

1 Vulnerability of island insect pollinator communities to pathogens

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12
13 *Abstract*

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

29
30 *Keywords*

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

32
33 *1. Introduction*

34
35 Invertebrates play key roles in maintaining ecosystem stability and diversity, with perhaps the
36 most obvious example being insect pollinators which have driven floral evolution (e.g.

37 Stebbins, 2013; Dilcher, 2000) and mediate much of plant reproduction today. Globally,
38 insect pollinators are in decline and this has been reviewed extensively elsewhere (e.g.
39 Helmer, 2020; Ollerton, 2017) and, whilst the biggest factor is generally understood to be
40 habitat loss, another key reason is an increased spread and occurrence of pathogens (Potts et
41 al., 2010). Globalisation has resulted in the increased ability of pathogens to spread between
42 populations and this is especially evident with pathogens that cause human disease where we
43 are seeing an increase in the frequency of epidemics and pandemics, e.g. SARS, MERS and
44 COVID-19 have all emerged within the past 20 years (Anderson et al., 2020). The same
45 pattern is applicable to diverse pathogens and hosts, including insect pollinators, and can
46 have far greater implications than merely upon the health status of a single species.

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

68
69 Whilst insect populations and associated ecosystem functions will always be at risk from
70 infectious disease regardless of geography, island populations are especially vulnerable.

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

88

89 2. *What makes islands special*

90

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

101

102 Much of what makes islands important ecosystems, lies in what we do not know. Our poor
103 knowledge of the true biodiversity, due to the ‘Linnaean shortfall’ of incomplete biodiversity
104 characterisation, applies most strikingly to invertebrates, largely because of their vast

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

110

111 As described by Whittaker et al (2008) in their “general dynamic theory of island
112 biogeography”, species distribution is shaped by immigration, extinction and speciation. For
113 oceanic islands, this is largely driven by the availability of unoccupied niches. Over time,
114 habitat complexity increases, endemics accumulate and local populations differentiate, whilst
115 at the same time populations on other islands become extinct. Assuming equilibrium has been
116 reached and extinction rates are relatively low, the species diversity will increase as further
117 colonizations occur (Steinbauer et al., 2012). Fragment islands, on the other hand, would
118 have had their ecological space filled prior to insularisation (Gillespie and Roderick, 2002).

119 Upon separation from mainlands, they initially experience a decline in species numbers.

120 Then, over time, relic taxa which remain may evolve to become new endemics. Elevation
121 often drives comparable changes to island age in species diversity, where environmental
122 gradients drive speciation creates . Higher altitudes represent habitats further from reservoirs
123 of adapted populations, compared to lowland coastal areas (Steinbauer et al., 2012).

124 Generally, lower lying coastal areas will be more suitable to invaders than higher elevation
125 areas (due to differences in distance from comparable mainland habitats). This may afford
126 some level of protection from extinction to the lowland taxa, as they may continually receive
127 arrivals from overseas source populations, although, conversely, these areas are often the
128 most amenable to agricultural use, so may face greater habitat modification threat, as well as
129 pest and pathogen introductions, often via ports (where the vast majority of accidental
130 introductions occur).

131

132 Islands are particularly susceptible to the effects of climate change (Nurse et al., 2014) and
133 thus, island pollinator communities are particularly at risk (e.g. through the removal of low-
134 lying habitats with rises in sea level). The interaction between climate change and altitude is
135 particularly interesting. Whereas with mainland populations, species can often shift their host
136 ranges latitudinally to escape rising temperatures, island species need to move toward higher
137 elevations to achieve the same effect. This means that the available habitat area is likely to

138 decrease and may not even exist, as the plants they may need may not be able to respond as
139 quickly.

140

141 *3. Island pollinators and pollination networks*

142

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

161

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

169

170 Biological traits of different pollinators play a key role in how likely they are to be successful
171 on islands. For instance, stingless bees (Meliponinae) appear unable to cross water barriers,

172 and social insects may find it more difficult to establish on islands due to high resource
173 requirements. Further, smaller insects may be good colonisers because of their high dispersal
174 abilities; e.g. Spengler et al (2011) observed a decrease in insect body size with increasing
175 island isolation. However, these smaller insects may be less able to establish on islands that
176 already harbour larger competitors.

177

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

195

196 4. Introductions of managed pollinators

197 4.1. Honey bees

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

202

203 The traits that make the western honey bee so successful as a managed pollinator (generalist
204 foraging behaviour and large numbers per hive [$<30,000$]) are also those which have
205 transformed it into one of the world's most successful invasive species. Irrespective of any

206 pathogens, this can, and has had a big effect on ecosystems in itself. For example, honey bees
207 have been shown to outcompete native pollinators in Tasmania (Goulson et al., 2002), the
208 Bonin Islands (Kato et al., 1999) and Tenerife (Dupont et al., 2004).

209

210 Islands can, however, also provide interesting opportunities. Honey bees were introduced to
211 Santa Cruz Island, California, in the 1880s and were very successful in colonizing the island.
212 They were found to forage on one third of the island's plants, with their abundance negatively
213 correlated with that of native bees (Wenner, 1993). In this case, the parasitic mite *V.*
214 *destructor* was introduced as a biological control agent and successfully eradicated honey
215 bees from the eastern part of the island (Wenner et al., 2009). On the island of Gotland,
216 Sweden, the honey bee population was subjected to a natural selection experiment. Fries et al.
217 (2006), allowed *Varroa* to establish in 150 colonies (and an additional 38 swarms), which
218 resulted in the death of all but 13 colonies. These became resistant to *Varroa* by evolving
219 behavioural traits that confer resistance to *Varroa* (Oddie et al., 2018) and viruses (Thaduri et
220 al., 2019). Here, being isolated on an island allowed selection to take place in a closed system
221 without the introduction of any further honey bee genetic diversity, although the same *Varroa*
222 resistant behavioural traits have now been also found in mainland populations across the
223 world (Grindrod & Martin, 2012), although intail isolation of populations remains important.

224

225 While honey bees and their pathogens have been reviewed extensively elsewhere (e.g.
226 Genersch & Aubert, 2010; Nazzi & Le Conte, 2016; Martin & Brettell, 2019), they constitue
227 the majority of what we know about island pollinator health. Thus, these studies provide vital
228 information on how island populatons cope with pathogens. The number one enemy of the
229 honey bee in recent times has been the ecto-parasitic *Varroa* mite (*V. destructor*), along with
230 DWV that the mite vectors (Martin et al., 2012; Wilfert et al., 2016). A number of studies
231 have clearly shown that when *Varroa* invades honey bee populations on an island (or
232 archipelago), there is a dramatic increase in DWV prevalence and titre in honey bee colonies
233 (Martin et al., 2012; Mondet et al., 2014) and this has been associated with large scale colony
234 losses, including in feral populations (Kraus & Page, 1995). However, this is not always the
235 case. Indeed, when comparing colony loss data for mainland and island populations generally
236 (Brodschneider et al., 2018; Gray et al., 2020), there do not appear to be any strong
237 differences. Nonetheless, island studies again have shown some interesting outcomes.

238

239 For example, a small honey bee population was introduced onto the small isolated island of
240 Fernando de Noronha, 350 km off the coast of Brasil. The colonies were accidentally infested
241 with *Varroa* mites, but surprisingly, DWV levels were at the limit of detection i.e. very low.
242 For over 35 years the bees and mites have survived without any need for control measures
243 (Brettell & Martin, 2017). Similarly, a recent study by Roberts et al. (2020) showed *Varroa*-
244 infested (in this case *Varroa jacobsoni*) honey bee populations in Papua New Guinea and the
245 Solomon Islands were also free of DWV and were able to survive with no mite control.
246 Whilst we do not know for certain why these populations remain stable with high *Varroa*
247 prevalence, they indicate the critical role of DWV in honey bee mortality.

248

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

260

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

272 pre- and post- *Varroa* introduction. They found the same reduction in DWV variation as
273 previously reported in honey bees (Martin et al., 2012).

274

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

286

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

293

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

303

304 *4.2 Bumblebees*

305 Another pollinator group that are now commonly utilised for commercial pollination are the
306 bumble bees (*Bombus* spp.). While bumble bees are primarily used for pollination of
307 glasshouse crops, they commonly escape and establish feral populations. Similarly to honey
308 bees, these have been shown to drive the extinction of native species via direct competition,
309 reproductive interference (Kanbe et al., 2008) or pathogen spillover (Colla et al., 2006). For
310 example; following introduction to the island of Tasmania, *B. terrestris* has been implicated
311 in increasing the invasiveness of an alien plant species, *Agapanthus praecox* subsp. *orientalis*
312 (Hingston, 2006) and has a greater plant species foraging range than many native pollinators,
313 so has the potential for further disruptions to Tasmanian ecosystems (Kingston and
314 McQuillan, 1998). Its introduction to the Japanese island of Hokkaido directly impacted
315 native pollinators by displacing two species of *Chalicodoma* (megachilid bees) from visiting
316 *Gompholobium huegelii* (McQuillan & Hingston, 1999). On Hokkaido, *B. terrestris* has
317 potentially also displaced a native bumble bee species (Inari et al., 2005), although the
318 authors suggest habitat suitability could also have played a role. The fact that *B. terrestris*
319 was found more in agricultural landscapes and gardens with introduced exotic plants
320 highlights the fact that it is a combination of (largely human-driven) factors that serve to
321 disrupt island ecosystems.

322
323 As with honey bees, bumble bee introductions have been accompanied by the introduction of
324 their parasites and pathogens. When *B. terrestris* was introduced to Japan, the tracheal mite,
325 *Locustacarus buchneri* was also introduced and may now colonise native *Bombus*
326 populations (Goka et al., 2000). Again, the follow-on impacts can be complex; in this case, *B.*
327 *impatiens* infected with *L. buchneri* showed increased floral constancy (Otterstatter et al.,
328 2005).

329
330 Bumble bees are frequently infected with other microbial pathogens. While the vast majority
331 of studies to date have focussed on mainland populations, the threat of their introduction to
332 islands, particularly through infected managed bumble bee colonies, is substantial.
333 Experimental infections show that the native Japanese species *B. hypocrita* and *B. diversus*
334 can be infected by *Nosema bombi*, a known pathogen common in *B. terrestris* populations
335 (Niwa et al., 2004). Again, there can be knock-on effects; *B. terrestris* has been shown to
336 visit fewer flowers when infected with the common bumble bee pathogen *Crithidia bombi*
337 (Otterstatter et al., 2005). Both *C. bombi* and *Nosema* spp. have been experimentally
338 demonstrated to be transmissible across species through the shared use of floral resources (in

339 this case from honey bees to bumble bees) (Graystock et al., 2015). It is thought that
340 *Crithidia expoeki* may also spillover from managed bumble bees (Meeus et al., 2011).

341

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

356

357 4.3 Other managed pollinators

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

368

369 5. Threats from other invertebrates

370

371 In addition to invasive managed bees, other invasive species, especially other social insects
372 such as ants and wasps, can be a source of disease. One particular group of interest are the

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

381

382 Numerous studies have found that social wasps harbour a range of bee-associated viruses
383 (Dalmon et al., 2019; Singh et al., 2010; Yang et al., 2020). For example, the yellowjacket
384 wasp, *V. germanica*, has become established in New Zealand, where individuals have tested
385 positive for KBV, DWV (Brenton-Rule et al., 2018) and MKV (Dobelman et al., 2020), a
386 recently discovered virus known to infect honey bees, wasps and also their mite pests
387 (Mordecai et al., 2016; Felden et al., 2020). Additionally, the invasive yellow-legged hornet
388 (*V. velutina*) has been shown to harbour replicating *Israeli acute paralysis virus* (IAPV)
389 (Yañez et al., 2012), DWV (Mazzei et al., 2018), MKV (Highfield et al., 2020), IAPV and
390 BQCV (Mazzei et al., 2019). Furthermore, KBV and *Moku Virus* have both been detected in
391 diseased *Vespula vulgaris* individuals (Quinn et al., 2018).

392

393 The majority of studies investigating viruses in wasps have focussed on honey bee-associated
394 viruses and have hypothesised spillover in the direction of honey bee to wasp. As wasps are
395 honey bee predators, this is the most obvious transmission pathway, but transmission could
396 also be possible from wasp to bee, for example through flower sharing (Proesmans et al.,
397 2021). So far, there have been few studies investigating viruses harboured by wasps, however
398 the apparent frequency that honey bee-associated viruses have been detected suggests for
399 these viruses at least, that wasps could be reservoirs and that virus spillover may occur from
400 wasps to other insects. Much more research in this area is needed if we are to gain a fuller
401 understanding of pollinator health. In particular, understanding the prerequisites for spillover
402 between wasps and other insects, including determining how and when spillover happens in
403 the field, will be important if we are to develop strategies to protect at risk populations.

404

405 Ants are one of the most successful groups of invaders and are commonly found in high
406 densities. Honey bee-associated viruses were detected in invasive big-headed ants (*Pheidole*

407 *megacephala*) and ghost ants (*Tapinoma melanocephalum*) in Hawaii (Brettell et al., 2019),
408 and invasive Argentine ants (*Linepithema humile*) have been shown to be a reservoir of
409 honey bee-associated viruses in New Zealand (Sébastien et al., 2015, Dobelman et al., 2020).
410 Interestingly, Lester et al. (2019) showed that Argentine ants do not show the same immune
411 response to the common honey bee-associated viruses, DWV and KBV, as to *Linepithema*
412 *humile* virus 1 (LHUV-1), an ant-associated pathogen with which they have presumably co-
413 evolved for longer time.

414

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

429

430 Another successful invader is the diamond back moth, *Plutella xylostella*, a common pest of
431 brassica crops with long range dispersal abilities (Chapman et al., 2002). This moth is
432 commonly infected with *Zoophthora radicans*, a multi host pathogen capable of infecting
433 other Lepidoptera and Diptera (Xu et al., 2006; Milner & Mahon, 1985), so represents yet
434 another species with the capacity to transport pathogens across a distance. Delgado & Cook
435 (2009) found that the same strain of a locally rare *Wolbachia* infection, correlated with DBM
436 sex ratio distortion (probably a male-killer), was present in both Malaysia and Kenya, but
437 absent from most localities. This most likely reflects human-assisted movement of this pest
438 and its pathogen between continents.

439

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

450

451 *6. Plant and other environmental pathogens*

452

453 There are many routes by which pathogens can enter or maintain themselves in environments.
454 For example, numerous plant viruses are now frequently being detected in both honey bees
455 and their hive materials (e.g. Roberts et al., 2018; Schoonavaere et al., 2018; Granberg et al.,
456 2013), which is not surprising given bees need to collect pollen to provision their young. In
457 this way, pollinators can transmit pathogens between individual plants and whilst plant
458 viruses do not generally replicate in their insect vectors (Gray et al., 1999), plant disease can
459 cause indirect effects on pollinators through resulting depletions of the floral resources.
460 However, it has become apparent that some of these viruses can infect insects, despite insects
461 and plants belonging to different kingdoms of life. The first such virus shown to do this,
462 *Tobacco ringspot virus* (TRSV), was not only shown to replicate in honey bees, but its
463 incidence was greater among weak colonies (Li et al., 2014). Whether the virus was more
464 successful when colonies were already weak, or whether it caused the health declines is
465 unknown but the finding certainly warrants further investigation.

466

467 Many bee species are known to collect fungal spores, both as an incidental component of
468 nectar and pollen and separately, as a target source of protein (Shaw, 1990; Takahashi et al.,
469 2019), including spores of *Podosphaera xanthii*, the causal agent of powdery mildew disease
470 in cucurbits (Parish et al., 2020). Whilst collection of fungal spores does not seem to cause
471 significant health problems for bees, the presence of toxic chemicals in mildews (Spencer et
472 al., 1994) could conceivably become a health issue if ingested in sufficient quantities.
473 Further, insect pollinators have been shown to be vectors of fungal pathogens of plants, e.g.

474 *Monilinia vaccinii-corymbosi*, the causative agent of mummy-berry disease in blueberry
475 (Batra & Batra, 1985) and *Microbotryum violaceum*, the causative agent of anther smut
476 disease in the white campion (Shykoff & Bucheli, 1995). Similarly to their vectoring of viral
477 plant pathogens, the fungal pathogens cause disease in the host plant which have the potential
478 to result in pollination network disruptions.

479

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

489

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

495

496 7. Conclusions and future directions

497

498 The biggest threat to island insect pollinator communities isn't one particular pathogen, but
499 the combination of pathogens and the invasive species that will likely introduce them. The
500 pathogens with the most potential to cause harm are probably the viruses (especially RNA
501 viruses), due to their generally broader host ranges, high rates of mutation and evolution and
502 frequent interspecies transmission. These pathogens have the potential to cause widespread
503 declines in diverse hosts, which, in turn, could result in broader disruption of island
504 ecosystems through disruption of plant-pollinator networks, many of which we still do not
505 fully understand. Further, our lack of understanding of plant-pollinator networks in itself adds
506 to the threats faced by island communities. In order to better understand the health of
507 pollinators, we need to further characterise island pollinator communities, including

508 identification of endemic taxa which may be at greater risk. Much more research is also
509 needed to understand the pathogens which do, or have the capacity to, cause pathology in
510 pollinators, especially wild pollinators which have received little attention to date. There is
511 always the threat of newly arising interactions such as that of *Varroa* and DWV (and recently
512 with SARS-CoV2 in humans); events in which a microbe has quickly changed in its
513 biology/interactions with other species, and, thereby, transformed to a deadly pathogen.
514 While we cannot predict when or where the next emergence will take place, an improved
515 understanding of pollinator health and interactions will provide the best opportunity to deal
516 with such a situation. Where particular species or pathogens of concern are identified,
517 targeted biosecurity efforts may need to be implemented to reduce the risk of importation at
518 ports and airports, and aid conservation of at risk populations. Furthermore, being integral to
519 the function of many island ecosystems, understanding and monitoring insect pollinator
520 health may lead us to better informed conservation strategies.

521

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533

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