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Differentiating nectar from pollen foraging affects estimates of specialization in plant-pollinator networks: a case study from the Bornean peat swamp forest canopy

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Abstract

Specialization is a core concept in the study of flowering plants and their relationships with floral visitors. In recent decades, researchers have increasingly used bipartite floral interaction networks to study these relationships. Networks are typically built from simple observations of floral visitation and ignore which resources visitors acquire during visits. However, flowers can provide nectar, pollen, or both, and floral visitor species may only forage for one or the other on a given plant. Here, using data we collected which differentiates nectar from pollen foraging for floral visitors to 15 Bornean rainforest tree species, we investigate whether estimates of specialization change when multiple floral resources are accounted for. We find that the same visitors have different estimated values of specialization when calculated using the overall visitation data (the standard approach), versus only nectar or pollen foraging. Differences in specialization estimates for flower-visiting taxa scale up to affect estimates of specialization for the whole community of floral visitors, with greater specialization found in nectar than pollen foraging. Our findings highlight some important considerations when using resource-agnostic visitation data in network-based studies of plant-pollinator relationships. In addition, this study represents one of the first network analyses of plant-pollinator interactions in a tropical rainforest canopy.

Introduction

Specialization is a core dimension of the relationships between flowering plants and floral visitors (Armbruster 2016; Waser and Ollerton 2006). While ecological specialization has been defined in many ways in the literature (Devictor *et al.* 2010), in the context of anthecology (the study of flowers, floral visitors, and their relationships), it broadly refers to how restrictive an organism is in terms of the partners it interacts with (Armbruster 2016; Baker 1983; Robertson 1895). The degree to which either participant in a plant-pollinator mutualism is specialized has implications for how reliant those species are on each other, whether that be a plant's dependency on a visitor as a pollinator, or a visitor's dependency on a flower as a source of nutritional resources. As such, specialization is at the centre of ongoing research on population dynamics, competition, community assembly, response to disturbance, co-evolutionary trajectories, and speciation in both flowering plants and anthophilous animals (Armbruster 2014, 2016; Benadi *et al.* 2013; Biesmeijer *et al.* 2006; Lomáscolo *et al.* 2019; Valdovinos and Marsland 2021). Given the central role that specialization plays in our understanding of the ecology and evolution of flowers and their visitors, it is important that we be able to measure it accurately and consistently.

In recent decades, researchers have increasingly used bipartite network analyses to assess specialization in communities of flowering plants and anthophilous animals (Knight *et al.* 2018). Anthecological systems are often highly diverse, and the relationships within them are complex. Analyzing these systems as ecological networks allows for the roles and positions of multiple taxa to be evaluated simultaneously, as well as enabling the investigation of emergent, system-level properties that might not be apparent from the study of individual taxa or smaller system sub-components (Bascompte 2009; Vizentin-Bugoni *et al.* 2018). Methods for quantifying specialization in bipartite networks facilitate its evaluation at multiple levels of organization, including the whole network, either 'party' (i.e., either all the plants or all the visitors in the network), the guild/functional group (e.g. 'bee', 'hummingbird'), and the individual species (Blüthgen *et al.* 2006; Fründ *et al.* 2016). These network-derived measures of specialization are integral to current research on a broad range of topics and provide the foundation for theoretical relationships between specialization and the dynamics of plant and pollinator communities. For example, network analyses have been used to show changes in community-level specialization in

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response to environmental drivers such as changing climate or land use (Chesshire *et al.* 2021; Kaiser-Bunbury *et al.* 2017; Shinohara *et al.* 2019), and in simulated networks, more specialized organisms and communities are less resilient to disturbance and experience higher extinction rates (Clavel *et al.* 2011; Weiner *et al.* 2014).

However, because the bipartite networks used in anthecological studies are typically built from observations of visits to flowers and do not include information on what resources visitors are acquiring, estimates of specialization from these networks may not accurately depict visitors' dependencies on floral hosts. In bipartite floral interaction networks, floral visitors and flowering plants are represented by nodes, which are connected by links that represent the presence and/or strength of a relationship between those nodes. In most published plant-pollinator network studies, the strength (or 'weight', in network parlance) of links is determined by rates of observed visitation and does not incorporate information on what resources visitors are acquiring. This is potentially problematic because floral visitors frequently require multiple floral resources, such as nectar, pollen, or floral oils, and may specialize to different degrees on each of the floral resources they use. For example, many bee species have specialized pollen diets, meaning they acquire pollen to provision their young from flowers of a limited set of plant taxa (typically referred to as 'oligolectic' bees, Danforth *et al.*, 2019; Waser and Ollerton, 2006). However, adults of these oligolectic bees often visit flowers of additional species to search for the nectar they need to fuel their foraging activity (Cane and Sipes 2006; Robertson 1925). In a network built from observations of visitation, oligolectic bees can appear to be generalized, while in reality their persistence hinges on access to a narrow subset of the flowers they visit (e.g. Gibson *et al.* 2024). Similar variation in resource-specific specialization may occur in other taxa that use multiple floral resources, such as the many flower-visiting beetle, fly, and bug species (Haslett 1989; Wäckers *et al.* 2007; Wedmann *et al.* 2021), although knowledge on floral resource specialization in these groups is relatively sparse.

While most anthecologists will be aware of examples where observed patterns of floral visitation are a poor proxy for the ecological specialization of a flower-visiting taxon, investigations of how this impacts the inferences made from floral visitation networks have been limited. Given the widespread use of network-derived measures of specialization, it is important to evaluate whether estimates of visitors' specialization from visitation networks are representative of their actual specialization on the resources they are foraging for, and how this propagates to community-level measures of specialization. One approach to answering this question is to compare visitation networks to pollen-use networks inferred from the pollen found on visitors' bodies (Tourbez *et al.* 2024), or in bee nests (Dorado *et al.* 2011; Gresty *et al.* 2018). However, direct comparisons of visitation networks to pollen-identification networks are complicated by difficulties in ensuring that both networks encapsulate the same spatial scale (Bosch *et al.* 2009), are sampled to a similar level of completeness (De Manincor *et al.* 2020), the fact that non-bee pollinators do not generally carry pollen destined for consumption externally, and the contamination of body pollen from sources that are not associated with pollen foraging (Vaknin *et al.* 2000). Furthermore, pollen-identification networks offer little insight into nectar specialization, and many floral visitors discriminate between nectar sources (Cronk and Ojeda 2008; Heinrich 2004). An analogous question from the plants' point of view, of how well visitation approximates specialization on specific pollinators, has been investigated several times (Ballantyne *et al.* 2015, 2017; Cirtwill *et al.* 2024; De Santiago Hernández *et al.* 2019; Jędrzejewska-Szmek and Zych 2013). These phytocentric studies typically find that visitation networks have more connections than networks of pollen deposition, and that plants in actuality rely on a subset of visiting species to achieve successful pollination. Thus, plants are more specialized than is implied by visitation data alone.

In this study, we use observations of floral interactions from the canopy of a tropical rainforest to compare the structure of a network built on visitation to that of networks built using only records of nectar or pollen foraging, respectively. Our study and data set are novel in several ways. Previously, only a handful of studies globally (across both temperate and tropical zones) have applied a network approach to study floral interactions in the forest canopy, and/or evaluated specialization of canopy pollinators (Swart *et al.* 2024; Wardhaugh *et al.* 2015). Furthermore, the Asian tropics are generally under-represented in the plant-pollinator network literature (Vizentin-Bugoni *et al.* 2018) (but see Hass *et al.* 2018; Simla *et al.* 2022; Sritongchuay *et al.* 2019a, 2019b for recent ground-level networks from the region). Historically, most tropical canopy plant pollinator research has been conducted using the handful of fixed canopy-access structures scattered around the world (e.g. Roubik 1993; Roubik *et al.* 2003, 2005; Van Dulmen 2001). By using rope-access techniques, we expand our research to a habitat type (tropical peat swamp forest) lacking such infrastructure, and to larger spatial scales than are accessible from fixed structures.

Specifically, we use our floral interaction data set to ask the following questions:

1. How different are estimates of flower visitor specialization when they are based on a visitation network versus a nectar-foraging or pollen-foraging network?
2. How different are estimates of specialization for the visitor community as a whole when they are based on a visitation network versus a nectar-foraging or pollen-foraging network?

Materials and methods

Study system and species

This study uses floral interaction data collected in the canopy and sub-canopy of a tropical peat swamp forest in Central Kalimantan, a province in Indonesian Borneo. Observations of floral interactions were made on locally occurring species of tree and woody shrub in the genus *Syzygium* (Myrtaceae, P. Browne ex Gaertn.). *Syzygium* is one of the world's most diverse genera of woody plant (Ahmad *et al.* 2016; Low *et al.* 2022), and it reaches peak diversity in the tropical rainforests of southeast Asia, where it is the most abundant and diverse tree genus in many types of forest (Cannon and Lerdau 2015; Slik *et al.* 2003). The open and accessible brush-like flowers are used as a source of pollen and nectar by a remarkably broad range of anthophilous taxa, including birds, bees, beetles, and butterflies (Boulter *et al.* 2005; Kuriakose *et al.* 2018; Lughadha and Proenca 1996). In Bornean peat swamp forests, the flowering of *Syzygium* species is not seasonally restricted, instead providing irregular resource pulses year-round (Harrison *et al.* 2016), including during seasons where alternative floral resources are lacking (as high as 38% of flowering trees during months with low overall flowering, unpubl. data). Thus, *Syzygium* species represent a key resource for the anthophilous communities within peat swamp forests.

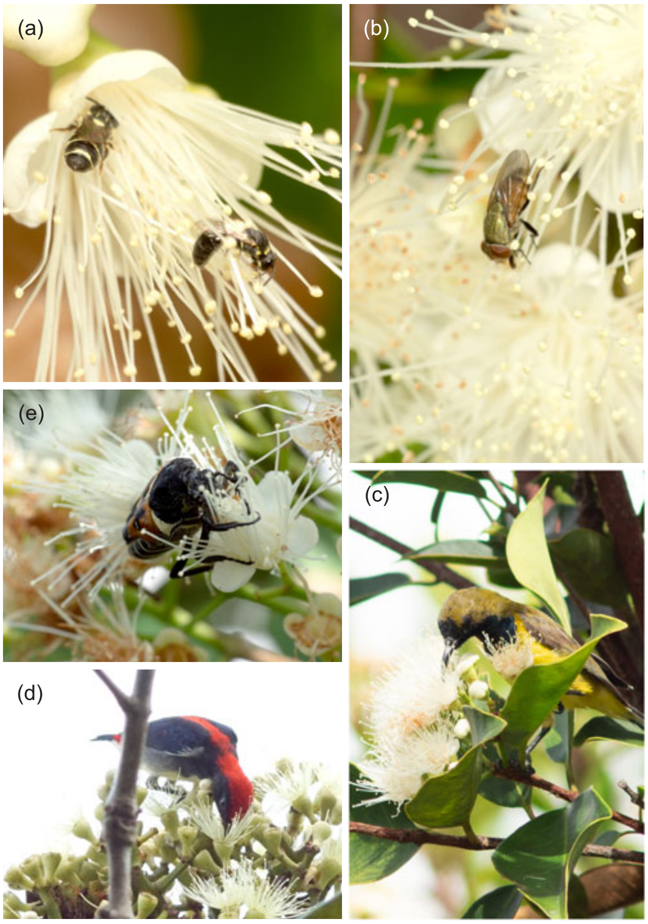

Figure 1. Examples of pollen and nectar foraging on *Syzygium* flowers. Clockwise from top-left: a. *Hylaeus penangensis* Cockerell and *Ceratina cf. nigrolateralis* foraging for pollen and nectar, respectively; b. nose fly (Rhiniidae sp.) consuming pollen; c. Olive-backed Sunbird (*Cinnyris jugularis* L.) nectaring; d. Scarlet-backed Flowerpecker (*Dicaeum cruentatum* L.) nectaring on *Syzygium oligmyrum* Diels; and e. flower chaffer (*Taeniodera sp.*) consuming *Syzygium* pollen.

We decided to restrict data collection to this single genus for several reasons. First, the deep hypanthium cup and filamentous stamens of *Syzygium* flowers facilitate the classification of resource use by floral visitors, enabling differentiation between flower visitors foraging for pollen versus nectar (Figure 1). Second, different species flower throughout the year, their flowers are easy to spot, and they attract high rates of visitation, enabling continuous data collection over the study period. Third, the wood qualities and branching architecture of *Syzygium* species facilitate safe access to canopy inflorescences, unlike many tropical peat swamp forest tree species. Studying a network restricted to interactions within a single plant genus may result in different estimates of visitor specialization than studying interactions across a whole community of plants, or even across a less closely related subset of the community, as pollinators often specialize on specific plant lineages while demonstrating generalized foraging patterns within those lineages (Robertson 1925; Waser and Ollerton 2006). However, the main objective of this work is not to estimate specialization for specific taxa or to compare specialization across different communities, but rather to explore how different approaches to building networks can influence our understanding of specialization in a single community.

Data collection was conducted in the vicinity of the Tuanan Research Center, which is located within the recently listed Mawas Protected Area, one of the largest remnant patches of peat swamp forest in Central Kalimantan. Study trees were distributed across a mixture of primary peat swamp forest, recovering (post-fire) forest edge, and recently deforested/burnt habitat. Each individual study tree was assigned to a species by experts in the genus (see Acknowledgements), although determining the correct scientific binomial was not always possible given the unresolved state of taxonomy for the genus in the region (Ahmad *et al.* 2016).

Few studies of floral visitors have been conducted in Bornean peat swamp forests, and as such, their identities and taxonomies remain largely unknown. Vertebrate visitors, including nectarivorous birds in several families and nectarivorous bats in the Pteropodidae, are important pollinators in many Bornean forests (Kato 1996; Roubik *et al.* 2005; Sakai 2000). They tend to be well described and can consistently be identified to the species level (Phillipps and Phillipps 2014, 2016). Conversely, invertebrate floral visitors at Tuanan are likely to belong to poorly understood groups with incomplete taxonomies, for which comprehensive identification resources don't exist. Indeed, a few recent invertebrate surveys at Tuanan have encountered species new to science, as well as new records for the region (Dow and Silvius 2014; Widowati *et al.* 2023, Issa Bettencourt pers. comm.)

Data collection

Between October 2022 and July 2023, AA observed visitation and resource-foraging on flowers of 15 co-occurring *Syzygium* species at Tuanan (Table 1). Walking surveys for blooming trees were conducted weekly, and once discovered, trees were selected for inclusion based on ease-of-access, safety for climbing, and the amount of data already collected for that species. Ultimately, 37 individual flowering trees located within a 1.6 km radius of the station were included in the study. Observations were carried out from shortly after sunrise to shortly after sunset, as long as it was not raining. Typically, 2–3 trees were visited during a field day with good weather. Visitors to *Syzygium* flowers were observed in 30-minute periods, during which all visitors to a clump of 1–3 inflorescences (5–200 flowers) were recorded. Visitors were assigned to consistently identifiable and mutually exclusive visual morphogroups (Table 2). For each visitor morphogroup, we recorded the number of individuals that visited flowers (defined as any visitor that touched the perianth or floral reproductive parts), and among those, how many foraged for pollen and/or nectar. As such, the pollen- and nectar-foraging data are subsets of the visitation data. A total of 152 such observation periods were conducted (76 hours). Observations were conducted at a maximum distance of 3 m from the inflorescences, using insect binoculars (Pentax Papilio II 6.5×21). Most observations were conducted in the canopy, which was accessed using ropes. On the forest edge, where flowers extend to near ground level, and on some shrubby *Syzygium* species, observations were conducted from the ground. Immediately after visual observations, voucher specimens of invertebrate visitors were collected from the same part of the tree for 15 minutes (total netting time, excluding processing time), to provide higher taxonomic resolution information on visual morphogroup composition (Table S2).

In the first days of canopy observations, it became apparent that vertebrate visitors were affected by the observer's presence in the canopy. Thereafter, all observations of vertebrate visitors were conducted from the ground or lower canopy using 10×42 birding

Table 1. *Syzygium* trees in included in this study. *Syzygium* species were identified by AA, Dr. Yee Wen Low (Singapore Botanic Gardens), Dr. Peter Ashton (Arnold Arboretum, Harvard University, emeritus), and Bina Swasta Sitepu (Wanariset Harbarium) from pressed specimens. Pressed specimens for each tree included in the study were deposited at the Wanariset Herbarium in Samboja, Indonesia

Scientific name	Local name	# of indv.	# obs. rds.
Syzygium indet. sp. 2	Galam tikus	3	30
Syzygium subgenus *Syzygium* sp. 2	Galam tikus daun besar	1	3
Syzygium aff. *travancoricum*	Galam tikus jangkar	1	5
Syzygium subgenus *Syzygium* sp. 3	Jambu burung	1	12
Syzygium cf. *incarnatum*	Tapuhut putih	3	18
Syzygium subgenus *Oborapi* sp. 1	Tapuhut ungu	3	15
Syzygium subgenus *Syzygium* sp. 1	Tatumbu kalepang	3	27
Syzygium cf. *syzygioides*	Tatumbu kasar	4	32
Syzygium cf. *nigricans*	Tatumbu pohon merah	2	9
Syzygium oligomyrum	Tatumbu putih	7	55
Syzygium zeylanicum	Tatumbu tabaras	2	13
Syzygium cf. *pyrifolium*	Tatumbu tabatik	2	10
Syzygium subgenus *Sequestratum* sp. 1	Tatumbu rohat	1	15
Syzygium acuminatissimum	Tatumbu ungu	1	2
Syzygium indet. sp. 1	Tatumbu buah merah #2	1	5

binoculars, either prior to climbing into the canopy to observe the insects or after canopy work was completed. In these vertebrate observation rounds (100 in total, or 50 hours), which were separate from and in addition to the invertebrate observation rounds, all vertebrates that drank nectar from flowers on the visible part of the tree were recorded. No vertebrates were observed to consume pollen or purposefully interact with stamens and anthers.

To assess the potential importance of nocturnal flower visitors such as bats and moths, AA conducted 13 hours of crepuscular/nocturnal observation in 2022–2023. Nocturnal invertebrate and vertebrate observation rounds were conducted in the same way as their diurnal counterparts, including canopy observations, but a high-power red-light headlamp was used to illuminate inflorescences. Bats and most nocturnal invertebrates (including moths) have been shown not to respond to red light sources (Brehm *et al.* 2021; Briscoe and Chittka 2001; Spoelstra *et al.* 2017), minimizing behavioural interference. No nocturnal vertebrate pollinators were observed, and mean rates of invertebrate visitation were very low (<4 per hour, compared with ~23 per hour for diurnal sampling). Nonetheless, to ascertain the absence of nocturnal vertebrate pollinators, field workers conducted an additional 36 hours of nocturnal observations from July to December 2024, using red-light headlamps and night-vision cameras, during which no nocturnal vertebrate visitors were recorded. The 2024 observations were limited to the subcanopy and or canopies on the forest edge with a clear line-of-sight from the ground.

Analytical approach

To investigate how estimates of specialization from resource-indiscriminate visitation data compare to estimates of specialization based exclusively on nectar or pollen foraging, we built three separate weighted (i.e., including information about interaction frequency) bipartite networks and calculated the same set of specialization metrics for each. In the first network, weights of interactions were determined by the number of times a visitor morphogroup (Table 2) was observed visiting a *Syzygium* species (Table 1, see Tables S1–S3 for detailed information on *Syzygium* species and visitor morphogroup compositions). In the two resource-specific networks, only visits that included the observed use of either nectar or pollen were included ('nectar-foraging' and 'pollen-foraging' networks, respectively).

To compare visitor specialization across networks, we calculated d', a commonly used specialization metric, for each visitor morphogroup in each network (Blüthgen *et al.* 2006). For visitor nodes (which typically represent a visitor taxon, such as a species or genus), d' is a measure of the Shannon diversity of the 'community' of plant species it interacts with, rescaled between 0 (least specialized) and 1 (most specialized). A visitor node's specialization is assessed relative to the 'availability' of the plant species in the network, which is measured as the frequency with which each plant is visited by all the visitors in the network. A d' of 0 signifies that a flower visitor interacts with plant species exactly proportionally to how often they interact with all the visitors in the network (i.e. proportionally to their weighted degrees). A high d' indicates that a visitor species interacts with plant species non-randomly, and typically corresponds to the observed use of just one interaction partner. Since plants' weighted degrees are calculated independently in each of the three networks we consider here (all visitation, nectar foraging, and pollen foraging), a visitor species' resource-specific foraging may be more proportional to availability for one resource, and therefore score as less specialized (lower d'), even if it visits fewer *Syzygium* species for that resource than it does for the other. This differs from classical measures of specialization based on raw counts of the number of interaction partners (Armbruster 2016; Waser and Ollerton 2006), where a visitor would not be able to measure as less specialized in a network where it had fewer interaction partners. The classical, count-based metrics are highly sensitive to sample size (i.e., the number of plant-pollinator interactions observed in the network), which has led to their decline in use in favour of d' and related measures (Dormann 2011; Fründ *et al.* 2016).

Table 2. Visitor morphogroups used in this study. All groups are mutually exclusive (e.g. ‘other flies’ does not include members of the family Culicidae). Tax. res. indicates the smallest taxonomic level that encompasses all group members. Information on the composition of morphogroups according to collected voucher specimens can be found in supplementary Tables S2–3

Invertebrate group	Order	Taxon name	Tax. res.	Total obs.
elaterids + cerambycids	Coleoptera	Elateridae/ Cerambycidae	superfamily/ family	133
scarabs	Coleoptera	Scarabaeidae	family	27
tiny beetles	Coleoptera	Coleoptera	order	37
small beetles	Coleoptera	Coleoptera	order	109
medium beetles	Coleoptera	Coleoptera	order	30
mosquitos	Diptera	Culicidae	family	15
other flies	Diptera	Diptera	order	140
Apis	Hymenoptera	*Apis*	genus	13
Megachile	Hymenoptera	*Megachile*	genus	25
Nomia	Hymenoptera	*Nomia*	genus	36
stingless bees	Hymenoptera	Meliponini	tribe	251
Xylocopa	Hymenoptera	*Xylocopa*	genus	48
tiny bees	Hymenoptera	Anthophila	suprafamilial clade	181
small bees	Hymenoptera	Anthophila	suprafamilial clade	178
medium bees	Hymenoptera	Anthophila	suprafamilial clade	20
large bees	Hymenoptera	Anthophila	suprafamilial clade	6
ants	Hymenoptera	Formicidae	family	200
hover wasps	Hymenoptera	Stenogastrinae	subfamily	77
other wasps	Hymenoptera	Hymenoptera	order	79
butterflies	Lepidoptera	Rhopalocera	suborder	43
moths	Lepidoptera	Lepidoptera	order	23
roaches	Blattodea	Blattodea	order	7
bugs	Hemiptera	Hemiptera	order	6
Vertebrate group	Class	Taxon name	Tax. res.*	Total obs.
spiderhunters	Aves	*Arachnothera*	genus	32
sunbirds	Aves	Nectariniidae	family	178
flowerpeckers	Aves	Dicaeidae	family	63
other birds	Aves	Passeriformes	order	15
squirrels	Mammalia	*Callosciurus*	genus	5

After computing d’ for each visitor morphogroup in each network, we calculated the difference in visitor morphogroup specialization values between the nectar-foraging network and the visitation network ($d'_{nectar} - d'_{visits} = \Delta d'_{nectar}$) and between the pollen-foraging network and the visitation network ($d'_{pollen} - d'_{visits} = \Delta d'_{pollen}$) (Figure 2). We also tested whether morphogroups were significantly more or less specialized, on average, in the resource-specific networks than the visitation network using paired *t*-tests on the d’ values of morphogroups that were present in both the visitation network and each resource-specific network. Additionally, because raw values of d’ are difficult to interpret ecologically, we graphically demonstrate differences in how each network ranks visitor morphogroups in terms of specialization in Figure 3.

To assess how differences in estimates of visitor morphogroup specialization scale up to affect estimates of specialization at higher levels of biological organization, we calculated the weighted mean d’ for the entire flower visitor community in each network ($\langle d'_{visitors} \rangle$, following Blüthgen *et al.* 2006). Because this community-level metric can be sensitive to differences in network size (i.e., differences in the number of included taxa and their interaction totals) (Fründ *et al.* 2016), which varied across our three networks, we generated null expectations of specialization for the visitation network at different sizes by randomly removing interactions and recalculating $\langle d'_{visitors} \rangle$. We then compared the observed $\langle d'_{visitors} \rangle$ for each resource-specific network to the distribution of rarefied null $\langle d'_{visitors} \rangle$ values (Figure 4). The whole-network equivalent of $\langle d'_{visitors} \rangle$, which includes both plants and visitors and is known as H2’, is more frequently encountered in the literature. However, we opt to report $\langle d'_{visitors} \rangle$ here because it is more directly related to our question of *visitor* specialization. Evaluating H2’ instead of $\langle d'_{visitors} \rangle$ did not qualitatively change the results (Figure S1).

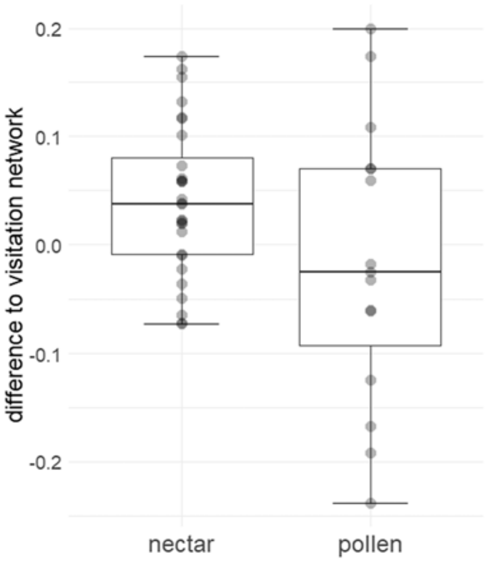

Figure 2. Boxplots of the difference in visitor morphogroup specialization between resource-specific networks and the visitation network. The y-axis values are the differences in d' value for the same morphogroups between the visitation and the nectar foraging networks ($d'_{nectar} - d'_{visits}$) and the visitation and the pollen foraging networks ($d'_{pollen} - d'_{visits}$), respectively. Each point represents a single visitor morphogroup. Nectar specialization was significantly higher than visitation specialization on average (paired *t*-test *p* value = 0.005), while pollen specialization often differed in magnitude, but was not significantly higher or lower on average (paired *t*-test *p* value = 0.648).

All analyses were conducted in R (R Core Team 2023), and the following packages were used to conduct analyses and generate figures: dplyr, ggplot2, bipartite, igraph, tidyr, forcats, ggpubr, rstatix (Csárdi *et al.* 2024; Dormann *et al.* 2008; Kassambara 2023a, 2023b; Wickham 2016, 2023; Wickham *et al.* 2023a, 2023b).

Results

We observed a total of 1977 visits by individuals from 28 visitor morphogroups to 15 *Syzygium* species. Individuals from all 28 visitor morphogroups foraged on nectar, and all 15 *Syzygium* species served as a source of nectar for at least one visitor morphogroup. A total of 1112 nectar foraging visits were observed. The pollen-foraging network was smaller, with 614 pollen foraging visits by 15 visitor morphogroups to 11 *Syzygium* species. Identification of vertebrate visitors in the field and of voucher specimens of invertebrates in the lab resulted in 297 unique visitor species and morphospecies (Tables S2–3). Invertebrate visitors were predominant, with 766 visits by bees (Hymenoptera: Anthophila), 337 by beetles (Coleoptera), 200 by ants (Hymenoptera: Formicidae), 157 by wasps (Hymenoptera), 155 by flies (Diptera), and a handful of visits by a diversity of other insect orders (e.g. Lepidoptera, Blattodea, Hemiptera). Floral visits by invertebrates that were exclusively ambush predators and did not consume nectar or pollen were excluded from the networks (Mantodea [4 visits] and Salticidae [1]), as were visits by invertebrate orders with fewer than 5 total recorded visits (Orthoptera [2] and Dermaptera [1]). Vertebrate observation rounds recorded 260 visits by birds from several families and one species of squirrel (Table S3).

Visitors in the nectar-foraging network were more specialized (paired *t*-test $p = 0.005$), and visitors in the pollen-foraging network similarly specialized (paired *t*-test $p = 0.648$), as compared with the network based on all flower visitation (Figure 2). For the 28 visitor morphogroups included in the nectar-foraging network, mean $\Delta d'_{nectar}$ was 0.04 (range: −0.07 to 0.17), indicating that they were, on average, more specialized for nectar foraging than for all flower visitation. Overall, 71% of morphogroups (20/28) were more specialized in the nectar-foraging network than they were in the all visitation network. For the 15 visitor morphogroups included in the pollen-foraging network, mean $\Delta d'_{pollen}$ was −0.02 (range: −0.24 to 0.2), indicating that species were, on average, less specialized for pollen foraging than for all flower visitation. Overall, 40% (6/15) of morphogroups were less specialized in the pollen-foraging network than they were in the all visitation network.

One way to assess how much accounting for the type of floral resource a visitor forages on during visits affects estimates of its specialization is to ask whether the rank order of groups, from most to least specialized, changes across the interaction networks. For the 15 visitor morphogroups observed foraging on both pollen and nectar, we compared rankings based on the all visitation network with those based on resource-specific networks. Most morphogroups changed rank across these networks, and in many cases, the shifts were substantial. On average, the same morphogroup's specialization rank differed by 3.3 positions between any two networks, with differences as large as 12 ranks (Figure 3). These shifts indicate that a visitor considered relatively generalized when all visits are treated equally might appear much more specialized when only pollen or nectar foraging is considered.

The visitor community as a whole was more specialized in the nectar-foraging network than it was in all visitation network ($<d'_{poll}> = 0.287$ and 0.253 for the observed nectar-foraging and all visitation networks, respectively). Comparison to rarefaction null visitation networks of the same size as the nectar-foraging network found the difference in specialization to be highly significant ($p \leq 0.001$) (Figure 4). The visitor community also scored as more specialized in the pollen-foraging network than in the all visitation network ($<d'_{poll}> = 0.277$ in the pollen-foraging network). However, that score was well within the range of rarefied null visitation networks of the same size as the pollen-foraging network ($p = 0.90$), indicating the difference in specialization was non-significant.

Discussion

The extent to which a flower-feeding animal is specialized — that is, how restrictive it is in terms of the diversity of flowering plant species it acquires resources from — is an important dimension of its ecology and natural history. Yet the plant-pollinator networks used to evaluate specialization are typically based upon observations of flower visits, and do not distinguish whether the flower visitor is foraging for pollen or nectar. In reality, visitors may be more selective about where they acquire one or the other resource, creating an opportunity for resource-indiscriminate visitation data to misrepresent visitors' dependencies on the plants they visit. Research on the analogous potential for visitation networks to misrepresent plants' dependencies on visitors as pollinators has shown that plants are frequently more specialized than is implied by visitation networks (Ballantyne *et al.* 2015, 2017; De Santiago-Hernández *et al.* 2019; King *et al.* 2013). Surprisingly, given the attention devoted to the phytocentric perspective, analogous investigations from the visitors' point of view have been limited.

We accessed the canopy of a tropical rainforest to collect a floral interaction dataset that differentiates pollen and nectar foraging, and compared how a traditional visitation-based network differed from networks built on pollen- or nectar-foraging in their estimates of floral visitor specialization. We found that a floral

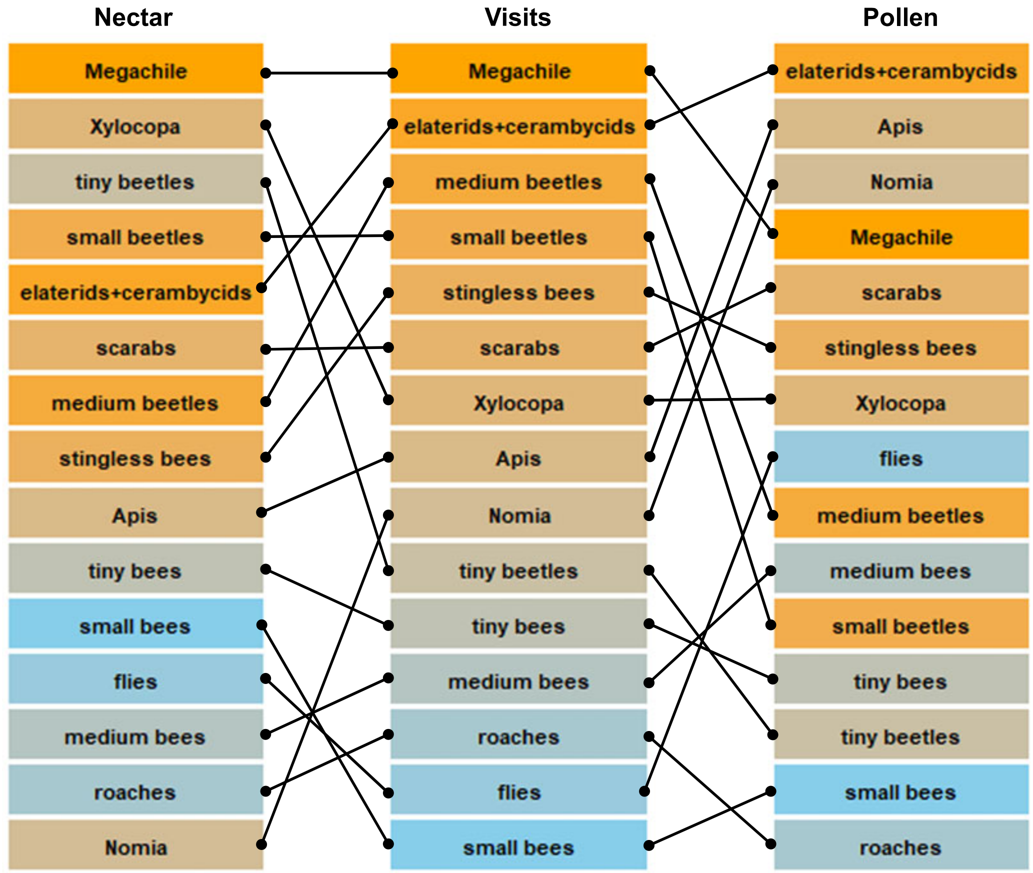

Figure 3. Visitor morphogroups ranked in decreasing order of specialization in each network. Fill colour represents relative specialization in the visitation network (orange = most specialized, blue = least specialized). Lines connect the same visitor morphogroups between networks. Only the 15 morphogroups that foraged on both nectar and pollen are included.

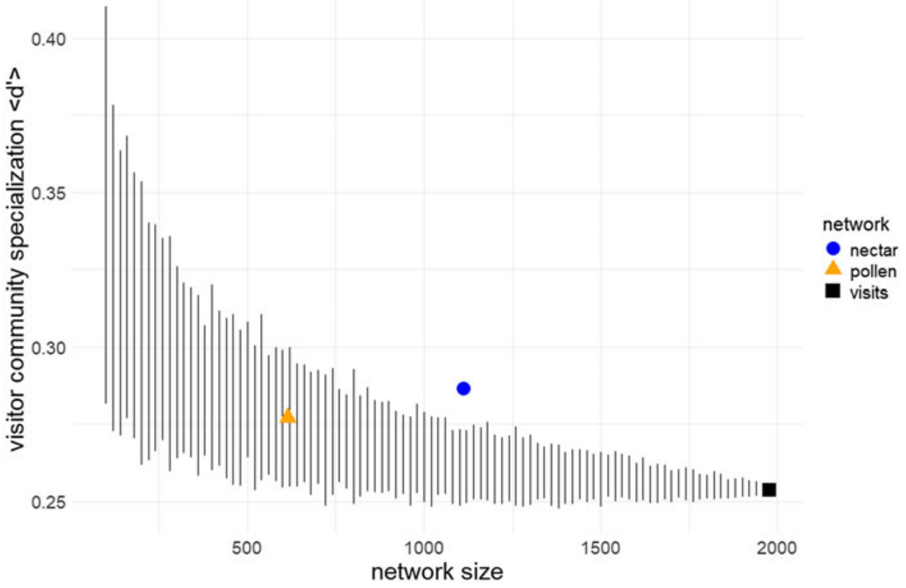

Figure 4. $\langle d'_{\text{visitors}} \rangle$ (visitor community weighted mean d') plotted against network size (total number of observed interactions) for the visitation, nectar-foraging, and pollen-foraging networks. Error bars represent the inner 95% of $\langle d'_{\text{visitors}} \rangle$ values for 99 rarefactions of the visitation network repeated at 20-interaction intervals.

interaction network built on resource-agnostic visitation data resulted in markedly different estimates of visitor specialization than did networks that reflect resource use (Figures 2 and 3). Likewise, specialization as measured for the entire flower-visitor community differed between the visitation-based network and the pollen- and nectar-foraging networks (Figure 4). Previously, significant differences between visitation-based and resource-specific specialization have been found when comparing visitation networks to networks inferred from the scopal pollen loads of bees (Tourbez *et al.* 2024). However, it has been unclear to what degree observed differences in specialization between visitation networks and pollen-identification networks is attributable to bees foraging for pollen unevenly on the plants they visit, as opposed to the tendency for pollen identification to provide more complete sampling of interactions (De Manincor *et al.* 2020), especially for rare visitor species (Dorado *et al.* 2011). By using a system where nectar and pollen foraging can be differentiated during visits, we minimize the influence of sampling at different scales and levels of completeness, expand our analysis beyond the realm of bees, and compare nectar-specific foraging networks to pollen-foraging and visitation-derived networks for the first time.

As well as differences in the estimated values of specialization between networks, there were pronounced differences among our networks in terms of how flower visitors were *ranked* for specialization. The most specialized morphogroups in either of the resource-foraging networks were often amongst the more generalized morphogroups in the visitation network, and vice versa. This is well exemplified by the bee genus *Nomia* Latreille. Of the 15 visitor morphogroups that foraged on *Syzygium* for both pollen and nectar, *Nomia* were the least specialized nectar foragers, firmly in the middle of the pack in the visitation network (9th most specialized), and the 3rd most specialized pollen foragers (Figure 3). These findings highlight the potential for visitation networks to misidentify the most specialized taxa in a community of floral visitors.

Most visitors were more specialized in the nectar-foraging network than they were in the visitation network. The tendency for visitors to be more specialized nectar-foragers carried through to affect estimates of specialization for the whole visitor community, with the result that nectar-foraging was more specialized than either pollen-foraging or visitation at the network level. While the sign of the difference in specialization between the pollen-foraging and visitation networks was less predictable, the magnitudes of those differences were often large, with visitor morphogroups differing by as much as 24% of the maximum range of the d’ metric between the two. Though our findings appear to contradict the established theory that pollen-foraging is, on average, more specialized than nectar foraging (at least for bees) (Cane and Sipes 2006; Danforth *et al.* 2019; Strickler 1979), it is perhaps not that surprising for a network which includes members of only one plant genus. From the point of view of pollen-foragers, *Syzygium* flowers may be largely interchangeable, with similar floral morphology to deal with when collecting pollen, and potentially similar pollen nutrient composition (insofar as pollen composition may be a phylogenetically conserved trait [Ruedenauer *et al.* 2019], though as far as we are aware that has not been studied in the Myrtaceae). Conversely, we observed substantial variation in per-flower nectar volume and nectar sugar concentrations amongst the *Syzygium* species in this study (Figure S2). Resulting differences in the economics of foraging on different *Syzygium* flowers may explain the increased specialization in nectar foraging (Heinrich 2004; Roubik 1996). Further studies that consider a wider taxonomic range of plant species are needed to establish the generality of our findings.

The inability of the undifferentiated visitation data to accurately represent the resource-specialization of floral visitors questions the findings of a large body of network-based literature on specialization in plant and pollinator communities. Interestingly, many early studies on specialization in anthophilous animals did distinguish between floral resources, including foundational research by 19th and early 20th-century anthecologists (Robertson 1925; Waser 2006). For instance, early research on temperate bees showed that they tended to be more selective about sources of larval provisions (typically pollen) than they were about sources of nectar. As a result, bees are defined as specialists or generalists based on the diversity of larval provision sources alone (Cane and Sipes 2006; Danforth *et al.* 2019; Strickler 1979). However, with the advent of network approaches easier-to-collect visitation data have become the norm, and these data are now frequently used to compare specialization both within the same network and across different visitor communities (Petanidou and Potts 2006, provides an example of both). The growing availability of published visitation networks has also stimulated meta-analysis of network-derived specialization metrics (Knight *et al.* 2018; López-Vázquez *et al.* 2024; Vizentin-Bugoni *et al.* 2018). Because, as we have shown, the links between plants and animals in a visitation network may not be representative of their true interdependencies, comparisons across systems that provide different resources, or between taxa with different floral resource requirements, may be affected. For example, a global comparison of specialization of insect pollinator taxa found that in warm climates bee species had a broader set of floral interaction partners, on average, than other insect pollinators (Saunders *et al.* 2023). However, because bee species on average visit flowers for more different resources (including pollen and nectar, but in some cases also floral oils or volatiles) than species from other insect groups included in the analysis (such as wasps or butterflies, which rarely consume pollen), there is more opportunity for them to appear generalized while in fact specializing on a more restricted set of plants for at least one floral resource.

The literature on geographic gradients in plant and pollinator specialization also relies heavily on visitation networks, despite clear differences across latitudes and regions in the diversity of floral resource types provided to floral visitors. As noted by Armbruster (2006), pollen and nectar rewards are ubiquitous across latitudes, whereas floral oils and brood-site provision are restricted to subarctic latitudes, and the provision of fragrant volatiles or resins as rewards is restricted to the tropics and subtropics. Consequently, opportunities for specialized mutualisms to be masked by resource-agnostic visitation data may increase with decreasing latitude. There are also trends in the identities and resource requirements of major pollinating taxa (Armbruster 2006), which may affect biases in visitation networks—for example, primarily nectivorous bats and birds are absent from higher latitudes, and there are often strong altitudinal gradients in the functional diversity of pollinator taxa (Dellinger *et al.* 2023). Thus, conclusions that pollinator communities at lower latitudes (Saunders *et al.* 2023; Schleuning *et al.* 2012) and lower elevations (Olesen and Jordano 2002) are more generalized should be revisited, taking into account correlated trends in diversity of resources provided by flowers and utilized by visitors.

By using data collected in the canopy of a Southeast Asian tropical forest, this study helps fill geographic, biome, and forest-stratal gaps in the plant-pollinator network literature (Vizentin-Bugoni *et al.* 2018; Zanata *et al.* 2017). We found only two previous studies that applied a network approach to studying floral interactions in the forest canopy, both of which also used Bluthgen’s family of network specialization metrics to evaluate the specialization of canopy pollinators. Wardhaugh *et al.* (2015) used a canopy crane in tropical forests in northern Australia to study beetle assemblages and found similar degrees of specialization in anthophilous and folivorous beetles, contrary to theoretical expectations. Swart *et al.* (2024) used rope access to study network structure and specialization amongst visitors to four tree species with similar floral morphology in a temperate montane forest in South Africa, using observations of visits to estimate pollinator specialization (pollen from visitor bodies was also identified, but not used to estimate specialization of visitor taxa). While most pollinators visited all four tree species and scored relatively low (highly generalized) values of d’, they showed clear preferences for some trees over others, despite the generalized morphology of the flowers. The latter study, along with the work we present here, is representative of a growing movement amongst anthecologists to escape the confines of fixed canopy infrastructure by using elevated traps (Roubik 1993; Ulyshen *et al.* 2010; Urban-Mead *et al.* 2021), canopy cameras (Droissart *et al.* 2021), or rope access (Reyes *et al.* 2021; Swart *et al.* 2024), which has led to significant gains of knowledge on canopy pollination and pollinator ecology in recent years. Nonetheless, despite the increasing flexibility offered by these methods and the proliferation of anthecological research in recent decades (Knight *et al.* 2018), as far as we are aware this study represents the first published plant-pollinator network study from the canopy of an Asian forest, the first study of floral interactions in a Bornean peat swamp forest, and one of only a handful of published plant-pollinator networks from tropical Asia, generally.

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References

Ahmad B, Baider C, Bernardini B, Biffin E, Brambach F, Burslem D, Byng JW, Christenhusz M, Florens FBV, Lucas E, Ray A, Ray R, Smets E, Snow N, Strijk JS, Wilson PG and Syzygium Working Group (2016) *Syzygium* (Myrtaceae): monographing a taxonomic giant via 22 coordinated regional revisions. *PeerJ Preprints* **4**, e1930v1.

Armbruster S (2006) *Evolutionary and ecological aspects of specialized pollination: views from the arctic to the tropics*. In Waser N and Ollerton J (eds), *Plant-Pollinator Interactions: from Specialization to Generalization*. Chicago: University of Chicago Press, 260–282.

Armbruster WS (2014) Floral specialization and angiosperm diversity: phenotypic divergence, fitness trade-offs and realized pollination accuracy. *AoB PLANTS* **6**, plu003. https://doi.org/10.1093/aobpla/plu003.

Armbruster WS (2016) The specialization continuum in pollination systems: diversity of concepts and implications for ecology, evolution and conservation. *Functional Ecology* **31**(1), 88–100. https://doi.org/10.1111/1365-2435.12783.

Baker HG (1983) *An outline of the history of anthecology, or pollination biology*. In Jones CE and Little RJ (eds), *Pollination Biology*. New York: Elsevier, 7–28.

Ballantyne G, Baldock KCR, Rendell L and Willmer PG (2017) Pollinator importance networks illustrate the crucial value of bees in a highly speciose plant community. *Scientific Reports* **7**(1), 8389. https://doi.org/10.1038/s41598-017-08798-x.

Ballantyne G, Baldock KCR and Willmer PG (2015) Constructing more informative plant–pollinator networks: visitation and pollen deposition networks in a heathland plant community. *Proceedings of the Royal Society B: Biological Sciences* **282**(1814), 20151130. https://doi.org/10.1098/rspb.2015.1130.

Bascompte J (2009) Mutualistic networks. *Frontiers in Ecology and the Environment* **7**(8), 429–436. https://doi.org/10.1890/080026.

Benadi G, Blüthgen N, Hovestadt T and Poethke H-J (2013) Contrasting specialization–stability relationships in plant–animal mutualistic systems. *Ecological Modelling* **258**, 65–73. https://doi.org/10.1016/j.ecolmodel.2013.03.002.

Biesmeijer JC, Roberts SPM, Reemer M, Ohlemüller R, Edwards M, Peeters T, Schaffers AP, Potts SG, Kleukers R, Thomas CD, Settele J and Kunin WE (2006) Parallel declines in pollinators and insect-pollinated plants in Britain and the Netherlands. *Science* **313**(5785), 351–354. https://doi.org/10.1126/science.1127863.

Blüthgen N, Menzel F and Blüthgen N (2006) Measuring specialization in species interaction networks. *BMC Ecology* **6**(1), 9. https://doi.org/10.1186/1472-6785-6-9.

Bosch J, Martín González AM, Rodrigo A and Navarro D (2009) Plant–pollinator networks: adding the pollinator’s perspective. *Ecology Letters* **12**(5), 409–419. https://doi.org/10.1111/j.1461-0248.2009.01296.x.

Boulter SL, Kitching RL, Howlett BG and Goodall K (2005) Any which way will do – the pollination biology of a northern Australian rainforest canopy tree (Syzygium sayeri; Myrtaceae). *Botanical Journal of the Linnean Society* **149**(1), 69–84. https://doi.org/10.1111/j.1095-8339.2005.00430.x.

Brehm G, Niermann J, Jaimes Nino LM, Enseling D, Jüstel T, Axmacher JC, Warrant E and Fiedler K (2021) Moths are strongly attracted to ultraviolet and blue radiation. *Insect Conservation and Diversity* **14**(2), 188–198. https://doi.org/10.1111/icad.12476.

Briscoe AD and Chittka L (2001) The evolution of color vision in insects. *Annual Review of Entomology* **46**(1), 471–510. https://doi.org/10.1146/annurev.ento.46.1.471.

Cane JH and Sipes J (2006) *Characterizing floral specialization by bees*. In *Plant-Pollinator Interactions: from Specialization to Generalization*. Chicago: University of Chicago Press.

Cannon CH and Lerdau M (2015) Variable mating behaviors and the maintenance of tropical biodiversity. *Frontiers in Genetics* **66**, 183. https://doi.org/10.3389/fgene.2015.00183.

Chesshire PR, McCabe LM and Cobb NS (2021) Variation in plant–pollinator network structure along the elevational gradient of the San Francisco Peaks, Arizona. *Insects* **12**(12), 1060. https://doi.org/10.3390/insects12121060.

Cirtwill AR, Wirta H, Kaartinen R, Ballantyne G, Stone GN, Cunnold H, Tiusanen M and Roslin T (2024) Flower-visitor and pollen-load data provide complementary insight into species and individual network roles. *Oikos* **2024**(4), e10301. https://doi.org/10.1111/oik.10301.

Clavel J, Julliard R and Devictor V (2011) Worldwide decline of specialist species: toward a global functional homogenization? *Frontiers in Ecology and the Environment* **9**(4), 222–228. https://doi.org/10.1890/080216.

Cronk Q and Ojeda I (2008) Bird-pollinated flowers in an evolutionary and molecular context. *Journal of Experimental Botany* **59**(4), 715–727. https://doi.org/10.1093/jxb/ern009.

Csárdi G, Nepusz T, Müller K, Horvát S, Traag V, Zanini F and Noom D (2024, February 20) igraph for R: R interface of the igraph library for graph theory and network analysis. (Version v2.0.2). Zenodo. https://doi.org/10.5281/ZENODO.7682609.

Danforth BN, Minckley RL, Neff JL and Fawcett F (2019) *The Solitary Bees: Biology, Evolution, Conservation*. Princeton: Princeton University Press.

De Manincor N, Hautekèete N, Mazoyer C, Moreau P, Piquot Y, Schatz B, Schmitt E, Zélazny M and Massol F (2020) How biased is our perception of plant-pollinator networks? A comparison of visit- and pollen-based representations of the same networks. *Acta Oecologica* **105**, 103551. https://doi.org/10.1016/j.actao.2020.103551.

De Santiago-Hernández MH, Martén-Rodríguez S, Lopezaraiza-Mikel M, Oyama K, González-Rodríguez A and Quesada M (2019) The role of pollination effectiveness on the attributes of interaction networks: from floral visitation to plant fitness. *Ecology* **100**(10), e02803. https://doi.org/10.1002/ecy.2803.

Dellinger AS, Hamilton AM, Wessinger CA and Smith SD (2023) Opposing patterns of altitude-driven pollinator turnover in the tropical and temperate Americas. *The American Naturalist* **202**(2), 152–165. https://doi.org/10.1086/725017.

Devictor V, Clavel J, Julliard R, Lavergne S, Mouillot D, Thuiller W, Venail P, Villéger S and Mouquet N (2010) Defining and measuring ecological specialization. *Journal of Applied Ecology* **47**(1), 15–25. https://doi.org/10.1111/j.1365-2664.2009.01744.x.

Dorado J, Vázquez DP, Stevani EL and Chacoff NP (2011) Rareness and specialization in plant–pollinator networks. *Ecology* **92**(1), 19–25. https://doi.org/10.1890/10-0794.1.

Dormann CF (2011) How to be a specialist? Quantifying specialisation in pollination networks. *Network Biology* **1**(1), 1–20.

Dormann CF, Gruber B and Fründ J (2008) Introducing the bipartite package: analysing ecological networks. *R News* **8**(2), 8–11.

Dow RA and Silvius M (2014) Results of an Odonata survey carried out in the peatlands of Central Kalimantan, Indonesia, in 2012. *Journal of the International Dragonfly Fund* **7**, 41.

Droissart V, Azandi L, Onguene ER, Savignac M, Smith TB and Deblauwe V (2021) PICT: a low-cost, modular, open-source camera trap system to study plant–insect interactions. *Methods in Ecology and Evolution* **12**(8), 1389–1396. https://doi.org/10.1111/2041-210X.13618.

Fründ J, McCann KS and Williams NM (2016) Sampling bias is a challenge for quantifying specialization and network structure: lessons from a quantitative niche model. *Oikos* **125**(4), 502–513. https://doi.org/10.1111/oik.02256.

Gibson SD, Onuferko TM, Myers L and Colla SR (2024) Determining the plant-pollinator network in a culturally significant food and medicine garden in the Great Lakes region. *PeerJ* **12**, e17401. https://doi.org/10.7717/peerj.17401.

Gresty CEA, Clare E, Devey DS, Cowan RS, Csiba L, Malakasi P, Lewis OT and Willis KJ (2018) Flower preferences and pollen transport networks for cavity-nesting solitary bees: Implications for the design of agri-environment schemes. *Ecology and Evolution* **8**(15), 7574–7587. https://doi.org/10.1002/ece3.4234.

Harrison ME, Zweifel N, Husson SJ, Cheyne SM, D'Arcy LJ, Harsanto FA, Morrogh-Bernard HC, Purwanto A, Rahmatd, Santiano, Vogel ER, Wich SA and Noordwijk MA (2016) Disparity in onset timing and frequency of flowering and fruiting events in two Bornean peat-swamp forests. *Biotropica* **48**(2), 188–197. https://doi.org/10.1111/btp.12265.

Haslett JR (1989) Interpreting patterns of resource utilization: randomness and selectivity in pollen feeding by adult hoverflies. *Oecologia* **78**(4), 433–442. https://doi.org/10.1007/BF00378732.

Hass AL, Liese B, Heong KL, Settele J, Tscharntke T and Westphal C (2018) Plant-pollinator interactions and bee functional diversity are driven by agroforests in rice-dominated landscapes. *Agriculture, Ecosystems & Environment* **253**, 140–147. https://doi.org/10.1016/j.agee.2017.10.019.

Heinrich B (2004) *Bumblebee Economics*, 2nd edn. Cambridge: Harvard University Press.

Jędrzejewska-Szmek K and Zych M (2013) Flower-visitor and pollen transport networks in a large city: structure and properties. *Arthropod-Plant Interactions* **7**(5), 503–516. https://doi.org/10.1007/s11829-013-9274-z.

Kaiser-Bunbury CN, Mougal J, Whittington AE, Valentin T, Gabriel R, Olesen JM and Blüthgen N (2017) Ecosystem restoration strengthens pollination network resilience and function. *Nature* **542**(7640), 223–227. https://doi.org/10.1038/nature21071.

Kassambara A (2023a) ggpubr: 'ggplot2' based publication ready plots. https://rpkgs.datanovia.com/ggpubr/

Kassambara A (2023b) rstatix: Pipe-friendly framework for basic statistical tests. https://rpkgs.datanovia.com/rstatix/

Kato M (1996) Plant-pollinator interactions in the understory of a lowland mixed dipterocarp forest in Sarawak. *American Journal of Botany* **83**(6), 732–743. https://doi.org/10.1002/j.1537-2197.1996.tb12762.x.

King C, Ballantyne G and Willmer PG (2013) Why flower visitation is a poor proxy for pollination: measuring single-visit pollen deposition, with implications for pollination networks and conservation. *Methods in Ecology and Evolution* **4**(9), 811–818. https://doi.org/10.1111/2041-210X.12074.

Knight TM, Ashman T-L, Bennett JM, Burns JH, Passonneau S and Steets JA (2018) Reflections on, and visions for, the changing field of pollination ecology. *Ecology Letters* **21**(8), 1282–1295. https://doi.org/10.1111/ele.13094.

Kuriakose G, Sinu PA and Shivanna KR (2018) Floral traits predict pollination syndrome in Syzygium species: a study on four endemic species of the Western Ghats, India. *Australian Journal of Botany* **66**(7), 575. https://doi.org/10.1071/BT18042.

Lomáscolo SB, Giannini N, Chacoff NP, Castro-Urgal R and Vázquez DP (2019) Inferring coevolution in a plant–pollinator network. *Oikos* **128**(6), 775–789. https://doi.org/10.1111/oik.05960.

López-Vázquez K, Lara C, Corcuera P, Castillo-Guevara C and Cuautle M (2024) The human touch: a meta-analysis of anthropogenic effects on plant-pollinator interaction networks. *PeerJ* **12**, e17647. https://doi.org/10.7717/peerj.17647.

Low YW, Rajaraman S, Tomlin CM, Ahmad JA, Ardi WH, Armstrong K, Athen P, Berhaman A, Bone RE, Cheek M, Cho NRW, Choo LM, Cowie ID, Crayn D, Fleck SJ, Ford AJ, Forster PI, Girmansyah D, Goyder DJ, Gray B, Heatubun CD, Ibrahim A, Ibrahim B, Jayasinghe HD, Kalat MA, Kathriarachchi HS, Kintamani E, Koh SL, Lai JTK, Lee SML, Leong PKF, Lim WH, Lum SKY, Mahyuni R, McDonald WJF, Metali F, Mustaqim WA, Naiki A, Ngo KM, Niissalo M, Ranasinghe S, Repin R, Rustiami H, Simbiak VI, Sukri RS, Sunarti S, Trethowan LA, Trias-Blasi A, Vasconcelos TNC, Wanma JF, Widodo P, Wijesundara DSA, Worboys S, Yap JW, Yong KT, Khew GSW, Salojärvi J, Michael TP, Middleton DJ, Burslem DFRP, Lindqvist C, Lucas EJ and Albert VA (2022) Genomic insights into rapid speciation within the world's largest tree genus Syzygium. *Nature Communications* **13**(1), 5031. https://doi.org/10.1038/s41467-022-32637-x.

Lughadha EN and Proenca C (1996) A survey of the reproductive biology of the Myrtoideae (Myrtaceae). *Annals of the Missouri Botanical Garden* **83**(4), 480. https://doi.org/10.2307/2399990.

Olesen JM and Jordano P (2002) Geographic patterns in plant–pollinator mutualistic networks. *Ecology* **83**(9), 2416–2424. https://doi.org/10.1890/0012-9658(2002)083[2416:GPIPPM]2.0.CO;2.

Petanidou T and Potts SG (2006) *Mutual use of resources in Mediterranean plant–pollinator communities: how specialized are pollination webs*. In Waser NM and Ollerton J (eds), *Plant–Pollinator Interactions: From Specialization to Generalization*. Chicago: University of Chicago Press, 220–244.

Phillipps Q and Phillipps K (2014) *Phillipps' Field Guide to the Birds of Borneo: Sabah, Sarawak, Brunei, and Kalimantan*, 3rd edn. Princeton: Princeton University Press.

Phillipps Q and Phillipps K (2016) *Phillipps' Field Guide to the Mammals of Borneo: Sabah, Sarawak, Brunei, and Kalimantan*. Princeton: Princeton University Press.

R Core Team (2023) *R: A Language and Environment for Statistical Computing*. Vienna, Austria: R Foundation for Statistical Computing. https://www.R-project.org/

Reyes HC, Draper D and Marques I (2021) Pollination in the rainforest: scarce visitors and low effective pollinators limit the fruiting success of tropical orchids. *Insects* **12**(10), 856. https://doi.org/10.3390/insects12100856.

Robertson C (1895) The philosophy of flower seasons, and the phaenological relations of the entomophilous glora and the anthophilous insect fauna. *The American Naturalist* **29**(338), 97–117. https://doi.org/10.1086/276089.

Robertson C (1925) Heterotropic bees. *Ecology* **6**(4), 412–436. https://doi.org/10.2307/1929107.

Roubik DW (1993) Tropical pollinators in the canopy and understory: field data and theory for stratum? preferences? *Journal of Insect Behavior* **6**(6), 659–673. https://doi.org/10.1007/BF01201668.

Roubik DW (1996) *Wild bees of Brunei Darussalam*. In Edwards DS, Booth WE, and Choy SC (eds), *Tropical Rainforest Research — Current Issues*, Vol. **74**. Dordrecht: Springer Netherlands, 59–66.

Roubik DW, Sakai S and Gattesco F (2003) *Canopy flowers and certainty: loose niches revisited*. In Lowman MD and Rinker HB (eds), *Tropical Forest Canopies: Ecology and Management*. New York: Springer, 261–282.

Roubik DW, Sakai S and Karim AAH (eds) (2005) *Pollination Ecology and the Rain Forest: Sarawak Studies*. New York: Springer.

Ruedenauer FA, Spaethe J, Van Der Kooi CJ and Leonhardt SD (2019) Pollinator or pedigree: which factors determine the evolution of pollen nutrients? *Oecologia* **191**(2), 349–358. https://doi.org/10.1007/s00442-019-04494-x.

Sakai S (2000) Reproductive phenology of gingers in a lowland mixed dipterocarp forest in Borneo. *Journal of Tropical Ecology* **16**(3), 337–354. https://doi.org/10.1017/S0266467400001449.

Saunders ME, Kendall LK, Lanuza JB, Hall MA, Rader R and Stavert JR (2023) Climate mediates roles of pollinator species in plant–pollinator networks. *Global Ecology and Biogeography* **32**(4), 511–518. https://doi.org/10.1111/geb.13643.

Schleuning M, Fründ J, Klein A-M, Abrahamczyk S, Alarcón R, Albrecht M, Andersson GKS, Bazarian S, Böhning-Gaese K, Bommarco R, Dalsgaard B, Dehling DM, Gotlieb A, Hagen M, Hickler T, Holzschuh A, Kaiser-Bunbury CN, Kreft H, Morris RJ, Sandel B, Sutherland WJ, Svenning J-C, Tscharntke T, Watts S, Weiner CN, Werner M, Williams NM, Winqvist C, Dormann CF and Blüthgen N (2012) Specialization of mutualistic interaction networks decreases toward tropical latitudes. *Current Biology* **22**(20), 1925–1931. https://doi.org/10.1016/j.cub.2012.08.015.

Shinohara N, Uchida K and Yoshida T (2019) Contrasting effects of land-use changes on herbivory and pollination networks. *Ecology and Evolution* **9**(23), 13585–13595. https://doi.org/10.1002/ece3.5814.

Simla P, Chaianunporn T, Sankamethawee W, Hughes AC and Sritongchuay T (2022) Effect of landscape composition and invasive plants on pollination networks of Smallholder Orchards in Northeastern Thailand. *Plants* **11**(15), 1976. https://doi.org/10.3390/plants11151976.

Slik JWF, Poulsen AD, Ashton PS, Cannon CH, Eichhorn KAO, Kartawinata K, Lanniari I, Nagamasu H, Nakagawa M, Van Nieuwstadt MGL, Payne J, Purwaningsih, Saridan A, Sidiyasa K, Verburg RW, Webb CO and Wilkie P (2003) A floristic analysis of the lowland dipterocarp forests of Borneo. *Journal of Biogeography* **30**(10), 1517–1531. https://doi.org/10.1046/j.1365-2699.2003.00967.x.

Spoelstra K, Van Grunsven RHA, Ramakers JJC, Ferguson KB, Raap T, Donners M, Veenendaal EM and Visser ME (2017) Response of bats to light with different spectra: light-shy and agile bat presence is affected by white and green, but not red light. *Proceedings of the Royal Society B: Biological Sciences* **284**(1855), 20170075. https://doi.org/10.1098/rspb.2017.0075.

Sritongchuay T, Hughes AC and Bumrungsri S (2019a) The role of bats in pollination networks is influenced by landscape structure. *Global Ecology and Conservation* **20**, e00702. https://doi.org/10.1016/j.gecco.2019.e00702.

Sritongchuay T, Hughes AC, Memmott J and Bumrungsri S (2019b) Forest proximity and lowland mosaic increase robustness of tropical pollination networks in mixed fruit orchards. *Landscape and Urban Planning* **192**, 103646. https://doi.org/10.1016/j.landurbplan.2019.103646.

Strickler K (1979) Specialization and foraging efficiency of solitary bees. *Ecology* **60**(5), 998–1009. https://doi.org/10.2307/1936868.

Swart RC, Geerts S, Pryke JS and Coetzee A (2024) Generalist southern African temperate forest canopy tree species have distinct pollinator communities partially predicted by floral traits. *Austral Ecology* **49**(5), e13523. https://doi.org/10.1111/aec.13523.

Tourbez C, Gómez-Martínez C, González-Estévez MÁ and Lázaro A (2024) Pollen analysis reveals the effects of uncovered interactions, pollen-carrying structures, and pollinator sex on the structure of wild bee–plant networks. *Insect Science* **31**(3), 971–988. https://doi.org/10.1111/1744-7917.13267.

Ulyshen MD, Soon V and Hanula JL (2010) On the vertical distribution of bees in a temperate deciduous forest. *Insect Conservation and Diversity* **3**, 222–228. https://doi.org/10.1111/j.1752-4598.2010.00092.x.

Urban-Mead KR, Muñiz P, Gillung J, Espinoza A, Fordyce R, Van Dyke M, McArt SH and Danforth BN (2021) Bees in the trees: diverse spring fauna in temperate forest edge canopies. *Forest Ecology and Management* **482**, 118903. https://doi.org/10.1016/j.foreco.2020.118903.

Vaknin Y, Gan-Mor S, Bechar A, Ronen B and Eisikowitch D (2000) *The role of electrostatic forces in pollination*. In Dafni A, Hesse M and Pacini E (eds), *Pollen and Pollination*. Vienna: Springer Vienna, 133–142.

Valdovinos FS and Marsland R (2021) Niche theory for mutualism: a graphical approach to plant-pollinator network dynamics. *The American Naturalist* **197**(4), 393–404. https://doi.org/10.1086/712831.

Van Dulmen A (2001) Pollination and phenology of flowers in the canopy of two contrasting rain forest types in Amazonia, Colombia. *Forestry Sciences* **153**, 73–85. https://doi.org/10.1007/978-94-017-3606-0_7.

Vizentin-Bugoni J, Maruyama PK, De Souza CS, Ollerton J, Rech AR and Sazima M (2018) *Plant-pollinator networks in the tropics: a review*. In Dáttilo W and Rico-Gray V (eds), *Ecological Networks in the Tropics*. Cham: Springer International Publishing, 73–91.

Wäckers FL, Romeis J and Van Rijn P (2007) Nectar and pollen feeding by insect herbivores and implications for multitrophic interactions. *Annual Review of Entomology* **52**(1), 301–323. https://doi.org/10.1146/annurev.ento.52.110405.091352.

Wardhaugh CW, Edwards W and Stork NE (2015) The specialization and structure of antagonistic and mutualistic networks of beetles on rainforest canopy trees: network structure and specialization. *Biological Journal of the Linnean Society* **114**(2), 287–295. https://doi.org/10.1111/bij.12430.

Waser NM (2006) *Specialization and generalization in plant-pollinator interactions: a historical perspective*. In *Plant-Pollinator Interactions: from Specialization to Generalization*. Chicago: Univ. Chicago Press, 3–17.

Waser NM and Ollerton J (eds) (2006) *Plant-Pollinator Interactions: from Specialization to Generalization*. Chicago: University of Chicago Press.

Wedmann S, Hörnschemeyer T, Engel MS, Zetter R and Grímsson F (2021) The last meal of an Eocene pollen-feeding fly. *Current Biology* **31**(9), 2020–2026.e4. https://doi.org/10.1016/j.cub.2021.02.025.

Weiner CN, Werner M, Linsenmair KE and Blüthgen N (2014) Land-use impacts on plant–pollinator networks: interaction strength and specialization predict pollinator declines. *Ecology* **95**(2), 466–474. https://doi.org/10.1890/13-0436.1.

Wickham H (2016) *ggplot2: Elegant Graphics for Data Analysis*. New York: Springer-Verlag.

Wickham H (2023) forcats: Tools for working with categorical variables (factors). https://forcats.tidyverse.org/

Wickham H, François R, Henry L, Müller K and Vaughan D (2023a) dplyr: A grammar of data manipulation. https://CRAN.R-project.org/package=dplyr

Wickham H, Vaughan D and Girlich M (2023b) tidyr: Tidy messy data. https://CRAN.R-project.org/package=tidyr

Widowati R, Maulana RG and Atmoko SSU (2023) Inventory of stingless bees based on nesting and nest trees at Tuanan Orangutan Research Station Central Kalimantan Indonesia. *European Chemical Bulletin* **12**(S3), 2246–2256.

Zanata TB, Dalsgaard B, Passos FC, Cotton PA, Roper JJ, Maruyama PK, Fischer E, Schleuning M, Martín González AM, Vizentin-Bugoni J, Franklin DC, Abrahamczyk S, Alárcon R, Araujo AC, Araújo FP, Azevedo-Junior SMDE, Baquero AC, Böhning-Gaese K, Carstensen DW, Chupil H, Coelho AG, Faria RR, Hořák D, Ingversen TT, Janeček Š, Kohler G, Lara C, Las-Casas FMG, Lopes AV, Machado AO, Machado CG, Machado IC, Maglianesi MA, Malucelli TS, Mohd-Azlan J, Moura AC, Oliveira GM, Oliveira PE, Ornelas JF, Riegert J, Rodrigues LC, Rosero-Lasprilla L, Rui AM, Sazima M, Schmid B, Sedláček O, Timmermann A, Vollstädt MGR, Wang Z, Watts S, Rahbek C and Varassin IG (2017) Global patterns of interaction specialization in bird–flower networks. *Journal of Biogeography* **44**(8), 1891–1910. https://doi.org/10.1111/jbi.13045.