Functional and taxonomic responses of tropical moth communities to deforestation

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Yenny Correa Carmona[1,2], Rodolphe Rougerie[3], Pierre Arnal[3], Liliana Ballesteros-Mejia[3,4,5], Jan Beck[6,7], Sylvain Dolédec[8], Chris Ho[9], Ian J. Kitching[10], Patrick Lavelle[11], Solen Le Clec'h[12], Carlos Lopez Vaamonde[13,14], Marlúcia B. Martins[15], Jérôme Murienne[16], Johan Oszwald[17], Sujeevan Ratnasingham[9], Thibaud Decaëns[1*]

1. CEFE, Univ Montpellier, CNRS, EPHE, IRD, Univ Paul Valéry Montpellier 3, Montpellier, France
2. Grupo de Entomología Universidad de Antioquia (GEUA). AA 1226. Medellín, Colombia
3. Muséum national d'Histoire naturelle, Institut de Systématique, Évolution, Biodiversité, UMR 7205 ISYEB, MNHN, CNRS, EPHE, Sorbonne Univ, Univ Antilles, Paris, France
4. CESAB, Centre de Synthèse et d'Analyse sur la Biodiversité, Montpellier, France
5. Grupo de Investigación Diseño, Imagen y Comunicación. Facultad de Creación y Comunicación. Universidad El Bosque. Bogotá – Colombia
6. Department of Environmental Sciences, Univ Basel, Basel, Switzerland
7. Museum of Natural History, Univ Colorado, Boulder, Colorado
8. Univ Lyon, Université Claude Bernard Lyon 1, CNRS, ENTPE, UMR 5023 LEHNA, F-69622, Villeurbanne, France
9. Centre for Biodiversity Genomics, Univ Guelph, Guelph, Ontario, Canada
10. Department of Life Sciences, Natural History Museum, London, UK
11. Univ Paris Sorbonne, IEES-BIODIS, Paris, France
12. Environmental Systems Analysis Group, Wageningen University, Wageningen, the Netherlands
13. INRAE, UR0633 Zoologie Forestière, Orléans, France
14. Institut de Recherche sur la Biologie de l'Insecte UMR 7261, CNRS – Univ Tours, Tours, France

15. Laboratório de Ecologia de Invertebrados, Coordenacão de Zoologia, Museu Paraense Emilio Goeldi, Belém, Pará, Brazil

16. Laboratoire Evolution et Diversité Biologique (UMR5174) - Université de Toulouse, CNRS, IRD, UPS - Toulouse, France

17. COSTEL, UMR CNRS 5654, Univ Rennes 2, Rennes, France

* Corresponding author: Thibaud.Decaens@cefe.cnrs.fr

Abstract

1. Global insect decline has recently become a cause for major concern, particularly in the tropics where the vast majority of species occurs. Deforestation is suggested as being a major driver of this decline, but how anthropogenic changes in landscape structure affect tropical insect communities has rarely been addressed.

2. We sampled Saturniidae and Sphingidae moths on 27 farms located in Brazilian Amazonia (Pará state) and characterized by different deforestation histories. We used functional traits (forewing length, body mass, wing load, trophic niche breadth and resource use strategy), analysed by combining RLQ and null model analyses, to investigate the responses of their taxonomic and functional diversity to landscape change dynamics and current structure.

3. We found that communities had a higher proportion of large and polyphagous species with low wing load in landscapes with low forest quality and relative cover and high land use turnover. This was mainly due to a significant response to deforestation by saturniids, whereas the more mobile sphingids showed no significant landscape-related pattern. We also observed an overall increase of species richness and functional dispersion in landscapes that have been deforested for a long time when compared with more recent agricultural settlements.

4. Our results highlight the complex way in which landscape structure and historical dynamics interact to shape Neotropical moth communities and that saturniid moths respond clearly to the structure of the surrounding landscape, confirming their potential use as an indicator group for environmental monitoring programs.

Key words: community ecology, landscape ecology, functional traits, Neotropical insect decline, Lepidoptera

Introduction

Understanding how species adapt to human-impacted landscapes, and how ecological communities are modified in response, are important ecological questions (Gardner et al., 2010) traditionally addressed by analysing variations in taxonomic diversity along gradients of deforestation or landscape anthropization. This approach enables the quantification of human impacts on biodiversity, but does not provide information on the mechanisms involved in biodiversity erosion (Majekova et al., 2016), for which studies of the functional and phylogenetic components of biodiversity are required (Devictor et al., 2010; Mouillot et al., 2013). At a landscape scale, species traits (e.g. body size, dispersal capacity, diet and habitat specialization) are fundamental for explaining how species may adapt to their environment, and can help assess the conservation value of agricultural landscapes for their consideration into conservation strategies (Gamez-Virues et al., 2015).

The Amazonian rainforest is the largest remaining frontier forest on Earth (i.e. large, ecologically intact, and relatively undisturbed natural forests; Bryant et al., 1997), long recognized for its outstanding biodiversity (Cardoso Da Silva et al., 2005; Wilson, 2002). However, it faces alarming rates of deforestation, mainly from expanding agricultural encroachment and timber production, and increasingly frequent large-scale forest fires (Kelly et al., 2020; Newbold et al., 2014). Among agricultural activities, small-scale subsistence agriculture has been identified as a powerful driver of landscape transformation and deforestation in the Amazon, second after cattle ranching (Kalamandeen et al., 2018). Recent estimates report a loss of about 710,000 km^2 of forest from 1970-2018, almost 20% of the original forest cover (Butler, 2020). This conversion is known to have dramatic consequences for biodiversity, but potential non-linear and threshold effects are still poorly understood (Barlow et al., 2016; Decaëns et al., 2018). Agro-conversion is also likely to affect the environmental stability of the entire region with potential negative effects on key ecosystem services for local human populations (Lavelle et al., 2016).

The conservation of Amazonian biodiversity also faces the challenge of the choice of biological models to document the response of biological communities to environmental change. Most studies have focused on a few exemplar groups of organisms whose responses are assumed to be representative of all biodiversity (Fazey et al., 2005; Gardner et al., 2009). This has generated a strong bias towards vertebrates and flowering plants, with other important components of terrestrial biodiversity, such as invertebrates, being under-represented (Collen et al., 2009). Therefore, there is a critical need to broaden the taxonomic spectrum of research into biodiversity-disturbance relationships, and to strengthen the representation of the most speciose groups in these kinds of studies. Of these, insects represent a major component of biodiversity (over 1,000,000 named species; Stork, 2018) and their accelerating decline has recently caused major concern (Wagner, 2020). Deforestation is one of the major drivers of this decline (Eggleton, 2020), but most studies have focused on temperate forests (Thom & Seidl, 2016). This is partly due to the challenges posed by sampling tropical insects (Hanski et al., 2009; Ros & Pineda, 2009), resulting in many groups being largely undocumented, together with a strong taxonomic impediment plaguing most insect orders (Cardoso Da Silva et al., 2005). We thus need more studies to better understand the processes at play behind deforestation effects on tropical insect communities, especially at the landscape scale and by integrating the temporal dynamics of landscape elements. Indeed, the dynamics of landscape patches, which is recognised as an important factor affecting biodiversity in temperate regions (Ernoult et al., 2006; Fischer, 2001; Vogt-Schilb et al., 2018), has so far not been considered to explain the response of tropical insects to deforestation.

Saturniidae (wild silkmoths) and Sphingidae (hawkmoths) are some of the most charismatic insects. They are phylogenetically sister lineages with contrasting life-histories (Janzen, 1984). Sphingids are mostly income-breeders (*sensu* Jonsson, 1997), with short life cycles, mono-/oligophagous larvae, and adult females ovipositing only a few eggs per hostplant. Adult moths of most species are active flower foragers and excellent fliers, some species exhibiting migratory behaviour (Ballesteros-Mejia et al., 2017). In contrast, saturniids are typically capital-breeders with non-feeding adults, long life cycles, polyphagous larvae, and adult females ovipositing many eggs per hostplant; they are considered poor dispersers (Tuskes et al., 1996).

Here, we investigate the responses of the taxonomic and functional diversity of saturniid and sphingid communities to the structure of agroecosystems in a recently deforested area of Brazilian Amazonia. Moth communities were sampled in three different landscapes representing distinct deforestation dynamics, from young agricultural settlements to areas with a longer history of agro-conversion. We test three hypotheses: (1) Taxonomic and functional diversity decrease with deforestation; (2) Due to lower dispersal abilities, capital-breeders are more sensitive to deforestation than income-breeders; (3) Following deforestation, moth communities become increasingly dominated by species that are generalist/polyphagous and/or have high dispersal capabilities.

Materials and Methods

Study sites

The study was undertaken in three areas of Brazilian Amazonia in Pará state (Fig. 1), all characterized by recent and rapid agricultural dynamics but with different deforestation histories and subsequent agricultural dynamics (Oszwald et al., 2011):

1) The Pacajá area (51°0'9"W, 3°39'36"S) was occupied by highway settlers from the early 1990s, who delimited 100 ha agricultural plots along tertiary roads. Most deforestation took place in the decade before sampling.
2) Palmares II (5°46'8"S, 49°53'43"W) is a large cattle farm from the late 1980s, later invaded in 1994 by farmers from the Landless Worker Movement, who expropriated the owner and divided the farm into 520 plots of 25 ha. Subsequent deforestation culminated within the 20 years before sampling.
3) The Maçaranduba area (49°18'34"W, 4°45'5"S) was first impacted in the 1970s by the Amazonian deforestation front, the forest remnants then underwent secondary deforestation during the 1990s. It is currently occupied by an agro-extractivist community that has largely shifted towards cattle ranching.

The study areas are distant from each other by 120 and 230 km respectively, and were all originally covered by the same type of tropical rainforest (Xingu/Tocantins/Araguaia and Tocantins/Pindare moist forests; Silva-Souza & Souza, 2020) within the Belém centre of endemism (Cardoso Da Silva et al., 2005).

Landscape structure variables

In each study area, we selected nine non-contiguous farms that best represent the local production systems (Lavelle et al., 2016). These farms were then used as replicated elementary units to describe landscape structure from Landsat images taken in five different years between 1990 and 2007 (Table 1; SI table 1). We calculated six landscape metrics that we considered important in structuring moth communities: i) the amount of habitat, measured as the % cover of mature forest within each farm in 2007; ii) landscape fragmentation, estimated from total edge density; iii) landscape dynamics, determined as the mean between-year land-use turnover (i.e., change in land-use composition); iv) an index of forest patch stability, calculated from the temporal dynamics of the forest mean patch density during the 1990-2007 period; v) an index of habitat quality, measured as the proportion of forest on a given farm that was undisturbed during the 1990-2007 period; and vi) the diversity of potential hostplants, assessed using tree diversity recorded at five equidistant points along a 1 km transect within each farm (Decaëns et al., 2018).

Moth sampling and taxonomic assignments

On each farm, moths were sampled between April and June 2008 using light trapping on a single moonless night (i.e., 9 collecting nights per study area). The light trap consisted of a white sheet (2 m×3 m) illuminated with a 175W mercury vapour bulb powered by a portable generator. The trap was placed near the centre of the farm and about 50m from the largest forest remnant. Collecting took place from 18h00 to 06h00 to enable the detection of species with different flight behaviours (de Camargo et al., 2016; Lamarre et al., 2015). Specimens were killed by ammonia injection, dried with silica gel and stored in labelled paper envelopes.

Species identifications were initially based on wing patterns, but confirmed by DNA barcoding (Hebert et al., 2003), which was particularly useful for damaged specimens, where diagnostic characters were unavailable, or in taxonomically complex genera (see Supporting Information for details; accounting for unnamed/undescribed taxa using Barcode Index Numbers (BINs, see Ratnasingham & Hebert, 2013).

Functional trait measures

We considered five functional traits for analyses. Morphological features were measured for 1-3 individuals per moth species (a number considered sufficient for multi-species trait-based analyses; Beck, pers. comm.), on specimen images using the image annotation tool specifically implemented for that purpose in BOLD (see Supplementary Information; Ratnasingham & Hebert, 2007). For this purpose, the images used represented the dorsal side of specimens prepared according to entomological museum standards (see example in Supplementary Information). In total, we measured seven morphometric traits on 301 images (SI Table 2) that were then used to calculate three morphological functional traits: i) the forewing length (cm), a commonly-used measure of body size in Lepidoptera (Beck & Kitching, 2007), defined as the maximum distance between the base of the costa and the apex of the forewing; ii) the product of thorax width and body length (cm^2), which was used as a proxy for body mass; and iii) the wing load, which was estimated as the ratio of thorax width to wing surface (forewing + hindwing), used as a surrogate for flight strength (species with high wing loads are expected to have more powerful flight than species with low wing loads; Beck & Kitching, 2007). To maintain consistency in the dataset, we used only images of males, so that we could also include species whose females are not documented in our dataset.

We quantified the trophic niche breadth as the average count of plant genera consumed by caterpillars for each moth genus (Ballesteros-Mejia et al., 2020). For each species, the resource use strategies were categorized into capital and income breeding strategies to differentiate species whose adults do not feed and rely on reserves accumulated during larval instars, thereby reproducing independently of adult stage resource availability (capital breeders), from species able to feed during adulthood and thus able to allocate adult stage resources directly for reproduction (income breeders) (Beck et al., 2006; Jonsson, 1997). Assignment to either of these two categories can be made by examining the presence or absence of a functional proboscis in adult specimens. In South America, saturniids are exclusively capital breeders while the majority of sphingids are income breeders.

Statistical analyses

In a first step, we compared regional species richness among the three study areas by plotting rarefaction and extrapolation curves with number of collecting nights as a measure of sampling intensity ('iNEXT' package in R v.3.5.3; Hsieh et al., 2019; R Core Team, 2019). Second, we calculated for each farm, the observed richness (total number of species observed) and the incidence-based Chao index, which estimates the lower bound for the expected asymptotic species richness (Gotelli & Chao, 2013) ('estimateR' and 'diversity' functions of the 'vegan' package; Oksanen et al., 2019). Finally, we calculated the average Sorensen beta-diversity among pairs of farms within each study area using the 'betadiver' function ('vegan' package). To avoid any overestimation of beta-diversity due to the presence of singletons (i.e. species represented by a single specimen in the dataset), analyses were done using successively the whole dataset and a subset without singletons. As we could not find any significant differences between the two ways of calculating, we finally decided to keep the singletons in the analyses.

In a second step, we analysed the links between functional traits and landscape metrics using RLQ analysis, a multivariate tool that maximizes the covariance between linear combinations of traits and environmental variables mediated by species abundances (Dolédec et al., 1996; Dray et al., 2014). Three different RLQ were computed (see Supporting Information), for the two families together using the complete set of functional traits, and for each family independently after removing the resource use trait, which was constant within each family ('ade4' package in R; Dray & Dufour, 2007). The overall statistical significance of the analysis was tested using the function 'fourthcorner2'. The links between traits and landscape metrics and their association with the axes of covariation were tested through a fourth-corner analysis using adjusted p-values to control for false discovery rate, with the functions ‘fourthcorner’, and ‘fourthcorner.rlq’ (Dray et al., 2014; Dray & Legendre, 2008; Legendre et al., 1997).

In a final step, for each moth community (i.e. species assemblage described at the farm-scale), we calculated six functional diversity indices: functional richness (FRic), which is the amount of functional space filled by the community; functional evenness (FEve), which highlights the regularity of abundance distributions in the functional space; functional divergence (FDiv), which estimates the proportion of the total abundance that is supported by the species with the most extreme functional traits; functional dispersion (FDis), which is the abundance-weighted average distance of species to the centroid of the functional space; and the Rao’s quadratic entropy (RaoQ), which is the abundance-weighted sum of pairwise functional distances between species (‘dbFD’ function of the ‘FD’ package for R; Laliberté et al., 2014). We then calculated community-level weighted means (CWM; Lavorel et al., 2008) for all the functional traits of the trait table. To determine whether functional diversity indices and trait CWMs were different from those expected by chance, we recalculated them all using 999 randomized community tables (‘randomizeMatrix’ function of the ‘picante’ package; Kembel et al., 2010) under the ‘independentswap’ null model; (Kembel et al., 2010). We then used the standard deviation of the 999 simulated indices to calculate the standardized effect size (SES) as suggested by Gotelli & McCabe (2002). We analysed the variations of these indices along the gradient described by the RLQ first axis through linear mixed-effects models (LMM) with study area as the random effect (‘lmer’ function of the ‘lme4’ package in R, and ‘lmerTest’ package for associated p values; Bates et al., 2015; Kuznetsova et al., 2017).

Results

Effect of deforestation on biodiversity metrics of moth communities

A total of 1210 specimens was collected from the three study areas, for which 602 DNA barcodes were obtained, representing 120 species (SI Table 3), of which 111 corresponded to previously named species, 9 were unnamed BINs of saturniids (i.e., three *Hylesia* species, and one unnamed BIN in six other genera). Most of the regional diversity comprises saturniids (71 species, 26 genera), whereas sphingids are less diverse (49 species, 20 genera). We found a perfect match between morphological and molecular (BINs) identifications, except for two species of saturniids (i.e., *Dirphia panamensis* and *Ptiloscola cinerea*) and two species of sphingids (*Erynnyis ello* and *Manduca diffissa*), which were each split into two distinct BINs.

The rarefaction and extrapolation curves, adjusted for the three study areas, clearly showed that Palmares had a lower overall cumulative species richness compared with Pacajá and Maçaranduba (Fig. 2). This is driven by variations in saturniid diversity across the three study areas; no difference was observed for sphingids (SI Fig. 3). This trend was confirmed by the cumulative asymptotic indices for each study area, and the average Sorensen index for each moth family, highlighting that beta-diversity was highest in Pacajá and lowest in Palmares (Table 2).

Effects of deforestation on functional moth diversity

The fourth corner analysis indicated a significant link between species and landscape metrics (simulated-p = 0.034), between traits and species distribution (simulated-p = 0.008), and between traits and landscape metrics (simulated-p = 0.036). The fourth corner analysis detected a marginally significant link between forewing length and forest cover (p = 0.094). It also highlights that the combination of landscape metrics synthesized by the first RLQ axis was significantly linked with wing load, forewing length and polyphagy level (Fig. 3A), and that the combination of traits synthetized by the first RLQ axis was significantly linked with percentage forest cover, forest quality, and temporal turnover of land uses (Fig 3B).

The first RLQ axis explained up to 98% of the total variance of the matrix that crosses landscape metrics and species functional traits (Fig. 3D). It revealed a difference between more recently deforested areas (i.e. Pacajá and Palmares with positive scores on the first RLQ axis) with high quality forest habitats still covering significant land surface despite being fragmented, and the more anciently deforested farms of Maçaranduba presenting a dynamics toward degraded forests and fallow extension (with negative scores on the first RLQ axis; Fig. 3C). The first RLQ axis also revealed differences between the sites, in terms of moth communities (Fig. 3A). Moth communities on the farms in Maçaranduba were characterised by large and polyphagous species with a small wing load. Farms in Pacajá and Palmares were characterized by smaller and less polyphagous species, with a higher wing load (Fig. 3A).

RLQ analyses computed for each family separately highlighted a similar gradient along the first axis setting the less recently deforested area (Maçaranduba) against the two other areas. In saturniids (SI Fig. 4), the results were globally significant and showed the same links between traits and environmental variables as the global RLQ analysis. In contrast, the RLQ analysis computed for sphingids showed no significant association between the traits and landscape variables (SI Fig. 5).

Community diversity and functional trait composition

Significant variations in several of the metrics used to describe taxonomic and functional diversity occurred along the first RLQ axis deforestation gradient (SI Fig. 6). For example, there was a significant decrease in estimated richness (Chao index) along the first RLQ axis (Fig. 4A), as well as a decrease in the SES of functional dispersion, with individual values lower than expected by chance for some communities at the recently deforested areas (Fig. 4B). As evidenced by the RLQ analysis, CWM of forewing length (Fig. 4C) and of the degree of polyphagy (Fig. 4D) decreased significantly along the first RLQ axis, showing higher values than expected by chance in some communities of Maçaranduba, and lower than expected by chance in some others at Pacajá and Palmares. Conversely, wing load CWM significantly increased along the RLQ axis, reaching values higher than expected by chance in some of the more recently deforested farms (Fig. 4E).

Discussion

Contrary to the expectation of our first hypothesis, we did not find any clear decrease in either taxonomic or functional diversity with increased deforestation. Instead, we found that both estimated species richness and functional trait dispersion were higher in the anciently deforested landscapes. In agreement with our second hypothesis, we found different patterns of responses between saturniid and sphingid communities, likely explained by the broad functional differences that distinguish these two moth families. Finally, our results only partially validate our third hypothesis, since they reveal that moth communities in the formerly deforested landscapes, although dominated as expected by generalist species, are also composed of species that are on average larger and with a lower dispersal capacity.

Trait composition in response to landscape structure

The first RLQ axis showed a significant link between landscape structure and trait composition of moth communities, both for the pooled families and for saturniids alone. This link reveals that the most deforested landscapes (i.e., with less forest cover, lower forest quality and higher land-use temporal dynamics) comprised of larger and more polyphagous species with lower wing load. Conversely, farms with a more recent deforestation history harboured communities composed of smaller and less polyphagous species with higher wing load. For these traits, some communities in the most extreme areas of the deforestation gradient had CWMs significantly different from expected by chance.

Our finding that species were on average larger in the most deforested landscapes was surprising. Indeed, it is commonly accepted that body size in most arthropod taxa tends to decrease with the intensification of land-use and the increased simplification of the landscape (Gamez-Virues et al., 2015; Simons et al., 2016). In Lepidoptera, Rabl et al. (2020) showed that two moth taxa (i.e. Arctiinae and Geometridae) were much smaller-sized in oil palm plantations than in nearby old-growth forest. Some studies however, while supporting a significant effect of land-use intensity on arthropod body size, also noted that the direction of this effect may vary substantially among taxonomic groups (Birkhofer et al., 2017). In our study, the observed increase in moth size with increased deforestation could suggest that larger species are more efficient dispersers than smaller ones, as an increase in average dispersal capacity is an expected response of Lepidoptera communities along gradients of anthropogenic disturbances (Boerschig et al., 2013). However, it is also possible that the response of this trait is caused by factors not fully captured by our set of landscape metrics. For example, Nino et al. (2019) proposed that microclimate modification in more open landscapes could favour large species with better tolerance to desiccation. It is also possible that large moth species may benefit from positive cascading effects following a decline in predator assemblages in deforested landscapes. Insectivorous birds and bats, for instance, are known to be negatively affected by tropical rainforests fragmentation, especially those that are more specialised and larger (Farneda et al., 2015; Sekercioglu et al., 2002, 2004).

In flying insects such as Lepidoptera, it is generally accepted that wing length and thorax size are positively associated with flight ability and dispersal (Beck & Kitching, 2007). Higher wing load is assumed to indicate more muscle mass per wing area, hence greater flight strength and agility, and the community-level average of this trait is therefore expected to increase with landscape fragmentation. We found, however, that wing load CWM was higher in landscapes with the lowest levels of deforestation. This result was particularly significant in the case of saturnids, whereas no significant trend was observed for sphingids. This might suggest that wing load is not an appropriate indicator of flight efficiency in saturniids, but rather that variation in this trait is actually explained by a stronger representation of subfamily Ceratocampinae within less deforested study areas. Ceratocampinae often have high wing loads compared with other saturniids, but their position on the environmental gradient of the first RLQ axis might, however, be explained by other functional traits (wing size or trophic specialization). Alternatively, it is also possible that the fragmentation of the forest landscape that takes place at the beginning of the deforestation gradient can act as an environmental filter by disfavouring the presence of species with low dispersal capacity within communities. This hypothesis is supported by the decrease in functional dispersal observed in the most recently deforested farms, which we discuss below.

The observed increase in the degree of polyphagy within moth communities in the most intensely deforested landscapes corroborates our third hypothesis and is consistent with other similar studies. Indeed, the decline of specialists, and their gradual replacement by more generalist species, is recognized as one of the main mechanisms leading to biotic homogenization as a response to landscape disturbance (Gamez-Virues et al., 2015). At the habitat patch scale, it results directly from the increase in disturbance caused by agricultural practices and changes in vegetation composition, which tend to favour generalist life-history traits to the detriment of specialists (Boerschig et al., 2013; Mangels et al., 2017). At the landscape scale, the size of patches has also been predicted to be important for specialized feeders, which have larger home-range requirements (Gamez-Virues et al., 2015). Therefore, traits such as trophic niche breadth, and, as mentioned previously, dispersal capacity are expected to increase as the landscape deforestation intensifies.

Taxonomic and functional diversity in deforested landscapes

We found differences in regional species richness among the different study sites, especially for saturniids, which was less diverse in one of the more recently deforested area (Palmares) than in the two other study areas. At the local scale of individual communities, species richness decreased along the environmental gradient identified by the RLQ analysis, showing highest values for the less recently deforested farms and the lowest for recently deforested farms. Such an increase in alpha diversity with tropical forest disturbance has already been reported for some groups of moths (e.g. Geometridae in Borneo, Arctiidae and Geometridae in Ecuador), while opposite responses, or an absence of response, have been reported for other groups (Fiedler et al., 2007; Hilt & Fiedler, 2008). In our study, the high regional diversity at one of the recently deforested areas (Pacajá) can be readily explained by good quality forest still covering a significant proportion of the landscape, creating suitable conditions for a large number of species at this scale. The comparatively low local diversity, and the average Sorensen index of dissimilarity, together highlighted that moth communities in this area were characterised by a higher beta-diversity compared with the two other areas, which could result from heterogeneity in forest composition among forest remnants. In the other recently deforested area (Palmares), the forest cover is similar to that observed in Pacajá, but this site has a higher landscape fragmentation (edge density) and a lower species richness of plant communities (Decaëns et al., 2018). A reduction of the diversity of available food plants, together with a homogenization of forest cover composition, may thus explain the decrease in local and regional species richness at this site. Finally, high levels of species richness at the highly deforested area (Maçaranduba) might be attributed to the landscape structure, formed by a patchwork of diversified habitats, including stable forest remnants in large patches, but also fallows of different ages and well established pastures (Oszwald et al., 2011). Additionally, species richness of shrubs and trees in this site is high, both at local and regional scales (Decaëns et al., 2018). The structurally complex landscape, combined with high diversity of potential food plants, likely provides more niches and diverse ways of exploiting environmental resources, thus allowing co-occurrence of a higher number of species (Fahrig et al., 2011; Tews et al., 2004).

Functional richness and equitability did not show any variation along the first RLQ axis, yet functional dispersion tended to increase from the least to the more deforested farms. This suggests a strong effect of environmental filters on the structuring of moth communities in the least deforested landscapes, and a decrease of this effect along the deforestation gradient, which contradicts both theoretical and empirical evidence (Mouillot et al., 2013), and expectations of our first hypothesis. This suggests that the same drivers proposed to explain the high species diversity in the more deforested sites triggered an increase in niche complementarity among co-occurring species, enhancing species occurrence probabilities and/or abundances (Mason et al., 2013). In the least deforested sites, recent vegetation clearings generated a significant fragmentation of forest patches, separated from each other by sparsely vegetated areas. This early landscape transformation is likely to have generated a significant filtering of species, leading to functional under-dispersion within communities.

Differential responses of saturniid and sphingid moths to landscape structure

The most significant changes in moth communities observed in our study were due to an effect of landscape structure on saturniid communities, contrasting with the weak response of sphingid communities. This corroborates our third hypothesis, which predicted different responses by both families to deforested landscapes, because of differences in the life-histories of these moths. Sphingids are generally characterized by high mobility and an ability to forage on many flowering plant species as adults, including those in disturbed ecosystems (Hawes et al., 2009). While it is likely that some sphingids are negatively impacted by habitat disturbance, its effects seem to be counteracted and balanced by other subgroups not affected in this way, thereby explaining how the overall species richness of the family remains unchanged in different types of agricultural landscapes (Beck et al., 2006; Schulze & Fiedler, 2003). Saturniids are therefore more likely to show significant responses to anthropogenic disturbances. Recently, Basset et al. (2017) proposed Saturniidae as a potential model taxon for studying the long-term effects of climate change on tropical insects. Our results support this suggestion by demonstrating that these moths can also be used to study the effects of disturbances at finer time scales.

Conclusion

Our study demonstrates the subtle responses of Amazonian moth communities to changes in the structure of landscapes as a result of deforestation. First, the complexity and specificity of the socioeconomic situations prevailing in each study area resulted in nonlinear change of landscape features along the gradient, which induced unexpected responses in species richness and functional diversity. Although moth communities in more recently deforested sites were structured in response to environmental filters, local conditions specific to older sites allowed for the maintenance of larger numbers of species and higher functional dispersion. We further confirmed the expected response in functional trait composition, corresponding to a progressive replacement of small and specialist species with reduced mobility by generalists of larger size along the deforestation gradient. Saturniids in particular appear a suitable indicator group to monitor forest disturbance in the Amazon, as their communities show significant responses to landscape changes linked to agricultural activities. This confirms our prediction that the contrasting eco-evolutionary characteristics of these two moth families (as already discussed by Janzen, 1984), and especially their resource use strategies, imply different responses to landscape disturbance in the context of Amazonian deforestation.

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Conflicts of interest

The authors have no conflict of interest to declare.

Data availability statement

All relevant data are within the paper or stored in Zenodo repository under DOI: 10.5281/zenodo.4507401.

References

Ballesteros-Mejia, L., Arnal, P., Hallwachs, W., Haxaire, J., Janzen, D., Kitching, I. J., & Rougerie, R. (2020). A global food plant dataset for wild silkmoths and hawkmoths, and its use in documenting polyphagy of their caterpillars (Lepidoptera: Bombycoidea: Saturniidae, Sphingidae). *Biodiversity Data Journal*, *8*, e60027. https://doi.org/10.3897/BDJ.8.e60027

Ballesteros-Mejia, L., Kitching, I. J., Jetz, W., & Beck, J. (2017). Putting insects on the map: Near ‐ global variation in sphingid moth richness along spatial and environmental gradients. *Ecography, 40*, 698–708. https://doi.org/10.1111/ecog.02438

Barlow, J., Lennox, G. D., Ferreira, J., Berenguer, E., Lees, A. C., Mac Nally, R., Thomson, J. R., de Barros Ferraz, S. F., Louzada, J., Fonseca Oliveira, V. H., Parry, L., de Castro Solar, R. R., Vieira, I. C. G., Aragao, L. E. O. C., Begotti, R. A., Braga, R. F., Cardoso, T. M., de Oliveira, R. C., Souza, C. M., … Gardner, T. A. (2016). Anthropogenic disturbance in tropical forests can double biodiversity loss from deforestation. *Nature*, *535*(7610), 144–147. https://doi.org/10.1038/nature18326

Basset, Y., Lamarre, G. P. A., Ratz, T., Segar, S. T., Decaëns, T., Rougerie, R., Miller, S. E., Perez, F., Bobadilla, R., Lopez, Y., Ramirez, J. A., Aiello, A., & Barrios, H. (2017). The Saturniidae of Barro Colorado Island, Panama: A model taxon for studying the long- term effects of climate change? *Ecology and Evolution*, *7*, 9991–10004.

Bates, D., Maechler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, *67*(1), 1–48. https://doi.org/doi:10.18637/jss.v067.i01.

Beck, J., & Kitching, I. J. (2007). Correlates of range size and dispersal ability: A comparative analysis of sphingid moths from the Indo-Australian tropics. *Global Ecology and Biogeography*, *16*(3), 341–349. https://doi.org/10.1111/j.1466-8238.2007.00289.x

Beck, J., Kitching, I. J., & Linsenmair, K. E. (2006). Effects of habitat disturbance can be subtle yet significant: Biodiversity of hawkmoth-assemblages (Lepidoptera: Sphingidae) in

Southeast-Asia. *Biodiversity and Conservation*, *15*(1), 465–486. https://doi.org/10.1007/s10531-005-0306-6

Birkhofer, K., Gossner, M. M., Diekoetter, T., Drees, C., Ferlian, O., Maraun, M., Scheu, S., Weisser, W. W., Wolters, V., Wurst, S., Zaitsev, A. S., & Smith, H. G. (2017). Land-use type and intensity differentially filter traits in above- and below-ground arthropod communities. *Journal of Animal Ecology*, *86*(3), 511–520. https://doi.org/10.1111/1365-2656.12641

Boerschig, C., Klein, A.-M., von Wehrden, H., & Krauss, J. (2013). Traits of butterfly communities change from specialist to generalist characteristics with increasing land-use intensity. *Basic and Applied Ecology*, *14*(7), 547–554. https://doi.org/10.1016/j.baae.2013.09.002

Bryant, D., Nielsen, D., & Tangley, L. (1997). *The last frontier forests: Ecosystems and economies on the edge*. World Resources Institute.

Butler, R. (2020). *Calculating deforestation figures for the Amazon*. https://rainforests.mongabay.com/amazon/deforestation_calculations.html

Cardoso Da Silva, J. M., Rylands, A. B., & Da Fonseca, G. A. B. (2005). The fate of the Amazonian areas of endemism. *Conservation Biology*, *19*, 689–694.

Collen, B., Loh, J., Whitmee, S., McRae, L., Amin, R., & Baillie, J. E. M. (2009). Monitoring Change in Vertebrate Abundance: The Living Planet Index. *Conservation Biology*, *23*(2), 317–327. https://doi.org/10.1111/j.1523-1739.2008.01117.x

de Camargo, A. J. A., de Camargo, N. F., Correa, D. C. V., de Camargo, W. R. F., Vieira, E. M., Marini-Filho, O., & Amorim, F. W. (2016). Diversity patterns and chronobiology of hawkmoths (Lepidoptera, Sphingidae) in the Brazilian Amazon rainforest. *Journal of Insect Conservation*, *20*(4), 629–641. https://doi.org/10.1007/s10841-016-9894-6

Decaëns, T., Martins, M. B., Feijoo, A., Oszwald, J., Doledec, S., Mathieu, J., de Sartre, X. A., Bonilla, D., Brown, G. G., Cuellar Criollo, Y. A., Dubs, F., Furtado, I. S., Gond, V., Gordillo, E., Le Clec'h, S., Marichal, R., Mitja, D., de Souza, I. M., Praxedes, C., … Lavelle, P. (2018). Biodiversity loss along a gradient of deforestation in Amazonian agricultural landscapes. *Conservation Biology*, *32*(6), 1380–1391. https://doi.org/10.1111/cobi.13206

Devictor, V., Mouillot, D., Meynard, C., Jiguet, F., Thuiller, W., & Mouquet, N. (2010). Spatial mismatch and congruence between taxonomic, phylogenetic and functional diversity: The need for integrative conservation strategies in a changing world. *Ecology Letters*, *13*(8), 1030–1040.

https://doi.org/10.1111/j.1461-0248.2010.01493.x

Dolédec, S., Chessel, D., terBraak, C. J. F., & Champely, S. (1996). Matching species traits to environmental variables: A new three-table ordination method. *Environmental and Ecological Statistics*, *3*(2), 143–166. https://doi.org/10.1007/BF02427859

Dray, S., Choler, P., Dolédec, S., Peres-Neto, P. R., Thuiller, W., Pavoine, S., & ter Braak, C. J. F. (2014). Combining the fourth-corner and the RLQ methods for assessing trait responses to environmental variation. *Ecology*, *95*(1), 14–21. https://doi.org/10.1890/13-0196.1

Dray, S., & Dufour, A.-B. (2007). The ade4 package: Implementing the duality diagram for ecologists. *Journal of Statistical Software*, *22*(4), 1–20. https://doi.org/10.18637/jss.v022.i04

Dray, S., & Legendre, P. (2008). Tresting the species traits-environment relationships: The fourth-corner problem revisited. *Ecology*, *89*(12), 3400–3412. https://doi.org/10.1890/08-0349.1

Eggleton, P. (2020). The state of the World's insects. *Annual Review of Environment and Resources*, *45*, 7–20.

Ernoult, A., Tremauville, Y., Cellier, D., Margerie, P., Langlois, E., & Alard, D. (2006). Potential landscape drivers of biodiversity components in a flood plain: Past or present patterns? *Biological Conservation*, *127*(1), 1–17. https://doi.org/10.1016/j.biocon.2005.07.008

Fahrig, L., Baudry, J., Brotons, L., Burel, F. G., Crist, T. O., Fuller, R. J., Sirami, C., Siriwardena, G. M., & Martin, J.-L. (2011). Functional landscape heterogeneity and animal biodiversity in agricultural landscapes. *Ecology Letters*, *14*(2), 101–112. https://doi.org/10.1111/j.1461-0248.2010.01559.x

Farneda, F. Z., Rocha, R., Lopez-Baucells, A., Groenenberg, M., Silva, I., Palmeirim, J. M., Bobrowiec, P. E. D., & Meyer, C. F. J. (2015). Trait-related responses to habitat fragmentation in Amazonian bats. *Journal of Applied Ecology*, *52*(5), 1381–1391. https://doi.org/10.1111/1365-2664.12490

Fazey, I., Fischer, J., & Lindenmayer, D. B. (2005). What do conservation biologists publish? *Biological Conservation*, *124*(1), 63–73. https://doi.org/10.1016/j.biocon.2005.01.013

Fiedler, K., Hilt, N., Brehm, G., & Schulze, C. H. (2007). Moths at tropical forest margins—How mega-diverse insect assemblages respond to forest disturbance and recovery. In T. Tscharntke, C. Leuschner, M. Zeller, E. Guhardja, & A. Bidin (Eds.), *Stability of Tropical*

Rainforest Margins: Linking Ecological, Economic and Social Constraints of Land Use and Conservation (pp. 39-+).

Fischer, M. (2001). Landscape dynamics can accelerate metapopulation extinction. *Trends in Ecology & Evolution*, *16*(5), 225–226. https://doi.org/10.1016/S0169-5347(01)02175-9

Gamez-Virues, S., Perovic, D. J., Gossner, M. M., Boersching, C., Bluethgen, N., de Jong, H., Simons, N. K., Klein, A.-M., Krauss, J., Maier, G., Scherber, C., Steckel, J., Rothenwoehrer, C., Steffan-Dewenter, I., Weiner, C. N., Weisser, W., Werner, M., Tscharntke, T., & Westphal, C. (2015). Landscape simplification filters species traits and drives biotic homogenization. *Nature Communications*, *6*, 8568. https://doi.org/10.1038/ncomms9568

Gardner, T. A., Barlow, J., Chazdon, R., Ewers, R. M., Harvey, C. A., Peres, C. A., & Sodhi, N. S. (2009). Prospects for tropical forest biodiversity in a human-modified world. *Ecology Letters*, *12*(6), 561–582. https://doi.org/10.1111/j.1461-0248.2009.01294.x

Gardner, T. A., Barlow, J., Sodhi, N. S., & Peres, C. A. (2010). A multi-region assessment of tropical forest biodiversity in a human-modified world. *Biological Conservation*, *143*(10), 2293–2300. https://doi.org/10.1016/j.biocon.2010.05.017

Gotelli, N., & Chao, A. (2013). Measuring and Estimating Species Richness, Species Diversity, and Biotic Similarity from Sampling Data. In S. A. Levin (Ed.), *Encyclopedia of Biodiversity* (2nd ed., Vol. 5, pp. 195–211). Academic Press.

Gotelli, N. J., & McCabe, D. J. (2002). Species co-occurrence: A meta-analysis of J.M. Diamond's assembly rules model. *Ecology*, *83*(8), 2091–2096.

Hanski, I., Meyke, E., & Miinala, M. (2009). Deforestation and tropical insect extinctions Reply. *Biology Letters*, *5*(5), 653–655. https://doi.org/10.1098/rsbl.2009.0457

Hawes, J., Motta, C. da S., Overal, W. L., Barlow, J., Gardner, T. A., & Peres, C. A. (2009). Diversity and composition of Amazonian moths in primary, secondary and plantation forests. *Journal of Tropical Ecology*, *25*, 281–300. https://doi.org/10.1017/S0266467409006038

Hebert, P. D. N., Cywinska, A., Ball, S. L., & DeWaard, J. R. (2003). Biological identifications through DNA barcodes. *Proceedings of the Royal Society B-Biological Sciences*, *270*(1512), 313–321. https://doi.org/10.1098/rspb.2002.2218

Hilt, N., & Fiedler, K. (2008). Successional stages of faunal regeneration—A case study on megadiverse moths. In *Gradients in a tropical mountain ecosystem ot Ecuador* (pp. 443–449).

Springer-Verlag.

Hsieh, T. C., Ma, K. H., & Chao, A. (2019). *iNEXT: iNterpolation and EXTrapolation for species diversity. R package version 2.0.19.*

Janzen, D. H. (1984). Two ways to be a tropical big moth: Santa Rosa saturniids and sphingids. *Oxford Surveys in Evolutionary Biology*, *1*, 85–140.

Jonsson, K. I. (1997). Capital and income breeding as alternative tactics of resource use in reproduction. *Oikos*, *78*(1), 57–66. https://doi.org/10.2307/3545800

Kalamandeen, M., Gloor, E., Mitchard, E., Quincey, D., Spracklen, D., Spracklen, B., Spracklen, B., Adami, M., Aragão, L. E. O. C., & Galbraith, D. (2018). Pervasive rise of small-scale deforestation in Amazonia. *Scientific Reports*, *8*(1600). https://doi.org/DOI:10.1038/s41598-018-19358-2

Kelly, L. T., Giljohann, K. M., Duane, A., Aquilue, N., Archibald, S., Batllori, E., Bennett, A. F., Buckland, S. T., Canelles, Q., Clarke, M. F., Fortin, M.-J., Hermoso, V., Herrando, S., Keane, R. E., Lake, F. K., McCarthy, M. A., Moran-Ordonez, A., Parr, C. L., Pausas, J. G., … Brotons, L. (2020). Fire and biodiversity in the Anthropocene. *Science (New York, N.Y.)*, *370*(6519). https://doi.org/10.1126/science.abb0355

Kembel, S. W., Cowan, P. D., Helmus, M. R., Cornwell, W. K., Morlon, H., Ackerly, D. D., Blomberg, S. P., & Webb, C. O. (2010). Picante: R tools for integrating phylogenies and ecology. *Bioinformatics*, *26*, 1463–1464.

Kitching, I. J., Rougerie, R., Zwick, A., Hamilton, C. A., St Laurent, R. A., Naumann, S., Mejia, L. B., & Kawahara, A. Y. (2018). A global checklist of the Bombycoidea (Insecta: Lepidoptera). *Biodiversity Data Journal*, *6*, UNSP e22236. https://doi.org/10.3897/BDJ.6.e22236

Kuznetsova, A., Brockhoff, P. B., & Christensen, R. H. B. (2017). lmerTest package: Tests in linear Mixed effects models. *Journal of Statistical Software*, *82*(13), 1–26. https://doi.org/10.18637/jss.v082.i13

Laliberté, E., Legendre, P., & Shipley, B. (2014). *FD: measuring functional diversity from multiple traits, and other tools for functional ecology. R package version 1.0-12.*

Lamarre, G., Mendoza, I., Rougerie, R., Decaëns, T., Hérault, B., & Béneluz, F. (2015). Stay out (almost) all night: Contrasting responses in flight activity among tropical moth assemblages. *Neotropical Entomology*, *44*, 109–115.

Lavelle, P., Doledec, S., de Sartre, X. A., Decaens, T., Gond, V., Grimaldi, M., Oszwald, J., Hubert, B., Ramirez, B., Veiga, I., de Souza, S., de Assis, W. S., Michelotti, F., Martins, M., Feijoo, A., Bommel, P., Castaneda, E., Chacon, P., Desjardins, T., … Velasquez, J. (2016). Unsustainable landscapes of deforested Amazonia: An analysis of the relationships among landscapes and the social, economic and environmental profiles of farms at different ages following deforestation. *Global Environmental Change-Human and Policy Dimensions*, *40*, 137–155. https://doi.org/10.1016/j.gloenvcha.2016.04.009

Lavorel, S., Grigulis, K., McIntyre, S., Williams, N. S. G., Garden, D., Dorrough, J., Berman, S., Quetier, F., Thebault, A., & Bonis, A. (2008). Assessing functional diversity in the field—Methodology matters! *Functional Ecology*, *22*(1), 134–147. https://doi.org/10.1111/j.1365-2435.2007.01339.x

Legendre, P., Galzin, R., & HarmelinVivien, M. L. (1997). Relating behavior to habitat: Solutions to the fourth-corner problem. *Ecology*, *78*(2), 547–562.

Majekova, M., Paal, T., Plowman, N. S., Bryndova, M., Kasari, L., Norberg, A., Weiss, M., Bishop, T. R., Luke, S. H., Sam, K., Le Bagousse-Pinguet, Y., Leps, J., Goetzenberger, L., & de Bello, F. (2016). Evaluating Functional Diversity: Missing Trait Data and the Importance of Species Abundance Structure and Data Transformation. *Plos One*, *11*(2), e0149270. https://doi.org/10.1371/journal.pone.0149270

Mangels, J., Fiedler, K., Schneider, F. D., & Bluethgen, N. (2017). Diversity and trait composition of moths respond to land-use intensification in grasslands: Generalists replace specialists. *Biodiversity and Conservation*, *26*(14), 3385–3405. https://doi.org/10.1007/s10531-017-1411-z

Mason, N. W. H., de Bello, F., Mouillot, D., Pavoine, S., & Dray, S. (2013). A guide for using functional diversity indices to reveal changes in assembly processes along ecological gradients. *Journal of Vegetation Science*, *24*(5), 794–806. https://doi.org/10.1111/jvs.12013

Mouillot, D., Graham, N. A. J., Villeger, S., Mason, N. W. H., & Bellwood, D. R. (2013). A functional approach reveals community responses to disturbances. *Trends in Ecology & Evolution*, *28*(3), 167–177. https://doi.org/10.1016/j.tree.2012.10.004

Newbold, T., Hudson, L. N., Phillips, H. R. P., Hill, S. L. L., Contu, S., Lysenko, I., Blandon, A., Butchart, S. H. M., Booth, H. L., Day, J., De Palma, A., Harrison, M. L. K., Kirkpatrick, L., Pynegar, E., Robinson, A., Simpson, J., Mace, G. M., Scharlemann, J. P. W., & Purvis, A.

(2014). A global model of the response of tropical and sub-tropical forest biodiversity to anthropogenic pressures. *Proceedings of the Royal Society B-Biological Sciences*, *281*(1792), 20141371. https://doi.org/10.1098/rspb.2014.1371

Nino, L. M. J., Moertter, R., & Brehm, G. (2019). Diversity and trait patterns of moths at the edge of an Amazonian rainforest. *Journal of Insect Conservation*, *23*(4), 751–763. https://doi.org/10.1007/s10841-019-00168-4

Oksanen, J., Blanchet, F. G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P. R., O'Hara, r. B., Simpson, G. L., Solymos, P., Stevens, M. H. H., Szoecs, E., & Wagner, H. (2019). *Vegan: Community Ecology Package. R package version 2.5-4.*

Oszwald, J., Gond, V., Dolédec, S., & Lavelle, P. (2011). Identification d'indicateurs de changement d'occupation du sol pour le suivi des mosaïques paysagères. *Bois et Forêts Des Tropiques*, *307*(1), 8–21.

R Core Team. (2019). *R: A language and environment for statistical computing. Version 3.5.3*. R Foundation for Statistical Computing. https://www.R-project.org/

Rabl, D., Alonso-Rodriguez, A. M., Brehm, G., & Fiedler, K. (2020). Trait Variation in Moths Mirrors Small-Scaled Ecological Gradients in A Tropical Forest Landscape. *Insects*, *11*(9), 612. https://doi.org/10.3390/insects11090612

Ratnasingham, S., & Hebert, P. D. N. (2007). BOLD: The Barcode of Life Data System (www.barcodinglife.org). *Molecular Ecology Notes*, *7*(3), 355–364. https://doi.org/10.1111/j.1471-8286.2007.01678.x

Ratnasingham, S., & Hebert, P. D. N. (2013). A DNA-Based Registry for All Animal Species: The Barcode Index Number (BIN) System. *Plos One*, *8*(7), e66213. https://doi.org/10.1371/journal.pone.0066213

Ros, M., & Pineda, E. (2009). Apparent extinction or insufficient sampling?: Comment on "Deforestation and apparent extinctions of endemic forest beetles in Madagascar." *Biology Letters*, *5*(5), 651–652. https://doi.org/10.1098/rsbl.2009.0341

Schulze, C. H., & Fiedler, K. (2003). Hawkmoth diversity in northern Borneo does not reflect the influence of anthropogenic habitat disturbance. *Ecotropica*, *9*, 99–102.

Sekercioglu, C. H., Daily, G. C., & Ehrlich, P. R. (2004). Ecosystem consequences of bird declines. *Proceedings of the National Academy of Sciences of the United States of America*, *101*(52), 18042–18047. https://doi.org/10.1073/pnas.0408049101

Sekercioglu, C. H., Ehrlich, P. R., Daily, G. C., Aygen, D., Goehring, D., & Sandi, R. F. (2002). Disappearance of insectivorous birds from tropical forest fragments. *Proceedings of the National Academy of Sciences of the United States of America*, *99*(1), 263–267. https://doi.org/10.1073/pnas.012616199

Silva-Souza, K. J. P., & Souza, A. F. (2020). Woody plant subregions of the Amazon forest. *Journal of Ecology*, *108*(6), 2321–2335. https://doi.org/10.1111/1365-2745.13406

Simons, N. K., Weisser, W. W., & Gossner, M. M. (2016). Multi-taxa approach shows consistent shifts in arthropod functional traits along grassland land-use intensity gradient. *Ecology*, *97*(3), 754–764. https://doi.org/10.1890/15-0616.1

Stork, N. E. (2018). How many species of insects and other terrestrial arthropods are there on Earth? *Annual Review of Entomology*, *63*, 31–45.

Tews, J., Brose, U., Grimm, V., Tielborger, K., Wichmann, M. C., Schwager, M., & Jeltsch, F. (2004). Animal species diversity driven by habitat heterogeneity/diversity: The importance of keystone structures. *Journal of Biogeography*, *31*(1), 79–92. https://doi.org/10.1046/j.0305-0270.2003.00994.x

Thom, D., & Seidl, R. (2016). Natural disturbance impacts on ecosystem services and biodiversity in temperate and boreal forests. *Biological Reviews*, *91*(3), 760–781. https://doi.org/10.1111/brv.12193

Tuskes, P. M., Tuttle, J. P., & Collins, M. M. (1996). *The wild silk moths of North America: A natural history of the Saturniidae of the United States and Canada*. Cornell University Press.

Vogt-Schilb, H., Moreau, P.-A., Malaval, J.-C., Schatz, B., & Richard, F. (2018). Effects of long-term landscape dynamics and city growth on biodiversity in the Mediterranean: The case study of Montpellier, France. *Urban Ecosystems*, *21*(5), 921–932. https://doi.org/10.1007/s11252-018-0780-8

Wagner, D. L. (2020). Insect declines in the Anthropocene. *Annual Review of Entomology*, *65*, 457–480.

Wilson, E. (2002). *The future of life*. Vintage Books.

Figures

Figure 1. Geographical location and landscape structure of the three study areas in South America (A), in Brazil relative to the deforestation front (B) and in the State of Pará, Brazil (B). The lower panel shows interpreted 2007 Landsat images; black lines indicate the boundaries of the nine farms in each study area; yrs = age of the peak deforestation in each area.

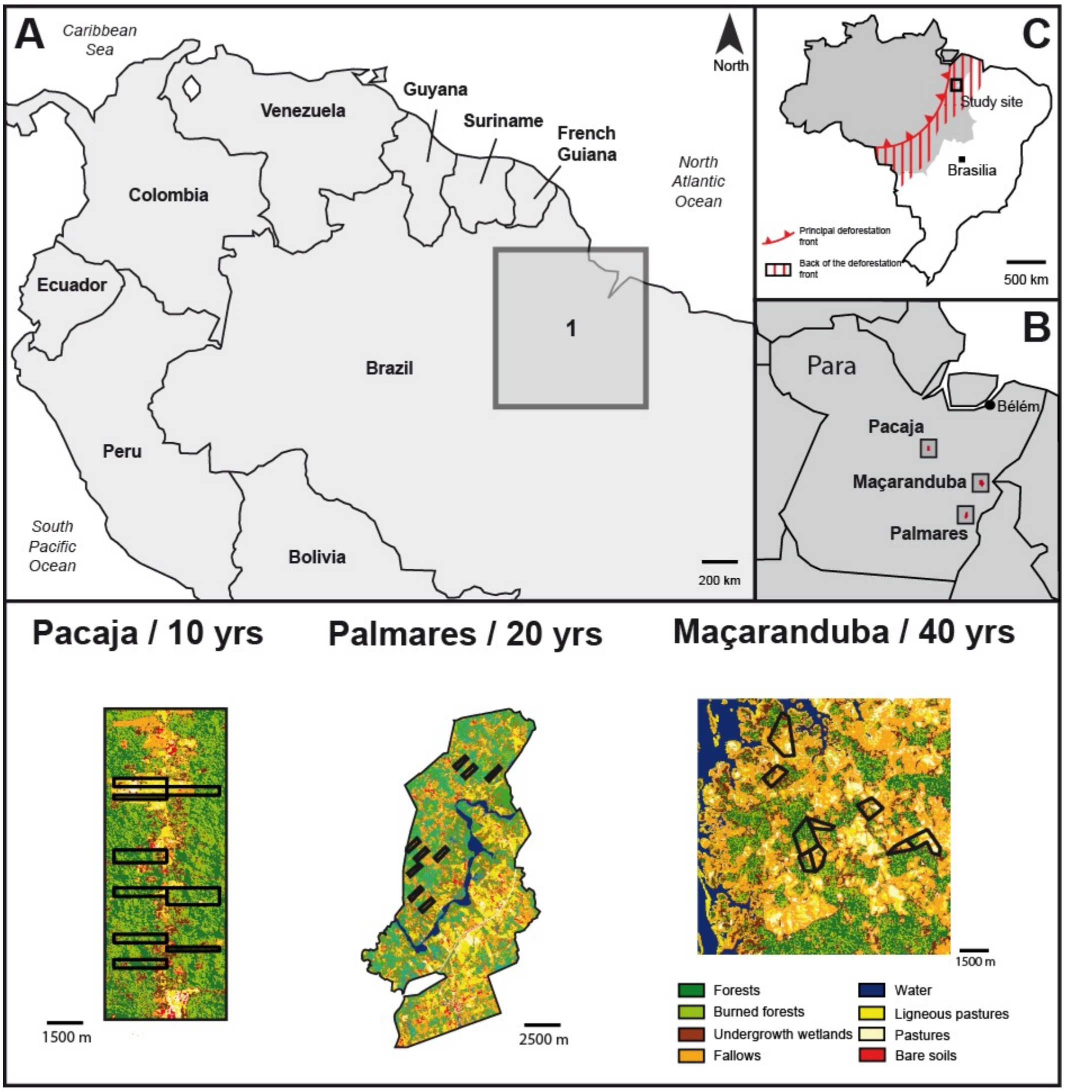

Figure 2. Individual-based rarefaction and extrapolation curves of moth species (Saturniidae + Sphingidae) pooled for the three sampling areas. Solid lines represent rarefaction curves whereas dashed lines represent extrapolation curves; shaded areas are 95% confidence intervals based on a bootstrap with 200 replications.

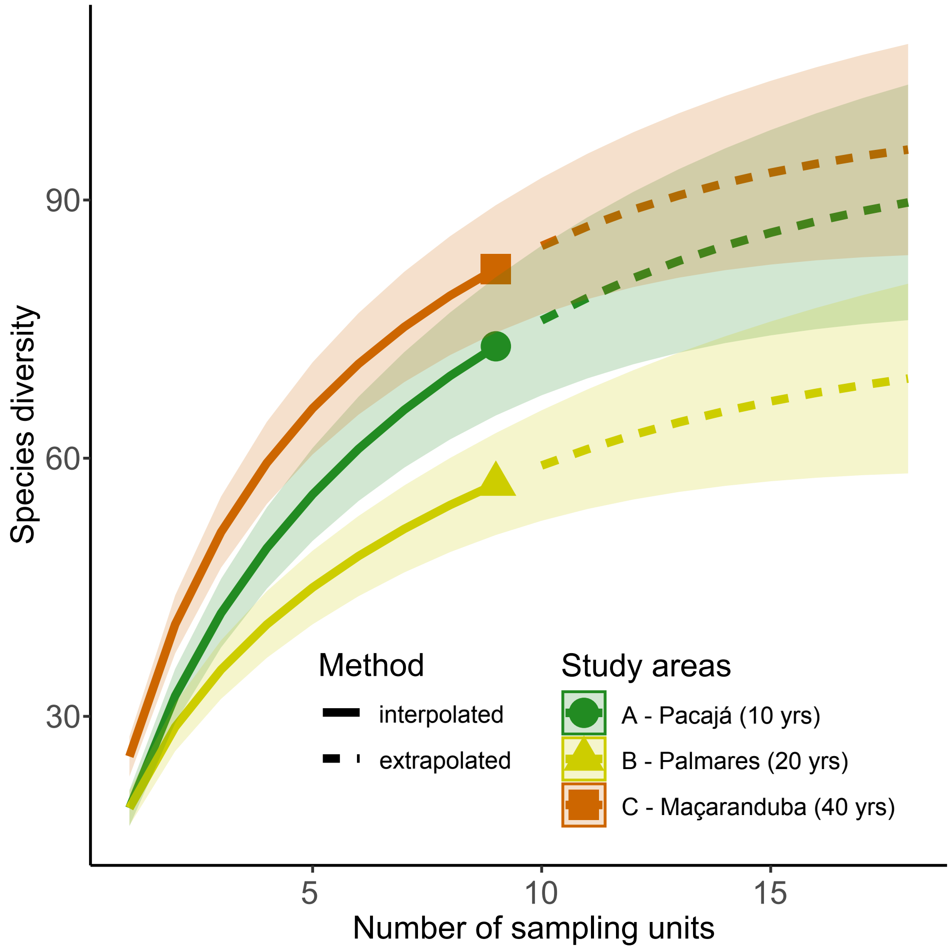

Figure 3. First-two axes of a RLQ performed between functional traits and landscape metrics showing: (A) functional trait loadings; (B) landscape metric loadings; (C) Study site factorial coordinates, grouped by study areas. Red arrows on figures (A) and (B) indicate traits or environmental variables significantly linked with RLQ axes ($p < 0.05$).

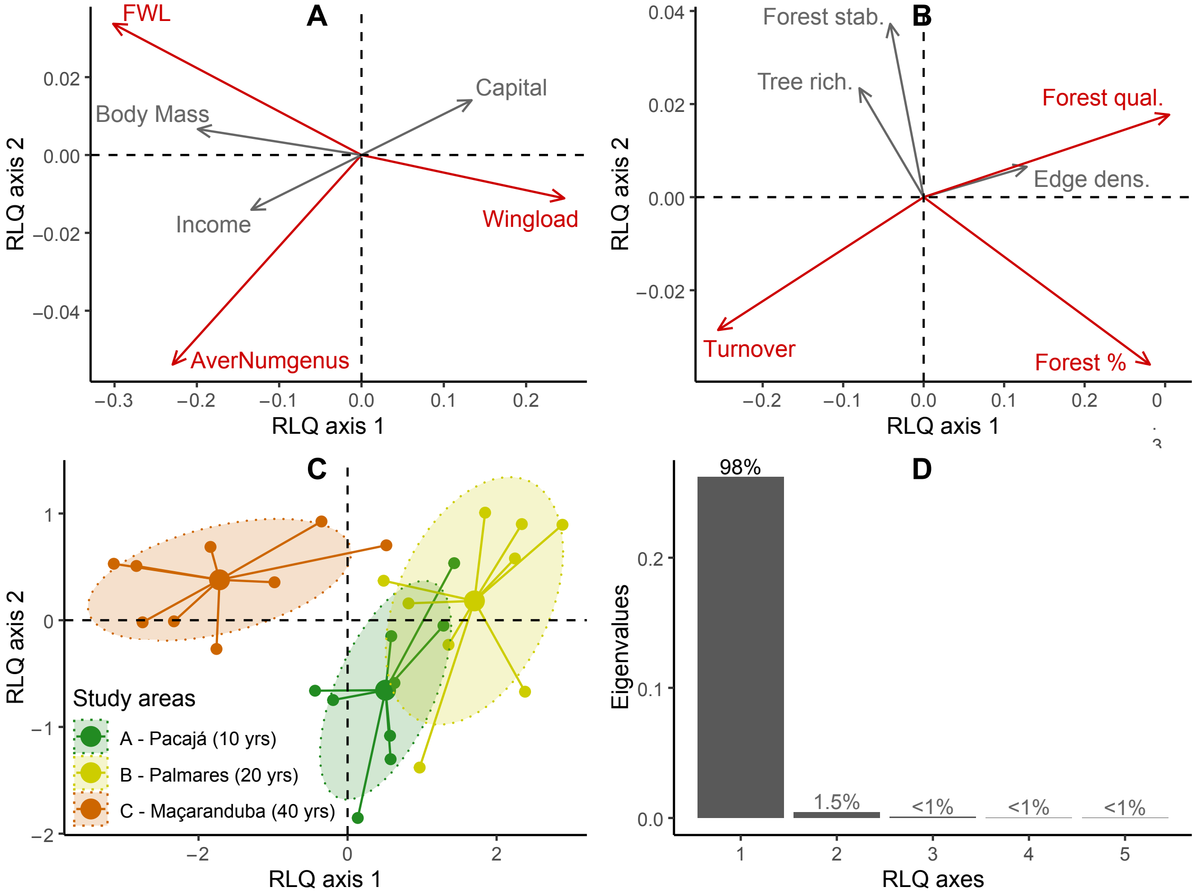

Figure 4. Significant variations of standardized effective sizes (SES) of functional diversity indices and community weighted means (CWM) of functional traits along the gradient on the first RLQ axis: (A) Chao-based estimates of species richness; (B) Functional dispersion; (C) Forewing length; (D) Polyphagy index. Dots represent farms colored according to their study area. Blue lines represent adjusted linear mixed-effect models, with their respective confidence intervals in grey areas. The horizontal dashed lines indicate standardized effect sizes of -2.0 and 2.0, which correspond approximately to the 5% significance level. Significance codes for linear mixed-effect models: 0 '***' 0.001 '**' 0.01 '*' 0.05.

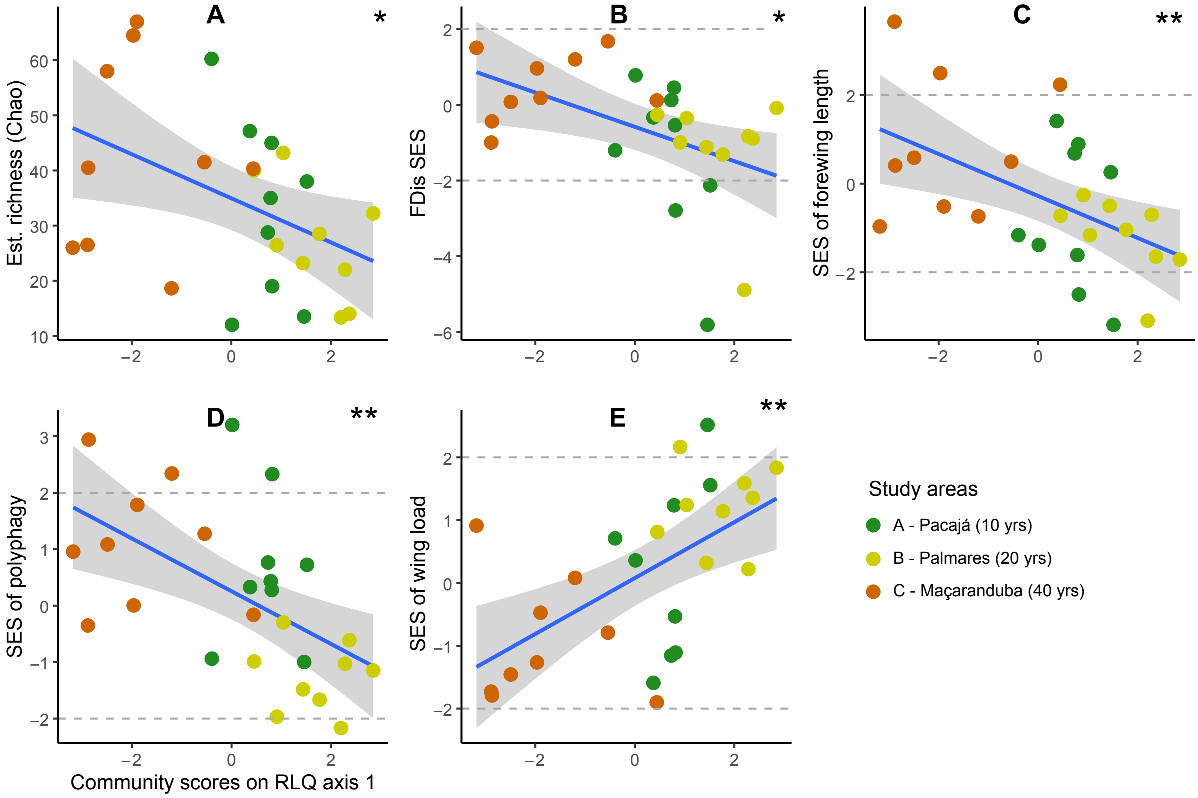

Table 1. Average landscape characteristics in the three study areas. Forest % = forest cover; Turnover = average 1990-2007 land use turnover; ED = total edge density; For Qual = forest quality index; R Trees = rarefied species richness of trees; Forest stab. = index of forest stability.

	Forest %	**Turn Over**	**ED**	**For Qual**	**R Trees**	**Forest stab.**
A - Pacajá (10 yrs)	96.49	19.79	476	0.74	21.46	0.09
B - Palmares (20 yrs)	92.20	15.01	689	0.88	15.35	0.35
C - Maçaranduba (40 yrs)	33.68	31.90	622	0.42	19.34	0.88

Table 2. Average characteristics of saturniid and sphingid moth communities in the three study areas. n = number of specimens collected; S.obs = observed number of species; Chao = estimated species numbers; SE.Chao = standard error of the Chao index; Sorensen = average pair-wise Sorensen index of beta-diversity among sampling point within each study area; SE.Sorensen = standard error of the Sorensen index.

	n	**S.obs**	**Chao**	**SE.Chao**	**Sorensen**	**SE.Sorensen**
A - Pacaja (10 yrs)						
Saturniidae	189	47	57.0	6.1	0.73	0.02
Sphingidae	158	26	58	29.8	0.70	0.03
Total	347	73	96.7	11.3	0.71	0.02
B - Palmares (20 yrs)						
Saturniidae	231	32	37.6	4.6	0.50	0.02
Sphingidae	117	25	41	12.8	0.54	0.02
Total	348	57	74.9	10.1	0.51	0.01
C - Maçaranduba (40 yrs)						
Saturniidae	257	52	61.0	5.7	0.67	0.02
Sphingidae	258	30	44.8	13.3	0.58	0.03
Total	515	82	100.3	9.2	0.63	0.02