

Forest fragments, primary and secondary forests harbour similar arthropod assemblages after 40 years of landscape regeneration in the Central Amazon

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Abstract

1. Large-scale deforestation leads to habitat loss and fragmentation with major consequences for biodiversity. However, the impacts of these environmental disturbances can be mitigated by forest regeneration. We evaluated the effects of forest fragmentation and vegetation recovery on arthropod assemblages in human-modified landscapes in the Amazon.
2. Arthropods were sampled in 10-ha forest fragments, continuous primary forests, and secondary forests using Malaise traps. We identified arthropods in multiple taxonomic resolutions from order to species.
3. We collected 25,230 arthropods belonging to 17 orders. Coleoptera and Hemiptera were more abundant in secondary forests compared to other habitats. A dipteran family (Clusiidae) and a horse fly species (*Dichelacera cervicornis*—Tabanidae) were identified as indicators of forest fragments and continuous forests, respectively. Similar levels of taxonomic diversity between habitats were documented. The taxonomic composition also was similar between studied habitats in all taxonomic resolutions.
4. Although the studied landscapes suffered strong environmental disturbances four decades ago, the vegetation has been in continuous regeneration since then, favouring the dispersal of arthropods throughout habitats.
5. Forest fragments and old secondary forests contribute to the maintenance of a rich and diverse arthropod assemblage in landscapes composed of large tracts of continuous primary forests.

KEYWORDS

altered landscapes, beetles, biological corridors, degraded forests, Diptera, true bugs

INTRODUCTION

In the last 30 years, the world has lost 78 million hectares of forests and recently about 130 million forest fragments have been identified on three continents (FAO & UNEP, 2020; Taubert et al., 2018). Most

forest losses, degradation and fragmentation worldwide resulted from human activities such as agriculture, cattle ranching and timber extraction (FAO & UNEP, 2020). Vegetation recovery in these human-disturbed landscapes has led to the expansion of secondary forests, which currently account for a substantial portion of the tropical region

(Aide et al., 2013; Almeida et al., 2016; Chazdon, 2014; Chazdon et al., 2017). Investigating how organisms are being affected by habitat disturbance is essential to assess the importance of forests with different levels of degradation to biodiversity conservation and recovery (Chazdon et al., 2009; Mendenhall et al., 2013).

Local extinction, abundance reduction, and changes in taxonomic composition are the main responses of biological assemblages to forest disturbance (Alroy, 2017; Barlow et al., 2016; Newbold et al., 2015). Those major impacts of forest disturbances on biodiversity, however, can be mitigated by the vegetation recovery (Chazdon et al., 2017). Moreover, the effects of forest degradation on biodiversity are context and taxon dependent (Barlow et al., 2007; Doherty et al., 2021; Solar et al., 2015). Then, examining a diverse array of organisms in distinct regions and ecological contexts is essential to understanding the consequences of forest disturbance to biodiversity, especially in highly biodiverse regions such as the Amazon basin.

Arthropods are among the organisms affected by habitat disturbance in the Amazon region. For example, in the Eastern Brazilian Amazon research has found that fruit-eating butterflies, dung beetles and spiders have higher species richness in primary than secondary forests and *Eucalyptus* plantations while fruit flies and grasshoppers had similar species richness between those habitats (Barlow et al., 2007). In contrast to species richness and abundance, the species composition of some arthropod groups that occupy secondary forests is distinct from primary forests (Barlow et al., 2007; Cajariba & Silva, 2017; Solar et al., 2015). These examples indicate that Amazonian arthropod responses to forest disturbance depend on how its diversity is measured across time, habitat types and taxa identity.

Most information about arthropod response to forest disturbance in the Amazon region was collected in areas subjected to long-term and large-scale forest disturbance (e.g., França et al., 2020; Oliveira-Junior & Juen, 2019; Solar et al., 2015; Solar et al., 2016). Nonetheless, it remains poorly documented how the results of those studies could be applied in landscapes occupied by large tracts of continuous and low-disturbed forests, which cover most of the central portion of the Amazon basin (Matricardi et al., 2020).

In the Central Amazon, many studies on the influence of forest disturbances on biodiversity, especially forest regeneration and fragmentation, have been conducted in the Biological Dynamics of Forest Fragments Project (BDFFP) sites (Laurance et al., 2018). The landscapes in BDFFP are composed of experimental forest fragments with standard sizes (1, 10 and 100 ha), pastures and large extensions of primary forests and old secondary forests providing a unique opportunity to investigate the consequences of forest fragmentation and regeneration for tropical biodiversity (Laurance et al., 2018; Mesquita et al., 2015).

In addition, long-term biological monitoring highlights the BDFFP as a remarkable region to investigate the effects of habitat disturbance on tropical arthropod assemblages (Didham, 1997; Vasconcelos & Bruna, 2012). Investigating arthropods is constrained by difficulties in identifying these organisms to species level and involves decisions about gain and loss of information about taxa's identity (Basset et al., 2004; Godfray et al., 1999; Timms et al., 2013).

Traditionally, arthropod studies in BDFFP sites have focused on specific taxonomic groups such as butterflies (Brown Jr. & Hutchings, 1997), beetles (Didham et al., 1998; Klein, 1989) and ants (Vasconcelos, 1999) identified to species or genus resolution. Here, we provide the first analyses at multiple taxonomic resolutions to evaluate the simultaneous consequences of forest fragmentation and regeneration on arthropod assemblages. The study was designed to answer the following questions:

- i. Are there differences in arthropod abundance and taxonomic diversity between forest fragments, secondary and primary continuous forests in the studied landscape? Hypothetically, forest fragments harbour lower taxonomic diversity than continuous habitats since they host a lower abundance of individuals and an incomplete sample of regional habitats (Rosenzweig, 1996). Indeed, several arthropod groups in BDFFP's forest fragments present lower species diversity and abundance than continuous forests (Leidner et al., 2010; Vasconcelos & Bruna, 2012). Arthropod diversity and abundance are also positive correlated with plant species diversity and habitat structure (Randlkofer et al., 2010; Salman & Blaustein, 2018; Schaffers et al., 2008). The influence of plant diversity and vegetation structure on arthropod assemblages, however, could be diminished along the time of forest regeneration (Newbold et al., 2015). For example, old-aged secondary forests present minor differences in diversity and abundance of arthropods compared with primary forests in the Amazon (Barlow et al., 2007; Cajariba & Silva, 2017; Quintero & Roslin, 2005). Therefore, we expected to find lower taxonomic diversity and abundance in forest fragments compared to continuous forests, but no substantial differences in those diversity metrics between old secondary forests and continuous primary forests.
- ii. Are there differences in arthropod taxonomic composition between forest fragments, secondary and primary continuous forests? Taxonomic composition is more sensitive than richness and abundance to detected differences in arthropod assemblages between secondary and primary forests (Barlow et al., 2007). Primary and secondary forests are quite distinct in vegetation structure and floristic composition (Almeida et al., 2019; Chazdon, 2014; Longworth et al., 2014). The taxonomic composition of arthropod assemblages is affected by floristics, and vegetation structure (Randlkofer et al., 2010; Salman & Blaustein, 2018; Schaffers et al., 2008). Since plant species composition and vegetation structure are quite distinct between secondary and primary forests in the study region (Almeida et al., 2019; Laurance, 2001; Longworth et al., 2014), we expected that the arthropod taxonomic composition will also distinct between those habitats. In contrast, influences of forest fragmentation on arthropod taxonomic composition are variable and more pronounced in small 1-ha fragments (Didham, 1997; Didham et al., 1998; Laurance et al., 2018). Nuclear areas of larger fragments (10 and 100 ha) in the study region tend to remain similar to primary forests in tree species composition and structure (Laurance et al., 2006). Given that we sampled 10-ha

forest fragments, we do not expect to find marked differences in arthropod taxonomic composition between forest fragments and continuous primary forests.

MATERIALS AND METHODS

Study site

The BDFFP field camps are located 80 km north of Manaus city, in the Central Amazon (2°25'S; 59°50'W; Figure 1). The BDFFP's study sites are one of the few places in the world where forest fragments have been experimentally isolated from continuous forests in such a manner to maintain standard sizes and shapes (Haddad et al., 2015). In the early 1980s, the fragments were isolated from the nearby intact forest by clearing and burning the surrounding forests (Laurance et al., 2018). The BDFFP's experimental design includes 11 forest fragments (five of 1 ha, four of 10 ha and two of 100 ha) and several study sites in the continuous primary forest used as experimental controls (Laurance et al., 2018).

The regional climate is tropical humid, with an average temperature of 26°C and annual rainfall of 1900–2300 mm, characterized by a rainy season extending from December to May and a dry season from June to November (Vasconcelos & Bruna, 2012). The landscape in the study region is dominated by large tracts of continuous primary forests, along with active and abandoned pastures, secondary forests and square-shaped forest fragments (Figure 1).

The disturbed vegetation around the fragments has been in secondary succession during the last 40 years (Mesquita et al., 2015). Secondary forests are occupied by disturbance-tolerant plants whose species composition depends on the previous management of the felled vegetation (Mesquita et al., 2001). Secondary forests growing in heavily burned sites used for pasture implementation are dominated by *Vismia* plants (Mesquita et al., 2001). In contrast, secondary forests are dominated by *Cecropia* trees in abandoned sites where the primary forests have only been cleared, with no use of fire to burn the vegetation (Mesquita et al., 2001). Moreover, secondary forest sites had more open understory and a lower tree canopy height than primary forests and forest fragments (Almeida et al., 2019; Mokross et al., 2018).

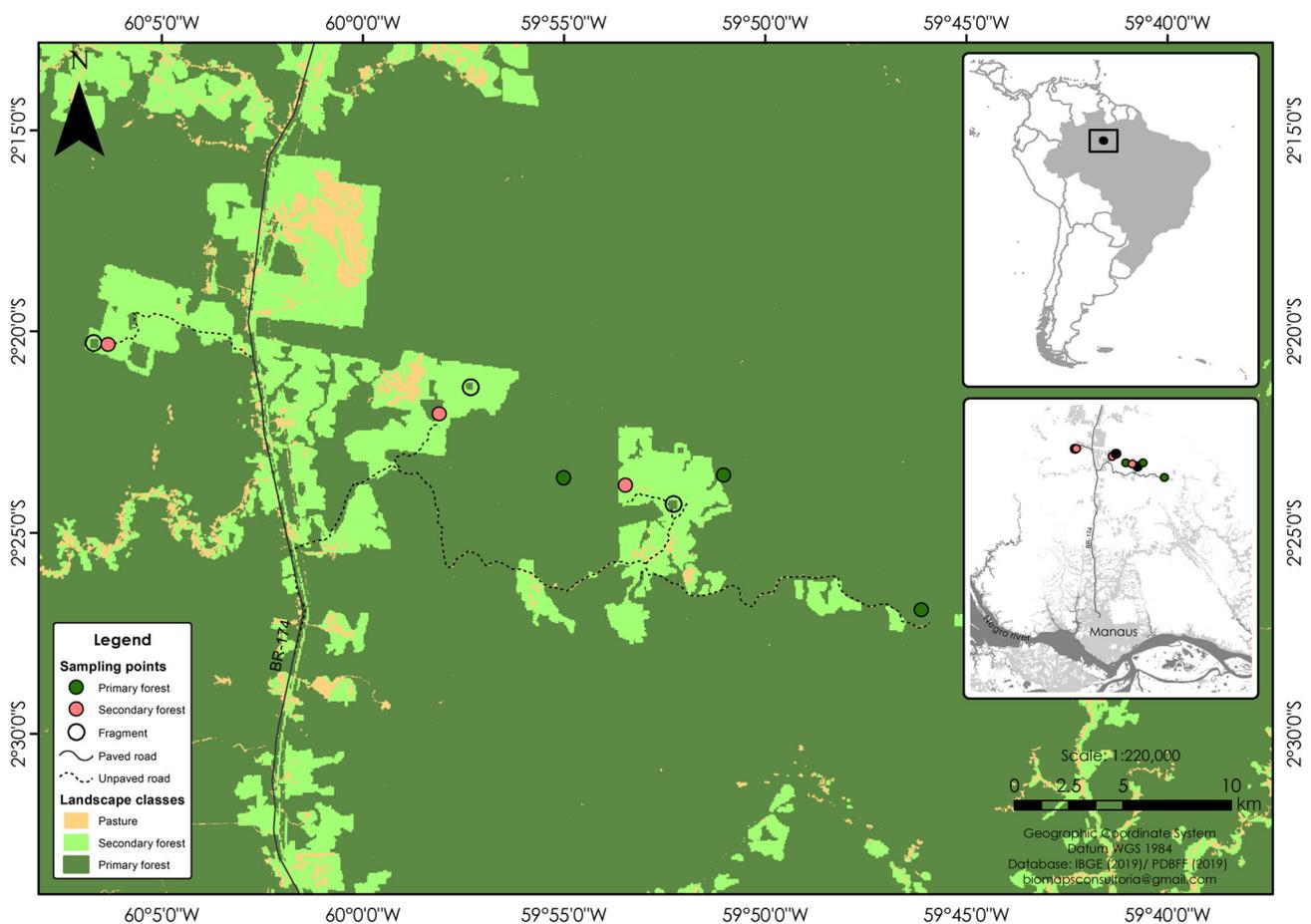


FIGURE 1 Biological Dynamics of Forest Fragments Project study region. Symbols show the location of continuous primary forests (dark-green circles), 10-ha forest fragments (black open circles) and secondary forests (pink circles). In this scale, the small 1-ha forest fragments could not be observed. The polygon has an approximate area of 256,000 ha, covered by low-disturbed forests (dark green, 90% of the area), secondary forests (light green, 8%) and pastures (salmon colour, 2%). Land-use classes were defined from a supervised classification of a Landsat 8 OLI/TIRS image obtained from 30 July 2017

The secondary vegetation growing around the forest fragments was regularly cleared (and sometimes burned), temporarily isolating the fragments through a 100-m band of cleared vegetation, with the most recent re-isolation happening in 2013–2014 (Laurance et al., 2011; Rocha et al., 2017; Vasconcelos & Bruna, 2012).

Arthropod sampling and study design

Arthropods were sampled in forest fragments, primary continuous forests and secondary forests with three sampling sites in each habitat (Figure 1). We concentrated our sampling efforts in mid-size forest fragments (10 ha) and did not collect arthropods in 1- and 100-ha fragments.

We used Malaise traps (1.60 m height \times 1.50 m long) to capture arthropods (Townes, 1972). Malaise traps are relatively easy to use, produce standard sampling units while capturing a great variety and abundance of arthropods (Missa et al., 2009; Yi et al., 2012). Each sampling site consisted of four Malaise traps separated by 20 m and distributed at the cardinal compass points. Sampling sites were set in the proximity of the base camps to permit the daily traps monitoring. The traps were positioned at least 1 km distant from the edges of secondary and primary forests and placed in the centre of the 10-ha forest fragments to minimize the chances of collecting arthropods from the secondary forests along the fragment edges.

Sampling sites were visited on two different occasions with a minimum interval of 30 days between them. Each sampling occasion consisted of 84 h of continuous arthropod trapping in each site. Fieldwork took place from July to December 2018, covering the entire dry season. Arthropods were preserved in bottles containing 90% alcohol properly labelled and taken to the Animal Biology Laboratory of the Federal University of Amazonas (UFAM) for sorting and identification.

Identifying thousands of individuals and taxa represents a significant challenge for arthropod assemblage investigation. Researchers suggest order (Biaggini et al., 2007), family (Høye et al., 2021; Lamarre et al., 2016; Timms et al., 2013) or genus (Souza et al., 2016) as the most cost-efficient identification levels. We adopted a multiple resolution strategy to identify arthropods. Initially, the arthropods were identified to order (all individuals) and family (only Diptera—58% of collected individuals). In this phase, we used the identification keys of Rafael et al. (2012) and consultation with entomologists from the National Institute for Amazonian Research (INPA). Posteriorly, we selected the Tabanidae flies (Diptera) for identification at genus and species levels due to their high abundance in the samples and because one of the authors (Augusto Loureiro Henriques) is a taxonomist specialist in this group of flies.

Data analysis

For the analysis, we combined the contents of the four Malaise traps at each study site and used each sampling occasion (two occasions) and site as sampling units. One pooled sample of the first sampling

occasion from a secondary forest site and another from a primary forest site had to be discarded due to problems of label identification in the bottles. Thus, analyses were performed with 16 sampling units sampled with equal trapping/hour effort: five in secondary forests, five in primary forests and six in forest fragments. Sampling occasion is not independent within site; therefore, we used linear mixed models (LMMs) to take into account the dependence in the data.

The number of individuals collected in the sampling units was used as an indicator of arthropod abundance. The abundance of arthropod taxonomic groups (species to order) was the response variable, the habitat was the fixed predictor variable and the temporal replicates within sites were selected as a random variable in LMM models. We restricted these analyses to the most abundant taxonomic groups: order (>200 individuals), family (>100 individuals), genus (>36 individuals) and species (>10 individuals). We checked if the model's assumptions were met by visual inspection of the residuals.

In complement to LMM tests, we applied an indicator species analysis to identify arthropod taxa associated with a particular habitat (primary forests, secondary forests or forest fragments). The indicator values (Indval) were calculated using the taxa's relative abundance and frequency in each habitat. The Indval varies from 0 to 1 and the statistical inferences are based on 999 permutation tests (Dufrene & Legendre, 1997).

Differences in alpha diversity between habitats were accessed through Fisher's alpha index, calculated at the four taxonomic resolutions. This index was chosen because it is less biased by differences in sample size (Rosenzweig, 1996). We then used the same analytical framework (LMM) to test for differences in alpha diversity between habitats.

The indicator analysis and LMM tests were run in R (R Core Team, 2021), using the packages “indicspecies” (De Cáceres et al., 2010) and afex (Singmann et al., 2021), respectively.

The compositional analyses were based on nonmetric multidimensional scaling ordinations using the Bray–Curtis index as a measure of dissimilarity between samples. The data were standardized by the total number of individuals from each sampling unit, and square root transformed to balance the contributions of abundant and rare taxa (Clarke & Warwick, 2001). Matrices were analysed through analysis of similarity (ANOSIM) to test hypotheses of differences in taxonomic composition between the three habitat types. Ordinations and ANOSIM analysis we carried out in Primer software (Clarke & Warwick, 2001).

RESULTS

Arthropod assemblages: Orders and families

We collected 25,230 arthropods distributed in 17 orders and 30 families of Diptera (Appendix S1). There were few differences in the number of orders and the total number of individuals collected between habitats: 10-ha forest fragments (15 orders and 8768 individuals),

primary continuous forests (15 orders and 8415 individuals) and secondary forests (17 orders and 8047 individuals).

The most abundant arthropod groups were Diptera (58% of individuals), followed by Hymenoptera (21%), Collembola (8%), Lepidoptera (5%), Hemiptera (3%), Coleoptera (3%) and Trichoptera (3%). The overall abundance of major arthropod groups did not differ between habitat types ($F = 0.188$, $p = 0.831$, NumDF = 2, DenDF = 13; Figure 2). However, indicator species analysis showed that Coleoptera (Indval = 0.42, $p = 0.004$) and Hemiptera (Indval = 0.41, $p = 0.005$) had higher relative abundances and frequencies in secondary forests compared to other habitats (Figure 2).

The number of families and the total abundance of Diptera were both similar between continuous forests (27 families and 5028 individuals) and forest fragments (26 families and 5027 individuals), but abundance was considerably lower in secondary forests (27 families and 3739 individuals). Except for the family Clusiidae, identified as an indicator of forest fragments (Indval = 0.78, $p = 0.009$), no other fly family showed differences in relative frequency or abundance between habitats.

Fisher's alpha diversity was not different between the habitats for orders (LMM, $F = 0.346$, $p = 0.714$, NumDF = 2, DenDF = 13) and families (LMM, $F = 1.045$, $p = 0.384$, NumDF = 2, DenDF = 13), indicating similar levels of local diversity in these taxonomic resolutions

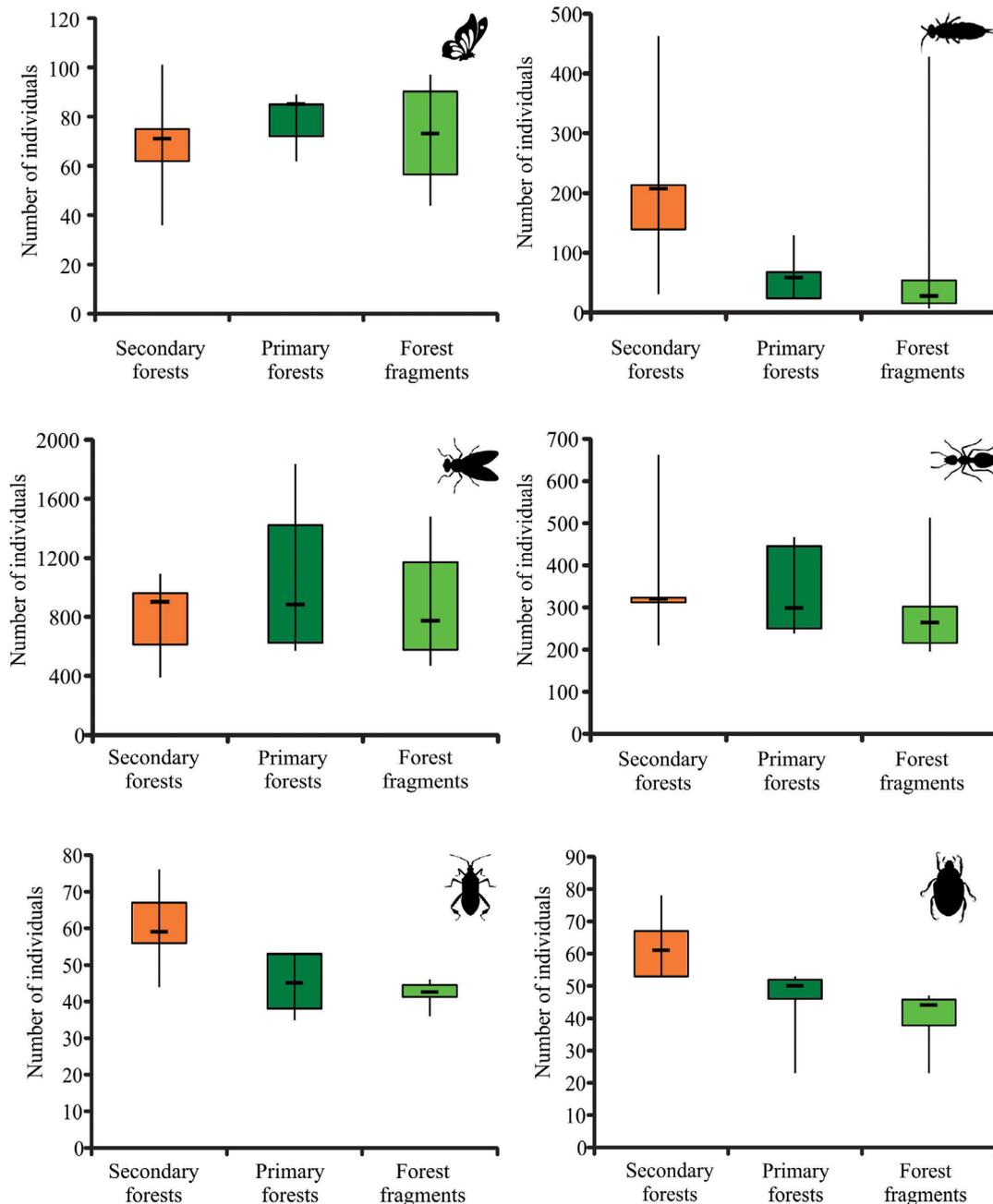


FIGURE 2 Abundance variations of major arthropod groups between studied habitats. (a) Lepidoptera; (b) Collembola; (c) Diptera; (d) Hymenoptera; (e) Hemiptera; (f) Coleoptera. Dashes represent the median, vertical lines represent the minimum and maximum values and boxes represent the 25% and 75% quartiles

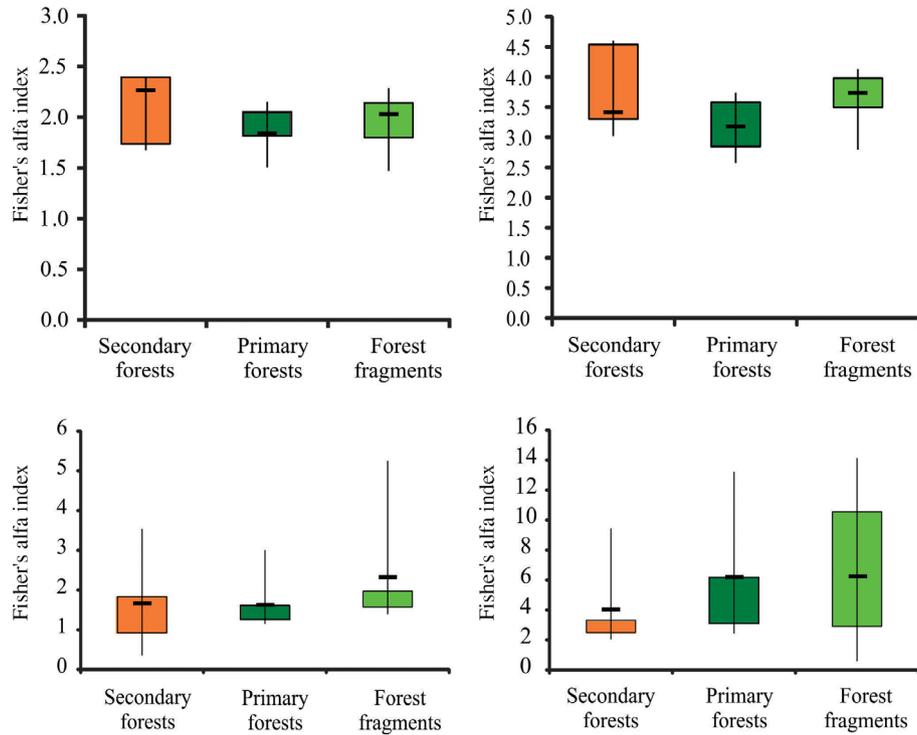


FIGURE 3 Variation in alpha diversity (Fisher's alpha) between studied habitats in the taxonomic resolutions of (a) order, (b) family (Diptera), (c) genus (Tabanidae) and (d) species (Tabanidae). Dashes represent the median, vertical lines represent the minimum and maximum values and boxes delimit the 25% and 75% quartiles

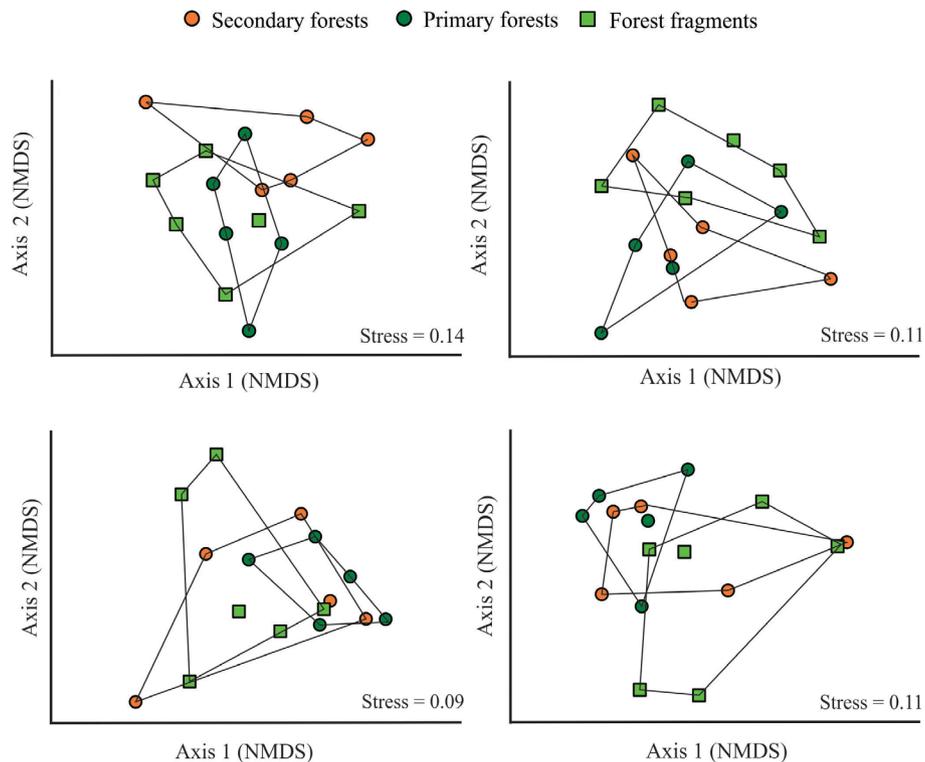


FIGURE 4 Ordination of sampling units in the multidimensional space using the taxonomic resolutions of (a) order, (b) family (Diptera), (c) genus (Tabanidae) and (d) species (Tabanidae). All collected individuals were included in this analysis. NMDS, nonmetric multidimensional scaling

(Figure 3). Also, taxonomic composition at the levels of order and family were not different between habitats (global $R = 0.04$, $p = 0.32$ for order and global $R = 0.08$, $p = 0.18$ for family) with ordination plots showing extensive overlaps in taxonomic composition between sites and habitats (Figure 4).

Arthropod assemblages: Genera and species

The average number of horse fly species (Tabanidae) was similar between forest fragments ($n = 21$ species) and secondary forests ($n = 23$ species), but was slightly higher in continuous forests ($n = 26$ species). Horse fly assemblages are characterized by the high dominance of a few species. Indeed, only three species (*Stypommisa glauddicolor*, *Tabanus trivittatus* and *Pityocera cervus*) were responsible for 84% of all collected individuals.

The total number of horse fly individuals was quite different between habitats: continuous forests (849 individuals), secondary forests (467 individuals) and forest fragments (219 individuals). However, no significant differences were detected in the average abundances between habitats (LMM, $F = 1.321$, $p = 0.306$, NumDF = 2, DenDF = 13), which can be explained by the large variations in individual species abundance within each sampling unit (Appendix S1).

Individuals from *Dichelacera* genus were more abundant and frequent in continuous forests (Indval = 0.78, $p = 0.006$), with no species from this genus collected in the forest fragments. Consequently, the species *Dichelacera cervicornis* was identified as an indicator species of continuous forests (Indval = 0.78, $p = 0.009$) being rarely detected in secondary forests ($n = 8$ individuals) and absent in forest fragment samples.

No differences were detected in Fisher's alpha diversity between the studied habitats in the resolutions of genus (LMM, $F = 0.647$, $p = 0.647$, NumDF = 2, DenDF = 13) and species (LMM, $F = 0.399$, $p = 0.681$, NumDF = 2, DenDF = 13) (Figure 3). Similarly, taxonomic compositions of horse flies were not different between habitats in the resolutions of genus (global $R = 0.01$, $p = 0.38$) and species (global $R = 0.09$, $p = 0.16$) with little distinction in the taxonomic composition between sites and habitats (Figure 4).

DISCUSSION

In this study, we collected diversified arthropod samples composed of many taxonomic and functional groups (Lamarre et al., 2016). We expected to find differences in the abundance, diversity and taxonomic composition of arthropods between major studied habitats as documented from the study region (Didham, 1997; Vasconcelos & Bruna, 2012) and other parts of the Amazon (Barlow et al., 2007; Cajariba & Silva, 2017). For instance, we expected to find lower taxonomic diversity in forest fragments compared to continuous forests as previewed by the species-area relationships (Rosenzweig, 1996), and that secondary and primary forests harboured distinctive arthropod

composition as found in Eastern Amazon (Barlow et al., 2007). However, we documented only minor differences in taxonomic and compositional diversities between forest fragments, primary and second forests suggesting that these habitats support similar arthropod assemblages.

In the study region, reductions in arthropod species richness and abundance were more evident in 1-ha fragments and pastures (Klein, 1989; Leidner et al., 2010; Morato & Campos, 2000); two habitats not sampled in this study. Our choice to sample only 10-ha fragments may have masked the effects of more drastic fragment area reduction and vegetation structure simplification on arthropod assemblages.

The regional land-use history and previous studies are relevant to put our results into perspective. Forest fragments in the BDFFP were isolated from continuous forests from 1980 to 1984, when the cleared vegetation was burned for pasture implementation in three major cattle ranches (Laurance et al., 2018; Vasconcelos & Bruna, 2012). Afterwards, there were no intensive interventions on the vegetation, such as regular large-scale burning or deforestation of secondary or primary forests. Therefore, the secondary vegetation in the study region has been in regeneration for nearly 40 years. Our results suggest that forest regeneration over this relatively long time period promotes increased flows of arthropods between habitats as documented in a variety of taxa, including Euglossini bees (Becker et al., 1991), butterflies (Brown Jr. & Hutchings, 1997), beetles (Quintero & Roslin, 2005), birds (Mokross et al., 2018; Stouffer et al., 2011) and bats (Rocha et al., 2018).

The influence of forest regeneration in arthropod assemblages is well illustrated from previous studies in Scarabaeinae beetles and Euglossini bees. Species richness and abundance of Scarabaeinae beetles decreased in a gradient from continuous forests, forest fragments of 10 and 1 ha soon after the fragments had been isolated (Klein, 1989), with these differences practically disappeared after 14 years (Quintero & Roslin, 2005). Similarly, the positive correlation in the abundance of Euglossini bees with fragment size reported in 1983 was no longer detected after 5–6 years (Becker et al., 1991; Powell & Powell, 1987).

The recovery of Scarabaeinae beetles and Euglossini bee's assemblages is related to secondary forest growth favouring the connection between forest fragments and continuous forests (Becker et al., 1991; Quintero & Halffter, 2009). Our study suggests that secondary forests also represent favourable habitats for several other lineages of arthropods. Apparently, the studied habitats seem to offer enough and adequate resources and microhabitats, allowing several arthropods lineages to retain similar diversity levels between these habitats.

We emphasize, however, that pattern of subtle differences in arthropod assemblages between habitats found in our study may not be replicated in regions of the Amazon that suffer severe and continuous disturbances. Secondary forests in regions heavily degraded by recurrent deforestation and burning (Carvalho et al., 2019; Nunes et al., 2020) may not perform well as biological corridors between forest fragments and less disturbed forests, an aspect that deserves further investigation.

Arthropod's groups responses to habitat disturbances

We expected that coarse taxonomic resolutions (orders and families) would perform poorly compared to more finely resolutions (genus and species) in revealing differences in diversity metrics between habitats. However, minor differences between sampled habitats were observed in all taxonomic resolutions. Indeed, only two orders (out of 17), one family (out of 30) and one species (out of 31) showed significant differences in abundance between habitats.

We emphasize, however, that arthropod response to habitat disturbance could be largely taxa-dependent (e.g., Alonso-Rodríguez et al., 2017; Barlow et al., 2007), and the patterns not evident in a coarser taxonomic resolution could be detected only in a more refined taxonomic and ecological assessment of the sampled taxa (Rosser, 2017). However, our approach is practical because it permits sorting all specimens collected in a reasonable time period, and helps to identify taxa candidates for further in-depth studies.

Greater abundance of beetles (Coleoptera) and true bugs (Hemiptera) were recorded in secondary forests than in forest fragments and continuous forests. It is possible that specific resources (e.g., decaying wood, soft tissue plants) used by these insects are more abundant in secondary vegetation than in forest fragments and continuous forests. Indeed, secondary forests showed marked differences in biomass and floristic composition compared to primary forests in the study region (Laurance, 2001; Longworth et al., 2014; Roeder et al., 2010). Further detailed taxonomic and ecological assessment of Coleoptera and Hemiptera is necessary to understand the abundance differences between habitats reported here.

Most flies lineages appear to be successfully colonizing disturbed environments, given that out of 30 families of Diptera, only one (Clusiidae) showed significant association to a particular habitat. Clusiidae was identified as indicator taxa of forest fragments, with 80% of the individuals (13/16) collected in this habitat. Flies of this family are found in various open or wooded habitats (Garcez, 2009; Lonsdale & Marshall, 2012). It is possible that sampled Clusiidae flies were associated with open vegetation and benefited from re-isolation of the fragments and their proximity to pasture areas. During the first years after fragments isolation, typical open-area fruit flies (Drosophilidae) invaded the forest fragments (Martins, 1989), and perhaps a similar situation could be happening with Clusiidae flies.

The higher number of individuals collected in primary continuous forests suggests that horse flies (Tabanidae) prefer less disturbed environments. Two numerically dominant species (*S. glandicolor*, *T. trivittatus*) were abundant in primary forests (Appendix S1; see also Barbosa et al., 2005). The species *D. cervicornis* was identified as an indicator of primary forests (Gorayeb, 1993; Henriques & Rafael, 1999), reinforcing the association between Tabanidae and primary forests (Gorayeb, 1993; Henriques et al., 2007).

Horse fly abundance is strongly affected by seasonality in temperature, humidity and rainfall, with some species more abundant in wet and others in the dry season (Baldacchino et al., 2014; Ferreira-Keppler et al., 2010; Krüger & Krolow, 2015). Also, several species are associated with forest canopy in the Central Amazon (Oliveira

et al., 2007). We underestimated the regional diversity of Tabanidae because our study was conducted on the forest understory during the dry season. Indeed, at least 29 horse fly species not found during our sampling were recorded in the study region (INPA Entomological Collection, unpublished data). Even with incomplete inventory, our data suggest that horse fly assemblages were not distinct between habitats, suggesting that secondary forests and forest fragments can also host a diversified assemblage of these insects.

CONCLUSION

Four decades ago, the landscapes of the BDFFP were permanently altered by large-scale deforestation and burning. However, these severe disturbances have not been recurrent and secondary forests have been regenerating for a long time. Some arthropod taxa had specific responses to habitat disturbance, with some of them being favoured in secondary forests (Coleoptera and Hemiptera), forest fragments (Clusiidae) or primary forests (*D. cervicornis*). Overall, however, we did not detect substantial differences in arthropod assemblages between habitats suggesting that forest regeneration in the studied region favours the dispersal of arthropods between major regional habitats. Thus landscapes composed of large tracts of low-disturbed forests, mid-size forest fragments, and old secondary forests are relevant for maintaining a rich assemblage of tropical arthropods.

Long-term regeneration of secondary forests is fundamental to biodiversity recovery in such disturbed landscapes. Unfortunately, only 16% of secondary forests of the Brazilian Amazon were aged between 20 and 32 years (Smith et al., 2020). Conservation policies that value secondary forests as carbon storage and biodiversity repositories must be more widely adopted. Protection of mid- to large-size forest fragments is also a relevant strategy due to its conservation value to arthropods. Incentives to private landowners to protect the old secondary forests and forest fragments in their properties could help to maintain these forests in continuous regeneration, improving their conservation value.

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CONFLICT OF INTEREST

The authors declare that there is no conflict of interest.

DATA AVAILABILITY STATEMENT

Data available in article supplementary material

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

Appendix S1: Supporting Information.

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