Article

Canopies drive the reassembly of pollinator communities and interaction networks along tropical forest succession

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ABSTRACT

Vertical stratification is a prominent driver of biodiversity in forests. As the proportion of successional forests increases worldwide and canopies are lost at a fast pace, it is crucial to understand the role of stratification as a driver of community recovery and ecological processes during succession, particularly for important plant mutualist groups essential for forest recovery. Within a well-resolved chronosequence in the northwestern Ecuadorian rainforest, we compiled an extensive database of over 20,000 diurnal and nocturnal pollinators and 2,000 interactions with plants and examined the interacting effects of recovery age and stratification on pollinator community and interaction network reassembly. In late successional and old-growth forests, stratification was a stronger predictor of pollinator abundance, alpha-diversity, functional richness and beta-diversity than forest legacy. While most groups were strongly associated with canopies (moths, social bees, and nocturnal bees), orchid bees exhibited an inverse pattern, also presenting the strongest functional response to stratification and recovery status. Within the entire chronosequence (0-38 years of recovery, plus old-growth forests), recovery status and stratification, alongside landscape features, acted synergistically as predictors of pollinator community parameters. Although structurally stable across the chronosequence and between strata, Interaction networks were richer and most distinct in canopies, while the highest pollinator and interaction diversity were found in old-growth canopies. In successional forests, networks were only comparable in size to active disturbances and early recovery with both strata combined, whereas complete networks in old-growth forests were more than twice as large as those in other recovery statuses. Our study underlines the importance of stratification in leveraging pollinator diversity during forest succession. By serving as havens for canopy-adapted species, tropical canopies may thus help safeguard pollination processes in disturbed landscapes.

Keywords: Chocó, chronosequence, disturbance legacy, forest recovery, functional traits, passive restoration, vertical stratification

1. INTRODUCTION

Forests are remarkably diverse ecosystems that harbor most of the Earth's biota [1]. 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) [2] and a wide range of microhabitats and resources associated with trees, epiphytes, and other midstory components [3]. One of the most prominent drivers of forest heterogeneity and biotic composition is vertical stratification, characterized by distinct niches formed through the interplay of microclimatic conditions, microhabitats, and resources [4,5].

While the forest understory offer a variety of resources associated with the soil (e.g., dung, deadwood, carrion, and soil microfauna) and with low-laying vegetation (herbs and bushes in deciduous forests or pioneers in clearings) [6], resources essential to certain consumer guilds are concentrated in the forest's upper layer, particularly in tropical rainforests where a clear degree of vertical stratification is present [6]. The canopy, a photosynthetic hotspot in the forest due to increased radiation, excels in resource offer for primary consumers [7]. Large and productive trees have a much higher resource yield (e.g., flowers and fruits) than understory plants [8], 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 [9,10]. Indeed, a quarter of all invertebrates are expected to be canopy specialists [6].

Nonetheless, canopies are fragile and affected not only by acute forest clearings but also by the chronic targeted logging of slow-growing, large hardwood trees that comprise a significant portion of canopies [11]. Furthermore, canopies suffer from an inherently low resilience, as veteran trees may take centuries to establish, grow, and provide their ecosystem functions [12]. Tropical forests are particularly critical in this regard. They foster an estimated three-quarters of Earth's biodiversity and account for most of the world's current Biodiversity Hotspots [13]. In these ecosystems, the loss of vertical complexity through selective logging, combined with forest fragmentation and reduction in patch size, significantly reduces the incidence of essential low-mobility canopy specialists, such as fruit-dispersing primates [5]. However, these stressors also filter out a relevant proportion of important starters and maintainers of forest succession and recovery from the landscape, such as mobile canopy-specialist pollinators and seed dispersers [14,15]. Even partial canopy

losses may lead to significantly higher exposure in forest understories due to increased heat and light incidence, which further affects species occurrences in forests affected by targeted logging, especially among desiccation-prone animals such as many arthropod groups [6].

Therefore, it is crucial to understand the impact of canopy loss on arthropod groups that partake in essential ecosystem processes necessary for forest recovery. Insect pollinators, for instance, are critical for the regeneration of tropical forests [16]. The consequences of losing canopy-associated habitats, however, are still relatively little understood for insects. Most of our current knowledge of invertebrate diversity is still based on understory sampling [17], which stems from logistical limitations in sampling canopies, often leading to small sample sizes and replication issues [17,18]. While there is evidence that several insect communities, including pollinators, may be more diverse in canopies [19–21], data are sparse and often conflicting, and the ecological drivers of pollinator stratification are understudied [17,22–25]. Pollinators may be particularly associated with the presence of resource-dense canopy trees in primary or old successional forests, as they provide abundant and year-round resources for several groups of flower-visiting insects [9,20,26]. The role of canopy formation as a driver of pollinator communities and the pollination service they provide during the process of forest succession has, to date, not been explicitly investigated, thereby precluding our understanding of the reassembly of plant-pollination networks.

Therefore, we examined whether stratification significantly affects pollinator communities and their interaction networks with plants along a tropical forest regeneration gradient. Ultimately, we sought to understand the role of canopy formation on the recovery of a key mutualistic ecosystem process. Specifically, we expected:

(i) Stratification to enhance pollinator diversity along forest recovery by supplying a distinct environment in successional forests that can be colonized by canopy-adapted species. Therefore, canopies shall yield communities complementary to understories, leading to higher overall abundance and (functional) diversity in canopy-bearing forests. This effect will be evident after the first few decades of recovery but will be stronger in older forests, where floral resource stratification is more pronounced.

(ii) Pollinator community complementarity to be driven by pollinators' interaction, dispersal, and response traits. Given the different and presumably richer assemblage of flowering species in the canopy, we expect interaction traits (e.g., proboscis length) to be more variable in canopies. Accordingly, dispersal traits in canopy-loving insect assemblages

(e.g., larger body size and high flight efficiency), as well as response traits (e.g., incidence of aposematism and crypticism), will reflect the drier, warmer, and windier conditions found in canopies, as well as an increased exposure to predators.

(iii) Interaction networks will be larger and more diverse in canopies due to larger pools of pollinator and plant species interacting, and present the most distinct interactions due to being composed of canopy-specialist species. Network size will be considerably larger in old-growth forests due to increased community divergence between strata, resulting in higher complementarity.

METHODS

Study site

The study was conducted in 2022 and 2023 in the Río Canandé (0°31'33.4"N, 79°12'46.0" W) and the Tesoro Escondido (0°32'30.9"N, 79°08'41.9"W) Reserves, Esmeraldas province, northwestern Ecuador (Fig. 1A). The site is a lowland forest ecosystem within the Chocó-Darien ecoregion, 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 well-resolved chronosequence of 62 50x50 m plots ranging from active disturbance agricultural sites to regenerating secondary forests and old-growth forests [27] (Fig. 1B).

The plots are divided into 12 active disturbances (active cacao plantations or pastures), 19 early recovery plots marked by the absence of canopy cover (1-14 years of recovery), 14 late recovery plots (15-38 years), and 17 old-growth forests with no evidence of recent disturbance. Plots were separated by a minimum distance of 350 m and a maximum distance of 12.8 km (Fig. 1B). 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 of each year). All plots were sampled in the understory, and late recovery and old-growth plots were also sampled in the canopy. Five late recovery plots (ranging from 15 to 26 years) could not be sampled in the canopy due to unfavorable conditions for setting canopy pulley ropes (see below). The permit to conduct research on

the site and to sample insects was granted by the Ministry of Environment of Ecuador (Contrato Marco MAE-DNB-CM-2021-0187).

Canopy pulley system

In order to sample the canopy of late-successional and old-growth forests, we installed a pulley system in a single canopy tree with the assistance of bow-and-arrow shooting (Fig. 1C-F). For the rope installation, we selected an accessible and somewhat horizontal branch 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) (Fig. S1). We used a 29-inch 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). Once successfully placed, the fishing line was replaced by a 5 mm polypropylene braided plastic rope, the final pulley rope to which traps were attached. A troubleshooting guide for the canopy setting is available in the Supplementary Information (Box S1).

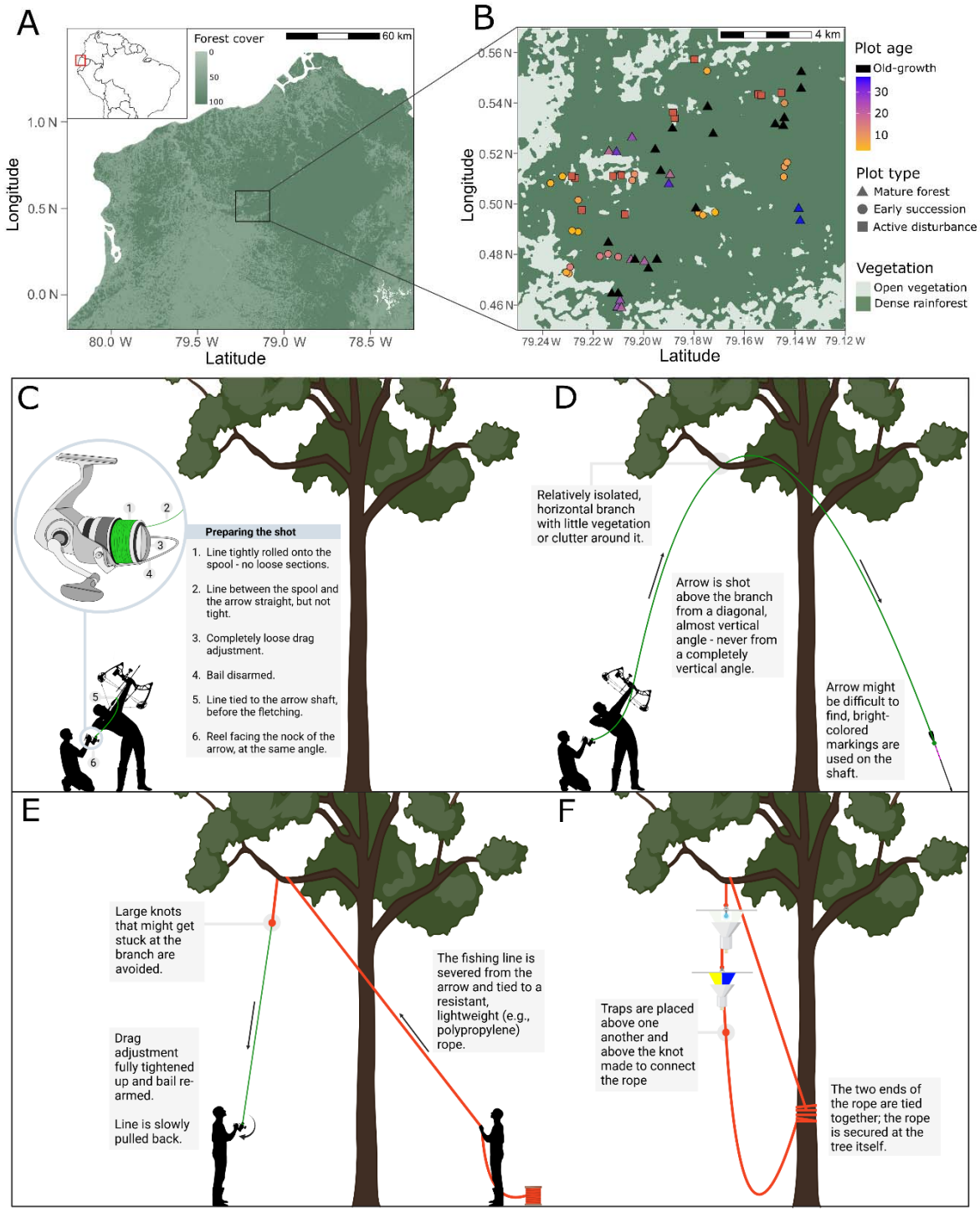

Figure 1. A-B: Research sites and sampling plots. C-D: A step-by-step process of installing the canopy rope that constitutes the pulley system used to lift the traps. A: location of the research area in northwestern Ecuador. B: Plots where pollinator and interaction data were collected. Plots are colored according to their recovery ages, and different shares represent recovery stages. C: preparations for the shot and setup of the fishing reel and arrow. The inset box outlines the technical requirements for a successful shot. D: Selection of a fitting branch at

the canopy, shooting, and arrow retrieval. See Box S1 for a list of potential issues and their respective solutions in this step. E: Replacement of the fishing line with the final pulley rope. F: Overview of the successfully set rope and traps. Persons, traps, and trees are not to scale. Created with elements from BioRender (https://BioRender.com/i24e291).

Pollinator sampling

We employed three different trap types in all 62 understories and all 26 canopies to capture a variety of pollinator groups. In 2022, we used nocturnal white vane traps equipped with mixed white and UV LED lights [28] to capture moths and nocturnal bees (Fig. S1A, Box S2 for trap details). All nocturnal bees (all belonging to the *Megalopta* genus, Halictidae) were taken and processed, while for moths, two focal groups were chosen for further processing and analysis: Hawkmoths (Sphingidae) and tiger moths (Arctiinae). The former is a frequently studied and key pollinator group with a functional morphology highly adapted to floral visitation [29], while the latter is a highly diverse group of often aposematic moths that have recently been suggested to play a key role in pollination [30]. Alongside nocturnal traps, we also set diurnal blue-yellow vane traps [31] to attract diurnal bees (Fig. S1B, Box S2). All bees were kept for processing. Both traps were set once in each plot and stratum and were left for 24h. Unlike regular vane traps, both models were adapted with a dry-killing chamber that allowed for the collection of pollen samples.

In 2023, diurnal vane traps were set again in all plots to increase bee capture numbers. In addition, fragrance traps were set to capture male orchid bees, a prominent group of pollinators in the Neotropics [32] (Fig. S1C, Box S2). Four fragrance traps were set at a time, each containing a different compound to capture species with different affinities towards fragrances: 1,8-cineole, eugenol, methyl salicylate, and skatol. In total, 616 traps were set (88 light vane traps, 176 colored vane traps, and 352 fragrance traps), of which 182 were set in the 26 canopies of late recoveries and old growths.

Insect determination and trait measurements

After sorting, insects were identified to the lowest possible level. Moths were 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

196 the Natural History Museum (London). Identification supported by COI barcoding of ca. 90%
197 of all moth species [33]. Nearly all moth species could be assigned a genus, and most were
198 identified to species level. Bees were identified using specialized literature [32,34,35]. All bees
199 could be assigned a genus and most (>90%) a species.

200 From each species, we collected three morphological traits: body size (BS), relative
201 proboscis length (RPL), and wing aspect ratio (AR). BS is an indicator of dispersal ability and
202 resistance to desiccation in insects [36], and was measured as the length between the tip of
203 the head and the tip of the last abdominal segment of moths. The intertegular distance was
204 used as a proxy for size in bees [37]. Proboscis length is related to morphological coupling
205 with flowering plants and is an interaction trait associated with feeding specialization [38].
206 RPL It was measured as the proboscis length (combined extended length of the prementum
207 and glossa in bees, and the entire extended length of the galeae in moths) divided by BS to
208 account for the allometric relationship between proboscis length and body size in insects
209 [39]. AR is a measure of flight performance, with a higher AR indicating longer and narrower
210 wings, which serve as a proxy of gliding capability and flight speed, and may influence
211 habitat use [40]. It was measured as the ratio between the square root of the forewing length
212 and the wing area for moths; for bees, the formula was simplified to the ratio between wing
213 length and the wing's mean chord (widest wing width) due to a relatively conserved wing
214 shape across groups [40]. Traits were measured manually with a caliper for larger bees (e.g.,
215 Euglossini) and with the aid of microscopy and linear morphometric analysis via the ImageJ
216 software [41] for smaller (> 5 mm of body length) bees. For the latter, the proboscises were
217 dissected and mounted on slides for further image analysis. All moth traits were collected
218 via standardized photography and processed using image analysis, with a modified version
219 of the mothseg algorithm [42]. We supplemented this data with individual measurements of
220 photographs with scale bars for proboscis length. Up to ten individuals were measured per
221 species.

222 In moths, we measured two additional and important traits related to coloration,
223 which is linked to thermoregulation and predation avoidance [43] and thus potentially a
224 driver of the vertical distribution of species. For both, we also used standardized moth
225 photographs and the modified version of the mothseg algorithm: (i) Lightness was measured
226 as the median pixel value of four main color channels (red, green, blue, and UV) of the
227 dorsal side of fully spread individuals, which represents overall brightness (e.g., high values

228 for white species and low values for dark species), (ii) Contrast, measured as the
229 interquartile distance (25th-75th percentiles) of the distribution of pixel values, representing
230 coloration variability with high values often associated with conspicuousness to predators
231 and aposematism.
232

233 *Pollen DNA metabarcoding*

234 After capture, all insects were checked under a stereomicroscope for the presence of
235 pollen, and any significant pollen load (10 or more grains) was collected. In bees, pollen was
236 collected both from the specialized structures of females (entire legs from corbiculate
237 species or by scraping the pollen out of scopae), or, when present, by scraping other body
238 surfaces, such as the head, thorax, and abdomen, of both males and females. In male orchid
239 bees, the entire pollen sacs deposited by orchids were collected. As for moths, due to the
240 large number of individuals in the traps and a higher chance of contamination, only
241 proboscises, which remain coiled between the palps, were checked for pollen and collected.
242 Samples were pooled per pollinator species and per plot, and preserved dry at -20°C.
243 Sample extraction, amplification, and sequencing were performed at Ludwig-
244 Maximilians-Universität München, Germany. Extraction, quality control, and library
245 preparation were done as described in [44] and [45], followed by multiplexed next-generation
246 DNA metabarcoding for the ITS2 region [46]. The bioinformatics pipeline is available at [47]
247 (version 8c8536b). We used VSEARCH [48] for quality filtering, merging, dereplication, and
248 definition of amplicon sequence variants (ASVs). We first classified ASVs through global
249 alignments (97% threshold) against an Ecuadorian plant database using BCdatabaser [49]. We
250 then identified unclassified ASVs using a global vascular plant database [50] with VSEARCH,
251 again at a 97% threshold. We hierarchically identified the remaining unclassified reads to the
252 lowest possible taxonomic level at a threshold of 0.8 with SINTAX [51]. Contaminations (e.g.,
253 Eurasian or cultivated genera not found in the area) and other potential contaminations
254 observed in the negative controls were removed with *phyloseq* [52]. Finally, we merged ASVs
255 at the species level and transformed them into relative read abundances (RRAs) per sample.
256 Following [30], the throughput of each pool was multiplied by the number of individuals in
257 the pool (median = 1, range = 1–65), then randomly subsampled and unevenly rarefied
258 based on sample size, before being multiplied again to account for uneven pool sizes that

may affect sequence detection probabilities. Low RRAs (<10%) were then removed from the samples according to the results of the positive control samples to further exclude possible contamination or non-legitimate interactions (e.g., low-abundance pollen deposited on pollinators by wind). RRAs were then used as interaction weights between plant species and pollinator species per sample, which avoids overemphasizing rare species in pollen pools [30]. Final interaction weights thus corresponded to the rarefied RRAs multiplied by 1000 to obtain integers that approximate observation counts.

Data analysis

1. Response variables

All data were analyzed in R 4.5.0 [53], using the packages *vegan* for community-level analyses [54], *bipartite* for network analyses [55], *FD* for estimating functional richness [56], and *betapart* for estimating beta-diversity [57]. The following response variables from pollinator communities were measured per sample (each pollinator group was analyzed independently):

(i) Abundance: the total sum of individuals.

(ii) Alpha-diversity: measured as the exponential Shannon diversity (e*H'*) (effective diversity, q = 1), which corresponds to the number of equally common species that would yield the same diversity value [58].

(iii) Beta-diversity: measured by two parameters, $\beta_{DISTINCTIVENESS}$ and $\beta_{DISPERSAL}$. Both metrics are based on a non-metric multidimensional scaling (NMDS) (k = 2, minimum of 10000 iterations) of the samples based on a Bray-Curtis distance matrix. $\beta_{DISTINCTIVENESS}$ was measured as a sample's mean total abundance-weighted dissimilarity in relation to all other samples, being a proxy for the uniqueness of the sample's composition in relation to the entire sample pool [57]. $\beta_{DISPERSAL}$ was measured as the distance of each sample to its within-group centroid (i.e., recovery status and stratum), indicating whether a certain sample group has a conserved and predictable species composition or shows high variation [57].

287 (iv) Functional richness: measured via a distance-based and multi-trait framework.
288 Functional richness represents the volume of the minimum convex hull
289 encompassing all species in a Principal Correspondence Analysis reduction based on
290 community-weighted trait means [59]. High functional richness thus represents a
291 sample where species occupy a large area of the trait space. All bee traits (RPL, BL,
292 AR) and all moth traits measured (RPL, BS, AR, lightness, and coloration) were
293 employed. The index could only be calculated for samples with three or more
294 species.

295 (v) Community-weighted traits means (CwMean) and coefficient of variation (CwCV):
296 in order to also examine trait-specific responses, we measured mean values and
297 coefficient of variation of pollinator traits (RPL, BS, AR, lightness, and contrast) in
298 each sample, weighted by species abundances.

299 Additionally, the following variables were measured for each plot's interaction
300 network (here, interaction networks were built with all pollinator groups combined):

301 (vi) Interaction diversity (H'): Shannon's diversity of network entries.

302 (vii) Interaction specialization: measured as the H_2' index of niche differentiation [60].
303 H_2' varies from zero to one and quantifies how unique, on average, the interactions
304 between species are. High values ($H_2' \rightarrow 1$) indicate a low interaction overlap
305 between pollinator species and thus high network specialization.

306 (viii) Interaction beta-diversity: measured as in (iii). The dissimilarity matrix was
307 constructed based on an occurrence matrix, where species corresponded to unique
308 interaction pairs found in each sample, and their weights represented their
309 abundance. Dimensionality reduction and $\beta_{DISTINCTIVENESS}$ and $\beta_{DISPERSAL}$ calculation were
310 then performed accordingly.

311

312 **2. Independent variables and linear models**

313 *Plot recovery age* (years after the last disturbance) and *stratum* (understory or canopy)
314 were used as explanatory variables for the variables above along the recovery gradient.
315 Because old-growth forests do not have a determined age, we transformed *plot recovery*

age into the discrete variable *recovery status* by separating plots into the following groups: active disturbance (0, plots still undergoing disturbance), early regeneration (1, plots between one and 14 years of regeneration), late regeneration (2, plots between 15 and 38 years of regeneration), and old growth (3). Besides these two main variables, we also included potential landscape features that might affect insect abundance and diversity patterns: plot elevation a.s.l., which may affect plot temperature and thus the microclimatic niches in both strata, and the proportion of forest within a 500 m buffer around the plot, a proxy for landscape isolation and fragmentation, which may affect species pools due to dispersal limitations. The ESRI World Imagery basemap was used as a source for recent landcover and sourced from Escobar et al. (2024).

Data were analyzed in two ways: first, we examined the paired differences in pollinator community parameters, interaction network parameters, and community-weighted traits in canopy-bearing forests (late successional and old-growth) to first determine whether parameters differ between forest strata and/or recovery legacies. Linear mixed-effects models (LMMs) were fitted for each response variable, setting stratum (canopy vs. understory) and recovery stage (successional vs. old growth) as independent variables and collection plot as a random variable to account for paired samples. Models were fit as generalized mixed-effect models (GLMMs) with a Poisson error family in all instances of pollinator abundance, and with a Gaussian error fit (regular LMMs) in all other instances. Residual normality and homoscedasticity were checked for all models. Second, all chronosequence samples (62 understory and 26 canopy samples) were analyzed together to assess the effect of stratification, recovery status, and their interaction on pollinator community and interaction network reassembly. Similarly, LMMs were fitted for each variable, with stratum, recovery status, and their interaction as independent variables, alongside plot elevation and the proportion of surrounding forest. Again, the collection plot was set as a random variable. Error family selection, as well as residual normality and homoscedasticity checks, were performed as above.

RESULTS

1. Pollinators sampled

346 A total of 20,245 target insects from 424 species were collected in the 88 samples (62
347 understories and 26 canopies): 8,615 bees of 86 species and 11,630 moths of 338 species.
348 Moths were represented by the two focal groups Arctiinae and Sphingidae, with the former
349 accounting for the vast majority of individuals (98.1%). Therefore, all results concerning
350 moths hereafter refer to both groups together. The samples from diurnal vane traps
351 consisted almost exclusively of stingless bees (Apidae: Meliponini) (3,607 individuals of 29
352 species), while orchid bees (Apidae: Euglossini) were the only group collected by fragrance
353 traps (4,530 individuals of 53 species). Nocturnal *Megalopta* (Halictidae: Augochlorini) bees
354 were collected from light traps (488 individuals of four species). Other bee groups (e.g.,
355 Colletidae, diurnal Halictidae) accounted for 0.27% of the total bee captures and were thus
356 not included in further analyses.
357
358 **2. The role of stratification and disturbance legacy in mature forests**
359 In paired canopy and understory samples from mature forests (old growth and late
360 successional forests), stratification was a stronger driver of pollinator communities than
361 recovery legacy (Tab. 1, Fig. 2). Abundance, alpha diversity, functional richness, and beta
362 diversities varied significantly between canopy and understory in all groups, but rarely
363 between old-growth and successional forests (Tab. 1). Moths and nocturnal bees were more
364 abundant and diverse in canopies (Fig. 2A, D, Tab. 1). Nocturnal bees were additionally more
365 abundant in old-growth forests (Fig. 2D). Moth beta diversity, however, was not affected by
366 none of the two predictors (Fig. 3C, Tab. 1).
367 Stingless bees were more abundant in canopies, but not more diverse or functionally
368 rich (Tab. 1, Fig. 2 B). Moreover, their communities were more conserved in canopies, being
369 less distinct and exhibiting less dispersal than those in the understories (Tab. 1, Fig. 3A).
370 In contrast to other groups, orchid bees showed an opposite pattern, being strongly
371 associated with the understory in abundance, diversity, and functional richness, with
372 canopies presenting the most distinctive communities (Tab. 1, Fig. 2C, Fig. 3B). Communities
373 of these bees in old-growth forests also presented higher dispersal (Tab. 1, Fig. 3B).
374
375 **3. The effect of stratification in pollinator community reassembly**
376 In the context of the chronosequence, stratification and recovery status were significant
377 drivers of the abundance of all pollinator groups. Stingless bees were more abundant in

canopies of older forests, as well as more diverse in older forests in general, while nocturnal bees were both more abundant and diverse in the canopies of older forests (Tab. 2, Fig. 2 B, C). None of these two groups was affected by the amount of surrounding forest or elevation.

Orchid bees, conversely, were significantly less abundant in canopies in general but associated with late successional forests and old growth (Tab. 2, Fig. 2C), and the canopies of older forests had the most distinct communities (Tab. 2, Fig. 3B). The amount of surrounding forest also affected these bees, with community composition presenting less variation and higher functional richness in plots near higher proportions of forest (Tab. 2).

Moths, despite being associated with canopies, were also abundant and diverse in active disturbances and early regenerating forests, therefore being significantly associated with early successional understories when inserted into a chronosequence context (Tab. 2, Fig. 2). The surrounding forested area was a strong driver of all moth community parameters, with moths being more abundant, diverse, and functionally rich in more connected plots, while presenting more conserved and predictable communities (Tab. 2, Fig 3C).

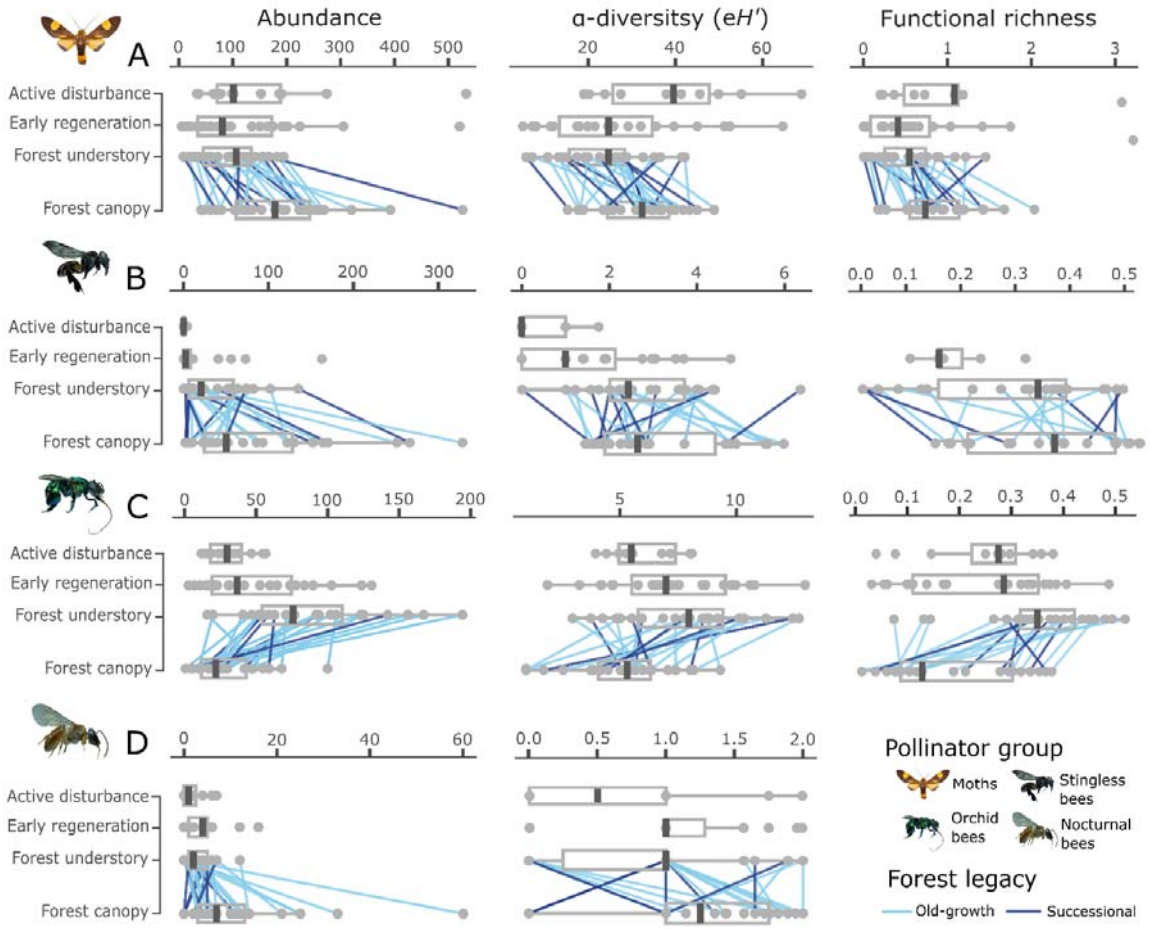

Figure 2. The abundance (left), alpha diversity (exponential Shannon diversity) (middle), and functional richness (right) of different diurnal and nocturnal pollinator groups along a forest recovery chronosequence and between forest strata. A: tiger moths, B: stingless bees (Meliponini), C: orchid bees (Euglossini) and D: nocturnal bees (*Megalopta* genus). Forests (plots older than 15 years and with a clear vertical structure) are separated into understory and canopy samples. Lines between points indicated paired samples from the same plot, and line color represents disturbance legacy (old growth in light blue and successional forests between 15 and 38 years of age in dark blue). Functional richness and values are not shown for samples with fewer than three species, as was always the case with nocturnal bees.

Table 1. The role of stratification and disturbance legacy as drivers of pollinator abundance, alpha diversity (Rarefied e*H'*), and functional richness (R) in paired undergrowth and canopy samples in vertically structured tropical forests (>15 years). The mixed-effect linear models' marginal R-squared is shown ($_mR^2$), as well as the SD-standardized estimate coefficients (β) and standard errors (SE) for each explanatory variable, i.e., (canopy vs. understory) and disturbance legacy (old growth vs. late successional). The fit used for each model's error family is specified. Bold values denote significance. *p < 0.05, **p < 0.05, ***p < 0.001.

			Canopy vs. Understory	Old growth vs. Successional
	Error fit	$_mR^2$	β (SE)	β(SE)
Moths				

Abundance	Poisson	0.24	**0.003 (0.0001)*****	0.0002 (0.001)
α-diversity (e*H′*)	Gaussian	0.20	**0.39 (0.10)*****	-0.05 (0.16)
Functional R	Gaussian	0.13	**0.37 (0.11)****	0.02 (0.16)
β-Dispersal	Gaussian	0.05	-0.20 (0.13)	-0.12 (0.15)
β-Distinctiveness	Gaussian	0.03	-0.11 (0.13)	-0.14 (0.15)
Stingless bees				
Abundance	Poisson	0.23	**0.006 (0.0003)*****	0.005 (0.003)
α-diversity (e*H′*)	Gaussian	0.06	0.12 (0.12)	0.21 (0.16)
Functional R	Gaussian	0.03	0.18 (0.12)	0.002 (0.19)
β-Dispersal	Gaussian	0.10	**-0.33 (0.10)*****	0.008 (0.17)
β-Distinctiveness	Gaussian	0.19	**-0.44 (0.12)*****	0.03 (0.14)
Orchid bees				
Abundance	Poisson	0.59	**-0.01 (0.001)*****	0.001 (0.002)
α-diversity (e*H′*)	Gaussian	0.23	**-0.49 (0.13)*****	0.02 (0.13)
Functional R	Gaussian	0.34	**-0.56 (0.11)*****	-0.18 (0.14)
β-Dispersal	Gaussian	0.15	0.19 (0.14)	**0.35 (0.14)***
β-Distinctiveness	Gaussian	0.14	**0.39 (0.14)****	-0.01 (0.14)
Nocturnal bees				
Abundance	Poisson	0.50	**0.06 (0.006)*****	**0.03 (0.01)***
α-diversity (e*H′*)	Gaussian	0.13	**0.30 (0.12)***	0.22 (0.14)

Table 2. Drivers of abundance, alpha diversity (exponential Shannon diversity – e*H'*), functional richness (R), and beta diversity (dispersal and distinctiveness) of different diurnal and nocturnal groups along a tropical forest recovery chronosequence. Drivers: Stratification (Understory vs. Canopy); Recovery: recovery status (active disturbance, early regeneration, late regeneration forest, or old-growth forest); Rec:Strat: the interaction between stratification and recovery status; Elevation: elevation a.s.l.; ForestArea: plot isolation (proportion of forest within a 500m buffer). The mixed-effect linear models' marginal R-squared is shown ($_mR^2$), as well as the SD-standardized estimate coefficients (β) and standard errors (SE) for every explanatory variable in each model. Bold values denote significance. *p < 0.05, **p < 0.01, ***p < 0.001.

			Stratification	Recovery	Strat:Rec	Elevation	ForestArea
	Error fit	$_mR^2$	β (SE)	β (SE)	β (SE)	β (SE)	β (SE)
Moths							
Abundance	Poisson	0.30	**0.006 (6x10^{-4})*****	**-0.003 (0.001)****	**-0.004 (6x10^{-4})*****	-0.001 (0.001)	**0.004 (0.001)*****
α-diversity (e*H'*)	Gaussian	0.21	0.03 (0.41)	**-0.61 (0.15)*****	0.26 (0.41)	0.10 (0.12)	**0.39 (0.15)***
Functional R	Gaussian	0.19	-0.14 (0.43)	**-0.46 (0.15)****	0.40 (0.43)	0.23 (0.12)	**0.33 (0.15)***
β-Dispersal	Gaussian	0.20	-0.92 (0.49)	0.05 (0.14)	0.72 (0.50)	**0.31 (0.11)*****	**-0.34 (0.13)****
β-Distinctiveness	Gaussian	0.20	-0.76 (0.49)	-0.07 (0.14)	0.70 (0.50)	0.11 (0.11)	**-0.38 (0.14)****
Stingless bees							
Abundance	Poisson	0.62	0.001 (0.002)	**0.02 (0.004)*****	**0.005 (0.001) ****	0.005 (0.003)	0.004 (0.004)
α-diversity (e*H'*)	Gaussian	0.38	-0.19 (0.41)	**0.46 (0.12) *****	0.30 (0.41)	-0.11 (0.10)	0.15 (0.12)
Functional R	Gaussian	0.15	0.43 (0.67)	0.23 (0.18)	-0.25 (0.69)	0.11 (0.17)	0.11 (0.18)
β-Dispersal	Gaussian	0.06	0.06 (0.43)	-0.12 (0.34)	0.20 (0.42)	0.09 (0.16)	0.11 (0.18)
β-Distinctiveness	Gaussian	0.18	0.48 (0.50)	-0.09 (0.15)	-0.89 (0.51)	-0.09 (0.13)	0.22 (0.16)
Orchid bees							
Abundance	Poisson	0.40	**-0.01 (0.002)*****	**0.008 (0.002)*****	-0.002 (0.003)	-0.004 (0.002)	0.004 (0.003)
α-diversity (e*H'*)	Gaussian	0.17	-0.38 (0.56)	0.32 (0.24)	-0.11 (0.57)	0.02 (0.11)	-0.10 (0.57)
Functional R	Gaussian	0.24	0.51 (0.51)	0.16 (0.14)	-1.04 (0.52)	-0.04 (0.11)	**0.28 (0.14)***
β-Dispersal	Gaussian	0.21	**-1.86 (0.53)*****	-0.01 (0.13)	**2.14 (0.54)*****	0.15 (0.11)	**-0.30 (0.13)***
β-Distinctiveness	Gaussian	0.19	0.08 (0.54)	-0.07 (0.14)	0.36 (0.55)	0.20 (0.11)	-0.23 (0.13)
Nocturnal bees							
Abundance	Poisson	0.40	**-0.17 (0.04)*****	0.006 (0.02)	**0.23 (0.04)*****	0.024 (0.01)	-0.002 (0.02)
α-diversity (e*H'*)	Gaussian	0.16	-0.75 (0.48)	0.12 (0.15)	**1.02 (0.49)***	-0.14 (0.12)	-0.03 (0.14)

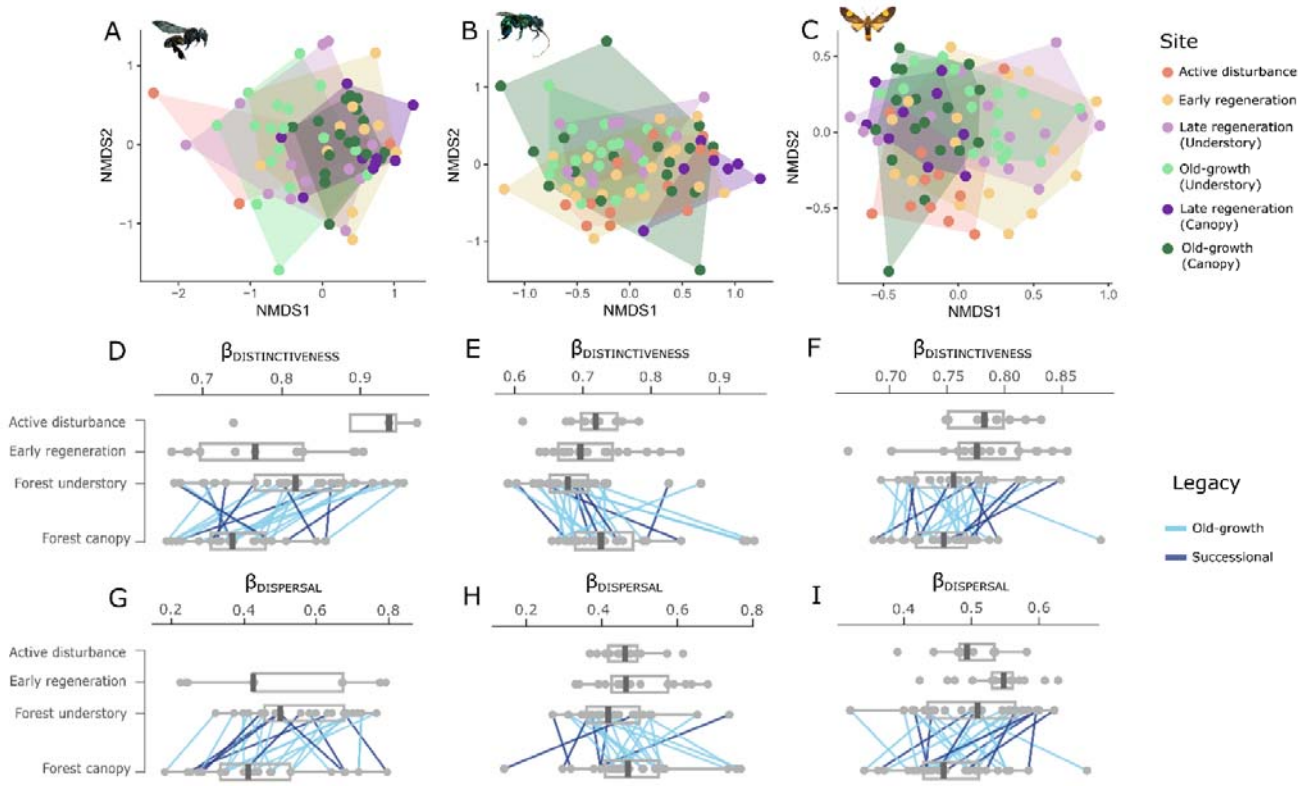

Figure 3. The composition of pollinator communities in understory and canopy samples across the recovery chronosequence. On the top row (A-C), the ordination of samples according to pollinator communities based on non-metric multidimensional scaling (NMDS). The first two axes are shown. Samples are colored according to recovery status and, in late successional forests, are divided into canopy and understory. A – stingless bees (Meliponini), B – orchid bees (Euglossini), C – moths. On the middle row (D-E), values of beta diversity are shown per sample in terms of distinctiveness (mean distance to shared centroid). On the bottom row (G-I), values of beta diversity are shown per sample in terms of dispersal (within-group mean distance from centroid). In D-I, samples are divided by recovery status, and forest samples (old growth and successional) are paired between canopy and understory.

4. The role of functional traits

Forest recovery and stratification had different effects on the functional traits of pollinators. Moths were the least affected functionally by both variables, as most traits did not vary between recovery stages or between canopy and understory (Fig. 4A). However, older canopies contained moths with a significantly higher aspect ratio (narrow and long wings), and canopies in general presented moths with more variable contrasts in coloration.

Orchid bees were the group whose functional morphology was most affected by both variables (Fig. 4 B). Bees in older canopies had relatively longer proboscises, had higher aspect ratios, and were smaller. Additionally, bees had more variable proboscis lengths in older forests and in understories. Body size also varied more frequently in the understories of younger forests or disturbances.

Finally, the functional traits of stingless bees did not vary in function of the recovery stage, but rather stratification or its interaction with recovery stage (Fig. 4 C). Bees were larger and had relatively shorter proboscises in the understory, but body size was more variable in canopies. Moreover, aspect ratios were larger in the understories of younger forests, as well as the variation in proboscis length.

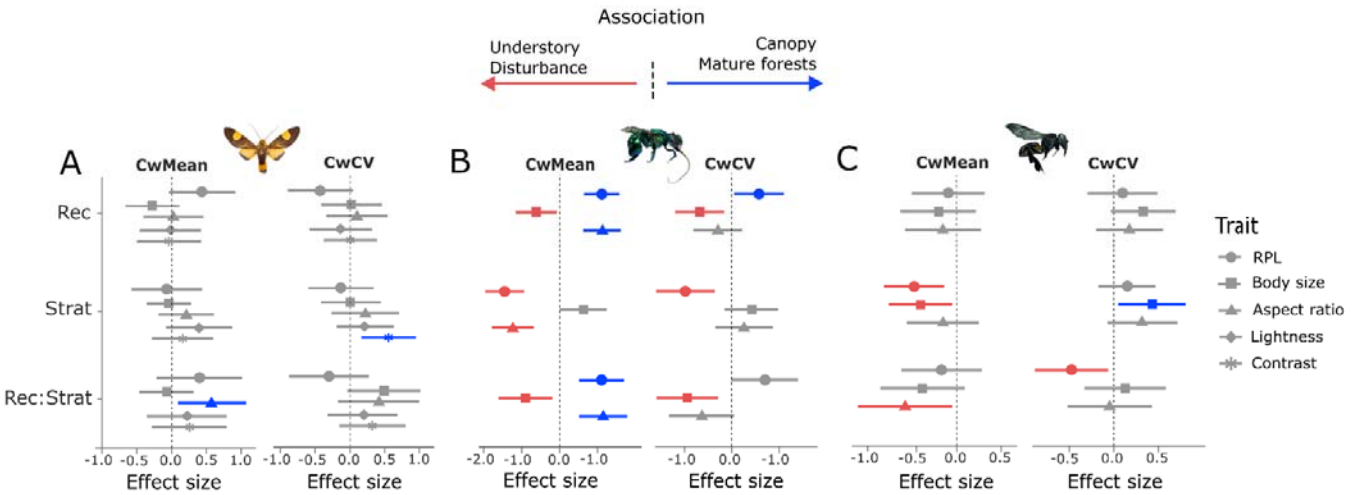

Figure 4. Effect sizes (standardized estimate coefficients) of recovery stage (Rec), stratification (Strat), and their interaction (Rec:Strat) on the community-weighted means (CwMean) and community-weighted coefficient of variation (CwCV) of different functional traits from pollinators. A: moths, B: orchid bees (Euglossini), C: stingless bees (Meliponini). The mean effect size and 95% confidence intervals are shown. Significant effects are shown in blue (positive association with canopies and older plots) or red (positive association with understories and disturbance or early regeneration).

5. Reassembly of interaction networks

Stratification had significant effects on plant-pollinator interactions. Paired samples from canopy-bearing forests showed that interaction diversity was higher in canopies ($R^2 = 0.11$, $\beta = 0.3$, se = 0.1, $p < 0.01$) (Fig. 5A) but not network specialization ($R^2 = 0.01$, $\beta = -0.02$, se = 0.1, $p = 0.08$) (Fig. 5B). In terms of beta-diversity, interactions were the most distinct in canopies ($R^2 = 0.49$, $\beta = 0.67$, se = 0.1, $p < 0.001$) (Fig. 5C) but not more dispersed ($R^2 = 0.05$, $\beta = -0.19$, se = 0.13, $p = 0.15$) (Fig. 5D). Forest legacy did not affect any of the parameters in paired forest samples ($p > 0.05$ in all instances).

When setting interactions within the chronosequence setting, networks were primarily driven by landscape features. Interaction diversity was positively affected by the proportion of surrounding forest only ($R^2 = 0.18$, $\beta = 0.42$, se = 0.15, $p < 0.01$). Network specialization ($R^2 = 0.13$) was higher in higher elevations ($\beta = 0.26$, se = 0.13, $p < 0.05$) and in sites with less surrounding forest ($\beta = -0.40$, se = 0.15, $p < 0.05$). As for beta-diversity, interactions were the most distinct in plots with less surrounding forest ($R^2 = 0.19$, $\beta = -0.38$, se = 0.14, $p < 0.005$), and

more dispersed ($R^2 = 0.20$) at higher elevations ($\beta = 0.31$, se = 0.11, $p < 0.005$) and in plots with less surrounding forest ($\beta = -0.34$, se = 0.13, $p < 0.05$). Stratification and recovery status, as well as their interaction, did not have significant effects on any of the parameters within the chronosequence ($p > 0.05$ for all estimates).

Pooled networks were stable across recovery statuses and strata, remaining similar in terms of diversity and specialization despite clear changes in size (Fig. 5E). Late-recovery networks were the smallest and dominated by settling moths, particularly the canopy. Old-growth forests contained the largest, least specialized networks, as well as the highest diversity of pollinator groups. The old-growth canopy network was marked by its large size and the participation of meliponine bees, nocturnal bees, and hawkmoths while maintaining the dominance of settling moths (Fig. 5E).

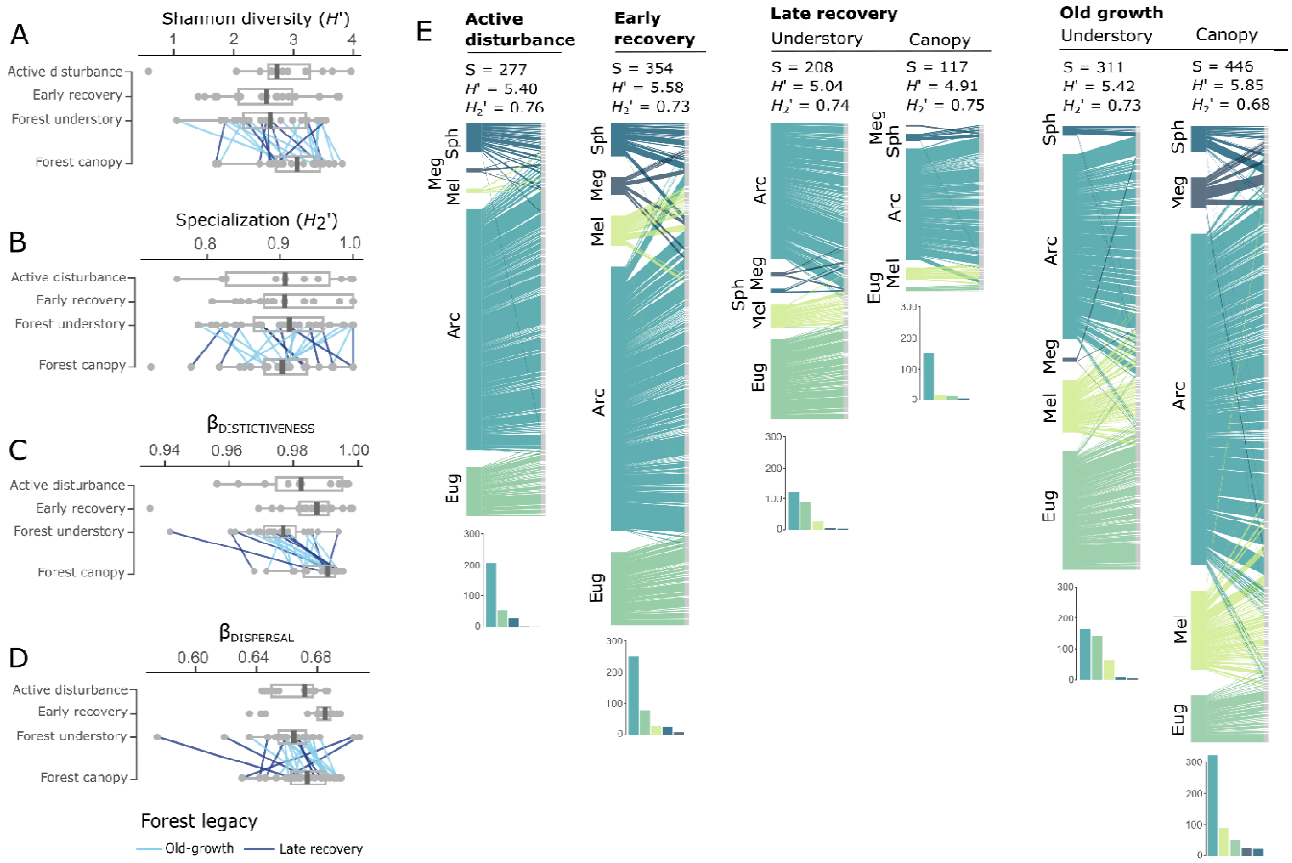

Figure 5. The diversity and structure of Interaction networks between pollinators and plants along the recovery gradient and forest strata. A – plot-level interaction Shannon diversity (H'), B – Network specialization (H_2'), C – interaction distinctiveness (beta diversity measured as mean distance to shared centroid), and D – Interaction dispersal (beta diversity measured as within-group mean distance from centroid). E – The structure of networks formed by interactions pooled by the recovery stage and stratum, followed by network size (S), interaction Shannon diversity (H') and network specialization (H_2'). Pollinators and their interactions are colored according to major groups (Sph: Sphingidae, Meg: *Megalopta*, Arc: Arctiinae moths, Mel: Meliponini bees, Eug: Euglossini bees). At the bottom of each network, bar plots show the frequency of pollen samples collected for each pollinator group. Although

networks in E are illustrated with pooled pollinator groups, all metrics in A-E were measured in species-level networks (pollinator species and plant ASVs).

DISCUSSION

The vertical stratification of resources in forests is a key driver of the distribution of various animal functional groups, ranging from non-flying mammals [61] to butterflies [62], as well as ground predators and flying insectivores [63,64]. Resource stratification thus permeates different ecosystem processes. For pollinators, floral resource stratification has been reported to influence the abundance and diversity of bees and wasps in temperate forests [65,66] and of moths in Paleotropical forests [67], for instance. Moreover, large, highly energy-dense canopy trees sustain populations of tropical bees and beetles [9,20,26,62], and an overall higher diversity of flowering resources has been recorded in tropical canopies compared to understories [7–10]. These premises suggest that canopies are essential to sustain pollinator populations in the landscape, especially in highly disturbed areas with decreasing forest cover. However, the role of canopies in the reassembly of pollinator communities and their interaction networks along forest recovery and succession had thus far not been explored.

Our study revealed that all pollinator groups studied exhibited some degree of stratification in their abundance, diversity, and functional richness within the chronosequence. Most groups showed an association with canopies, except for the understory-associated orchid bees. In canopy-bearing forests (successional and old-growth), forest stratum was a stronger predictor of pollinator community parameters than forest legacy, suggesting that resource stratification towards the canopy (e.g., flowers, host plants, or nesting sites) may already occur within a few recovery decades. The canopy-closure phase of succession (10-25 years) is characterized by rapid species turnover, an increase in basal area, maturity of pioneer trees, exclusion of understory pioneers, and the establishment of an epiphytic flora [69], all of which may influence pollinator stratification. Even though several veteran tree species may take centuries to reestablish, leading to distinct communities in old-growth forests compared to those in successional [12], sufficient resource density may already be

525 present in old secondary forests to sustain pollinators [70], and these resources seem
526 to stratify rather soon.

527 However, contrary to trends observed in pollinator communities, interaction
528 networks were large and complex in active disturbances and early-recovery plots and
529 relatively small in successional forests. Only when both strata were combined were
530 the networks in successional forests comparable to those of earlier stages. Old-
531 growth forests, on the other hand, presented large and rich networks in each stratum,
532 which led to their complete network being twice as large as those of other recovery
533 statuses. Therefore, we can assume that pollinators are flexible in terms of foraging
534 and diet as they are able to exploit disturbed sites within a landscape. They are likely
535 to profit from increased herb and forb density in pastures, as well as pioneer bushes
536 and trees in early succession (e.g., the pioneer tree genus *Cecropia* was the most
537 abundant in pollen pools), potentially buffering pollinator groups against disturbance.
538 This resistance to disturbance can be best observed in moths, which stand out as the
539 group least affected by the recovery gradient. Tiger- and hawkmoths thrived in
540 pastures and plantations, essentially acting as indicators of disturbance. Such
541 resistance has been previously noted and associated with the high mobility of most
542 species, which allows movement across the matrix during milder nighttime
543 conditions, as well as with the feeding generalism of adults and caterpillars of many
544 species [42,71]. Moths might thus be important drivers of network reassembly in
545 recovering forests [30].

546 However, pollinators in general appear to still be associated with old-growth
547 forests to some extent, likely due to both a more diverse pool of floral resources [72]
548 and a higher likelihood of finding nesting sites and refuge [65,73]. Tiger moths, the
549 leading group in the pollination networks and the one that showed the strongest
550 affinity towards the canopy, were strongly influenced by the proportion of
551 surrounding forests, being more abundant, diverse, and functionally richer in less
552 isolated plots. Their communities were also more predictable and less variable in
553 plots surrounded by more forest cover. Indeed, forest cover and plot elevation, two
554 variables linked to plot isolation, were also the best predictors of network structure
555 and diversity. Old-growth forests may thus provide suitable habitats and act as a
556 source of pollinator species that are able to forage within the matrix (i.e., areas

557 without canopy cover), which underscores the importance of maintaining forest
558 connectivity and a minimum proportion of forest on the landscape to sustain
559 pollinator populations [72]. This importance also extends to secondary forests, given
560 the abundance and diversity of pollinators in their canopies. Despite small networks
561 in late-recovery sites, canopy interactions were still overall more distinct and variable,
562 suggesting that canopies in both legacies contain plant and pollinator species not
563 observed in forest understories, indicating the presence of canopy-specialized species
564 [see 74]. These species appear to be the most representative among tiger moths,
565 which account for the majority of interactions in late-recovery canopies.

566 This network recovery pattern warrants a careful examination of the types of
567 resources beyond flowers that drive the vertical distribution of floral visitors. Tiger
568 moths, for instance, are also affected by the availability of host plants for larvae, and
569 many species specialize in canopy-specialized lianas [19]. An increased (functional)
570 diversity of host plants in canopies, driven largely by epiphytes and climbers that add
571 to the crown cover of large trees, may thus also drive the vertical distribution and
572 potentially the recovery of other herbivores. Canopy-associated substrates and
573 microenvironments (e.g., nesting cavities, phytotelmas, and trunk roosts) may also
574 influence the distribution of a plethora of other animals and their recovery patterns,
575 encompassing small insects to vertebrates [17,65,75,76]. The benefits of these non-
576 nutritional resources and microenvironmental niches are already present in late-
577 successional forests and can enhance faunal recovery [77]. For pollinators specifically,
578 the observed high resilience associated with newly formed canopies highlights the
579 role of vertical stratification for pollinator community reassembly and further
580 evidences the relevance of secondary forests as alternate providers of nutritional and
581 non-nutritional resources [70].

582 Some pollinators, however, were absent in active disturbances and particularly
583 dependent on old canopies in primary forests. The eusocial stingless bees and the
584 facultatively social nocturnal *Megalopta* were positively influenced by recovery time
585 and stratification, both of which also exhibited the most interactions in old-growth
586 canopies. Both groups are likely limited by the availability of nesting and food
587 resources found in forests. The former are dominant pollinators in tropical
588 ecosystems and typically live in colonies that host hundreds to thousands of

589 individuals [32]. They show a high susceptibility to forest cover loss [78,79], which can
590 be attributed to the cavity-nesting habit of many species [32], the need for large trees
591 (> 50 cm in diameter at breast height) to establish nests [79], and their reliance on
592 forest-associated resources, such as floral or bark resin [80]. In our study, canopy
593 specialists primarily consisted of small (ca. 2 mm), gregarious, and wood-nesting
594 *Trigonisca* bees. These would theoretically be classified as "shade-loving" bees
595 according to [74] due to their small size and resulting susceptibility to heat and
596 desiccation. Nonetheless, stingless bees were on average smaller and had shorter
597 proboscises in the canopy, which suggests that the interplay between functional traits
598 and abiotic factors is not always straightforward and may interact with an animal's
599 need for food and nesting resources. For instance, nesting and foraging close to the
600 canopy may enable small stingless bees with large colonies and short flight ranges
601 (e.g., *Trigonisca*, less than 100 m from colonies) to compensate for lower mobility [81]
602 and optimize foraging. Furthermore, establishing a nest may also be more successful
603 in upper strata, where the abundance of natural substrate for cavity-nesting
604 pollinators such as stingless bees and *Megalopta* (e.g., natural crevices in wood) is
605 higher [65]. *Megalopta* bees also exhibit remarkably low heat tolerance [82], which
606 may also be linked to their reliance on forests with canopy cover.

607 Although also more diverse and abundant in late-successional and old-growth
608 forests, orchid bees stand out as relatively resistant to disturbance and remarkably
609 canopy-avoidant, a trait previously observed before but not ubiquitous across studies
610 [83]. Male orchid bees require wide dispersal and foraging ranges to search for
611 particular and specific volatile compounds used in courtship that are sparsely
612 distributed across the forest [84]. This need, combined with a good dispersal ability
613 [85], may lead to a low response to the successional gradients, as bees are able to
614 transit between forest patches. In this regard, orchid bees may contribute to the
615 stability and reassembly of pollination networks by facilitating pollen flow across the
616 matrix. However, the underlying causes of the repeating canopy-avoidant behavior
617 are unknown. A prominent hypothesis is that the dissipation of floral volatiles (both
618 synthetic and natural ones produced by host plants) by sunlight and wind in the
619 canopy hinders detection by Euglossines, which would explain canopy avoidance [74].
620 Interestingly, these bees also showed the strongest functional response to recovery

621 and stratification. Functional richness was significantly higher in forest understories of
622 less isolated plots, where communities were the most conserved, comprising smaller,
623 fast-flying bees with relatively longer proboscises. The small and filtered subset of
624 species in canopies was variable but tended to contain larger bees more apt to
625 maneuverability, such as those in the genus *Eulaema*. Unlike stingless bees, these
626 bees seem to adhere to the shade-loving pattern shown by Bawa [[74]], with larger and
627 hairier bees such as *Eulaema* more prone to successful thermoregulation in more
628 exposed conditions [87]

629 While different pollinator groups exhibited their own idiosyncratic recovery
630 trajectories and functional responses to stratification, our study reaffirms the
631 importance of both primeval and successional forests in maintaining animal diversity
632 in disturbed landscapes, as documented for a range of ecosystems [[70,88]]. A high
633 abundance and diversity of pollinators in recently stratified successional forests, as
634 well as unique communities interacting with distinctive sets of plants, underscore the
635 importance of structural complexity in both secondary and primary forests in
636 maintaining and recovering biodiversity [[89]]. However, interaction networks in
637 secondary forests did not resemble those in old growth. Therefore, while passive
638 restoration can be seen as an effective process for fostering pollinator communities in
639 disturbed landscapes, safeguarding a sufficient cover of old primary forests remains
640 necessary to preserve a diverse source of pollinators and plant species in
641 regenerating landscapes. Whenever selective logging cannot be regulated, allowing
642 patches of forest to naturally recover may still significantly increase resilience in
643 disturbed landscapes by providing refuge and non-nutritional resources to pollinators
644 [[90]]. Furthermore, the group-specific interactions between stratification, recovery, and
645 environmental factors highlight the need for comprehensive biodiversity assessments
646 that consider canopies as species-rich sections of the landscape.

647

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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.

DATA AVAILABILITY

All the raw data and code scripts used to produce the results of this manuscript will be made publicly available in an online Zenodo repository upon acceptance.

ADDITIONAL INFORMATION

The authors declare no competing interests.

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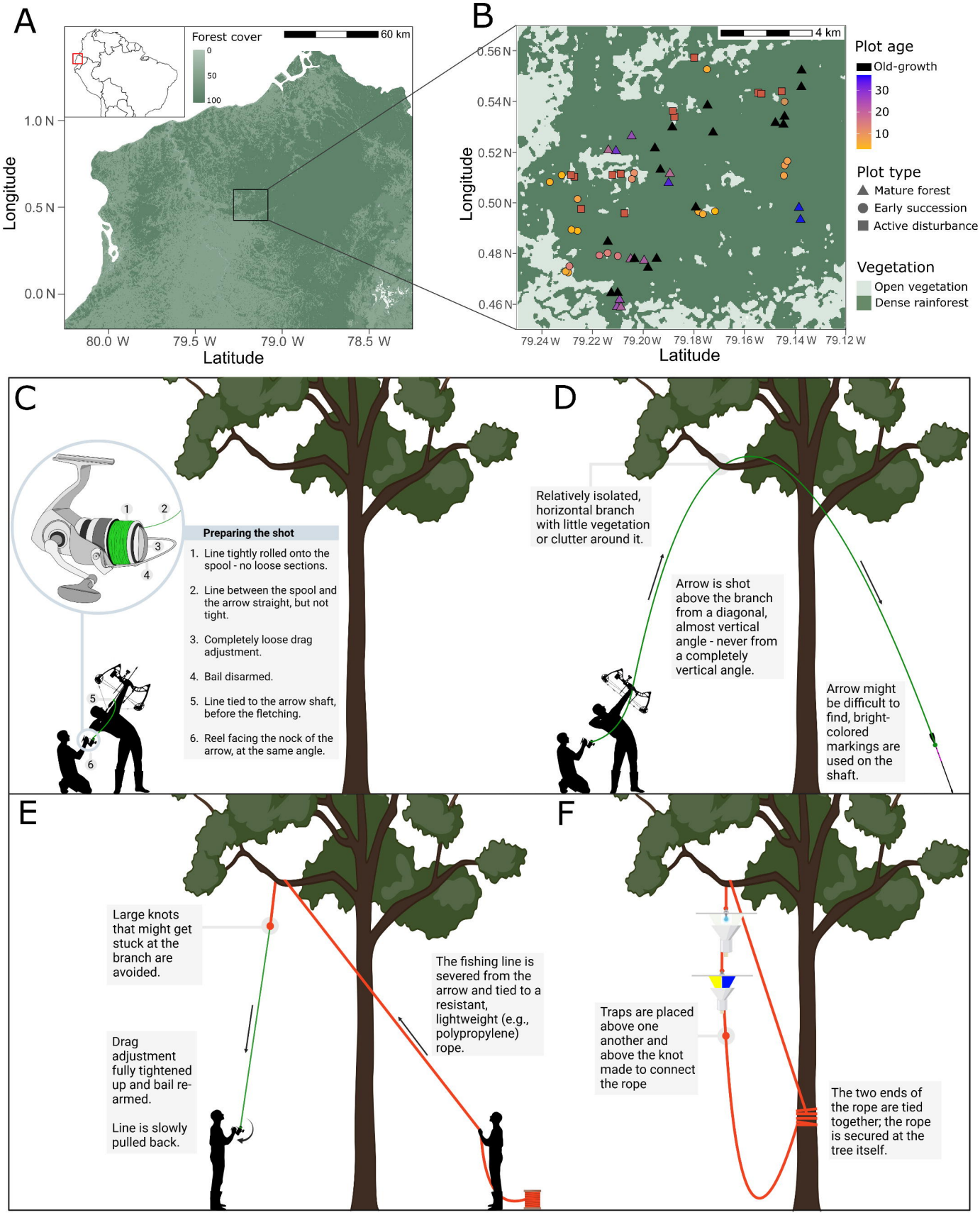
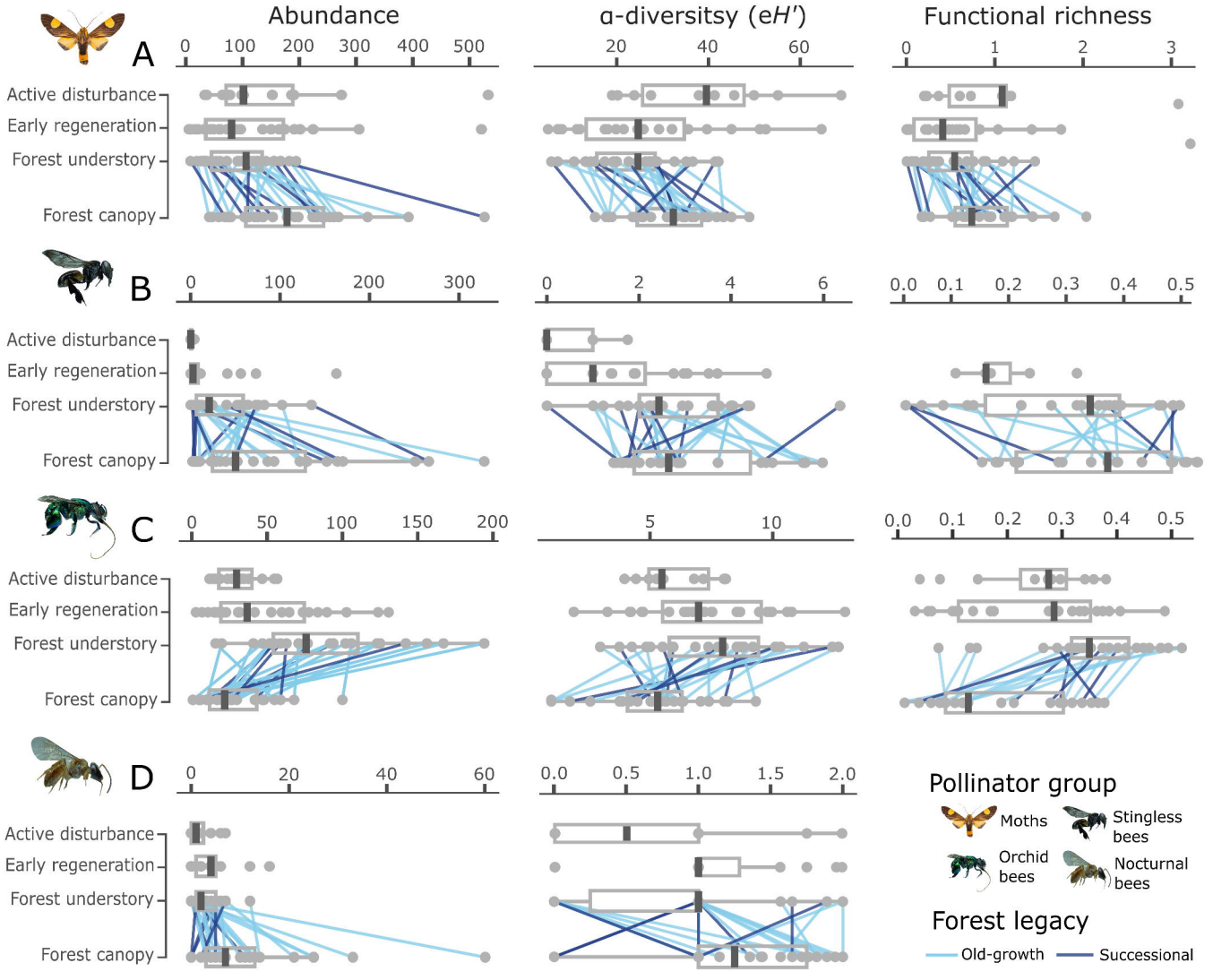
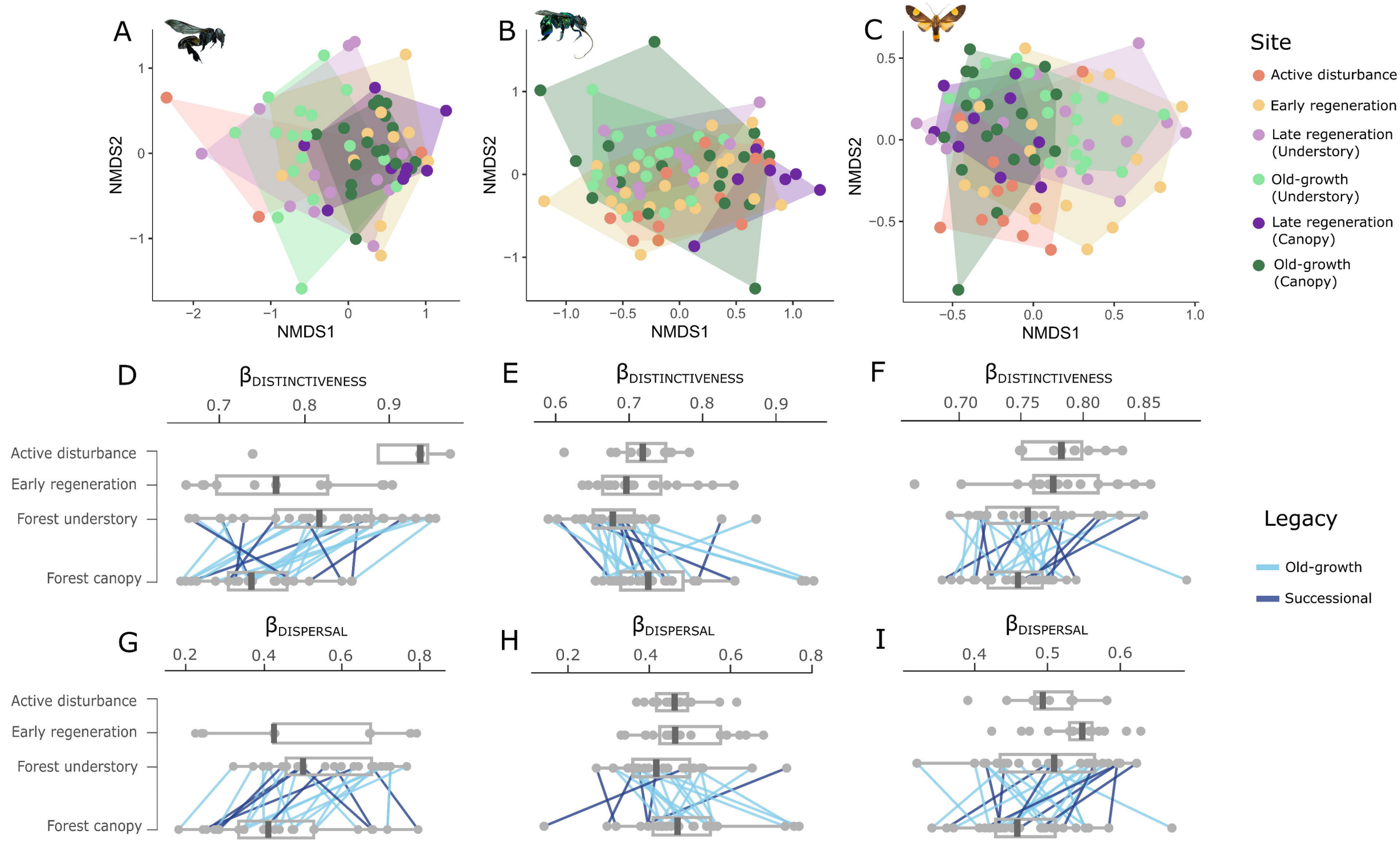
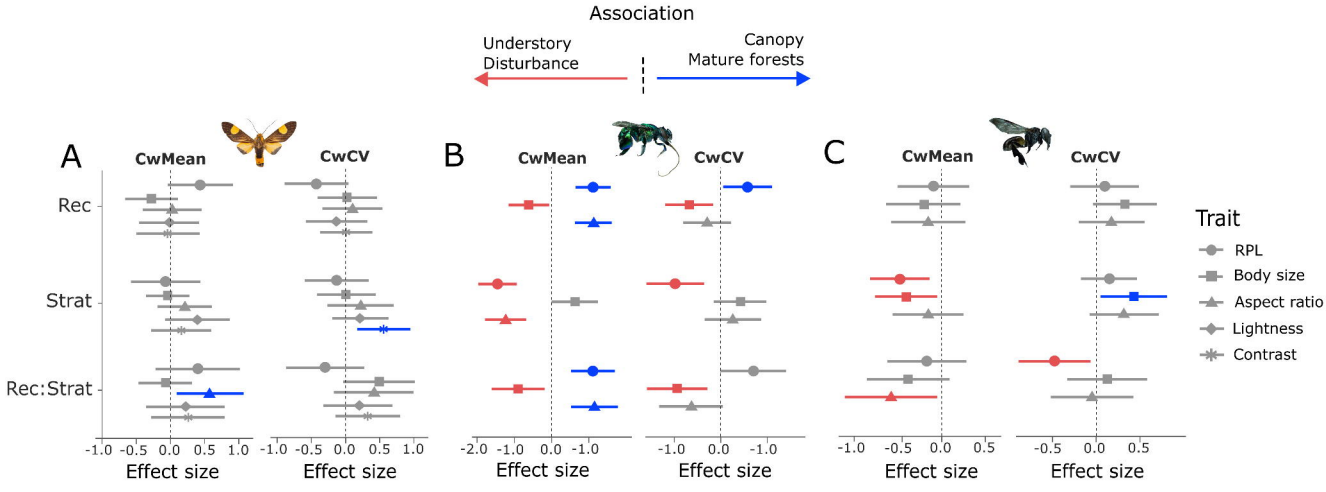
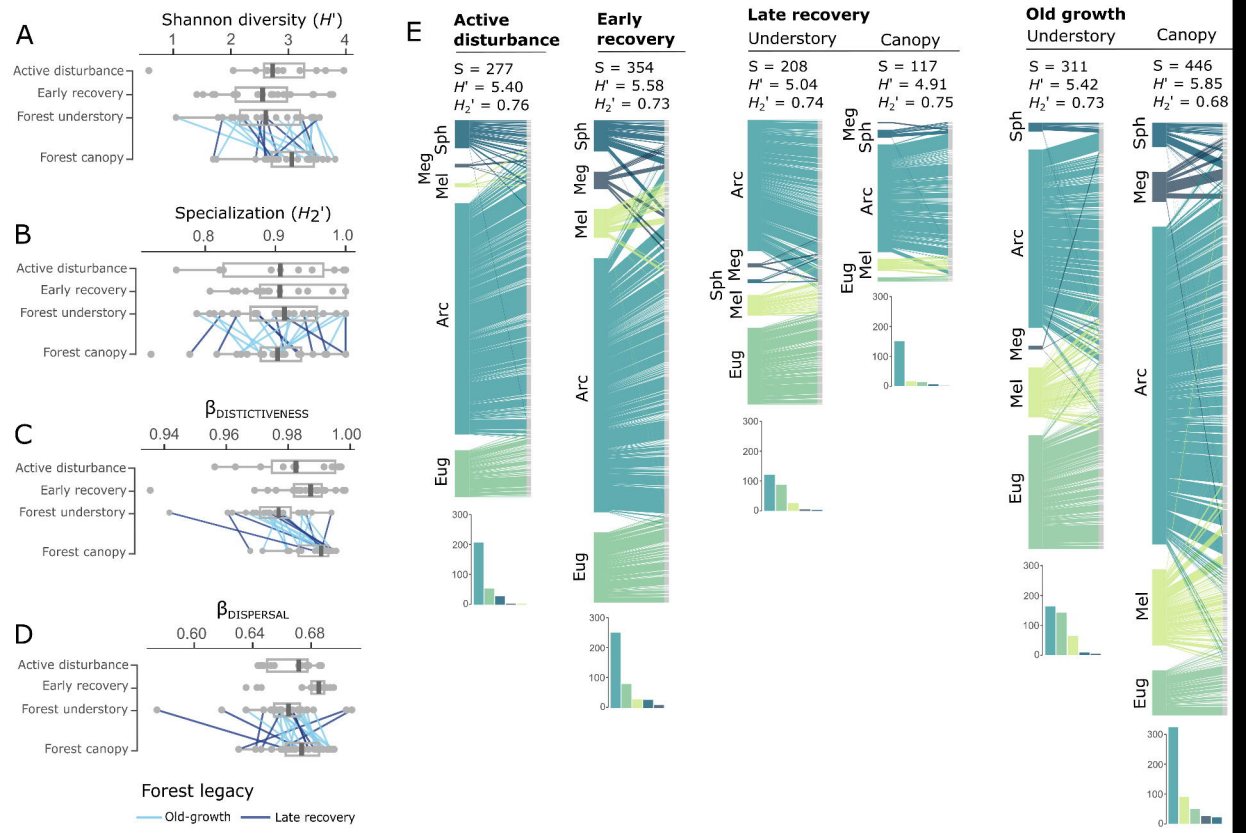

A
Forest cover
0
50
100
60 km
1.0 N
0.5 N
0.0 N
Longitude
80.0 W
79.5 W
79.0 W
78.5 W
Latitude
B
4 km
0.56 N
0.54 N
0.52 N
0.50 N
0.48 N
0.46 N
Longitude
79.24 W
79.22 W
79.20 W
79.18 W
79.16 W
79.14 W
79.12 W
Latitude
Plot age
Old-growth
30
20
10
Plot type
Mature forest
Early succession
Active disturbance
Vegetation
Open vegetation
Dense rainforest
C
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.
D
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.
E
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.
F
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.


Abundance
α-diversitsy (eH′)
Functional richness
A
B
C
D
Active disturbance
Early regeneration
Forest understory
Forest canopy
0 100 200 300 400 500
20 40 60
0 1 2 3
0 100 200 300
0 2 4 6
0.0 0.1 0.2 0.3 0.4 0.5
0 50 100 150 200
5 10
0 20 40 60
0.0 0.5 1.0 1.5 2.0
Pollinator group
Moths
Stingless bees
Orchid bees
Nocturnal bees
Forest legacy
Old-growth
Successional


A
B
C
NMDS1
NMDS2
Site
Active disturbance
Early regeneration
Late regeneration (Understory)
Old-growth (Understory)
Late regeneration (Canopy)
Old-growth (Canopy)
D
E
F
G
H
I
βDISTINCTIVENESS
βDISPERSAL
Active disturbance
Early regeneration
Forest understory
Forest canopy
Legacy
Old-growth
Successional


Association
Understory Disturbance
Canopy Mature forests
A
CwMean
CwCV
Rec
Strat
Rec:Strat
-1.0 -0.5 0.0 0.5 1.0
Effect size
B
CwMean
CwCV
-2.0 -1.0 0.0 -1.0
-1.0 0.0 -1.0
Effect size
C
CwMean
CwCV
-1.0 -0.5 0.0 0.5
-0.5 0.0 0.5
Effect size
Trait
RPL
Body size
Aspect ratio
Lightness
Contrast


A
Shannon diversity (H')
1
2
3
4
Active disturbance
Early recovery
Forest understory
Forest canopy
B
Specialization (H2')
0.8
0.9
1.0
Active disturbance
Early recovery
Forest understory
Forest canopy
C
βDISTICTIVENESS
0.94
0.96
0.98
1.00
Active disturbance
Early recovery
Forest understory
Forest canopy
D
βDISPERSAL
0.60
0.64
0.68
Active disturbance
Early recovery
Forest understory
Forest canopy
Forest legacy
Old-growth
Late recovery
E
Active disturbance
S = 277
H' = 5.40
H2' = 0.76
Early recovery
S = 354
H' = 5.58
H2' = 0.73
Late recovery
Understory
S = 208
H' = 5.04
H2' = 0.74
Canopy
S = 117
H' = 5.04
H2' = 0.75
Old growth
Understory
S = 311
H' = 5.42
H2' = 0.73
Canopy
S = 446
H' = 5.85
H2' = 0.68
Meg
Sph
Mel
Arc
Eug
300
200
100
0