1   **Complex networks of parasites and pollinators: moving towards a healthy balance**
2
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6

7   **Abstract**
8   Parasites are viewed as a major threat to wild pollinator health. While this may be true for
9   epidemics driven by parasite spillover from managed or invasive species, the picture is more
10   complex for endemic parasites. Wild pollinator species host and share a species-rich,
11   generalist parasite community. In contrast to the negative health impacts that these
12   parasites impose on individual hosts, at a community level they may act to reduce
13   competition from common and abundant pollinator species. By providing rare species with
14   space in which to exist, this will act to support and maintain a diverse, and thus healthier
15   pollinator community. At this level, and perhaps paraxodically, parasites may be good for
16   pollinators. This stands in clear contrast to the obvious negative impacts of epidemic and
17   spillover parasites on wild pollinator communities. Research into floral resources that
18   control parasites could be best employed to help design landscapes that provide pollinators
19   with the opportunity to moderate their parasite community, rather than attempting to
20   eliminate specific parasites from wild pollinator communities.
21
22

"I love parasites. I can't get enough of them" Gary Larson

"Parasites are absolutely a bad thing if you're the individual infected by them. But they are a very natural component of ecosystems. Parasitism is the most popular animal lifestyle on the planet" Kevin Lafferty

Introduction

Parasites, here defined broadly to range from brood parasites to viruses, are a fundamental aspect of the health of their hosts. As such, it is not surprising that they have often taken centre stage in the discussion of pollinator health (Vanbergen et al 2013; Goulson et al 2015). While the role they play in the health of managed bees has been clear for centuries, their relationship to the health of wild bees, and other insect pollinators, remains unclear. There is a strong tendency in the published literature to view all parasites in wild insect pollinators as negative drivers of pollinator health, with the consequent conclusion being that we need to control them to support wild pollinator populations. However, from an ecological perspective, a rich and abundant parasite community may be not just a sign of a healthy host community (Hudson et al 2006), but an actual positive driver of this health (Ashby & King 2017). Here my aim is to dissect the complex relationship between parasites and wild pollinator health, focusing on bees due to a general lack of knowledge for other insect pollinators and on health at the level of the pollinator community (López-Uribe et al 2020 ; Stevenson et al, this issue). A more holistic approach to the relationship between pollinators and their parasites is essential to the future support and maintenance of healthy pollinator assemblages.

Parasites and the health of managed insect pollinators – a misleading model for wild pollinator health?

The relationship between parasites and the health of managed insect pollinators – a diverse and species rich group that includes bumble bees (*Bombus* spp.), honey bees (*Apis* spp.), solitary bees (e.g., *Megachile*, *Osmia*), and stingless bees (e.g., *Melipona* spp.), amongst others (Osterman et al. 2021) – has been known for centuries, particularly with respect to honey bees (Fleming 1871). Parasites negatively impact the health of individuals and, in social species, the colony (reviewed by Schmid-Hempel 1998). Perhaps the most well-known example is the nexus of the parasitic mite *Varroa destructor* and the viruses (particularly Deformed Wing Virus) that it transmits, which together are the major challenge faced by keepers of the honey bee *Apis mellifera* in Europe and North America (Wilfert et al 2016). Similarly, the microparasite *Nosema bombi* has been blamed for a collapse in commercial breeding of the bumble bee *Bombus occidentalis* in North America (Thorp & Sheperd 2005), while managed populations of the alfalfa leaf-cutting bee (*Megachile rotundata*) are threatened by chalkbrood disease (causative agent: *Ascosphaera aggregata*)(Evison & Jensen 2018). Unsurprisingly, individual beekeepers and commercial producers of insect pollinators have addressed the threat that parasites pose to the health of their bees from the perspective of management and elimination (Kane & Faux 2021). This approach sits within the broader world of the management and elimination of parasites in agricultural systems, pets, and the human population itself. Here, health is often defined as an absence of parasitism. However, even in humans this is controversial, with the relationship between allergies, autoimmune diseases, and the elimination of parasites being a key example of where parasites might actually have a positive role in individual human health (the 'hygiene'

and 'old friends' hypotheses (see below); Strachan 1989; Rook et al 2003; Bloomfield et al 2016). In honey bees, recent work suggests that management and elimination approaches may even stand in the way of the evolution of a less impactful relationship between parasites and their social hosts (Grindrod and Martin 2021).

However, managed insect pollinators are, in fundamental ways, different to wild insect pollinators. Management and commercialisation, just like monoculture farming, provide ideal conditions for the spread and population growth of parasites. For example, honey bees and stingless bees are kept in apiaries and meliponaries at artificially high densities, eliminating the natural social distancing between colonies that would happen in the wild. This enables the rapid spread of parasites and disease, and enhances their negative impacts. Consequently, while parasites may have similar impacts on the health of individual managed and wild insect pollinators, this need not extrapolate to impacts on the health of colonies, or wider populations and communities of these insects. Perhaps more importantly, managed pollinators are approached from a single species perspective, with any reduction in individual or colony health being viewed as purely negative. However, wild pollinators live in complex ecological networks of species, and consequently impacts on individual health need to be viewed through a more holistic lens.

Parasite spillover and wild pollinator health
Before examining the interaction between pollinators and their natural parasites, it is important to distinguish this from emerging parasites, which in pollinators are largely driven through parasite spillover (Meeus et al 2011). The impact of such emerging parasites in managed pollinators is clear (see discussion of *V. destructor* and DWV above). Whether emerging parasites are factors in wild pollinator health remains unclear. Parasite spillover from managed bumble bees and honey bees has been demonstrated (e.g., Fürst et al 2014) or suggested based on available evidence (Thorp & Shepherd 2005; Cameron et al 2011; Cameron et al 2016). However, whether these emergent parasites are having a meaningful impact on wild pollinator populations is unclear, and currently relies upon the interpretation of correlational evidence (Cameron et al 2011; Cameron et al 2016; Schmid-Hempel et al 2014). Regardless, the dynamics and impacts of emergent parasites are likely to be quite different to the impacts of natural parasite communities.

Parasites and wild pollinator health, *sensu stricto*
Bee health can be examined across a range of scales (López-Uribe et al 2020 ; Stevenson et al, this issue), from the individual to the community. Almost by definition, parasites should negatively impact the health of individual pollinators, as noted above, so here I largely focus on health at the levels of populations, species and pollinator communities. However, before doing so there are two potential ways in which parasites might directly, and positively, impact the health of individual pollinators. The first of these relates to the 'hygiene hypothesis' (Strachan 1989) or, more recently, the 'old friends hypothesis' (Rook et al 2003, Bloomfield et al 2016), both of which were developed in response to challenges to human health. The 'hygiene hypothesis' proposed that lower incidence of infections in young children, and thus exposure to infectious microbes, could explain increases in allergic diseases in European and North American populations (e.g., asthma, hay fever; Strachan, 1989). The argument here is that normal development of the immune system requires interactions with the challenges (bacteria, etc.) that it has evolved with. The 'old friends

119   hypothesis' suggests that, rather than development and function of the immune system
120   relying solely on these antagonistic interactions, it is ambient microbiomes (on the skin, gut,
121   etc.) and parasites that cause chronic infections, that are essential for development and
122   maintenance of normal immune function. In humans this has led to the development of
123   therapies that deliberately re-introduce parasites into humans to regulate the immune
124   system (e.g., Broadhurst et al 2010).
125
126   How might these hypotheses apply to insect pollinators? Recent evidence for the presence
127   of an adaptive anti-viral immune system in insects (Tassetto et al 2017) shows that insect
128   immune systems are more similar to mammalian immune systems than had been supposed.
129   Consequently, infectious microbes – as suggested by the 'hygiene hypothesis' – may have a
130   similar role in the development of the insect immune system, and their absence may lead to
131   maladaptive responses to adult infections. Experiments that eliminate antagonistic
132   microbes during development are required to test this idea. However, as is the case with
133   humans (Rook et al. 2003, Bloomfield et al 2016), the 'old friends hypothesis' may be more
134   applicable to understanding insect immunity. A co-evolved gut microbiome has been
135   identified in key insect pollinators (honey bees: Kwong & Moran 2016, bumble bees:
136   Hammer & Moran 2021) and interactions between the insect immune system and the gut
137   microbiome are well-documented (Horak et al 2020, Lesperance & Broderick 2020), as are
138   interactions between the gut microbiome and parasites (Koch & Schmid-Hempel 2011),
139   both of which can be viewed as prerequisites for the 'old friends hypothesis' to apply.
140   Consequently, microbes may play a key role in the development, maintenance, and function
141   of the immune system of insect pollinators, and thus have a positive impact on individual
142   health (Horak et al 2020). A final aspect of the 'old friends hypothesis' argues that parasites
143   that cause chronic infections could have evolved a regulatory relationship with the immune
144   system. An analogy for this in insect pollinators emerges from the concept of immune
145   priming. In bumblebees, an initial exposure to a low-dose of a bacterial pathogen gave
146   specific protection against secondary exposure (Sadd & Schmid-Hempel 2006). Similar, but
147   perhaps less specific effects could result in prior exposure to a low virulence but abundant
148   pathogen providing protection against subsequent exposure to a high virulence pathogen
149   that interacts similarly with the immune system. Consequently, such low virulent pathogens
150   could actually confer health benefits on individual insect pollinators, depending upon the
151   relative prevalence and thus opportunities to encounter parasites across a range of
152   virulence levels. Whether such interactions exist in wild insect pollinators deserves
153   investigation. Overall, investigating how and where the 'old friends hypothesis' maps on to
154   insect pollinators could be a productive area to mine for researchers of bee health.
155
156   **Parasites and wild pollinator health, *sensu lato***
157   Turning to the level of population or community health in wild pollinators (López-Uribe et al
158   2020 ; Stevenson et al, this issue), a useful analogy can be made with the extensive
159   literature on pollinator-plant networks (Bennett et al 2018; Vizentin-Bugoni et al 2018).
160   Empirical and theoretical studies of the relationship between pollinators and the plants that
161   they pollinate show that a robust, resilient, or perhaps healthy network is one that contains
162   many pollinator species, with redundancy in their plant visitation patterns (Bennett et al
163   2018; Vizentin-Bugoni et al 2018). Here it is the pollinators that are driving the health of the
164   plant community. Similarly, in the relationship between parasites and pollinators, a diverse
165   parasite community species may drive the health of the pollinator community. Parasites are

known to exert bottom-up control over host population size and dynamics (Hudson et al 1998), and as such could play an important role in limiting the populations of dominant generalist pollinators, enabling the survival and success of their rarer competitors (Hatcher et al 2006). Such apparent competition has been experimentally identified in parasitoid-leaf miner communities (Morris et al 2004). Consequently, the structure, robustness, and resilience of pollinator communities may well depend, to some degree, on their associated parasite community. From this perspective, parasites have to be recognised not just as negative influences on the physiological and reproductive health of individuals and colonies, but also positive influences on the health of pollinator communities. Thus, a healthy parasite community is likely a sign of a healthy pollinator community (Hudson et al 2006).

This perspective obviously depends upon the biology of the system. Wild insect pollinators support a natural parasite community, which has been best described in bumblebees (Alford 1975, Schmid-Hempel 1998). Key features of this community are that it is species rich, taxonomically rich (meaning that it encompasses parasites from viruses to trypanosomes to nematode worms to parasitoids and cuckoo bees), and largely made up of generalist parasites that can infect multiple host species (Alford 1975, Schmid-Hempel 1998). In fact, recent work has shown that at least some of these parasites have an even broader host range, being capable of infecting solitary bees (e.g., Figueroa et al 2021). As such, this parasite community has the potential to play a significant role in structuring host communities and thus the broader health of the pollinator community. What evidence is there that such structuring might be taking place? In a multi-site, two year study, common bumblebee species in Alpine meadows had consistently higher parasite richness and load than rare species (Durrer & Schmid-Hempel 1995), despite the fact that these parasites are generalists that can either directly attack or spread between multiple host species (Figueroa et al 2020; Graystock et al 2020; Ruiz-González et al 2012; Salathé & Schmid-Hempel 2011). Similar patterns were found in a single-year study in North America, where common species of bumblebee were more parasitised by a trypanosome parasite and conopid fly parasitoids than were their rarer congeners (Malfi & Roulston 2014). These patterns in parasite richness and load suggest that parasites could suppress common pollinator species and, by extension, enable rare species to maintain their populations as a result of reduced competition, resulting in a more diverse, and thus healthier pollinator community. Evidence for such dynamics was found in a 39-year data set of 6 species of cuckoo bumble bees (*Bombus* subgenus *Psythirus*) and their bumble bee host assemblage (6 focal host species and 10 potential host species) across the island of Great Britain (Antonovics & Edwards 2011). They found that parasites had a negative impact on host population dynamics, driving down their host species and thus potentially reducing competition for non-focal host species. Importantly, the cuckoo bumblebees disappeared when their hosts became rarer (seen most obviously at range edges for the host), so enabling the bounce back of host species required for such long-term host-parasite cycles. Similar fluctuations in parasite populations have been seen across an 11-year study of the trypanosome gut parasite *Crithidia bombi* in bumblebee queens (*B. terrestris*), but in the absence of host abundance data these fluctuations are hard to interpret (Schmid-Hempel et al 2019). Together, these studies suggest that parasite communities could be playing a positive role in the health of pollinator communities through apparent or parasite-mediated competition (Hatcher et al 2006).

213 In addition to differential prevalence, differential virulence across host species could also
214 help to support a more species-rich pollinator assemblage. Again, this has been identified in
215 the endemic parasites of bumblebees, where the microsporidian *Nosema bombi* and the
216 castrating nematode *Sphaerularia bombi* vary in their virulence depending upon the
217 bumblebee species they are parasitising (Rutrecht & Brown 2009, Jones & Brown 2014, Kelly
218 2009). However, it is an open question as to how such variation in virulence maps to
219 background host abundance, and thus whether such variation will act to enhance or
220 decrease pollinator species richness. Theory suggests that the relationship between
221 parasites and multiple hosts is complex and varied, and so patterns of virulence across
222 multiple pollinator species cannot easily be predicted (e.g., Osnas & Dobson 2011).
223 Consequently, further empirical studies of virulence across a broader range of host species
224 are needed to address this.
225
226 An important caveat to the discussion above is that we still have a severe knowledge gap on
227 the actual impact of parasites on wild pollinators. Laboratory studies have found significant
228 impacts on colony (Brown et al 2003; Yourth et al 2008; Otti & Schmid-Hempel 2007;
229 Rutrecht & Brown 2009) and population-level health (Brown et al 2003), but how these
230 translate into real impacts in the field remains unknown, apart from the case of cuckoo bees
231 described above. However, given the prevalence of parasites such as *Crithidia bombi*
232 (Shykoff & Schmid-Hempel 1991; Gillespie 2010; Kissinger et al 2011; Cordes et al 2012;
233 Jones & Brown 2014; Gamboa et al 2015; Gallot-Lavallee et al 2016; Plischuk et al 2020) and
234 *S. bombi* (Kelly 2009) that are known to have dramatic impacts on host species (Brown et al
235 2003; Kelly 2009; Jones & Brown 2014), it seems likely that they are having at least some
236 impact on their host populations in the wild.
237
238 Along with their potential role in structuring pollinator communities, and as emphasised in
239 a series of seminal publications, parasites are a natural part of food webs, playing important
240 roles as consumers of and redistributors of biomass and nutrients, and drivers of stability
241 (e.g., Lafferty et al 2006, Lafferty et al 2008). Removals of, or declines in parasites, could
242 thus have negative impacts on host population health through further disruption of the
243 structure of trophic relationships. Finally, from an evolutionary perspective, hosts have
244 coevolved with their parasites, as can be seen from the existence of immune systems,
245 positive selection on host immune genes (Barribeau et al 2015), as well as the evolution of
246 behavioural responses to reduce parasite impacts (Müller & Schmid-Hempel 1993).
247 Consequently, declines or removals of parasites could dramatically change the selective
248 landscape in which pollinators continue to evolve.
249
250 **Parasite epidemiology and its control in wild pollinators**
251 Despite the potential importance of parasites to pollinator diversity and community health,
252 as detailed above, current research on the role of parasites in wild bee health has focused
253 largely on either understanding transmission dynamics (Ruiz-Gonzalez et al 2012; Adler et al
254 2018; Figueroa et al 2019; Bailes et al 2020; Figueroa et al 2020; Graystock et al 2020), or
255 how floral resources can be used to control natural endemic parasites in bumble bees (see
256 below). Identification of parasite sources (Graystock et al 2020), sinks (Jones and Brown
257 2014), and reservoirs of infection (Graystock et al 2020) can help to predict whether
258 parasites will enhance pollinator species richness or actually depress populations of rare

259 species even further. However, how these transmission dynamics map onto patterns of
260 species abundance remains to be determined.
261
262 Transmission dynamics are not solely driven by properties of the parasite or the host. One
263 of the most exciting recent branches of research into pollinator health has been the
264 discovery that numerous compounds that occur as non-nutritive components in nectar and
265 pollen (Manson et al 2010; Anthony et al 2015; Baracchi et al 2015; Biller et al 2015; Palmer-
266 Young et al 2016; Palmer-Young et al 2017; Giacomini et al 2018; Koch et al 2019; LoCascio
267 et al 2019; Folly et al 2020; Folly et al 2021), as well as particular flowering plant species
268 (Giacomini et al 2018; LoCascio et al 2019; Giacomini et al 2021), have been identified as
269 reducing or preventing infections of pollinator parasites, including the trypanosome
270 *Crithidia bombi* in two species of bumble bee (*B. terrestris* and *B. impatiens*)(Manson et al
271 2010; Anthony et al 2015; Baracchi et al 2015; Biller et al 2015; Palmer-Young et al 2016;
272 Palmer-Young et al 2017; Giacomini et al 2018; Koch et al 2019; LoCascio et al 2019), and
273 the microsporidia *Nosema apis* and *N. bombi* in honey bees and bumble bees respectively
274 (Folly et al 2020; Folly et al 2021). Importantly, these discoveries are of much broader
275 relevance than the pollinator species in which they have been documented, as these
276 parasites are now known to infect a much broader array of species outside of bumblebees
277 and honey bees. In at least some of these cases, these natural medicines are either under
278 threat due to habitat loss (Koch et al 2019) or come from species that are naturally
279 important forage sources for wild bees (LoCascio et al 2019). One way to take advantage of
280 these compounds to enhance pollinator health is to include them in the supplementary
281 diets of managed pollinators, which could result in a reduction of pathogen spillover (see
282 above). However, it has also been suggested that they could be used in floral enhancement
283 schemes to provide a natural pharmacy for wild bees (Folly et al 2021).
284
285 How such non-nutritive floral resources could be provided at a landscape level for wild
286 insect pollinators is unclear. Floral enrichment schemes in agricultural landscapes need to
287 balance availability of high quality nectar and pollen sources to serve a diversity of polylectic
288 and oligolectic insect pollinators. Incorporating species that provide compounds or pollen
289 types that can act to reduce parasite infection or load has to be balanced against the need
290 to provide this complex nutrition. In addition, if parasites are acting to reduce competition
291 from numerically dominant insect pollinators, and thus enabling a richer pollinator
292 community (as discussed above), then the provision of natural pharmaceuticals should be
293 targeted through plants that are not visited, or significantly less visited by dominant insect
294 pollinator species. In non-agricultural environments, where recent habitat loss has led to
295 the loss of plants that provide these pharmaceutical services to insect pollinators (e.g., Koch
296 et al 2019), ecological restoration is obviously a much simpler business.
297
298 **What might a healthy parasite-pollinator network look like?**
299 Efforts to maximise pollinator health at the community scale through the manipulation of
300 parasites are limited by a fundamental gap in knowledge. Arguably the biggest challenge in
301 understanding what a healthy assemblage of pollinators and parasites would be is gathering
302 the real-world data to answer this question. By their very nature, host-parasite associations
303 are dynamic in space and time (Thompson 2005). Consequently, snapshots from a single
304 season, single year, or single site are limited in what they can tell us. In addition, pollinator
305 assemblages themselves have been significantly altered by anthropogenic forces, such as

306   intensive agriculture, urbanisation, and climate change, which may have implications for the
307   structure and health of the host-parasite community. Ecological network theory provides
308   tools to assess the structure and stability of bi-partite networks (Runghen et al 2021), and a
309   first step therefore might be to apply network analyses to already collected host-parasite
310   data in pollinators, or to new data collected from targeted habitats, to gain an
311   understanding of how pollinator-parasite communities vary across different ecosystems.
312   Information on how pollinator-parasite communities are structured, in terms of nestedness,
313   redundancy, etc., and how this relates to robustness and resilience, will provide unique
314   insights into pollinator community health.
315
316   **Parasites in pollinators: a right to life?**
317   Notwithstanding their potential positive impacts on wild pollinator community structure,
318   specific targeted conservation actions may still require the removal of pollinator parasites.
319   For example, reintroduction of locally extinct pollinators, like the large blue butterfly
320   *Phengaris arion* or the short-haired bumblebee *B. subterraneus*, falls under IUCN
321   regulations, and these often require quarantine to enable the elimination of parasites (e.g.,
322   Brown et al 2017). Increasingly, the more research is done the more generalist pollinator
323   parasites appear to be, suggesting that such parasite elimination may not have any
324   consequences for the survival of individual parasite species. However, losses of other
325   parasite species during reintroductions (e.g., the California condor louse; see Dunn (2009)
326   for a review) argues against complacency. Conservation is not a zero sum game, and while
327   pollinators are important across a range of values, parasites have the same ethical right to
328   life and conservation as any other organism. This is not questioned when parasites are of
329   the same taxonomic group as their hosts – for example, cuckoo and kleptoparasitic bees,
330   which themselves can be categorised as endangered under IUCN criteria (Fitzpatrick et al
331   2007; Nieto et al 2014) – or when they fit the definition of parasitoids – for example,
332   conopid flies and syntretic wasps – demonstrating a very specific kind of chauvinism
333   towards the broad array of life that has evolved to parasitise pollinators. Future re-
334   introduction schemes and conservation actions for pollinators should explicitly recognise
335   and incorporate their natural parasite community (Dougherty et al 2016, Carlson et al 2020),
336   rather than treating them simply as threats to pollinator conservation.
337
338   **Conclusion**
339   Parasites are a natural part of wild pollinator biology, but their important role in structuring
340   wild pollinator communities has been largely ignored, with a focus instead on their control
341   and elimination. While this focus has been driven by the important issue of pathogen
342   spillover, the dynamics of natural host-parasite associations are fundamentally different,
343   and consequently require an approach that reflects our knowledge of host-parasite
344   community dynamics. Unfortunately, evidence for the role of parasites in structuring
345   pollinator communities, or even driving the dynamics of individual pollinator species, is
346   limited. However, what evidence there is suggests that generalist parasites may enable
347   richer and more diverse pollinator assemblages through their impacts on more abundant
348   host species. Further work, both empirical and theoretical, is needed to determine whether
349   this is the case. In the meantime, the potential utilisation of natural pharmaceuticals for
350   wild pollinators needs to be carefully considered, to make sure that it does not undermine
351   the forces that are maintaining rarer pollinator species within the community. In conclusion,
352   the potential role of parasites as signals for, and drivers of pollinator community health

353 needs to be confirmed if we are to take a holistic approach to managing and maintaining
354 healthy pollinator communities.
355

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