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Disparate continental scale patterns in floral host breadth of Australian colletid bees (Colletidae: Hymenoptera)

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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.

Euryglossinae / Hylaeinae / Neopasiphaeinae / Pollination / Myrtaceae

1. INTRODUCTION

Myriad studies have examined the biogeography of bees at varying spatial scales while considering historical scenarios leading to their current distributions (e.g. Almeida et al. 2012;

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 and Hogendoorn 2009; Dorey et al. 2021; Hallmann et al. 2017).

While some studies have examined how historical biogeographic events have shaped the continental distributions of some individual bee

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taxa (e.g. de Camargo and de Pedro 1992; Leys et al. 2002; Hines 2008; Tierney et al. 2008; Rehan et al. 2010; Chenoweth and 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 are associated with some of the most unusual flora and fauna in the world, with many endemic and endangered taxa (e.g. 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. 2006). 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 and Mackay 1998; Houston 2018; Taylor and 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. 2012). 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 ~230 Australian species (Almeida et al. 2012; 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 plants (Cane 2021) through 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 utilise 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 bees that lack scopae or corbiculae (specialised pollen-carrying setae on the hind legs or the underside of the metasoma), and these bees oftentimes have a diminutive body form. 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, which 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 and 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. 2006; 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.

2. MATERIALS AND METHODS

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 2022). 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 et al. 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 NODEF, 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 randomised 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.

3. RESULTS

Our bee-plant interaction data (Table I) included 6907 recorded interactions for Neopasiphaeinae, 6568 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 I).

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 summarises 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.

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

Table I 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	6568	26	141
Neopasiphaeinae	6907	30	193

diagrams are presented in Supplementary Materials 1, 2, and 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 summarised in Table II 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

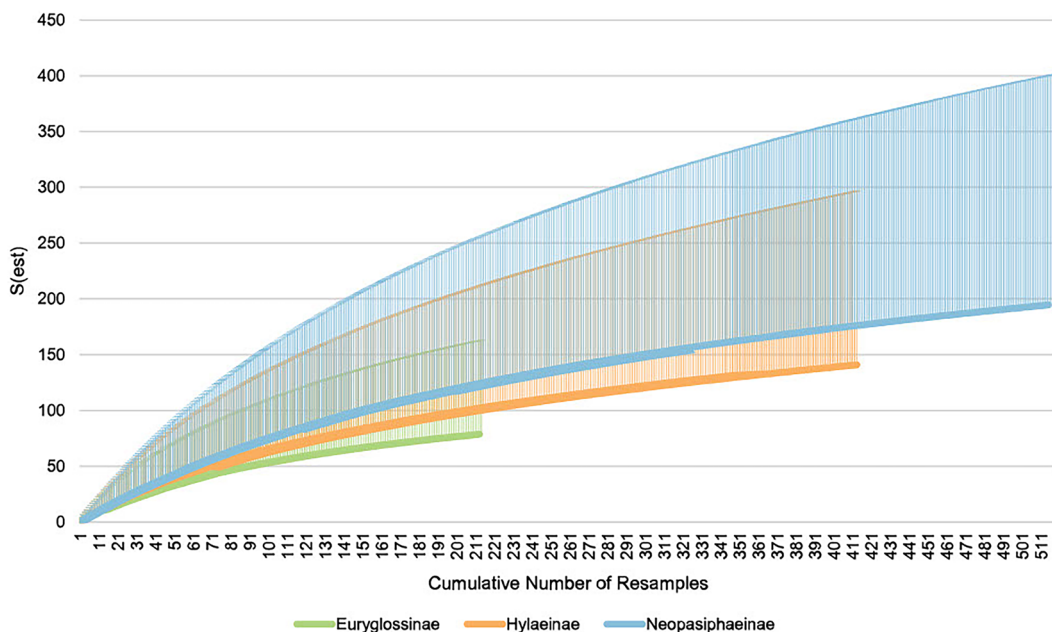


Figure 1. Rarefaction curves for colletid bee subfamilies Euryglossinae, Hylaeinae and Neopasiphaeinae used to calculate estimated total floral host breadth ($S(est)$), run for 1000 iterations. Upper 95% CI are indicated by the shaded sections.

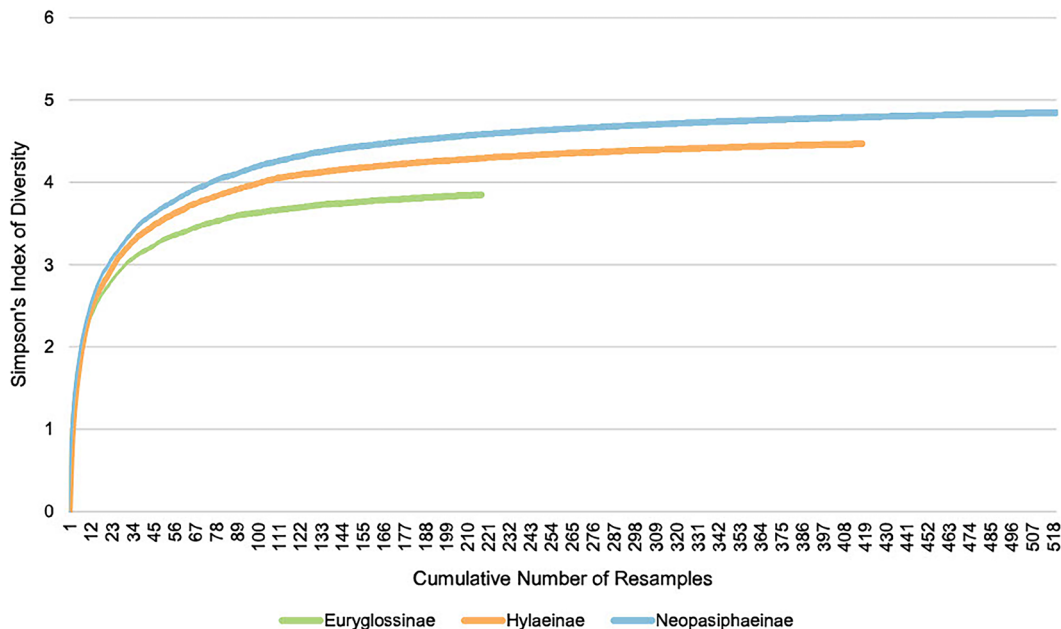


Figure 2. Rarefaction curves for colletid bee subfamilies Euryglossinae, Hylaeinae and Neopasiphaeinae, used to calculate Simpson’s index of diversity in floral host breadth, run for 1000 iterations.

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 mostly the same floral hosts. 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.

4. DISCUSSION

The colletid subfamilies Euryglossinae, Hylaeinae, and Neopasiphaeinae comprise approximately 53% of all described bee species in Australia (Batley and Hogendoorn 2009), so

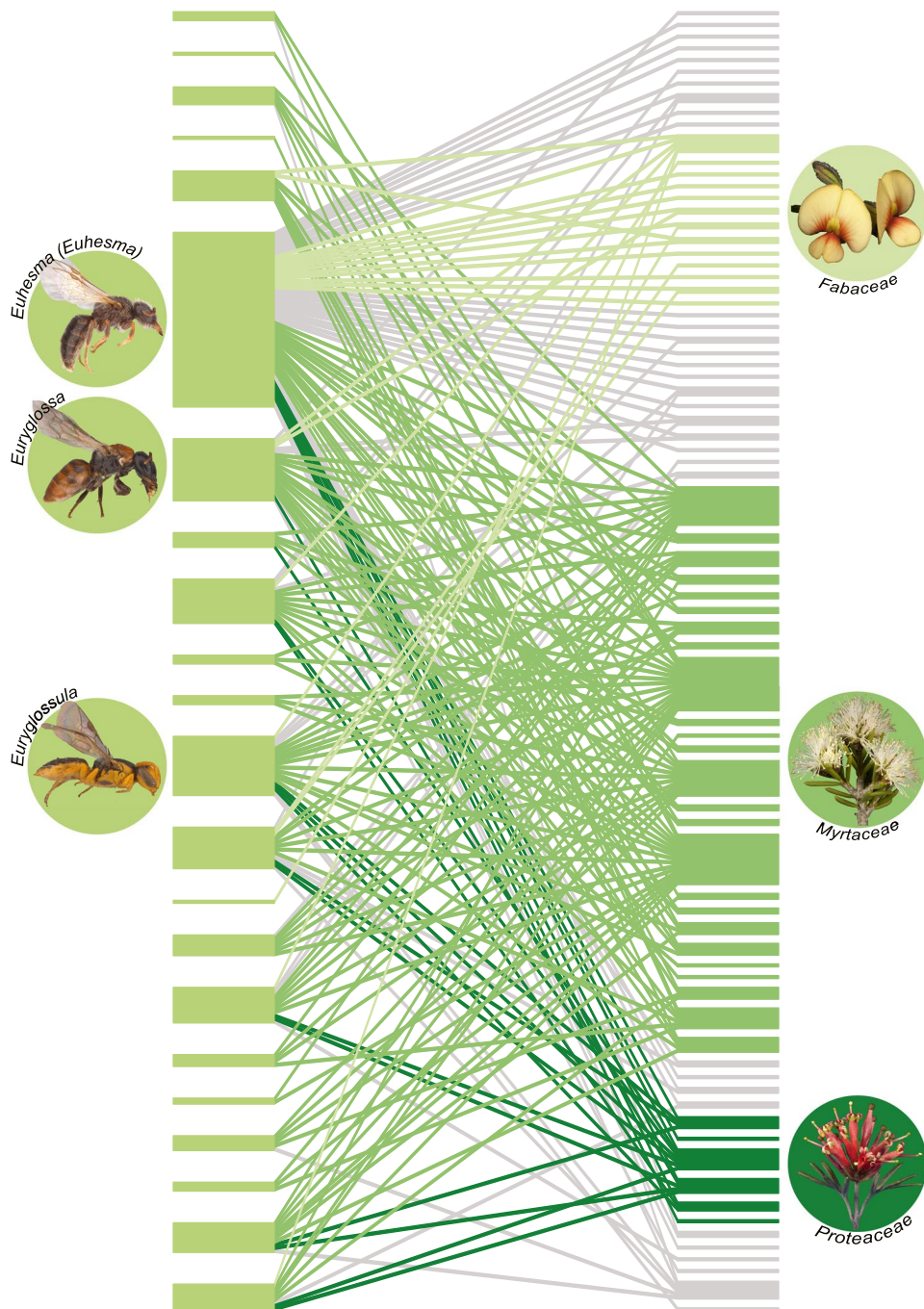


Figure 3. Floral host breadth network for the Australian colletid subfamily Euryglossinae. Bee subgenera are on the left, plant genera on the right with three families of interest colour coded (Fabaceae=lightest green/top, Myrtaceae=medium green/middle, Proteaceae=darkest green/bottom). Thickness of horizontal 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.

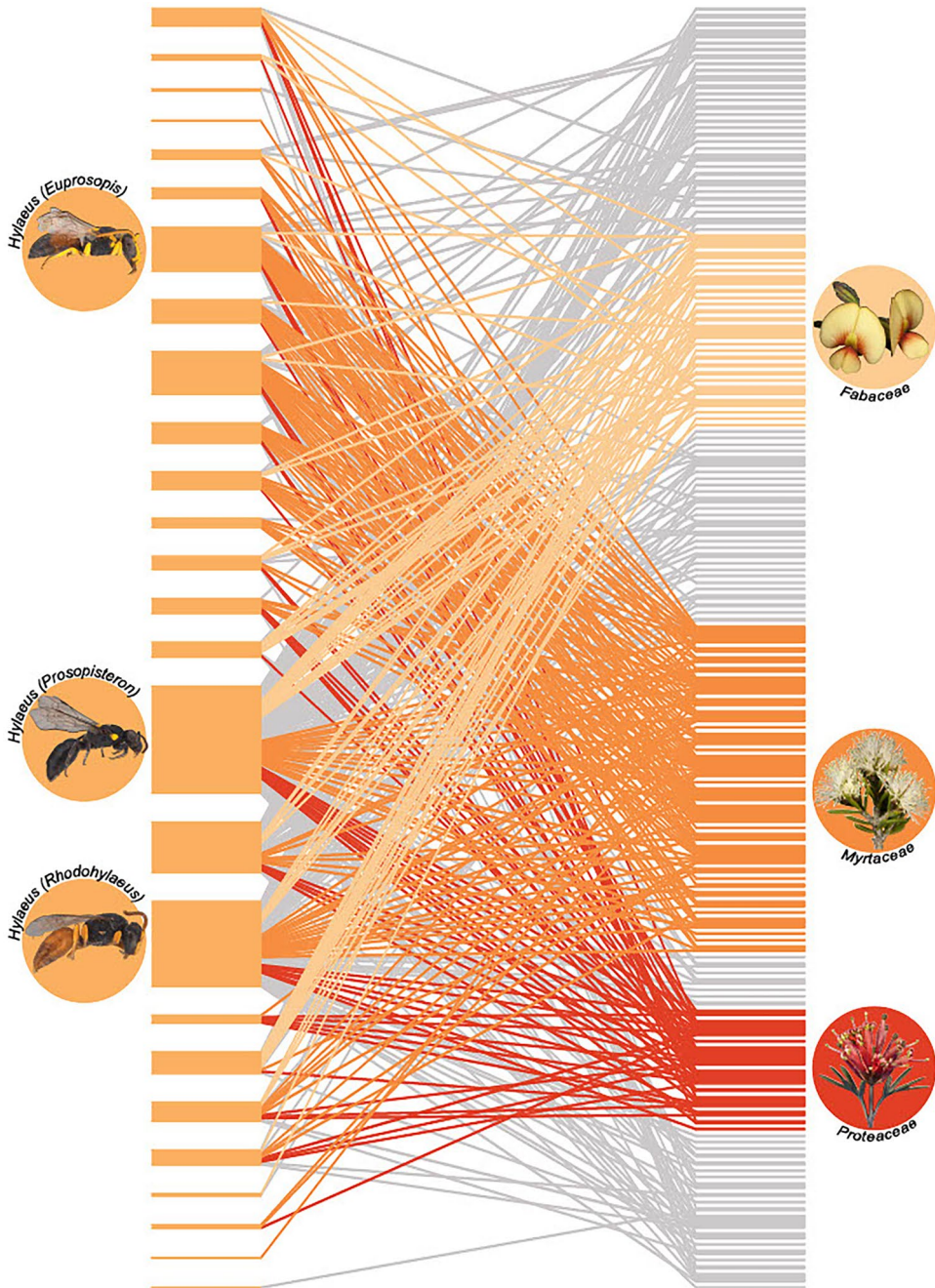


Figure 4. Floral host breadth network for the Australian colletid subfamily Hylaeinae. Bee subgenera are on the left, plant genera on the right with three families of interest colour coded (Fabaceae=lightest orange/top, Myrtaceae=medium orange/middle, Proteaceae=darkest orange/bottom). Thickness of horizontal bars 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.

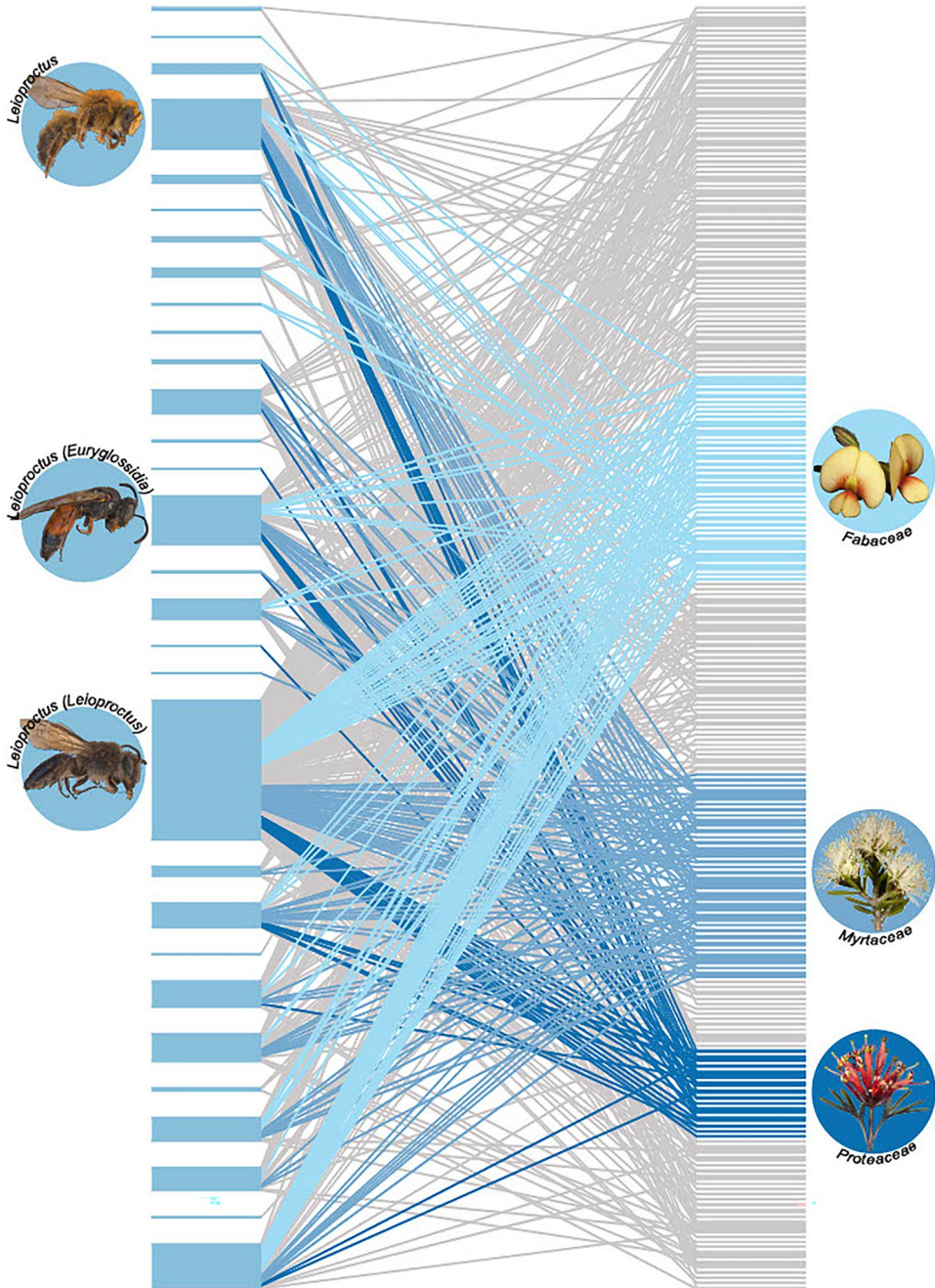


Figure 5. Floral host breadth network for the Australian colletid subfamily Neopasiphaeinae. Bee subgenera are on the left, plant genera on the right with three families of interest colour coded (Fabaceae=lightest blue/top, Myrtaceae=medium blue/middle, Proteaceae=darkest blue/bottom). Thickness of horizontal bars 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.

Table II A summary table of network indices for each of the bee subfamily networks, detailing the level of interest and the indices itself

	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

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.

4.1. 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. 2012), 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. 2012, 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 (Supplementary Material 4). Differences in species diversity of the three subfamilies are, 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 (6907 records for Neopasiphaeinae, 6568 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 (Figures 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 are not a result of inadequate sampling.

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 are markedly lower than either of the other two subfamilies (Table II). This statistic, combined with their lower partner diversity and higher niche overlap, all suggest that euryglossines are more frequently utilising similar plant genera (Table II). Unlike Neopasiphaeinae, Euryglossinae, and Hylaeinae lack scopae and carry pollen internally in their crops. 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 and allow them to specialise on *Calothamnus* species, despite these flowers being adapted for avian pollination (Houston 1983, 2018). The subgenus *Leioproctus* (*Filiglossa*) is 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 to 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.

4.1.1. 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*, *Syzygium*, 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 lorries (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.

4.2. 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.

4.2.1. 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 and 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.

4.2.2. 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.

4.2.3. *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 do not 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, multi-voltine bees would benefit from a more expansive floral host breadth, so there are floral hosts available throughout their flight season. Future research should include assessment if there is any phylogenetic inertia or climatic factors that influence on the voltinism of these groups.

4.2.4. *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.

SUPPLEMENTARY INFORMATION

The online version contains supplementary material available at <https://doi.org/10.1007/s13592-023-00996-z>.

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AUTHOR CONTRIBUTION

Patricia S. Slattery, Michael S.Y. Lee, Michael P. Schwarz, and Ben A. Parslow contributed to study conception and design. Data collation and analyses were performed by Patricia S. Slattery, who wrote the first complete draft. All the authors contributed to the writing of the manuscript, and all the authors read and approved the final version of this manuscript.

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DATA AVAILABILITY

The datasets generated during and/or analysed during the current study are available from the corresponding museum on reasonable request.

CODE AVAILABILITY

All code will be provided upon reasonable request through contact with the corresponding author.

DECLARATIONS

Ethics approval This study did not require any ethics approval.

Consent to participate This manuscript had no human participants.

Consent for publication Data contributors were all contacted for, and received, consent to use their data prior to the submission of this manuscript.

Competing interests The authors declare no competing interests.

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