

1 ***Manuscript title: Functional and taxonomic responses of tropical moth***
2 ***communities to deforestation***

3 ***Running title: Moth communities in deforested landscapes***

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35 **Abstract**

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

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

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

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

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

57 **Introduction**

58 Understanding how species adapt to human-impacted landscapes, and how ecological
59 communities are modified in response, are important ecological questions (Gardner et al., 2010)
60 traditionally addressed by analysing variations in taxonomic diversity along gradients of
61 deforestation or landscape anthropization. This approach enables the quantification of human
62 impacts on biodiversity, but does not provide information on the mechanisms involved in
63 biodiversity erosion (Majekova et al., 2016), for which studies of the functional and
64 phylogenetic components of biodiversity are required (Devictor et al., 2010; Mouillot et al.,
65 2013). At a landscape scale, species traits (e.g. body size, dispersal capacity, diet and habitat
66 specialization) are fundamental for explaining how species may adapt to their environment, and
67 can help assess the conservation value of agricultural landscapes for their consideration into
68 conservation strategies (Gamez-Virues et al., 2015).

69 The Amazonian rainforest is the largest remaining frontier forest on Earth (i.e. large,
70 ecologically intact, and relatively undisturbed natural forests; Bryant et al., 1997), long
71 recognized for its outstanding biodiversity (Cardoso Da Silva et al., 2005; Wilson, 2002).
72 However, it faces alarming rates of deforestation, mainly from expanding agricultural
73 encroachment and timber production, and increasingly frequent large-scale forest fires (Kelly
74 et al., 2020; Newbold et al., 2014). Among agricultural activities, small-scale subsistence
75 agriculture has been identified as a powerful driver of landscape transformation and
76 deforestation in the Amazon, second after cattle ranching (Kalamandeen et al., 2018). Recent
77 estimates report a loss of about 710,000 km² of forest from 1970-2018, almost 20% of the
78 original forest cover (Butler, 2020). This conversion is known to have dramatic consequences
79 for biodiversity, but potential non-linear and threshold effects are still poorly understood
80 (Barlow et al., 2016; Decaëns et al., 2018). Agro-conversion is also likely to affect the
81 environmental stability of the entire region with potential negative effects on key ecosystem
82 services for local human populations (Lavelle et al., 2016).

83 The conservation of Amazonian biodiversity also faces the challenge of the choice of biological
84 models to document the response of biological communities to environmental change. Most
85 studies have focused on a few exemplar groups of organisms whose responses are assumed to
86 be representative of all biodiversity (Fazey et al., 2005; Gardner et al., 2009). This has generated
87 a strong bias towards vertebrates and flowering plants, with other important components of
88 terrestrial biodiversity, such as invertebrates, being under-represented (Collen et al., 2009).
89 Therefore, there is a critical need to broaden the taxonomic spectrum of research into

90 biodiversity-disturbance relationships, and to strengthen the representation of the most speciose
91 groups in these kinds of studies. Of these, insects represent a major component of biodiversity
92 (over 1,000,000 named species; Stork, 2018) and their accelerating decline has recently caused
93 major concern (Wagner, 2020). Deforestation is one of the major drivers of this decline
94 (Eggleton, 2020), but most studies have focused on temperate forests (Thom & Seidl, 2016).
95 This is partly due to the challenges posed by sampling tropical insects (Hanski et al., 2009; Ros
96 & Pineda, 2009), resulting in many groups being largely undocumented, together with a strong
97 taxonomic impediment plaguing most insect orders (Cardoso Da Silva et al., 2005). We thus
98 need more studies to better understand the processes at play behind deforestation effects on
99 tropical insect communities, especially at the landscape scale and by integrating the temporal
100 dynamics of landscape elements. Indeed, the dynamics of landscape patches, which is
101 recognised as an important factor affecting biodiversity in temperate regions (Ernoul et al.,
102 2006; Fischer, 2001; Vogt-Schilb et al., 2018), has so far not been considered to explain the
103 response of tropical insects to deforestation.

104 Saturniidae (wild silkmoths) and Sphingidae (hawkmoths) are some of the most charismatic
105 insects. They are phylogenetically sister lineages with contrasting life-histories (Janzen, 1984).
106 Sphingids are mostly income-breeders (*sensu* Jonsson, 1997), with short life cycles, mono-
107 /oligophagous larvae, and adult females ovipositing only a few eggs per hostplant. Adult moths
108 of most species are active flower foragers and excellent fliers, some species exhibiting
109 migratory behaviour (Ballesteros-Mejia et al., 2017). In contrast, saturniids are typically
110 capital-breeders with non-feeding adults, long life cycles, polyphagous larvae, and adult
111 females ovipositing many eggs per hostplant; they are considered poor dispersers (Tuskes et al.,
112 1996).

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

122 **Materials and Methods**

123 ***Study sites***

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

- 127 1) The Pacajá area (51°0'9"W, 3°39'36"S) was occupied by highway settlers from the early
128 1990s, who delimited 100 ha agricultural plots along tertiary roads. Most deforestation
129 took place in the decade before sampling.
- 130 2) Palmares II (5°46'8"S, 49°53'43"W) is a large cattle farm from the late 1980s, later
131 invaded in 1994 by farmers from the Landless Worker Movement, who expropriated
132 the owner and divided the farm into 520 plots of 25 ha. Subsequent deforestation
133 culminated within the 20 years before sampling.
- 134 3) The Maçaranduba area (49°18'34"W, 4°45'5"S) was first impacted in the 1970s by the
135 Amazonian deforestation front, the forest remnants then underwent secondary
136 deforestation during the 1990s. It is currently occupied by an agro-extractivist
137 community that has largely shifted towards cattle ranching.

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

142 ***Landscape structure variables***

143 In each study area, we selected nine non-contiguous farms that best represent the local
144 production systems (Lavelle et al., 2016). These farms were then used as replicated elementary
145 units to describe landscape structure from Landsat images taken in five different years between
146 1990 and 2007 (Table 1; SI table 1). We calculated six landscape metrics that we considered
147 important in structuring moth communities: i) the amount of habitat, measured as the % cover
148 of mature forest within each farm in 2007; ii) landscape fragmentation, estimated from total
149 edge density; iii) landscape dynamics, determined as the mean between-year land-use turnover
150 (i.e., change in land-use composition); iv) an index of forest patch stability, calculated from the
151 temporal dynamics of the forest mean patch density during the 1990-2007 period; v) an index
152 of habitat quality, measured as the proportion of forest on a given farm that was undisturbed
153 during the 1990-2007 period; and vi) the diversity of potential hostplants, assessed using tree

154 diversity recorded at five equidistant points along a 1 km transect within each farm (Decaëns et
155 al., 2018).

156 *Moth sampling and taxonomic assignments*

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

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

169 *Functional trait measures*

170 We considered five functional traits for analyses. Morphological features were measured for 1-
171 3 individuals per moth species (a number considered sufficient for multi-species trait-based
172 analyses; Beck, pers. comm.), on specimen images using the image annotation tool specifically
173 implemented for that purpose in BOLD (see Supplementary Information; Ratnasingham &
174 Hebert, 2007). For this purpose, the images used represented the dorsal side of specimens
175 prepared according to entomological museum standards (see example in Supplementary
176 Information). In total, we measured seven morphometric traits on 301 images (SI Table 2) that
177 were then used to calculate three morphological functional traits: i) the forewing length (cm), a
178 commonly-used measure of body size in Lepidoptera (Beck & Kitching, 2007), defined as the
179 maximum distance between the base of the costa and the apex of the forewing; ii) the product
180 of thorax width and body length (cm²), which was used as a proxy for body mass; and iii) the
181 wing load, which was estimated as the ratio of thorax width to wing surface (forewing +
182 hindwing), used as a surrogate for flight strength (species with high wing loads are expected to
183 have more powerful flight than species with low wing loads; Beck & Kitching, 2007). To
184 maintain consistency in the dataset, we used only images of males, so that we could also include
185 species whose females are not documented in our dataset.

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

196 *Statistical analyses*

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

209 In a second step, we analysed the links between functional traits and landscape metrics using
210 RLQ analysis, a multivariate tool that maximizes the covariance between linear combinations
211 of traits and environmental variables mediated by species abundances (Dolédec et al., 1996;
212 Dray et al., 2014). Three different RLQ were computed (see Supporting Information), for the
213 two families together using the complete set of functional traits, and for each family
214 independently after removing the resource use trait, which was constant within each family
215 ('ade4' package in R; Dray & Dufour, 2007). The overall statistical significance of the analysis
216 was tested using the function 'fourthcorner2'. The links between traits and landscape metrics
217 and their association with the axes of covariation were tested through a fourth-corner analysis

218 using adjusted p-values to control for false discovery rate, with the functions ‘fourthcorner’,
219 and ‘fourthcorner.rlq’ (Dray et al., 2014; Dray & Legendre, 2008; Legendre et al., 1997).

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

239 **Results**

240 *Effect of deforestation on biodiversity metrics of moth communities*

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

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

256 *Effects of deforestation on functional moth diversity*

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

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

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

281 *Community diversity and functional trait composition*

282 Significant variations in several of the metrics used to describe taxonomic and functional
283 diversity occurred along the first RLQ axis deforestation gradient (SI Fig. 6). For example, there
284 was a significant decrease in estimated richness (Chao index) along the first RLQ axis (Fig.
285 4A), as well as a decrease in the SES of functional dispersion, with individual values lower than
286 expected by chance for some communities at the recently deforested areas (Fig. 4B). As
287 evidenced by the RLQ analysis, CWM of forewing length (Fig. 4C) and of the degree of
288 polyphagy (Fig. 4D) decreased significantly along the first RLQ axis, showing higher values
289 than expected by chance in some communities of Maçaranduba, and lower than expected by
290 chance in some others at Pacajá and Palmares. Conversely, wing load CWM significantly
291 increased along the RLQ axis, reaching values higher than expected by chance in some of the
292 more recently deforested farms (Fig. 4E).

293 **Discussion**

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

303 *Trait composition in response to landscape structure*

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

312 Our finding that species were on average larger in the most deforested landscapes was
313 surprising. Indeed, it is commonly accepted that body size in most arthropod taxa tends to

314 decrease with the intensification of land-use and the increased simplification of the landscape
315 (Gamez-Virues et al., 2015; Simons et al., 2016). In Lepidoptera, Rabl et al. (2020) showed that
316 two moth taxa (i.e. Arctiinae and Geometridae) were much smaller-sized in oil palm plantations
317 than in nearby old-growth forest. Some studies however, while supporting a significant effect
318 of land-use intensity on arthropod body size, also noted that the direction of this effect may
319 vary substantially among taxonomic groups (Birkhofer et al., 2017). In our study, the observed
320 increase in moth size with increased deforestation could suggest that larger species are more
321 efficient dispersers than smaller ones, as an increase in average dispersal capacity is an expected
322 response of Lepidoptera communities along gradients of anthropogenic disturbances
323 (Boerschig et al., 2013). However, it is also possible that the response of this trait is caused by
324 factors not fully captured by our set of landscape metrics. For example, Nino et al. (2019)
325 proposed that microclimate modification in more open landscapes could favour large species
326 with better tolerance to desiccation. It is also possible that large moth species may benefit from
327 positive cascading effects following a decline in predator assemblages in deforested landscapes.
328 Insectivorous birds and bats, for instance, are known to be negatively affected by tropical
329 rainforests fragmentation, especially those that are more specialised and larger (Farneda et al.,
330 2015; Sekercioglu et al., 2002, 2004).

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

346 hypothesis is supported by the decrease in functional dispersal observed in the most recently
347 deforested farms, which we discuss below.

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

360 *Taxonomic and functional diversity in deforested landscapes*

361 We found differences in regional species richness among the different study sites, especially
362 for saturniids, which was less diverse in one of the more recently deforested area (Palmares)
363 than in the two other study areas. At the local scale of individual communities, species richness
364 decreased along the environmental gradient identified by the RLQ analysis, showing highest
365 values for the less recently deforested farms and the lowest for recently deforested farms. Such
366 an increase in alpha diversity with tropical forest disturbance has already been reported for
367 some groups of moths (e.g. Geometridae in Borneo, Arctiidae and Geometridae in Ecuador),
368 while opposite responses, or an absence of response, have been reported for other groups
369 (Fiedler et al., 2007; Hilt & Fiedler, 2008). In our study, the high regional diversity at one of
370 the recently deforested areas (Pacajá) can be readily explained by good quality forest still
371 covering a significant proportion of the landscape, creating suitable conditions for a large
372 number of species at this scale. The comparatively low local diversity, and the average Sorensen
373 index of dissimilarity, together highlighted that moth communities in this area were
374 characterised by a higher beta-diversity compared with the two other areas, which could result
375 from heterogeneity in forest composition among forest remnants. In the other recently
376 deforested area (Palmares), the forest cover is similar to that observed in Pacajá, but this site
377 has a higher landscape fragmentation (edge density) and a lower species richness of plant
378 communities (Decaëns et al., 2018). A reduction of the diversity of available food plants,

379 together with a homogenization of forest cover composition, may thus explain the decrease in
380 local and regional species richness at this site. Finally, high levels of species richness at the
381 highly deforested area (Maçaranduba) might be attributed to the landscape structure, formed by
382 a patchwork of diversified habitats, including stable forest remnants in large patches, but also
383 fallows of different ages and well established pastures (Oszwald et al., 2011). Additionally,
384 species richness of shrubs and trees in this site is high, both at local and regional scales (Decaëns
385 et al., 2018). The structurally complex landscape, combined with high diversity of potential
386 food plants, likely provides more niches and diverse ways of exploiting environmental
387 resources, thus allowing co-occurrence of a higher number of species (Fahrig et al., 2011; Tews
388 et al., 2004).

389 Functional richness and equitability did not show any variation along the first RLQ axis, yet
390 functional dispersion tended to increase from the least to the more deforested farms. This
391 suggests a strong effect of environmental filters on the structuring of moth communities in the
392 least deforested landscapes, and a decrease of this effect along the deforestation gradient, which
393 contradicts both theoretical and empirical evidence (Mouillot et al., 2013), and expectations of
394 our first hypothesis. This suggests that the same drivers proposed to explain the high species
395 diversity in the more deforested sites triggered an increase in niche complementarity among co-
396 occurring species, enhancing species occurrence probabilities and/or abundances (Mason et al.,
397 2013). In the least deforested sites, recent vegetation clearings generated a significant
398 fragmentation of forest patches, separated from each other by sparsely vegetated areas. This
399 early landscape transformation is likely to have generated a significant filtering of species,
400 leading to functional under-dispersion within communities.

401 *Differential responses of saturniid and sphingid moths to landscape structure*

402 The most significant changes in moth communities observed in our study were due to an effect
403 of landscape structure on saturniid communities, contrasting with the weak response of sphingid
404 communities. This corroborates our third hypothesis, which predicted different responses by
405 both families to deforested landscapes, because of differences in the life-histories of these moths.
406 Sphingids are generally characterized by high mobility and an ability to forage on many
407 flowering plant species as adults, including those in disturbed ecosystems (Hawes et al., 2009).
408 While it is likely that some sphingids are negatively impacted by habitat disturbance, its effects
409 seem to be counteracted and balanced by other subgroups not affected in this way, thereby
410 explaining how the overall species richness of the family remains unchanged in different types
411 of agricultural landscapes (Beck et al., 2006; Schulze & Fiedler, 2003). Saturniids are therefore

412 more likely to show significant responses to anthropogenic disturbances. Recently, Basset et al.
413 (2017) proposed Saturniidae as a potential model taxon for studying the long-term effects of
414 climate change on tropical insects. Our results support this suggestion by demonstrating that
415 these moths can also be used to study the effects of disturbances at finer time scales.

416 **Conclusion**

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

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442 **Conflicts of interest**

443 The authors have no conflict of interest to declare.

444 **Data availability statement**

445 All relevant data are within the paper or stored in Zenodo repository under DOI:
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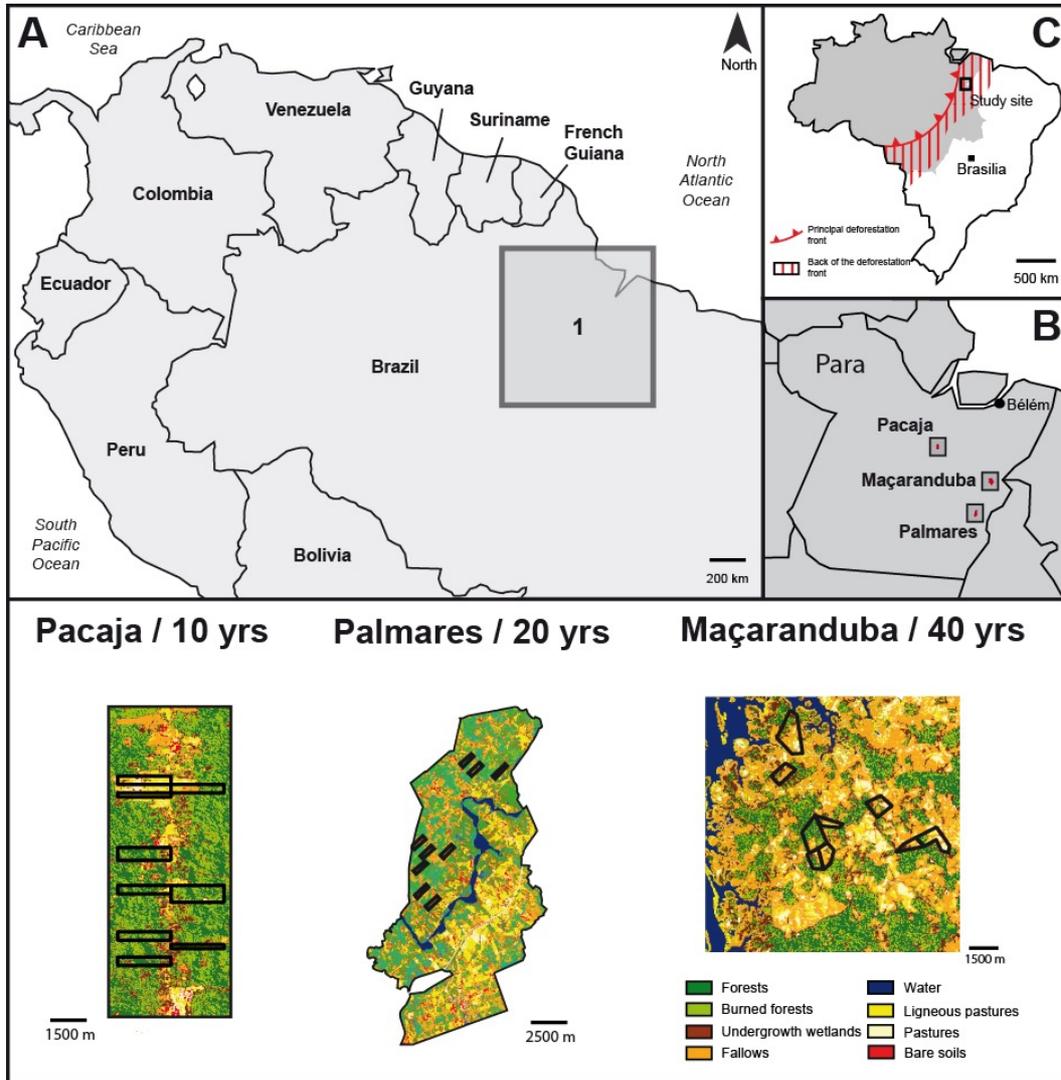
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685 **Figures**

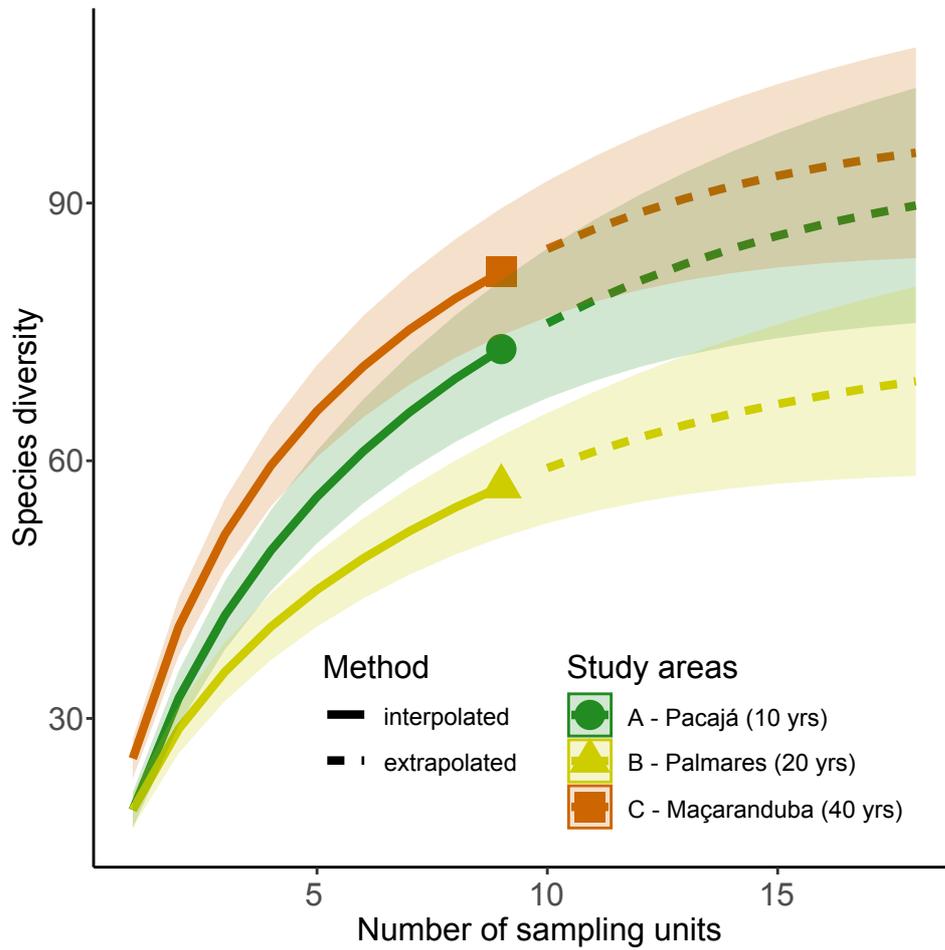
686 **Figure 1.** Geographical location and landscape structure of the three study areas in South
687 America (A), in Brazil relative to the deforestation front (B) and in the State of Pará, Brazil (B).
688 The lower panel shows interpreted 2007 Landsat images; black lines indicate the boundaries of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



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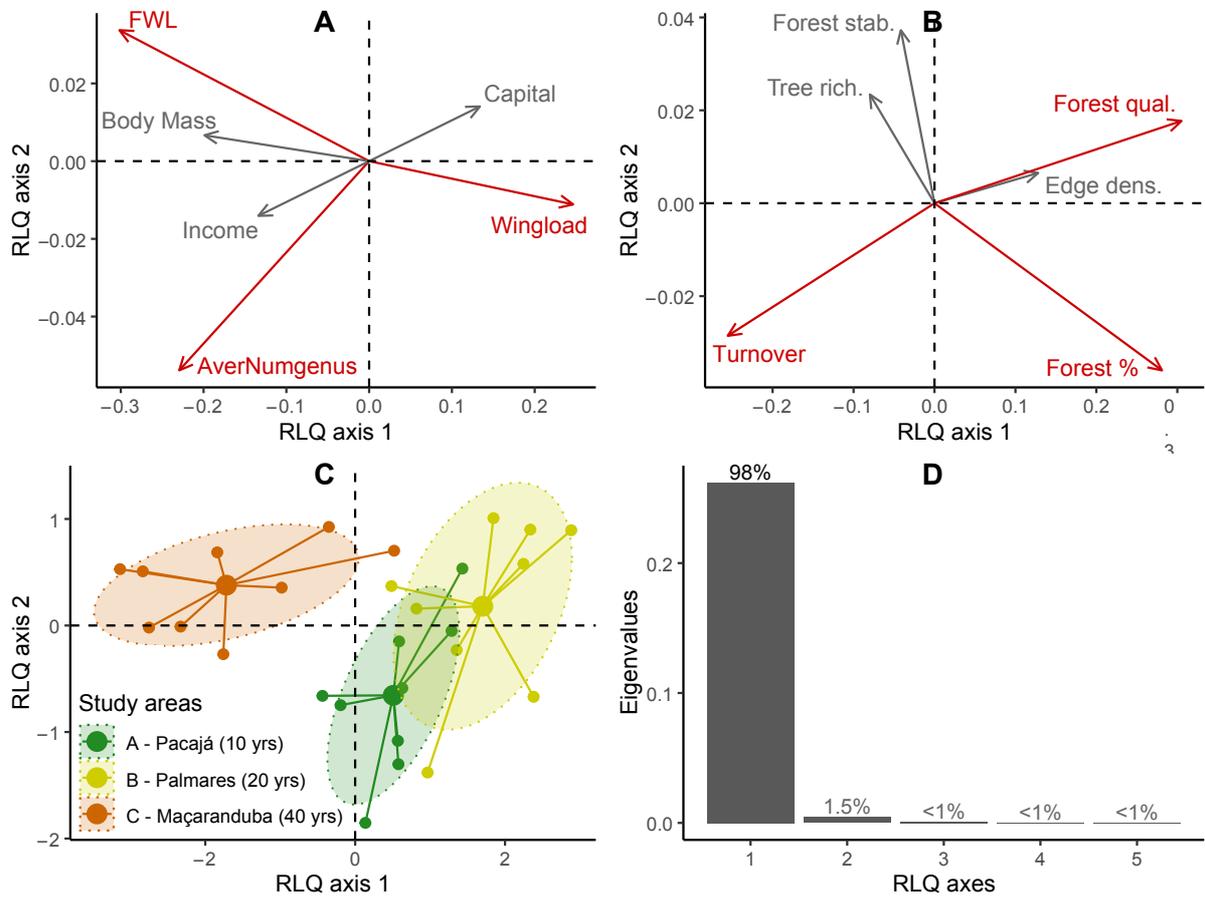
692 **Figure 2.** Individual-based rarefaction and extrapolation curves of moth species (Saturniidae +
693 Sphingidae) pooled for the three sampling areas. Solid lines represent rarefaction curves
694 whereas dashed lines represent extrapolation curves; shaded areas are 95% confidence intervals
695 based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



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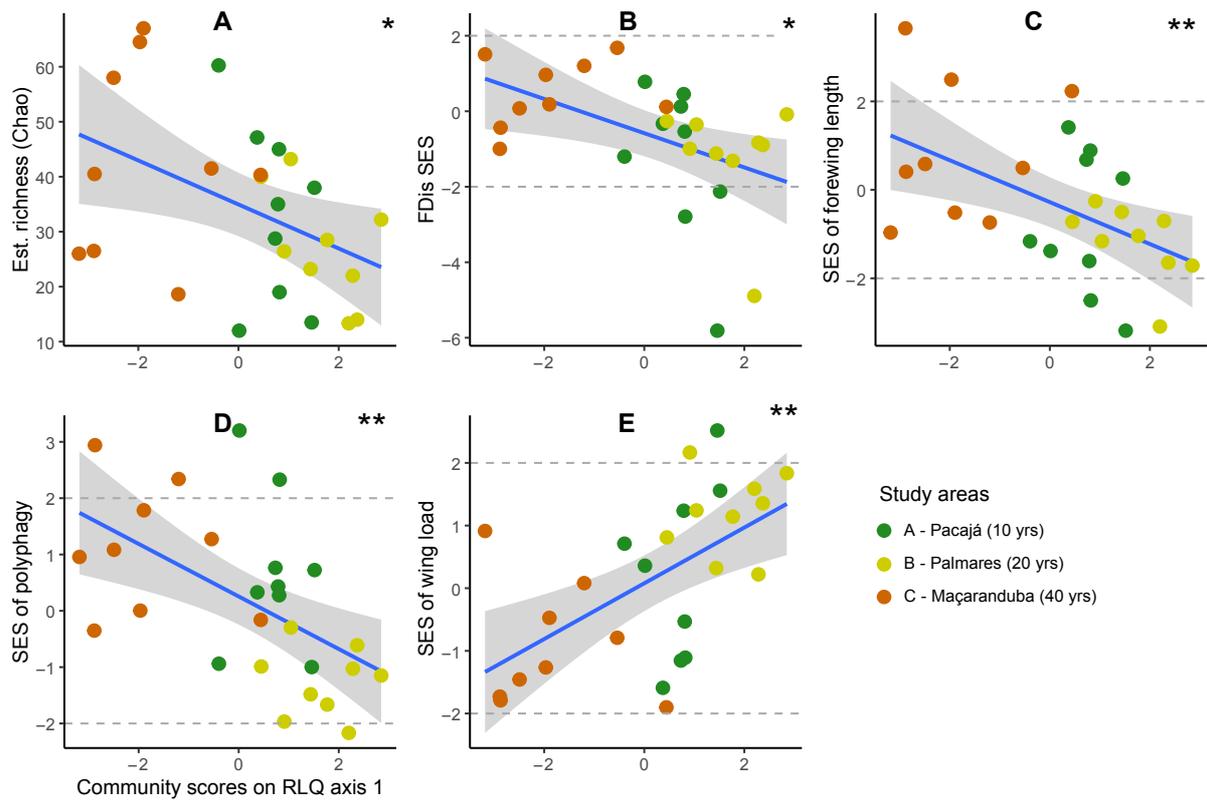
698 **Figure 3.** First-two axes of a RLQ performed between functional traits and landscape metrics
 699 showing: (A) functional trait loadings; (B) landscape metric loadings; (C) Study site factorial
 700 coordinates, grouped by study areas. Red arrows on figures (A) and (B) indicate traits or
 701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



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



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

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

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

	n	S.obs	Chao	SE.Chao	Sorensen	SE.Sorensen
<i>A - Pacaja (10 yrs)</i>						
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
<i>B - Palmares (20 yrs)</i>						
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
<i>C - Maçaranduba (40 yrs)</i>						
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

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