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The reassembly of plant-pollinator interactions along tropical forest succession

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ABSTRACT

Pollination sustains ecosystem recovery but is among the processes most vulnerable to disturbance. Tropical forests rely on animal-mediated pollen flow and may be unable to recover from large-scale disturbance if plant-pollinator interactions break down. Using a dataset of over 24,000 insect and vertebrate pollinators from 500 species, we examined the post-disturbance resistance, recovery rates, and reassembly pathways of plant-pollinator networks along a recovery chronosequence spanning nearly four decades in a rainforest biodiversity hotspot. While floral resource abundance, diversity, and composition took up to three decades to recover to old-growth levels, pollinator abundance and diversity were highly resistant, often enhanced in agricultural sites, and promptly recovered to old-growth levels. Pollinators covered a broader range of the recovery gradient than host plants, resulting in resistant network structural properties in agricultural sites and suggesting pollen flow across successional stages. Consequently, network reassembly was mediated by a pollinator community that was not strongly bottom-up regulated. Pollinators may thus sustain tropical forest recovery through network rewiring supported by their resource generalism and mobility. Furthermore, the stability of reassembly along succession was secured through complementary functional turnover, as disturbance-adapted taxa gave way to forest-adapted ones. Nonetheless, pollinator composition recovered much more slowly than other community attributes, and their interaction networks, although resistant in agricultural sites, became smaller and more specialized in successional forests and did not fully recover to old growth levels. Therefore, despite the potential of pollinators to cross and forage within the agricultural matrix, thereby maintaining animal-mediated pollen flow across the landscape, secondary forests lack conditions found in old growth and exhibit impoverished networks that may take decades to recover.

Keywords: pollination, lowland rainforest, Ecuador, chronosequence, functional diversity, resilience, flowering plants, floral resources, forest succession, metabarcoding, old-growth forests

MAIN

Pollination sustains gene flow within and among plant communities, defines plant community structure, and underpins ecosystem function and resilience¹⁻³. Tropical plant communities are particularly dependent on animal-mediated pollination, with up to 94% of tropical trees relying on animal-mediated pollen flow, their pollinators encompassing a wide range of diurnal and nocturnal insects as well as vertebrates⁴. Therefore, maintaining functionally diverse pollinator communities is pivotal to preventing inbreeding depression, ensuring the persistence of tropical ecosystems, and securing ecological restoration^{3,5}. Given the scale of disturbance to the world's tropical forests, with over half of primary forests lost or degraded⁶, examining the role of pollinators in post-disturbance dynamics should help provide a better grasp of their contribution to achieving restoration goals⁷. Furthermore, up to 70% of current forests consist of successional stands⁶, which exhibit great potential as enhanced carbon sinks and providers of livelihoods to people⁸⁻¹⁰. Thus, there is a need to assess whether recovering forests can sustain pollinator communities and plant-pollinator interactions in regenerating landscapes, particularly in the face of ongoing global pollinator decline¹¹, and given that pollination is one of the most heavily affected processes of plant regeneration¹².

Passive, or unassisted, restoration is recognized as the most cost-efficient and successful route towards tropical forest recovery¹³. However, the ecology of passive restoration in the tropics has historically focused on the plant community component, e.g., plant diversity and community structure, functional traits, and biomass^{9,14-19}, which collectively suggest rapid turnover of functional groups and quick recovery of diversity and biomass, while species composition usually lags by decades^{16,19,20}. The often predictable replacement of a post-disturbance, *r*-strategist, light-tolerant, wind-dispersed, and wind-pollinated community with a shade-tolerant, slow-growing, animal-dispersed, animal-pollinated, and vertically structured community usually occurs within a few decades^{17,21}, especially in areas with high forest cover⁷. From the perspective of primary and secondary consumers, secondary tropical forests may even be more energetically productive than old-growth forests (OG), indicating that recovering forests may equally sustain communities of insectivores, herbivores, frugivores, and nectarivores²².

However, the resistance (i.e., the proportion of the remaining pre-disturbance-state community or process) and resilience (i.e., recovery rate of such community or process to a pre-disturbance state) (definitions *sensu* Nimmo *et al.*²³) of animal communities are comparatively

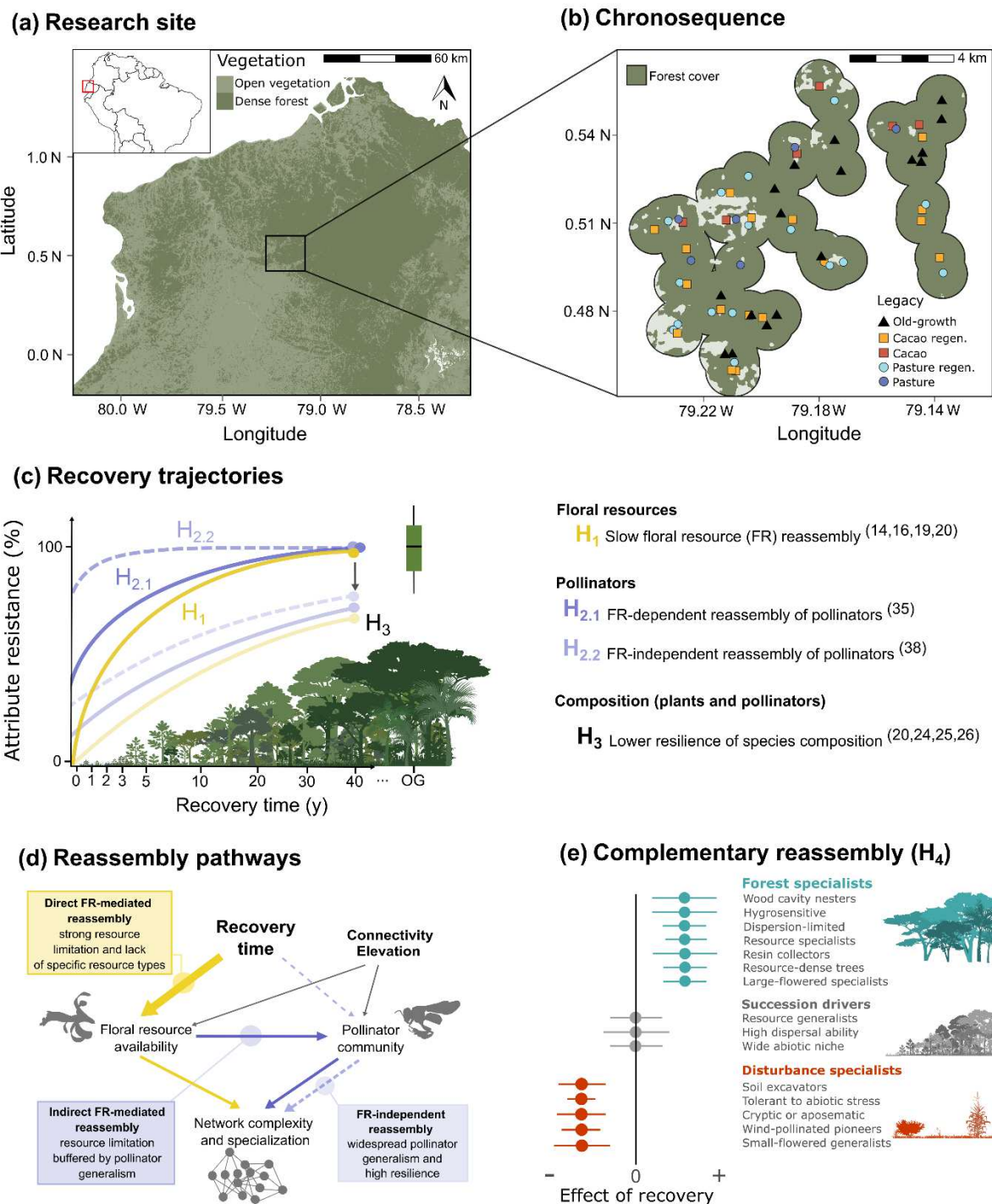
less studied. Vertebrate and invertebrate communities seem to follow a similar trend of rapid diversity but delayed composition recovery, as seen in plants ^{24–27}. Whether animals persist in disturbed forests seems to depend on niche-based processes, such as dispersal ability as well as resource and habitat requirements ^{26,28}. Delayed composition recovery has been hypothesized to be driven by animals that depend on OG forest structural traits or on plant species that recover slowly, such as pollinators and saproxylic beetles ²⁵. However, the resistance and resilience of pollinators and their interactions in tropical forests have not been sufficiently explored. A large body of work, particularly but not exclusively on bees in temperate ecosystems, indicates that restoration successfully recovers pollinator communities and interaction networks and highlights the important role of habitat connectivity in restoration ^{29–34}.

Nonetheless, the causal pathways (e.g., a recovery process involving bottom-up regulation of pollinators and interaction recovery through floral resource availability ³⁵) among floral resources, pollinators, and network structure have, to our knowledge, not been explored under the lens of succession and over the first decades of tropical forest recovery. As tropical pollinator communities often entail a large proportion of generalists, which confer interaction niche redundancy ³⁶, tropical plant-pollinator interaction networks may be buffered against disturbance ³⁷. Such redundancy, coupled with the high mobility provided by flight, may confer some resistance and resilience to plant-pollinator networks, depending on the scale of the disturbance and habitat connectivity ³¹. However, several variables may hinder pollination recovery in a regenerating landscape, such as insufficient primary habitats and the lack of specific resources associated with OG (e.g., nesting substrates, resin, volatiles) ^{5,34}. It is thus important to (i) describe recovery trajectories of floral resources, pollinators, and their interactions with plants to shed light on whether and when pollination network structure stabilizes along forest succession, and (ii) identify reassembly pathways, i.e., the mechanism through which networks recover (e.g., forest structure, floral resource availability, pollinator generalism, landscape connectivity).

In a well-resolved recovery chronosequence (space-for-time substitution) spanning nearly four decades and two disturbance legacies in the biodiversity hotspot of the Ecuadorian Chocó rainforest (Figure 1a-b), we examined the recovery trajectories and reassembly pathways of plant-pollinator interactions at multiple levels: floral resources, animals, and interaction network structure, which have shown to be linked to visitation rates and seed set and thus suitable indicators of pollination quality ³⁰. To obtain a comprehensive picture of the recovery of plant-pollinator interactions, we undertook a multi-taxon sampling approach that included a wide range of diurnal

and nocturnal insects as well as vertebrate pollinators and reconstructed their interaction networks with plants through pollen DNA metabarcoding.

Given known patterns of plant community succession^{14,16,19,20}, we hypothesized low resistance of floral resource availability due to simplified communities in agricultural sites and early recovery, dominated by abundant, disturbance-adapted, but resource-poor (e.g., small-flowered individuals with low nectar yield) pioneer herbs and shrubs, vines, and lianas. A steady recovery trajectory should follow, with community attributes and resource density reaching OG levels within a few decades (H₁, Figure 1c). In contrast, pollinators should exhibit greater resistance to disturbance due to resource generalism and mobility provided by flight^{5,36} (H₂, Figure 1c), and their recovery may be mediated either by plot-level resource availability (bottom-up recovery, e.g., Potts *et al.*³⁵) (H_{2.1}). Alternatively, their recovery may be largely independent of localized resource availability (e.g., Griffins *et al.*³⁸) due to widespread feeding generalism and cross-plot mobility, resulting in high resistance and fast recovery (H_{2.2}, Figure 1c) driven mainly by landscape variables such as forest connectivity^{31,38}. Regardless of the trophic level, community composition should take longer to recover than other parameters^{20,24–26} (H₃, Figure 1c). Based on these hypotheses, we propose three different potential recovery pathways for pollination networks (Figure 1d): direct floral resource-mediated recovery, where network structure is dependent on local floral resource availability and diversity; indirect floral resource-driven recovery mediated by pollinators, where network structure is dependent on a bottom-up regulated pollinator community; or floral resource-independent and pollinator-mediated recovery, where rapid pollinator community reassembly translates into high network resistance and resilience. Moreover, we expect reassembly to be driven by a functional turnover of flowering plants (e.g., pollination system, floral accessibility, resource type offered) and pollinators (e.g., body size and dispersal ability, feeding morphology specialization, nesting requirements) (H₄, Figure 1e)^{17,21,25,26}, which should confer stability to network recovery. Finally, disturbance legacies should leave distinct imprints on the recovery trajectories of plant-pollinator interactions due to differing starting conditions for recovery, such as vertical structure, shading, and the presence of remnant trees³⁹ (H₅).



157 **Figure 1. Study design and conceptual depiction of the hypothesized recovery trajectories and reassembly**
158 **pathways.** (a) The location of the research site (red rectangle, inset) in the Chocó-Darien ecoregion in Northwestern
159 Ecuador. (b) Study site within the Reassembly research unit, showing the 62 plots that compose the recovery

chronosequence. Plots are accompanied by 1-km-radius buffers showing the proportion of forested area within them. (c) Hypothesized recovery trajectories of floral resources and pollinators within the chronosequence: low-resistance, linear recovery of floral resource diversity and density (H_1); floral resource-dependent reassembly of the pollinator community ($H_{2.1}$) or, alternatively, a floral resource-independent recovery marked by widespread pollinator generalism and complementary trait-based recovery ($H_{2.2}$); and low resilience (slower recovery) of species composition of both floral resources and pollinators in comparison to other community attributes, preventing full recovery (H_3). (d) The multiple hypothesized pathways (differently colored arrows) through which plant-pollinator interactions may recover. Path color and style are linked to hypotheses in (c). Landscape variables (such as forest connectivity and elevation a.s.l.) may influence these pathways by influencing plant and pollinator dispersal across the landscape. (e) The hypothesized complementary trait-based recovery of the community (H_4), where, within the chronosequence, species can be separated into disturbance specialists, forest specialists, and succession drivers, based on functional traits.

RESULTS

Sampled community and interaction network

In the recovery chronosequence in the northwestern Ecuadorian Chocó rainforest, we sampled a total of 24,188 pollinators from 500 species and 184 genera belonging to the major groups of tiger and lichen moths (Erebidae: Arctiinae), hawkmoths (Sphingidae), diurnal bees (families Apidae, Halictidae, Megachilidae and Colletidae), nocturnal solitary bees (Halictidae: *Megalopta*), and bats (Chiroptera) (Supplementary Dataset 1). From these pollinators, 5,051 interactions with 514 amplicon sequence variants (ASVs, henceforth called plant species) from 317 genera and 92 families were extracted via pollen DNA metabarcoding. The most prominent pollinator groups were moths (Arctiinae and Sphingidae, 339 species and 2,189 interactions), followed by stingless bees (Apidae: Meliponini, 47 species and 1159 interactions) and orchid bees (Apidae: Euglossini, 50 species and 583 interactions). Less frequent groups included nocturnal and diurnal sweat bees (Halictidae: Augochlorini), anthophilous bats (Chiroptera: Phyllostomidae), leafcutter bees (Megachilidae), plasterer bees (Colletidae), honeybees (*Apis mellifera*), and mason bees (Apidae: Xylocopinae). Additionally, 12,831 individuals from 436 plant (morpho)species across 179 genera and 71 families were recorded as flowering in the chronosequence plots (Supplementary Dataset 2).

Resistance and recovery of resources, pollinators, and interactions

Floral resources, pollinator communities, and interaction networks displayed disparate resistance levels and recovery trajectories (Figure 2, Table 1). Floral resource community parameters (flowering individual abundance, resource density, alpha diversity, and functional diversity), showed a moderate average resistance ($62.6 \pm 13.7\%$) (expressed as the percentage of a parameter's value that remains in agricultural plots relative to OG) and a significant recovery rate towards OG in all parameters. Functional dispersion recovered the fastest (2 and 13 years in ex-pastures and ex-cacaos, respectively), and abundance and resource density recovered the slowest (20 – 22 years) (Figure 2a-e, Table 1). All parameters increased over time, except abundance, which decreased rapidly due to the exclusion of pioneer species such as grasses (Figure 2a), and all parameters recovered to OG levels within the chronosequence, with an average recovery time of 15.25 ± 5.7 years. The upper confidence interval (CI) of alpha diversity, however, estimates a recovery time of 48 years (Table 1), but the wide CI suggests uncertainty due to the spread of the data. Disturbance legacy – ex-cacao plantations or ex-pastures – led to different trajectories for functional dispersion only, which recovered faster in pastures (1 – 5 years) than in cacao plantations (3 – 30 years).

In stark contrast, pollinator community parameters (abundance, alpha diversity, and functional diversity) were more resistant ($80.2 \pm 12.6\%$) and recovered in less time (4.0 ± 7.1 years) than floral resources. Pollinator abundance and alpha diversity showed no significant recovery trajectory, retaining OG values after disturbance, with diversity being higher in agricultural sites than in OG (Figure 2f-g, Table 1). Functional evenness and dispersion were also highly resistant and resilient, recovering within the first decade (Figure 2h-i). Legacies did not affect recovery trajectories. Community similarity to OG was the only parameter with a steep recovery curve, taking between 11 and 33 years for ex-pastures, and 7 and 27 years for ex-cacao plantations to fully recover (Figure 3d, Table 1). These patterns, i.e., weak, non-significant effects of the chronosequence on abundance, alpha diversity, and functional diversity, were consistent across taxonomic groups. Most groups were represented in agricultural plots, particularly moths, bats, and sweat bees (Figure S1, supplementary material).

Pollination networks were consequently resistant in linkage density, specialization, and interaction similarity to OG (72.5%–98.2 %), but to a lesser extent in interaction diversity (50.1%–69.6%) (Table 1). However, none of the network parameters showed significant recovery rates, and, by the end of the chronosequence, none fully recovered to OG levels (Table 1, Figure 2j-l). In all parameters and legacies, OG plots overlapped with agricultural plots ($p > 0.05$ for all cases, t-

tests) but not with chronosequence plots (1-38 years) ($p < 0.05$ for all cases, t-tests) (Figure 2j-l, Figure 3f). Specialization (H_2') in pastures was the only variable exhibiting a significant recovery trend but plateaued before reaching OG levels (Figure 2l).

Table 1. Resistance and recovery of floral resource availability, pollinator community, and interaction network parameters. Resistance is expressed as the percentage of the parameter value that remains in agricultural plots relative to old growth (OG) (PA: pastures; CA: cacao plantations), while years until full recovery are expressed as the number of years necessary for the parameter in each legacy to reach 90% of the OG median (Metz et al., 2026). Numbers in brackets represent the 95% confidence intervals of the fitted models. An absence of these values indicates that recovery could not be estimated as the parameter reached an asymptote beyond the OG median, possibly representing an alternate state or very long recovery time. On the right, the slope estimate (β) and standard error (SE) of the intrinsic recovery rate λ , obtained using negative exponential recovery models, are shown. Bold values indicate significant recovery rates ($p < 0.05$).

Parameter	Resistance (%)		Years until full recovery (95% CI) *		Recovery rate (λ) (β , SE)	
	PA	CA	PA	CA	PA	CA
Floral resources						
Resource density	69.6	67.4	22 (16 – 30)	21 (17 – 25)	0.05 (0.009)	0.06 (0.008)
Effective diversity	37.4	36.1	12 (2 – 48)	14 (9 – 22)	0.16 (0.07)	0.13 (0.03)
Functional evenness	72.7	64.2	16 (8 – 28)	12 (8 – 16)	0.07 (0.02)	0.11 (0.03)
Functional dispersion	82.4	70.4	2 (1 – 5)	13 (3 – 30)	0.45 (0.41)	0.10 (0.04)
Abundance (log)	60.1	55.8	22 (13 – 27)	20 (13 – 26)	0.09 (0.02)	0.11 (0.03)
Similarity to OG	67.6	67.1	14 (11 – 26)	15 (10 – 27)	0.08 (0.01)	0.08 (0.02)
Pollinators						
Abundance (log)	93.4	91.1	0 (0 – 0)	0 (0 – 0)	0.01 (0.02)	0.02 (0.03)
Effective diversity*	66.7	71.6	0 (0 – 0)	0 (0 – 0)	0.04 (0.03)	0.05 (0.03)
Functional evenness	91.2	90.0	0 (0 – 0)	2 (1 – 3)	0.08 (0.04)	0.07 (0.02)
Functional dispersion	88.6	87.7	1 (0 – 5)	3 (2 – 13)	0.07 (0.08)	0.19 (0.42)
Similarity to OG	66.5	61.4	20 (11 – 33)	14 (7 – 27)	0.04 (0.008)	0.10 (0.03)
Interactions						
Effective diversity	69.6	50.1	–	–	0.36 (1.01)	0.13 (0.31)
Linkage density	94.6	72.5	–	–	0.06 (0.03)	0.02 (0.02)
Specialization	98.2	89.8	–	–	0.04 (0.02)	0.02 (0.03)
Similarity to OG	97.1	95.4	–	–	-0.01 (0.03)	-0.02 (0.01)

* Results based on quadratic model, see methods

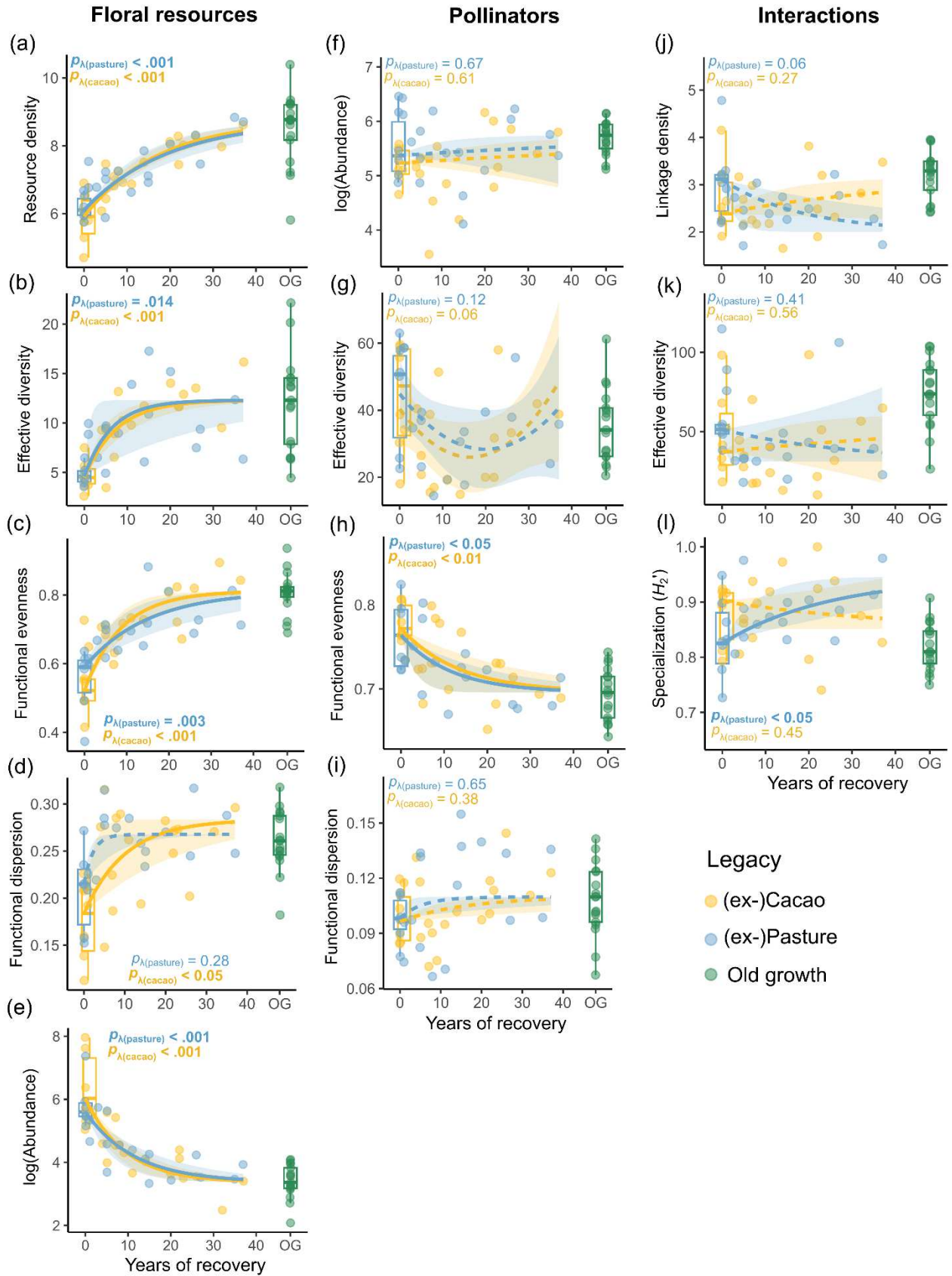


Figure 2. The recovery trajectories of floral resources, pollinators, and interaction networks along a regeneration chronosequence. (a-e): floral resource availability parameters, (f-i): pollinator community parameters, (j-l): interaction network structural metrics. Plots are divided by their disturbance legacies: (ex-)pastures in blue, (ex-)cacao plantations in yellow, and old-growth forests (OG) in green on the right as the reference state. Shaded areas correspond to each model's 95% confidence intervals. Boxplots on the left correspond to the parameter distribution in agricultural sites. The p -values of each model's intrinsic recovery rate (λ) are shown in each graph. Solid lines and dashed lines indicate significant and non-significant models, respectively.

Species and interaction composition and recovery niches

While community similarity steadily approached OG plots for floral resources and pollinators (Figure 3d-e) or showed high resistance but incomplete recovery in networks (Figure 3f), the trends in composition recovery differed. For floral resources, composition varied in function both of the recovery stage (plants: PERMANOVA $R^2 = 0.13$, $F_{55,6} = 1.37$, $p < 0.0001$) and legacy ($R^2 = 0.06$, $F_{59,6} = 1.76$, $p < 0.0001$), with both legacies showing no overlap in agricultural sites and gradually converging towards OG (Figure 3a). OG plots were, however, widely variable in composition, and many did not overlap with late recovery forests (Figure 3a). A similar pattern was observed for pollinators (recovery stage: $R^2 = 0.17$, $F_{55,6} = 1.87$, $p < 0.0001$; legacy: $R^2 = 0.06$, $F_{59,2} = 1.74$, $p < 0.01$), but composition turnover was relatively weaker, with OG fully overlapping with late recovery forests (Figure 3b). Pollinator communities in OG were also more conserved, presenting less variation across plots (Figure 3b). The observed turnover was mostly driven by bees, which showed relatively distinct old-growth communities, but not by moths and bats, where a high overlap among successional stages was observed (Figure S1). While interaction composition varied significantly with recovery stage ($R^2 = 0.15$, $F_{55,6} = 1.09$, $p < 0.01$) and legacy ($R^2 = 0.04$, $F_{59,2} = 1.11$, $p < 0.01$), recovery stages and the legacies largely overlapped in the interaction space (Figure 3c), as evidenced by the high resistance of interaction similarity (Figure 3f).

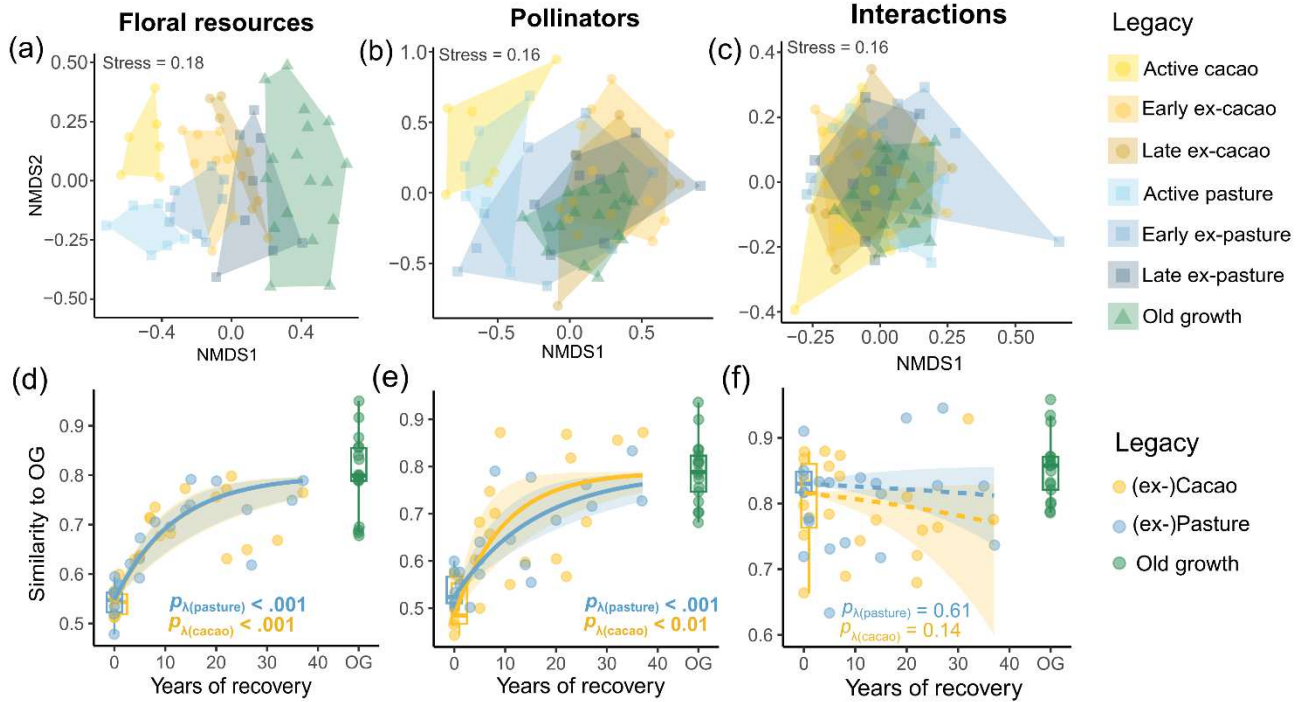


Figure 3. The composition of floral resources, pollinators, and plant-pollinator interactions along the chronosequence. (a), (d): floral resources; (b), (e): pollinators; (c), (f): interactions. The top graphs show the non-metric multidimensional scaling (NMDS) dimension reduction of the communities of each level. Plots are separated by legacy. Graphs on the bottom show the recovery of community composition similarity to OG. OG plots are shown on the right as a reference state in green, and chronosequence plots are divided by legacy: (ex-)cacao plantations in yellow, and (ex-)pastures in blue. Shaded areas correspond to 95% confidence intervals. The p -values of each model's intrinsic recovery rate (λ) estimates are shown at the bottom of each graph. Solid lines and dashed lines indicate significant and non-significant models, respectively.

Patterns in recovery niche optima and breadth, i.e., the position in the recovery gradient where a species peaks in abundance and its variation around this optimum, respectively, further indicate the stronger composition partitioning in plants compared to pollinators and interactions. Plants offering floral resources had, on average, a significantly narrower recovery niche breadth (showing an average abundance-weighted standard deviation of 0.084 ± 0.062 around their recovery optima) than pollinators (0.181 ± 0.057) and interactions inferred from pollen loads (0.171 ± 0.053) (Figure 4a-c). That means plant species offering resources were more restricted to narrow intervals along the recovery gradient than pollinators and interactions. Recovery niche optima

reveal that most plants peak in abundance in the middle of the recovery gradient, but with wide
 variation in recovery optima (0.543 ± 0.181) (Figure 4d), while pollinators and interactions peak
 at a slightly yet significantly later position and show less variation in optima (pollinators: $0.624 \pm$
 0.113 , interactions: 0.629 ± 0.098) (Figure 4e-f). Together, the two recovery niche attributes
 indicate higher turnover of flowering species than of pollinators. Pollinator species tended to
 exhibit the highest abundances at mid-recovery stages, but showed much broader recovery niches,
 thus facilitating pollen flow across different stages of the chronosequence.

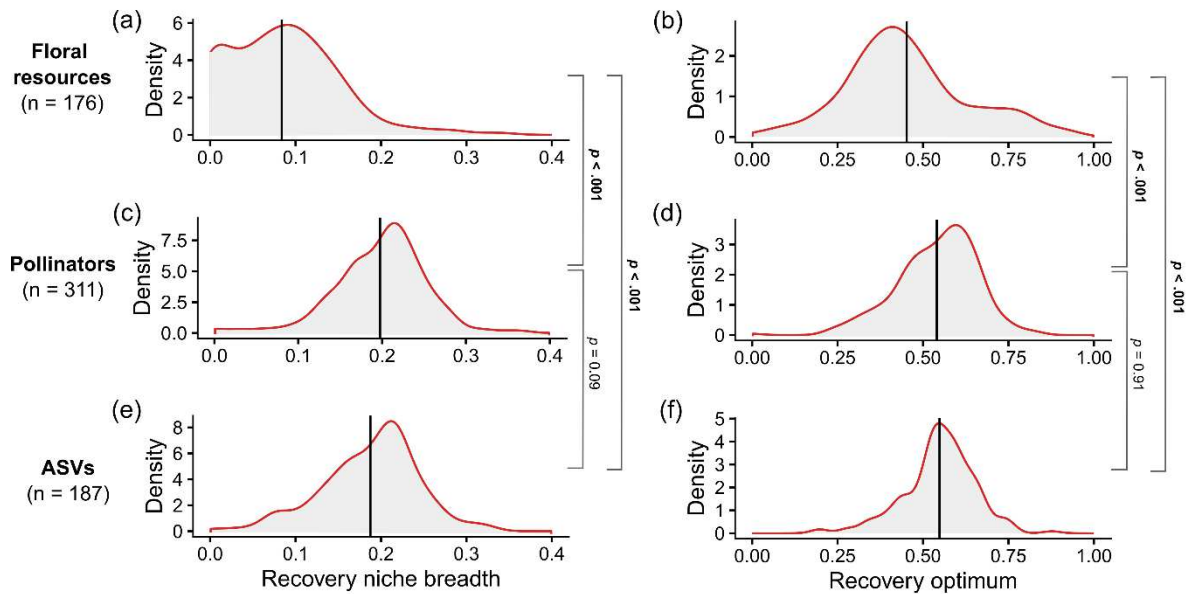


Figure 4. The recovery niche optima and breadths of species and interactions along the recovery gradient. Graphs on the left represent the density of recovery niche breadths (the variation in a species' occurrence along the recovery gradient), and, on the right, recovery niche optima (the location along the recovery gradient where a species is abundant). (a, b) Plants offering floral resources, (c, d) pollinators, and (e, f) Amplicon Sequence Variants (ASVs) extracted from pollen loads on pollinators, representing the plant species pollinators interacted with. Numbers in the top-right corner indicate the sample sizes by species (only species with a total abundance of 5 or more individuals were included). The recovery gradient was measured using the forest Recovery Index, which accounts for several biotic and abiotic plot attributes (see Methods). Vertical lines indicate the distribution means. *p*-values of the cross-group comparisons (Tukey post-hoc test) are shown.

3.2 Recovery drivers and reassembly pathways

The output of the Structural Equation Models, which test the direct and indirect effects between sets of dependent (pollinator and floral resource community attributes) and independent variables (plot and landscape attributes), suggests that the recovery of pollinator communities was driven by both floral resource availability and landscape connectivity, and that interaction network reassembly was not driven directly by floral resources (Figure 5a). In order properly to quantify forest recovery, floral resource availability, and forest connectivity along the chronosequence, we derived three indexes. The recovery index (RI) was used to quantify forest recovery, a composite index derived from forest structural attributes (aboveground biomass, mean tree height, and circumference) and abiotic variables (temperature and humidity) that better represent the recovery gradient than simple recovery age. Similarly, the floral resource recovery index (FRRI) and the connectivity index (CI) provide a composite, more informative measure of the overall (functional) diversity and density of resources on a plot, and the proportion of surrounding forest at different scales, respectively (see methods for details on composite indices). There was a strong effect of RI on FRRI, which, in turn, led to a decrease in pollinator diversity but to a recovery of pollinator community similarity to OG (Figure 5a). RI also directly and positively affected the recovery of community composition. Moreover, pollinator abundance and community composition recovery were positively affected by forest connectivity (CI). Composition was indeed the pollinator community attribute most well-explained by its driving variables ($R^2 = 0.64$), compared to the others ($R^2 = 0.08$ – 0.13). Network structure was not directly affected by FRRI; rather, interactions were more diverse with increased pollinator abundance and diversity, but no effect was observed in interaction specialization or composition (Figure 5a). Together, these outcomes provide strong support for our hypothesized reassembly framework (Figure 1c-d), particularly a resource-independent and pollinator-mediated interaction network reassembly (H_1 and $H_{2.2}$), and a slow recovery of community composition (as shown by pollinators) (H_3). Full model outputs are available in the supplementary material (Table S1), as well as model quality statistics (Table S2).

Divergent recovery pathways are evident among individual pollinator groups (Figure 5b-f), providing initial evidence for a complementary, trait-based reassembly (H_4). Some functional groups were strongly associated with disturbance, some with older recovering forests, and some showed neutral responses. Moths (Figure 5b) belonged to the latter group. Communities were unaffected by FRRI or by forest recovery in general, but rather directly and positively by landscape connectivity and elevation. Interactions with plants, in turn, became more diverse as moth diversity increased. Interestingly, this was the only group where a direct, albeit weak, effect of FRRI on

interaction networks was observed (Figure 5b). Stingless bees (Figure 5c) were partially driven by floral resource recovery: bee abundance and compositional similarity to OG increased with FRRI. Interaction diversity increased with bee diversity, which was independent of the recovery gradient. This group was also particularly sensitive to elevation, with elevation positively affecting bee abundance but negatively affecting bee diversity (Figure 5c). Orchid bees (Figure 5d) were remarkably unaffected by forest recovery in general: only elevation negatively affected orchid bee abundance, while their abundance was positively associated with interaction diversity and composition similarity to OG. Interestingly, the abundance and diversity of nocturnal bees (Figure 5e) were most strongly and directly affected by RI, not by FRRI. The diversity of these bees was also negatively affected by elevation. Their diversity of interactions with plants was positively associated with their abundance (Figure 5e). Finally, other bees, such as diurnal sweat bees, honeybees, mason, leafcutter, oil, and plasterer bees (Figure 5f) were strongly and negatively affected by forest recovery, indicating an association with disturbance. Their abundance and diversity both strongly decreased with increasing FRRI, and their diversity further decreased with CI. Their interactions with plants were most diverse in disturbed sites, where their abundance was highest (Figure 5f).

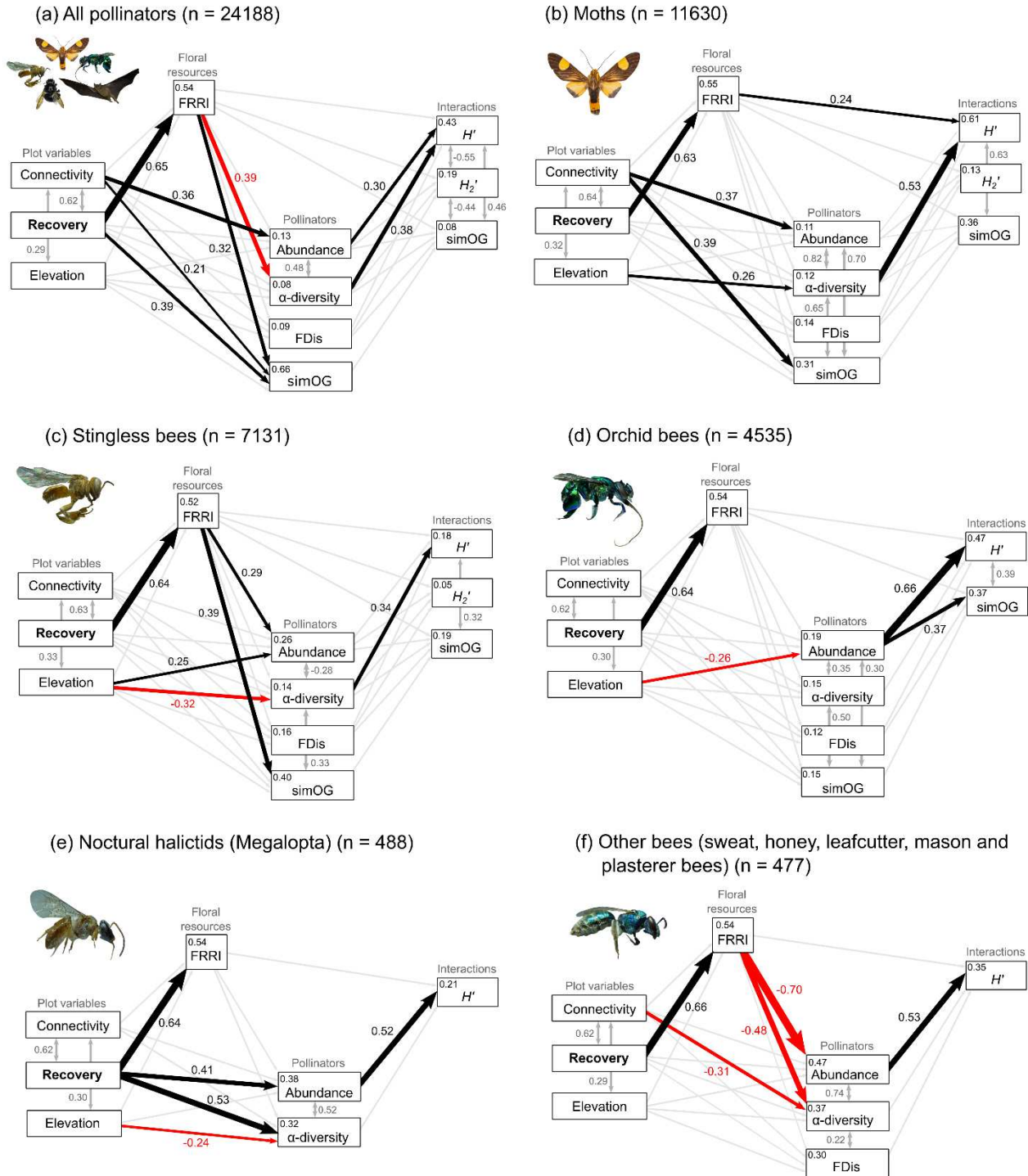


Figure 5. Path diagrams derived from Structural Equation Models depicting reassembly pathways of plant-pollinator interactions. (a) All pollinators, (b) moths (Erebidae: Arctiinae and Sphingidae), (c) stingless bees (Apidae: Meliponini), (d) orchid bees (Apidae: Euglossini), (e) nocturnal bees (Halictidae: Augochlorini: *Megalocta*), (f) other relevant bee groups, including diurnal sweat bees (Halictidae: Augochlorini), leafcutter bees (Halictidae), mason bees (Apidae: Xylocopinae), plasterer and oil bees

(Colletidae), and honeybees (*Apis mellifera*). Single-headed arrows represent hypothesized causal paths between a predictor and a response variable. Black arrows indicate positive effects, and red arrows negative effects. Arrow width indicates effect size, and numbers alongside arrows are the standardized effect estimates. Grey arrows indicate non-significant effects. Double-headed grey arrows represent significant and relevant (equal or higher than 0.3 estimate) covariation between variables. R-squared values of each response variable are shown within their respective boxes. FRRI: Floral resource recovery index; FDis: functional dispersion; simOG: community or interaction similarity to old-growth forests; H' : interactions Shannon diversity. H_2' : network specialization.

3.3 Trait-driven recovery

Despite a slight tendency for larger and longer-tubed flowers in older forests, there was no significant effect of the forest recovery index on community-weighted (CW) tube length ($\beta = 1.32$, $se = 0.80$, $p = 0.10$) or floral size ($\beta = 0.39$, $se = 0.25$, $p = 0.13$) (Figure 6a). No significant effect was found for the overall pollinator CW functional feeding length ($\beta = 0.04$, $se = 0.07$, $p = 0.60$) or body size ($\beta = -0.30$, $se = 0.31$, $p = 0.32$) either; however, individual groups showed distinct trends (Figure 6b). The CW functional feeding length of moths, the most abundant pollinator group, increased with recovery ($\beta = 0.02$, $se = 0.007$, $p < 0.05$), while that of stingless bees, the second most abundant group, decreased ($\beta = -0.10$, $se = 0.03$, $p < 0.05$). No other groups showed any significant linear trend. Stingless bees also showed a significant decrease in body size with recovery ($\beta = -0.08$, $se = 0.02$, $p < 0.05$), and the group encompassing honey, sweat, leafcutter, mason, and plasterer bees showed an increase ($\beta = 0.22$, $se = 0.11$, $p = 0.050$), but no other group (Figure 6b).

Meanwhile, life-history functional traits provided additional insight into species partitioning within the chronosequence. Bilateral, accessible, nectar- and pollen-offering plants from wind-, bee-, butterfly-, and settling moth-pollination systems were associated with disturbance and earlier recovery stages, opposing those belonging to hawkmoth-, and beetle-pollination systems, which were associated with older forests (Figure 6c). Radial flowers with restrictive morphologies (e.g., tubular), flowers offering rare resources (resin, oil, scent, fleshy parts), and species with vertebrate-pollination or generalized small-diverse-insect-pollination systems were not affected by recovery. As for bee recovery, soil excavators, aposematically colored bees, and kleptoparasitic bees were associated with disturbance, opposed to aboveground wood

nesters that require pre-existing cavities or are aerial nesters, as well as bees of all other colorations,
 those showing eusocial or semi-social behavior, those with sparse pilosity, and those requiring non-
 floral resources (resin, oils, volatiles) (Figure 6d). Wood-excavating bees, belowground nesters in
 pre-existing cavities, cavity generalist bees (wood, soil, and insect nest users), as well as densely
 pilose bees and bees not requiring rare resources were not affected by recovery. Moths were
 remarkably unaffected by forest recovery in general with regard to the selected functional traits
 (coloration pattern, lightness, and contrast) (Figure 6e). While a large portion of pollinators showed
 neutral functional responses to the recovery gradient, the turnover of functional groups of flowering
 plants and bees provides further evidence for a complementary functional trait-based reassembly
 (H₄).

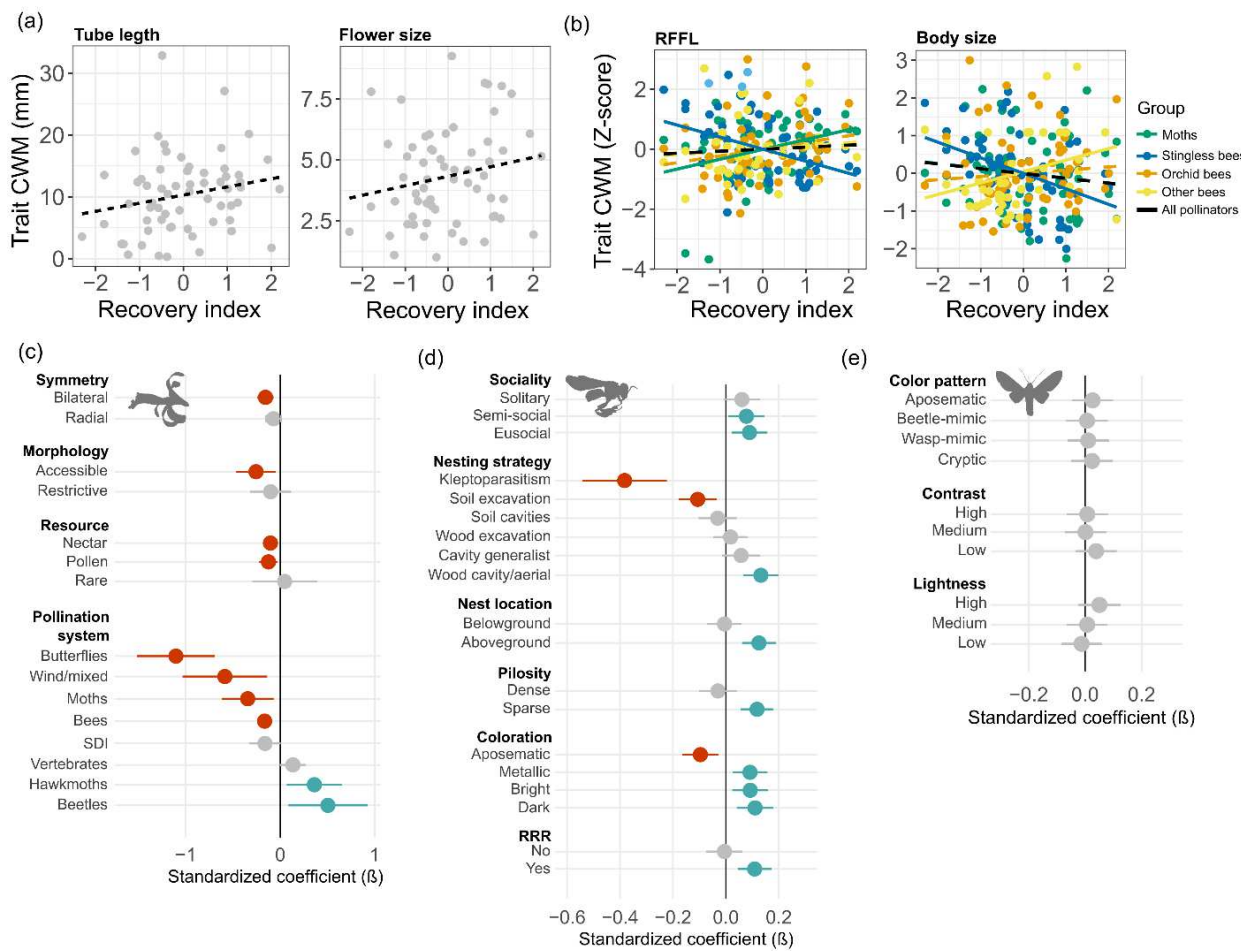


Figure 6. Effect of forest Recovery Index on the functional traits of plants and pollinators along the regeneration chronosequence. (a) The variation of community-weighted means (CWM) of floral morphological functional traits (floral tube length and floral size) and of (b) pollinator functional traits (relative functional feeding[SL1.1] length – RFFL, measured as the relative proboscis length – and body

size) along the regeneration gradient. In (a) and (b), solid lines indicate significant effects, and dashed lines indicate non-significance. In (b), Z-scores are shown to enable cross-group comparisons. Pollinator groups are shown separately, with the overall trend of the entire pollinator community shown in black. In the second row, the effects of the recovery gradient on qualitative traits of (c) plants, (d) bees, and (e) moths are shown through standardized effect coefficients (β). Horizontal bars represent 95% confidence intervals. Significant negative effects are shown in red, positive effects in blue, and non-significant effects in grey. Abbreviations: SDI = small diverse insects. RRR = reliance on rare resources (resin, oil, scent, fleshy parts).

DISCUSSION

In this study, we examined the recovery trajectories of tropical pollinator communities, floral resource availability, and pollination networks during the first decades of succession, as well as the recovery pathways leading to pollination network reassembly. We found that pollinators are resistant to disturbance, often thriving in agricultural sites despite low resistance and slower recovery of floral resource availability. Pollinators exhibited broader recovery niches by moving across different successional stages. Consequently, we also observed high resistance in plant-pollinator interactions at agricultural sites and early recovery, with variations in network structure mediated by a resistant pollinator community that was not strongly bottom-up regulated.

These outcomes confirm our first prediction (H_1): floral resource density and diversity mirror plant community successional dynamics by recovering steadily within the first three decades of succession^{14,16,19,20}. Furthermore, a rapid, floral resource-independent recovery of pollinators ($H_{2.2}$) was corroborated. These patterns have important implications for forest recovery dynamics, as pollinators appear to sustain pollen flow within and across old-growth patches, maintaining gene flow between climax assemblages and within the matrix itself. By feeding on and promoting pollination in pioneer communities at agricultural or early successional sites, pollinators ensure a continuous supply of seeds from entomophilous and pioneer grasses that do not compose seed banks to neighboring anthropogenically or naturally created clearings, while also contributing to the establishment of early successional species and pioneer trees in seed banks⁴⁰. Moreover, pollinators may sustain themselves in secondary forests, which already exhibit floral diversity and density comparable to OG at the canopy-closure period (15-20 years²¹), further evidencing that tropical logged forests are energetically rewarding for secondary consumers²². Therefore, even in regions where primary forests are scarce, pollination services may still be assured, provided that

sufficient cover of structurally mature secondary forests is present, adding to the array of valuable biological, social, and economic attributes of regenerating forests ^{8,9}.

In addition, our results strengthen the body of evidence that mutualistic animals, particularly mobile ones, can drive tropical forest recovery by maintaining ecosystem processes across different successional stages. Mobile seed dispersers, such as bats and birds, and large dung beetles, facilitate the colonization of pioneer species and the maintenance of seed banks in adjacent disturbed sites ^{26,41–43}. Pollinators seem to follow the same trend, particularly large, wide-ranging ones that show weaker responses to small-scale disturbance, such as bats ⁴⁴, large solitary bees ⁴⁵, and hawkmoths ⁴⁶. Such potential as “succession drivers” will, however, be limited in groups of small-ranged, low-mobility consumers, including detritivores ²⁵, as well as small insect pollinators with complex life cycles ⁴⁷ or territorial ones (e.g., many hummingbird species) ⁴⁸. Several tropical pollinators are considered dispersal-limited, particularly the small, eusocial, and highly diverse stingless bees, which tend to forage only short distances around nests often established in tree hollows in conserved forests ^{49,50}. Our results support this notion: stingless bees, which encompass species as small as 2 mm (e.g., *Trigonisca* spp.), were on average smaller in old, conserved forests (Figure 5b), and their similarity to OG increased over time (Figure 4c), supporting that OG communities are taxonomically and functionally unique in comparison to successional forests. Even this group, however, was largely unaffected by the recovery gradient (Figure 4c), suggesting some plasticity in foraging habitat. Resource generalism also likely plays a role in pollinator resistance. Although tropical pollinators can be resource specialists, such as oligolectic solitary bees ⁵¹, abundant and important groups in the tropics, such as stingless bees, moths, birds, and bats, tend to visit a wide range of plants ^{52–55}. Despite initial conditions in the two disturbance legacies (e.g., shading, initial vertical structure, and presence of remnant trees that influence recovery via nucleation ⁵⁶) and consequent differences in initial plant communities (Figure 3a), recovery of pollinators and network rates were similar in cacao plantations and pastures, reinforcing the notion of foraging generalism and resource redundancy for pollinators. Therefore, pollinators may eventually require mature forests to roost, find nesting resources or substrates, and seek refuge, but seem able to traverse the matrix to feed on pioneers in disturbed sites, a pattern clearly illustrated by nocturnal bees in the research site ⁵⁶.

As supported by the SEM (Figure 4a), plant-pollinator interactions reassembled through a resource-independent, pollinator-mediated pathway. The abundance and diversity of pollinators were the main variables dictating network interaction diversity. Pollinators were, in fact, most

abundant and diverse in agricultural sites, perhaps because of the abundance of flowering individuals (Figure 2e) and consequent enhanced attractiveness of resources ⁵⁷, which drew pollinators to open areas. However, pollinator abundance and diversity were poorly explained by their predicted variables, as were interaction specialization and interaction similarity to OG, further evidencing pollinator dispersal and generalism. Furthermore, these reassembly pathways varied considerably among pollinator groups (Figure 4). Thus, a stable trend in pollinator abundance and diversity appears to reflect a shift from disturbance-adapted to forest-adapted pollinators, accompanied by a substitution of life-history traits (Figure 5). These results support our hypothesis of trait complementarity (H₄) and suggest that the maintenance of network diversity and structure (and, potentially, of pollination service) is being achieved through pollinator multifunctionality and diverse responses to disturbance ⁵⁸. That is, a stable assemblage of pollinators and their services appear to be assured along succession by two mechanisms: (i) pollinators with wide recovery niches and little functional response to the recovery gradient (particularly moths, Figure 5e, whose importance in tropical pollination networks due to widespread generalism, hyper diversity, connective potential, and pollination of pioneers has been attested ⁵³) and (ii) the complementary substitution of functional groups. Bilateral, accessible flowers offering nectar and pollen and pollinated by wind, lepidoptera, and bees were associated with agricultural sites and early succession, due to the dominance of herbs and shrubs from families like Lamiaceae, Verbenaceae, and Poaceae, which gave way to a more balanced community containing more vertebrate, hawkmoth, and beetle-pollination systems (Figure 5c). Aposematic, kleptoparasites, and soil excavators were gradually replaced by non-aposematic, wood-cavity nesters with higher degrees of sociality and an increased need for rarer resources (resin, oil, mud, feces, and volatiles), reflecting the nesting substrates and resources available in forests. However, while multifunctionality is suggested by the turnover of functional groups, whether that translates into pollination effectiveness along succession, which varies among pollinator groups ⁵⁹, remains to be assessed.

The functional turnover of bees suggests a decoupling of needs: foraging generalism seems to be accompanied by stricter requirements for refuge and nesting. Eusocial bees nesting above ground and in natural wood cavities are more susceptible to habitat loss and distance from preserved forests than solitary, belowground soil-nesting ones have often been reported ^{5,34}. Stricter needs for refuge would also explain why the recovery index, which summarizes several forest structural attributes, had a direct effect on pollinator composition independently (Figure 4a), and

also such a strong direct effect on nocturnal bees, which are resource generalists but highly dependent on natural cavities in logs and epiphytes for nesting⁵⁶. Such decoupling likely explains why pollinator composition recovered much more slowly than other community parameters, exhibited the strongest response to its predicting variables, being dependent on floral resource availability, landscape connectivity, and the recovery of forest structure (Figure 4a). Our hypothesis (H₃) was thus partially corroborated, because, although slowly, both plant and pollinator community compositions recovered within the four decades. Community composition has been repeatedly shown to recover slowly in animal communities^{25–27} and to be considered a better metric of community response to restoration⁶⁰. A slower recovery of pollinator composition is likely a result of the strong compositional gradient of floral resources observed here (Figure 3a), which leads to a lack of distinct floral resources, but also non-nutritional resources associated with an old-growth flora (e.g., nesting cavities in wood, host plant diversity for larvae, floral and extra-floral resin, volatiles for mating), that may be absent in successional forests. Furthermore, although large, diverse, and more generalized in agricultural sites, networks became smaller, less diverse, and more specialized in successional forests and did not converge towards old growth within four decades. Therefore, while pollinator resistance may help maintain animal-mediated pollen flow during tropical forest recovery, early successional stands seem to lack conditions found in either disturbed sites or old-growth forests and exhibit impoverished networks, which may take several decades to recover. A slow recovery of species composition and delays in network recovery are not unique to pollination but also occur in plant dispersal networks⁶¹, thereby reinforcing the vulnerability of mutualisms¹² and underscoring the irreplaceability of primary forests for biodiversity conservation⁶².

While plant-pollinator networks display remarkable resistance and resilience, the success of pollinator restoration requires less isolated, less fragmented, more connected landscapes that still contain some extent of forest cover^{31,63,64}. In our study, connectivity and/or elevation, variables that influence plot isolation, affected the recovery of all groups, to some extent (Figure 4). Therefore, it can be assumed that the role of functional turnover in assuring pollination may thus break down if disturbance reaches a point where the landscape can no longer provide suitable habitats and corridors for forest pollinators. Although some groups thrive under disturbance (e.g., sweat bees and other solitary bees), their presence alone may not be sufficient to avoid pollen limitation in landscapes where forests have been thoroughly cleared. Even pollinators known to be robust against fragmentation (e.g., orchid bees, which were not affected by recovery – Figure 4d)

may be unable to cope with increasing patch isolation⁶⁵. Our study site still exhibits a high degree of forest cover (Figure 1b) and a high proportion of OG forests⁶⁶, likely facilitating recovery. Succession is considerably slower in regions under more intense disturbance regimes, with low and fragmented primary forest cover⁶⁷. Future studies should therefore subject the reassembly of plant-pollinator interactions to stronger connectivity gradients to assess their resistance to varying degrees of landscape-scale disturbance. Furthermore, studies should assess plant fitness as a direct correlate of network structure (e.g., Kaiser-Bunbury *et al.*³⁰) and therefore test whether network stability in successional forests translates into stable pollination services.

METHODS

Study site and chronosequence

This research was conducted in 2022 and 2023 in the Río Canandé and Tesoro Escondido reserves in northwestern Ecuador (0.5° N 79.2° W, 130–540 m a.s.l.) (Fig. 1a-b of the main text). The site lies on the western foothills of the Andes and is a lowland rainforest within the Chocó-Tumbes-Magdalena ecoregion, characterized by high precipitation (ca. 5000 mm/year), a stable mean temperature of ca. 25°C, and a dry midyear season (Af climate)⁶⁶. Data collection took place in a well-resolved chronosequence (space-for-time substitution) composed of 62 50x50m plots, which included active disturbances in the form of pastures (PA, n = 6) and cacao plantations (CA, n = 6), a regeneration gradient ranging from one to 38 years of recovery in the form of regenerating ex-pastures (PR, n = 16) or ex-cacao plantations (CR, n = 17), and old-growth forests that served as a pre-disturbance reference state (OG, n = 17)⁶⁶ (Fig. 1b). Plot size was limited by the topological features of the area, and plot number per legacy was limited by the land use patterns of local farmers in the previous decades⁶⁶. Old-growth forests were identified as areas with minimal to no evidence of recent disturbance, as indicated by variables such as mean tree height, mean basal area, aboveground biomass, and tree richness⁶⁶. The shortest distance between plots was 184 m, the largest distance 14 km, and the mean distance between plots within the same recovery stage ranged between 4.6 and 5.5 km (Fig. 1b). Plot elevation above sea level ranged between 159 and 615 m and was not correlated with recovery age⁶⁶. Research in the reserves and data collection were permitted by the Ministry of Environment of Ecuador (Contrato Marco MAE-DNB-CM-2021-0187).

Data collection

Data collection took place between March and June (32 plots) and October and December (30 plots) of 2022 and 2023, totaling four fieldwork campaigns. In each period, half of the plots of each recovery stage were sampled, so that recovery stages were evenly sampled between the two seasons. Nocturnal pollinators and their interactions were sampled in all plots in 2022 using light traps (see *Data collection: pollinators* below), as well as diurnal pollinators and their interactions using colored vane traps. In 2023, all plots were sampled once for floral resources, and additional diurnal pollinators and their interactions (using fragrance traps, active netting, and a repetition of vane trap sampling due to low catch rates in 2022). Bats were sampled in both years, with a quarter of the plots sampled in each period (15 plots in March-June 2022; 16 in October-December 2022; 15 in March-June 2023; and 16 in October-December 2023). Floral resources and plot characteristics are unlikely to vary substantially over the 6- to 12-month interval between nocturnal pollinator and floral resource sampling, and we expect the change in recovered plots to be negligible.

Data collection: floral resources

We assessed the entire 2500 m² area of each plot by walking ten 50 x 5 m parallel transects (2.5 m on each side) to quantify floral resource availability. The 62 plots totaled a sampled area of 15,5 ha. During walks, all plant individuals bearing at least one flower in active anthesis (or active in the previous night) were recorded. Each flowering individual was assigned a morphotype, had the number of flowers counted or estimated (see below), and had vegetative and reproductive organs collected for identification and trait measurement. This procedure was performed for all observable and reachable understory plants, and direct observations were also possible in the midstory (5-10 m). For canopy plants (trees, climbers, and epiphytes), fallen flowers and floral traces were observed and collected. In the case of large canopy trees that produce a large number of flowers at once (e.g., *Turpinia occidentalis*, *Banara guianensis*, *Carapa* spp.) and leave a large radius of floral traces around the trunk, transects were disregarded for the individual abundance count, and a space of at least 5 m between two floral trace circles was considered for different individuals to be counted. While this method likely underestimates canopy resource occurrence, especially epiphytes, there is no established way to sample canopy resources in large forest areas,

and in all cases, floral traces overlapped with the pre-existing tree inventories conducted in the plots⁶⁶.

To measure floral abundance per individual, we employed a method similar to the floral abundance scanning of Szigeti *et al.*⁶⁸ by assigning a logarithmic floral abundance factor to each morphotype to serve as a proxy for floral density: a factor of 1 for morphotypes with observable individuals that produce one flower or floral head only (e.g., herbs, small shrubs and epiphytes, e.g., *Burmeistera* spp.); 10 for observable herbs, shrubs, epiphytes or trees that produce few flowers (< 10 per plant, e.g., *Gasteranthus villosus*); 100 for shrubs, trees and epiphytes with a sparse amount of flowers (10 – 100 per plant, e.g., *Miconia centronioides*); 1,000 for trees or epiphytes with a dense amount of flowers (100 – 1000 per plant, e.g., *Wettinia quinaria*); and 10,000 to dense-canopy trees with practically uncountable flowers (e.g., *Banara guianensis*). Floral abundance factors were assigned to morphotypes in the field based on the average number of flowers per individual (10 individuals per morphotype, when available), and, if necessary, later corrected for canopy plants and epiphytes using photographs and literature after species identification.

Morphotypes were identified to the lowest possible level based on external vegetative and floral morphology via field guides and catalogs for the region^{69–71}. A tree species database (all individuals with a diameter at breast height ≥ 7.95 cm) was available for all plots⁶⁶ and used to cross-check and identify all marked individuals of trees flowering within the plot. The Plants of the World Online (powo.science.kew.org) and iNaturalist (inaturalist.org) platforms were used as complementary, confirmatory tools, and the Global Biodiversity Information Facility (GBIF) (gbif.org) was used to confirm the geographical ranges of putative species. Vouchers are stored in the Biological Collection of the School of Life Sciences, Technical University of Munich, Freising, Germany.

For each morphotype, we measured six functional traits (criteria and detailed definitions of the traits described in Table S3 of the Supplementary Material): (i) Flower width (mm), measured as the diameter of the perianth at its outermost position, (ii) flower length (mm), measured as the vertical length of the perianth, valid for gamopetalous or gamosepalous flowers forming any vertical structure (otherwise zero), (iii) the presence or absence of bilaterality (zygomorphy), (iv) pollination unit morphology (16 categories, adapted from Durka^{72,73}, Table S3), and (v) the main floral reward: nectar, pollen, nectar and pollen, and rare resources (oil, fleshy parts, resin, volatiles, or absent/deception). Finally, species were assigned (vi) pollination syndromes, the convergent suites of floral traits (including morphology, color, anthesis time, and scent emission), which

indicates the likely most effective pollinator agent⁷⁴. The considered syndromes were: anemophily (wind), ambophily (wind and insects), cantharophily (beetles), chiropterophily (bats), melittophily (diurnal bees), ornithophily (birds), phalaenophily (settling moths), psychophily (butterflies), sphingophily (hawkmoths), and small diverse insects (SDI), which refer to small and generalist flowers without a clear syndrome that attract taxonomically diverse small insects⁷⁵. Syndrome classification was based on the floral traits listed by Faegri and Pijl^{76,77}. Rarer syndromes were not present on the site (e.g., therophily and sapromyophily) or were grouped within SDI (i.e., myrmecophily, myophily, tripophily) (Table S3 for detailed criteria).

Data collection: pollinators

We employed distinct capture methods in each plot to sample different functional groups of pollinators: (i) mixed blue and yellow vane traps⁷⁸ were set 1.8 m above ground at the center of the plot to capture diurnal pollinators. The traps contained a dry killing chamber that operated on chloroform fumes, allowing for pollen collection. The trap was left in the field for 24 h. (ii) Fragrance traps aimed at male orchid bees (Apidae: Euglossini), a dominant group of Neotropical pollinators⁷⁹. Four traps, each consisting of 1.5 L perforated bottles containing a different synthetic fragrance (1,8-cineol, eugenol, skatole, and methyl salicylate), were set in each plot to attract a wider variety of bees. Traps were also set for 24 h at the center of the plot, 1.8 m above ground. (iii) Four hours of active netting were performed within the entire plot area to capture additional diurnal bees foraging on the plot. (iv) Vane traps equipped with Lepi-LED light set to the mixed UV and visible light setting to capture nocturnal pollinators⁸¹. These traps, similar in structure and function to the diurnal vane traps, remained in the plot for 24h. The light was timed to operate between 18:00 and 06:00. From the traps, we collected all nocturnal bees, as well as all moths from Sphingidae, a relevant pollinator group known for its role in the pollination of tropical plants, and Arctiinae (Erebidae), a large and conspicuous group of tiger and lichen moths whose important role in pollination networks has been attested⁵³. (v) Six 6x3m mist nets were installed at ground level near natural corridors within the plot to capture bats, and remained open between 18:30 and 00:00.

Insects often exhibit vertical stratification in tropical forests, with many showing an affinity for the canopy⁸². Therefore, we sampled both the understory and the canopy of plots containing clear vertical stratification (>15 years of recovery and OG). For that, traps from methods (i), (ii), and (iv) were set in the canopy (mean height 25.8 ± 5.3 m, median 25.2 m, range 15–38.0 m) of

plots simultaneously to understory traps by using a pulley system installed through a bow-and-arrow shooting⁸³. From the 62 chronosequence plots, 26 presented suitable conditions for setting traps in the canopy. Traps were always set at the tallest or one of the tallest trees in the plot and operated similarly to understory traps.

Specialized taxonomic keys were used to identify bats⁸⁴, stingless bees^{85,86}, orchid bees⁸⁷, and nocturnal bees⁸⁸. Bee identification was further aided by CR's personal collection (Aarhus University, Denmark). Diurnal sweat bees (Halictidae: Augochlorini), among other smaller groups found at the site (e.g., Megachilidae), were identified to the subgenus level⁸⁹ and separated into morphotypes, as no dedicated taxonomic material is available for identifying these bees in the region. Moths were identified using a dedicated catalog for the Canandé reserve⁹⁰ and GB's collection at the Phyletisches Museum Jena (Germany) with material from Costa Rica, Ecuador, and Perú, as well as photographs taken in the Natural History Museum (London). Nearly all moth species could be assigned a genus, and most were identified to the species level. All (morpho)species were barcoded (COI region, Canadian Centre for DNA Barcoding) to assist identification.

We measured two functional traits from all pollinator species: body size (BS) and functional feeding length (FFL). BS, an important dispersal and interaction trait, corresponded to body length in moths (distance between the tip of the head and the tip of the abdomen), intertegular distance in bees, and forearm length in bats. FFL, an interaction trait associated with feeding specialization, was measured as the uncoiled and straightened proboscis in moths, the glossa plus prementum in bees, and the longest skull length in bats. Because BS and FFL are often allometrically related⁹¹, we calculated the relative functional feeding length (RFFL) as FFL/BS to replace FFL and avoid collinearity. In addition to these quantitative traits, we assigned a set of qualitative, life-history functional traits to insect pollinators (bees and moths) that may affect their occurrence and survival along forest regeneration.

Bees were classified in terms of:

- Sociality: strictly solitary, eusocial, or semi-social (encompassing facultatively social, communal, and primitively eusocial species).
- Nesting strategy: kleptoparasitism, soil excavation, pre-existing cavities in soil, wood excavators, pre-existing cavities in wood or aerial nesters (both grouped together due to the dependence on a pre-existing structure), or cavity generalists (usage of different substrates, including soil, wood, and pre-existing insect nests).

- Nest location: aboveground or belowground.
- Reliance on rare resources: presence or absence. Rare resources are here classified as any resource other than pollen or nectar needed for survival, which include: floral or extra-floral resin, oils, scents, vegetative parts (e.g., leaves), mud, and feces.
- Dense pilosity: presence or absence. Dense pilosity was classified as the presence of hair covering a significant proportion of the thorax and/or abdomen, to the extent that the cuticle below is not visible.
- Body coloration: metallic, aposematic (stark dark-clear contrasts with vibrant colors, or the presence of color patterns associated with Müllerian mimicry), dull (i.e., not metallic or aposematic) and dark (black or dark brown), or dull and clear-colored (yellow or light brown).

All qualitative bee traits, except for pilosity and coloration, were gathered from the literature, either from pre-existing reviews or datasets (⁹²), or from species- or group-specific sources. Precise details on the source of each species' traits, as well as an overview of all bee traits collected, can be found in Supplementary Dataset 1. Pilosity and coloration were classified based on prepared specimens collected from the site.

For moths, we compiled information on three quantitative traits: Body coloration, lightness, and contrast. These traits were chosen as they could be collected directly from preserved specimens and represent important responses to abiotic conditions and predation pressure ⁹³:

- Body coloration: Aposematic (stark dark-clear contrasts with vibrant colors, or the presence of color patterns associated with Müllerian mimicry), wasp mimics (Batesian mimicry found in many *Euchromiina* moths, which mimic black-and-yellow banded hymenopteran species), beetle mimics (Batesian mimicry found in many *Ctenuchina* moths, which mimic the color and shape of coleopteran elytra), or cryptic species, which do not present the abovementioned strategies and are marked by dull white or brown coloration.
- Lightness: the median pixel value of four main color channels (red, green, blue, and UV) of the dorsal side of fully spread individuals, which represents overall brightness, and thus conspicuity, of the animal (e.g., high values for bright white species). Species were divided into low (33rd percentile), medium (33rd-66th percentile), and high lightness (66th percentile).

- Contrast: measured as the interquartile distance (25th-75th percentiles) of the distribution of pixel values, representing coloration variability with high values often associated with conspicuousness to predators. Similar to lightness, species were divided into low (33rd percentile), medium (33rd-66th percentiles), and high (66th percentile).

Lightness and contrast values were obtained via standardized photography following⁹⁴ and processed using image analysis with the LEPY pipeline⁹⁵. Due to the paucity of species- or genus-level information on tropical moths in the literature and the fact that most species at the site are undescribed⁹⁰, other important life-history traits (e.g., host plant specificity) could not be collected. All trait details can be found in Supplementary Dataset 1.

Data collection: plant-pollinator interactions

All collected insect pollinators were checked under a stereomicroscope for pollen load. Pollen loads were collected and pooled per pollinator species per plot, and only samples with a significant pooled pollen load were considered for analysis (> 10 grains) to ensure enough throughput. Pollen was collected by extracting the proboscis (moths), corbiculae (corbiculate bees, Apinae), or by scraping other body surfaces (e.g., scopa when present) and storing the loads in 96% ethanol. As for male Euglossini bees, which normally carry pollen sacs from orchids, the entire sack was collected. For bats, pollen loads were assessed in the field, and bats carrying visible pollen were swabbed over their entire body surface. Bat pollen samples were also pooled by species and plot, then stored in 96% ethanol. Pollen samples were then transported to Germany (Ludwigs-Maximilians-Universität München), where they underwent multiplexed next-generation DNA metabarcoding of the ITS2 region⁹⁶. The procedures listed below are the same as those described in Diniz *et al.*⁹⁷: extraction, quality control, and library preparation were performed following Sickel *et al.*⁹⁸ and Campos *et al.*⁹⁹, and we used the pipeline described in Leonhardt *et al.*¹⁰⁰ (v. 8c8536b). Quality filtering, merging, dereplication, and definition of amplicon sequence variants (ASVs), as well as ASV classification, were done with VSEARCH¹⁰¹. SINTAX¹⁰² was used for the hierarchical classification of remaining unidentified reads. Classification was performed using alignments from a plant database for Ecuador with BCdatabaser¹⁰³. Low abundance and contamination filtering, and relative read abundance (RRA) treatment are detailed in Diniz *et al.*⁹⁷. An RRA cutoff of 0.05 per sample was used to include interactions. An adjacency interaction

matrix A_{ij} was built for each plot, where interaction frequencies corresponded to the RRA of plant species i in the pollen loads of pooled pollinator samples of pollinator species j .

Data analysis

Response parameters

All analyses were carried out in R 4.5.0¹⁰⁴. The recovery of the flowering plant and pollinator communities, as well as interaction networks, was assessed through the following nine response parameters estimated per plot:

(i) Abundance (plants and pollinators). The sum of all individuals in each plot. Due to a highly left-skewed distribution, the variable was log-transformed for flowering plants before analysis. As pollinator samples were collected from the canopy and understory of canopy-bearing plots, we obtained the mean pollinator abundance whenever canopy samples were present.

(ii) Effective Shannon diversity (eH) (plants and pollinators), or the rarefied exponent of the Shannon entropy ($q = 1$), corresponds to the effective number of species¹⁰⁵. To better account for species relative abundances and the doubled pollinator samples in canopy-bearing plots, communities underwent abundance-based rarefaction in all plots using the *i.NEXT* package¹⁰⁶, and the asymptotic eH value for each community was estimated.

(iii) Resource density (RD) (plants only), measured as the estimated amount of floral resources produced by all individuals in the 2500 m² area of the plot, considering plant abundance, diversity, and floral size, calculated as:

$$RD = \frac{\sum_{i=1}^n (\log(FS_i \times a_i \times s_i))}{n}$$

where n_i is the number of flowering species on the plot's area, FS is the floral size of species i , a is the abundance of species i in the plot, and s is the flower abundance scaling factor (see above) of species i . FS was calculated as the diameter of the flower's perianth base, which applied for tubeless, dialipetalous flowers, as well as composite influences (where FS corresponded to the diameter of the floral head). In the case of tubular flowers, FS was measured as the product between corolla diameter (outermost diameter of the tube) and corolla depth (tube length). FS was used as

a proxy for the amount of floral resources, as floral size is positively correlated with the amount of resources offered ¹⁰⁷.

(iv) Functional evenness (FEve) and (v) functional dispersion (FDis) (plants and pollinators), measured using a distance-based multivariate trait framework in the *FD* package ¹⁰⁸. After a principal component analysis (PCoA) ordination, a minimum spanning tree was constructed for all species in the community using Euclidean distances. FEve corresponded to the homogeneity of the trait-weighted abundances among branches ¹⁰⁹. A high evenness (FEve $\rightarrow$ 1) indicates that the functional space is regularly filled by species with even abundances. As for FDis, the Euclidean distance of all species to a common centroid weighted by species' relative abundance is calculated. A high dispersion (FDis $\rightarrow$ 1) thus indicates high average trait dissimilarity within a community ¹⁰⁸. FDis and FEve were estimated with all plant traits (corolla length and width, presence of bilaterality, morphology of the pollination unit, and the presence or absence of different floral rewards), except for pollination syndrome, as it is an amalgamation of other floral traits that may introduce redundancy. As for pollinators, only body size and relative functional feeding length were used, as these are the only common traits across all pollinator species studied. The entire pool of species (understory and canopy species) was assessed for pollinators.

(vi) Interaction diversity (networks). Measured as the effective Shannon diversity (eH) of interactions, similarly to pollinators and plants. For this, an interaction adjacency matrix was constructed for each chronosequence plot, and eH was estimated for each plot's network using network entries (unique interaction pairs).

(vii) Linkage density (networks). Measured as the marginal totals-weighted diversity of interactions per species in the network, indicating how many partners from the other level, on average, species in the network interact with ¹¹⁰.

(viii) Interaction specialization (interactions). Measured as H_2' , a network-level metric of niche discrimination, indicating how exclusive, on average, interactions are in a network while accounting for network size ¹¹¹. H_2' was estimated for each plot's network separately, including all pollinator groups.

(ix) Community similarity to old growth (plants, pollinators, and interactions): measured as the similarity of the community in each chronosequence plot to the OG median (reference pre-disturbance state) by calculating the inverse Euclidean distance (1/1-ED) from each plot to the OG centroid in a non-metric multidimensional scaling (NMDS, Bray-Curtis distance) dimensionality reduction, resulting in a similarity value ranging from zero to one, with one meaning that a plot lies

on the OG forest centroid. By including the distance of OG plots to their own centroid, we can also assess the variability in species composition among OG forests. To build the occurrence matrices for the NMDSs, the abundance of plant morphotypes, pollinator species, and unique interaction pairs between plants and pollinator species were converted to proportions per plot. For the plant community NMDS, two dimensions (k2) were used. For pollinators, three dimensions (k3) were used to keep stress below acceptable levels (< 0.2), and the increased dimensionality was supported by a Procrustes analysis (correlation with k2 = 0.85, $p = 0.001$). For interaction networks, four dimensions (k = 4) were used (correlation with k2 = 0.71, $p = 0.001$).

Resistance and recovery time

In order to examine the reassembly of floral resources, pollinators and interaction networks, we assessed the recovery of the ten response parameters listed above by (i) estimating their resistance to disturbance, and (ii) estimating their recovery rate and the amount of time necessary to reach pre-disturbance OG levels. We used the resistance-resilience framework built by Metz *et al.*²⁶ and Poorter *et al.*¹⁹. Resistance, here defined as the proportion of a biodiversity parameter that remains after disturbance in relation to a pre-disturbance state, was calculated as the negative exponential of the Kullback–Leibler divergence²⁶:

$$R = \exp(-|\ln(\frac{\varphi_0}{\varphi_{Ref}})|),$$

where R is the parameter's resistance, φ_0 and φ_{Ref} are the medians of the parameter in the active disturbance and in the reference state (OG), respectively. R ranges from 0% to 100%, with 100% meaning that the median of the parameter in disturbances equals the reference state. Resistance was calculated separately for pastures and cacao plantations. With this formula, resistance can also be calculated for parameters that are higher in active disturbances than in the reference state, or equivalent, which can occur in a system with disturbance-tolerant species²⁶.

Next, recovery trajectories and the time necessary for full recovery were estimated by fitting a negative exponential function, which is suitable for variables that recover non-linearly (e.g., as observed in saturating recovery curves along recovery^{19,26}):

$$\varphi(t) = \varphi_0 + (\varphi_{Ref} - \varphi_0)(1 - e^{-\lambda t})$$

where, $\varphi(t)$ is the value of the response parameter at time t , φ_0 is the parameter's median in agricultural plots, φ_{Ref} the parameter's median in old-growth plots, and λ is the parameter's constant recovery rate. The equation models recovery as a saturating curve, with the difference between φ_{Ref} and φ_0 decreasing at a constant rate of λ ²⁶. Additionally, it allows φ_0 to be both higher or lower than φ_{Ref} , and asymptotically reach φ_{Ref} in both ways.

Full recovery time was then estimated as the predicted number of years required for the response parameter to reach either 90% (if φ_0 below φ_{Ref}) or 110% (if φ_0 above φ_{Ref}) of the OG median (see above)²⁶, which suggests that the parameter has reached a value within the expected range for OG forests. For each model, we obtained 95% confidence intervals via bootstrapping (1000 permutations), and the two legacies (cacao plantations and pastures) were analyzed separately. If no significant recovery rate was found (estimate $p > 0.05$) and the distribution of the parameter in OG did not differ from those in agricultural plots or the chronosequence (1–38 years) (both tested via t-tests), the time until full recovery was set to zero. If no significant recovery rate was found, and the distribution of the parameter in OG overlapped with agricultural plots but not with the chronosequence (1-38 years), recovery was deemed as indeterminate and potentially involving an alternate state (e.g.,¹¹²).

In special cases, the negative exponential function could not be fit to the data because the recovering parameter saturated beyond the OG median (floral resource FDis, and network specialization, diversity, and linkage density). In these cases, the median of the parameter at the end of the chronosequence (>30 years of recovery) was used as the reference instead of the OG median, and recovery was also deemed potentially to involve an alternate state. However, the spread of the data was taken into consideration. If the parameter distribution across the chronosequence (1-38 years) overlapped with that of OG, the alternate-state scenario was discarded, and the saturation point above OG was considered a data artifact. In one case (pollinator alpha diversity), the model did not converge because the data exhibited a non-asymptotic U-shaped distribution (decreasing towards early regeneration, then increasing towards late regeneration). Therefore, a quadratic polynomial model was fitted. In this case, the time to full recovery was defined as the point at which predicted values reached OG levels after the initial decrease. One plot was excluded from the network data (cacao regeneration, 9 years) because it was a strong outlier.

The removal of the outlier did not significantly affect the results and helped greatly reduce estimated standard errors (Fig. S2).

Recovery of community composition

With the occurrence matrices built and the NMDS reductions obtained in step (ix) of section 2.3.1, we assessed the recovery trajectory of community and interaction composition by dividing plots into seven categorical recovery stages: PA (active pastures), CA (active cacaos), early PR or early CR (generations, 1 – 15 years), late PR or late CR (16 – 38 years), and OG. After the dimension reduction and the resulting two main NMDS axes, permutational multivariate analyses of variance (PERMANOVAs) were performed to test whether recovery stages and recovery legacies [(ex-)cacao plantations, (ex-)pastures, and OG] vary in species and interaction composition.

Recovery niche breadth

To complement our understanding of how species composition recovered over time, we calculated the recovery breadth (RNB) for all plant and pollinator species, as well as for the ASVs (interactions) found in pollen loads. A species' RNB is the abundance-weighted standard deviation of a species along the recovery gradient in relation to its recovery optimum (or the point in the recovery gradient where the species is most abundant), with a low RNB ($RNB \rightarrow 0$) indicating that a species occurs only at a single point in the recovery gradient, and a high RNB ($RNB \rightarrow 1$) indicating that a species' abundance is equally distributed along the recovery gradient. RNB was calculated as:

$$RNB = \sqrt{\frac{\sum p_i (x_i - \bar{x})^2}{\sum p_i}}$$

where p_i is the species' abundance at the position i of the recovery gradient, x_i is the value of the recovery gradient on that position and $\bar{x}$ is the mean abundance-weighted niche position (i.e., recovery optimum). To obtain positions in the recovery gradient, we did not use recovery age, which excludes old-growth forests, but rather created a recovery index (RI). The RI was created as a comprehensive index that summarizes biotic and abiotic conditions in the plot to reflect its

recovery status, rather than relying solely on recovery years. With this approach, OG plots could be included in the analysis, and recovery could be expressed as a forest's structural and abiotic characteristics. The index was derived from plot aboveground biomass (t/ha), yearly average temperature and humidity, mean tree height (m), and mean stem circumference (cm), all sourced from Escobar *et al.*⁶⁶ and Newell *et al.*¹¹³. RI was derived through a principal component analysis (PCA), following Landim *et al.*¹¹⁴ and Peres-Neto *et al.*¹¹⁵. The number of retained axes from the PCA was determined using a permutation test on the correlation matrix of the eigenvalues of plot variables. One component (PC1) was sufficient (Fig. S3a) and significantly correlated with plot recovery age ($r = 0.72$, $p < .001$) and aboveground biomass ($r = 0.83$, $p < 0.001$), thereby largely representing the recovery gradient. RI was scaled to range from 0 to 1 prior to analysis.

Only species with a total abundance of five or more individuals were included. After obtaining recovery optima and RNB values for each species of flowering plant, pollinator, and ASV, both variables were plotted as density graphs, and the means of each group were compared (ANOVA and post-hoc Tukey test) to examine which group (plants or pollinators) more closely approached the niche optima and breadth distribution of interactions (ASVs) and was thus driving recovery more strongly.

Recovery pathways and drivers

Apart from examining recovery trajectories, we sought to identify recovery pathways and the direct and indirect drivers of plant-pollinator interactions by employing Structural Equation Models (SEMs) using the *lavaan* package¹¹⁶. SEMs are multivariate inferential tools that allow the integration of causal direct and indirect effects between variables within a defined path structure¹¹⁷. With this framework, we could simultaneously examine the direct effects of plot variables (e.g., recovery) on floral resource availability and the pollinator community, as well as the subsequent cascading effects on interaction networks.

The exogenous variables in the SEMS were the plot recovery index (RI, see above), connectivity, and elevation a.s.l.. Plot connectivity, which plays a role in forest recovery by determining the efficiency of colonization by plant and pollinator species originating from forest sources¹¹⁸, was measured using the same approach used for RI. The variables used for deriving connectivity were the forest cover in 100m, 500m, and 1000m buffers around the plot, distance to the nearest forest's edge, as well as the proportion of active and regenerating pastures and cacao

plantations in a 1000m buffer, measured using Landsat and Sentinel Imagery and sourced from Landim *et al.*¹¹⁴ and Escobar *et al.*⁶⁶. This connectivity index captured both small-scale plot connectivity and landscape-scale habitat selection¹¹⁴. Again, the first component was sufficient, and connectivity was moderately correlated with RI ($r = 0.65$, $p < 0.001$). Elevation a.s.l. (m) was included in the set of response variables as it may also serve as an abiotic barrier to species dispersal, thereby affecting colonization and recovery processes¹¹⁹.

The endogenous variables in the model were floral resource availability, pollinator community parameters, and interaction network structure parameters. As all floral resource parameters were moderately correlated ($r = -0.55$ to 0.71 ; Fig. S4a), we employed the same multivariate approach described above to derive the floral resource recovery index (FRRI). One component was sufficient (Fig. S4b), and FRRI was significantly correlated with all floral resource parameters (Fig. S4a). As for pollinator community parameters, abundance (log-transformed), alpha diversity (rarefied eH), functional dispersion (FDis), and community similarity to OG (simOG) were included in the model. As for the interaction network structure, interaction diversity (H'), specialization (H_2'), and similarity to OG (simOG) were included. Functional evenness (FEve) and network linkage density were excluded from the models due to correlations with other parameters within their respective groups, resulting in poor model fits. All variables were rescaled to range from 0 to 1 prior to analysis.

The causal paths tested in the SEMs are summarized in Fig. 1. FRRI and all pollinator community parameters were hypothesized to be affected by exogenous plot variables, and all pollinator variables were hypothesized to be affected by FRRI. These paths allow testing whether pollinator recovery is a direct result of exogenous variables or an indirect result via floral resources, and which parameter drives pollinator community reassembly (Fig. 1a). All network parameters were hypothesized to be affected by FRRI and by pollinator abundance, diversity, and functional dispersion (Fig. 1b), which allows testing whether network structure is driven by resource availability (directly or indirectly via exogenous variables) or by different parameters of the pollinator community (directly or indirectly via resource availability). Network similarity simOG was also hypothesized to vary as a function of pollinator simOG.

An SEM was fit to the entire pooled pollinator community and interaction network to assess the overall recovery of plant-pollinator interactions as a process. Five other SEMs were fit for each major pollinator group individually to assess taxon-specific processes: stingless bees, orchid bees, moths, nocturnal bees, and other bees (leafcutter, plasterer, honey, mason, and sweat bees). H_2'

was not included in the models for orchid, nocturnal, and other bees due to the limited network size in several plots. Network simOG was not included for nocturnal or sweat bees due to a lack of interactions in OG (sweat bees) or outside OG (nocturnal bees), which hinders the calculation of similarity values. Due to low alpha diversity in several plots, pollinator community simOG could not be estimated for nocturnal and sweat bees, and FDis could not be estimated for nocturnal bees. All final SEMs presented good fit indicators (tser test model $p = 0.12 - 0.90$) (Tab S4).

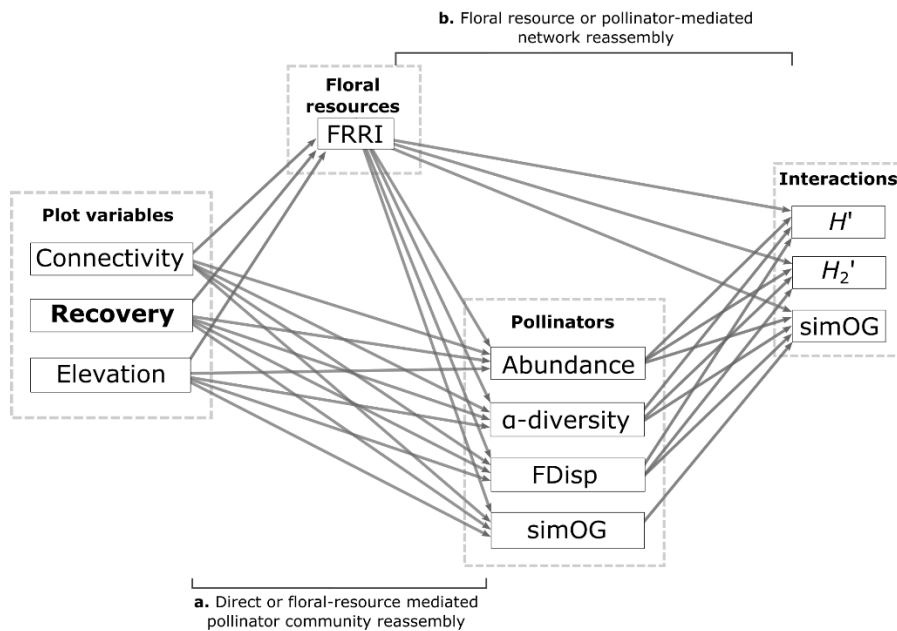


Fig. 1. The defined path structure for the Structural Equation Models (SEMs) used to disentangle reassembly drivers and pathways. Exogenous variables (plot variables) and different groups of endogenous variables (floral resource recovery parameters, pollinator community parameters, and interaction network parameters) are separated by groups in boxes. Arrows indicate hypothesized causal relationships. (a) and (b) describe the two different reassembly processes at play. FRRI: floral resource recovery index, FDis: functional dispersion, simOG: similarity to old growth, H' : interaction Shannon diversity, H_2' : network specialization.

Trait-driven recovery

We assessed the role of species' functional traits in community recovery along the chronosequence by examining variation in quantitative and qualitative traits across plant and pollinator communities. For quantitative traits (floral length and width, and pollinator BS and

RFFL), we calculated the community-weighted mean (CWM) of each trait per plot and tested whether these traits were affected by the Recovery Index using linear regressions (residual normality and homoscedasticity were checked in all instances). For pollinators, we first calculated CWMs of both traits for the whole plot community to assess the general recovery trend, and subsequently for each major pollinator group separately [moths, stingless bees, orchid bees, and other bees that did not have high enough diversity for an individual analysis (mason, plasterer, leafcutter, nocturnal, and sweat bees)]. Pollinator trait CWMs were Z-score standardized prior to analyses to enable cross-group comparisons.

For qualitative traits, species occurrence matrices were filtered by trait category, and the effect of plot Recovery Index on the total abundance of species belonging to that category was assessed. The seven qualitative bee functional traits and the three moth functional traits listed in the section “*Data collection: pollinators*” were included. As in previous steps, abundance was averaged between the two strata in plots where the canopy was sampled. Abundance was log-transformed in all instances to account for left-skewed distributions and outliers, and the effect of the Recovery Index on pollinator abundances was assessed with linear regressions. Zero-inflated models were employed in cases with high incidences of sampling zeros using the *glmmTMB* package ¹²⁰, and, in these cases, the results of the conditional model are shown. For pollinators, zero-inflated models were used only for kleptoparasitic bees. Unlike pollinators, flowering plant species richness was assessed as a response variable rather than abundance, because abundance exhibited an extremely left-skewed distribution due to the dominance of several pioneer species, particularly in early regeneration plots, whereas richness was normally distributed. The four qualitative plant functional traits listed in the section “*Data collection: flowering plants*” were included. All pollination systems were assessed, but bat- and bird-pollination were grouped together as “vertebrates” due to the rarity of the former. As for pollination unit morphology, due to the large number of categories, two groups were defined: restrictive flowers (i.e., those that impose a barrier to the resource, such as a floral tube or a specific blocking mechanism, as in labiate or orchid flowers) and non-restrictive flowers. The restrictive group included funnelform, tubulate, papilionate, urceolate, saccate, labiate, coronate, orchid, and trapping flowers/inflorescences, while the non-restrictive group included rotate, campanulate, crateriform, capitulate, cruciform, cyanthiform, and spadix flowers/inflorescences. The effect of the Recovery index on flowering plant richness was assessed with Poisson-fitted generalized linear models. Zero-inflated models

were used for the following groups: beetle-, wind-, settling moth-, butterfly-, and hawkmoth-pollination system, as well as plants offering rare resources.

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Conflicts of Interest

The authors have no conflicts to declare.

Author Contributions

U.M.D.: Conceptualization, data collection, data curation, data analysis, writing. A.K.: Conceptualization, funding acquisition, data collection, data curation, reviewing. G.B.: Conceptualization, data collection, data curation, reviewing. C.R.: Data collection, reviewing. K.V.: data collection, data curation, data analysis, reviewing. S.Er.: data collection, reviewing. S.B.: funding acquisition, reviewing. M.T.: funding acquisition, reviewing. N.B.: Conceptualization, funding acquisition, reviewing. S.Es.: data collection, data curation, reviewing. M-J.E.: funding acquisition, reviewing. J. E. G-A.: funding acquisition, reviewing. S.D.L.: Conceptualization, funding acquisition, data collection, reviewing.

Availability of Data and Materials

All data and code used in the analyses will be made available in a public repository upon acceptance. During review, data and code are deposited in Zenodo and can be accessed using the following link:

https://zenodo.org/records/2172883?token=eyJhbGciOiJIUzUxMiJ9.eyJpZCI6IjQ0MzU0NmU0LWM2NGQtNGU1MC04NjQ4LTkzN2EzYzY0OTNmYSIsImRhdGEiOnt9LCJyYW5kb20iOiIwNTZlMmZiZTI5ZWVjMzdkNjAyZmFhOTc0Yjc0NDIxNiJ9.037-dA3409xmpdrJu7dCEoRBaKhHKBK1dlUnnuIkDKGHKqMjRZdJ6-_g-Or0dTotusqK5s9B6bilkBFhhFwAA

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