Honey bees (Hymenoptera: Apidae) outnumber native bees in Tasmanian apple orchards: Perspectives for balancing crop production and native bee conservation

Kit S Prendergast,^{1*} Nicolas Leclercq² and Nicolas J Vereecken²

¹Molecular and Life Sciences, Curtin University, Bentley, WA 6102, Australia.

²Agroecology Lab, Free University of Brussels, Boulevard du Triomphe CP 264/02, Brussels B-1050, Belgium.

Abstract

Apples are a major crop globally, including in Tasmania (Australia) – known as ‘the Apple Isle’ owing to the key role of apples in Tasmania’s history and economy. Most apple cultivars are obligate entomophilous species, and fruit quantity, quality and economic value are enhanced under insect pollination. Whilst the introduced European honey bee (*Apis mellifera*) is often assumed to be the main pollinator of apple in most regions of the world, including Australia, there is an increasing interest in alternative pollinators. The pollinator community of Tasmanian apple crops, however, has never been assessed. In this study, we surveyed four apple orchards for 3 days each during peak bloom in the Huon Valley region to characterise bee assemblages visiting blooming apple trees and the native bee fauna associated with surrounding flowering vegetation. Our results show that honey bees were the predominant visitors to apple blossoms (90.7% of visits), followed by the introduced bumble bee *Bombus terrestris* (5.9% of visits), with only a minor contribution by native bees (3.3% of visits). Twenty-six species of native bees were collected in total, of which only 10 species (five *Exoneura* (Apidae), four *Lasioglossum* (Halictidae) and one *Euryglossa* (Colletidae) species) were collected from apple blossoms, with *Exoneura* being the most abundant visitors. Few native bees were captured on apple blossoms, however co-blooming surrounding native vegetation, as well exotic flowers, hosted a high diversity and abundance of native bees. Site conditions influenced community composition, including abundance and representation of introduced bees compared to native bees visiting apples. Additionally, warmer temperatures favoured native bees. Collectively, our results suggest that Tasmania’s apple production in its current state is unlikely to rely exclusively on native pollinators. Native bees nevertheless warrant conservation in such an insular crop production system. This can be achievable through retaining native flowering plants and even exotic non-crop flowers in and around orchards. Promoting the diversity and abundance of native bees through habitat enhancement may have additional benefits, such as filling current and future pollination demands and gaps, a key strategy under scenarios of climate change.

Key words apple, bee, bumblebee, honey bee, native bee, Tasmania, weather, weed, wild bee, wildflower.

INTRODUCTION

Apples (*Malus domestica* varieties: Rosaceae) are a major food crop across the world, including in Australia where it has been introduced by colonists and cultivated since the late 17th century (Luby 2003; Keogh *et al.* 2010a). The majority of apple cultivars are self-incompatible (Dulta & Verma 1987), produce seeds through obligate entomophily, and insect pollination is reported to enhance yield, fruit quality and overall crop economic value (Klein *et al.* 2007; Garratt *et al.* 2014; Miñarro & García 2018; Pardo & Borges 2020). Honey bees (*Apis* spp., predominantly *Apis mellifera*, but also *Apis cerana* in southern, south-eastern and eastern Asia) are traditionally used as the main pollinators of apples (Pardo & Borges 2020), yet there is increasing interest in alternative pollinators, including in Australia, owing to the similar or higher per-visit performance in pollen transfer by native or other managed species (Hogendoorn *et al.* 2006; Rader *et al.* 2009; Mader *et al.* 2010; Christmann & Aw-Hassan 2012).

Although honey bees are usually considered to be the most important pollinator of apple flowers, there is evidence to suggest that solitary native bees have proven as effective, if not more effective, than honey bees as pollinators of apple flowers (Vicens & Bosch 2000; Bosch & Kemp 2002; Mallinger & Gratton 2015; Park *et al.* 2016). This is due to comparatively low pollination efficiency at the individual level in honey bees because they move between flowers on the same plant or because the pollen they collect is no longer available for plant sexual reproduction, making them poor pollinators for plants such as self-incompatible apple varieties (Free 1966). Honey bees may even be detrimental to successful pollination as they have been observed to primarily visit petal-less or even wilted flowers with dehiscing anthers (Williams & Brain 1985). In addition, pollinator diversity has been found to positively affect apple yield (Martins *et al.* 2015; Blitzer *et al.* 2016; Földesi *et al.* 2016), and more generally, reports indicate that diverse wild bee communities are of overarching importance for effective pollination and inter-annual yield stability for many crops (Garibaldi *et al.* 2011; Garibaldi *et al.* 2013), particularly in a context of global change

*kit.prendergast21@gmail.com

(Potts *et al.* 2010; Potts *et al.* 2016; Settele *et al.* 2016). Differences in body size and thermal niche may mean that different bee taxa are differentially affected by weather and climatic conditions (Buckley & Kingsolver 2012), and so an understanding of how temperate-origin introduced bees, and the endemic Australian bees, respond to variations in temperature and other environmental conditions can provide more stable pollination services (Tuell & Isaacs 2010) and help predict how pollination assemblages may be influenced by variable weather conditions, as well as ongoing climate change (Grose *et al.* 2010; Rader *et al.* 2013).

It is estimated in Australia that apple yield would decline by 90% in the absence of honey bees (Gibbs & Muirhead 1998). However, Australia has a rich diversity of native bees, comprising over 2000 species, including pollen generalist taxa (Houston 2018), with the potential to forage on apple flowers. Despite the economic importance of the crop pollination services, management guidelines for pollination to focus primarily on honey bee management (Goodman 1994; Department of Primary Industries and Regional Development 2017). To date, the few studies documenting the bee visitors to apple flowers in Australia have been limited to coarse taxonomic levels (Saunders & Luck 2016; Brown *et al.* 2020). Furthermore, in a recent study by Saunders and Luck (2018), honey bees were excluded on the assumption that they were managed, which may be inappropriate given that feral honey bees are often present in Australian ecosystems (Paton 1996) and which has hindered the possibility to properly evaluate the relative contribution of honey bees to crop pollination. Another introduced pollinator species of interest in the Tasmanian context besides the European honey bee is the bumblebee *Bombus terrestris*, which was first recorded in Tasmania in 1992 as an illegally introduced species. Today, *B. terrestris* is well established in the Apple Isle and occupies much of the territory (Semmens *et al.* 1993; Hingston 2006). Although known to be effective pollinators of apple flowers (Goodell & Thomson 1997; Thomson & Goodell 2001; Pérez-Méndez *et al.* 2020), bumblebees have potential negative impacts on both native bees and honey bees through competition (Kingston & McQuillan 1998; McQuillan & Hingston 1999) and can promote the spread of invasive weeds (Stout *et al.* 2002).

Insular landscapes are theoretically expected to be characterised by a depauperate fauna compared to the neighbouring continent (Michener 1979), but the extent to which the 'Apple Isle' of Australia (McConnell & Servant 1999; Hall 2014) harbours diverse communities of native bees and what flora they rely on (apples as well as alternative foraging resources) remains virtually unknown. This is however particularly relevant to the economy of the Tasmanian pome fruit industry, which is dominated by apple production, has a farm-gate value of AUD\$32.2M (Fruit Growers Tasmania 2019) and, in 2002, accounted for approximately 18% of the total Australian production and 65% Australian apple exports (Salter 2002).

In this study, we aimed to contribute to filling the above-mentioned gaps in our knowledge by investigating the community structure of bees associated to commercial apple orchards in Tasmania. Specifically, we assessed the contributions

of bee taxa – both Australian native bees and introduced bees (honey bees and *B. terrestris*) as visitors to apple orchards, and identify the native bees visiting the apple flowers as well as other flowering plant species in the vicinity. Results from this study will go towards identifying the importance of different bee taxa to apple pollination in Tasmania and provide management recommendations for enhancing on-farm native bee diversity.

MATERIALS AND METHODS

Survey methods

K. S. P. surveyed four apple orchards in October 2019, three of which were 'Certified Organic' (Australian Organic Ltd 2019) and one which used Integrated Pest Management (IPM) (Table S1). Only the IPM orchard had managed honey bee colonies (30 colonies, at densities of approximately 2.5 colonies/ha). Each orchard was surveyed for three consecutive days during the flowering season on days that were suitable for bee activity, namely, when temperatures were >15 °C, partly cloudy to sunny condition, with wind speeds <20 km/h, and no rain.

Orchards were surveyed both passively using bee bowls (also known as pan traps in the literature) (Westphal *et al.* 2008; Prendergast *et al.* 2020) and sweep netting with an entomological sweep net. Across all study sites, the same 500 mL plastic bowls (AVA[®]) were used, and they were all painted the same way, first using a primer (white Motip[®] primer) and then with white, fluorescent yellow and blue spray paints (white and yellow Rocol[®] paints and fluorescent blue Liquitex[®] paint). Three sets of bee bowls were set out at 9:00 h and collected at 16:00 h (7 h duration). Each set consisted of a triplet of each colour placed 3 m apart from each other flush on open grassland. Each triplet set was placed at least 30 m distant. Bowls were half filled with water and unscented liquid soap (1:0.01 water:soap). For 1.5 h in the morning, and again in the afternoon, K. S. P. slowly traversed the orchard and netted bees from apple blossoms, amounting to a total of 3 h per survey.

Due to differences in orchard layout, fixed transects were not used, but rather, the sampling effort was standardised by duration. Effort was made to collect all bees observed; although the introduced bees can be identified on the wing, counts were based on collections so as to standardise sampling among the three bee taxa, given that observational counts can greatly exceed numbers of specimens collected (Tangtorwongsakul *et al.* 2018; Prendergast *et al.* 2020).

Interspersed between the apple blossom surveys, a total of 3 h was spent netting native bees from other flowering plants within and surrounding the orchard (within a radius of 50 m from the border of the apple orchard). Thus, each orchard and the surrounding vegetation were surveyed for a total of 6 h/day, totalling 18 h over the 3 days of surveying each orchard. All specimens were stored in labelled jars in ethanol and pinned later in the lab prior to identification. Specimens were identified by K. S. P. using published keys where available (Exley 1976; Walker 1986; Walker 1995; Batley & Houston 2012), consulting published descriptions (Cockerell 1914, 1918, 1905, 1930) and PaDIL (<http://www.padil.gov.au/pollinators/>). Native flower

species were identified using Simmons *et al.* (2009). Maximum daily temperature was determined from recordings for the region provided by the Bureau of Meteorology (<http://www.bom.gov.au/tas/>).

Statistical analyses

Statistical analyses were performed in R version 3.6.2 (R Core Team 2019). The effect of predictor variables on response variables was analysed using mixed-effect models (package *lme4* (version 1.1-24) (Bates *et al.* 2015), with orchard included as a random factor to account for repeated visits. For each model, each survey represented an observation ($N = 12$), and netting data from the morning and afternoon period were pooled. The low sample size precluded testing interaction effects. As the response variables – abundance and species richness – were count data, generalised linear mixed-effect (glmer) models with a Poisson distribution were first constructed and checked for overdispersion and normality using the `dispersion_glmer` function (package *blme4* (version 1.4) (Korner-Nievergelt *et al.* 2015) and `qqPlot(resids())` function (Fox 2015). These assumptions were met for models where the response variable was native bee species richness and *Bombus* abundance. For models where the response variable was honey bee abundance and native bee abundance, these assumptions were not met, and consequently, negative binomial mixed-effect models (*glmmTMB* function) were used (package *glmmTMB* (version 1.0.2.1) (Brooks *et al.* 2017), and residual diagnostics (KS test, dispersion test, outlier test and residual vs. predicted tests) were assessed with the package *DHARMa* (version 0.3.2.0) (Hartig 2020).

Estimates of the effect size of categorical variables of interest were obtained through a summary output of the model, and for continuous variables, this also indicated the direction of the effect. For categorical variables found to be significant, when the number of levels exceeded two, pairwise contrasts were calculated using Tukey's *post hoc* tests (*lsmeans* package (version 2.30-0); Lenth 2016). R^2 values from glmer models were calculated with the `r.squaredGLMM` function (package *MuMIn* (version 1.43.15); Barton 2019) and with the function `r2_nakagawa` function (package *performance* (version 0.4.7); Lüdtke *et al.* 2020) for *glmmTMB* models.

The significance of explanatory variables was determined using a chi-squared likelihood ratio approach, where an ANOVA was performed between two models with and without the explanatory variable being evaluated, where a chi-squared value corresponding to $P < 0.05$ indicated significance.

Effect of temperature

Temperature was first plotted against sampling date, which revealed that temperature did not vary consistently across the surveys (Fig. S1) and therefore did not confound analyses between orchards. Prior to investigating patterns of visitation between native bees and introduced bees to apple orchards, the effect of temperature was investigated separately for honey bees, bumble bees and native bees.

Differences in visits to apple blossoms between honey bees, bumblebees and native bees

To determine whether relative abundances of honey bees, bumble bees and native bees in apple orchards differed, we modelled differences in relative abundance between these bee taxa. Separate models were used for bees captured in bee bowls and by sweep netting. A number of specimens (response variable) according to bee taxon (explanatory variable, levels honey bees, bumblebees and native bees) were evaluated using a negative binomial mixed-effect models (*glmmTMB* function) with orchard site as a random effect to account for repeated visits to each orchard.

Native bees in orchards vs. on surrounding vegetation

Bees in and around orchards may not necessarily be those visiting the crop blossoms. To investigate this, abundance and species richness of native bees netted on apple blossoms, netted on surrounding non-apple flowers (i.e. native flowers, exotics and weeds) and caught in bee bowls was analysed using mixed-effect models. In addition, to test if there was a 'spillover' of bees present on surrounding flowers to apples, we assessed whether there was an association between native bees on the surrounding vegetation with native bees visiting apple blossoms. This was modelled for both abundance and species richness of native bees, with native bees on non-apple flowers as the predictor variable, and native bees on apple flowers as the response variable, with orchard site as a random effect. Additionally, we visualised the overlap in apples with other flowers for each bee species with a bipartite plant–pollinator interaction network using the R package *bipartite* (version 2.15) (Dormann *et al.* 2008).

Associations between introduced bees and native bees

Introduced species may outcompete native species, resulting in negative associations. This potential for competition between introduced bees (*Apis mellifera* and *Bombus terrestris*) with native bees was evaluated by analysing whether introduced bee abundance during a survey influenced native bees present. This was analysed using total abundance of native bees across all methods in relation to total abundance of honey bees and bumblebees recorded (collected on apple blossoms and in the bee bowls) combined, as well as for native bees collected in each location independently (apple blossoms, bee bowls and surrounding flowers). This tested whether introduced bees were excluding native bees from the apple blossoms, as well as at the site scale, respectively.

Turnover among sites

We assessed beta diversity of native bee assemblages and its partitioning into species replacement (turnover) vs. species richness (nestedness) components using the R package *BAT* (version 2.4.0) (Cardoso *et al.* 2015). We calculated total beta diversity, as well as its two components, species replacement and species

richness effects (Carvalho *et al.* 2012) based on a species x site matrix with species abundances pooled for all 3 days at each site, and used the Sørensen family of beta diversity.

RESULTS

Across all surveys combining all collection methods, a total of 1247 honey bees, 81 bumblebees (69 queens and 12 workers) and 358 native bees belonging to 26 species in seven genera and three families were collected (Table 1) (Prendergast 2020b, 2020c).

Differences among bee taxa in apple orchards

Regarding bees visiting the blossoms of the apple trees, across the 12 surveys, a total of 1236 honey bees were recorded foraging on the apple blossoms, 81 bumble bees and 45 native bees (Table 1). The introduced bees (honey and bumble bees) therefore dominated the bees foraging on apple blossoms, comprising 98.2% of bees. There were significant differences between numbers of bees foraging on apple blossoms according to bee taxon (i.e. honey bee, bumble bee and native bee) ($P < 0.001$; Table 2). On average across all surveys, more honey bees were collected than other taxa (honey bees vs. bumble bees: $P < 0.001$; honey bees vs. native bees: $P < 0.001$), where there were no significant differences between *Bombus terrestris* and native bees ($P = 0.116$) (Fig. 1a).

In contrast, whilst there were significant differences between taxa in numbers of bees caught in bee bowls ($P < 0.001$; Table 2), their relative representation differed from the patterns of bees foraging on the apples: no bumble bees were caught in bee bowls, whereas more native bees than honey bees were caught in the bee bowls ($P = 0.002$, Fig. 1b).

Native bees

The taxonomic composition of native bees in the orchards pooling all collection methods was dominated by species in the family Halictidae (genera *Lasioglossum* and *Homalictus*) and in the genus *Exoneura* (Apidae) – both polylectic taxa displaying varying degrees of sociality (Houston 2018) (Fig. 2a,c–e) (see also Prendergast 2020b, 2020c [Correction added on 11 February 2021, after first online publication: the ‘semi-social and polylectic taxa’ has been corrected]). Taxa that are more specialised in their pollen foraging preferences were restricted to the orchard A, which had large amounts of native flora in the surroundings (Figs. 2b and 3) (see also Prendergast 2020b). Of the 26 species recorded, only 10 were recorded foraging on apples (Fig. 3) (Prendergast 2020b). These belonged primarily to the genera *Exoneura* (Apidae, five species) – social species that nest in reeds and hollow stems (Fig. 2a), and *Lasioglossum* (Halictidae, four species) – semi-social ground-nesting species (e.g. Fig. 2c–e). Only one solitary bee species (*Euryglossa* sp., Colletidae) was collected foraging on apple blossoms (Fig. 3) (Prendergast 2020c). On average, only one species was recorded foraging on apple blossoms per survey (Table 1), and no species was recorded foraging exclusively on the apple blossoms; however, for five of these species, more individuals were collected on apples than the other flora species (Fig. 3) (Prendergast 2020b). The number of species recorded per survey ranged from 0 to 9, with an average of 5.5 ± 0.89 species collected per survey.

There were significant differences in both abundance and species richness of native bees according to sampling method ($P = 0.003$ and $P < 0.001$, respectively) (Fig. 4 and Table 1). There also appeared to be substantial variation in abundance and species richness among orchards (Fig. 4). For both abundance and species richness, more native bees were collected from surrounding flowers than from apple blossoms (abundance: $P = 0.006$; species richness: $P < 0.001$), whereas bee bowls and

Table 1 Average abundance $\pm$ SE of bee taxa collected on the apple blossoms, in bee bowls, and for native bees, on the surrounding flowers, and overall, and the average species richness of native bees ($N = 12$)

	Honey bees	Bumblebees	Native bee abundance	Native bee species richness
Apple blossoms	103 $\pm$ 13.7	6.75 $\pm$ 1.92	3.75 $\pm$ 2.10	1 $\pm$ 0.35
Bee bowls	0.91 $\pm$ 0.50	0	10.91 $\pm$ 5.80	1.83 $\pm$ 0.76
Surrounding flowers	—	—	15.17 $\pm$ 3.55	4.5 $\pm$ 0.87
Overall	1247	81	358	26

Table 2 Differences in abundance among bee taxa (honey bees, bumble bees and native bees) collected foraging on apple blossoms and captured passively in bee bowls in apple orchards

Bees netted on apples	Main effect	χ^2	df	P	R_m^2	R_c^2
	Taxon	58.0	2	<0.001	0.888	0.916
	Residual variation	Variance	SD			
	Orchard	0.07	0.27			
Bees captured in bee bowls	Main effect	χ^2	df	P	R_m^2	R_c^2
	Taxon	26.4	2	<0.001	0.951	0.992
	Residual variation	Variance	SD			
	Orchard	5.08	2.25

Fig. 1. Relative abundance of the European honey bee, introduced bumblebee (*Bombus terrestris*) and native bees on (a) apple blossoms and (b) captured in bee bowls. $N = 12$. The box plots display the median (horizontal line), 25th and 75th percentiles (upper and lower hinges of the box), with the whiskers extending $1.5 \times$ the interquartile range (range between the upper and lower hinges). Circles represent outliers.

apple blossoms however did not differ (abundance: $P = 0.571$; species richness: $P = 0.206$) (Table 3). More species were collected from surrounding flowers than bee bowls ($P = 0.001$), whereas differences in abundance of native bees collected on surrounding flowers vs. bee bowls did not differ statistically ($P = 0.117$) (Table 3).

There was no relationship between native bees recorded on surrounding flowers with native bees recorded foraging on apple blossoms for both abundance ($\chi^2 = 0.062$, $P = 0.803$, estimate = -0.008 , SE = 0.03 and $R_m^2 = 0.001$) and species richness ($\chi^2 = 0.004$, $P = 0.951$, estimate = -0.02 , SE = 0.33 and $R_m^2 < 0.001$).

Relationship between introduced bees and native bees

Neither abundance nor species richness of native bees was significantly associated with abundance of introduced bees (both

$P > 0.05$). This lack of an association was consistent for native bees collected in bee bowls, on apple blossoms and on surrounding flowers (all $P > 0.05$) (Table 4).

Weather conditions

Abundance of both introduced bee taxa exhibited non-significant relationships with temperature ($P > 0.05$; Table 5). In contrast, native bee abundance and species richness was positively related to temperature (abundance: $P = 0.034$; species richness: $P = 0.017$; Table 5). Native bees were not observed foraging when conditions were cloudy or raining, whereas although introduced bees did not exhibit a relationship with temperature, they appeared to be more tolerant of such weather conditions. In particular, bumble bees still foraged during periods when it was overcast or there was light drizzle.

Fig. 2. Examples of native bees collected: (a) *Exoneura* (*Exoneura*) *tasmanica* nesting in an exotic blackberry stem; (b) *Euhesma* (*Euhesma*) *fasciatella* on native *Acacia*; (c) *Lasioglossum* (*Chilalictus*) sp. on the exotic ornamental *Dimorphotheca ecklonis*; (d) small halictid on the weed *Taraxicum officinale*; (e) *Lasioglossum* (*Chilalictus*) sp. on the exotic *Trifolium repens* (considered a ‘weed’ in apple orchards); and (f) *Exoneura* (*Exoneura*) *tasmanica* with an introduced queen *Bombus terrestris*. Images by Kit Prendergast.

Fig. 3. Bipartite plant-bee network showing floral associations of all native bees collected across four Tasmanian apple orchards. Native bee species are on the top, and plants are on the bottom. Apple blossoms are in red, exotic plants in dark green and Australian native plants in light green. Thickness of the grey bars represents the number of bees collected on the plant.

(a)

(b)

Fig. 4. Mean abundance and species richness ($\pm$ SE) of native bees collected on apple blossoms, in bee bowls and on the surrounding flora across four apple orchards in the Huon Valley region of Tasmania. Each orchard was surveyed three times in October. Orchards A–C were Certified Organic, and Orchard D was managed under Integrated Pest Management.

Variation among sites

Although honey bees dominated assemblages across all four sites, the native bee fauna and their representation on apples, on surrounding vegetation and caught in bee bowls varied (Fig. 4), with bee bowls being relatively ineffective in the organic orchards with larger amounts of native vegetation but

Table 4 Relationship between abundance of introduced bees (*Apis mellifera* and *Bombus terrestris*) and native bee abundance and species richness ($N = 12$)

Native bee abundance	χ^2	P	Estimate	SE	R_m^2
Total	0.49	0.485	0.005	0.007	0.042
Apples	0.17	0.680	−0.004	0.009	0.016
Bee bowls	0.02	0.807	−0.002	0.012	0.001
Surrounding flowers	1.28	0.259	0.008	0.007	0.132
Native bee species richness	χ^2	P	Estimate	SE	R_m^2
Total	0.06	0.809	−0.0007	0.003	0.006
Apples	0.25	0.621	0.003	0.007	0.021
Bee bowls	2.97	0.085	0.019	0.012	0.176
Surrounding flowers	0.112	0.738	0.003	0.009	0.042

χ^2 and P values are based on ANOVAs between a model with and without introduced bee abundance as the explanatory variables. Orchard was included as a random effect in all models. Native bee abundance was modelled with negative binomial models, whereas species richness was modelled with generalised linear mixed-effect models with a Poisson distribution. The estimate and associated standard error (SE) were produced from a summary of the model containing introduced bee abundance as a main effect. R_m^2 (marginal R^2) provides the variance explained by introduced bee abundance.

were effective in the IPM orchard D, which lacked native flora in or around the orchard.

Each orchard had at least one species found exclusively at that site (Fig. 5). The greatest number of bees exclusive to a site (eight species) was recorded at orchard A, including genera not recorded elsewhere (*Euhesma* and *Trichocolletes*). In addition to the introduced honey bees and bumble bees, two native species – *Lasioglossum* (*Chilalictus*) *orbatum* and *Lasioglossum* (*Chilalictus*) *cleandi* – were shared between all sites, both of which are medium-sized, generalised, ground-nesting halictids (Prendergast 2020b). [Correction added on 11 February 2021, after first online publication: ‘cleandi’ has been corrected].

Beta diversity was fairly low, with only moderate differentiation among orchard in their bee assemblage, with almost an equal contribution of turnover and nestedness (i.e. replacement and richness beta-diversity components) to the overall differentiation among sites (Table 6).

DISCUSSION

In some landscapes and for some crops, honey bees contribute only a fraction of pollination services (Garibaldi *et al.* 2013; Garratt *et al.* 2016). Yet our results found honey bees to be the

Table 3 Differences between sampling location (apple blossoms, surrounding flowers and bee bowls) in abundance and species richness of native bees

Native bee abundance	Main effect	χ^2	df	P	R_m^2	R^2_c
	Sampling location	11.7	2	0.003	0.239	0.431
	Residual variation	Variance	SD			
	Orchard	0.33	0.58			
Native bee species richness	Main effect	χ^2	df	P	R_m^2	R^2_c
	Sampling location	31.8	2	<0.001	0.435	0.547
	Residual variation	Variance	SD			
	Orchard	0.10	0.32			

Table 5 Relationship between bees and daily maximum temperature

Taxon	χ^2	df	P	Estimate	SE	R_m^2
<i>A. mellifera</i>	0.21	1	0.648	−0.01	0.03	0.014
<i>B. terrestris</i>	0.12	1	0.726	−0.01	0.04	0.006
Native bee abundance	4.59	1	0.032	0.12	0.05	0.277
Native bee species richness	5.67	1	0.017	0.07	0.03	0.334

For *Bombus terrestris* and native bee species richness, generalised linear mixed-effect models were used, whereas negative binomial glmers were used for *Apis mellifera* and native bee abundance.

Fig. 5. Venn diagram showing shared and unique bee species between the four Tasmanian apple orchards.**Table 6** Beta diversity among the four Tasmanian apple orchards

Beta-diversity component	Average	Variance
Btotal	0.419	0.003
Brepl	0.192	0.002
Brich	0.227	0.002

Calculated beta diversity of the four sites simultaneously, with average and variance among all pairwise comparisons (Legendre 2014).

Brepl, beta diversity explained by replacement of species alone; Brich, beta diversity explained by species loss/gain (i.e. richness differences) alone; Btotal, total beta diversity, which reflects both species replacement and loss/gain.

main visitors to Tasmanian apple flowers and therefore suggest that honey bees are likely to be the main pollinators. This result is consistent with other research where honey bees have been found to be the primary pollinators of apple (Free 1993; Ramírez & Davenport 2013; Pardo & Borges 2020), or even their sole visitors (Geslin *et al.* 2017).

There has been little published research on apple flower visitors in Australia; however, research to date in other states of Australia has found that honey bees are also the main visitors to apple blossoms (Somerville 1999; Keogh *et al.* 2010b). Research conducted in New South Wales revealed that honey bees comprise 97% of insect visitors to apple blossoms (Somerville 1999). Furthermore, honey bee exclusion from apple trees causes significant reductions in fruit set and yield per tree (Langridge & Jenkins 1970). In New Zealand, the only pollinating insects across seven apple varieties were honey bees,

and to a lesser extent *Bombus terrestris*, with bee exclusion likewise resulting in only trace fruit set (Palmer-Jones & Clinch 1966, 1967, 1968). It therefore appears that in Australia, and particularly in Tasmania as our results seem to suggest, pollinators other than *Apis mellifera* are unlikely to satisfy the pollination requirements of commercial apple orchards.

The discrepancy between studies documenting a rich native bee pollinator assemblage visiting apple orchards (e.g. Földesi *et al.* 2016; Szabolcs-Szatmár-Bereg, Hungary; Russo *et al.* 2015; New York, USA) and the present study where native bees were scarce is likely to stem from the biogeography of the Australian continent, which has experienced long periods of evolution in isolation from other flora and fauna (Michener 1979; Hopper 2009; Brown & Cunningham 2019). The plant family Rosaceae is only a minor component of the Australian flora, with only 26 native species out of an estimated 21 000 species of native flora (Australian National Botanic Gardens and Centre for Australian National Biodiversity Research (ANBGANBR) 2015; Messina 2020), and thus not a major component in the evolutionary history of Australian native bees. Many native bees instead are specialists on native flora, many of which are endemic (Houston 2018). Furthermore, bees often prefer native flora over exotic flora (Williams *et al.* 2011; Morandin & Kremen 2013). Our results suggest that honey bees may be required to fulfil the pollination needs of apple in geographical regions where this crop is an introduced species and where the native bee communities are infrequent visitors; however, whether this applies to other regions of the world still needs to be investigated.

Honey bees comprised the vast majority of visits to apples, yet managed honey bee colonies were kept on the premises only in orchard D. As surrounding properties were not known to host managed honey bee colonies in the organic orchards (orchards A–C) (based on discussion with the orchard owners), it appears that a substantial proportion of the honey bee visitors were likely to be feral honey bees. This situation does not appear to be unusual: many apple growers achieve adequate pollination by relying on feral bees or honey bees from colonies managed for honey production in the landscape (Somerville 1999). However, feral honey bees can be detrimental to wildlife by usurping nesting hollows of hollow-nesting birds and mammals (New 2005; Berris & Barth 2020) and can pose a risk to managed bees through competition for food resources and disease transmission (Pirk *et al.* 2017). More intensive surveys into the reliance of apple production on feral honey bee colonies are required, and an investigation into the economics of removal of feral colonies and partnerships between growers and apiarists in having managed hives on site to achieve optimal yield and/or quality. Partnerships between apiarists and apple growers may be fruitful in this respect (Keogh *et al.* 2010a), whilst ensuring that temporary honey bee hives are not at levels that can cause competitive impacts on resident native bees or spread diseases.

Previous studies on the relative pollination efficiency of different bee taxa have often found that even when honey bees are as efficient, or less efficient, than native bees, their overall pollination services are superior by virtue of their greater abundances (Park *et al.* 2016). Indeed, honey bees far outnumbered

native bees on the apple orchards, emphasising the need for ongoing research in Australia into bee biosecurity against introduced parasites and diseases (e.g. *Varroa* mite) (Iwasaki *et al.* 2015) and improving honey bee management for apple pollination services (Stern *et al.* 2001).

Bombus terrestris were common visitors to apple blossoms, including under weather conditions that were suboptimal foraging conditions for most other bees (Linsley 1978; Riessberger & Crailsheim 1997; Goulson 2003; Joshi & Joshi 2010; Tuell & Isaacs 2010; Brittain *et al.* 2013; Güler & Dikmen 2013). Periods of inclement weather are common in Tasmania during the period of apple bloom; hence, this introduced species may be providing consistent pollination services. This must be weighed up against the potential negative environmental impacts of bumble bees (Stout & Goulson 2000).

With the majority of bumble bees collected being queens, this suggests sampling coincided with the period in which queens had recently emerged from winter hibernation and were in early establishment of colonies (Goulson 2003). This points to a potential control strategy, whereby queens can be targeted and eliminated to reduce propagation of new colonies. Blue vane traps have been demonstrated to be particularly attractive to *Bombus* (Stephen & Rao 2005; Prendergast *et al.* 2020); however, by-catch of non-target bees in Tasmania needs to be established.

The differential activity of bee taxa in relation to temperature is in line with differential sensitivity based on origin and body size, with the activity of the larger, hairy, temperate-origin introduced bees being unaffected by temperature, whereas the activity of smaller-sized native bees, better adapted to the warmer climate of Australia, was positively related (Fig. 3f). The increased activity of native bees has implications for climate change, where it may be that native bees play an increasingly important role under predicted higher temperatures (Antarctic Climate and Ecosystems Cooperative Research Centre (ACE CRC) 2010). There was considerable variation between orchards in wild bee abundance and diversity (Fig. 4), and although temperature did not consistently co-vary with orchard surveyed (Fig. S1), this may explain some of the variation between sites.

Wild bees often augment pollination services (Viana *et al.* 2014; Blitzer *et al.* 2016; Park *et al.* 2016; Miñarro & García 2018) and may enhance honey bee pollination services by altering their foraging behaviour (Greenleaf & Kremen 2006). Planting alternative foraging plants in and among the apple trees and ensuring there are adequate nesting resources in the orchards may enhance native bee populations and encourage native bee visitation (Campbell *et al.* 2017). For example, *Exoneura* were observed visiting apple flowers, and their populations can be enhanced by providing bundles of reeds and pithy stems, whereas for *Lasioglossum*, they require patches of bare soil for nesting (Houston 2018). That *Exoneura* and *Lasioglossum* were the main native bee visitors to apples, with other taxa such as *Homalictus* being present but foraging only on weedy understorey flora are consistent with Brown *et al.* (2020). This suggests that *Exoneura* and *Lasioglossum* are the best candidates in Australia to focus on for wild bee pollination services to apple. The main native bee visitors, *Exoneura*, were most abundant at

the orchard, which had lots of blackberry, with the *Exoneura* using the old pithy stems for nesting (Fig. 3a). This suggests that provision of nesting resources is important for encouraging these native apple visitors (Lye *et al.* 2009; Roulston & Goodell 2011). Blackberry, however, is a highly invasive species in Tasmania (Department of Primary Industries, Parks, Water and Environment (DPIPWE) (Tasmania) 2019). Recommendations from this research would be to (i) ensure bees are not nesting in blackberry stems before removing it and (ii) provide alternative native substrates for these native bees to use if blackberry removal is to take place, e.g. pithy centres of dead stems, reeds and/or twigs of native plants, e.g. *Xanthorrhoea* (Schwarz & Blows 1991; Sugden & Pyke 1991; Silberbauer 1992).

For sustainable apple production in Tasmania, and indeed abroad, beekeeping practices need to be integrated with promoting the biodiversity of native bees in farm systems to include non-crop species (Kleijn *et al.* 2015; Senapathi *et al.* 2015; Prendergast 2020a). Although we did not find negative associations between introduced bees and native bees, honey bees always dominated the assemblages and there was little variation in the relative proportions of honey bees and native bees, making determining potential competitive impacts difficult in this study.

Although native bees were only minor components during most surveys of the apple orchards, a relatively high diversity and abundance of native bees was collected on native flowers surrounding the apple orchards. This reveals that in this region, provided native vegetation is retained, native bees can still persist. If native flora are planted interspersed among the apple trees, this may encourage native bees to move into the orchards and also forage on the apple flowers (Campbell *et al.* 2017; Wu *et al.* 2019). Even if this does not result in spillover into apples (Nicholson *et al.* 2020), supporting bee biodiversity is important for wildflowers in native ecosystems and the ecosystem services these habitats provide (Kremen *et al.* 2007) and also has high intrinsic value (Kleijn *et al.* 2015; Prendergast 2020a). The floral associations of native bees observed in the present study are similar to those by Hingston (1999), who found that Halictidae visited a taxonomically diverse range of flowers, and native Fabaceae and Ericaceae were important floral resources for a range of native bee species in Tasmania. Future studies are required to perform floristic surveys concurrently with bee surveys to evaluate how the floristic community (abundance, species richness and composition) influence native bee communities in and around apple orchards. Bees in the family Megachilidae are known to be effective apple pollinators (Vicens & Bosch 2000; Wei *et al.* 2002) and frequent visitors to apple orchards (Sheffield *et al.* 2008). Yet no megachilids were observed. This is likely due to (i) megachilids not being active at this time of year (based on surveys conducted in Western Australia; Prendergast 2020d); (ii) the fact that alternative foraging resources, or nesting resources, were not present in the vicinity; and (iii) the fact that megachilids are rare, being only a minor component of the Tasmanian bee fauna (Hingston 1999; PaDIL 2020). Installing trap nests (bee hotels) (Sheffield *et al.* 2008; Prendergast 2018; Prendergast *et al.* 2020) and more regular field surveys in the region could establish the cause of their absence during this survey.

Numerous other studies have revealed the importance of wildflower plantings and native vegetation in supporting diverse wild bees, and even honey bees, around apple orchards (Sheffield *et al.* 2013; Földesi *et al.* 2016; Joshi *et al.* 2016; Campbell *et al.* 2017; Wu *et al.* 2019). Diversification of non-crop resources should support a greater diversity and abundance of native bees, both those that visit the apple crop and those that contribute to the biodiversity of native bees in the region (Guzman *et al.* 2019).

In orchard D, there was virtually no native vegetation in the immediate vicinity; however, a very high abundance of halictids were collected in the bee bowls and, in particular, foraging on the weeds in and around the apple orchard. This may represent a concentrating effect, whereby with less native vegetation, the bees were concentrated on the prolific weeds. There is also evidence to suggest that conversion of forest to open agricultural habitats can favour halictids – ground-nesting generalist bees – by enhancing nesting substrates (open ground) and floral resources (Lentini *et al.* 2012; Harrison *et al.* 2018; Hall *et al.* 2019; Brown *et al.* 2020). The high abundance of native bees on ‘weeds’ (Fig. 2c–e) emphasises the value of ‘weedy’ species in agricultural settings and argues against eliminating these species (Marshall *et al.* 2003; Frankie *et al.* 2013; Bretagnolle & Gaba 2015; Requier *et al.* 2015; Lowenstein *et al.* 2019; Brown *et al.* 2020).

Although low sample size limits the confidence in conclusions, a number of points can be made comparing the turnover among sites that warrant further investigation. Firstly, it appears that bee bowls appear most effective in relatively ‘poor’ habitat from the point of view for supporting a more diversified and specialised bee assemblage. This has implications when exclusively using bee bowls to gauge the relative value of habitats, and indeed, previous studies have suggested that bee bowls are more effective in resource-poor habitats (Mayer 2005; Roulston *et al.* 2007; Baum & Wallen 2011; Prendergast *et al.* 2020), and are biased towards sampling halictids in habitats where there are few alternative flowering resources (e.g. crop fields), but perform poorly at sampling species-rich native bee assemblages in floristically rich habitats (Prendergast *et al.* 2020). Bee bowls were moreover ineffective at collecting the dominant apple flower visitors, consistent with other studies that have found that bee bowls are ineffective at accurately sampling honey bees and bumble bees (Wagner *et al.* 2014; Buchanan *et al.* 2017; Prendergast *et al.* 2020). It is evident that if bee bowls had been deployed only, this would have completely mischaracterised that bee assemblage visiting the apple orchards.

Secondly, contrasting with species–area relationships (Taki *et al.* 2018), the smallest orchard had the greatest number of species unique to that habitat. This may be attributed to the high amounts of native flora in the surroundings. Indeed, the two genera exclusively found in this orchard (*Euhesma*, represented by *Euhesma fasciatella*, and *Trichocolletes*, represented by *Trichocolletes venustus*) both were collected exclusively on native pea plants (Fabaceae).

Amazingly, each site, despite being in the same geographical region and representing same dominant habitat type (apple orchard), had at least one species unique to that site. Although

greater sampling effort may have uncovered a greater similarity among sites, this nevertheless high turnover indicated that each orchard had its own unique contribution to the regional diversity in this habitat type. As expected, honey bees occurred across all sites, as well as two generalist halictids and bumble bees. This latter finding underscores the establishment of this introduced species across Tasmania.

The results presented here also are important in contributing to the documenting of Australia’s native bee diversity (Batley & Hogendoorn 2009). Indeed, there have been very few surveys of native bees in Tasmania, and these have largely been conducted in solely natural habitats (McQuillan & Hingston 1999; Hingston 2002). Moreover, results here also provide information on what native flora the bees around orchards forage on, and by documenting which bees occur, their specific requirements, including not just food resources but also nesting habitats, can be catered for. This will go towards creating orchards that support native bee biodiversity. Such advice to growers is severely lacking in Tasmania, and Australia in general, which contrasts with the wealth of information about supporting wild native bee taxa around apple orchards overseas (e.g. Park 2012; Földesi *et al.* 2016; Sheffield *et al.* 2016).

ACKNOWLEDGEMENTS

K. S. P. would like to firstly thank the orchard owners who kindly permitted her to survey their orchards: Roslyn and Anthony Mangold of Old Post Office Farm; Matthew and Coreen Tack of Our Mate’s Farm; Christine and Mark Duggan of Duggan’s Apples; and Andrew Hall of Reid’s Fruit. K. S. P. would also like to thank Geoff Allen of University of Tasmania for kindly loaning her field equipment, Andrew Smith of Willie Smith’s Apples for providing her information about the Tasmanian apple industry, her family in Tasmania for providing such a warm welcome, her hosts for being so accommodating and letting her babysit joeys, and Rob Manning and Liz Barbour for feedback on a draft of the manuscript. K. S. P. would like to thank Freda and John Hamblin for their financial contribution to funding this project. We received financial support from the FNRS/FWO joint programme ‘EOS – Excellence of Science’ for the project ‘CLiPS: Climate change and its impact on Pollination Services’ (project 30947854), which made the apple surveys in Tasmania possible. We would also like to thank the three reviewers for their constructive feedback for improving the manuscript.

REFERENCES

- Antarctic Climate and Ecosystems Cooperative Research Centre (ACE CRC). 2010. *Climate Futures for Tasmania General Climate Impacts: The Summary*. Antarctic Climate and Ecosystems Cooperative Research Centre, Hobart, Tasmania.
- Australian National Botanic Gardens and Centre for Australian National Biodiversity Research (ANBGANBR). 2015. Australian flora statistics, in *Australian National Botanic Gardens and Centre for Australian*

- National Biodiversity Research. Available from: <https://www.anbg.gov.au/aust-veg/australian-flora-statistics.html> [Accessed 18 Nov 2020]
- Australian Organic Ltd (2019). Australian Certified Organic Standard: the requirements for organic certification 2019 – version 1. Australian Organic Ltd. Nundah, QLD. Available from: https://aco.net.au/Downloads/ACOS_2017_V1.pdf [Accessed 18 Feb 2020]
- Barton K. 2019. MuMIn: multi-model inference. R package version 1.43.15. Available from: <https://CRAN.R-project.org/package=MuMIn> [Accessed 2 May 2020]
- Bates D, Maechler M, Bolker BM & Walker S. 2015. Fitting linear mixed-effects models using lme4. *Journal of Statistical Software* **67**, 1–48.
- Batley M & Hogendoorn K. 2009. Diversity and conservation status of native Australian bees. *Apidologie* **40**, 347–354.
- Batley M & Houston TF. 2012. Revision of the Australian bee genus *Trichocolletes* Cockerell (Hymenoptera: Colletidae: Paracolletini). *Records of the Australian Museum* **64**, 1–50.
- Baum KA & Wallen KE. 2011. Potential bias in pan trapping as a function of floral abundance. *Journal of the Kansas Entomological Society* **84**, 155–115.
- Berris KK & Barth M. 2020. PVC nest boxes are less at risk of occupancy by feral honey bees than timber nest boxes and natural hollows. *Ecological Management and Restoration* **21**, 155–157.
- Blitzer EJ, Gibbs J, Park MG & Danforth BN. 2016. Pollination services for apple are dependent on diverse wild bee communities. *Agriculture, Ecosystems & Environment* **221**, 1–7.
- Bosch J & Kemp WP. 2002. Developing and establishing bee species as crop pollinators: the example of *Osmia* spp. (Hymenoptera: Megachilidae) and fruit trees. *Bulletin of Entomological Research* **92**, 3–16.
- Bretagnolle V & Gaba S. 2015. Weeds for bees? A review. *Agronomy for Sustainable Development* **35**, 891–909.
- Brittain C, Kremen C & Klein A-M. 2013. Biodiversity buffers pollination from changes in environmental conditions. *Global Change Biology* **19**, 540–547.
- Brooks ME, Kristensen K, van Benthem KJ et al. 2017. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *The R Journal* **9**, 378–400.
- Brown J, Barton PS & Cunningham SA. 2020. Flower visitation and land cover associations of above ground- and below ground-nesting native bees in an agricultural region of south-east Australia. *Agriculture, Ecosystems & Environment* **295**, 106895.
- Brown J & Cunningham SA. 2019. Global-scale drivers of crop visitor diversity and the historical development of agriculture. *Proceedings of the Royal Society B: Biological Sciences* **286**, 20192096. <https://doi.org/10.1098/rspb.2019.2096>.
- Buchanan A, Gibbs J, Komondy L & Szendrei Z. 2017. Bee community of commercial potato fields in Michigan and *Bombus impatiens* visitation to neonicotinoid-treated potato plants. *Insects* **8**, 30.
- Buckley LB & Kingsolver JG. 2012. Functional and phylogenetic approaches to forecasting species' responses to climate change. *Annual Review of Ecology, Evolution, and Systematics* **43**, 205–226.
- Campbell AJ, Wilby A, Sutton P & Wäckers FL. 2017. Do sown flower strips boost wild pollinator abundance and pollination services in a spring-flowering crop? A case study from UK cider apple orchards. *Agriculture, Ecosystems & Environment* **239**, 20–29.
- Cardoso P, Rigal F & Carvalho JC. 2015. BAT – Biodiversity Assessment Tools, an R package for the measurement and estimation of alpha and beta taxon, phylogenetic and functional diversity. *Methods in Ecology and Evolution* **6**, 232–236.
- Carvalho JC, Cardoso P & Gomes P. 2012. Determining the relative roles of species replacement and species richness differences in generating beta-diversity patterns. *Global Ecology and Biogeography* **21**, 760–771.
- Christmann S & Aw-Hassan AA. 2012. Farming with alternative pollinators (FAP) – an overlooked win-win-strategy for climate change adaptation. *Agriculture, Ecosystems & Environment* **161**, 161–164.
- Cockerell TDA. 1905. Descriptions and records of bees. V. *Annals and Magazine of Natural History* **7** (16), 465–477.
- Cockerell TDA. 1914. New Australian bees. *Entomologist* **47**, 197–201.
- Cockerell TDA. 1918. Some bees collected in Queensland. *Memoirs of the Queensland Museum* **6**, 112–120.
- Cockerell TDA. 1930. New Australian bees. *Memoirs of the Queensland Museum* **10**, 37–50.
- Department of Primary Industries and Regional Development. 2017. Recommendations for successful apple pollination. In *Agriculture and Food – Pome fruit*. Government of Western Australia, Western Australia.
- Department of Primary Industries, Parks, Water and Environment (DPIPWE) (Tasmania). 2019. Blackberry. In *Invasive Species*. Department of Primary Industries, Parks, Water and Environment (Tasmania), Tasmania.
- Dulta P & Verma L. 1987. Role of insect pollinators on yield and quality of apple fruit. *Indian Journal of Horticulture* **44**, 274–279.
- Exley EM. 1976. Revision of the subgenus *Euryglossa* Smith (Apoidea: Colletidae: Euryglossinae). *Australian Journal of Zoology Supplementary Series* **24** (41), 1–72.
- Földesi R, Kovács-Hostyánszki A, Körösi Á et al. 2016. Relationships between wild bees, hoverflies and pollination success in apple orchards with different landscape contexts. *Agricultural and Forest Entomology* **18** (1), 68–75. <https://doi.org/10.1111/afe.12135>
- Fox J. 2015. *Applied Regression Analysis and Generalized Linear Models*. Sage Publications, Thousand Oaks, California.
- Frankie GW, Vinson SB, Rizzardi MA et al. 2013. Relationships of bees to host ornamental and weedy flowers in urban Northwest Guanacaste Province, Costa Rica. *Journal of the Kansas Entomological Society* **86**, 325–351.
- Free JB. 1966. The pollinating efficiency of honey-bee visits to apple flowers. *Journal of Horticultural Science* **41** (1), 91–94.
- Free JB. 1993. *Insect Pollination of Crops*. Academic Press, London, UK.
- Fruit Growers Tasmania. 2019. Fruit Growers Tasmania: about Tasmania. Fruit Growers Tasmania, Tasmania.
- Garibaldi LA, Steffan-Dewenter I, Kremen C et al. 2011. Stability of pollination services decreases with isolation from natural areas despite honey bee visits. *Ecology Letters* **14** (10), 1062–1072.
- Garibaldi LA, Steffan-Dewenter I, Winfree R et al. 2013. Wild pollinators enhance fruit set of crops regardless of honey bee abundance. *Science* **339** (6127), 1608–1611.
- Garratt MP, Breeze T, Boreux V et al. 2016. Apple pollination: demand depends on variety and supply depends on pollinator identity. *PLoS ONE* **11**, e0153889.
- Garratt MP, Breeze TD, Jenner N, Polce C, Biesmeijer JC & Potts SG. 2014. Avoiding a bad apple: insect pollination enhances fruit quality and economic value. *Agriculture, Ecosystems & Environment* **184**, 34–40.
- Geslin B, Aizen MA, Garcia N, Pereira A-J, Vaissière BE & Garibaldi LA. 2017. The impact of honey bee colony quality on crop yield and farmers' profit in apples and pears. *Agriculture, Ecosystems & Environment* **248**, 153–161.
- Gibbs DM & Muirhead IF. 1998. The economic value and environmental impact of the Australian beekeeping industry.
- Goodell K & Thomson JD. 1997. Comparisons of pollen removal and deposition by honey bees and bumble bees visiting apple, pp. 103–108. International Society for Horticultural Science (ISHS), Leuven, Belgium.
- Goodman R. 1994. Honey bee pollination of fruit tree crops (ed. Agriculture Victoria). Victoria State Government, Victoria.
- Goulson D. 2003. In: *Bumblebees, Their Behaviour and Ecology*, pp. 235. Oxford University Press, Oxford, UK ISBN 0-19-852607-5.
- Greenleaf SS & Kremen C. 2006. Wild bees enhance honey bees' pollination of hybrid sunflower. *Proceedings of the National Academy of Sciences* **103**, 13890–13895.
- Grose MR, Barnes-Keogh I, Corney SP et al. 2010. *Climate Futures for Tasmania: General Climate Impacts Technical Report*. Antarctic Climate & Ecosystems Cooperative Research Centre, Hobart, Tasmania.
- Güler Y & Dikmen F. 2013. Potential bee pollinators of sweet cherry in inclement weather conditions. *Journal of the Entomological Research Society* **15**, 9–19.
- Guzman A, Chase M & Kremen C. 2019. On-farm diversification in an agriculturally-dominated landscape positively influences specialist pollinators. *Frontiers in Sustainable Food Systems* **3**, 87.
- Hall B. 2014. Apple of the Huon. In *Tasmanian Geographic*. Tasmanian Geographic.
- Hall MA, Nimmo DG, Cunningham SA, Walker K & Bennett AF. 2019. The response of wild bees to tree cover and rural land use is mediated by species' traits. *Biological Conservation* **231**, 1–12.
- Harrison T, Gibbs J & Winfree R. 2018. Forest bees are replaced in agricultural and urban landscapes by native species with different phenologies and life-history traits. *Global Change Biology* **24** (1), 287–296.

- Hartig F. 2020. DHARMA: residual diagnostics for hierarchical (multi-level/mixed) regression models. The Comprehensive R Archive Network (CRAN), R package version 0.3. 2.0.
- Hingston AB. 1999. Affinities between southern Tasmanian plants in native bee visitor profiles. *Australian Journal of Zoology* **47**, 361–384.
- Hingston AB. 2002. Pollination ecology of *Eucalyptus globulus* subsp. *globulus* and *Eucalyptus nitens* (Myrtaceae). In *School of Geography and Environmental Studies* vol. Doctor of Philosophy. University of Tasmania, Tasmania.
- Hingston AB. 2006. Is the exotic bumble bee *Bombus terrestris* really invading Tasmanian native vegetation? *Journal of Insect Conservation* **10**, 289–293.
- Hogendoom K, Gross CL, Sedgley M & Keller MA. 2006. Increased tomato yield through pollination by native Australian *Amegilla chlorocyanea* (Hymenoptera: Anthophoridae). *Journal of Economic Entomology* **99**, 828–833.
- Hopper SD. 2009. OCBIL theory: towards an integrated understanding of the evolution, ecology and conservation of biodiversity on old, climatically buffered, infertile landscapes. *Plant and Soil* **322**, 49–86.
- Houston TF. 2018. *A Guide to the Native Bees of Australia*. CSIRO Publishing, Clayton South, Victoria.
- Iwasaki JM, Barratt BI, Lord JM, Mercer AR & Dickinson KJ. 2015. The New Zealand experience of varroa invasion highlights research opportunities for Australia. *Ambio* **44**, 694–704.
- Joshi NC & Joshi P. 2010. Foraging behaviour of *Apis* spp. on apple flowers in a subtropical environment. *New York Science Journal* **3**, 71–76.
- Joshi NK, Otieno M, Rajotte EG, Fleischer SJ & Biddinger DJ. 2016. Proximity to woodland and landscape structure drives pollinator visitation in apple orchard ecosystem. *Frontiers in Ecology and Evolution* **4**, 38.
- Keogh RC, Mullins IJ & Robinson AP. 2010a. Pollination aware case study: apple. In *Pollination Aware*, vol. RIRDC Publication No 10/109 (ed. AgriFutures Australia). AgriFutures.
- Keogh RC, Robinson AP & Mullins IJ. 2010b. Pollination aware – the real value of pollination in Australia (ed. RIRaD Corporation). Rural Industries Research and Development Corporation.
- Kingston AB & McQuillan PB. 1998. Does the recently introduced bumble bee *Bombus terrestris* (Apidae) threaten Australian ecosystems? *Australian Journal of Ecology* **23**, 539–549.
- Kleijn D, Winfree R, Bartomeus I *et al.* 2015. Delivery of crop pollination services is an insufficient argument for wild pollinator conservation. *Nature Communications* **6** (1), 1–9.
- Klein A-M, Vaissiere BE, Cane JH *et al.* 2007. Importance of pollinators in changing landscapes for world crops. *Proceedings of the Royal Society of London B: Biological Sciences* **274**, 303–313.
- Korner-Nievergelt F, Roth T, Felten S, Guelat J, Almasi B & Korner-Nievergelt P. 2015. *Bayesian Data Analysis in Ecology Using Linear Models with R, BUGS and Stan*. Elsevier, London, UK.
- Kremen C, Williams NM, Aizen MA *et al.* 2007. Pollination and other ecosystem services produced by mobile organisms: a conceptual framework for the effects of land-use change. *Ecology Letters* **10** (4), 299–314.
- Langridge D & Jenkins P. 1970. The role of honey bees in pollination of apples. *Australian Journal of Experimental Agriculture* **10**, 366–368.
- Legendre P (2014) Interpreting the replacement and richness difference components of beta diversity. *Global Ecology and Biogeography*, **23** (11), 1324–1334. <https://doi.org/10.1111/geb.12207>
- Lenth RV. 2016. Least-squares means: the R package lsmmeans. *Journal of Statistical Software* **69**, 1–33.
- Lentini PE, Martin TG, Gibbons P, Fischer J & Cunningham SA. 2012. Supporting wild pollinators in a temperate agricultural landscape: maintaining mosaics of natural features and production. *Biological Conservation* **149**, 84–92.
- Linsley EG. 1978. Temporal patterns of flower visitation by solitary bees, with particular reference to the southwestern United States. *Journal of the Kansas Entomological Society* **1978**, 531–546.
- Lowenstein DM, Matteson KC & Minor ES. 2019. Evaluating the dependence of urban pollinators on ornamental, non-native, and ‘weedy’ floral resources. *Urban Ecosystem* **22**, 293–302.
- Luby J. 2003. Taxonomic classification and brief history. In: *Apples – Botany, Production and Uses* (eds D Ferree & I Warrington). Cabi Publishing, Oxon.
- Lüdecke D, Makowski D, Waggoner P & Patil I. 2020. Performance: assessment of regression models performance, 2020. *CRAN, R package*. DOI: <https://doi.org/10.5281/zenodo.3952174>, R package. Available from URL: <https://easystats.github.io/performance/> [Accessed 2 May 2020]
- Lye G, Park K, Osborne J, Holland J & Goulson D. 2009. Assessing the value of Rural Stewardship schemes for providing foraging resources and nesting habitat for bumble bee queens (Hymenoptera: Apidae). *Biological Conservation* **142**, 2023–2032.
- Mader E, Spivak M & Evans E. 2010. Managing alternative pollinators: a guide for growers, beekeepers, and conservationists. *Sustainable Agriculture Research and Education. Handbook* 11.
- Mallinger RE & Gratton C. 2015. Species richness of wild bees, but not the use of managed honey bees, increases fruit set of a pollinator-dependent crop. *Journal of Applied Ecology* **52**, 323–330.
- Marshall E, Brown V, Boatman N, Lutman P, Squire G & Ward L. 2003. The role of weeds in supporting biological diversity within crop fields. *Weed Research* **43**, 77–89.
- Martins KT, Gonzalez A & Lechowicz MJ. 2015. Pollination services are mediated by bee functional diversity and landscape context. *Agriculture, Ecosystems & Environment* **200**, 12–20.
- Mayer C. 2005. Does grazing influence bee diversity?. In: *African Biodiversity: Molecules, Organisms, Ecosystems* (eds BA Huber, BJ Sinclair, K-H, Lampe) pp. 173–179. Springer Verlag US, Boston, MA.
- McConnell A & Servant N. 1999. The history and heritage of the Tasmanian apple industry – a profile Queen Victoria Museum and Art Gallery, Launceston.
- Rader R, Reilly J, Bartomeus I & Winfree R. 2013. Native bees buffer the negative impact of climate warming on honey bee pollination of water-melon crops. *Global Change Biology* **19**, 3103–3110 <https://doi.org/10.1111/gcb.12264>.
- McQuillan PB & Hingston AB. 1999. Displacement of Tasmanian native megachilid bees by the recently introduced bumble bee *Bombus terrestris* (Linnaeus, 1758) (Hymenoptera: Apidae). *Australian Journal of Zoology* **47**, 59–65.
- Messina A. 2020. Rosaceae, in Phillip G. Kodela (ed.), *Flora of Australia*. Australian Biological Resources Study, Department of Agriculture, Water and the Environment: Canberra. Available from URL: <https://profiles.ala.org.au/opus/foa/profile/Rosaceae> [Date Accessed: 18 November 2020]
- Michener CD. 1979. Biogeography of the bees. *Annals of the Missouri Botanical Garden* **66** (3), 277–347.
- Miñarro M & García D. 2018. Complementarity and redundancy in the functional niche of cider apple pollinators. *Apidologie* **49**, 789–802.
- Morandin LA & Kremen C. 2013. Bee preference for native versus exotic plants in restored agricultural hedgerows. *Restoration Ecology* **21**, 26–32.
- New TR. 2005. *Invertebrate Conservation and Agricultural Ecosystems*. Cambridge University Press, Cambridge, UK.
- Nicholson CC, Ward KL, Williams NM *et al.* 2020. Mismatched outcomes for biodiversity and ecosystem services: testing the responses of crop pollinators and wild bee biodiversity to habitat enhancement. *Ecology Letters* **23** (2), 326–335.
- PaDIL. 2020. Australian pollinators: Tasmania search. Available from: <https://www.padil.gov.au/pollinators/search?sortType=ScientificName&viewType=Details&pageSize=10&queryText1=Tasmania&queryType1=all> Accessed 27/09/2020
- Palmer-Jones T & Clinch PG. 1966. Observations on the pollination of apple trees (*Malus sylvestris* Mill.) I. Variety Cox’s Orange Pippin. *New Zealand Journal of Agricultural Research* **9** (2), 191–196.
- Palmer-Jones T & Clinch PG. 1967. Observations on the pollination of apple trees (*Malus sylvestris* Mill.) II. Varieties Granny Smith, Sturmer, Jonathan, and Cox’s Orange Pippin. *New Zealand Journal of Agricultural Research* **10** (1), 143–149.
- Palmer-Jones T & Clinch PG. 1968. Observations on the pollination of apple trees (*Malus sylvestris* Mill.) III. Varieties Granny Smith, Kidd’s

- orange red, and golden delicious. *New Zealand Journal of Agricultural Research* **11** (1), 149–153.
- Pardo A & Borges PA. 2020. Worldwide importance of insect pollination in apple orchards: a review. *Agriculture, Ecosystems & Environment* **293**, 106839.
- Park M. 2012. Wild pollinators of Eastern apple orchards and how to conserve them (ed. TX Society). Cornell University
- Park MG, Raguso RA, Losey JE & Danforth BN. 2016. Per-visit pollinator performance and regional importance of wild *Bombus* and *Andrena* (*Melandrena*) compared to the managed honey bee in New York apple orchards. *Apidologie* **47**, 145–160.
- Paton DC. 1996. *Overview of Feral and Managed Honey Bees in Australia: Distribution, Abundance, Extent of Interactions with Native Biota, Evidence of Impacts and Future Research*. Australian Nature Conservation Agency, Canberra.
- Pérez-Méndez N, Andersson GK, Requier F et al. 2020. The economic cost of losing native pollinator species for orchard production. *Journal of Applied Ecology* **57** (3), 599–608.
- Pirk CW, Crewe RM & Moritz RF. 2017. Risks and benefits of the biological interface between managed and wild bee pollinators. *Functional Ecology* **31**, 47–55.
- Pollinator Partnership Canada. n.d. Bee friendly farmer registration. Pollinator Partnership Canada, Canada.
- Potts SG, Biesmeijer JC, Kremen C, Neumann P, Schweiger O & Kunin WE. 2010. Global pollinator declines: trends, impacts and drivers. *Trends in Ecology & Evolution* **25**, 345–353.
- Potts SG, Imperatriz-Fonseca V, Ngo HT et al. (2016) Safeguarding pollinators and their values to human well-being. *Nature*, **540** (7632), 220–229. <https://doi.org/10.1038/nature20588>
- Prendergast KA. 2018. Nesting biology of *Megachile ignita* Smith, 1853 (Hymenoptera: Megachilidae) in artificial nesting blocks in urbanised southwestern Australia. *Australian Entomologist* **45**, 139–148.
- Prendergast K. 2020a. Beyond ecosystem services as justification for biodiversity conservation. *Austral Ecology* **45** (2), 141–143.
- Prendergast K. 2020b. Native bees and their floral host associations in Tasmania apple orchards. Curtin University. Dataset. <https://doi.org/10.25917/5ee9d9bde413c>
- Prendergast K. 2020c. Native bees collected in Tasmania apple orchards October 2019. Curtin University. Dataset. <https://doi.org/10.25917/arw1-te90>
- Prendergast K. 2020d. Species of native bees in the urbanised region of the southwest Western Australian biodiversity hotspot. Dataset. <https://doi.org/10.1002/ecs2.3076>
- Prendergast K, Menz MH, Bateman B & Dixon K. 2020. The relative performance of sampling methods for native bees: an empirical test and review of the literature. *Ecosphere* **5**, e03076. <https://doi.org/10.1002/ecs2.3076>.
- R Core Team. 2019. *R: A Language and Environment for Statistical Computing*, R version 3.6.2. R Foundation for Statistical Computing, Vienna, Austria.
- Rader R, Howlett BG, Cunningham SA et al. 2009. Alternative pollinator taxa are equally efficient but not as effective as the honey bee in a mass flowering crop. *Journal of Applied Ecology* **46**, 1080–1087.
- Ramírez F & Davenport TL. 2013. Apple pollination: a review. *Scientia Horticulturae* **162**, 188–203.
- Requier F, Odoux J-F, Tamic T et al. 2015. Honey bee diet in intensive farmland habitats reveals an unexpectedly high flower richness and a major role of weeds. *Ecological Applications* **25**, 881–890.
- Riessberger U & Crailsheims K. 1997. Short-term effect of different weather conditions upon the behaviour of forager and nurse honey bees (*Apis mellifera carnica* Pollmann). *Apidologie* **28**, 411–426.
- Roulston TH & Goodell K. 2011. The role of resources and risks in regulating wild bee populations. *Annual Review of Entomology* **56**, 293–312.
- Roulston TH, Smith SA & Brewster AL. 2007. A comparison of pan trap and intensive net sampling techniques for documenting a bee (Hymenoptera: Apiformes) fauna. *Journal of the Kansas Entomological Society* **80**, 179–181.
- Russo L, Park M, Gibbs J & Danforth B. 2015. The challenge of accurately documenting bee species richness in agroecosystems: bee diversity in eastern apple orchards. *Ecology and Evolution* **5**, 3531–3540.
- Salter M. 2002. Senate review of Australia's quarantine function: submission by Tasmania Apple & Pear Growers Association Inc. Tasmania Apple & Pear Growers Association Inc., Tasmania.
- Saunders ME & Luck GW. 2016. Combining costs and benefits of animal activities to assess net yield outcomes in apple orchards. *PLoS ONE* **11**, e0158618.
- Saunders ME & Luck GW. 2018. Interaction effects between local flower richness and distance to natural woodland on pest and beneficial insects in apple orchards. *Agricultural and Forest Entomology* **20**, 279–287.
- Schwarz MP & Blows MW. 1991. Kin association during nest founding in the bee *Exoneura bicolor*: active discrimination, philopatry and familiar landmarks. *Psyche: A Journal of Entomology* **98**, 241–250.
- Semmens T, Turner E & Buttermore R. 1993. *Bombus terrestris* (L.) (Hymenoptera: Apidae) now established in Tasmania. *Australian Journal of Entomology* **32**, 346–346.
- Senapathi D, Biesmeijer JC, Breeze TD, Kleijn D, Potts SG & Carvalheiro LG. 2015. Pollinator conservation – the difference between managing for pollination services and preserving pollinator diversity. *Current Opinion in Insect Science* **12**, 93–101.
- Settle J, Bishop J & Potts SG. 2016. Climate change impacts on pollination. *Nature Plants* **2**, 1–3.
- Sheffield C, Ngo HT & Azzu N. 2016. *A manual on apple pollination*. Pollination Services for Sustainable Agriculture. Food and Agriculture Organization of the United Nations (FAO), Rome.
- Sheffield CS, Kevan PG, Pindar A & Packer L. 2013. Bee (Hymenoptera: Apoidea) diversity within apple orchards and old fields in the Annapolis Valley, Nova Scotia, Canada. *The Canadian Entomologist* **145**, 94–114.
- Sheffield CS, Kevan PG, Westby SM & Smith RF. 2008. Diversity of cavity-nesting bees (Hymenoptera: Apoidea) within apple orchards and wild habitats in the Annapolis Valley, Nova Scotia, Canada. *The Canadian Entomologist* **140**, 235–249.
- Silberbauer L. 1992. Founding patterns of *Exoneura bicolor* Smith in Cobboboonee State Forest, southwestern Victoria. *Australian Zoologist* **28**, 67–73.
- Simmons M, Wapstra H & Wapstra A, eds. 2009. *A Guide to Flowers & Plants of Tasmania*. New Holland Publishers, Chatswood, NSW.
- Somerville DC. 1999. Pollination of apples by honey bees. In *agnote*, vol. DAI. NSW Agriculture, NSW.
- Stephen WP & Rao S. 2005. Unscented color traps for non-*Apis* bees (Hymenoptera: Apiformes). *Journal of the Kansas Entomological Society* **78**, 373–380.
- Stem R, Eisikowitch D & Dag A. 2001. Sequential introduction of honey bee colonies and doubling their density increases cross-pollination, fruit-set and yield in 'Red Delicious' apple. *The Journal of Horticultural Science and Biotechnology* **76**, 17–23.
- Stout JC, Kells AR & Goulson D. 2002. Pollination of the invasive exotic shrub *Lupinus arboreus* (Fabaceae) by introduced bees in Tasmania. *Biological Conservation* **106**, 425–434.
- Stout JC, Goulson D (2000) Bumble bees in Tasmania: their distribution and potential impact on Australian flora and fauna. *Bee World*, **81** (2), 80–86. <https://doi.org/10.1080/0005772x.2000.11099475>
- Sugden EA & Pyke GH. 1991. Effects of honey bees on colonies of *Exoneura asimillima*, an Australian native bee. *Australian Journal of Ecology* **16**, 171–181.
- Taki H, Murao R, Mitai K & Yamaura Y. 2018. The species richness/abundance–area relationship of bees in an early successional tree plantation. *Basic and Applied Ecology* **26**, 64–70.
- Tangtorwongsakul P, Warrit N & Gale GA. 2018. Effects of landscape cover and local habitat characteristics on visiting bees in tropical orchards. *Agricultural and Forest Entomology* **20**, 28–40.
- Thomson JD & Goodell K. 2001. Pollen removal and deposition by honey bee and bumble bee visitors to apple and almond flowers. *Journal of Applied Ecology* **38**, 1032–1044.
- Tuell JK & Isaacs R. 2010. Weather during bloom affects pollination and yield of highbush blueberry. *Journal of Economic Entomology* **103**, 557–562.
- Viana BF, da Encarnação Coutinho JG, Garibaldi LA, Gastagnino GLB, Gramacho KP & da Silva FO. 2014. Stingless bees further improve apple pollination and production. *Journal of Pollination Ecology* **14**, 261–269.

- Vicens N & Bosch J. 2000. Pollinating efficacy of *Osmia cornuta* and *Apis mellifera* (Hymenoptera: Megachilidae, Apidae) on 'Red Delicious' apple. *Environmental Entomology* **29**, 235–240.
- Wagner DL, Ascher JS & Bricker NK. 2014. A transmission right-of-way as habitat for wild bees (Hymenoptera: Apoidea: Anthophila) in Connecticut. *Annals of the Entomological Society of America* **107**, 1110–1120.
- Walker K. 1986. Revision of the Australian species of the genus *Homalictus* Cockerell (Hymenoptera: Halictidae). *Memoirs of the Museum of Victoria* **47**, 105–200.
- Walker K. 1995. Revision of the Australian native bee subgenus *Lasioglossum* (*Chilalictus*) (Hymenoptera: Halictidae). *Memoirs of the Museum of Victoria* **55**, 1–423.
- Wei S-G, Wang R, Smirle MJ & Xu H-L. 2002. Release of *Osmia excavata* and *Osmia jacoti* (Hymenoptera: Megachilidae) for apple pollination. *The Canadian Entomologist* **134**, 369–380.
- Westphal C, Bommarco R, Carré G *et al.* 2008. Measuring bee diversity in different European habitats and biogeographical regions. *Ecological Monographs* **78**, 653–671.
- Williams NM, Cariveau D, Winfree R *et al.* 2011. Bees in disturbed habitats use, but do not prefer, alien plants. *Basic and Applied Ecology* **12**, 332–341.
- Williams RR & Brain P. 1985. Honey-bee activity when visiting flowers of the apple cultivars Cox's Orange Pippin and Golden Delicious. *Journal of Horticultural Science* **60**, 25–28.
- Wu P, Axmacher JC, Li X *et al.* 2019. Contrasting effects of natural shrubland and plantation forests on bee assemblages at neighboring apple orchards in Beijing, China. *Biological Conservation* **237**, 456–462.

Accepted for publication 17 January 2021.

SUPPORTING INFORMATION

Additional supporting information may/can be found online in the supporting information tab for this article.

Table S1. Tasmanian apple orchards surveyed (A–D): geographic information, dates surveyed, management type, size and apple varieties.

Figure S1. Maximum daily temperature during each survey.