








## RESEARCH ARTICLE

# Using plant–pollinator interactions to identify key species for planning tropical forest restoration

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There is still a lack of practical guidelines for understanding species roles and planning restoration strategies to enhance plant–pollinator interactions and support ecosystem functioning. We applied a network approach to understand the evolution of plant–pollinator restoration patterns and identify priority species, thus advancing restoration planning. Specifically, we compared species composition and network metrics along a gradient of time postdisturbance, from the initial stage of restoration to pristine forest in the Eastern Amazon. We found that mining type is a predictor of species composition. We observed the recovery of interaction diversity and pollinator specialization in the early stages of restoration. Mining type affected connectance, interactions, and species richness, and the restoration stage affected the number of links. From the interactions, we built a trait-based framework to select manageable native species for initial restoration. The species selection framework proposed here is useful not only for forest restoration but also for the restoration of other areas and case studies (e.g. agroecosystems, conservation units, and ecological corridors) and can be adapted depending on the goals of each project. Here, we provide practical information for the management of mined land restoration in the Eastern Amazon and for restoration planning across broader scales.

**Key words:** mining, pollination, restoration of interactions, restoration planning, species selection, tropical forests

## Implications for Practice

- A network approach is applied to monitor and inform mine-land restoration.
- Species restoration is related to the mine type and local landscape in the Amazon.
- Network diversity and specialization recover in the early stages of restoration.
- Restoration of network size, species richness, and connectance are related to mining type.
- Interaction networks and species traits can inform restoration planning.

## Introduction

Ecosystem restoration is instrumental in supporting biodiversity conservation, climate stabilization, ecosystem service provisioning, and safeguarding human well-being (Díaz et al. 2019). Restoration practices involve diverse components, including landscape planning and species selection, monitoring, and governance, which are needed to safeguard long-term successful programs (Gann et al. 2019). Thus, understanding the key biodiversity components of ecosystems is fundamental for proposing practical guidance for restoration planning to support the reestablishment of functional and stable ecosystems (Gann et al. 2019).

Ecosystem structure refers to the biophysical components of an ecosystem that dynamically interact to produce ecosystem

functions (La Notte et al. 2017). An important ecosystem function to be considered in restoration projects is the interaction between plants and their pollinators (Forup et al. 2008; Devoto et al. 2012; Kaiser-Bunbury et al. 2017); these interactions are directly responsible for the reproductive success of plants and the maintenance of pollinator communities in restored fields, also indirectly contributing to food availability for frugivore species and soil health (Carvalho et al. 2021; Lam et al. 2024). Interaction patterns are better studied with the use of network theory, which provides important insights for understanding ecosystem functioning and the processes inherent to it

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(Bascompte et al. 2003). Interaction network metrics, measured from plant–animal networks, can provide an understanding of historical and contemporary ecosystem functions as well as the actors shaping community functioning, which includes monitoring the success of restoration practices (Kaiser-Bunbury & Blüthgen 2015; Harvey et al. 2017).

A range of network metrics (e.g. interaction strength, diversity, specialization, nestedness, modularity, connectance, and stability) have been used as indicators of ecosystem health and pollination restoration (Tylianakis et al. 2010; Kaiser-Bunbury et al. 2017), and at a global scale, restoration practices effectively support ecosystem functions, such as pollination and seed dispersal, leading to a better state compared with degraded landscapes (Genes & Dirzo 2022). However, contrasting results are found when studies are analyzed at local scales. Old-growth stages of successfully restored Scottish woodlands presented greater interaction diversity, similar to reference sites (Devoto et al. 2012), whereas in restored heathlands in the United Kingdom, plant–pollinator networks are less complex and less resilient than those in ancient sites are (Forup et al. 2008). Therefore, landscape restoration is susceptible to the formation of new and simplified plant–pollinator networks (Cariveau et al. 2020), and a correct strategy for restoration planning is needed to select species that support pollination restoration and avoid biotic simplification and homogenization in the long term (Holl & Luong 2022). Although each species is needed to support biodiversity and ecosystem functions (BEFs) in a community, not all species contribute equally to ecosystem functioning and network stability (Blüthgen et al. 2006; Poisot et al. 2012), and monitoring practices are important for understanding restoration success and species roles.

A key element to start ecosystem restoration and provide the necessary structure for biodiversity reestablishment is selecting priority species (Massante et al. 2023). Species selection has historically focused on the reintroduction of dominant commercial plant species (Leger et al. 2021), which may be challenged by local environmental filtering (Holl & Brancalion 2020). Species traits are useful for selecting native plant species when aiming to restore BEFs and enable long-term stability of restored ecosystems (Devoto et al. 2012; Elle et al. 2012; Montoya et al. 2012; Pockock et al. 2012; Campbell et al. 2019; Coutinho et al. 2023). By using broad-scale data, generalist and phylogenetically diverse plant species can support pollination restoration in areas with low coverage of biodiversity data (Campbell et al. 2019). With the use of local data, previous studies have also indicated the importance of species traits for the selection of plants for restoring pollination functions (e.g. interaction diversity, phenology, seed dispersal and germination requirements, conservation status, and biocultural importance) (Giannini et al. 2017; Sabatino et al. 2021; Bergamo et al. 2023). However, previous species selection frameworks focused only on plant species, and no previous attempt has been made to include the selection of both plants and pollinators in tropical forests to support the restoration of plant–pollinator interactions with a framework that can be

applied by practitioners that rely on secondary data (e.g. those provided by environmental licensing and regional-level data).

In this study, we applied a network approach to understand the dynamics of plant–pollinator restoration patterns and identify species roles to inform restoration planning. Our approach aimed at understanding the restoration status (monitoring) and providing a species selection framework that can bridge science into practice for restoration practitioners. We investigate whether the postrestoration period affects species composition and interaction metrics and how interaction patterns can be applied to prioritize species for restoration and to support decision-making in restoration planning. We hypothesized that more advanced stages of restoration would present species composition and interaction patterns more similar to those at pristine sites than early stages of restoration. We sampled two different mined land restoration sites in the Eastern Amazon and built a species selection framework (from the interactions) for selecting species that enhance interactions and safeguard ecosystem functioning through the restoration process (Fig. 1), thus building an evidence-based practice for the restoration of interactions in tropical forests (FAO et al. 2023).

## Methods

### Study Site and Research Design

This study was carried out at the Carajás National Forest (CNF) (Fig. 2), one of the largest remnants of Amazon forest in the Eastern Amazon, located in the southeastern region of Pará State, Brazil (Souza-Filho et al. 2016). The CNF is home to one of the largest mineral extraction projects in the world (Vale 2023), and we selected a chronosequence of mined land restoration areas following two types of mineral extraction (sand, SM1–SM3, and iron ore, IM1–IM3) in the CNF (Fig. 2) and compared these chronosequences to pristine forest sites (Table S1). All sand and two (of the three) iron restoration areas were surrounded by evergreen submontane Amazon forest, which was the restoration target for all the sites. Restoration chronosequences followed different but standardized restoration protocols, which enabled comparisons between sites since time was the main driver of the differences among the restoration stages.

We sampled 25 sites in total, with eight sites in the three sand mines (SM1–SM3, two initial, three intermediate, and three advanced), nine sites in the three waste piles of the iron mine (IM1–IM3, 3 areas of each state) and eight sites in pristine forest (Fig. 2, Table S1). Sampling was conducted three times at each site between April 2018 and October 2019 (details in Supplement S1 and Gastauer et al. 2020a, 2020b).

### Floral Visitors

We surveyed each site and collected all floral visitors from all plants with open flowers in the understory (up to 3 m above-ground). We applied an adapted protocol from the standardized method proposed by Sakagami et al. (1967). At each sampling

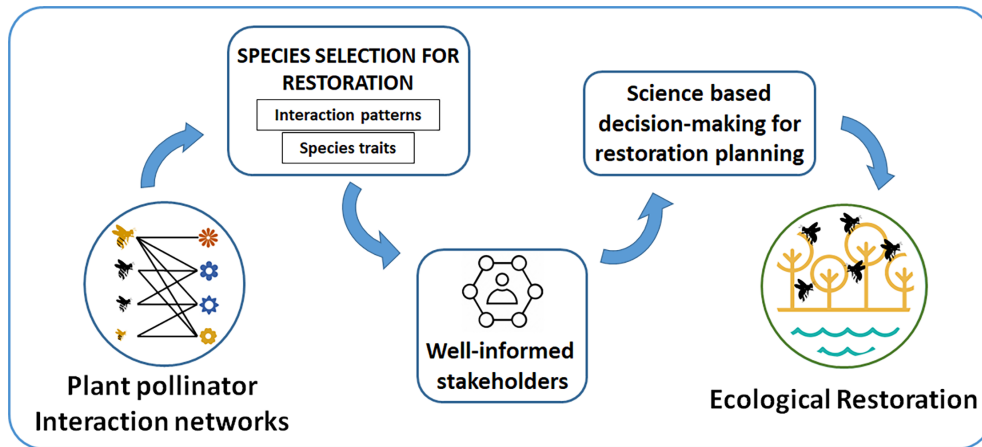


Figure 1. Pathways from plant–pollinator interaction networks that promote ecological restoration.

site, a transect of approximately 1 km was covered for 1 hour, where all open flowers were observed for 5 minutes and all floral visitors were collected. We considered a visitor (henceforth

pollinator) when the bee or wasp individual touched the reproductive organs of the flower and only after that visitor was collected. From the recorded visits, for each sampling site (25),

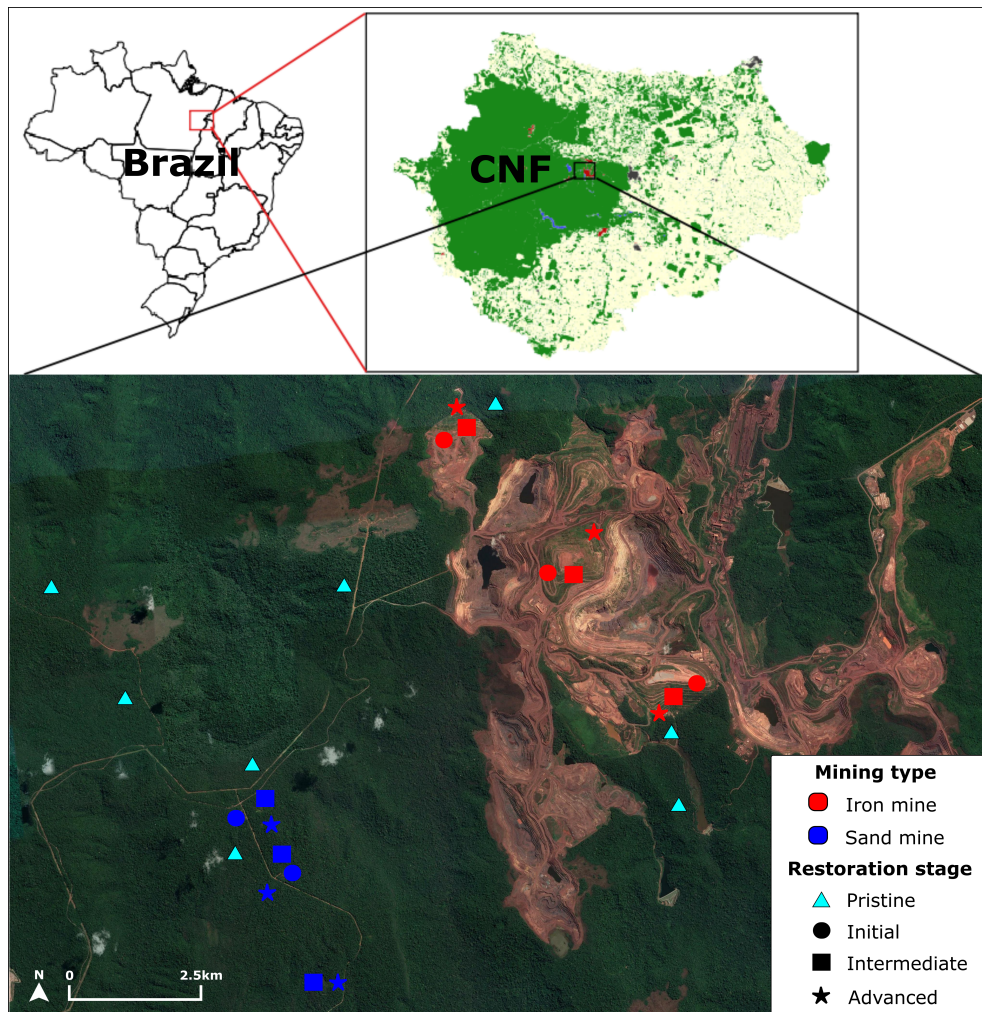


Figure 2. Location of the study sites inside the Carajás National Forest (CNF). The pristine sites are shown in light green; the sand mine restoration sites are shown in blue; and the iron mine restoration sites are shown in red.

we built a weighted matrix of interactions. With pollinator species as columns and plants as rows, the number of visits observed from a pollinator species to a plant species was noted in the intersection cells.

### Interaction Composition

To evaluate the species assemblage composition (plant and pollinator species based on interactions), we visualized the data by performing principal coordinate analysis (PCoA, “cmdscale” function in the vegan package) (Legendre et al. 2012) using a Bray–Curtis dissimilarity matrix based on the log-transformed  $(x + 1)$  species abundances per site (“vegdist” function in the vegan package). Species abundances for both levels (plants and pollinators) were obtained from the interactions. To test for differences in species composition among the restoration and pristine sites, we performed permutational multivariate analysis of variance (PERMANOVA, “adonis” function in the vegan package) (Anderson 2001), which is defined by a Monte Carlo test with 9999 permutations and is based on a log-transformed Bray–Curtis dissimilarity matrix (Legendre & Legendre 2012).

### Interaction Networks

For each study site (25), we calculated network-level metrics (interaction diversity, connectance, number of links, interaction richness, and species richness for both levels) using the “networklevel” function and species-level metrics (d’pol) in the bipartite package (Dormann 2022). The choice of network metrics followed previous indicators highlighted to monitor and assess restoration and management practices (Kaiser-Bunbury et al. 2017). We provide a description of each metric and its behavior in Supplement S1. None of the interaction metrics indicated spatial autocorrelation (Table S2), and sampling completeness was acceptable for network comparison (details in Supplement S1). In addition, as we were only able to sample understory plants, we evaluated the completeness of vegetation sampling to allow for among-site comparisons. We used a Chao–Hill approach to evaluate among-site richness and diversity estimators (Chao et al. 2020). We obtained high and similar sampling coverage for all areas (Fig. S1), which also allows us to perform comparisons demonstrating that not all estimated species have been sampled (as expected), but comparable efforts have been made across study sites (details in Supplement S1).

To evaluate the effects of restoration on interaction metrics, we used generalized linear mixed-effects models (GLMMs) (Zuur et al. 2009), with interaction metrics as response variables (Table S3). To evaluate the fixed effects on these metrics, we used the mine type (control, iron, and sand) and regeneration stage (control, initial, intermediate, and advanced). As a random effect, we used the sampling site and event (1|site + sampling) to indicate the variance from sampling effects in space and time. All the models were performed in the “lme4” package (Bates et al. 2015). The adjusted models were subjected to analysis of variance (ANOVA) and pairwise comparisons using Tukey’s test (“multcomp” package, Hothorn et al. 2008). The

assumptions of normality and homogeneity of the residuals of the adjusted models were observed. All analyses were performed in the R environment (R Core Team 2021), and a graphical view was generated with the “ggeffects” package (Lüdtke 2018).

### Species Selection Framework

To build the species selection framework, we considered only plant–bee interactions, as bee species have much greater management potential and provide much lower risk potential for accidents. To understand the role of each plant and bee species in the plant–bee interaction networks, we calculated species partner diversity (Pd) (i.e. Shannon’s diversity of interactions for each species; “specieslevel” function in the bipartite package) (Dormann 2022) to identify the most generalist species (which interact with more partners and, thus, can sustain the restoration of the network).

To select and indicate the plant and bee species to use in the restoration, we built a two-criteria framework based on (1) species interactions and (2) species traits, as high bee functional diversity contributes to higher pollination service provision (Woodcock et al. 2019). First, we assessed Pd to include species with high local Pd, which will potentially support the restoration of interactions. Second, we assessed each species’ management potential to increase the resource allocation efficiency and long-term maintenance of the species in the restoration environment (Table S6). From the complete list of species, we retrieved only those with Pd values above zero ( $Pd > 0$ ) (27% of bees and 64% of plants). Next, we calculated the mean and median Pd for each species, considering the values for all areas where each species was present. The mean values were calculated to select species with high Pd values across all the study sites (species present in various areas and with Pd greater than 0 receive higher values). The median value was calculated to select species with high absolute values of Pd (where they are present) that were not present at many of the study sites and, therefore, would present low mean values despite presenting high single Pd values. The combination of these metrics (mean and median) was applied to maximize the selection of species with high Pd values (regardless of their occurrence pattern).

To assess the management potential of each species ( $Pd > 0$ ), we selected species traits to assess the feasibility of species application and maintenance in restoration areas. For the plants, we selected three traits that have previously been applied for selecting plants for restoration strategies: [1p] potential as nurse plants, [2p] reproductive capacity from seeds, and [3p] wind dispersal ability (anemochory) (Table S6) (further details in Gianini et al. 2017). For the bees, nine traits were used: (1a) nesting in cavities, (2a) adaptation to a wooden beehive, (3a) no plundering behavior, (4a) commonly maintained by local breeders, (5a) crop pollinator, (6a) suitable for honey production, (7a) suitable for pollen production, (8a) suitable for wax production, and (9a) suitable for propolis production (a list of traits with their justifications and sources is presented in Table S6). For each species, a value ranging from 0 to 1 was assigned for each of the evaluated characteristics, with

0 (zero) indicating that the species did not present the trait of interest and 1 (one) indicating that the species presented the trait. The selection of species at the restoration sites with high potential for management was performed on the basis of an index calculated for each species; this index consists of the sum of the mean and median values of Pd and the values assigned to each of the abovementioned traits (three traits for plants and nine traits for bees).

Only the taxa identified at the species level were considered for the species selection framework. All exotic species were excluded from the species selection process (Supplement S1; Table S8). Restoration practices in the Amazon need to overcome a 60% mortality rate, which makes it more interesting to use a small subset of species in initial stages and incorporate more species with time (Salomão et al. 2020). Thus, in our study, we chose to indicate a set of 10 species to be used for supporting plant–pollinator interaction restoration, as this number can be added by practitioners for practical restoration. All analyses were performed in the R environment with R version 4.0.1 (R Core Team 2021).

## Results

We recorded 1260 interactions among the 25 studied sites (Fig. 3A). A total of 118 plant species, 137 bee species (1090 individuals), and 51 wasp species (170 individuals) were collected (Table S8). Across all the study sites, only five species of bees and 12 plant species were responsible for more than half of the observed interactions. Ten sites (out of 25) accounted for more than half of the total interactions.

### Interaction Composition

The different species presented the greatest number of interactions at the different types of sites (restoration areas after sand mining, after iron mining, and pristine forest). In the sand mining areas, the plant and bee species with the greatest number of interactions were *Borreria verticilata* and *Trigona chanchamayoensis*, which accounted for 14 and 17% of the total interactions in these areas, respectively (Fig. 3B). In the iron mining areas, *Muntingia calabura* (plant) and *Apis mellifera* (bee) had the greatest number of interactions, accounting for 37 and 52% of the local interactions, respectively (Fig. 3C). Among the pristine forest sites, the plant and bee species with the greatest number of interactions were *B. ocymifolia* (13% of interactions) and *T. pallens* (15%) (Fig. 3D), respectively.

When the mining types (sand and iron) and restoration stages (initial, intermediate, and advanced) were compared with those of the pristine forest, the pollinator and plant community compositions differed between both the mining types and the restoration stages (Fig. 4;  $p < 0.001$ ). In a pairwise comparison between the mining types and pristine forest, the pollinator and plant interaction compositions differed between the iron and (both) sand mines and pristine forest but did not differ between the sand mines and pristine forest (Table S5;  $p < 0.003$ ). In a pairwise comparison between the restoration stages and the pristine forest, the pollinator interaction composition differed between the initial

and intermediate stages compared with the pristine sites (Table S5;  $p < 0.006$ ), and the plant community composition differed between the intermediate and advanced stages compared with the pristine forest sites (Table S5;  $p < 0.03$ ).

### Interaction Networks

*Interaction diversity* and pollinator specialization ( $d'_{\text{pol}}$ ) did not significantly differ with respect to mine type or restoration stage (Table S4). *Connectance* was affected by mine type ( $\chi^2 = 10.612$ ,  $p = 0.004$ ; 43% fixed effect explanation, random effect = 46% explanation) (Table S4), and iron mine areas had higher connectance values than pristine areas ( $p = 0.013$ , Fig. 5A). The *number of links* was affected by the restoration stage ( $\chi^2 = 24.956$ ,  $p < 0.001$ ; 14% fixed effects) (Table S4); however, random effects also provided a high explanation for the overall variance (65%). The control areas presented a greater number of links than did the advanced ( $p < 0.001$ ) and intermediate-stage ( $p < 0.001$ ) areas, and the initial-stage areas presented higher values than did the advanced-stage ( $p = 0.041$ ) and intermediate-stage ( $p = 0.013$ ) areas (Fig. 5B). The *interaction richness* was affected only by mine type ( $\chi^2 = 12.208$ ,  $p = 0.002$ ), with a 21% explanation of fixed effects (38% explanation of random effects) (Table S4). The control areas presented greater interaction richness than the iron mine restoration areas ( $p < 0.001$ ) (Fig. 5C). *Bee species richness* differed only by mine type ( $\chi^2 = 12.926$ ,  $p = 0.001$ ), with a 17% explanation of fixed effects (32% explanation of random effects). The control areas presented greater bee species richness than the iron mine areas ( $p = 0.002$ ) (Fig. 5D). *The plant species richness* did not differ between any of the treatments (Table S4).

### Species Selection

Among the 116 bee species, 32 (27%) had Pd values above zero. Among the 111 plant species sampled, 65 (58%) had Pd values above zero. Only six bee species were present in at least five sampled sites, and these species also presented higher mean Pd values. Four plant species were present in at least five sites. Among the bee species, only the exotic honeybee *A. mellifera* was excluded from the species selection process. Among the plants, eight exotic species were excluded (Table S6).

From our species selection framework, we selected the 10 species of bees and 10 species of plants that presented the highest potential to be used in the initial stages of restoration projects aimed at the restoration of plant–pollinator interactions (Table 1). Based on the Pd values and the evaluated species traits associated with management, it was possible to select 10 bee species with the potential to be managed and used in the restoration (Table 1). In addition, we also provide a list of all species with rank scores above zero (Table S7).

## Discussion

In this study, we show that mining type is a predictor of bee species restoration and that older stages of restoration present

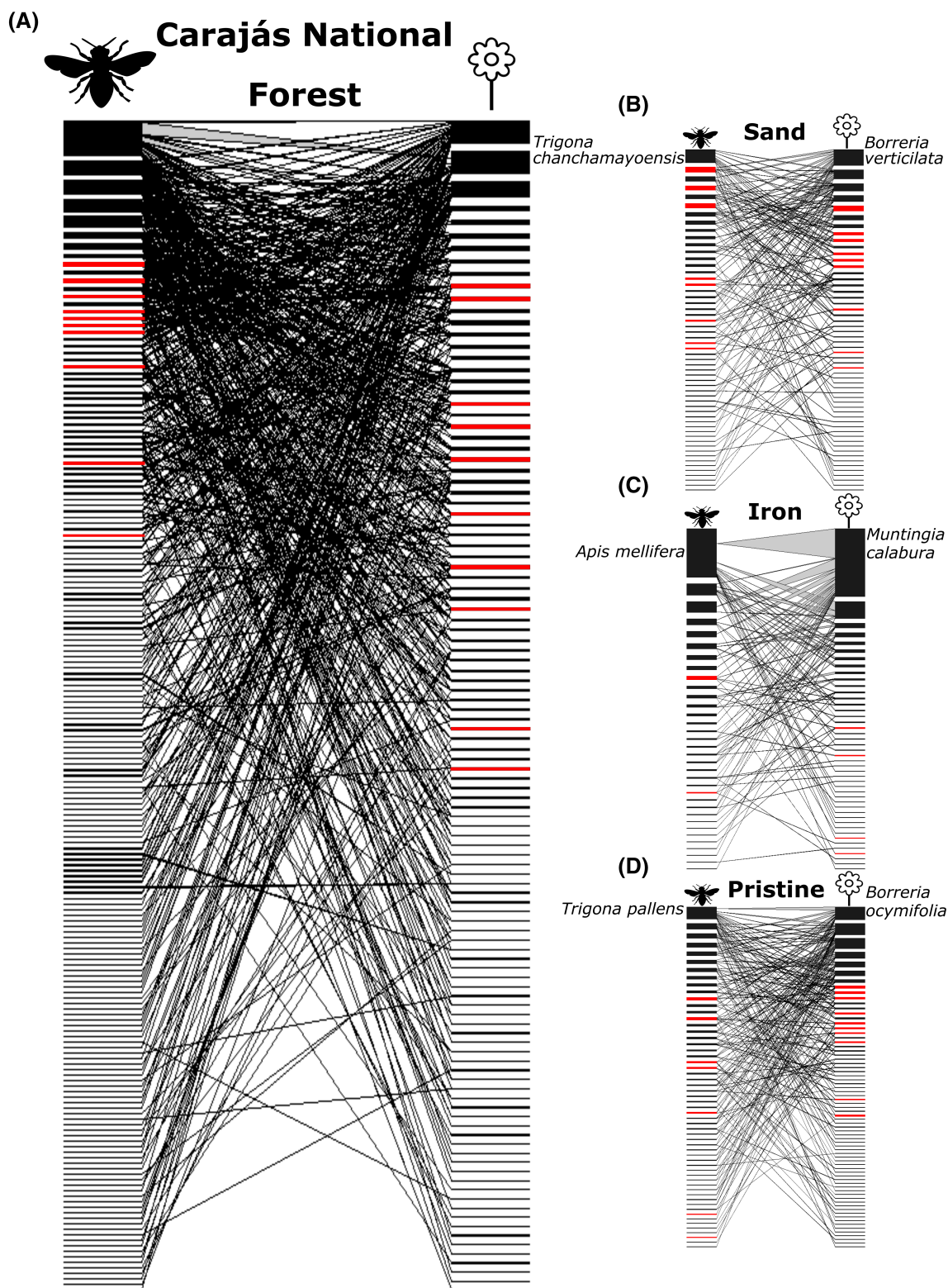


Figure 3. Complete interaction network from the Carajás National Forest (A), interaction networks from the sand mine (B), iron mine (C) and pristine forest sites (D). The species selected for enhancing the restoration of plant–pollinator interactions are in red. All networks represent pollinators on the left and plants on the right (the network size is 1260 links between 188 pollinator species and 118 plant species). The most generalist pollinators and plant species from each site are provided.

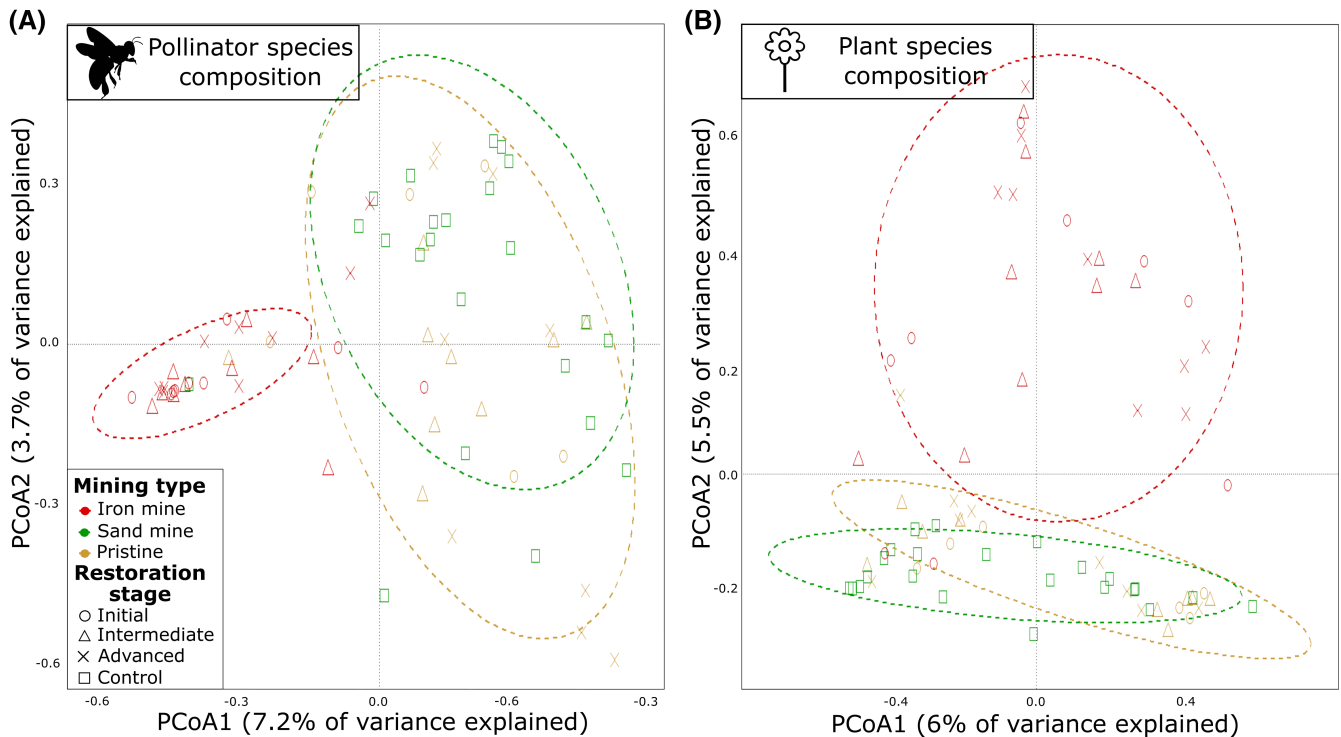


Figure 4. Plant and pollinator interaction compositions. Differences in (A) pollinator and (B) plant community composition between the pristine forest (yellow symbols) and mining sites (iron mining in red and sand mining in green) as determined via principal coordinate analysis (PCoA). The initial, intermediate, advanced, and control restoration stages for each mining type are shown as circles, triangles, X, and squares, respectively.

similar pollinator species compositions to those of pristine forests, supporting pollinator species return in active mined land restoration areas. Interaction patterns such as interaction diversity and pollinator specialization ( $d'_{\text{pol}}$ ) are rapidly recovered in mined land restoration areas in the Amazon, contrary to the restoration patterns found in other ecosystems (Kaiser-Bunbury et al. 2017; Cortés-Flores et al. 2023). Connectance, interaction richness, and bee species richness are affected by mining type, and the number of links in plant–pollinator networks is affected by the restoration stage, indicating patterns of plant–pollinator interaction restoration in the Amazon forest. Although interaction metrics did not show a spatial effect (Moran's  $I > 0.05$ ), we observed a relevant effect of sampling location and time in the analyzed models. For example, regarding connectance, the model explained 42% of the variation (mine type), but if sampling events and location (random effects) are considered, the explanation reaches 89%. Therefore, we emphasize that in addition to environmental variation, factors related to seasonality and location also affect these interactions, regardless of the geographic distance between sampling locations, as expected when accounting for the heterogeneity of tropical forests (Santiago et al. 2022; Flores et al. 2024).

Our species selection framework highlights 10 species of plants and 10 species of bees to be managed in the initial stages of restoration projects aimed at enhancing the restoration of plant–bee interactions and supporting the restoration of BEFs in the community (Hua et al. 2022). This is the first species selection framework to consider the roles of species at both

levels of local interaction networks and species traits selected to safeguard the restoration of interactions and inform and support decision-making and resource allocation in restoration planning in the Amazon (Holl & Brancalion 2020), incorporating stakeholder needs for practical guidance and support for pollinators (Samnegård et al. 2024).

### Interaction Composition

Our study revealed that species composition was influenced by mining type. While sand mine restoration is initiated by topsoil application (returning pristine forest soil to restoration fields), the waste piles being restored in the iron mine still harbor iron. Restoration areas in iron mines are more exposed, reaching higher temperatures, and are more isolated from pristine forests by other active mining sites than are sand mines (Gastauer et al. 2020b). Thus, soil characteristics, local climate, and landscape structure (i.e. habitat amount and isolation) appear to be the main differences for explaining species composition among mining types; this finding is consistent with previous discussions about the ability of species to colonize new habitats (Cariveau et al. 2020; Dambros et al. 2020). As our restored sites matured, their species composition tended to resemble that of pristine forests, which is supported by the results of other studies on the evolution of not only species diversity but also several environmental properties that sustain local species (Gastauer et al. 2020a). In our study, pollinator species composition differed between sites in the early stages of restoration (initial and intermediate) and pristine forests but was not

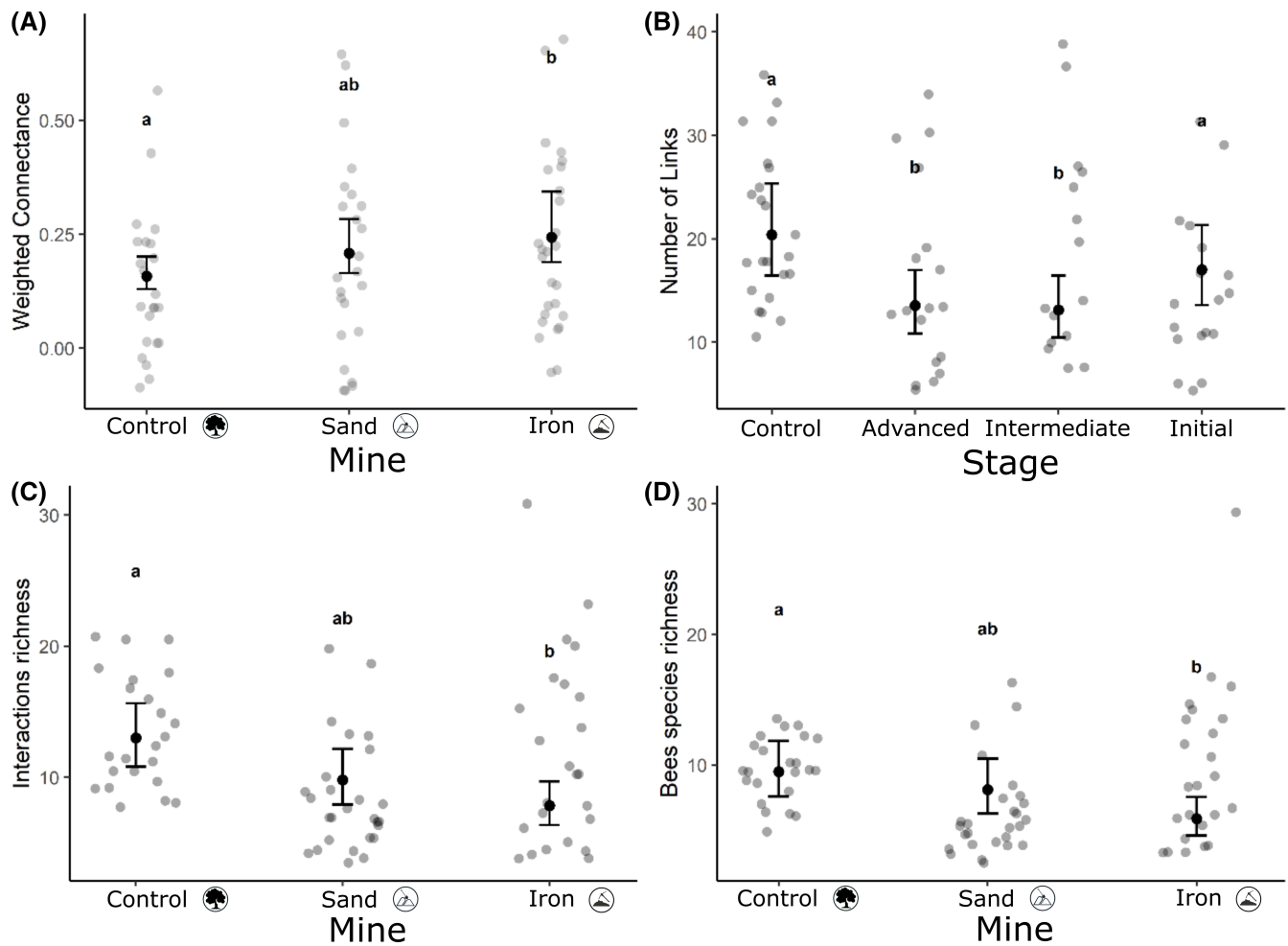


Figure 5. Differences in plant-pollinator interaction patterns. Partial residuals and marginal averages estimated from the mixed effect model for interaction metrics modeled by mine type and restoration stage: weighted connectance (A), number of links (B), interaction richness (C), and bee species richness (D). Marginal averages by a common letter are not significantly different according to Tukey's test ( $p$  value  $< 0.05$ ). The error bars represent 95% CI.

different between advanced-stage sites and pristine forests, demonstrating the recovery of species composition and ecosystem functionality in older stages of restoration (Santiago et al. 2022; Novotny & Goodell 2020; Carvalho et al. 2022). Plant species composition followed the opposite trend, with only sites in advanced stages being different from those in pristine forests. This finding demonstrates that after initial stages, when plant composition is driven mainly by planted species, sites in advanced stages appear to form a novel and functional community by receiving new species from the surrounding environment and supporting new BEFs (e.g. seed dispersal) (Medeiros-Sarmiento et al. 2021; Castro et al. 2022). Future studies should evaluate the evolution of the functional and phylogenetic diversity of pollinators through the restoration process, as these features of the community rarely respond similarly (Guiden et al. 2021).

### Interaction Networks

Regardless of the recovery in interaction diversity and pollinator specialization ( $d'_{\text{pol}}$ ) across mine types and restoration stages,

different species were responsible for the greatest number of interactions, and a small set of species (5 of 117 bee species and 12 of 102 plant species) was responsible for more than half of the interactions recorded. Thus, different cores of highly generalist species are responsible for supporting interaction networks at different sites (Bascompte et al. 2003; Lewinsohn et al. 2006). The most generalist plant species (genera *Borreria* and *Muntingia*) are well known to attract diverse pollinators (bees, wasps, flies, butterflies, and beetles) (Figueiredo et al. 2008; Fernández et al. 2009). Among the pollinators, *Trigona* (*Trigona pallens* and *T. chanchamayoensis*) and *Apis mellifera*, were responsible for the majority of the interactions. These are eusocial species and trophic generalists that build large nests (>1000 individuals) capable of housing many individuals who fly into the surrounding environment (Rasmussen & Camargo 2008). *Apis mellifera* and *Trigona* species are relatively unselective of the cavities in which they build their nests, with some species constructing exposed nests around tree branches and lianas and in association with termites (Roubik 1983; Rasmussen & Camargo 2008). *Apis mellifera* is a habitat generalist capable of pollinating local plants in

**Table 1.** List of plant and bee species selected for enhancing plant–pollinator interactions during the restoration process in the Eastern Amazon and their respective sampled partner diversities.

Family	Species	Partner diversity	
		Mean	Median
<b>Plants</b>			
Bixaceae	<i>Bixa orellana</i> L.	0.0814	1.0178
Fabaceae	<i>Senna latifolia</i> (G. Mey.) H. S. Irwin & Barneby	0.0755	1.8867
Malpighiaceae	<i>Lophanthera lactescens</i> Ducke	0.0277	0.6931
Malpighiaceae	<i>Stigmaphyllon paraense</i> C. E. Anderson	0.0653	1.6326
Asteraceae	<i>Vernonanthura brasiliiana</i> (L.) H. Rob.	0.1758	1.1412
Euphorbiaceae	<i>Aparisthium cordatum</i> (A. Juss.) Baill.	0.1477	1.0114
Fabaceae	<i>Senegalia multipinnata</i> (Ducke) Seigler & Ebinger	0.0439	1.0986
Melastomataceae	<i>Miconia alata</i> (Aubl.) DC.	0.0416	1.0397
Malpighiaceae	<i>Byrsonima stipulacea</i> A. Juss.	0.0788	0.9854
Fabaceae	<i>Senna alata</i> (L.) Roxb.	0.1074	0.9503
<b>Bees</b>			
Apidae	<i>Melipona (Michmelia) seminigra</i> (Friese, 1903)	0.0779	0.6931
Apidae	<i>Tetragona clavipes</i> (Fabricius, 1804)	0.0994	0.6931
Apidae	<i>Tetragonisca angustula</i> (Latreille, 1811)	0.0809	0.6931
Apidae	<i>Tetragona quadrangula</i> (Lepeletier, 1836)	0.0439	1.0986
Apidae	<i>Ptilotrigona lurida</i> (Smith, 1854)	0.0656	0.8196
Apidae	<i>Nannotrigona punctata</i> (Smith, 1854)	0.0717	0.8959
Apidae	<i>Plebeia alvarengai</i> Moure, 1994	0.0277	0.6931
Apidae	<i>Tetragona dorsalis</i> (Smith, 1854)	0.0277	0.6931
Apidae	<i>Frieseomelitta portoi</i> (Friese, 1900)	0.0532	0.6648
Apidae	<i>Xylocopa (Neoxylocopa) frontalis</i> (Olivier, 1789)	0.0200	0.5004

degraded landscapes (Giannini et al. 2015). In the short term, a high abundance of *A. mellifera* is important for supporting the whole network; however, long-term interactions between native fauna are needed to safeguard the restoration of specialized interactions in the ecosystem.

Overall, the restoration areas in the iron mine lands are more connected (higher values of connectance) and present lower richness (of interactions and pollinators), which supports colonization by super generalist species to the detriment of specialists (Bersier et al. 2002). Generalist pollinators are highly flexible and capable of surpassing local environmental filters, leading to the selection of a novel community, potentially resulting in the need for a longer period to fully recover ecosystem functionality (Holl 2002; Carvalho et al. 2022). In fact, our results of the restoration status are similar to those of previous studies that focused on the full arthropod communities from sterile piles in iron mines, where advanced stages did not reach a similar state as the reference sites did (Lynggaard et al. 2020). Thus, given the severity of impacts on these areas, it is important to consider different time frames and a more intense set of restoration practices to support the provision of ecosystem functions (Xu et al. 2023).

We found a greater number of links in the pristine forest and sites in the initial stages of restoration. Floral resources are densely supplied in relatively small areas in their initial restoration stages compared with the extensive temporal and spatial distributions of floral resources in tropical forests (Silva et al. 2021; Ren et al. 2023). Our results suggest the rapid recovery of plant–pollinator interactions in sand mine restoration areas. As pollinators are mobile agents, their fast recovery in

early successional stages can be explained mainly by the arrival of species from adjacent pristine forests (Lázaro & Alomar 2019). Other studies have reported similar fast recoveries of plant–pollinator interactions (Griffin et al. 2017; Onuferko et al. 2018; Novotny & Goodell 2020; Araújo et al. 2021), which are associated with the high abundance of floral resources that attract diverse pollinators from the surrounding forest matrix (Cusser & Goodell 2013).

To support the long-term maintenance and recovery of pollinators at restoration sites, it is essential to consider how landscapes can support pollinator nesting requirements (Coutinho et al. 2018). Thus, an important restoration practice may be the additional management of trap nests in restoration fields to attract nesting bees (Oliveira et al. 2013; Staab et al. 2018). In addition, understanding the role of supergeneralist and alien species in mined land restoration is important (Gaiarsa & Bascompte 2022), thus preventing the risk of local biotic homogenization in the long term (Carvalho et al. 2013). An important caveat to be considered in our study is related to pollinator sampling. Although we applied standardized efforts across study sites and compared the completeness of the vegetation coverage, we evaluated plant–pollinator communities in the understory, up to 3 m. High vegetation structure was a limiting factor for pollinator sampling, especially in pristine forests, where we found canopies 30 m high, and currently, we are not able to quantify how much of the interacting community we were not able to assess, which may indicate that pristine forests are actually in a different (better) state from initial areas, as they have a full set of undetected interactions occurring in the canopy. This is a recurrent problem for surveying plant–pollinator

interaction networks in tropical forests (Ferreira et al. 2020), and additional methods (e.g. the use of flower environmental DNA and pollen adhered to pollinator body parts) are needed for a better understanding of canopy interactions (Banerjee et al. 2022; Newton et al. 2023; Romeiro et al. 2023).

### Species Selection for Pollinator Restoration

Our framework provides strong support for stakeholders to select species aligned with project goals and improve resource allocation at the start of the restoration process. Plant management characteristics were based on a previous study (Giannini et al. 2017), and here, for the first time, a set of bee species traits was proposed and applied to select bee species that can be managed in restored landscapes. Our bee and plant selection structure is robust and can be adapted to different strategies focused on regional sustainable development, such as native beekeeping (for honey, pollen, wax, and propolis production), crop pollination, agroforestry systems, or other scenarios in which pollinators are needed and can provide an alternative source of income for the local population (Jaffé et al. 2015). In addition, pollination restoration supports the reproduction of flowering plants and the indirect positive effects of sustaining a functional community to safeguard ecosystem restoration (Leclère et al. 2020).

The species selected with our framework are generalist species that may act as hubs to increase visitation rates, supporting both plant (fruit set) and pollinator (resource supply) species, in addition to supporting other ecosystem functions such as seed dispersal, soil quality, and carbon storage through indirect effects (Carvalho et al. 2021; Weiskopf et al. 2023; Lam et al. 2024). The selected bee species present both social and solitary behavior and represent seven different genera of native stingless bees and one carpenter bee with different nest architectures, colors, foraging behaviors, and sizes. Both very small (*Tetragonisca angustula*) and very large (*Xylocopa frontalis*) bees found in the CNF were selected (Borges et al. 2020). Local nurseries are capable of supplying most of the selected bees, improving income distribution in the region, and preventing genetic invasion in the region. These bees are also supplied from areas under deforestation (through the bee rescue process), and their management is well known in the region (Villas-Bôas 2012). The selected plants can also be found in local nurseries, and their germination and seedling transport are known in the region (Zappi et al. 2018), safeguarding local populations. The plants are fast growing and flowering. For example, the species *Bixa orellana* starts flowering after 15 months (EMBRAPA 2009). The 10 plant species selected in our study belong to six botanical families, 60% of which are shared with the selection system proposed by Giannini et al. (2017), and 100% are shared with the selection proposed by Zappi et al. (2018) for the CNF. The presence of shared taxa among these different approaches is highly important and increases support for integrative strategies (species, traits, functionality, and ecosystem functions) aimed at the sustainability of the restored ecosystem (Bommarco et al. 2018).

Selecting botanical families to support pollinator restoration is an innovative and important approach to informing

decision-making during restoration planning and safeguarding phylogenetic diversity in the restored environment. Among the six botanical families selected in our framework, one is among the most important for the restoration of pollinators (Malpighiaceae), and five are among the most common families (in terms of the number of species) in plant–pollinator interaction networks in Brazil (Campbell et al. 2019). Network metrics can provide an understanding of historical and contemporary ecosystem processes as well as the species that shape community functioning (Kaiser-Bunbury & Blüthgen 2015; Harvey et al. 2017); thus, the methods applied in this study can also support practical guidance for restoration monitoring. This is the first study to assess the restoration of interactions in the Amazon forest, and although we were able to shed light on the trends of interaction restoration, future studies should incorporate the functional space occupied during the restoration process, compare it to reference sites, and assess the percentage of the interacting community that is restricted to the canopies to provide a more complete understanding of the restored ecosystems.

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## Supporting Information

The following information may be found in the online version of this article:

**Supplement S1.** Details on study methods and results.

**Figure S1.** Sampling completeness profile for each treatment.

**Table S1.** List of the sampled sites, mining types, and restoration stages with respect to the number of interactions.

**Table S2.** Moran index values observed for the studied region for each of the interaction metrics.

**Table S3.** Asymptotic diversity estimates along with related statistics (Fig. S1).

**Table S4.** Analysis of variance (ANOVA) results for the mixed-effects model of interaction metrics modeled by mine type and regeneration stage.

**Table S5.** Results of the permutational multivariate analysis of variance (PERMANOVA) of bee and plant species in the different site types and restoration stages.

**Table S6.** Plant and pollinator traits (and their justification) for selecting species for restoration.

**Table S7.** Complete list of species selected with rank values above zero (>0).

**Table S8.** Complete list of plants and pollinator species collected in the Carajás National Forest, Eastern Amazon, Brazil.

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