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Pollination and dispersal networks in the Amazonian tree flora

Hans ter Steege[1,2] ✉, Caio S. Ballarin[3,4], Carlos Eduardo Pinto[5], Lorena B. Valadão-Mendes[6], Pablo Stevenson[7], Diego F. Correa[7,8], Tereza Cristina Giannini[9], Vitor H. F. Gomes[10], Matt McGlone[11] & Renato A. F. de Lima[5]

We collected flower-visiting data for 5,201 Amazonian trees species, corresponding to 50% of all known tree species and 94% of all estimated individuals in Amazonia. Bees are the most common flower-visitors responsible for 74% of all studied tree genera and 74.1% of all individual trees, followed by generalist flower-visitors (39.2%). Sixteen tree genera make up 50% of all interactions between tree genera and their flower-visitors. Two of those: *Inga, Miconia*, each provide more than 2% of all interactions at genus level while six: *Protium, Eschweilera, Inga, Pouteria, Ocotea*, and *Virola* each provide more than 2% of all interactions at the estimated tree population level, underscoring the importance of these tree genera in the forest. Forty hyperdominant genera are responsible for half of the fruit resources of the Amazonian disperser community. Nearly 80% of these Amazonian tree species rely on animals for both pollination and seed dispersal, and less than 1% are free from animal involvement in these key life stages. This strong biotic dependence highlights a critical point: animal-mediated interactions are not peripheral but central to the maintenance, regeneration, and spatial structure of Amazonian forests, which makes halting of defaunation in these forests a priority.

The Amazonian forests host approximately 392 billion trees with an estimated 15,000 to 16,000 tree species[1,2]. Trees form the basic structure of a forest, providing functions for many interstitial species. This ranges from support for epiphytes and lianas, food for animal species in the form of leaves, fruits, seeds, floral rewards (e.g. nectar and pollen), to living space and shelter for animals. Pollination and dispersal are two important stages of the life cycle of plants where they may need animals to fulfil these two processes[3,4]. Pollination and dispersal may have had a significant influence on diversity - the increase of angiosperm diversity suggested to be closely linked with that of its pollinators[5,6] and its dispersers[7]. As a consequence, tree species interact with a large number of animal species and their relationships can be viewed as interaction networks[8]. While several studies have been carried out on localized networks in the American tropics e.g.[9–13], less were carried out at the regional level[14,15], and while data for the Brazilian Cerrado and Atlantic forest is abundant e.g[14]. and several references therein[15,16],, data for Amazonia is scarce[13,17,18]. Understanding these interactions is fundamental for comprehending the maintenance of diversity and the dynamics of Amazonian tree communities, particularly within a biome of remarkable ecological and functional complexity.

Pollination and seed dispersal initiate the renewal of plant populations by enabling reproduction and propagule movement[19,20]. These processes precede seedling recruitment and later-stage interactions such as belowground mutualisms and herbivory, which become more relevant for the survival and performance of successfully established recruits[21,22]. Hence, they represent crucial steps a plant must undergo to successfully promote its population maintenance and spread.

In tropical forests it has been documented that over 90% of species rely on animals for pollination—considerably more than in temperate forests,

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[1]Naturalis Biodiversity Center, LeidenPO Box 9517, 2300 RA, The Netherlands. [2]Quantitative Biodiversity Dynamics, Utrecht University, Padualaan 8, Utrecht, 3584 CH, The Netherlands. [3]Laboratório de Ecologia da Polinização e Interações – LEPI, Departamento de Biodiversidade e Bioestatística, Instituto de Biociências, Universidade Estadual Paulista 'Júlio de Mesquita Filho' (IBB - UNESP), Rua Prof. Dr Antonio Celso Wagner Zanin, Botucatu, SP, CEP 18618-689, Brazil. [4]Programa de Pós-graduação em Biologia Vegetal, IBB - UNESP, Rua Prof. Dr Antonio Celso Wagner Zanin, Botucatu, SP, CEP 18618-689, Brazil. [5]Departamento de Ciências Biológicas, ESALQ, Universidade de São Paulo, Brazil, Avenida Pádua Dias, 11, CEP 13418-900 Piracicaba, Brazil. [6]Programa de Pós-graduação em Biologia Animal, Universidade Federal dos Vales do Jequitinhonha e Mucuri, Diamantina, MG, Brazil. [7]Laboratorio de Ecología de Bosques Tropicales y Primatología, Universidad de los Andes, Carrera 1 # 18a- 10, Bogotá, DC, 111711, Colombia. [8]Centre for Biodiversity and Conservation Science CBCS, The University of Queensland, Brisbane, QLD, 4072, Australia. [9]Instituto Tecnológico Vale, Rua Boaventura de Silva 955, Belém, Pará, Brazil. [10]Department of Biology, University of Turku, Turku, Finland. [11]Manaaki Whenua – Landcare Research, PO Box 69040 Lincoln, 7640, New Zealand. ✉e-mail: hans.tersteege@naturalis.nl

where wind pollination is more common[4,23]. Although wind pollination is generally less frequent in tropical forests, it remains prominent in specific Amazonian clades, such as Moraceae and Urticaceae, which contribute substantially to airborne pollen loads[24].

Plants attract pollinators by offering a diverse array of rewards—nectar, pollen, oils, resins, and fragrances—each closely tied to specific floral traits[16,25–27]. Among these, nectar is the most prevalent, present in approximately 74% of animal-pollinated flowering plant species[28]. As a readily accessible energy source, nectar supports a wide range of floral visitors, including bees, birds, bats, and other vertebrates and invertebrates[29,30]. It is metabolically inexpensive and low in nitrogen, and thus favoured as a reward under conditions marked by high light availability, abundant moisture, and low soil fertility[31,32]. Pollen, in turn, is another key reward, particularly for bees, some of which rely on vibrational foraging (buzz pollination) to extract it, a widespread feature across angiosperm lineages[33]. Even wind-pollinated species may contribute to the floral resource pool by producing abundant, nitrogen-rich pollen[34] that attracts insect visitors.

Despite the ecological importance of non-nectar rewards such as pollen, oils, and resins—especially for specialized bee lineages—their diversity, prevalence, and distribution in Amazonian tree species remain largely unexplored and significant knowledge gaps remain. Challenges in accessing tall forest canopies and sampling sufficient individuals of rare or scattered species have limited our understanding of pollination systems in the region. As a result, the diversity of pollination modes—spanning multiple clades and floral traits such as colour, symmetry, shape, and reward type—remains largely undocumented. This scarcity of data hinders our ability to assess the prevalence and ecological importance of distinct systems, including those involving non-nectar rewards or less-studied pollinator groups. For example, beetles and thrips play vital roles in the pollination of early-diverging angiosperms such as Annonaceae, Myristicaceae, and Arecaceae[35–41] which are abundant in Amazonia. Understanding the distribution and ecological roles of these specialized interactions is essential, as they support the reproduction of both wild and culturally important species and are key to forest regeneration. Therefore, linking pollination systems, floral traits, and rewards to tree distribution in Amazonia may open new avenues to integrate evolutionary and ecological perspectives underlying tree community assembly and population dynamics, ultimately informing conservation and restoration efforts in this biome.

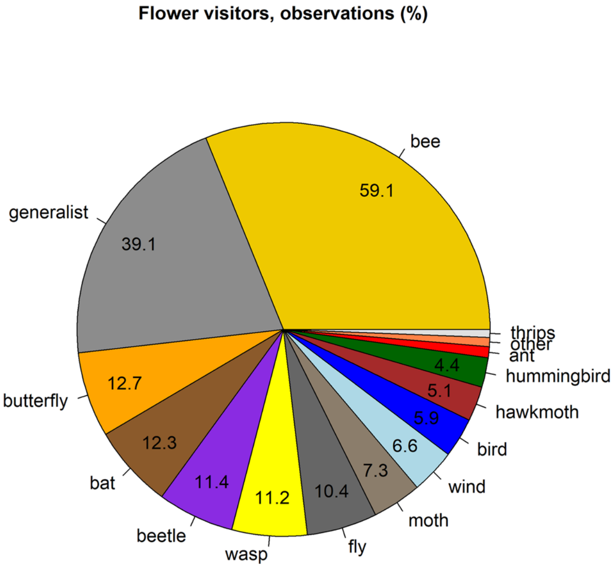

Fig. 1 | Flower visitation in the Amazonian tree flora. The percentage of Amazonian tree species visited by the various potential pollinators (see Supplementary Table 1 for actual data). Colours are an approximate representation of the colour of the visitor group and used throughout the paper. The last three groups have a percentage lower than 4%.

In tropical regions, previous studies indicate that over 75–90% of tree species rely on vertebrate dispersers such as birds, primates, reptiles, bats, and rodents[42–45]. This proportion is substantially higher than in temperate areas, where vertebrate dispersal accounts for 40–60% of species[45]. Such differences reflect the greater species richness, variation in fruit traits, and environmental conditions characteristic of tropical ecosystems[10,46–48]. Fruits vary widely in morphology and composition, with fleshiness being a major determinant of dispersal mode. Species with fleshy fruits, mostly endozoochorous, rely on arboreal vertebrates to transport seeds, while dry-fruited species typically depend on abiotic dispersal or terrestrial mammals[32,49,50]. Seed mass also may influence dispersal distance, but the evidence is mixed[51].

Despite its central role, seed dispersal in Amazonia remains insufficiently studied, particularly regarding the diversity of animal dispersers and their interactions under different disturbing regimes[52]. For example, although dispersal networks may include many tree and vertebrate species, a few key animals—such as the bearded saki (*Chiropotes satanas* Hoffmannsegg) and tapir (*Tapirus terrestris* L.)—dominate observed interactions in the Guianas[10]. In Amazonia, several other vertebrate species have been recorded as frugivores and seed dispersers[53,54]. Understanding these relationships is crucial because seed dispersal reduces density-dependent mortality near parent trees, promotes colonization of new habitats, supports seedling survival, and influences forest composition and resilience[55–57].

To explore the pollination and dispersal networks in Amazonian trees, we compiled data on 5,201 species observed in forest plots (amounting to 30% of the estimated species in Amazonia[58] and representative of over 99% of all individual trees there)[1,2], including estimates of population size and comprehensive trait information[1,2]. Our dataset encompasses functional traits linked to pollination - floral rewards, flower colour, size, and symmetry, and breeding system – and fruit/seed dispersal - fruit fleshiness, seed mass. We also report on flower-visitors and dispersal mode for the majority of tree species represented in our dataset, reflecting patterns observed across species and genera. Although we recognize inherent taxonomic and sampling limitations, this represents the first large-scale compilation of plant–animal reproductive interactions for Amazonian trees, providing the most comprehensive assessment currently available. With this information, we address two core questions:

i) What are the most common pollination and dispersal strategies in Amazonian trees?
ii) Are these strategies associated with specific floral/fruit traits?

Additionally, we quantify the diversity and abundance of flower-visitors and seed dispersers based on our population estimations, shedding light on the complexity and functional significance of these interaction networks in this megadiverse biome. This is essentially a descriptive study, bringing together the fruit and dispersal, and flower and flower-visitor information – data that was available for Amazonian trees at this moment. We understand that this is a start and hope that this will inspire others to gather more data, test, support and/or falsify our findings.

Results

Flower visitation and floral traits

Using just the species-level observations, our compiled data on flower visitation covers 797 species, of 5,201 Amazonian tree species (15.3%) in from 2,054 tree inventory plots of the Amazon Tree Diversity Network (ATDN)[2]. At genus level, the data provides pollination information for 536 genera (66.7% of all genera in those plots).

When we scale up the compiled species and genus data to Amazonian tree population level[1,2], the species are representative for 34.1% of all estimated Amazonian tree individuals and the compiled genera for 94.4% of all estimated Amazonian tree individuals).

Based on the compiled data (Fig. 1, Supplementary Table 1), bees are the most common flower-visitors with 59.1% of the tree species in the data and 74.8% of all genera with observed bee visitation. Butterflies, beetles, flies, and wasps all visited more than 10% of the tree species and around 40% of tree genera. Bat and hummingbird visitation has been observed in 98 (12.3%) and 35 (4.4%) of the studied species, and 15.4 and 15.5% of all studied genera, respectively. Wind pollination is reported in 53 species (6.6%).

Scaling up to Amazonian tree population level this may suggest that 84.3% of the estimated individual trees potentially are being visited by bees, followed by generalist flower-visitors (66.1%, Supplementary Table 1).

The percentage of genera, visited by a specific potential pollinator, is slightly higher than the percentage of species but strongly correlated ($R^2 = 98\%$, data in Supplementary Table 1).

The ten tree families with the highest number of flower-visitors, based on the genus level data, are): Fabaceae, Rubiaceae, Malvaceae, Arecaceae, Euphorbiaceae, Lauraceae, Chrysobalanaceae, Melastomataceae, and Lecythidaceae (Table 1, Supplementary Table 2). Based on the Shannon index, Malvaceae has the highest flower visitor diversity, followed by Rubiaceae, Fabaceae, Rutaceae, Euphorbiaceae. Fabaceae is the only family with all 13 flower visitor types (incl. wind pollination, Table 1, Supplementary Table 2).

The ten orders with the highest number of flower interactions at genus level are Fabales, Malpighiales, Gentianales, Sapindales, Malvales, Myrtales, Ericales, Rosales, Magnoliales, and Lamiales (Table 2, Supplementary Table 3).

The network structure for tree families and flower-visitors is rather congested (Supplementary Fig. 1). For tree orders the main patterns are a little easier to visualize (Fig. 2). Thrips and beetles are strongly linked to the early land plants (Magnoliales). Beetles are also prominent flower-visitors of the Arecales (Arecaceae). The most frequent flower-visitors (bees, generalist visitors, and butterflies) have links to most families and orders (Supplementary Figs. 1–3, Supplementary Tables 2 and 3).

In the 5,201 species used in this study, 215 are Amazonian hyperdominants, making up 50% of the total number of stems in Amazonia. Of those we have pollination data for 83 species, or 38.6% (Supplementary Table 4). Sixteen (species-rich) tree genera make up 50% of all interactions between tree genera and their flower-visitors. Two very species-rich genera: *Inga* and *Miconia* each provide more than 2% of all interactions at the genus level (Fig. 3a).

Scaling up to estimated Amazonian tree population level, seven genera: *Protium, Eschweilera, Inga, Pouteria, Ocotea*, *Virola*, and *Euterpe* each potentially provide more than 2% of all interactions at the estimated tree population level (Fig. 3b). The sixteen genera that are estimated to make up 50% of all interactions at the estimated tree population level (Fig. 3c) can be considered the hyperdominants in flower – flower-visitor interactions. Fifteen of these are also hyperdominant in terms of population size (Supplementary Table 4). The importance of a genus for the region is based on the total number of interactions estimated at genus level (based on the number of species Fig. 3a) and, perhaps even more, at tree population level (Fig. 3b) and, as species numbers and populations of genera are related, this results in a positive (but not very strong) relationship between the percentage of interactions at the two levels (Fig. 3d).

In the compiled data, we found colour information for 3,269 species (68.2%, Fig. 4a). Most flowers are (or have) white (68.2%), followed by cream (25.4%), yellow (19.1%), and green(ish) (9.1%), together good for 88.6% of all flowers. Red (5.7%), pink (4.6%), purple (3.3%), brown (1.3%), orange (0.9%), and blue (0.4%) are much less common colours in the flowers of Amazonian trees. As a result of the majority of flowers being white, most flower visitor groups visit white flowers for almost 50%. Bees visit white flowers significantly less than expected by chance (Fig. 5a, Supplementary Table 5). Moths, hawkmoths and bats visit white flowers more than expected, while visiting cream coloured flowers less than expected. Hummingbirds, birds, and bats visit white flowers for 50% or their flower visits but visit red and pink (and violet for birds) flowers more than expected by their presence. Beetlee and thrips visit green flower more than expected,

Table 1 | Number of Amazonian tree genera per flower-visitor type by tree family

Family	bee	generalist	butterfly	beetle	fly	wasp	hummingbird	moth	bat	wind	hawkmoth	bird	thrips	# visitor types	Shannon
Fabaceae	90	58	32	14	17	18	11	10	24	8	10	19	2	13	2.196
Rubiaceae	25	15	19	3	6	6	11	12	1	0	14	11	0	11	2.200
Malvaceae	19	11	5	10	11	6	8	8	18	1	6	4	0	12	2.317
Euphorbiaceae	10	13	1	3	3	4	3	0	3	12	1	1	0	11	2.046
Arecaceae	13	5	1	20	4	2	0	0	0	4	0	0	0	7	1.570
Annonaceae	3	4	0	25	2	0	0	0	0	0	1	0	14	6	1.287
Myrtaceae	13	12	1	5	6	3	2	0	1	0	0	1	1	10	1.881
Lauraceae	10	16	7	3	4	2	0	1	0	0	0	0	0	7	1.639
Sapotaceae	9	8	7	2	5	2	0	2	0	0	0	0	0	7	1.777
Rutaceae	5	9	4	0	3	2	3	1	0	1	2	3	0	10	2.102

The table is ordered by the number of interactions. Data for all families is found in Supplementary Table 2. Generalist include the categories small diverse insects, generalist, insects; other includes bug, cockroach, cricket, green lacewing, lizard, mammal, flowerbug, and mosquito; bird is birds without hummingbirds; mammal includes all mammals except bats; # visitor types, the number of flower visitor type observed; Shannon, flower visitor diversity as estimated by the Shannon index. The 90 in the Fabaceae/bee combination means that 90 genera of Fabaceae have reported bee flower visitation.

Table 2 | Number of Amazonian tree genera per flower-visitor combinations by order

Order	bee	generalist	butterfly	beetle	fly	wasp	hummingbird	moth	bat	wind	hawkmoth	bird	thrips	other	ant	# visitor types	Shannon
Fabales	90	59	32	14	17	18	11	10	24	8	10	19	2	4	5	13	2.280
Malpighiales	64	50	12	9	11	17	11	4	10	17	5	5	1	4	5	13	2.222
Gentianales	32	20	26	3	7	7	12	19	2	0	19	12	0	4	2	11	2.282
Sapindales	31	36	12	5	11	6	5	8	0	5	7	4	2	0	1	11	2.155
Malvales	22	13	5	10	11	6	8	8	18	1	6	4	0	4	1	12	2.397
Myrtales	33	17	6	7	10	7	6	3	4	0	4	5	3	2	4	12	2.295
Ericales	28	16	9	4	9	6	2	5	1	2	0	0	0	1	3	10	2.040
Rosales	14	16	0	4	6	6	0	0	1	21	0	0	1	0	0	6	1.737
Magnoliales	5	6	0	31	3	0	0	0	0	0	1	0	19	0	1	5	1.394
Lamiales	14	7	6	2	8	3	8	0	2	0	2	3	0	1	0	9	2.144

Data for all orders is found in Supplementary Table 3. Generalist include the categories small diverse insects, generalist, and insect; other includes bug, cockroach, cricket, green lacewing, lizard, mammal, flowerbug, and mosquito; bird is birds without hummingbirds; mammal includes all mammals except bats; # visitor types, the number of flower visitor types observed; Shannon, flower visitor diversity as estimated by the Shannon index. The 90 in the Fabales/bee combination means that 90 genera of Fabales have reported bee flower visitation.

while wind pollinated flowers are also more often green than their average in the flower community.

We found pollination rewards for 4,243 species (81.6%, Fig. 4b). Nectar is the most common pollination reward (60.0%), followed by pollen (42.5%). Other rewards: volatiles, tissue, brood, oil, and resin follow at a considerable distance (5.2%, 4.2%, 1.4%, 1.3%, and 0.9% respectively). In 0.9% of the tree species no reward is offered (Fig. 4b, Supplementary Table 6). Most flower visitors show the highest visitiation for flowers that provide nectar as reward, except beetles, ants and the group 'other' (Fig. 5b, Supplementary Table 6). The groups hummingbird, bird, moth, hawkmoth and bat also favor flowers providing nectar and visit flowers providing pollen less than expectd by chance. The groups beetle, fly, other and thrips visit flowers providing nectar less flowers offering pollen, volatiles, tissue, and brood more than expected.

White, red, and purple flowers provide nectar and pollen more often than expected, while yellow and green flowers provide both resources less than expected. Green and yellow flowers provide volatiles and tissue as reward more often than expected (Supplementary Table 7).

Flower symmetry was found for 5,199 species (~100%, Fig. 4c). Most flowers are actinomorphic (83%). Strong zygomorphy is found in 11.8% of the species, while 5.2% are slightly zygomorphic. Flower symmetry appears to have little influence on visitation (Supplementary Table 8) and the few significant Pearson residuals are rather small (Fig. 5c, Supplementary Table 8).

Breeding system was found for 5,196 species (~100%, Fig. 4d). Two thirds of the tree species are bisexual, thus the average ratio bisexual / (monoecious+dioecious) is around 2. This is the case for the majority of types of flower-visitor (Supplementary Table 9). However, for flowers visited by hawkmoths, hummingbirds, bats, ants, and birds, hermaphroditism is much more common (ratio's from 3.5-7.5). The groups hawkmoth, hummingbird, ant, bat, bird have significant positive residuals for hermaphroditic flowers, and roughly 80% of the flowers visted by them are hermaphroditic (Fig. 5d, Supplementary Table 9). The groups generalist, beetle and, especially, wind have significant negative residuals for hermaphrodicy. More than 60% of monoecious + dioecious flowers are wind pollinated (sign. positive residuals).

All floral traits we studied are largely conserved within genera, possibly reflecting similar strategies to attract and reward the same pollinator groups at this taxonomic level (Supplementary Fig. 4). This means that most species within a genus have similar flower colour (or the same combination), the same reward (or in a few cases two [nectar + pollen]); equal symmetry, and breeding system; mostly the same one or two flower visitors, and, finally, the same dispersal syndrome.

Dispersal

We used two dispersal classifications (see methods). Dispersal was established for all 5,201 known species. Based on the 2023 classification, 4,097 tree species (77.8%) used in this study, are animal dispersed (Table 3, Supplementary Table 10). Anemochory is relatively common with 13.7% of all species. Explosive dehiscence is found in 5.2% of all species and 9% of all individuals.

Scaling up to estimated Amazonian tree populations 78% of all estimated Amazonian trees are potentially animal dispersed (Supplementary Table 11).

Based on the Shannon index, Fabaceae shows the highest diversity of dispersal types, followed by Malvaceae, Rutaceae, and Moraceae (each with Shannon index > 1, and 4 dispersal types, Supplementary Table 10). Fabaceae is also the only family where at least 7 types of dispersal are found.

Because animal dispersal and especially endozoochory is so common, it is found among almost all families (Fig. 6). In several families, where the majority of fruits are fleshy (Supplementary Table 11) it is the only dispersal mode. In families with high diversity in dispersal, fleshy fruits are less prominent (Supplementary Table 11). In most animal dispersed species (96%) fruits are fleshy (Supplementary Table 12), for synzoochorous species this percentage is somewhat lower (87%). For most non-animal dispersed

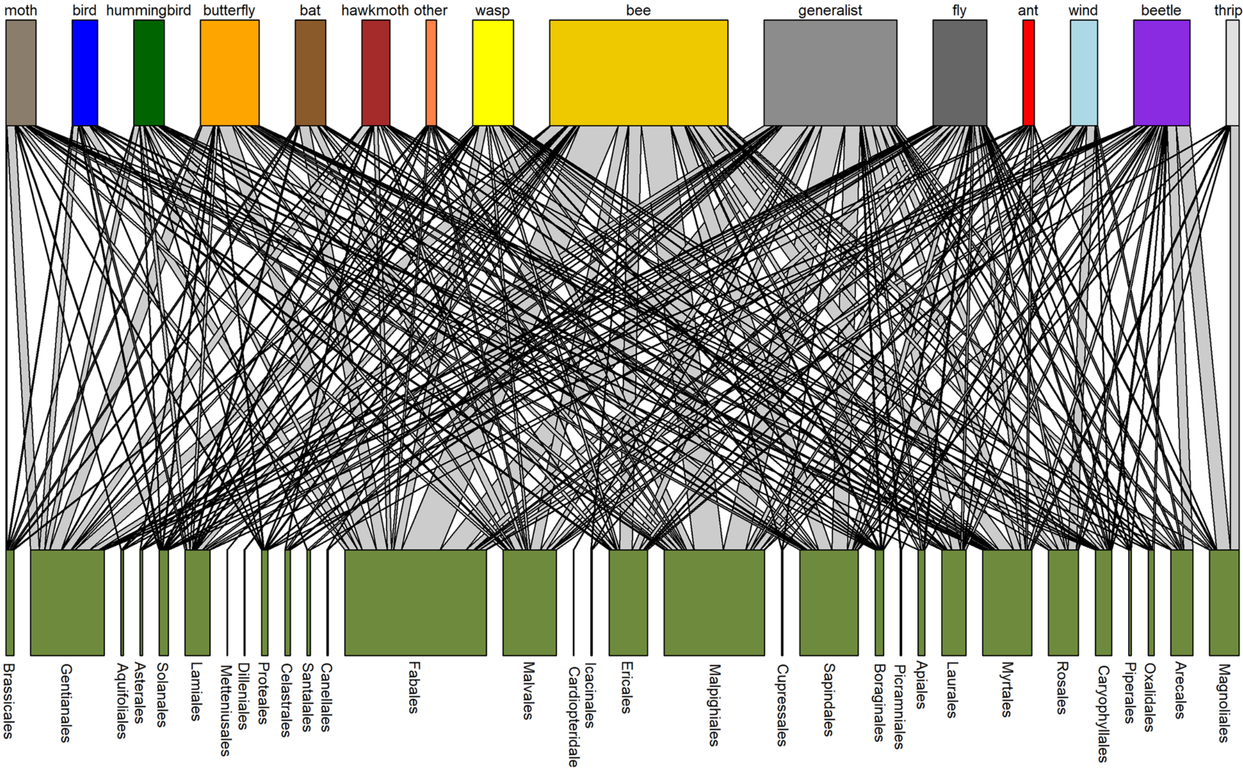

Fig. 2 | Pollination network of Amazonian trees. Network of flower-visitors/pollinators and Amazonian tree orders based on the number of tree species – flower-visitor interactions. The width of the bars indicate the sum of the interactions of the flower visitor category (top) and the families (bottom). They are in fact the sums of the columns and rows of the crosstab they are based on (Supplementary Table 3).

species (97%) fruits are dry. Most seeds have a seed mass between 0.1 g and 10 g (Supplementary Table 13). The average of seed mass for almost all dispersal types falls within this range. Only seeds with synzoochorous dispersal have a considerably larger average seed mass (10-100 g).

Using the 2025 dispersal classification, 83% of tree species are animal dispersed, mainly by arboreal vertebrates (primates, bats, birds, Supplementary Fig. 5).

Dispersal network for A) dispersal 2023[59] and B) 2025, shows that arboreal dispersal (primates, bats, birds) and endozoochory are by far the largest classes and largely overlapping (Supplementary Fig. 6). It is important to note that by far the largest part of Amazonian tree species is dispersed by animals (4097 or 77.8%) in the 2025 scheme and 4,046 (77.7%) in the 2023 scheme.

Scaling up, forty genera make up 50% of all Amazonian trees that provide fruit to dispersers (Supplementary Table 10). Of these the most abundant genera are *Eschweilera, Protium, Pouteria, Inga, Virola, Euterpe, Pseudolmedia, Iryanthera, Oenocarpus, Brosimum*, *Ocotea*, which together make up 25% of the fleshy fruit providers for the Amazonian disperser community. Such genera either have a few widely spread species (e.g. *Pseudolmedia, Socratea, Attalea, Iriartea*), or many species (e.g. *Eschweilera, Protium, Pouteria, Inga, Virola, Ocotea*). The first thirty-two of the hyperdominant fruit providers are also hyperdominant in terms of population, except for *Socratea*, which is very close to the hyperdominant genera (Supplementary Table 10). The other genus population hyperdominants (*Pachira, Eperua, Tachigali, Aspidosperma, Macrolobium, Rinorea*, and *Mabea*) lack fleshy fruits and have few interactions with dispersers, although some species of *Pachira* may be dispersed by animals (Supplementary Table 10).

Combinations of data of pollination vs dispersal

In 79.5% of all interactions estimated for Amazonian tree individuals, animals are responsible for both pollination and dispersal, in 19.9% they are responsible for either pollination or dispersal. Only in 0.6% of all the interactions animals are neither involved in pollination nor in dispersal (Table 4).

Discussion

Our synthesis of pollination and dispersal networks in Amazonian trees reveals the dominant role of animals in sustaining the reproduction and dispersal of the region's tree flora. By compiling data on flower-visitors and dispersal agents for 5,201 species—spanning ca. 50% of known Amazonian tree diversity[58] and 99% of the estimated number of individual trees (Fig. 2 of[1]), we provide one of the most comprehensive overviews to date of how reproductive and dispersal mutualisms shape Amazonian forests. A striking result is that, based on the studied tree species, nearly 80% of Amazonian tree species rely on animals for both pollination/flower visitation and seed dispersal, and less than 1% of species are free from animal involvement in these key life stages. This strong biotic dependence highlights a critical point: animal-mediated interactions are central to the maintenance, and spatial structure of Amazonian forests. This dependency suggests that any disruption to animal populations—especially frugivores, and pollinators such as bees, bats, and birds—may have cascading consequences for forest composition, diversity, and resilience[60–62]. On the other hand, trees are also a resource for animals and a few, widely spread and/or species rich genera are responsible for 50% of the interactions with flower-visitors and dispersers. As predicted[1], hyperdominant taxa play a very prominent role in providing resources to the flower visitor and disperser community.

One potential limitation concerns the breadth of our empirical flower-visitation data coverage. Flower-visitation data at the species level is available for 15% of the tree species occurring in the ATDN plots, representing 34% of all estimated individuals. Such data is available for 66.7% of all genera, that have been found in the ATDN plots. First, as we have floral attributes for a large part of the 5201 species found in the forest plots (Fig. 4), and as most

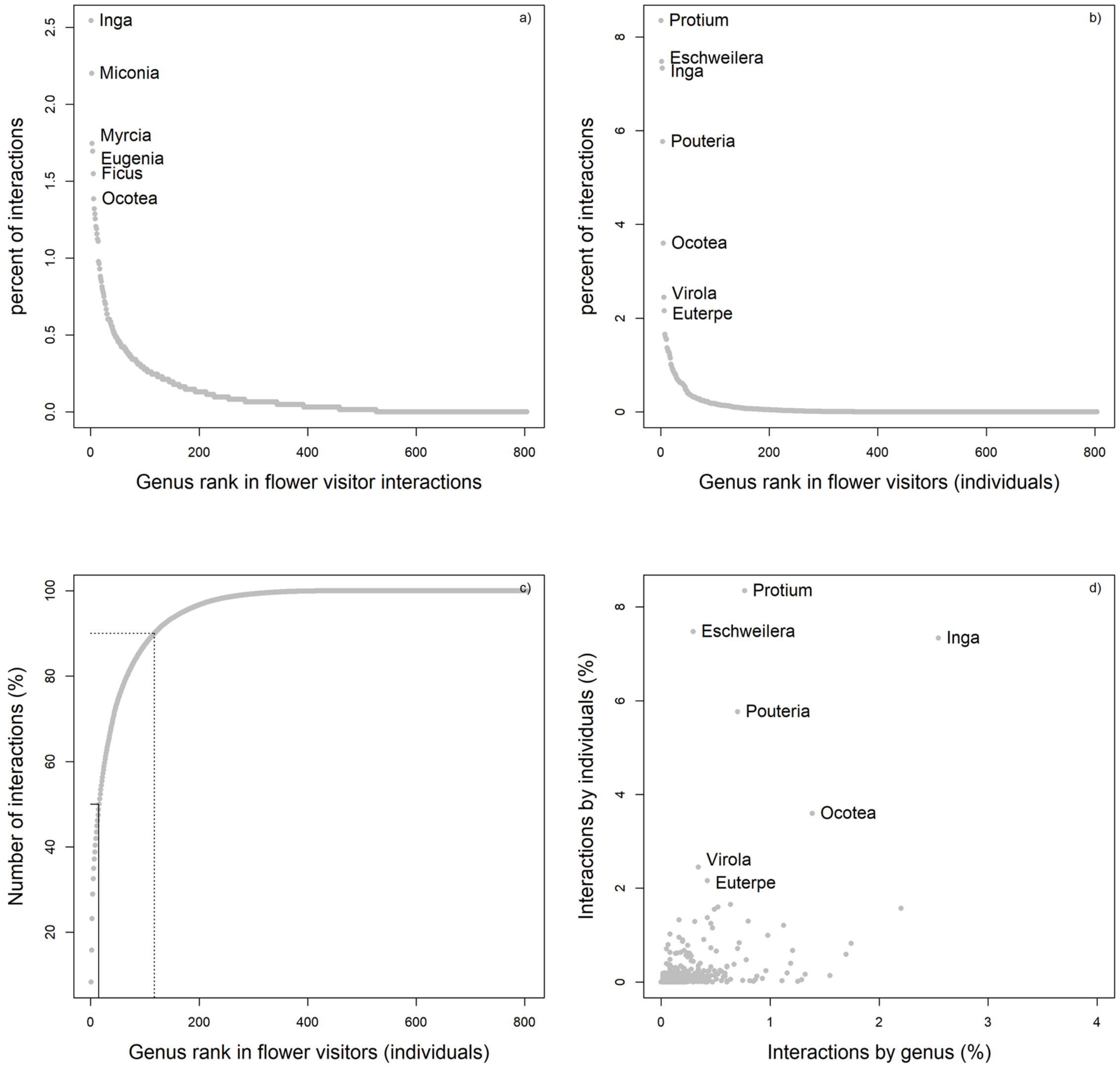

Fig. 3 | Rank abundance curves of Amazonian trees providing pollination services. **a** Genera rank order in percentage of interactions between tree genera and flower-visitors. Six genera with more than 1.4% of all interactions are indicated. **b** Same for the percentage at level of estimated population sizes of tree species. Seven genera with more than 2% of all interactions are indicated. **c** Cumulative flower flower-visitor interactions at the estimated population level. Sixteen genera make up 50% of all interactions, 116 genera make up 90% of all interactions. **d** The relationship between the interactions of the at genus level (**a**) and population level (b); data in Supplementary Table 4.

floral attributes, associated with pollinator visitation and pollination, such as colour, reward type, breeding system, and floral symmetry, are highly conserved within the genera represented in our dataset (Supplementary Fig. 4), this allows our upscaling approach to reflect the high probability that species and individuals belonging to the same genus are visited by similar guilds of floral visitors. We also explicitly considered the potential visitation by multiple pollinator guilds, acknowledging that many plant systems attract a very diverse assemblage of floral visitors. Finally, our study does not seek to quantify frequency or efficiency for each species individually; instead, by incorporating population sizes[1,2], we provide an overview of pollination systems across the Amazon basin. We also tested the compiled data by bootstrapping the 251 publications that made up our data (Supplementary Fig. 7). For the more common flower visitor types the spread is fairly low. Because our data included some outliers the percentage genera reported by pollinator groups in Supplementary Table 1 are somewhat higher that the bootstraps of the means (Supplementary Table 14). This is caused by the fact that our web searches for pollinators only had positive interactions for rare genera that had not been found in the single studies. Also, as some studies only dealt with one pollinator group only, the bootstraps of the means show bimodality for these groups (particularly birds, thrips, Supplementary Fig. 8). The bi-modality for ants is likely due to its very low occurrence.

As bees are sometimes the only investigated flower visitor, there are more outliers, as is the case for wasps (fig-wasps being exclusive pollinators of figs, but other wasps visiting several other flower types) and generalist flower visitors. While this variation may be more important for the flower visitor that are rarer, as all but one (wind) are based on animal visitors, this has little effect on the total number of species and estimated individual trees that are visited by animals or not (wind pollination). As several wind-pollinated species are also visited by insects, this suggests that the number of species and estimated tree individuals that are animal pollinated may be even higher.

For seed dispersal, we assigned dispersal modes to all species based on direct observations and fruit and seed traits, and we consider the accuracy of this classification to be even higher (Supplementary Fig. 4 f). Still, we acknowledge that, given the scarcity of available literature on Amazonian floral and fruit traits, as well as on their visitors, many of the species–animal associations in our dataset were inferred through cross-referencing rather than direct evidence. We also acknowledge that fruits and seeds may have

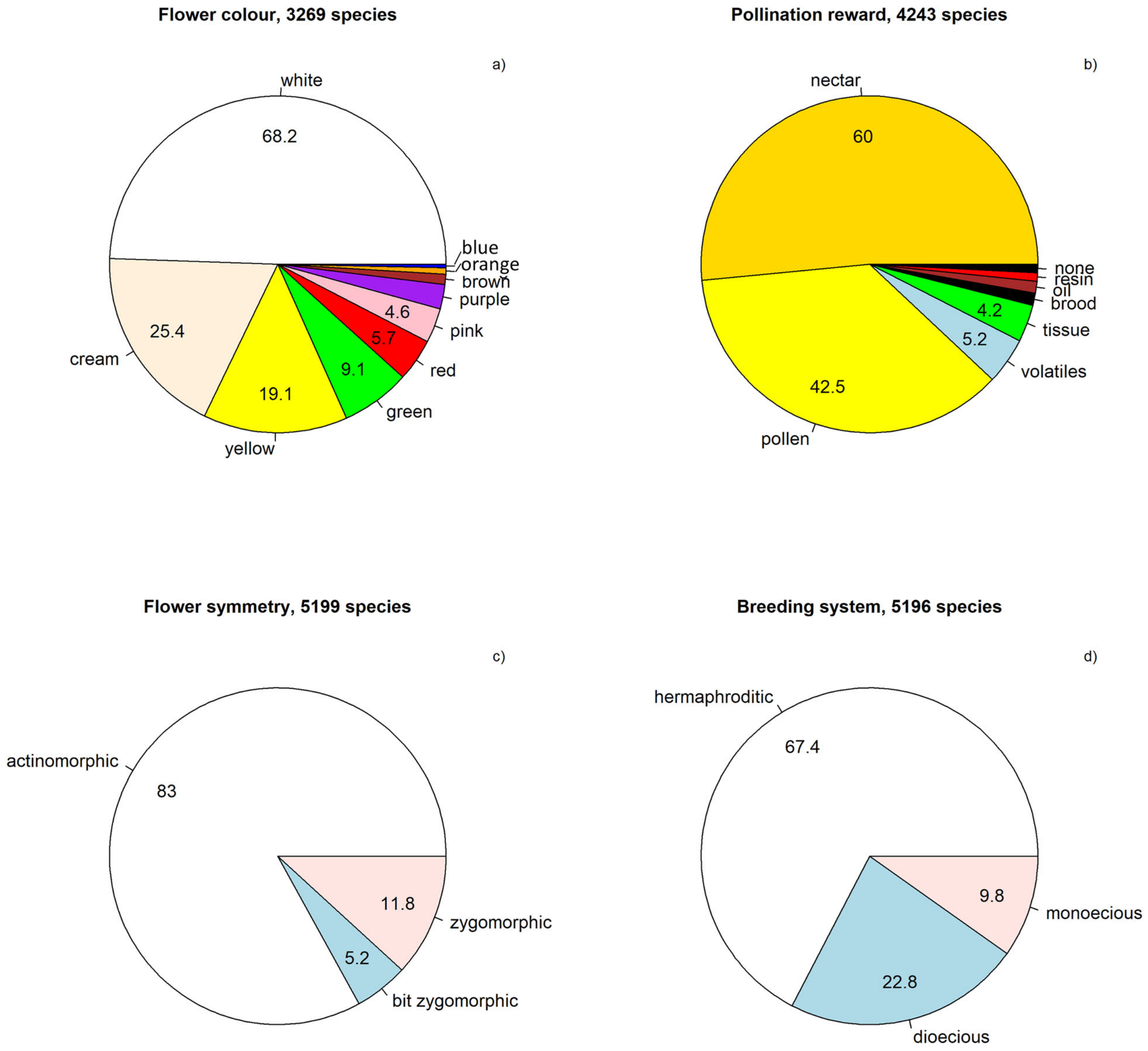

Fig. 4 | Flower characteristic of Amazonian trees. **a** Flower colour, **b** pollination reward, **c** Flower symmetry, and **d** breeding system for Amazonian tree species. Colours: Flower colour, colour following flower colour; reward colour, more or less representative to the colour of the substrate offered.

more than one dispersal mechanism. Barochorous seeds can de be dispersed by rodents and become synzoochorous, and hydrochorous seeds falling on land may become synzoochorous too. Correa et al[59] provide an interesting example – fruits of *Spondias mombin*, are eaten and moved by primates and dropped on the ground (synzochorous), where they can be swallowed by Tapir (endozoochorous), defecated in water and thus become hydrochorous. Many species may have such primary, secondary and perhaps tertiary dispersal. This highlights a substantial gap in research on the links between plant reproduction and animal partners in the region. Although numerous floristic and zoological inventories have been conducted in Amazonia, relatively few studies explicitly connect these two components through direct observation of ecological interactions. Addressing this gap is critical, as the disruption of plant–animal mutualisms is likely to generate cascading effects on community functioning that extend far beyond the loss of individual species[63].

It is also important to recognize that not all floral visitors are effective pollinators and this study did not assess the actual dependence of tree species on their pollinators or seed dispersers. Such information would require reproductive experiments, including pollinator or disperser exclusion and germination trials, to determine the degree of plant reliance on biotic pollination (e.g., compatibility systems and pollen limitation[64,65], the effectiveness of different animal groups in providing these services (pollinator performance[66]) and the contribution of dispersers to actual seedling establishment[67].

However, our findings at least indicate two complementary aspects: (i) the dependence of floral visitors and dispersers on these trees as sources of trophic resources (e.g., floral rewards and other floral tissues not typically considered resources, as well as seeds and fruits) and (ii) the importance of these animals for plant reproductive success, either by enhancing reproduction—through legitimate flower visits and effective pollen transfer for pollinators, or by facilitating seed dispersal for frugivores—or by reducing reproductive potential. Negative effects may occur through depletion of floral resources available to pollinators[68], consumption of floral tissues (e.g., pollen) that decreases attractiveness to other visitors[69], deposition of heterospecific pollen on stigmas[70], or through interactions with fruits and seeds, including seed predation[71], fruit consumption without effective seed dispersal, and the accumulation or caching of seeds for later use (scatter-hoarding)[68], which may limit seedling establishment.

We also recognize that our extrapolation of interactions from population size may introduce limitations in how precisely interaction frequency and identity can be inferred because: (i) inter- and intraspecific variation in flower production can span several orders of magnitude; (ii) energetic

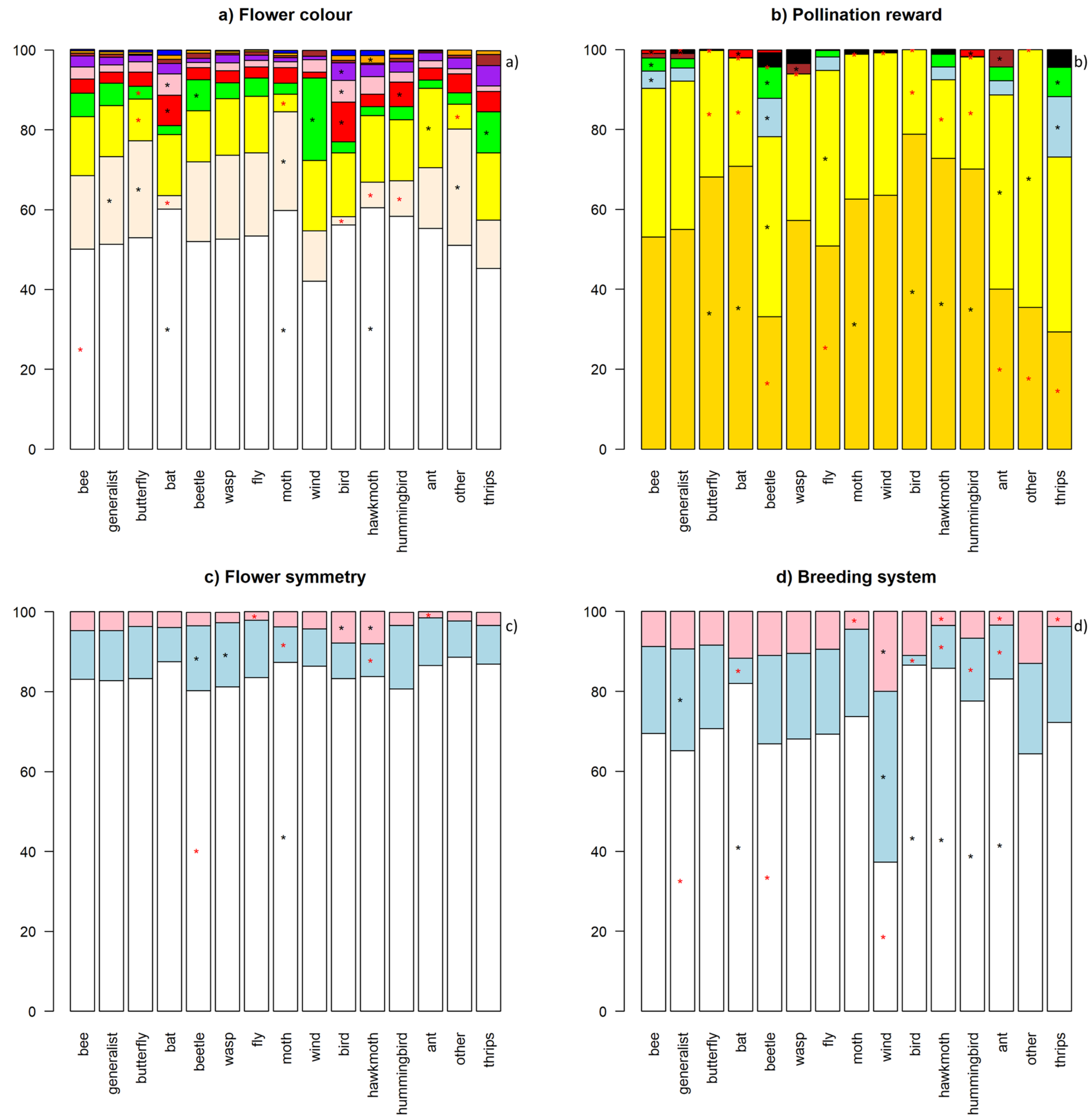

Fig. 5 | Interaction between flower visitors and flower traits (percentages). **a** Flower colour. Colours as in Fig. 4a. **b** Pollination reward. Colours as in Fig. 4b. **c** Flower symmetry: actinomorphic, slightly zygomorphic, zygomorphic. **d** Breeding: hermophroditic, dioecious, monoecious. Stars indicate significant Pearson residuals; black, positive; red, negative. See Supplementary Tables 5–9 for more information.

content of floral resources, fruits and seeds provided by different species may likewise vary greatly; and (iii) species with larger floral displays and greater resource abundance are not necessarily those receiving the highest visitation rates, as neighbourhood context, seasonality, climatic conditions, and even neutral effects can strongly influence visitation frequencies. In addition, grouping animal partners into broad categories may be simplistic, as taxonomic subsets within these groups can display distinct preferences. In pollination, this is particularly evident among bees, which differ in their ability to buzz-pollinate or collect floral oils and thereby exploit different resource niches. For other groups, such as bats and hummingbirds, these within-group differences are likely less pronounced.

Finally, we have assumed that pollination and dispersal interactions remain constant over different biomes, as we included flower visitation data from Cerrado, Atlantic rainforest and central American rainforests, while the Amazonian data was concentrated (but not unique) in two areas: Carajás, Para and central Amazonia. While understory and lower canopy trees are easier accessible and may be a larger part of our tree data, several studies did access canopy trees and specific canopy genera (e.g. *Pouteria*, genera of Lecythidaceae, *Ocotea*) are well presented in the data.

Our findings indicate bees to be the most common flower-visitors, consistent with global patterns in tropical forests[4,69]. However, the prevalence of multiple floral visitor groups (butterflies, flies, beetles, hummingbirds, bats) across a large proportion of the flora suggests that pollination systems in Amazonian trees are mostly generalized, with occasional specialization tied to particular flower morphology or rewards. The prevalence of generalist pollination systems may reflect an adaptive strategy

Table 3 | Nr of Amazonian tree species per dispersal category by family

Family	Endozoochory	Anemochory	Synzoochory	Explosive.dehiscence	Hydrochory	Unassisted	Myrmecochory	Epizoochory	shannon index	# dispersal types
Fabaceae	363	192	52	98	116	18	6	0	1.511	7
Lauraceae	324	0	10	0	0	0	0	0	0.135	2
Annonaceae	256	0	7	8	0	0	0	0	0.252	3
Rubiaceae	222	88	0	2	1	1	0	0	0.670	5
Sapotaceae	214	0	1	0	0	0	0	0	0.030	2
Myrtaceae	192	0	0	0	0	0	0	0	0.000	1
Melastomataceae	184	8	0	0	0	0	0	0	0.173	2
Euphorbiaceae	139	0	1	0	0	0	0	0	0.042	2
Chrysobalanaceae	129	0	73	0	0	0	0	0	0.654	2
Burseraceae	101	0	0	0	0	0	0	0	0.000	1

Last two columns give diversity of dispersal type, expressed as Shannon index, and the number of dispersal types found in the family. Table is ordered in flower-visitor interactions. Full family list in Supplementary Table 10.

in the face of diversity and spatial and temporal unpredictability of pollinators in tropical forests. So, in hyper-diverse environments such as Amazonia, we suggest that the dependence on multiple groups of visitors may increase the reproductive resilience of plant species in the face of variability in pollinator abundance.

Considering the pattern of the pollination systems of the species evaluated, biotic pollination prevailed, reinforcing the importance of pollinators in this studied biome. In fact, recent studies have shown that approximately 90% of plant species depend on animal pollinators to ensure their sexual reproduction[23,70,72]. The pattern tends to be stronger and more complex in tropical ecosystems. The large proportion of trees pollinated by bees — encompassing 60% of the species, 74% of the genera and up to 84% of the estimated number of individuals of our dataset — reinforces the central importance of bees as pollinators in the maintenance of biodiversity and ecological functioning. This dominance of bees recorded here as floral visitors is similar to previous studies[4,14,69]. However, it is worth noting that, among pollinators, bees also have the most species[73,74], and are among the best studied groups of pollinators in pollination systems in Brazil[14]. Our result may in part reflect this focus on bees.

Surprisingly, white and cream flowers dominate the colour spectrum even among bird pollinated species, which traditionally are associated with bright red or purple corollas (to which they still have an extra positive association in the data here, Supplementary Table 5). This pattern may further suggest that red coloration functions primarily as a bee-avoidance signal rather than as a bird-attraction cue[75,76]. As argued by Givnish and Patterson[77], low levels of narrow-spectrum, greenish light in rainforest do not favour the evolution of large, brightly coloured petals. Selection for small, visually inconspicuous flowers in forest subcanopy and understories presumably puts a premium on the use of scents rather than colour as floral attractants[77]. Most flowers are actinomorphic and bisexual which aligns with the generalist pattern of pollination observed[78], possibly reflecting evolutionary pressures to maximize visitation opportunities in a diverse but spatially dynamic pollinator community[79,80].

Whereas specialized pollination may drive plant speciation[81,82], species rich tree genera such as *Licania* s.l., *Pouteria* s.l. and *Inga*, have rather unspecialized pollination. In *Inga* and *Protium* the richness may be more driven by insect herbivory[83,84]. The 15 most species-rich genera (*Miconia*, *Myrcia*, *Palicourea*, *Eugenia*, *Inga*, *Pouteria*, *Ocotea*, *Swartzia*, *Ouratea*, *Clusia*, *Piper*, *Guatteria*, *Ficus*, *Solanum*, and *Protium*) exhibit a gradient from specialized to generalist pollination systems. On one end, *Miconia*, *Ouratea*, *Solanum*, and most Myrtaceae are buzz-pollinated; *Clusia* is frequently visited by resin-collecting bees; and *Ficus* relies on highly species-specific wasps. On the other end, genera such as *Inga* and *Palicourea* can be visited by multiple animal groups, ranging from insects like bees to vertebrates such as hummingbirds and bats. *Piper*, in contrast, may exhibit ambophily in many species, simultaneously relying on wind pollination and pollination by small generalist insects. Several of these genera have high levels of dioecy (*Protium*, *Pouteria*, *Ocotea*, *Clusia*), a sexual system associated with plain, small (except *Clusia* here), and actinomorphic flowers. Tree species with more generalized pollination and dispersal systems, *Pouteria* s.l., *Licania* s.l., and *Ocotea* s.l. may function as ecological buffers under disturbance. These generalists can maintain ecosystem functions when specialist interactions are disrupted and may act as hubs in mutualistic networks, contributing to the stability and resilience of ecological systems[8].

Despite the growing recognition and increase in studies of pollination systems, Amazonia still lacks in-depth studies on the spatial patterns and stability of these interactions. Given the increasing anthropogenic threats to the Amazonian biome — including deforestation, fragmentation, and the intensification of extreme events associated with climate change — it is of great importance to develop research that explores how these pressures affect the structure and resilience of pollination networks.

Conserving the forest and its pollinators will have positive consequences for people, as many wild pollinators will visit crops. In the Eastern Amazon, pollinators contribute nearly USD 1 billion to crop production[85]. Most fruits used by traditional communities within the forest depend on

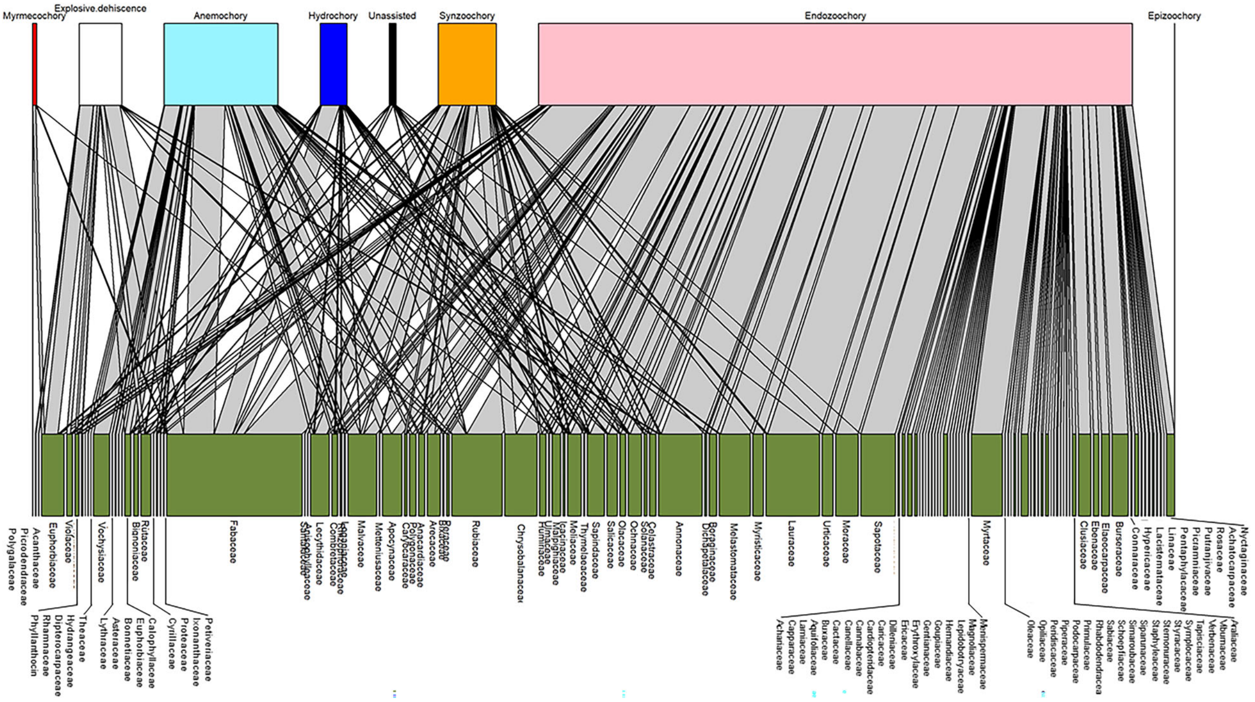

Fig. 6 | Network of disperser syndromes of Amazonian tree species by family. Based on the 2023 dispersal data[59]. The width of the bars indicate the sum of the interactions of the dispersal category (top) and the families (bottom).

insect pollination[17], with bees playing a key role in maintaining stable pollination services despite increasing deforestation across the biome[86].

Our results also confirm the overwhelming importance of animals in Amazonian tree dispersal, with 78–83% of species used in our dataset relying on frugivores, mainly primates, bats, and birds, and most fruits being fleshy with small to medium-sized seeds. These patterns mirror the findings that animal-mediated dispersal dominates even in human-modified Amazonian forests and that seed traits such as size and fleshiness might be tightly linked to dispersal mode[87]. A small subset of hyperdominant genera (e.g., *Eschweilera*, *Protium*, *Pouteria*, *Inga*, *Virola*, *Ocotea*) account for a disproportionate share of dispersal interactions, providing key resources for frugivores and potentially stabilizing dispersal networks[54]. Together, these results highlight the central role of animals in sustaining Amazonian tree populations, emphasizing that the loss of frugivores or hyperdominant fruiting trees could have cascading consequences for forest regeneration and community structure[53,60].

However, as other studies reviewing plant-frugivore interactions in Amazonia[88], there is a large gap in the knowledge of community-wide fruit–frugivore interactions, because most observational studies have focused on single or a few species. Although our knowledge on this type of interactions has increased[89,90], a wider coverage of plant species and its seed dispersal agents are still needed, as basic studies still find surprising discoveries. For example, on how parrots may play dispersal services by epizoochory[91] or how most seed predators may also act as effective seed dispersers[92,93]. Although seed dispersal networks are usually characterized as generalist systems, where dispersal modes depend on the abundance and efficiency of the dispersal agents[49], these systems are not randomly organized[88] and in many cases the plants may generate filters in terms of morphology and chemistry[94–96], which merit further attention.

The overwhelming reliance on animals for both key reproductive stages underscores a critical vulnerability: the ongoing defaunation in the Amazon—driven by habitat fragmentation, overhunting, infrastructure expansion, and climate change—may disrupt plant–animal mutualisms with consequences at multiple trophic levels[61,97,98]. Network-based conservation approaches, which prioritize the integrity of mutualistic relationships rather than species alone, offer a promising framework to anticipate cascading effects of species loss[63,99]. Large-bodied frugivores and specialized pollinators—often the first to disappear from disturbed landscapes—play disproportionately important roles in maintaining connectivity within these networks[60,100]. As such, conservation planning must integrate interaction redundancy and network robustness into forest management and restoration strategies[101,102].

Our upscaling approach highlights the disproportionate importance of certain genera, which, based on our extrapolation from population size, account for the majority of potential floral visitation and fruit/seed dispersal events among Amazonian trees. These species concentrate most interactions—engaging with a greater diversity of visitors and dispersal modes—and often provide key resources that span multiple ecological niches[103], a pattern that is not necessarily linked to their abundance. Identifying such species can reveal critical contributors to ecosystem functioning and the maintenance of plant–animal mutualisms, offering valuable guidance for conservation efforts, as their loss could trigger particularly strong cascading effects across the community.

Methods

Population sizes, range size, dominance, were obtained from published data of the Amazon Tree Diversity Network[1,2], and corrected for recent name changes, using the December 2023 WFO data (https://www.wfoplantlist.org/)[104].

Flower visitation

Flower visitation was obtained from Valadão-Mendes, et al.[14]. The database of Valadão-Mendes contained 7,778 plant-flower-visitor observations, which was extended by 54 new references and web searches (Amazonia, Central America, Atlantic Forest), to now include 19,799 records. For Amazonian tree species[58] it includes 14,076 records at genus level (for 542 of 808 genera) and 9,619 at species level (for 797 of 5,201 species). We selected all 797 species occurring in the Amazonian tree flora, and sub-selected those occurring in the ATDN lists[1,2], responsible for 34.1% of the number of Amazonian trees. With this data we generated a species level interaction matrix. Similarly, we made a matrix of genus level interaction matrix for flower visitation. In the matrices of flower visitation, the classes were: ant,

Table 4 | Dispersal and pollination interactions in the Amazonian tree community

	Endozoochory	Synzoochory	Myrmecochory	Epizoochory	Anemochory	Explosive.dehiscence	Hydrochory	Unassisted	Endozoochory	Synzoochory	Myrmecochory	Epizoochory	Anemochory	Explosive.dehiscence	Hydrochory	Unassisted
bee	2922	294	11	0	548	143	90	18	72.6	7.3	0.3	0.0	13.6	3.6	2.2	0.5
generalist	2606	154	6	1	418	101	53	15	77.7	4.6	0.2	0.0	12.5	3.0	1.6	0.5
beetle	1743	118	0	0	82	38	18	3	87.1	5.9	0.0	0.0	4.1	1.9	0.9	0.2
butterfly	1543	87	4	0	207	60	27	8	79.7	4.5	0.2	0.0	10.7	3.1	1.4	0.4
fly	1403	128	0	0	254	58	77	15	72.5	6.6	0.0	0.0	13.1	3.0	4.0	0.8
wasp	1283	122	4	0	210	30	18	8	76.6	7.3	0.2	0.0	12.5	1.8	1.1	0.5
moth	812	59	0	0	132	13	11	4	78.8	5.7	0.0	0.0	12.8	1.3	1.1	0.4
hawkmoth	546	62	1	0	211	5	10	2	65.2	7.4	0.1	0.0	25.2	0.6	1.2	0.2
hummingbird	518	12	0	0	165	68	9	8	66.4	1.5	0.0	0.0	21.2	8.7	1.2	1.0
ant	578	57	0	0	74	27	4	0	78.1	7.7	0.0	0.0	10.0	3.7	0.5	0.0
bat	356	65	6	0	162	85	36	2	50.0	9.1	0.8	0.0	22.8	11.9	5.1	0.3
bird	394	5	0	0	126	47	44	4	63.6	0.8	0.0	0.0	20.3	7.6	7.1	0.7
other	386	19	0	0	16	0	5	0	90.6	4.5	0.0	0.0	3.8	0.0	1.2	0.0
thrips	350	3	0	0	25	50	3	1	81.0	0.7	0.0	0.0	5.8	11.6	0.7	0.2
wind	326	4	12	0	84	30	34	1	66.4	0.8	2.4	0.0	17.1	6.1	6.9	0.2
wind	289	3	11	0	68	24	32	1	67.5	0.7	2.6	0.0	15.9	5.6	7.5	0.2

The cells provide species numbers (right) and percentages (left). Light brown, both pollination and dispersal are animal mediated (17,173 interactions, 79.5%); light green, either pollination or dispersal is animal mediated (4,303 interactions, 19.9%); light blue, neither pollination nor dispersal are animal mediated (125 instances, 0.6%).

bat, bee, beetle, bird, bug, butterfly, cockroach, cricket, flower bug, fly, generalist, green lacewing, hawkmoth, hummingbird, insect, lizard, mammal, mosquito, moth, small diverse insects, thrips, wasp, wind. We combined small diverse insects, generalist insects, and insect into generalist flower-visitor, and bug, cockroach, cricket, flower bug, green lacewing, lizard, mammal, and mosquito into the category 'other', as these had very few interactions. So alphabetically we used ant, bat, bee, beetle, bird, butterfly, fly, generalist, hawkmoth, hummingbird, moth, other, thrips, wasp, and wind. Although our search may not have been exhaustive, the last data that was included: "Atlantic flower invertebrate interactions"[15], added over 4,000 records for Amazonian tree species but hardly improved the quantitative information in the dataset from 89.7 to 90%. Finding the last 10% of flower/flower-visitor interaction data is likely very challenging at this moment, yet also is unlikely to massively change our results.

Flower characters

No standardization for flower characters, important for pollination, exist and databases for such characters are scarce[105]. So, we used various floras to obtain the minimum set of traits for which we were able to obtain information. Flower colour and size (either above or below 1 cm) were taken from a variety of flora's, notably[106–113] and web searches. If two colours were observed, both were scored in the data matrix. For analyses, if flower colour was creamy-white, or creamy-yellow the colour was taken as cream. If the flower was predominantly green, all other colours were ignored and the colour was taken as greenish. Nectar production was taken from[28] and scored as a percentage by genus. We first scored the percentage of species by genus and, if not available, we used the information by family. Information on other floral rewards was compiled from datasets[28] and[114] or extracted for each plant species based on studies describing floral traits and the distribution of rewards across plant families and genera[37,115,116]. Because species-level information was often lacking, rewards were primarily assigned at the genus level, supported by evidence from floral morphology (e.g., poricidal anthers data from[33]), floral visitor records, or known patterns of reward production within genera. Each species was then categorized into one of eight floral reward types: nectar, pollen, oil, resin, volatiles/tissue, brood, or no reward. Volatiles and floral tissues were grouped together due to the high representation of beetle-pollinated species, which are typically attracted by floral fragrances (with a reproductive function) and/or feed on tissues (with a trophic function).

Fruit, seed and dispersal data

Dispersal data was gathered by Pablo Stevenson and Diego Correa[59], and Matt McGlone, each at species level. Diego Correa and Pablo Stevenson[49,59] assigned dispersal modes to morphospecies, identified to the genus level if no variation in dispersal modes was found for species within genera. Dispersal modes were assigned to over 10,000 species and morphospecies. Both Stevenson and Correa, and McGlone created dispersal groups at species level but with different classes. Stevenson and Correa used: Anemochory, Hydrochory, Explosive dehiscence, Unassisted dispersal, Endozoochory, Synzoochory, Epizoochory, and Myrmecochory. McGlone used: Wind, Explosive dehiscence, Water dispersal, Unassisted dispersal, and dispersal by Ants, Terrestrial dispersal (mainly mammals and large birds), and finally Arboreal vertebrate dispersers (mainly primates, bats, birds).

Seed mass was taken from[117–119] and various floras and tree guides[106,107,120–122]. Because seed mass varies over several orders of magnitude, we used logarithmic classes for seed mass[118,123].

Fleshiness, which is a strong indicator of arboreal vertebrate dispersal was a combination of data from ter Steege, Stevenson, McGlone, at species level and gleaned from a large number of tree guides and floras, as above.

Breeding system

Breeding system may vary considerably in some genera and was taken at species level from[124] and descriptions from floras and monographs (in particular, *Flora e Funga do Brasil*. Jardim Botânico do Rio de Janeiro (http://floradobrasil.jbrj.gov.br/) issues of *Flora Neotropica* (https://www.springer.com/series/16365); and the Springer book series *The Families and Genera of Vascular Plants*[125–127], and other published revisions.

Analysis

Assuming that our sample is representative, in the results, percentages are based on the number of species for which data was observed per trait (the number of which is given).

Combining the above data resulted in a data matrix of 5,201 species and 68 data columns and one for 808 genera and 55 data columns. To obtain the number of estimated individuals for the comparisons, matrices (e.g for pollination or dispersal alone), were converted to matrices, only consisting of 0 and 1 values, which were multiplied by the vector of total Amazonian population size per species (or genus), resulting in matrices of the estimated number of individuals for each species-trait or genus-trait combination. Interaction results for the estimated number of Amazonian trees per species are based on the matrix with population estimates by species.

Statistics and reproducibility

We used mainly crosstabs and network analyses based on the crosstabs, using the R package *bipartite*[128]. We analysed the crosstabs with species count data, as contingency tables, with Chi square analysis. We assessed individual relationships in the tables with the Pearson residuals[129], the significance level based on a Bonferroni correction: $p < 0.05/(\text{number of cells in the table})$. Bootstraps of the percentage of genera visited by pollinator groups were carried out by selecting 251 publications with replacement from the 251 available publications, 10,000 times. We analysed the bootstrapped data with the package "bcaboot"[130]. *P*-values for Chi square Pearson residuals were calculated with standard R functions (Chitest()). Reproducibility was maintained by use of versioned scripts. All analyses were carried out with custom made R[131] scripts.

Reporting summary

Further information on research design is available in the Nature Portfolio Reporting Summary linked to this article.

Data availability

All data used is publicly available in the publications cited and available through https://doi.org/10.6084/m9.figshare.28417586.

Code availability

The code to reproduce the analyses and all figures are publicly available through https://doi.org/10.6084/m9.figshare.28417586.

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Author contributions

HtS conceived the study. HtS collected new literature with flower visitation data. RL provided new flower visitation data from the TreeCo database. TG added bee flower-visitation data. HtS, CB, and LVM added flower colour and size. CB collected data on pollination reward. PS, DC, HtS reviewed dispersal data and harmonized the two dispersal schemes. MM provided the plant breeding systems. HtS added seed mass. Fleshiness was collected by HtS and MM. HtS carried out the analyses and wrote the first version of the manuscript with contributions from CB and CEP. CB, CEP, LVM, PS, DC, TG, VG, RL, MM provided comments on and new text to the various manuscript versions and all authors approved the final version of the manuscript.

Competing interests

The authors declare no competing interests.

Additional information

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Correspondence and requests for materials should be addressed to Hans ter Steege.

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