Stratification along tropical forest succession enhances pollinator diversity via functionally unique canopies

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ABSTRACT

Vertical stratification is among the main drivers of biodiversity in forests. Canopies are a key spatial component for primary consumers due to a higher concentration of resources, but methodological constraints impair a proper assessment of canopy communities. Therefore, the occupancy of key animal groups along the forest's vertical axis and the role of stratification in forest succession remains little understood. In this work, we investigated the stratification of pollinator abundance, (functional) diversity, and composition along a succession chronosequence in a lowland rainforest ecosystem. Moths, social diurnal bees, and nocturnal bees were more abundant and diverse in canopies, while orchid bees showed an inverse trend across parameters, suggesting taxa-specific responses. Late successional and old-growth forests were similarly diverse, suggesting that stratification establishes fast. Moreover, canopy-bearing successional and old-growth forests were more diverse than early successional plots across all groups. For moths and partially for bees, stratification enhanced diversity in old-growth and late-successional forests via species turnover between canopy and understory. Plot isolation, elevation, and canopy height had overall little effect on the variance between canopy and understory, potentially indicating a more prominent role of resource composition than environmental and local plot variables. Moreover, canopies harbored different pollinator compositions than understories. In particular, smaller, shorter-tongued, slower-flying, light-colored bees, and cryptic moths were associated with the canopy, suggesting that the relative role of interaction, dispersal and response traits in pollinator stratification is also group-dependent. Our study underlines the importance of stratification in leveraging diversity along forest succession, with a trait-driven, group-specific divergence of pollinator communities

between forest strata. These results highlight the importance of considering canopies to improve sampling completeness and fully assess ecosystem biodiversity.

1. INTRODUCTION

Forests are remarkably diverse ecosystems that harbor most of the Earth's biota (Gaston, 2000). The diversity of biological niches offered by forests can ultimately be linked to their multidimensional complexity in the form of habitat heterogeneity (clearings, edges, and patch-matrix dynamics) (Forman & Godron, 1986; Watson, 1998) and a wide range of microhabitats and resources associated with trees and epiphytes (Nadkarni, 1994). Moreover, a prominent driver of forest heterogeneity and diversity is vertical stratification, with each forest stratum characterized by distinct niches formed by the interplay of microclimatic conditions and microhabitats (Shaw, 2004), as well as different sets of nutritional resources and nesting or roosting sites for animals (Jachowski et al., 2016; Nadkarni et al., 2013).

While the forest under- and midstories offer a variety of niches and resources associated with the soil (e.g., dung, deadwood, and carrion) and with low-laying vegetation (herbs and bushes in deciduous forests or pioneers in clearings) (Basset et al., 2003; Kudo et al., 2008), the concentration of resources in the upper layers is an important driver of animal distribution, particularly in tropical rainforests where a clear degree of vertical stratification is present (Basset et al., 2003). The canopy, a photosynthetic hotspot in the forest due to increased radiation, excels in resource yield for primary consumers (Ozanne et al., 2003). Large and productive trees have a much higher resource yield (e.g., flowers and fruits) than understory plants (Baker et al., 1983), while the accumulation of epiphytes, lianas, and tree crown results in a higher taxonomical and functional diversity of primary resources and turns canopies into optimal foraging areas for herbivores, frugivores and nectarivores (Ramalho, 2004; Schowalter & Chao, 2021).

Nonetheless, canopies are fragile sections of the landscape marked by low resistance due to the targeted logging of slow-growing, large hardwood trees (Asner et al., 2006), and low resilience, as such trees sometimes take centuries to establish, grow, and provide their ecosystem functions (Xu et al., 2015). Abandoned logged forests may take several decades to achieve a similar structural and biological complexity as old-growth forests (Finegan, 1996). Tropical forests are particularly critical in this regard. They foster an estimated three-quarters of Earth's biodiversity (Stork, 2018) and account for most of the world's current Biodiversity Hotspots (Myers et al., 2000). In these ecosystems, the loss of vertical complexity through selective logging further hinders forest succession by filtering out canopy-specialist pollinators and seed dispersers from the landscape (Silva et al., 2020; Whitworth et al., 2016).

The sensitivity of fauna to canopy removal and the consequent effects on forest recovery is, however, context- and taxa-dependent. Enhanced forest connectivity and concentrated losses of canopy cover may still allow for the occurrence of canopy specialist and their movement across the landscape (Cadavid-Florez et al., 2020). Meanwhile, highly fragmented and logged forests will have a perceptive impact on canopy specialists, even removing canopy-restricted animals with low mobility (e.g., canopy primates, Shaw, 2004). Moreover, a higher exposure associated with canopy cover loss, such as increased heat and light incidence also selectively removes smaller, desiccation-prone animals from the landscape (Basset et al., 2003), underlining the role of dispersal and response traits in defining canopy dependence and response to disturbance.

The effect of canopy loss and the role of traits in defining canopy usage is, however, still relatively little understood for insects, despite half of the world's

arthropods estimated to occur in canopies (Ozanne et al., 2003; Schowalter & Chao, 2021) and up to a quarter of invertebrates expected to be canopy specialists (Basset et al., 2003). Most of our current knowledge of invertebrate diversity is still based on understory sampling (Nakamura et al., 2017). While there is evidence that several insect communities, including pollinators, are more abundant and diverse in canopies (Brehm, 2007; Roubik, 1992a; Stangler et al., 2016; Watanabe et al., 2017), evidence is sparse and often conflicting. Pollinators are expected to be particularly sensitive to the loss of old-growth canopies. Mass-flowering canopy trees serve as abundant and year-round resources for several groups of canopy-restricted bees and beetles, for instance (Kirmse & Chaboo, 2020; Ramalho, 2004; Roubik, 1992a), underlining the critical role of old forests with dense canopy cover in maintaining pollinator communities. Pollinators, critical for the reproduction of more than 95 % of tropical plants (Ollerton et al., 2011) and consequently essential for forest regeneration (López-Cubillos et al., 2023), are thus an exceptional model group to assess the importance of the canopy for ecosystem processes and the effects of canopy loss on biodiversity, yet the ecological drivers of pollinator stratification are largely understudied (Allen & Davies, 2023; Ashton et al., 2016; Nakamura et al., 2017; Roubik, 1993; Smith et al., 2012).

Most of these gaps are due to the logistical limitations of sampling canopies (Ulyshen et al., 2010). While several methods exist, ranging from tree climbing to cranes and scaffoldings (Schowalter & Chao, 2021), they are often cumbersome and expensive, thus only occasionally used and consequently suffer from sample size and replication issues (Barker & Pinard, 2001; Nakamura et al., 2017). Shooting methods used to rig pulley ropes on trees for passive trapping became progressively more popular since early canopy research (Barker & Pinard, 2001), particularly slingshots

127 and hand catapults (Allen & Davies, 2023; Yusah et al., 2012). Bows and crossbows,
128 however, entail the most precision and potency and allow for placing traps in higher
129 strata (Ellwood & Foster, 2001), while still being relatively simple and cheap.
130 Although the use of bows is frequently mentioned (Ashton et al., 2016; R. L. Kitching
131 et al., 2001; Morris et al., 2015; Sobek et al., 2009), the method has never been
132 described in detail, hindering its reproducibility, and has also not yet been used in
133 large biodiversity assessments.

134 We employed and provided technical details on the archery-assisted pulley system
135 method in a comprehensive sampling of diurnal and nocturnal pollinators in tropical
136 canopies to assess their abundance, diversity, composition, and functional uniqueness
137 in comparison to the understory, focusing on bees and moths. We aimed to investigate
138 how stratification contributes to and enhances diversity along forest succession in a
139 disturbed landscape. Considering the accumulation of floral resources in the canopy,
140 we expect that (i) pollinator (functional) diversity and abundance will be higher in the
141 canopy than in the understory, particularly as the degree of stratification increases in
142 older forests. Due to higher exposure in the canopy, as well as differing assemblages
143 of floral resources (e.g., epiphytes and crown trees), we expect (ii) differing
144 community compositions of pollinator species between strata. The resulting turnover
145 will lead to (iii) a higher overall diversity in old-growth forests in relation to the early
146 stages of forest recovery. Turnover, in turn, should be driven by (iv) dispersal traits,
147 e.g., larger (less desiccation-prone) insects with a better flying performance (higher
148 wind resistance) insects associated with the canopy; by their (v) response traits, with
149 light-colored or aposematic species associated with the canopy to resist overheating
150 and avoid predation; and by their (vi) interaction traits, with the packing of more
151 variable floral resources allowing for the occurrence of longer proboscises.

2. METHODS

2.1. Study area

The study was conducted between 2022 and 2023 in the Río Canandé Reserve (0°31'33.4"N, 79°12'46.0"W) and the Tesoro Escondido Reserve (0°32'30.9"N, 79°08'41.9"W), Esmeraldas province, northwestern Ecuador. The site is a lowland forest ecosystem within the Chocó-Darien ecoregion and a biodiversity hotspot on the western foothills of the Andes (Fagua & Ramsey, 2019), with a mean annual temperature of 24°C and annual rainfall of ca. 2100 mm, (Af climate, Köppen scale). The study was carried out in an ~7800 ha area within the REASSEMBLY research unit, a chronosequence of 62 50x50 m plots ranging from active disturbance agricultural sites, to regenerating secondary forests and old-growth forests (Escobar et al., 2024). From these plots, we sampled the canopy at 27 plots which had a defined vertical structure, at least one tree 15 m in height or taller, and significant canopy closure (section *2.2* below). All these plots were located in old-growth (OG) primary forests (N = 16) and late successional forests (LS), formerly pastures, or cacao plantations (N = 11, 9-37 years of regeneration). The remaining 35 plots were sampled at the understory only. These plots were either active plots (AC), i.e. cacao plantations or pastures (N = 12), or early successional (ES) forests without clear vertical stratification (N = 23, 1-8 years of regeneration). All plots were separated by at least 350 m (maximum distance 12.8 km) and were within comparable elevations (224-615m, average 388 ± 119,3).

Four insect sampling campaigns were carried out in total with each plot sampled twice: two campaigns in 2022, and two campaigns in 2023 (half of the plots were sampled between March and May and the respective other half between October and

December). Three LS plots were removed from the 2023 campaigns as canopy ropes could not be installed (the only usable tree fell or there were no more suitable branches). The permit to conduct research on the site and to sample insects was granted by the institutions in charge (Ministry of Environment of Ecuador, Contrato Marco MAE-DNB-CM-2021-0187).

2.2. Installation of pulley system and canopy traps

In each LS and OG plot, a pulley system was installed in a single tree in the canopy with the assistance of bow-and-arrow shooting (Fig. 1). For the rope installation we selected an accessible branch without much surrounding clutter or vegetation from the tallest or among the tallest trees within the plot (mean height 25.8 ± 5.3 m, median 25.2 m, range 15 – 37.0 m) to allow for a clean shot and avoid arrow tangling.

For installing the rope, we used a 29-inches glass fiber and aluminum Strongbow GECKO compound bow (BogenSportWelt, Germany) and 70 cm glass fiber arrows with rounded points (Toparchery, Germany). A 0.32 mm 4-strands braided polyethylene fishing line (Mounchain, Japan) was attached to the arrows and set onto a TP500 double-drag brake system fishing reel (YJIU, China, see Fig. 1 A for technical adjustments made to the reel). After selecting a fitting branch and successfully shooting the fishing line over it (Fig. 1, B – C), the fishing line was replaced by a ca. 5 mm polypropylene braided plastic rope, the final pulley system to which traps were attached (Fig. 1, D). A troubleshooting guide for the canopy setting can be found in the Appendix S1: Box S1. After the rope installment, traps (section *2.3* below) were attached to it using carabiners on the trap roofs and pulled up into the canopy. Traps

were separated by approximately 30 cm from one another and lifted to the maximum height possible, i.e. ideally directly below the branch where the rope was installed.

2.3. Insect trapping

We employed several types of traps to capture a variety of pollinator groups. In 2022, we sampled nocturnal insects (moths and bees), as well as diurnal bees. On each plot, we installed one light trap and one vane trap at each stratum level (one set of traps at AC and ES plots, two sets in LS and OG plots) within the plot area. Traps were left in the field for 24 hours. At the understories, traps were always ca. 2 m apart and ca. 1.5 m above ground. At the canopy, vane traps were always placed directly below light traps, separated by ca. 1 m. The traps employed were as follows:

(i) Light vane traps: target nocturnal insects; they were modified funnel traps consisting of a roof, three white vanes and a funnel of white polypropylene (Singh et al., 2022), equipped with a LepiLED mini Switch light (Brehm, 2017) and connected to a power bank battery. We used the mixed light setting (UV and visible light spectrums). The funnel traps were attached to a collection chamber which was connected to a 5 L bucket (wrapped in aluminum foil) with chloroform used to fast-kill trapped insects. The traps were timed to start light emission at 1800h and stop at 0600h. All trapped insects were collected the following day.

(ii) Color vane traps: target diurnal bees; the traps were in principle adaptations of a common and commercially-available used vane trap model (Prendergast et al., 2020) but due to the rainy environment, they had a roof and were equipped with both a yellow and a blue plastic vane attached transversally, forming an alternating color pattern designed to visually attract bees. Insects were collected in a connected 1 L plastic bucket wrapped in aluminum foil.

In 2023, color vane traps were set up once more in all plots, now with the addition of sugar baits (small quantities of honey smeared on the interior walls of the funnels) to increase capture rates. Additionally, we set up (iii) fragrance traps targeting fragrance-collecting male orchid bees (Apidae: Euglossini) (Eltz et al., 1999), a dominant pollinator group in the Neotropics (Michener, 2007). These traps were adaptations of those used by (Ferreira et al., 2013), using two lateral entrance holes (ca. 3 cm) equipped with plastic funnels and a piece of cotton imbibed in household insecticide (Raid, USA) as a fast-killing agent. On each plot, we placed four fragrance traps at the canopy and understory, each containing one of the following compounds: 1,8-cineole, eugenol, methyl-salicylate, and skatol (Carl Roth GmbH, Germany). This combination was chosen to attract a diverse range of orchid bee species (Cancino & Damon, 2007). As in the previous year, each set of traps (one vane trap, four fragrance traps) was simultaneously installed at the canopy and understory. In total, 348 traps (54 light vane traps, 102 color vane traps, and 192 fragrance traps) were set up, half at each strata level of the 27 LS and OG plots, and 245 (35 light vane traps, 70 color vane traps, and 140 fragrance traps) in the understory of AC and ES plots.

2.4. Focal insect groups and processing

After collection, insect samples were sorted, and target groups were selected for light traps: hawkmoths (Sphingidae) and tiger moths (Erebidae: Arctiinae). The first are large, fast-flying moths known for their importance as pollinators (Renner & Feil, 1993), while the latter are a large and diverse clade of conspicuous and often aposematic moths, which are likely underestimated as pollinators (Van Zandt et al., 2020). After sorting, insects were identified to the lowest possible level. Moths were sorted to morphospecies (referred to as species hereafter) and identified using the

collections in the Phyletisches Museum Jena, Germany and the research collection of GB from Costa Rica, Ecuador, and Perú, as well as photographs taken by GB in the Natural History Museum (London). Identification supported by COI barcoding of ca. 90% of all moth species (GB unpublished catalogue). Nearly all moth species could be assigned a genus, and most were identified to species level. Bees were identified using specialized literature (Bonilla-Gómez & Nates-Parra, 1992; Michener, 2007; Roubik, 1992b; L. M. Santos & Melo, 2015). All bees could be assigned a genus, and nearly all (> 95%) a (morpho)species.

From each insect species, we collected four morphological traits: body size (BS), proboscis length (PL), effective proboscis length (EL), and wing aspect ratio (AR). BS is an indicator of dispersal ability and resistance to desiccation in insects (Bailey et al., 2018) and was measured as the length between the tip of the head and the tip of the last abdominal segment of moths. The inter-tegular distance was used as a proxy for size in bees (Cane, 1987). PL is related to morphological coupling with flowering plants and is an interaction trait associated with feeding specialization (Johnson et al., 2017). It was measured as the combined extended length of the prementum and glossa for bees, and the entire extended length of the galeae. EL was calculated as the ratio between PL and BS, which accounts for the allometric relationship between PL and BS. AR is a measure of flight performance, with a higher AR indicating a better gliding capability (faster flyers) (Bhat et al., 2019). It was measured as the ratio between the square root of the forewing length and the wing area for moths; and for bees, the formula was simplified to the ratio between wing length and the wing's mean chord (widest wing width) due to a relatively conserved wing shape across groups (Bhat et al., 2019). Traits were measured manually with a caliper for larger bees (e.g., Euglossini) and with the aid of microscopy and linear

276 morphometric analysis via the ImageJ software (Collins, 2007) for smaller (> 5 mm of
277 body length) bees. For the latter, the proboscises were dissected and mounted on slides
278 for further image analysis. All moth traits were collected via a standardized
279 photography (Brehm, submitted) and processed via image analysis, using a modified
280 version of the mothseg algorithm (Jaimes Nino et al., 2019). We supplemented this
281 data with individual measurements of photographs with scale bars for proboscis length
282 (Brehm, submitted). We used measurement data from all species and used mean values
283 when more than one individual was present (up to ten).

284 We additionally measured coloration, which is linked to thermoregulation and
285 predation avoidance (Badejo et al., 2020). Coloration is thus an important response
286 trait that might affect the vertical distribution of species. For moths, we measured two
287 variables, also via standardized moth photographs and the modified version of the
288 mothseg algorithm: (1) Lightness was measured as the median pixel value of four
289 main color channels (red, green, blue, and UV) of the dorsal side of fully spread
290 individuals, which represents overall brightness (e.g., high values for white species
291 and low values for dark species), (2) Contrast, measured as the interquartile distance
292 (25th-75th percentiles) of the distribution of pixel values, representing coloration
293 variability with high values often associated with conspicuousness to predators and
294 aposematism. Trait measurements will be described in detail separately (GB, DB,
295 Yenny Correa Carmona, Dimitri Korsch, unpublished data). Finally, external visual
296 appearance was established as a set of categorical variables. Following Fiedler and
297 Brehm (2021), moths were classified as aposematic, hymenopteran mimic, beetle
298 mimic, and cryptic (none of the aforementioned). Bees, which did not show strong
299 mimicry patterns, were visually assessed and separated into five categories based on
300 the predominant color of their bodies, with the dorsal side of the head, thorax, and

abdomen used as reference: “dull-dark” (matte bees ranging from dark brown to black), “dull-clear” (matte bees of orange or yellow color), “iridescent-blue”, “iridescent-green”, “iridescent-red” and “aposematic” (the latter four strictly Euglossines).

2.4. Data analysis

All analyses were performed in R Studio 4.1.0 (R Core Team, 2021). To assess the variation in the occurrence of pollinators between canopies and understories, we tested for differences in four community parameters as response variables: (i) abundance (A), or the total sum of individuals in each sample; (ii) exponential Shannon diversity (effective diversity, q = 1), which corresponds to the effective number of common species (Magurran, 2013). To account for the effect of abundance and allow for a better cross-sample comparison, the asymptotic diversity of each sample was estimated via abundance-based rarefaction (Chao et al., 2014); (iii) functional richness (FRic) and (iv) functional dispersal (FDis), both measured via a distance-based and multi-trait framework to estimate functional diversity through the *FD* package (Laliberté & Legendre, 2010; Villéger et al., 2008). FRic estimates functional richness as the volume of the minimum convex hull encompassing all species in a PCoA reduction (Villéger et al., 2008), while FDis measures the distance of all species to a common centroid, thus estimating the average dispersal in functional profiles in comparison to a common mean (Laliberté & Legendre, 2010). All numeric traits were used to calculate FDis and FRic. Because these two indices could not be properly estimated for communities with less than three species, species-poor groups in the samples (i.e., *Megalopta* bees) did not undergo functional analysis. These four parameters were calculated for the canopy and understory of all LS and OG plots, and

326 each main pollinator group was analyzed separately. Paired t-tests were used to assess
327 whether the canopies and understories differed significantly for each of these
328 parameters. The normality of the data was checked in all instances.

329 To understand whether diversity in stratified LS and OG is enhanced via
330 species turnover between strata, we compared the rarefied diversity of canopy
331 samples, understory samples, and pooled canopy and understory samples of both
332 forest legacies through generalized linear models (GLMs) fit with a gaussian error
333 family and log link function, accounting for residual overdispersion. The same
334 analysis was used along the entire chronosequence gradient, i.e., rarefied diversity of
335 pollinators was compared among AC, ES, LS (pooled), and OG (pooled) to assess
336 whether canopy-bearing plots were more diverse in pollinators than early successional
337 and active plots. Main pollinator groups were analyzed separately so group-specific
338 trends could be considered. To ensure the lack of effect of plot proximity on diversity,
339 the lack of spatial autocorrelation of residuals of the diversity models for each group
340 was checked via Moran's I index calculated with the *ape* package (Paradis & Schliep,
341 2019) (Appendix S1: Table S1).

342 To find possible drivers of pollinator community stratification in the canopy-
343 bearing plots, we assessed how absolute differences in abundance, diversity, FDis, and
344 FRic between canopy and understory were affected by the following environmental
345 and landscape variables: (i) disturbance legacy (LS or OG), which may affect the
346 forest vertical structure and plant community found in the plot; (ii) canopy height,
347 using the height of canopy traps as a proxy; (iii) elevation a.s.l., which may affect plot
348 temperature and thus the microclimatic niches in both strata (Rapp & Silman, 2012);
349 and (iv) the proportion of forest within a 500 m buffer around the plot, a proxy for
350 landscape isolation and fragmentation, which affects pollinator occurrence and

dispersal (Didham et al., 1996). The ESRI World Imagery basemap was used as source for recent landcover and sourced from Escobar et al. (2024). We examined the effect estimates of the four normalized community parameters by GLMs adjusted with a quasibinomial error distribution to account for the ratio values of the community parameters and residual overdispersion. In order to assess legacy-specific patterns, the data from the three disturbance legacies (old-growth, former cacao plantations, and former pastures) were separated and analyzed independently as described above.

Finally, we examined whether species composition differed significantly between canopies and understories though Non-metric Multidimensional Scaling (NMDS) using the Bray-Curtis distance. A PERMANOVA (1000 permutations) followed to assess whether the canopy and understory groups differed significantly in composition. To understand how species composition was influenced by functional traits (PL, BS, EL, and AR, plus lightness and contrast for moths), we employed a Canonical Correspondence Analysis (CCA) using each trait's community-weighted mean as constraining. The significance variance explained by the main CCA axes, as well as the six constraining variables, were assessed via Monte Carlo permutation tests (1000 permutations). The main pollinator groups were analyzed separately. The occurrence (presence of absence) of visual categories was analyzed independently, with estimates of the effect of stratification on color occurrence obtained via GLMs set with a binomial error family. Similarly to the previous section, the three disturbance legacies were separated and analyzed independently (old growth, former cacao plantations, and former pastures).

3. RESULTS

3.1. Stratification and its effect on pollinator diversity

A total of 13997 target insects were collected in the 27 LS and OG plots, encompassing 7614 moths from 302 species and 6383 bees from 89 species. Of these, 5727 (41%) were captured in the understory, and 8270 (59%) in the canopy. Moths were represented by the two focal groups Arctiinae and Sphingidae, with the former accounting for the vast majority of individuals (98.1%). Therefore, all results concerning moths hereafter refer to both groups analyzed together. The samples from diurnal traps were dominated by stingless bees (Apidae: Meliponini) (51% of bee individuals) collected exclusively from vane traps, orchid bees (Apidae: Euglossini) (43%) collected from fragrance traps, and nocturnal *Megalopta* (Halictidae: Augochlorini) bees (6%) from light traps. Other bee groups (e.g., Colletidae, diurnal Halictidae) accounted for 0.27% of the total bee captures and were thus not included in further analyses.

Abundance and diversity were significantly higher in the canopy relative to the understory for moths (abundance: $t = 4.48$, $p < 0.001$; diversity: $t = 7.16$, $p < 0.001$), stingless bees ($t = 2.95$, $p < 0.01$; $t = 3.19$, $p < 0.01$) and *Megalopta* bees ($t = 3.01$, $p < 0.01$; $t = 2.97$, $p < 0.01$). Moths showed the strongest preference towards the canopy (Fig. 2). Orchid bees, however, showed an inverse pattern, with a stark decrease in abundance ($t = -5.23$, $p < 0.001$) and diversity ($t = -3.36$, $p < 0.01$) in the canopy relative to the understory. Moreover, moths showed a significantly higher functional richness ($t = 3.85$, $p < 0.001$) and dispersion ($t = 4.13$, $p < 0.001$) in the canopy, while orchid bees again showed a strong and inverse pattern (FRic, $t = -5.60$, $p < 0.001$; FDIs, $t = -2.29$, $p < 0.05$) (Fig. 2). There was no significant difference between the strata for stingless bees ($p > 0.05$ for both variables).

Additionally, 4997 bees and 4263 moths were collected in the remaining AC and ES plots, summing up to 23257 target insects captured in total. Along the

succession gradient, the canopy-bearing LS and OG forests always had similar species diversity vales, and both forest legacies were significantly more diverse than ES and AC for Meliponini bees and more diverse than ES for moths (Fig. 3, Tab. 1). Moths were also highly diverse in AC plots and did not differ between late and old-growth forest plots (Fig. 3 A-B, Tab.1). Overall, nocturnal *Megalopta* bees were also more diverse in older forests, particularly OGs (Fig. 3 D). However, Euglossines showed no significant pattern along the successional gradient, although they were on average most diverse in LS and OG (Fig. 3 C).

In terms of the turnover between canopy and understory, pooled LS and OG samples were significantly more diverse than individual canopy and/or understory samples for moths, particularly in late successional forests (Fig. 3 A, Tab. 1), suggesting high turnover and a complementary interaction between strata and increase in total diversity. Meliponini showed no turnover between canopy and understory in both forest types (Fig. 3, B). The diversity of Euglossini in forest plots was similar to that of understory samples, especially in OG plots (Fig. 3 C). *Megalopta* showed an inverse trend (Fig. 3, D), although their low diversities likely impaired proper estimation.

3.2. The role of forest legacy, canopy height, and environmental features

Plot environmental variables and disturbance legacy only explained little variation between canopy and understory in terms of abundance, diversity, and functional diversity for most pollinator groups. Neither canopy height, legacy, elevation nor the proportion of forest around the plots had a significant effect on the variation of Meliponines and moths ($p > 0.05$ for all variables) (Fig. 4). The proportion of forested area around sampling plots, however, had a significant and negative effect

426 on the variation in diversity (χ^2 = 9.47, p = 0.002) and the functional dispersal (χ^2 =
427 3.88, p = 0.04) of Euglossines (Fig. 4), i.e., canopy and understory communities
428 became more similar taxonomically and functionally with increasing proportions of
429 forest around plots. *Megalopta* bees showed a sharp decrease in the variation in
430 abundance (χ^2 = 4.83, p = 0.02) and diversity (χ^2 = 6.06, p = 0.01) between canopy and
431 understory in LS plots, i.e., strata were more similar in successional forests than in
432 old-growth forests. Abundance variation was further positively affected by plot
433 elevation (χ^2 = 5.43, p = 0.02); and diversity variation was negatively affected by
434 canopy height (χ^2 = 6.63, p = 0.01) (Fig. 4), i.e., bees were more evenly distributed
435 between strata at lower elevations and in plots with shorter canopies.
436
437 *3. 5. Species composition and the influence of traits*

438 Species composition differed significantly between canopy and understory for
439 both bees (F = 8.63, R^2 = 0.15, p < 0.001) and moths (F = 4.29, R^2 = 0.008, p <
440 0.001), with a most noticeable divergence within bees following a phylogenetic signal
441 due to differences in strata preferences of Meliponini and Euglossini. The entire bee
442 community varied significantly in their functional profiles, with larger, longer-
443 tongued, and faster-flying bees strongly associated with the understory (CCA1: Eigenv
444 = 0.54, F = 6.63, p < 0.001; CCA2: Eigenv = 0.28, F = 3.45, p < 0.01). All traits
445 significantly affected the distribution of pooled bee species (Fig. 5, A, Tab. 2).
446 Proboscis length and wing aspect ratio, which are likely associated with the long-
447 tongued and fast-flying orchid bees, explained the most variance, although with an
448 overall low variance explained (Tab. 2).
449 Meliponini, when isolated, showed a stronger association with the understory
450 for all traits (CCA1: Eigenv = 0.72, F = 10.60, p < 0.001; CCA2: Eigenv = 0.69, F =

10.20, $p < 0.001$) (Fig. 5, B; Tab. 2). Euglossini presented a less clear yet significant signal of functional trait distribution between canopy and understory (CCA1: Eigenv = 0.33, F = 6.39, $p < 0.001$; CCA2: Eigenv = 0.19, F = 3.71, $p < 0.001$), yet bees in the canopy tended to be larger, slower flyers with shorter effective proboscis lengths (Fig. 5, C; Tab. 2). Traits significantly influenced moth composition (CCA1: Eigenv = 0.26, F = 3.93, $p < 0.001$; CCA2: Eigenv = 0.21, F = 3.20, $p < 0.001$), yet to a smaller extent and with the least clear distinction between canopy and understory. Most notably, moths in canopy samples tended to show a lighter coloration, while contrast did not significantly vary across samples (Fig. 5, D; Tab. 2).

The different color categories of bees and moths differed significantly between canopy and understory. Canopy-associated bees fell into the dull bright category, followed by the dull dark bees. Across all forest legacies, both groups were represented mainly by small social stingless bees (Fig. 6, A). All other colors tied to euglossines were more associated with the understory, i.e., aposematism on old-growth plots, and iridescent colors, particularly red, in all legacies (Fig. 6, A). Cryptic moths were much more common in the canopy across all three legacies, while aposematic and beetle mimics were associated with the understory (Fig. 6, B). These patterns were stronger in old-growth forests and relatively weak in former cacao plantations. Hymenopteran mimics were strongly and significantly associated with the canopy in old-growth plots, but not in successional forests (Fig. 6, B).

4. DISCUSSION

4.1 Patterns of pollinator stratification

Our study provides new insight into the vertical stratification of insect pollinators along forest succession. We found an overall increase in pollinator abundance and diversity in canopies, as well as different species composition between strata, which led to a diversity-enhancing effect in successional and primary forests for moths and, to a lesser extent for orchid and stingless bees. Our expectations (i-iii) were, however, only partially confirmed, as canopy preferences were group-dependent and driven by taxa-specific functional traits.

Positive associations with canopies were observed for moths, meliponines, and *Megalopta* bees, all of which are driven, to some extent, by the vertical stratification of resources. Arctiinae moths increase in abundance and diversity in canopies, likely influenced by the availability of resources for liana- and vine-specialized caterpillars (Brehm, 2007), suggesting a bottom-up regulation of this group by vegetative resources. In addition, a concentration of floral resources in the canopy has also been suggested as a potential driver of stratification in tropical Arctiinae and Sphingidae (Schulze et al., 2001). Such associations have not been observed for other groups of moths (e.g., Geometridae), indicating that group-specific canopy preferences operate even within a given feeding guild (Brehm & Axmacher, 2006). In addition, in temperate forests, the inverse pattern was observed for several groups including tiger moths (Böttger et al., 2025), suggesting that the stratifying effect of resource availability is more prominent in the tropics and likely related to components not present in temperate forests (e.g., lianas and epiphytes). Meanwhile, a high abundance and diversity of Meliponines is likely related to their specialization on mass-flowering canopy trees (Calaça et al., 2022; Ramalho, 2004), which provide abundant food resources for their partly large colonies. *Megalopta*, in turn, is a highly understudied group but scarce evidence shows a dietary preference towards a few veteran bat-

499 pollinated canopy trees (Smith et al., 2012), which is further supported here by their
500 spike in occurrence in old-growth canopies.

501 The observed canopy preferences suggest a key role of resource availability in
502 the vertical distribution of tropical insects, as often reported in temperate forests
503 (Sobek et al., 2009; Ulyshen et al., 2010). The stratifying effect of resources has also
504 been observed in a variety of functional groups, including seed dispersers and non-
505 obligate floral visitors, ranging from non-flying mammals (Rader & Krockenberger,
506 2006), birds and frugivorous bats (Chmel et al., 2016; Thiel et al., 2021) to butterflies
507 (Fermon et al., 2005), as well as ground predators and flying insectivores (Basham et
508 al., 2023; Kalko & Handley, 2001), indicating that resource stratification permeates
509 different ecosystem processes. In our study site, several slow-growth, mass-flowering
510 trees and palms with accessible flowers were likely driving the increased abundance of
511 pollinators, particularly stingless bees, in canopies, including *Miconia*
512 (Melastomataceae), *Wettinia* (Arecaceae), *Banara* (Salicacaea), and resin-rewarding
513 *Clusia* (Clusiaceae) (Lozano et al., 2024). On top, the abundant night-blooming *Inga*
514 (Fabaceae) and Meliaceae (e.g., *Guarea*, *Tapirira*) (Lozano et al., 2024) might further
515 explain the canopy preference of *Megalopta* bees in OG plots and why stratification in
516 this group was lower in successional forests.

517 Euglossines, in contrast, showed a notable aversion towards the canopy, as
518 frequently noted (Feitosa Ribeiro et al., 2024; Ramos et al., 2022; Vega-Hidalgo et al.,
519 2020), but underlying causes are unknown. A prominent hypothesis is the dissipation
520 of floral volatiles (synthetic and natural) by sunlight and wind in the canopy, which
521 hinders detection by Euglossines and would explain why these bees avoid the canopy
522 (Ramos et al., 2022), as well as the low occurrence of Euglossini-pollinated orchids in
523 canopies (Hernández-Pérez et al., 2018). A further and more detailed examination of

resource (functional) diversity stratification might shed light on the role of various resources (food, nests, scent) on the vertical distribution of orchid bees and other pollinators in general (e.g., Silva et al., 2021). Beyond the role of resources, the composition shift from larger, longer-tongued Euglossines with good flying performance towards small and light-colored eusocial Meliponines in the canopy may shed some light onto the role of traits on the stratification of pollinators and the influence of abiotic factors.

4.2 The influence of traits

Our results also only partially confirmed our expectations (iv-vi) of large, light-colored, or aposematic pollinators with longer proboscises and better flying performance in the canopy. Size had the most notable variation between strata, and against our expectations, the canopy was dominated by small Meliponines with relatively broad wings and smaller proboscis. Most of this variation reflects the canopy aversion of the large, dispersal-capable, and long-tongued Euglossines, but this pattern repeats also within stingless bees. Canopy specialists mainly comprised small (ca. 2 mm), gregarious, and wood-nesting *Trigonisca* bees (Michener, 2007), especially the bright-colored and highly abundant *T. atomaria*, while larger genera, such as *Partamona,* were more common in the understory (as also seen by Roubik, 1993).

This outcome is the opposite of the "shade-loving" bees associated with the understory described by Bawa (1990) and Kato (1996) and suggests that the interplay between dispersal and response traits and abiotic factors is not always straightforward and may be related to other variables to the usage of the landscape by a given animal, such as finding food and nesting resources. For instance, nesting and foraging close to

549 the canopy may enable small Meliponines with very short flight ranges (e.g.,
550 *Trigonisca*, less than 100 m from colonies) to account for both smaller size and lower
551 mobility (Grüter & Hayes, 2022) and may consequently represent a tradeoff between
552 exposure, such as stronger winds, low humidity, and heat (which may be partially
553 buffered by brighter colors), and foraging optimization. Establishing a nest may also
554 be easier in upper strata, as the abundance of natural substrate for cavity bees (e.g.,
555 natural crevices in wood) (Sobek et al., 2009) provides an advantage to most
556 Meliponines and many solitary bees (Batra, 1984; Wille & Michener, 1973).
557 Therefore, while functional traits may explain bee stratification to some extent, much
558 of the variation seems to be tied to group- and genera-specific preferences. Within
559 Euglossini, for instance, a slight shade-loving bee pattern (more robust bees in the
560 exposed canopy) emerged mainly due to large *Eulaema* bees that often ventured
561 beyond the understory, as also seen by Roubik (1993). The importance of accounting
562 for genera or species when assessing canopy preference is thus clear, as suggested for
563 organisms ranging from bees (Roubik, 1993) to bats (Kalko & Handley, 2001).
564 Life-history traits may provide additional insight. The nomadic and long-range
565 movement of solitary Euglossini males, as opposed to the localized colony life of
566 Meliponini, makes this group vulnerable to habitat fragmentation if patch sizes are too
567 small (Powell & Powell, 1987). In our study system, this negative effect of
568 fragmentation manifested in more homogeneous strata, with less (functionally) diverse
569 canopies in more isolated plots. This outcome suggests an interaction between canopy
570 usage and fragmentation for isolation-sensitive groups, as assumed by Ramos et al.
571 (2022). Nocturnal bees, in turn, naturally intolerant to heat and desiccation (Gonzalez
572 et al., 2023), were less stratified when canopies were higher (thus potentially drier)

and a higher stratification in more elevated plots, where colder temperatures likely buffered the effect of exposure on these bees.

As for moths, specific adult functional traits showed a limited influence on the community composition, further suggesting a stronger role of larval stages in stratification. An exception was the occurrence of visual deception. Light-colored, cryptic, and hymenopteran mimic moths were associated with the canopy, indicating that canopy-specialist adult moths require some form of protection from predators to compensate for their exposure (Brehm, 2007) when, e.g., searching for ovipositing sites. The occurrence of this specific form of mimicry in the canopy might be related to cavity-nesting wasps and bees, common in canopies (Sobek et al., 2009), while the frequent occurrence of coleopteran mimicry and aposematism in the understory further reinforces genus-specific preferences for strata (e.g., Coleoptera mimicry is mainly represented by genera *Correbia*, *Correbidia*, and *Lycomorphodes*, Rabl et al., 2020) possibly driven by the vertical stratification of different predator guilds (Basham et al., 2023).

Therefore, the varying importance of dispersal, response, and protective traits across taxa, allied to tribe- or genus-specific patterns, suggest accounting for both morphological and life-history traits (e.g., roosting and nesting requirements, feeding specialization of adults and larval stages, sociality, period of activity) for a more comprehensive understanding of animal stratification and recovery (see Montoya-Pfeiffer et al., 2020).

4.3 The diversity-leveraging effect of stratification

Despite the different stratification patterns and signal of functional traits across groups, the overall increased pollinator diversity in canopy-bearing underlines the

relevance of both primeval and successional forests in maintaining animal diversity in disturbed landscapes, as attested for a range of ecosystems (Taki et al., 2013; Ulyshen et al., 2024). Pollinator diversity was consistently similar between LS and OG forests and significantly higher than early successional plots, except for Euglossini bees. Male Euglossines require wide dispersal and foraging ranges to search for particular and specific volatile compounds used in courtship that are sparsely distributed across the forest (Eltz et al., 1999). On top of being an essential part of their reproductive cycle, a good dispersal capability grants them a notably high resistance to disturbance (Aguiar & Gaglianone, 2012; Botsch et al., 2017), consequently leading to a low response to the successional gradients (Rasmussen, 2009). High resistance and resilience to the loss of habits have been linked to dispersal ability, more vagile being often less sensitive (Meyer et al., 2009). Low dependence on canopy-specific resources and a solitary life likely also played a role in their prolific nature, unlike other social bee groups that are more dependent on resources closer to colonies.

For instance, social Meliponines and facultatively social *Megalopta* (Smith, 2021) are more tied to forested plots and are much more sensitive to disturbance. Consequently, these groups must be more strongly tied to the resources, in terms of both quantity and composition, found in LS and OG forests. Although the plant composition of primary forests may take centuries to recover (Finegan, 1996), older secondary forests (20-35 years) harbor insect communities similar to that of old-growth forests, successfully sustaining associated ecosystem processes (Taki et al., 2013). Most Meliponines and many solitary bees are known to be polylectic, i.e., to consume nectar and pollen from a wide range of plant species (Michener, 2007; Wcislo & Cane, 1996), thus allowing for the colonization of LS plots when canopy

closure starts to establish and plant diversity increases (10-25 years, Chazdon, 2008) as observed for stingless bees and *Megalopta*.

Moths showed the strongest turnover and complementary effect between canopy and understory, particularly in LS forests. This group may serve as a good example to illustrate the effect of resource turnover during forest succession on pollinator diversity. The high moth diversity seen in disturbed plots, which has repeatedly been found for Arctiinae and Sphingidae moths, is probably associated to a high mobility of most species that allows movement across the matrix during milder nighttime conditions, as well as with the feeding generalism of caterpillars of many species (Fiedler et al., 2007; Jaimes Nino et al., 2019; Kitching et al., 2000; Nöske et al., 2008). Colonizing bushes and herbs, however, are then quickly removed during early forest succession due to the establishment of the first light-tolerant pioneer trees, and plant diversity only significantly increases again and is at its highest after the first decade during the stem exclusion phase (*sensu* Chazdon, 2008), when plant species suppression, turnover, and growth are the highest stratification starts to take place. Thus, high plant (functional) diversity may explain both the stronger stratification of moths in LS plots and the lower diversity in ES plots, where a structured plant community is still not established.

Whether due to the higher availability of leaf or floral resources, a high pollinator diversity starting at recently stratified LS forests underlines the importance of structural complexity in secondary forests in maintaining biodiversity (Hilmers et al., 2018). Moreover, it signals that the positive effects of forest regeneration in recovering ecosystem processes are quick to reap. Whenever selective logging cannot be regulated, allowing patches of forest to naturally recover may thus significantly increase the resilience of disturbed landscapes (Meli et al., 2017). In conclusion, the

varying patterns of stratification and recovery across taxa highlight the need for comprehensive biodiversity assessments that consider the different forest strata. For this purpose, we stress that the archery-assisted pulley system was highly suitable for the quick setup of traps at heights up to 37 m. Note that this limit was set by the study site and longer shooting ranges are certainly possible. This method can thus be applied for primary or successional rainforests with no access to infrastructure, such as canopy cranes and platforms, or where topography (e.g., inclination) precludes their setup, thereby aiding in reducing sample size issues (Barker & Pinard, 2001).

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AUTHOR CONTRIBUTIONS

SDL, GB, AK, and UMD conceptualized the research. SDL, AK and GB acquired and managed the funding. UMD, DB, SVL, and JW performed fieldwork and data collection. UMD, DB, SVL, JW, MP and KF performed sample processing and data curation. CR, GB, UMD, DB, SVL, JW, MP, KF identified insects. UMD performed data analysis and wrote the manuscript draft. All authors contributed critically to the last manuscript draft.

CONFLICT OF INTERST

The authors declare no conflicts of interest.

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1058 **TABLES**

1059

1060 **Table 1.** Estimates (β) and standard errors (SE) of differences in diversity (q = 1)
1061 between plot types along the successional gradient (top), and between isolated strata
1062 and pooled samples of late successional forests (middle) and old-growth forests
1063 (bottom). The reference plot type is always the first in the couplet, followed by the
1064 compared plot type, hence positive and negative values indicate an increase or
1065 decrease in diversity in the compared plot type in relation to the reference plot,
1066 respectively.

	β (SE)					
Succession gradient	AC - ES	AC - LS	AC - OG	ES – LS	ES - OG	LS - OG
Moths	**-0.29 (0.11)**	0.11 (0.11)	0.04 (0.10)	**0.40 (0.10)**	**0.33 (0.10)**	-0.08 (0.10)
Meliponini	**1.06 (0.36)**	**2.18 (0.45)**	**2.47 (0.39)**	**1.12 (0.40)**	**1.41 (0.33)**	0.28 (0.42)
Euglossini	0.10 (0.09)	0.19 (0.11)	0.19 (0.10)	0.09 (0.09)	0.09 (0.07)	-0.01 (0.09)
Megalopta	0.34 (0.21)	**0.68 (0.26)**	**0.90 (0.22)**	0.34 (0.23)	**0.57 (0.19)**	0.23 (0.24)

	β (SE)		
Late succession (LS)	Pooled - Understory	Pooled - Canopy	Understory - Canopy
Moths	**-0.22 (0.10)**	**-0.20 (0.09)**	0.03 (0.10)
Meliponini	-0.41 (0.44)	-0.47 (0.43)	-0.06 (0.43)
Euglossini	-0.48 (0.87)	**-2.96 (0.87)**	**-2.49 (0.87)**
Megalopta	-0.38 (0.26)	-0.43 (0.26)	-0.06 (0.26)

	β (SE)		
Old growth (OG)	Pooled - Understory	Pooled - Canopy	Understory - Canopy
Moths	**-0.33 (0.09)**	-0.15 (0.08)	0.18 (0.09)
Meliponini	-0.16 (0.13)	-0.07 (0.12)	0.09 (0.13)
Euglossini	-0.11 (0.10)	**-0.32 (0.11)**	-0.21 (0.11)
Megalopta	**-0.64 (0.19)**	-0.04 (0.19)	**0.59 (0.18)**

1067 Notes: Bold values indicate significant values ($p < 0.05$).
1068 Abbreviations: AC – active disturbance; ES – Early succession; LS – late succession, OG –
1069 old-growth forests.

1070 **Table 2.** Summary of variance explained by different functional traits obtained by a

1071 Canonical Correspondence Analysis (CCA) analyzing differences in the distribution of

1072 all pollinator groups between canopy and understory. F-statistics and p-values are

1073 based on 999 random Monte Carlo permutations.

Parameter	Moths		Bees (pooled)		Meliponini		Euglossini	
	Variance (%)	F (*p*)	Variance (%)	F (*p*)	Variance (%)	F (*p*)	Variance (%)	F (*p*)
PL	6.17	3.71 **(.001)**	9.64	5.75 **(.001)**	12.16	9.35 **(.001)**	6.53	3.77 **(.001)**
BS	3.70	2.23 **(.009)**	4.44	2.65 **(.001)**	12.03	9.25 **(.001)**	6.25	3.61 **(.001)**
EPL	3.79	2.28 **(.001)**	4.10	2.45 **(.002)**	7.94	6.10 **(.001)**	4.38	2.53 **(.003)**
AR	3.03	1.83 **(.001)**	6.46	3.86 **(.001)**	10.65	8.19 **(.001)**	8.29	4.78 **(.001)**
Lightness	3.23	1.95 **(.001)**	-	-	-	-	-	-
Contrast	2.04	1.43 (.085)	-	-	-	-	-	-
Total	21.96		24.65		42.78		25.46	

1074 Abbreviations: PL - proboscis length, BL - body size (body length for moths, intertegular

1075 distance for bees), AR - wing aspect ratio, EL - effective proboscis length, Lightness -

1076 coloration lightness (moths only), Contrast - coloration contrast (moths only), Total – total

1077 cumulative variance explained

FIGURE CAPTIONS

Figure 1. A step-by-step process of installing the canopy rope that constitutes the pulley system used to lift the traps. **a** – preparations for the shot and set up of the fishing reel and arrow. The inset box lists the technical requirements of the fishing reel, bow, and arrow for a successful shot. **b** – Selection of a fitting branch at the canopy, shooting, and arrow retrieval. This step entails most of the difficulties that may arise during the process. See Box for a list of issues that can occur and respective solutions. **c** – replacement of the fishing line with the final pulley rope. **d** – Overview of the successfully set rope and traps. Persons, traps, and trees are not to scale. Created in BioRender (https://BioRender.com/i24e291).

Figure 2. Paired differences in abundance, diversity (rarefied exponential Shannon diversity), functional richness (FRic) and functional dispersion (FDis) of moth and bee pollinators between the understory and the canopy of the sampled plots. Asterisks indicate significance levels reported by the t-tests (ns = not significant, * = < 0.05, ** = < 0.01, *** < 0.001), and lines between paired points indicate the plot legacy. Functional richness and dispersion values are not shown for *Megalopta* bees due to low diversity in most plots (<3 species). Horizontal lines within boxes indicate the distribution's median, box edges the 25th and 75th percentiles, and whiskers the minimum and maximum values.

Figure 3. Rarefied diversity (q = 1) of the four major pollinator groups captured along the successional gradient: active disturbances (AC), early successional plots (ES), late successional forests (LS), and old-growth forests (OG). LS and OG are further separated into understory (U) samples, canopy samples (C), and pooled samples, for

which diversity was measured independently. Asterisks indicate significant differences ($p < 0.05$) between the means of pooled, understory, and canopy samples within the latter two groups. The dashed lines indicate the mean diversity across all plots. A: moths, B: Meliponini, D: Euglossini, E: *Megalopta.* Horizontal lines within boxes indicate the distribution's median, box edges the 25th and 75th percentiles, whiskers the minimum and maximum values, and the shaded area datapoint density.

Figure 4. Model estimates for the effects of plot variables on the community parameters (abundance, Shannon's exponential diversity, functional dispersal (FDis) and functional richness (FRic)) of the four main pollinator groups sampled. Points and bars depict estimate means and error bars, respectively, which are colored according to the direction of the association between variables [positive (blue) or negative (red)] and significance ($p < 0.05$). Plot variables: **Leg** – disturbance legacy (successional forests compared to old-growth forests), **Hei** – canopy height, For – proportion of forest in a 500 m buffer, **Ele** – plot elevation. For the legacy variables, old-growth plots are set as the reference group.

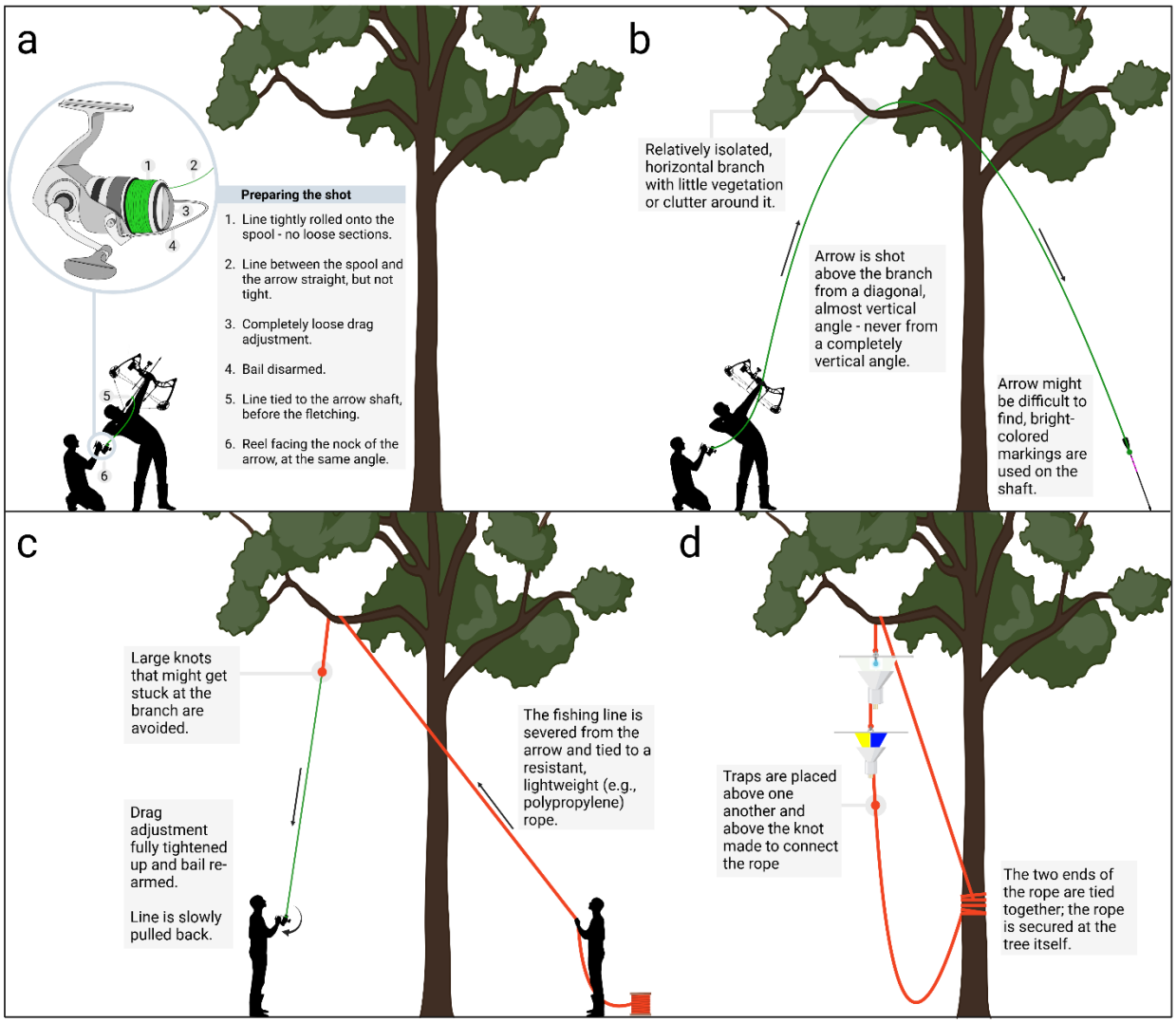
Figure 5. The effect of functional parameters on the divergence of all bee groups pooled (a), as well as specifically on the two dominant bee groups Meliponini (b) and Euglossini (c), and moths (d). Canopy and understory plot samples are separated by shape and color, and grey crosses represent species. Axes correspond to the two main components of the Canonical Correspondence Analysis (CCA), and percentages are the variance explained by each axis. Vectors indicate the direction and intensity (length) of the constrained variables: **PL** = proboscis length, **BS** = body size, **EPL** =

effective proboscis length, **AR** = wing aspect ratio, **contrast** = coloration contrast, **lightness** = coloration lightness.

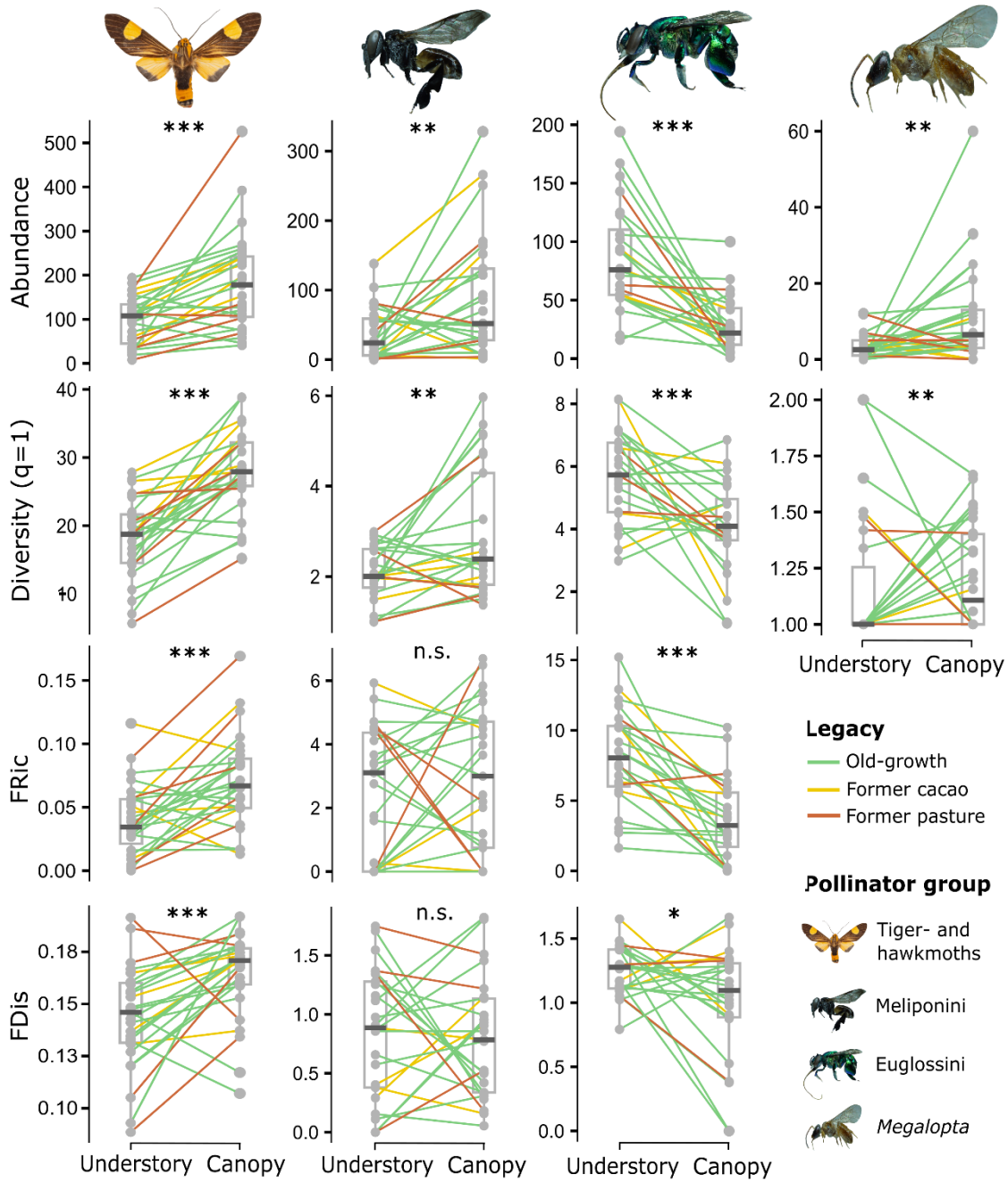
Figure 6. Model estimates of the occurrence probability of different visual categories of bees (A) and moths (B) at the canopies of the studied plots relative to the understories (positive and negative values indicate an association with canopy and understory, respectively) in the three disturbance legacy classes (old-growth forests, former cacao plantations, and former pastures). Bars indicate standard errors. Estimates are significant ($p < 0.05$) unless stated otherwise (n.s. on top of the estimate). Categories: **Apo** – aposematic, **Dar** – dull dark, **Bri** – dull bright, **Blu** – iridescent blue, **Gre** – iridescent green, **Red** – iridescent red, **Cry** – cryptic, **Col** – coleoptera mimic, **Hym** – hymenoptera mimic.

FIGURES

Figure 1

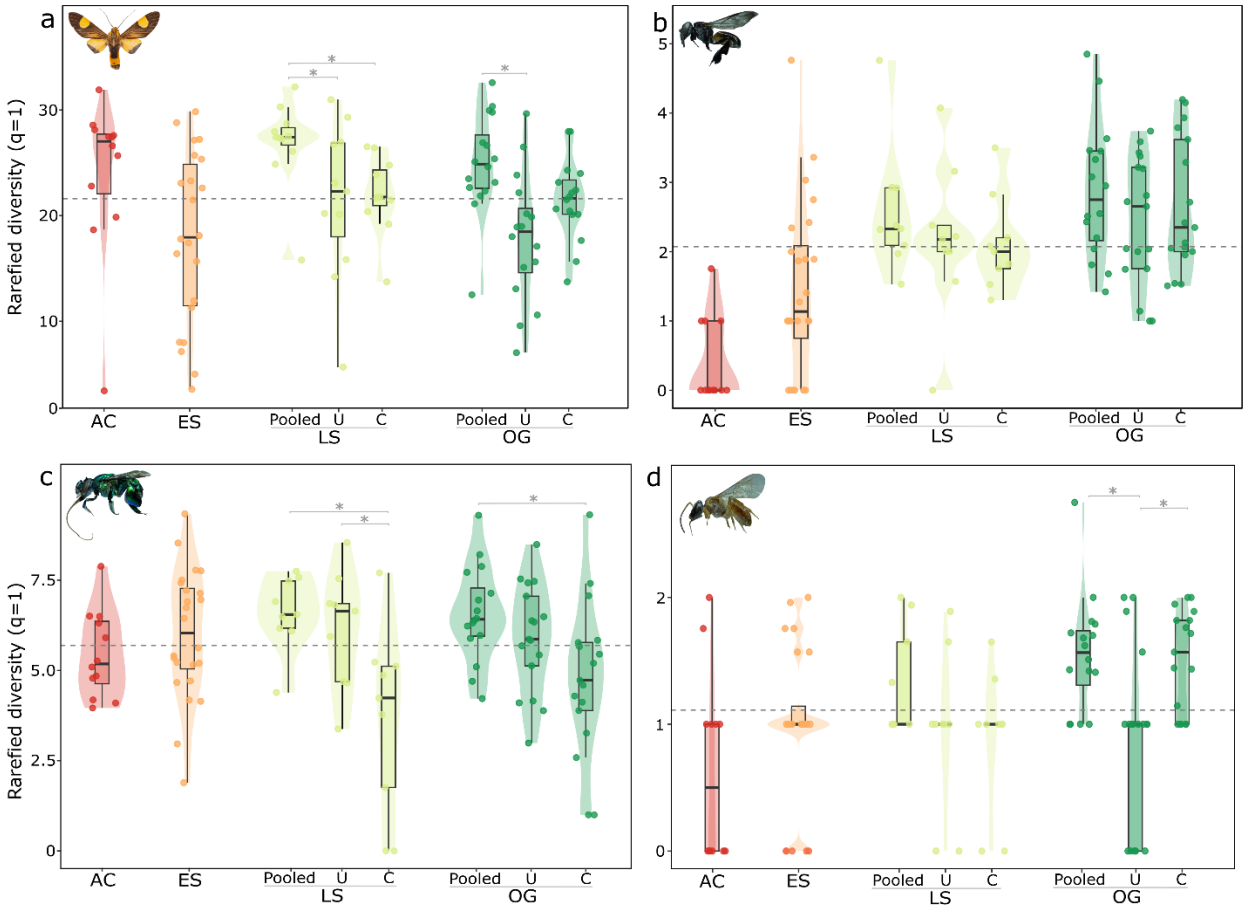


1144 **Figure 2**



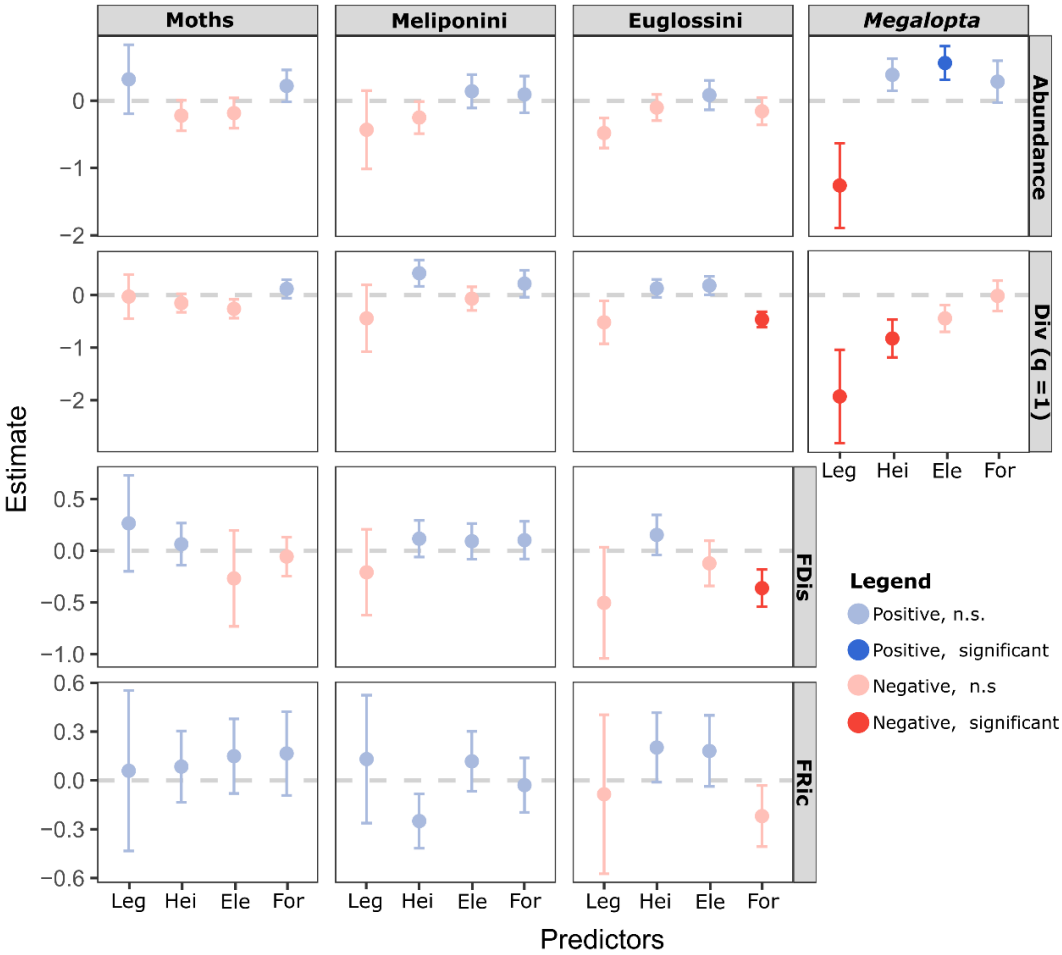
1145

1146 **Figure 3**



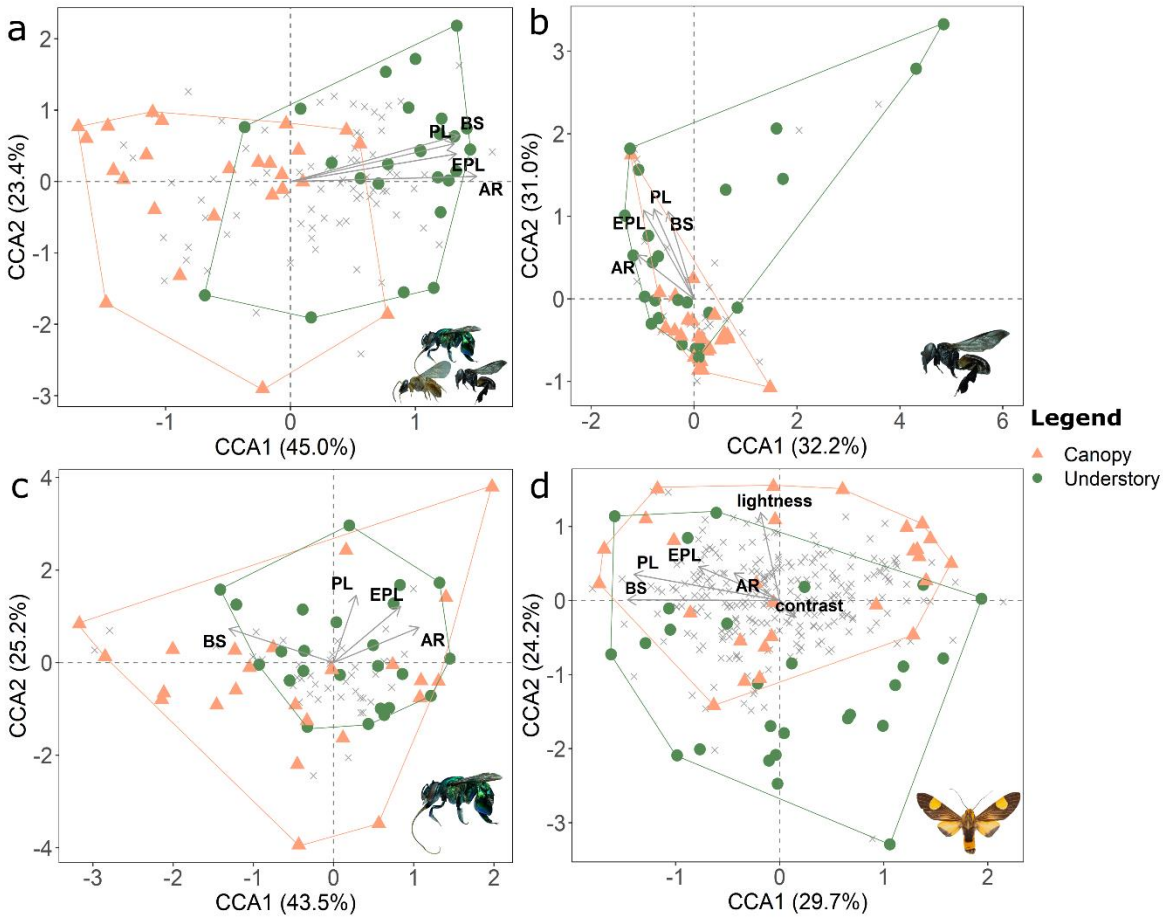
11

1148 **Figure 4**



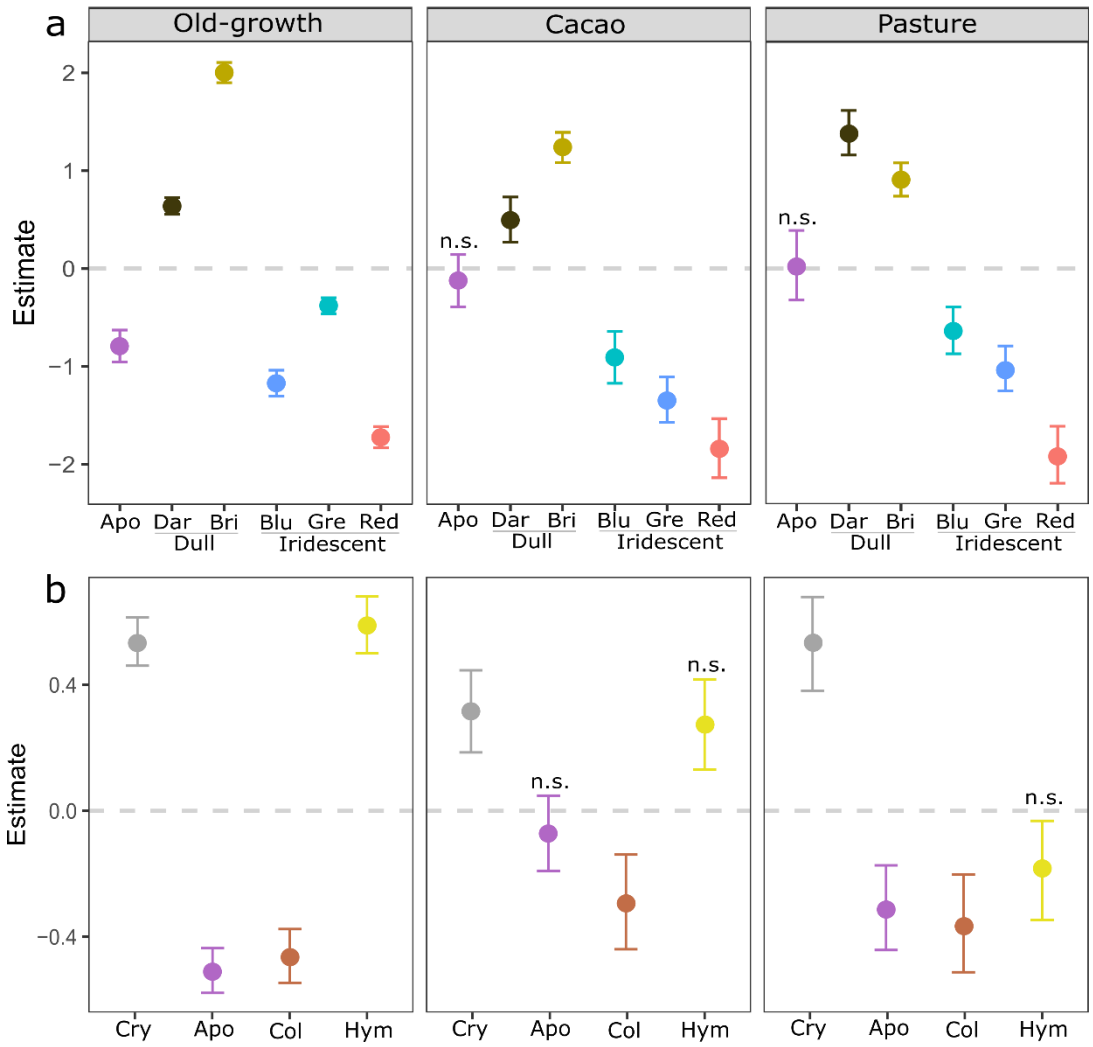
1149

1150 **Figure 5**



1151

1152 **Figure 6**



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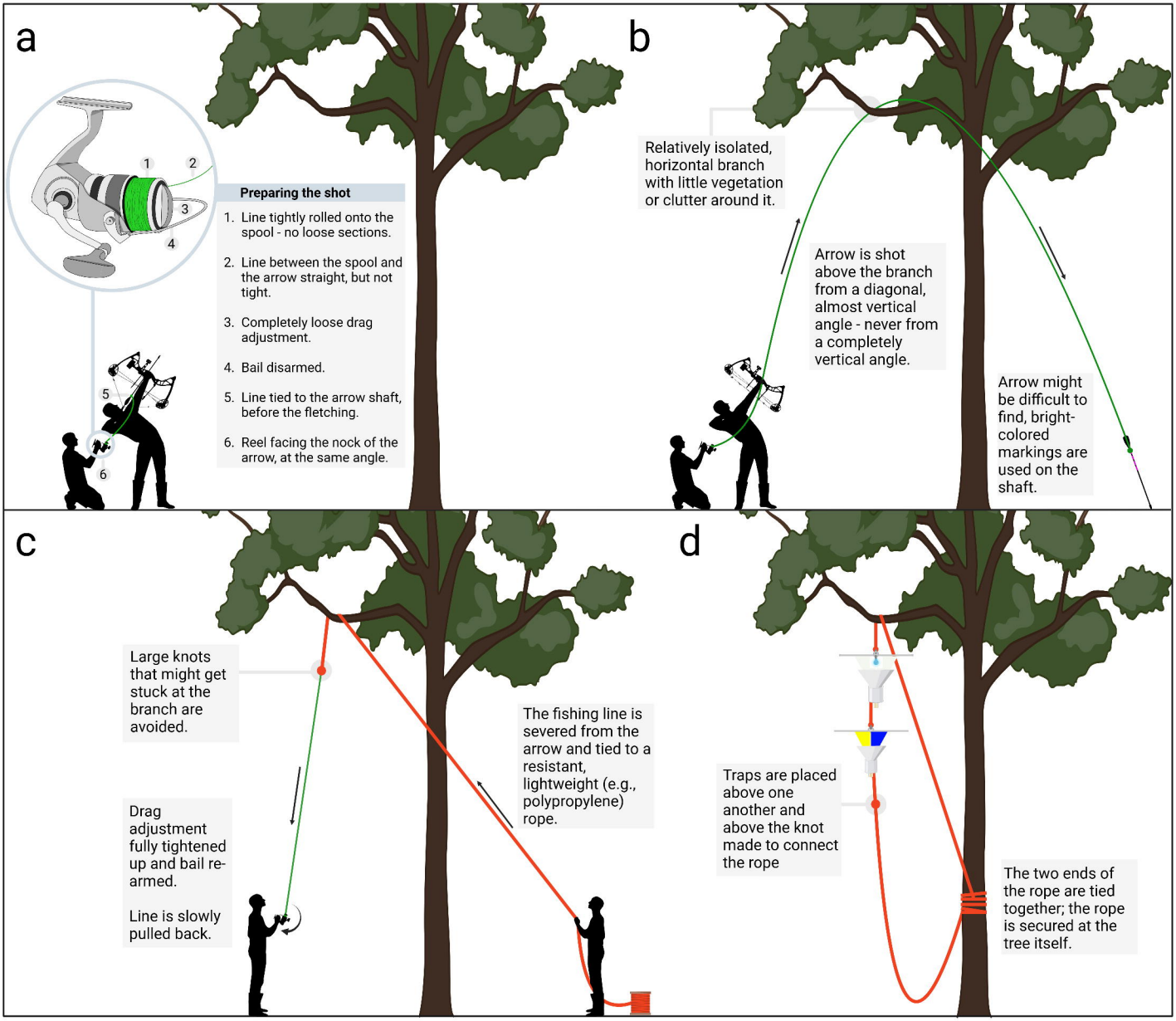
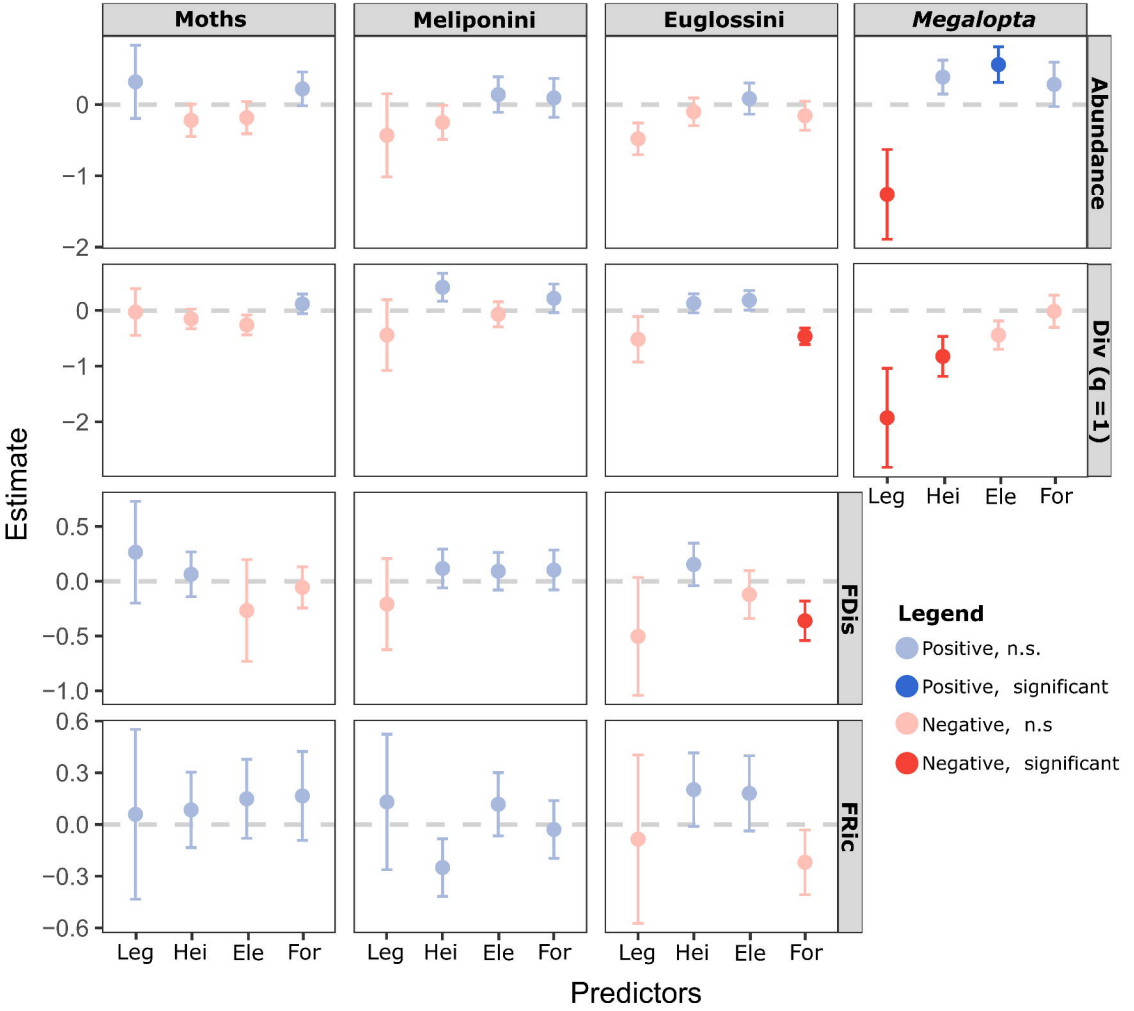
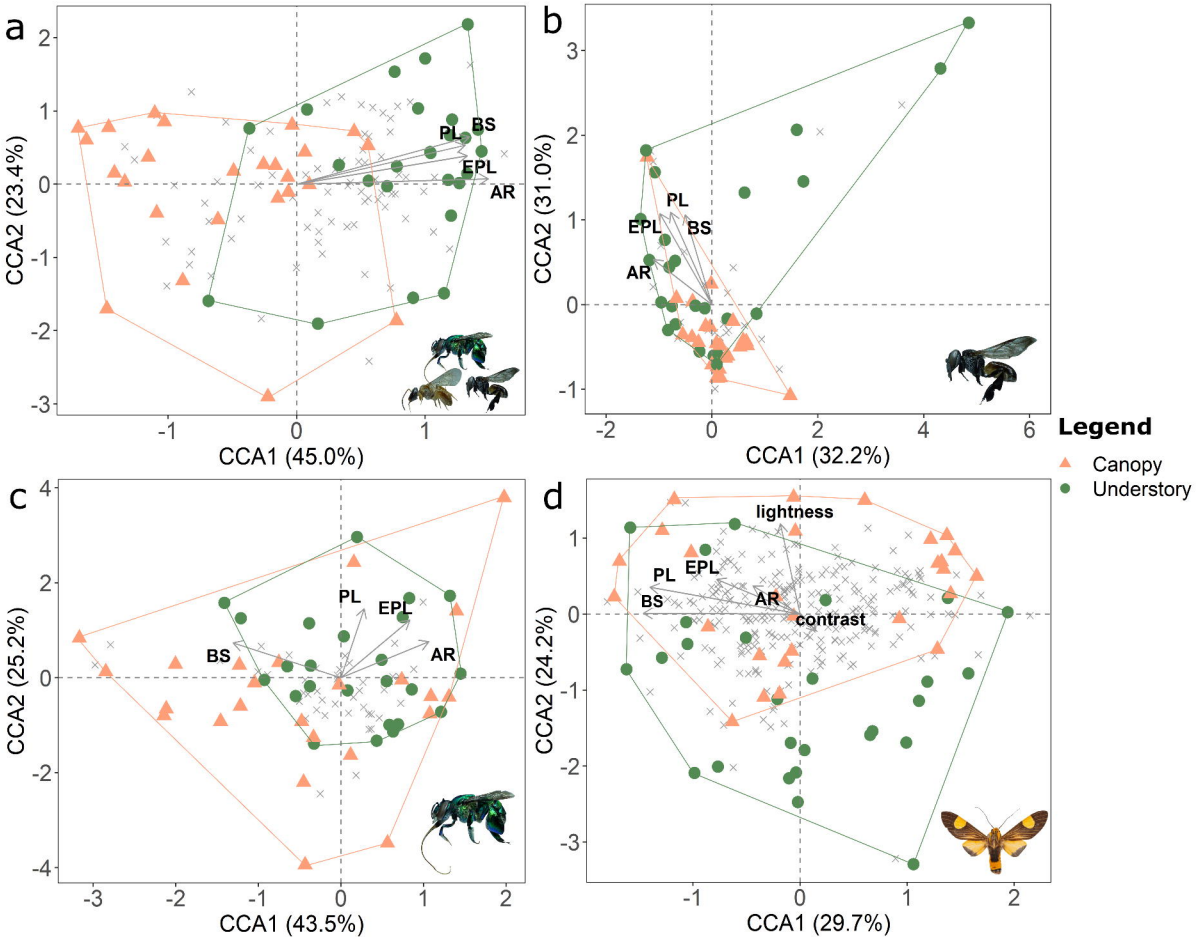
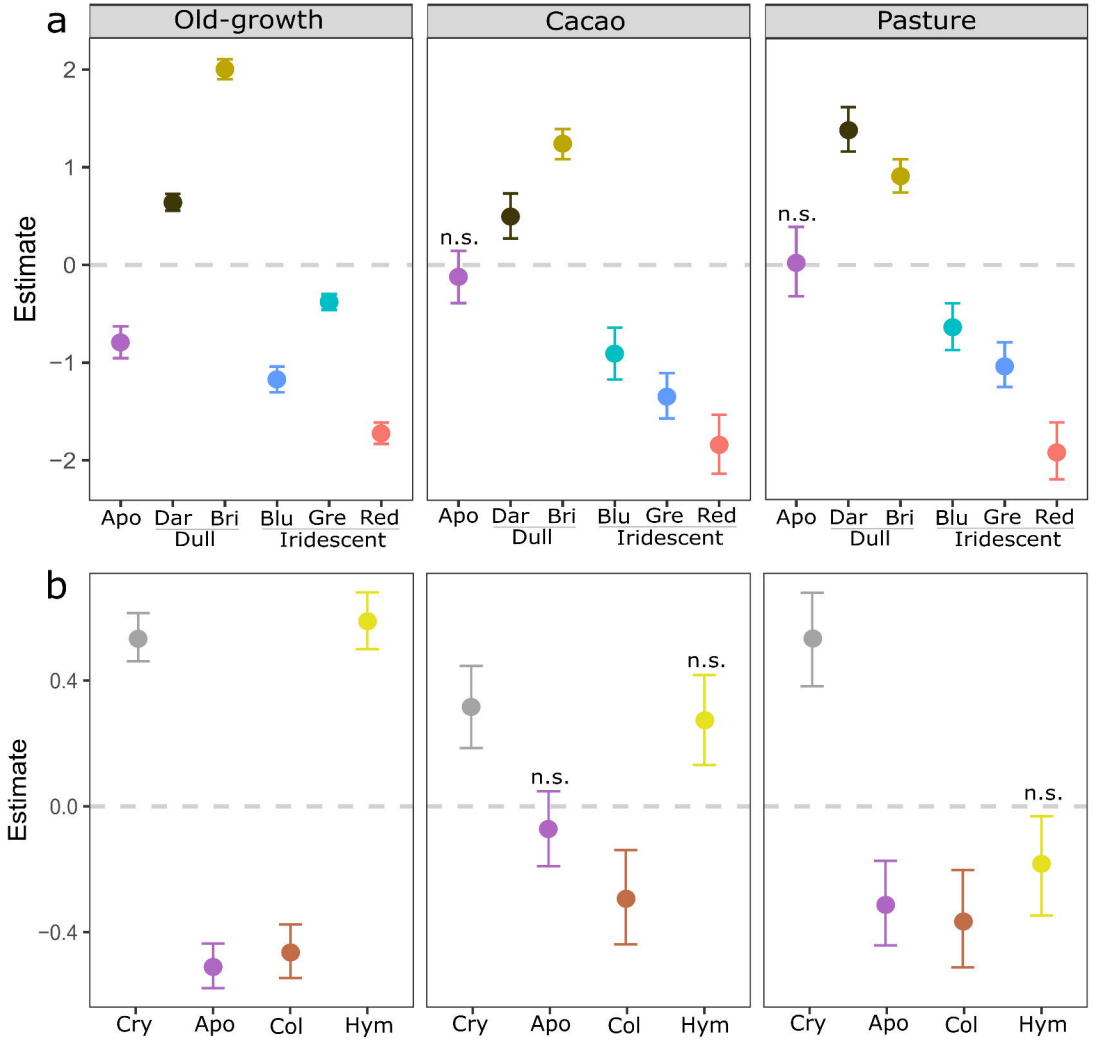
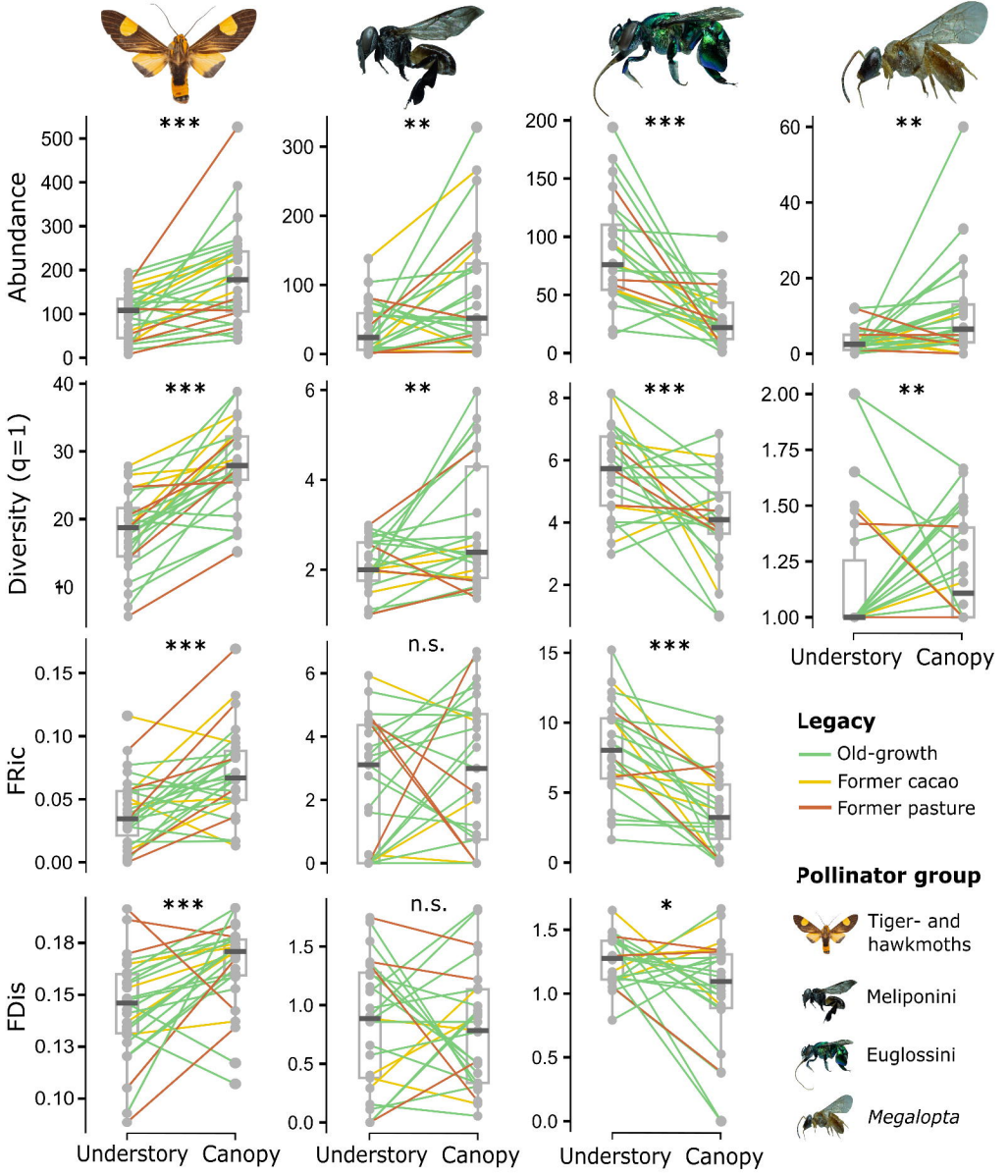
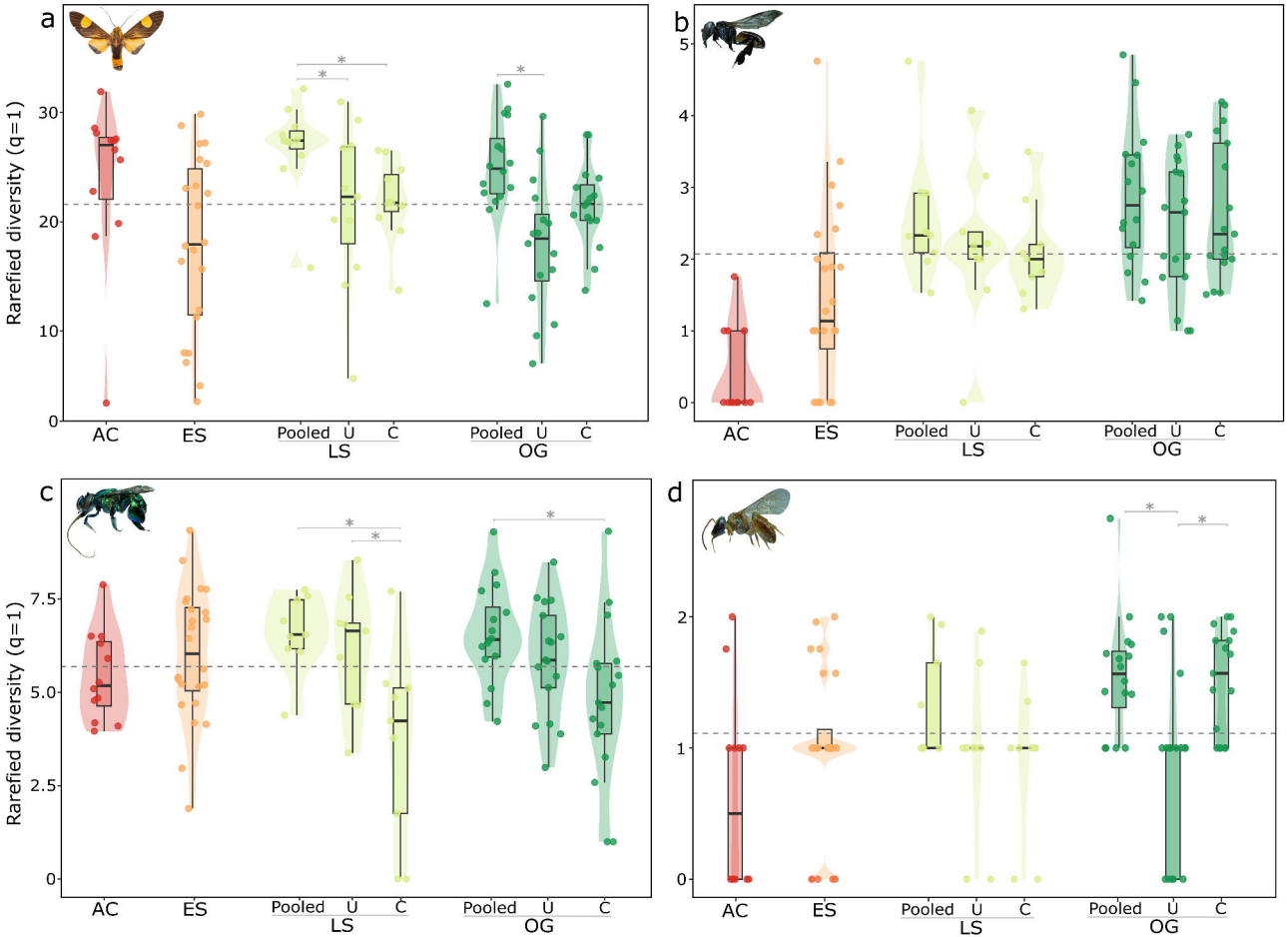

a
1
2
3
4
5
6
Preparing the shot
1. Line tightly rolled onto the spool - no loose sections.
2. Line between the spool and the arrow straight, but not tight.
3. Completely loose drag adjustment.
4. Bail disarmed.
5. Line tied to the arrow shaft, before the fletching.
6. Reel facing the nock of the arrow, at the same angle.
b
Relatively isolated, horizontal branch with little vegetation or clutter around it.
Arrow is shot above the branch from a diagonal, almost vertical angle - never from a completely vertical angle.
Arrow might be difficult to find, bright-colored markings are used on the shaft.
c
Large knots that might get stuck at the branch are avoided.
The fishing line is severed from the arrow and tied to a resistant, lightweight (e.g., polypropylene) rope.
Drag adjustment fully tightened up and bail re-armed.
Line is slowly pulled back.
d
Traps are placed above one another and above the knot made to connect the rope
The two ends of the rope are tied together; the rope is secured at the tree itself.


Moths
Meliponini
Euglossini
Megalopta
Abundance
Div (q =1)
FDis
FRic
Estimate
Predictors
Leg
Hei
Ele
For
Legend
Positive, n.s.
Positive, significant
Negative, n.s
Negative, significant


a
CCA2 (23.4%)
CCA1 (45.0%)
PL
BS
EPL
AR
b
CCA2 (31.0%)
CCA1 (32.2%)
PL
EPL
BS
AR
Legend
Canopy
Understory
c
CCA2 (25.2%)
CCA1 (43.5%)
PL
EPL
BS
AR
d
CCA2 (24.2%)
CCA1 (29.7%)
lightness
PL
EPL
BS
AR
contrast


a
Old-growth
Cacao
Pasture
Estimate
2
1
0
−1
−2
n.s.
n.s.
Apo
Dar
Bri
Blu
Gre
Red
Dull
Iridescent
b
Estimate
0.4
0.0
−0.4
n.s.
n.s.
n.s.
Cry
Apo
Col
Hym


Abundance
Diversity (q=1)
FRic
FDis
***
**
n.s.
*
Understory
Canopy
Legacy
Old-growth
Former cacao
Former pasture
Pollinator group
Tiger- and hawkmoths
Meliponini
Euglossini
Megalopta


a
b
c
d
Rarefied diversity (q=1)
AC
ES
Pooled
U
C
LS
OG
*