Continental Scale Patterns in the Floral Host Breadth of Australian Native Bees

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Cover image:

A euryglossine photographed on a Myrtaceae flower by James B. Dorey
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SUMMARY

As a biogeographically isolated continent, there have been limited dispersal opportunities for biota into Australia in the last 35 million years. Consequently, the Australian biota has evolved a high degree of endemism, with unique adaptations and specialisations. This is reflected well in both our native bees and their visitations to various flora in the landscape. The Australian native bee fauna is distinct at even the global scale, and made up of five families including: Colletidae, Megachilidae, Apidae, Halictidae, and the entirely Australian endemic family, Stenotritidae. The short-tongued colletids are the most species-rich family in Australia but are not common outside of South America and Australia. Conversely, the most species-rich family at the global scale, the long-tongued Apidae, is outnumbered by any one of the major colletid subfamilies in Australia. Therefore, while their endemism and floral visitation habits are a part of what makes our native bees so interesting, what factors could be driving these unusual patterns?

I introduce this thesis with a broad review of the native bee fauna’s varied biogeographic histories, potential drivers of diversity, and discuss their future in the Australian environment. Much of the literature, however, is consistently evaluating species or populations at only the regional scale. Building an understanding of how native bees utilise floral resources at the larger continental scale could inform on potential evolutionary drivers that might have impacted their diversity. This is most feasible to assess in an island-continent such as Australia, where inward and outward dispersals are limited and likely less important than any potential co-evolutionary relationships. Determining the use of floral hosts can highlight any reliance on certain flora (*i.e.* specialisation), or more generalist visitation habits, which can help inform future practices or management.

Using records that encompass more than 100 years of museum collections from across Australia, we conducted the first continental-scale research into the floral host breadth (visited floral genera) of two major Australian bee families: the Colletidae and the Apidae. These bees make up over half of our native bee fauna and comprise a range of different morphologies and social structures. Colletidae are generally small to tiny, solitary, short-tongued bees, which we would expect to somewhat limit their floral host breadth. Contrastingly, Apidae, enabled by their long tongues and variable sociality, might be able to visit a broader range of floral hosts and have a greater floral host breadth. Our data and analyses rejected these hypotheses, with colletid bees displaying a much greater floral host breadth, even when correcting for differences in sampling effort (i.e., record numbers) and species number. I discuss the preponderance of a hyper-diverse colletid subfamily on one plant family and explore how drivers other than morphological differences might be affecting the floral host breadth of our native bee fauna.

DECLARATION

I certify that this thesis:

1. does not incorporate without acknowledgment any material previously submitted for a degree or diploma in any university

2. and the research within will not be submitted for any other future degree or diploma without the permission of Flinders University; and

3. to the best of my knowledge and belief, does not contain any material previously published or written by another person except where due reference is made in the text.

Signed: Patricia Slattery

Date: 7th March 2024

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PUBLICATIONS

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THE AUSTRALIAN NATIVE BEE FAUNA: BIOGEOGRAPHY, SPECIALISATIONS, AND THEIR FUTURE IN OUR SYSTEMS (HYMENOPTERA: APOIDEA)

The Australian context

Australia is a unique biogeographical landscape: a largely isolated island continent that, since its final break up from the supercontinent Gondwana, has resulted in ~35 million years of largely independent evolution (Frakes, 1999). As a result of this prolonged separation, many Australian flora and fauna have evolved unique interactions within this continental landscape. In terms of flora, this can be seen through the dominance of certain families and genera (*i.e.* Myrtaceae and *Acacia*), or specific adaptations such as woody plants with long lived leaves or fire-dependence for germination (Crisp & Cook, 2013). Australia's faunal biodiversity is also distinct and diverse, and similarly to other continents insects make up a large component of our ecosystems, while simultaneously being some of the least understood (Raven & Yeates, 2007). Within the various insect orders, some of the most reliant on our native flora are the Australian native bees, some of which are, in turn, important pollinators of angiosperms (Houston, 2018; Prendergast, 2023).

The Australian native bee fauna are some of the most taxonomically unusual in the world, and include representatives from five of seven families, one of which is entirely endemic to Australia (Michener, 2007). Colletidae, a short-tongued bee family (~2,600 spp. globally), is primarily distributed in the southern hemisphere and makes up over half of the described bee species in Australia (Almeida et al., 2023; Batley & Hogendoorn, 2009; Danforth et al., 2019; Slattery et al., 2023). Halictidae, sometimes known as sweat bees, are the second largest bee family in Australia (and worldwide) (~4,500 spp. globally), and present on every continent except Antarctica (Danforth et al., 2008). Apidae, the most speciose bee family in the world (~6,000 spp. globally), includes some of the most iconic Australian native bees: stingless bees (Meliponini), blue-banded and teddy bear bees (*Amegilla*), as well as some social parasites like cuckoo bees (*i.e.*, *Thyreus* or *Inquilina*). Megachilidae are resin or leaf-cutter bees (~4,000 spp. globally), so-called for lining their nests with soil, leaves or resin, and are similarly found on all continents except for Antarctica (Paini, 2004b). Stenotritidae is the only entirely endemic Australian family (~21 spp.). They are large, fast-flying, hairy bees that were previously thought to belong within Colletidae, but were assigned family status in 1980 (McGinley, 1980). Australia's bee fauna is distinct and diverse due to both an unusually large diversity of colletids, and high degree of endemism (*e.g.,* Stenotritidae and Euryglossinae), with representatives from five of the seven global bee families (Andrenidae and Mellittidae are absent).

Biogeographic histories

Michener's (1979) seminal biogeographic research on bees was framed on a global scale and was, until recently, the most comprehensive research available on why bee diversity varies across the continents, and why Australia's bee fauna is so unique. Michener hypothesised in this work that bees originated in Gondwana, in what is now Africa and South America, before dispersing elsewhere (Michener, 1979). In the 40 years since this publication our understanding of these systems and regions has improved significantly, with key knowledge advancements such as the inclusion of molecular research that can inform on dispersals out of and into Australia.

The common ancestor of colletids and Stenotritidae arose before the K-T boundary (66 million years ago) and likely had an origin in South America before transantarctic dispersal into Australia (Almeida et al., 2012a). Colletidae underwent much of their diversification before Australia had its final break-up from Antarctica and this, combined with their South American origin, help explain their much greater diversity in the southern hemisphere (Almeida et al., 2012a, 2023). Australia has three major subfamilies of colletids: Neopasiphaeinae, Hylaeinae and Euryglossinae, but also includes the (recently reassigned) subfamily of Callomelittinae (containing only one genus, *Callomelittia*), and the previously *incertae sedis* genus *Paracolletes* (formerly the tribe Paracolletini), that has been reassigned to the predominantly South American colletid subfamily, Diphaglossinae (Almeida et al., 2012a, 2019; Houston, 2020; Rozen Jr. & Houston, 2022). The biogeographic history of Euryglossinae is the simplest within this family, with an estimated crown age of 48 million years, and an origin and current distribution in Australia (Almeida et al., 2012a). Callomelittinae likely have the same origin and share a similar current distribution, but their most informative crown age (Neopasiphaeinae + Callomelittinae) was 60 million years ago (Almeida et al., 2012a, 2019). *Paracolletes* arrived in Australia sometime before the end of the Eocene (34 million years ago), and their closest crown age (Diphaglossinae + *Paracolletes*) is 65 million years old (Almeida et al., 2012a, 2019). Hylaeinae have a strong Australian diversity and crown age of 45 million years, before rapid expansion outside of the continent (albeit entirely belonging to a single genus, *Hylaeus*) (Almeida et al., 2019; Kayaalp et al., 2013). *Anthoglossa*, *Trichocolletes* and the Australian clade of Neopasiphaeinae were separated from the neotropics before the final break-up of Gondwana, but might have moved freely between South America, Australia and Antarctica throughout the Palaeocene until the Oligocene, when they officially separated into the South American and Australian clades of Neopasiphaeinae (Almeida et al., 2012a, 2019). The distribution of the colletid sister family Stenotritidae likely never expanded out of their east Gondwanan origin, and as the family crown age is in the late Oligocene, stenotritids probably arose just before or coincided with the dispersal of many other extant bee families into Australia (Almeida et al., 2023).

The diversity of Australian Apidae is often best considered at the tribal level, with some very distinct patterns in their arrival into Australia and biogeographic history. The tribe Meliponini of the Apinae subfamily has a seemingly vicariant split between 'New World' and 'Old World' clades, and all of Australia's Meliponini belong to the mostly tropical 'Old World' clade. These 'Old World' ancestors apparently dispersed into Australia via the Indo-Malayan region, resulting in our *Tetragonula* species (Rasmussen, 2008; Rasmussen & Cameron, 2007). Australian and New Guinea *Austroplebeia* species originated via dispersal from Africa through this same route, or some other passage through Sundaland, like the Sula Spur, while the Australian plate moved toward the Asian continent (Engel et al., 2021).

The subfamily Anthophorinae was previously assigned as a tribe within Apinae (Anthophorini); but more recent phylogenetic evidence has reassigned it as a subfamily within Apidae (Bossert et al., 2019). The Australian diversity of this subfamily includes several subgenera of *Amegilla* (which originated later than other anthophorines), arising in South-East Asia and then dispersing down through Sahul into Australia via geographic connections (Dubitzky, 2007; Leijs et al., 2017). They are primarily parasitised by the kleptoparasitic tribe Melectini (Australian representation only includes genus *Thyreus*): which was previously assigned under the Apinae subfamily, before being reassigned to Nomadinae with other kleptoparasitic tribes (Bossert et al., 2019). Sless et al. (2022) has more recently suggested that they act as a sister taxon to Nomadinae, rather than nested within it, so an accurate biogeographic history is currently unexplored.

Nomadinae are an Apidae subfamily of kleptoparasites, and of the over 850 species worldwide, only one is native to Australia (*Nomada australensis*) (Walker et al., 2020). Litman et al. (2013) determined a crown age of 92.9 million years for the subfamily, while Cardinal, Straka and Danforth's (2010) phylogeny of Apidae bees had a crown age of ~85 million years. *Nomada*, specifically, have a Holarctic origin ~65 million years ago that resulted in three dispersals to the southern hemisphere, with an eventual dispersal into Australasia during the late Miocene ~10 million years ago (Odanaka et al., 2022).

The Apidae subfamily Xylocopinae includes the tribe Allodapini, which has an African origin, and their trans-continental biogeographic history falls into two very separate dispersal events. The Australian "exoneurine" clade (comprising *Exoneura, Exoneurella, Brevineura* and *Inquilina*) had a single origin that involved dispersal from Africa to Australia, most likely via Antarctica in the Eocene (Chenoweth & Schwarz, 2011a). In contrast, the allodapine genus *Braunsapis* dispersed from Africa to Asia, and diversified there prior to a single dispersal into Australia in the late Miocene (Fuller et al., 2005).

Ctenoplectra are oil collecting bees that were previously assigned under the Apinae subfamily (Michener, 2007). However, Bossert et al.'s (2019) apid phylogeny inferred the genus as a sister group to Xylocopinae and reassigned the tribe Ctenoplectrini to within Xylocopinae. This tribe, which has only one Australian species (*Ctenoplectra australica*), had an origin in Africa in the early Eocene, before moving into Asia ~30-40 million years ago, and from there into the Indonesian archipelago and northern Sahul before establishing within Australia ~13 million years ago (Schaefer & Renner, 2008).

The Xylocopinae tribe Ceratinini have a crown age of ~40 million years (Cardinal et al., 2010), of which we only have one Australian species: *Ceratina (Neoceratina) australensis*. This tribe also had an African origin followed by worldwide dispersals, with only a single colonisation event of Australia (Dew et al., 2016; Oppenheimer et al., 2018).

The final tribe of Australian Xylocopinae is the Xylocopini, which contains only a single genus, *Xylocopa*, but with multiple subgenera (Leys, 2000; Leys et al., 2002). Only two subgenera occur in Australia: *Xylocopa (Lestis)* and *Xylocopa (Koptortosoma),* and both have a Eurasian origin with post-Gondwanan dispersal into Australia (Leys et al., 2002).

Our understanding of the biogeographic history for Megachilidae in Australia is also limited and constrained to a single genus (*Megachile*) in the Australian fauna. Despite poor resolution in the clade, the Australian *Megachile* subgenera likely arrived to the Australian continent via Asia in the early Miocene (Trunz et al., 2016). This coincides with the upwards shift of the Australian plate towards Asia and the increase in the Antarctic Ice Sheet, which could have facilitated movement between the continents (Beddow et al., 2016).

The final family of Australian native bees for which we have molecular biogeographic data is Halictidae, though considering the global diversity of this family, our knowledge of its Australian origins is very sparse. The subfamily Halictinae seemingly dispersed into Australia from Laurasia through the Sunda Arc approximately 30 million years ago (Chenoweth & Schwarz, 2011a; Danforth et al., 2008). The subgenus *Lasioglossum (Homalictus)* of this subfamily may have diversified in the tropics of Australia, South-East Asia or the Indo-Malayan region before dispersals into the Pacific (including remote islands) followed by the rest of Australia (Ibalim et al., 2020). More generally, the biogeographic origins of other Australian halictids are very unclear and will likely remain so until broader geographic sampling and the resolution of generic and subgeneric relationships.

To summarise, Colletidae are Australia's oldest bee family, and along with Stenotritidae (much later in their habitation) were potentially the only bee fauna in Australia until the late Oligocene or early

Neogene (Almeida et al., 2023). Colletid ancestors likely arose in what is now South America, whereas most other Australian bee fauna seem to have dispersed into Australia via several routes through the Indo-Malay region separating the Pacific and Indian Oceans in northern Australia. Using ~800 ultra-conserved elements from across the bee genome for 216 different species and fossil records assigned to modern groups, Almeida and Bossert et al. (2023) were able to create the most comprehensive phylogeny we have to date. With this research, they supported that the most recent common ancestor of bees lived ~124 million years ago and originated in Western Gondwana (Almeida et al., 2023), verifying Michener's (1979) biogeographic hypothesis.

Despite this, there are several major gaps in our knowledge about the timing of arrival and distribution of certain bee groups in the continent, from the finer taxonomic scale to entire families (Megachilidae) with no to minimal research published about their biogeographic histories in Australia. Many of these groups comprise a major part of the Australian bee fauna (*e.g.*, Halictidae is the second most speciose family in Australia), but with little understanding of their arrival into, and consequent distribution within, Australia. Interpreting the distribution of these groups over evolutionary time at the larger scale is important for understanding what key drivers (*e.g.*, biogeographic, anthropogenic, or floral resources) may have impacted their diversification.

Pollination syndromes and networks

One of these potential drivers of bee diversity, floral resources, is of great importance when considering pollination — a (usually) mutualistic relationship wherein flowers are fertilised in exchange for resources such as nectar, oil and the pollen itself (Michener, 2007). Angiosperms may attract pollinators through showy flowers, often with specific pollination syndromes, which represent a floral trait that is responsible for the attraction of a specific group of animals as pollinators (Fenster et al., 2004). These floral traits can be convergent over time in different plant species via co-evolution driven by a similar pollinator suite. Conversely, different pollinators can drive divergences in angiosperm floral traits. Consequently, these syndromes are helpful in understanding floral evolution, and they can often inform on potential primary pollinators for a species (Rosas-Guerrero et al., 2014). Pollination syndromes, connecting pollinators with floral hosts, can involve anything from the shape and colour of the flower to the scent that it releases (Reverté et al., 2016) and certain traits are oftentimes better predictors of primary pollinators than others (*i.e.* flower colour vs. corolla shape) (Dellinger, 2020). Their usefulness as predictors is highly controversial and largely dependent on the syndrome itself, but it is usually not enough to inform on all visiting pollinators for any one floral species (Hingston & McQuillan, 2000; Ollerton et al., 2009; Wang et al., 2020).

Pollination networks refer to the complex web of interactions between pollinators (of any kind) and the floral resources that they visit and pollinate. These networks are a preferred method for assessing the visitation breadth of flora, or the pollinators themselves, but are also often somewhat controversial. The scale of the analysis, for example, can impact the interpretation of the relationship between plant and pollinator, both spatially and temporally (Prendergast & Ollerton, 2022b). However, many of these controversies come from the issues involved with the assumption that visitation equates to pollination, which is often not the case (Ballantyne et al., 2015; King et al., 2013). Inclusion of parameters such as time of ‘visit’, pollinator efficacy or their importance in the network, as well as the consideration of temporal and spatial impacts on data acquisition, all provide greater detail on relationships in the network, making the network itself more representative of the natural system (Ballantyne et al., 2015; Prendergast & Ollerton, 2022b).

Both pollination networks and syndromes can be informative for understanding the links between pollinators and angiosperms. This can, in turn, reveal the fragility or robustness of these pollination relationships, which is particularly important in the contemporary climate where extremes are becoming more common, and anthropogenic disruptions to ecosystems are frequent and increasingly more severe (Elle et al., 2012). Pollinator declines have been well discussed at the global scale with the data available, for both agricultural and natural systems (Potts et al., 2010; Pyke et al., 2023). At a finer scale, temperature fluctuations have already caused phenological mismatches between plants and their pollinators (Fabina et al., 2010; Kudo & Ida, 2013; Solga et al., 2014). Invasive bee species are becoming more and more prevalent, even in more remote regions, while their impacts on native species are not fully understood (Elliott et al., 2021; Goulson, 2003; Huryn, 1997; Iwasaki & Hogendoorn, 2022; Paini, 2004a; Prendergast et al., 2022; Prendergast & Ollerton, 2022a). A better understanding of the dependency of our native pollinators on native flora and how the inclusion of non-native species into those networks might impact those relationships will provide meaningful data for conservation of biodiversity. This is especially so when native flora requires specific specialisations for successful pollination, which have likely evolved with our native bee fauna (Bernhardt & Weston, 1996).

Specialised visitation roles

Specialisation of visitation can differ substantially, even within generic groups, and different degrees of specialisation have been given different definitions based on how specific their visitations are. Pollinators can visit only a single species of plant in very specialised pollination relationships, like those of some *Euhesma* species (Table 1) (Houston, 1992), or they can be super-generalists, such as the introduced European Honeybee (*Apis mellifera*). A species that visits only a single species of angiosperm has previously been referred to as monolectic, but this definition has recently been updated to describe the visitation of (at most), a single genus (Cane, 2021). Cane and Sipes (2006) defined oligolectic as the visitation of up to four genera within one plant family, mesolecty as the visitation of more than four genera across three families, and polylecty as a greater visitation breadth than either of the latter. Exact definitions of these categories are somewhat blurred, as visitation patterns can depend on several factors including: the species that are flowering in any one area, pollinator specific behaviours such as floral constancy (*i.e.*, when bees visit only one species when foraging), the records available for bee species (some species are better researched than others), the pollinator's target resource (as bees may be more generalist in their visitations for nectar resources, than for pollen), and even the environment where they are foraging (Fernandes et al., 2022).

Our Australian bee fauna has some unique examples of these visitation specialisations and species have been able to exploit new niches and floral hosts by evolving unusual adaptations and behaviours (Table 1). A clear example of specialised pollination requirements is the diverse, endemic plant genus *Eremophila*. These plants are mostly arid adapted, and of the over 250 species, the majority are insect pollinated (Chinnock, 2007). Flowers are often shaped with a long corolla, with a constriction somewhere along the corolla tube. This requires that either: i) the insect pollinators are tiny enough to fully insert themselves past the constriction; ii) have long tongues that can fit through the constriction; or like in the case of some colletids iii) adapt elongated mouthparts to act as modified glossae (Houston, 1983) (Table 1).

Table 1: A summary of some unusual morphological and behavioural adaptations for specialised visitation in the Australian native bee fauna on angiosperms for pollination or floral resource acquisition. Bee placements and names in the first column are updated to current taxonomy and may seem dissimilar to references.

Bees	***Angiosperm***	***Specialisation***	***References***
Halictidae, Apidae, Colletidae	*Solanum, Hibbertia, Dianella, Agrostocrinum, Conostephium,*some Fabaceae, Epacridaceae, and Myrtaceae	Buzz pollination requires that the anthers of the flower be vibrated at specific frequencies to release their pollen. This sonication behaviour has been observed in three out of five native Australian bee families.	• Houston and Ladd, 2002 • Proença, 1992 • Stone *et al.*, 2003
Leioproctus, Trichocolletes, Hylaeus* and *Euhesma	*Eremophila*	Elongation of the maxillary or labial palpi (part of the tongue/glossae) means they can be inserted through the narrow corolla tubes of *Eremophila* species and draw the nectar up. There are several colletid species in Australia that have elongated mouthparts to facilitate this process, despite being a short-tongued family.	• Exley, 1998 • Houston, 1983 • Houston, 1990 • Krenn, Plant and Szucsich, 2005 • Maynard, 1994
Euhesma	*Verticordia*	*Verticordia* plants have very oily pollen, so very few bees can harvest it. *Euhesma*, which lack scopae, are able to lick the pollen and ingest it.	• Houston, 1992 • Houston *et al.*, 1993
Leioproctus (Cladocerapis)	*Persoonia*	These bees have a strongly modified clypeus and are large, and strong enough to force apart the stiff tepals of *Persoonia* species to access nectar at the base of the flower.	• Bernhardt and Weston, 1996 • Rayment, 1950 • Wallace, Maynard and Trueman, 2002
Leioproctus (Filiglossa)	*Persoonia*	Small body size with elongated and filament-like palpi that can be slipped between tepals to access nectaries.	• Bernhardt and Walker, 1996 • Bernhardt and Weston, 1996 • Maynard, 1995
Leioproctus (Leioproctus) conospermi	*Conospermum*	Short maxillary palpi and sparse scopae in females to collect the large pollen grains. Males also have dense, long, white hairs and white compound eyes	• Delnevo *et al.*, 2020 • Maynard, 1995 • Houston, 1989

species-group (inc. *conospermi*, *pappus* and *tomentosus*)		and wings, thought to help with camouflage on the plant when motionless.	
Lasioglossum (Chilalictus) platychilum	Goodeniaceae	Modified frontal tarsi with specialised bristles that rake pollen from the top of the cup-shaped style.	• Walker, 1995 • Houston, 2018
Euhesma tubulifera	*Calothamnus*	Labial palpi that are 80% the length of the body can be used as a straw-like organ that is inserted between the stamens.	• Houston, 1983
Leioproctus (Leioproctus) macmillani	*Astroloma xerophyllum*	Elongation of the head below the compound eyes and proboscis allows for deeper access into the elongated corolla tube of this winter flowering plant. Females have only been recorded visiting this species and have unusual buzz pollination behaviours.	• Houston, 1991

Australian native bees as crop pollinators

At the global level, insect pollination (primarily bees) was valued at USD$200 billion per year (Lebuhn et al., 2013). In Australia, the number of commercial beekeepers is in decline but the number of hives each maintains is increasing, and recreational beekeepers have increased tenfold since the 1960's (Clarke & Le Deuvre, 2021). Combined, the value of recreational beekeepers, commercial beekeepers, honeybees and pollination in Australia is estimated at AUD$437.5 million (Clarke & Le Deuvre, 2021). Previous valuation reports of the Australian pollination and honeybee industry have accumulated enough data to assess the dependence and economic importance of thirty-five Australian crops (Clarke & Le Deuvre, 2021; Gordon & Davis, 2003). Of the crops investigated, eighteen are 100% reliant on pollination by flying insects, with honeybees the most commonly employed (Clarke & Le Deuvre, 2021). Comparatively to the global scale, the pollination and honeybee industry in Australia is well researched and managed (Hein, 2009). So, what are the benefits of utilising native bees as pollinators in comparison to introduced species?

Both native and managed populations of bees are in decline (Cunningham et al., 2002; Slaa et al., 2006), and with the now very real threat of the *Varroa* mite being spread within the Australian honeybee industry, developing an understanding of potential alternative pollination strategies could prove vital (Bernauer et al., 2022; Chapman et al., 2023; Cunningham et al., 2002; Garibaldi et al., 2013; Owen et al., 2021). While the positive relationship between wild pollination and fruit set is demonstrated globally, oftentimes more effective than that of honeybees (Garibaldi et al., 2013), the utility of using native bee species as pollinators of agricultural crops, can be problematic. One *Tetragonula* species proved ineffective pollinators of watermelon and cucumber (Nacko et al., 2022), although another species of this genus (*Tetragonula carbonaria*) was a more effective pollinator of *Macadamia* than honeybees (Heard, 1994). Native insects and *Tetragonula* species proved effective at pollinating mango in northern Australia, the flowers of which are unattractive to honeybees (Anderson et al., 1982). Stingless bees also increased both the fruit yield and quality for a *Capsicum* species (Greco et al., 2011). Bernauer *et al.* (2022) found that native allodapine and halictine bees were efficient pollinators of Pink Lady apples, while the eusocial *Tetragonula carbonaria* had low efficiency, but high pollination effectiveness due to their abundance. Native *Amegilla* species pollination of greenhouse tomatoes increased fruit set and weight, comparable to that of bumblebees (*Bombus* species) overseas, and were more effective than mechanical or wand pollination (Bell et al., 2006; Hogendoorn et al., 2006). Native green carpenter bee (*Xylocopa (Lestis) aerata*) pollination of tomato plants also increased fruit yield (Hogendoorn et al., 2000).

One of the biggest issues faced in the potential transition to use of native bees as primary pollinators of Australian crops is the rate of reproduction. Honeybees are abundant, with a quick rate of reproduction and a large thermal tolerance (Jaboor et al., 2022). Contrastingly, while voltinism (*i.e.*, generations produced per year) is understudied in Australian native bees (Schwarz et al., 1998; Slattery et al., 2023), it is recorded as being impacted by a number of different environmental conditions (Cronin & Schwarz, 2001; Forrest et al., 2019). Native bees are slower to reproduce than honeybees (Slaa et al., 2006) and their abundance is often lower than that of native bees in agricultural regions (Prendergast et al., 2021). Therefore, while they are effective pollinators of several Australian crops, without new protocols for mass rearing of native bees, it is unlikely that they would be able to fill the role of primary pollinators for those industries (Hogendoorn et al., 2000; Prendergast et al., 2021).

Conservation concerns

Worldwide, based on the admittedly sparse data available in many regions, there has been a decline in flying insects at the both the regional and global scale (Braby et al., 2021; Hallmann et al., 2017; Lebuhn et al., 2013; Sánchez-Bayo & Wyckhuys, 2019, 2021; Wagner, 2020; Pyke et al., 2023). These declines are driven by a number of anthropogenic factors, both direct (such as the use of pesticides and fragmentation of habitat associated with a growing population) or indirect through the exacerbation of climatic change (*i.e.* increasing extreme weather conditions and events) (Dorey et al., 2021; Wagner et al., 2021).

Urbanisation is a continual development in the modern world, and its rapid and increasing rate of growth is one of the largest threats to our native systems. Li et al. (2022) found that Australia is consistently predicted to have one of the five greatest habitat losses as a direct result of increased urbanisation. This expansion into natural systems has resulted in 0.9% of the world's terrestrial biodiversity hotspots being urbanised in 2015, compared to the 0.5% of the rest of the globe (Li et al., 2022). In both regional, agricultural landscapes (Rix et al., 2017) and the suburbs of major cities in Australia (Braby et al., 2021), terrestrial invertebrates are in decline as a result of urban expansion and associated landscape changes.

A thirty-three-year study in Britain found disturbing patterns in the loss of pollinators: 33% of insect pollinator species declined in growth rate year-by-year with a 25% decline in bees overall (Powney et al., 2019). Eusociality, however, played a major role in occupancy success of bees with an overall increase of 38%, while solitary species (which comprise a majority of Australia's bee fauna) faced a decline of 32% (Powney et al., 2019). This decreasing diversity in less common, solitary species (*e.g.* colletids) and increasing eusocial species (*e.g.* stingless bees) is also observed in the city of Curitiba, southern Brazil, where human population increased from 140,000 to almost 2 million with a 55.6% increase in urbanisation (Pereira et al., 2021). While there is a distinct lack of long-term entomological surveys within Australia, very few studies show no change in diversity, or those that do belong to non-bee insect fauna (*e.g.* Hemiptera or Formicidae) (Sánchez-Bayo & Wyckhuys, 2019).

Urban areas are an increasingly pervasive part of our landscapes, so understanding how native pollinators interact with them is important for managing and conserving populations. Green spaces in our cities generally include a few major habitats (golf courses, public parks and residential gardens, streetscapes, and remnant bushland), all of which provide different levels of floral diversity, native floral abundance and nesting substrate (Prendergast et al., 2022a; Threlfall et al., 2015). Native bees in our urban environments have demonstrated preferences for increased native flora and less built spaces, with increased rare or unique species in bushland remnants (Prendergast, Tomlinson, et al., 2022; Threlfall et al., 2015). Introduced bees like honeybees are more likely to utilise introduced flora than native bees, which tend to rely primarily on native plants (Goulson, 2003; Slattery et al., 2023; Threlfall et al., 2015).

These considerations very briefly address the impacts of only one of the threats to our native bees at the larger scale. Further conservation concerns include other global threats to flying insects (Wagner et al., 2021), and a poor understanding of the diversity of our native bees and the services they provide in a broader context, especially when compared to honeybees. In major Australian newspapers from November 2006 to September 2015, less than 20% of articles on “pollination” mentioned native bees as pollinators; conversely, a majority (80%) discussed honeybees as pollinators (Smith & Saunders, 2016). Generally, we can surmise that Australian native bee conservation issues are understudied when compared to impacts on honeybees (Batley & Hogendoorn, 2009), but even the study of these impacts is subject to underdeveloped research protocols (Paini, 2004a).

Future research

One of the largest obstacles for developing deeper insights into Australian pollinators in their native systems can be ascribed to a paucity of research effort and resources: we have a large bee fauna and geographic area, and a small population. Continual declines in specialised taxonomists and insect ecologists mean that in the onset of the sixth mass extinction, species are disappearing at a rate faster than they can be described (Batley & Hogendoorn, 2009; Rix et al., 2017; Sands, 2018). Australia, with its ancient, endemic lineages, undescribed diversity and new pressures in the face of climate change, has a long way to go in filling the gaps (Austin et al., 2004; Taylor et al., 2018).

While there is literature on some of the unusual specialisations that can be found in Australian plant-pollinator relationships, they are often at the generic (or lower) level in smaller localities (like many of those in Table 1). There are no studies that have looked at these relationships at larger scales, despite our understanding that bee faunal compositions do vary across continents. The obvious question then is *why* is there such a difference, and *how* has it driven these discrepancies? For example, if there are differences in how our native bee fauna utilise different floral resources or prefer certain syndromes, then they are not equal pollinators within the larger network, as not all bee fauna will (or are able to) visit the same angiosperms. Therefore, developing an understanding of these continental-scale bee-plant relationships has the potential to inform on how these assemblages may have evolved over time, or even suggest areas of concern in future conservation management.

DISPARATE CONTINENTAL SCALE PATTERNS IN FLORAL HOST BREADTH OF AUSTRALIAN COLLETID BEES (HYMENOPTERA: COLLETIDAE)

This chapter was published on the 28th February 2023 in the journal Apidologie *by myself (Patricia S. Slattery (PSS)), Ben A. Parslow (BAP), Michael S.Y. Lee (MSYL), Michael Batley (MB), Ken L. Walker (KLW) and Michael P. Schwarz (MPS).*

PSS, BAP, MSYL and MPS all contributed to the conception and design of this chapter. PSS collated all data, completed all analyses and wrote the first complete draft. All authors contributed to the writing of this publication and approved the final submission of the manuscript, which was completed by PSS. The figures and tables have been adjusted to match other chapters for this thesis submission, and minor stylistic improvements incorporated.

Abstract

Plant-bee networks are rarely, if ever, studied quantitatively at continental scales, yet these have the potential to inform how biota and ecosystems are assembled beyond narrower regional biomes. The short-tongued bee family Colletidae comprises the major component of bee diversity in Australia, with three key subfamilies: the Neopasiphaeinae, Hylaeinae and Euryglossinae. We use museum data (>27,000 records) to record binary interactions between these bees (from each of these subfamilies, resolved to subgenera) and plants (resolved to genera). The resulting networks were analysed using bipartite graphs and associated indices of network structure. The three bee subfamilies showed markedly different network structures with their floral hosts. Euryglossinae had strong interactions with Myrtaceae and an otherwise relatively narrow host breadth, Neopasiphaeinae had little signal of host specialisation above genera and a very broad host breadth, and Hylaeinae appeared intermediate in network structure. Furthermore, Euryglossinae is more speciose within Australia (404 species, or ~ 25% of described Australian bee fauna) than Hylaeinae and Neopasiphaeinae, but these differences do not correspond to the stem ages of the three subfamilies, suggesting that time-since-origin does not explain bee species diversity or floral host breadth. Patterns of host breadth persist after rarefaction analyses that correct for differing numbers of observation records. We suggest that visitation networks could be influenced by evolutionary constraints to expansion of floral host breadth, but it is also possible that many bee-plant interactions are shaped by bees exploiting floral traits that are driven by non-bee fauna operating at large biogeographical scales.

Keywords

Euryglossinae; Hylaeinae; Neopasiphaeinae; Pollination; Myrtaceae

Introduction

Myriad studies have examined the biogeography of bees at varying spatial scales while considering historical scenarios leading to their current distributions (Almeida et al., 2012b; Kayaalp et al., 2013, 2017; Michener, 1979, 2007). These studies have broad ecological implications because of the crucial roles that bees play as terrestrial pollinators, and recent declines in bee abundance and diversity may have alarming consequences for both agriculture and native ecosystems (Batley & Hogendoorn, 2009; Dorey et al., 2021; Hallmann et al., 2017).

Whilst some studies have examined how historical biogeographic events have shaped the continental distributions of some individual bee taxa (*e.g.* Camargo & Pedro, 1992; Leys et al., 2002; Hines, 2008; Tierney et al., 2008; Rehan et al., 2010; Chenoweth & Schwarz, 2011; Dew et al., 2016) there are no studies that quantitatively examine how these distributions translate into plant-pollinator networks at continental scales; yet such networks may be important for understanding how terrestrial ecosystems are assembled and evolve. If the floral host breadth of bee taxa exhibits long-term phylogenetic inertia, then rare bee dispersal or origin events have the potential to influence ecosystems at continental scales.

Discerning continental scale patterns in bee diversity and bee-plant networks is likely to be easier for continents that have, or had, limited connections with surrounding regions such that recent dispersals do not override historical co-evolutionary events. The unusual geography and geological history of the island-continent of Australia is associated with some of the most unusual flora and fauna in the world, with many endemic and endangered taxa (Dickman, 2018; Dorey et al., 2021). Indeed, Michener (1965) referred to Australia as having the most distinctive bee fauna in the world, with one family (Stenotritidae) being entirely restricted to Australia while two other families (Andrenidae and Melittidae) are entirely absent (Bossert et al., 2022; Danforth et al., 2006a) . Much of the diversity we observe in Australian flowering plants today is associated with interactions involving bees (Toon et al., 2014), and these bees can play critical pollinator roles (Gross & Mackay, 1998; Houston, 2018; G. Taylor & Whelan, 2014).

Colletidae, the most diverse bee family in Australia, makes up more than half the named species, and is found in every biome in the continent. Colletids have a broad global distribution – found on every major landmass except Antarctica and with a centre of diversity in the southern hemisphere (Almeida et al., 2012b). This family includes the Australasian endemic subfamily Euryglossinae, comprising ~400 species, or almost 25% of the Australian bee fauna. The second major colletid subfamily, Hylaeinae, is found on every continent except Antarctica and consists of ~200 Australian species (Kayaalp et al., 2013; Walker, 2006). The Neopasiphaeinae also has a Gondwanan origin and whilst not as globally widespread as Hylaeinae, also occurs in Neotropical and Holarctic regions and consists of ~300 Australian species (Almeida et al., 2012b; Walker, 2006). All three subfamilies have stem ages in the Eocene, shortly after the last fragmentation stages of Gondwana, but prior to the collision of the Australian plate with southern Asia. Early diversification of these subfamilies therefore likely occurred when Australia was mostly isolated from other continents but prior to the major Miocene period of aridification (Byrne et al., 2008).

Floral visitations by bees can fall anywhere from monolectic, in which species will visit only a single species or genus of flowering plant (Cane, 2021), through to oligolectic, visiting only a few members of a plant family or a genus, and polylectic, visiting numerous host plants across multiple genera or families, to super-generalism where bees can exploit nearly all angiosperms in their habitat. Many of Australia's solitary bees have restricted breadths of floral hosts ranging from monolecty or oligolecty and associated restrictions in flight seasons (Houston, 2018) to polylectic visitation breadths such as observed in *Lasioglossum (Chilalictus) cognatum* (Walker, 1995). Floral host preference can also be the result of physiological constraints such as the size of the pollen, or inherent neurological preferences (González-Varo et al., 2016). Morphological constraints could be as simple as bee tongue length (effectively, length of the glossa), or the shape of the flower itself.

Another factor that may impact upon the visitation habits of bees is the resource that the flower provides, and nectar and pollen may not be the only substances that bees use (Westerkamp, 1996). *Acacia* species are both widespread and abundant in the Australian landscape, but their flowers lack nectaries, and in this case, exploiting *Acacia* pollen for brood rearing will require non-*Acacia* sources of nectar. Bees that utilize nectarless plants for pollen acquisition will also require co-flowering plants that provide nectar or nectar-like liquid carbohydrates, in which case simple binary bee-plant interactions may fail to capture important ecological constraints. This multiple dependency has the potential to impact bee-plant relationships at large geographical scales, directly relevant for Australian systems.

Hylaeinae and Euryglossinae also have the distinction of being the only pollen-collecting bee subfamilies that completely lack scopae or corbiculae (specialized pollen-carrying setae on the hind legs or the underside of the metasoma), and these bees oftentimes have a diminutive body form. However, partial reduction of scopae occurs in some African *Colletes* species (Kuhlmann, 2006) and in one Australian neopasiphaeine bee, *Leioproctus (Euryglossidia)*, scopae is reduced to sparse, simple hairs (Houston, 1981). These characteristics may play key roles in determining floral host ranges: small body size may limit the ability to effectively sonicate poricidal anthers (Mesquita-Neto et al., 2021) and lack of scopae may make it difficult for bees to capture sonicated pollen as it descends. The short tongues of colletids may also exclude them from accessing the nectaries of plants with long corolla tubes, unless their body size is small enough to crawl into the corolla tube itself. Floral taxa, such as Myrtaceae, that present pollen in open anthers and nectar in shallow cups, may be more accessible to a wider range of bee species, including tiny species with short tongues.

The diversity of bee subfamilies could also be a function of their stem ages – the elapsed time since they originated, providing more time available to both expand niches and to speciate. At the same time, as suggested for *Acacia* thrips by McLeish et al. (2007), diversification of hosts could directly impact radiation of those taxa that rely upon them. In this context we could expect an associated increase in bee species diversity as their floral hosts become more specialised and speciation occurs.

Many studies (*i.e.*, Abrahamson et al., 2001; Drès & Mallet, 2002; Forbes et al., 2017) have also linked the speciation of phytophagous and parasitic insect groups to host shifts via adaptive radiation, and such host shifts have been implicated in the very early diversification of bee lineages (Danforth et al., 2006b; Michez et al., 2008; Murray et al., 2018). Conversely, *lack* of host shifts – *i.e.*, phylogenetic inertia in host breadth - could also be a driver of speciation if host plants have fragmented distributions that promote allopatric speciation in the bees that rely on them (Avrani et al., 2012). These considerations highlight the importance of bee-plant networks as an important tool for understanding how pollinator guilds first evolved and how coevolutionary entanglements have shaped biodiversity.

Here we present, at a continental scale, a synthesis of observed floral hosts for the major Australian colletid bee subfamilies Euryglossinae, Neopasiphaeinae and Hylaeinae. Whilst previous studies, most notably Michener (1965), have noted floral host breadth for some Australian bee taxa, no studies have attempted to explore this quantitatively at a continental level that explicitly compares major bee taxa. We combine extensive museum records to explore plant-bee interactions for the three major colletid subfamilies in Australia and then explore why floral host breadth might differ between the three bee groups.

Methodology

Floral visitation datasets were developed from museum records (Western Australian Museum, Australian Museum and Museums Victoria) from >100-year span covering an extensive geographical range in Australia. Our data only include records where bees could be identified to subgeneric level (or generic level where subgenera are not currently recognised) and plants identified to generic level. Individual records that did not have this degree of specificity were excluded from analyses. Distinction of the sexes was not included due to the number of records that did not include this information. Plant taxa were updated to their current taxonomic status: *Dryandra* records were organised into *Banksia*, *Nemcia* are regarded as *Gastrolobium*, *Morgania* are in *Stemodia* and *Derwentia* are re-recorded as *Veronica*.

Bee subfamily placement was based on the Australian Faunal Directory (AFD) for both Hylaeinae and Euryglossinae (Australian Biological Resources Study, 2022b). Neopasiphaeinae placement was based on Almeida et al. (2019), wherein the subfamily Callomelittinae and tribe *Paracolletini* are reassigned outside of the subfamily.

Bee-plant networks were developed in R version 4.0.4 (R Core Team, 2021) using the packages *bipartite* (Dormann, Gruber and Fründ, 2008) and *vegan* (Oksanen et al., 2020). Network level analyses (Dormann et al., 2009) were undertaken and the following parameters were estimated for each subfamily: (i) niche overlap (for both the bees in a subfamily, and for all the host plants exploited by that subfamily) which measures the similarity in niche use; values closer to 0 indicate few or no common niches and 1 equals perfect niche overlap. (ii) The C-score (both bees and plants) measures aggregation, with values close to 0 indicating aggregation of species in use of a common resource (*e.g.*, plant genera) and values closer to 1 demonstrating disaggregation (which could flag competitive exclusion). We also estimated (iii) a nestedness metric, indicating the extent to which the host breadth of taxa with narrower resource spans forms nested subsets of the host breadth of other taxa with broader resource spans. Nestedness was based on overlap and decreasing fill, or NODF, at the network level. (iv) Togetherness (bees only) which measures the number of co-occupancies, which are matches of co-absence and co-presence in the matrix (*i.e.*, two bee subgenera are both visiting the same plant genera, and both not visiting the neighbouring plant genus). Finally, (v) Partner diversity (bees only), which is an indication of the mean Shannon diversity of the floral hosts that the subfamily is visiting (the higher the value the greater the diversity of floral hosts in that subfamily).

IBM SPSS version 25.0.0.2 (IBM Corp, 2017) was used to assess the skew and kurtosis of visitation numbers for each subfamily.

Variation in the number of records for specific bee taxa is a potentially important confounding factor in our data: scarcity of records could suggest limited floral host ranges, but might instead reflect bee rarity with consequent inability to 'capture' true floral host ranges. We explored these possibilities using rarefaction analyses implemented in EstimateS version 9.1.0 (Colwell, 2013) where floral host richness (S) and diversity (measured as Shannon's diversity index) were the dependent variables and sampling effort, measured as the number of interaction records, was the independent variable. We did not extrapolate rarefaction curves, knots were estimated for every bee subgenus, the bias-corrected formula was used for Chao 1 and Chao 2 and bee subgenera were randomized without replacement.

These analyses were run for 1000 iterations and the output modelled in MS Excel (Microsoft, 2022). For these analyses asymptotic rarefaction curves for species richness suggest that true floral host ranges are estimated with current sample sizes, whereas steeper curves indicate that sample sizes underestimate host breadths.

Results

Our bee-plant interaction data (Table 2) included 6,907 recorded interactions for Neopasiphaeinae, 6,568 for Hylaeinae and 13,601 for Euryglossinae. Neopasiphaeinae subgenera were recorded visiting 193 floral host genera, Hylaeinae visited 141 and Euryglossinae 78 genera, with the number of recorded subgenera within each bee subfamily ranging from 22 to 30 (Table 2).

Table 2: The total number of included interactions before creating the binary matrix, the total number of bee subgenera represented in this study, and the total number of floral host genera recorded in this study for each subfamily.

Subfamily	***Total number of recorded interactions***	***Number of subgenera represented***	***Recorded floral host genera***
Euryglossinae	13,601	22	78
Hylaeinae	6,568	26	141
Neopasiphaeinae	6,907	30	193

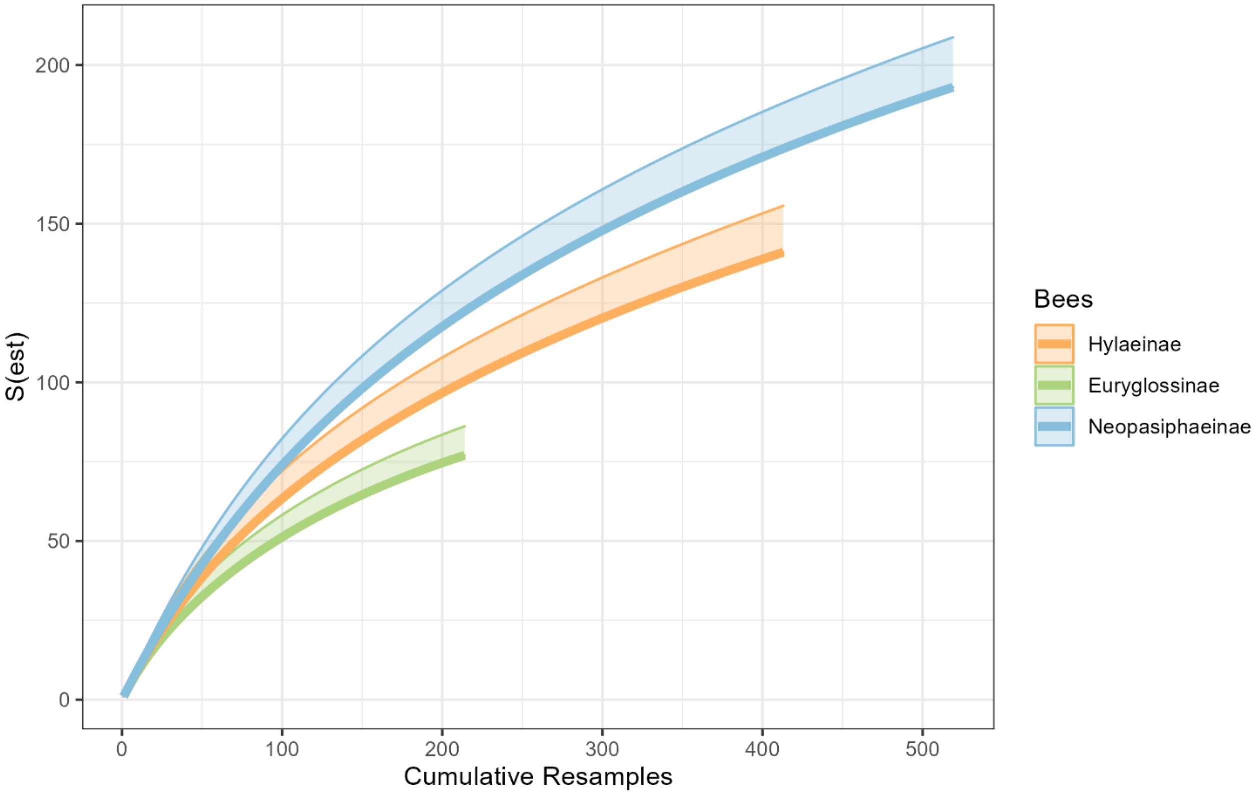

Figure 1: Rarefaction curves for colletid bee subfamilies Euryglossinae, Hylaeinae and Neopasiphaeinae used to calculate estimated total floral host breadth (S(est)), run for 1,000 iterations. Upper 95% CI are indicated by the shaded sections.

Figure 1 shows how the number of floral interaction observations is related to the number of host records, summarising the results of our rarefaction analyses. It shows the expected number of plant genera that each subfamily could visit, S_{est} as a function of sampling effort and with upper 95% confidence limit for rarefaction curves. Neopasiphaeinae has the largest floral host breadth, Hylaeinae intermediate, and Euryglossinae the smallest host breadth, with the steepness of the rarefaction curve declining more rapidly as a function of sampling effort. Figure 2 summarizes Shannon's diversity index for the three bee groups using the same rarefaction analyses as for S_{est} and indicates that floral host diversity is highest for the Neopasiphaeinae and lowest for the Euryglossinae.

Table 3: A summary of network indices for each of the bee subfamily networks, detailing the level of interest and the indices themselves.

	Network Level	*Neopasiphaeinae*	*Hylaeinae*	*Euryglossinae*
Niche overlap	*Bee*	0.08	0.16	0.37
	Plant	0.29	0.23	0.36
C-score	*Bee*	0.76	0.58	0.37
	Plant	0.46	0.54	0.34
NODF	*Network*	0.42	0.38	0.48
Togetherness	*Bee*	0.03	0.06	0.11
Partner diversity	*Bee*	3.64	3.27	1.46

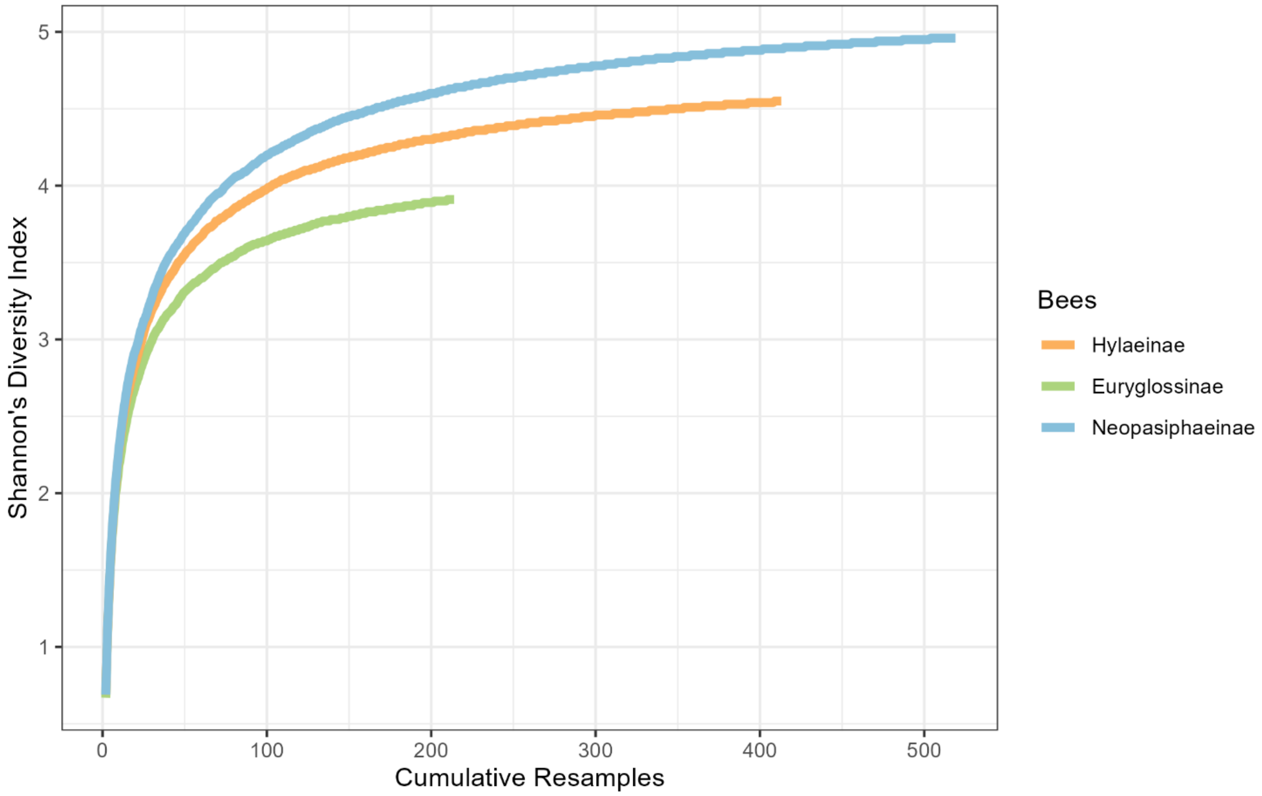

Figure 2: Rarefaction curves for colletid bee subfamilies Euryglossinae, Hylaeinae and Neopasiphaeinae, used to calculate Shannon's diversity index in floral host breadth, run for 1,000 iterations.

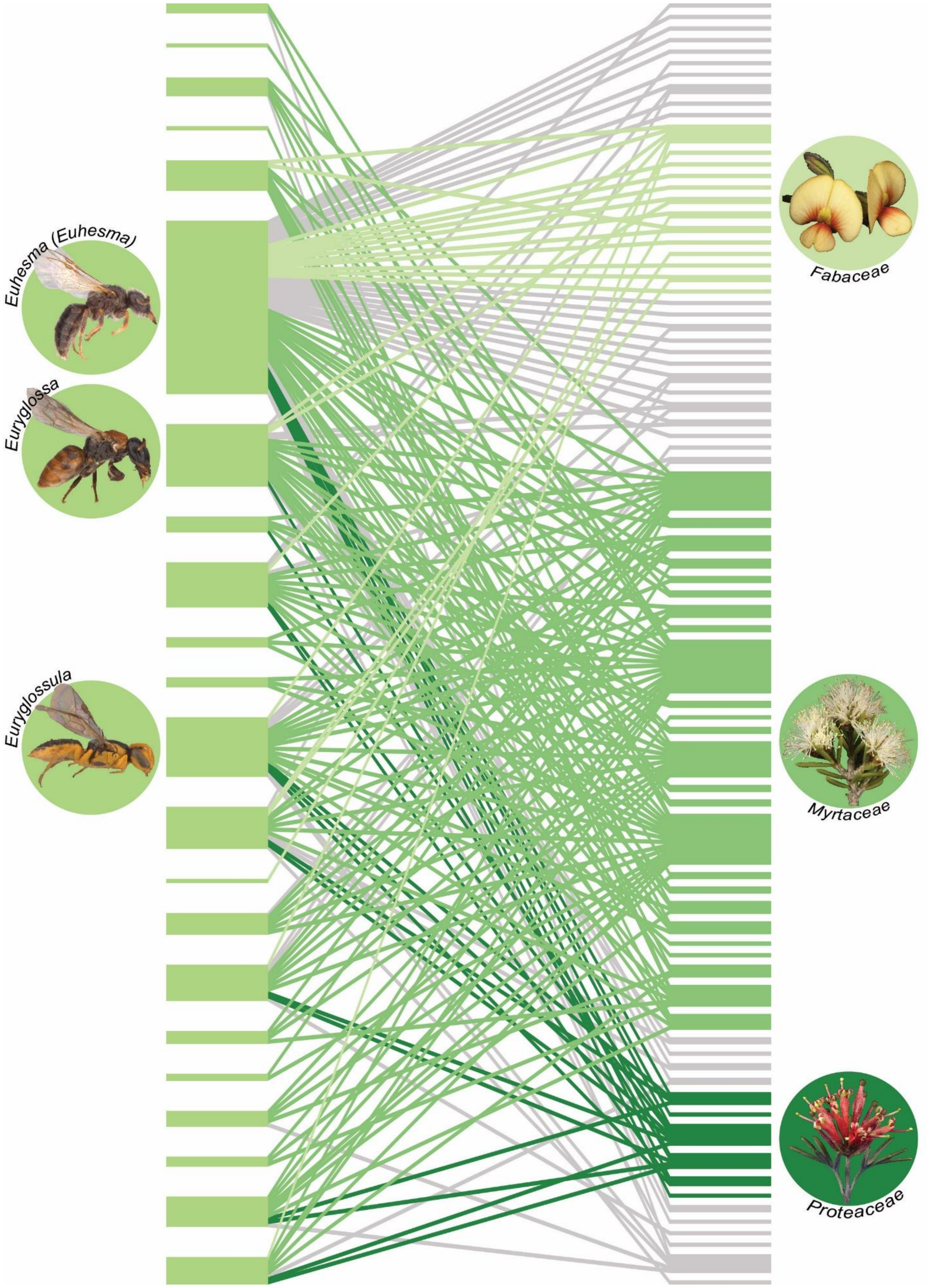

Figure 3: Floral host breadth network for the Australian colletid subfamily Euryglossinae. Bee subgenera are on the left, plant genera on the right with three families of interest colour coded (Fabaceae = lightest green/top, Myrtaceae = medium green/middle, Proteaceae = darkest green/bottom). Thickness of horizontal lines denotes the total number of linkages for each bee or plant subgenus/genus in the dataset. One line indicates one binary visitation record between the bee subgenera and the plant genera.

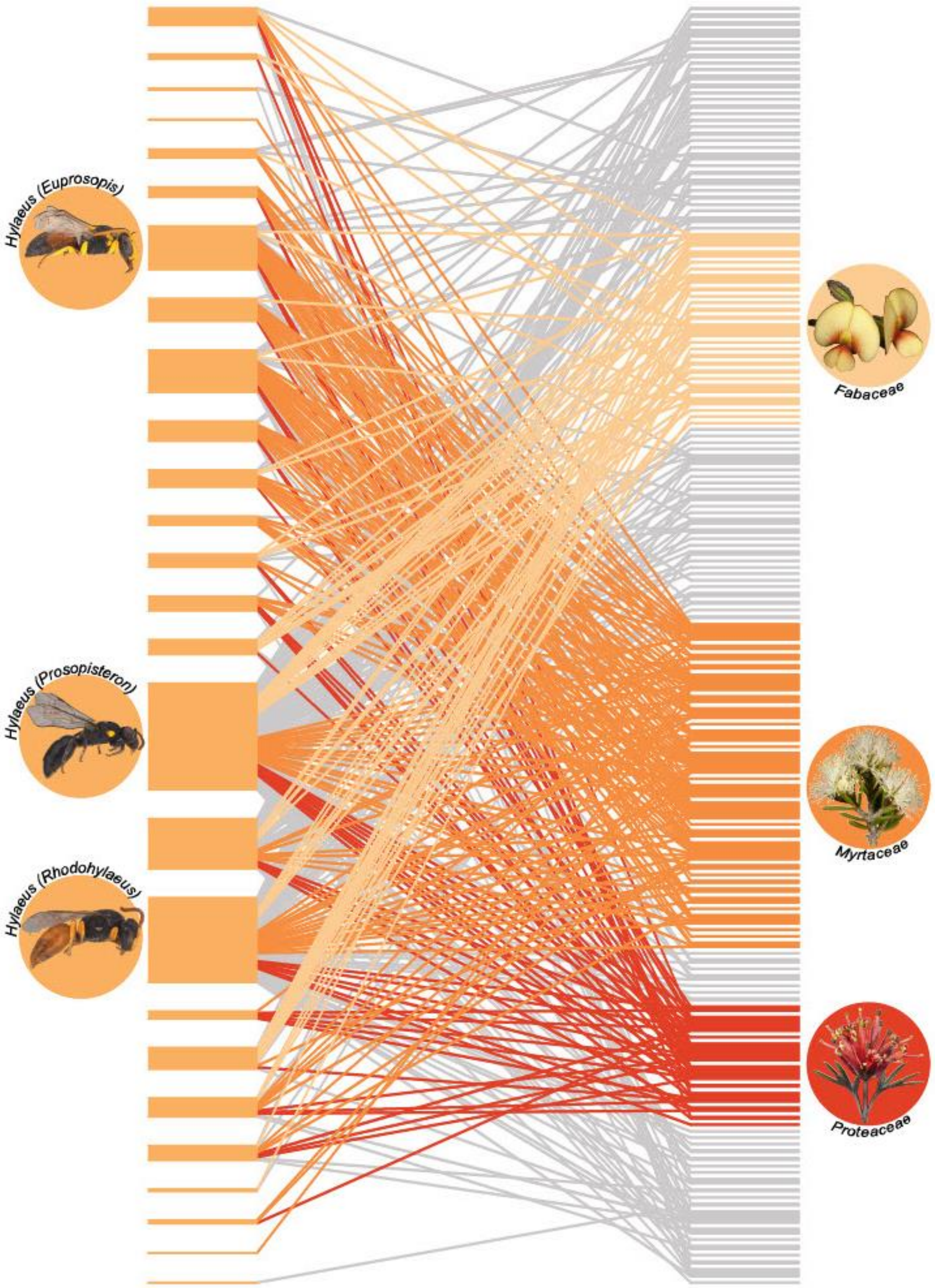

Figure 4: Floral host breadth network for the Australian colletid subfamily Hylaeinae. Bee subgenera are on the left, plant genera on the right with three families of interest colour coded (Fabaceae = lightest orange/top, Myrtaceae = medium orange/middle, Proteaceae = darkest orange/bottom). Thickness of horizontal lines denotes the total number of linkages for each bee or plant subgenus/genus in the dataset. One line indicates one binary visitation record between the bee subgenera and the plant genera.

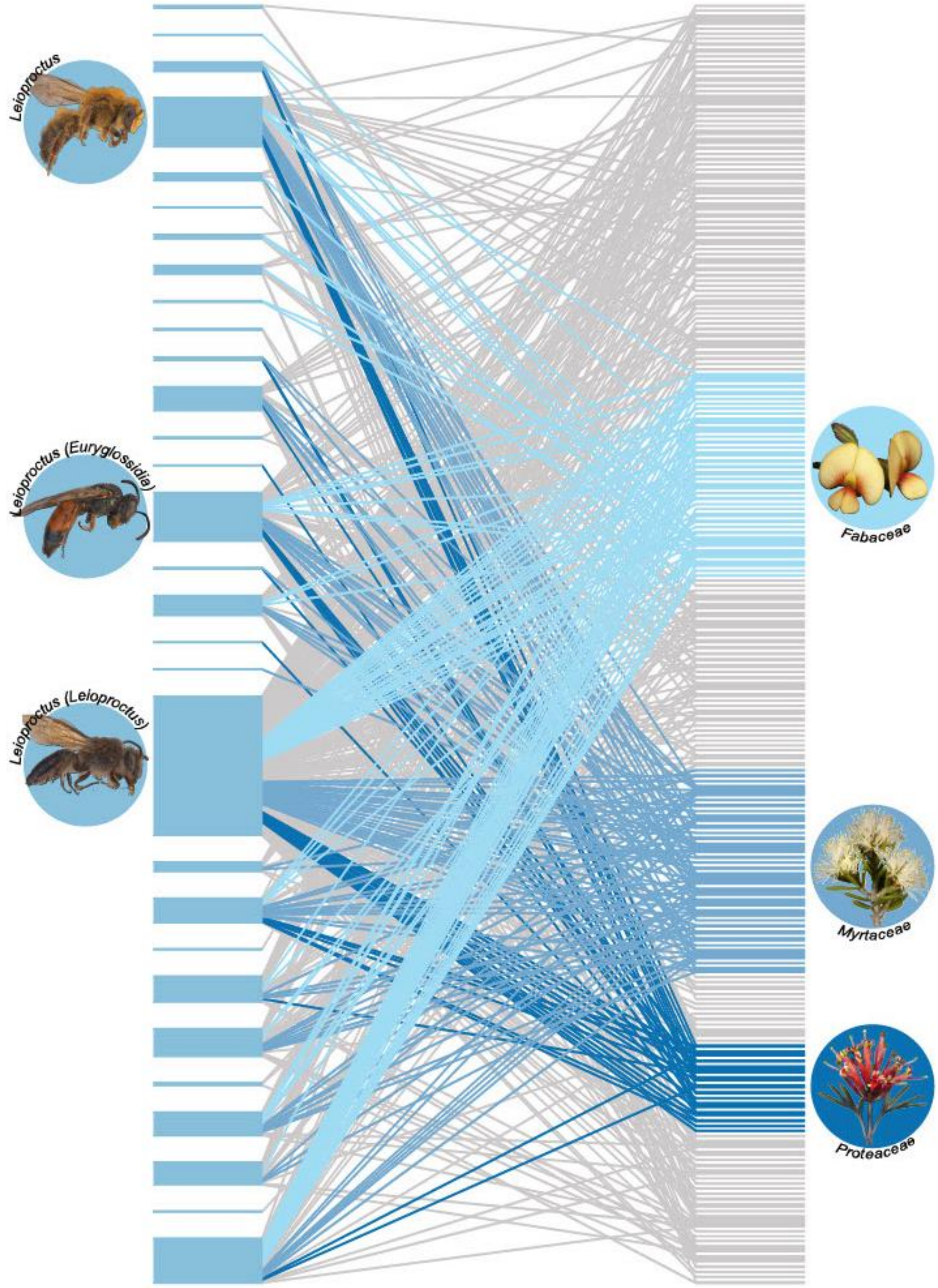

Figure 5: Floral host breadth network for the Australian colletid subfamily Neopasiphaeinae. Bee subgenera are on the left, plant genera on the right with three families of interest colour coded (Fabaceae = lightest blue/top, Myrtaceae = medium blue/middle, Proteaceae = darkest blue/bottom). Thickness of horizontal lines denotes the total number of linkages for each bee or plant subgenus/genus in the dataset. One line indicates one binary visitation record between the bee subgenera and the plant genera.

Network diagrams developed in bipartite are shown for Euryglossinae (Figure 3), Hylaeinae (Figure 4) and Neopasiphaeinae (Figure 5) where key plant families are colour-coded to flag the most common plant groups. More detailed diagrams are presented in Appendix A (Supplementary Material 1-3), where bee and plant subgenera are indicated for every node. These diagrams suggest that Euryglossinae had the most skewed floral host range (Figure 3), with a high proportion of bee taxa linked to Myrtaceae visitations. Hylaeinae had a larger visitation breadth than that of Euryglossinae, with a less marked preference for any one plant family. Neopasiphaeinae had the largest floral host breadth of the subfamilies, with no clear preferences for specific plant families or genera (Figure 5). In direct comparison to the other two subfamilies, most of their interactions occurred outside of the three plant families highlighted (Fabaceae, Myrtaceae and Proteaceae). These observations were then further analysed using network indices, to assess if the apparent patterns were of interest.

Network indices, broken down into bee subfamilies, are summarized in Table 3 where indices are calculated separately for bees and plants where appropriate. Niche overlap was greatest for euryglossines (0.37) and least for neopasiphaeines (0.08), which fits with the bipartite diagrams showing preponderance for Myrtaceae hosts in Euryglossinae and the wider host range of Neopasiphaeinae. Interestingly, when calculated for plant hosts, niche overlaps did not mirror the pattern for bees, with values being generally greater. This suggests that plants had wider bee host ranges than *vice versa*, but non-equivalence of bee and plant taxa categories means this result needs to be regarded cautiously. C-scores for bees were lowest for euryglossines (0.37) and highest for neopasiphaeines (0.76) and provide a measure of aggregation/disaggregation in host use. Our C-score values therefore suggest a similar trend as found for niche overlap where euryglossine records tend to be concentrated on Myrtaceae. Togetherness was highest for euryglossines (0.11), with a greater number of co-occupancies in the matrix, suggesting that most of the bee subgenera are visiting the same floral host genera. Hylaeinae (0.06) were again intermediate between euryglossines and neopasiphaeines (0.03). Partner diversity was highest for the Neopasiphaeinae (3.64), followed by the hylaeines (3.27) and lowest for euryglossines (1.46).

NODF was highest for Euryglossinae, suggesting a greater nestedness in their interaction matrix, with Hylaeinae having the lowest NODF score. Togetherness was highest and partner diversity was lowest for Euryglossinae, indicating that many bee subgenera are visiting the same plant genera. Conversely, Neopasiphaeinae scored lowest for togetherness and highest for partner diversity suggesting this subfamily demonstrates a greater floral visitation diversity. These analyses support our other results suggesting more limited host ranges for Euryglossinae.

Discussion

The colletid subfamilies Euryglossinae, Hylaeinae and Neopasiphaeinae comprise approximately 53% of all described bee species in Australia (Batley & Hogendoorn, 2009), so understanding their potential roles as pollinators at a continental scale is important. Multiple research projects have focussed on the use of native bees for crop and ecosystem pollination, in Australia and more globally (*e.g.* Heard, 1999; Kremen et al., 2002; Winfree et al., 2007; Prendergast et al., 2021), but these studies are unable to be informed of broader pollination networks at higher taxonomic levels. Yet these broader kinds of patterns may be critical: they may indicate the wider utility of higher taxa as potential pollinators before having to explore particular species in detail. These patterns could also help understand how pollinator networks are shaped by phylogenetic constraints and the assembly of pollinator suites from key inter-continental dispersal events or *in situ* origins of highly divergent clades. Because bees are such important pollinators in most terrestrial ecosystems (Danforth, 2007), higher-level pollinator networks may also help understand how continental-scale differences in floral diversity have arisen.

Floral host ranges

When exploring broader pollinator patterns a key question concerns the age of clades: older clades should have had more time in which to undergo both speciation and radiation in floral host range. Euryglossinae and Hylaeinae both have Australian origins with approximate stem ages of 54 and 58 mya, respectively, in the late Paleocene or early Eocene (Almeida et al., 2012b), although larger taxon sampling is likely to increase those ages slightly (Kayaalp et al., 2013, 2017). Neopasiphaeinae has a stem age of ~60 mya, with a Gondwanan heritage, involving several South American and Australian interchanges through Antarctica (Almeida et al., 2012b, 2019). The differences in stem ages of these subfamilies are not large and are not obviously related to species richness of the subfamilies. Hylaeinae and Neopasiphaeinae have ~200 and ~300 Australian species, respectively, compared to ~400 euryglossine species, despite these similar stem ages. Differences in species diversity of the three subfamilies is therefore likely to be due to factors other than clade age.

We found major differences in the floral host ranges of the three subfamilies, with the Euryglossinae having the narrowest range and the least diversity (measured using Shannon’s index) of host plants despite being the most speciose subfamily. This low diversity coincides with the preponderance of Myrtaceae hosts and could suggest some form of ecological connection that can influence a continental-scale pattern of bee diversity. It is therefore important to ask whether this pattern is robust to our protocols for data acquisition or whether it may be explained by sampling artefacts.

Estimates of taxonomic richness and diversity are clearly impacted by both sampling effort and taxonomic resolution. We were not able to meaningfully identify bees to species level because of limits to current identification tools and taxonomist capacities, and we therefore limited taxonomic resolution to subgeneric level (treating monotypic genera as subgenera). At present there is no accepted protocol for deciding whether generic and subgeneric-level designations of colletid bees are equivalent (*e.g.* in clade age) and it is unlikely that any such scheme could be developed without extensive molecular studies.

Comparing levels of sampling effort for the three Australian subfamilies is more straightforward than issues concerning equivalence of subgenera because identifying subfamily membership is trivial for Australian species (Michener, 1965, 2007). Museum records were unequal for the three bee subfamilies (6,907 records for Neopasiphaeinae, 6,568 for Hylaeinae and 13,601 for Euryglossinae). The much lower floral host range and diversity of Euryglossinae – the taxon with the most records - thus cannot be explained by differences in sampling efforts (= museum records). Our rarefaction analyses (Figure 1 and 2) corroborate this, with euryglossines approaching taxon richness and diversity plateaux as a function of sampling effort much sooner than Neopasiphaeinae, with Hylaeinae being intermediate. Consequently, we conclude that the lower host plant richness and diversity for Euryglossinae is not a result of different sampling intensity. Sampling also covered a good spread of subgenera diversity in all three subfamilies, with all speciose subgenera being sampled. Thus, the different patterns retrieved are also unlikely to be artefacts of patchiness in sampling across subgenera.

When stem ages for the three subfamilies are considered, the lower diversity of plants used by Euryglossinae suggests some kind of barrier for adaptive radiation in host use, supported by our analyses of network statistics. In particular, the C-scores for both the plant and bee level in the Euryglossinae network is markedly lower than either of the other two subfamilies (Table 3). This statistic, combined with their lower partner diversity and higher niche overlap all suggest that euryglossines are more frequently utilising similar plant genera (Table 3). Unlike Neopasiphaeinae, Euryglossinae and Hylaeinae lack scopae and carry pollen internally in their crop. A *priori*, we might expect this to influence floral host breadth; for example, scopal morphology and density might affect the ability to harvest different pollen types, and the ability to swallow and then regurgitate pollen from the crop might vary with pollen grain size. Many Australian bees have developed unique adaptations or behaviours in order to exploit plants that otherwise might be outside their floral host breadth; *Euhesma tubulifera* have elongated maxillary palpi that can be up to 80% of their body length allow them to specialise on *Calothamnus* species, despite these flowers being adapted for avian pollination (Houston, 1983, 2018). The subgenus *Leioproctus* (*Filiglossa)* are even able to exploit the nectaries of *Persoonia* species by using hairs from the galeae to slip between the petals and access the nectaries (Maynard, 1994). A large number of euryglossine and hylaeine species have small body sizes that have allow them exploit narrow corolla tubes in plant groups like *Eremophila* by crawling into the flower itself (Houston, 2018). But regardless of the similarities between euryglossines and hylaeines, we found that host range and diversity were more similar between neopasiphaeines and hylaeines, with euryglossines showing distinctly divergent patterns.

Why are Euryglossinae so abundant and diverse in Australasia, but absent everywhere else?

The above considerations indicate a much narrower floral host breadth in Euryglossinae than the two other major groups, but one which does not seem to be explained by phylogenetic stem ages or methods of pollen transport. Hylaeinae have very successfully dispersed outside of Australia with *Hylaeus* even found on remote islands in the Pacific and Indian oceans (Michener 1965, 2007), yet despite their ubiquity and abundance in Australia, euryglossines are scarce in neighbouring New Guinea and New Zealand and absent everywhere else (Michener, 2007).

One possibility for the restricted distribution of Euryglossinae might be their preponderance for Myrtaceae floral hosts. This preferential visitation could be due to the morphology of eucalypt flowers (especially *Eucalyptus*, *Corymbia* and *Angophora*), along with other Myrtaceae such as *Leptospermum*, *Callistemon*, *Syzigium* and *Melaleuca*, which present shallow cup-like nectaries readily accessible to short-tongued and small bees. As Michener (2007) noted, “short-tongued or minute bees take nectar from shallow flowers”. Myrtaceae are diverse and abundant in Australia (14 out of 17 tribes), but less abundant elsewhere (Michener, 1979; Thornhill et al., 2015). Importantly, most eucalypt subgenera had arisen by the late Eocene or early Oligocene (Thornhill et al., 2019), which is later than the stem age of Euryglossinae but roughly coincides with an accelerated divergence of euryglossine subgenera approximately 35-25 mya (Kayaalp et al., 2013). Many Australian Myrtaceae are adapted for bird pollination (Beardsell et al., 1993), especially parrots (Psittaciformes), via shallow nectaries: it is possible that the shallow cup-like nectaries and brush-like flowers in many Australian Myrtaceae genera are partly adaptations for pollination by parrots and that this floral morphology has allowed secondary exploitation by short-tongued bees. Interestingly, although parrots have an ancient Gondwanan origin, they show an elevated rate of diversification in the late Eocene and early Oligocene, especially for the Australian lories (Schweizer et al., 2011). These considerations raise the possibility that many euryglossines may rely on floral resources whose nectary morphologies are partly or mainly responses to bird pollination. If this is the case, then the diversity and abundance of Euryglossinae may be linked to radiation of Myrtaceae in Australia and the role of bird pollinators in that family’s evolutionary history. At the same time, the seemingly coincident radiation of Myrtaceae, parrots and euryglossines might be linked to major climate changes at the Eocene/Oligocene boundary (Nge et al., 2020).

In summary, our data indicate strong patterns in the higher-level diversity of colletid bees and their floral host ranges in Australia, and we can propose hypotheses for these patterns, which can be further tested with additional data. Identifying those broad patterns opens up a series of questions that need to be addressed if we are to ask why pollination ecosystems differ at large geographic scales.

Outstanding Issues and Future Directions

Our study reveals some major continental-scale patterns in colletid bee diversity and floral host ranges in Australia. These patterns prompt a number of questions that need more detailed studies to be addressed.

(i) *What are the drivers of species diversity and floral host range in Australian colletid bees?* Clade stem ages in the three key Australian colletid subfamilies do not explain differences in species diversity or floral host ranges, but teasing apart multiple potential causal factors will be challenging. Quantitatively assessing those factors at purely higher taxonomic levels, (*e.g.* subfamily level) is problematic because of limited statistical degrees of freedom in analyses. Phylogenetic comparative approaches (*e.g.* Pagel & Harvey, 1988; Pagel, 1999) that use full phylogenetic information will likely offer the most powerful way forward, but for continental-scale patterns this would require (1) detailed and robust phylogenies for most Australian bee species, as well as (2) ecological information (*e.g.* on floral hosts) for each species. The former is not currently available, but the current study is a contribution towards the latter.

(ii) *To what extent do plant-bee interaction observations reflect 'real' pollination networks?* As discussed by King et al. (2013), visitation does not always equal pollination, thus floral host breadth does not indicate pollination breadth (though the two are correlated, and floral host breadth sets an upper limit on pollination breadth). With up to 40% of visitations not entailing effective pollination, these networks should be interpreted as simply visitation breadth, rather than evidence of true pollination. If some bees, especially those that transport pollen internally, are common visitors to plants but ineffective pollinators, their inclusion in pollinator networks may lead to misleading measures of network connectedness and resilience. As concerns about pollination network resilience rise in the face of changing climates and land use, it will be important that network analyses discriminate between actual pollinators and simple visitors.

(iii) *How might voltinism impact the floral host breadth of Australian colletids?* Currently, there is very little information known about the number of generations per year that Australian bees can produce. We also don't know how much of a role genetics would play in controlling this voltinism. Are there patterns across genera or families, or climatic effects?

There is likely to be a strong link between voltinism and floral host breadth; specialist bees are likely to be univoltine with much less opportunity to expand their floral host range. This would be true for both temperate and tropical species unless their preferred floral resource is in flower for an extensive time period. Likewise, multivoltine bees would benefit from a more expansive floral host breadth, so there are floral hosts available throughout their flight season. Future research should include assess if there is any phylogenetic inertia or climatic factors that influence on the voltinism of these groups.

(iv) *How do adaptive radiations, phylogenetic inertia and rare dispersal events combine to shape continental patterns?* Our analyses suggest limits to adaptive radiation in floral host use at the level of subfamilies, otherwise we would find homogeneity across those taxa in terms of diversity and floral host breadth. But the existence of phylogenetic inertia means that rare inter-continental dispersal events – of particular but random taxa - have the potential to shape pollination networks by allowing or preventing novel bee-plant interactions to be introduced into a region. In continental regions like Australia, where dispersal barriers from surrounding landmasses have been geologically high, we might expect regional diversity to be higher than for more-connected continents. Michener (1965, 2007) has noted how exceptional the Australian bee fauna is, and future studies need to explore whether unusual regional bee faunas, and their floral host ranges, can be explained by rare stochastic dispersal events and limits to adaptive radiation.

HOW DOES BEE TONGUE-LENGTH AFFECT FLORAL HOST BREADTH? COMPARISONS OF AUSTRALIAN APIDAE (HYMENOTPERA)

Abstract

Flowering plants and their pollinators are a quintessential example of the benefits of a mutualistic relationship. These associations at times rely on specialised interactions or preferences that can drive evolutionary processes like adaptation or speciation. Despite this, network analyses of plant-pollinator interactions are nearly always restricted to narrow biomes such as, for example, specific mountain ranges, geographically limited forest types or European urban landscapes. Yet much broader, geographically widespread network analyses have the potential to inform how plant and pollinator interactions have helped assemble biota on very large scales. A recent continental-scale study (Slattery et al., 2023) on plant-pollinator networks involving short-tongued colletid bees in Australia indicated that the three key subfamilies exhibited very different network structures, both in floral-host species richness and host diversity. Here we use similar analyses to explore floral host richness and diversity for several key Australian long-tongued bee groups in the family Apidae. We hypothesised that long-tongued bees would have greater host richness and diversity because of their ability to access nectar rewards that are often unavailable to short-tongued bees. Instead, we found much narrower host ranges and lower diversities than for that of the Australian Colletidae. This counter-intuitive result cannot be explained by simple morphological differences, like tongue length, for the key colletid and apid bee groups, and we discuss how it may be related to bee speciation and historical biogeography. We present several hypotheses that may help explain our puzzling results, including the notion that access to a wider variety of host plants may decrease opportunities for allopatric speciation in bees and, counter-intuitively, limit expansion of host ranges. Our results also show that network analyses at continental scales can help reveal ecological patterns that are otherwise opaque at smaller scales.

Keywords

Anthophorinae, Xylocopinae, Meliponini, Allodapini and Colletidae

Introduction

Network analyses are an efficient approach for quantifying interactions between angiosperms and pollinators to generate an overview of the visitation habits from either perspective. These networks can be focussed on the visitation or visitor breadth of a single species or include several taxa at each level in community or ecosystem studies. Resulting webs are most frequently used to understand extant interactions and dependencies in ecological networks, and vulnerabilities to disruption if any particular elements are lost (Dormann et al., 2008; Schleuning et al., 2016; Vanbergen et al., 2017; Weiner et al., 2014). Due to these links between tropic levels, they can also be used to infer how ecosystems might have more broadly evolved over time via the introduction of new elements from dispersal events, and development of new co-evolutionary relationships. In other words, these network analyses can be used to explore both current ecosystem dynamics and the historical processes that have generated them.

Plant-pollinator network analyses are nearly always applied to restricted regions or biomes, such as islands (Crichton et al., 2018; Draper et al., 2021; Groutsch et al., 2019; Hayes et al., 2019), altitudinal bands (Adedoja et al., 2018; Montaño-Centellas, 2020; Ramos-Jiliberto et al., 2010) or urban and agricultural ecosystems (Maruyama et al., 2019; Morrison & Dirzo, 2020; Parra-Tabla et al., 2017; Theodorou et al., 2017). However, regional ecosystems are never completely isolated from surrounding areas (Wyborn, 2011), so defining geospatial limits for network analyses can become arbitrary.

Slattery et al. (2023) recently investigated bee-plant networks for colletid bees in Australia, in what was the first study to examine such networks at a continental scale. The study found that three subfamilies in the short-tongued bee family Colletidae differed strongly in their interactions with host plant genera, which suggested that deep evolutionary drivers for these bees impacted networks at a continental scale. Slattery et al. (2023) raised the possibility that some colletid bee networks may be vicariously driven by vertebrates, particularly psittaciform birds (parrots) that can only access nectar via shallow cups. Under this hypothesis, the evolution of shallow-cup nectaries driven by vertebrate pollinators provides a resource that is then exploited by short-tongued bees. These bees would at best provide only secondary pollination services, breaking our assumptions of expected co-evolutionary pollination relationships between plants and specific bees. This scenario would have major consequences, such as suggesting that bees cannot be assumed to always be important pollinators, as they might instead be ‘parasitic’ on other co-evolved plant-animal relationships. More recent research has supported this non-mutualistic relationship with other plants and pollinators, with pollinators acting in an exploitative manner through destructive visitations (Sakhalkar et al., 2023; Varma et al., 2020) or the exclusion of more effective pollinators (Unni et al., 2021). These non-mutualistic interactions can also take place at the plant level by changing the chemical make-up of the pollen available (Feng et al., 2024; Rivest & Forrest, 2020).

Apidae includes some of the largest and hairiest of the Australian bee fauna (*e.g.*, Carpenter bees,) and are one of two long-tongued families native to the continent. While their global diversity is the greatest of any family, they are represented by fewer than 200 Australian species and make up less than 12% of our native bees (Australian Biological Resources Study, 2022a; Batley & Hogendoorn, 2009). Despite their relatively moderate Australian richness, the family includes several iconic Australian species (*e.g.*, blue-banded or teddy bear bees in *Amegilla*) and a diverse spectrum of sociality. Many apid bees are solitary (like the majority of the Australian bee fauna), but the family also includes kleptoparasites (*e.g.* Cuckoo bees), quasisocial species with related nesting behaviour (*e.g.*, exoneurines) and entirely eusocial species like the stingless bees in the Meliponini tribe.

Slattery et al. (2023) only examined colletid bees, which are short-tongued and almost completely solitary nesters. However, tongue length (usually measured as the length of glossae) should partially determine the kinds of flowers from which bees can obtain nectar. If nectaries occur at the bottom of long, narrow corolla tubes, tongue length would directly impact the likelihood of feeding success and, consequently, visitation (B. Anderson & Johnson, 2008; Harder, 1983; Nilsson, 1988; Van Der Kooi & Ollerton, 2020; Wei et al., 2020, 2023). Therefore, we might expect that long-tongued bees like Apidae would have access to a wider range of angiosperms and consequently, broader floral host ranges. Of course, multiple factors may impact the floral host ranges of bees, including the specific floral resources obtained, activity phenologies, climate adaptations, and competitive interactions, to name a few. Another potentially confounding driver in floral host ranges is the amount of evolutionary time that bee lineages have had to adapt to native flora, and how those flora adapt to different bees. Older bee clades should have had more opportunities to evolve the ability to exploit a wider range of possible hosts through adaptive responses like niche partitioning (Finke & Snyder, 2008), and this should manifest as a larger range of exploited plants across the entire clade, a separate concept from niche breadth of individual species. This is especially important when considering these interactions at the higher taxonomic level, with described preferences in floral resources (Casanelles-Abella et al., 2023; Iwasaki et al., 2018; Nyman et al., 2010).

When combined, the above considerations suggest hypotheses for the breadth of floral host ranges for specific bee groups. In Australian native bees, we would expect that: (1) Long-tongued bees should have broader floral host ranges than short-tongued bees; and (2) Floral host ranges of major bee clades should be positively linked with clade ages. Here, we test these hypotheses by developing bee-plant interaction networks for the major long-tongued native Australian bees in the family

Apidae. We compare these networks with those for the Australian native bees of the short-tongued Colletidae. If either or both predictions are inconsistent with broad network patterns, this would require re-evaluating some core assumptions about the evolutionary assembly of bee-pollinator elements.

Methodology

Data collation

Methodology for this study closely followed that of Slattery et al. (2023). Digitised floral visitation records from Australian museums (Western Australian Museum, Australian Museum and Museums Victoria [all available upon reasonable request to the corresponding institution]) were collated and filtered for Apidae interactions resolved to subgeneric (or generic, where there are no relevant subgenera) level for bee taxa, and to generic level for floral hosts. Records that did not have this degree of specificity were excluded from the analyses. Plant genera and bee subgenera were updated to their current taxonomic status and sex was not distinguished due to the number of records that did not include this information. Interaction data were also recorded into binary (presence vs. absence for each bee-plant combination) connections to help reduce the effects of unequal sampling effort (*e.g.*, the effect of having hundreds of specimens obtained in a single collection episode). Unique collection locations from the filtered dataset covered a broad geographical distribution of records, demonstrated in Figure 6, created with QGIS Geographical Information System version 3.22 (QGIS Development Team, 2024).

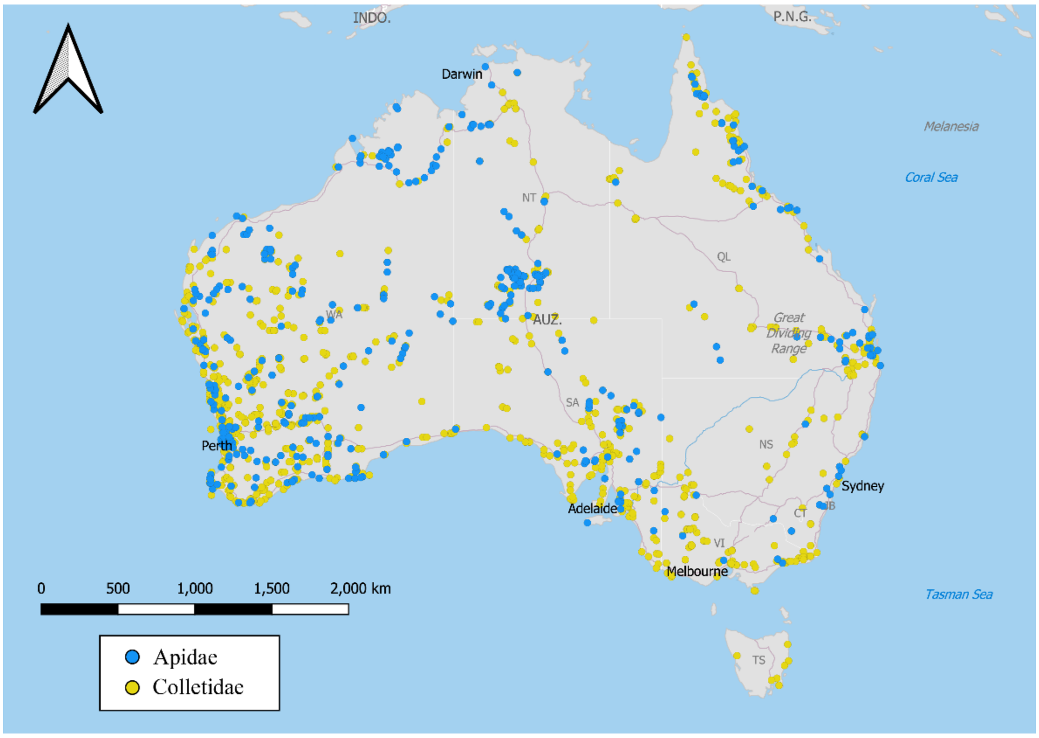

Figure 6: Unique collection location records for Apidae and Colletidae datasets, demonstrating the geographical spread of this study. Created with QGIS Geographical Information System version 3.22 (QGIS Development Team, 2024).

Network Statistics

There was a total of three Apidae subfamilies from the filtered data: Anthophorinae (consisting of only *Amegilla* subgenera), Apinae (represented by only the tribe Meliponini) and Xylocopinae. Each of these subfamilies' networks were analysed independently, but network indices in the Xylocopinae were broken down into smaller taxonomic units. The genus *Xylocopa* was analysed independently, while the tribe Allodapini was separated into two monophyletic groups (i) the genus *Braunsapis*, and (ii) the other combined exoneurine genera *Exoneura*, *Exoneurella*, *Brevineura* and *Inquilina*, due to these clades having different evolutionary origins and occupying different climatic niches (Chenoweth & Schwarz, 2011b; Fuller et al., 2005). In Australia, the Xylocopinae tribe Ceratinini is represented by only a single species, *Ceratina (Neoceratina) australensis*, and was not included in statistical analyses, though we do report a floral host range for this species (Table 4).

Networks were created in R version 4.0.4 (R Core Team, 2021) using the packages *bipartite* (Dormann et al., 2008) and *vegan* (Oksanen et al., 2020). Network statistics included: niche overlap (similarity at the bee level, *i.e.* similarity between bee subgenera in terms of the plant genera visited, and at the plant level, *i.e.* similarity between the plant genera in terms of their visitation from bee genera/subgenera), C-score (measures disaggregation in the network so that values closer to one suggest repelling forces [*i.e.* competition] on the same level), NODF (nestedness based on overlap and decreasing fill), togetherness (co-occupancies and co-absences in the data matrix, *i.e.* at the bee level, where two subsequent bee genera/subgenera are recorded as both visiting a particular plant genus, and then both not visiting the different plant genus) and partner diversity for bees (the mean Shannon diversity of the floral hosts that each bee subfamily is visiting) (Dormann et al., 2009). These statistics were assessed for significance using the *vegan* function 'oecosimu', run for 1,000 simulations with the "r00" model, which maintains the number of filled cells, but randomises their replacement in the matrix.

Rarefaction Analyses

A major issue in developing estimates of floral host richness and diversity is unequal sampling (or record) density. This could arise from differences in taxon abundance, but also unequal sampling of environments. We assessed the impact of sample sizes using rarefaction analyses in EstimateS version 9.1.0 (Colwell, 2013) for each bee group with sufficient interaction data. These bee groups were: Meliponini, *Amegilla*, Melectini, *Xylocopa*, exoneurines and *Braunsapis*. These curves could be used to explore the impact of sampling density on estimates of floral host richness (S) and diversity, as measured by Shannon's diversity index. We extrapolated rarefaction curves at a factor of three times (three times the total number of resamples for each group); but patterns persisted even when extrapolated to a cumulative resample of 13,601 interaction records (the largest number of interaction records for a single colletid subfamily in Slattery et al. (2023)). In these rarefaction analyses, a curve that reaches the asymptote (or a plateau) suggests that the true floral host range of that bee taxa is well-estimated by the actual sampled data, while a curve that does not reach asymptote suggests total floral host breadth remains underestimated. Knots of these curves were estimated, and the bias-corrected formula was used for Chao 1 and Chao 2, with samples randomised without replacement. All rarefaction curves were run for 1000 iterations and the consensus was modelled in R (R Core Team, 2021) using the packages *ggplot2* (Wickham, 2016), *dplyr* (Wickham et al., 2022) and *tidyverse* (Wickham et al., 2019).

Comparisons to Colletidae

To further simplify comparisons between the Apidae floral host breadth presented here, and the Colletidae floral host breadth presented in Slattery et al. (2023), we plotted the log10 number of the highest potential floral host breadth (presented in the rarefaction curves) against the log10 described Australian species for each of these groups (based on: Australian Biological Resources Study (2022)). Then, to explore the presence of possible outliers in our model, we assessed the standardised residuals of these same variables. Residuals greater than |2| indicate a significant deviation from the mean and observed values. These scatter plots were developed in R (R Core Team, 2021) again using the packages *ggplot2* (Wickham, 2016), *tibble* (Müller & Wickham, 2022) and *dplyr* (Wickham et al., 2022).

Results

Network Statistics

The Apinae tribe Meliponini had 356 recorded interactions with 23 different plant genera in the two bee genera present in Australia (*Austroplebeia* and *Tetragonula*) (Table 4). Three *Amegilla* subgenera visited 59 different plant species in a total of 416 interaction records (Table 4). The final subfamily, Xylocopinae, had four bee fauna of interest with the largest number of interactions recorded in the exoneurine group with 532 interactions from four bee genera recorded across 39 plant genera (Table 4).

In the networks statistics *Amegilla* had the most nested matrix (NODF = 40.04) while the smallest degree of nestedness was in the Xylocopinae subgenera *Xylocopa* (NODF = 0) (Table 5). Niche overlap for the bee level (bee subgenera/genera) was highest in the stingless bees in the Meliponini (0.308), with significant overlap in plant genera visitations, and lowest in the *Xylocopa*, where there were no similarities in floral host breadth (Table 5).

Table 4: Total number of interactions (before binary transformation) for bee faunal groups, with specific numbers for each based on the number of bee subgenera, recorded number of floral hosts and the total number of interactions.

	Total number of recorded interactions	*Number of subgenera represented*	*Recorded floral host genera*
Meliponini	356	2	23
Melectini	66	1	19
Amegilla	416	3	59
Exoneurines	532	4	39
Braunsapis	175	1	22
Ceratinini	17	1	3
Xylocopa	20	2	11

Table 5: Network level indices separately calculated for all bee faunal groups that had sufficient interaction data for analysis (*i.e.* more than one be genus/subgenus). Table details the level of interest (Plant/Bee) and the result of the statistic for each of the bee faunal groups. Bolded values indicate significance (p-value = <0.05(* = <0.01, ** = <0.001)) in 'oecosimu' output.

	NODF	*Niche overlap*		*C-score*		*Togetherness*		*Partner diversity*	
	Network	*Plant*	*Bee*	*Plant*	*Bee*	*Plant*	*Bee*	*Plant*	*Bee*
Meliponini	**31.281***	0.701	**0.308**	0.294	1	**0.468****	0	**0.213***	**2.676****
Amegilla	40.040	**0.733****	**0.258****	**0.137****	0.409	**0.626****	0.178	**0.344****	**3.596****
Exoneurines	**27.436***	0.384	0.301	**0.245***	0.169	0.557	0.472	**0.463****	**2.691***
Xylocopa	**0****	**0.491**	**0****	0.509	1	**0.491***	0	**0****	1.742

Comparatively, the niche overlap for plant level (plant genera) was higher than that of the bee level in every matrix, which might suggest that plant genera have a greater bee visitation breadth, compared to bee subgenera floral host breadths (Table 5). The results of the mean co-occupancies and co-absences in the togetherness indices also corroborate the values in the niche overlap, with the highest values at the bee level in the exoneurine group (Togetherness = 0.472) (Table 5). C-scores at the bee level were mixed, with *Xylocopa* subgenera and Meliponini having values of 1, indicating total disaggregation in the matrix and reflecting Togetherness values; *Amegilla* had a moderate score of 0.409, and the exoneurine group had the lowest at 0.169, which might suggest very little competition between bee genera for floral resources (Table 5). The final statistic of interest was partner diversity, where *Amegilla* subgenera (3.596) had the greatest diversity and richness in their floral host breadth, while the two *Xylocopa* subgenera (1.742) had the smallest diversity and richness in floral hosts (Table 5).

Floral Networks

The floral networks for each subfamily are depicted in Figures 6, 7 and 8: three predominant plant families of interest are colour-coded in both networks (Fabaceae, Myrtaceae and Proteaceae), due to their prevalence in the Australian system (Crisp & Cook, 2013). In the Meliponini network (Figure 6) *Austroplebeia* visited the most plant genera, with the visitation breadth of *Tetragonula* not expanding outside of Myrtaceae or Proteaceae.

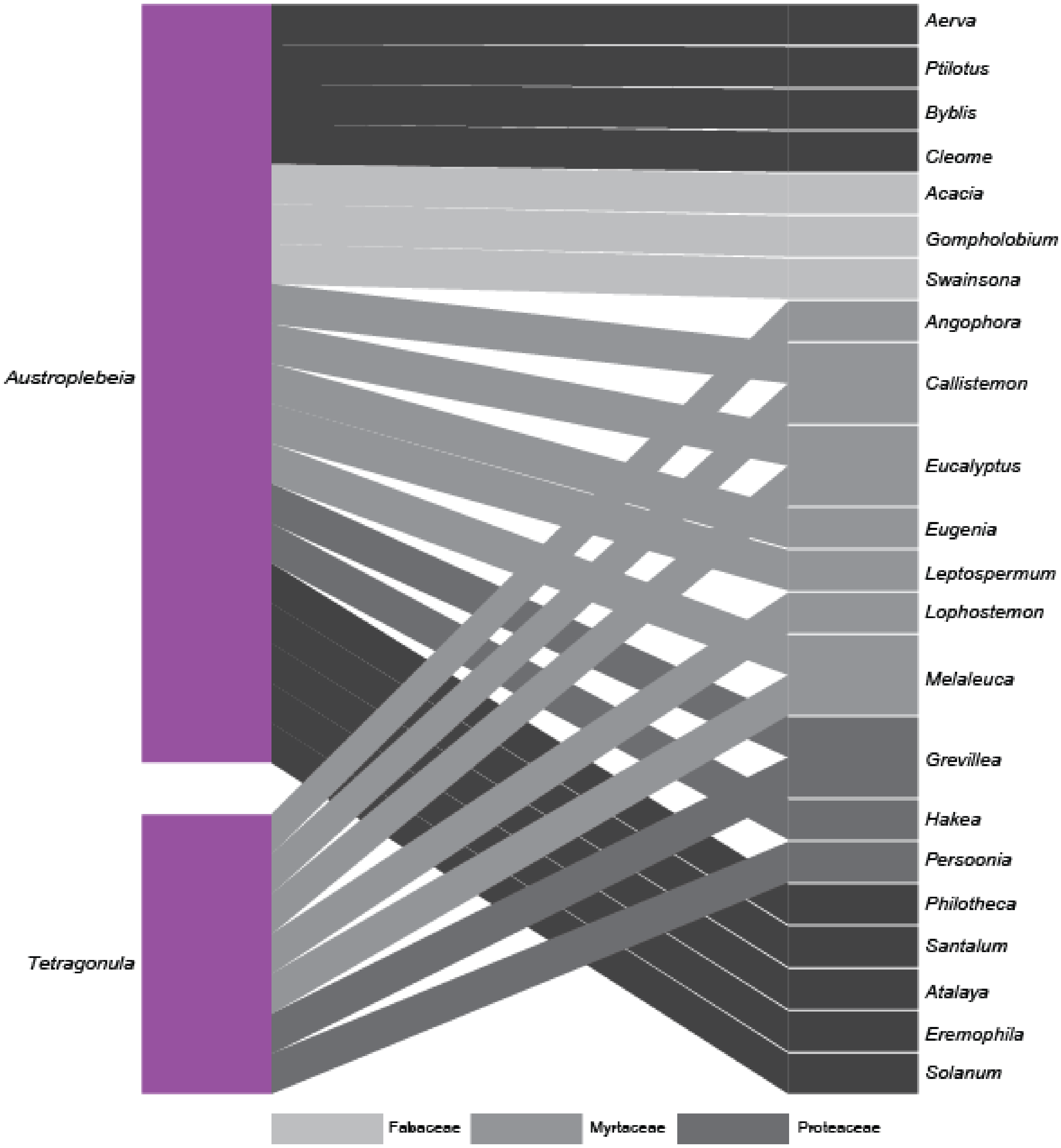

Figure 7: Floral host breadth network for the Australian Apidae tribe Meliponini. Bee subgenera are on the left and plant genera on the right with three families of interest colour coded according to the legend below. Each diagonal or horizontal line indicates one binary connection between a bee and plant taxon, unweighted for the number of actual recorded interactions.

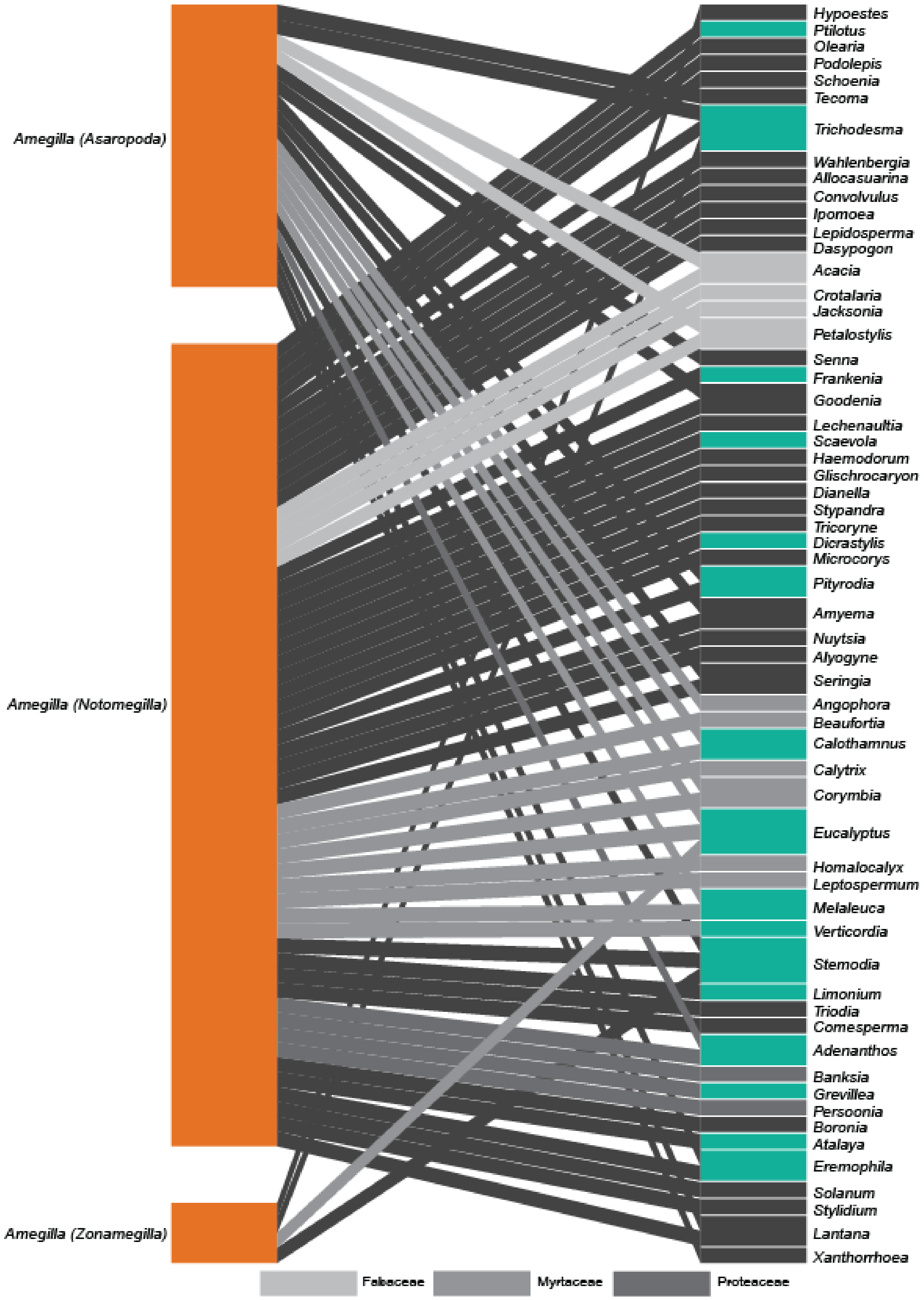

Figure 8: Floral host breadth network for the Australian Apidae subfamily Anthophorinae, represented by only *Amegilla*. Bee subgenera are on the left and plant genera on the right with three plant families of special interest coloured as described in the legend. Colours on the right-hand band indicate visitations by the genus *Thyreus*, from the tribe Melectini, which are kleptoparasitic on anthophorine bees. Each diagonal or horizontal line indicates one binary visitation record between the bee subgenus and the associated plant genus.

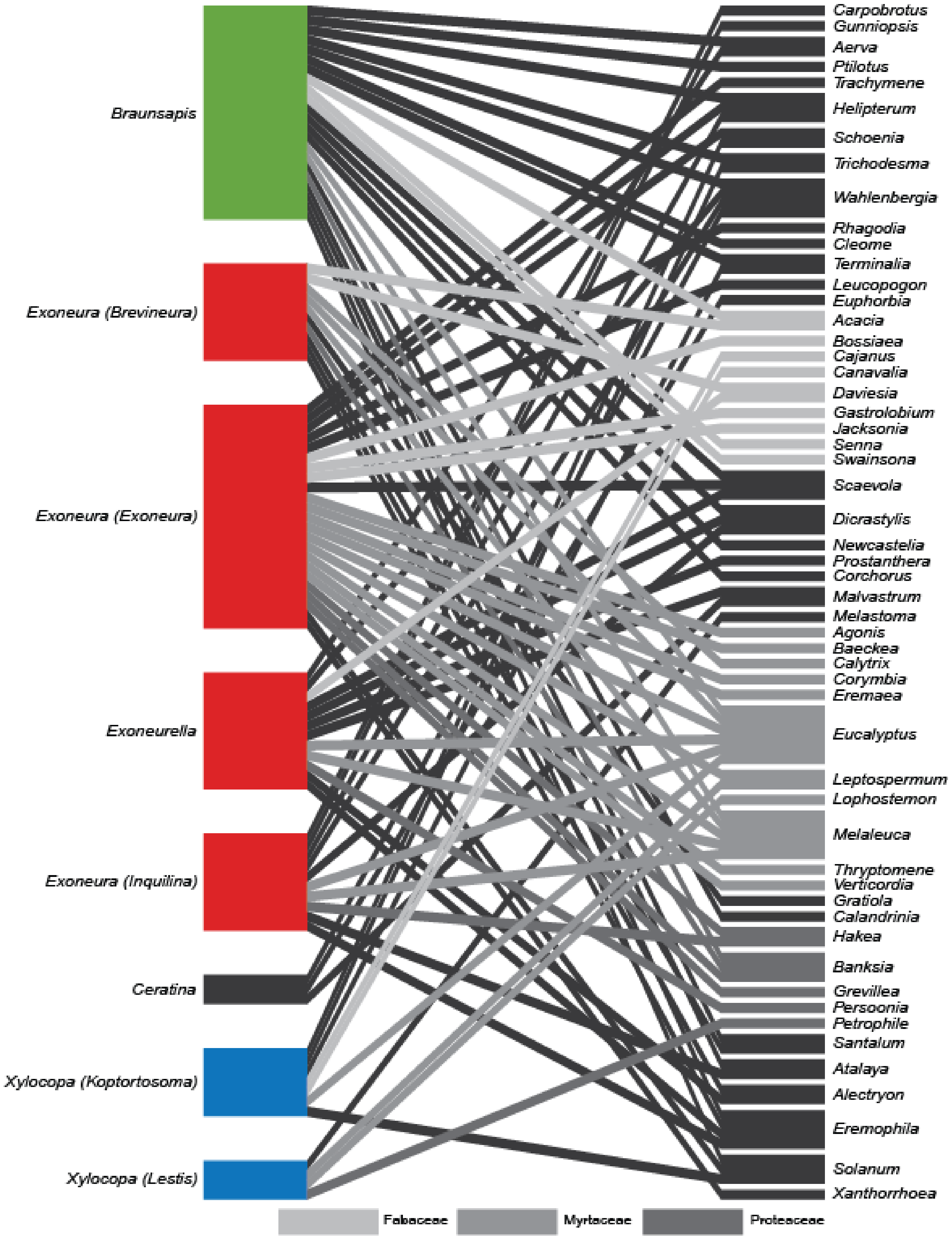

Figure 9: Floral host network for the Australian Apidae subfamily Xylocopinae. Bee genera/subgenera are on the left with different colours denoting the different group allocations used for further analyses (*Braunsapis* = green, exoneurines = red and *Xylocopa* = blue). Plant genera are coloured based on 3 families of interest, described in the legend at the bottom of the figure. Each diagonal or horizontal line indicates one binary visitation record between the bee genus/subgenus and the plant genus.

Amegilla (Notomegilla) (Figure 7) had the broadest floral host breadth among the *Amegilla* subgenera, with numerous visitations outside of the three plant families of interest. In the remaining network for Xylocopinae (Figure 8), exoneurine genera visited 39 plant genera that gave them the broadest floral host breadth in the Xylocopinae network, with many of these comprising Myrtaceae genera. The Ceratinini, which has only one Australian species, *Ceratina (Neoceratina) australensis*, has recorded interactions with only three plant genera.

Rarefaction Analyses

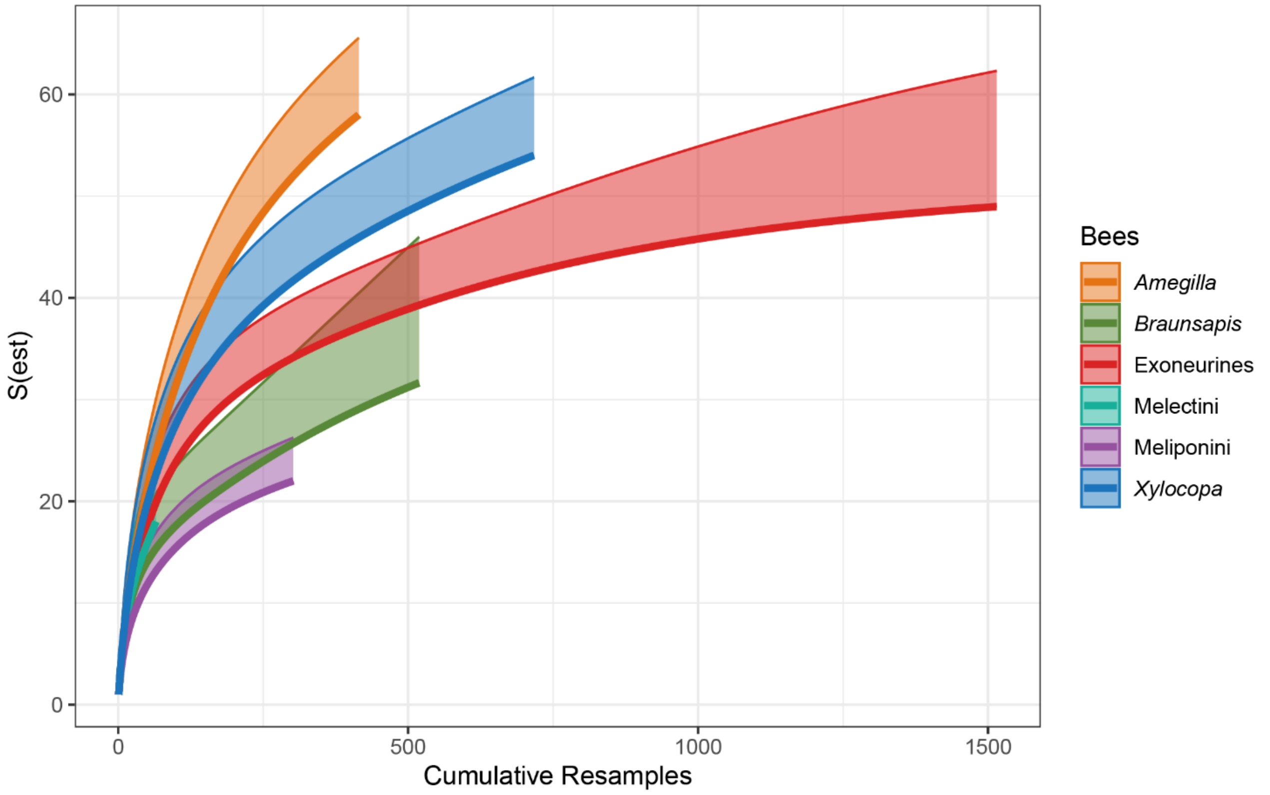

Figure 10: Rarefaction curves for Apidae bee fauna used to calculate estimated total genera floral host breadth (S(est)) extrapolated at a factor of 3x, run for 1,000 iterations. Upper 95% CI are indicated by the shaded sections.

Figures 9 and 10 summarise rarefaction analyses for each of the bee tribes/genera: wherein Figure 9 demonstrates S(est) on the y-axis as a function of sampling effort, showing the expected number of plant genera that each bee group can visit, fitted with upper 95% confidence limits. Extrapolated at a factor of 3x, *Amegilla* subgenera again have the broadest floral host breadth, followed by *Xylocopa* subgenera as the next broadest. Figure 10 depicts the highest possible Shannon's index of diversity value for each tribe/genus' floral host breadth extrapolated at a factor of 3x. The tribe/genus with the highest possible diversity of floral host breadth is again *Amegilla*, followed by *Xylocopa* with Melectini having the lowest floral host diversity, with an upper limit of 18 estimated plant genera in their floral host breadth.

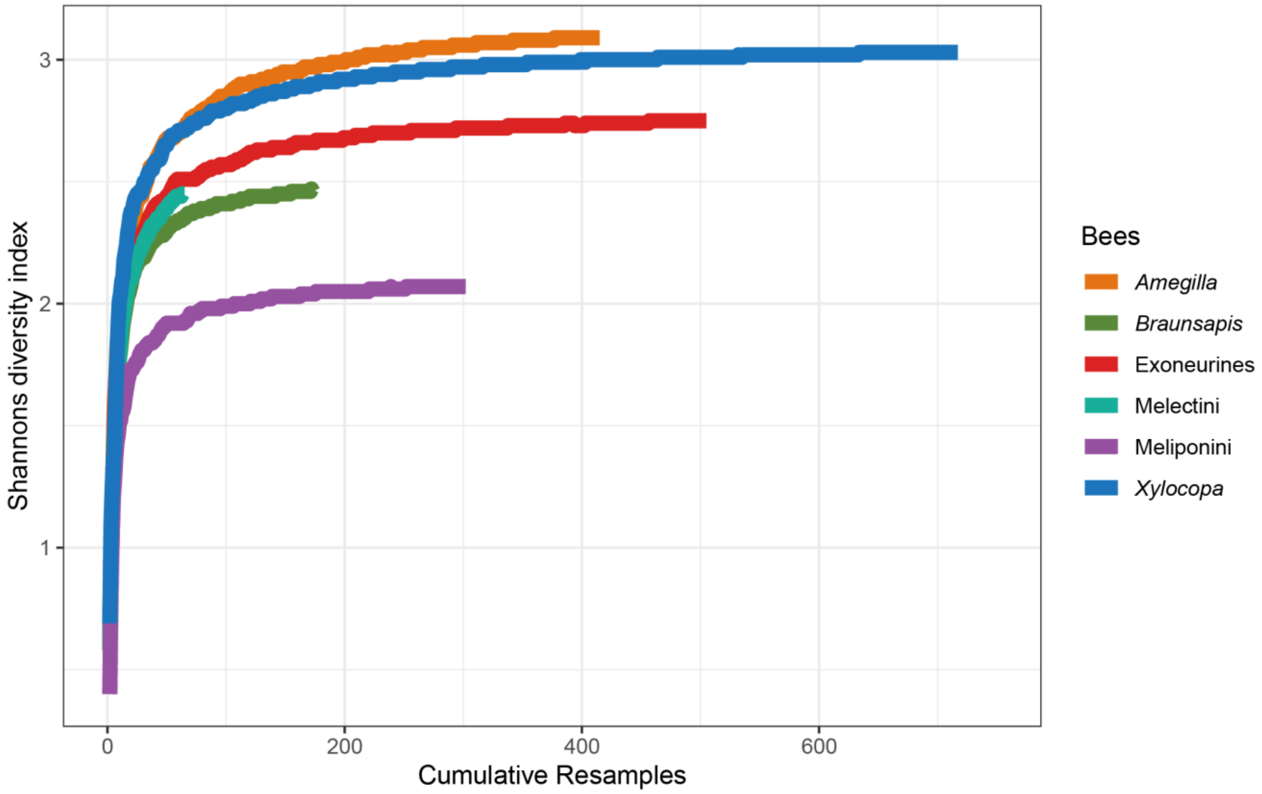

Figure 11: Rarefaction curves for Apidae bee fauna used to calculate Shannon's index of diversity in genera floral host breadth, extrapolated at a factor of 3x and run for 1,000 iterations.

Comparisons to Colletidae

Figure 11 summarises the combined results of the rarefaction curves of the Apidae subfamilies and the major Australian subfamilies of Colletidae (Slattery et al., 2023). The estimated total number of potential floral host genera (including 95% confidence intervals) is presented in Figure 11a for each of the bee faunal groupings. Comparatively, Colletidae subfamilies have a greater potential floral host breadth than any of the Apidae bee faunas. Figure 11b is the combined Colletidae and Apidae potential floral host generic diversity, which shows a greater potential diversity for all colletid subfamilies than any of the Apidae groups.

The estimated potential floral host breadth ($\log_{10}$) of Colletidae and Apidae is again presented in Figure 12, plotted against the described species diversity for each bee fauna ($\log_{10}$) (as available at Australian Biological Resources Study, 2022a, 2022b)). Fitting a linear model to these values gave an adjusted $R^2 = 0.67$ (p-value = 0.004) and looking at the standardised residuals of this same model in Figure 7, the closest bee faunal group to a significant deviation (*i.e.*, more than two standardised residuals) is Euryglossinae.

a)

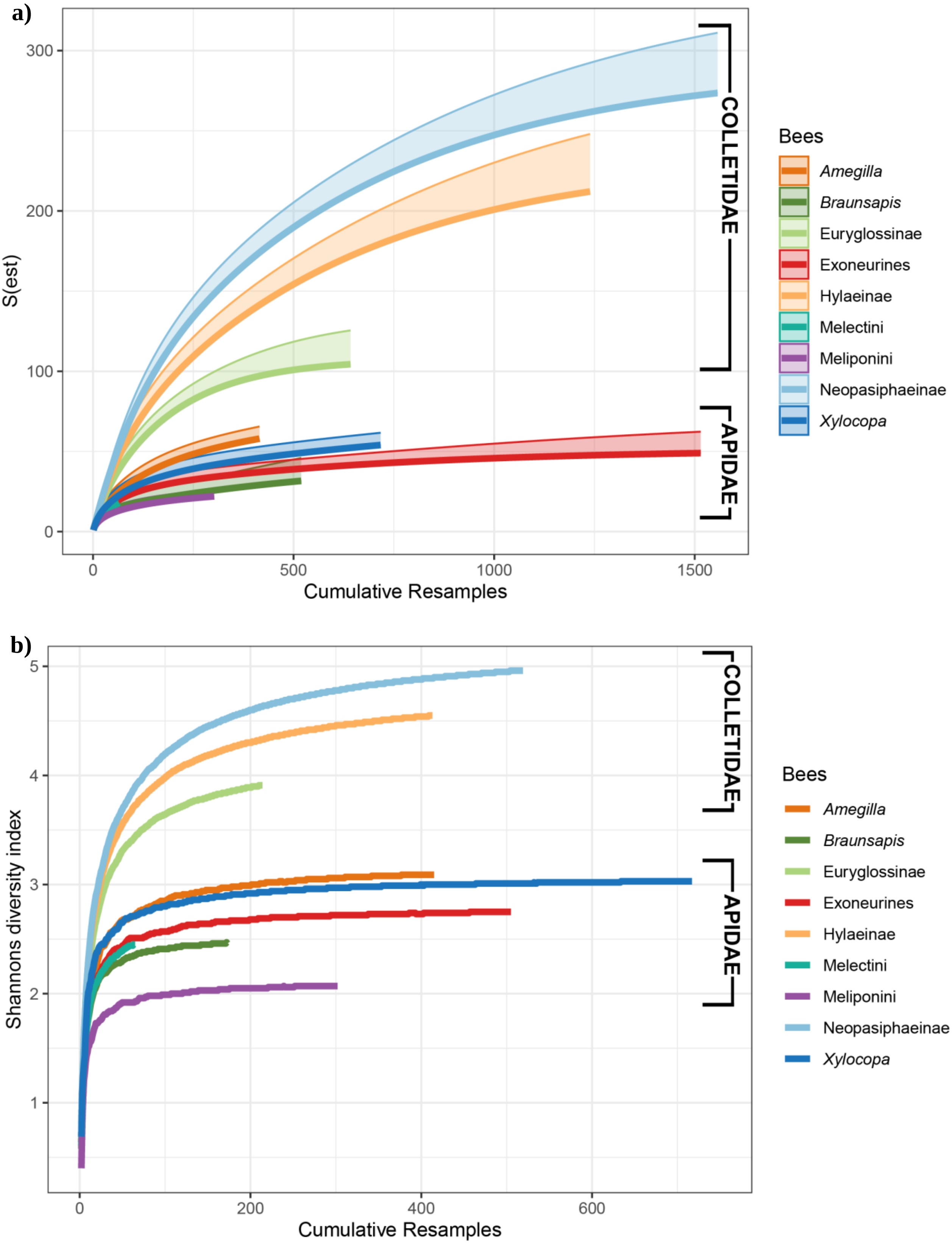

Figure 12: a) Rarefaction curves of Apidae and Colletidae bee fauna used to calculate estimated total genera floral host breadth (S(est)) extrapolated at a factor of 3x, run for 1,000 iterations. Upper 95% CI are indicated by the shaded sections. **b)** Rarefaction curves for Apidae and Colletidae bee fauna used to calculate Shannon's index of diversity in genera floral host breadth, extrapolated at a factor of 3x and run for 1,000 iterations.

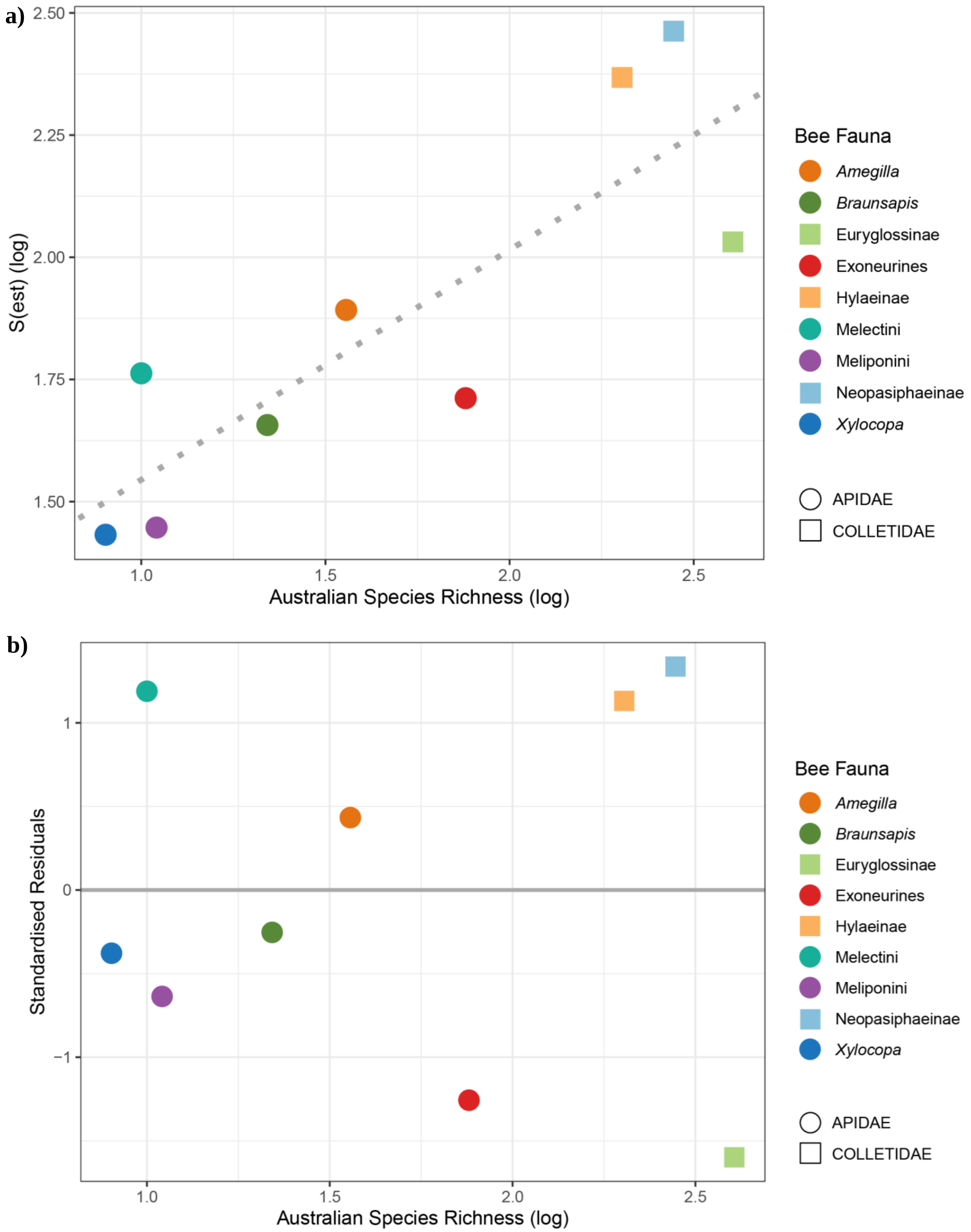

Figure 13: a) Estimated floral host breadth ($\log_{10}$) of Apidae and Colletidae bee fauna plotted against total Australian bee species richness ($\log_{10}$). The grey linear regression model plotted has an adjusted $R^2 = 0.67$ (p-value = 0.004). **b)** Standardised residuals of Apidae and Colletidae from the regression model against the total Australian species richness for each bee faunal group ($\log_{10}$).

Discussion

Our analyses provide insight into the variation among network structures within the Australian Apidae, enabling comparisons with networks for the short-tongued Australian Colletidae. Below, we elaborate on the implications of these issues separately.

Apidae networks

Rarefaction curves for the apid floral host breadths were based off weighted data (non-binary interaction records) extrapolated at a factor of three for 1,000 iterations to assess the impacts of record scarcity in the networks and associated statistics. *Amegilla* had the broadest floral host breadth in the floral networks, and the greatest partner diversity for any of the apid bee groups, which is corroborated in the results of our rarefaction analyses (Figures 9 and 10). Meliponini, however, had the least diversity and richness of floral hosts in their rarefaction analyses (Figures 9 and 10), reflective of the high niche overlap at the plant level in their network, suggesting both genera of Australian stingless bee are visiting primarily the same floral hosts (Table 5 and Figure 6).

The rarefaction analyses presented in Figures 9 and 10 suggest that there may be some underestimation in the total floral host richness for the apid bee faunal groups, but these weighted outputs reflect the results of binary network statistics. Even when extrapolated further (to 13,601 resamples – the greatest number of interactions for any bee group across both families), both measures of floral host diversity and richness were smaller than any of the colletid subfamilies.

Network statistics closely reflected both the matrices and bipartite networks. High significance in low C-scores at the plant level could indicate that there is little competition between plant genera for bees (other than *Xylocopa*) (Table 5). High significance in low partner diversity statistics at the plant level are reflective of bee subgenera diversity in these networks. Togetherness scores at the bee level for both Meliponini and *Xylocopa* are a result of only two subgenera in the networks (co-absences in plant visitations cannot exist for only two bee subgenera), linked to the C-score output of these bee faunal groups at the same level (Stone & Roberts, 1992). However, while there was some overlap in visitation between the two meliponine genera, *Xylocopa* subgenera had no similarities in their floral host breadth, which explains their low NODF, niche overlap and partner diversity on the plant level. The most nested network was for the *Amegilla* subgenera, with only six plant genera visited by bees not belonging to *Amegilla (Notomegilla)*. *Amegilla* had the broadest floral host breadth of any of the apid bee faunal groupings.

Comparisons between colletid and apid networks and floral host breadths

We hypothesised that the long-tongued Australian Apidae, when compared to short-tongued Australian colletids, would have a greater floral host breadth, because greater tongue length would allow them to exploit a broader range of angiosperm floral morphologies (Johnson & Anderson, 2010; Nilsson, 1988; Wei et al., 2023). Although sample sizes differed between the bee groups, rarefaction analyses indicated that this variation in the number of records is not sufficient to explain the much greater floral host richness and diversity of colletids compared to apids. Our data therefore suggest a counterintuitive result: long-tongued Apidae have a smaller floral host breadth than short-tongued colletids, and this cannot be explained as an artefact of sample sizes.

There are numerous additional differences between apids and colletids. Tongue length could potentially be correlated with other causal factors, such as voltinism or sociality, which are perhaps the stronger drivers of floral host range of these bee families.

In terms of sociality, colletids are almost entirely comprised of solitary bees (only one colletid bee, a hylaeine species, has been reliably reported as social (Hearn et al., 2022)), while many Australian Apidae are social to some extent, ranging from quasisocial, semisocial and eusocial to parasitic (Cronin & Schwarz, 2001; Schwarz et al., 2007, 2010). This can impact floral host breadth in different ways. For example, cuckoo bees (the kleptoparasitic genera included in these networks, *Inquilina* (Figure 8) and *Thyreus* (Figure 7)) had overlap in their floral visitation with the floral host breadth of their bee host. As kleptoparasites, these genera rely on their bee hosts to obtain resources, so overlap in floral breadth with their hosts is expected, with visitations outside of their hosts' breadth limited. These differences in sociality can also impact the rate of reproduction (number of generations produced each year), as well as the total brood produced and surviving in each of those generations (Tierney et al., 2000; Yagi & Hasegawa, 2012). Eusocial bees have also been described as reverting to solitary nesting in response to their foraging behaviours in another bee family, Halictidae (Danforth, 2002). However, some of these same bees can also demonstrate intraspecific differences in sociality associated changes in altitude and latitude (Plateaux-Quénu et al., 2000; Soucy & Danforth, 2002).

Differences in the voltinism of these families could also explain their disparity in floral host breadth. Voltinism in Australian bee fauna is understudied, but while most colletids are likely univoltine, many apid species are multivoltine or active year-round. Under this hypothesis, multivoltinism and more extensive seasonal activity windows should promote an increase in the floral host breadth of Apidae due to greater foraging opportunities. However, this is the opposite of what we saw in comparisons to colletid floral host breadths (Figure 11) (Slattery et al., 2023).

Alternatively, floral host breadth could be related to the total Australian species richness in each of our bee faunal groups (Figure 11a). In our networks bees were allocated into subgeneric/generic ranks, but these somewhat arbitrary categories may ‘hide’ the true biological species richness, and individual species level adaptations could drive floral host breadth in these taxonomic categories. For example, while in our networks *Exoneura* might appear to have a greater floral host breadth than *Brevineura* (Figure 8), this might simply be due to the variation in number of described species in each of these generic groups. If this is the case, then variation in floral host breadth across bee subgenera would be an artefact of species numbers.

We therefore explored this possible relationship between floral host breadth and described species number in Figure 11. All bee faunal groups fall within two standard residuals of the linear model (Figure 11b), and Euryglossinae has the greatest departure from this model. As discussed in Slattery et al. (2023), the hyper-diversity of this subfamily, along with their more restricted floral host breadth, could be driven by their reliance on Myrtaceae genera, whose own diversification and distribution are likely driven by non-bee fauna.

Biogeographic histories in the Australian landscape

The biogeographic histories of Colletidae and Apidae are also very different: colletids had dispersed into Australia before the late Cretaceous, likely via a trans-Antarctic route when South America and Australia were still connected as a part of Gondwana. Representatives of this family had free movement between these continents until the Eocene. Colletidae were probably the only bee fauna on the continent until the late Oligocene and Neogene boundary, when the most recent common ancestor of the endemic bee family Stenotritidae arose, and other families began to disperse down into Australia through Asia (Almeida et al., 2023). This is the historical dispersal route of most Australian Apidae fauna, with the exception of the allodapine genus *Braunsapis* (Chenoweth & Schwarz, 2011b). As a result, the colletid subfamilies have had longer occupation of the Australian continent to develop diverse interactions with dominant native angiosperms such as Fabaceae, Myrtaceae and Proteaceae, families that are ancient and abundant in the landscape (Crisp & Cook, 2013). The reliance of Australian colletid bees on these flora, before the continent moved towards the Asian plate that allowed the introduction of many Apidae bee fauna, could help explain their expansive floral host breadth in comparison to the more recent Australian history of Apidae (Almeida et al., 2023). Prolonged interactions with these angiosperms may explain the preference of colletids for these families. Under this hypothesis, Australian apid visitations to these plant families could be explained by their abundance in the Australian landscape, rather than the same preponderance or reliance on them that we see within the Colletidae.

Finally, in addition to historical distributions in the Australian landscape based on dispersal time, there could be differentiation in the current distribution within these families. If apids and colletids occupy different biomes that vary in their floral host diversity, then these floral breadth differences could reflect the different biomes that these bee families are distributed within. If long-tongued bees are mainly occupying areas with lower floral host diversity, their lower floral host breadth could result from a lack of *access* to a greater diversity of floral resources. A proportional increase of Australian apids in the occupation of these floristically diverse biomes might then drive a correlated increase in their floral host breadth. This would require specific floral diversity data from across Australia that could be cross referenced with locational data of the Australian bee families, and while an interesting area for future research (with the increase in publicly available bee and plant datasets), it is currently outside the scope of this research.

To conclude, while the original hypotheses of tongue length and clade ages driving floral host breadth were not supported here, this in turn suggests other factors potentially influencing bee family visitation preferences at the continental scale. Species richness and time since dispersal into, or origin in Australia, seem to better explain the differences between floral host breadth of Australian colletid and apid bees. We suggest that further, more detailed, research into the biogeographic histories of the Australian bee fauna could better unveil correlations between habitation age on the continent and floral host breadth.

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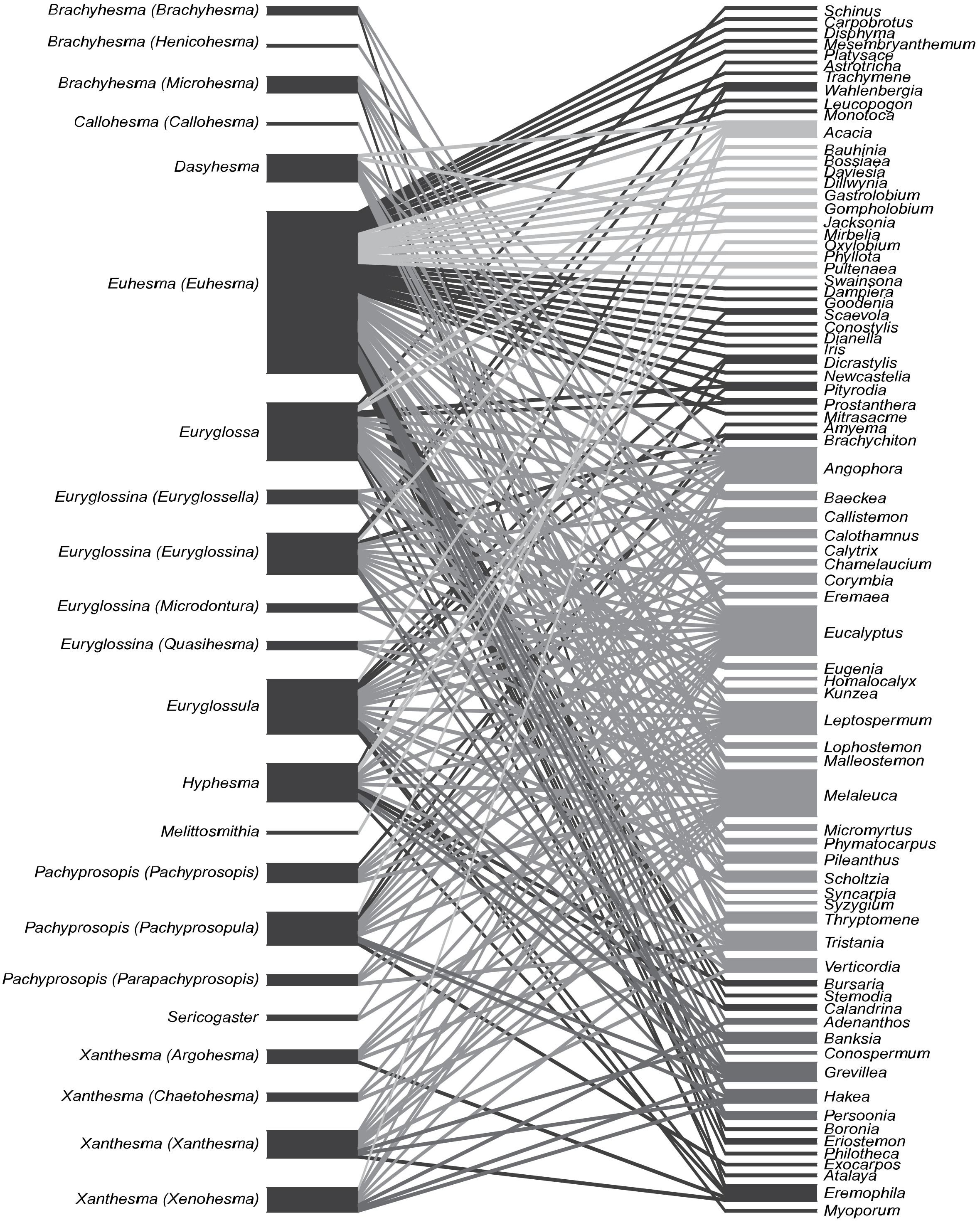
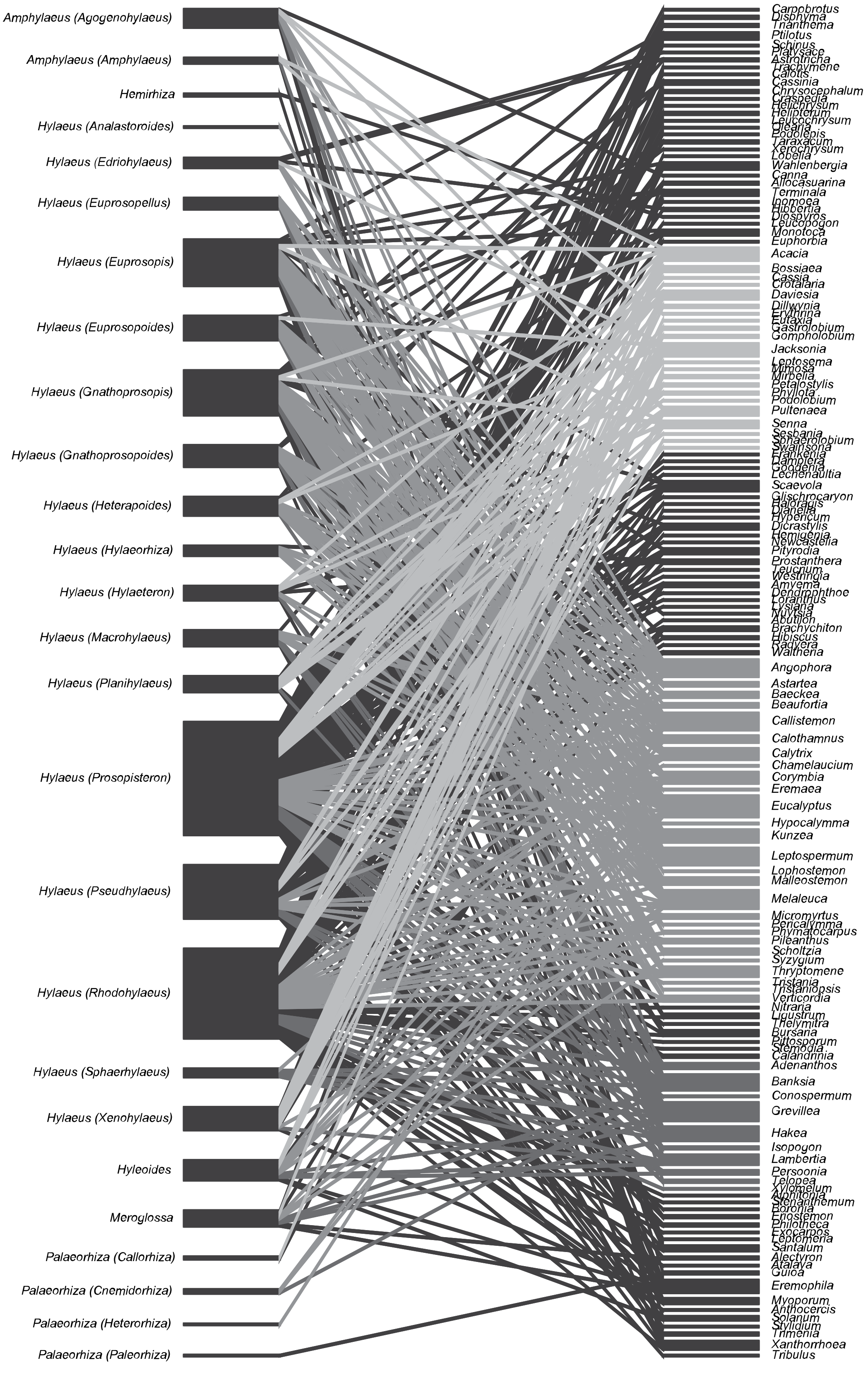
APPENDICES

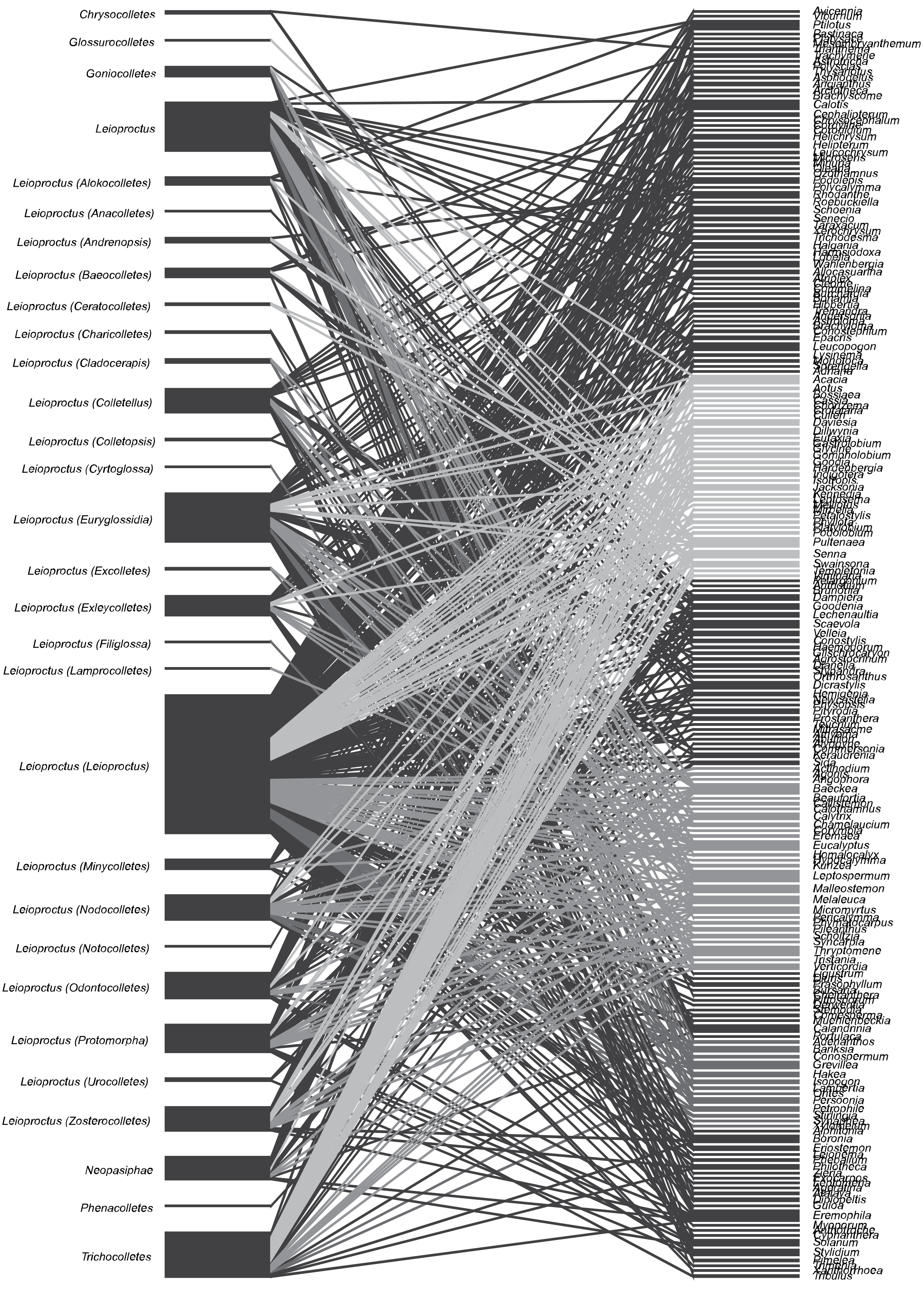
Appendix A: Supplementary Materials



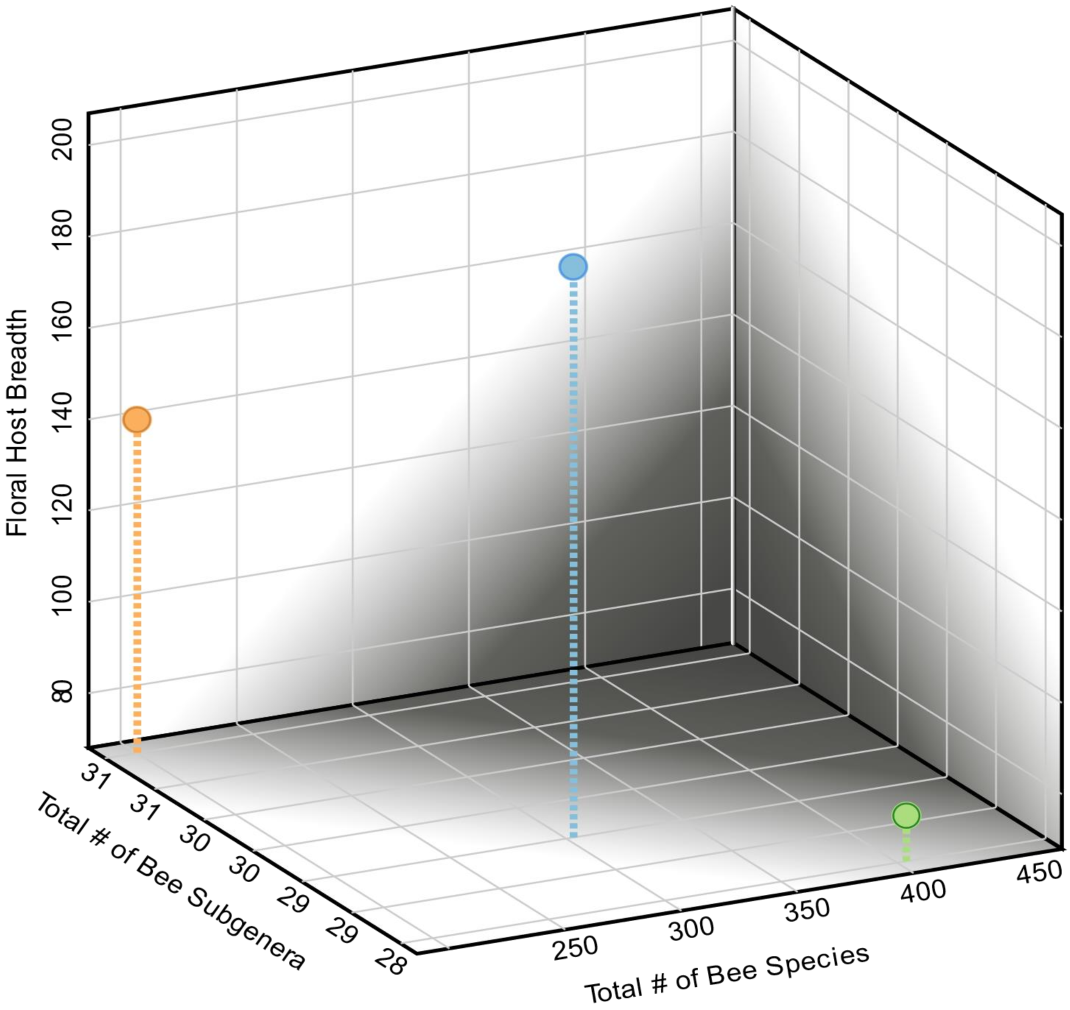
Supplementary Material 1: Floral host breadth network for the Australian colletid subfamily Euryglossinae. Bee subgenera are on the left, plant genera on the right with three families of interest colour coded (Fabaceae = lightest grey/top, Myrtaceae = medium grey/middle, Proteaceae = darkest grey/bottom). Thickness of horizontal lines denotes the number of linkages that subgenus/genus is linked to in the dataset. One line indicates one binary visitation record between the bee subgenera and the plant genera.



Supplementary Material 2: Floral host breadth network for the Australian colletid subfamily Hylaeinae. Bee subgenera are on the left, plant genera on the right with three families of interest colour coded (Fabaceae = lightest grey/top, Myrtaceae = medium grey/middle, Proteaceae = darkest grey/bottom). Thickness of horizontal lines denotes the number of linkages that subgenus/genus is linked to in the dataset. One line indicates one binary visitation record between the bee subgenera and the plant genera.



Supplementary Material 3: Floral host breadth network for the Australian colletid subfamily Neopasiphaeinae. Bee subgenera are on the left, plant genera on the right with three families of interest colour coded (Fabaceae = lightest grey/top, Myrtaceae = medium grey/middle, Proteaceae = darkest grey/bottom). Thickness of horizontal lines denotes the number of linkages that subgenus/genus is linked to in the dataset. One line indicates one binary visitation record between the bee subgenera and the plant genera.



Supplementary Material 4: 3-D scatterplot of floral host breadth against the number of species and number of subgenera for each colletid subfamily. Species and subgeneric richness do not clearly predict floral host breadth.

Appendix B: R Script – Colletidae Networks and Rarefaction Curves

```
####Bipartite Floral Networks - Colletidae ####
#Created by Patricia Slattery (patricia.slattery@flinders.edu.au)
#for floral networks of Australian colletids

####1.0 Load packages####
library("vegan")
library("bipartite")

####2.0 Euryglossinae####
#####2.1 set working directory#####
setwd("C:/Users/patri/OneDrive/Documents/Uni/P5_FloralNetworksColletidae/Euryglo
ssinae")
#####2.2 read in .csv files#####
#variables should be across the top and in the first column (can be binary or
actual numbers)
Eury <- read.csv(file = "Euryglossinae.csv", row.names = 1)
BinaryEury <- read.csv(file = "BinaryEuryglossinae.csv", row.names = 1)
#check data
Eury
BinaryEury
#Set font style to italics for genera names
par(font=3)
#####2.3 begin analyses#####
######2.3.1 Bipartite network######
EuryWeb <- plotweb(BinaryEury, method = "normal")
######2.3.2 Nestedness matrix######
EuryMatrix <- visweb(Eury, type="nested")

#####2.4 stats of interest#####
NLstatsEury <- networklevel(BinaryEury)
SLstatsEury <- specieslevel(BinaryEury)
NODFEury <- nestednodf(BinaryEury)
DegreeDistEury <- degreedistr(BinaryEury)

#####2.5 export stats of interest#####
capture.output(NLstatsEury, file = "NLstatsEury.txt")
capture.output(SLstatsEury, file = "SLstatsEury.txt")
capture.output(NODFEury, file = "NODFEury.txt")
capture.output(DegreeDistEury, file = "DegreeDistEury.txt")

####3.0 Hylaeinae####
#####3.1 set working directory#####
setwd("C:/Users/patri/OneDrive/Documents/Uni/P5_FloralNetworksColletidae/Hylaein
ae")
#####3.2 read in .csv files#####
#variables should be across the top and in the first column (can be binary or
actual numbers)
Hylae <- read.csv(file = "Hylaeinae.csv", row.names = 1)
BinaryHylae <- read.csv(file = "BinaryHylaeinae.csv", row.names = 1)
#check the numbers
Hylae
BinaryHylae
#####3.3 begin analyses#####
######3.3.1 Bipartite network######
HylaeWeb <- plotweb(BinaryHylae, method = "normal")
######3.3.2 Nestedness matrix######
visweb(Hylae, type="nested")

#####3.4 stats of interest#####
NLstatsHylae <- networklevel(BinaryHylae)
SLstatsHylae <- specieslevel(BinaryHylae)
```

```
NODFHylae <- nestednodf(BinaryHylae)
DegreeDistHylae <- degreedistr(BinaryHylae)

#####3.5 export stats of interest#####
capture.output(NLstatsHylae, file = "NLstatsHylae.txt")
capture.output(SLstatsHylae, file = "SLstatsHylae.txt")
capture.output(NODFHylae, file = "NODFHylae.txt")
capture.output(DegreeDistHylae, file = "DegreeDistHylae.txt")

####4.0 Neopasiphaeinae####
#####4.1 set working directory#####
setwd("C:/Users/patri/OneDrive/Documents/Uni/P5_FloralNetworksColletidae/Neopasiphaeinae")
#####4.2 read in .csv files#####
#variables should be across the top and in the first column (can be binary or actual numbers)
Neo <- read.csv(file = "Neopasiphaeinae.csv", row.names = 1)
BinaryNeo <- read.csv(file = "BinaryNeopasiphaeinae.csv", row.names = 1)
#check data
Neo
BinaryNeo
#####4.3 begin analyses#####
######4.3.1 Bipartite network######
NeoWeb <- plotweb(BinaryNeo, method = "normal")
######4.3.2 Nestedness matrix######
visweb(Neo, type="nested")

#####4.4 stats of interest#####
NLstatsNeo <- networklevel(BinaryNeo)
SLstatsNeo <- specieslevel(BinaryNeo)
NODFNeo <- nestednodf(BinaryNeo)
DegreeDistNeo <- degreedistr(BinaryNeo)

#####4.5 export stats of interest#####
capture.output(NLstatsNeo, file = "NLstatsNeo.txt")
capture.output(SLstatsNeo, file = "SLstatsNeo.txt")
capture.output(NODFNeo, file = "NODFNeo.txt")
capture.output(DegreeDistNeo, file = "DegreeDistNeo.txt")

####5.0 Colletidae Rarefaction Analyses####
#####5.1 Load packages#####
library(ggplot2)
library(reshape)
library(dplyr)
library(tidyverse)
setwd("C:/Users/patri/OneDrive/Documents/Uni/P5_FloralNetworksColletidae/RarefactionCurves")

#####5.2 Read in the Estimate S stats as a tibble to play with#####
#create a path to tell the list and function where to look
dataPath2 <-
"C:/Users/patri/OneDrive/Documents/Uni/P5_FloralNetworksColletidae/RarefactionCurves"
#The list of what to look for based on the pattern
#i.e. this one created a list of every file in the dataPath2 folder that was a .txt
ColletidTSVs <- list.files(dataPath2, pattern = "\\.txt")
#create an empty list with a name
Colletids <- list()
#the function that will read in all of the .txts and put them in that list
for (i in seq_along(ColletidTSVs)) {
      Colletids[[i]] <- readr::read_tsv(ColletidTSVs[i])
}
#change the names based on the file names to group them by when you combine it
```

```
names(Colletids) <- stringr:: str_replace(ColletidTSVs, pattern = "\\.txt",
                                          replacement = "")

#####5.3 Combine the .txt files into a single tibble####
#create the combined tibble, .id is where the names of each file will go
Colletid_ES_DI <- dplyr:: bind_rows(Colletids, .id = "Bees") %>%
        #rename the columns to make it a bit easier to navigate
        dplyr::rename(Cum_R = Individuals,
                      Sest = `S(est)`,
                      Sest_lower = `S(est) 95% CI Lower Bound`,
                      Sest_upper = `S(est) 95% CI Upper Bound`,
                      Shannons = `Shannon Mean`) %>%
        #select only the columns we care about
        dplyr::select(Bees, Cum_R, Sest, Sest_lower, Sest_upper, Shannons) %>%
        #turn all 0 into NA so the curves look better
        dplyr::mutate(Shannons = na_if(Shannons, 0))

#####5.4 Create a colour palette for each subfamily #####
COLLcolPal <- c(Hylaeinae = '#FCB05D', Euryglossinae = '#ACD47D',
                Neopasiphaeinae = '#86BFDB')

#####5.5 Create the S(est) plot#####
Colletid_Sest <- Colletid_ES_DI %>%
        dplyr::group_by(Bees) %>%
        ggplot(., aes(x = Cum_R, colour = Bees, y = Sest)) +
        geom_ribbon(aes(ymax = Sest_upper, ymin = Sest,
                        fill = Bees), alpha = 0.3) +
        geom_line(size = 1.75) +
        labs(x="Cumulative Resamples",
             y="S(est)") +
        theme_bw() +
        scale_color_manual(values = COLLcolPal) +
        scale_fill_manual(values = COLLcolPal)

Colletid_Sest

######5.5.1 Save the Plot in whatever size and format you want ######
ggplot2::ggsave(Colletid_Sest,
                file = "1.0_Colletid_S_est.png",
                width = 19, height = 12, units = "cm")

#####5.6 Create the Shannons DI plot#####
Colletid_Shannons <- Colletid_ES_DI %>%
        dplyr::group_by(Bees) %>%
        ggplot(., aes(x = Cum_R, colour = Bees, y = Shannons)) +
        geom_line(size = 1.75) +
        labs(x="Cumulative Resamples",
             y="Shannon's Diversity Index") +
        theme_bw() +
        scale_color_manual(values = COLLcolPal) +
        scale_fill_manual(values = COLLcolPal)

Colletid_Shannons

######5.6.1 Save the Plot in whatever size and format you want ######
ggplot2::ggsave(Colletid_Shannons,
                file = "1.0_Colletid_Shannons.png",
                width = 19, height = 12, units = "cm")
```

Appendix C: R Script – Apidae Networks, Rarefaction Curves and Comparisons to Colletidae

```
####Bipartite Floral Networks - Apidae####
#Created by Patricia Slattery (patricia.slattery@flinders.edu.au)
#began November 2022

####1.0 Load packages####
library("bipartite")
library("vegan")

####2.0 Apinae####
#####2.1 set working directory#####
setwd("C:/Users/patri/OneDrive/Documents/Uni/P6_FloralNetworksApidae/Apinae/Combined")
#####2.2 read in .csv files#####
#variables should be across the top and in the first column (can be binary or actual numbers)
Apinae <- read.csv(file = "Apinae.csv", row.names = 1)
BinaryApinae <- read.csv(file = "Bin_Apinae.csv", row.names = 1)
#check data
Apinae
BinaryApinae
#Set font syle to italics for genera names
par(font=3)
#####2.3 begin analyses#####
######2.3.1 Bipartite network######
ApinaeWeb <- plotweb(BinaryApinae, method = "normal")
######2.3.2 Nestedness matrix######
ApianeMatrix <- visweb(Apinae, type="nested")

#####2.4 stats of interest#####
#these functions use bipartite
NLstatsApinae <- networklevel(BinaryApinae)
SLstatsApinae <- specieslevel(BinaryApinae)
#these functions use vegan (but NODF are included in the network level stats?)
nestednodf(Apinae)
DegreeDistApinae <- degreedistr(BinaryApinae)
oecosimuApinae <- oecosimu(BinaryApinae, nestfun = networklevel,
                           method = "r00", nsimul = 1000)

#####2.6 export stats of interest#####
capture.output(NLstatsApinae, file = "NLstatsApinae.txt")
capture.output(SLstatsApinae, file = "SLstatsApinae.txt")
capture.output(NODFApinae, file = "NODFApinae.txt")
capture.output(DegreeDistApinae, file = "DegreeDistApinae.txt")
capture.output(oecosimuApinae, file = "oecosimuApinae.txt")

####3.0 Xylocopinae####
#####3.1 set working directory#####
setwd("C:/Users/patri/OneDrive/Documents/Uni/P6_FloralNetworksApidae/Xylocopinae/Older")
#####3.2 read in .csv files#####
#variables should be across the top and in the first column (can be binary or actual numbers)
Xylocopinae <- read.csv(file = "Det_Xylocopinae.csv", row.names = 1)
BinaryXylocopinae <- read.csv(file = "Bin_Xylocopinae.csv", row.names = 1)
#check data
Xylocopinae
BinaryXylocopinae
#Set font syle to italics for genera names
par(font=3)
#####3.3 begin analyses#####
```

```
######3.3.1 Bipartite network######
XylocopinaeWeb <- plotweb(BinaryXylocopinae, method = "normal")
######3.3.2 Nestedness matrix######
XylocopinaeMatrix <- visweb(Xylocopinae, type="nested")

#####3.4 stats of interest#####
NLstatsXylocopinae <- networklevel(Xylocopinae)
SLstatsXylocopinae <- specieslevel(BinaryXylocopinae)
NODFXylocopinae <- nestednodf(BinaryXylocopinae)
DegreeDistXylocopinae <- degreedistr(BinaryXylocopinae)
oecosimuXylocopinae <- oecosimu(BinaryXylocopinae, nestfun = networklevel,
                                method = "r00", nsimul = 1000)

#####3.6 export stats of interest#####
capture.output(NLstatsXylocopinae, file = "NLstatsXylocopinae.txt")
capture.output(SLstatsXylocopinae, file = "SLstatsXylocopinae.txt")
capture.output(NODFXylocopinae, file = "NODFXylocopinae.txt")
capture.output(DegreeDistXylocopinae, file = "DegreeDistXylocopinae.txt")
capture.output(oecosimuXylocopinae, file = "oecosimuXylocopinae.txt")

####4.0 Allodapini (minus Braunsapis)####
#####4.1 set working directory#####
setwd("C:/Users/patri/OneDrive/Documents/Uni/P6_FloralNetworksApidae/Xylocopinae
/Allodapini")
#####4.2 read in .csv files#####
#variables should be across the top and in the first column (can be binary or
actual numbers)
Allodapini <- read.csv(file = "Allodapini.csv", row.names = 1)
BinaryAllodapini <- read.csv(file = "Bin_Allodapini.csv", row.names = 1)
#check data
Allodapini
BinaryAllodapini

#####4.3 stats of interest#####
NLstatsAllodapini <- networklevel(BinaryAllodapini)
SLstatsAllodapini <- specieslevel(BinaryAllodapini)
NODFAllodapini <- nestednodf(BinaryAllodapini)
DegreeDistAllodapini <- degreedistr(BinaryAllodapini)
oecosimuAllodapini <- oecosimu(BinaryAllodapini, nestfun = networklevel,
                                 method = "r00", nsimul = 1000)

#####4.4 export stats of interest#####
capture.output(NLstatsAllodapini, file = "NLstatsAllodapini.txt")
capture.output(SLstatsAllodapini, file = "SLstatsAllodapini.txt")
capture.output(NODFAllodapini, file = "NODFAllodapini.txt")
capture.output(DegreeDistAllodapini, file = "DegreeDistAllodapini.txt")
capture.output(oecosimuAllodapini, file = "oecosimuAllodapini.txt")

####5.0 Xylocopa####
#####5.1 set working directory#####
setwd("C:/Users/patri/OneDrive/Documents/Uni/P6_FloralNetworksApidae/Xylocopinae
/Xylocopini")
#####5.2 read in .csv files#####
#variables should be across the top and in the first column (can be binary or
actual numbers)
Xylocopini <- read.csv(file = "Xylocopini.csv", row.names = 1)
BinaryXylocopini <- read.csv(file = "Bin_Xylocopini.csv", row.names = 1)
#check data
Xylocopini
BinaryXylocopini

#####5.3 stats of interest#####
NLstatsXylocopini <- networklevel(BinaryXylocopini)
NLstatsXylocopini
```

```
SLstatsXylocopini <- specieslevel(BinaryXylocopini)
NODFXylocopini <- nestednodf(BinaryXylocopini)
NODFXylocopini
DegreeDistXylocopini <- degreedistr(BinaryXylocopini)
oecosimuXylocopini <- oecosimu(BinaryXylocopini, nestfun = networklevel,
                               method = "r00", nsimul = 1000)

#####5.4 export stats of interest#####
capture.output(NLstatsXylocopini, file = "NLstatsXylocopini.txt")
capture.output(SLstatsXylocopini, file = "SLstatsXylocopini.txt")
capture.output(NODFXylocopini, file = "NODFXylocopini.txt")
capture.output(DegreeDistXylocopini, file = "DegreeDistXylocopini.txt")
capture.output(oecosimuXylocopini, file = "oecosimuXylocopini.txt")

####6.0 Anthophorinae####
#####6.1 set working directory#####
setwd("C:/Users/patri/OneDrive/Documents/Uni/P6_FloralNetworksApidae/Anthophorin
ae")
#####6.2 read in .csv files#####
#variables should be across the top and in the first column (can be binary or
actual numbers)
Anthophorinae <- read.csv(file = "Anthophorinae.csv", row.names = 1)
BinaryAnthophorinae <- read.csv(file = "Bin_Anthophorinae.csv", row.names = 1)
#check data
Anthophorinae
BinaryAnthophorinae
######6.3.1 Bipartite Network######
AnthophorinaeWeb <- plotweb(BinaryAnthophorinae, method = "normal")
######6.3.2 Nestedness matrix######
AnthophorinaeMatrix <- visweb(Anthophorinae, type="nested")

#####6.4 stats of interest#####
NLstatsAnthophorinae <- networklevel(BinaryAnthophorinae)
SLstatsAnthophorinae <- specieslevel(BinaryAnthophorinae)
NODFAnthophorinae <- nestednodf(BinaryAnthophorinae)
DegreeDistAnthophorinae <- degreedistr(BinaryAnthophorinae)
oecosimuAnthophorinae <- oecosimu(BinaryAnthophorini, nestfun = networklevel,
                                method = "r00", nsimul = 1000)

#####6.6 export stats of interest#####
capture.output(NLstatsAnthophorinae, file = "NLstatsAnthophorinae.txt")
capture.output(SLstatsAnthophorinae, file = "SLstatsAnthophorinae.txt")
capture.output(NODFAnthophorinae, file = "NODFAnthophorinae.txt")
capture.output(DegreeDistAnthophorinae, file = "DegreeDistAnthophorinae.txt")
capture.output(oecosimuAnthophorinae, file = "oecosimuAnthophorinae.txt")

####7.0 Meliponini####
#####7.1 set working directory#####
setwd("C:/Users/patri/OneDrive/Documents/Uni/P6_FloralNetworksApidae/Apinae/Meli
ponini")

#####7.2 read in .csv files#####
#variables should be across the top and in the first column (can be binary or
actual numbers)
Meliponini <- read.csv(file = "Meliponini.csv", row.names = 1)
BinaryMeliponini <- read.csv(file = "Bin_Meliponini.csv", row.names = 1)
#check data
Meliponini
BinaryMeliponini

MeliponiniWeb <- plotweb(BinaryMeliponini)

#####7.3 stats of interest#####
NLstatsMeliponini <- networklevel(BinaryMeliponini)
```

```
SLstatsMeliponini <- specieslevel(BinaryMeliponini)
NODFMeliponini <- nestednodf(BinaryMeliponini)
WNODAMeliponini <- nest.smdm(BinaryMeliponini)
#too few data points for lower level
DegreeDistMeliponini <- degreedistr(BinaryMeliponini)
oecosimuMeliponini <- oecosimu(BinaryMeliponini, nestfun = networklevel,
                              method = "r00", nsimul = 1000)

#####7.4 export stats of interest#####
capture.output(NLstatsMeliponini, file = "NLstatsMeliponini.txt")
capture.output(SLstatsMeliponini, file = "SLstatsMeliponini.txt")
capture.output(NODFMeliponini, file = "NODFMeliponini.txt")
capture.output(WNODAMeliponini, file = "WNODAMeliponini.txt")
capture.output(DegreeDistMeliponini, file = "DegreeDistMeliponini.txt")
capture.output(oecosimuMeliponini, file = "oecosimuMeliponini.txt")

####8.0 Compare bee species diversty to S(est)####
#####8.1 Set working Directory and load packages#####
setwd("C:/Users/patri/OneDrive/Documents/Uni/P6_FloralNetworksApidae")
library(ggplot2)
library(tidyr)
library(dplyr)
#####8.2.1 Read in the data frame#####
Compare <- read.csv("Compare.csv") %>%
  tibble::as_tibble(.) %>%
  dplyr::rename(Bees = X,
                Richness = bee_diversity)
#####8.2.2 Log10 the tibble#####
#trying to normalise the data for a better adj. R^2.
logCompare <- Compare %>%
  #create log versions of variables
  mutate(logS_est = log10(S_est),
         logRichness = log10(Richness)) %>%
  #merge the new variables with the original tibble
  full_join(., Compare)
#check the output
logCompare
#####8.3.1  Create the colour Palette####
colPal <- c(Exoneurines = '#DB2323', Amegilla = '#E57213',
            Hylaeinae = '#FCB05D', Euryglossinae = '#ACD47D',
            Braunsapis = '#588938', Melectini = '#17AF99',
            Neopasiphaeinae = '#86BFDB', Xylocopa = '#1C75BC',
            Meliponini = '#9652A0')
colPalApidae <- c(Exoneurines = '#DB2323', Amegilla = '#E57213',
                  Braunsapis = '#588938', Melectini = '#17AF99',
                  Xylocopa = '#1C75BC', Meliponini = '#9652A0')
#####8.4 Regression Equation#####
#original dataset
regression <-lm(S_est~Richness, data = Compare)
regression
CompareRegression <- summary(regression)
#the log version
logRegression <-lm(logS_est~logRichness, data = logCompare)
logRegression
logCompareRegression <- summary(logRegression)
#check for outliers in the model for original
boxplot(regression[['residuals']])
summary(regression)
summary(regression)$adj.r.squared
capture.output(CompareRegression, file = "CompareRegression.txt")
#and then for the log
boxplot(logRegression[['residuals']])
summary(logRegression)
summary(logRegression)$adj.r.squared
```

```
capture.output(logCompareRegression, file = "logCompareRegression.txt")
#####8.5 Print the damn Plot####
logComparePlot <- ggplot(logCompare, aes(x=logRichness, y=logS_est,
colour=Bees)) +
          labs(x="Australian Species Richness (log)", y="S(est) (log)",
               col="Bee Fauna") +
          geom_point(size = 5) +
          geom_abline(intercept = 1.075, slope = 0.47, colour = "dark grey",
                      linetype = "dotted", linewidth = 1.5) +
          theme(legend.position = "bottom",
                legend.direction = "horizontal") +
          theme_bw() +
          scale_color_manual(values = colPal)
logComparePlot
ggplot2::ggsave(logComparePlot, file = "2.0_logCompare.pdf",
                width = 19, height = 12, units = "cm")

#####8.6 Standardised Residuals#####
#original data
standard_res <- rstandard(regression)
standard_res
Compare_res <- cbind(Compare, standard_res)
Compare_res
capture.output(Compare_res, file = "CompareResiduals.txt")
#for the log values
logstandard_res <- rstandard(logRegression)
logstandard_res
logCompare_res <- cbind(logCompare, logstandard_res)
logCompare_res
capture.output(logCompare_res, file = "logCompareResiduals.txt")
#If you want to easily see most significant deviations, remove # below
#Compare_res[order(-standard_res),]

#####8.7 Plot the residuals####
logCompareResiduals <- ggplot(logCompare_res, aes(x=logRichness,
y=logstandard_res,
                          colour=Bees)) +
                          labs(x="Australian Species Richness (log)",
                               y="Standardised Residuals",
                               col="Bee Fauna") +
                          geom_hline(yintercept = 0, colour = "dark grey",
                                     linetype = "solid", size = 1) +
                          geom_point(size = 5) +
                          theme(legend.position = "bottom",
                                legend.direction = "horizontal") +
                          theme_bw() +
                          scale_color_manual(values = colPal)
logCompareResiduals
ggplot2::ggsave(logCompareResiduals, file = "2.0_logCompareResiduals.pdf",
                width = 19, height = 12, units = "cm")

####9.0 Colletidae and Apidae Rarefaction Analyses####
#####9.1 Load package and dataset#####
setwd("C:/Users/patri/OneDrive/Documents/Uni/P6_FloralNetworksApidae/Rarefaction
Curves")

##### 9.2 Read in data #### (James' code)
# Select the folder where the estimateS files are stored
dataPath <-
"C:/Users/patri/OneDrive/Documents/Uni/P6_FloralNetworksApidae/RarefactionCurves
/ES_DI"
# Extract .tsv and .csv file names
tsvPaths <- file.info(list.files(dataPath, full.names = TRUE,
                                pattern = "\\.txt", recursive = TRUE)) %>%
```

```
  rownames(.)
csvPaths <- file.info(list.files(dataPath, full.names = TRUE,
                                 pattern = "\\.csv", recursive = TRUE)) %>%
  rownames(.)

# read in the .tsv files
loopTibble <- tibble::tibble()
for(i in 1:length(tsvPaths)){
  loopTibble <- loopTibble %>%
    dplyr::bind_rows(readr::read_tsv(tsvPaths[i])%>%
                       dplyr::mutate(Bees =
                                       stringr::str_extract(tsvPaths[i],
                                                            "[A-Z]+[a-
z]+\\.")%>%
                                       stringr::str_remove("\\."),
                                     .before = 1))
}
# copy the function and read in the .csv files
for(i in 1:length(csvPaths)){
  loopTibble <- loopTibble %>%
    dplyr::bind_rows(readr::read_csv(csvPaths[i])%>%
                       dplyr::mutate(Bees =
                                       stringr::str_extract(csvPaths[i],
                                                            "[A-Z]+[a-
z]+\\.")%>%
                                       stringr::str_remove("\\."),
                                     .before = 1))
}

#####9.3 combine the .csv and .tsv files #####
dataCombined <- loopTibble %>%
  dplyr::rename(Cum_R = Individuals,
                Sest = `S(est)`,
                Sest_lower = `S(est) 95% CI Lower Bound`,
                Sest_upper = `S(est) 95% CI Upper Bound`,
                Shannons = `Shannon Mean`)

#####9.4 Make combined R dataset ####
CollApi_ES_DI <- dataCombined %>%
  dplyr::select(Bees, Cum_R, Sest, Sest_lower, Sest_upper, Shannons)

######9.4.1 Make the 0 in the Shannons column NA so we don't get weird lines####
CollApi_ES_DI_NA <- CollApi_ES_DI %>%
  dplyr::select(Cum_R, Bees, Shannons) %>%
  mutate(Shannons = na_if(Shannons, 0))

######9.4.1 Read the datasets to make sure they're long format #####
CollApi_ES_DI
CollApi_ES_DI_NA
#just checking the names, because my figures are a bit weird
mutatedbees <- CollApi_ES_DI %>%
  dplyr::select(Bees) %>%
  mutate()
mutatedbees
unique(mutatedbees)
#should only be 9

#####9.5 Create the S(est) plot#####
ColletidaeApidae_EX_DI_3x_Sest <- CollApi_ES_DI %>%
  dplyr::group_by(Bees) %>%
  ggplot(., aes(x = Cum_R, colour = Bees, y = Sest)) +
  geom_ribbon(aes(ymax = Sest_upper, ymin = Sest,
                  fill = Bees), alpha = 0.3) +
  geom_line(size = 1.75) +
```

```
  labs(x="Cumulative Resamples",
       y="S(est)") +
  theme_bw() +
  scale_color_manual(values = colPal) +
  scale_fill_manual(values = colPal)

ColletidaeApidae_EX_DI_3x_Sest

######9.6.1 Save the Plot in whatever size and format you want ######
ggplot2::ggsave(ColletidaeApidae_EX_DI_3x_Sest,
                file = "3.0_ColletidaeApidae_EX_DI_3x_Sest.pdf",
                width = 19, height = 12, units = "cm")

#####9.7 Create the Shannons DI plot#####
ColletidaeApidae_EX_DI_3x_Shannons <- CollApi_ES_DI_NA %>%
  dplyr::group_by(Bees) %>%
  ggplot(., aes(x = Cum_R, colour = Bees, y = Shannons)) +
  geom_line(size = 1.75) + xlim(0, 750) +
  labs(x="Cumulative Resamples",
       y="Shannons diversity index") +
  theme_bw() +
  scale_color_manual(values = colPal) +
  scale_fill_manual(values = colPal)

ColletidaeApidae_EX_DI_3x_Shannons

######9.7.1 Save the Plot in whatever size and format you want ######
ggplot2::ggsave(ColletidaeApidae_EX_DI_3x_Shannons,
                file = "3.0_ColletidaeApidae_EX_DI_3x_Shannons.pdf",
                width = 19, height = 12, units = "cm")

####10.0 JUST Apidae Rarefaction Analyses####
#####10.1 Can just use the same tibble and remove the colletid rows####
Apidae_ES_DI <- CollApi_ES_DI %>%
  dplyr::group_by(Bees) %>%
  dplyr::filter(., Bees == "Exoneurines"| Bees == "Amegilla"|
                Bees == "Braunsapis"| Bees == "Melectini"|
                Bees == "Xylocopa"| Bees == "Meliponini") %>%
  dplyr::mutate(Shannons = na_if(Shannons, 0))
#double check things look ok
Apidae_ES_DI

#####10.2 Create the S(est) plot#####
Apidae_ES_DI_3x_Sest <- Apidae_ES_DI %>%
  ggplot(., aes(x = Cum_R, colour = Bees, y = Sest)) +
  geom_ribbon(aes(ymax = Sest_upper, ymin = Sest,
                fill = Bees),alpha = 0.5) +
  geom_line(size = 1.5) +
  labs(x="Cumulative Resamples",
       y="S(est)") +
  theme_bw() +
  scale_color_manual(values = colPalApidae) +
  scale_fill_manual(values = colPalApidae)

Apidae_ES_DI_3x_Sest

#####10.5 Save the Plot in whatever size and format you want ######
ggplot2::ggsave(Apidae_ES_DI_3x_Sest,
                file = "3.0_Apidae_ES_DI_3x_Sest.pdf",
                width = 19, height = 12, units = "cm")

#####10.6 Create the Shannons DI plot#####
Apidae_ES_DI_3x_Shannons <- Apidae_ES_DI %>%
  dplyr::group_by(Bees) %>%
```

```
  ggplot(., aes(x = Cum_R, colour = Bees, y = Shannons)) +
  geom_line(size = 3) + xlim(0, 750) +
  labs(x="Cumulative Resamples",
       y="Shannons diversity index") +
  theme_bw() +
  scale_color_manual(values = colPalApidae) +
  scale_fill_manual(values = colPalApidae)

Apidae_ES_DI_3x_Shannons

#####10.7 Save the Plot in whatever size and format you want ######
ggplot2::ggsave(Apidae_ES_DI_3x_Shannons,
                file = "3.0_Apidae_EX_DI_3x_Shannons.pdf",
                width = 19, height = 12, units = "cm")
```