

**Could pollination networks be applied for biological conservation and monitoring of threatened plant communities? – Examples from an endangered ecological community, the Howell Shrublands.**

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I certify that the substance of this thesis has not already been submitted for any degree and is not currently being submitted for any other degree or qualification.

I certify that any help received in preparing this thesis and all sources used have been acknowledged in this thesis.

Signature: \_\_\_\_\_



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## **Abstract:**

Plant-pollinator interactions play a pivotal role in the structure and persistence of biological communities. Despite this, plant-pollinator relationships are rarely considered in applied conservation, potentially resulting in counterproductive or ineffective management practices. By allowing interactions between plants and pollinators to be quantitatively assessed, network analyses may offer valuable information for applied conservation. To demonstrate the potential utility of network analyses in conservation, this study will attempt to inform management for an endangered ecological community in eastern Australia using a multi-year pollination network. Over six seasons, 1,633.4 hours of floral visitation data were collected for 103 plant species to construct a network of plant-pollinator interactions. Asymptotic richness estimates were used to evaluate sampling efficacy, and predict the amount of effort required to complete sampling. Network analyses were conducted using the Bipartite package for RStudio, allowing species of high conservation value to be identified in terms of interaction strength, and the pollinator service index (*PSI*). Network specialisation ( $H_2'$ ), nestedness ( $wNODF$ ), robustness, and modularity were assessed as potential indicators of community stability. Sampling was estimated to detect up to 90.05% of floral visitors, and 66.66% of interactions, with floral species predicted to require an average of 18.03 hours observation to sample a majority of interactions. This was also found to coincide with stable asymptotic richness estimates for a separate sample of species subject to relatively intensive sampling efforts and is therefore recommended as a baseline for future testing and sampling. Exotic honeybees (*Apis mellifera*) were identified as an important pollinator within the network, which was generally more specialised, modular, and robust to floral extinctions than could be explained by null models. Dividing the network into temporal sub-networks revealed late winter and early summer flowering plants were significantly less robust to pollinator extinction in spite of high interaction nestedness. This level of risk is likely to increase significantly if honeybees become locally extinct due to the parasite *Varroa destructor*. Therefore, conservation efforts should focus on late winter pollinators as a means of preserving the floral community.



## **Introduction:**

As primary producers, plants form the basis upon which most, if not all terrestrial species depend (Robbins 1944). Consequently, the preservation of diverse plant communities is frequently considered a pre-requisite for the conservation or restoration of entire ecosystems. However, without maintaining the plant-pollinator interactions upon which 87.5% of all flowering plants rely, or at least benefit from (Ollerton et al. 2011), few efforts are likely to be successful long-term (Gross 2017). Indeed, the loss of mutualistic interactions may already have contributed to plant population declines (Jackson et al. 1988; Cramer et al. 2007), and will likely result in further trophic disturbances, with terrestrial communities seemingly more sensitive to plant, than animal extinctions (Scherber et al. 2010; Schleuning et al. 2016). Likewise, failure to recognize the importance of specific interactions may lead to unsuccessful or counterproductive management practices (Tylianakis et al. 2010; Gross 2017). For instance, removing an invasive plant species may threaten co-occurring native species if it reduces the abundance of their shared pollinators (Carvalheiro et al. 2008a).

Despite this, most conservation is species-based, focusing on population demographics, and resource limitations to identify processes that cause decline, or prevent recovery (e.g. Gross & Caddy 2006; Cramer et al. 2007; Gross & Mackay 2014). At the community scale, this means that monitoring is limited to species richness or abundance attributes that, due to the extreme longevity (Patrut et al. 2018), or seed viability (Shen-Miller et al. 1995) of some plants, may not reflect long-term population viability (Helm et al. 2006; Vellend et al. 2006). This approach also fails to disclose whether functional interactions are maintained alongside biodiversity, as species presence provides no guarantee of interaction without spatio-temporal co-occurrence and mutual obligation (Memmott et al. 2004; Hegland et al. 2009; Tylianakis et al. 2010). Thus, with growing concern about the broader implications of recent pollinator declines (Potts et al. 2010), we need to consider methods capable of monitoring both species and interactions (Elle et al. 2012).

Until recently, analytic constraints have largely restricted the study of biological interactions to the level of species or populations. However, recent developments drawing on graph and ecological food web theories allow communities of interacting

species to be examined as a series of ‘nodes’ linked together to form an ecological network (Jordano 1987; Bascompte & Jordano 2007; Bascompte 2009; Vazquez et al. 2009; Bascompte 2010). These networks provide a means of representing the functional relationships within ecological communities, allowing inferences to be made about their structure and stability. To date, most research has been preoccupied with the theoretical implications of network analysis (Bascompte 2007). However, given the potential to provide valuable monitoring and insight into community scale responses to disturbance, practical applications of network theory are increasingly being discussed (Tylianakis et al. 2010; Elle et al. 2012).

Unlike other interactions, pollination is readily observable in the field, involves mutually exclusive functions (i.e. species can be pollinated, or pollinator, but not both), and instances of pollen moving between pollinators are rare. This makes pollination networks relatively simple to construct using a variety of cost-effective, and potentially non-destructive methods (Hegland et al. 2010; Gibson et al. 2011). As a result, pollination networks have been suggested as a potential alternative to traditional biodiversity assessment methods (Hegland et al. 2010; Tylianakis et al. 2010; Elle et al. 2012). However, biological communities are difficult to sample comprehensively (Chao et al. 2009; Chacoff et al. 2012; Costa et al. 2016), with many aspects of network analysis prone to sampling bias (Fründ et al. 2016; Vizentin-Bugoni et al. 2016). Indeed, substantially greater effort may be necessary to sample a community of interactions than species (Chacoff et al. 2012), as each species may participate in multiple interactions. Therefore, practical implementation of network analyses will require methods capable of evaluating total interaction diversity, and community stability from an incomplete sample.

Asymptotic richness estimates have been used extensively to approximate regional or geographic biodiversity, but have only recently been used to evaluate interaction sampling (Chacoff et al. 2012; Costa et al. 2016; Souza et al. 2018). For such purposes, the Chao2 equation is least biased with respect to sample size, and type-I error (Walther & Moore 2005; Gwinn et al. 2016), and is therefore often used among network studies. However, this method assumes that all sampling units are equivalent in effort, and therefore have equal opportunity to sample all species and interactions (Colwell & Coddington 1994). This will not always be the case however; as most

network studies used a species-based sampling approach, meaning interactions can only be observed when samples are based on either interaction partner. Consequently, in order to accurately estimate the total diversity of interactions within a network, sampling must be evaluated at the species-level. Despite this, of the few studies that have attempted to evaluate the proportion of interactions sampled, most have failed to do so, instead electing to provide collective evaluations of their sampling effort at network-level (Chacoff et al. 2012; Costa et al. 2016; Souza et al. 2018).

Similarly, while researchers have identified several network attributes as potential indicators of community robustness or stability, the exact correlation between these network attributes and community robustness is often unclear, with empirical evaluation often lacking (Tylianakis et al. 2010). Connectance (the proportion of realized interactions) frequently correlates with network stability (Thebault & Fontaine 2010), but exhibits considerable bias relative to network size and sampling effort (Jordano 1987; Nielsen & Bascompte 2007; Fründ et al. 2016). Conversely, specialisation ( $H_2'$ ), nestedness ( $wNODF$ ), and modularity are relatively insensitive to sampling effort (Vizentin-Bugoni et al. 2016), but their relationship with network stability is less clear, and often interrelated (Tylianakis et al. 2010; Elle et al. 2012). Specialisation, for example, measures the extent of each species' dependence on a particular resource or interaction (Blüthgen et al. 2006), and is therefore expected to reduce network robustness, due to the increased sensitivity of specialist species to disturbance (Henle et al. 2004).

Nestedness measures the extent of interaction overlap between specialist and generalist species within a network, and it is therefore assumed to increase community robustness by allowing generalists to replace the functions lost through specialist extinctions (Memmott et al. 2004; Nielsen & Bascompte 2007). Likewise, modularity measures to the proportion of interactions that form discrete sub-networks or modules that are more densely linked internally than externally (Olesen et al. 2007; Dupont et al. 2009). In highly modular networks, disturbances are more likely to be contained within modules, and less likely to cascade through the entire network (Thebault & Fontaine 2010). Thus, both nestedness and modularity can increase the stability of highly specialised network. Yet they may also decrease stability, as highly nested communities may be particularly vulnerable to generalist extinctions

(Memmott et al. 2004), while disturbances may have especially severe consequences within modules (Olesen et al. 2007). Without clear correlation between network structure and community stability, then, applying such analyses for conservation provides a challenging prospect.

Species-level metrics may have more immediate utility, as means to identify species critical to maintain community structure. This may be particularly valuable for invasive species management, where an insufficient understanding of interspecific relationships can lead to counterproductive management practices (Carvalho et al. 2008a; Carvalho et al. 2008b; Gross et al. 2017). Many invasive plants and pollinators are generalists that attract a broad range of native pollinators, or forage indiscriminately. This allows them to rapidly integrate into native pollination networks, often becoming important interaction hubs that increase community nestedness (Olesen et al. 2002; Aizen et al. 2008; Bartomeus et al. 2008). Since nestedness is often associated with community robustness (Memmott et al. 2004; Bascompte et al. 2006; Aizen et al. 2008), any attempt to suppress or remove these invaders, may negatively affect the native species that share the network (Valdovinos et al. 2009). Therefore, by allowing quantitative evaluation of a species functional significance, pollination networks may lead to better-informed management decisions.

This thesis will attempt to address some of the limitations preventing application of network analyses in biological conservation. Using examples from an endangered ecological community in eastern Australia, a method to evaluate sampling effort via the Chao2 equation (Chao et al. 2009) is outlined, with recommendations about sample sizes and procedure. Network specialisation, nestedness, robustness, and modularity were assessed across multiple phenological phases in order to identify conservation priorities, and potential keystone and umbrella species identified using species strength and the pollination services index (PSI). Finally, network analyses are used to predict the potential impacts of an invasive pollinator (*Apis mellifera*) declining from the network.

## **Chapter 1. Sampling floral visitation and pollination networks – How do we determine when enough is enough?**

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### **Abstract**

Sampling effort can have a significant effect on the perceived properties of an interaction network. Despite this, few studies standardise effort across species, or evaluate sampling effort. This could severely limit the use of network analyses in biodiversity management, where standardised resampling is necessary to assess conservation outcomes. To address this issue, here we outline a method used to estimate the sampling effort for an east Australian floral visitation network. Floral visitations were recorded over six flowering seasons using a combination of video surveillance and timed stationary observations. Effort was divided into discrete sampling hours, and the total number of unobserved visitors and interactions estimated via the Chao2 method. Chao2 estimates were used to predict the mean sampling effort required to observe increasing proportions of interactions per floral species. Predictions were compared against comprehensively sampled visitation datasets, and the stability of interaction richness estimates assessed. Sampling was estimated to account for 90% of floral visitors and 67% of interactions, and would need to increase by 333% to 50 +/- 74 hours per floral species in order to reach completion. This meant that the observed connectance of 7% underestimated the total estimated connectance of 9%, but not significantly so. We predict that 18 hours of sampling are needed to observe a majority of interactions for each floral species. When tested for a sample of comprehensively sampled species, Chao2 estimates were found to stabilise within 18 hours of sampling. Practical sampling limitations mean that few network studies will sample all interactions. Asymptotic richness estimates may be used to estimate the total richness of species or interactions, and therefore provide more accurate representations of network diversity and connectance. Pending further investigation, it is therefore recommended that future pollination studies observe each floral species for a minimum of 18 hours, in order to provide an adequate sample.

**Keywords:** biodiversity, conservation, interaction, network, pollination, sampling.

### **Introduction:**

Bipartite analyses involving ecological networks are an increasingly common means of quantifying interspecific interactions and their importance within ecological communities (Blüthgen 2010). To attain meaningful results, sampling methods must provide an accurate representation of the relative richness, abundance or quality of interactions occurring within a community (Gibson et al. 2011). Subsequently, the relative effort and comprehensiveness of sampling can have a significant impact on many common network metrics (Nielsen & Bascompte 2007; Blüthgen 2010; Rivera-Hutinel et al. 2012; Falcão et al. 2016; Fründ et al. 2016; Vizentin-Bugoni et al. 2016). For example, connectance refers to the proportion of possible interactions realised within a network (Gardner & Ashby 1970), and is commonly used to assess the relative stability or specialisation within and between ecological communities (May 1972; Blüthgen et al. 2008). Nevertheless, as a function of both interaction and species diversity, connectance has been shown to fluctuate with increasing detection of new species or interactions (Nielsen & Bascompte 2007; Rivera-Hutinel et al. 2012; Vizentin-Bugoni et al. 2016), and therefore prone to sampling bias, which limits comparison between ecological communities (Blüthgen 2010).

Most study of plant interactions involves sampling a selection of plant species or individuals within a community and recording the frequency and identity of their interaction partners within a time period (Korine et al. 2000; Petanidou et al. 2008; Baldock et al. 2011; Donatti et al. 2011; Souza et al. 2018). Thus, while these interactions may be retroactively sampled (Bosch et al. 2009; Devoto et al. 2011; Costa et al. 2016), by collecting and identifying the pollen loads carried by individual pollinators, for instance, the diversity of interactions observed will depend upon the relative diversity of interacting species, extent of co-occurrence (Olesen et al. 2008), and comprehensiveness of sampling (Costa et al. 2016; Fründ et al. 2016). As such, the probability of recording any given species or interaction will depend upon its relative abundance, phenological state, degree of specialization, and the number of sample replicates. For instance, the low abundance of rare species means they often go under sampled, resulting in a poor estimation of their role and significance within interaction networks (Dorado et al. 2011). Similarly, species may go under sampled

when sampling is limited to a single season (Alarcón et al. 2008; Dupont et al. 2009) or narrow geographic range (Dicks et al. 2002; Devoto et al. 2005), particularly when abundance is determined by stochastic events (Olesen et al. 2008).

Nevertheless, it should be possible to provide an accurate representation of the interaction diversity through the use of regular sampling intervals, replication over multiple seasons and stratified sampling procedures (Dupont et al. 2003; Petanidou et al. 2008; Gibson et al. 2011). However, the efficacy of sampling will still need evaluation, as interactions may still go un-sampled due to restricted sampling periods, protracted sampling intervals, or simple misfortune. Yet while numerous studies have demonstrated a link between sampling effort and bipartite network metrics (Nielsen & Bascompte 2007; Blüthgen 2010; Rivera-Hutinel et al. 2012; Falcão et al. 2016; Fründ et al. 2016; Vizentin-Bugoni et al. 2016), few have provided any assessment of the sample sizes required to calculate them. This is problematic because the relative frequency of rare or trivial interactions within a community may appear similar regardless of sampling depth (Colwell & Coddington 1994). Therefore, without statistical evaluation it is almost impossible to accurately compare networks and communities, as there are no standardised methods to minimize sampling bias.

When network researchers have attempted to evaluate their sampling effort, they've used a combination of post-hoc species accumulation and asymptotic richness estimators to calculate the proportion of the total species or interaction richness observed at the community-level (Chacoff et al. 2012; Souza et al. 2018). This assumes that all sampling is equivalent, meaning all species or interactions within the community have the opportunity to be recorded within each sample (Colwell & Coddington 1994). In a plant interaction network, sampling may be considered equivalent for species richness, as each potential interaction partner is capable of visiting all floral species. However, interactions are tied to specific species, and cannot be recorded in samples that may not include either species. Therefore, sampling must be evaluated at the species-level to provide an accurate estimate of the total interaction richness. Concurrently, while post-hoc analysis ensures the best possible sample is used to estimate the total species or interaction richness (Colwell & Coddington 1994; Chao et al. 2009), there is an inherent disadvantage. Because of their nature, post-hoc analyses cannot be used to inform the initial study

methodology. This may present a significant issue when circumstances prevent additional sampling (e.g. when comparing pre- and post-disturbance), as there is no opportunity for supplementary sampling if the initial sampling effort is found to be unsatisfactory. Thus, any prior information regarding the minimum number of samples needed to record a significant proportion of the total interaction diversity may be highly beneficial.

Here, we use species accumulation and asymptotic species/interaction richness estimates to assess the efficacy of a floral visitation sampling over six years in temperate woodland on the Northern Tablelands of New South Wales, Australia. Accounting for variability in sampling effort between species, we predict the minimum sampling effort required to observe a majority of the total interaction richness for each floral species. Our predictions are tested using floral visitation datasets for *Begonia danumensis* from tropical rainforest in Sabah, Malaysia (Whitehead *et al.* unpublished data), *Brachyscome stuartii* from temperate woodland in New South Wales (NSW), Australia (Whitehead unpublished data), and *Chrysanthemoides monilifera* from coastal heath in NSW, Australia (Gross *et al.* 2017). Current methods of floral visitation and network sampling are also reviewed.

## **Materials and Methods:**

### *Study Area:*

The study was conducted over 15 hectares of granite outcropping to the east of Copeton Dam (29° 56' 08" S, 151° 02' 11" E) in northern New South Wales (NSW), Australia. Located within a temperate region, the area experiences hot summers and no dry season (Stern *et al.* 2000), meaning the majority of flowering occurs during the warmer part of the year, between August and February. Vegetation within the site broadly represents a layered, open low-woodland (Specht 1970), despite the predominance of low shrub species, particularly *Homoranthus prolixus* (Myrtaceae). This unusual structure and floristic composition is characteristic of the Howell Shrublands, a listed Endangered Ecological Community (EEC) within the New South Wales Biodiversity Conservation Act (NSW Government 2016). Consequently, understanding the network of biotic interactions that serve to threaten or sustain the long-term community viability is, we contend, an ongoing priority for conservation.



### *Sampling Methods:*

Floral visitation data was compiled over six non-successive flowering seasons from August through November in 2007, September through November in 2011, August through October in 2012, October in 2014, and August through February in 2015/16 and 2016/17. We attempted to survey the community as comprehensively as possible, by observing a random sample of individuals from as many species over as many different sampling periods as possible. Observations were made via a combination of video camera (Sony Handycam models HDR-155 XR160, HDR-PJ540, and FDR-AXP35 4K) and timed stationary observations conducted at roughly weekly intervals between 06:00 and 18:00 hours Australian Eastern Standard Time (AEST). Stationary observations consisted of a single observer recording all floral interactions occurring within the floral display of a single plant over a 15-60 minute period. Cameras (up to 15 at a time) were deployed for up to 4 hours per plant, with the field of view adjusted in order to provide reliable visitor identifications, and a representative sample of the observed plant's total floral display. Conspecific sampling was structured to ensure no two individuals were observed simultaneously within a 50-metre radius of one another.

A visit was recorded whenever a visitor contacted the reproductive structures of a flower (indicating the visitor may act as a potential pollinator) or otherwise consumed or collected floral resources (e.g. nectar and/or pollen) without contacting the reproductive structures (non-pollinating trophic interaction). This approach has previously been used to identify and distinguish between different floral interaction types (Inouye 1980; Irwin et al. 2010), and is considered pragmatic for revealing potential mutualistic (pollination) and antagonistic interactions within a floral visitation network (Inouye 1980; Jacobs et al. 2009). However, further investigation is needed to confirm whether visits result in effective pollen transfer, and to what extent (Gross & Mackay 1998; Ballantyne et al. 2015; Gross et al. 2017). For any plant or visitor species that could not be identified from video observations or directly in the field, voucher specimens were collected for laboratory identification, and later lodged as vouchers with the N. C. W. Beadle Herbarium or Natural History Museum respectively at the University of New England, NSW, Australia. All species

identifications were made via relevant field guides (e.g. Braby 2004), online resources (e.g. [www.ala.org.au/](http://www.ala.org.au/), [www.padil.gov.au/](http://www.padil.gov.au/), <http://plantnet.rbgsyd.nsw.gov.au>) or expert knowledge (see acknowledgements).

*Estimating Species/Interaction Richness and Additional Sampling Requirements:*

Observations were divided into discrete hours of observation, and the sampling effort (hours) evaluated using species accumulation, and the Chao2 (Chao 1987) asymptotic richness estimator. As no single estimation method has yet been found to be superior across all community types or sampling designs (Gwinn et al. 2016), we elected to use the Chao2 asymptotic richness estimator due to its previous application in floral interaction studies (Chacoff et al. 2012; Souza et al. 2018), and broad applicability in biodiversity analysis (Gotelli & Colwell 2001; Chao et al. 2009).

The Chao2 estimator is one of the least biased methods for estimating richness from small sample sizes (Walther & Moore 2005; Gwinn et al. 2016), meaning estimates remain relatively stable despite changes in sample size. It therefore avoids one of the most common criticisms of asymptotic richness estimation, in that estimates are significantly affected by sampling bias (Colwell & Coddington 1994; Chao et al. 2009). It also has a low type-I error rate when dealing with high community richness (Gwinn et al. 2016), making it suitable for estimating community interaction richness. The Chao2 estimator applies a non-parametric approach to estimate richness based on the hypothesis that rarely observed species/interactions can be used to infer the probability that additional species/interactions remain unobserved (Chao 1987; Chao et al. 2009). As such, the total species richness ( $S_E$ ) can be estimated as:

$$S_E = S_O + (U^2/2D) \quad (\text{Chao et al. 2009})$$

Where  $S_O$  = the observed species richness,  $U$  = the number of unique species (that were recorded in only one sample) and  $D$  = the number of duplicate species (that were recorded in two samples). This allows estimation of the observed proportion of the total species or interaction richness via the following:

$$\%S_O = 100 \times S_E / S_O \quad (\text{Chao et al. 2009})$$

All asymptotic richness estimates were calculated using 100 random permutations in EstimateS (Colwell 2013). This enabled observations to be made with respect to estimate stability with increasing sample size, and species or interaction accumulation. Species accumulation curves were produced using 100 random sampling permutations with the Vegan package (Oksanen et al. 2010) in RStudio (RStudio Team 2015).

Using the methods outlined in Chao et al. (2009), we also estimated the minimum number of samples ( $m$ ) required to detect a given proportion ( $g$ ) of the total asymptotic species or interaction richness from an existing sample size ( $n$ ) as follows:

$$m_g = nU/2D \times \log[(U^2/2D) / (S_E(1-g))] \quad (\text{Chao et al. 2009})$$

#### *Evaluation of Sampling Effort:*

We evaluated three measures of sampling efficacy: (1) the proportion of the total estimated floral visitor community sampled, (2) the proportion of the total estimated community interaction richness sampled, and (3) the proportion of the total estimated interactions sampled per floral species. Measure (1), allows evaluation of whether sampling was sufficient with regard to the total community of floral visitors. Measure (2) has previously been used to evaluate sampling sufficiency with regard to community level interaction richness (Chacoff et al. 2012; Souza et al. 2018).

However, the probability of recording any given interaction depends on the relative sampling effort devoted to each of the species involved. Consequently, by pooling observations for all species within the community, this method falsely assumes that all samples are equivalent, meaning results are predisposed to sampling bias (Colwell & Coddington 1994). Measure (3) attempts to minimize sampling bias, by using the aggregate estimated interaction richness for each floral species observed. Parity of interaction richness estimated using methods (2) and (3), was assessed via chi-square analysis, with the null hypothesis that both methods were equivalent.

#### *Sampling Effort and Network Connectance:*

Connectance (C) is one of the most commonly used network metrics to assess stability or degree of specialisation within ecological networks (May 1972; Blüthgen et al. 2008), and in floral visitation networks is calculated using the formula:

$$C = I/AP \quad (\text{May 1972})$$

Where I = the richness of interactions observed, A = the richness of floral visitors observed, and P = the richness of plant species observed. However, connectance tends to fluctuate with sampling intensity as a greater proportion of species and interactions are recorded (Nielsen & Bascompte 2007; Rivera-Hutinel et al. 2012; Vizentin-Bugoni et al. 2016). This limits potential opportunities for comparison between ecological communities, as it is difficult to determine whether variability is due to differences in community structure or sampling bias (Blüthgen 2010). However, as a finite number of species and interactions can occur within a community, it should be possible to compare ecological networks provided the total species and interaction richness can be estimated accurately. In order to determine whether sampling efficacy and asymptotic richness estimates could significantly effect connectance values, chi-square analyses were used to compare our observed connectance with values calculated using asymptotic species and interaction richness estimates.

#### *Estimating a Minimum Sample Size:*

Using the methods previously used to estimate the minimum number of samples to observe a proportion of the total asymptotic interaction richness (Chao et al. 2009), we calculated the average number of sampling hours required to observe increasing proportions of the total estimated interaction richness and the results plotted using Microsoft Excel. This was conducted only for plants with  $\geq 10$  samples and  $\geq 5$  visitor species in order to minimize inaccuracies due to sampling bias, as asymptotic estimators are less accurate when sample sizes are low (Gwinn et al. 2016).

To determine whether Chao2 estimates vary significantly with sampling effort, datasets with a relatively high ( $>50$  hours) sampling effort, and ( $>90\%$ ) estimated sampling efficacy (Table 1) were divided into sampling hours and subject run through 100 random permutations in EstimateS (Colwell 2013). Estimates were deemed to have stabilized when means consistently fell within a 95% confidence interval of the

final estimate. We also used chi-square analyses to test whether significantly more sampling was required to reach each threshold based on the average floral visitor accumulation.

### **Results:**

In total we sampled 108 floral species for 15.12 +/- 16.74 (SD) hours giving a combined total of 1,633.40 hours observation. From these observations we recorded 16,699 visits from 199 floral visitor species resulting in 1,453 distinct interaction combinations. Sampling efficacy varied considerably across the three measures. Our total estimated asymptotic floral visitor richness was 220.77 +/- 9.91. We therefore observed 90.05% of the floral visitor community (Figure 1). However, to observe the remaining floral visitors, we estimate a minimum of 1442.50 additional sampling hours are needed.

When observations were pooled for all species (2), we observed an estimated 76.74% of the total interaction richness, meaning an additional 3351.37 sampling hours would be needed to observe all 1893.47 +/- 48.34 interactions (Figure 2). When interaction richness was estimated for each species individually (3), the proportion of interactions observed (66.66%) was significantly lower ( $\chi^2 = 40.90$ ,  $p < 0.01$ ). The sampling effort to observe all 2179.71 +/- 21.99 estimated interactions was also significantly greater ( $\chi^2 = 14.34$ ,  $p < 0.01$ ), requiring each species to be sampled for 50.35 +/- 73.90 hours, or 3804.40 hours total. Network connectance increased from an observed 6.76% to 8.81% (2) and 8.85% (3) respectively, however did not change significantly regardless of the analytical method ( $\chi^2 = 0.23$ ,  $p = 0.63$ ). The estimated effort required to observe successive proportions of the total interaction richness was found to increase exponentially (Figure 3) across  $n = 65$  floral species. A majority of floral interactions are predicted to have been observed within 18.03 +/- 18.51 hours of sampling, however upwards of 50.35 +/- 73.90 sampling hours may be required for complete sampling.

A similar pattern was observed for species datasets with >50 hours sampling effort, however predictions became less accurate with increased sampling. A majority of interactions were observed within 18.03 hours as expected in *Begonia danumensis* and *Brachyscome stuartii*, however significantly greater ( $\chi^2 = 7.95$ ,  $p < 0.01$ ) effort

was needed for *Chrysanthemoides monilifera* (Table 2). Nevertheless, in *B. stuartii* and *C. monilifera* mean Chao2 estimates remain within a 95% confidence interval when sampling is greater than 18.03 hours. Estimates did not fall within a 95% confidence interval for *B. danumensis*, despite varying < 1 species after 8 hours of sampling.

### **Discussion:**

We estimate that the sampling undertaken was sufficient to observe 90.05% of the expected diversity of floral visitors, but only 66.66% of the total range of interactions for the 108 floral species observed. This is likely a result of the species to interaction ratio, and the frequency of generalist to specialist floral visitors (Stang et al. 2009), with a sizeable portion of interactions likely to result from generalist opportunistic interactions (Chacoff et al. 2012). In order to observe the remaining diversity of species and interactions, we estimate that our current sampling effort would need to increase by more than 332.91% to over 5,438 hours. However, such extensive efforts are likely too impractical for conservation applications, where time and resources are frequently limited (Hegland et al. 2010).

Fortunately, metrics derived from incidence data (e.g. connectance, nestedness, and modularity) tend to approach stable asymptotes relatively quickly (Nielsen & Bascompte 2007; Costa et al. 2016; Vizentin-Bugoni et al. 2016). In a relatively specialized plant-hummingbird network, Vizentin-Bugoni et al. (2016) found these began to stabilize after 10-15 hours of sampling, when the number of additional species and interactions observed began to diminish. This point of diminishing return (Grantham et al. 2008) is likely to be greater for generalist than specialist species, though orchid pollination systems may provide a notable exception, as their specialized interactions rarely occur (Ackerman et al. 1994; Gross et al. unpublished).

The point at which this milestone occurs is likely to be difficult to define. One method may be to use incidence-based estimates of species and interaction richness that should stabilize at a similar point in time. For instance, the Chao2 estimate is prone to sampling bias when calculated from a small sample (Colwell & Coddington 1994; Chao et al. 2009; Costa et al. 2016), but becomes increasingly stable as the benefit from additional sampling decreases. Therefore, the point at which estimates begin to

stabilise is likely to be analogous with incidence-based metrics. From a small sample of comprehensively sampled floral visitation datasets, we found that Chao2 estimates fall within a 95% confidence interval of one another within 18 hours of sampling. This also coincided with our estimated mean effort required to sample a majority of floral interactions per species of 18.0 +/- 18.5 hours. Pending further investigation, this is likely to represent an important sampling milestone. We therefore recommend that future floral visitation studies aim to observe each species for a minimum of 18 hours. This should ensure that the most frequent, thus presumably the most significant (Vázquez et al. 2005; Sahli & Conner 2006), interactions will be recorded while the remaining diversity can be estimated effectively. However, it is worth noting that this may not be sufficient for all species, and is therefore intended only as a guide for standardization.

*Previous Use of Asymptotic Richness Estimates:*

Asymptotic richness estimates, particularly the Chao2 equation, are increasingly being used as a tool to evaluate sampling efficacy in network studies (Chacoff et al. 2012; Costa et al. 2016; Vizentin-Bugoni et al. 2016; Souza et al. 2018). However, most studies appear to ignore that these estimates assume all samples to be equivalent (Gotelli & Colwell 2001; Chao et al. 2009). This is unlikely to occur in network studies, particularly when sampling is species-based. Other than Chacoff et al. (2012) this is the first interaction study to evaluate interaction sampling at the level of species, and the first to recognize the significance of the differences that may result from collective estimates. We found that sampling efficacy increased significantly from 66.66% to 76.74% of interactions when observations were pooled for all species. Previous studies are therefore likely to have overestimated the proportion of interactions sampled and underestimated community diversity.

Accurately estimating the proficiency of a network's sampling is likely to be an important precursor for comparative studies. However, it's often assumed that networks of similar size and sampling effort provide accurate comparison (Olesen & Jordano 2002; Ollerton & Cranmer 2002; Dalgaard et al. 2011; Souza et al. 2018). Yet, despite almost no variation in sampling effort or floral species richness, Souza et al. (2018) observed 26.5% and 99.2% of plant-pollinator interactions in Cerrado and Pantanal networks respectively. Therefore, any resulting differences in observed

network structure are as likely to reflect sampling biases, as environmental variance. Moreover, these estimates may also be misleading given the vulnerability of asymptotic richness estimates to insufficient sample sizes (Gwinn et al. 2016). For instance, Souza et al. (2018) sampled each floral species for an average of 5.38 and 5.59 hours in Cerrado and Pantanal respectively. This is considerably less than the 18 hours we found were necessary to achieve a reliable estimate, and may therefore exhibit significant bias (Costa et al. 2016; Gwinn et al. 2016).

#### *Importance of Sampling Methods:*

To allow accurate comparison of networks across different spatial timeframes, networks need to be comparable in terms of both sampling effort and methodology. Previous meta-analyses have sought to identify generalised network patterns throughout time and space (Jordano 1987; Olesen & Jordano 2002; Blüthgen et al. 2008), but been limited by a lack of methodological standardisation. At present floral visitation and pollination networks are primarily studied using two different methods (transect, and timed observation), which result in significant variability at both species- and community-level (Gibson et al. 2011). Transect sampling generally involves an observer walking a linear transect at a constant speed while recording all interactions observed within a predetermined radius (Memmott 1999; Basilio et al. 2006; Alarcón et al. 2008). Thus the sampling of floral species occurs relative to their abundance. By contrast, timed observations generally involve a stationary observer recording interactions for a single flower, individual or group of conspecifics within a period of time (Morales & Aizen 2006; Olesen et al. 2008; Vizentin-Bugoni et al. 2016; Gross et al. 2017; Souza et al. 2018), allowing effort to be controlled for each species (Stang et al. 2009). Both methods are therefore uniquely biased, and result in an observed network that differs from the reality (Vazquez et al. 2009; Gibson et al. 2011).

Ultimately, the most suitable method will depend on the hypotheses being tested and the study environment (Gibson et al. 2011). However, in most circumstances, timed



observations offer three notable advantages. Firstly, by allowing observations to be allocated evenly between species, timed observations provide a much more even comparison of interaction significance (Vazquez et al. 2009). Secondly, observations can be weighted by the relative abundance of the species observed, thereby allowing observations to better account for the importance of common versus rare species within the network (Carvalho et al. 2008a; Kaiser-Bunbury et al. 2009; Gibson et al. 2011). This also produces results that are more directly comparable to transect observations (Gibson et al. 2011). Finally, timed observations are less likely to over- or under-sample certain floral visitor taxa, as the presence of an observer, particularly when moving, is likely to result in some degree of floral visitor disturbance. For instance, Coleopteran pollinators often spend long periods foraging at the same flower, and are less frequently disturbed by a moving observer than other floral visitors. Consequently, Coleopterans are more likely to be sampled repeatedly, and therefore over-sampled in transect surveys (Ballantyne et al. 2017).

The extent to which observations may be biased by the presence of a stationary versus motile observer is poorly resolved. However, in a pairwise comparison of transect and timed observations, Gibson et al. (2011) reliably detected more unique interactions via timed observations, suggesting the presence of a motile observer may bias the diversity of interactions sampled. Meanwhile, the observer-impact of timed observations may be further reduced through the use of digital video cameras, which provide a digital record of observations for review, and allow a single researcher to make multiple observations simultaneously (Gilpin et al. 2017). As digital cameras and other technologies become more affordable, and more easily incorporated into the study of ecological networks, the sampling procedures and methods of evaluation used are likely to be of increasing importance. Given our present understanding, the most reliable data is likely to result from stationary observations standardised to a minimum of 18 hours per species.

### **Acknowledgements:**

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Mackay, E. Mackay, and C. Silveira de Souza for their assistance in the field, and editorial comments, and thank Dan Bickel (*Entomology Department, Australian Museum, Sydney, NSW, Australia*) and Tobias Smith (*Ecosystem Management, University of New England, Armidale, NSW, Australia*) for their assistance with insect identifications. The study was funded by a student research grant provided by the University of New England (UNE).

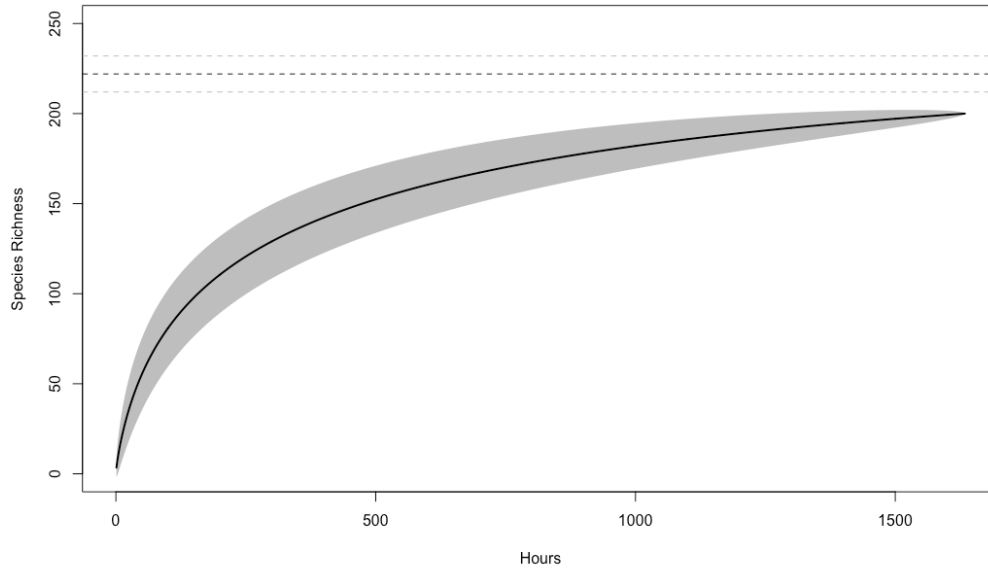
## Tables and Figures:

**Table 1:** Floral visitation datasets used to test minimum sampling threshold, with Chao2 asymptotic richness estimates. Sampling methods are analogous with the present study.

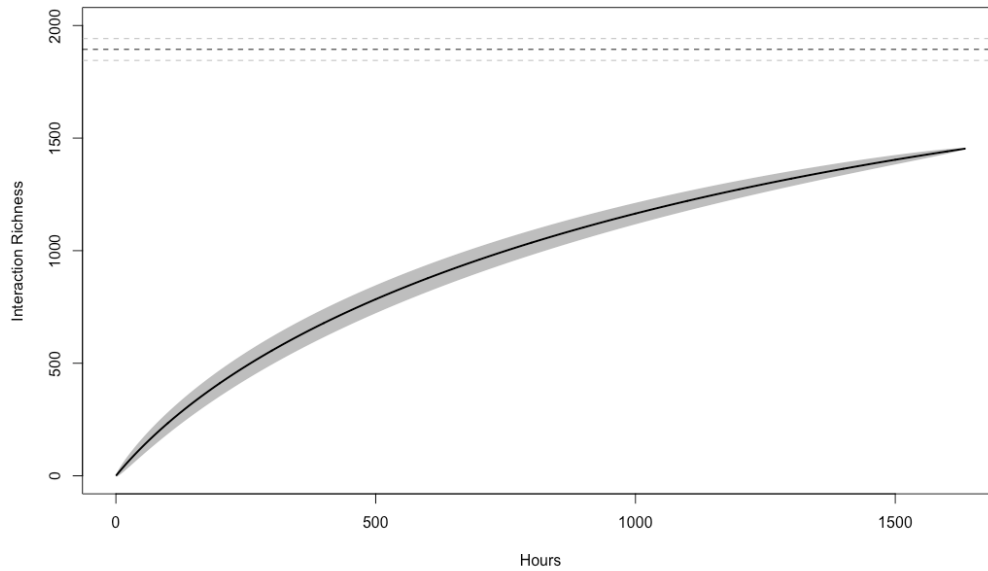
Dataset:	Floral Species:	Habitat Type:	Location:	Sampling Effort (Hours):	Interactions Observed (S <sub>0</sub> ):	Chao2 Estimate (S <sub>E</sub> ):	Estimated Efficacy (%):
Whitehead <i>et al.</i> unpublished data	<i>Begonia danumensis</i>	Tropical Rainforest	Sabah, Malaysia.	67	6	6	100.00
Whitehead unpublished data	<i>Brachyscome stuartii</i>	Temperate Woodland	New South Wales, Australia.	79	39	43	90.70
(Gross <i>et al.</i> 2017)	<i>Chrysanthemoides monilifera</i>	Coastal Heath	New South Wales, Australia.	150	35	38	92.11

**Table 2:** Mean effort to reach sampling milestones in three floral visitation datasets with >50 hours of sampling effort and >90% estimated sampling completeness. Values represent the mean of 100 random sampling permutations, and are rounded to the next whole hour. Values found to be significantly higher than our sample mean are marked with an asterisk (\*). Chao2 estimates for *Begonia danumensis* were between 5.1 and 5.96 within eight hours of sampling. Since sampling was estimated to be complete for this species, the lower 95% confidence interval was equal with the observed total of six floral visitors.

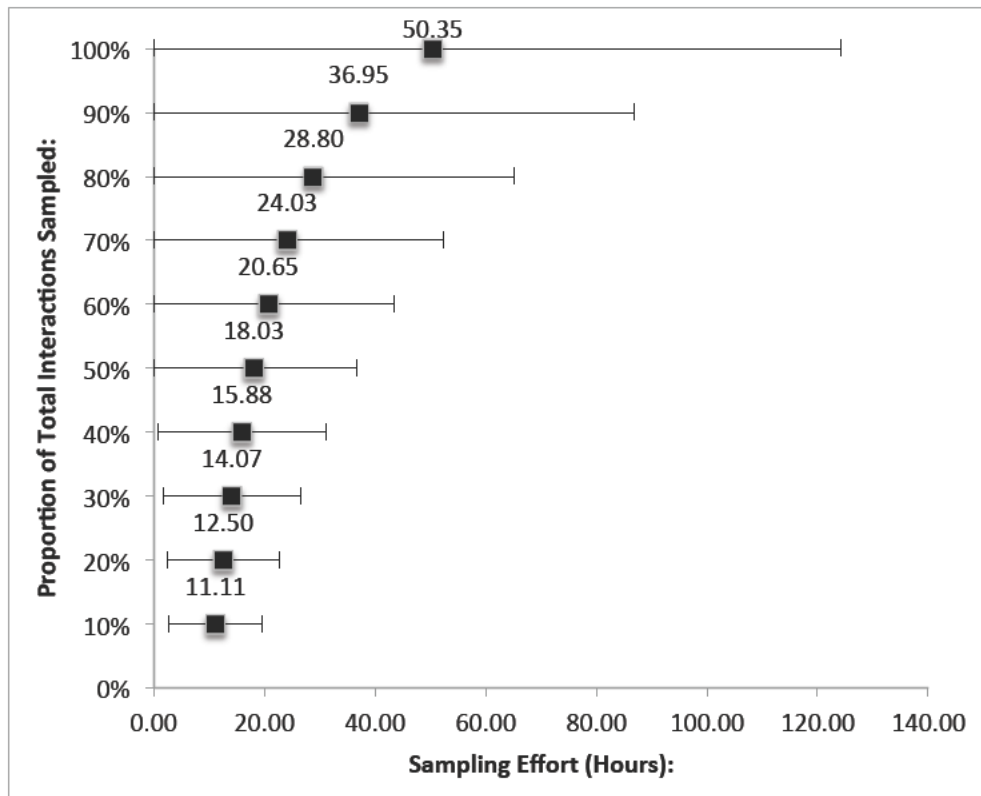
Dataset:	Floral Species:	Hours to Sample a Proportion of Estimated Interaction Richness (Mean):										Hours before Chao2 Means fall within a 95% CI (Hours):
		10%	20%	30%	40%	50%	60%	70%	80%	90%	100%	
Whitehead <i>et al.</i> unpublished data	<i>Begonia danumensis</i>	1	2	4	5	7	9	13	20	36	67*	~ 67(8)
Whitehead unpublished data	<i>Brachyscome stuartii</i>	2	5	8	11	17	25	35*	49*	73*	97*	16
(Gross <i>et al.</i> 2017)	<i>Chrysanthemoides monilifera</i>	4	8	14	21	30*	45*	61*	93*	143*	191*	18
<b>Sample Mean:</b>		<b>11.11</b>	<b>12.50</b>	<b>14.07</b>	<b>15.88</b>	<b>18.03</b>	<b>20.65</b>	<b>24.03</b>	<b>28.80</b>	<b>36.95</b>	<b>50.35</b>	-



**Figure 1:** Accumulation floral visitor species with increased community-level sampling of the Howell Shrublands floral community. Mean (black) and range (grey) of species accumulation based on 100 random sampling arrangements. Chao2 asymptotic species richness estimate (black) and standard deviation (grey) are represented as dashed horizontal lines.



**Figure 2:** Accumulation of floral interactions with increasing community-level sampling of the Howell Shrublands floral community. Mean (black) and range (grey) of species accumulation based on 100 random sampling arrangements. Chao2 asymptotic species richness estimate (black) and standard deviation (grey) are represented as dashed horizontal lines.



**Figure 3:** Scatterplot of the mean sampling effort to observe increasing proportions of the asymptotic floral visitor richness estimated for  $n = 65$  species of the Howell Shrublands floral community. Error bars represent one standard deviation, and data labels are positioned above corresponding data points.

**Higher Degree Research Thesis by Publication  
University of New England**

**STATEMENT OF AUTHORS' CONTRIBUTION**

(To appear at the end of each thesis chapter submitted as an article/paper)

We, the Research Master/PhD candidate and the candidate's Principal Supervisor, certify that all co-authors have consented to their work being included in the thesis and they have accepted the candidate's contribution as indicated in the *Statement of Originality*.

	<b>Author's Name (please print clearly)</b>	<b>% contribution</b>
Candidate	Joshua Whitehead	85%
Other Authors	Caroline Gross	15%

Name of Candidate: **Joshua Whitehead**

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\_\_\_\_\_  
Candidate

23/09/2018  
Date

  
\_\_\_\_\_  
Principal Supervisor

28 Sept 2018  
Date

**Higher Degree Research Thesis by Publication  
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	<b>Author's Name (please print clearly)</b>	<b>% contribution</b>
Candidate	Joshua Whitehead	85%
Other Authors	Caroline Gross	15%

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Name/title of Principal Supervisor: **Prof. Caroline Gross**

  
Candidate

23/09/2018  
Date

  
Principal Supervisor

28 Sept 2018  
Date

## Chapter 2. Using pollination networks to identify conservation priorities in the Howell Shrublands EEC.

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### Abstract:

The persistence of most floral species, and the communities they support, depends upon a network of mutualistic interactions that facilitate the production and dispersal of seed. Despite this, few biodiversity assessments account for biological interactions, meaning their functional significance is often overlooked in conservation. Network analyses may address this issue by providing opportunities to identify and monitor functional interactions. Here we demonstrate the potential utility of network analyses in biological conservation using examples from an endangered floral community in eastern Australia. Over six seasons between 2007 and 2017, we observed 103 floral resources for a total of 1,633.4 hours, and recorded 1,453 unique interactions with 199 floral visitor taxa. Using the Bipartite package for R, we compared specialisation ( $H_2'$ ), nestedness ( $wNODF$ ), modularity, and robustness with Vazquez null models to determine the community's resilience to disturbance throughout the course of a season. Possible keystone or umbrella species for conservation were identified using species strength and the pollination services index (PSI). *Leptospermum novae-angliae*, *L. polygalifolium*, and *Eucalyptus prava* were identified as the most important floral resources, with *Melangyna* spp., *Lasioglossum (Chilalictus)* spp., and introduced *Apis mellifera* the most important pollinators, though each species varied in significance over the course of a season. The entire network was significantly more specialised, modular, and robust to pollinator loss than expected, despite consistently lower robustness to plant, than pollinator extinctions. Dividing the network in temporal sub-units revealed that late winter and early summer flowering plants had significantly lower robustness to pollinator loss despite high community nestedness. In light of these findings, we suggest that conservation efforts at the site should focus on maintaining and improving the late winter and early summer pollinator communities in order to promote floral robustness. Results also suggest that nestedness may be an unreliable indicator of community robustness.



**Keywords:** conservation, pollination network, modularity, nestedness, specialisation.

### **Introduction:**

Plant-pollinator interactions play an important role in the reproduction of an estimated 87.5% of all flowering plants (Ollerton et al. 2011). These plants are by and large, the main source of terrestrial primary production (Robbins 1944), making pollination a key contributor to ecosystem function. Despite this, plant-pollinator interactions are often overlooked in biological conservation (Gross 2017), occasionally leading to counterproductive management decisions (Carvalho et al. 2008a; Carvalho et al. 2008b; Gross et al. 2017). However, recent disruption of plant-pollinator mutualisms due to pollinator decline (Potts et al. 2010), has emphasized the need to include pollination in the decision-making process. Nevertheless, part of the issue is that most conservation planners use species-specific data (e.g. Gross & Caddy 2006; Cramer et al. 2007; Gross & Mackay 2014), or biodiversity assessments that rely upon species richness or abundance (Tylianakis et al. 2010) to make inferences about community resilience. However, such methods often fail to determine whether ecosystem functions are maintained along with biodiversity (Elle et al. 2012; Gross 2017), as the presence of two species may not guarantee interaction without spatio-temporal co-occurrence or shared biological obligation (Memmott et al. 2007; Hegland et al. 2009; Tylianakis et al. 2010).

Network analyses have been proposed as a potential solution to this issue, by allowing community-level assessment of both species and interaction data in order to provide more meaningful interpretation of community structure and its impact on resilience. However, as species often participate in multiple interactions, the effort required to sample interactions is greater than sampling species alone (Chacoff et al. 2012). This may be why network analyses rarely see practical application, with most research instead focused on theoretical advancement (Bascompte 2007). Nevertheless, due to their functional significance, pollination networks may be well suited for biological conservation (Hegland et al. 2010; Tylianakis et al. 2010; Elle et al. 2012). This is because plant-pollinator interactions are readily observable, occur between mutually exclusive species assemblages, and involve few, if any, secondary or tertiary interactions. Thus, unlike other predator-prey or host-parasite networks, pollination

networks are relatively easily sampled via several non-destructive, and cost-effective means (Hegland et al. 2010; Gibson et al. 2011).

The main advantage of network analyses over traditional biodiversity assessments is that they allow species to be considered in terms of their functional significance, rather than just abundance. This makes them especially effective at identifying keystone or umbrella species (Bascompte et al. 2006), which due to their disproportionate influence over other species, provide indirect benefit to other species through conservation (Paine 1969; Roberge & Angelstam 2004). Network analyses also allow communities to be viewed as more than just their component parts (Bascompte & Jordano 2007; Tylianakis et al. 2010), allowing structural attributes to be quantified as potential indicators of stability (Tylianakis et al. 2010). This may become an increasingly valuable in future conservation, with plant-pollinator mutualisms likely to experience disruptions due to global climate change (Memmott et al. 2007; Hegland et al. 2009; Etterson & Mazer 2016). Yet, although these structural attributes of pollination networks theoretically serve as indicators of community stability, empirical evidence may be lacking (Tylianakis et al. 2010).

For instance, increasing connectance (proportion of realized interactions) is often associated with network stability (Thebault & Fontaine 2010), but exhibits considerable bias with respect to network size or sampling effort (Jordano 1987; Nielsen & Bascompte 2007; Fründ et al. 2016), limiting its reliability as an indicator. Conversely, specialisation ( $H_2'$ ), nestedness ( $wNODF$ ), and modularity are relatively insensitive to sampling effort (Vizentin-Bugoni et al. 2016), but their correlation with network stability is less apparent, and may be integrative (Tylianakis et al. 2010; Elle et al. 2012). Since specialisation measures the relative degree to which species depend upon specific resources or interactions (Blüthgen et al. 2006), more specialized networks are expected to be less robust, due to the increased sensitivity of specialist species to disturbance (Henle et al. 2004). However, nestedness and modularity may increase the robustness of a specialized network (Memmott et al. 2004; Olesen et al. 2007; Elle et al. 2012).

Nestedness relates to the extent of interaction overlap between specialists and generalists within a network, and it is assumed to provide a buffer against specialist extinctions, by allowing them to be functionally replaced by generalists (Memmott et

al. 2004; Nielsen & Bascompte 2007). Likewise, modularity measures to the proportion of interactions that form discrete sub-networks or modules that are more densely linked internally than externally (Olesen et al. 2007; Dupont et al. 2009). In highly modular networks, disturbances are more likely to be contained within modules, and less likely to cascade through the entire network (Thebault & Fontaine 2010). However, nestedness and modularity may also decrease stability, as highly nested communities may be particularly sensitive to generalist extinctions (Memmott et al. 2004), while disturbances may have disproportionately severe impacts on species within modules (Olesen et al. 2007). Thus, incorporating community-level network attributes into management may be a challenging prospect.

Understanding and monitoring aspects of network structure that promote stability may be made more difficult by the temporal dynamics of ecological communities, with trophic and climatic fluctuations likely to promote important shifts in community structure over time (Olesen et al. 2008; Petanidou et al. 2008; Dupont et al. 2009; Baldock et al. 2011; Burkle et al. 2013; Trøjelsgaard et al. 2016). Despite this, most interaction networks are treated like static entities. This potentially misrepresents the significance of specific interactions, particularly when partners are shared over different time frames (Poisot et al. 2015). In order to demonstrate the potential utility of network analyses for biological conservation, this paper will assess community resilience and identify possible umbrella species for an endangered floral community in eastern Australia. To demonstrate the significance of temporal variation, networks are divided into discrete sub-networks that reflect local variation in flowering phenology on a monthly basis.

## **Materials and Methods:**

### *Study Area:*

Sampling was conducted over 15 hectares of granite outcropping to the east of Copeton Dam (29° 56' 08" S, 151° 02' 11" E) in northern New South Wales (NSW), Australia. The area forms part of the New England Batholith; a circa 282 million year old plutonic geological formation (Phillips et al. 2011) encompassing an estimated 175,000 hectares of eastern Australia north from Tamworth, New South Wales to Stanthorpe, Queensland (Leigh 1968).

The structural and taxonomic diversity of granite vegetation communities has been recognised worldwide (Burbank & Platt 1964; Hambler 1964; Wyatt & Fowler 1977; Porembski et al. 1994; Hopper et al. 1997; Main 1997; Porembski et al. 1997; Hunter & Clarke 1998; Meirelles et al. 1999; Porembski 2005). Yet, few studies have investigated the diversity of biotic interactions within. The granite floristic communities of eastern Australia, and the New England Batholith in particular, contain many rare, threatened and endemic taxa of potentially significant conservation or economic value (Kirkpatrick et al. 1988; Norris & Thomas 1991; Hunter & Clarke 1998; McGann 2002). Previous study within the New England Batholith floristic region has primarily focused on community structure and taxonomic variability (Kirkpatrick et al. 1988; Richards & Hunter 1997; Hunter & Clarke 1998; McGann 2002), or the ecology of specific species (Benson 1992; Hunter et al. 1998).

Like most of the New England Batholith, vegetation within the study area exhibits significant structural and taxonomic heterogeneity (Hunter & Clarke 1998). Nevertheless, vegetation throughout the site typically represents a low open woodland (Specht 1970), with structural layering and composition contingent on recent disturbance history and successional age. Occupying a southerly altitudinal gradient ranging from 714 m to 745 m above sea level (a.s.l), the community is characteristic of the Howell Shrublands, an endangered ecological community (EEC), listed under the New South Wales Biodiversity Conservation Act (NSW Government 2016), and distinguished by a dense shrub layer of *Homoranthus prolixus*. The Howell Shrublands currently occupy a fragmented distribution along the New England Batholith currently threatened by inadequate fire regimes and increased grazing pressure due to the presence of feral goats (*Capra aegagrus hircus*). Therefore, any information regarding the mechanisms of community persistence is potentially of significant conservation value. To our knowledge, this is the first study to investigate community-scale plant–pollinator interactions within the region.

#### *Floral IDs/Flowering Phenology:*

Vegetation surveys were conducted once a month from August to December in 2011 and 2012, to recorded the identity of any species within a 20m radius at four locations within the study area. From August 2015 to April 2017, vegetation surveys were conducted once a week, and the number of sampling locations was increased to nine.

During this time, we also recorded the proportion of flowering to non-flowering individuals observed for any species observed within the nine sampling locations, allowing us to observe seasonal variation and phenology patterns. Reference specimens were collected to identify any floral species encountered within the sampling locations, with vouchers lodged at the N. C. W. Beadle Herbarium, at the University of New England, NSW, Australia.

#### *Floral Visitation:*

We recorded floral visitation interactions using a combination of digital camera (Sony Handycam models HDR-155 XR160, HDR-PJ540, and FDR-AXP35 4K) video and timed field observations recorded over six non-successive flowering seasons. Field observations involved a single observer recording all the floral interactions to occur within a 15-60 minute period at the floral display of an individual plant. Up to 15 cameras at a time were recording video for up to 4 hours per plant, with the field of view adjusted in order to provide reliable visitor identifications, and a representative sample of the observed plant's total floral display. Conspecific sampling was structured to ensure no two individuals were observed simultaneously within a 50-metre radius of one another. Observations were recorded from August to December in 2007, September to December in 2011, August to October in 2012, October 2014, and August to February in 2015/2016 and 2016/2017. For each interaction, floral visitors were identified as either a potential pollinator (PP), or non-pollinator (NP) depending upon behavioural observations previously used to identify floral larceny (Inouye 1980; Irwin et al. 2010). Such an approach is considered pragmatic for revealing likely pollinators within a system (Jacobs et al. 2009); however further investigation is needed to confirm whether effective pollination actually occurs (Gross & Mackay 1998; Gross et al. 2017).

Visitors classified as PP, were observed to make consistent contact with both male and female reproductive structures whilst moving within and between flowers on separate individuals of the same species. Whilst this ignores the potential for some floral visitors to facilitate self pollination despite limited pollen dispersal capabilities, without supplementary evidence regarding floral breeding systems, discrimination of pollinating from non-pollinating interactions relies on demonstrated capacities for pollen receipt, transfer, and dispersal (Inouye 1980; Irwin et al. 2010). Any floral

visitor unable to meet the criteria for classification as a PP was considered a NP. Previous studies have further sub-classified non-pollinating floral visitors according to their behaviour and impact on floral fecundity (Irwin & Brody 1999; Burkle et al. 2007; Stein & Hensen 2011), however this was deemed unnecessary given the nature of study and potential for overlap in classification (Fumero-Cabán & Melendez-Ackerman 2007; Stein & Hensen 2011).

#### *Pollinator/Visitor IDs:*

Floral visitor reference specimens were collected for identification throughout the study using a combination of pan trap and net sampling. We employed a combination of methods to ensure the greatest potential diversity of species were sampled, as each method is likely to sample a significantly different assortment of species (Popic et al. 2013). Pan traps were constructed from opaque white polyethylene bowls (110mm diameter, 70mm high) coloured with UV-bright fluorescent spray-paint, to form a tricolour arrangement of blue, white and yellow. Traps were deployed in groups of three (one of each colour) at ground level within the vicinity of flowering plants. Each group was placed at least 20m apart, and filled with water to a depth of 1cm, before adding a drop of non-odorous detergent to reduce the surface tension. Traps were left undisturbed for 4-8 hours between 06:00 and 18:00 Australian Eastern Standard Time (AEST) before returning to collect any captures.

Net sampling occurred haphazardly throughout the study, and involved an observer using an entomological net to capture any floral visitors observed within a 20m transect of flowering plants over a 30 minute period. Floral visitors were then euthanized with ethyl acetate, and transferred to 70 mL specimen bottles for transportation. All captures were pin-mounted within 24 hours or stored in 70% ethanol (and later pin-mounted) for identification. All floral visitors were identified to generic level, unless reliable species level identifications could be made from the video recordings and in the field. Identifications were made using relevant field guides (e.g. Braby 2004), online resources (e.g. [www.ala.org.au/](http://www.ala.org.au/), [www.padil.gov.au/](http://www.padil.gov.au/), <http://plantnet.rbgsyd.nsw.gov.au>) or expert knowledge (see acknowledgements) and cross-referenced with photographs, and video recordings.

#### *Network Analysis:*

Floral visitation data was organised into seven bipartite matrices to reflect observed flowering phenology patterns (or seasons) occurring throughout the course of a year (Figure 1). This was done in order to minimise the number of potentially ‘forbidden interactions’ (Jordano et al. 2003), rendered impossible by a lack of temporal overlap between species, represented within a network. Within each matrix, we used rows to represent floral species, columns to represent visitor species, and entries to represent the observed rate of interaction per hour of sampling. We used interaction rates, as opposed to raw abundance, in order to account for variation in sampling effort between floral species, and therefore provide a more accurate representation of each species’ importance within the network. Each network was then rebuilt with and without NP floral visitors to determine the extent to which interaction type affected network and species relationships.

Networks were analyzed using the “bipartite” package (Dormann et al. 2008), in RStudio (RStudio Team 2015) and compared using a selection of descriptive, quantitative (Dormann et al. 2009), and species-specific metrics (Dormann 2011). Descriptive characteristics included the number of floral and faunal species, and the number of unique interactions (links). These descriptors may be strongly influenced by sampling effort & network size (Nielsen & Bascompte 2007; Blüthgen et al. 2008; Dormann et al. 2009). Thus, we utilised the methods outlined in chapter one (Whitehead & Gross unpublished) to estimate network descriptors using the Chao2 equation (Chao et al. 2009). For the same reasons, we also elected to use quantitative metrics with minimal sensitivity to sampling bias (Fründ et al. 2016; Vizentin-Bugoni et al. 2016), such as specialisation, nestedness, modularity, and robustness.

Specialisation was calculated via the  $H_2'$  index, which estimates the degree of interaction partitioning based on the observed frequency of potentially interacting species (Blüthgen et al. 2006). Networks with low specialisation, are therefore expected to have high interaction redundancy, making them more resilient to species decline or random extinctions (Blüthgen et al. 2007; Elle et al. 2012). Nestedness was quantified using the  $wNODF$  index (Almeida-Neto & Ulrich 2011) and relates to the extent of interaction overlap between specialist and generalist species. Nestedness may therefore improve resilience in highly specialized networks, by increasing the proportion of redundant interactions (Memmott et al. 2004; Tylianakis et al. 2010;

Elle et al. 2012). Similarly, modularity relates to the prevalence of discrete sub-networks within a community (Olesen et al. 2007). Highly modular networks are therefore less likely to experience significant trophic cascades, as the impact of species loss or extinction is more likely to be contained within a specific module or sub-network (Dupont et al. 2009; Thebault & Fontaine 2010). Weighted modularity was calculated via the DIRTLPAwb+ algorithm (Beckett 2016), which is notably faster, and more consistent than other methods (e.g. Dormann et al. 2014). Analyses were replicated ten times to account for any potential variability due to the algorithms initial configuration (Dormann et al. 2014; Vizentin-Bugoni et al. 2016; Souza et al. 2018). Finally, robustness was used to measure the resilience of a network to species loss by calculating the area under a secondary extinction curve (Memmott et al. 2004; Burgos et al. 2007). This was based on the assumption that extinctions in one guild (e.g. pollinators) would promote co-extinctions in the other (e.g. plants) following a loss of obligate interactions.

The significance of quantitative metrics was determined by comparison with 1,000 iterations of the Vazquez null model (Vázquez et al. 2005), which randomly assigns interactions while retaining network connectance (Vázquez et al. 2007). This was deemed to provide a more informative comparison than Patefield null models (Patefield 1981), which maintained network size, but not connectance, producing networks that were significantly less specialized, more nested, and less modular (Table 1). Results were deemed significant if they fell outside a 95% confidence interval of the Vazquez null mean.

Pollinators potentially acting as keystone, or umbrella species within the community were identified using species-level metrics including species strength, and pollination services index (PSI). Species strength was used to quantify a pollinators' importance in terms of its cumulative share of interactions across all interaction partners (Bascompte et al. 2006). Since pollinators may utilize, or even depend upon plant species they do not pollinate, key plant species were identified via their mean species strength for all floral visitors, and not simply those which serve as potential pollinators. Similarly, PSI was used to estimate the likelihood of conspecific pollen transfer based on the observed proportion of visits within and between species. However, as species strength and PSI are both derived from an observed interaction



frequency at sampled individual plants, some over or under-estimation may occur due to variability in the constancy of individual pollinators. This is particularly likely when a specific individual or sex within a sampled population concentrates a greater portion of interactions within a particular floral resource than the rest of that species' population as a whole. For instance, due to differences in pollen and nectar foraging behaviours in male and female solitary bee species (Ne'eman et al. 2006).

### **Results:**

We identified 186 floral species; of which 147 produce flowers adapted for zoophilous pollination. From 1633.4 hours of observation we recorded floral visitation data for 103 of these species (Table 2), resulting in 1453 unique interactions involving 199 identifiable taxa (Table 3; Figures 2-3). This included 162 species potentially acting as pollinators of one or more plant species, peaking in diversity between the middle of spring and the beginning of summer (Figure 1). Observations were estimated to account for 90.05% of floral visitor species and 66.66% of interactions present within the sampled community, though this wasn't consistent across all sub-networks (Table 4).

The resulting networks (Figures 4-11) identified several possible keystone or umbrella species, of which *Leptospermum novae-angliae*, *L. polygalifolium*, and *Eucalyptus prava* were the most important floral species (Table 5), while *Melangyna* spp., *Lasioglossum (Chilalictus)* spp., and *Apis mellifera* were among the most important pollinators in terms of strength (Table 5), and PSI (Table 6). However, no species were consistently among the most important in terms of either metric across all sub-networks.

When all observations were considered, the resulting network was significantly more specialised, less nested, more modular and more resilient to plant extinctions than expected (Table 1). Despite this, the community was consistently more vulnerable to plant, than pollinator extinctions, with higher plant than pollinator robustness across all sub-networks. Dividing the network into temporal sub-networks revealed a similar pattern in terms of specialisation and modularity, with all networks significantly more specialised and modular than expected by the null models (Table 1). Early spring was the only period significantly less nested than the null models, while significantly more

robust pollinator communities were observed from late winter to the middle of spring, and in early summer. Plants flowering in the middle of summer were the only species observed to be significantly more resilient to pollinator loss, with significantly greater nestedness coinciding with reduced robustness in late winter and early summer (Table 1).

### **Discussion:**

This is one of the first studies to identify conservation priorities through network analysis and for a plant-pollinator network in particular. Using network analyses we were able to identify multiple plant and pollinator species whose frequency of interaction with other species, suggests they may be suitable keystone or umbrella species for conservation (Paine 1969; Roberge & Angelstam 2004). These include, *L. novae-angliae*, *L. polygalifolium*, and *E. prava*, or *Melangyna* spp., *Lasioglossum (Chilalictus)* spp., and *A. mellifera*, which provided the greatest impact in terms of floral resources (Table 5) and pollination services (Tables 5-6) respectively, over the entire sampling period. Though the transiency of floral resources (Figure 1) ensures that multiple species may act as keystones at different times of the year.

Conserving populations of floral keystone species might therefore appear to be a logical pre-requisite for conserving the network as a whole. However, the transience of floral resources means pollinators are likely to rely upon a variety of floral resources scattered throughout the course of a season. Therefore, it may be necessary to divide the network into shorter temporal sub-units in order to identify when and where management is likely to have the greatest benefit. As a whole, the network was significantly more modular, more specialised, and more robust to plant extinctions than the null models could predict, though like most ecological networks, was less resilient to floral than faunal extinctions in general (Schleuning et al. 2016). When the network was divided into shorter sampling intervals, most sub-networks observed similarly significant specialisation, modularity, and pollinator robustness compared with the null models (Table 1). However, this was not consistent, as late winter and early summer flowering plants were observed to be significantly less robust than the null models could predict, suggesting they may be at risk of future disturbances that result in pollinator extinctions.

Lower robustness within the early summer flowering plants, may be an artefact of the relative considerable sampling bias experienced, having sampled the lowest estimated proportion of floral visitors (72.34%) and interactions (57.04%) respectively. For comparison, sampling of the late winter network was estimated to be considerably more complete, detecting 89.97% of floral visitors, and 71.71% of interactions. Plants flowering at this time of the year might also be expected to have lower robustness, with a climate-driven trend toward earlier flowering potentially leading to the dissociation of plant-pollinator mutualisms (Fitter & Fitter 2002; Hegland et al. 2009; McEwan et al. 2010). Consequently, network analyses suggest conservation of the Howell Shrublands may be best achieved via the management of its most important late winter pollinators; *Trichocolletes* spp., *Apis mellifera*, *Melangyna* spp., *Lichenostomus melanops*, and *Brychosoma* spp. (Tables 5-6).

Despite their potential as research and conservation tools, networks are frequently limited by the scale of effort involved in sampling them (Hegland et al. 2010). This is to some extent inevitable, as each species may engage in multiple interactions, with more or less effort required to observe a similar number or proportion of interactions per species (Chapter 1). As a result, significantly greater effort may be necessary to achieve similar samples of interaction versus species richness (Chacoff et al. 2012). However, since time and associated costs of sampling are likely to be major deterrents in applied conservation (Hegland et al. 2010; Tylianakis et al. 2010), network analyses will need to provide significant advantages over current monitoring foci even at low sampling intensity.

In the case of the Howell Shrublands, assessments relying upon species richness and abundance may have identified the late winter pollination network as a priority due to its relatively low species richness. However, as rarity may be an unreliable indicator of extinction risk (Rabinowitz 1981; Harnik et al. 2012), their tendency to prioritise rare species, may be at odds with the preservation of network function (Smith & Knapp 2003; Memmott et al. 2004). For instance, the long-term survival of a rare plant may be more dependent upon the presence of common species that constitutes a majority of resources for their shared pollinators (Gibson et al. 2006; Carvalheiro et al. 2008a).

Unfortunately, many network parameters are extremely sensitive to species richness or sample size (Blüthgen et al. 2007; Nielsen & Bascompte 2007; Vizentin-Bugoni et al. 2016), creating issues in terms of their reliability, and suitability for comparison. Assessments are therefore likely to be limited to metrics such as specialisation, nestedness, or modularity, which approach a relatively stable asymptote within a short period of sampling (Vizentin-Bugoni et al. 2016). However, the relationship between these metrics and network robustness is often unclear. Increasing specialisation is expected to reduce robustness, by reducing the degree of interaction redundancy (Blüthgen et al. 2007; Blüthgen et al. 2008). This also assumes that specialists are at higher risk of extinction, and while there is evidence to support this theory (Henle et al. 2004), such an assumption is not guaranteed. Similarly, increasing nestedness is presumed to confer robustness by increasing the likelihood that generalist interactions can replace those of specialists (Memmott et al. 2004; Bascompte et al. 2006). Once again, this assumes that specialists are more likely to succumb to extinction. Finally, modularity is assumed to increase robustness by containing the spread of extinctions throughout a network (Olesen et al. 2007; Dupont et al. 2009; Thebault & Fontaine 2010).

However, each of these metrics may integrate with one another to variable extents. For instance, networks may be highly modular, yet nested within modules (Olesen et al. 2007). Meanwhile, some degree of specialisation is required to form modular and nested interactions, potentially obscuring the relationship between these metrics and community robustness. In this study, specialisation and modularity observed a remarkably similar pattern (Table 1) and are likely to be closely correlated, while nestedness was much more variable. No metric served as a reliable indicator of robustness, though counter-intuitively, higher nestedness often coincided with lower robustness. Indeed, the two sub-networks with significantly lower plant robustness were also the only networks to have significantly higher nestedness scores. Nevertheless, relationships between these metrics and their impact on community robustness will require further investigation.

It is worth noting that this study did not account for variability in pollinator effectiveness, and therefore may not accurately reflect the relative importance of each pollinator visit. Experimentally measuring the effectiveness of each interaction is a

time consuming process and unlikely to be feasible under the constraints of most conservation initiatives. However, interaction frequency may provide a practical alternative, assuming that the most frequent pollinators are also the most likely to effect seed set (Vázquez et al. 2005; Sahli & Conner 2006). One alternative may be to construct pollination networks retroactively, through sampling the pollen loads carried by floral visitors (Bosch et al. 2009; Alarcón 2010; Devoto et al. 2011). However, while this may provide more accurate interpretations of pollinator efficiency, the assumption that pollen loads accurately reflect floral visitation and pollinator effectiveness may be erroneous due to the presence of self-incompatible pollen, or larcenous interactions. For instance, when honeybees (*Apis mellifera*) have been observed to collect pollen from other bee species rather than flowers (Laroca & Winston 1978; Thorp & Briggs 1980; Jean 2005), or reduce floral fecundity by removing the pollen from *Melastoma affine* stigmas (Gross & Mackay 1998).

Likewise, accurate pollen identifications may be extremely difficult (Godwin 1934; Mander et al. 2014), particularly when closely related or congeneric species co-occur. This may present an issue, as circumstances may deem species identifications necessary. For instance, when particular species are of known extinction risk, legal status, or the focus of monitoring programs due to their economic or ecological importance. This may also prove an issue with invertebrate pollinators, whose species identities are frequently unknown or poorly resolved. Though this is more likely to reflect taxonomic limitations rather than the identification of unique morphospecies (Elle et al. 2012). Nevertheless, as this study suggests, network analyses may be able to provide a more valuable conservation tool than traditional species-based approaches, by prioritising functional interaction over specific identifications.

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## Tables and Figures:

**Table 1.** Observed network metrics compared with mean and 95% confidence intervals for 1,000 replications of the Patefield and Vazquez null models. Observations that were significantly different from the Vazquez null mean are marked with an asterisk (\*), and all values are provided to two decimal places.

$H_2'$ :	Observed:	Patefield Mean:	Patefield 95%CI Lower:	Patefield 95%CI Upper:	Vazquez Mean:	Vazquez 95%CI Lower:	Vazquez 95%CI Upper:
Late Winter	0.52*	0.19	0.13	0.25	0.19	0.13	0.23
Early Spring	0.52*	0.12	0.09	0.15	0.13	0.09	0.17
Mid Spring	0.54*	0.07	0.07	0.08	0.12	0.09	0.14
Late Spring	0.58*	0.15	0.11	0.18	0.20	0.18	0.24
Early Summer	0.68*	0.12	0.06	0.18	0.42	0.36	0.49
Mid Summer	0.62*	0.17	0.13	0.21	0.19	0.15	0.24
Late Summer	0.56*	0.18	0.13	0.23	0.20	0.15	0.25
ALL	0.55*	0.10	0.09	0.11	0.12	0.10	0.13

wNODF:	Observed:	Patefield Mean:	Patefield 95%CI Lower:	Patefield 95%CI Upper:	Vazquez Mean:	Vazquez 95%CI Lower:	Vazquez 95%CI Upper:
Late Winter	20.43*	26.05	17.70	34.75	11.36	7.52	16.12
Early Spring	15.26	40.74	32.45	48.78	19.74	15.97	23.44
Mid Spring	13.64	30.68	25.02	36.09	13.80	11.58	16.21
Late Spring	15.11	29.42	26.67	32.61	12.91	9.93	15.84
Early Summer	14.67*	28.81	27.46	30.09	10.24	8.69	12.07
Mid Summer	10.08	19.42	13.86	24.95	9.75	7.06	12.84
Late Summer	13.32	28.11	20.02	36.98	13.64	9.77	18.81
ALL	12.29*	27.46	25.03	29.96	18.47	16.00	20.83

Modularity:	Observed:	Patefield Mean:	Patefield 95%CI Lower:	Patefield 95%CI Upper:	Vazquez Mean:	Vazquez 95%CI Lower:	Vazquez 95%CI Upper:
Late Winter	0.50*	0.29	0.25	0.34	0.43	0.39	0.47
Early Spring	0.46*	0.16	0.14	0.19	0.26	0.23	0.28
Mid Spring	0.51*	0.17	0.15	0.20	0.26	0.25	0.28
Late Spring	0.60*	0.32	0.30	0.35	0.42	0.41	0.44
Early Summer	0.68*	0.50	0.46	0.54	0.53	0.51	0.54
Mid Summer	0.57*	0.32	0.28	0.36	0.42	0.39	0.46
Late Summer	0.55*	0.27	0.22	0.32	0.40	0.36	0.45
ALL	0.55*	0.17	0.19	0.21	0.27	0.26	0.28

<b>Robustness (Plants):</b>	<b>Observed:</b>	<b>Patefield Mean:</b>	<b>Patefield 95%CI Lower:</b>	<b>Patefield 95%CI Upper:</b>	<b>Vazquez Mean:</b>	<b>Vazquez 95%CI Lower:</b>	<b>Vazquez 95%CI Upper:</b>
Late Winter	<b>0.69*</b>	0.74	0.72	0.77	<b>0.73</b>	<b>0.70</b>	<b>0.76</b>
Early Spring	<b>0.75</b>	0.75	0.72	0.78	<b>0.72</b>	<b>0.70</b>	<b>0.75</b>
Mid Spring	<b>0.79</b>	0.73	0.70	0.75	<b>0.78</b>	<b>0.76</b>	<b>0.80</b>
Late Spring	<b>0.77</b>	0.72	0.70	0.73	<b>0.79</b>	<b>0.77</b>	<b>0.81</b>
Early Summer	<b>0.74*</b>	0.69	0.68	0.71	<b>0.81</b>	<b>0.78</b>	<b>0.83</b>
Mid Summer	<b>0.77*</b>	0.75	0.73	0.77	<b>0.74</b>	<b>0.71</b>	<b>0.76</b>
Late Summer	<b>0.72</b>	0.76	0.73	0.78	<b>0.74</b>	<b>0.71</b>	<b>0.77</b>
ALL	<b>0.83</b>	0.75	0.73	0.76	<b>0.82</b>	<b>0.80</b>	<b>0.83</b>

<b>Robustness (Pollinators):</b>	<b>Observed:</b>	<b>Patefield Mean:</b>	<b>Patefield 95%CI Lower:</b>	<b>Patefield 95%CI Upper:</b>	<b>Vazquez Mean:</b>	<b>Vazquez 95%CI Lower:</b>	<b>Vazquez 95%CI Upper:</b>
Late Winter	<b>0.65*</b>	0.72	0.70	0.74	<b>0.62</b>	<b>0.60</b>	<b>0.64</b>
Early Spring	<b>0.63*</b>	0.76	0.73	0.78	<b>0.61</b>	<b>0.58</b>	<b>0.62</b>
Mid Spring	<b>0.68*</b>	0.66	0.65	0.68	<b>0.65</b>	<b>0.63</b>	<b>0.67</b>
Late Spring	<b>0.63</b>	0.73	0.71	0.75	<b>0.62</b>	<b>0.60</b>	<b>0.64</b>
Early Summer	<b>0.62*</b>	0.65	0.64	0.66	<b>0.60</b>	<b>0.58</b>	<b>0.61</b>
Mid Summer	<b>0.63</b>	0.68	0.66	0.70	<b>0.63</b>	<b>0.61</b>	<b>0.65</b>
Late Summer	<b>0.61</b>	0.74	0.71	0.76	<b>0.61</b>	<b>0.59</b>	<b>0.64</b>
ALL	<b>0.74*</b>	0.72	0.71	0.73	<b>0.70</b>	<b>0.69</b>	<b>0.71</b>

**Table 2.** Observed plant species. Naturalised exotic species are marked with an asterisk (\*).

<b>ID Number:</b>	<b>Order:</b>	<b>Family:</b>	<b>Species:</b>
1	Apiales	Apiaceae	<i>Actinotus helianthi</i>
2	Apiales	Araliaceae	<i>Trachymene incisa</i>
3	Apiales	Pittosporaceae	<i>Bursaria spinosa</i>
4	Apiales	Pittosporaceae	<i>Cheiranthra telfordii</i>
5	Asparagales	Asparagaceae	<i>Anthropodium milleflorum</i>
6	Asparagales	Asparagaceae	<i>Dichopogon fimbriatus</i>
7	Asparagales	Asparagaceae	<i>Thysanotus tuberosus</i>
8	Asparagales	Asphodelaceae	<i>Bulbine bulbosa</i>
9	Asparagales	Asphodelaceae	<i>Dianella caerulea</i>
10	Asparagales	Asphodelaceae	<i>Tricoryne elatior</i>
11	Asparagales	Hypoxidaceae	<i>Hypoxis hygrometrica</i>
12	Asparagales	Iridaceae	<i>Patersonia sericea</i>
13	Asparagales	Orchidaceae	<i>Caladenia fuscata</i>
14	Asparagales	Orchidaceae	<i>Diuris abbreviata</i>
15	Asparagales	Orchidaceae	<i>Glossodia major</i>
16	Asparagales	Orchidaceae	<i>Microtis parviflora</i>
17	Asparagales	Orchidaceae	<i>Spiranthes australis</i>
18	Asterales	Asteraceae	<i>Brachyscome multifida</i>
19	Asterales	Asteraceae	<i>Brachyscome nova-anglica</i>



<b>ID Number:</b>	<b>Order:</b>	<b>Family:</b>	<b>Species:</b>
20	Asterales	Asteraceae	<i>Brachyscome stuartii</i>
21	Asterales	Asteraceae	<i>Cassinia copensis</i>
22	Asterales	Asteraceae	<i>Cassinia laevis</i>
23	Asterales	Asteraceae	<i>Cassinia quinquefaria</i>
24	Asterales	Asteraceae	<i>Chrysocephalum apiculatum</i>
25	Asterales	Asteraceae	<i>Hypochaeris radicata*</i>
26	Asterales	Asteraceae	<i>Olearia elliptica</i>
27	Asterales	Asteraceae	<i>Olearia ramosissima</i>
28	Asterales	Asteraceae	<i>Ozothamnus obcordatus</i>
29	Asterales	Asteraceae	<i>Podolepis neglecta</i>
30	Asterales	Asteraceae	<i>Senecio diaschides</i>
31	Asterales	Asteraceae	<i>Vittadinia cuneata</i>
32	Asterales	Campanulaceae	<i>Isotoma anethifolia</i>
33	Asterales	Campanulaceae	<i>Lobelia andrewsii</i>
34	Asterales	Campanulaceae	<i>Wahlenbergia stricta</i>
35	Asterales	Goodeniaceae	<i>Goodenia bellidifolia</i>
36	Asterales	Goodeniaceae	<i>Goodenia hederacea</i>
37	Asterales	Goodeniaceae	<i>Goodenia macbarronii</i>
38	Asterales	Menyanthaceae	<i>Nymphoides geminata</i>
39	Asterales	Stylidiaceae	<i>Stylidium graminifolium</i>
40	Caryophyllales	Droseraceae	<i>Drosera burmanni</i>
41	Caryophyllales	Droseraceae	<i>Drosera glanduligera</i>
42	Caryophyllales	Droseraceae	<i>Drosera peltata</i>
43	Commelinales	Commelinaceae	<i>Commelina cyanea</i>
44	Commelinales	Commelinaceae	<i>Murdannia graminea</i>
45	Dilleniales	Dilleniaceae	<i>Hibbertia acicularis</i>
46	Dilleniales	Dilleniaceae	<i>Hibbertia kaputarensis</i>
47	Dilleniales	Dilleniaceae	<i>Hibbertia riparia</i>
48	Dilleniales	Dilleniaceae	<i>Hibbertia</i> sp. aff. <i>riparia</i>
49	Ericales	Ericaceae	<i>Brachyloma daphnoides</i>
50	Ericales	Ericaceae	<i>Leucopogon melaleuroides</i>
51	Ericales	Ericaceae	<i>Leucopogon muticus</i>
52	Ericales	Ericaceae	<i>Leucopogon neoanglicus</i>
53	Ericales	Ericaceae	<i>Leucopogon virgatus</i>
54	Ericales	Ericaceae	<i>Lissanthe strigosa</i>
55	Ericales	Ericaceae	<i>Melichrus urceolatus</i>
56	Ericales	Primulaceae	<i>Anagallis arvensis*</i>
57	Fabales	Fabaceae	<i>Acacia decora</i>
58	Fabales	Fabaceae	<i>Acacia granitica</i>
59	Fabales	Fabaceae	<i>Acacia neriifolia</i>
60	Fabales	Fabaceae	<i>Acacia penninervis</i>
61	Fabales	Fabaceae	<i>Acacia pruinosa</i>
62	Fabales	Fabaceae	<i>Acacia triptera</i>
63	Fabales	Fabaceae	<i>Acacia viscidula</i>
64	Fabales	Fabaceae	<i>Bossiaea obcordata</i>

<b>ID Number:</b>	<b>Order:</b>	<b>Family:</b>	<b>Species:</b>
65	Fabales	Fabaceae	<i>Bossiaea scortechinii</i>
66	Fabales	Fabaceae	<i>Dillwynia sericea</i>
67	Fabales	Fabaceae	<i>Dillwynia sieberi</i>
68	Fabales	Fabaceae	<i>Glycine clandestina</i>
69	Fabales	Fabaceae	<i>Hardenbergia violacea</i>
70	Fabales	Fabaceae	<i>Hovea heterophylla</i>
71	Fabales	Fabaceae	<i>Hovea lanceolata</i>
72	Fabales	Fabaceae	<i>Mirbelia pungens</i>
73	Fabales	Fabaceae	<i>Pultenaea myrtoides</i>
74	Gentianales	Gentianaceae	<i>Centaurium tenuiflorum*</i>
75	Lamiales	Lamiaceae	<i>Prostanthera nivea</i>
76	Lamiales	Lentibulariaceae	<i>Utricularia dichotoma</i>
77	Liliales	Colchicaceae	<i>Wurmbea biglandulosa</i>
78	Malpighiales	Hypericaceae	<i>Hypericum gramineum</i>
79	Malpighiales	Violaceae	<i>Viola betonicifolia</i>
80	Malvales	Thymelaeaceae	<i>Pimelea linifolia</i>
81	Myrtales	Myrtaceae	<i>Callistemon linearis</i>
82	Myrtales	Myrtaceae	<i>Callistemon pungens</i>
83	Myrtales	Myrtaceae	<i>Calytrix tetragona</i>
84	Myrtales	Myrtaceae	<i>Eucalyptus dealbata</i>
85	Myrtales	Myrtaceae	<i>Eucalyptus prava</i>
86	Myrtales	Myrtaceae	<i>Harmogia densifolia</i>
87	Myrtales	Myrtaceae	<i>Homoranthus prolixus</i>
88	Myrtales	Myrtaceae	<i>Kunzea parvifolia</i>
89	Myrtales	Myrtaceae	<i>Leptospermum brevipes</i>
90	Myrtales	Myrtaceae	<i>Leptospermum novae-angliae</i>
91	Myrtales	Myrtaceae	<i>Leptospermum polygalifolium</i>
92	Myrtales	Myrtaceae	<i>Micromyrtus sessilis</i>
93	Oxalidales	Oxalidaceae	<i>Oxalis radicata</i>
94	Poales	Xyridaceae	<i>Xyris complanata</i>
95	Proteales	Proteaceae	<i>Grevillea floribunda</i>
96	Proteales	Proteaceae	<i>Grevillea triternata</i>
97	Proteales	Proteaceae	<i>Hakea microcarpa</i>
98	Proteales	Proteaceae	<i>Persoonia cornifolia</i>
99	Rosales	Rhamnaceae	<i>Cryptandra amara</i>
100	Santalales	Santalaceae	<i>Choretrum candollei</i>
101	Sapindales	Rutaceae	<i>Correa reflexa</i>
102	Sapindales	Rutaceae	<i>Crowea exalata</i>
103	Sapindales	Rutaceae	<i>Zieria odorifera</i>

**Table 3.** Observed floral visitor taxa. Naturalised exotic species are marked with an asterisk. Numbers reflect the number of morphospecies where reliable species identification wasn't possible under general observation.

<b>ID:</b>	<b>Class:</b>	<b>Order:</b>	<b>Family:</b>	<b>Species:</b>
A	Aves	Passeriformes	Melpigidae	<i>Anthochaera carunculata</i>

<b>ID:</b>	<b>Class:</b>	<b>Order:</b>	<b>Family:</b>	<b>Species:</b>
<b>B</b>	Aves	Passeriformes	Melpigidae	<i>Lichenostomus melanops</i>
<b>C</b>	Aves	Passeriformes	Melpigidae	<i>Lichenostomus penicillatus</i>
<b>D</b>	Aves	Passeriformes	Melpigidae	<i>Melithreptus lunatus</i>
<b>E</b>	Aves	Passeriformes	Melpigidae	<i>Philemon corniculatus</i>
<b>F</b>	Aves	Psittaciformes	Psittaculidae	<i>Glossopsitta concinna</i>
<b>G</b>	Aves	Psittaciformes	Psittaculidae	<i>Glossopsitta pusilla</i>
<b>H</b>	Aves	Psittaciformes	Psittaculidae	<i>Trichoglossus chlorolepidotus</i>
<b>I</b>	Aves	Psittaciformes	Psittaculidae	<i>Trichoglossus moluccanus</i>
<b>J</b>	Insecta	Coleoptera	Buprestidae	<i>Castiarina parallela</i>
<b>K</b>	Insecta	Coleoptera	Buprestidae	<i>Castiarina skusei</i>
<b>L</b>	Insecta	Coleoptera	Buprestidae	<i>Ethonion</i> spp. <sup>1</sup>
<b>M</b>	Insecta	Coleoptera	Buprestidae	<i>Melobasis</i> spp. <sup>1</sup>
<b>N</b>	Insecta	Coleoptera	Buprestidae	<i>Stigmodera macularia</i>
<b>O</b>	Insecta	Coleoptera	Cantharidae	<i>Heteromastix</i> spp. <sup>1</sup>
<b>P</b>	Insecta	Coleoptera	Chrysomelidae	<i>Aporocera</i> spp. <sup>1</sup>
<b>Q</b>	Insecta	Coleoptera	Chrysomelidae	<i>Edusella</i> spp. <sup>1</sup>
<b>R</b>	Insecta	Coleoptera	Chrysomelidae	<i>Nisotra</i> spp. <sup>2</sup>
<b>S</b>	Insecta	Coleoptera	Cleridae	<i>Eleale lepida</i>
<b>T</b>	Insecta	Coleoptera	Cleridae	<i>Eleale</i> spp. <sup>2</sup>
<b>U</b>	Insecta	Coleoptera	Coccinellidae	<i>Coccinella transversalis</i>
<b>V</b>	Insecta	Coleoptera	Coccinellidae	<i>Micraspis frenata</i>
<b>W</b>	Insecta	Coleoptera	Curculionidae	<i>Leptopius</i> spp. <sup>1</sup>
<b>X</b>	Insecta	Coleoptera	Dermestidae	<i>Anthrenus</i> spp. <sup>1</sup>
<b>Y</b>	Insecta	Coleoptera	Lycidae	<i>Porrostoma</i> spp. <sup>2</sup>
<b>Z</b>	Insecta	Coleoptera	Melyridae	<i>Dicranolaius</i> spp. <sup>2</sup>
<b>AA</b>	Insecta	Coleoptera	Mordellidae	<i>Hoshihananomia</i> spp. <sup>1</sup>
<b>AB</b>	Insecta	Coleoptera	Mordellidae	<i>Mordella</i> spp. <sup>2</sup>
<b>AC</b>	Insecta	Coleoptera	Mordellidae	<i>Tomoxioda</i> spp. <sup>1</sup>
<b>AD</b>	Insecta	Coleoptera	Nitidulidae	<i>Aethina</i> spp. <sup>1</sup>
<b>AE</b>	Insecta	Coleoptera	Scarabaeidae	<i>Aplopsis</i> spp. <sup>1</sup>
<b>AF</b>	Insecta	Coleoptera	Scarabaeidae	<i>Diphucephala</i> spp. <sup>1</sup>
<b>AG</b>	Insecta	Coleoptera	Scarabaeidae	<i>Eupoecila australasiae</i>
<b>AH</b>	Insecta	Coleoptera	Scarabaeidae	<i>Neorrhina punctatum</i>
<b>AI</b>	Insecta	Coleoptera	Scarabaeidae	<i>Phyllotocus</i> spp. <sup>1</sup>
<b>AJ</b>	Insecta	Coleoptera	Tenebrionidae	<i>Homotrysis</i> spp. <sup>1</sup>
<b>AK</b>	Insecta	Diptera	Bibionidae	<i>Dilophus</i> spp. <sup>2</sup>
<b>AL</b>	Insecta	Diptera	Bombyliidae	<i>Anthrax</i> spp. <sup>2</sup>
<b>AM</b>	Insecta	Diptera	Bombyliidae	<i>Balaana</i> spp. <sup>2</sup>
<b>AN</b>	Insecta	Diptera	Bombyliidae	<i>Brychosoma</i> spp. <sup>1</sup>
<b>AO</b>	Insecta	Diptera	Bombyliidae	<i>Comptosia</i> spp. <sup>2</sup>
<b>AP</b>	Insecta	Diptera	Bombyliidae	<i>Eusurbus</i> spp. <sup>1</sup>
<b>AQ</b>	Insecta	Diptera	Bombyliidae	<i>Geron</i> spp. <sup>2</sup>
<b>AR</b>	Insecta	Diptera	Bombyliidae	<i>Meomyia</i> spp. <sup>1</sup>
<b>AS</b>	Insecta	Diptera	Bombyliidae	<i>Staurostichus</i> spp. <sup>4</sup>
<b>AT</b>	Insecta	Diptera	Bombyliidae	<i>Villa</i> spp. <sup>3</sup>
<b>AU</b>	Insecta	Diptera	Calliphoridae	<i>Amenia</i> spp. <sup>1</sup>

<b>ID:</b>	<b>Class:</b>	<b>Order:</b>	<b>Family:</b>	<b>Species:</b>
AV	Insecta	Diptera	Calliphoridae	<i>Calliphora (Australocalliphora) spp.</i> <sup>1</sup>
AW	Insecta	Diptera	Calliphoridae	<i>Calliphora (Paracalliphora) spp.</i> <sup>2</sup>
AX	Insecta	Diptera	Calliphoridae	<i>Chrysomya spp.</i> <sup>2</sup>
AY	Insecta	Diptera	Lauxaniidae	<i>Poecilohetaerus spp.</i> <sup>1</sup>
AZ	Insecta	Diptera	Lauxaniidae	<i>Sapromyza spp.</i> <sup>1</sup>
BA	Insecta	Diptera	Muscidae	<i>Dichaetomyia spp.</i> <sup>2</sup>
BB	Insecta	Diptera	Muscidae	<i>Helina spp.</i> <sup>2</sup>
BC	Insecta	Diptera	Muscidae	<i>Hydrotaea spp.</i> <sup>1</sup>
BD	Insecta	Diptera	Muscidae	<i>Musca spp.</i> <sup>2</sup>
BE	Insecta	Diptera	Muscidae	<i>Neomyia spp.</i> <sup>1</sup>
BF	Insecta	Diptera	Nemestrinidae	<i>Trichophthalma spp.</i> <sup>2</sup>
BG	Insecta	Diptera	Rhiniidae	<i>Stomorhina spp.</i> <sup>2</sup>
BH	Insecta	Diptera	Sarcophagidae	<i>Amobia spp.</i> <sup>1</sup>
BI	Insecta	Diptera	Sarcophagidae	<i>Protomiltogramma spp.</i> <sup>1</sup>
BJ	Insecta	Diptera	Sarcophagidae	<i>Sarcophaga spp.</i> <sup>3</sup>
BK	Insecta	Diptera	Sepsidae	<i>Parapalaeosepsis spp.</i> <sup>1</sup>
BL	Insecta	Diptera	Stratiomyidae	<i>Odontomyia spp.</i> <sup>3</sup>
BM	Insecta	Diptera	Syrphidae	<i>Eristalinus spp.</i> <sup>2</sup>
BN	Insecta	Diptera	Syrphidae	<i>Eumerus spp.</i> <sup>1</sup>
BO	Insecta	Diptera	Syrphidae	<i>Melangyna spp.</i> <sup>1</sup>
BP	Insecta	Diptera	Syrphidae	<i>Melanostoma apicale</i>
BQ	Insecta	Diptera	Syrphidae	<i>Simosyrphus grandicornis</i>
BR	Insecta	Diptera	Syrphidae	<i>Sphaerophoria macrogaster</i>
BS	Insecta	Diptera	Tabanidae	<i>Copidapha vicina</i>
BT	Insecta	Diptera	Tabanidae	<i>Ectenopsis spp.</i> <sup>1</sup>
BU	Insecta	Diptera	Tabanidae	<i>Myioscaptia calliphora</i>
BV	Insecta	Diptera	Tabanidae	<i>Scaptia auriflua</i>
BW	Insecta	Diptera	Tabanidae	<i>Tabanus spp.</i> <sup>2</sup>
BX	Insecta	Diptera	Tachinidae	<i>Carcelia spp.</i> <sup>3</sup>
BY	Insecta	Diptera	Tachinidae	<i>Cylindromyia spp.</i> <sup>1</sup>
BZ	Insecta	Diptera	Tachinidae	<i>Eurygastropsis spp.</i> <sup>1</sup>
CA	Insecta	Diptera	Tachinidae	<i>Exorista spp.</i> <sup>2</sup>
CB	Insecta	Diptera	Tachinidae	<i>Linnaemya spp.</i> <sup>1</sup>
CC	Insecta	Diptera	Tachinidae	<i>Phasia spp.</i> <sup>2</sup>
CD	Insecta	Diptera	Tachinidae	<i>Rutilia (Ameniamima) spp.</i> <sup>1</sup>
CE	Insecta	Diptera	Tachinidae	<i>Rutilia (Chrysorutilia) spp.</i> <sup>1</sup>
CF	Insecta	Diptera	Tachinidae	<i>Rutilia (Donovanius) lepida</i>
CG	Insecta	Diptera	Tachinidae	<i>Rutilia (Donovanius) regalis</i>
CH	Insecta	Diptera	Tachinidae	<i>Rutilia (Rutilia) spp.</i> <sup>1</sup>
CI	Insecta	Diptera	Tachinidae	<i>Senostoma spp.</i> <sup>2</sup>
CJ	Insecta	Diptera	Tachinidae	<i>Winthemia spp.</i> <sup>1</sup>
CK	Insecta	Diptera	Tephritidae	<i>Spathulina acroleuca</i>
CL	Insecta	Diptera	Tephritidae	<i>Trupanea spp.</i> <sup>1</sup>
CM	Insecta	Diptera	Therevidae	<i>Acupalpa spp.</i> <sup>1</sup>
CN	Insecta	Diptera	Therevidae	<i>Anabarhynchus spp.</i> <sup>1</sup>
CO	Insecta	Diptera	Therevidae	<i>Bonjeania spp.</i> <sup>1</sup>

<b>ID:</b>	<b>Class:</b>	<b>Order:</b>	<b>Family:</b>	<b>Species:</b>
CP	Insecta	Hemiptera	Lygaeidae	<i>Nysius</i> spp. <sup>1</sup>
CQ	Insecta	Hemiptera	Lygaeidae	<i>Thunbergia</i> spp. <sup>1</sup>
CR	Insecta	Hemiptera	Miridae	<i>Setocoris</i> spp. <sup>1</sup>
CS	Insecta	Hemiptera	Pentatomidae	<i>Cuspicona</i> spp. <sup>1</sup>
CT	Insecta	Hemiptera	Pentatomidae	<i>Ocirrhoe</i> spp. <sup>1</sup>
CU	Insecta	Hemiptera	Pentatomidae	<i>Poecilometis</i> spp. <sup>1</sup>
CV	Insecta	Hemiptera	Scutelleridae	<i>Scutiphora</i> spp. <sup>1</sup>
CW	Insecta	Hymenoptera	Apidae	<i>Amegilla</i> spp. <sup>2</sup>
CX	Insecta	Hymenoptera	Apidae	<i>Apis mellifera</i> *
CY	Insecta	Hymenoptera	Apidae	<i>Braunsapis</i> spp. <sup>2</sup>
CZ	Insecta	Hymenoptera	Apidae	<i>Exoneura</i> spp. <sup>2</sup>
DA	Insecta	Hymenoptera	Apidae	<i>Exoneurella</i> spp. <sup>2</sup>
DB	Insecta	Hymenoptera	Apidae	<i>Thyreus caeruleopunctatus</i>
DC	Insecta	Hymenoptera	Apidae	<i>Xylocopa (Lestis) aeratus</i>
DD	Insecta	Hymenoptera	Braconidae	<i>Campyloneurus</i> spp. <sup>1</sup>
DE	Insecta	Hymenoptera	Chalcididae	<i>Brachymeria</i> spp. <sup>1</sup>
DF	Insecta	Hymenoptera	Colletidae	<i>Hylaeus (Euprosopis) honestus</i>
DG	Insecta	Hymenoptera	Colletidae	<i>Hylaeus (Gnathoprosopis) euxanthus</i>
DH	Insecta	Hymenoptera	Colletidae	<i>Hylaeus (Gnathoprosopoides) philoleucus</i>
DI	Insecta	Hymenoptera	Colletidae	<i>Hylaeus (Pseudhylaeus) albocuneatus</i>
DJ	Insecta	Hymenoptera	Colletidae	<i>Leioproctus (Cladocerapis) spp.</i> <sup>1</sup>
DK	Insecta	Hymenoptera	Colletidae	<i>Leioproctus (Filiglossa) spp.</i> <sup>1</sup>
DL	Insecta	Hymenoptera	Colletidae	<i>Leioproctus (Leioproctus) maculatus</i>
DM	Insecta	Hymenoptera	Colletidae	<i>Leioproctus (Leioproctus) spp.</i> <sup>2</sup>
DN	Insecta	Hymenoptera	Colletidae	<i>Meroglossa impressifrons</i>
DO	Insecta	Hymenoptera	Colletidae	<i>Meroglossa plumifera</i>
DP	Insecta	Hymenoptera	Colletidae	<i>Paracolletes (Paracolletes) crassipes</i>
DQ	Insecta	Hymenoptera	Colletidae	<i>Trichocolletes</i> spp. <sup>1</sup>
DR	Insecta	Hymenoptera	Crabronidae	<i>Bembix palmata</i>
DS	Insecta	Hymenoptera	Crabronidae	<i>Cerceris</i> spp. <sup>1</sup>
DT	Insecta	Hymenoptera	Crabronidae	<i>Sphecius pectoralis</i>
DU	Insecta	Hymenoptera	Crabronidae	<i>Tachysphex</i> spp. <sup>2</sup>
DV	Insecta	Hymenoptera	Formicidae	<i>Campanotus</i> spp. <sup>1</sup>
DW	Insecta	Hymenoptera	Formicidae	<i>Crematogaster</i> spp. <sup>1</sup>
DX	Insecta	Hymenoptera	Formicidae	<i>Iridomyrmex</i> spp. <sup>3</sup>
DY	Insecta	Hymenoptera	Formicidae	<i>Polyrhachis</i> spp. <sup>1</sup>
DZ	Insecta	Hymenoptera	Formicidae	<i>Rhytidoponera</i> spp. <sup>1</sup>
EA	Insecta	Hymenoptera	Gasteruptiidae	<i>Gasteruption</i> spp. <sup>2</sup>
EB	Insecta	Hymenoptera	Halictidae	<i>Homalictus</i> spp. <sup>3</sup>
EC	Insecta	Hymenoptera	Halictidae	<i>Lasioglossum (Australictus) spp.</i>
ED	Insecta	Hymenoptera	Halictidae	<i>Lasioglossum (Chilalictus) spp.</i> <sup>4</sup>
EE	Insecta	Hymenoptera	Halictidae	<i>Lasioglossum (Parasphecodes) spp.</i> <sup>2</sup>
EF	Insecta	Hymenoptera	Halictidae	<i>Lipotriches (Austronomia) australica</i>
EG	Insecta	Hymenoptera	Halictidae	<i>Lipotriches (Austronomia) flavoviridis</i>
EH	Insecta	Hymenoptera	Halictidae	<i>Lipotriches (Austronomia) muscosa</i>
EI	Insecta	Hymenoptera	Halictidae	<i>Lipotriches (Austronomia) phanerura</i>

<b>ID:</b>	<b>Class:</b>	<b>Order:</b>	<b>Family:</b>	<b>Species:</b>
EJ	Insecta	Hymenoptera	Ichneumonidae	<i>Hyposoter</i> spp. <sup>1</sup>
EK	Insecta	Hymenoptera	Ichneumonidae	<i>Labium</i> spp. <sup>2</sup>
EL	Insecta	Hymenoptera	Ichneumonidae	<i>Lissopimpla excelsa</i>
EM	Insecta	Hymenoptera	Megachilidae	<i>Megachile (Austrochile) modesta</i>
EN	Insecta	Hymenoptera	Megachilidae	<i>Megachile (Eutricharaea) maculariformis</i>
EO	Insecta	Hymenoptera	Megachilidae	<i>Megachile (Eutricharaea) simplex</i>
EP	Insecta	Hymenoptera	Megachilidae	<i>Megachile (Hackeriapis) tosticauda</i>
EQ	Insecta	Hymenoptera	Megachilidae	<i>Megachile (Rhodomegachile) deanii</i>
ER	Insecta	Hymenoptera	Megachilidae	<i>Megachile aurifrons</i>
ES	Insecta	Hymenoptera	Megachilidae	<i>Megachile eucalypti</i>
ET	Insecta	Hymenoptera	Megachilidae	<i>Megachile ferox</i>
EU	Insecta	Hymenoptera	Megachilidae	<i>Megachile lucidiventris</i>
EV	Insecta	Hymenoptera	Megachilidae	<i>Megachile semiluctuosa</i>
EW	Insecta	Hymenoptera	Pergidae	<i>Pterygophorus</i> spp. <sup>1</sup>
EX	Insecta	Hymenoptera	Pompilidae	<i>Cryptocheilus</i> spp. <sup>1</sup>
EY	Insecta	Hymenoptera	Pompilidae	<i>Turneromyia</i> spp. <sup>1</sup>
EZ	Insecta	Hymenoptera	Scoliidae	<i>Austroscolia soror</i>
FA	Insecta	Hymenoptera	Scoliidae	<i>Radumeris</i> spp. <sup>1</sup>
FB	Insecta	Hymenoptera	Scoliidae	<i>Scolia (Discolia) verticalis</i>
FC	Insecta	Hymenoptera	Sphecidae	<i>Sphex</i> spp. <sup>1</sup>
FD	Insecta	Hymenoptera	Tiphiidae	<i>Anthobosca</i> spp. <sup>2</sup>
FE	Insecta	Hymenoptera	Tiphiidae	<i>Catocheilus</i> spp. <sup>1</sup>
FF	Insecta	Hymenoptera	Tiphiidae	<i>Epactiothynnus</i> spp. <sup>1</sup>
FG	Insecta	Hymenoptera	Tiphiidae	<i>Tachyphron</i> spp. <sup>1</sup>
FH	Insecta	Hymenoptera	Tiphiidae	<i>Thynnoides</i> spp. <sup>1</sup>
FI	Insecta	Hymenoptera	Torymidae	<i>Torymoides</i> spp. <sup>1</sup>
FJ	Insecta	Hymenoptera	Vespidae	<i>Abispa ephippium</i>
FK	Insecta	Hymenoptera	Vespidae	<i>Delta</i> spp. <sup>1</sup>
FL	Insecta	Hymenoptera	Vespidae	<i>Paralastor</i> spp. <sup>2</sup>
FM	Insecta	Hymenoptera	Vespidae	<i>Polistes</i> spp. <sup>2</sup>
FN	Insecta	Hymenoptera	Vespidae	<i>Pseudabispa</i> spp. <sup>1</sup>
FO	Insecta	Hymenoptera	Vespidae	<i>Ropalidia</i> spp. <sup>1</sup>
FP	Insecta	Hymenoptera	Vespidae	<i>Stenodyneriellus</i> spp. <sup>1</sup>
FQ	Insecta	Lepidoptera	Erebidae	<i>Amata</i> spp. <sup>2</sup>
FR	Insecta	Lepidoptera	Erebidae	<i>Donuca lanipes</i>
FS	Insecta	Lepidoptera	Hesperiidae	<i>Hesperilla donnysa</i>
FT	Insecta	Lepidoptera	Hesperiidae	<i>Ocybadistes walkeri</i>
FU	Insecta	Lepidoptera	Hesperiidae	<i>Taractrocera papyria</i>
FV	Insecta	Lepidoptera	Hesperiidae	<i>Toxidia parvulus</i>
FW	Insecta	Lepidoptera	Lycaenidae	<i>Lampides boeticus</i>
FX	Insecta	Lepidoptera	Lycaenidae	<i>Nacaduba biocellata</i>
FY	Insecta	Lepidoptera	Lycaenidae	<i>Zizina otis</i>
FZ	Insecta	Lepidoptera	Noctuidae	<i>Helicoverpa</i> spp. <sup>1</sup>
GA	Insecta	Lepidoptera	Nymphalidae	<i>Danaus plexippus</i>
GB	Insecta	Lepidoptera	Nymphalidae	<i>Heteronympha merope</i>
GC	Insecta	Lepidoptera	Nymphalidae	<i>Hypocysta pseudirius</i>

ID:	Class:	Order:	Family:	Species:
GD	Insecta	Lepidoptera	Nymphalidae	<i>Junonia villida</i>
GE	Insecta	Lepidoptera	Nymphalidae	<i>Vanessa kershawi</i>
GF	Insecta	Lepidoptera	Oecophoridae	<i>Aeolocoma</i> spp. <sup>1</sup>
GG	Insecta	Lepidoptera	Oecophoridae	<i>Barea</i> spp. <sup>1</sup>
GH	Insecta	Lepidoptera	Oecophoridae	<i>Philobota</i> spp. <sup>2</sup>
GI	Insecta	Lepidoptera	Oecophoridae	<i>Snellenia</i> spp. <sup>1</sup>
GJ	Insecta	Lepidoptera	Pieridae	<i>Belenois java</i>
GK	Insecta	Lepidoptera	Pieridae	<i>Delias argenthona</i>
GL	Insecta	Lepidoptera	Pieridae	<i>Elodina angulipennis</i>
GM	Insecta	Lepidoptera	Pieridae	<i>Eurema smilax</i>
GN	Insecta	Lepidoptera	Pieridae	<i>Pieris rapae</i>
GO	Insecta	Lepidoptera	Pterophoridae	<i>Stenoptilia</i> spp. <sup>1</sup>
GP	Insecta	Lepidoptera	Zygaenidae	<i>Pollanisus cyanota</i>
GQ	Reptilia	Squamata	Scincidae	<i>Liopholis modesta</i>

**Table 4:** Proportion of floral visitor and floral interaction richness observed based on the Chao2 estimation method. Estimated values are rounded to the nearest whole number and percentages to two decimal places.

Floral Network:	Floral Visitors:			Interactions:		
	Observed:	Chao2 Estimate:	% Observed:	Observed:	Chao2 Estimate:	% Observed:
Late Winter	41	46	89.97%	96	134	71.71%
Early Spring	63	79	79.69%	186	256	72.62%
Mid Spring	122	134	91.02%	531	835	63.57%
Late Spring	131	165	79.24%	449	687	65.31%
Early Summer	117	162	72.34%	251	440	57.04%
Mid Summer	57	70	81.66%	143	240	59.46%
Late Summer	40	43	93.02%	89	120	74.07%
All Seasons	199	221	90.05%	1453	2180	66.66%

**Table 5:** The most important plants and pollinators in order of species strength for each Howell Shrublands pollination network. Species strength serves as a cumulative measure of a species' share of interactions across all interaction partners, and thus it's relative importance to the network as a whole.

Network:	Plant:	Species Strength:	Pollinator:	Species Strength:
Late Winter	<i>Acacia neriifolia</i>	13.77	<i>Trichocolletes</i> spp.	3.65
	<i>Leucopogon melaleuroides</i>	4.71	<i>Apis mellifera</i>	2.95
	<i>Acacia pruinosa</i>	3.08	<i>Melangyna</i> spp.	2.85
	<i>Olearia ramosissima</i>	2.71	<i>Lichenostomus melanops</i> .	1.67
	<i>Acacia viscidula</i>	2.02	<i>Brychosoma</i> spp.	0.88
Early Spring	<i>Acacia decora</i>	9.55	<i>Melangyna</i> spp.	8.79
	<i>Acacia granitica</i>	6.15	<i>Apis mellifera</i>	5.81
	<i>Micromyrtus sessilis</i>	5.40	<i>Trichocolletes</i> spp.	2.57
	<i>Hakea microcarpa</i>	4.76	<i>Lasioglossum (Chilalictus)</i> spp.	2.24

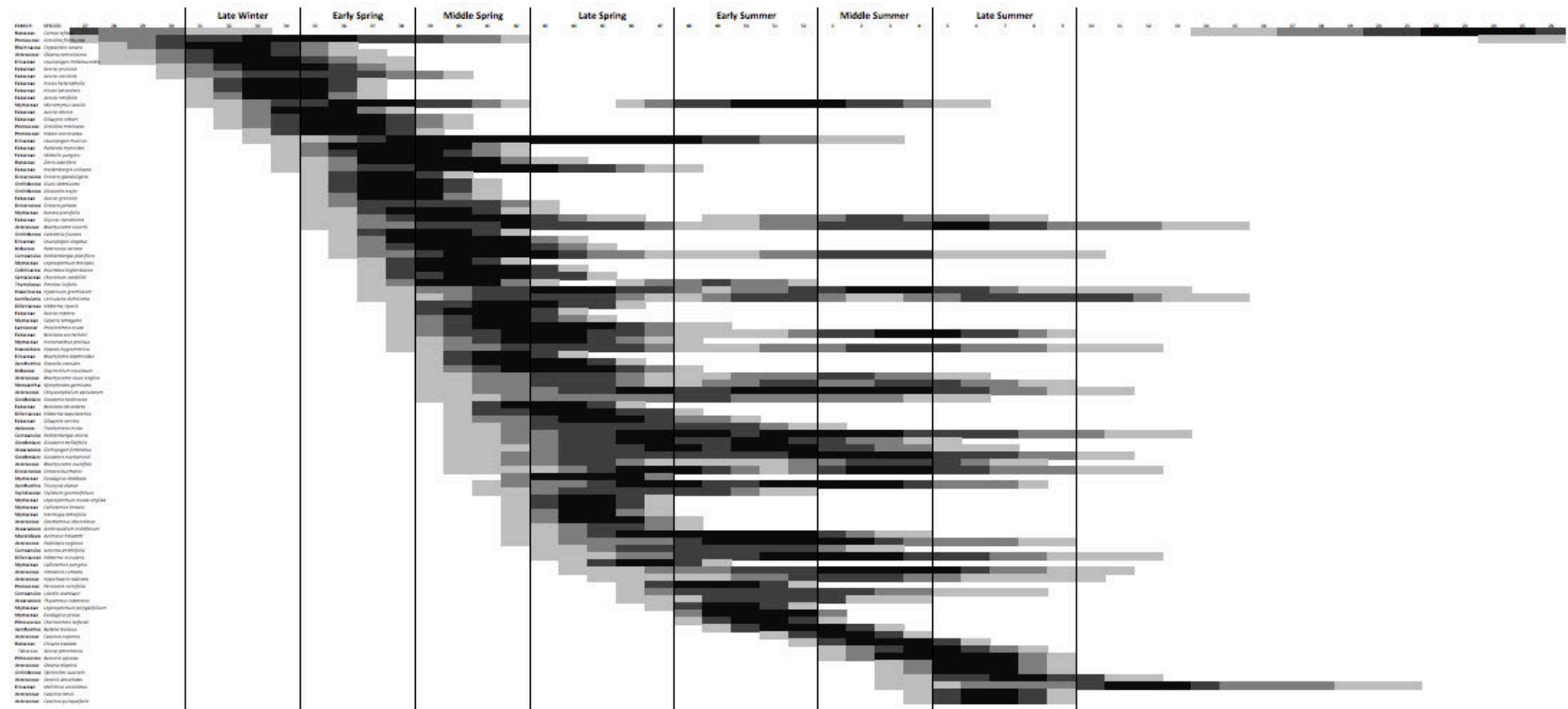
	<i>Leucopogon virgatus</i>	4.39	<i>Simosyrphus grandicornis</i>	1.22
<b>Mid Spring</b>	<i>Leptospermum brevipes</i>	18.60	<i>Melangyna</i> spp.	10.26
	<i>Eucalyptus dealbata</i>	10.08	<i>Apis mellifera</i>	6.18
	<i>Homoranthus prolixus</i>	9.71	<i>Simosyrphus grandicornis</i>	3.46
	<i>Acacia triptera</i>	8.11	<i>Homalictus</i> spp.	2.96
	<i>Brachyscome stuartii</i>	7.47	<i>Lipotriches (Austronomia) flavoviridis</i>	2.77
<b>Late Spring</b>	<i>Leptospermum novae-angliae</i>	45.81	<i>Lasioglossum (Chilalictus)</i> spp.	7.86
	<i>Harmogia densifolia</i>	8.11	<i>Homalictus</i> spp.	7.79
	<i>Homoranthus prolixus</i>	6.93	<i>Simosyrphus grandicornis</i>	3.27
	<i>Callistemon pungens</i>	5.33	<i>Lipotriches (Austronomia) flavoviridis</i>	2.11
	<i>Leucopogon muticus</i>	4.81	<i>Melangyna</i> spp.	2.05
<b>Early Summer</b>	<i>Leptospermum polygalifolium</i>	44.40	<i>Braunsapis</i> spp.	3.59
	<i>Eucalyptus prava</i>	16.20	<i>Lasioglossum (Chilalictus)</i> spp.	3.34
	<i>Actinotus helianthii</i>	7.48	<i>Lipotriches (Austronomia) flavoviridis</i>	2.85
	<i>Leucopogon muticus</i>	7.17	<i>Homalictus</i> spp.	2.21
	<i>Micromyrtus sessilis</i>	3.59	<i>Simosyrphus grandicornis</i>	1.97
<b>Mid Summer</b>	<i>Micromyrtus sessilis</i>	9.68	<i>Homalictus</i> spp.	3.87
	<i>Cassinia copensis</i>	7.54	<i>Braunsapis</i> spp.	2.63
	<i>Brachyscome stuartii</i>	5.49	<i>Lasioglossum (Chilalictus)</i> spp.	2.53
	<i>Crowea exalata</i>	5.16	<i>Taractrocera papyria</i>	1.59
	<i>Leucopogon muticus</i>	4.65	<i>Amegilla</i> spp.	1.36
<b>Late Summer</b>	<i>Bursaria spinosa</i>	14.16	<i>Braunsapis</i> spp.	4.16
	<i>Brachyscome stuartii</i>	5.59	<i>Megachile ferox</i>	2.02
	<i>Olearia elliptica</i>	3.22	<i>Exoneurella</i> spp.	1.85
	<i>Brachyscome multifida</i>	2.68	<i>Apis mellifera</i>	1.64
	<i>Cassinia quinquefaria</i>	2.62	<i>Lasioglossum (Chilalictus)</i> spp.	1.63
<b>ALL:</b>	<i>Leptospermum novae-angliae</i>	20.20	<i>Melangyna</i> spp.	12.10
	<i>Leptospermum polygalifolium</i>	16.66	<i>Lasioglossum (Chilalictus)</i> spp.	12.04
	<i>Eucalyptus prava</i>	10.36	<i>Apis mellifera</i>	10.64
	<i>Bursaria spinosa</i>	7.98	<i>Homalictus</i> spp.	8.16
	<i>Leptospermum brevipes</i>	7.17	<i>Braunsapis</i> spp.	5.81
	<i>Eucalyptus dealbata</i>	5.84	<i>Simosyrphus grandicornis</i>	5.79
	<i>Acacia decora</i>	5.79	<i>Trichocolletes</i> spp.	4.69
	<i>Micromyrtus sessilis</i>	5.16	<i>Lipotriches (Austronomia) flavoviridis</i>	4.65
	<i>Leucopogon muticus</i>	4.36	<i>Megachile ferox</i>	3.10
<i>Crowea exalata</i>	4.18	<i>Lichenostomus melanops</i>	2.14	

**Table 6:** The most important pollinators in order of pollinator services index (PSI) for each Howell Shrublands pollination network. Here, PSI serves to estimate the probability that specific pollinators will be carrying conspecific pollen, and therefore the probability of successful pollen transfer, based on the observed proportion of visits within and between floral species.

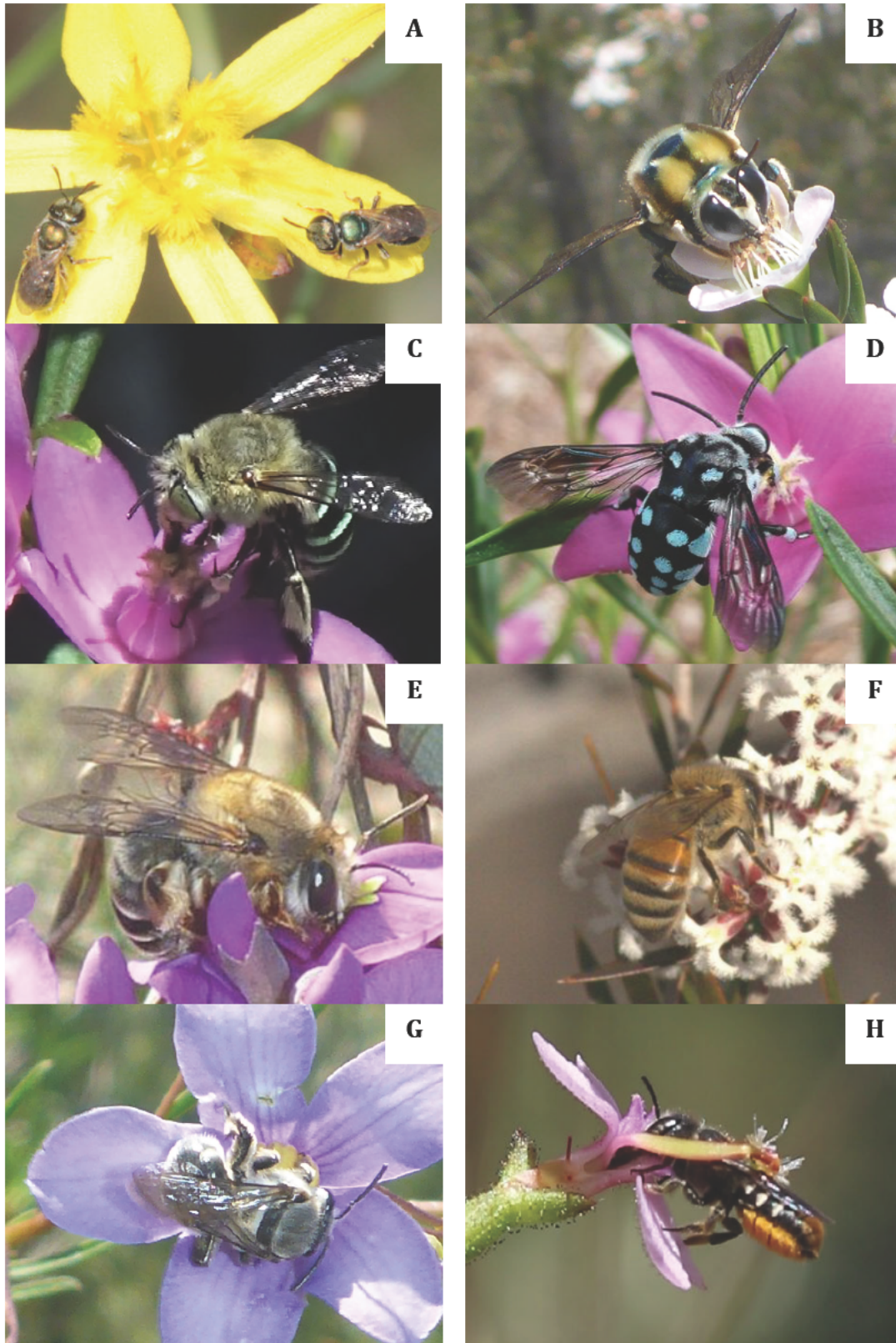
Network:	Pollinator:	PSI:
<b>Late Winter</b>	<i>Lichenostomus melanops.</i>	0.766
	<i>Trichocolletes</i> spp.	0.674
	<i>Melangyna</i> spp.	0.665
	<i>Apis mellifera</i>	0.501



	<i>Lasioglossum (Chilalictus) spp.</i>	0.484
<b>Early Spring</b>	<i>Lichenostomus melanops</i>	1.000
	<i>Sapromyza spp.</i>	0.764
	<i>Melangyna spp.</i>	0.689
	<i>Aeolocosma spp.</i>	0.664
	<i>Lasioglossum (Chilalictus) spp.</i>	0.603
<b>Mid Spring</b>	<i>Melangyna spp.</i>	0.729
	<i>Braunsapis spp.</i>	0.689
	<i>Eleale spp.</i>	0.598
	<i>Apis mellifera</i>	0.578
	<i>Lipotriches (Austronomia) flavoviridis</i>	0.542
<b>Late Spring</b>	<i>Homalictus spp.</i>	0.623
	<i>Hylaeus (Gnathoprosopis) euxanthus</i>	0.619
	<i>Megachile (Hackeriapis) tosticauda</i>	0.562
	<i>Belenois java</i>	0.553
	<i>Lasioglossum (Chilalictus) spp.</i>	0.503
<b>Early Summer</b>	<i>Comptosia spp.</i>	0.857
	<i>Leioproctus (Cladocerapis) spp.</i>	0.844
	<i>Lasioglossum (Chilalictus) spp.</i>	0.636
	<i>Megachile ferox</i>	0.636
	<i>Lipotriches (Austronomia) muscosa</i>	0.634
<b>Mid Summer</b>	<i>Melangyna spp.</i>	0.600
	<i>Lipotriches (Austronomia) flavoviridis</i>	0.532
	<i>Amegilla spp.</i>	0.521
	<i>Homalictus spp.</i>	0.470
	<i>Megachile (Hackeriapis) tosticauda</i>	0.403
<b>Late Summer</b>	<i>Amegilla spp.</i>	1.000
	<i>Megachile ferox</i>	0.698
	<i>Lasioglossum (Chilalictus) spp.</i>	0.505
	<i>Braunsapis spp.</i>	0.502
	<i>Gasteruption spp.</i>	0.346
<b>ALL:</b>	<i>Leioproctus (Cladocerapis) spp.</i>	0.667
	<i>Melangyna spp.</i>	0.626
	<i>Heteromastix spp.</i>	0.582
	<i>Eleale spp.</i>	0.577
	<i>Apis mellifera</i>	0.507
	<i>Brychosoma spp.</i>	0.498
	<i>Lasioglossum (Chilalictus) spp.</i>	0.466
	<i>Trichocolletes spp.</i>	0.465
	<i>Hylaeus (Gnathoprosopis) euxanthus</i>	0.431
<i>Amegilla spp.</i>	0.415	

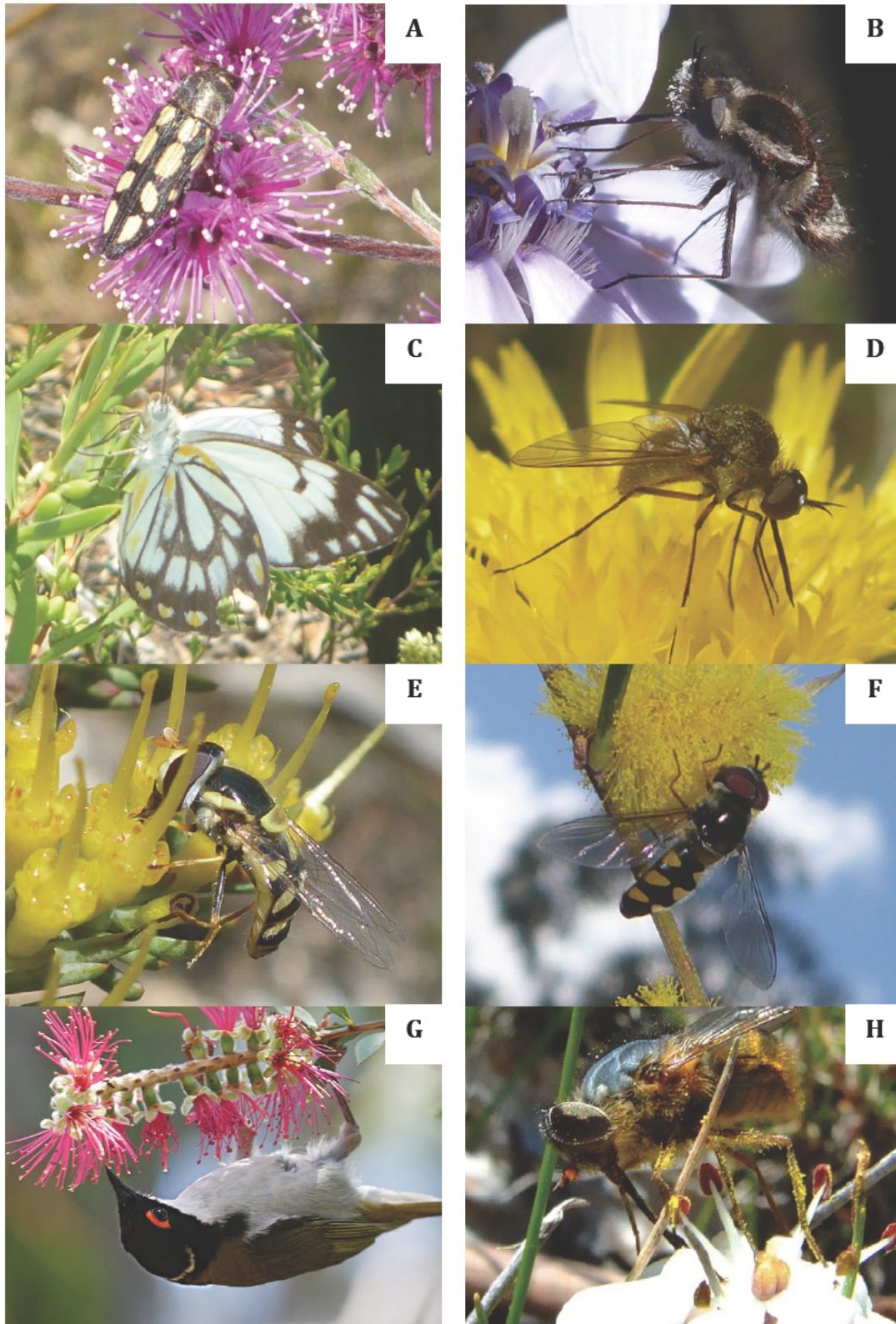


**Figure 1.** Howell Shrublands flowering phenology patterns. Grey scale bars represent the average proportion of mature individuals in flower over the 2015 to 2017 flowering seasons. Colour changes represent incremental increases of 25% from white (0%) to black (75-100%). The species list provided on the left-hand side is reproduced for clarity in **Appendix 2.1**.

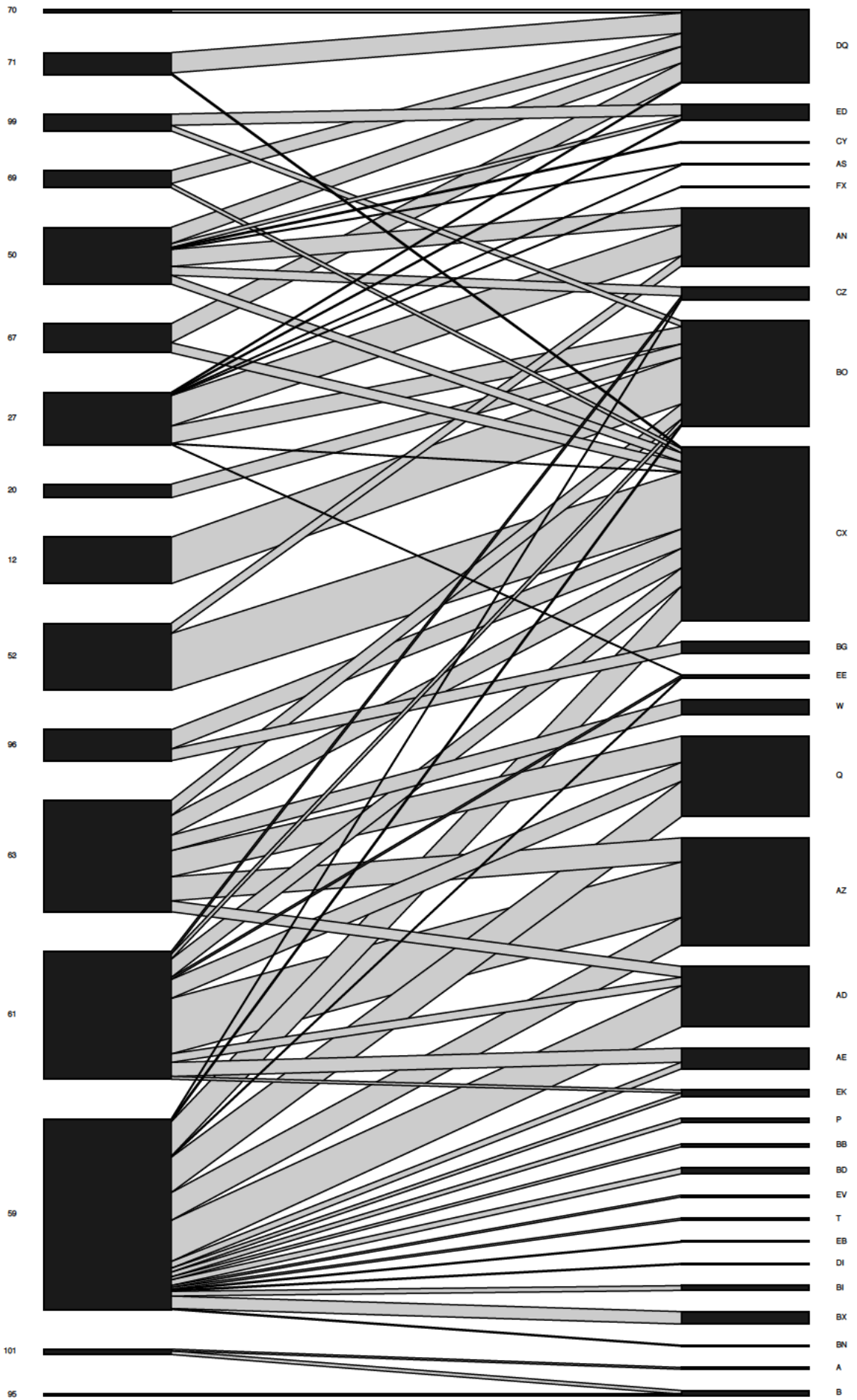


**Figure 2.** Images of selected bee pollinators: **A** = Two *Homalictus* sp. (Hymenoptera: Halictidae) on *Tricoryne elatior*; **B** = *Xylocopa aeratus* (Hymenoptera: Apidae) on *Leptospermum novae-angliae*; **C** = *Amegilla* sp. (Hymenoptera: Apidae) on *Crowea exalata*; **D** = *Thyreus caeruleopunctatus* (Hymenoptera: Apidae) on *C. exalata*; **E** = *Trichocolletes* sp. (Hymenoptera: Colletidae) on *Hardenbergia violacea*; **F** = *Apis mellifera* (Hymenoptera: Apidae) on *Leucopogon melaleucoides*; **G** = *Lipotriches muscosa* (Hymenoptera: Halictidae) on *Cheiranthra telfordii*; and **H** = *Megachile ferox* (Hymenoptera: Megachilidae) on *Stylidium graminifolium*. All images by J. D. Whitehead, or C. L. Gross.

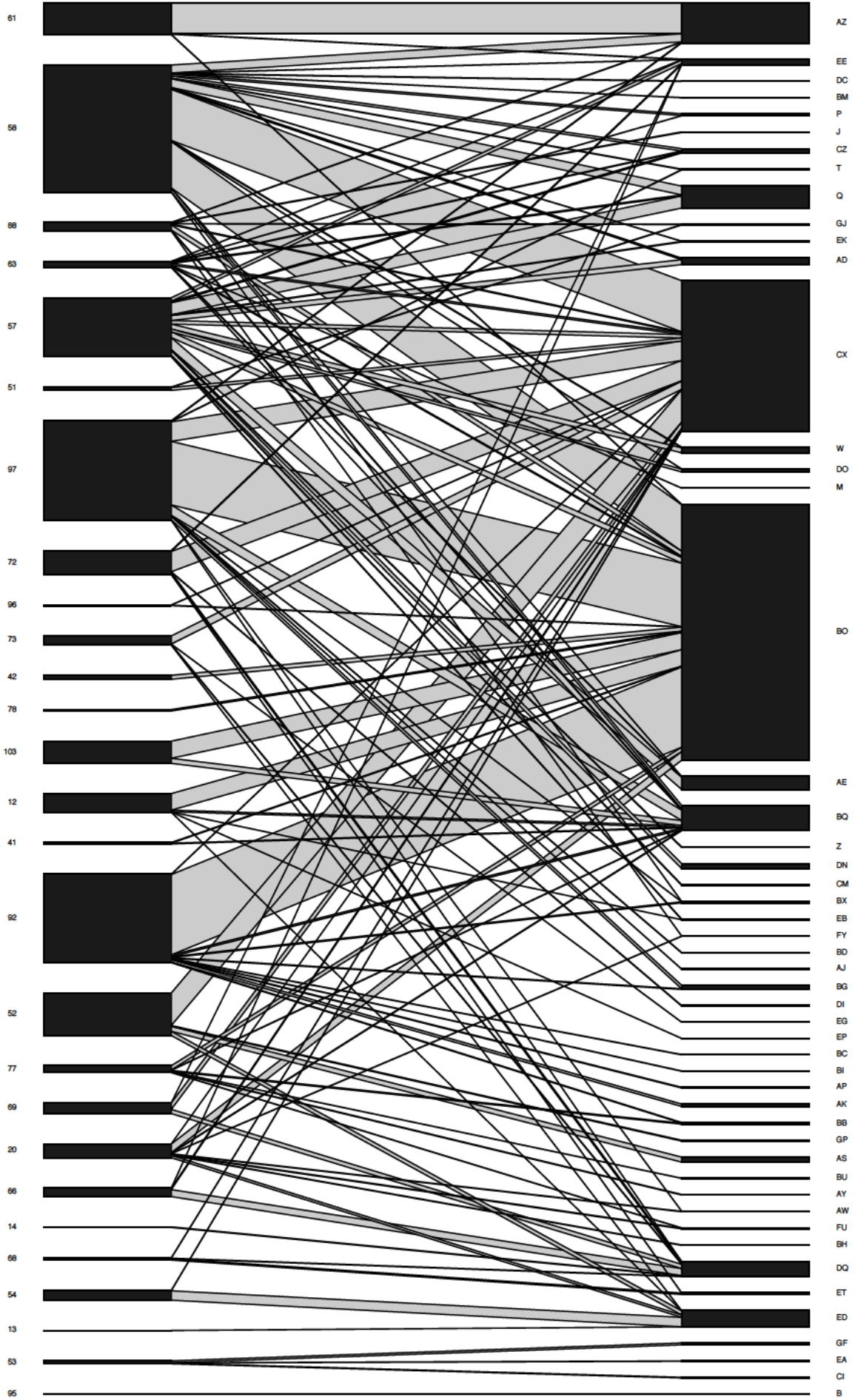


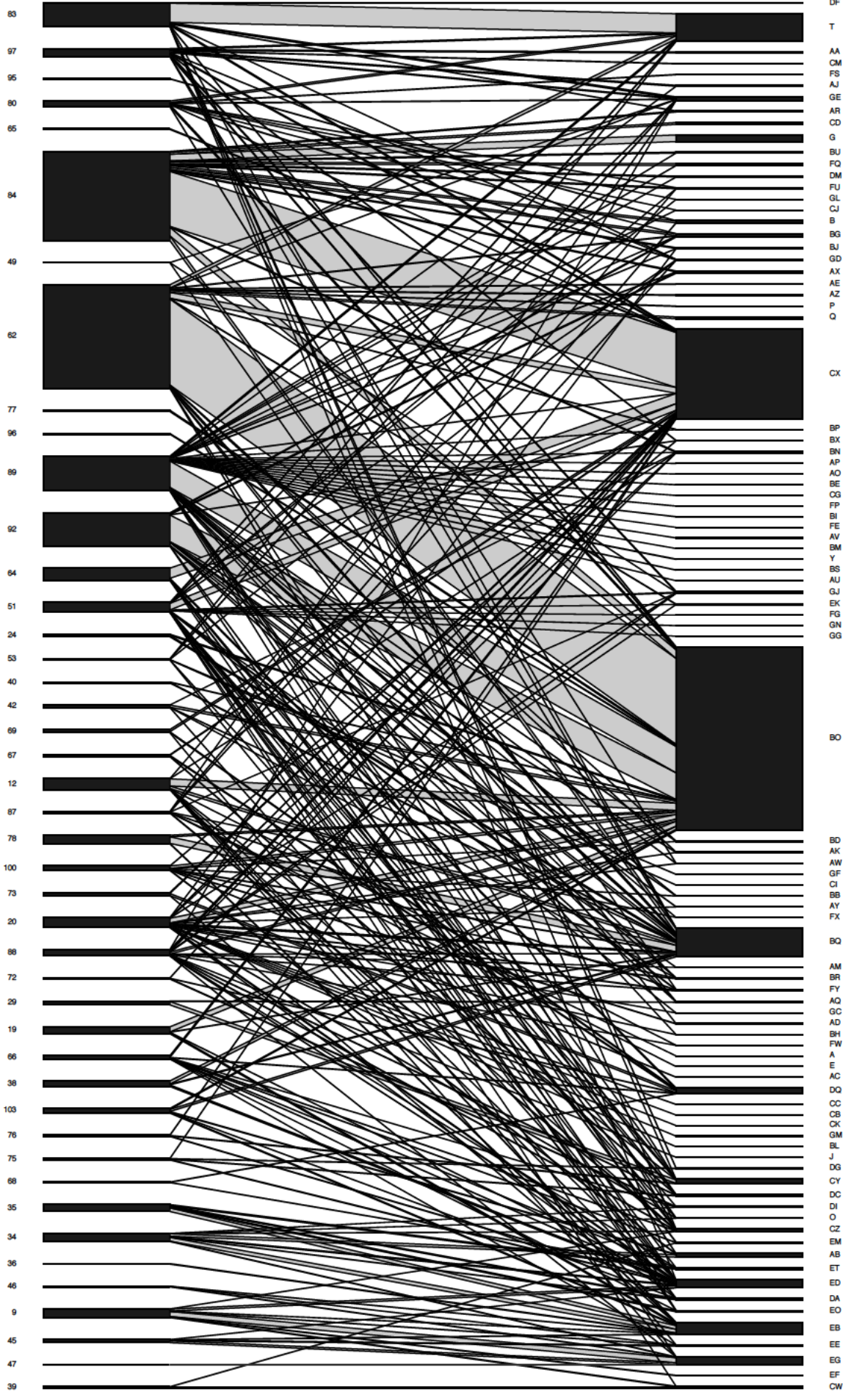


**Figure 3.** Images of selected pollinator taxa: **A** = *Castiarina parallela* (Coleoptera: Buprestidae) on *Kunzea parvifolia*; **B** = *Brychosoma* sp. (Diptera: Bombyliidae) on *Olearia ramosissima*; **C** = *Belenois java* (Lepidoptera: Pieridae) on *Leucopogon muticus*; **D** = *Geron* sp. (Diptera: Bombyliidae) on *Podolepis neglecta*; **E** = *Simosyrphus grandicornis* (Diptera: Syrphidae) on *Homoranthus prolixus*; **F** = *Melangyna* sp. (Diptera: Syrphidae) on *Acacia granitica*; **G** = *Melithreptus lunatus* (Passeriformes: Melpigidae) on *Callistemon pungens* (Image by K. D. Mackay); and **H** = *Myioscaptia calliphora* (Diptera: Tabanidae) on *Wurmbea biglandulosa* (Image by W. Waters). All images by J. D. Whitehead, or C. L. Gross, unless otherwise attributed.

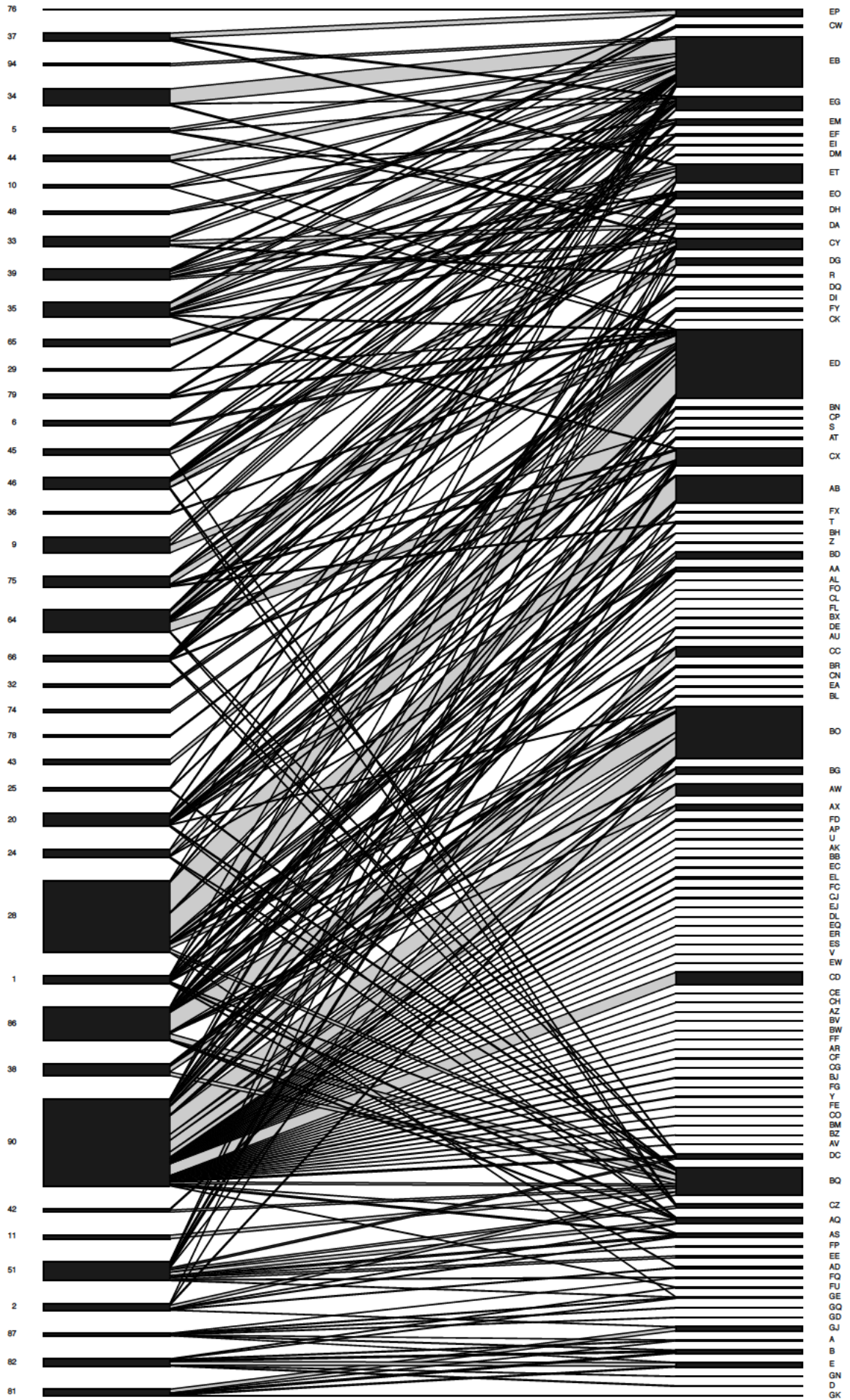




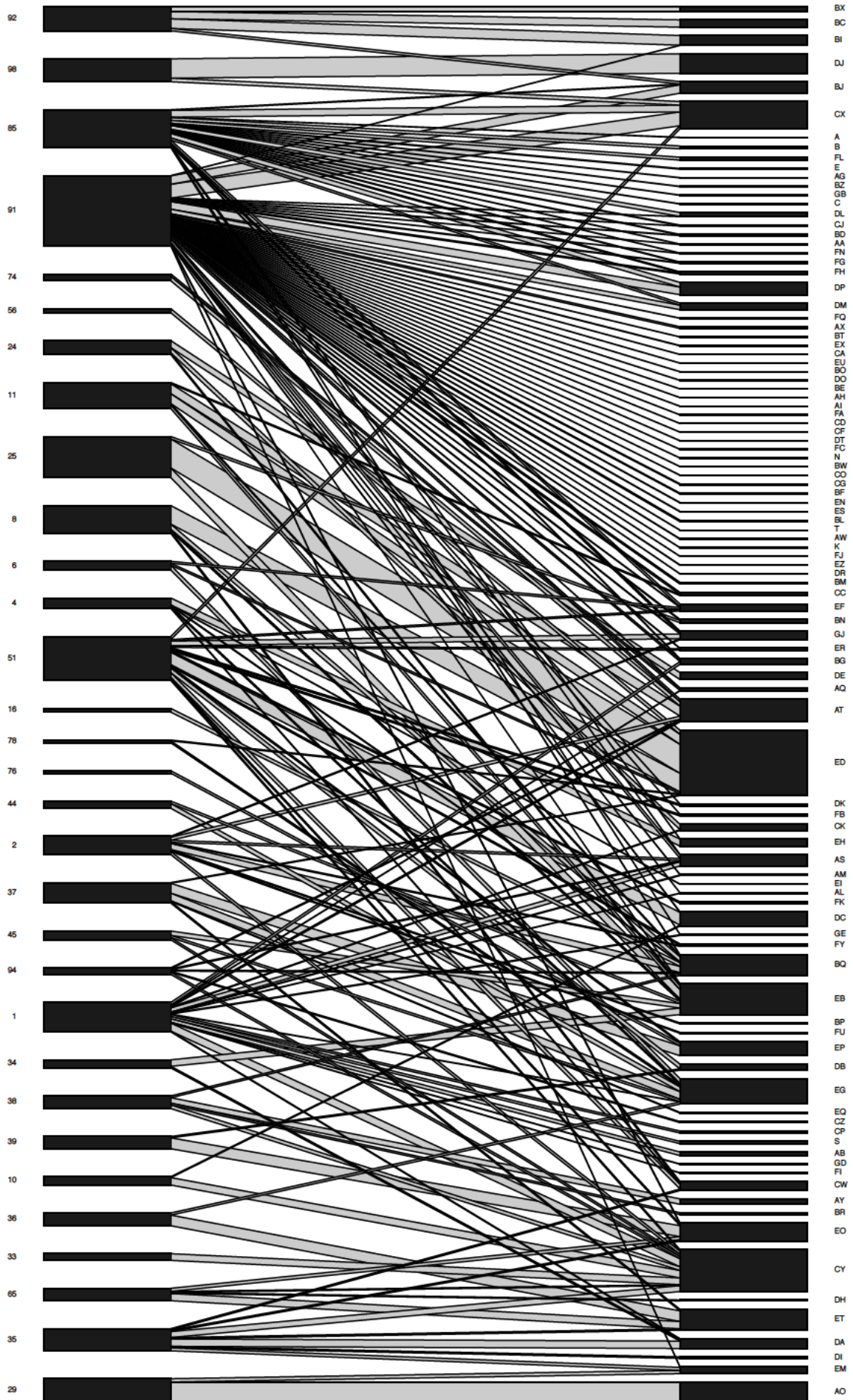




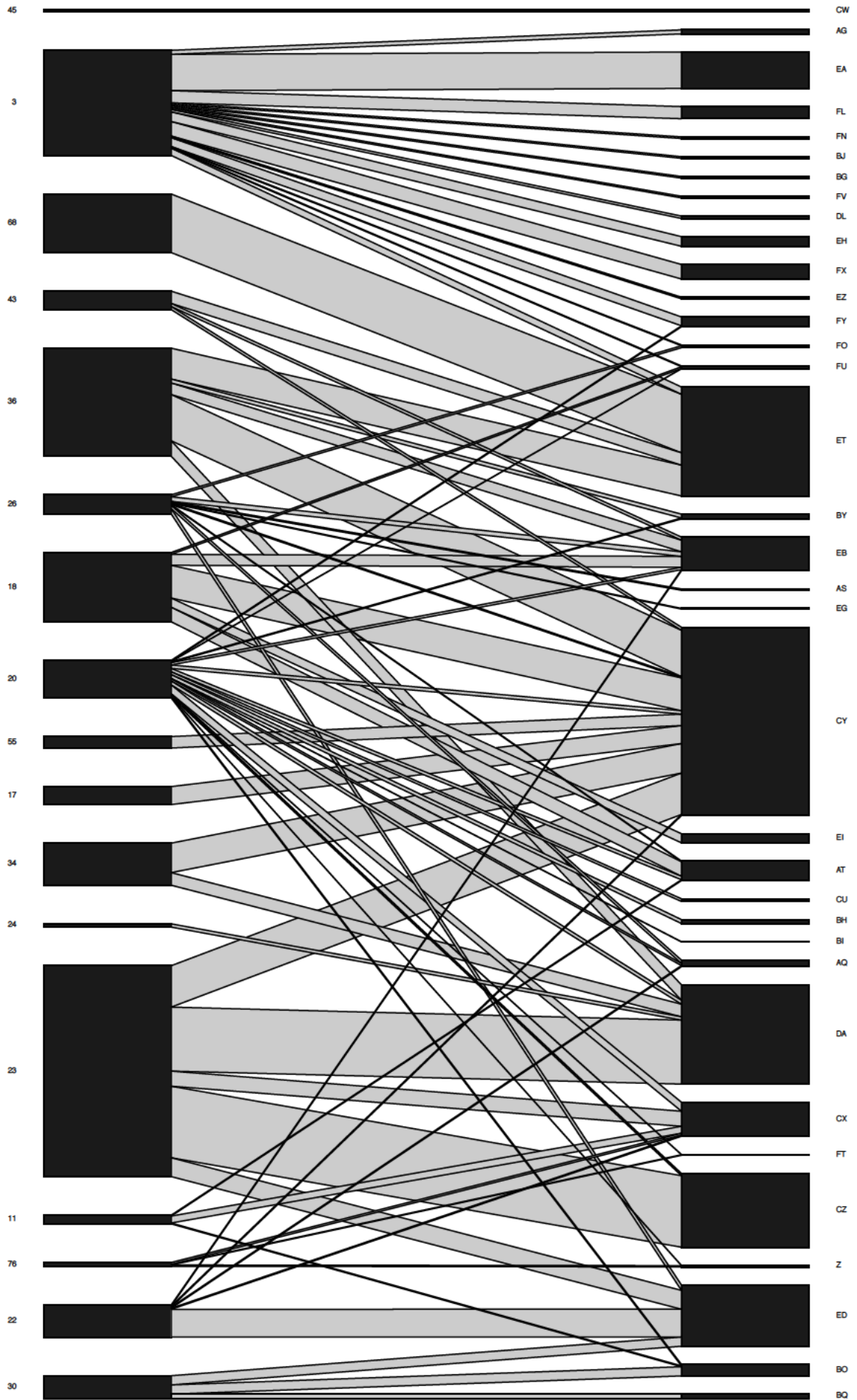






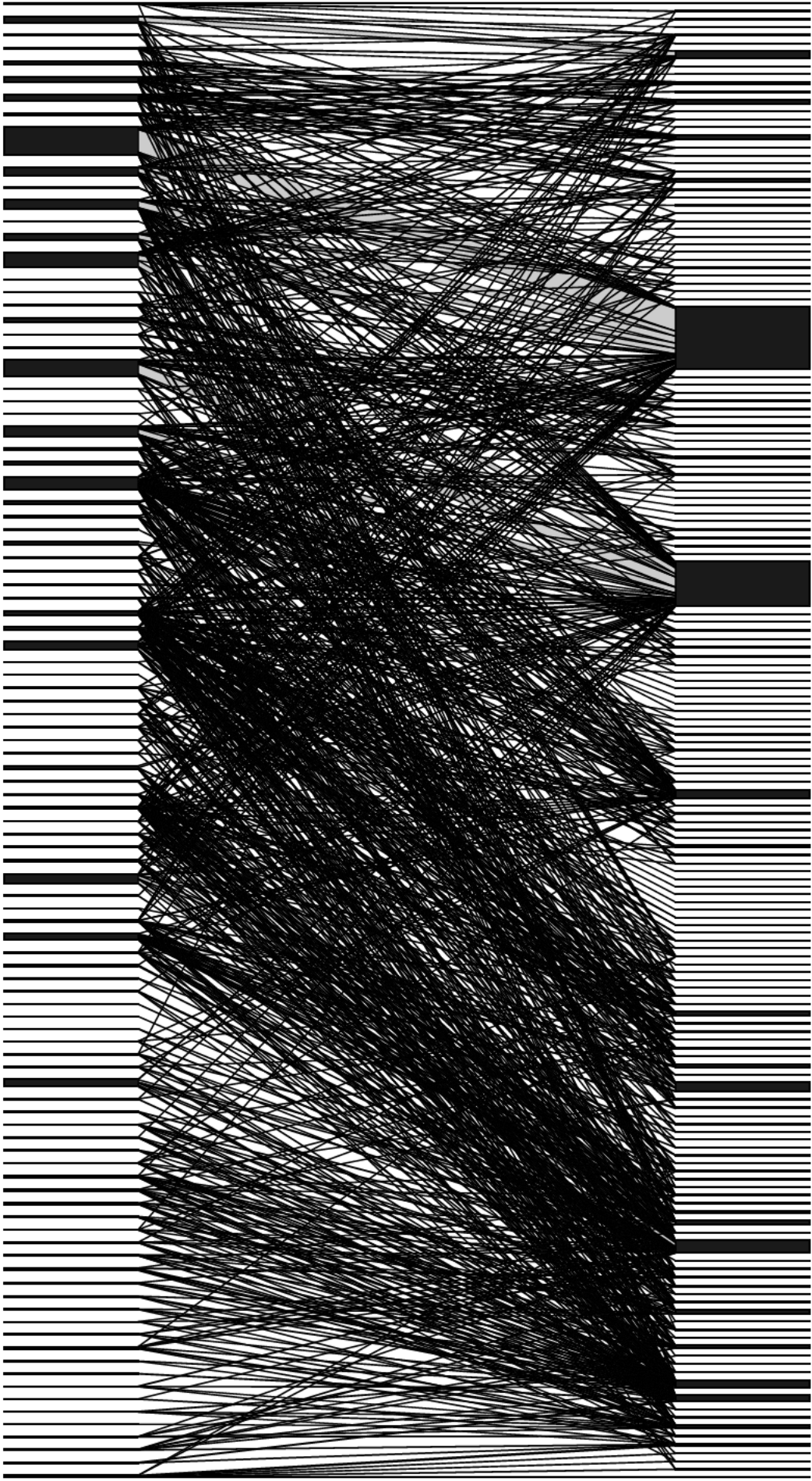








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**Higher Degree Research Thesis by Publication  
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**STATEMENT OF AUTHORS' CONTRIBUTION**

(To appear at the end of each thesis chapter submitted as an article/paper)

We, the Research Master/PhD candidate and the candidate's Principal Supervisor, certify that all co-authors have consented to their work being included in the thesis and they have accepted the candidate's contribution as indicated in the *Statement of Originality*.

	<b>Author's Name (please print clearly)</b>	<b>% contribution</b>
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Other Authors	Caroline Gross	15%

Name of Candidate: **Joshua Whitehead**

Name/title of Principal Supervisor: **Prof. Caroline Gross**

  
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Candidate

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Date

  
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Principal Supervisor

28 Sept 2018  
Date

### **Chapter 3. Exotic honeybee decline may threaten the resilience of fragmented floral communities in Australia.**

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#### **Abstract:**

The role of invasive species in biological conservation is often portrayed in black and white, though they more often resemble shades of grey. In Australia, naturalized populations of the Western honeybee (*Apis mellifera*) are one such species, threatened by another. The ectoparasitic mite, *Varroa destructor*, though yet to reach Australia, has been responsible for significant decline of honeybee populations in other countries, with ecological consequences that may both help and hinder the conservation of biodiversity. To better understand the potential consequences of *Varroa* mediated honeybee decline, we investigated the influence of *A. mellifera* on an endangered plant-pollinator community in eastern Australia. Using a combination of timed stationary, and video observations we recorded 1,633.4 hours of floral visitation data over six flowering seasons. Models based on an Australian pollination network were used to determine the significance of *A. mellifera* as a pollinator, while its direct impact on native pollinator foraging was classified in terms of positive (+), negative (-), or neutral (0) impact on native foraging efficiency during field observations. Network visitation rates were manipulated in order to investigate the consequences of honeybee extinction or decline, and assessed in terms of network specialisation ( $H_2'$ ), nestedness ( $wNODF$ ), and secondary extinction function using the Bipartite package for R. Honeybees were found to utilize 31.87% of flowering species within the community, serving as a potential pollinator for the majority (79.31%) of those species. Physical encounters between *A. mellifera* and native pollinators coincided with 4.10% of honeybee visits, and were significantly more likely to have negative consequences for the native species ( $t = -5.81442422$ ,  $df = 92$ ,  $p < 0.001$ ). Reducing or removing honeybees from the network resulted in significantly increased specialization and decreased nestedness of the network, increasing the risk of secondary floral extinctions. In light of these results, we discuss the various impacts of *A. mellifera* on Australian fauna and flora, and identify

possible management concerns and opportunities regarding the impacts of *V. destructor*.

**Keywords:** *Apis mellifera*, conservation, invasive species, pollination, *Varroa destructor*.

### **Introduction:**

In spite of our best efforts, the scientific perception of exotic species is often subjective (Schlaepfer et al. 2011), giving particular emphasis to negative impacts over contradictory evidence (Rodriguez 2006; Pysek et al. 2008). However, it is important for effective species management that these impacts are not considered in isolation. In the southwest United States, invasive salt cedar (*Tamarix* spp.) threatens to replace the native riparian vegetation. However, systematic removal of *Tamarix* would be ill-advised, potentially resulting in increased stream erosion, and native bird decline, with up to 75% of the nests of endangered South-western Willow Flycatcher (*Empidonax traillii* ssp. *extimus*), for example, constructed in *Tamarix* (Zavaleta et al. 2001; Shafroth et al. 2008; Sogge et al. 2008). Similarly, a non-native population of Banteng (*Bos javanicus*) in northern Australia threatens the native grassland fire ecology (Bowman et al. 1990), but may be of considerable conservation value given the species rarity within its natural range (Bradshaw et al. 2006). Exotic species management therefore needs to be pragmatic. Both positive and negative impacts need to be considered and evaluated, within the broader environmental context (Rodriguez 2006; Maris & Béchet 2010; Schlaepfer et al. 2011).

In Australia, the Western honeybee (*Apis mellifera*) has generated a range of conflicting perspectives with regard to an invasive species management. Introduced circa 1822, naturalized populations of *A. mellifera* now occur in almost all non-arid environments (Paton 1993). Though the variability and density of these populations is poorly understood, estimates suggest there may be  $50 \pm 150$  colonies per square kilometre of native vegetation (Oldroyd et al. 1997), comprising approximately 30,000 individuals each (Winston 1991). Effectively managing such high density populations would be logistically unfeasible, requiring an estimated annual contribution of AUD \$5,524/km<sup>2</sup>, before Australian apiculture is considered (Oldroyd 1998). Thus, *A. mellifera*'s presence in the Australian environment is largely

condoned, owing to the assumption that it provides pollination services that compliment native pollinators (Paton 1993). Indeed, the presence of naturalised honeybees may even be encouraged, for they provide free pollination services worth an estimated \$21.3-50.5 million AUD to the Australian economy each year (Cook et al. 2007).

The majority of Australia's flora and fauna evolved independently of social pollinators, particularly *Apis*, and may be particularly vulnerable in their presence (Michener 1979; Paton 1993). Indeed, several studies have shown exotic honeybees may compete with native fauna for floral resources (Paton 1993; Sugden et al. 1996; Gross & Mackay 1998; Paton 2000; Gross 2001; Goulson et al. 2002; Paine 2004) and nest sites (Oldroyd et al. 1994; Wood & Wallis 1998; Pyke 1999), exploit native floral resources (Taylor & Whelan 1988; Vaughton 1996; Gross & Mackay 1998), or facilitate invasive flora (Goulson & Derwent 2004; Simpson et al. 2005; Gross et al. 2010; Gross et al. 2017). As a result, honeybees have been recognized as a significant threat to Australia's native biota within the New South Wales Biodiversity Conservation Act (NSW Government 2016). However, these observations are not unique. In Asia and the Americas, where social bee species are naturally common, naturalized *A. mellifera* has similar effects on the local flora (Barthell et al. 2001; Hansen et al. 2002; do Carmo et al. 2004; Dupont et al. 2004) and fauna (Sakagami 1959; Laroca & Winston 1978; Roubik 1978, 1980; Schaffer et al. 1983; Kato et al. 1999). Nevertheless, exotic honeybees may be of significant conservation value. In Brazil, *A. mellifera* is able to maintain gene flow between forest fragments that would otherwise be isolated even when native pollinators are present (Dick 2001; Dick et al. 2003).

Habitat fragmentation is a major cause of population decline, biodiversity loss, and community modification in Australia (Saunders et al. 1991; NSW Government 2016); where in some areas over 93% of native vegetation has been removed (Hobbs & Yates 2003). As a result, many native plants now subsist within remnant populations at risk of genetic drift and inbreeding due to their relative isolation (Young et al. 1996). In these modified landscapes, *A. mellifera* may be of particular significance. As generalist pollinators, Western honeybees visit a broad range of Australian flora (Wills et al. 1990; Paton 1993), and may functionally replace native pollinators when



displaced by fragmentation (Dick et al. 2003). Unlike most solitary bees, honeybees are capable of foraging many kilometres from their nest (Beekman & Ratnieks 2000; Zurbuchen et al. 2010). This may enable them to traverse the necessary distances to maintain viable gene flow between remnant floral populations (Dick 2001; Dick et al. 2003). Thus, in spite of their negative impacts on native biota, honeybees may still have an important role to play in the conservation of threatened plant communities. Recent declines in Europe and North America suggest *A. mellifera* may be vulnerable to novel parasites, pathogens and pesticides (Stokstad 2007; Goulson et al. 2015), which may threaten naturalised populations and their future contribution to this role.

First described in 2000 (Anderson & Trueman 2000), *Varroa destructor* is an ectoparasite that evolved following a successful host switch from *Apis cerana* to *A. mellifera* circa 1958 (Anderson & Trueman 2000; Dobrynin et al. 2013). Acting as a common vector of honeybee viruses (Martin et al. 2012), *V. destructor* causes significant mortality within host populations (Martin et al. 2012; Goulson et al. 2015; Wegener et al. 2016) and has been implicated in significant wild colony losses (Kraus & Page 1995). Though *V. destructor* has yet to establish in Australia, given the global scale of infestation, it's likely only a matter of time before this happens (Cook et al. 2007; Rinderer et al. 2013; Iwasaki et al. 2015). While this may provide new opportunities for invasive species management (Simpson et al. 2005; Gross et al. 2010; Paynter et al. 2010), or benefit specific species (Paton 1993; Oldroyd et al. 1994; Vaughton 1996; Gross & Mackay 1998; Wood & Wallis 1998; Paine & Roberts 2005), the broader ecological impacts of honeybee decline on native plant fecundity are unknown.

Here, the functional significance and ecological impact of *A. mellifera* on an endangered ecological community from eastern Australia is assessed using plant-pollinator and pollinator-pollinator interactions to predict the potential ecological impacts of *V. destructor*.

## **Materials and Methods:**

### *Study Area:*

Observations were conducted within 15 hectares of dry subtropical granite vegetation to the east of Copeton Dam (29° 56' 08" S, 151° 02' 11" E) in northern New South

Wales (NSW), Australia. Vegetation within the site is dominated by low shrubs; particularly *Homoranthus prolixus* (Myrtaceae), and generally represents a layered, low open-woodland (Specht 1970) despite considerable structural and taxonomic heterogeneity. Vegetation of this type is often highly fragmented, and is currently recognised as the Howell Shrublands Endangered Ecological Community (EEC) currently listed under the New South Wales Biodiversity Conservation Act (NSW Government 2016). Maintaining pollination services and gene flow among fragmented occurrences of this community are likely to be important for maintaining its floristic diversity, structure, and function.

#### *Sampling Design:*

Data was compiled over six non-successive flowering seasons from August through November in 2007, September through November in 2011, August through October in 2012, October in 2014, and August through February in 2015/16 and 2016/17. Observations were recorded using a combination of camera (Sony Handycam models HDR-155 XR160, HDR-PJ540, and FDR-AXP35 4K) surveillance and timed stationary observations. Field observations involved a single observer recording all the floral interactions to occur during a 15-60 minute period within the floral display of a flowering individual. Meanwhile, up to 15 cameras at a time were used to record videos of up to 4 hours per individual, with the field of view adjusted so to enable reliable visitor identifications, and provide a representative sample of the observed floral display. Since floral visitation studies are prone to spatio-temporal bias due to phenological variability (Olesen et al. 2008) consistent sampling is needed to prevent biased sampling (Colwell et al. 2004). Sampling was therefore randomly stratified to include as many individuals, over as many sampling periods and locations per species, and observations were conducted at roughly weekly intervals between 06:00 and 18:00 hours Australian Eastern Standard Time (AEST). Conspecific sampling was conducted so as to ensure no two individuals were observed simultaneously within a 50-metre radius of each other.

Plant-pollinator interactions were recorded whenever a floral visitor made contact with both male and female reproductive structures of the flower, and had demonstrated an ability to transport pollen within and between flowers on separate individuals. Such an approach offers a pragmatic means of identifying prospective

pollinators (Inouye 1980; Jacobs et al. 2009), notwithstanding further study to confirm effective pollen transfer (Gross & Mackay 1998; Ballantyne et al. 2015; Gross et al. 2017).

At times multiple floral visitors could be observed utilising the same floral resource simultaneously, or in rapid succession. Whenever this resulted in heterospecific encounters between *A. mellifera* and a native floral visitor, the outcome was scored on a positive to negative scale according to the perceived impact on native foraging efficiency. A positive (+1) interaction was scored whenever *A. mellifera* served to facilitate a native floral visitor by providing access to otherwise inaccessible resources. For example, when a buzz-pollinator releases pollen from a poricidal anther, successive visitors may scavenge any pollen that is left behind (Gross & Mackay 1998; Newstrom & Robertson 2005). Negative (-1) interactions were scored whenever the presence of a resident or incoming honeybee caused a native floral visitor to deter from, leave, or defend a floral resource (Gross *et al.* unpublished). When no direct impact could be observed, interactions were scored as neutral (0).

Any species that couldn't be identified direct from the field or videos were collected for laboratory identification. All identifications were confirmed using relevant field guides (e.g. Braby 2004), online resources (e.g. [www.ala.org.au/](http://www.ala.org.au/), [www.padil.gov.au/](http://www.padil.gov.au/), <http://plantnet.rbgsyd.nsw.gov.au>) or expert knowledge (see acknowledgements), and voucher specimens lodged with the N. C. W. Beadle Herbarium and Natural History Museum at the University of New England, NSW, Australia respectively.

#### *Network Analysis:*

Floral visitation data was compiled into bipartite matrices representing seven, roughly month-long patterns of flowering episodes. This was done to minimise the number of interactions forbidden or isolated by a lack of phenological overlap (Jordano et al. 2003; Olesen et al. 2011). Such interactions can have a notable impact on network metrics such as nestedness and robustness, and imply greater stability than otherwise anticipated. For example, a specialist pollinator relying on two floral species that flower asynchronously over successive months is at high risk of extinction due to an obligate dependence on each species in succession (Gross 2017). However, network analyses treat all species as synchronous, meaning that networks spanning the entire

flowering period will suggest the pollinator is of reduced risk due to an apparent decrease in dependency on either floral species.

Within each matrix, rows and columns were used to represent plant, and pollinator species respectively. To account for sampling bias, data was standardised as the rate of interaction per hour of sampling, before analysis via the Bipartite package (Dormann et al. 2008) in RStudio (RStudio Team 2015). The relative importance of *A. mellifera* as a pollinator within the floral community was estimated in terms of species strength and the pollinator service index (PSI). Species strength refers to a species' cumulative share of interactions for all interaction partners (Bascompte et al. 2006). PSI estimates the likelihood a pollinator will be carrying conspecific pollen. It therefore differs, in that it rates a pollinator on a scale of zero (completely irrelevant), to one (obligate), based on the observed proportionate of interactions within and between partners.

To determine the potential impact of honeybee decline on floral communities, we compared network specialisation (Blüthgen et al. 2006), and nestedness at decreasing proportions of the observed *A. mellifera* interaction frequency. Specialisation was measured using the  $H_2'$  index (Blüthgen et al. 2006), which evaluates the relative concentration of interactions from completely diffuse (0) to completely obligate (1). Nestedness was measured via the weighted *NODF* index (Almeida-Neto & Ulrich 2011), which ranks the extent of interaction overlap between specialist and generalist species on a scale from zero to complete (100) overlap. Both metrics are possible determinants of community stability, though the evidence is inconclusive (Tylianakis et al. 2010; Elle et al. 2012). Additionally, we compared the likelihood of pollinator mediated secondary extinctions (Memmott et al. 2004) with and without *A. mellifera* using 1,000 randomizations.

#### *Statistical Analysis:*

The direct impact of *A. mellifera* on native pollinators was assessed via a series of one sample t-tests where our null hypothesis was a neutral (0) outcome. Chi-square analyses were used to determine whether *A. mellifera* decline or removal had a significant impact on network specialisation, nestedness, or secondary extinction risk relative to what is expected at the observed interaction frequency.

## Results:

*Apis mellifera* foraged continuously from August through February at 58 (31.86%) of the 182 flowering plants identified. Of these, *Dodonaea falcata* (dioecious), and *Myriophyllum lophatum* (monoecious) were morphologically adapted for wind-pollination (anemophilous), while the remaining 56 species were animal-pollinated (zoophilous). *Apis mellifera* served as a potential pollinator for 46 (82.14%) of the zoophilous species visited, but otherwise behaved as a floral larcenist. In 1,633.4 hours of observation, *A. mellifera* was the second most abundant floral visitor in the community, participating in 2,271 total visits, and recorded the highest visitation rate at 41.72 visits per hour on *Eucalyptus dealbata*. Direct interactions between *A. mellifera* and native pollinators were infrequent, occurring once per 17.56 hours of observation, or 24.39 *A. mellifera* visits. Interactions were significantly more likely to have a negative impact on native foraging efficiency ( $t = -5.81442422$ ,  $df = 92$ ,  $p = 0.00000009$ ), though net impacts varied between pollinator orders (Table 1).

Over the entire sampling period, *A. mellifera* is the third most important pollinator in terms of species strength, and fifth most in terms of PSI, though both metrics varied between seasons (Figure 1). Reducing the observed visitation rate of *A. mellifera* increased specialisation (Figure 2), and decreased nestedness (Figure 3) in all networks, but not to a significant extent. Though no plant species were solely reliant on *A. mellifera* for pollination, removing the species increased the likelihood of floral extinctions as a result of random pollinator losses in all networks (Figure 4). However, this increase was only significant ( $\chi^2 = 5.896226415$ ,  $p = 0.000836$ ) for species within the late winter pollination network (Figure 4).

## Discussion:

This study is one of the first to synthesize information concerning the ecological ramifications of a possible *Varroa* infestation in Australia, and one of the first to use network analyses to predict the potential impacts of species decline. In the 3 years following detection in California, *Varroa* was implicated in losses of up to 75% of wild honeybee colonies (Kraus & Page 1995), with losses of a similar magnitude predicted for Australia (Rinderer et al. 2013). If this were to occur, our results suggest the Howell Shrublands pollination network will become more specialized and less nested, reducing its capacity to withstand further pollinator declines (Tylianakis et al.

2010; Elle et al. 2012). These observations are likely to be repeated elsewhere in Australia, with *A. mellifera* recorded visiting similar quantities of floral species in Western (Wills et al. 1990), and South Australia (Paton 1993). However, the impacts of *Varroa* are likely to be diverse, affecting all aspects of honeybee interaction. Thus in order to understand the potential impacts of *Varroa*, we must first investigate the broader impacts of its host.

#### *Impact of Honeybees on Native Fauna:*

The physical presence of *A. mellifera* at a floral resource was found to significantly impede native foragers, with roughly a third of all encounters resulting in competitive interference. This likely reflects the relative size asymmetry between *A. mellifera* and native pollinators, with theory predicting the smaller species will concede resources rather than risk injury through confrontation with the larger (Smith & Parker 1976). Indeed, previous studies support this prediction, with larger, more aggressive pollinators often preventing access to, or acquiring flowers from smaller, less aggressive competitors (Nagamitsu & Inoue 1997; Thomson 2004; Dworschak & Blüthgen 2010; Gross et al. unpublished). Since the majority of Australian bees are smaller than *A. mellifera* (Paton 1993), under most circumstances, they would be expected to avoid physical confrontation. Conversely, the respective size and armor protection of avian and coleopteran pollinators, may explain their relative resilience to interference detected in this study.

Nevertheless, *A. mellifera* may also compete with native pollinators indirectly by consuming limited resources. Under such circumstances, and assuming no net benefit is derived through interference, competition may be expected to favour smaller native pollinators due to the relative scaling of resource limitations (Persson 1985; Amarasekare 2002). However, most native pollinators are solitary, with foraging activities concentrated during the middle of the day when ambient temperatures are highest (Paton 1993). *Apis mellifera*'s social foraging, ability to stockpile resources draw upon them in times of scarcity, and capacity for foraging at lower temperatures, may therefore provide a significant advantage, particularly when resources are replenished overnight (Bond & Brown 1979; Paton 1993; Horskins & Turner 1999).

Yet competition for floral resources may be difficult to quantify, for although *A. mellifera* may be observed to consume over 80% of nectar produced (Paton 2000), rapid replenishment (Lou et al. 2014) may reduce the impact on native foragers. Foraging efficiency can have a significant effect on the reproduction of many native pollinators, and is therefore likely to be reflected in their reproductive success. For example, increasing the abundance of *A. mellifera* colonies reduced the number of *Hylaeus alcyoneus* present by 23% (Paini & Roberts 2005), presumably because the added competition reduced the number of larvae that could be provisioned. Similarly, higher abundances of *A. mellifera* almost doubled the number of *Callistemon rugulosus* flowers defended by New Holland honeyeaters (*Phylidonyris novaehollandiae*) in South Australia (Paton 1993). This likely reflects the scale of resource exploitation by *A. mellifera*, with several studies linking honeyeater densities to nectar availability (Ford 1979, 1981; Pyke 1983; Paton & Turner 1985; Pyke & Recher 1986).

Honeybees may also compete with native fauna for nesting habitat (Saunders et al. 1982; Oldroyd et al. 1994; Wood & Wallis 1998; Pyke 1999; Gibbons et al. 2002), preferring to inhabit tree hollows with a volume of approximately 40 litres, located more than a metre above the ground (Seeley & Morse 1978). Such hollows represent an important source of shelter for many Australian birds, mammals, and reptiles (Pyke 1999; Gibbons et al. 2002), which due to their slow formation (Gibbons et al. 2000) are a critically limited resource. Yet despite this, the presence of *A. mellifera* colonies may also benefit native species by providing a reliable source of trophic resources even in times of hardship (Bellis & Profke 2003; Silvester et al. 2017). Indeed, commercial apiaries have been observed to attract a range of native and invasive insectivores, as well as higher order predators in search of insectivore prey (Silvester et al. 2017).

Least understood are *A. mellifera*'s epizootic impacts, which are likely to have gone unnoticed given the paucity of relevant research. *Apis mellifera* is host to a broad range of parasites and pathogens that may pose a potential risk to native fauna. These include fungal (Vandenberg & Stephen 1983; Gilliam et al. 1992; Gilliam et al. 1994; Maxfield-Taylor et al. 2015; Reynaldi et al. 2015), viral (Genersch et al. 2006; Celle et al. 2008), and parasitic (Spiewok & Neumann 2006; Halcroft et al. 2010;

Villalobos 2016) infections that have demonstrated transmissibility with naïve species, genera, and families. For instance, the chalkbrood fungus (*Ascosphaera apis*) has been detected in naïve species of *Apis* (Gilliam et al. 1992), *Bombus* (Maxfield-Taylor et al. 2015), *Megachile* (Vandenberg & Stephen 1983), and *Xylocopa* (Gilliam et al. 1994; Reynaldi et al. 2015) following the introduction of *A. mellifera*. Yet such instances are likely just the tip of the iceberg. In unrelated taxa, epizootic transmissions have had disastrous consequences for native species. The crayfish plague fungus (*Aphanomyces astaci*), for instance, has all but eliminated many European crayfish populations following its transmission from species introduced from North America (Unestam & Weiss 1970; Kozubikova et al. 2009).

#### *Impacts of Honeybees on Native Flora:*

Any change in the number or behaviour of native pollinators due to competition with *A. mellifera* is likely to decrease floral fecundity unless *A. mellifera* can provide pollination services comparable to those lost. We found *A. mellifera* to be an important pollinator in terms of both frequency (species strength) and fidelity (PSI), though it remains to be determined whether pollen transfer is proficient (Ballantyne et al. 2015; Gross et al. 2017). Australia's flora evolved in isolation from honeybees (Michener 1979), meaning few species are morphologically suited for honeybee pollination. Consequently, honeybees have often been found to reduce native seed set due to inefficient pollen transfer (Paton 1993; Bernhardt & Weston 1996; Vaughton 1996; Richardson et al. 2000), as may occur in the naturally bird pollinated shrub *Callistemon rugulosus* (Paton 1993, 1997).

Honeybees may also reduce native seed set by directly or indirectly reducing the amount of pollen deposited by native pollinators. In the pioneer shrub, *Melastoma affine*, honeybees reduced floral fecundity by removing pollen directly from the stigma following its deposition by a bona fide pollinator (Gross and Mackay 1998). Conversely, by removing the majority of available pollen, honeybees significantly reduced the amount of *Correa reflexa* pollen carried by, and subsequently deposited by native pollinators (Paton 1993, 1997). Despite such cases, honeybees may have neutral or even positive impacts when native pollinators are scarce (Paton 1997, 2000), having been observed to facilitating between 6.7% and 17.1% seed set in *C. reflexa* although significantly less than the native pollinators (Paton 1993, 1997).



With recent pollinator declines (Potts et al. 2010) and habitat fragmentation potentially acting as drivers of future biodiversity loss (Saunders et al. 1991; NSW Government 2016), any such pollination is likely to be beneficial, or at least better than none.

Indeed, we found that losing *A. mellifera* could significantly increase the risk of floral extinctions due to pollinator loss, particularly among species flowering early in the season. Since many of these species exhibit a long-term trend toward earlier flowering in response to climate change (Fitter & Fitter 2002; Hegland et al. 2009; McEwan et al. 2010), honeybees may provide an important buffer against future disruption of plant-pollinator mutualisms. Under current conditions, evidence suggests that the direction and magnitude of honeybee impacts will depend heavily upon the degree of anthropogenic disturbance and habitat fragmentation (Butz Huryn 1997; Kato et al. 1999; Lomov et al. 2010). Our results support this by suggesting that the presence of *A. mellifera* may buffer plant communities against fragmentation-driven pollinator decline, having previously been shown to maintain pollination services within and between remnant plant populations (Dick 2001; Dick et al. 2003).

#### *Potential Impacts of Varroa:*

Australian honeybees exhibit similar susceptibility to *Varroa* as American varieties (Rinderer et al. 2013), meaning comparable losses of up to 75% over three years may be expected should the parasite reach Australia (Kraus & Page 1995; Rinderer et al. 2013). Since honeybees compete with native pollinators for limited resources, any subsequent decline is likely to provide short-term competitive release and subsequent benefit to reproductive success. However, the prevalence of honeybee viral infections may also be linked with *Varroa* infestations (Martin et al. 2012; Mondet et al. 2014; Iwasaki et al. 2015), increasing the likelihood of interspecific transmissions (Genersch et al. 2006; Furst et al. 2014; Ravoet et al. 2014) that may have a significant impact on native species.

The influence of *Varroa* on floral communities is likely to vary depending on the local significance of *A. mellifera* as a pollinator. In stable communities with a diverse assembly of native pollinators, the presence of *Varroa* is likely to improve floral fecundity by suppressing *A. mellifera* and thus increasing opportunities for more

efficient pollinators. However, in fragmented or degraded communities, where *A. mellifera* may be one of few pollinators able to provide adequate services, the viability of some species may be jeopardized entirely (Dick 2001; Dick et al. 2003; Lomov et al. 2010). The absence of honeybee pollination may also provide opportunities for invasive species management, with a reduction in seed set likely to facilitate more effective control mechanisms (Simpson et al. 2005; Gross et al. 2010; Paynter et al. 2010). Nevertheless, the persistence of wild honeybees in Europe, and the Americas despite *Varroa* infestation (Rinderer et al. 2001; Fries et al. 2006; Seeley 2006; Le Conte et al. 2007; Brettell & Martin 2017) implies that populations may recover over time. Indeed, behavioral adaptations linked to colony size and swarming frequency that reduce the rate of *Varroa* infestation are believed to have evolved fairly rapidly (Mikheyev et al. 2015; Loftus et al. 2016), adding a temporal aspect for conservationists to consider.

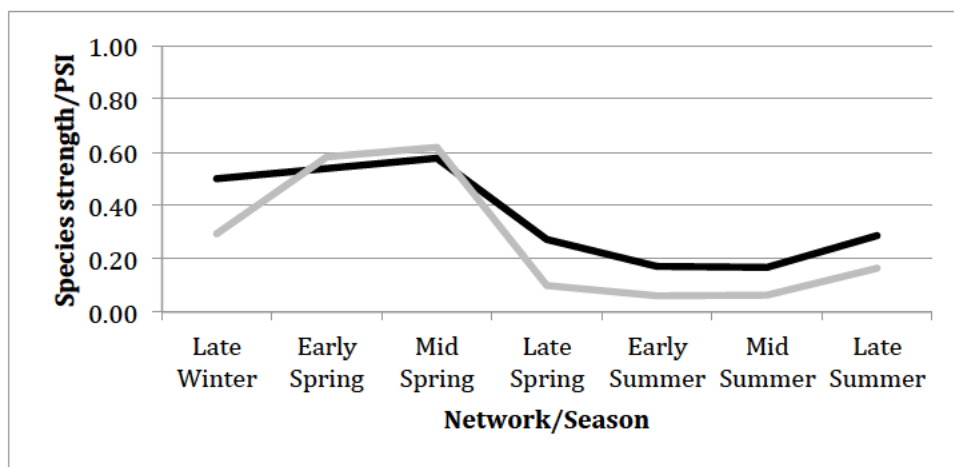
#### **Acknowledgements:**

Video recordings were collected by W. Waters, and C. L. Gross in 2007; L. B. Vary, I. Simpson, and C. L. Gross in 2011, 2012, and 2014; and J. D. Whitehead and C. L. Gross in 2015, 2016, and 2017. All data from the videos were gathered, collated, and analysed by J. D. Whitehead. The authors would also like to acknowledge K. D. Mackay, E. Mackay, and C. Silveira de Souza for their assistance in the field, and editorial comments, and thank Dan Bickel (*Entomology Department, Australian Museum, Sydney, NSW, Australia*) and Tobias Smith (*Ecosystem Management, University of New England, Armidale, NSW, Australia*) for their assistance with insect identifications. The study was funded by a student research grant provided by the University of New England (UNE).

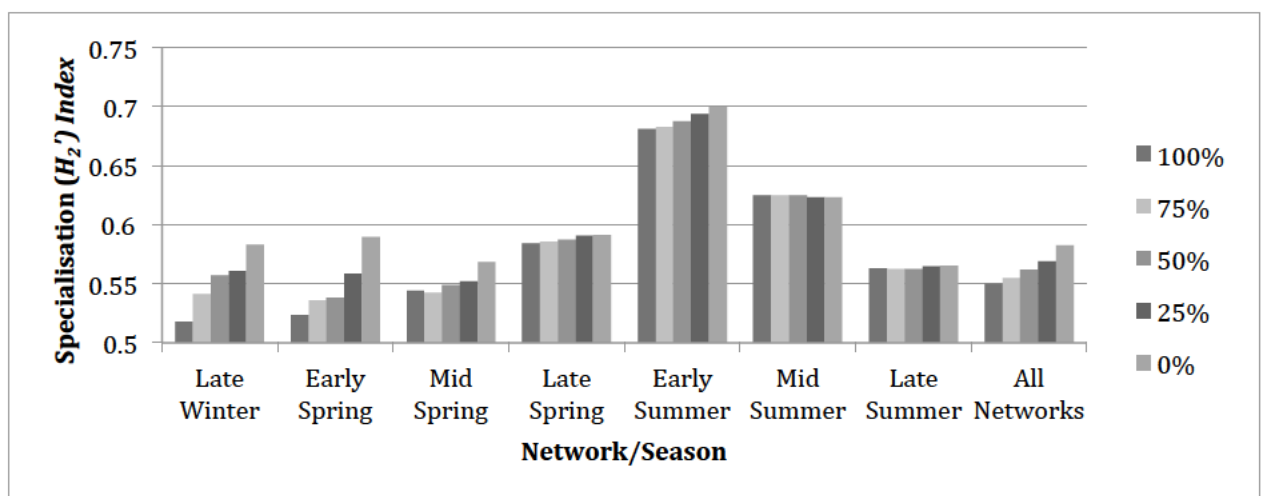
## Tables and Figures:

**Table 1.** Mean impact and significance of direct foraging interactions between *Apis mellifera* and native floral visitors. Individual interactions could be competitive = -1, neutral = 0, or facilitative = 1; with data provided to 2 decimal places where relevant.

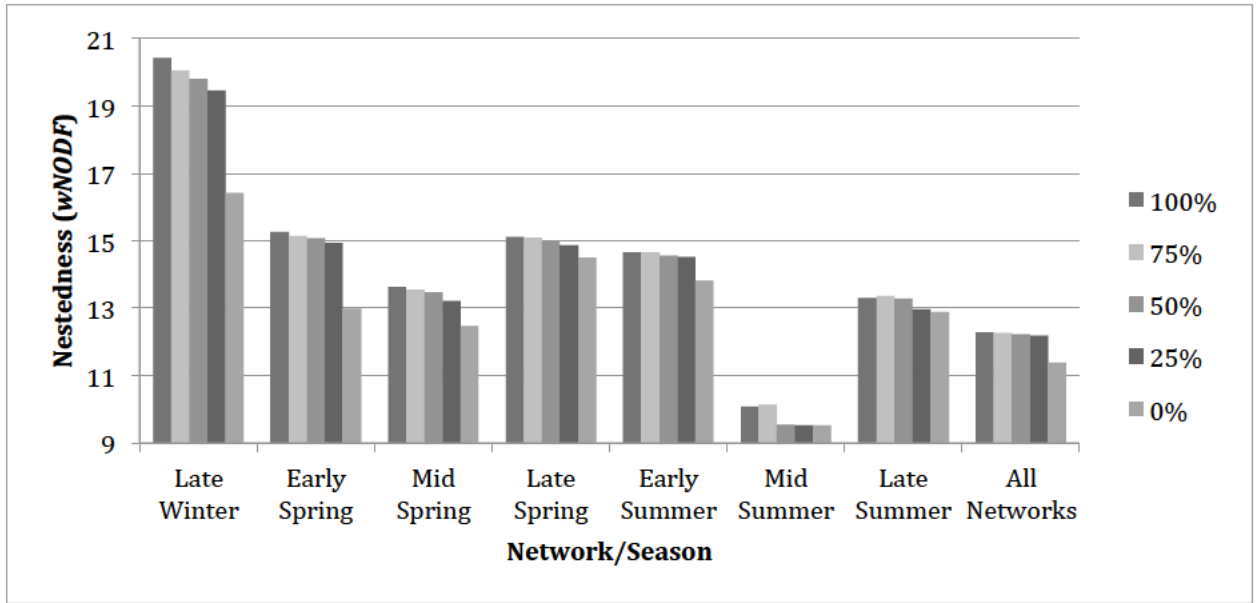
ORDER:	Mean:	SD:	df:	T-statistic:	p-value:
Aves	0.00	0.00	7	0.00	1.00
Coleoptera	-0.06	0.25	15	-1.00	0.33
Diptera	-0.36	0.62	41	-3.75	<0.01
Hymenoptera	-0.52	0.51	26	-5.29	<0.01
All Orders	-0.32	0.53	92	-5.81	<0.01



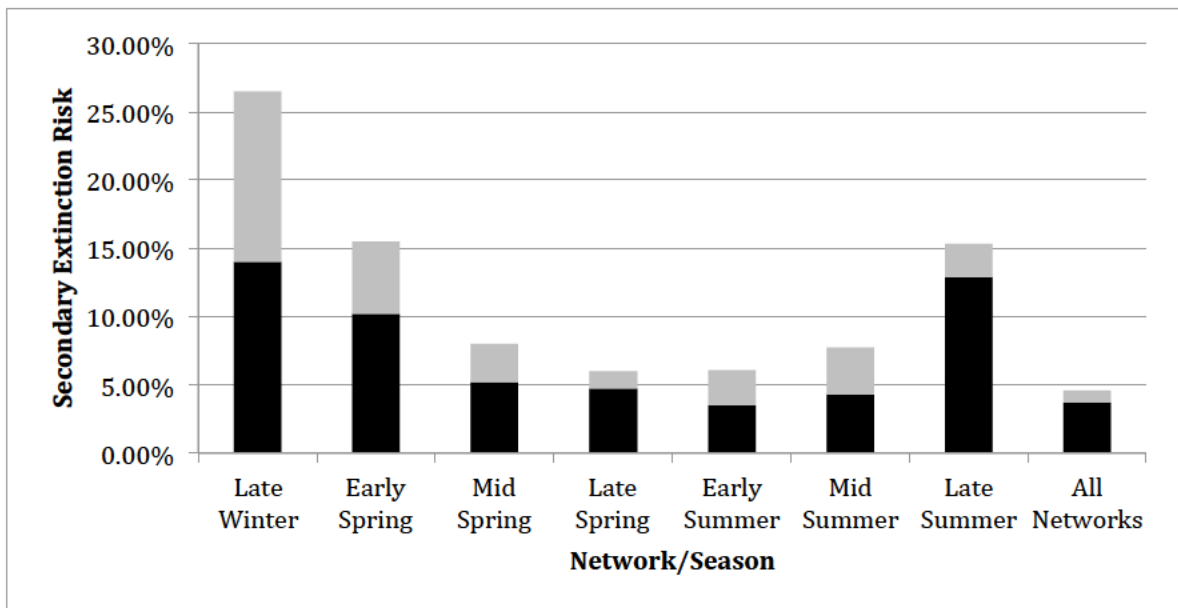
**Figure 1.** Change in *Apis mellifera* species strength (grey) and pollinator service index (black) scores between late winter and late summer pollination networks. Species strength has been reduced by a factor of 10 to ease comparison. Data was pooled for all years of sampling.



**Figure 2:** Network specialisation ( $H_2'$ ) at different proportions of the *Apis mellifera* visitation rate observed for the Howell Shrublands floral community. Data was pooled for all years of sampling.



**Figure 3:** Network nestedness ( $wNODF$ ) at different proportions of the observed *Apis mellifera* visitation rate for the Howell Shrublands floral community. Data was pooled for all years of sampling.



**Figure 4.** Likelihood of a random pollinator extinction triggering secondary plant extinctions when *Apis mellifera* is present (black) or absent (grey) from the Howell Shrublands pollination network. Data was pooled for all years of sampling.

**Higher Degree Research Thesis by Publication  
University of New England**

**STATEMENT OF AUTHORS' CONTRIBUTION**

(To appear at the end of each thesis chapter submitted as an article/paper)

We, the Research Master/PhD candidate and the candidate's Principal Supervisor, certify that all co-authors have consented to their work being included in the thesis and they have accepted the candidate's contribution as indicated in the *Statement of Originality*.

	<b>Author's Name (please print clearly)</b>	<b>% contribution</b>
Candidate	Joshua Whitehead	85%
Other Authors	Caroline Gross	15%

Name of Candidate: **Joshua Whitehead**

Name/title of Principal Supervisor: **Prof. Caroline Gross**

  
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Candidate

23/09/2018  
Date

  
\_\_\_\_\_  
Principal Supervisor

28 Sept 2018  
Date

## **Conclusion:**

Growing concern about the recent declines and disruption of pollination systems around the world has accentuated the need to understand how they respond to disturbance. This thesis demonstrates that network analyses can be a valuable research and conservation tool, by allowing the species and functional diversity of plant-pollinator communities to be visualized and quantified. By focusing on what species do, rather than their presence or absence, network analyses may help conservationists identify functionally significant species, and provide more tangible assessments of ecosystem health. However, the absence of standardised methodologies and the relative degree of effort involved in sampling a plant-pollinator network may significantly limit their utility (Hegland et al. 2010; Tylianakis et al. 2010; Elle et al. 2012).

In this thesis I describe a method that accounts for a methodological oversight in previous studies, and enables sampling to be evaluated post-hoc. Another way to address this may be the development of a standardised sampling procedure with a baseline threshold known to provide a relatively reliable sample. This study found that approximately 18 hours of stationary observations were required to sample a majority of interactions and produce a reliable estimate of the total interaction richness for each species. Nevertheless, the effort required to reach this threshold is likely to vary considerably between species or environments, and will therefore require further investigation to determine its reliability in different systems.

Determining when stable estimates occur is also likely to be important for quantifying community structure, with several network metrics likely to stabilize at a similar level of effort (Fründ et al. 2016; Vizentin-Bugoni et al. 2016). However, practitioners will also require a clearer understanding of the roles these attributes play in community stability, and how they may be manipulated in conservation.

This thesis has shown that species-specific metrics such as species strength, and pollinator service index (*PSI*), may be used to identify keystone or umbrella species for conservation. Meanwhile, network robustness may be used to identify communities, or subsets within a community that may be vulnerable to disturbance. For instance, the Howell Shrublands pollination network was found to be significantly less robust to pollinator extinctions in late winter and early summer. Conservation

efforts can therefore be focused on species likely to provide the greatest return on investment for restoration efforts. In this case, the likelihood of exotic honeybees declining from the system following the arrival of a novel parasite (Rinderer et al. 2013) may serve to further threaten late winter flowering plants, whose plant-pollinator mutualisms may already be threatened due to climate change (Fitter & Fitter 2002; Hegland et al. 2009; McEwan et al. 2010). Thus, conserving the pollinator populations that may contribute most to the floral fecundity of late winter flowering plants (e.g. *Trichocolletes* spp., *Melangyna* spp., *Lichenostomus melanops*, and *Brychosoma* spp.) may be an important priority.

Although this suggests pollination networks may be a useful alternative to traditional biodiversity assessment methods, further work is needed to determine which aspects of network structure contribute most to community robustness. For instance, specialisation ( $H_2'$ ), nestedness ( $wNODF$ ), and modularity are all predicted to influence robustness (Tylianakis et al. 2010; Elle et al. 2012), though the exact relationships remain unclear. Given the variability of these metrics when observed across different time scales, flowering phenology may have a significant effect on network structure. It is therefore recommended that future studies conducted in seasonal environments use temporal snapshots to provide a more accurate representation of network transience and minimise the accumulation of forbidden interactions (Olesen et al. 2011).

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## Appendix:

Appendix 2.1: Howell Shrublands floral species in order of appearance from Chapter 2 - Figure 1.

FAMILY:	SPECIES:
Rutaceae	<i>Correa reflexa</i>
Proteaceae	<i>Grevillea floribunda</i>
Rhamnaceae	<i>Cryptandra amara</i>
Asteraceae	<i>Olearia ramosissima</i>
Ericaceae	<i>Leucopogon melaleuroides</i>
Fabaceae	<i>Acacia pruinosa</i>
Fabaceae	<i>Acacia viscidula</i>
Fabaceae	<i>Hovea heterophylla</i>
Fabaceae	<i>Hovea lanceolata</i>
Fabaceae	<i>Acacia neriifolia</i>
Myrtaceae	<i>Micromyrtus sessilis</i>
Fabaceae	<i>Acacia decora</i>
Fabaceae	<i>Dillwynia sieberi</i>
Proteaceae	<i>Grevillea triternata</i>
Proteaceae	<i>Hakea microcarpa</i>
Ericaceae	<i>Leucopogon muticus</i>
Fabaceae	<i>Pultenea myrtoides</i>
Fabaceae	<i>Mirbelia pungens</i>
Rutaceae	<i>Zieria odorifera</i>
Fabaceae	<i>Hardenbergia violacea</i>
Droseraceae	<i>Drosera glanduligera</i>
Orchidaceae	<i>Diuris abbreviata</i>
Orchidaceae	<i>Glossodia major</i>
Fabaceae	<i>Acacia granitica</i>
Droseraceae	<i>Drosera peltata</i>
Myrtaceae	<i>Kunzea parvifolia</i>
Fabaceae	<i>Glycine clandestina</i>
Asteraceae	<i>Brachyscome stuartii</i>
Orchidaceae	<i>Caladenia fuscata</i>
Ericaceae	<i>Leucopogon virgatus</i>
Iridaceae	<i>Patersonia sericea</i>
Campanulaceae	<i>Wahlenbergia planiflora</i>
Myrtaceae	<i>Leptospermum brevipes</i>
Colchicaceae	<i>Wurmbea biglandulosa</i>

Santalaceae	<i>Choretrum candollei</i>
Thymelaeaceae	<i>Pimelea linifolia</i>
Asparagaceae	<i>Laxmannia gracilis</i>
Campanulaceae	<i>Wahlenbergia gracilis</i>
Hypericaceae	<i>Hypericum gramineum</i>
Lentibulariaceae	<i>Utricularia dichotoma</i>
Asteraceae	<i>Triptilodiscus pygmaeus</i>
Dilleniaceae	<i>Hibbertia riparia</i>
Fabaceae	<i>Acacia triptera</i>
Myrtaceae	<i>Calytrix tetragona</i>
Lamiaceae	<i>Prostanthera nivea</i>
Fabaceae	<i>Bossiaea scortechinii</i>
Myrtaceae	<i>Homoranthus prolixus</i>
Hypoxidaceae	<i>Hypoxis hygrometrica</i>
Ericaceae	<i>Brachyloma daphnoides</i>
Xanthorrhoeaceae	<i>Dianella caerulea</i>
Iridaceae	<i>Sisyrinchium rosulatum</i>
Asteraceae	<i>Brachyscome nova-anglica</i>
Menyanthaceae	<i>Nymphoides geminata</i>
Asteraceae	<i>Chrysocephalum apiculatum</i>
Goodeniaceae	<i>Goodenia hederacea</i>
Fabaceae	<i>Bossiaea obcordata</i>
Dilleniaceae	<i>Hibbertia kaputarensis</i>
Fabaceae	<i>Dillwynia sericea</i>
Apiaceae	<i>Trachymene incisa</i>
Campanulaceae	<i>Wahlenbergia stricta</i>
Goodeniaceae	<i>Goodenia bellidifolia</i>
Asparagaceae	<i>Dichopogon fimbriatus</i>
Goodeniaceae	<i>Goodenia macbarronii</i>
Asteraceae	<i>Brachyscome multifida</i>
Droseraceae	<i>Drosera burmanni</i>
Haemodoraceae	<i>Haemodorum planifolium</i>
Orchidaceae	<i>Calochilus robertsonii</i>
Myrtaceae	<i>Eucalyptus dealbata</i>
Xanthorrhoeaceae	<i>Tricoryne elatior</i>
Stylidiaceae	<i>Stylidium graminifolium</i>
Myrtaceae	<i>Leptospermum novae-angliae</i>
Myrtaceae	<i>Callistemon linearis</i>
Myrtaceae	<i>Harmogia densifolia</i>

Asteraceae	<i>Ozothamnus obcordatus</i>
Asparagaceae	<i>Anthropodium milleflorum</i>
Mackinlayaceae	<i>Actinotus helianthi</i>
Asteraceae	<i>Podolepis neglecta</i>
Campanulaceae	<i>Isotoma anethifolia</i>
Dilleniaceae	<i>Hibbertia acicularis</i>
Myrtaceae	<i>Callistemon pungens</i>
Portulacaceae	<i>Portulaca bicolor</i>
Montiaceae	<i>Calandrinia pickeringii</i>
Asteraceae	<i>Vittadinia cuneata</i>
Asteraceae	<i>Hypochaeris radicata</i>
Proteaceae	<i>Persoonia cornifolia</i>
Campanulaceae	<i>Lobelia andrewsii</i>
Asparagaceae	<i>Thysanotus tuberosus</i>
Myrtaceae	<i>Leptospermum polygalifolium</i>
Myrtaceae	<i>Eucalyptus prava</i>
Pittosporaceae	<i>Cheiranthra telfordii</i>
Xanthorrhoeaceae	<i>Bulbine bulbosa</i>
Asteraceae	<i>Cassinia copensis</i>
Rutaceae	<i>Crowea exalata</i>
Pittosporaceae	<i>Bursaria spinosa</i>
Asteraceae	<i>Olearia elliptica</i>
Orchidaceae	<i>Spiranthes australis</i>
Asteraceae	<i>Senecio diaschides</i>
Ericaceae	<i>Melichrus urceolatus</i>
Asteraceae	<i>Cassinia laevis</i>
Asteraceae	<i>Cassinia quinquefaria</i>