

1 **Phenology of a bee (Hymenoptera: Apoidea) community over a ten-year period in**
2 **south- eastern Australia.**

3 Running title: decade-long bee monitoring

4 Michael J. Neave ¹, Julian Brown^{2*}, Michael Batley ³, Sujaya Rao ⁴, Saul A. Cunningham ²

5 1 CSIRO Ecosystem Sciences, Box 1700, Canberra, ACT 2601, Australia

6 2 Australian National University, Fenner School of Environment and Society, 141 Linnaeus
7 Way, Acton, ACT, 2601.

8 3 The Australian Museum, 1 William Street, Sydney, New South Wales 2010, Australia.

9 4 Department of Entomology, University of Minnesota, 1980 Folwell Avenue, St Paul, MN,
10 55108, USA.

11 *julian.macpherson.brown@gmail.com

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13
14 **Abstract**

15 Bee responses to anthropogenic disturbances have received much recent attention in scientific
16 literature. These studies typically involve one to three years of sampling along spatial
17 gradients of disturbance, though occasionally greater temporal replication and/or longer time
18 periods are used at the expense of spatial replication. We surveyed bees using a blue vane
19 trap during spring, summer, and autumn from 2008 to 2017 at one location in Canberra,
20 Australia. To the best of our knowledge, this is the longest near-continuous record of bee
21 activity in the southern hemisphere. We use these data to describe the temporal dynamics of
22 the bee community, which was characterised by high annual variability in overall abundance,
23 richness, and composition, and a negative correlation between spring rainfall and bee activity.
24 The phenologies of abundant species are also described. Our findings relate only to our study
25 site, but are similar to findings from other long-term studies conducted in the northern
26 hemisphere which collectively present a picture of high natural variability in bee
27 communities that must be considered when interpreting findings of bee responses to
28 anthropogenic disturbances.

29
30 **Introduction**

31 Population declines of wild pollinators have led to growing concern for these animals and the
32 pollination services they provide (Potts et al., 2010, Garibaldi et al., 2011). To understand
33 how best to conserve and manage populations of wild pollinators we need basic information
34 about the biology of native species and their responses to anthropogenic disturbances.
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35 There is typically a trade-off between spatial and temporal sampling of ecological
36 communities, given limited funding and resources, and researchers investigating bee
37 communities have balanced this trade-off in different ways. Most field studies of bees are
38 short-term, typically focusing on spring-active bees over one to three years across multiple
39 sites. These studies often describe changes in bee communities along spatial gradients of
40 anthropogenic disturbance (e.g. agricultural land cover), and combine these descriptions with
41 knowledge of historical and projected anthropogenic disturbances to infer temporal trends in
42 bee communities (Winfrey et al., 2009, Kennedy et al., 2013). This kind of study may fail to
43 detect responses of bees to anthropogenic disturbances against the background of natural
44 spatial variability, including spatially asynchronous temporal dynamics of typically unknown
45 magnitude. Other studies have repeated historical surveys, or used museum collections and
46 data repositories spanning decades to infer responses of bee communities to anthropogenic
47 pressures over long time scales (Bartomeus et al., 2013, Scheper et al., 2014, Biesmeijer et
48 al., 2006, Burkle et al., 2013, Grixti and Packer, 2006). These studies are typically conducted
49 at coarse spatial and temporal resolutions, aggregating specimens collected across a large
50 area in different years, or collecting specimens decades apart without collection in the
51 intervening periods. They primarily provide insight into broad-scale changes in bee faunas
52 that can be interpreted in light of anthropogenic disturbances occurring over similar spatial
53 and temporal scales. A small number of studies have been longitudinal, repeatedly surveying
54 bees at one or few nearby locations over a decade or more of consecutive years (Iserbyt and
55 Rasmont, 2012, Onuferko et al., 2018, Roubik, 2001). In addition to describing long-term
56 trends, these longitudinal studies characterise the natural temporal variation of bee
57 communities against which the signal and biological significance of anthropogenic impacts
58 must be detected and assessed. The present study is a decade-long, near continuous
59 longitudinal study of an Australian bee community.

60 While short-term multi-site studies of bee communities have been conducted on all southern
61 continents except Antarctica (Kennedy et al., 2013), to the best of our knowledge there have
62 been no long-term studies in the southern hemisphere that characterise annual and seasonal
63 community dynamics. Australia has approximately 1600 species of native bees, and the
64 majority of these are solitary and nest in soil, hollow stems, or woody debris (Schwarz and
65 Hogendoorn, 1999). However, their population and community dynamics, as well as their
66 phenology remain poorly understood (Batley and Hogendoorn, 2009). Information about
67 emergence dates, development times, periods of activity, number of generations per year or
68 population variation from year-to-year is limited and obtaining such data can be protracted
69 and difficult.

70 The Australian bee fauna is dominated by the families Colletidae (53% of named species) and
71 Halictidae (23%), with Apidae, Megachilidae, and the endemic Stenotritidae comprising only
72 12, 10, and 1% respectively, and the otherwise widespread Andrenidae and Melittidae absent
73 (Batley and Hogendoorn, 2009). Life cycle studies do not reflect these relative proportions,
74 with most detailed studies focusing on Apidae. The most detailed account is of the life cycle
75 of *Amegilla (Zonamegilla) pulchra* (Apidae) in Brisbane (Cardale, 1968b, Cardale, 1968a,
76 Cardale, 1968c). This species overwinters as mature larvae (prepupae) and adults emerge in

77 summer. Females require a minimum of seven weeks for development and produce up to
78 three generations per year. Allodapine bees (Schwarz et al., 2007) have also been studied
79 extensively, largely because of interest in their primitively social status. Active throughout
80 the warmer months, they overwinter as adults and most feed their larvae progressively. Egg
81 laying, however, varies (Silberbauer, 1997) from a single burst, or two bursts (Tierney et al.,
82 1997) to progressive laying throughout the active season (Hogendoorn et al., 2001).
83 Reproductive females may have relatively long lives, reportedly as long as 18 months
84 (Schwarz et al., 2007). The two *Xylocopa* (*Lestis*) species mass provision their brood cells
85 and show a much lower level of cooperativity than the allodapines, but they also overwinter
86 as adults (Steen and Schwarz, 2000). *Xylocopa aeratus* is predominantly univoltine, while *X.*
87 *bombylans* is bivoltine.

88 With two exceptions, the life histories of Australian Halictidae are undocumented. In other
89 parts of the World, inseminated females hibernate in winter, emerging in spring to forage and
90 produce offspring. Most of the males are produced in late summer when they mate with
91 young females that will hibernate and found the next generation (Michener, 2007). Long-
92 lived queens have also been reported in social species of halictines, (Michener, 1990), but
93 similar sociality is unknown in Australian representatives of the subfamily (Danforth and
94 Shuqing, 2001). The Australian species *Lasioglossum* (*Chilalictus*) *hemichalceum* has been
95 studied (Kukuk, 1996). Up to 20 females live in communal groups in which all individuals
96 are reproductively active. In spring (November) females that have overwintered as mated
97 adults rear brood consisting of males and females. After mating, these first-generation
98 females go on to rear a second brood consisting of males and females (Kukuk et al., 2005).
99 Second-generation females mate then overwinter (March-October in Victoria) to begin the
100 cycle in the following year. A second Australian species, *Lipotriches* (*Austronomia*)
101 *australica*, was studied by (Vogel and Kukuk, 1994). Colonies comprised two-three
102 reproductive females, all of which foraged in spring. A general spring–early summer peak in
103 Halictidae activity was reported from Hobart, Tasmania, though some species exhibited
104 bimodal flight patterns peaking in spring and autumn (Hingston, 1998).

105 For families Colletidae, Stenotritidae or Megachilidae, inferences about emergence times and
106 number of generations per annum have been drawn, with varying degrees of confidence, from
107 collection data and field observations (Houston, 1987, Houston, 1991, Houston and Maynard,
108 2012). *Leioproctus plumosus* has been shown to be multivoltine (Batley and Brandley, 2014),
109 while *Leioproctus fulvus*, whose nests are accompanied by conspicuous tumuli, is apparently
110 univoltine (MB pers. obs.). Because adult activity of univoltine species lasts for no more than
111 eight weeks, observation of activity over significantly longer periods is interpreted as
112 evidence of multivoltinism (Houston, 1971, Houston, 1975a). While this assumption is
113 reasonable in many cases, it should be used with care as *Amphylaeus morosus* (Colletidae)
114 females have been reported as surviving for up to a year (Spessa et al., 2014). Similar
115 inferences can be drawn from collection data found in taxonomic publications (Walker, 1995)
116 or data repositories like Atlas of Living Australia. The information from such sources is
117 averaged over many collection sites and different collection methods, which may provide a

118 distorted picture as demonstrated by the observation that the activity periods of the univoltine
119 species *Amegilla dawsoni* at different localities were widely out of phase (Houston, 1991).

120 There is also a dearth of information regarding the range and drivers of inter-annual variation
121 in Australian bee activity. Some anecdotal evidence exists, such as the observation that *L.*
122 *hemichalceum* reproductive activity terminated early in a year with above average rainfall
123 and below average temperature (Kukuk, 1996). Moisture and temperature are known to
124 influence bee behavior and demography in other parts of the world (Stone and Willmer, 1989,
125 Richards and Packer, 1995), and ground-nesting bees may be particularly susceptible to
126 flooding and soil moisture which makes broods more susceptible to fungal attacks (Richards
127 and Packer, 1995, Packer and Knerer, 1986). On the other hand, the emergence of
128 *Leioproctus plumosus* was not strongly correlated with rainfall, but was affected by
129 parasitism (Batley and Brandley, 2014).

130 The present study provides the first near-continuous, long-term (ten years) longitudinal study
131 of bee activity in the southern hemisphere. Specifically, we describe: 1) seasonal and annual
132 variation in overall bee abundance, species richness, and community composition; 2) overall
133 bee abundance as it relates to rainfall; and 3) seasonal phenologies of abundant species. We
134 also explore associations between species-specific emergence date and two bee traits: 1) total
135 abundance, to test the hypothesis that more abundant bees are more likely to be detected
136 earlier (as they reach detection levels at earlier stages of emergence), and 2) body size which
137 may influence the range of temperatures over which bee species are active (Stone and
138 Willmer 1989). Finally, we compared two trapping methods in terms of the bee species they
139 detect as different trapping methods have been shown to detect different bee taxa (Hall,
140 2018).

141

142 **Methods and Materials**

143 *Study site*

144 We trapped bees at one location in the Commonwealth Scientific and Industrial Research
145 Organisation (CSIRO) Ginninderra Experimental station, Canberra ACT (35° 20' south, 149°
146 09' east) which is used as a mixed cropping/grazing farm of approximately 5.5km x 1.0km.
147 Most of the land cover within 1 km of this site is urban, and some of this development
148 occurred during the ten year study period. A single blue vane bee trap (SpringStar Inc.,
149 Woodinville, USA) was attached to a steel star picket using a right angled bracket at a height
150 of 1.3 m as these have been effective in previous surveys of Australian bees (Lentini et al.,
151 2012, Hall, 2018). No liquids, pheromones, or killing agents were used in this trap. A pan
152 trap was also placed 150m away from the blue vane trap that consisted of a yellow plastic
153 wash tub (37cm x 31cm x 14cm) with a 1cm hole drilled 2cm from the top of the tub and
154 covered with fine gauze mesh to avoid overflowing during rain events, filled with water and
155 detergent. In addition, we replaced all the blue coloured bee-attracting parts on an annual
156 basis (the beginning of each season) to eliminate any possibility that the blue coloured parts
157 would fade in sunlight and therefore become less attractive.

158

159 *Data collection*

160 Blue vane trapping started in early October 2008 and concluded at the end of November
161 2017. The trap was emptied of bees every 4 to 22 (mean = 7.69, SD = 2.7) days, and
162 operation of the trap ceased over winter (June, July, and August) except in 2011, 2013 and
163 2015, when colder temperatures from mid April onwards produced a zero catch for two or
164 more weeks in a row (excluding *Apis mellifera*). We also have no data for December 2008.
165 Single trapping events sometimes included days on either side of the change of month. When
166 summarising data by month we assigned samples to whichever month accounted for the most
167 days. Once collected the bees were sorted to species, sexed and then counted. Species were
168 named according to the Australian Faunal Directory, because this directory is used by other
169 Australian databases (e.g. the Atlas of Living Australia) as the definitive checklist of species
170 names. As a result, *Lasioglossum (Homalictus)* was treated as *Homalictus (Homalictus)*.
171 Inter-tegular measurements (IT distance) were made from up to five male and five female
172 bees (depending on numbers caught) of each species as an indicator of bee size (Cane, 1987).

173 The yellow pan trap was opened for one week periods coinciding with a blue vane trap
174 weekly trapping event. These traps were open for one week for each of the months from
175 October 2015 to November 2016 (excluding winter).

176 Rainfall and temperature data were collected onsite from the Ginninderra farm
177 meteorological station situated 1.5 km from the trap.

178 *Data analysis*

179 Descriptive statistics are provided for 1) seasonal and annual variation in overall bee
180 abundance and species richness, 2) overall bee abundance as it relates to rainfall, and 3)
181 seasonal phenologies of abundant species averaged across years. Spearman correlation was
182 used when there was evidence of non-linearity (for relationships between bee abundance and
183 seasonal rainfall, see Figure 4), Pearson correlation was used when assumptions of linearity
184 were met.

185 Regression analyses were used to model species-specific emergence date as a function of
186 body size and total abundance of each species, with individual species (only those detected
187 during at least two sample periods) as replicates. Emergence data for each species was the
188 earliest date of detection across all years, measured as the number of days since the end of
189 July (the coldest month in Canberra). Response and predictor variables were log transformed
190 to normalise data (Poisson models were over-dispersed, and there were too few observations
191 to estimate the theta parameter of negative binomial models). Two models with different data
192 sets were used: 1) one data set containing all native bee species to explore overall
193 relationships, and 2) one data set containing only native Halictidae species to account for the
194 possibility of phylogenetic effects on seasonal activity (there were too few Apidae). Mixed
195 effects models with a random effect for year were used to account for the fact that different
196 bees emerged earliest in different years, using the glmmTMB package (Magnusson et al.,

2017) in the R statistical environment (R Core Team, 2013). Data transformation could not overcome the influence of one outlier species in each data set, so they were removed. *Hylaeus honestus*, the only Colletidae species, was removed from the data set containing all native species, while *Lipotriches sp.*, the only representative of the Nomiinae subfamily, was removed from the Halictidae data set leaving only species of the Halictinae subfamily.

Because the pan trap was open for a limited period, only results from the blue vane trap have been used for statistical analysis.

Results

We collected 3742 individuals comprising 31 species in the blue vane trap (Table 1a). All the species are native, except for *Apis mellifera*. Halictid bees accounted for 94% of all individuals caught. Four of the five most abundant Halictid species were in the genus *Lasioglossum*, *L. clelandi* (49.3%), *L. cognatum* (19.0%) and *L. lanarium* (16.5%). The fifth most abundant bee *Homalictus (Homalictus) sphecodoides* comprised 6.0% of the total bees caught.

Only 197 males, representing 5.5% of the total catch, were caught in the blue vane trap. Of these 132 (67%) were *L. lanarium*. This species had a relatively high male abundance of 132♂:450♀, as did *Amegilla asserta* 9♂:16♀ and *A. chlorocyanea* 1♂:3♀. All other species combined (excluding *A. mellifera*) had relatively low male ratios that changed throughout the year from 17♂:2261♀ in spring to 26♂:457♀ in summer and 12♂:188♀ in autumn. It is unclear why blue vane traps should be so inefficient at sampling males, which are expected to be more numerous than females (Fisher, 1958, Helms, 1994). The reason for the particularly high proportion of males of *L. lanarium*, which has been reported previously (Walker, 1995), is also unclear. Collection records from Atlas of Living Australia (ALA, 2018) show that, as for almost all Australian *Lasioglossum* species, variation in abundance with time is the same for both sexes of *L. lanarium* (unpub. results).

We collected 294 individuals from the pan trap, which included six species, all *Lasioglossum* and two individuals of *Apis mellifera* (Table 1b). No additional species were caught in the pan trap.

Seasonal variation

Total bee abundance (i.e. summed across all species) typically peaked in spring (September-November), with a secondary peak in summer (December-February) (Figure 2). Total bee abundance was highly correlated with the abundance of *Lasioglossum clelandi* (Pearson correlation = 0.92, p-value = <0.001), the most abundant species (Table 1a).

Species richness appeared to peak in summer during the first few observation years, but in spring thereafter, which might be explained by the loss of summer and autumn active species

234 in the second half of the sampling period (see below). Most of the halictids peaked in spring
235 (Table 1; Figure 3), whereas larger-bodied Apidae and Megachilidae peaked or were not
236 detected until after spring.

237 Several species of bees were caught in high enough numbers (22 minimum) that we were
238 able to assess the phenology of these species individually over the multiple years of survey
239 (Figure 3). All but two halictine species showed activity periods longer than eight weeks
240 suggesting they are multivoltine. The exceptions were *L. clelandi* and *L. orbatum* which were
241 active mostly in spring, though neither species was completely absent later in the year.
242 *Amegilla asserta* did not appear until summer, but remained active until the colder months,
243 which is consistent with the multigenerational behaviour reported for *A. pulchra* (Cardale,
244 1968b).

245 *Phenology, abundance, and body size*

246 Whether all bee species or only halictid species were analysed there was a significant
247 negative relationship ($\alpha = 0.05$) between bee abundance and earliest detection date, such
248 that more abundant species tended to be detected earlier in the season (Table 2). Using all bee
249 species there was a marginally significant ($0.1 < p\text{-value} > 0.05$) positive relationship between
250 earliest date of detection and inter-tegular distance, but a non-significant negative relationship
251 when only Halictidae bees were included (Table 2).

252 *Annual variation*

253 Year-to-year variation in total bee abundance was high, species richness was less variable
254 (Figure 2). The ratio of bee abundance per day (i.e. total number of bees trapped divided by
255 total number of sample days in each year) in one year relative to the previous year ranged
256 from 0.16 to 5.70 (Table 3), while the ratio of species richness per day in each year compared
257 to the previous year ranged from 0.49 to 1.95.

258 Similarity in bee community composition, calculated as the Bray-Curtis (using abundance
259 data) and Jaccard (using presence-absence data) similarity indices between consecutive years
260 averaged 45% and 38% respectively (Table 3). Of the 31 species detected across the entire
261 ten-year sampling period, five were detected in all years, *L. clelandi*, *L. cognatum*, *L.*
262 *lanarium*, *L. orbatum*, and *Apis mellifera*. These five species collectively comprised >74% of
263 specimens in every year. *Lasioglossum clelandi* was the most abundant species in nine out of
264 ten years, *L. cognatum* was dominant in the remaining year. Fourteen species were detected
265 in only one year. The mean number of years in which a given species was detected was 3.4.
266 Species that were more abundant tended to be detected more frequently (Pearson correlation
267 between number of years each species was present and the average abundance of each species
268 = 0.66, $p\text{-value} = < 0.001$, across all species).

269 There was a large decline in bee abundance and richness following the first year of sampling
270 (Figure 2). Of the 14 species observed in only one year, eight were observed only in the first
271 year of sampling (spring 2008–autumn 2009), three of which were spring and/or summer
272 active Halictids and five were summer or autumn active Colletids. Four species were

273 observed only in the 2010–2011 sampling period (one Halictidae, two Megachilidae, one
274 Colletidae), another only in 2011–2012 (Halictidae), and another only in 2012–2013
275 (Colletidae). Thus, the decline in bee species across the first half of the ten-year sample
276 period may have partly arisen from the loss of rare, predominantly Colletidae species (all but
277 one colletid species disappeared in this period).

278 Seasonal rainfall appeared to play a role in determining overall bee abundances from year-to-
279 year (Figure 4). The greatest numbers of bees were detected in springs with low rainfall
280 (Spearman correlation between total bee abundance in spring and total rainfall in spring = -
281 0.72, p-value = 0.02). Spring rainfall was almost identical (and below average) in the first
282 two sampling years, making lack of rain an unlikely candidate for causing the initial decline
283 in bee numbers (data not shown). There were no statistically significant correlations between
284 autumn bee abundance and autumn rainfall (Spearman correlation = -0.18, p-value = 0.64), or
285 summer bee abundance and summer rainfall (Spearman correlation = -0.30, p-value = 0.44).

286

287 Discussion

288 We used a near-continuous bee monitoring program of a single site over ten years to gain a
289 better understanding of the basic biology of native Australian bees and long-term community
290 dynamics at this site. To the best of our knowledge, this is the longest such monitoring period
291 published in the southern hemisphere. While our results cannot be generalised to other sites,
292 when considered in the context of existing literature they contribute to our understanding of
293 Australian bee biology and the nature of temporal variation in bee communities.

294 *Bee biology*

295 There were clear patterns of taxonomic variation in phenology over the ten year sample
296 period at our study site. Most Apidae and Megachilidae species were detected in summer
297 and/or autumn, whereas most Halictidae species were spring and/or to a lesser extent summer
298 active. The colletid bees sampled were also collected later in the year, but these numbers
299 were very small and this pattern is not typical of colletids (Maynard, 2014, Houston, 1975b).
300 Other Australian studies (Cardale, 1968b, Cardale, 1968a) also observed the Apidae genus
301 we detected (*Amegilla*) emerging late in the year, though other Apidae genera are known to
302 be active in spring (Schwarz *et al.*, 2007) highlighting the limits to generalisations that can be
303 made from studying a single location. Most of the larger-bodied species were Apidae and
304 Megachilidae, such that spring was dominated by small halictid bees and large bees were
305 active mostly after spring.

306 There was also variation in the shape of activity patterns. Some species were unimodal while
307 others appeared to be bimodal. *Lasioglossum hemichalceum* is one of the few species of bee
308 whose phenology has been studied in Australia, and appeared to be bimodal in western
309 Victoria, except in an unusually wet and cold year where it was unimodal (Kukuk, 1996). In
310 the present study *L. hemichalceum* appeared to be multivoltine.

311 *Lasioglossum* species are likely to be important crop pollinators in the study area and
312 surrounding regions. *Lasioglossum* was the most speciose and abundant genus at our study
313 site, and four of five species detected in all ten sample years were *Lasioglossum* (the fifth was
314 *Apis mellifera*). These and other species of this genus were also the most abundant in blue
315 vane traps in agricultural regions of inland New South Wales (Lentini *et al.*, 2012), north-east
316 Victoria (Hall *et al.*, 2019), and south-east Victoria (Brown *et al.*, 2020), where in the latter
317 study they were also relatively frequent visitors to apple, pear, plum, cherry, raspberry,
318 blueberry, and blackberry flowers. *Lasioglossum* species may thus be temporally reliable at
319 sites other than ours (i.e. because they are abundant) and may also provide spatially reliable
320 pollination services (i.e. are present in most years at most sites). Most Australian
321 *Lasioglossum* species are generalist in their foraging habits (Walker, 1995, Batley, 2019) so
322 are likely to visit a range of crops.

323 *Homalictus sphecodoides* was detected in nine of ten years and was the fourth most abundant
324 species. Similarly, *H. urbanus* was the most abundant species in agricultural landscapes of
325 south-east Queensland (Cunningham *et al.*, 2013). Given the very small size of these species,
326 they are likely to be pollinators of Asteraceae and other flowers in which the pollen is readily
327 accessible, and have been observed to visit these flowers more frequently than others in
328 agricultural landscapes of south-east Victoria (Brown *et al.*, 2020).

329 *Amegilla asserta* was detected in six of ten years, at a relatively low abundance. For some
330 flowers, bee body size is important to pollination function (Hoehn *et al.*, 2008) such that the
331 large-bodied *A. asserta* may play an important role in the pollinator community.

332 *Trapping*

333 The pan trap detected a nested subset of the species detected with the blue vane trap. This
334 suggests these alternative methods do not detect different sections of the bee assemblage, and
335 is in agreement with previous research from the northern hemisphere (Joshi *et al.*, 2015,
336 Buchanan *et al.*, 2017).

337 *Annual variation*

338 One important advantage of long-term longitudinal studies such as ours over coarser long-
339 term studies, or studies with high spatial replication but not temporal replication, is they
340 provide insight into annual variation in bee communities. We observed that total bee
341 abundance more than halved between some consecutive years, and more than quadrupled
342 between other years. Species richness halved between some consecutive years and doubled
343 between others. While our results are not generalizable beyond our study site, similarly high
344 annual variation in bee communities has been reported from long-term studies in the northern
345 hemisphere, even in undisturbed nature preserves (Roubik, 2001). Caution should therefore
346 be taken in inferring trends in bee abundance and richness from a small number of points in
347 time. Further, multi-site short-term studies may be subject to large amounts of unexplained
348 spatial variation when bee communities at different sites fluctuate asynchronously through
349 time in response to a range of spatio-temporally variable factors such as rainfall (a potential
350 contributor to annual variation at our site).

351 We also found that bee community composition was highly variable between years, being on
352 average 45% (based on abundance data) and 38% (based on presence-absence data) similar
353 between consecutive years. Fourteen of 31 species (45%) were detected in only one year,
354 spread across the first five years of sampling, and these tended to be the less abundant
355 species. However, community composition was more stable in terms of the dominant species,
356 with >74% of all specimens in every year consisting of the same five species, one of which
357 (*L. clelandi*) was the most abundant species in all but one year. Again our results are not
358 generalizable beyond our study site, but some long-term studies of bee communities from the
359 northern hemisphere also found that less abundant species were detected in one sample
360 period only, while highly abundant species persisted across decades (Cane et al., 2005).
361 Multi-site, short-term studies might thus be subject to inflated compositional differences as a
362 result of missing rarer species, while capturing the dominant species across sites.

363 There was a large decline in bee abundance and richness following the first year of sampling.
364 Interestingly, long-term longitudinal studies of bee communities in the northern hemisphere
365 have also reported declines in abundance and/or diversity through time, which the authors
366 attributed to long-term weather patterns or landscape change (Onuferko et al., 2018, Iserbyt
367 and Rasmont, 2012). Landscape change could have been important at our study site as a large
368 urban development (the suburb of Crace) commenced within 1 km in the second year of
369 sampling. Long-term decline could also be due to any number of unmeasured environmental
370 factors, or possibly an effect of trapping, but without spatial replication at the appropriate
371 scale it is only possible to speculate.

372 Regardless of whether studies of bee responses to anthropogenic disturbances favour spatial
373 or temporal replication, they often provide some evidence of decline (Scheper et al., 2014,
374 Biesmeijer et al., 2006, Bartomeus et al., 2013, Burkle et al., 2013). These declines would
375 tend to represent declines in average abundance, richness, and or composition, but to fully
376 appreciate extinction risk the natural variation around this average must be ascertained
377 because more variable populations are more likely to go extinct (Vucetich et al., 2000). The
378 considerable natural annual variability reported here and in other studies of bee communities
379 (Roubik, 2001, Iserbyt and Rasmont, 2012) suggests that bees in decline could be closer to
380 extinction than trends of average abundance suggest.

381

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386

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Tables

Table 1a. Abundance of each bee species collected, organised by family. Counts are assigned to three different periods: Spring (September, October, November) Summer (December, January, February) and Autumn (March, April, May). IT span records the inter-tegular distance (mm), as a guide to body size (Cane 1987). We have measured the mean IT distance for both males and females.

Species	Spring		Summer		Autumn		Total	IT span	
	Females	Males	Females	Males	Females	Males		♀	♂
Blue Trap									
Apidae									
<i>Amegilla (Notomegilla) chlorocyanea</i> (Cockerell, 1914)			1	1	2		4	3.40	3.04
<i>Amegilla (Zonamegilla) asserta</i> (Cockerell, 1926)			8	6	8	3	25	3.55	3.31
<i>Apis mellifera</i> L.	19		53		98		170	3.14	
Megachilidae									
<i>Megachile erythropyga</i> Smith, 1853			2		1		3	3.20	
<i>Megachile (Hackeripis) oblonga</i> Smith, 1879					4		4	2.40	
<i>Megachile sp.</i> Latreille, 1802					1		1	2.96	
Colletidae									
<i>Leioproctus (Leioproctus) spatulatus</i> (Cockerell, 1905)					1		1	1.44	
<i>Leioproctus (Leioproctus) maculatus</i> (Rayment, 1930)					1		1	2.24	
<i>Leioproctus (Minycolletes) wahlenbergiae</i> Michener, 1965					1		1	1.84	
<i>Euryglossina (Euryglossina) hypochroma</i> Cockerell, 1916					1		1	0.80	
<i>Euhesma (Euhesma) wahlenbergiae</i> (Michener, 1965)			1				1	1.12	
<i>Hylaeus (Euprosopis) honestus</i> (Smith, 1879)	2						2	2.96	
<i>Hylaeus (Gnathoprosopis) euxanthus</i> (Cockerell, 1910)			1				1	1.36	
Halictidae									

<i>Homalictus (Homalictus) sphecodoides</i> (Smith, 1853)	129	1	53	8	20	1	212	1.06	0.80
<i>Homalictus (Homalictus) urbanus</i> (Smith, 1879)			3				3	1.12	
<i>Homalictus (Homalictus) sphecodopsis</i> (Cockerell, 1905)						1	1	1.12	
<i>Lasioglossum (Chilalictus) mundulum</i> (Cockerell, 1916)	2					1	3	1.12	
<i>Lasioglossum (Chilalictus) clelandi</i> (Cockerell, 1910)	1671	3	52	2	9	1	1738	1.71	1.57
<i>Lasioglossum (Chilalictus) cognatum</i> (Smith, 1853)	321	4	247	11	81	8	672	1.36	1.18
<i>Lasioglossum (Chilalictus) expansifrons</i> (Cockerell, 1914)	10		9			3	22		
<i>Lasioglossum (Chilalictus) hemichalceum</i> (Cockerell, 1923)	21		70	4	56	1	152	1.12	0.82
<i>Lasioglossum (Chilalictus) lanarium</i> (Smith, 1853)	329	68	98	38	23	26	582	2.08	1.74
<i>Lasioglossum (Chilalictus) orbatum</i> (Smith, 1853)	91	8	6			2	107	1.76	1.50
<i>Lasioglossum (Chilalictus) mediopolitum</i> (Cockerell, 1914)			5				5	1.26	
<i>Lasioglossum (Chilalictus) imitans</i> (Cockerell, 1914)	8		2				11	1.52	
<i>Lasioglossum (Chilalictus) biceps</i> Walker, 1995						1	1	1.12	
<i>Lasioglossum (Chilalictus) globosum</i> (Smith, 1853)	2	1					3	1.28	1.04
<i>Lasioglossum (Chilalictus) greavsi</i> (Rayment, 1930)	4						4	1.16	
<i>Lasioglossum (Chilalictus) willsi</i> (Cockerell, 1906)						1	1	1.52	
<i>Lasioglossum (Parasphecodes) imitator</i> Michener, 1965				1			1		2.00
<i>Lipotriches sp.</i> Gerstaecker, 1858			6		3		9	1.97	
Total species =31	2609	85	617	71	319	41	3742		

Table 1b. Abundance of each bee species collected in the pan trap only. Note the trap was only open from October 2015 to November 2016.

Species	Spring		Summer		Autumn		Total
	Early	Peak	Peak	Late	Late	Late	
Pan Trap (Oct 2015 to Nov 2016 only)							
Apidae	♀	♂	♀	♂	♀	♂	
<i>Apis mellifera</i> L.	1			1			2
Halictidae							
<i>Lasioglossum (Chilalictus) lanarium</i> (Smith, 1853)	3	4	3	5			15
<i>Lasioglossum (Chilalictus) cognatum</i> (Smith, 1853)	3		4		1		8
<i>Lasioglossum (Chilalictus) clelandi</i> (Cockerell, 1910)	121	2	3		1		127
<i>Lasioglossum (Chilalictus) orbatum</i> (Smith, 1853)	32	4			2		38
<i>Homalictus (Homalictus) sphecodoides</i> (Smith, 1853)	76	2	21		4		103
<i>Lasioglossum (Chilalictus) expansifrons</i> (Cockerell, 1914)	1						1
Total species =6	237	12	31	6	8	0	294

Table 2: Parameter estimates and p-values from linear mixed effects models with (log transformed) earliest date of detection (number of days since July) for either all bee species ($n = 17$) or Halictidae bee species ($n = 12$) as the response variable, and both (log transformed) inter-tegular distance (IT) and (log transformed) total number of individuals detected for each species as predictor variables. (DF is residual degrees of freedom).

Data set	Parameters	DF	Estimate	p-value
All bees	log(IT)	13	0.75	0.078
	log(abundance)	13	-0.24	<0.001
Halictidae	log(IT)	8	-1.34	0.192
	log(abundance)	8	-0.26	<0.001

Table 3: comparisons of total bee abundance, species richness, and compositional similarity between consecutive years. Abundance and richness ratios were calculated as the total number of bee individuals or species caught per day in one year (i.e. total number of individuals or species trapped divided by the total number of trapping days) divided by the total number of individuals or species caught per day in the previous year. Similarity was calculated as the Bray-Curtis (using abundance data) and Jaccard (using presence-absence data) similarity indices between consecutive years.

	Abundance ratio	Richness ratio	Bray-Curtis similarity	Jaccard similarity
2009 vs 2008	0.32	0.49	48%	33%

2010 vs 2009	0.24	0.92	35%	62%
2011 vs 2010	1.92	0.66	33%	47%
2012 vs 2011	2.46	1.10	54%	33%
2013 vs 2012	0.52	0.92	47%	39%
2014 vs 2013	0.89	0.74	82%	36%
2015 vs 2014	2.84	1.32	48%	30%
2016 vs 2015	0.16	0.77	27%	30%
2017 vs 2016	5.70	1.95	27%	29%
Average	1.67	0.99	45%	38%

Figure legends

Fig 1. Ginninderra Farm surrounded on three sides by Canberra Australia. Black star indicates position of trap.

Figure 2. Number of bees caught divided by the number of trapping days, and total number of species caught, for each month across the entire sampling period (trapping did not occur in December 2008 and most winter months). Grey bars highlight spring months.

Figure 3: Phenology of the eight most abundant bees caught. White bars = total number of female specimens, black bars = total number of male specimens.

Figure 4: Total number of bees caught per day as a function of rainfall for Autumn, Spring, and Summer.

Figures

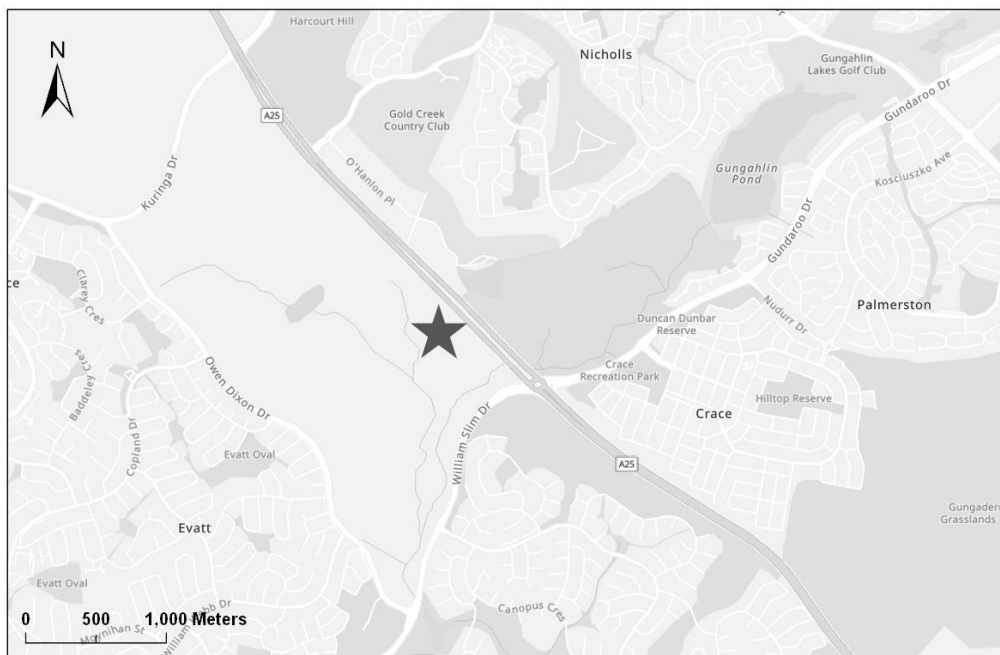


Figure 1.

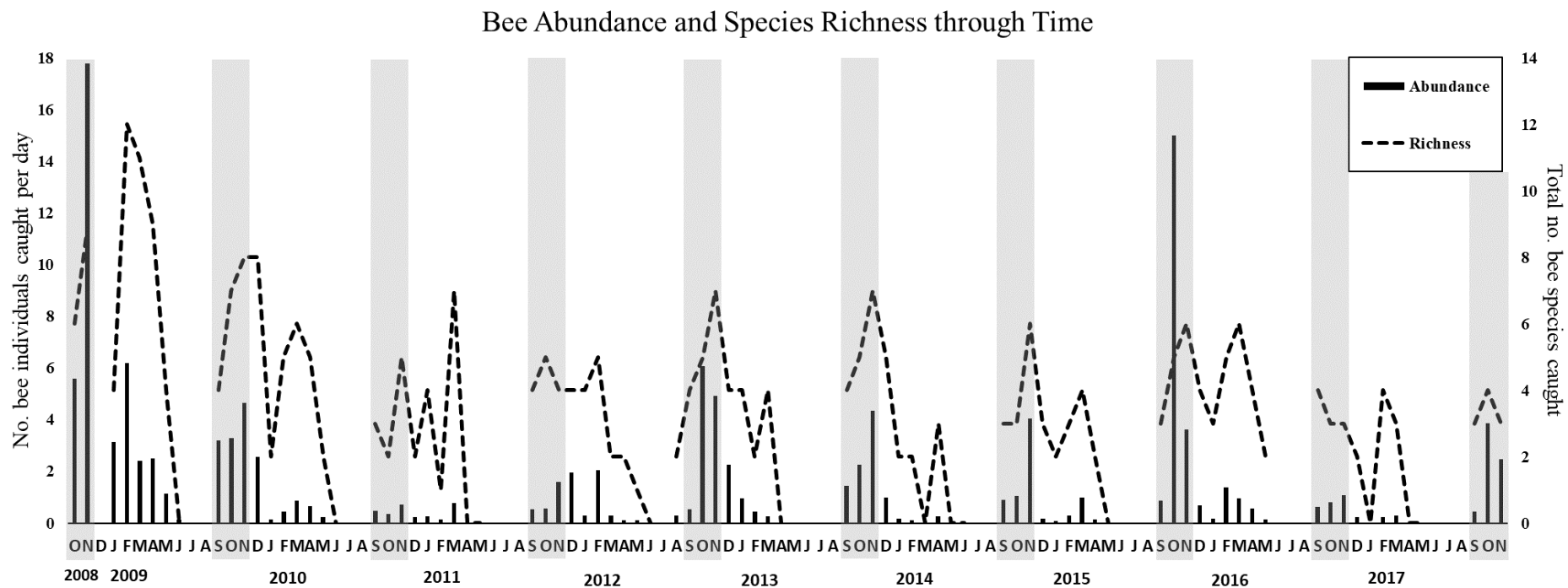


Figure 2.

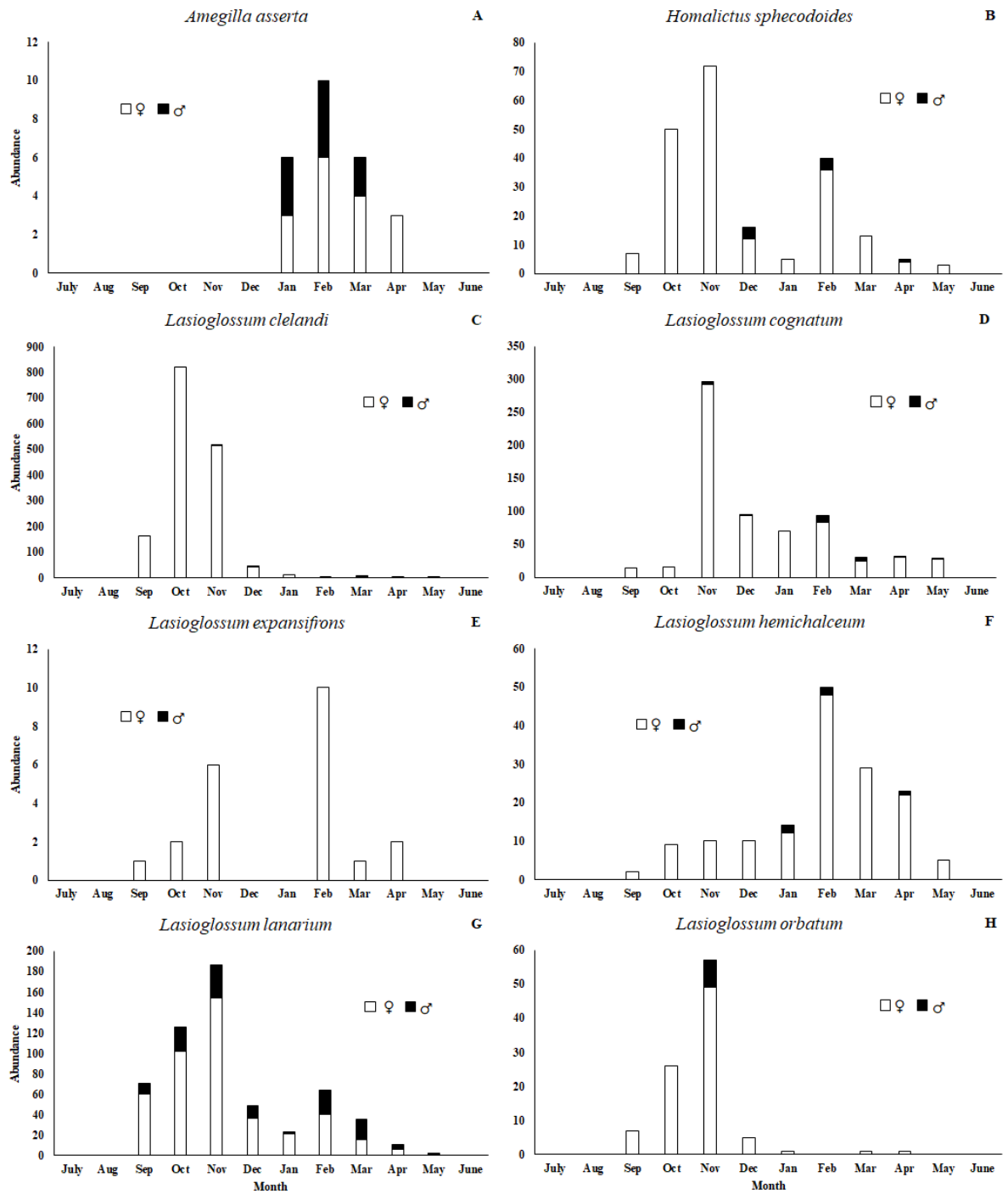


Figure 3

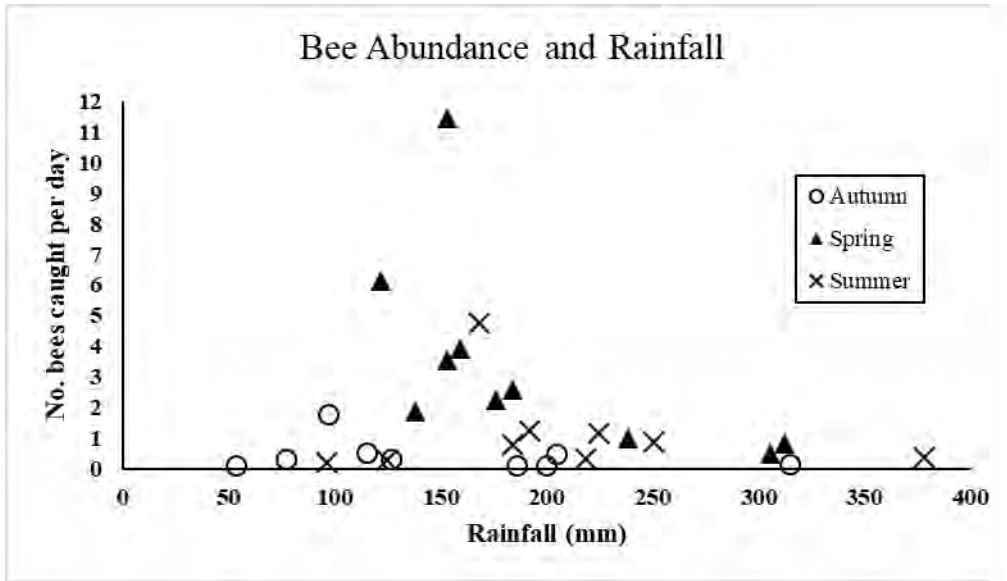


Figure 4



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Author/s:

Neave, MJ;Brown, J;Batley, M;Rao, S;Cunningham, SA

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