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Bees of the Victorian Alps: network structure and interactions of introduced species

Running title: Bees of the Victorian Alps

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Abstract

Bees are considered the most important plant pollinators in many ecosystems, yet little is known about pollination of native plants by bees in many Australian ecosystems including the alpine region. Here we consider bee pollination in this region by constructing a bee visitation network and investigating the degree of specialism and network “nestedness”, which are related to the robustness of the network to perturbations. Bees and flowers were collected and observed from 10 sites across the Bogong High Plains/Mt Hotham region in Victoria. Low nestedness and a low degree of specialism were detected, consistent with patterns in other alpine regions. Twenty-one native and one non-indigenous bee species were observed visiting 46 of the 67 flower species recorded. The introduced *Apis mellifera* had a large floral overlap with native bees, which may reduce fecundity of native bees through competition. The introduced plant, *Hypochaeris radicata* (Asteraceae), had the largest and most sustained coverage of any flower and had the most visitations and bee species of any flower. The network developed in this study is a first step in understanding pollination patterns in the alpine/sub alpine region and serves as a baseline for future comparisons.

Keywords: Bees, Australian Alps, *Apis mellifera*, *Hypochaeris radicata*, pollination network.

Introduction

Bees are considered to be an indicator species group for ecosystem health. While their necessity to human survival is often overstated (Rader *et al.* 2016; Garibaldi *et al.* 2013), they are an excellent species group for studying changes in pollination processes within an ecosystem due to their dependence on flowers for nutrition (Vanbergen *et al.* 2017), whereas other pollinators, such as flies or wasps, exploit other resources (Burkle *et al.* 2013).

The interrelationship of bees with flowers results in a structural organisation that forms a network, which can then be quantified for its properties, importance and strength (Bascompte *et al.* 2003; Popic *et al*. 2013; Nielsen & Bascomte 2007). One component of networks involves specialisation, characterised by the number of links a species encounters in a network (Almeida-Neto *et al.* 2008; Bluthgen *et al.* 2006; Dorman 2011). Abundant generalists can cover a wide range of floral resources with high connectivity and are therefore important for network stability (Vanbergen *et al.* 2017). Specialist pollinators are rare (Bascompte *et al.* 2003; Nielsen & Bascompte 2007; Popic *et al.* 2013), and considered less redundant than generalists given that their loss can potentially have a greater effect on the plant community (Dorman 2011), however generalists have a greater effect on the networks structure (Vanbergen *et al.* 2017) particularly when generalists represent newly introduced, non-indigenous species.

Another related commonly-used network metric, "nestedness", is the degree of asymmetry of the network, and indicates its stability against perturbations; that is, the ability to function when individual species become extinct (Alimeida-Neto *et al.* 2007; Bascompte *et al.* 2003; Nielsen & Bascompte 2007; Popic *et al.* 2013). Nestedness reflects a nonrandom structure (Bascompte et al. 2003) that measures niche width and niche interactions (Dorman 2011; Dormann *et al.* 2009; Guimaraes & Guimaraes 2006). The presence of nestedness within interactive networks is hypothesized to arise due to uneven distribution of interacting species (Burkle *et al.* 2013; Nielsen & Bascomte 2007). Highly nested networks occur where specialised species interact with generalized ones (Almeida-Neto et al. 2008; Bascompte *et al.* 2003; Nielsen & Bascompte 2007). Although debated (Strona & Fattorini 2014), a high degree of nestedness is thought to indicate that a species is less likely to be vulnerable even when other species are eliminated from a network (Almeida-Neto *et al.* 2007; Bascompte *et al.* 2003; Nielsen & Bascompte 2007; Vanbergen *et al.* 2017).

Non-indigenous species in an environment are considered one of the biggest threats to global biodiversity (Goulson 2003; Valdovinos *et al.* 2009). Together with climate change and habitat deterioration, invasions by non-indigenous species constitute the three main anthropogenic threats to ecosystem processes, including pollination networks (Memmott & Waser 2002; Valdovinos *et al.* 2009, Memmott *et al.* 2007). Non-indigenous species can impact directly by predating on native species, or indirectly by causing behavioural shifts, niche displacement and competitive exclusion of natives (Mooney & Cleland 2001; Goulson 2003). The removal of a pollinator species can change foraging specialisation in unpredictable ways, such as through reduced floral fidelity and plant reproductive function (Brosi & Briggs 2013). These impacts can cause trophic cascades through an ecosystem that lowers resilience, including through altered nestedness (Folke *et al*. 2004). However, once established non-indigenous species can become an integral part of the network (Memmott & Waser 2002) and important for species persistence (Valdovinos *et al.* 2009).

There are two groups of non-indigenous species in the Australian Alps, the honeybee *Apis mellifera* L. 1758 (Apidae) and several non-indigenous plant species (McDougall *et al*. 2005) that could influence alpine networks. *Apis mellifera* is a prolific, polylectic forager that influences networks (Giannini *et al.* 2015; Santos *et al*. 2012), often being considered either detrimental or potentially beneficial to native plants (Paini & Roberts 2005). Negative impacts include displacement of native pollinators through resource competition, inefficient pollination of native flowers, and an increase in non-indigenous plant populations due to preferential visitation (Goulson 2003; Hanley & Goulson 2003; Kearns *et al*. 1998: Paini 2004; Paini & Roberts 2005; Paton 1993). Each of these effects has the potential to lower network nestedness (Strona & Fattorini 2014). *Apis mellifera* is considered competitive because of its large size, aggressive behaviour and social structure which provides an advantage over solitary species (Paton 1993; Manning 1997). There are no studies on the impact of honeybees on network structures in Australia, although they can indirectly alter the structure of a network by changing the connectivity and strength of interactions (Ginnini *et al.* 2015; Vanbergen *et al.* 2017).

Introduced plants continue to increase in abundance in the Australian Alps, with 175 species now recorded above 1500 m (McDougall *et al.* 2005). Invasive angiosperms often bloom for long periods, attracting pollinators (Memmott & Waser 2002). With strong presence within a pollination web, such species can potentially increase pollinator populations by increasing resources, thereby competitively reducing native flower fecundity and eroding asymmetric structure of networks to cause instability (Aizen et al. 2008, Memmott et al. 2004, Muñoz & Cavieres 2008).

Developing and quantifying a visitation network on the relationship between bees and flowers is a first step in determining pollinator / plant community structure. When species interconnections have been established, they provide a baseline to assess how any new invasive species might interact within the network, helping to assess their role as a threatening process in alpine ecosystems. Therefore, a visitation network of Victorian alpine/subalpine bee species and their angiosperm hosts across open heathland/grasslands (McDougall & Walsh 2007) is developed. We consider the potential impact of *Apis mellifera*, which has recently been detected (Nash 2013), on the structure of the network. The likely impact of the dominant non-indigenous plant species on bees and the network is discussed.

Methods

Study Sites

Ten sites were selected to have similar vegetation and flowering species from across the Bogong High Plains and Mt Hotham / Dinner Plain region, within the Victorian Alps. Sites were from 700m to 27.9 km apart (Table 1) across alpine (3) and sub alpine (7) ecosystems from 1400-1870 m a.s.l (Fig 1). Varying levels dissimilarity between site flowering vegetation, excluding wind pollenated species, were observed (Table 1), with the three alpine sites being less dissimilar compared with the subalpine sites. All sites shared at least 9 flowering species.

Field Methods

A stratified sample design was used. At all sites, surveys were conducted 3 times each month from November 2013 to March 2014 (N = 15) within the same pre-defined 100 x 100 m areas. Each survey consisted of 8 randomly placed 5 m x 2 m transects within this area. Percentage abundance of each flowering species was estimated in each transect and each transect patrolled for 15 minutes to record visitation; that is, a total of 2 hours was spent on observations per site. Air temperature was recorded at the start of each sampling at each site. Only bees were recorded, although it is acknowledged that flies, moths and other insects can also be important pollinators. Individual bees observed on a flower were caught with a butterfly net. For each capture, the bee and flower species were recorded. If the individual was not identifiable, a voucher was retained for subsequent identification. As permit restrictions did not allow for destructive sampling, the collection of pollen from flowers and bees did not yield results adequate for properly quantifying floral resources or a pollination network, hence the focus of this study was on visitation networks despite their limitations (Popic *et al.* 2013).

Flowers

Flowers in plots were measured in three ways: 1) total coverage as estimated by the number of floral units / m^2; 2) floral unit that bees were known to visit; and 3) floral unit on which bees were caught. Floral units were defined as are defined as non-connected florets, with flowering occurring when the flower is open and more than 50% of the anthers are showing or more than 50% of the ray florets have opened.

Network Analysis

Due to the low number of visitations per individual survey at each site and non-significance of networks (Appendix I), a network was created by pooling all observed visitation data to create a matrix, showing the number of times each bee species (A) visited each plant species (P) for Victorian alpine/subalpine open heathland/grasslands of the Bogong High Plains and Mt Hotham region. The network was constructed with the Bipartite package (Dormann *et al.* 2009) in R (R Core Team 2014), with nestedness and associated significance analysed in the ANINHADO program. Only bipartite connections between the two groups were considered, as unconnected pollinator species can skew results towards specialism due to a lack of information (Dormann 2011). To visualise networks, rectangles were generated in two columns that represent species, with their width proportional to how many interactions they have with the opposing group. Lines linking the two groups show the number of interactions. GIMP (GNU Image Manipulation Program 2001-2013) was used to colour the network, to make it easier to interpret and to arrange family phylogenies (Fig 2).

The network analysis involves two levels of indices. The first order indices look at the number of plant and bee species, the average number of links per species and how many visits and number of species were observed. The second order indices are calculated from qualitative data and affected by network size (Dormann *et al.* 2009; Popic *et al.* 2013), and represent the degree of the networks' nestedness and connectance. Connectance is the proportion of all possible links within the network (Dormann *et al.* 2009). Nestedness is a measure of the temperature (T) of a matrix. If a matrix is cold (0) then it has high nestedness, but if it is hot (100) then it is random. T was converted into the nestedness index, N, where N=(100–T)/100. In this index 0 is random and 1 is perfectly nested (Bascompte *et al.* 2003). In a perfectly nested network the most generalist bee visits all flowers and the most generalist flower is visited by every bee (Almeida-Neto *et al.* 2008). When these distributions of occurrence are arranged into a matrix, it is considered 'perfectly nested' if most of the presences are in the top left corner of the matrix, forming a triangle (Ulrich *et al.* 2009). Any metric that quantifies the arrangement of a network aims to determine how much it deviates from the perfectly nested arrangement (Almeida-Neto *et al.* 2008). Nestedness is relatively insensitive to sampling effort (n) and is more affected by the number of species and links in the network (Nielsen & Bascompte 2007).

A null network model was used to compare the structure of networks with varying size (Popic et al., 2013); this accounts for sensitivity to the number of species in the higher and lower trophic levels, the asymmetry of network dimensions and the number of interactions, when determining statistical significance of the degree of nestedness of the matrix (Dormann et al., 2009). Matrix T was recalculated using a Monte Carlo randomization analysis (1,000 randomisations) to create null networks, and compared with actual networks to determine how often the network could be produced by chance (Dormann, 2011). A nestedness metric based on Overlap and Decreasing Fill (NODF) (Guimaraes & Guimaraes 2006) and CE null model (Strona & Fattorini 2014) were also used to test whether observing an interaction between bees and flowers being specialised was greater than expected by chance (Alarcón 2010).

The second order indices included a measure of the degree of specialisation of species in a network (H2') and specialisation at the species level (d'). Both indices are robust to variation in sampling effort and variation in the matrix (Blüthgen *et al*. 2006). H2' is based on how much each species deviates from its actual number of interactions to an expected number, given the total interactions within the web. If there is no specialisation H2'will be close to 0, but if there is high specialisation H2' is closer to 1. The d' measure accounts for the importance of the availability of each niche proportionally (Dormann 2011). If a pollinator uses all niches in the same proportion available in the environment, it is a more generalist species, being more opportunistic. If a pollinator uses few niches in contrast to their availability in the environment, it is a specialist. For the most generalized bee species d' = 0, and for the most specialist bee species d' = 1 (Blüthgen *et al.* 2006, Dormann 2011).

Two factors were thought to influence bee activity directly, hence likely to influence network measures. Temperature has a direct influence on bee activity, hence the association between temperature recorded when bees were sampled was tested directly using a Pearson correlation. Regression analysis did not indicate elevation being a significant factor for either the indices of nestedness ($F_{1,9} = 0.77$; $P = 0.406$) or connectiveness ($F_{1,9} = 0.02$; $P = 0.889$). ANOVA was used to determine the effect of flower coverage, as quantified by flora units / m^2 on visitation by a bee. The coverage of native and introduced flowers were kept as separate independent variables, and the percentage of native and introduced flowers bees were caught on relative to their coverage was used to test if non-indigenous bees favour non-indigenous flowers.

Results

Structure of the visitation network

A total 2,262 captures for 22 bee species (Table 2) was recorded on 15 flower families (Table 3 & Fig. 2). Four families were represented (relative abundance): Apidae (63.09%), Colletidae (15.69%), Halictidae (18.66%) and Megachilidae (2.56%) (Fig. 2). Two species of Apidae visited the most flower species: *A. mellifera* (37.98% of all bees) and *Exoneura bicolor* (25.11% of all bees). Four species of Colletidae were recorded (Fig. 2), with *Leioproctus chalybeatus* (Colletidae, Erichson 1842) a relatively common species representing 95% of Colletidae caught (14.99% of all bees). Halictidae had the most species (Fig. 2), with *Lasioglossum subrussatum* (Cockerell 1922) the most common (6.81% of all bees), followed by *L. baudini* (3.76% of all bees). Five *Lasioglossum* spp. were not observed on invasive plant species, however three of these species were least abundant: *L. gynochilum* (Michener 1965) (0.09% of all bees), *L. imitans* (Cockerell 1914) (0.09% of all bees) and *L. mundulum* (Cockerell 1916) (0.13% of all bees). Two species of Megachilidae, *Megachile aurifrons* (Smith 1853) and *M. macularis* (Torre 1896), were recorded preferring Fabaceae flowers (1.72% coverage).

Bees were captured on 46 of the 67 flower species recorded. Visited flowers had greater coverage within sites than non-visited flowers (92.06% of total coverage including non-visited flowers). The plant family Asteraceae had the most species and the most bee visits (55.53%; Fig. 2). The second largest family, Fabaceae, had fewer than half the bee visits of the Asteracea (18.7%). The other families of flowers had very low coverage and bee visits, except for Ranunculaceae; 10.71% coverage, 6.59% total bee visitation.

The network had low connectance, mid-range nestedness, with H2’ being of mid-range specialisation and the network being more generalist (Table 3). The monthly nestedness data (N = 1) contradicted overall nestedness (N = 0.528), which is most likely due to the low number of species and links in the network (Nielsen & Bascompte 2007), hence the pooling of data. The d’ index for bees and plants was low (Table 3), suggesting alpine species maximize niche utilisation. Overall bees were found to be opportunists, but for individual species the d’ index had a large range (Table 2). The most generalist bee species was *L. sculpturatum* (Halictidae, Cockerell 1930) and the least opportunistic was *M. macularis*.

The non-indigenous honeybee, *A. mellifera,* was caught on more flower species than any other bee (30); three of the species visited were not visited by other bee species (Fig. 2). Three invasive flowering species were visited by *A. mellifera* (42.5% of its visits), whilst native bees visited 6 non-indigenous species (24.23% of native bee visits). *Apis mellifera* was the only visitor to the non-indigenous *Triflolium repens* L. (Fabaceae) (6.81% of its visits), but was also caught on the native species *Podolobium alpestre* (F.Muell.) (Fabaceae) (6.19%), *Wahlenbergia gloriosa* Lothian (Campanulaceae)(3.05%), *Hovea montana* (Hook.f.) (Fabaceae) (0.75%), *Orites lancifolia* F.Muell (Proteaceae) (3.27%) and *Stylidium armeria* (Labill.) (Stylidiaceae)(1.02%).

Temperature was associated with the number of bees observed visiting a flower, with native bees having a slightly stronger correlation (0.339, $R^2 = 0.115$, N = 108, $P < 0.01$) than *A. mellifera* (0.23, $R^2 = 0.53$, N = 108, $P = 0.016$).

Non-indigenous flower visitations

Though non-indigenous flowering plant species (7) were present across all 10 sites in varying amounts, all except *Hypochaeris radicata* L. (Asteraceae) were in low abundance. Bees visited five non-indigenous species (Fig. 2). Coverage of native and non-indigenous species influenced bee choice (ANOVA $F_{2,133}=74.83$, P<0.01); that is, the greater flower coverage, the more bees visited that species. *Hypochaeris radicata* had the most coverage (9.82%) and was the only species flowering every month of this study, hence it had the greatest number of pollinator species caught on it (14) and highest percentage of visitations (17.95%; Fig. 2). Other introduced flowers had relatively low coverage and few visits. The non-indigenous *Viola bicolor* Pursh (Violaceae) and *Verbascum thapsus* L. (Scrophulariaceae) were not visited within the study plots. *Apis mellifera* and native bees visited *H. radicata* to a similar extent (*A. mellifera* 51.23%, natives 48.77%). *Exoneura bicolor* was caught on more flowers than any other native bee and favoured *Achillea millefolium* L. (Asteraceae) (4.2%); it was the only bee caught on *Hieracium praealtum* L. (Asteraceae)(0.13%), which had low coverage (0.06%). *Leioproctus chalybeatus* visited 19 flowers (41.3%), favouring *H. radicata* (3.54%), and was the only visitor to *Leucanthemum vulgare* Lam. (Asteraceae) (0.04%). Megachilidae (2 spp.) were the only group observed on *Lotus corniculatus* L. (Fabaceae) (0.93% coverage).

Discussion

Nature of the visitation network

Bees found in the Victorian Alps have a strong, positive visitation rate associated with the amount of floral coverage, have low connectivity, low specialism and mid-range nestedness. Comparison with other alpine networks is difficult due to the most efficient pollinators in alpine ecosystems, *Bombus* spp. (Bergman, Molau & Holmgren 1996; Bingham 1998), not being present on the Australian mainland as confirmed in this study. This is compounded by limited information from the southern hemisphere (e.g. Primack 1978; Primack 1983), with only one study from the Australian mountains (Inouye & Pyke 1988). That study recorded 13 bee species from the Snowy Mountains, NSW, on 43 flowering species. Of the bee species recorded, only two were considered polylectic, with the other 11 species monolectic (Inouye & Pyke 1988). However, the data available in that study were not used in a network analysis, precluding a direct comparison.

Our results (Table 3) can be loosely contrasted with a visitation network from the Simpson Desert, Australia (Popic *et al*. 2013). That visitation network had nearly twice the bee species (50) detected from a similar number of plant species (52), but half the number of sites (5); a similar mid-range degree of specialisation was found in this study (H2' 0.493), with a slightly higher degree of bee (d’ 0.46-0.56) and plant (d’ 0.33-0.47) specialisation and a lower realised proportion of links (connectance 0.065); however, nestedness in that network was very high (0.948) (Popic *et al*. 2013).

Although not as low as a desert network, the low connectivity observed here is consistent with observations from other alpine regions. In a comparison of networks from altitudinal gradient studies (Olesen & Jordano 2002), connectivity was found to decrease with an increase in altitude. Aizen *et a*l (2008) found a negative correlation between connectance and altitude. Species richness can influence indices from a network limiting comparisons between networks (Blüthgen *et al*. 2006), in that smaller networks have fewer asymmetric interactions potentially influencing this pattern (Fang & Huang 2012).

Low nestedness is thought to be largely due to plant species being more generalized at higher altitudes (Olesen & Jordano 2002), due to the limited period in which flowering (and thus pollination) can occur. This contrasts with the mid-range nestedness value (0.528) for our Victorian Alps visitation network (Table 3), and other alpine pollination networks such as Fang and Huang (2012) who found nestedness of approximately 0.96 at 3500 m. This demonstrates that the literature doesn't unequivocally support low nestedness in alpine areas. It does, however, support low connectance (Aizen et al 2008).

Influence of non-indigenous *Hypochaeris radicata*

Hypochaeris radicata was a consistent presence across the survey period and was the most visited flower, particularly favored by the introduced bee *A. mellifera*. Originally from Morocco, *H. radicata* (Asteraceae) is considered naturalised across temperate Australia (Ortiz et al. 2008). This dominant species has spread from roadsides to become established across alpine/ sub alpine grasslands and is now a dominant species across the Australian Alps. Non-indigenous plants in pollinator networks are primarily generalists that seemingly persist by being attractive to pollinators (Memmott & Waser 2002). In pollination networks, these plants may compete with other flowers and/or facilitate pollinator populations, or have no impact (Valdovinos et al. 2009). All of these factors have the potential to lower the nestedness strength of a network so other perturbations have a greater negative effect that can lead to species extinction and ultimate collapse of the whole network (Memmott & Waser 2002).

The higher the coverage an introduced flower species has, the greater its attraction to pollinators (Primack 1983; Kearns *et al*. 1998; Packer *et al.* 2005; Aizen *et al*. 2008; Muñoz & Cavieres 2008). This changes visitation rates and connectance within a network (Valdovinos et al. 2009). Aizen & Harder (2008) found that networks with high introduced flower presence exhibited weaker nestedness than networks with fewer introduced flowers. Introduced flowers can change the strength of asymmetrical mutualism within the pollination network, particularly if they have a large coverage, as was the case in this study for *H. radicata*.

This is an issue for oligolectic bees that not only visit fewer flowers, but also have reduced genetic variation compared with polylactic bees, so are at greater risk in a network (Aarssen 1981; Packer *et al.* 2005). With higher nestedness, an oligolectic species is less likely to become isolated and its extinction risk decreases. Therefore, the bees in the Victorian Alps network may be at a higher risk of becoming extinct, because of the instability of the network as a whole. However, although nestedness of the network is unusually low, *H. radicata* may also be having a positive effect on the bees that visit it. Introduced flowers are known to increase populations and redistribute pollinators because they offer large rewards for extended periods of time (Memmott & Waser 2002;

Lopezaraiza-Mikel et al. 2007). Sustained availability is attractive to bees because of floral constancy, but also because bees need large amounts of nectar and pollen. Müller *et al.* (2006) found that for the 41 bee species found in Europe, 85% needed all of the pollen from 30 flowers to rear a single larva. One female bee needs 28,475 flower heads over a lifetime. The nutritional content of pollen is also important, and proteins are essential for a bee to reproduce and for its longevity (Weiner *et al.* 2010). This can be an issue in monoculture crops, where bees are forced to feed on flowers that are low in protein and amino acids (Vanenglesdorp *et al.* 2007). *Hypochaeris radicata* has high levels of protein and amino acids (Weiner et al. 2010), and is therefore particularly suitable for bee populations.

Such findings suggest that once introduced species become established in an ecosystem, their removal should be considered carefully from many angles, beyond the simplified perception that they have negative effects (Lopezaraiza-Mikel et al. 2007). In fact, the removal of introduced flowers can increase extinction risk of pollinators, particularly if they have generalised effects (Valdovinos *et al.* 2009). Because *H. radicata* was the most connected in the network, it forms the core of the visitation network. The removal of a core species increases the extinction risk for bee species (Vanbergen & Initiative 2013). Of course, removal of *H. radicata* may have a positive effect on native plants for other reasons, but there are also many other non-indigenous species incursions in this region that could benefit from its removal.

With invasive, non-indigenous species impacting alpine environments along with other factors including climate change and associated fire incidence effecting vegetation (Wahren *et al.* 2013; Camac *et al.* 2017), local extinctions of bee species are probably inevitable, but this may be buffered by the presence of additional energy sources provided by naturalised flowers. With warmer conditions habitat resistance lowers, hence increasing the invasion potential of non-indigenous plants (Beaumont *et al.* 2009). Though such flowers may sustain bee populations, they can change the dynamics of an ecosystem, increasing the risk of a regime shift and extinction cascade (Memmott & Waser 2002; Folke *et al.* 2004). Ultimately, long term monitoring will be required to measure these changes and identify potential shifts in the network that threaten particular plant species. Competition experiments would also be useful to assess the impact of *Apis mellifera* on native populations both in the presence and absence of non-indigenous flowering species.

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Table 1. Geographic distances between individual sites (top right) and Jaccard dissimilarity indices for flowering plant species between sites (bottom left). Sites are given in Figure 1.

	Buckety	**ITEX**	**Lang**	**Mt McKay**	**Cult**	**Mt Nelse**	**WH**	**JB**	**Mt Hotham**	**Baldy**
Buckety		6.9 km	8.7 km	11.3 km	9.5 km	10.7 km	10.0 km	14.1 km	19.1 km	20.0 km
ITEX	62%		5.3 km	4.4km	9.1 km	9.4 km	14.0 km	13.8 km	15.2 km	15.8 km
Lang	66%	49%		7.5 km	3.8 km	4.3 km	6.8 km	18.1 km	20.7 km	21.4 km
Mt McKay	63%	59%	44%		10.3 km	9.3 km	14.0 km	16.5 km	15.3 km	15.9 km
Cult	45%	57%	55%	71%		1.9 km	4.1 km	22.0 km	24.5 km	25.1 km
Mt Nelse	62%	55%	36%	50%	58%		5.6 km	22.3 km	23.8 km	24.7 km
WH	60%	66%	67%	76%	58%	75%		23.0 km	27.0 km	27.9 km
JB	69%	74%	65%	59%	76%	70%	67%		9.5 km	10.0 km
Mt Hotham	61%	60%	48%	44%	56%	38%	81%	76%		0.7 km

Baldy	68%	80%	73%	62%	74%	67%	76%	74%	69%	

Table 2 Bee species of the Bogong High Plains and Mt Hotham region including degree of specialization.

Apidae: *Apis mellifera* L. (1758)	0.470
Apidae: *Exoneura (Exoneura) bicolor* (Smith, F. 1854)	0.449
Colletidae: *Hylaeus (Euprosopsis) honestus* (Smith, 1879)	0.458
Colletidae: *Hyphesma atromicans* (Cockerell, 1913)	0.359
Colletidae: *Leioproctus (Lamprocolletes) chalybeatus* (Erichson, 1842)	0.452
Colletidae: *Leioproctus (Lamprocolletes) clarki* (Cockerell, 1929)	0.370
Halictidae: *Homalictus (Homalictus) sphecodoides* (Smith, 1853)	0.391
Halictidae: *Lasioglossum (Chilalictus) disclusum* (Cockerell, 1914)	0.337
Halictidae: *Lasioglossum (Chilalictus) asperithorax* (Cockerell, 1910)	0.365
Halictidae: *Lasioglossum (Chilalictus) baudini* (Cockerell, 1915)	0.284
Halictidae: *Lasioglossum (Chilalictus) brazier* (Cockerell, 1916)	0.254
Halictidae: Lasioglossum (Chilalictus) clelandi (Cockerell, 1910)	0.396
Halictidae: *Lasioglossum (Chilalictus) gynochilium* (Michener, 1965)	0.266
Halictidae: *Lasioglossum (Chilalictus) littleri* (Cockerell, 1914)	0.389
Halictidae: *Lasioglossum (Chilalictus) mundulum* (Cockerell, 1916)	0.247
Halictidae: *Lasioglossum (Chilalictus) sculpturatum* (Cockerell, 1930)	0.161
Halictidae: *Lasioglossum (Chilalictus) seductum* (Cockerell, 1914)	0.304
Halictidae: *Lasioglossum (Pharasphecodes) subrassatum* (Cockerell, 1922)	0.310
Halictidae: *Lasioglossum hilactum* (Smith, 1853)	0.428
Halictidae: *Lasioglossum imitans* (Cockerell, 1914)	0.524
Halictidae: *Lasioglossum culpturatum* (Cockerell, 1930)	Not Calculated
Megachilidae: *Megachile aurifrons* (Smith, 1853)	0.271
Megachilidae: *Megachile macularis* (Torre, 1896)	0.579

Table 3. Indices of the network of bees and the flowers they visit, in the Bogong High Plains.

Significance of the network is indicated as P(Ce). Indices are described in the text and listed below.

	Network (all months)
Number of bee species	**22**
Number of plant species	**46**
Links per species	**2.956**
Visits	**2,262**
C (Connectance)	**0.199**
Nestedness Index (N)	**0.528**
P(Ce)	**<0.01**
H2'	**0.406**
Mean bee specialisation index d'	**0.367**

C (Connectance): the proportion of all possible links within the network

N (Nestedness): an index reflecting the temperature of a matrix. Under high nestedness (N=1), generalist bees visit all flowers and generalist flowers are visited by all bees. Under low nestedness (N=0) the association is random.

P(Ce): represents probability of an interaction between bees and flowers being specialised was greater than expected by chance.

H2’: degree of specialisation of species in a network. If there is no specialisation the index approaches 0.

d’: degree of specialisation at the species level taking into account available niches. If species have a high level of specialisation, d’ approaches 1.

Figure 1. Location of field sites in the Victorian Alps, Australia.

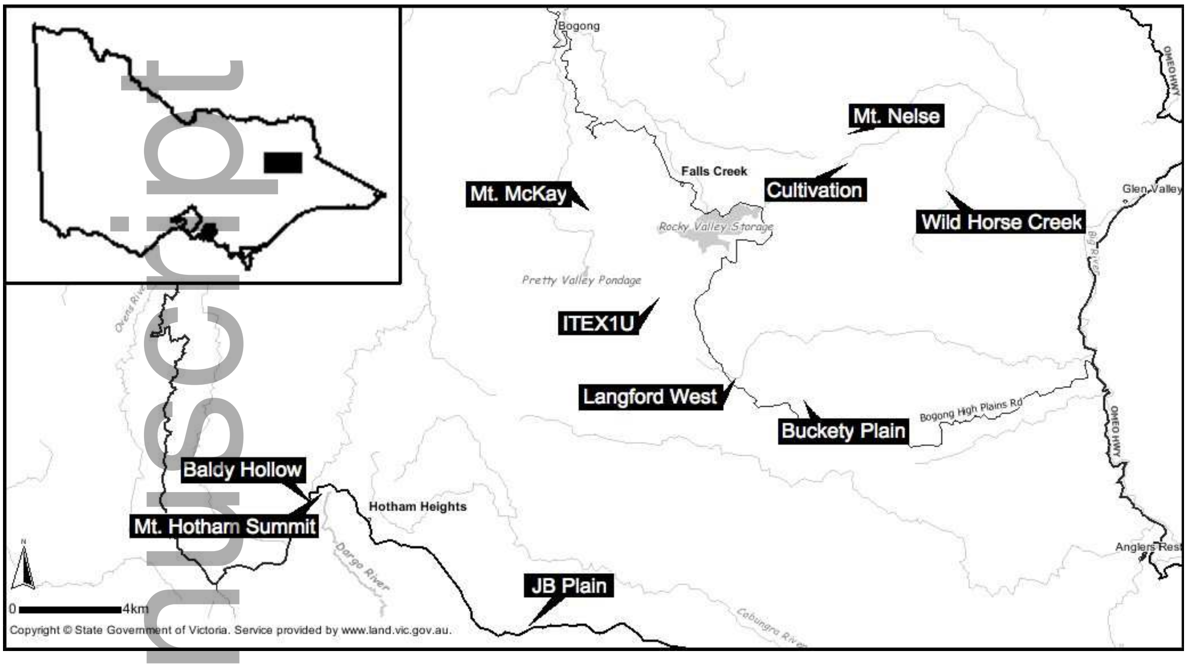


Figure 2. Quantitative bee and flower visitation network. The width of lines reflects the number times individuals of different bee species (left side) were observed to visit flowers of different plant species (right side). Size of the blocks for each bee and flower species are representative of the number of bees caught and of the times a flower was visited. Brackets show the family of that species. Asterisks indicate non-indigenous species.

Appendix 1. Individual site data with Indices of the network of bees and the flowers they visit, across the Bogong High Plains. Significance of the network is indicated as P(Ce). Indices are described in the text and listed below.

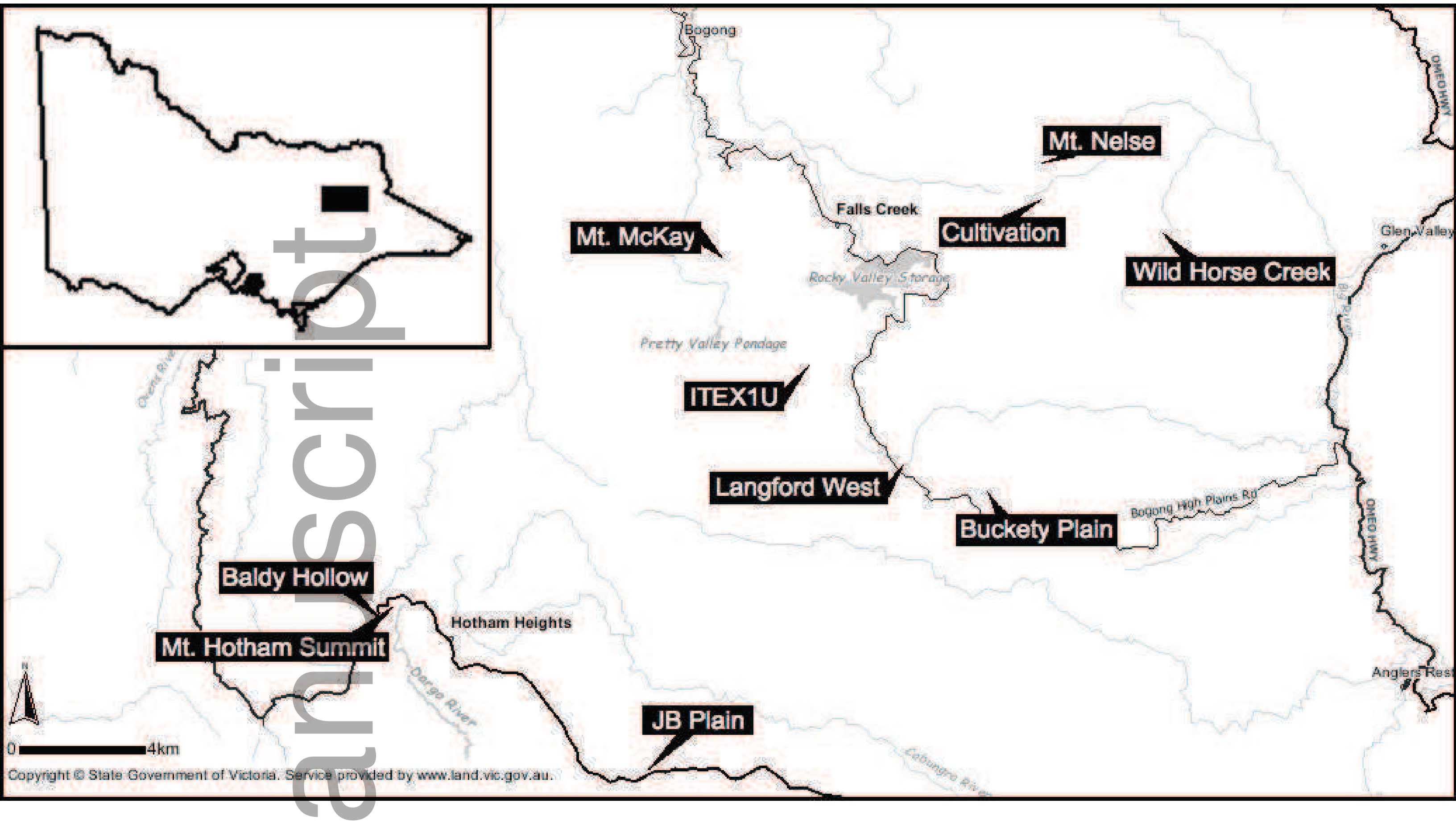
Site	Elevation m a.s.l.	Bee spp.	Flower spp. visited	Links per species	Visits	N	P(Ce)	H2’	C
Wild Horse Creek	1400	9	8	1.05	100	0.35	0.97	0.77	0.22
Buckety Plain	1550	14	12	1.46	291	0.49	0.99	0.50	0.23
Langford West	1625	16	20	1.64	318	0.35	0.93	0.52	0.18
JB plain	1636	14	13	1.59	401	0.71	0.66	0.39	0.24
Baldy Hollow	1650	19	19	1.39	394	0.54	0.92	0.64	0.15
Cultivation	1685	10	11	1.43	102	0.19	0.81	0.45	0.27
Pretty Valley	1757	9	12	1.57	179	0.49	0.91	0.51	0.31
Mt Hotham summit	1810	14	11	1.20	245	0.47	0.89	0.45	0.19
Mt McKay	1820	8	12	1.00	142	0.27	0.92	0.56	0.21
Mt Nelse	1880	11	11	1.18	88	0.19	0.88	0.60	0.21

N (Nestedness): an index reflecting the temperature of a matrix. Under high nestedness (N=1), generalist bees visit all flowers and generalist flowers are visited by all bees. Under low nestedness (N=0) the association is random.

P(Ce): represents probability of an interaction between bees and flowers being specialised was greater than expected by chance.

H2’: degree of specialisation of species in a network. If there is no specialisation the index approaches 0.

C (Connectance): the proportion of all possible links within the network



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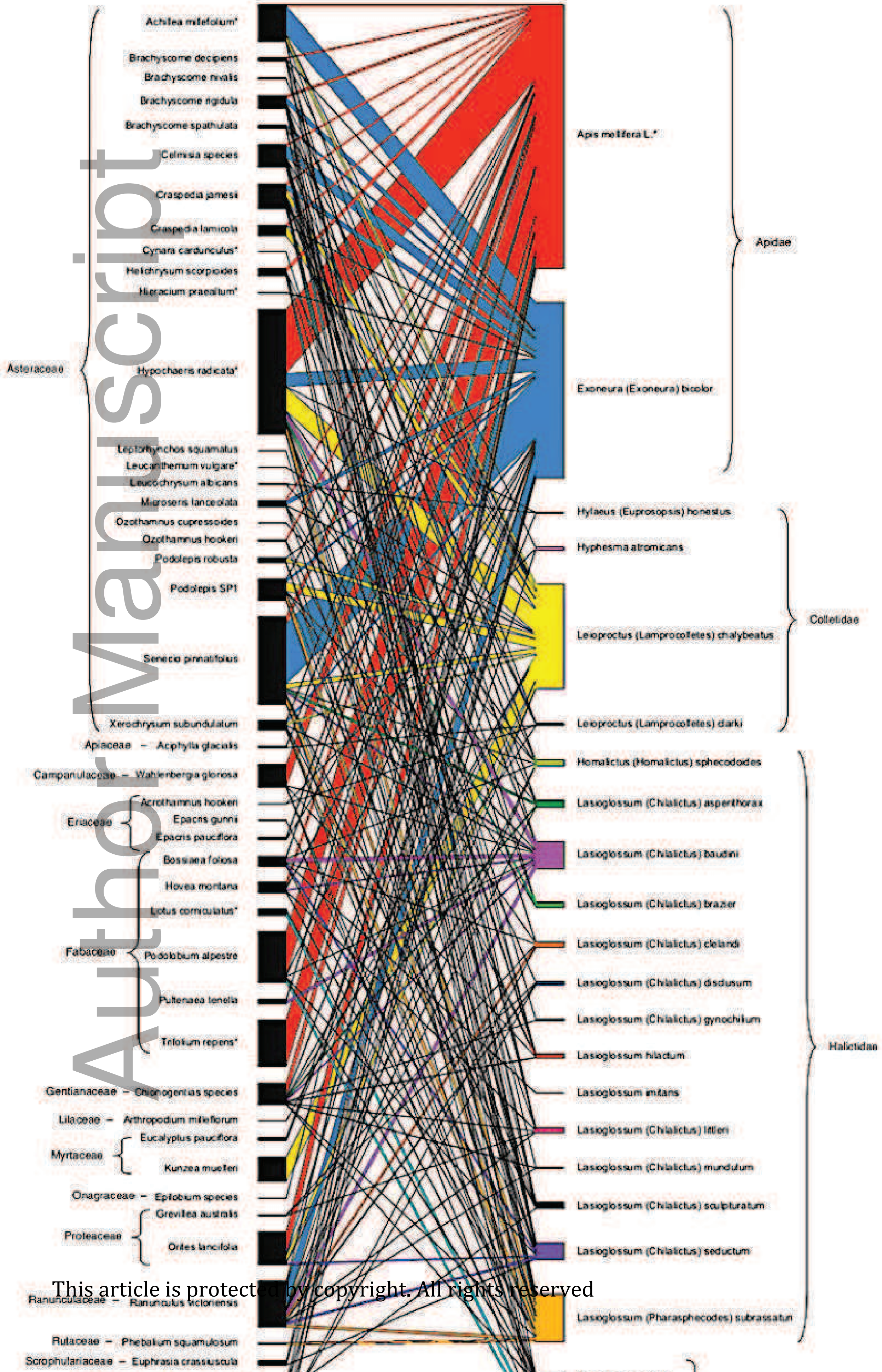
Asteraceae
Achillea millefolium*
Brachyscome decipiens
Brachyscome nivalis
Brachyscome rigidula
Brachyscome spathulata
Celmisia species
Craspedia jamesii
Craspedia lamicola
Cynara cardunculus*
Helichrysum scorpioides
Hieracium praealtum*
Hypochaeris radicata*
Leptorhynchos squamatus
Leucanthemum vulgare*
Leucochrysum albicans
Microseris lanceolata
Ozothamnus cupressoides
Ozothamnus hookeri
Podolepis robusta
Podolepis SP1
Senecio pinnatifolius
Xerochrysum subundulatum
Apiaceae – Aciphylla glacialis
Campanulaceae – Wahlenbergia gloriosa
Ericaceae
Acrothamnus hookeri
Epacris gunnii
Epacris pauciflora
Fabaceae
Bossiaea foliosa
Hovea montana
Lotus corniculatus*
Podolobium alpestre
Pultenaea tenella
Trifolium repens*
Gentianaceae – Chionogentias species
Liliaceae – Arthropodium milleflorum
Myrtaceae
Eucalyptus pauciflora
Kunzea muelleri
Onagraceae – Epilobium species
Proteaceae
Grevillea australis
Orites lancifolia
Ranunculaceae – Ranunculus victoriensis
Rutaceae – Phebalium squamulosum
Scrophulariaceae – Euphrasia crassiuscula
Apis mellifera L.*
Exoneura (Exoneura) bicolor
Apidae
Hylaeus (Euprosopsis) honestus
Hyphesma atromicans
Leioproctus (Lamprocolletes) chalybeatus
Leioproctus (Lamprocolletes) clarki
Colletidae
Homalictus (Homalictus) sphecodoides
Lasioglossum (Chilalictus) asperithorax
Lasioglossum (Chilalictus) baudini
Lasioglossum (Chilalictus) brazieri
Lasioglossum (Chilalictus) clelandi
Lasioglossum (Chilalictus) disclusum
Lasioglossum (Chilalictus) gynochilum
Lasioglossum hiltacum
Lasioglossum imitans
Lasioglossum (Chilalictus) littleri
Lasioglossum (Chilalictus) mundulum
Lasioglossum (Chilalictus) sculpturatum
Lasioglossum (Chilalictus) seductum
Lasioglossum (Pharasphecodes) subrassatum
Halictidae