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RESEARCH ARTICLE

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# The role of tropical forest fragment vegetation in maintaining arthropod diversity and spillover to adjacent sugarcane fields

# O papel da vegetação de fragmentos de floresta tropical na manutenção da diversidade de artrópodes e na sua disseminação para campos de cana-de-açúcar adjacentes

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## Abstract

1. The degradation of forests in tropical agricultural landscapes has reduced biodiversity and may negatively affect ecosystem services. However, the role of forest fragments in the provision of ecosystem services for agroecosystems, such as biological control, is still not well understood.
2. This study analyses the relationship between tree diversity and arthropod communities in forest fragments and adjacent sugarcane fields around Jaboticabal (São Paulo, Brazil) to evaluate the benefits of preserving Atlantic Forest fragments.
3. We tested the hypotheses: (1) arthropod diversity and the abundance of key functional groups in forest fragments are favoured by tree diversity, (2) diversity and abundance of these functional groups in sugarcane fields depend on adjacent forests and (3) the insect community composition of forest fragments and sugarcane fields is similar due to spillover effects.
4. Arthropods were sampled in 10 forest fragments over 2 years (2020 and 2022) using traps (Malaise, yellow pan) and direct tree sampling. We identified arthropods to morphospecies (2020) and family level (2022) and associated families to functional groups.
5. We found that the quality of forest fragments, particularly tree species richness, was positively related to forest arthropod richness and frequency (occupied samples) of functional groups involved in ecosystem services such as predators, but also of phytophagous insects. There was also a strong positive correlation between insect family richness and functional groups of forest fragments and adjacent sugarcane fields, indicating potential spillover and spatial connectivity between habitats. Although insect community composition was significantly different between forest

fragments and sugarcane fields, NMDS ordination revealed partial overlap of family communities, suggesting many shared taxa in both habitats.

6. This study highlights the importance of diverse forest fragments in preserving insect biodiversity and related ecosystem services in tropical agricultural landscapes and advocates for the conservation and restoration of these habitats. However, the benefits in terms of crop damage reduction and yields remain to be confirmed.

**KEYWORDS**
agroecology, biocontrol, biodiversity, ecosystem services, insects, natural enemies, woodlands

## INTRODUCTION

Human land use has caused the loss and fragmentation of natural and semi-natural habitats, affecting the stability of ecosystems (Jacobson et al., 2019; Newbold et al., 2015). Fragmentation is the division of such habitats into more or less distant native remnants, characterised by the emergence of ecological discontinuities within the ecosystem (Fahrig, 2003). Fragmentation is often the result of partial transformation to arable land (Heisswolf et al., 2009; Wilson et al., 2016). The replacement of semi-natural habitats by simplified agricultural systems negatively affects ecosystems, including the loss of biodiversity and related services (Asbjornsen et al., 2014; Wilson et al., 2016). To maintain or improve ecosystem services in agricultural landscapes, it is necessary to conserve and/or restore biodiversity (Garbach et al., 2014). However, efficient conservation and restoration require the understanding of interactions and mechanisms driving biodiversity and abundance of taxonomic or functional groups providing such services (Gutierrez-Arellano & Mulligan, 2018).

Arthropods, in particular insects, are key organisms providing many ecosystem services such as pollination, biological control of pests and organic matter decomposition (Millennium Ecosystem Assessment, 2005; Ramos et al., 2020). However, arthropod populations and the services they provide can be negatively affected by habitat degradation (Gagic et al., 2018; Schowalter et al., 2018). Several studies have documented the decline in abundance, species diversity and quality of ecosystem services in disturbed environments, in particular the decline in pollinator and seed-dispersing ant abundance (Leal et al., 2014; Mata & Tidon, 2013; Winfree et al., 2009). This decline is related to the degradation of plant communities, such as species loss and spread of exotic plants, that directly affect insect populations (Diniz et al., 2010). Conversely, increased plant diversity increases the availability and variety of resources, which in turn promotes greater insect abundance, diversity and the provision of ecosystem services (Brockerhoff et al., 2017). Therefore, ecosystem services provided by arthropods are increasingly considered in land management decisions including practices that protect biodiversity (Losey & Vaughan, 2006).

Maintaining or enhancing ecosystem services in agricultural landscapes may be facilitated by preserving non-crop areas, particularly semi-natural vegetation zones near crop fields sustaining beneficial insect populations (Gagic et al., 2018; Parry et al., 2015; Pywell et al., 2015). This facilitation can be explained by movements of insects between habitats (habitat spillover), and among them several groups represent important ecological functions and services (Blitzer et al., 2012; Rand et al., 2006). Forest fragments are examples of natural or semi-natural habitats that influence the provision of multiple ecosystem services in adjacent fields (Decocq et al., 2016; Mitchell et al., 2014). Several studies have shown that arthropods involved in biological control of tropical crops are favoured by adjacent natural forests (Klein et al., 2006; Santos et al., 2018; Sousa et al., 2011) but they did not take into account habitat quality. Areas with high plant species diversity are key drivers of insect diversity and abundance (Rowe & Holland, 2013; Zhang et al., 2016), contributing to the overall ecological quality of the habitat. The biodiversity and ecosystem services provided by forest fragments depend on their ecological quality, including resource availability, vegetation structure and connectivity (Haddad et al., 2015; Hertzog et al., 2019). A more comprehensive understanding of the specific habitat and vegetation characteristics that promote insect biodiversity and the abundance of beneficial arthropods is crucial to preserve or improve related ecosystem services (Bartual et al., 2019).

The Brazilian Atlantic Forest, in particular the semi-deciduous forest vegetation of Southeastern Brazil, has been largely fragmented, and agriculture is one of the main drivers of fragmentation and loss of forest area (Rezende et al., 2018). Forests were mostly replaced by sugarcane fields, resulting in a sugarcane-dominated agricultural landscape with a low proportion of remnant forest fragments (Haddad et al., 2015; Ribeiro et al., 2009). Recent estimates indicate that only 28% of the original Atlantic Forest cover remains, of which an unknown part is highly disturbed by previous cutting or burning (Rezende et al., 2018). The size of these fragments is usually small (<50 ha), and they are often isolated. We consider them as natural habitats since, contrary to European forests (Decocq et al., 2016), they are not managed. Despite disturbance and fragmentation, these forest fragments may still represent an important reservoir of beneficial arthropods and potentially contribute to the provision of ecosystem services in adjacent crop fields through spillover effects (Castro & Moraes, 2010). A deeper knowledge of interactions between forest quality and arthropod communities in forests and the spillover to adjacent agroecosystems is needed to support beneficial arthropod populations and their associated ecosystem services. Thus, this study aims at improving the knowledge of the arthropod communities in fragments of the Atlantic Forest and their influence on communities of adjacent sugarcane fields. We further relate arthropod occurrence

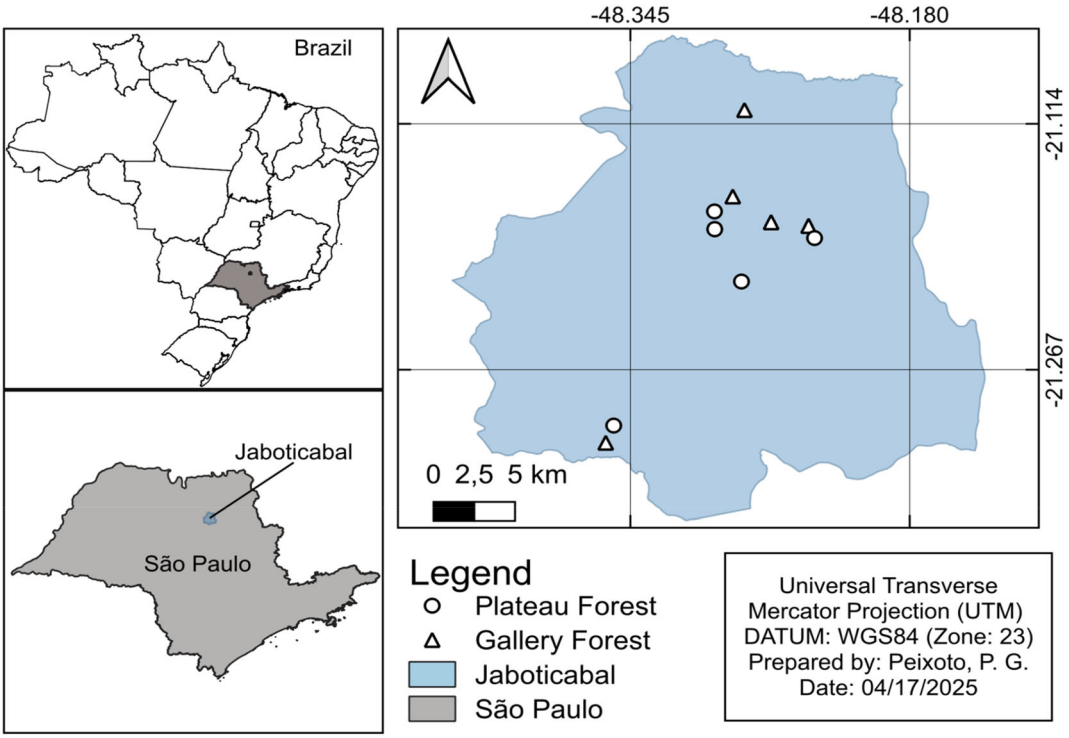


**FIGURE 1** Study area and geographical position of the 10 studied forest fragments.

and community composition to characteristics of forest fragment vegetation. We tested the following hypotheses: (1) insect diversity and the abundance of key functional groups are favoured by tree diversity; (2) richness and/or abundance of insect functional groups in sugarcane fields depend on richness and/or abundance of the same functional groups in adjacent forests and (3) the insect family composition of forest fragments and sugarcane fields is similar due to spillover effects.

## MATERIALS AND METHODS

### Study sites and design

The study was conducted in fragments of the Atlantic rain forest (Mata Atlantica) and adjacent sugarcane fields in the municipality of Jaboticabal, São Paulo state, Brazil (21°15′19″ S, 48°19′21″ W). The study area is characterised by a dominance of sugarcane fields with a small percentage of remnant gallery and plateau forests. The climate is mesothermic with dry winters and a rainy summer season, an annual rainfall of 1300 mm and a mean temperature of 22°C. The western, more continental parts of the Atlantic rain forest are semi-deciduous and represent a transition zone to the drier savanna systems (Brazilian Cerrado). Atlantic rain forest was the prevailing vegetation of the study area before European colonisation.

Arthropods were sampled in April 2020 and August 2022, using direct and indirect (trapping) collection methods. The 2020 samples served as a preliminary baseline to support and refine our 2022 sampling design. In 2020, 10 forest fragments (Figure 1) were selected according to the following selection criteria: >50 m width and length, no commercial tree plantation in the fragments, and a minimum distance of 1 km from each other. Five fragments were situated on shallow slopes (plateau fragments), and five were gallery forest remnants close to rivers and creeks (river valley or gallery fragments). Plateau fragments typically exhibited a greater cover of shrub and liana species compared to river valley fragments because disturbance by fire or cutting was more frequent. River valley fragments are protected as Permanent Preservation Areas (PPAs), in particular to preserve the water quality of tap water catchment areas (Santos et al., 2018). Three fragments had to be replaced in 2022 due to access problems and wildfires. In each forest fragment, we collected data in a randomly selected 50 × 20 m plot, 5 m from the edge.

Arthropods were also sampled in sugarcane fields adjacent to forest fragments (5 m from the field edge). Sugarcane is usually harvested during the dry season between May and September and resprouts from rhizomes afterwards. Regrowth is slow until the beginning of the rainy season in November. Herbicide treatments are common, but no insecticides were applied during the study period.

### Tree species and habitat quality index

At the end of the rainy season in 2020, we set up a preliminary study focusing on arthropod biodiversity of forest fragments. We defined woody plants of more than 5 cm diameter at breast height as trees and identified them to species level. Sampling was limited to 20 trees

associated with five subplots of 1 $m^2$ in each plot (closest tree to each corner). We used a simple habitat quality index to characterise forest fragments suggested by Felfili et al. (2011). The index uses tree cover as a positive criterion and climber and grasses cover as negative criteria. Forest disturbance by tree cutting or fire increases the cover of climbers (lianas, vines) and grasses relative to tree cover. The cover was estimated as the vertical projection of aboveground plant organs using a modified Londo scale (Londo, 1976) reaching from 0 (bare ground) to 1 (full cover) with 0.1 intervals. The quality index was calculated as the sum of the three parameters, with liana and grass cover fitted as negative and tree cover as positive values. In August 2022, a more detailed method was used to obtain more information on plant and arthropod community characteristics. Instead of selecting 20 trees, all trees of the 1000 $m^2$ plots were identified and insects were sampled from all trees in the dry season.

## Arthropod sampling

On each tree, we carefully cut a randomly selected branch at 2–5 m height with long-reach pruning shears and manually captured all arthropods. If insects flew away or fell to the ground during cutting, another branch was collected to reduce losses by escape. Sampled arthropods were transferred to 70% diluted alcohol prior to identification. In 2020, insects and spiders were identified to morphospecies level. In 2022, we identified sampled insects individually to family level in order to obtain more information on taxonomic and functional groups (Báldi, 2003) but we did not include spiders. We assigned all insects sampled in 2022 to the following functional groups using knowledge on life-history feeding features of the majority of species in each family: parasitoids, predators, omnivores and phytophagous arthropods (Brown et al., 2009; Brown et al., 2010; Fernandez & Sharkey, 2006). Families that could not be clearly assigned to a functional group were considered omnivorous and finally removed from analyses of functional groups. For insects that change feeding between larval and adult stages, we used the larval feeding behaviour, as larvae generally have higher resource demands and are the primary consumers in the life cycle (Kaleka et al., 2019). In August 2022, we additionally used trapping to sample flying insects. A Malaise-type trap was positioned in each forest fragment plot. The catching recipient of the traps was filled with 400 mL of 70% alcohol solution, and the insects were collected after 48 h. In sugarcane fields, we placed two yellow pan traps (42 × 28 × 8 cm) 15 m apart and 5 m from the field edge. Each pan trap was filled with 2 L of water and 10 drops of detergent before exposure for a duration of 48 h. Likewise, the insects were preserved in 70% alcohol, identified at family level and classified into functional groups.

## Data analysis

We ran generalised linear mixed models (GLMM) to analyse the effects of habitat quality (2020 habitat quality index, 2022 tree richness) on arthropod richness (2020 morphospecies, 2022 insect family), family frequency and functional group frequency. Frequency was calculated as the number of occupied branches per fragment (only 2022). We fitted fragment type (plateau or gallery) as a random effect to account for variation among different fragments, resulting in the following model structure: diversity measure ~ habitat quality + (1|fragment type). Poisson distribution with log-link was used when data were not overdispersed, and negative binomial error distribution in the case of overdispersion. We also tested the relationship between the 2020 habitat quality index and 2022 tree species richness using a linear mixed-effects model (LMM) with Gaussian errors and fragment type as a random effect. We further calculated the marginal and conditional $R^2$ using the *r*-squared GLMM function of the MuMIn package to analyse model fit.

Similar models were run to analyse the influence of insect family richness (total and within functional groups) in forest fragments on the same variables in adjacent sugarcane fields following the model structure: sugarcane family richness ~ forest family richness + (1|fragment type). Additionally, insect family composition of forest fragments and sugarcane fields was compared using non-metric multidimensional scaling (NMDS) based on Jaccard dissimilarity in presence-absence data. The NMDS was run using the metaMDS function from the *vegan* package with a maximum of 100 random starts (trymax = 100) to avoid local minima. The NMDS ordination was visualised with convex hulls representing each habitat–forest type combination, and point colours and shapes were used to differentiate forest types and habitat types. We tested differences between the sugarcane and forest fragment habitat using permutational multivariate analysis of variance (PERMANOVA). Statistical tests were run using the *adonis2* functions of the vegan package with 999 permutations and Jaccard distance as the dissimilarity metric. All analyses were performed using R 3.6.2 software (R Core Team, 2024).

# RESULTS

In the 10 forest fragments of our study, we found 115 tree species of 35 plant families. *Croton floribundus* (Euphorbiaceae), *Astronium graveolens* (Anacardiaceae) and *Acacia polyphylla* (Fabaceae) were the most frequent tree species (Table S1). Tree density was on average 79.1 (29–125) per 1000 $m^2$ plot (only measured in 2022).

In 2020, we collected 200 arthropod morphospecies including 148 insect morphospecies (Table S2). In 2022, we found 33 insect families in direct collections, of which six families were predatory, seven were parasitoids and fifteen were phytophagous (Table S3). Trapping in 2022 provided 121 insect families, of which 20 families were predators, 26 were parasitoids and 40 were phytophagous. Seventy families occurred in both habitats, 36 only in forest fragments and 15 only in sugarcane fields (Table S4).

The influence of forest fragment quality measured as habitat quality index was significant for overall arthropod morphospecies richness (estimate = 0.384, $\chi^2(1) = 13.659$, $p < 0.001$, marginal/conditional $R^2 = 0.59$; Figure 2a), but not for insect morphospecies

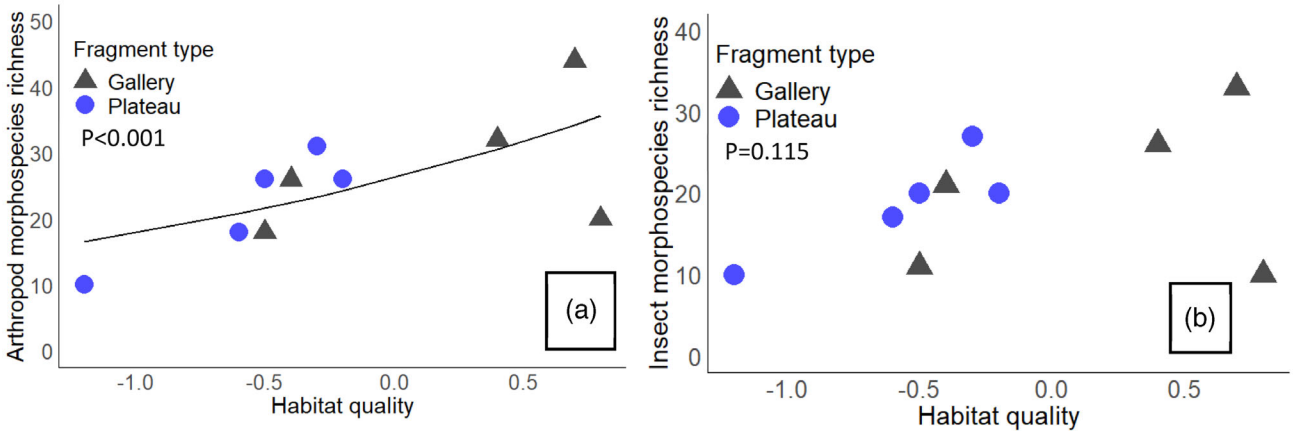


**FIGURE 2** Relationship between habitat quality index and 2020 invertebrate morphospecies richness in gallery and plateau forest fragments. (a) Total arthropod morphospecies richness, (b) Insect morphospecies richness. Lines show predictions from linear mixed-effects models (LMM) with habitat quality as a fixed effect and fragment type as a random effect.

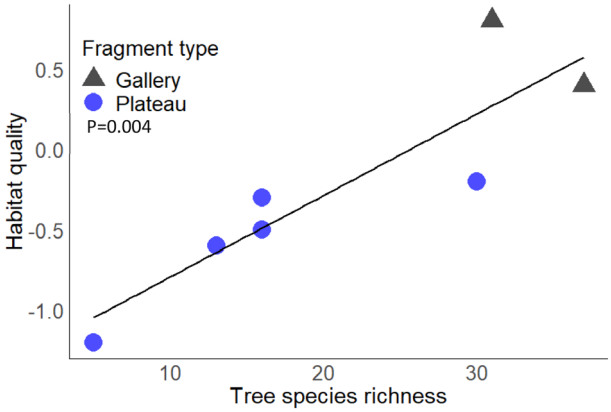


**FIGURE 3** Relationship between habitat quality index estimated in 2020 and tree species richness in 2022. Regression lines are drawn according to GLMM, including habitat quality as fixed and fragment type as random effect.

richness (estimate = 0.267, $\chi^2(1) = 2.490$, $p = 0.115$, marginal/conditional $R^2 = 0.23$; Figure 2b) in 2020.

The habitat quality index of 2020 was positively correlated with tree species richness of 2022 in seven fragments analysed in both years (estimate = 0.040, $\chi^2(1) = 8.2824$, $p = 0.004$, marginal $R^2 = 0.53$, conditional $R^2 = 0.79$) indicating that the index was a reliable estimate of tree diversity (Figure 3).

The family richness of insects (Figure 4a), as well as the frequency of phytophagous (Figure 4b) and predatory insects (Figure 4c) were positively related to tree species richness whereas the relationship with parasitoids (Figure 4d) was not significant (Table 1).

Relationships between family richness of insects in forest fragments and family richness in sugarcane fields were significantly positive for total richness, phytophagous family, and predator family richness, indicating that insect diversity of sugarcane fields depends on adjacent forest fragments (Table 2; Figure 5). The relationship between family richness of parasitoids in forest fragments and that in sugarcane fields was also positive but only marginally significant (Table 2).

NMDS separated sugarcane insect communities from those of forest fragments (Figure 6). Despite different trap types, there was, however, an overlap between both habitats. Habitat and forest fragment type explained 8.55% and 6.67% of the total variation, respectively. PERMANOVA still revealed a significant difference between sugarcane fields and forest fragments ($F = 1.6837$, $p = 0.011$).

## DISCUSSION

We found a positive influence of forest habitat quality (tree species richness and forest quality index) on arthropod richness and the frequency of functional groups involved in ecosystem services such as predators but also of phytophagous insects that may attack crop plants. While the preliminary data of 2020 showed significant relationships with habitat quality index only when spiders were included, the more detailed analyses of 2022 revealed significant relations for insect family richness and the frequency of several functional insect groups. We further demonstrated that the richness of insect families and functional groups in sugarcane fields were highly correlated to those of adjacent forest fragments, suggesting a causal relationship and insect movements between the two habitats. However, although NMDS showed some overlap of insect family composition in forest fragments and sugarcane fields, the differences were still significant.

Previous studies have already identified a positive effect of tree species richness on arthropod diversity (Ampoorter et al., 2020; Schuldt et al., 2019), as well as a positive relationship between tree productivity and arthropod richness (Li et al., 2023). Such a positive influence of plant diversity on arthropod richness across multiple trophic groups is known to improve ecosystem multifunctionality and promote a wide range of ecosystem services (Soliveres et al., 2016). As diversity increases, the number of available niches increases and organisms are more likely to use resources in diverse, complementary,

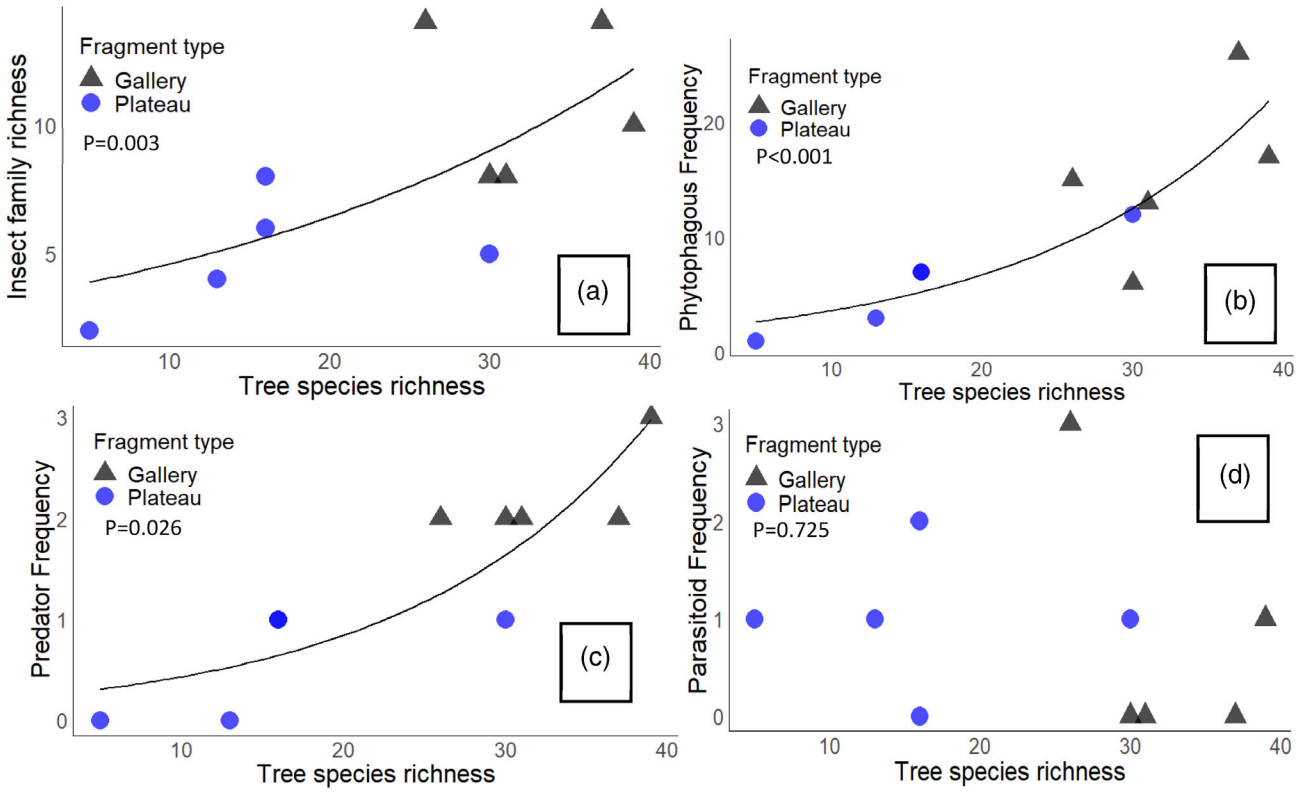


**FIGURE 4** Relationship between tree species richness and insect family richness and frequency in 1000 $m^2$ forest fragment plots (2022). (a) Insect family richness, (b) Phytophagous family frequency, (c) Predator family frequency, (d) Parasitoid family frequency. Regression lines are drawn according to GLMM, including tree species richness as fixed effect and fragment type as a random effect.

**TABLE 1** Generalized linear mixed model (GLMM) testing the effects of tree species richness on insect family richness and the frequency of phytophagous, predatory and parasitoid insects in 1000 $m^2$ in forest fragment plots (2022).

| | Estimate | $Chi^2$ | *p* | Marginal $R^2$ | Conditional $R^2$ |
|---|---|---|---|---|---|
| All families (richness) | 0.035 ± 0.012 | $\chi^2(1) = 9.010$ | **0.003** | 0.549 | 0.549 |
| Phytophagous (frequency) | 0.062 ± 0.011 | $\chi^2(1) = 30.05$ | **<0.001** | 0.837 | 0.837 |
| Predators (frequency) | 0.067 ± 0.030 | $\chi^2(1) = 4.989$ | **0.026** | 0.438 | 0.438 |
| Parasitoids (frequency) | 0.012 ± 0.034 | $\chi^2(1) = 0.124$ | 0.725 | 0.047 | 0.047 |

*Note*: *p*-values in bold are significant at $p < 0.05$.

**TABLE 2** Generalized linear mixed model (GLMM) testing the influence of insect family richness in forest fragments on the same variable in adjacent sugarcane fields.

| | Estimate | $Chi^2$ | *p* | Marginal $R^2$ | Conditional $R^2$ |
|---|---|---|---|---|---|
| All families | 0.008 ± 0.004 | $\chi^2(1) = 4.907$ | **0.027** | 0.226 | 0.713 |
| Phytophagous | 0.059 ± 0.028 | $\chi^2(1) = 4.56$ | **0.034** | 0.349 | 0.349 |
| Predators | 0.075 ± 0.036 | $\chi^2(1) = 4.33$ | **0.038** | 0.296 | 0.296 |
| Parasitoids | 0.064 ± 0.036 | $\chi^2(1) = 3.22$ | *0.073* | 0.441 | 0.560 |

*Note*: *p*-values in bold are significant at $p < 0.05$, in italics at $p < 0.1$.

or mutually facilitative ways (Haan et al., 2021). Furthermore, biodiversity plays a crucial role in maintaining the stability of ecosystem processes by supporting different species that occupy similar functional niches but respond differently to environmental changes. The absence of a particular species may be compensated by the presence of another species with a similar functional role (Cadotte et al., 2011; Elmqvist et al., 2003). Thus, our findings support the hypothesis that tree diversity and forest habitat quality are key drivers of arthropod

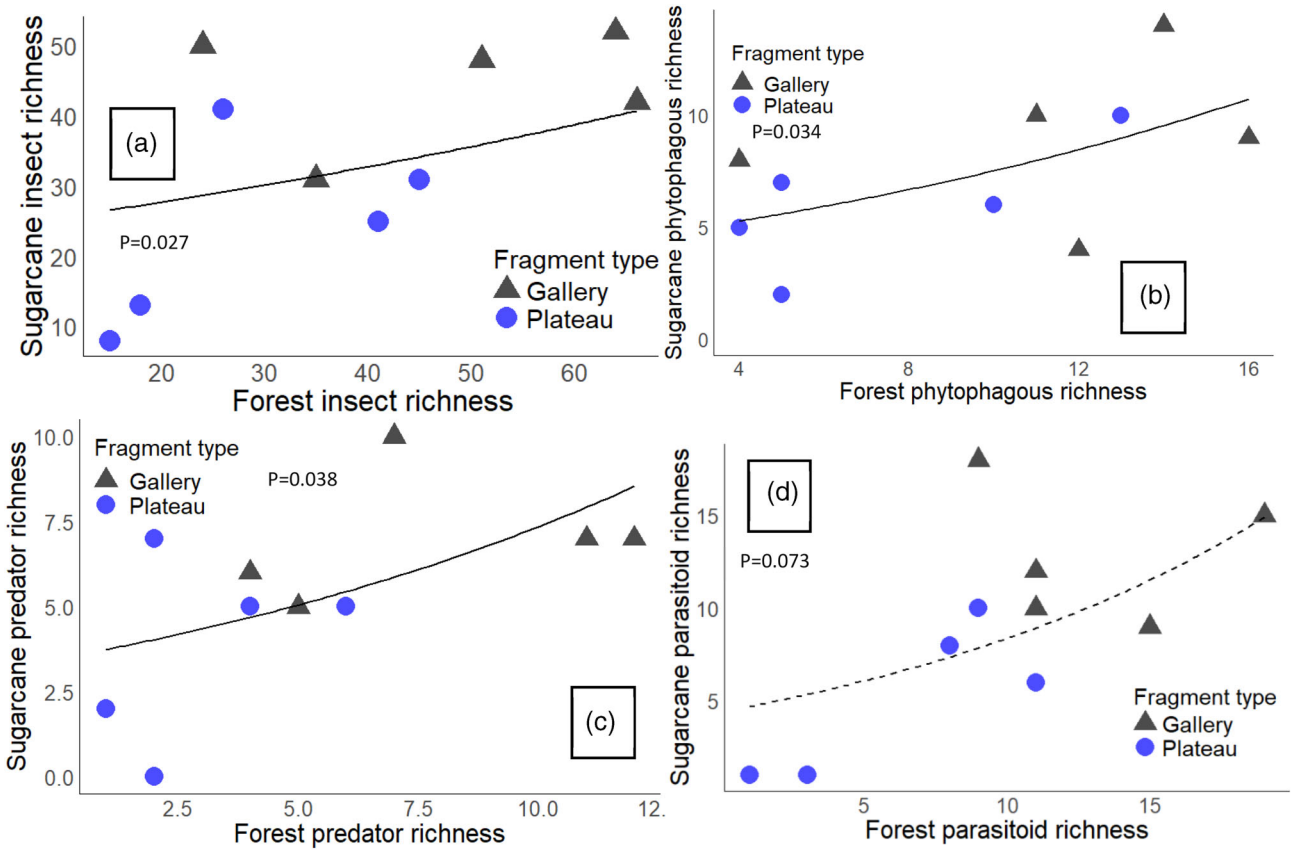


**FIGURE 5** Influence of forest total insect family richness and functional group richness on the same parameters in sugarcane fields (2022). (a) Total insects, (b) Phytophagous, (c) Predators and (d) Parasitoids. Regression lines are drawn according to GLMM including forest family richness as fixed and fragment type as random effect.

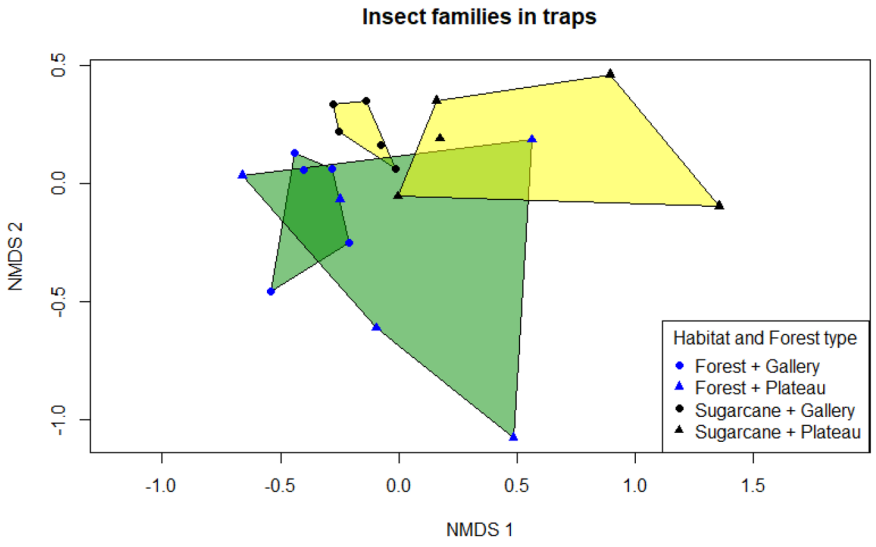


**FIGURE 6** Non-metric Multidimensional Scaling (NMDS) of the insect family community in forest fragments and adjacent sugarcane fields. Yellow polygons: Sugarcane, green polygons: Forest fragments.

diversity. In addition to the conservation of habitats, it is thus also important to preserve or restore habitat quality in order to support complex arthropod communities sustaining ecosystem services across landscapes.

The influence of tree species richness on phytophagous insects was expected as they directly depend on plants. Other studies found that habitats with greater tree diversity harbour more diverse and abundant herbivore communities (Leal et al., 2016; O'Brien

et al., 2017). A higher number of plant species provides a greater variety of resources facilitating the coexistence of more herbivorous species (Leal et al., 2016; Lewinsohn & Roslin, 2008). However, increased plant diversity may also hamper insects' ability to locate their host plants (Silva & Clarke, 2020). Hence, plant species richness may limit the negative effects of herbivorous insects on individual plant species, but other factors such as the taxonomic distance of tree species and the proportion of non-host trees may be equally or more influential than species richness (Gougherty & Davies, 2024; Jactel et al., 2021). Although phytophagous insects are commonly perceived as pests in agriculture, they represent a vital trophic group in maintaining ecosystem services (Soliveres et al., 2016). They are prey for predators, and a higher abundance of prey supports greater species richness and abundance of natural enemies (Dominik et al., 2018; Fenoglio et al., 2012). Additionally, most phytophagous insect species are not considered pest insects since they do not attack crop plants. The major pest insects of sugarcane, sugarcane borer, spittle bugs and sugarcane weevil are oligophagous, feeding either only on sugarcane or on very few other grass species (Buitrago et al., 2022; Li et al., 2024). It is thus unlikely that they use forest fragments as habitats. Therefore, the increase of phytophagous insects with increasing tree diversity cannot necessarily be considered a disservice to the ecosystem.

The effect of tree or plant species is generally less pronounced than on phytophagous arthropods, as natural enemies do not feed directly on plants (O'Brien et al., 2017). However, several important predator and parasitoid groups change nutrition from larval to adult stages. While larvae are carnivorous, adults feed on floral resources such as pollen and nectar (Gardarin et al., 2018). Although food consumption is much higher during carnivorous larval stages, adult access to floral and extrafloral nectar can enhance longevity, fecundity and host searching activity (Benelli et al., 2017; Gillespie et al., 2016). This is particularly relevant in tropical forests, where many trees have extrafloral nectaries that produce nectar to favour ants and parasitoids protecting plants from herbivory (Câmara et al., 2017; Miranda et al., 2022). Furthermore, several predator groups such as ladybirds use floral resources and extrafloral as complementary food (Gardarin et al., 2018; Holm et al., 2021; Stowe et al., 2021). Finally, herbivores feeding on forest fragment vegetation represent alternative prey for predators including natural enemies feeding on pest insects (Gillespie et al., 2016; Stemmelen et al., 2022). Accordingly, our results showed an increase in predator richness in forest fragments of higher tree species richness. However, the frequency of parasitoid families was not significantly affected. Since many parasitoids are limited by their ability to access floral nectar, especially from deep flowers, they may rely on specific nectar sources not analysed in our study, such as lianas or understory herbs (Garcia et al., 2014; Russell, 2015). Complete vegetation analysis is required to better understand relationships with insects at higher trophic levels (Garcia et al., 2014).

Although our study revealed relationships between tree species richness and the richness of certain insect functional groups, such as predators, we acknowledge that family richness alone may not fully reflect the functional contribution of these groups to ecosystem services. Therefore, it remains unclear whether the observed increase in predator richness translates into improved biological control (Chaplin-Kramer et al., 2011; Tscharntke et al., 2016). Furthermore, different predator families vary considerably in their hunting strategies, prey specificity and efficiency, which limits the interpretation of potential impacts on pest suppression (Tylianakis & Romo, 2010). Our results suggest that species with potential for biological control are favoured, but future studies need to include identification to species level and abundance measurements to better assess the relationship between biodiversity and ecosystem service provision in agroecosystems.

The positive relationship between insect richness in forest fragments and sugarcane fields confirms that natural habitats in agricultural landscapes favour species richness in crop fields and may thus promote the associated ecosystem services (Bartual et al., 2019; Medeiros et al., 2019). This positive effect can be explained by the movement of insects between habitats to search for resources, protection and a suitable microclimate (González et al., 2016; Sorribas et al., 2016). However, the comparison of community differences using PERMANOVA also showed that insect family composition is different between forests and agricultural habitats. These differences in community composition reflect habitat differences in terms of food resource availability, microclimate and predator abundance limiting interaction between forests and agricultural habitats (Schneider et al., 2016; Alves et al., 2020). Although spillover likely results in shared taxa between habitats, habitat-specific conditions maintain distinct community assemblages. The placement of traps at different distances from the forest fragments may help to better understand movements between forest fragments and sugarcane fields. Additionally, the use of different trap types in our study may have overestimated the differences between both habitats. Although yellow pan traps are not optimal for forest habitats, their use in both habitats may improve the comparison of insect communities and should be included in future studies. Directional traps or even capture-mark-recapture studies are required to ultimately evaluate spillover from forest fragments to sugarcane fields (Pollier et al., 2016).

Another limitation of our study is the use of larval feeding preference for functional group classification. This choice is justified by the amount of food consumption but may bias spillover dynamics, as adults are usually more mobile than larvae. In particular, holometabolous insects often change nutrition during their life cycle, such as Lepidoptera, of which larvae are typically herbivorous while adults are pollinators (Wang et al., 2024). The separation of larvae and adults in different functional groups may help to overcome this limitation in future studies.

Our findings highlighted the critical role of natural habitats to preserve insect biodiversity and their associated ecosystem services within agricultural landscapes. The diversity and quality of forest fragments had a significant influence on arthropod community composition. Beyond tree species richness, understory vegetation and climbers may also play an important role that needs to be considered in future studies (Ampoorter et al., 2020; Staab & Schuldt, 2020). Our study does not only emphasise the necessity for policies and management strategies improving the conservation of natural habitats, such as forest fragments in tropical agricultural landscapes, but also shows

the importance of examining the characteristics of these fragments, such as plant species composition, floral resource provision and phenology, more closely. Further studies are needed to fully understand the effects of tropical forest fragments on ecosystem service provision and to develop strategies for improving these services.

## AUTHOR CONTRIBUTIONS

**Sabrina Cesarin de Oliveira:** Conceptualization; formal analysis; investigation; methodology; writing – original draft. **Noelline Tsafack:** Formal analysis; validation; writing – review and editing. **Maëlle Cario:** Conceptualization; formal analysis; methodology. **Davi Rodrigo Rossatto:** Conceptualization; methodology; writing – review and editing. **Armin Bischoff:** Conceptualization; formal analysis; writing – original draft; writing – review and editing. **Odair Aparecido Fernandes:** Conceptualization; formal analysis; methodology; resources; supervision; writing – review and editing.

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## CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

## DATA AVAILABILITY STATEMENT

The data that supports the findings of this study are available (Oliveira et al., 2025): https://doi.org/10.5061/dryad.c866t1gjv.

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## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

**Table S1.** Frequency of plant species: number of occupied forest fragments ($n = 10$).

**Table S2.** Frequency of arthropod morphospecies sampled in 2020.

**Table S3.** Frequency of insect families sampled in 2022.

**Table S4.** Insect families sampled in traps of 2022.

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