Complex networks of parasites and pollinators: moving towards a healthy balance

Mark J F Brown
Centre for Ecology, Evolution, and Behaviour; Department of Biological Sciences; School of Life Sciences and the Environment; Royal Holloway University of London; UK
Abstract
Parasites are viewed as a major threat to wild pollinator health. While this may be true for epidemics driven by parasite spillover from managed or invasive species, the picture is more complex for endemic parasites. Wild pollinator species host and share a species-rich, generalist parasite community. In contrast to the negative health impacts that these parasites impose on individual hosts, at a community level they may act to reduce competition from common and abundant pollinator species. By providing rare species with space in which to exist, this will act to support and maintain a diverse, and thus healthier pollinator community. At this level, and perhaps paradoxically, parasites may be good for pollinators. This stands in clear contrast to the obvious negative impacts of epidemic and spillover parasites on wild pollinator communities. Research into floral resources that control parasites could be best employed to help design landscapes that provide pollinators with the opportunity to moderate their parasite community, rather than attempting to eliminate specific parasites from wild pollinator communities.

Keywords
Bumblebees, Bombus, apparent competition, ecological networks, food webs
“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 (causal 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 (Thorpe & 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
hypothesis’ suggests that, rather than development and function of the immune system relying solely on these antagonistic interactions, it is ambient microbiomes (on the skin, gut, etc.) and parasites that cause chronic infections, that are essential for development and maintenance of normal immune function. In humans this has led to the development of therapies that deliberately re-introduce parasites into humans to regulate the immune system (e.g., Broadhurst et al. 2010).

How might these hypotheses apply to insect pollinators? Recent evidence for the presence of an adaptive anti-viral immune system in insects (Tassetto et al. 2017) shows that insect immune systems are more similar to mammalian immune systems than had been supposed. Consequently, infectious microbes – as suggested by the ‘hygiene hypothesis’ – may have a similar role in the development of the insect immune system, and their absence may lead to maladaptive responses to adult infections. Experiments that eliminate antagonistic microbes during development are required to test this idea. However, as is the case with humans (Rook et al. 2003, Bloomfield et al. 2016), the ‘old friends hypothesis’ may be more applicable to understanding insect immunity. A co-evolved gut microbiome has been identified in key insect pollinators (honey bees: Kwong & Moran 2016, bumble bees: Hammer & Moran 2021) and interactions between the insect immune system and the gut microbiome are well-documented (Horak et al. 2020, Lesperance & Broderick 2020), as are interactions between the gut microbiome and parasites (Koch & Schmid-Hempel 2011), both of which can be viewed as prerequisites for the ‘old friends hypothesis’ to apply. Consequently, microbes may play a key role in the development, maintenance, and function of the immune system of insect pollinators, and thus have a positive impact on individual health (Horak et al. 2020). A final aspect of the ‘old friends hypothesis’ argues that parasites that cause chronic infections could have evolved a regulatory relationship with the immune system. An analogy for this in insect pollinators emerges from the concept of immune priming. In bumblebees, an initial exposure to a low-dose of a bacterial pathogen gave specific protection against secondary exposure (Sadd & Schmid-Hempel 2006). Similar, but perhaps less specific effects could result in prior exposure to a low virulence but abundant pathogen providing protection against subsequent exposure to a high virulence pathogen that interacts similarly with the immune system. Consequently, such low virulent pathogens could actually confer health benefits on individual insect pollinators, depending upon the relative prevalence and thus opportunities to encounter parasites across a range of virulence levels. Whether such interactions exist in wild insect pollinators deserves investigation. Overall, investigating how and where the ‘old friends hypothesis’ maps on to insect pollinators could be a productive area to mine for researchers of bee health.

**Parasites and wild pollinator health, sensu lato**

Turning to the level of population or community health in wild pollinators (López-Uribe et al. 2020; Stevenson et al., this issue), a useful analogy can be made with the extensive literature on pollinator-plant networks (Bennett et al. 2018; Vizentin-Bugoni et al. 2018). Empirical and theoretical studies of the relationship between pollinators and the plants that they pollinate show that a robust, resilient, or perhaps healthy network is one that contains many pollinator species, with redundancy in their plant visitation patterns (Bennett et al. 2018; Vizentin-Bugoni et al. 2018). Here it is the pollinators that are driving the health of the plant community. Similarly, in the relationship between parasites and pollinators, a diverse 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).
In addition to differential prevalence, differential virulence across host species could also help to support a more species-rich pollinator assemblage. Again, this has been identified in the endemic parasites of bumblebees, where the microsporidian *Nosema bombi* and the castrating nematode *Sphaerularia bombi* vary in their virulence depending upon the bumblebee species they are parasitising (Rutrecht & Brown 2009, Jones & Brown 2014, Kelly 2009). However, it is an open question as to how such variation in virulence maps to background host abundance, and thus whether such variation will act to enhance or decrease pollinator species richness. Theory suggests that the relationship between parasites and multiple hosts is complex and varied, and so patterns of virulence across multiple pollinator species cannot easily be predicted (e.g., Osnas & Dobson 2011). Consequently, further empirical studies of virulence across a broader range of host species are needed to address this.

An important caveat to the discussion above is that we still have a severe knowledge gap on the actual impact of parasites on wild pollinators. Laboratory studies have found significant impacts on colony (Brown et al 2003; Yourth et al 2008; Otti & Schmid-Hempel 2007; Rutrecht & Brown 2009) and population-level health (Brown et al 2003), but how these translate into real impacts in the field remains unknown, apart from the case of cuckoo bees described above. However, given the prevalence of parasites such as *Crithidia bombi* (Shykoff & Schmid-Hempel 1991; Gillespie 2010; Kissinger et al 2011; Cordes et al 2012; Jones & Brown 2014; Gamboa et al 2015; Gallot-Lavallee et al 2016; Plischuk et al 2020) and *S. bombi* (Kelly 2009) that are known to have dramatic impacts on host species (Brown et al 2003; Kelly 2009; Jones & Brown 2014), it seems likely that they are having at least some impact on their host populations in the wild.

Along with their potential role in structuring pollinator communities, and as emphasised in a series of seminal publications, parasites are a natural part of food webs, playing important roles as consumers of and redistributors of biomass and nutrients, and drivers of stability (e.g., Lafferty et al 2006, Lafferty et al 2008). Removals of, or declines in parasites, could thus have negative impacts on host population health through further disruption of the structure of trophic relationships. Finally, from an evolutionary perspective, hosts have coevolved with their parasites, as can be seen from the existence of immune systems, positive selection on host immune genes (Barribeau et al 2015), as well as the evolution of behavioural responses to reduce parasite impacts (Müller & Schmid-Hempel 1993). Consequently, declines or removals of parasites could dramatically change the selective landscape in which pollinators continue to evolve.

**Parasite epidemiology and its control in wild pollinators**

Despite the potential importance of parasites to pollinator diversity and community health, as detailed above, current research on the role of parasites in wild bee health has focused largely on either understanding transmission dynamics (Ruiz-Gonzalez et al 2012; Adler et al 2018; Figueroa et al 2019; Bailes et al 2020; Figueroa et al 2020; Graystock et al 2020), or how floral resources can be used to control natural endemic parasites in bumble bees (see below). Identification of parasite sources (Graystock et al 2020), sinks (Jones and Brown 2014), and reservoirs of infection (Graystock et al 2020) can help to predict whether parasites will enhance pollinator species richness or actually depress populations of rare
species even further. However, how these transmission dynamics map onto patterns of species abundance remains to be determined.

Transmission dynamics are not solely driven by properties of the parasite or the host. One of the most exciting recent branches of research into pollinator health has been the discovery that numerous compounds that occur as non-nutritive components in nectar and pollen (Manson et al 2010; Anthony et al 2015; Baracchi et al 2015; Biller et al 2015; Palmer-Young et al 2016; Palmer-Young et al 2017; Giacomini et al 2018; Koch et al 2019; LoCascio et al 2019; Folly et al 2020; Folly et al 2021), as well as particular flowering plant species (Giacomini et al 2018; LoCascio et al 2019; Giacomini et al 2021), have been identified as reducing or preventing infections of pollinator parasites, including the trypanosome *Crithidia bombi* in two species of bumble bee (*B. terrestris* and *B. impatiens*) (Manson et al 2010; Anthony et al 2015; Baracchi et al 2015; Biller et al 2015; Palmer-Young et al 2016; Palmer-Young et al 2017; Giacomini et al 2018; Koch et al 2019; LoCascio et al 2019), and the microsporidia *Nosema apis* and *N. bombi* in honey bees and bumble bees respectively (Folly et al 2020; Folly et al 2021). Importantly, these discoveries are of much broader relevance than the pollinator species in which they have been documented, as these parasites are now known to infect a much broader array of species outside of bumblebees and honey bees. In at least some of these cases, these natural medicines are either under threat due to habitat loss (Koch et al 2019) or come from species that are naturally important forage sources for wild bees (LoCascio et al 2019). One way to take advantage of these compounds to enhance pollinator health is to include them in the supplementary diets of managed pollinators, which could result in a reduction of pathogen spillover (see above). However, it has also been suggested that they could be used in floral enhancement schemes to provide a natural pharmacy for wild bees (Folly et al 2021).

How such non-nutritive floral resources could be provided at a landscape level for wild insect pollinators is unclear. Floral enrichment schemes in agricultural landscapes need to balance availability of high quality nectar and pollen sources to serve a diversity of polylectic and oligolectic insect pollinators. Incorporating species that provide compounds or pollen types that can act to reduce parasite infection or load has to be balanced against the need to provide this complex nutrition. In addition, if parasites are acting to reduce competition from numerically dominant insect pollinators, and thus enabling a richer pollinator community (as discussed above), then the provision of natural pharmaceuticals should be targeted through plants that are not visited, or significantly less visited by dominant insect pollinator species. In non-agricultural environments, where recent habitat loss has led to the loss of plants that provide these pharmaceutical services to insect pollinators (e.g., Koch et al 2019), ecological restoration is obviously a much simpler business.

**What might a healthy parasite-pollinator network look like?**

Efforts to maximise pollinator health at the community scale through the manipulation of parasites are limited by a fundamental gap in knowledge. Arguably the biggest challenge in understanding what a healthy assemblage of pollinators and parasites would be is gathering the real-world data to answer this question. By their very nature, host-parasite associations are dynamic in space and time (Thompson 2005). Consequently, snapshots from a single season, single year, or single site are limited in what they can tell us. In addition, pollinator assemblages themselves have been significantly altered by anthropogenic forces, such as
intensive agriculture, urbanisation, and climate change, which may have implications for the structure and health of the host-parasite community. Ecological network theory provides tools to assess the structure and stability of bi-partite networks (Runghen et al 2021), and a first step therefore might be to apply network analyses to already collected host-parasite data in pollinators, or to new data collected from targeted habitats, to gain an understanding of how pollinator-parasite communities vary across different ecosystems. Information on how pollinator-parasite communities are structured, in terms of nestedness, redundancy, etc., and how this relates to robustness and resilience, will provide unique insights into pollinator community health.

Parasites in pollinators: a right to life?

Notwithstanding their potential positive impacts on wild pollinator community structure, specific targeted conservation actions may still require the removal of pollinator parasites. For example, reintroduction of locally extinct pollinators, like the large blue butterfly *Phengaris arion* or the short-haired bumblebee *B. subterraneus*, falls under IUCN regulations, and these often require quarantine to enable the elimination of parasites (e.g., Brown et al 2017). Increasingly, the more research is done the more generalist pollinator parasites appear to be, suggesting that such parasite elimination may not have any consequences for the survival of individual parasite species. However, losses of other parasite species during reintroductions (e.g., the California condor louse; see Dunn (2009) for a review) argues against complacency. Conservation is not a zero sum game, and while pollinators are important across a range of values, parasites have the same ethical right to life and conservation as any other organism. This is not questioned when parasites are of the same taxonomic group as their hosts – for example, cuckoo and kleptoparasitic bees, which themselves can be categorised as endangered under IUCN criteria (Fitzpatrick et al 2007; Nieto et al 2014) – or when they fit the definition of parasitoids – for example, conopid flies and syntretic wasps – demonstrating a very specific kind of chauvinism towards the broad array of life that has evolved to parasitise pollinators. Future reintroduction schemes and conservation actions for pollinators should explicitly recognise and incorporate their natural parasite community (Dougherty et al 2016, Carlson et al 2020), rather than treating them simply as threats to pollinator conservation.

Conclusion

Parasites are a natural part of wild pollinator biology, but their important role in structuring wild pollinator communities has been largely ignored, with a focus instead on their control and elimination. While this focus has been driven by the important issue of pathogen spillover, the dynamics of natural host-parasite associations are fundamentally different, and consequently require an approach that reflects our knowledge of host-parasite community dynamics. Unfortunately, evidence for the role of parasites in structuring pollinator communities, or even driving the dynamics of individual pollinator species, is limited. However, what evidence there is suggests that generalist parasites may enable richer and more diverse pollinator assemblages through their impacts on more abundant host species. Further work, both empirical and theoretical, is needed to determine whether this is the case. In the meantime, the potential utilisation of natural pharmaceuticals for wild pollinators needs to be carefully considered, to make sure that it does not undermine the forces that are maintaining rarer pollinator species within the community. In conclusion, the potential role of parasites as signals for, and drivers of pollinator community health...
needs to be confirmed if we are to take a holistic approach to managing and maintaining healthy pollinator communities.

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