

**Determining the pollinators of rare and  
endangered *Epacris* species:  
implications for conservation**

**Karen Johnson and Peter McQuillan**



**Final Report for Australian Flora Foundation**

**December 2012**

## 1.1 Abstract

There is little information available on the pollinators of Tasmania's threatened *Epacris* species. Our main objective was to determine the pollinators of eight *Epacris* species; and explore for relationships between pollinators, floral morphology, flowering time and habitat. In completing the objectives we undertook breeding system experiments, quantitatively documented pollinators, collated flowering time and habitat information; and assessed for the potential impact of introduced insects on the native *Epacris*-pollinator mutualisms. While *Epacris* species set very little seed in the absence of animals, seed set as a result of animal pollination was successful with up to 30% of capsules containing numerous viable seeds. *Epacris* species have generalised pollination systems attracting at least 33 different pollinators, including flies, bees and butterflies. Four introduced species also visited *Epacris*: honey bee, bumble bee, drone fly and cabbage white butterfly. The introduced drone fly and cabbage white butterfly have not previously been recorded as pollinators of the native flora of Tasmania. No statistically significant relationship was found between pollinators, floral attributes, flowering time or habitat. However, the introduced honey bee was the most frequent visitor to many *Epacris* species and its potential to impact on the native *Epacris*-pollinator relationships is discussed.

## 1.2 Introduction

Many vascular plants require the services of an animal pollinator if they are to reproduce by seed which appears to be the case for at least some *Epacris* species (Keith, 1997; Fripp, 1982; O'Brien and Calder 1989). As natural habitat is increasingly fragmented and converted to human uses, the diversity of native plant and native pollinator interactions is likely to decline (Buchmann and Nabhan, 1996; Aizen and Feinsinger, 1994a; Aizen and Feinsinger, 1994b; Winfree *et al.*, 2009). In addition, introduced flower visitors, such as the highly social honeybee and bumblebee, can competitively displace native solitary pollinators, and both of these species are present in Tasmania (Celebrezze and Paton, 2004; Hingston *et al.*, 2002; Hingston, 2005).

With small ranges and low numbers of individuals, rare plants are potentially most at risk from pollinator decline, particularly if they rely on a single or small number of pollinators (Spira, 2001; Liu and Koptur, 2003). For rare species requiring pollinators,

conservation managers need to know the animals involved so that they may consider their habitat and foraging requirements (Kearns *et al.*, 1998; Cane, 2001). Although much effort has gone into the conservation of *Epacris* species in Tasmania there is no specific information on *Epacris*-pollinator relationships (Keith, 1998). Thus, there remains a critical gap in our knowledge of the reproduction of these threatened plants, and in our consideration of the conservation requirements of their potential pollinators.

Tasmania supports 28 *Epacris* species of which almost half (12 spp.) are listed on the Tasmanian *Threatened Species Protection Act 1995* and/or Commonwealth *Environment Protection and Biodiversity Conservation Act 1999*. Six are nationally endangered and 3 are critically endangered species (Buchanan, 2009; Department of Primary Industries Parks Water and Environment, 2010). Knowledge regarding the current status of key populations of threatened *Epacris* and an understanding of critical life history parameters were specific objectives of the Forest Epacrid Recovery Plan (Keith, 1998).

This report aims to increase our understanding of critical life history parameters. The main objectives are (1) determine the pollinators of Tasmania's threatened *Epacris* species; (2) examine the relationships between pollinators, floral morphology, flowering time and habitat; (3) outline the potential impacts of introduced insects, such as the bumblebee and honeybee; and (4) assess the implications of this new knowledge for the conservation of *Epacris* species and pollinators.

### **1.3 Methods**

#### ***Study sites***

Pollinator observations for all threatened *Epacris* species were undertaken in Tasmania in 2011-12. Studies were undertaken for *E. apsleyensis* on Crown Land near the Douglas-Apsley National Park; *E. barbata* at the disused tin mines and on Mt. Amos in Freycinet National Park; *E. exserta* at Cataract Gorge and Corra Linn Gorge near Launceston; *E. glabella* on the west coast between the townships of Zeehan and Renison; *E. graniticola* on Mt. Stronach near Scottsdale; *E. limbata* on

the east coast near Hardings Falls; *E. virgata* Kettering at Humphries Rivulet in Wellington Park; and *E. virgata* in State Forest near Beaconsfield in north.

### ***Breeding system and open pollination experiments***

*Autonomous- selfing*— To investigate whether *Epacris* species could self-pollinate, we examined seed set in the absence of animals in *E. apsleyensis*, *E. exserta*, and *E. virgata* Kettering. One branch in bud on ten plants (6 for *E. exserta*) of each species was chosen. In total, 510 *Epacris apsleyensis* buds; 389 *E. exserta* buds; and 433 *E. virgata* Kettering buds were bagged. Buds were bagged with Terylene® mesh bags (approximately 20 cm by 30 cm, with ¼ mm mesh) to exclude animal visitors. No other manipulation was undertaken. Capsules were collected prior to dehiscence. A cut-test performed under a dissecting microscope was used to assess seed for the presence of endosperm. To standardise for comparison between the different numbers of flowers in each sample and treatment, capsules across all samples of a species were counted and converted to a percentage of the original number of bagged buds. Seven of the exclusion bags of *Epacris virgata* Kettering showed evidence of animal tampering and were excluded from analysis, thus only three samples were analysed.

*Open control*— To investigate whether pollination is occurring in the wild, we examined seed set in *Epacris* plants. One branch with good flowering on ten plants (6 for *E. exserta*) of each *Epacris* species was chosen and marked with a green twist tie and left open to all pollinators. Twist ties were located on the same branch as flowers but distant from them to minimise any influence on flower visitors. 905 *Epacris apsleyensis* flowers; 643 *E. exserta* flowers; 438 *E. limbata* flowers; and 457 *E. virgata* Kettering flowers were marked. (Note that seed set per capsule is grossly under estimated as some capsules dehisced prior to retrieval and some dehisced en route to the lab and were therefore not in their capsule any longer).



### ***Pollinators***

Over 85 hours of observations were made on the animal visitors to *Epacris* species during their peak flowering times. Observations were on *E. apsleyensis* (Sep 2011 & Mar-Apr 2012), *E. barbarta* (Sep 2011), *E. exserta* (Oct 2011), *E. glabella* (Oct 2012), *E. graniticola* (Oct 2011), *E. limbata* (Dec 2011 & Jan 2012), *E. virgata* Beaconsfield (Sep & Oct 2011), and *E. virgata* Kettering (Oct 2011). For a floral visitor to be designated a ‘pollinator’ the animal was necessarily observed to contact the reproductive organs, collect pollen and move between conspecific flowers.

Surveys were conducted between 10.00 and 16.00 hours on fine days with insect activity at *Epacris*. Flowers with available nectar and pollen were chosen for observation in person and by video camera (Panasonic Digital Video Camera, model no. NV-GS70, 1.7 MP, 500x digital zoom and /or JVC Digital Video Camera, model no. GZ-MG465, 1.07 MP, 32x optical zoom) on a tripod.

For the quantitative analysis, the identity of pollinators and the number of flowers visited were recorded. The number of flowers observed (either in person or by video camera) was documented. Where *Epacris* species were visited by the introduced honey bee or bumble bee, the mode of visitation (pollinator versus nectar-robber) was recorded. Additional pollinators were opportunistically recorded and added to the species list – these do not appear in the quantitative analysis.

Bees were identified using the key of Michener (1965) and the Hingston bee collection (housed at the School of Geography and Environmental Studies Laboratory, UTAS). Flies were identified using Colless and McAlpine (1991) and butterflies using Braby (2004). Other invertebrates were identified using Zborowski and Storey (2003), Daley (2007) and Shattuck (1999). Following Pizzey and Knight (1997), bird visitors were identified with binoculars as they visited flowers.

### **Floral traits, flowering times, and habitats**

Flowers were collected in the field for *E. apsleyensis*, *E. barbarta*, *E. exserta*, *E. glabella*, *E. graniticola*, *E. limbata*, *E. virgata* Beaconsfield, and *E. virgata* Kettering. One flower was collected from each of 15 plants for each species and measurements (accurate to 0.25mm) for floral attributes known to be important to the pollination process were documented under a dissecting microscope – length of corolla (from

floor of corolla to corolla mouth); width of corolla including petals; width of corolla mouth not including petals; anther length; corolla length/gynoecium; exertion or inclusion of anthers (measured from corolla mouth to most distal point). The median measurement was used for analysis.

Flowering time follows the Listing Statements found on the DPIPWE website. Habitat follows Keith (1998) and Listing Statements found on the DPIPWE website. Habitat includes four categories of vegetation type (dry sclerophyll forest, dry heath, wet heath, scrub); five categories of geology (dolerite, granite, alluvium, serpentinite, mudstone); and five categories of landform (river bank, mountain summit, slope, ridge, flat).

### **Pollen load analysis**

To determine if insects were faithful foragers on *Epacris* species the pollen loads of 24 insects collected while foraging on *Epacris* flowers were examined. Fourteen native flies, seven native bees and three honey bees were collected visiting *E. apasleyensis*, *E. limbata* and *E. virgata* Kettering and *E. virgata* Beaconsfield. A sample of pollen was removed from each animal, mounted on a slide, and microscopically examined. To determine pollen-type the sample was compared with pollen collected from *Epacris* flowers and other species in flower at the time of collection. An estimate was made of proportions of *Epacris* versus other pollen-types.

### **Data analysis**

Qualitative and quantitative Non-metric Multi-Dimensional Scaling (NMDS) analyses were performed on epacrid pollinator profiles using the ecodist library in R 2.15.1 (Goslee and Urban, 2007). Bray-Curtis dissimilarity matrices were used as input to the pollinator ordination. Quantitative Non-metric Multi-Dimensional Scaling (NMDS) analyses were also performed on *Epacris* floral profiles. A Euclidean dissimilarity matrix was used as input to the floral ordination. A Bray-Curtis matrix places less weight on shared zeros than the Euclidean approach. This recognises that pollinator information may be incomplete compared with information on floral features which are complete. Pollinator information was standardised as visits/flower/hour for the quantitative analysis.

To explore which individual pollinators influenced the variation in pollinator profiles, vectors indicating the direction and strength of pollinators in pollination ordination space based on the qualitative data set, were fitted. To explore which pollinators based on frequency of visits influenced the variation in pollinator profiles vectors indicating the direction and strength of pollinators in pollination ordination space based on the quantitative data set were fitted.

The Mantel test in the ecodist package in R 2.15.1 (Goslee and Urban, 2007), was used to test whether the Bray-Curtis distance matrix based on pollinators was significantly correlated ( $P \leq 0.05$ ) with the Euclidean matrix based on floral traits ( $P$ -values were for the two-tailed test and were based on 10,000 permutations); Euclidean matrix based on flowering times; and the Euclidean matrix based on habitat-type.

## 1.4 Results

### Breeding system and open pollination

*Autonomous- selfing*— No seed set occurred in *Epacris apseyensis* or *E. exserta* in the absence of animal pollinators. In contrast, *E. virgata* Kettering set some seed (Table 1).

*Open control*— Pollination is occurring in the wild with seed set recorded from *E. apseyensis*, *E. exserta*, and *E. virgata* Kettering. All plants produced capsules with various numbers of viable seeds.

Table 1:

Species	Autonomous selfing			Open pollination		
	% capsule with viable seed	Seed set range per capsule	Median seed set per capsule	% capsule with viable seed	Seed set range per capsule	Median seed set per capsule
<i>E. apseyensis</i>	0	0	0	30	1-35	6
<i>E. exserta</i>	0	0	0	22	1-41	4
<i>E. virgata</i> Kettering	11	1-3	1	47	1-76	7

### Pollinators

A total of 33 animal species were observed to visit *Epacris* flowers as pollinators (Table 2, Fig. 1 - 8). A total of 4896 animal visits to *Epacris* flowers were documented. No *Epacris* species was exclusively bee-, fly- or butterfly-pollinated

(Table 2, Fig. 1 photos of pollinators); and for each *Epacris* taxon, pollen was dispersed by more than one functional group of insects.

There was considerable overlap in the pollinator profiles of *Epacris* species. Flies and bees visited all of the study species. In particular, the red-bottomed bee (*Exoneura* sp.) and blow flies (*Calliphora* sp.) were pollinators of all species. Flies accounted for the greatest number of pollinating taxa. Butterflies were recorded from all species with the exceptions of *E. glabella* and *E. virgata* Beaconsfield. On one occasion, the blooms of *Epacris exserta* were observed to be visited by silvereyes (*Zosterops lateralis*). However, more evidence is required to confirm them as *Epacris* pollinators.

The introduced honey bee (*Apis mellifera*) dominated the visitor profile to *Epacris* flowers (Fig. 2). Over half of all the animal visits recorded were made by honey bees (2823 visits out of a total of 4896). With the exception of *E. virgata* Kettering, honey bees were observed to visit all species. Both the introduced honey bee and bumble bee (*Bombus terrestris*) were pollinators of *Epacris*. Bumble bees were only occasional visitors. The introduced drone fly (*Eristalis tenax*) and cabbage butterfly (*Pieris rapae*) also visited *Epacris* sp.

Other flower visitors included lycid beetles (*Porrostoma rhipidius*), clerid beetles (*Eleale* sp.) and soldier beetles (*Chauliognathus tricolor*). These species may play a relatively minor role in *Epacris* pollination by transporting pollen on their bodies as they move about a plant. Only beetles present in large numbers, carrying pollen obvious to the naked eye, and observed to move between plants have been included as pollinators in Table 2. Some midges and small flies (such as lauxaniid flies) may also be minor pollinators. However, they are so small that they do not necessarily contact the reproductive parts of a flower when probing for nectar or moving about a plant. Shield bugs (Pentatomidae) and flower spiders (*Diaea* sp.) also occupy *Epacris* sp. but are unlikely to play a role in pollination.



**Figure 1: Red-bottomed bee (*Exoneura* sp.) visits *E. barbarta***



**Figure 2: Introduced honeybee (*Apis mellifera*) visits *E. graniticola***



**Figure 3: Hoverfly (*Melangyna* sp.) visits *E. virgata* Beaconsfield**



**Figure 4: *Rutilla* (large) sp. visits *E. barbarta***



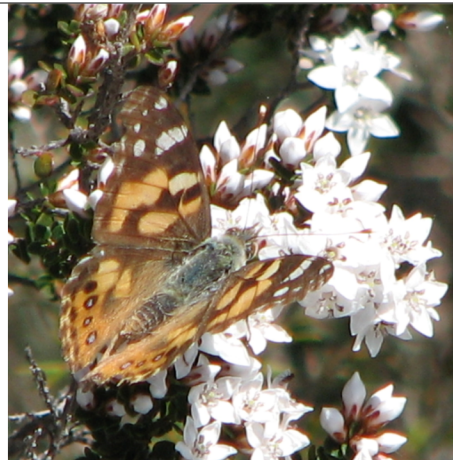
**Figure 5: Long-legged tachinid fly (*Prosenia* sp.) visits *E. virgata* Kettering**



**Figure 6: Long-tongued fly (*Scaptia* sp.) visits *E. barbarta***



**Figure 7: Australian admiral butterfly (*Vanessa itea*) visits *E. graniticola***



**Figure 8: Painted lady butterfly (*Vanessa kershawi*) visits *E. graniticola***

Table 2. Pollinators of *Epacris* sp. In Tasmania (Ea = *E. apsleyensis*, Eb = *E. barbarta*, Ee = *E. exserta*, Eg = *E. glabella*, Egr = *E. granitica*, El = *E. limbata*, EvB = *E. virgata* Beaconsfield, EvK = *E. virgata* Kettering, i = introduced species).

Pollinator			<i>Epacris</i> sp.							
Family	Species	Common name	Ea	Eb	Ee	Eg	Egr	El	EvB	EvK
<b>Bee</b>										
i	Apidae	<i>Apis mellifera</i>	honey bee	1	1	1	1	1	1	
	Bomblyiidae	<i>Aleucosia calophthalma</i>	beefly							1
i	Bomblyiidae	<i>Bombus terrestris</i>	bumble bee	1			1	1	1	
	Anthophoridae	<i>Exoneura</i> sp.	red-bottomed bee	1	1	1	1	1	1	1
	Anthophoridae	<i>Exoneura</i> –like (small) sp.	red-bottomed bee like				1			
	Colletidae	<i>Leioproctus</i> sp.	native bee					1	1	1
	Halictidae	<i>Homalictus</i> sp.	native bee			1		1		1
	Halictidae	<i>Lasioglossum (Parasphcodes)</i> sp.	native bee		1			1	1	1
	Halictidae	<i>Lasioglossum</i> sp.	native bee			1		1		1
<b>Fly</b>										
	Calliphoridae	<i>Calliphora</i> sp.	blow fly	1	1	1	1	1	1	1
	Empididae		native fly					1	1	
	Muscidae		muscid fly							1
	Nemestrinidae	<i>Pelecorrhynchus</i> sp.	native fly		1			1		
	Syrphidae	Eristalinae	drone fly					1	1	1
i	Syrphidae	<i>Eristalis tenax</i>	drone fly					1		
	Syrphidae	<i>Melangyna</i> sp.	hover fly	1			1		1	1
	Syrphidae	<i>Odontomyia</i> sp.								1
	Tabanidae	<i>Scaptia</i> sp.	long-tongued fly					1		
	Tachinidae	<i>Prosema</i> sp. ( long-legs)	long-legged tachinid	1	1			1		1
	Tachinidae	<i>Rutilla</i> (large) sp.	short-legged tachinid	1	1	1		1	1	
	Tachinidae	<i>Rutilla</i> (small) sp .	short-legged tachinid			1	1			
	Tachinidae	Tachinid (short-legs)	short-legged tachinid	1	1			1	1	1
<b>Butterfly</b>										
	Hesperiidae	<i>Hesperilla donnysa</i>	donnysa skipper						1	
	Hesperiidae	<i>Pasma tasmanicus</i>	Tasmanica skipper							1
	Nymphalidae	<i>Heteronympha penelope</i>	shouldered brown	1						
	Nymphalidae	<i>Vanessa itea</i>	Australian admiral			1		1		1
	Nymphalidae	<i>Vanessa kershawi</i>	Australian painted lady		1			1		
	Papilionidae	<i>Graphium macleayanus</i>	Macleay's swallowtail						1	
i	Pieridae	<i>Pieris rapae</i>	cabbage white	1						
<b>Beetle</b>										
	Alleculinae	<i>Atoichus bicolor</i>	alleculid beetle		1					
	Alleculinae		alleculid beetle					1		
	Oedemeridae		oedemerid beetle						1	
	Tenebrionidae	<i>Lepispilus sulcipennis</i>	darkling beetle							1



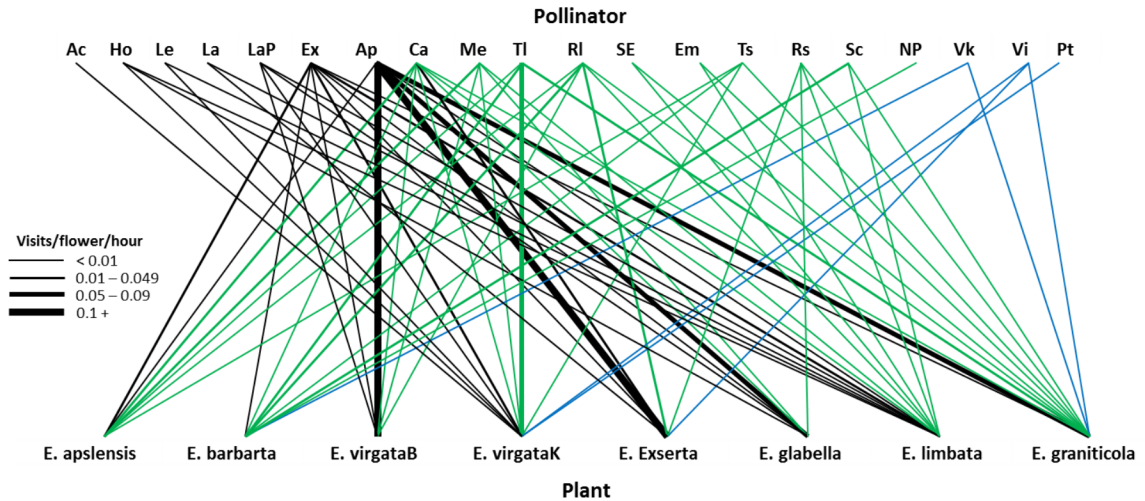


Figure 9. Frequency of pollinator visits to *Epacris* species (Visits are standardised to visits/flower/hour (Black line = bee; green = fly; blue = butterfly. Pollinators from left to right: **Bees** Ac = *Aleucosia calophthalma*, Ho = *Homalictus* sp., Le = *Leioproctus* sp., La = *Lasioglossum* sp., LaP = *Lasioglossum (Parasphecodes)* sp., Ex = *Exoneura* sp., Ap = *Apis mellifera*; **Flies** Ca = *Calliphora* sp., Me = *Melangyna* sp., Tl = *Prosenia* sp. ( long-legs), Rl = *Rutilia* (large) sp., SE = Eristalinae, Em = Empididae, Ts = Tachinid (short-legs), Rs = *Rutilia* (small) sp., Sc = *Scaptia* sp., NP = *Pelecorhynchus* sp.; **Butterflies** Vk = *Vanessa kershawi*, Vi = *Vanessa itea*, Pt = *Pasma tasmanicus*)

### Relationships between pollinators, floral traits, flowering times, and habitats

Three of the 20 pollinators exerted a major influence on the quantitative ordination of *Epacris* pollinator profiles: red-bottomed bees (*Exoneura* sp.), long-legged Tachinid flies and honey bees (*Apis mellifera*) with the vector for red-bottomed bee and long-legged Tachinid opposing that for honey bee (Fig. 10). In contrast, seven of the 20 pollinators exerted a major influence on the qualitative ordination of *Epacris* pollinator profiles: Hoverfly (*Melangyna* sp.), *Prosenia* sp. (long-legs), *Rutilia* (large) sp., Australian painted lady (*Vanessa kershawi*), Tachinid (short-legs), *Rutilia* (small) sp., and *Pelecorhynchus* sp. The vectors for *Prosenia* sp. (long-legs) and Tachinid (short-legs) were opposed to that for *Rutilia* (small) sp.; while Hoverfly was opposed to those for *Pelecorhynchus* sp. and Australian painted lady (Fig. 11).



No statistically significant relationship was found between the pollinator profiles (either quantitative or qualitative) and floral attribute profiles. No statistically significant relationships were found between either the qualitative or quantitative pollinator profiles and flowering times or habitats (Appendix 1).

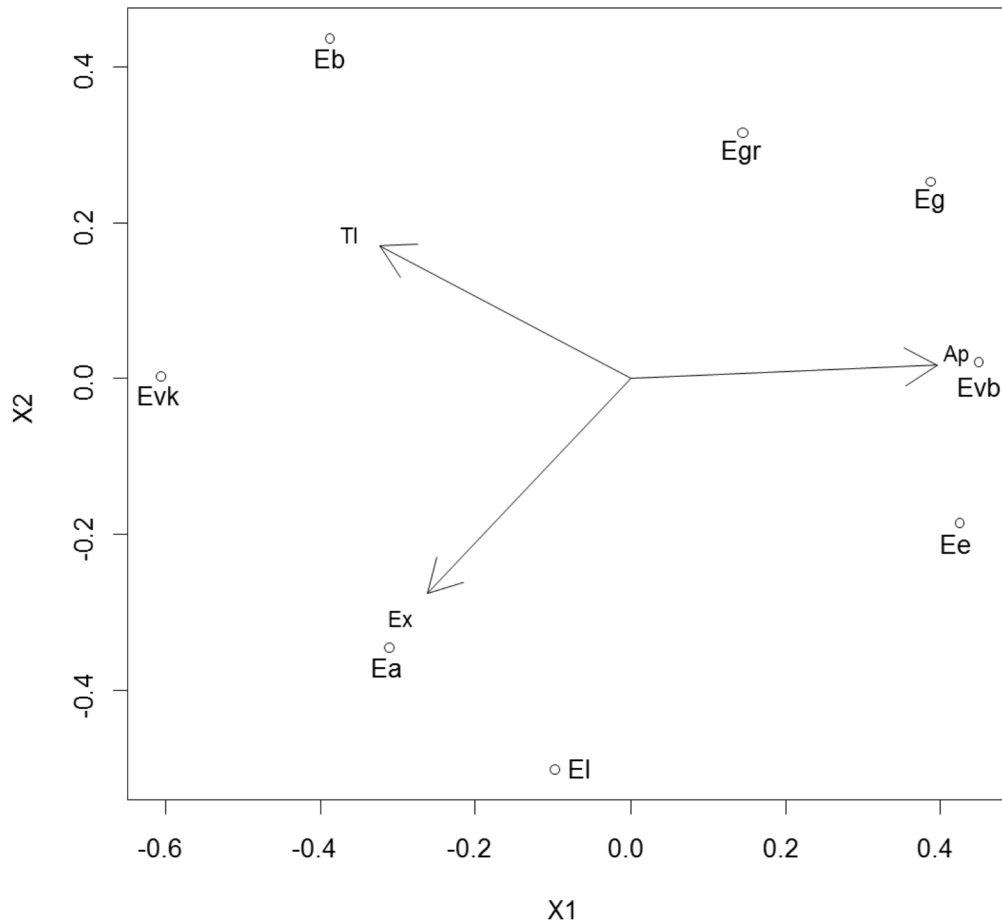


Figure 10. Ordination of *Epacris* according to quantitative pollinator profiles with pollinator groups influencing the variation between species fitted as vectors (Ea = *E. apasleyensis*, Eb = *E. barbarta*, Ee = *E. exserta*, Eg = *E. glabella*, Egr = *E. graniticola*, Evi = *E. virgata*Beaconsfield, Evk = *E. virgata*Kettering, Ap = *Apis mellifera* (honey bee), Ex = *Exoneura* sp. (red-bottomed bee), TI = Tachinid (long-legs) fly). Stress for 2D ordination = 0.17,  $r^2 = 0.82$ .

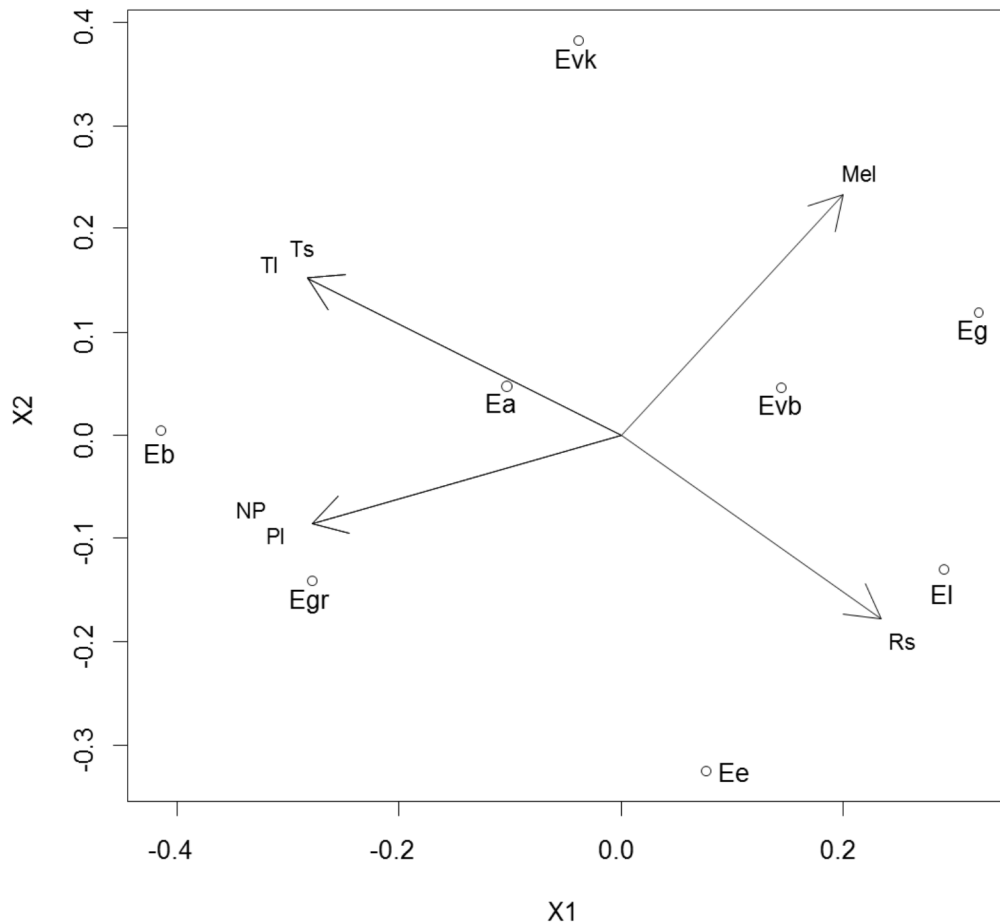


Figure 11. Ordination of *Epacris* according to qualitative pollinator profiles with pollinator groups influencing the variation between species fitted as vectors (Ea = *E. apseyensis*, Eb = *E. barbarta*, Ee = *E. exserta*, Eg = *E. glabella*, Egr = *E. graniticola*, Evb = *E. virgata*Beaconsfield, Evk = *E. virgata*Kettering, Mel = *Melangyna* sp. (hoverfly), Pl = Australian painted lady butterfly, Rs = *Rutilia* (small) sp. (fly), Tl = *Prosenia* sp. (Tachinid (long-legs) fly), Ts = Tachinid (short-legs) fly). Stress for 2D ordination = 0.15,  $r^2 = 0.83$ .

### Pollen load analysis

Fifteen of the 24 animals for which pollen loads were examined carried only *Epacris* pollen. Generally honeybees carried large amounts of pollen, predominantly on their legs. Native bees tended to have smaller pollen loads than honeybees and they were present on their legs and other parts of their bodies. Pollen was predominantly extracted from the mouthparts of flies with a small amount being trapped by body

hairs. The other pollen recorded was mostly *Hakea* and *Leptospermum* species from *E. limbata*; and *Hibbertia* species from *E. apsleyensis* and *E. virgata* Beaconsfield.

Table 3. Pollen loads carried by insects collected on *Epacris* species

Plant	Insect	% Pollen-type	
		<i>Epacris</i>	Other
<i>E. apsleyensis</i>	<i>Calliphora</i> sp.	100	0
	<i>Melangyna</i> sp.	80	20
	<i>Melangyna</i> sp.	100	0
	<i>Melangyna</i> sp.	100	0
	<i>Prosema</i> sp. ( long-legs)	60	40
	<i>Rutilia</i> (small) sp.	30	70
<i>E. limbata</i>	<i>Apis mellifera</i>	99	1
	<i>Calliphora</i> sp.	100	0
	<i>Exoneura</i> sp.	40	60
	<i>Lasioglossum</i> ( <i>Parasphcodes</i> ) sp.	90	10
	<i>Prosema</i> sp. ( long-legs)	40	60
	<i>Rutilia</i> (large) sp.	100	0
<i>E. virgata</i> Beaconsfield	<i>Apis mellifera</i>	100	0
	<i>Apis mellifera</i>	99	1
	<i>Calliphora</i> sp.	100	0
	<i>Calliphora</i> sp.	100	0
	Eristalinae	95	5
	<i>Exoneura</i> sp.	100	0
<i>E. virgata</i> Kettering	<i>Exoneura</i> sp.	100	0
	<i>Exoneura</i> sp.	100	0
	<i>Homalictus</i> sp.	100	0
	<i>Leioproctus</i> sp.	100	0
	<i>Prosema</i> sp. ( long-legs)	100	0
	<i>Prosema</i> sp. ( long-legs)	100	0

## DISCUSSION

Our data shows that *Epacris* species have generalised pollination systems attracting a range of pollinators, particularly flies, bees and butterflies. Red-bottomed bees (*Exoneura* sp.) and blow flies (*Calliphora* sp.) visited all *Epacris* species and these two taxa are known to be important pollinators of many other native plant species (Armstrong 1979). Hoverflies (*Melangyna* sp.) and Tachinid flies visited over half of the *Epacris* species, while native bees such as *Lasioglossum*, *Homalictus* and *Leioproctus* species were rarer. In addition, many lesser known pollinators were recorded including six native butterflies. Butterfly pollination has not been widely examined in Tasmania's flora but it is apparent that they are important pollinators of a

range of white tubular flowers, with recent records from *Epacris corymbifolia* and *Leucopogon collinus* (Johnson, 2012). Overall, most of the *Epacris* pollinators are geographically wide-spread generalist species that can occur across a range of habitat-types. As most *Epacris* species flower over spring there is not enough variation in flowering time within the species in this study to observe differences in seasonal pollinator availability. From the information available, we predict that other threatened *Epacris* species in Tasmania (*E. acuminata*, *E. curtisiae*, *E. grandis*, *E. moscaliana* and *E. stuartii*) are also likely to use the same generalist pollinators. The exploitation of a range of pollinators may promote robustness to pollinator loss. However, generalised relationships may also be more readily accessed by invasive ‘new’ species that are also generalists (Olesen *et al.* 2002).

Four introduced animals were observed to visit the flowers of *Epacris* species – honey bee, bumble bee, drone fly and cabbage butterfly. The introduced drone fly and cabbage butterfly have not previously been documented as pollinators of the native flora of Tasmania. All introduced animals visited *Epacris* flowers in ways indicative of pollinators rather than of nectar-robbers – legitimate accessing of flowers via the corolla mouth, contacting reproductive organs, and moving between conspecific plants. In contrast, nectar-robbing by bumble bees occurs in the common heath (*Epacris impressa*) (Hingston and McQuillan, 1998a). The common heath has longer corollas in its pink- and red-flowered races and shorter corollas in its white-flowered race exhibiting a bias towards bird and insect pollination respectively (Stace and Fripp, 1977; Hingston and McQuillan, 2000). In populations with longer corollas, bumble bees rob nectar by piercing the base of the corolla to obtain direct access to the nectaries without contacting the reproductive parts - thus circumventing the pollination process. It appears that the corolla lengths of the *Epacris* species in this study are short enough to facilitate legitimate pollination visits by the bumble bee. Furthermore, *E. barbarta* - with the longest of the floral tubes (of species in this study) has tightly packed bracts around the floral tube which may inhibit nectar-robbing access such as by piercing a hole in the corolla. Although the bumble bee was only observed in small numbers during this study if it becomes a more frequent visitor it could alter *Epacris* and native pollinator mutualisms by competing for floral resources.

Of the introduced species, only the honey bee was a frequent visitor to *Epacris* flowers. The qualitative and quantitative analyses give very different insights into *Epacris* pollinator profiles. Fig 11 (qualitative) shows the species variability that exists within *Epacris* pollinator profiles, while Fig. 10 (quantitative) indicates an inverse relationship between the numbers of visits by the red-bottomed bee (*Exoneura* sp.) and the introduced honey bee; and the long-legged Tachinid fly and honey bee. That is, the more honey bee visits an *Epacris* receives the fewer it gets from the native red-bottomed bee and long-legged Tachinid fly. As the red-bottomed bee visited all *Epacris* species the result is not due to the pollinator's absence from a site. In Australia, honeybees are frequent visitors at flowers and may remove up to 80% or more of the floral resources (Paton, 2000). This may result in competitive displacement of native fauna, including honeyeaters (Paton 1993) and native bees (Sugden and Pyke 1991; Schwarz and Hurst 1997; Paton, 2000). While it is known that native bees may experience lower forager returns and lower reproduction rates when exposed to competition with honeybees (Thomson, 2004) it has yet to be explored how honey bees impact on other pollinators. Our data suggests a potential impact on native flies as well.

Little work has been carried out on the ecological effects of feral and managed honey bee populations on the native flora of Tasmania. However, the frequency of visits we observed suggests that the honey bee has the capacity to aggressively compete with native pollinators for floral resources. The potential ecological impacts associated with the honey bee include the displacement of native pollinators and ineffective pollen transfer between conspecific plants (Hingston, 1998b). The potential for suppression of native pollinators suggests the potential of the honey bee to cause a cascade of impacts on native plant communities (Thomson, 2004). Both feral and managed populations have potential to impact on native flora and fauna. However, feral populations are likely to be most problematic, as unlike managed hives, they may remain on-site year-round.

*Epacris* species rely largely on a suite of animals for their reproduction, thus, pollinator conservation is crucial. This reliance is consistent with other Tasmanian epacrids including *Prionotes cerinthoides* and *Acrotriche aculeata* (Johnson, 2012, Johnson *et al.*, 2011, Johnson *et al.*, 2010), although, *Richea* species can undertake a

greater amount of self-pollination (Johnson, 2012). Autonomous selfing in *E. virgata* Kettering generated some seed, however, it was less than was set by open pollination where flowers were exposed to animal visitation. Clearly, successful animal pollination of threatened *Epacris* species is taking place at the study sites. Twenty to 30% of capsules had viable seed as a result of pollination by insects; and most capsules contained many viable seeds. However, insects were not always faithful foragers on *Epacris* with some pollen loads being a mixture of *Epacris* and other pollen-types. Pollen loads most likely reflect animal foraging behaviour (e.g. honey bees exhibit a high level of flower constancy (Waser 1986) and may visit many flowers on a single plant), time of insect collection (if collected early in their foraging bout pollen loads may under represent the number of plant species that would have been visited), and the presence of other flowers available for foraging. Many generalist visitors to flowers are drawn to the most locally abundant flower. Even though these pollinators may be common species, there may still be local competition for their services. Generalism in pollinating insects selects for floral uniformity at the regional level (Waser *et al.*, 1996) and this may explain in part the dominance of white, relatively shallow flowers in the Tasmanian flora.

That rare *Epacris* generally exploit common pollinators is a positive sign in a conservation sense. However, we have shown that most are obligate outcrossers. Complications may arise if populations of the *Epacris* are very scattered or rare, leading to inbreeding or poor pollinator service. The invasion of these breeding systems by the super-generalist honey bee is likely to be detrimental in the long term due to their efficiency in rapidly depleting nectar and pollen resources to the disadvantage of native co-adapted pollinators. Certainly, *Epacris* gene flows are probably already irreversibly changed by their activity over the last 150 years or so. We can only speculate on the consequences of this for the fitness of the populations in the face of ongoing habitat and environmental change.

Although further information is necessary to establish such things as whether *Epacris* floral resources are plentiful enough to accommodate the needs of both native pollinators and honey bees, the current high frequency of honey bee visitation is enough to cause concern. Over half of all visits to *Epacris* flowers (during this study) were undertaken by honey bees. They were the dominant visitors to *E. virgata*

Beaconsfield, *E. exserta*, *E. glabella* and *E. graniticola*, accounting for more visits than all the native pollinators combined. *Epacris virgata* Kettering was the only study species they did not visit. However, this is likely to be due to honey bees not being on-site during survey rather than to differences in floral attributes. There is a need to understand more about the mechanisms which keep generalist native pollinator populations at functionally useful levels. The profile of such species in our study is diverse and a multitude of biologies and life history attributes are represented. This represents a significant but important challenge to future conservation management.

## ACKNOWLEDGEMENTS

We thank the Australian Flora Foundation for funding this research.

## REFERENCES

- Aizen, M. A. and Feinsinger, P. 1994a. Habitat fragmentation, native insect pollinators, and feral honey bees in Argentine 'Chaco Serrano'. *Ecological Applications* 4(2): 378-392.
- Aizen, M. A. and Feinsinger, P. 1994b. Forest fragmentation, pollination, and plant reproduction in a Chaco Dry Forest, Argentina. *Ecology* 75(2): 330-351.
- Armstrong, J. A. 1979. Biotic pollination mechanisms in the Australian flora. *New Zealand Journal of Botany* 17: 467-508.
- Braby, M. F. 2004. The complete field guide to butterflies of Australia. CSIRO Publishing Victoria, Australia.
- Buchanan 2009: A Census of the Vascular Plants of Tasmania ([www.mag.tas.gov.au](http://www.mag.tas.gov.au)).
- Buchmann, S. L., and G. P. Nabhan. 1996. *The forgotten pollinators*. Island Press, Washington, D.C., USA.
- Cane, J. H. 2001. Habitat fragmentation and native bees: a premature verdict? *Conservation Ecology* 5(1): 3.
- Celebrezze, T. and Paton, D. C. 2004. Do introduced honeybees (*Apis mellifera*, Hymenoptera) provide full pollination service to bird-adapted Australian plants with small flowers? An experimental study of *Brachyloma ericoides* (Epacridaceae). *Austral Ecology* 29: 129-136.
- Colless, D. H. and McAlpine, D. K. 1991. Diptera. In CSIRO The Insects of Australia: a textbook for students and research workers Vol. 2. Melbourne University Press, Carlton.

- Daley, E. 2007. Wings: an introduction to Tasmania's winged insects. 40 Degrees South Pty Ltd, Hobart.
- Department of Primary Industries Parks Water and Environment. Threatened species list ([www.dpiw.tas.gov.au](http://www.dpiw.tas.gov.au)). Accessed 4 Feb 2010.
- Fripp, Y. J. 1982. Mating system and cross-compatibility of races of *Epacris impressa*. *Australian Journal of Botany* 30: 131-138.
- Goslee, S. C. and Urban, D. L. 2007. The ecodist package for dissimilarity-based analysis of ecological data. *Journal of Statistical Software* 22(7): 1-19.
- Hingston, A. B. 2005. Does the introduced bumblebee, *Bombus terrestris* (Apidae), prefer flowers of introduced or native plants in Australia? *Australian Journal of Zoology* 53: 29-34.
- Hingston, A., Marsden-Smedley, J., Driscoll, D. A., Corbett, S., Fenton, J., Anderson, R., Plowman, C., Mowling, F., Jenkin, M., Matsui, K., Bonham, K. J., Ilowski, M., McQuillan, P. B., Yaxley, B., Reid, T., Storey, D., Poole, L., Mallick, S. A., Fitzgerald, N., Kirkpatrick, J. B., Febey, J., Harwood, A. G., Michaels, K. F., Russell, M. J., Black, P. G., Emmerson, L., Visoiu, M., Morgan, J., Breen, S., Gates, S., Bantich, M. N. and Desmarchelier, J. M. 2002. Extent of invasion of Tasmanian native vegetation by the exotic bumblebee *Bombus terrestris* (Apoidea: Apidae). *Austral Ecology* 27: 162-172.
- Hingston, A. B. and McQuillan, P. B. 1998a. Nectar robbing in *Epacris impressa* (Epacridaceae) by the recently introduced bumblebee *Bombus terrestris* (Apidae) in Tasmania. *The Victorian Naturalist* 115: 116-119.
- Hingston, A. B. and McQuillan, P. B. 1998b. Does the recently introduced bumblebee *Bombus terrestris* (Apidae) threaten Australian ecosystems? *Australian Journal of Ecology* 23: 539-549.
- Hingston, A. B. and McQuillan, P. B. 2000. Are pollination syndromes useful predictors of floral visitors in Tasmania? *Austral Ecology* 25: 600-609.
- Johnson, K. A. 2012. Pollination ecology and evolution of epacrids, PhD Thesis. University of Tasmania.
- Johnson, K. A. and McQuillan, P. B., Kirkpatrick, J. B. 2010. Bird pollination of the climbing heath *Prionotes cerinthoides* (Ericaceae). *International Journal of Plant Sciences* 171: 147-157.
- Johnson, K. A., McQuillan, P. B. and Kirkpatrick, J. B. 2011. Nocturnal mammals, diurnal lizards and the pollination ecology of the cryptic flowering *Acrotriche serrulata* (Ericaceae) *International Journal of Plant Sciences* 172(2): 173-182.
- Kearns, C. A., Inouye, D. W. and Waser, N. M. 1998. Endangered mutualisms: The Conservation of Plant-Pollinator Interactions. *Annual Review of Ecological Systematics* 29:83-112.



- Keith, D. A. 1997. Combined effects of heat shock, smoke and darkness on germination of *Epacris stuartii* Stapf., and endangered fire-prone Australian shrub. *Oecologia* 112: 340-344.
- Keith, D. 1998. Recovery plan: Tasmanian forest epacrids 1999-2004. Tasmanian Parks and Wildlife Service, Hobart.
- Liu, H. and Koptur, S. 2003. Breeding system and pollination of a narrowly endemic herb of the Lower Florida Keys: impacts of the urban-wildland interface. *American Journal of Botany* 90: 1180-1187.)
- Michener, C. D. 1965. A classification of the bees of the Australian and South Pacific regions. *Bulletin of the American Museum of Natural History* 130: 1-362.
- O'Brien, S. P. and Calder, D. M. 1989. The breeding biology of *Epacris impressa*. Is this species heterostylous? *Australian Journal of Botany*. 37: 43-54.
- Olesen, J.M., Eskildsen, L.I. and Venkatasamy, S. 2002. Invasion of pollination networks on oceanic islands: Importance of invader complexes and endemic super generalists. *Diversity and Distributions* 8: 181- 192.
- Paton, D. C. 2000. Disruption of bird-plant pollination system in southern Australia. *Conservation Biology* 14: 1323-1324.
- Paton, D. C. 1993. Honey bees *Apis mellifera* in the Australian environment. Does *Apis mellifera* disrupt or benefit the native biota? *Bioscience* 43: 95-103.
- Pizzey, G. and Knight, F. 1997. *Field guide to the birds of Australia*. Pymble, NSW: HarperCollins.
- Schwarz, M. P. and Hurst, P. S. 1997. Effects of introduced honey bees on Australia's native bee fauna. *The Victorian Naturalist* 114: 7-12.
- Shattuck, S. O. 1999. *Australian ants: their biology and identification*. CSIRO Publishing, Victoria, Australia.
- Spira, T. P. 2001. Plant-pollinator interactions: a threatened mutualism with implications for the ecology and management of rare plants. *Natural Areas Journal* 21(1): 78-88.
- Stace, H. M., Fripp, Y. J. 1977. Racialization in *Epacris impressa*. II habitat differences and flowering times. *Australian Journal of Botany* 25: 315-323.
- Sugden, E. A. and Pyke, G. H. 1991. Effects of honey bees on colonies of *Exoneura asimillima*, an Australian native bee. *Australian Journal of Ecology* 16: 171-181.
- Thomson, D. 2004. Competitive interactions between the invasive European honey bees and native bumble bees. *Ecology* 85(2): 458-470.

Waser, N.M. 1986. Flower constancy: definition, cause, and measurement. *American Naturalist* 127: 593-603.

Waser, N.M., Chittka, L., Price, M.V., Williams N.M., and Ollerton, J. 1996. Generalization in pollination systems, and why it matters. *Ecology* 77: 1043-1060.

Winfree, R., Aguilar, R., Vázquez, D. P., LeBuhn, G. and Aizen, M. A. 2009. A meta-analysis of bees' responses to anthropogenic disturbance. *Ecology*: 90(8): 2068-2076.

Zborowski, P. and Storey, R. 2003. A field guide to insects in Australia (second edition). Reed New Holland, Sydney.

## APPENDIX

Quantitative pollinator data set showing visits/flower/hour (Ea = *E. apsleyensis*, Eb = *E. barbarta*, Ee = *E. exserta*, Eg = *E. glabella*, Egr = *E. granitica*, Evb = *E. virgata* Beaconsfield, Evk = *E. virgata* Kettering, Ap = *Apis mellifera*, Ex = *Exoneura* sp., Mel = *Melangyna* sp., Tl = *Prosenia* sp., Ca = *Calliphora* sp., Rl = *Rutelia* (large) sp., Pl = *Vanessa kershawi*, Ts = Tachinid (shor-legs) sp., LaP = *Lasioglossum* (*Parasphcodes*) sp., Ac = *Aleucosia calophthalma*, Aa = *Vanessa itea*, Tsk = *Pasma tasmanicus*, Ho = *Homalictus* sp., Le = *Leioproctus* sp., Rs = *Rutelia* (small) sp., La = *Lasioglossum* sp., NP = *Pelecorhynchus* sp., SE = Eristalinae, Em = Empididae, Sc = *Scaptia* sp.)

	Ap	Ex	Mel	Tl	Ca	Rl	Pl	Ts	LaP	Ac	Aa	Tsk	Ho	Le	Rs	La	NP	SE	Em	Sc
Ea	0.0078	0.0127	0.0354	0.0062	0.0112	0.0003	0.0000	0.0006	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Eb	0.0000	0.0004	0.0000	0.0179	0.0044	0.0140	0.0017	0.0002	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0004	0.0000	0.0000	0.0155
Evb	0.1044	0.0010	0.0007	0.0000	0.0069	0.0014	0.0000	0.0000	0.0002	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Evk	0.0000	0.0229	0.0018	0.0514	0.0008	0.0000	0.0000	0.0005	0.0050	0.0010	0.0003	0.0013	0.0005	0.0005	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Ee	0.1377	0.0073	0.0000	0.0000	0.0150	0.0381	0.0000	0.0000	0.0000	0.0000	0.0020	0.0000	0.0000	0.0000	0.0053	0.0004	0.0000	0.0000	0.0000	0.0000
Eg	0.0525	0.0009	0.0006	0.0000	0.0022	0.0000	0.0000	0.0000	0.0013	0.0000	0.0000	0.0000	0.0002	0.0000	0.0012	0.0000	0.0000	0.0000	0.0000	0.0000
El	0.0051	0.0111	0.0048	0.0000	0.0048	0.0059	0.0000	0.0000	0.0031	0.0000	0.0000	0.0000	0.0005	0.0005	0.0003	0.0002	0.0000	0.0021	0.0005	0.0005
Egr	0.0572	0.0012	0.0000	0.0171	0.0040	0.0002	0.0150	0.0025	0.0000	0.0000	0.0003	0.0000	0.0000	0.0012	0.0000	0.0000	0.0083	0.0000	0.0046	0.0000

Floral data set (Ea = *E. apsleyensis*, Eb = *E. barbarta*, Ee = *E. exserta*, Eg = *E. glabella*, Egr = *E. granitica*, Evb = *E. virgata* Beaconsfield, Evk = *E. virgata* Kettering, ft = length of corolla (from floor of corolla to corolla mouth), gy = gynoecium length, an = anther length, anei = exsertion or inclusion of anthers (measured from corolla mouth to most distal point), cm = width of corolla mouth not including petals; cmp = width of corolla including petals; ft/g = corolla length/gynoecium. All measurements in millimetres)

	ft	gy	an	anei	cm	cmp	ft/g
El	3.5	2.5	1.5	1.5	1.25	9	1.75
Eb	5	6.5	1.75	1.5	2	12.5	0.77
Ee	4	5.5	1.5	2	2	10.5	0.71
Ea	3	1.75	1.25	-0.25	1	8.5	1.71
EvB	3.25	5.25	1.5	2	1.5	8	0.64
EvK	3.5	5.5	1.5	2	2	9	0.65
Eg	3.5	5	1.5	2	2	9.75	0.7
Egr	3.25	5.5	1.5	2.25	2	9.5	0.62

Habitat data set (Ea = *E. apsleyensis*, Eb = *E. barbarta*, Ee = *E. exserta*, Eg = *E. glabella*, Egr = *E. graniticola*, Evb = *E. virgata*Beaconsfield, Evk = *E. virgata*Kettering, df = dry sclerophyll forest, he = dry heath, wh = wet heath, sc = scrub, do = dolerite, gr = granite, al = alluvium, se = serpentinite, me = mudstone, sl = slope, ri = ridge, rb = river bank, mt = mountain summit, fl = flat, 0 = no, 1 = yes)

	df	he	wh	sc	do	gr	al	se	mu	sl	ri	rb	mt	fl
Ea	1	0	0	0	1	0	0	0	0	1	0	0	0	0
Eb	1	1	0	1	0	1	0	0	0	1	1	0	0	0
Evb	1	0	0	0	1	0	0	0	0	1	0	0	0	1
Evk	1	0	0	0	1	0	0	0	1	1	0	0	0	0
Ee	1	0	0	1	1	0	1	0	0	0	0	1	0	1
Eg	1	1	0	1	0	0	0	1	0	1	1	0	0	0
EI	1	0	1	0	1	0	0	0	0	0	0	0	0	1
Egr	1	0	0	0	1	0	0	0	0	1	0	0	1	0

Flowering time data set (Ea = *E. apsleyensis*, Eb = *E. barbarta*, Ee = *E. exserta*, Eg = *E. glabella*, Egr = *E. graniticola*, Evb = *E. virgata*Beaconsfield, Evk = *E. virgata*Kettering, 0 = no, 1 = yes)

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Ea	1	1	1	1	1	1	1	1	1	1	1	0
Eb	0	0	0	0	0	0	0	0	1	1	1	0
EvB	0	0	0	0	0	0	0	0	1	1	1	0
EvK	0	0	0	0	0	0	0	0	1	1	1	0
Ee	0	0	0	0	0	0	0	0	1	1	0	0
Eg	0	0	0	0	0	0	0	0	1	1	0	0
EI	1	0	0	0	0	0	0	0	0	0	1	1
Egr	0	0	0	0	0	0	0	0	1	1	0	0