

1 Vulnerability of island insect pollinator communities to pathogens

2 Laura E Brettell^{1,2*}, Stephen J Martin³, Markus Riegler¹ and James M Cook¹

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4 ^{1.} *Hawkesbury Institute for the Environment, Western Sydney University, Locked Bag 1797,*
5 *Penrith, NSW, 2751, Australia.*

6 ^{2.} *Department of Vector Biology, Liverpool School of Tropical Medicine, Pembroke Place, L3*
7 *5QA, UK.*

8 ^{3.} *School of Environment and life Sciences, University of Salford, Manchester, M5 4WT, UK.*

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10 *Corresponding author. Email address: laura.brettell@lstmed.ac.uk

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12
13 *Abstract*

14
15 Island ecosystems, which often contain undescribed insects and small populations of single
16 island endemics, are at risk from diverse threats. The spread of pathogens is a major factor
17 affecting not just pollinator species themselves, but also posing significant knock-on effects
18 to often fragile island ecosystems through disruption of pollination networks. Insects are
19 vulnerable to diverse pathogens and these can be introduced to islands in a number of ways,
20 e.g. via the introduction of infected managed pollinator hosts (e.g. honey bees and their
21 viruses, in particular *Deformed wing virus*), long-range migrants (e.g. monarch butterflies and
22 their protozoan parasite, *Ophryocystit elektroscirrha*) and invasive species (e.g. social wasps
23 are common invaders and are frequently infected with multi-host viruses such as *Kashmir bee*
24 *virus* and Moku virus). Furthermore, these introductions can negatively affect island
25 ecosystems through outcompeting native taxa for resources. As such, the greatest threat to
26 island pollinator communities is not one particular pathogen, but the combination of
27 pathogens and introduced and invasive insects that will likely carry them.

28
29 *Keywords*

30 Island; pollinator; spillover; pathogen; invasive species; virus

31
32 *1. Introduction*

33
34 Invertebrates play key roles in maintaining ecosystem stability and diversity, with perhaps the
35 most obvious example being insect pollinators which have driven floral evolution (e.g.
36 Stebbins, 2013; Dilcher, 2000) and mediate much of plant reproduction today. Globally,

37 insect pollinators are in decline and this has been reviewed extensively elsewhere (e.g.
38 Helmer, 2020; Ollerton, 2017) and, whilst the biggest factor is generally understood to be
39 habitat loss, another key reason is an increased spread and occurrence of pathogens (Potts et
40 al., 2010). Globalisation has resulted in the increased ability of pathogens to spread between
41 populations and this is especially evident with pathogens that cause human disease where we
42 are seeing an increase in the frequency of epidemics and pandemics, e.g. SARS, MERS and
43 COVID-19 have all emerged within the past 20 years (Anderson et al., 2020). The same
44 pattern is applicable to diverse pathogens and hosts, including insect pollinators, and can
45 have far greater implications than merely upon the health status of a single species.

46

47 The western (or European) honey bee (*Apis mellifera*) exemplifies this. Over the past 50
48 years, this species has experienced massive losses in populations across the world,
49 particularly throughout mid-latitude regions of the Northern hemisphere. A key driver here
50 has been the spread of an ecto-parasitic mite (*Varroa destructor*, henceforth *Varroa*) that
51 provided a new viral transmission route which transformed a relatively rare and benign viral
52 pathogen (*Deformed wing virus*, DWV) to become one of the most widespread and deadly
53 insect pathogens among pollinator communities in the world (Martin & Brettell, 2019). Such
54 pollinator losses can dramatically impact the plants they pollinate, especially agricultural
55 crops, but also wild plants. Furthermore, it is not only the loss of a species from an ecosystem
56 that is of concern, disease can also change pollinator behaviour. For example, diseased
57 individuals can have altered foraging preferences (e.g. for nectar versus pollen) or impaired
58 foraging ability (reviewed by Koch et al., 2017). Such changing plant-pollinator interactions
59 can have follow on effects, such as altering plants' reproductive outputs. For example, the
60 disruption to pollination networks following introduction of *Bombus terrestris* to the island of
61 Hokkaido (initially introduced for glasshouse pollination, but which then escaped into the
62 wild) caused a reduction in seed set in the native tuberous flower *Corydalis ambigua*
63 (Dohzono et al., 2008). Pollinators can thus serve as biological indicators; their presence,
64 abundance and activities inform us about the state of an ecosystem (Kevan et al., 1999).
65 Consequently, given that each of those factors can be dramatically altered by pathogens,
66 understanding pollinator health is, arguably, vital for understanding ecosystem health.

67

68 Whilst insect populations and associated ecosystem functions will always be at risk from
69 infectious disease regardless of geography, island populations are especially vulnerable.
70 Being generally more isolated than mainland populations, they may be afforded some level of

71 protection as the frequency of colonisation by new pathogens may be lower. However, island
72 species by their very nature tend to maintain smaller population sizes and often lack
73 resistance to exotic pathogens and predators; these ecosystems are often fragile, so when
74 disruptions do happen, they typically have greater impacts. For example, due to
75 anthropogenic introduction of pest species and pathogens (especially avian malaria and pox
76 virus), Hawaiian endemic birds and plants make up 72% and 63% respectively of the total
77 USA species known to have gone extinct since the arrival of humans, despite Hawaii
78 comprising only 0.2% of the total USA land area (Vitousek et al., 1987). In particular, the
79 decline of Hawaiian endemic birds had the flow on effect of causing the extinction of 31
80 species of Bell flowers (Campanulaceae) (Cox & Elmqvist, 2000), suggesting similar effects
81 could be experienced following extinctions of insect pollinators. Island ecosystems have been
82 identified as a global priority due to their high human impact index (an indication of current
83 threat) (Kier et al., 2009). Understanding patterns of disease spread among island pollinators
84 and the knock-on effects on ecosystems can inform improved conservation management
85 plans, and monitoring the health of pollinators can give insights into the health of island
86 ecosystems more generally.

87

88 2. *What makes islands special*

89

90 Islands are frequently characterised by high levels of endemism and low species diversity
91 (Kier et al., 2009) and many maintain unique biodiversity. Along with other factors, such as
92 low genetic diversity due to bottlenecks at initial colonisation, genetic drift and adaptive loss
93 of traits such as flight (in birds and insects) and enemy resistance that are costly in the local
94 situation, island ecosystems are fragile. Consequently, islands show higher species extinction
95 rates (across many taxonomic groups, but most strikingly in birds) compared to mainland
96 populations (Manne et al., 1999; Ricketts et al., 2005), with cascades of extinctions following
97 disruptions of mutualisms (Vanbergen et al., 2017) and ecosystems generally. The majority
98 of recorded extinctions in the last four centuries have been oceanic island endemics
99 (Whittaker & Fernández-Palacios, 2007).

100

101 Much of what makes islands important ecosystems, lies in what we do not know. Our poor
102 knowledge of the true biodiversity, due to the ‘Linnaean shortfall’ of incomplete biodiversity
103 characterisation, applies most strikingly to invertebrates, largely because of their vast
104 diversity and their small size and diverse habitats making them difficult to study, so estimates

105 of losses are far from complete (Harvey et al., 2020; Pimm et al., 1995). It has been proposed
106 that a staggering 80% of insect species are yet to be described, the bulk of which are likely to
107 be found in tropical forests (Stork, 2018), making the many islands that harbour such forests
108 of particular concern.

109

110 As described by Whittaker et al (2008) in their “general dynamic theory of island
111 biogeography”, species distribution is shaped by immigration, extinction and speciation. For
112 oceanic islands, this is largely driven by the availability of unoccupied niches. Over time,
113 habitat complexity increases, endemics accumulate and local populations differentiate, whilst
114 at the same time populations on other islands become extinct. Assuming equilibrium has been
115 reached and extinction rates are relatively low, the species diversity will increase as further
116 colonizations occur (Steinbauer et al., 2012). Fragment islands, on the other hand, would
117 have had their ecological space filled prior to insularisation (Gillespie & Roderick, 2002).
118 Upon separation from mainlands, they initially experience a decline in species numbers.
119 Then, over time, relic taxa which remain may evolve to become new endemics. Elevation
120 often drives comparable changes to island age in species diversity, where environmental
121 gradients drive speciation. Higher altitudes represent habitats further from reservoirs of
122 adapted populations, compared to lowland coastal areas (Steinbauer et al., 2012). Generally,
123 lower lying coastal areas will be more suitable to invaders than higher elevation areas (due to
124 differences in distance from comparable mainland habitats). This may afford some level of
125 protection from extinction to the lowland taxa, as they may continually receive arrivals from
126 overseas source populations, although, conversely, these areas are often the most amenable to
127 agricultural use, so may face greater habitat modification threat, as well as pest and pathogen
128 introductions, often via ports (where the vast majority of accidental introductions occur).

129

130 Islands are particularly susceptible to the effects of climate change (Nurse et al., 2014) and
131 thus, island pollinator communities are particularly at risk (e.g. through the removal of low-
132 lying habitats with rises in sea level). The interaction between climate change and altitude is
133 particularly interesting. Whereas with mainland populations, species can often shift their host
134 ranges latitudinally to escape rising temperatures, island species need to move toward higher
135 elevations to achieve the same effect. This means that the available habitat area is likely to
136 decrease and may not even exist, as the plants they may need may not be able to respond as
137 quickly.

138

139 3. *Island pollinators and pollination networks*

140

141 Island plant-pollinator networks are largely comprised of (often endemic) super-generalists
142 (such as *Xylocopa darwini* on the Galápagos Islands [Traveset et al., 2013]), which confer
143 some protection against loss of a particular taxon; however, successful invasive generalists
144 (honey bees in particular) may be able to outcompete endemic taxa (Whittaker & Fernandez-
145 Palacios, 2007). The situation is exacerbated by the trend to import managed pollinators,
146 particularly honey bees and more recently bumblebees (*Bombus* spp.) to support commercial
147 crop production, which has also increased the number of invasive pests being accidentally
148 introduced to islands. For example, the Hawaiian Islands have no native species of ants, but
149 currently over 45 species have become established, including many serious pest species that
150 have impacted native flora and fauna (Krushelnycky et al., 2005). Such introductions will
151 have already altered ecosystem dynamics. Even the Galápagos, one of the most well-
152 preserved island chains, now has up to 40% of its pollination interactions involving alien
153 species (Traveset et al., 2013). Altered pollinator communities dominated by invasives can be
154 more resistant to disturbance but more susceptible to disease, often related to their high
155 abundances and degree of connectedness (Traveset et al., 2013). So, the few remaining
156 islands harbouring low numbers of invasive species (e.g. the Amami Islands [Kato, 2000])
157 are of particular research interest for characterisation of health status before likely
158 invasions/colonisations occur.

159

160 Island insect pollinator communities are largely made up of small, generalist solitary bees
161 and/or flies, with butterflies and social bees being far less common (Abe, 2006), although
162 through human-mediated movement, western honey bee now dominates pollination networks
163 on many islands across the world (e.g. Tenerife, Canary Islands [Dupont et al., 2004] and the
164 Hawaiian archipelago [Valenzuela, 2018]). There are exceptions, however, and many islands
165 are home to unique, specialised plant-pollinator interactions (Abe, 2006), perhaps the most
166 notable example being the island phenomenon of lizard pollination (Olesen & Valido, 2003).

167

168 Biological traits of different pollinators play a key role in how likely they are to be successful
169 on islands. For instance, stingless bees (Meliponinae) appear unable to cross water barriers,
170 and social insects may find it more difficult to establish on islands due to high resource
171 requirements. Further, smaller insects may be good colonisers because of their high dispersal
172 abilities; e.g. Spengler et al (2011) observed a decrease in insect body size with increasing

173 island isolation. However, these smaller insects may be less able to establish on islands that
174 already harbour larger competitors.

175

176 The majority of island pollinator communities are not well categorised, but the Amami
177 Islands in the Ryukyu archipelago (Japan) are an exception. The Amami Islands are
178 subtropical, comprise various vegetation types, and are florally diverse, harbouring 32
179 endemic vascular plants. Kato (2000), who surveyed insect visitors to 164 flowering plant
180 species between 1996-1999, showed flies (Diptera) to be the most abundant visitors (31.6%),
181 followed by Coleoptera (28.3%), then Hymenoptera (23.3%). The same pattern was seen
182 when comparing the number of different species within the orders (35.6%, 23.9% and 19.9%
183 respectively). Interestingly, when investigating pollination specifically, they found the
184 majority of flowering plants (61%) were pollinated by bees; mostly generalist small solitary
185 bees (e.g. *Lasioglossum*, *Hylaeus*), followed by larger, long tongued bees (e.g. *Xylocopa*,
186 *Tetralonia*), with Diptera-pollinated plants being next most common (13%). Although on
187 some Amari Islands both managed *A. mellifera* colonies and native *Apis cerana japonica* are
188 present, both species remain rare. Kato (2000) hypothesised that the limited numbers of
189 social bees may be due to challenging environmental conditions with frequent typhoons and
190 fluctuating floral resource availability, and the low numbers of *A. mellifera* specifically may
191 also be due in part to both competition with *A. cerana* and predation by the hornet *Vespa*
192 *analis* (Fujiwara et al., 2021).

193

194 4. Introductions of managed pollinators

195 4.1. Honey bees

196 The global transport of managed pollinators began over 500 years ago, with the first recorded
197 shipments of western honey bee (*A. mellifera*) colonies from Portugal to Brazil in 1530
198 (Crane, 1992). While this has facilitated global crop production, it has also dramatically
199 altered ecosystems the world over.

200

201 The traits that make the western honey bee so successful as a managed pollinator (generalist
202 foraging behaviour and large numbers per hive [$<30,000$]) are also those which have
203 transformed it into one of the world's most successful invasive species. Irrespective of any
204 pathogens, this can, and has had a big effect on ecosystems in itself. For example, honey bees
205 have been shown to outcompete native pollinators in Tasmania (Goulson et al., 2002), the
206 Bonin Islands (Kato et al., 1999) and Tenerife (Dupont et al., 2004).

207

208 While honey bees and their pathogens have been reviewed extensively elsewhere (e.g.
209 Genersch & Aubert, 2010; Martin & Brettell, 2019; Nazzi & Le Conte, 2016), they constitute
210 the majority of what we know about island pollinator health. Thus, these studies provide vital
211 information on how island populations cope with pathogens. The number one enemy of the
212 honey bee in recent times has been the *Varroa* mite, along with DWV that it vectors (Martin
213 et al., 2012; Wilfert et al., 2016). A number of studies have clearly shown that when *Varroa*
214 invades honey bee populations on an island (or archipelago), there is a dramatic increase in
215 DWV prevalence and titre in honey bee colonies (Martin et al., 2012; Mondet et al., 2014)
216 and this has been associated with large scale colony losses, including in feral populations
217 (Kraus & Page, 1995). However, this is not always the case. Indeed, when comparing colony
218 loss data for mainland and island populations generally (Brodschneider et al., 2018; Gray et
219 al., 2020), there do not appear to be any strong differences.

220

221 There are cases where the introduction of *Varroa* to islands does not appear to have been
222 detrimental to the honey bee population at all. For example, in the 1980s a small honey bee
223 population was introduced onto the small isolated island of Fernando de Noronha, 350 km off
224 the coast of Brasil. The colonies were accidentally infested with *Varroa* mites, but
225 surprisingly, DWV levels were at the limit of detection i.e. very low and for over 35 years the
226 bees and mites have survived without any need for control measures (Brettell & Martin,
227 2017). Similarly, a recent study by Roberts et al. (2020) showed *Varroa*-infested (in this case
228 *Varroa jacobsoni*) honey bee populations in Papua New Guinea and the Solomon Islands
229 were also free of DWV and were able to survive with no mite control. Whilst we do not know
230 for certain why these populations remain stable with high *Varroa* prevalence, they indicate
231 the critical role of DWV in honey bee mortality.

232

233 Islands can also provide interesting opportunities. Honey bees were introduced to Santa Cruz
234 Island, California, in the 1880s and were very successful in colonizing the island. They were
235 found to forage on one third of the island's plants, with their abundance negatively correlated
236 with that of native bees (Wenner, 1993). In this case, *Varroa* was introduced as a biological
237 control agent and successfully eradicated honey bees from the eastern part of the island
238 (Wenner et al., 2009). On the island of Gotland, Sweden, the honey bee population was
239 subjected to a natural selection experiment. Fries et al. (2006), allowed *Varroa* to establish in
240 150 colonies (and an additional 38 swarms), which resulted in the death of all but 13

241 colonies. These became resistant to *Varroa* by evolving behavioural traits that confer
242 resistance to the mite itself (Oddie et al., 2018) and the viruses it vectors (Thaduri et al.,
243 2019). Here, being isolated on an island allowed selection to take place in a closed system
244 without the introduction of any further honey bee genetic diversity. Although the same
245 *Varroa* resistant behavioural traits have now been also found in mainland populations across
246 the world (Grindrod & Martin, 2021), initial isolation of populations remains important.

247

248 One consideration with viral pathogens is that of varying effects of different variants and
249 strains. Recently there has been much focus in human disease on the differences in
250 transmission and virulence of different SARS-CoV-2 variants, which have the ability to result
251 in dramatically different outcomes in human populations (Jewell, 2021). This phenomenon is
252 not unique and many viruses encompass numerous variants that confer distinct phenotypes.
253 In particular, since the establishment of *Varroa*, DWV infections are dominated by two
254 variants (DWV-A and DWV-B), which have different (and still not fully understood)
255 etiologies; e.g. it seems that only DWV-B can replicate in *Varroa* mite tissues (Gisder &
256 Genersch, 2021). As such, it is likely that the outcomes of virus introductions to naïve
257 pollinator communities may differ considerably according to not only which virus is
258 introduced, but which variant(s).

259

260 The introduction of honey bee associated pathogens to an island has also resulted in spillover
261 to other insect taxa. The stark differences in DWV prevalence in honey bee populations on
262 Hawaiian islands with and without *Varroa* were mirrored in other Hymenoptera, including
263 the small carpenter bee (*Ceratina smaragdula*) and *Polistes* wasps (Santamaria et al., 2018).
264 A follow up study on insects found in Hawaiian apiaries infested with *Varroa* revealed DWV
265 in various hosts (Brettell et al., 2019), suggesting that *Varroa*'s introduction may impact upon
266 diverse taxa. Interestingly, the study also found a number of viral recombinants, suggesting
267 that whilst similar viral genotypes are being transmitted between taxa, there may be selection
268 occurring for recombinants better adapted to different hosts. Loope et al. (2019) investigated
269 DWV prevalence and diversity in honey bees and the yellowjacket wasp (*Vespula*
270 *pensylvanica*), a predator of bees (and which also at times shares floral resources) in Hawaii
271 pre- and post- *Varroa* introduction. They found the same reduction in DWV variation as
272 previously reported in honey bees (Martin et al., 2012).

273

274 Another study focussed on DWV prevalence and load in honey bees and *Bombus* spp. on UK
275 and French islands, again with and without *Varroa*, alongside corresponding mainland sites
276 where *Varroa* was present (Manley et al., 2019). This showed, as expected, that honey bees
277 living with *Varroa* had higher prevalence and titres of DWV and this resulted in spillover to
278 *Bombus* spp. on islands where *Varroa* was present. It is understood that insects can transmit
279 viruses such as DWV through the shared use of contaminated flowers (Alger et al., 2019;
280 Mazzei et al., 2014) and predation of infected individuals (Loope et al., 2019). The results of
281 these studies suggest this may be frequent and widespread, however the findings of Brettell et
282 al (2020), that the vast amount of DWV in honey bees (in Hawaii) was only resulting in
283 minimal spillover to other insects, suggest it isn't always the case and the frequency and
284 nature of interactions between taxa are important in determining the spillover risk.

285

286 Other common bee-associated pathogens are known to infect alternate hosts. The
287 microsporidian *Nosema ceranae* has been shown to be transmissible under laboratory
288 conditions from honey bees to the stingless bee *Tetragonula hockingsi* via shared floral
289 resources (Purkiss & Lach, 2019). Worryingly, in this study the pathogen caused a decrease
290 in longevity in the stingless bee, however data are currently lacking on whether pathology
291 and population declines are occurring in the field.

292

293 Our understanding of the ability of honey bee-associated pathogens to cause disease in
294 alternate hosts is severely lacking. So far, disease symptoms have only been identified in
295 *Bombus* spp. (Genersch et al., 2006; Fürst et al., 2014), *Vespa velutina* (Dalmon et al., 2019),
296 and *Lasius* spp. ants (Schlächli et al., 2020), but further research is needed. Potential sublethal
297 effects are of particular concern, such as effects on traits including longevity, fecundity and
298 foraging behaviour. These, if present, could alter population dynamics and subsequently
299 affect ecosystems. Furthermore, field surveys will always bias toward healthy (or at least
300 alive) individuals. Given insect populations are often not well characterised or quantified, our
301 capacity to detect increased deaths is minimal.

302

303 4.2 Bumblebees

304 Another pollinator group that is now commonly utilised for commercial pollination is the
305 bumble bees (*Bombus* spp.). While bumble bees are primarily used for pollination of
306 glasshouse crops, they commonly escape and establish feral populations. Similarly to honey
307 bees, they have been shown to drive the extinction of native species via direct competition,

308 reproductive interference (Kanbe et al., 2008) or pathogen spillover (Colla et al., 2006). For
309 example; following introduction to the island of Tasmania, *B. terrestris* has been implicated
310 in increasing the invasiveness of an alien plant species, *Agapanthus praecox* subsp. *orientalis*
311 (Hingston, 2006) and has a greater plant species foraging range than many native pollinators,
312 so has the potential for further disruptions to Tasmanian ecosystems (Kingston & McQuillan,
313 1998). Meanwhile, its introduction to the Japanese island of Hokkaido directly impacted
314 native pollinators by displacing two species of *Chalicodoma* (megachilid bees) from visiting
315 *Gompholobium huegelii* (McQuillan & Hingston, 1999). On Hokkaido, *B. terrestris* has
316 potentially also displaced a native bumble bee species (Inari et al., 2005), although the
317 authors suggest habitat suitability could also have played a role. The fact that *B. terrestris*
318 was found more in agricultural landscapes and gardens with introduced exotic plants
319 highlights the fact that it is a combination of (largely human-driven) factors that serve to
320 disrupt island ecosystems.

321

322 As with honey bees, bumble bee introductions have been accompanied by the introduction of
323 their parasites and pathogens. When *B. terrestris* was introduced to Japan, the tracheal mite,
324 *Locustacarus buchneri* was also introduced and may now colonise native *Bombus*
325 populations (Goka et al., 2000). Again, the follow-on impacts can be complex; in this case, *B.*
326 *impatiens* infected with *L. buchneri* showed increased floral constancy (Otterstater et al.,
327 2005).

328

329 Bumble bees are frequently infected with other microbial pathogens. While the vast majority
330 of studies to date have focussed on mainland populations, the threat of their introduction to
331 islands, particularly through infected managed bumble bee colonies, is substantial.

332 Experimental infections show that the native Japanese species *B. hypocrita* and *B. diversus*
333 can be infected by *Nosema bombi*, a pathogen common in *B. terrestris* populations (Niwa et
334 al., 2004). Again, there can be knock-on effects; *B. terrestris* has been shown to visit fewer
335 flowers when infected with the common bumble bee pathogen *Crithidia bombi* (Otterstater
336 et al., 2005). Both *C. bombi* and *Nosema* spp. have been experimentally demonstrated to be
337 transmissible across species through the shared use of floral resources (in this case from
338 honey bees to bumble bees) (Graystock et al., 2015). It is thought that *Crithidia expoeki* may
339 also spillover from managed bumble bees (Meeus et al., 2011).

340

341 The viruses that are commonly associated with honey bees are also frequently detected in
342 bumblebees. Further, Alger et al (2019) showed an increase in DWV- and *Black queen cell*
343 *virus* (BQCV)-positive bumble bees near apiaries where honey bees are infected and the
344 viruses are detected on flowers. Along with the finding that bumblebees in Tasmania only
345 tested positive for honey bee viruses where honey bees are present in the landscape (Fung et
346 al., 2017), this strongly suggests that honey bees are the source of these viruses. However,
347 once bumblebees become infected, they could potentially then go on to become sources for
348 new spillover events. Fung et al (2018) investigated whether the introduction of bumblebees
349 (*B. terrestris*) into the (*Varroa*-free) island of Tasmania had resulted in the co-introduction of
350 known honey bee viruses. Whilst it was shown that *Kashmir bee virus* (KBV) and *Sacbrood*
351 *virus* (SBV) were present in both honey bees and *B. terrestris* and were probably shared
352 between these species, it was not possible to determine whether the viruses were introduced
353 along with bumblebees or had previously been introduced with honey bees, as the same
354 viruses were also found in honey bees on the Australian mainland (the source of the
355 Tasmanian honey bee population).

356

357 *4.3 Other managed pollinators*

358

359 There are other managed pollinators which, while much less widely used than honey bees and
360 bumblebees, could still pose a threat to island pollinator communities if not managed
361 appropriately. One example of a pollinator introduction success story however, is that of the
362 weevil *Elaeidobius kamerunicus*, which was imported to Malaysia to pollinate oil palm
363 (*Elaeis*) (Kang & Karim., 1982). Before importation, experiments were undertaken to ensure
364 they would not pollinate any other local plant species and they were surface sterilised and
365 screened for nematodes before introduction. While parts of Malaysia are not an island, the
366 region was isolated enough to limit potential detrimental effects of the introduction
367 suggesting that if managed correctly, islands could provide further imported/managed
368 pollinator success stories.

369

370 *5. Threats from other invertebrates*

371

372 In addition to invasive managed bees, other invasive species, especially other social insects
373 such as ants and wasps, can be a source of disease. One particular group of interest are the
374 hornets (*Vespa* spp.), yellowjackets (*Vespula* spp.) and other invasive social wasps, e.g.

375 *Polistes* and *Ropalida*. While social wasps are not common pollinators, they are voracious
376 predators of pollinator larvae and adults and are successful invaders of many islands, e.g. the
377 Faroe Islands (Hammer & Jennsensen, 2019), Ascension Island, Canary Islands and New
378 Zealand (Martin, 2020), where they have had a dramatic effect. For example, in New Zealand
379 the predation of social wasps on some invertebrate species is so high that the probability of an
380 individual surviving through a single wasp season is virtually nil (Beggs, 2001). The wasps
381 have even been shown to outcompete honeydew specialist birds (Martin, 2020).

382

383 Numerous studies have found that social wasps harbour a range of bee-associated viruses
384 (Dalmon et al., 2019; Remnant et al., 2021; Singh et al., 2010; Yang et al., 2020). For
385 example, *Vespula germanica* has become established in New Zealand, where individuals
386 have tested positive for KBV, DWV (Brenton-Rule et al., 2018) and Moku virus (MKV)
387 (Dobelman et al., 2020) and *V. velutina* has been shown to harbour replicating *Israeli acute*
388 *paralysis virus* (IAPV) (Yañez et al., 2012), DWV (Mazzei et al., 2018), MKV (Highfield et
389 al., 2020), IAPV and BQCV (Mazzei et al., 2019). Furthermore, KBV and MKV have both
390 been detected in diseased *Vespula vulgaris* individuals (Quinn et al., 2018). Moku virus is a
391 recently discovered virus of particular interest; it was recently discovered in *V. pensylvanica*
392 transcriptome data (Mordecai et al., 2016), is now known to infect honey bees, multiple wasp
393 species, parasitic mites (Felden et al., 2020), ants and spiders (Dobelman et al., 2020) and has
394 been associated with a decrease in colony longevity in *V. pensylvanica* (Loope & Rankin,
395 2021). The recent discovery of a second virus closely related to MKV in *Vespula vulagris*,
396 which again is infective to honey bees (Remnant et al., 2021) suggests an emerging clade of
397 MKV-like viruses in *Vespula* spp. warranting further research attention.

398

399 The majority of studies investigating viruses in wasps have focussed on honey bee-associated
400 viruses and have hypothesised spillover in the direction of honey bee to wasp. As wasps are
401 honey bee predators, this is the most obvious transmission pathway, but transmission could
402 also be possible from wasp to bee, for example through flower sharing (Proesmans et al.,
403 2021). So far, there have been few studies investigating viruses harboured by wasps. However,
404 the apparent frequency with which honey bee-associated viruses have been detected in wasps
405 suggests that, for these viruses at least, wasps could be reservoirs and that virus spillover may
406 occur from wasps to other insects. Much more research in this area is needed if we are to gain
407 a fuller understanding of pollinator health. In particular, understanding the prerequisites for
408 spillover between wasps and other insects, including determining how and when spillover

409 happens in the field, will be important if we are to develop strategies to protect at risk
410 populations.

411

412 Ants are one of the most successful groups of invaders and are commonly found in high
413 densities. Honey bee-associated viruses were detected in invasive big-headed ants (*Pheidole*
414 *megacephala*) and ghost ants (*Tapinoma melanocephalum*) in Hawaii (Brettell et al., 2019),
415 and invasive Argentine ants (*Linepithema humile*) have been shown to be a reservoir of
416 honey bee-associated viruses in New Zealand (Sébastien et al., 2015, Dobelman et al., 2020).
417 Interestingly, Lester et al. (2019) showed that Argentine ants do not show the same immune
418 response to the common honey bee-associated viruses, DWV and KBV, as to *Linepithema*
419 *humile* virus 1 (LHUV-1), an ant-associated pathogen with which they have presumably co-
420 evolved for longer time.

421

422 Butterflies and moths are another pollinator group containing successful invasive species,
423 perhaps most notably, the monarch butterfly *Danaus plexippus*, which commonly harbours a
424 protozoan parasite, *Ophryocystis elektroscirrha*, that causes impaired wing development and
425 decreased longevity (Altizer et al., 2000). The monarch butterfly population now found on
426 the Hawaiian archipelago shows differences between islands in the prevalence of the parasite,
427 suggesting there may be differences in parasite or host genotypes which affect transmission
428 or virulence (Pierce et al., 2014). Furthermore, this parasite is also present in a New Zealand
429 monarch butterfly population, where it was established from an Australian source in
430 approximately 1870, and now has a latitudinal cline, where the parasite prevalence decreases
431 with increasing latitude (and cooler conditions) (Lester & Bulgarella, 2021). Interestingly,
432 this parasite is more prevalent in non-migratory than migratory populations, with
433 transmission being thought to occur over winter while the adults show clustering behaviour
434 and those individuals with the highest parasite burdens then being thought to not fly as far for
435 their spring/summer migration (Altizer et al., 2000).

436

437 Another successful invader is the diamond back moth, *Plutella xylostella*, a common pest of
438 brassica crops with long range dispersal abilities (Chapman et al., 2002). This moth is
439 commonly infected with *Zoophthora radicans*, a multi host pathogen capable of infecting
440 other Lepidoptera and Diptera (Xu et al., 2006; Milner & Mahon, 1985), so represents yet
441 another species with the capacity to transport pathogens across a distance. Delgado & Cook
442 (2009) found that the same strain of a locally rare *Wolbachia* infection, correlated with

443 diamondback moth (*Plutella xylostella*) sex ratio distortion (probably a male-killer), was
444 present in both Malaysia and Kenya, but absent from most localities. This most likely reflects
445 human-assisted movement of this pest and its pathogen between continents.

446

447 An additional issue resulting from the introduction of invasive species is their ability to
448 hybridise with native species. Experiments have shown that *Bombus canariensis*, an endemic
449 species of the Canary Islands, can produce fertile offspring when mated with *B. terrestris*
450 queens from the Netherlands (Eijnde & Ruijter, 2000). Furthermore, this may be happening
451 frequently; Tsuchida et al (2010) showed that 30% of field-caught indigenous bumble bees
452 had copulated with *B. terrestris* on the island of Honshu, Japan. Frequent hybridisation in the
453 field has also been documented in ants (Seifert, 1999) and hornets (Yamasaki et al., 2019),
454 suggesting this may be widespread. Hybridisation is a concern for conservation of
455 biodiversity generally, but little attention has thus far been given to the disease implication;
456 cross species matings could provide a new pathogen transmission route.

457

458 *6. Plant and other environmental pathogens*

459

460 There are many routes by which pathogens can enter, or maintain themselves, in
461 environments. For example, numerous plant viruses are now frequently being detected in
462 both honey bees and their hive materials (e.g. Roberts et al., 2018; Schoonavaere et al., 2018;
463 Granberg et al., 2013), which is not surprising given bees need to collect pollen to provision
464 their young. In this way, pollinators can transmit pathogens between individual plants and
465 whilst plant viruses do not generally replicate in their insect vectors (Gray et al., 1999), plant
466 disease can cause indirect effects on pollinators through resulting depletions of the floral
467 resources. However, it has become apparent that some of these viruses can infect insects,
468 despite insects and plants belonging to different kingdoms of life. The first such virus shown
469 to do this, *Tobacco ringspot virus* (TRSV), was not only shown to replicate in honey bees,
470 but its incidence was greater among weak colonies (Li et al., 2014). Whether the virus was
471 more successful when colonies were already weak, or whether it caused the health declines is
472 unknown, but the finding certainly warrants further investigation.

473

474 Many bee species are known to collect fungal spores, both as an incidental component of
475 nectar and pollen and, separately, as a target source of protein (Shaw, 1990; Takahashi et al.,
476 2019), including spores of *Podosphaera xanthii*, the causal agent of powdery mildew disease

477 in cucurbits (Parish et al., 2020). Whilst collection of fungal spores does not seem to cause
478 significant health problems for bees, the presence of toxic chemicals in mildews (Spencer et
479 al., 1994) could conceivably become a health issue if ingested in sufficient quantities.
480 Further, insect pollinators have been shown to be vectors of fungal pathogens of plants, e.g.
481 *Monilinia vaccinii-corymbosi*, the causative agent of mummy-berry disease in blueberry
482 (*Vaccinium* spp.) and huckleberry (*Gaylussacia* sp.) (Batra & Batra, 1985) and *Microbotryum*
483 *violaceum*, the causative agent of anther smut disease in the white campion (*Silene alba*)
484 (Shykoff & Bucheli, 1995). Similarly to their vectoring of viral plant pathogens, the fungal
485 pathogens cause disease in the host plant which have the potential to result in pollination
486 network disruptions.

487

488 There are other pathogens whose spores can persist in the soil or elsewhere in the
489 environment for extended periods of time. *Paenibacillus* spp. (the causative agent of
490 American foulbrood disease in honey bees) has been detected in wild pollinators
491 (Megachilidae and Halictidae bees [Keller et al., 2018]) and can remain in the soil for
492 decades. In addition, a recently discovered bacterial disease of the Australian stingless bee,
493 *Tetragonula carbonaria*, is caused by the common soil-borne pathogen *Lysinibacillus*
494 *sphaericus* (Shanks et al., 2017). These findings question whether there may be more soil-
495 borne microbes with the capacity to cause disease in diverse insect pollinators, especially
496 since this particular pathogen was also isolated from an *Austroplebeia australis* colony
497 (Shanks et al., 2017).

498

499 Additionally, the common bacterial genus, *Pseudomonas*, can also cause pathogenicity in
500 insects; *Pseudomonas* spp. are carried by ants where they elicit a strong immune response
501 (Lester et al., 2019), and are also virulent to other insects. For example, *P. aeruginosa* has
502 been shown to be virulent to the wax moth (*Galleria mellonella*), a common honey bee hive
503 pest (Williams, 1997).

504

505 7. Conclusions and future directions

506

507 The biggest threat to island insect pollinator communities isn't one particular pathogen, but
508 the combination of pathogens and the invasive species that will likely introduce them. The
509 pathogens with the most potential to cause harm are probably the viruses (especially RNA
510 viruses), due to their generally broader host ranges, high rates of mutation and evolution and

511 frequent interspecies transmission. These pathogens have the potential to cause widespread
512 declines in diverse hosts, which, in turn, could result in broader disruption of island
513 ecosystems through disruption of plant-pollinator networks, many of which we still do not
514 fully understand. Further, our lack of understanding of plant-pollinator networks in itself adds
515 to the threats faced by island communities. In order to better understand the health of
516 pollinators, we need to further characterise island pollinator communities, including
517 identification of endemic taxa which may be at greater risk. Much more research is also
518 needed to understand the pathogens which do, or have the capacity to, cause pathology in
519 pollinators, especially wild pollinators which have received little attention to date. There is
520 always the threat of newly arising interactions such as that of *Varroa* and DWV (and recently
521 with SARS-CoV2 in humans); events in which a microbe has quickly changed in its
522 biology/interactions with other species, and, thereby, transformed to a deadly pathogen.
523 While we cannot predict when or where the next emergence will take place, an improved
524 understanding of pollinator health and interactions will provide the best opportunity to deal
525 with such a situation. Where particular species or pathogens of concern are identified,
526 targeted biosecurity efforts may need to be implemented to reduce the risk of importation at
527 ports and airports, and aid conservation of at risk populations. Furthermore, being integral to
528 the function of many island ecosystems, understanding and monitoring insect pollinator
529 health may lead us to better informed conservation strategies.

530

531 *Acknowledgements*

532

533 We would like to thank Helen Hesketh and Grant Stentiford for inviting us to write this
534 review and contribute to what we believe is a very interesting and timely special issue. We
535 would like to thank the two anonymous reviewers who provided valuable comments and
536 feedback. We would also like to thank Jasmine Grinyer for help with editing. LB receives
537 funding from the project; “Healthy bee populations for sustainable pollination in horticulture”
538 which is funded by the Hort Frontiers Pollination Fund, part of the Hort Frontiers strategic
539 partnership initiative developed by Hort Innovation, with co-investment from Western
540 Sydney University, Bayer CropScience, Syngenta Asia-Pacific and Greening Australia, and
541 contributions from the Australian Government.

542

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