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Effects of habitat loss on three insect assemblages in modified ecosystems of foothills of the Colombian Orinoquia

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ABSTRACT

Introduction: The effects of habitat transformation have been widely studied and the effects are well-known at different levels of biological organization. However, few studies have focused on responses to this process at the level of multiple taxa in diverse taxonomic and functional groups.

Objective: Determine the variations in taxonomic and functional diversity of ants, butterflies, and dung beetles, at a spatial and temporal level in a landscape mosaic of the ecoregion of the Colombian foothills.

Methods: We assessed amount of natural habitat and landscape composition in four types of vegetation, during the highest and lowest rain periods. We collected butterflies with hand nets and used baited pitfall traps for dung beetles and ants.

Results: Habitat loss positively affected ant and butterfly species richness, and negatively affected dung beetles. The abundance of ants and butterflies had a positive effect on the dominance of species in the transformed vegetation, for dung beetles the abundance was negatively affected by the absence of canopy cover. Habitat loss had no negative effect on functional diversity as there is no difference between natural and transformed vegetation.

Conclusions: The amount of habitat, habitat connectivity and different types of vegetation cover were important factors in the maintenance of insect diversity in the modified ecosystems of foothills of the Colombian Orinoquia. The lack of a common spatial and temporal pattern shows that studies of multiple insect taxa should be carried out for biodiversity monitoring and conservation processes.

Key words: habitat fragmentation; habitat amount; ants; butterflies; dung beetles; neotropical landscape.

Habitat loss is the process by which natural vegetation is transformed by anthropogenic activities into any other type of land use such as crops, livestock, or urban growth (Collinge, 2009; Fahrig, 2019). These changes have negative effects on biodiversity, as seen by the decrease in the number of species, the reduction in their abundances, and by variations in the distribution of populations (Fahrig, 2003; Horváth et al., 2019). In extreme cases where the amount of natural vegetation remaining in a landscape is not suitable to support a population or assemblage (threshold habitat level) and the process of habitat loss increases over time, species extinction may occur (Collinge, 2009; Fahrig, 2001; Sardanyés et al., 2019). Thus, in landscapes with high levels of transformation, environmental parameters change in short periods of time, which is more noticeable in small patches of habitat (hyperdynamism)

(Laurance, 2002). Even so, the real impact of habitat loss on biodiversity seems to depend on the intensity, extent, and type of change in the vegetation (Arroyo-Rodríguez et al., 2019).

Recently, the global decline and increased pressures on biodiversity have been widely discussed (Arroyo-Rodríguez et al., 2019; Fahrig, 2019). It is evident that the decrease in biodiversity due to habitat loss is represented not only by the reduction of species richness (Macdonald et al. 2020), but also by changes in climate regulation, the supply of fertile soil and drinking water, erosion control, and food production (Skogen et al., 2018). Insects are not immune to the effects caused by the decrease of the habitats they occupy and functional loss of their communities, decrease in total biomass and reduction in the number of species, both of those that are specialists for a type of habitat, as well as those with wide distributions and abundant populations, have been documented. (Forister et al., 2019; Wagner, 2020). The main factors for the decline of insect assemblages have been quantified, from the greatest to the least impact and they are the loss and degradation of ecosystems, the excessive use of pesticides, and climate change (Jactel et al., 2021; Sánchez-Bayo & Wyckhuys, 2019). Other factors include disease, competition with invasive species, and light pollution caused by urbanization (Langevelde et al., 2018). As a result of the above, the main concerns regarding the decline of insects are focused on the loss of ecosystem services they provide such as cycling of organic matter (decomposition of wood, leaves, manure and carrion), pest control (arthropods, fungi and weeds), wildlife nutrition (primary base in trophic chains), and the main one, pollination (Forister et al., 2019; Losey & Vaughan, 2006; Noriega et al., 2018).

Although the effects of habitat transformation on response variables of communities such as alpha, beta, and gamma diversity have been widely studied (Arroyo-Rodríguez et al., 2019), studies that evaluate the responses of multiple taxa with contrasting ecological roles and habitat specializations in tropical forests are still very few (Filgueiras et al., 2019a). In addition to the above, studies focused on a single taxon may provide incomplete and less useful information for conservation plans, since the species differ in their sensitivity to habitat modification and so there are different responses in life cycle traits, such as dispersal capacity, reproductive potential and niche width (Díaz-García et al., 2020; Kellner et al., 2019). A multitaxon approach will be of great help for assessing with greater precision the patterns of biodiversity loss and the environmental factors that determine the response to these disturbances (Decaëns et al., 2018; Püttker et al., 2020). Such information is of great importance for understanding the drivers of the impacts of habitat loss (Carrié et al., 2017; Filgueiras et al., 2019a). Studies including traits at the functional level are few, even though the negative effects describing functional impoverishment of assemblages and the sensitivity of functional traits to habitat alteration are known (Ewers & Didham, 2006; Filgueiras et al. 2019a). Thus, research that studies the congruence of taxonomic and functional diversity together will improve our understanding of biodiversity patterns, the use of resources in ecosystems, habitat requirements of species, and environmental factors that function as filters (Castro et al., 2020; Nunes et al., 2016).

Insects are important components of biodiversity and in most terrestrial and aquatic ecosystems they are the most diverse group, both taxonomically and functionally (Parikh et al., 2020; Stork, 2018). We focus on the evaluation of the assemblages of three insect taxa: ants (Hymenoptera: Formicidae), dung beetles (Coleoptera: Scarabaeinae), and diurnal butterflies (Lepidoptera), groups that are traditionally used for the estimation of diversity, since they provide reliable information on the conservation status of a habitat (Andrade-C. et al., 2017; Fernández et al., 2019; Filgueiras et al. 2019a; Villarreal et al., 2006). These groups meet the criteria as good indicators of diversity and ecological processes: well-known and stable taxonomy, widely documented natural history, abundant species that are easy to observe and manipulate (little sampling effort), lower taxa (species and subspecies) with habitat specificity, sensitivity to changes, and high taxonomic and ecological diversity (Hayes et al., 2009; Parikh et al., 2020; Spector, 2006).

We compared the abundance, species richness and composition of three assemblages of insects (ants, dung beetles and diurnal butterflies) in a landscape mosaic that included fragments of secondary forest, riparian forests, pine plantations, and wooded pastures, in the foothills ecoregion to the east of the Eastern Cordillera of Colombia. Our objective was to determine variations in the diversity of species at the taxonomic and functional level, and their relationship to the number of available habitats and seasonal variation during the year (higher and lower rainfall). We started with the hypotheses that (1) In line with the documented importance of forest covers for the conservation of biodiversity, the highest values of taxonomic and functional diversity of assemblages will occur in secondary forests, followed by riparian forests, and finally plantations and wooded pastures; (2) the abundance values of the species assemblage in plantations and pastures will differ significantly from those in habitats with greater forest cover; (3) there will be marked variations between the periods of higher and lower rainfall in terms of the richness, composition and structure of the assemblages of dung beetles, butterflies and ants; and (4) the amount of habitat will positively influence the richness and abundance values, and these will be independent of the functional diversity values of the studied assemblages.

MATERIALS AND METHODS

Study area: This research was carried out in the foothills ecoregion, in the municipality of Villavicencio, East of the Eastern Cordillera of the Colombian Andes (4º8’34.588” S & 73º39’57.805” W), 723-774 m.a.s.l (Fig. 1). This ecoregion is considered as a transition

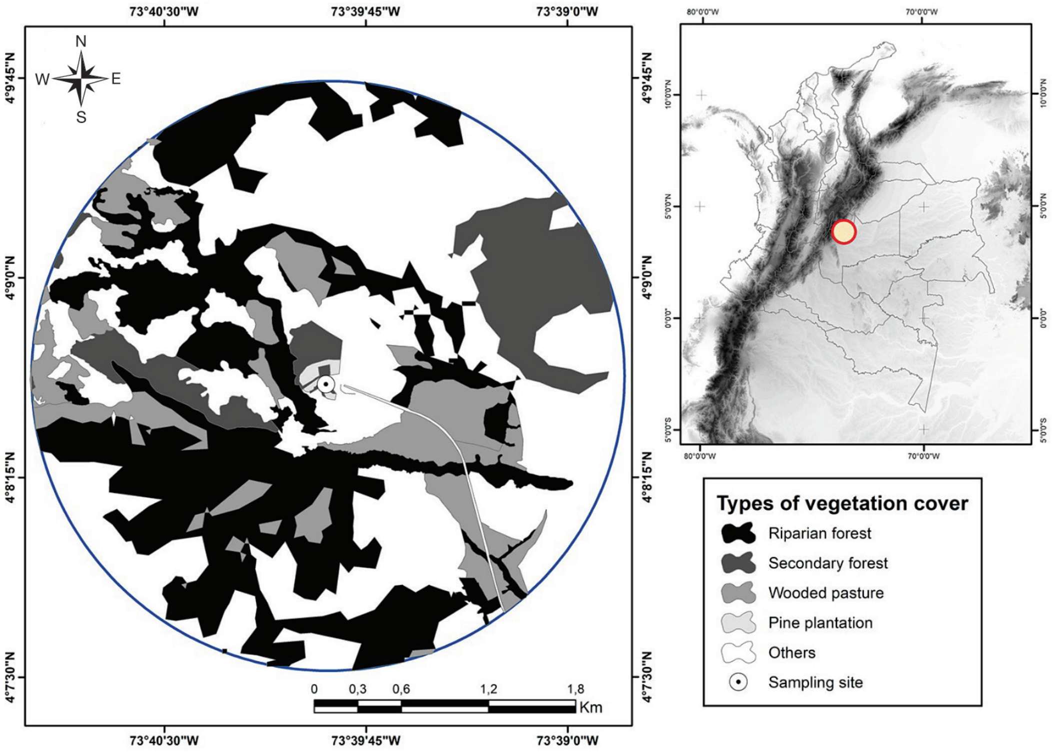

Fig. 1. Location of the sampling area in the ecoregion of the Colombian foothills, in the municipality of Villavicencio (Meta). The 2 000 m diameter circular buffer area centered on the sampling site is shown.

between the Andean life regions and the high plains of the Orinoquia region (Carvajal et al., 2007). The foothills are recognized as a center of endemism for fauna, called "Refugio de Villavicencio" (Brown, 1982; Romero et al., 2004) that extends along the lower slopes (the foothills) of the Eastern slope of the Eastern Cordillera in the Colombian Andes (Hernández et al., 1992). The annual temperature ranges between 24-32 °C, with precipitation between 24.2-84 mm per year, with minimums between the months of December and March and maximums between April and July (Minorta-C. & Rangel-Ch., 2015). Although the foothills are considered an ecoregion of high biodiversity (Rangel-Ch. 2014), its forests are in critical danger as they have only 16 % of their natural vegetation intact, 4 % semi-natural vegetation, and 80 % has been transformed (Etter et al., 2017; Latorre et al., 2014). The main activities of transformation and loss of habitat are of anthropic origin, such as large-scale agricultural crops (silvopastoral systems and monocultures), extensive livestock, illicit crops, and rapid urban growth (Hernández et al., 2021; Velosa et al., 2018).

We selected four types of vegetation for sampling:

Secondary forest (SF): tree cover with a discontinuous canopy and with a height greater than 15 m, where the most abundant species were *Clusia lineata* (Clusiaceae), *Miconia serrulata* (Melastomataceae) and *Phyllanthus attenuatus* (Phyllanthaceae).

Riparian forest (RF): tree cover located on the margins of running water, no more than 50 m wide and with a high abundance of tree species such as *Acalypha* aff. *diversifolia* (Euphorbiaceae), *Duroia hirsuta* (Rubiaceae), *Miconia serrulata* (Melastomataceae) and *Henriettella* aff. *seemannii* (Melastomataceae).

Wooded pasture (WP): dominated by Poaceae species, with dominance of *Panicum pilosum* (Poaceae), *Cyperus laxus* (Cyperaceae) and *Andropogon bicornis* (Poaceae), in addition to the presence of the tree *Vismia* aff. *lauriformis* (Hypericaceae).

Pine plantation (PP): monoculture consisting of *Pinus patula* (Pinaceae) and emerging species such as *Aphelandra pilosa* (Acanthaceae), *Tapirira* aff. *guianensis* (Anacardiaceae), *Philodendron* sp. (Araceae), *Costus* aff. *spiralis* (Costaceae) and *Alchornea glandulosa* (Euphorbiaceae). Pastures and pine plantations represent the most common anthropic pressures on the foothills ecosystems (Rangel-Ch. & Minorta-C., 2015).

Insect sampling: We carried out six sampling events, three during the season of greater precipitation in the months of May, June and July 2019, and three during the season of less precipitation in March, August and October of this same year (categories given according to the precipitation averages given by Minorta-C. & Rangel-Ch., 2015). During each sampling event we collected data on the assemblages of ants, dung beetles, and butterflies. For ants and dung beetles we used a baited pitfall trap design, while for butterflies we used nets standardized by hours/person, replicated in the landscape with spatial independence. We placed each set of pitfall traps 30 m away from the physical border of the fragment for the forest covers (Dröse et al., 2019; Martínez-Falcón et al., 2018), and away from the influence of forests or riparian vegetation by at least 100 m from wooded pasture and pine plantation (Da Silva & Hernández, 2015; Dröse et al., 2019).

Specifically, for each taxonomic group we followed the following protocols: for ants, we arranged three pitfall traps linearly and baited with tuna for each vegetation type, separated from each other by at least 60 m. Each of the traps was active for 48 hours in each of the sampling events, giving a total effort of 3 456 h/trap for the six sampling events; each trap was our sampling unit. For dung beetles we installed six pitfall traps in a straight line separated from each other by at least 30 m in each of the vegetation type; each trap was our sampling unit. Three traps were baited with approximately 30 g of human excrement and the other three with decomposing fish (Cultid et al., 2012). We checked and rebaited each of the traps every 12 hours, and they were kept active for 72 hours (Villarreal et al., 2006). This resulted in a sampling effort of 10 368 hours/trap for the six sampling events. For butterflies we used two methods for recollection of individuals. The first was the free search collection method with an insect nets (Andrade-C. et al., 2013). In each search we toured and collected the butterfly individuals that were perched on the vegetation or active in flight (Andrade-C. et al., 2013), with a total sampling effort of 2 hours/person/vegetation, in each of the six sampling events, and total 48 hours/person for the six sampling events; each hour was our sampling unit. The second method for collecting butterflies was the installation of two Van Someren-Rydon traps in each of the vegetation types, separated by at least 50 m from each other, one baited with decomposing fruit (banana, pineapple, mango, papaya and beer) and the other with pieces of decomposing fish (Andrade-C. et al., 2013). Each trap had an activation time of 48 hours and checked every 12 hours (DeVries, 1987). Thus, a sampling effort of 2 304 hours/trap was obtained for the six sampling events.

Ants and beetles collected from each trap were transported in hermetically sealed bags and preserved in 70 % alcohol for subsequent taxonomic determination (Fernández et al., 2019; Villarreal et al., 2006), and in envelopes for butterflies (Andrade-C. et al., 2013). The determination of ants was done following the keys for subfamily and genera of the book Introduction to the Ants of the Neotropical Region (Fernández, 2003) and Ants from Colombia (Fernández et al., 2019); the taxonomic update of the subfamilies and genera was done through the revision of the page: http://www.antweb.org (AntWeb, 2019). For the determination of dung beetles, the specialized keys were used: Edmonds & Zídek (2012), Génier (1998), Génier & Kohlmann (2003), Medina & Lopera-Toro (2000), Sarmiento-Garcés & Amat-García (2014) and Vaz de Mello et al. (2011). Butterfly determination was done with the help of the Lamas (2004) guide for neotropical butterflies and the illustrated list of butterflies of the Americas by Warren et al. (2017). The biological material is deposited in the insect collection of the Luis Gonzalo Andrade Natural History Museum. Collecting permits are from the Pedagogical and Technological University of Colombia, issued by the National Environmental Licensing Authority of Colombia.

Landscape metrics: We selected two landscape metrics to assess their influence on the species richness and functional diversity of the three groups of insects, (1) the amount of habitat and (2) the composition of the landscape (Collinge, 2009; Fahrig, 2013). The amount in hectares (ha) of each of the vegetation type is measured in a circular buffer area of 2 000 m diameter, based on the local landscape concept provided by Fahrig (2013). According to Fahrig (2013), the appropriate scale to test the habitat quantity hypothesis is the scale related to the average movement ranges of the study species. Following the previous idea, the buffer was selected taking into account dispersal studies of coprophagous beetles (Cultid-Medina et al., 2015) and butterflies (Marquez & Martínez, 2020) where they describe that the individuals of these groups can move up to 1.7 km and 1.3 km, respectively. Thus, the 2 km buffer was selected taking into account the greatest degree of dispersal of the groups, in this case, dung beetles. Landscape composition, defined as the types of habitats or vegetation present in the landscape (Collinge, 2009), was obtained according to the standardized Corine Land Cover methodology (IDEAM et al., 2011). The Corine Land Cover (CLC) methodology was born in Europe on june 27, of 1985, with the start of the CORINE program, “Coordination of Environmental Information”, which is an experimental type project that allows describing, characterizing, classifying and comparing land cover characteristics, interpreted from the use of medium resolution satellite images (Landsat), for the construction of land cover maps at different scales (Suárez-Parra et al., 2016).

These quantities were obtained through the ArcGIS v. 10.6 (ESRI, 2016) through landsat images using the GloVis system (USGS, 2019).

Data analysis. Taxonomic diversity: We used two measures to evaluate alpha diversity, both based on the effective number of species from the transformation of qD: diversity of order zero (q= 0) which is equivalent to the number of species and diversity of order one (q= 1), where the weight of each of the species is proportional to its abundance in the sample (Jost, 2006). The completeness of the sample was determined by calculating the coverage deficit using the bootstrap method with 95 % confidence intervals for interpolation and extrapolation (Chao & Jost, 2012). To graphically describe the abundance patterns of insect taxa in the vegetation types, we calculated range abundance curves with adjustment for undetected diversity (Chao et al. 2015). However, we would like to clarify that in the case of butterflies, we only used the records obtained from the insect net and omitted the individuals collected with Van Someren Rydon traps. This is due to the low number of individuals collected with the traps and to the fact that these species had already been recorded with the net method. For the development of the analyses, we used the R program (R Core Team, 2019) and the iNEXT packages for alpha diversity based on the effective number of species (Hsieh et al., 2016) and for the abundance range curves we followed Chao et al. (2015).

Assessment spatial and temporal change of the insect assemblages: We analyzed the degree of differentiation of the three groups of insects among the plant covers and seasons by calculating the Sorensen dissimilarity (βsor) and its replacement components (Simpson dissimilarity index, βsim) and nesting (βnes) (Baselga, 2010; Baselga, 2012). The exchange implies the substitution of species between sites or seasons mainly because of environmental limitations, while nesting implies that sites poor in species are actually subsets of sites or periods with greater richness (Baselga, 2010; Baselga, 2012). The differences between vegetation types and seasons were estimated by means of the non-parametric analysis of similarity ANOSIM (analysis of similarity of the abundance matrix) (Clarke & Warwick, 2001). We developed the analyses in the R program (R Core Team, 2019), using the betapart (Baselga et al., 2018) and Vegan for the ANOSIM analyses (Oksanen et al., 2019)

Functional diversity: For ants and dung beetles we used the ethological functional trait of food habits. The eating habits of ants were taken from Fernández (2003) and Fernández et al. (2019), where a species is a specialist if it feeds on a single resource, or a generalist if its feeding habits include both plant material and arthropods. We categorized dung beetle species as specialists if more than 70 % of the individuals were collected by means of a single type of bait and generalists if there was no difference between baits (Andresen, 2005). For butterflies we used and adapted habitat to categorize them as generalists (species with preference for non-forest matrices) or specialists (forest-dependent species), according to Filgueiras et al., (2019b). Thus, the butterfly species collected in open habitats, transformed habitats (wooded pasture and pine plantation) or natural habitats and transformed habitats all the same time, were categorized as generalists and the species captured in natural forest covers (riparian forest secondary forest) were categorized as specialists.

We evaluated functional diversity from a single-trait approach, through the indices of Functional Regularity (FRO) and multiple Functional Divergence (FDvar) (Mason et al., 2005; Pla et al., 2012). FRO is used to examine the extent to which effective use is made of the full range of resources available in each niche (Mason et al., 2005; Pla et al., 2012). FDvar is a measure of functional similarity between the dominant species of an assemblage, where a high value indicates a high niche differentiation between species, potentially reflecting low competition and a more efficient distribution and use of available resources (Córdova-Tapia

& Zambrano, 2015; Mason et al., 2005). We did these analyses with the FDivesity software (Casanoves et al. 2010), with extension to the R platform (R Core Team, 2019).

Landscape metrics vs taxonomic and functional diversity: To evaluate the effect of the amount of habitat and the type of vegetation on the richness and functional diversity of each group of insects, we performed a generalized linear model (GLM) with a Poisson error distribution for the q0 index. To observe if our model Y ~ amount habitat + vegetation (%) describes our response variable more than by chance, it was contrasted with a null model that represents the absence of some type of effect for the predictor variable (MacKenzie et al., 2018). Additionally, we performed a canonical correspondence analysis (CCA), where we compared a matrix of the response variables (richness of each taxon) and another with the explanatory variables (amount of coverage). To evaluate the significance of the CCA we performed a Wilk's Lambda test with 999 permutations. We did these analyses in the R program (R Core Team, 2019) through the CCA package (González & Déjean, 2021).

RESULTS

We recorded 17 126 ants, distributed in eight subfamilies, 35 genera and 75 species/morphospecies. The subfamily with the highest species richness was Myrmicinae, which together with Formicinae, group 73 % of the taxa found for ants. The most diverse genera were *Camponotus* and *Pheidole* with eight and seven morphospecies, respectively. For dung beetles we obtained records of 1 540 individuals, belonging to nine genera and 24 species/morphospecies. The most diverse genera were *Deltochilum* and *Dichotomius* with five and four species, respectively. For butterflies we registered 309 individuals belonging to six families, 80 genera and 117 species/morphospecies. The family with the highest number of species were Nymphalidae and Hesperiidae, which together accounted for 68 % of the species found. The most diverse genera were *Heliconius* and *Mesosemia* with six and five species, respectively.

The rarefaction-extrapolation estimators showed high sampling coverage for ants and dung beetles, which means that a high percentage of the species of these two groups present in the assemblages are represented in the sample, while for butterflies there was a low completeness. In this way, the ants had a coverage of 99 % for all the vegetation types. For dung beetles the representativeness ranged from 92 % in the wooded pasture to 98-99 % in the other vegetation types. For butterflies, the highest representation was in riparian forest and wooded pasture, both with 66 %, followed by secondary forest with 63 %, and pine plantation with 50 % (Table 1).

Taxonomic diversity: Ant species richness (q= 0) was higher in the transformed vegetation (pine plantation and wooded pasture) and lower in the conserved vegetation (secondary forest and riparian forest) (Table 1). When relative abundance was included in the diversity metric (q= 1), the same pattern was observed for the richness of species where the transformed vegetation was more diverse with the highest values of the effective number of abundant species (Table 1). Dung beetles had the highest richness (q= 0) in pine plantation and riparian forest, followed by secondary forest; and the wooded pasture had the lowest number of species. When considering the relative abundance (q= 1) the pine plantation shows a higher diversity, with the highest values of the effective number of abundant species, while the lowest values were in wooded pasture (Table 1). For butterflies, the wooded pastures and riparian forest were the vegetation types with the highest species richness (q= 0), and the secondary forest had the lowest number of species. Despite the above, when considering the relative abundances (q= 1), the vegetation types with the highest values of the effective number of abundant species were pine plantation and riparian forest (Table 1).

TABLE 1
Alpha diversity for each of the insects assemblages in sectors of foothills, Colombian Orinoquia

Taxa	Estimators	SF	RF	WP	PP
Ants	Q0	37	31	40	41
	Q1	7.827	7.649	8.670	11.811
	Abundance	2 345	1 271	7 035	2 616
	Sample coverage	0.9957	0.9929	0.9986	0.9962
	Deficit	0.0043	0.0071	0.0014	0.0038
Dung beetles	Q0	14	16	9	16
	Q1	4.020	4.037	3.593	4.242
	Abundance	329	620	48	553
	Sample coverage	0.9879	0.9952	0.9175	0.9928
	Deficit	0.0121	0.0048	0.0825	0.0072
Butterflies	Q0	32	46	47	39
	Q1	22.306	31.150	26.728	31.903
	Abundance	59	96	96	58
	Sample coverage	0.6300	0.6567	0.6578	0.5042
	Deficit	0.3700	0.3433	0.3422	0.4958

SF: secondary forest, RF: riparian forest, WP: wooded pasture, PP: pine plantation.

In general, the three groups had a hierarchical order of abundance with a few dominant species that changed between the plant covers, and many were represented by only a few individuals (Fig. 2). For ants, we showed a high dominance of *Ochetomyrmex neopolitus* (Fernández, 2003) and *Crematogaster tenuicula* (Forel, 1904) in riparian forest and wooded pasture. This second species was the most dominant in the pine plantation. In the secondary forest, *Ochetomyrmex semipolitus* (Mayr, 1878) and *Crematogaster limata* (Smith, 1858) were the most abundant, followed by *Ochetomyrmex neopolitus* and *Crematogaster tenuicula*. According to the analysis of imperfect detection of the abundance range curves, it was expected that 14, 8, 11 and 17 species of low abundances still remained to be recorded in the riparian forest, secondary forest, pine plantation and wooded pasture, respectively (Fig. 2).

For dung beetles a dominance of *Deltochilum* (*Deltohyboma*) sp. 1 was found in all vegetation types. In riparian forest we found *Onthophagus* gr. *clypeatus* and *Eurysternus caribaeus* (Herbst, 1789), in secondary forest *Eurysternus caribaeus,* and *Phanaeus cambeforti* (Arnaud, 1982) was found in pine plantations. Imperfect detection analyses showed that three more species can still be recorded for riparian forest and secondary forest, four for pine plantation, and eight for wooded pasture, all with low abundances (Fig. 2). For butterflies, the most abundant species in each of the vegetation types were different. For riparian forest *Napeogenes inachia johnsoni* (Fox & Real, 1971) had the highest abundance, followed by species such as *Hyposcada illinissa sinilia* (Herrich-Schäffer, 1865), *Oleria gunilla lubilerda* (Haensch, 1905), *Pteronymia* sp. 1 and *Posttaygetis penela* (Cramer, 1777). For secondary forest the most abundant species was *Oleria gunilla lubilerda* and for pine plantations it was *Mesosemia walteri* (Brévignon, 1998), and for wooded pasture it was *Hermeuptychia hermes* (Fabricius, 1775). The number of species represented by a single species (singletons) was high in all vegetation types. For the secondary forest 69 % of the species had only one individual in the sample, for wooded pasture 70 %, for riparian forest 72 %, and for pine plantation 74 %. Based on the imperfect detection analysis, 31 species were

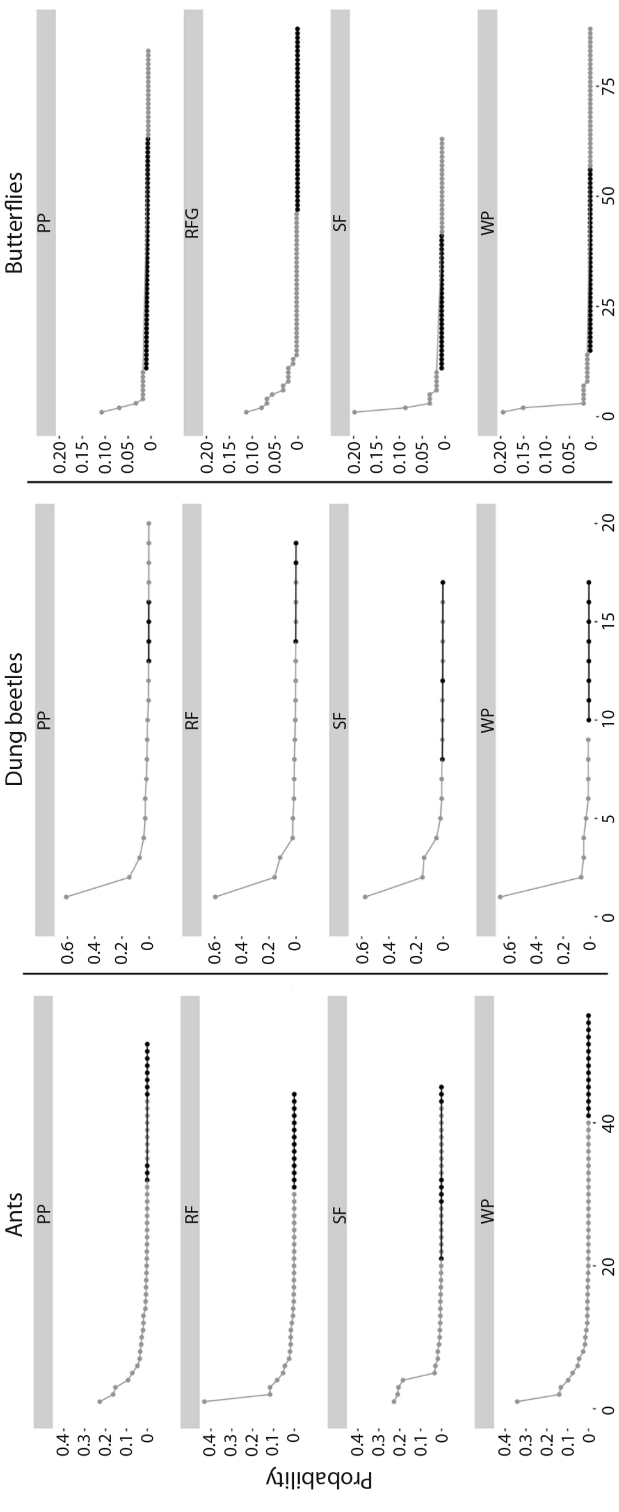

Fig. 2. Range abundance curves with probability of detection of the three assemblages of insects. The gray color reflects the species detected, while the black color reflects the species that are expected to be detected with increasing sampling effort. Riparian forest (RF), secondary forest (SF), wooded pasture (WP) and pine plantation (PP).

expected with low abundances that still need to be registered for secondary forest and for wooded pasture 42 are to be expected, for riparian forest 50 species, and for pine plantation 53 species (Fig. 2).

Spatial Assessment and temporal change of the insect assemblages: At the spatial and temporal level, the change in species composition was greater for butterflies than for ants and dung beetles (Fig. 3A, Fig. 3B). Among the plant covers, the assemblages of dung beetles (R= 0.389, P= 0.001) and of ants (R= 0.123, P= 0.003) was statistically different, while the composition for butterflies (R= 0.917, P= 0.413) did not have statistically significant differences. When considering the components of beta diversity for the three groups, the process that best explains the compositional changes between plant covers is species turnover (βsim), to a lesser extent for dung beetles than for ants and butterflies (Fig. 3C). Similarly, species composition changes between seasons were explained by species turnover (βsim) rather than by nesting (βnes) (Fig. 3D). However, there were no statistically significant differences among the assemblages, between the high and low rainfall season: ants (R= 0.083, P = 0.271), dung beetles (R= -0.115, P = 0.496) and butterflies (R= -0.374, P = 1).

Functional diversity: Functional regularity (FRO) showed differential behavior in each of the insect groups. For ants, the values

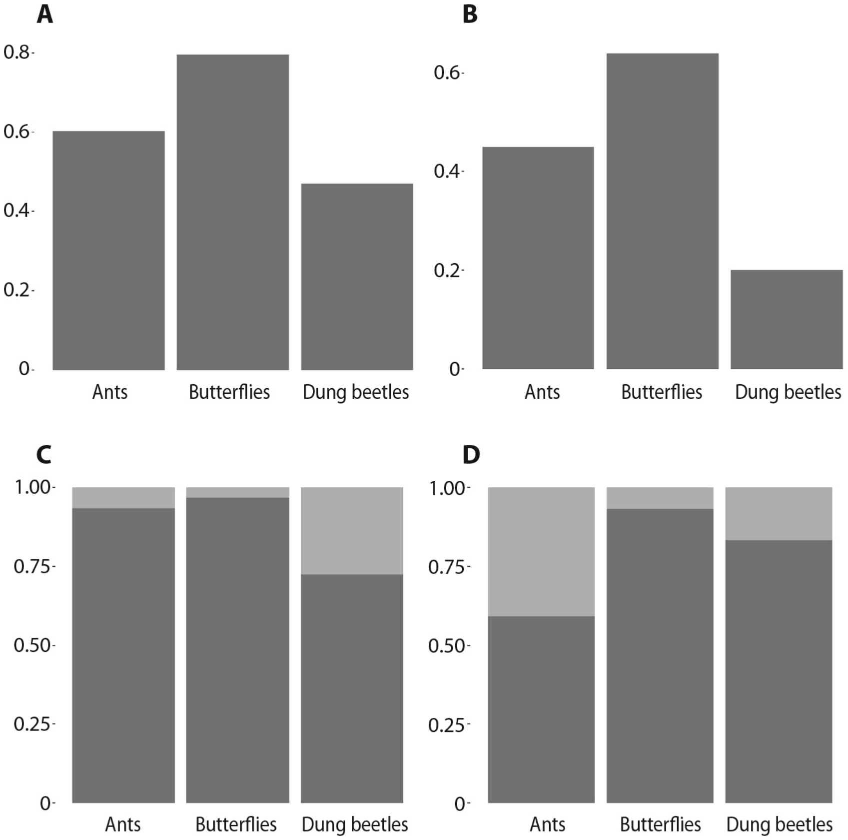

Fig. 3. Spatial and temporal beta diversity for insect assemblages: **a.** Spatial beta (βsor) diversity. **b.** Temporal beta (βsor) diversity. **c.** Percentage contribution of turnover (dark gray) and nesting (light gray) to spatial beta diversity. **d.** Percentage contribution of turnover (dark gray) and nesting (light gray) to temporal beta diversity.

were the same in all vegetation types. For dung beetles, the lowest values were in riparian forest and pine plantation, while the highest value was in wooded pasture. For butterflies, the wooded pasture had the lowest value, followed by riparian forest, and the secondary forest and the pine plantation had the same value (Table 2). Similarly, functional divergence (FDvar) had differential responses for the three groups in each vegetation type (Table 2). For ants, it had its highest values in riparian forest and secondary forest, while the lowest value was in pine plantation (Table 2). In dung beetles, the pine plantation and the secondary forest had the highest values, while the riparian forest had the lowest value. Finally, for butterflies, the secondary forest had the highest value, followed by the pine plantation, while the riparian forest and the wooded pasture had the lowest values.

Landscapes metrics vs taxonomic and functional diversity: Species richness and functional regularity showed a significant relationship with the amount of habitat, P = 0.0444 and P = 0.0442, respectively. While the functional divergence did not have statistically relationship with the amount of habitat (P= 0.0426) (Table 3). The total variance of the richness explained by the amount of habitat and vegetation type was 14 % (inertia) according to the CCA. In addition to the above, each assembly showed a significant relationship with the different variables (Wilk's Lambda= 0.2613, F= 0.6456, P= 0.0010). Thus, the richness of dung beetles had a significant relationship with the riparian forest and pine plantation, the richness of butterflies with the open pasture and the richness of ants with the secondary forest (Fig. 4).

DISCUSSION

Taxonomic and functional diversity: Contradicting our hypothesis, the natural forest covers of riparian forest and secondary forest did not have differential effects on species richness compared to pine plantation and wooded pasture. For insects, responses to habitat loss can be positive when there is evidence of an accumulation of individuals and intraspecific aggregation in fragments, or they can be

TABLE 2
Functional regularity (FRO) and functional divergence (FDvar) for the three groups of insects in each of the plant covers: riparian forest (RF), secondary forest (SF), pine plantation (PP) and wooded pasture (WP)

Taxa	FRO				FDvar			
	RF	SF	PP	WP	RF	SF	PP	WP
Ants	0.03	0.03	0.03	0.03	0.34	0.34	0.07	0.32
Dung beetles	0.07	0.08	0.07	0.13	0.11	0.21	0.25	0.16
Butterflies	0.02	0.03	0.03	0	0.2	0.31	0.23	0

TABLE 3
Results of the generalized linear model and the null model

Response variable	Model	AIC	∆AIC	ωi
Richness	~Amount	1 416.3	0.00	0.726
	~Null	1 418.3	1.95	0.274
FRO	~Amount	-952.8	0.00	0.738
	~Null	-950.7	2.07	0.262
FDvar	~Amount	-473.9	1.36	0.336
	~Null	-475.2	0.00	0.664

The Akaike information criterion (AIC) is shown, the difference between AIC of each model (∆AIC) and the Akaike weight (ωi).

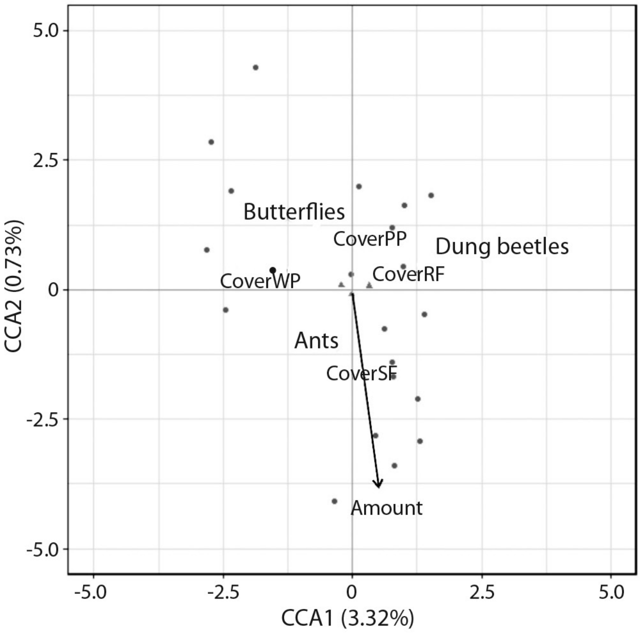

Fig. 4. Canonical correspondence analysis (ACC) between amount of habitat, amount of border, type of habitat, and richness of insects. RF (riparian forest), SF (secondary forest), PP (pine plantation), WP (wooded pasture).

negative when responses are associated with an increase in rare species (Crist et al., 2006; Davies et al., 2004). In accordance with the above and in a general way, the loss of habitat positively affected the species richness of ants and butterflies and negatively affected the dung beetles. On the other hand, the abundance of the ant and butterfly assemblages was positively affected by the loss of habitat by showing a high dominance of a few species that increased the abundance of individuals in the transformed vegetation, while for dung beetles the abundance of individuals was negatively affected in the wooded pasture and positively in the pine plantation. Ants and butterflies were congruent in the effects of habitat loss, while beetles had a differential response.

The high richness and abundance of dominant ant species in pine plantation and wooded pasture could be associated with the fact that these species belong to subfamilies of generalist habits such as Myrmicinae, Dolichoderinae and Formicinae, which can exploit a great diversity of microhabitats and resources by having superior colonization capacity (Cuezzo, 2003; Fernández et al., 2019). In this way, these generalist species may be displacing specialist species, since they have a greater tolerance to extreme conditions and are more efficient in the use of the remaining resources as a consequences of habitat loss (Sanabria-Blandón & de Ulloa, 2011). The simplification of ant assemblages due to habitat loss has been documented previously (Dias et al., 2008; González et al., 2018). However, the presence of monocultures and trees in pastures, can provide greater habitat heterogeneity and, therefore, an increase in the number of species, due to an increase in feeding sites and nesting sites (Bernardes et al., 2020; Dias et al., 2008; Rivera et al., 2008). This may also be a consequence of the microenvironmental similarities of wooded pastures with native vegetation, meaning that the vegetation structure in wooded pastures may supply the requirements of ant assemblages (Queiroz et al., 2020). In addition, the high diversity of ant assemblages, may also be determined by the distance to native habitats, which may drive the high richness values in transformed habitats (Queiroz & Ribas, 2016; Queiroz et al., 2020).

Dung beetles showed greatest richness and abundance in the canopy covers, including pine plantations, with species richness and abundance similar to riparian forest and secondary forest. Patterns where richness and abundance are greater in canopy plant covers than in open areas such as pastures is a pattern previously documented for this group of insects (Barragán et al., 2011; Davies et al., 2020; Giménez-Gómez et al., 2018; Scholtz et al., 2009). These changes in natural vegetation act as an environmental filter, reducing the diversity of dung beetle communities and causing changes in species composition (Cardinale et al., 2012). This pattern may be associated with the fact that forest vegetation provides better microenvironmental conditions than open areas: a greater supply of food resources due to a greater presence of fauna, a decrease in soil temperature, protection against excessive radiation, and a greater quantity of leaf litter which provides protection and improves soil conditions for nesting (Edwards et al., 2017; Nunes et al., 2018; Senior et al., 2017). This result shows that conservation of the canopy (native or exotic) in the ecosystems is an important factor in the preservation of an assemblage of dung beetles of native forests by improving microenvironmental conditions and soil quality (Giménez-Gómez et al., 2018; Gómez-Cifuentes et al., 2020)

As documented, the effect of habitat loss on butterfly assemblages can be positive and maintain high diversity rather than poor communities of individuals and low species richness (Filgueiras et al., 2016; Filgueiras et al., 2019b; Melo et al., 2019). However, the low representativeness for this group is demonstrated by the high number of singletons (60 % of the species) and doubletons (16 % of the species) present in the sample. In addition, these two groups represent 23 % and 12 % of the total abundance of the sample. This high number of singletons and doubletons in the sample has a negative influence on the sampling coverage, so there may be a degree of subsampling (Cultid-Medina & Escobar, 2019). This shows the adaptation of some species to disturbances and modification of natural habitats that promotes a decrease in sensitive species and an increase in generalist species (Filgueiras et al., 2019b). Also, the high species richness in the wooded pasture may be a result of an increase in pioneer plant species which in turn increases the availability of floristic resources that serve as a food source, both for adults and larvae, in comparison to forest cover (Melo et al., 2019; Vargas-Zapata et al., 2011).

The spatial turnover of the three groups in response to changes in the vegetation types may be associated with environmental and microhabitat variations that promote a loss and gain of species (Baselga & Leprieur, 2015; Baselga et al., 2018). These differences between the natural and transformed vegetation intensify the environmental filters for the typical species of natural habitats and allow an increase of generalist species and rare or highly sensitive species (Santoandré et al., 2019). This may explain the absence of differences for ant assemblages between plant covers, since the new environmental conditions favor the colonization of atypical species towards natural habitats from modified environments (Santoandré et al., 2019). For dung beetles, environmental filters are also a factor that determines the absence of differences in composition among the plant covers; however, the proximity between natural and transformed vegetation can cause the riparian forest to be a source of individuals for recolonization of the transformed vegetation and consequently, help in the maintenance of dung beetle diversity (Gilroy & Edwards, 2017). For butterflies, the low abundance of many species and the high number of rare (unique) species in the wooded pasture may indicate that they only use this area as a foraging area (Debinski & Holt, 2000).

Contrary to what we expected, functional diversity was low both in natural vegetation (riparian forest and secondary forest) and in transformed vegetation (pine plantation and wooded pasture) for the three groups of insects. At the ecosystem level, these low functional values could cause lower productivity, stability and resilience in the communities, since resources are not used in an optimal way due to low species complementarity (Kinzig et al., 2002; Mason et al., 2005).

Our results show that habitat loss does not have negative effects on functional diversity since there are no differences between natural and transformed vegetation. It can be assumed that the response relationship depends on various factors. (1) The functional trait considered: the high number of individuals of generalist species that we observed may be masking the true effects of habitat loss on the functional diversity of the insect species (Cadotte et al., 2011). Thus, generalist species that contribute disproportionately to ecosystem functions have unique functional traits that allow them to capture more resources available in the different plant covers (Mason et al., 2005; Mouillot et al., 2005). (2) Species richness does not greatly influence the results of the functional diversity, so our results show that there may be a high functional redundancy in the three groups of insects among the different vegetation types (Filgueiras et al., 2019a; Pla et al., 2012); consequently, the loss or gain of species caused by the loss of habitat, can be compensated due to the existence of functionally similar species (Cadotte et al., 2011). (3) The high dominance of generalist species over specialist species greatly affects the functional diversity of the three groups of insects, as has already been documented for these three groups (Filgueiras et al., 2019a). Consequently, the loss or decline of forest-dependent species (i.e., disturbance-sensitive species) can be offset by the proliferation of disturbance-adapted species that maintain community-level attributes (i.e., abundance, species richness) in tropical landscapes with anthropic intervention (Filgueiras et al., 2019a). Our results show a differential response of each insect group with respect to habitat transformation (quantity and type). The lack of congruence among the three insect groups provides information necessary to support multitaxon studies and for biodiversity monitoring, since a single taxon cannot provide a reliable view of biotic responses to habitat loss.

Does the amount of habitat affect the taxonomic and functional diversity of insects? Species richness and functional regularity were influenced by the amount of habitat in the study area. Thus, in landscapes where the level of habitat loss is low, the remnants of natural vegetation maintain high structural connectivity and therefore high diversity, contributing to the increase in migratory species between vegetation types and maintaining communities with high number of species (Fahrig, 2003; Püttker et al., 2011). However, it should be noted that our results should be interpreted as a first approach to the effect of the amount of habitat in this region of foothills, since the area that was chosen as a sample of the region. The foregoing may mean that this landscape metric (amount of habitat) is not the only one that may be acting on the diversity of insects and that there are other drivers that contribute to the richness of insect species, for example, proximity and composition of the vegetation in the landscape (Fahrig, 2013; Fahrig et al., 2019). This agrees with Watling et al. (2020), who describe the proximity between patches as one of the most important drivers of richness in a landscape, and with Fahrig et al. (2019) who describe low competition, diversity of habitats in the landscape, and a greater success of movement between patches, as factors that can counteract the negative effects due to habitat loss.

Similarly, another factor that differentially influences species richness in each of the insect assemblages is the composition of the vegetation, rather than the configuration of the patches in the landscape (i.e., size, shape, level of fragmentation) as has been demonstrated in other taxa (Arroyo-Rodríguez et al., 2016; Püttker et al., 2020). For example, for ants and butterflies the wooded pasture is a type of high-quality matrix that contains resources, facilitates movement between forest patches and buffers the negative effects of the loss of natural vegetation (Arroyo-Rodríguez et al., 2020). These shade-using species require less forest in the landscape to survive, resulting in an interaction between the amount of habitat and the quality of the matrix (Fahrig, 2001). Regarding the dung beetles and their relationship with the riparian forest, this type of coverage is of utmost importance for species that depend on humid environments for their reproduction, by maintaining minimal fluctuations in environmental conditions and, to a greater extent, by promoting biological connectivity between patches when used as biological corridors (Arroyo-Rodríguez et al., 2020; Fischer & Lindenmayer, 2007).

Our study provides evidence that the amount of habitat is a factor of great relevance for the maintenance of diversity in a landscape. However, habitat connectivity and heterogeneity of a landscape are important factors in the maintenance of insect diversity, both for species that are not very sensitive and for species highly sensitive to disturbances, as previously demonstrated in other studies (Filgueiras et al., 2016; Melo et al., 2019). Finally, we want to highlight the importance of the remnants of natural vegetation which function as sources and biological corridors that maintain patterns of diversity in the landscape. Thus, efforts at biodiversity conservation should be aimed at maintaining and increasing the connectivity of the landscape by increasing the amount of natural habitat, for example, through restoration or regeneration.

Temporaral variation: Although turnover explains the beta diversity between seasons, the absence of differences in the composition may be due to an overlap in the reproductive seasons of the insect species: cycles with irregular mortality but with constant reproduction (Kishimoto-Yamada & Itioka, 2015). This suggests that the communities are stable over time (Sackmann, 2006). These minimal changes in the composition of insects may be associated with the low monthly fluctuation in rainfall regimes that are characteristic of neotropical areas (Kishimoto-Yamada & Itioka, 2015). However, even though precipitation is an environmental variable that affects the dynamics of arthropod communities (Kishimoto-Yamada & Itioka, 2015; Mariottini et al., 2012), the composition and structure of insect assemblages over time may be influenced by other variables such as the structure and composition of the vegetation (Casas-Pinilla et al., 2017; Mahecha-Jiménez et al., 2011).

Implications for conservation: Our study contributes to an understanding of the patterns caused by habitat loss at the level of composition, species richness, abundance, and spatial and temporal change in groups of insects with different ecological roles in a transformed area with a deficit of information on biodiversity. Our results show that for insects, the amount of habitat and their connectivity, indicated by the proximity of natural vegetation to the transformed vegetation, are important factors for the maintenance of biodiversity in modified ecosystems of the foothills of Orinoquia. In addition to the above: (1) the type of pastures also plays an important role in maintaining the diversity of insects; that is, the quality of the matrix plays an important role in ecosystems with anthropic disturbances (Fahrig, 2001): (2) natural vegetation patches, which are relatively small in the landscape, can play an important role in maintaining the taxonomic and functional diversity of insect assemblages in the region, as has been demonstrated in other studies (Fahrig, 2017; Fahrig, 2019). In this way, conservation efforts should be aimed at restoring landscape connectivity and modifying transformed ecosystems so that they are more amenable to biodiversity, such as moving from clean cattle pastures to wooded pastures.

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RESUMEN

Efectos de la pérdida de hábitat en tres ensambles de insectos en ecosistemas modificados de Piedemonte en la Orinoquia colombiana

Introducción: Los efectos de la transformación del hábitat han sido ampliamente estudiados y son bien conocidos los efectos a diferentes niveles de organización biológica. Sin embargo, pocos estudios se han centrado en las respuestas a este proceso a nivel de múltiples taxones en diversos grupos taxonómicos y funcionales.
Objetivo: Determinar las variaciones en la diversidad taxonómica y funcional de hormigas, mariposas y escarabajos coprófagos, a nivel espacial y temporal en un mosaico paisajístico de la ecorregión del piedemonte colombiano.
Métodos: Evaluamos la cantidad de hábitat natural y la composición del paisaje en cuatro tipos de vegetación, durante los períodos de mayor y menor lluvia. Recolectamos mariposas con redes de mano y usamos trampas de caída con cebo para escarabajos coprófagos y hormigas.
Resultados: La pérdida de hábitat afectó positivamente la riqueza de especies de hormigas y mariposas y afectó negativamente a los escarabajos peloteros. La abundancia de hormigas y mariposas tuvo un efecto positivo sobre la dominancia de especies en la vegetación transformada, para los escarabajos coprófagos la abundancia se vio afectada negativamente por la ausencia de cobertura de dosel. La pérdida de hábitat no tuvo un efecto negativo sobre la diversidad funcional ya que no hay diferencia entre la vegetación natural y la transformada.
Conclusiones: La cantidad de hábitat, la conectividad del hábitat y los diferentes tipos de cobertura vegetal fueron factores importantes en el mantenimiento de la diversidad de insectos en los ecosistemas modificados del piedemonte de la Orinoquia colombiana. La falta de un patrón espacial y temporal común muestra que se deben realizar estudios de múltiples taxones de insectos para los procesos de monitoreo y conservación de la biodiversidad.

Palabras clave: fragmentación del hábitat; cantidad de hábitat; hormigas; mariposas; escarabajos peloteros; paisaje neotropical.

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