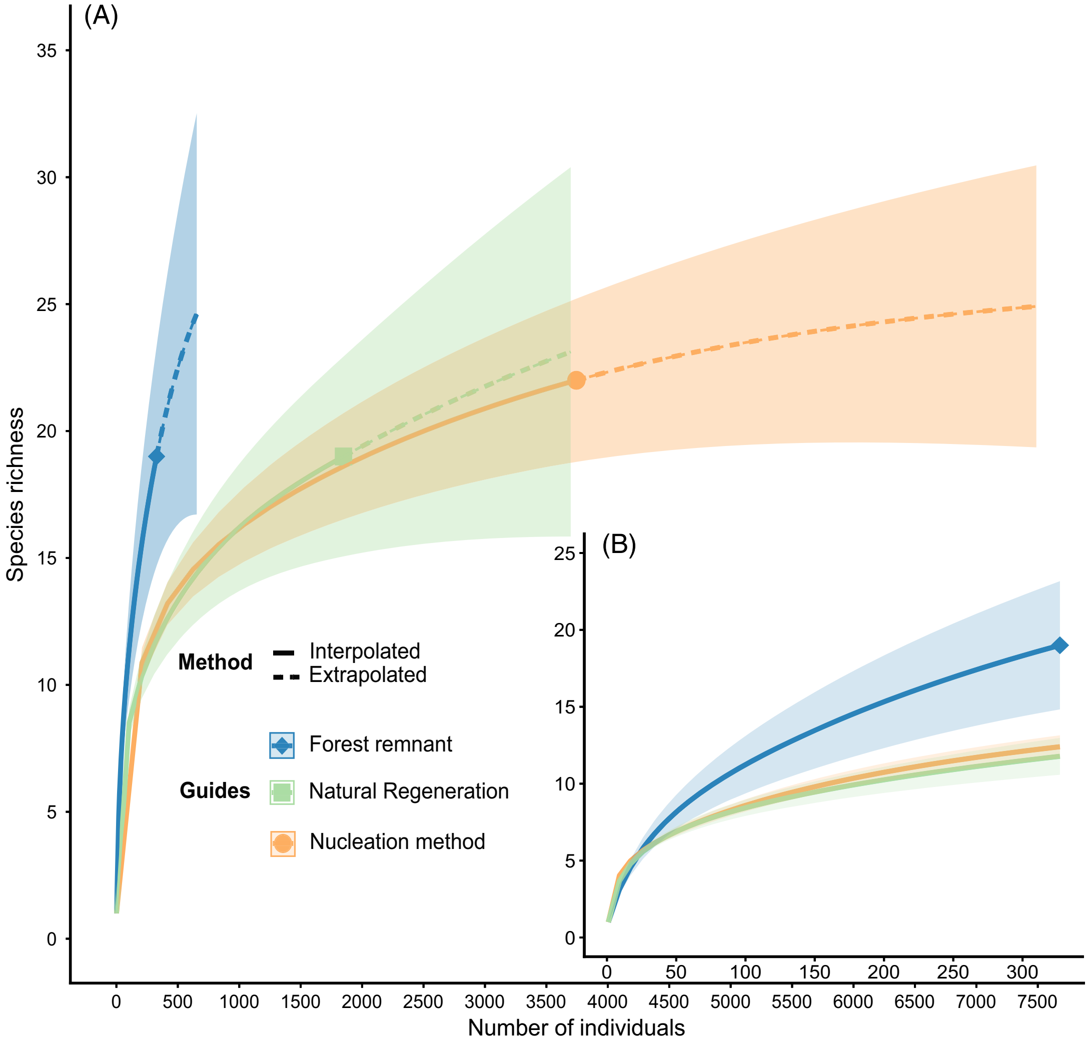

Figure 3. (A) Asymptotic richness curve of Drosophilidae, in the three study environments, at Hydro Mineração Paragominas, State of Pará, Brazil, based on number of individuals (solid lines) and extrapolation (dashed lines). In (B), richness curves based on the environment with the smallest number of individuals sampled.

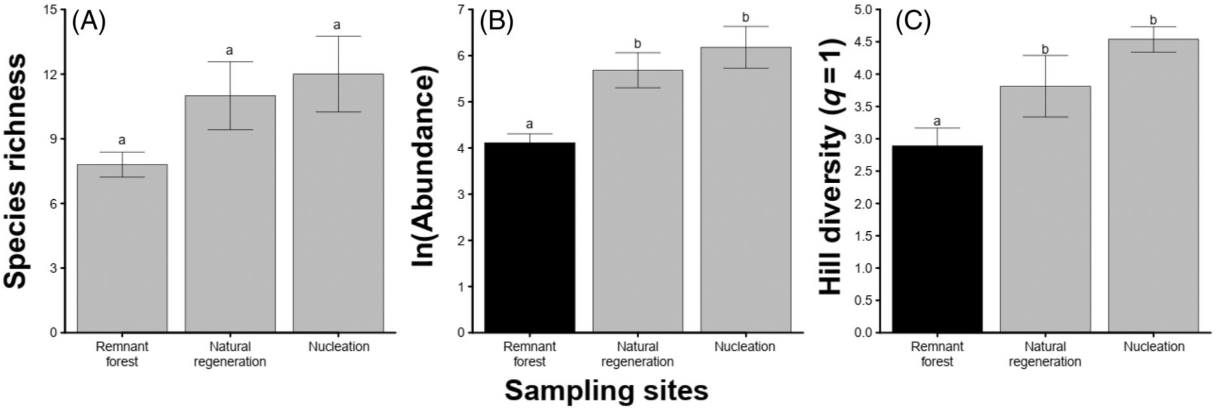

Figure 4. Mean (± SE) of the (A) observed species richness (Hill q0), (B) drosophilid abundance, and (C) diversity calculated by the Hill method among the different environments studied, at Hydro Mineração Paragominas, Pará, Brazil.

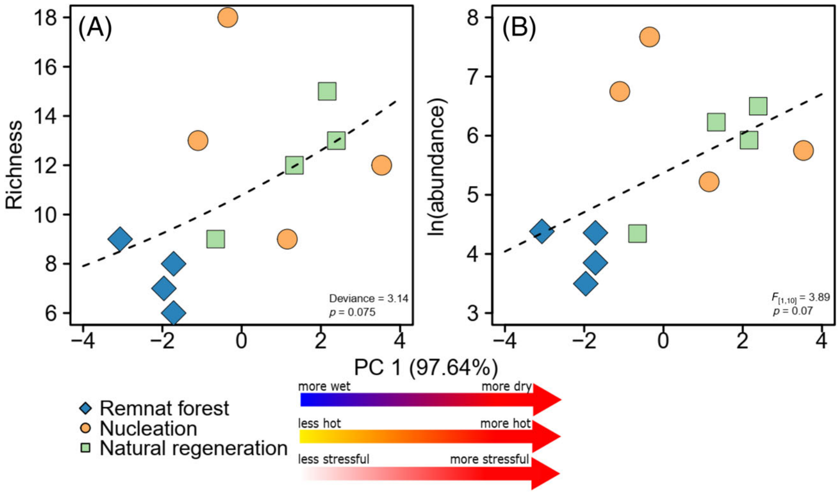

Figure 5. The effect of the local climate profile on the diversity attributes. (A) Drosophilid richness. (B) Drosophilid abundance, in different environments studied, at Hydro Mineração Paragominas, Pará, Brazil.

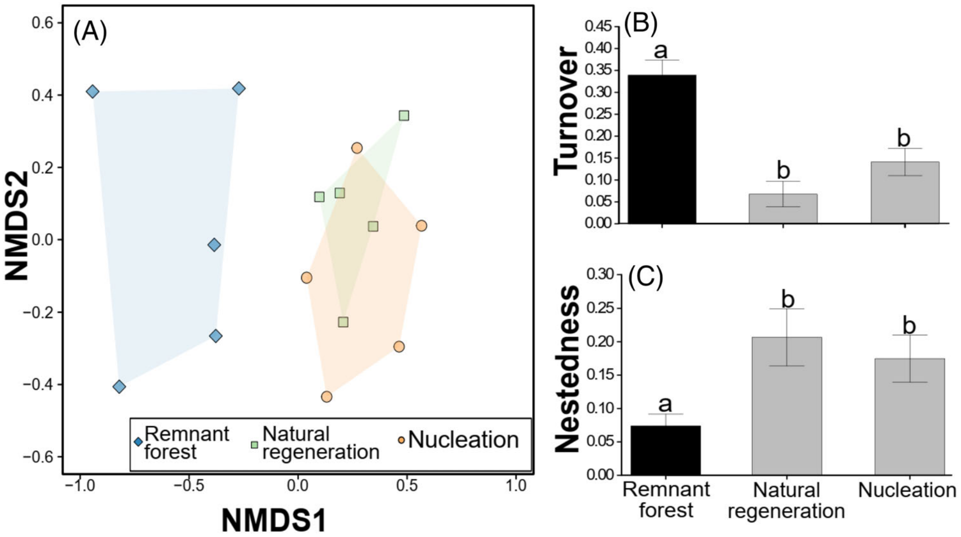

Figure 6. (A) Analysis of species composition using the nonmetric multidimensional scale (NMDS) and mean (± SE) of the beta diversity by (B) turnover and (C) nestedness in different environments at Hydro Mineração Paragominas, Pará, Brazil.

average richness, the accumulation curves showed that the richness in forest remnants is greater. In addition to the greater availability of resources that forest remnants offer, this can also occur due to the amenity and climate stability of these areas. It is important to observe the absence or small number of individuals of exotic species within the forest remnants, even in contiguous environments. Despite exotic species such, as *Zaprionus indianus*, being strong competitors and limiting the coexistence of native species (Oliveira et al. 2016), the forest seems to show resistance to the invasion of these species, maintaining the typical regional fauna. The regenerating environments, despite being dominated by exotic species, also denote the presence of typical forest species, which points to a positive trajectory of integration of these environments to the forest matrix, even if still incipient.

The fact that Hill diversity and abundance do not differ between areas under recovery is due to similarities in their composition in species with a predominance of those more cosmopolitan, mostly exotic. These species live in open areas, with greater tolerance to environmental changes and have reproductive strategies that lead to the production of large numbers of individuals per generation, such as *Z. indianus*, *Drosophila nasuta*, *Scaptodrosophila latifasciaeformis* (Penariol & Madi-Ravazzi 2013), and are usually associated with altered environments (da Mata et al. 2008; da Mata & Tidon 2013; Furtado & Martins 2018). Such species have been used as indicators of

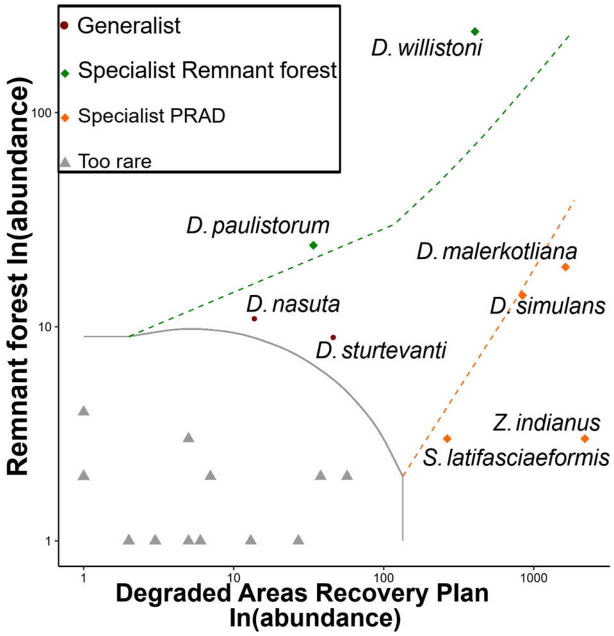

Figure 7. Species classification method result for the dataset between forest remnant and Degraded Area Recovery Program (PRAD) (natural regeneration and nucleation), using the supermajority specialization limit ($K = 2/3$). In dark red, they are generalist species, in green they are species that are specialists in the remnant forest, in orange they are specialists in the PRAD and in gray they are rare species.

environmental changes because they do not have affinity to forested environments in the Amazon, not occurring or being extremely rare in preserved forests (Martins 2001). These species together represented 41% of the total number of individuals sampled in the PRADs.

Despite the relationship between diversity and abiotic factors being statistically uncertain and presenting weak biological evidence in the present study, as discussed by Dushoff et al. (2019) and Muff et al. (2022) on the meaning of statistical significance, several works showed that the abundance and richness of drosophilids are significantly affected by abiotic conditions (climatological variables) (Dobzhansky 1957; Poppe et al. 2013; Furtado & Martins 2018). It is important to highlight that the evidence we found in our study is due to the time frame that we collected (a collection made in the rainy season). We know that the drosophilid community is seasonally structured (Roque et al. 2013; Coutinho-Silva et al. 2017), and possibly this effect could be more evident if our sampling time spectrum was larger, corroborating the findings of other studies. However, it is also important to point out that the rainy season is the time when more diversity is collected from drosophilids in tropical forests (Martins 1987; Tidon 2006; Garcia et al. 2014) and possibly there would not be much increase in diversity if we collected in the dry season. Our results raise the question about the temporal effort to find robust ecological patterns in the *Drosophila* community. Temperature and relative humidity can influence insect development (Winkler et al. 2020) and interfere with their fecundity (Nava et al. 2007). Works have reported that drosophilids are influenced by the stress of temperature and mean relative humidity in laboratory tests, showing the effect of climatic variables on the drosophilid community (Schou et al. 2017; Krüger et al. 2021). Torres and Madi-Ravazzi (2006), Nava et al. (2007), and Bombin and Reed (2016) show that climate variation, which occurs in subtropical areas of Brazil, has a strong influence on drosophilid species.

The distinction in composition between forest and areas under restoration demonstrate particular preferences of some species for certain environments, which facilitates the use of these species as indicators. The forest remnants comprise environments with a greater variety of niches and capable of hosting a greater variety of species, including species with a lower degree of tolerance to environmental variations (da Mata et al. 2008). Environments in early stages of recovery harbor species that are more general and have greater plasticity in relation to variations in temperature and humidity, such as those found in other types of altered environments in the Amazon (Furtado & Martins 2018). The results of the beta diversity components of this study make clear the strong effect of turnover in forest remnants. The forest remnants arranged between Hydro's forestry exploration and recovery areas may be contributing in a complementary way to each other, probably due to the high heterogeneity and variety of niches that these environments have with a great variety of resources that can be used by these flies (Cavasini et al. 2014), capable of providing a greater number of species coexisting (da Mata et al. 2008; Soares et al. 2015). The nestedness process observed in areas undergoing restoration is associated with the slow recolonization of environments (Dobrovolski et al. 2012), and the intensity of environmental filters defining favorable conditions for a certain set of species that is relatively more restricted. The highest nestedness values found in restoration areas, when compared with the areas of remaining forest, show that the losses and gains of species structure the community to processes of biotic homogenization (Socolar et al. 2016). These environments will have more or less the same species with a preference for open areas, which justifies the results found for the PRADs, that is, the beta diversity values analyzed here are strongly influenced by environmental characteristics (Soares et al. 2015; Soininen et al. 2018). And it reinforces how the structure of the drosophilid community can serve as a valuable indicator of an environment condition.

The species classified as typical of forested areas (*D. paulistorum* and *D. willistoni*) belong to the willistoni subgroup, of which they are known as indicators of forest environments and are occasionally found in open habitats (Torres & Madi-Ravazzi 2006; da Mata et al. 2008; Penariol & Madi-Ravazzi 2013). The records of these species in open habitats must be due to their high flight capacity, which makes it possible to cross great distances attracted by fruit baits (Dobzhansky 1957). Already, the predominance of species such as *S. latifasciaeformis*, *D. simulans*, *D. malerkotliana*, and *Z. indianus*, specialists in open areas, here represented by PRADs, is consistent with the literature. These species are exotic, and the last two recent invaders in the Amazon (Martins 1989, 2001), and show greater tolerances to environmental stress characteristic of the regeneration areas (da Mata et al. 2008; da Mata & Tidon 2013; Furtado & Martins 2018). The species *D. nasuta* and *D. sturtevanti*, classified as from both sites, have different biological and ecological aspects. *D. nasuta* is an exotic species, recently introduced in Brazil (first record in 2013, Leão et al. 2017; Silva et al. 2020), and first recorded in the Amazon in 2017 (from de de Medeiros et al. 2022). Its invasive potential causes concern to native species, as this species has a high reproductive capacity and can use a great diversity of habitats and resources (Silva et al. 2020; Montes et al. 2021). *D. sturtevanti* is a native neotropical species (da Conceicao Galego & Carareto 2005) and the structural characteristics of the environment do not seem to be a limiting factor for this species (Martins 1987). In fact, it is a very abundant species both in the Amazon biome, in the open cerrado and in gallery forests (Tidon 2006; Chaves & Tidon 2008), however, this species actually corresponds to a complex of cryptic species whose designation can be representing more than one species with complementary ecologies (Souza et al. 2014).

The similarities between richness, composition, diversity, and pattern of abundance of drosophilids in areas undergoing restoration show that these environments behave similarly in the initial trajectory of restoration (6 years), regardless of the technique applied. It also demonstrates the fidelity of the ecological behavior of the indicator species, giving consistency to the assessment of the evolution stage of forest restoration, regarding the recovery of biodiversity. This work represents a baseline for the progression of monitoring forest restoration. Continuous monitoring will make it possible to identify if there is variation in the degree of efficiency of biodiversity recovery between restoration techniques. Using drosophilids as indicators, it will be possible in the future to find a threshold at which the techniques used can be distinguished as to their effectiveness, if any. The big difference between these regeneration environments and the forest clearly reflects the initial phase of restoration. The future absence or reduction in the abundance of exotic species can be used as an easily measurable indicator of forest restoration. When these environments start to become more forest-like, the abundance of exotic species, such as *Z. indianus* and *S. latifascieformis*, will tend to decrease drastically, and typical forest species should predominate.

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LITERATURE CITED

Anderson MJ (2001) A new method for non-parametric multivariate analysis of variance. Austral Ecology 26:32–46. https://doi.org/10.1111/j.1442-9993.2001.01070.pp.x

Arbizu MP (2020) pairwise_adonis: pairwise multilevel comparison using adonis. R package, Accessed September 18, 2022. https://doi.org/10.1039/d0fo00487a

Bächli G, Vilela CR, Escher SA, Saura A (2004) The Drosophilidae (Diptera) of Fennoscandia and Denmark. Brill Academic Publishers, Leiden, The Netherlands

Baselga A, Orme CDL (2012) betapart: an R package for the study of beta diversity. Methods in Ecology and Evolution 3:808–812. https://doi.org/10.1111/j.2041-210X.2012.00224.x

Bishop TR, Robertson MP, van Rensburg BJ, Parr CL (2015) Contrasting species and functional beta diversity in montane ant assemblages. Journal of Biogeography 42:1776–1786. https://doi.org/10.1111/jbi.12537

Bombin A, Reed LK (2016) The changing biodiversity of Alabama *Drosophila*: important impacts of seasonal variation, urbanization, and invasive species. Ecology and Evolution 6:7057–7069. https://doi.org/10.1002/ece3.2452

Borges FLG, da Rosa Oliveira M, de Almeida TC, Majer JD, Garcia LC (2021) Terrestrial invertebrates as bioindicators in restoration ecology: a global bibliometric survey. Ecological Indicators 125:107458. https://doi.org/10.1016/j.ecolind.2021.107458

Brasil Neto AB, Schwartz G, Noronha NC, Gama MAP, Ferreira GC (2021) Natural regeneration for restoration of degraded areas after bauxite mining: a case study in the Eastern Amazon. Ecological Engineering 171:106392. https://doi.org/10.1016/j.ecoleng.2021.106392

Casimiro MS, Sansevero JBB, Queiroz JM (2019) What can ants tell us about ecological restoration? A global meta-analysis. Ecological Indicators 102:593–598. https://doi.org/10.1016/j.ecolind.2019.03.018

Cavasini R, Buschini M, Machado L, Mateus R (2014) Comparison of Drosophilidae (Diptera) assemblages from two highland Araucaria Forest fragments, with and without environmental conservation policies. Brazilian Journal of Biology 74:761–768. https://doi.org/10.1590/1519-6984.00113

Cerqueira RM, Jardim MAG, Silva Junior LLM, Paixão LP, Martins MB (2021) Fitossociologia do estrato arbóreo em floresta nativa e em áreas do programa de recuperação de áreas degradadas sob influência da mineração, Paragominas, Pará, Brasil. Nature and Conservation 14:22-41. https://doi.org/10.6008/CBPC2318-2881.2021.003.0002

Chang CC, Turner BL (2019) Ecological succession in a changing world. Journal of Ecology 107:503–509. https://doi.org/10.1111/1365-2745.13132

Chao A, Chiu C-H, Jost L (2014) Unifying species diversity, phylogenetic diversity, functional diversity, and related similarity and differentiation measures through Hill numbers. Annual Review of Ecology, Evolution, and Systematics 45:297–324. https://doi.org/10.1146/annurev-ecolsys-120213-091540

Chaves NB, Tidon R (2008) Biogeographical aspects of drosophilids (Diptera, Drosophilidae) of the Brazilian savanna. Revista Brasileira de Entomologia 52:340–348. https://doi.org/10.1590/S0085-56262008000300005

Chazdon RL, Chao A, Colwell RK, Lin S-Y, Norden N, Letcher SG, Clark DB, Finegan B, Arroyo JP (2011) A novel statistical method for classifying habitat generalists and specialists. Ecology 92:1332–1343. https://doi.org/10.1890/10-1345.1

Cole RJ, Holl KD, Zahawi RA, Wickey P, Townsend AR (2016) Leaf litter arthropod responses to tropical forest restoration. Ecology and Evolution 6:5158–5168. https://doi.org/10.1002/ece3.2220

Colwell RK, Chao A, Gotelli NJ, Lin S-Y, Mao CX, Chazdon RL, Longino JT (2012) Models and estimators linking individual-based and sample-based rarefaction, extrapolation and comparison of assemblages. Journal of Plant Ecology 5:3–21. https://doi.org/10.1093/jpe/rtr044

Corbin JD, Holl KD (2012) Applied nucleation as a forest restoration strategy. Forest Ecology and Management 265:37–46. https://doi.org/10.1016/j.foreco.2011.10.013

Coutinho-Silva RD, Montes MA, Oliveira GF, de Carvalho-Neto FG, Rohde C, Garcia ACL (2017) Effects of seasonality on drosophilids (Insecta, Diptera) in the northern part of the Atlantic Forest, Brazil. Bulletin of Entomological Research 107:634–644. https://doi.org/10.1017/S0007485317000190

da Conceicao Galego LG, Carareto CMA (2005) Intraspecific and interspecific pre-adult competition on the neotropical region colonizer *Zaprionus indianus* (Diptera: Drosophilidae) under laboratory conditions. Bragantia 64: 249–255. https://doi.org/10.1590/S0006-87052005000200012

da Cruz DC, Rey Benayas JM, Costa Ferreira G, Santos Ribeiro S (2020) Tree communities in three-year-old post-mining sites under different forest restoration techniques in the Brazilian Amazon. Forests 11:527. https://doi.org/10.3390/f11050527

da Mata RA, McGeoch M, Tidon R (2008) Drosophilid assemblages as a bioindicator system of human disturbance in the Brazilian Savanna. Biodiversity and Conservation 17:2899–2916. https://doi.org/10.1007/s10531-008-9403-7

da Mata RA, Tidon R (2013) The relative roles of habitat heterogeneity and disturbance in drosophilid assemblages (Diptera, Drosophilidae) in the Cerrado. Insect Conservation and Diversity 6:663–670. https://doi.org/10.1111/icad.12020

da Mata RA, Tidon R, Côrtes LG, de Marco P, Diniz-Filho JAF (2010) Invasive and flexible: niche shift in the drosophilid *Zaprionus indianus* (Insecta, Diptera). Biological Invasions 12:1231–1241. https://doi.org/10.1007/s10530-009-9542-0

da Silva PG, Lobo JM, Hensen MC, Vaz-de-Mello FZ, Hernández MIM (2018) Turnover and nestedness in subtropical dung beetle assemblages along an elevational gradient. Diversity and Distributions 24:1277–1290. https://doi.org/10.1111/ddi.12763

de Araujo RA, de Souza Silva JL, dos Santos Cugula J, Paschoal JP, Esteves VPP, do Rosário Vaz Morgado C (2021) Assessment of vegetation recomposition methods in a tropical forest using satellite images. Clean Technologies and Environmental Policy 23:797–810. https://doi.org/10.1007/s10098-020-01916-w

de Medeiros HF, Klaczko LB (2004) How many species of Drosophila (Diptera, Drosophilidae) remain to be described in the forests of São Paulo, Brazil?: species lists of three forest remnants. Biota Neotropica 4:1–12. https://doi.org/10.1590/S1676-06032004000100005

de Medeiros HF, Monteiro MP, Caçador AWB, Pereira CM, de Lurdes Bezerra Praxedes C, Martins MB, Montes MA, Garcia ACL (2022) First records of the invading species *Drosophila nasuta* (Diptera: Drosophilidae) in the Amazon. Neotropical Entomology 51:493–497. https://doi.org/10.1007/s13744-021-00938-3

de Oliveira MA, Gomes CFF, Pires EM, Marinho CGS, della Lucia TMC (2014) Bioindicadores ambientais: insetos como um instrumento desta avaliação. Revista Ceres 61:800–807. https://doi.org/10.1590/0034-737x201461000005

Dobrovolski R, Melo AS, Cassemiro FAS, Diniz-Filho JAF (2012) Climatic history and dispersal ability explain the relative importance of turnover and nestedness components of beta diversity. Global Ecology and Biogeography 21:191–197. https://doi.org/10.1111/j.1466-8238.2011.00671.x

Dobzhansky T (1957) Genetics of natural populations. XXVI. Chromosomal variability in island and continental populations of *Drosophila willistoni* from Central America and the West Indies. Evolution 11:280–293. https://doi.org/10.2307/2405791

Duarte LB, Gottschalk MS, Robe LJ (2018) Assemblage of drosophilids (Diptera, Drosophilidae) inhabiting flooded and nonflooded areas in the extreme South of Brazil. Revista Brasileira de Entomologia 62:29–35. https://doi.org/10.1016/j.rbe.2017.11.005

Dushoff J, Kain MP, Bolker BM (2019) I can see clearly now: reinterpreting statistical significance. Methods in Ecology and Evolution 10:756–759. https://doi.org/10.1111/2041-210X.13159

Ferreira LB, Tidon R (2005) Colonizing potential of Drosophilidae (Insecta, Diptera) in environments with different grades of urbanization. Biodiversity and Conservation 14:1809–1821. https://doi.org/10.1007/s10531-004-0701-4

Figueiredo RO, Markewitz D, Davidson EA, Schuler AE, Watrin ODS, de Souza Silva P (2010) Land-use effects on the chemical attributes of low-order streams in the eastern Amazon. Journal of Geophysical Research 115. https://doi.org/10.1029/2009JG001200

Furtado IS, Martins MB (2018) The impacts of land use intensification on the assembly of drosophilidae (Diptera). Global Ecology and Conservation 16:e00432. https://doi.org/10.1016/j.gecco.2018.e00432

Garcia ACL, Silva DMIDO, Monteiro AGF, Oliveira GF, Montes MA, Rohde C (2014) Abundance and richness of cryptic species of the *Willistoni* group of *Drosophila* (Diptera: Drosophilidae) in the biomes Caatinga and Atlantic Forest, Northeastern Brazil. Annals of the Entomological Society of America 107:975–982. https://doi.org/10.1603/AN14052

Gottschalk MS, de Toni DC, Valente VLS, Hofmann PRP (2007) Changes in Brazilian Drosophilidae (Diptera) assemblages across an urbanisation gradient. Neotropical Entomology 36:848–862. https://doi.org/10.1590/S1519-566X2007000600005

Harrison RJ, Muraszko J, Heslop D, Lascu I, Muxworthy AR, Roberts AP (2018) An improved algorithm for unmixing first-order reversal curve diagrams using principal component analysis. Geochemistry, Geophysics, Geosystems 19:1595–1610. https://doi.org/10.1029/2018GC007511

Holl KD, Reid JL, Cole RJ, Oviedo-Brenes F, Rosales JA, Zahawi RA (2020) Applied nucleation facilitates tropical forest recovery: lessons learned from a 15-year study. Journal of Applied Ecology 57:2316–2328. https://doi.org/10.1111/1365-2664.13684

Hsieh TC, Ma KH, Chao A (2016) iNEXT: an R package for rarefaction and extrapolation of species diversity (Hill numbers). Methods in Ecology and Evolution 7:1451–1456. https://doi.org/10.1111/2041-210X.12613

Hydro (2021) Hydro Paragominas: mina de bauxita. Accessed March 3, 2022. https://www.hydro.com/pt-BR/sobre-a-hydro/a-hydro-no-mundo/north-america/brasil/paragominas/mineracao-paragominas/

Ives AR (2015) For testing the significance of regression coefficients, go ahead and log-transform count data. Methods in Ecology and Evolution 6: 828–835. https://doi.org/10.1111/2041-210X.12386

Khan SAR, Sharif A, Golpîra H, Kumar A (2019) A green ideology in Asian emerging economies: from environmental policy and sustainable development. Sustainable Development 27:1063–1075. https://doi.org/10.1002/sd.1958

Krüger AP, Vieira JGA, Scheunemann T, Nava DE, Garcia FRM (2021) Effects of temperature and relative humidity on mating and survival of sterile *Drosophila suzukii*. Journal of Applied Entomology 145:789–799. https://doi.org/10.1111/jen.12894

Laurance WF, Sayer J, Cassman KG (2014) Agricultural expansion and its impacts on tropical nature. Trends in Ecology & Evolution 29:107–116. https://doi.org/10.1016/j.tree.2013.12.001

Leão BFD, Roque F, Deus P, Tidon R (2017) What happens when exotic species arrive in a new area? The case of drosophilids (Diptera) in the Brazilian Savanna. Drosophila Information Service 100:65–69. https://www.ou.edu/journals/dis/DIS100/Research/Leao%20et%20al%2065.pdf

Lue C-H, Borowy D, Buffington ML, Leips J (2018) Geographic and seasonal variation in species diversity and community composition of frugivorous Drosophila (Diptera: Drosophilidae) and their Leptopilina (Hymenoptera: Figitidae) parasitoids. Environmental Entomology 47:1096–1106. https://doi.org/10.1093/ee/nvy114

Magalhães LE, Bjornberg AJS (1957) Estudo da genitália masculina de 'Drosophila' do grupo 'saltans' (Diptera). Revista Brasileira de Biologia 17:435–450. http://www.drosophila.jp/jdd/class/030703/03070384.pdf

Malogolowkin C (1952) Sobre a genitália dos "Drosophilidae" (Diptera). III. Grupo willistoni do gênero Drosophila. Revista Brasileira de Biologia 12: 79–96. http://www.drosophila.jp/jdd/class/030703/03070388.pdf

Martins M (1987) Variação espacial e temporal de algumas espécies e grupos de Drosophila (Diptera) em duas reservas de matas isoladas, nas vizinhanças de Manaus (Amazonas, Brasil). Boletim do Museu Paraense Emilio Goeldi Serie Zoologia 3:195–218. https://repositorio.museu-goeldi.br/handle/mgoeldi/386

Martins MB (1989) Invasão de fragmentos florestais por espécies oportunistas de Drosophila (Diptera, Drosophilidae). Acta Amazonica 19:265–271. https://doi.org/10.1590/1809-43921989191271

Martins MB (2001) Drosophilid fruit-fly guilds in forest fragments. Pages 175–186. In: Bierregaard RO, Gascon C, Lovejoy TE, Mesquita R (eds) Lessons from Amazonia: the ecology and conservation of a fragmented forest. Yale University Press, New Haven, Connecticut

Martins MB, Bittencourt RN, Penna JAN (2008) Traps adapted to drosophilid collections in tropical rain forest. Drosophila Information Service 8:45–52. https://www.ou.edu/journals/dis/DIS91/Martins%20147.pdf

Martins WBR, Vale RL, Ferreira GC, Andrade VMS, Dionísio LFS, Rodrigues RP, Oliveira FA, Souza GMP (2018) Litterfall, litter stock and water holding capacity in post-mining forest restoration ecosystems, Eastern Amazon. Revista Brasileira de Ciências Agrárias – Brazilian Journal of Agricultural Sciences 13:1–9. https://doi.org/10.5039/agraria.v13i3a5546

Mechi A, Sanches DL (2010) Impactos ambientais da mineração no Estado de São Paulo. Estudos Avançados 24:209–220. https://doi.org/10.1590/S0103-40142010000100016

Mendes MF, Blauth ML, dos Santos LA, da Silva Valente Gaiesky VL, Gottschalk MS (2021) Temporal edge effects structure the assemblages of Drosophilidae (Diptera) in a Restinga forest fragment in Southern Brazil. Neotropical Biology and Conservation 16:299–315. https://doi.org/10.3897/neotropical.16.e61481

Mendes MF, Valer FB, Vieira JGA, Blauth ML, Gottschalk MS (2017) Diversity of Drosophilidae (Insecta, Diptera) in the Restinga forest of southern Brazil. Revista Brasileira de Entomologia 61:248–256. https://doi.org/10.1016/j.rbe.2017.05.002

Monteiro LS, Garcia ACL, Oliveira GF, Rohde C (2016) High diversity of Drosophilidae in high-altitude wet forests in Northeastern Brazil. Neotropical Entomology 45:265–273. https://doi.org/10.1007/s13744-016-0364-3

Montes MA, Neves CHCB, Ferreira AF, de Fátima Severina dos Santos M, Quintas JIFP, Manetta GDÂ, de Oliveira PV, Garcia ACL (2021) Invasion and spreading of *Drosophila nasuta* (Diptera, Drosophilidae) in the Caatinga biome, Brazil. Neotropical Entomology 50:571–578. https://doi.org/10.1007/s13744-021-00875-1

Mounsey CM, Stevens JC, Renton M, Dixon KW, Miller BP (2022) The influence of environmental drivers and restoration intervention methods on postmine restoration trajectories. Restoration Ecology 30:e13503. https://doi.org/10.1111/rec.13503

Muff S, Nilsen EB, O'Hara RB, Nater CR (2022) Rewriting results sections in the language of evidence. Trends in Ecology & Evolution 37:203–210. https://doi.org/10.1016/j.tree.2021.10.009

Nascimento E, Ambrogi B, Souto LS, Vilas-Bôas M, Uchôa M (2014) Efeito do envelhecimento de isca na captura de moscas (Diptera: Brachycera) em área de Caatinga. EntomoBrasilis 7:1–4. https://doi.org/10.12741/ebrasilis.v7i1.327

Nava DE, Nascimento AM, Stein CP, Haddad ML, Bento JM, Parra JR (2007) Biology, thermal requirements, and estimation of the number of generations of *Zaprionus indianus* (Diptera: Drosophilidae) for the main fig producing regions of Brazil. Florida Entomologist 90:495–501. https://doi.org/10.1653/0015-4040(2007)90[495:BTRAEO]2.0.CO;2

Oksanen J, Blanchet FG, Friendly M, Kindt R, Legendre P, McGlinn D, et al. (2020) Vegan: community ecology package. R package version 2.5-7. Accessed March 03, 2022. https://CRAN.R-project.org/package=vegan, https://doi.org/10.3389/fpsyg.2020.568256

Oliveira GF, Lauer Garcia AC, Montes MA, de Araújo Jucá JCL, da Silva Valente VL, Rohde C (2016) Are conservation units in the Caatinga biome, Brazil, efficient in the protection of biodiversity? An analysis based on the drosophilid fauna. Journal for Nature Conservation 34:145–150. https://doi.org/10.1016/j.jnc.2016.10.006

Onésimo CMG, Dias DD, Beirão M, Kozovits AR, Messias MCTB (2021) Ecological succession in areas degraded by bauxite mining indicates successful use of topsoil. Restoration Ecology 29:e13303. https://doi.org/10.1111/rec.13303

Padilha TCDS, Martins WBR, Ferreira GC, Ribeiro EGP, Rodrigues RP (2018) Deposição de micronutrientes da serapilheria em áreas de mineração submetidas a métodos de restauração florestal, Paragominas, PA. Solos nos biomas brasileiros – Ponta Grossa (PR): Atena Editora.

Palmer MA (2009) Reforming watershed restoration: science in need of application and applications in need of science. Estuaries and Coasts 32:1–17. https://doi.org/10.1007/s12237-008-9129-5

Parsons PA (1975) The effect of temperature and humidity on the distribution patterns of *Drosophila inornata* in Victoria, Australia. Environmental Entomology 4:961–964. https://doi.org/10.1093/ee/4.6.961

Parsons PA (1991) Biodiversity conservation under global climatic change: the insect Drosophila as a biological indicator? Global Ecology and Biogeography Letters 1:77. https://doi.org/10.2307/2997493

Penariol L, de Campos Bicudo HEM, Madi-Ravazzi L (2008) On the use of open or closed traps in the capture of drosophilids. Biota Neotropica 8:47–51. https://doi.org/10.1590/S1676-06032008000200004

Penariol LV, Madi-Ravazzi L (2013) Edge-interior differences in the species richness and abundance of drosophilids in a semideciduous forest fragment. Springerplus 2:114. https://doi.org/10.1186/2193-1801-2-114

Perillo LN, de Castro FS, Solar R, de Siqueira Neves F (2021) Disentangling the effects of latitudinal and elevational gradients on bee, wasp, and ant diversity in an ancient neotropical mountain range. Journal of Biogeography 48:1564–1578. https://doi.org/10.1111/jbi.14095

Piaia BB, Rovedder APM, Procknow D, Camargo B, Gazzola MD, Croda JP, de Moraes SM (2020) Natural regeneration as an indicator of ecological restoration by applied nucleation and passive restoration. Ecological Engineering 157:105991. https://doi.org/10.1016/j.ecoleng.2020.105991

Poppe JL, Valente VLS, Schmitz HJ (2013) Population dynamics of Drosophilids in the Pampa biome in response to temperature. Neotropical Entomology 42:269–277. https://doi.org/10.1007/s13744-013-0125-5

Ramírez-Soto A, Lucio-Palacio CR, Rodríguez-Mesa R, Sheseña-Hernández I, Farhat FN, Villa-Bonilla B, et al. (2018) Restoration of tropical montane cloud forests: a six-prong strategy. Restoration Ecology 26:206–211. https://doi.org/10.1111/rec.12660

Roque F, da Mata RA, Tidon R (2013) Temporal and vertical drosophilid (Insecta; Diptera) assemblage fluctuations in a neotropical gallery forest. Biodiversity and Conservation 22:657–672. https://doi.org/10.1007/s10531-013-0433-4

Rstudio Team (2021) RStudio: integrated development environment for R. Studio

Schou MF, Kristensen TN, Pedersen A, Karlsson BG, Loeschcke V, Malmendal A (2017) Metabolic and functional characterization of effects of developmental temperature in *Drosophila melanogaster*. American Journal of Physiology–Regulatory, Integrative and Comparative Physiology 312:R211–R222. https://doi.org/10.1152/ajpregu.00268.2016

Siddig AAH, Ellison AM, Ochs A, Villar-Leeman C, Lau MK (2016) How do ecologists select and use indicator species to monitor ecological change? Insights from 14 years of publication in ecological indicators. Ecological Indicators 60:223–230. https://doi.org/10.1016/j.ecolind.2015.06.036

Silva DG, Schmitz HJ, de Medeiros HF, Rohde C, Montes MA, Garcia ACL (2020) Geographic expansion and dominance of the invading species *Drosophila nasuta* (Diptera, Drosophilidae) in Brazil. Journal of Insect Conservation 24:525–534. https://doi.org/10.1007/s10841-020-00219-1

Skvarla MJ, Larson JL, Fisher JR, Dowling APG (2021) A review of terrestrial and canopy Malaise traps. Annals of the Entomological Society of America 114:27–47. https://doi.org/10.1093/aesa/saaa044

Soares CEA, Velho LFM, Lansac-Tôha FA, Bonecker CC, Landeiro VL, Bini LM (2015) The likely effects of river impoundment on beta-diversity of a floodplain zooplankton metacommunity. Natureza & Conservação 13:74–79. https://doi.org/10.1016/j.ncon.2015.04.002

Socolar JB, Gilroy JJ, Kunin WE, Edwards DP (2016) How should beta-diversity inform biodiversity conservation? Trends in Ecology & Evolution 31:67–80. https://doi.org/10.1016/j.tree.2015.11.005

Soininen J, Heino J, Wang J (2018) A meta-analysis of nestedness and turnover components of beta diversity across organisms and ecosystems. Global Ecology and Biogeography 27:96–109. https://doi.org/10.1111/geb.12660

Souza TAJ, Noll FB, de Campos Bicudo HEM, Madi-Ravazzi L (2014) Scanning electron microscopy of male terminalia and its application to species recognition and phylogenetic reconstruction in the *Drosophila saltans* group. PLoS One 9:e97156. https://doi.org/10.1371/journal.pone.0097156

Thompson ID, Okabe K, Tylianakis JM, Kumar P, Brockerhoff EG, Schellhorn NA, Parrotta JA, Nasi R (2011) Forest biodiversity and the delivery of ecosystem goods and services: translating science into policy. Bioscience 61:972–981. https://doi.org/10.1525/bio.2011.61.12.7

Tidon R (2006) Relationships between drosophilids (Diptera, Drosophilidae) and the environment in two contrasting tropical vegetations. Biological Journal of the Linnean Society 87:233–247. https://doi.org/10.1111/j.1095-8312.2006.00570.x

Torres FR, Madi-Ravazzi L (2006) Seasonal variation in natural populations of *Drosophila* spp. (Diptera) in two woodlands in the state of São Paulo, Brazil. Iheringia: Série Zoologia 96:437–444. https://doi.org/10.1590/S0073-47212006000400008

Viana-Junior AB, De-Souza CC, de Medeirosc HF, Carvalho-Filho F (2021) Diversity partitioning and distance-decay relationship of saprophytic flies (Insecta: Diptera) in the western Brazilian Amazon. Acta Oecologica 112: 103768. https://doi.org/10.1016/j.actao.2021.103768

Vilela CR (1983) A revision of the *Drosophila repleta* species group (Diptera, Drosophilidae). Revista Brasileira de Entomologia 27:1–114

Vilela CR, da Silva AFG, de Melo Sene F (2002) Preliminary data on the geographical distribution of *Drosophila* species within morphoclimatic domains of Brazil. III. The cardini group. Revista Brasileira de Entomologia 46:139–148. https://doi.org/10.1590/S0085-56262002000200006

Winkler A, Jung J, Kleinhenz B, Racca P (2020) A review on temperature and humidity effects on *Drosophila suzukii* population dynamics. Agricultural and Forest Entomology 22:179–192. Accessed March 03, 2022. https://doi.org/10.1111/afe.12381

Supporting Information

The following information may be found in the online version of this article:

Table S1. Pairwise test result of the permutational multivariate analysis of variance (PERMANOVA) for the Drosophilidae community across different environments.
Figure S1. Correlation matrix of measured climate variables.
Figure S2. Principal component analysis, in different environments studied, at Hydro Mineração Paragominas, Pará, Brazil.

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