



Occurrence of honey bee (*Apis mellifera*) pathogens in ants (Hymenoptera: Formicidae): a systematic review

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Abstract

Ants are ubiquitous insects that commonly coexist with honey bees in shared environments. The constant interactions between these species can facilitate the transmission of pathogens from honey bees to ants. If ants prove to be efficient carriers of pathogens, the situation may be exacerbated by spillback events. This systematic review gathers and summarizes instances of honey bee pathogen occurrences in ants. The reports are categorized based on host species, condition and stage, year and geographic area, as well as detection methods. A total of 22 studies have investigated the presence of 11 honey bee pathogens. Among nine detected viruses, five demonstrated replicative capability, suggesting that ants could potentially act as vectors for honey bee pathogens. Clinical symptoms were detected for acute bee paralysis virus (ABPV) in *Lasius niger* and deformed wing virus (DWV) in *Solenopsis invicta*. Additionally, multiple co-infections of honey bee pathogens have been observed in nine ant species. Understanding whether ants could act as incidental hosts, primary hosts, or vectors of these pathogens, facilitating transmission to other insects, is crucial. Further studies are necessary to clarify their role in the ecological dynamics of diseases, safeguarding the well-being not only of ants but also of other hymenopterans and insects.

Key words: Honey bee diseases, spillover, ants, honey bee pathogens, viral disease, invasive species.

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Introduction

Pathogens can spread across and affect multiple different host species (CLEAVELAND & al. 2001, WOOLHOUSE 2002). The pathogen jumps from one host (reservoir) to another (incidental and sympatric), causing damage not only at the individual level but also impacting populations, communities, and ecosystems (e.g., decreasing population density, reducing fitness, and potentially causing local extinctions) (POWER & MITCHELL 2004). At the individual level, the disease remains in the infected specimen without propagation (dead-end host), while at the population and community levels, the pathogens could be transmitted within the colony or environments leading to other species (FENTON & PEDERSEN 2005, NUGENT 2011). Pathogen outbreaks in new host species can lead to the occurrences of Emerging Infectious Diseases (EIDs) (DASZAK & al. 2000, PINILLA-GALLEGO & IRWIN 2022). The EIDs are caused

by pests and pathogens with higher incidences and that are able to infect new host species or to extend in another environment (DASZAK & al. 2000, ARISMENDI & al. 2021). The EIDs' spread is facilitated by human population growth, the encroachment into wildlife habitats, and the introduction and relocation of animals to unfamiliar geographic areas (DASZAK & al. 2001, OTTERSTATTER & THOMSON 2008). Among insect species, *Nosema ceranae* and deformed wing virus (DWV) have been recently defined as pathogens causing EIDs, due to their incidence and prevalence worldwide (FÜRST & al. 2014, BROWN 2017, MCMAHON & al. 2018).

The processes determining cross-species transmission are complex, involving several factors, such as host characteristics (e.g., immunological conditions, density, distribution, species interactions, phylogenetic distance),

pathogen attributes (e.g., transmission, viability, virulence, persistence, resistance), and the surrounding environment (e.g., habitat sharing, ecosystem boundaries, fragmentation) (PLOWRIGHT & al. 2017, BECKER & al. 2019, ELLWANGER & CHIES 2021). Once these multiple barriers are overcome, the transfer of a pathogen from a reservoir host to a recipient host occurs (PLOWRIGHT & al. 2017).

Interspecific transmission is a threat to entomofauna, necessitating the implementation of a One-Health approach for a comprehensive understanding of their processes, impacts, and effects (RUIZ-ARAVENA & al. 2021, WILFERT & al. 2021, PINILLA-GALLEGO & al. 2022). Within entomofauna, the One-Health approach is a paradigm that aims to ensure the ecosystem service of pollination and study the interaction of insects and their pathogens to understand infectious disease biology shared in the environment (MANLEY & al. 2015, WILFERT & al. 2021).

While extensively researched in humans, the consequences for biodiversity and wildlife populations, particularly in invertebrates, remain poorly documented (COLLA & al. 2006, OTTERSTATTER & THOMSON 2008, FÜRST & al. 2014). These concerns have become more pronounced following numerous insect monitoring efforts conducted over the past few decades, confirming a distressing decline in both biodiversity and insect abundance (FORISTER & al. 2019, EGGLETON 2020, DONKERSLEY & al. 2022). The relevance of diseases became apparent with the loss of thousands of honey bee colonies, contributing to Colony Collapse Disorder (CCD) (AIZEN & HARDER 2009, CORNMAN & al. 2012, LEVITT & al. 2013).

The honey bee (*Apis mellifera*) represents the most studied insect, also in terms of pathogens and pests, for its economic value, and its ecological and agricultural role. Besides, according to certain hypotheses, pathogens historically detected in honey bee colonies, shifted to other arthropods becoming generalists and triggering ecological effects due to the loss of biodiversity (LEVITT & al. 2013, DOBELMANN & al. 2020, OCEPEK & al. 2021, CILIA & al. 2022). The detection of honey bee pathogens in arthropods living near honey bee colonies suggests a potential environmental circulation of pathogens (LEVITT & al. 2013, NANETTI & al. 2021, CILIA & al. 2022). Sharing the same contaminated resources, such as flowers, honey, pollen, nectar, and the same environment poses a serious risk of infection for all pollinators as well as other insects (MANLEY & al. 2015, YAÑEZ & al. 2020, BURNHAM & al. 2021, PIOT & al. 2021).

Numerous monitored honey bee pathogens can infect various species as they are non-selective, making them easily transmissible among insects (GENERSCH & al. 2006, DOLEZAL & al. 2016). Indeed, several studies have corroborated the presence and replication of different honey bee pathogens in various orders of insects (Blattodea, Coleoptera, Dermaptera, Diptera, Hemiptera, Hymenoptera, Lepidoptera, Odonata, and Orthoptera) and arachnids (orders Araneae and Opiliones) (LEVITT & al. 2013, BRETTELL & al. 2020, DOBELMANN & al. 2020, NANETTI & al. 2021, SCHLÄPPI & al. 2023). However, due to the lower

economic interest in other insects compared with honey bees, information on the potential effects and symptoms of honey bee pathogens in non-*Apis* hosts is very limited, and there are still several knowledge gaps (GENERSCH & al. 2006, YAÑEZ & al. 2020, CILIA & al. 2021, NANETTI & al. 2021).

Concerning wild bees and other hymenopterans, the knowledge of the pathogen community within these species is limited, and this research area deserves further attention (TEHEL & al. 2016). Studies have already demonstrated the infectivity and pathogenicity of some honey bee pathogens to other hymenopterans (GENERSCH & al. 2006, LUCIA & al. 2014, FORZAN & al. 2017, CILIA & al. 2021). Both direct and indirect interactions between honey bees and other arthropods could play a crucial role in promoting the interspecific transmission of pathogens (PAYNE & al. 2020, YAÑEZ & al. 2020). Nevertheless, acquiring evidence of interspecific transmission is challenging, and frequently the pathways are unclear or undetermined (NANETTI & al. 2021).

Ants can also come into contact with honey bees, leading to infections with their pathogens. Additionally, they may contract other viruses, some of which are transmitted by different insects, such as *Drosophila C Virus*, *Aphid Lethal Paralysis Virus*, *Rhopalosiphum padi virus*, and *Hubei orthoptera virus 1* (BATY & al. 2020), although their effects and symptoms on hosts are mostly unknown. Ants emerge as dominant organisms in most terrestrial habitats, showcasing impressive adaptive radiation among social insects (HÖLLDOBLER & WILSON 2009). They can establish a complex network of interactions with virtually every component of their ecosystems, spanning from microorganisms to fungi and from other animals to plants (HÖLLDOBLER & WILSON 2009, NESS & al. 2010). As ubiquitous hymenopterans, ants are frequently encountered, even infiltrating hives, especially the invasive *Solenopsis*, *Anoplolepis*, *Pheidole*, and *Linepithema* species (PAYNE & al. 2020). They can be observed foraging around the landing board near hive entrances, scavenging deceased honey bee adults, preying on honey bee brood or robbing sugar and pollen resources (SPANGLER & TABER 1970, SCHLÄPPI & al. 2019, PAYNE & al. 2020, SCHLÄPPI & al. 2020).

All these direct interactions can promote the horizontal interspecific transmission of pathogens (YAÑEZ & al. 2020, PROESMANS & al. 2021), as evidenced by mainly honey bee viruses and also *Nosema* spp., found in ants residing inside or in proximity to apiaries (CELLE & al. 2008, LEVITT & al. 2013, SÉBASTIEN & al. 2015, GRUBER & al. 2017, BRETTELL & al. 2019, LESTER & al. 2019, DOBELMANN & al. 2020, PAYNE & al. 2020, SCHLÄPPI & al. 2020, ALLEN & RANKIN 2022). The diverse array of interactions that ants establish with plants, ranging from antagonism and opportunism to occasional mutualism and obligate symbiosis, may play a significant role for indirect pathogen transmission in various ecosystems (RICO-GREY & OLIVEIRA 2007, GRASSO & al. 2015).

Ant activities such as plant and flower patrolling as well as interactions with honeydew producers, driven by their

widespread nectar-feeding habit and trophobiotic and / or predatory behaviour (NESS & al. 2010, GRASSO & al. 2015, NEPI & al. 2018, SCHIFANI & al. 2020, CASTRACANI & al. 2023, SCHIFANI & al. 2024), could render ants susceptible to infections during their interactions with flowers and other plant parts previously visited by infected honey bees (HABER & al. 1981, JUNKER & al. 2007, DEL-CLARO & al. 2019, YAÑEZ & al. 2020, BURNHAM & al. 2021). Once infected, ants can transmit pathogens to other members of the colony, either through horizontal transmission, such as direct contact, the faecal-oral route, and trophallaxis, or through vertical transmission (ABRIL & JURVANSUU 2020, BATY & al. 2020). Similar to honey bees, ants exhibit a complex social immunity and structure, characterized by a high density of individuals within the colony, presenting both benefits and risks from an epidemiological perspective (CREMER & al. 2007, WALKER & HUGHES 2009, MALAGOCKA & al. 2019, BATY & al. 2020, SCHLÄPPI & al. 2021). Although studies have confirmed ants as biological hosts of some pathogens typically associated with honey bees (SÉBASTIEN & al. 2015, GRUBER & al. 2017, SCHLÄPPI & al. 2019, DOBELMANN & al. 2020, LIN & al. 2020, PAYNE & al. 2020), there is still a deficiency in data regarding potential effects and symptoms at both individual and colony levels (SCHLÄPPI & al. 2020). It is fundamental to investigate the possible routes and consequences of occurrence and interspecific pathogen transmission in ants (FOLGARAIT 1998, DEL TORO & al. 2012, SCHLÄPPI & al. 2020).

This systematic review aimed to collect, categorize, and summarize the documented studies of occurrences of honey bee pathogens in ants as reported in the literature. The spillover cases were grouped based on host species, condition and stage, geographical region, and co-infection in the same host.

Material and methods

Protocol and literature search

This systematic review was carried out according to the Preferred Reporting Items for Systematic Review and Meta-Analysis (PRISMA) protocols (MOHER & al. 2009). The research question guiding the review was: “Which honey bee pathogens may occur and / or infect ant species?”

The presence of pathogens was differentiated in occurrence (presence of pathogens in ant species) and infection (replicative pathogens or clinical symptoms). Also artificial infections were considered. Pathogen replication information was collected in each considered article, based on data reported, specific molecular techniques (strand-specific RT-PCR), or due to clinical symptoms found.

Only studies published in the English language were included. The article search encompassed PubMed, Web of Science (Web of Science Core Collection, BIOSIS Citation Index, BIOSIS Previews, Grants Index, KCI-Korean Journal Database, MEDLINE, Preprint Citation Index, ProQuest Dissertations & Theses Citation Index, SciEL Citation Index), Science Direct, Google Scholar, and

Scopus scientific databases, specifically targeting studies focused on the occurrence and / or infection of honey bee pathogens in ants. No restrictions were imposed on publication years, and the last search was conducted on 15 December 2023.

For each scientific database, the first screening was performed based on title, abstract, and keywords. For Web of Science, both “Authors keywords” and “Keywords Plus” were used for the articles search. In each database, the following search strategy was designed and utilized: “Honey Bee Pathogens” OR “Ant” OR “Ants” OR “Spillover” OR “Spill-over” OR “Inter Species Transmission” OR “Interspecific Transmission” OR “Inter Taxa Transmission” OR “Host Species Transmission” OR “Occurrence” OR “*Apis mellifera*” OR “Ant Species” OR “Social Insect” OR “Ant Larvae” OR “Ant Worker” OR “Ant Gynes” OR “Ant Queen” OR “Ant Colony” OR “Wild Ant” OR “Ant Nest” OR “Honey Bee Diseases” OR “Honey Bee Virus” OR “Honey Bee Bacteria” OR “Honey Bee Microsporidia” OR “Honey Bee Protozoa” OR “Managed Bees” OR “Commercial Bees” OR “Artificial Infection” OR “Replicative Virus” OR “Colony Collapse Disorder” OR “Deformed Wing Virus” OR “Acute Bee Paralysis Virus” OR “Israeli Acute Paralysis Virus” OR “Black Queen Cell Virus” OR “Sacbrood Virus” OR “*Apis mellifera* Filamentous Virus” OR “Kashmir Bee Virus” OR “Slow Bee Paralysis Virus” OR “Lake Sinai Virus” OR “*Varroa destructor*” OR “Macula-like Virus” OR “*Nosema apis*” OR “*Nosema ceranae*” OR “*Nosema bombi*” OR “*Spiroplasma*” OR “*Crithidia*” OR “*Crithidia mellificae*” OR “*Crithidia bombi*” OR “*Lotmaria passim*” OR “*Ascospaera*” OR “*Apicystis*” OR “Arthropods” OR “Entomofauna” OR “Hive Hosts” OR “Hive” OR “Free-Ranging Insect” OR “Bee Interaction”. Due to over 800.000 articles retrieved thereby, the logical operator “AND” was then used to combine descriptors in groups of two or three to decrease the number of articles, focusing on ant infection and ant pathogens.

Studies conducted in both field and laboratory conditions were included. Multiple hits of the same study were reduced to a single one. The search and screening for titles, abstracts, material and methods, and results were carried out independently by the authors. This encompassed all types of publications, such as articles, letters, notes, scientific notes, communications, and theses, with the specific aim of assessing cases of occurrence and interspecific transmission of honey bee pathogens in ants. Reviews, books, and book chapters were excluded from consideration. Potentially eligible research articles underwent independent reading and review by the authors, with data comparison to ensure integrity and reliability.

For each article incorporated into this review, relevant information, including author details, publication year, ant species, host conditions, host stage, pathogens, and prevalence was extracted. Instances of active replication of honey bee viruses were also documented. The data from the eligible studies are presented in tables and figures.

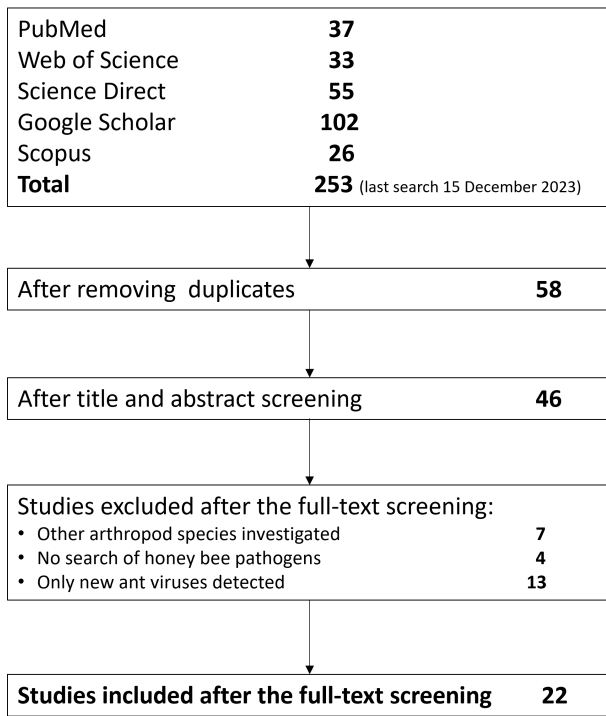


Fig. 1: Flow diagram reporting the number of retrieved studies from five databases after the title and abstract screening. In total, 22 studies were included in the systematic review after full-text screening, while 24 studies were excluded for the reasons provided.

Results

Following the PRISMA Protocol, 22 studies (Tab. S1, as digital supplementary material to this article, at the journal's web pages) were included in this systematic review (Fig. 1). No articles were published before 2008. The first article to investigate spillover from honey bees to ants was

published in 2008, and from that point onward, a total of 22 articles studied their occurrence (Fig. 2). Since 2008, the number of studies has consistently ranged from 1 to 2 per year, peaking at 6 in 2020, attributed to the rapid advancement of molecular genetic tools for pathogen detection. Although most pathogens were identified using quantitative PCR (qPCR) and Reverse Transcriptase-PCR (RT-PCR) (15 and 13, respectively; some studies investigated more than one pathogen), sequencing, metagenomics, and transcriptomics have also played significant roles in detecting the occurrence cases (Fig. 3).

For each article included in this review, pertinent information concerning the authors, geographical area, sampling year, host species, host conditions, host stage, pathogens and prevalence was extracted. The geographical distribution of pathogen occurrence in ants, as documented in the literature, reveals a significant number of studies in the USA and New Zealand (46 and 19, respectively), while cases from other countries were less frequent (Fig. 4).

A total of 11 different honey bee pathogens were detected in 32 different ant species, spanning 19 different genera (Fig. 5). The identified pathogens primarily consisted of viruses: acute bee paralysis virus (ABPV), black queen cell virus (BQCV), chronic bee paralysis virus (CBPV), both variants of deformed wing virus (DWV-A and DWV-B), Israeli acute paralysis virus (IAPV), Kashmir bee virus (KBV), sacbrood virus (SBV), two variants of Lake Sinai virus (LSV1 and LSV2), and Moku virus. Additionally, *Crithidia* spp. and *Nosema* spp. were detected. The predominant honey bee pathogen was DWV, accounting for 40 cases, inclusive of both DWV-A and DWV-B variants (Fig. 5). KBV, BQCV, ABPV, IAPV, and LSVs followed with 20, 13, 12, 7, and 7 cases, respectively, while other honey bee pathogens exhibited lower frequencies (fewer than 6 cases) (Fig. 5).

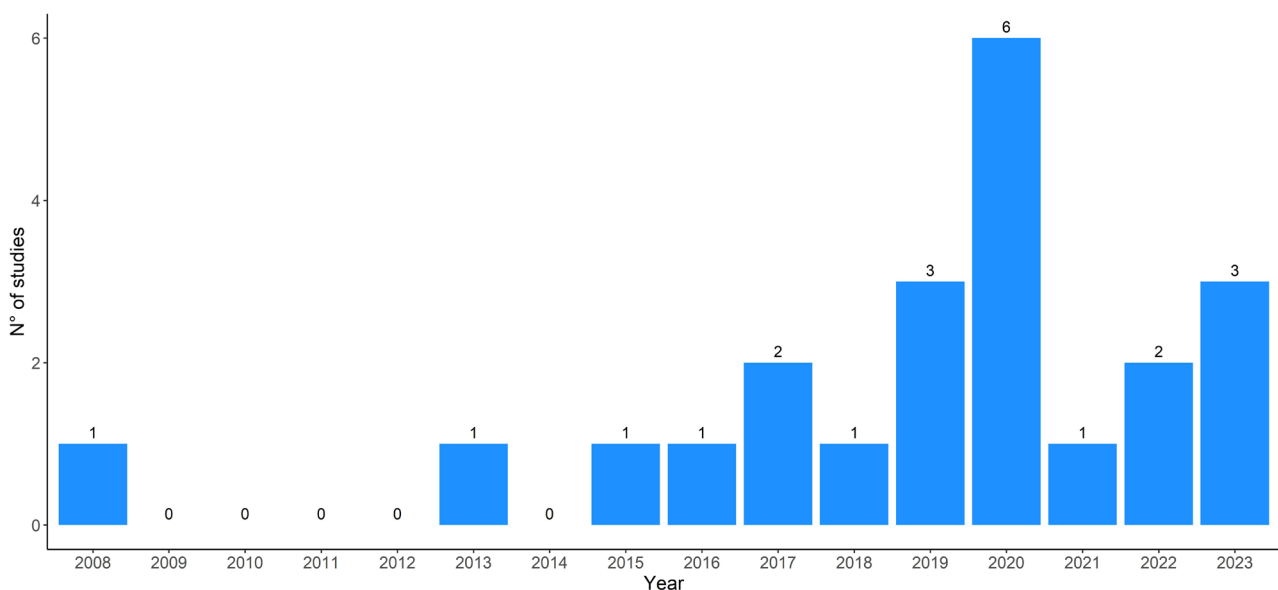


Fig. 2: The number of studies of honey bee pathogens in ants available in the literature until 2023.

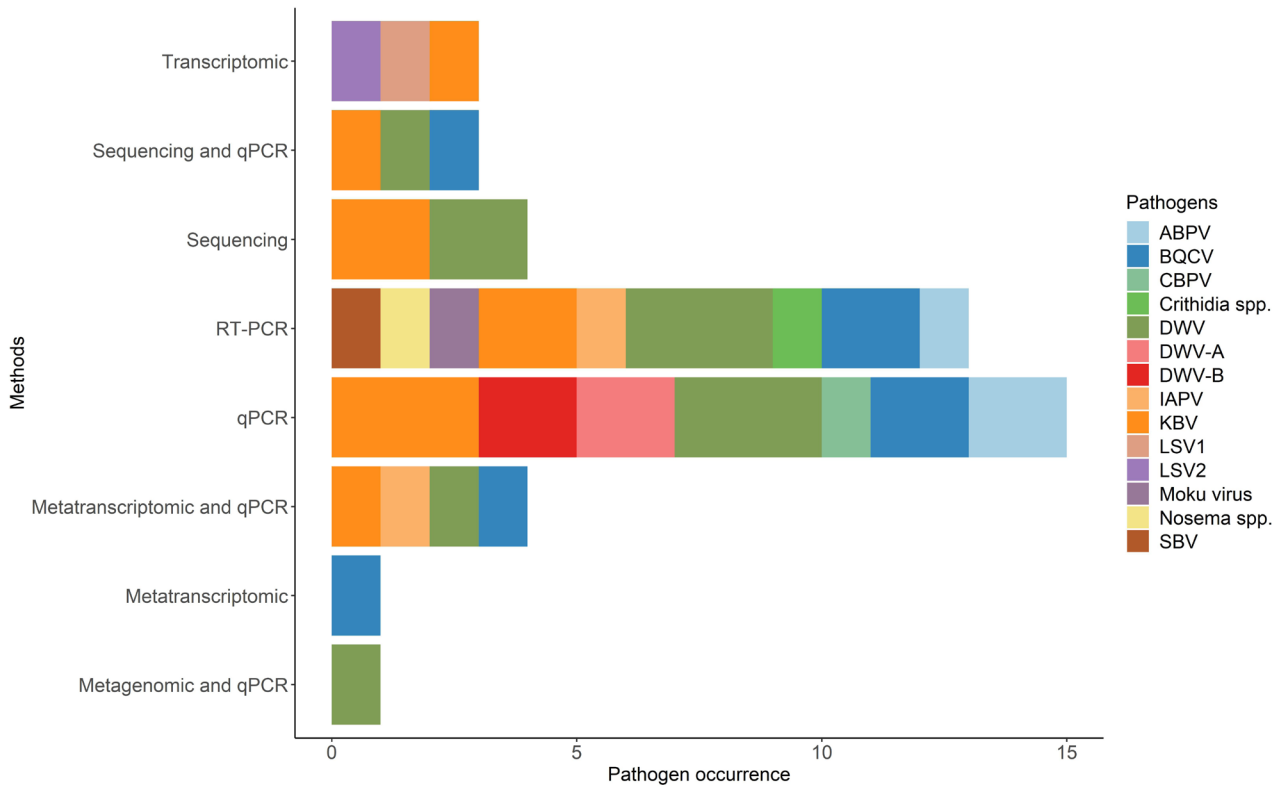


Fig. 3: The number of honey bee pathogens detected in ants related to the methods used for investigation (qPCR: quantitative PCR; RT-PCR: Reverse Transcriptase-PCR). Legend: ABPV: acute bee paralysis virus; BQCV: black queen cell virus; CBPV: chronic bee paralysis virus; DWV: deformed wing virus; DWV-A: deformed wing virus type A; DWV-B: deformed wing virus type B; IAPV: Israeli acute paralysis virus; KBV: Kashmir bee virus; LSV1: Lake Sinai virus type 1; LSV2: Lake Sinai virus type 2; SBV: sacbrood virus.

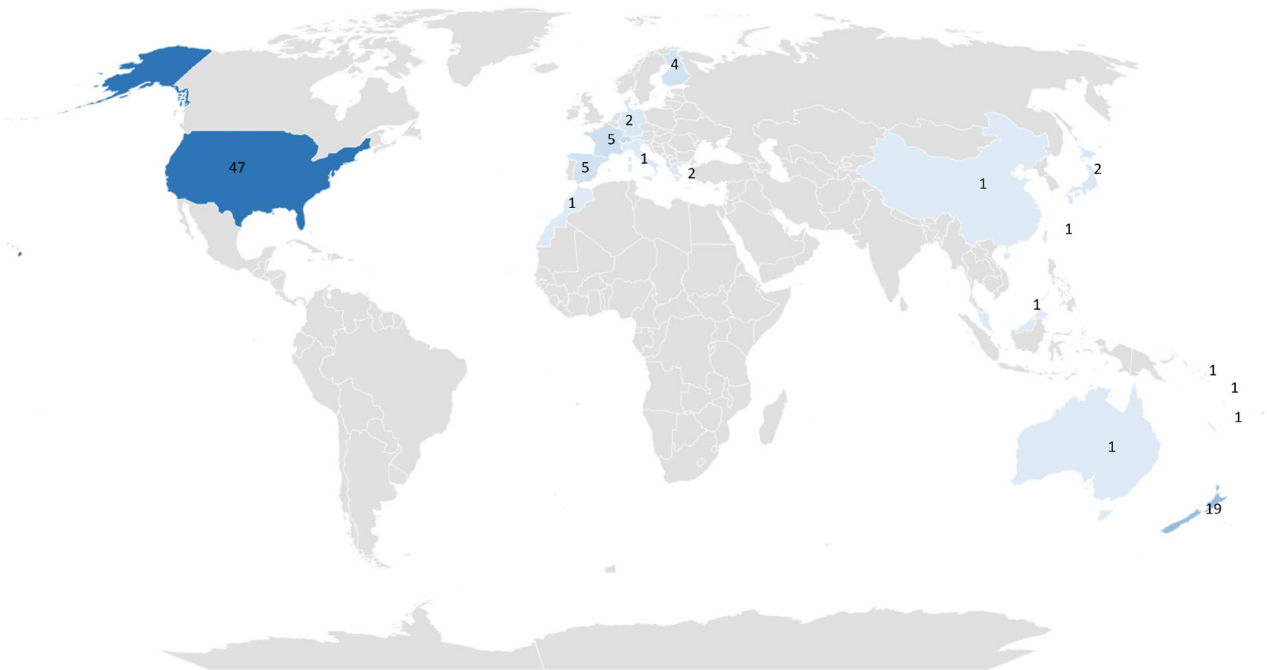


Fig. 4: Geographical distribution of the honey bee pathogen infections in ants, as reported in the literature. The number of occurrence cases is specified for each country and highlighted by different shades of blue.

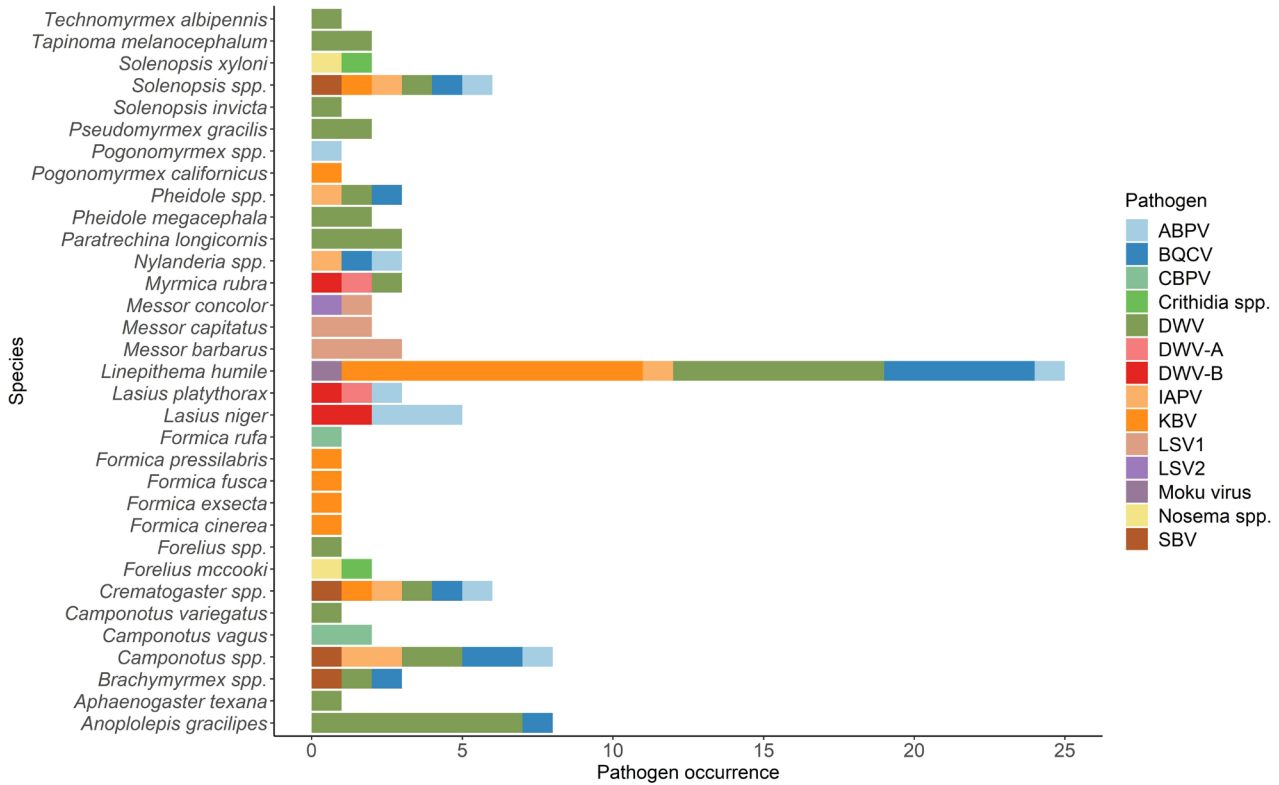


Fig. 5: Frequency of each honey bee pathogen occurrence in ant species. The predominant honey bee pathogen was DWV, accounting for 40 cases, inclusive of both DWV-A and DWV-B variants. Legend: ABPV: acute bee paralysis virus; BQCV: black queen cell virus; CBPV: chronic bee paralysis virus; DWV: deformed wing virus; DWV-A: deformed wing virus type A; DWV-B: deformed wing virus type B; IAPV: Israeli acute paralysis virus; KBV: Kashmir bee virus; LSV1: Lake Sinai virus type 1; LSV2: Lake Sinai virus type 2; SBV: sacbrood virus.

Tab. 1: Co-infection of honey bee pathogens detected simultaneously in ant individuals. Each line shows the co-infecting pathogens documented in a single individual of the host species. LSV1: Lake Sinai virus type 1; LSV2: Lake Sinai virus type 2; DWV: deformed wing virus; BQCV: black queen cell virus; SBV: sacbrood virus; IAPV: Israeli acute paralysis virus; ABPV: acute bee paralysis virus; KBV: Kashmir bee virus.

Host species	Co-infecting pathogens	Reference
<i>Messor concolor</i>	LSV1-LSV2	BIGOT & al. (2017)
<i>Brachymyrmex</i> sp.	DWV-BQCV	PAYNE & al. (2020)
	DWV-SBV	
<i>Nylanderia</i> sp.	BQCV-IAPV-ABPV	
<i>Pheidole</i> sp.	DWV-BQCV	
<i>Solenopsis invicta</i>	DWV-BQCV	
	DWV-SBV	
	DWV-IAPV	
<i>Camponotus</i> sp.	DWV-BQCV	
	DWV-IAPV	
	DWV-ABPV	
<i>Crematogaster</i> sp.	DWV-ABPV	
	DWV-BQCV	
<i>Linepithema humile</i>	DWV-KBV	DOBELMANN & al. (2020)
	DWV-Moku virus	
	KBV-Moku virus	
<i>Forelius mccooki</i>	<i>Crithidia</i> spp.- <i>Nosema</i> spp.	ALLEN & RANKIN (2022)

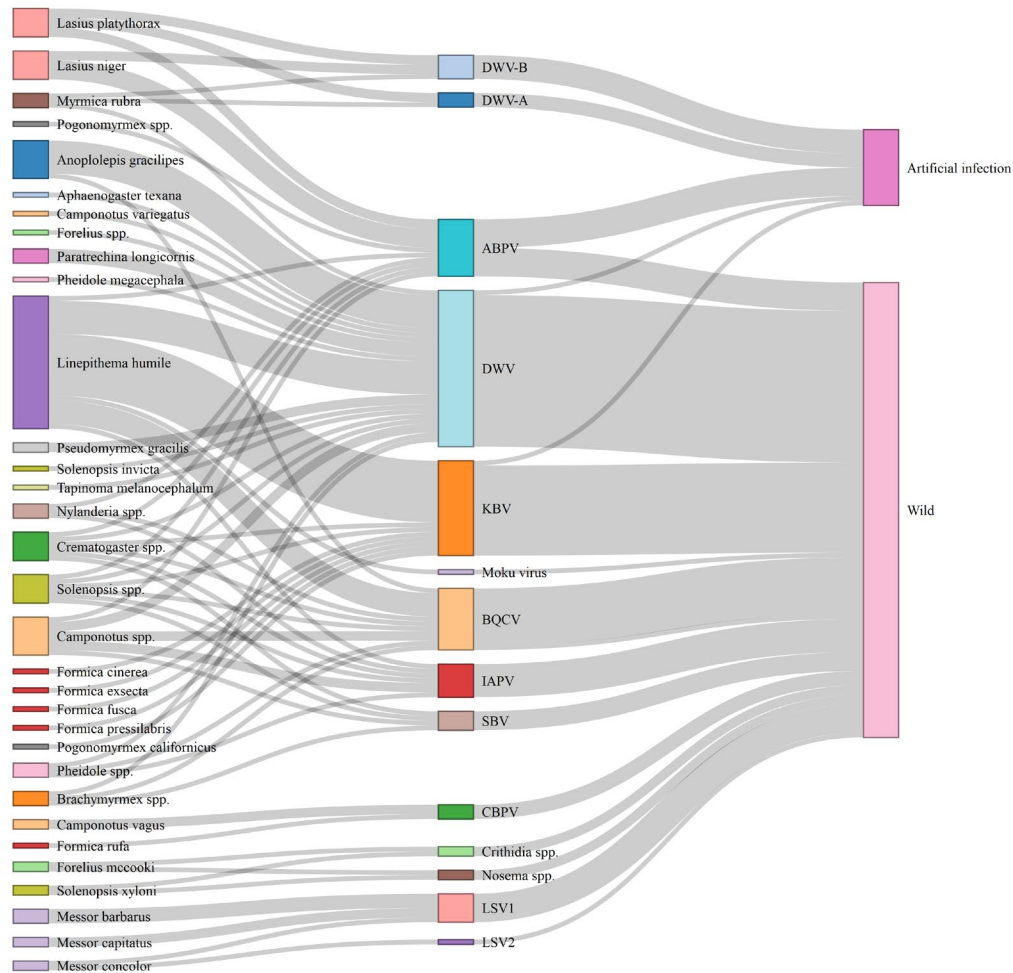


Fig. 6: Ant species tested positive for the pathogen in samples collected from the wild or through artificial infections. The thickness of connections (grey lines) and levels (rectangles) is proportional to the number of observations between nodes. Legend: ABPV: acute bee paralysis virus; BQCV: black queen cell virus; CBPV: chronic bee paralysis virus; DWV: deformed wing virus; DWV-A: deformed wing virus type A; DWV-B: deformed wing virus type B; IAPV: Israeli acute paralysis virus; KBV: Kashmir bee virus; LSV1: Lake Sinai virus type 1; LSV2: Lake Sinai virus type 2; SBV: sacbrood virus.

Overall, honey bee pathogens were detected in ants both in wild conditions and in artificial infection. All the reported pathogens were found in 94 cases in free-ranging individuals sampled in wild conditions (Fig. 6). On the other hand, experimental infections were conducted only on three viruses (DWV, ABPV, and KBV), revealing 14 cases (Fig. 6).

Finally, individuals from 9 ant species were discovered to be co-infected with multiple honey bee pathogens (Tab. 1). The most prevalent pathogens capable of co-infecting the ant hosts were DWV, BQCV, SBV, and ABPV. The highest incidence of co-infections was observed in *Solenopsis invicta*, *Camponotus* sp., and *Linepithema humile* individuals. Notably, *Nylanderia* sp. exhibited a high number of co-infections, with three pathogens (BQCV, IAPV, and ABPV) identified in the same individual.

Discussion

The results of this systematic review underscore the importance of occurrence of honey bee pathogens within

both native and non-native ant populations. The elevated incidence of spillover cases documented in the USA, New Zealand, and Europe may be attributed not only to the high density of honey bee colonies but also to the expertise in social insect and pathology research, while in the other countries there is a lack of documentation or surveys (INGRID & al. 1991, CRANE 2000, LODESANI & COSTA 2003, LÓPEZ-URIBE & SIMONE-FINSTROM 2019). The higher prevalence of pathogens occurrences in ants near apiaries indicates the disease circulation in their shared environment (CELLE & al. 2008, LEVITT & al. 2013, LESTER & al. 2019, BRETTELL & al. 2020, DOBELMANN & al. 2020, PAYNE & al. 2020, SCHLÄPPI & al. 2020, DOBELMANN & al. 2023). The detection of symptoms and other effects on alternative host populations remain unknown, underscoring the importance of expanding knowledge to comprehend the real impact on ant populations. Viruses vectored by *Varroa destructor* (DWV, KBV, ABPV, and IAPV) were most frequently involved in infection cases (LEVITT & al. 2013, SÉBASTIEN & al. 2015, GRUBER & al. 2017, VILJAKAINEN &

al. 2018, BRETTELL & al. 2019, LESTER & al. 2019, SCHLÄPPI & al. 2019, ABRIL & JURVANSUU 2020, BRETTELL & al. 2020, DOBELMANN & al. 2020, LIN & al. 2020, PAYNE & al. 2020, SCHLÄPPI & al. 2020, SCHLÄPPI & al. 2021, FELDEN & al. 2022, DOBELMANN & al. 2023, MILES & al. 2023). Similar to honey bees (BROMENSHENK & al. 2010, CORNMAN & al. 2012, HIGES & al. 2013), multiple infections were found in the investigated ant species, emphasizing the crucial role as incidental hosts of these social insects, which might contribute to the circulation and possible recirculation of pathogens within arthropod communities (WILFERT & al. 2021). Below, we provide a brief discussion of each honey bee pathogen reported in Tab. S1 and in relation to their spillover hosts.

Viruses

Deformed wing virus (DWV): DWV belongs to the *Iflavirus* genus within the Picornaviridae family and includes three distinct genetic variants (namely A, B, and C) (McMAHON & al. 2016, MORDECAI & al. 2016). This virus is among the most widespread honey bee viruses, with transmission often associated with the presence of the mite *Varroa destructor* in colonies (RYABOV & al. 2014, MARTIN & BRETTELL 2019). In honey bees, DWV can lead to pupal death or the emergence of adults with crippled and deformed wings, attributed to virus infection also in the brain and nervous system (DE MIRANDA & GENERSCH 2010, GISDER & GENERSCH 2017). DWV is considered a generalist virus due to its ability to infect different hosts, approximately 135 species across 8 orders (MARTIN & BRETTELL 2019, NANETTI & al. 2021, CILIA & al. 2022). The virus has been detected in 21 different ant species sampled in the USA, Europe, Asia, and Oceania. All three genomic variants were capable of infecting ants (BRETTELL & al. 2020). DWV exhibited infections across all castes and life stages, including workers, males, gynes, queens, larvae, and eggs (COOLING & al. 2017, BRETTELL & al. 2020, PAYNE & al. 2020, SCHLÄPPI & al. 2020). The replicative form was specifically found in *Crematogaster* spp., *Linepithema humile*, *Myrmica rubra*, *Paratrechina longicornis*, and *Solenopsis* spp., ants that are generally widespread, common around plants, and quite mobile (SÉBASTIEN & al. 2015, GRUBER & al. 2017, SCHLÄPPI & al. 2019, DOBELMANN & al. 2020, LIN & al. 2020). Besides, DWV clinical symptoms (crippled and deformed wings) and impaired mobility were detected in alate *S. invicta* males and gynes, highlighting a replicative infection of the virus (MILES & al. 2023). This is the first natural DWV infection showing clinical features in any ant species.

The DWV occurrence in ants was higher in individuals collected and observed living on or within bee hives, engaging in behaviour closely linked to honey bee colony development (e.g., robbing sugar resources, scavenging dead adult bees, or preying on bee brood) (PAYNE & al. 2020, DOBELMANN & al. 2023). The interactions between honey bees and ants sharing the same environment could promote an indirect pathway of pathogen transmission (BATY & al. 2020). Ants were found to have a higher vi-

ral load when collected in the presence of honey bees (GRUBER & al. 2017, LESTER & al. 2019). Additionally, phylogenetic analysis revealed that some DWV sequences were genetically identical to DWV isolated from honey bees (SÉBASTIEN & al. 2015, DOBELMANN & al. 2020, LIN & al. 2020).

AKI-complex (acute bee paralysis virus, Kashmir bee virus, Israeli acute paralysis virus): ABPV, KBV, and IAPV are three virulent and widespread viruses of honey bees (DE MIRANDA & al. 2010, McMAHON & al. 2018). They belong to the Dicistroviridae family and form a complex known as the AKI-complex due to the high similarity in their genetic sequences (DE MIRANDA & al. 2010). Usually, these viruses persist at low titers with a subclinical latent form, but they can become lethal when combined with other stress factors (DE MIRANDA & al. 2010, GISDER & GENERSCH 2017). Honey bees infected by ABPV and IAPV can exhibit symptoms such as trembling, inability to fly, and paralysis (DE MIRANDA & al. 2010). The AKI-complex is also associated with *Varroa destructor*, which can transmit the viruses through feeding (GENERSCH & al. 2010, YAÑEZ & al. 2020). The list of insects affected by these three viruses continues to increase, encompassing wild bees, wasps, ants, earwigs, beetles, roaches, and crickets (NANETTI & al. 2021). A total of 14 ant species tested positive for at least one of the three viruses; furthermore, all three viruses were detected in *Crematogaster* spp., *Linepithema humile*, and *Solenopsis* spp. (GRUBER & al. 2017, VILJAKAINEN & al. 2018, LESTER & al. 2019, ABRIL & JURVANSUU 2020, DOBELMANN & al. 2020, PAYNE & al. 2020, FELDEN & al. 2022, DOBELMANN & al. 2023). These viruses were investigated in ants only in the USA, New Zealand, Spain, and Switzerland. In artificial infection experiments, *Lasius niger* exhibited an ABPV load level of 10^4 in workers, 10^6 in queens and 10^2 in eggs, with infectious titers in the range of 9.57 ± 1.14 (mean \pm standard deviation; SCHLÄPPI & al. 2020). In the field, *L. humile* presented a KBV load ranging from 10^3 to 10^5 in workers (LESTER & al. 2019, ABRIL & JURVANSUU 2020). In most cases, ants were sampled in relation to the presence or absence of apiaries in proximity, and in one study, KBV viral concentrations were higher in ants collected within honey bee hives, reinforcing the possibility of the occurrence of these viruses (GRUBER & al. 2017). A replicative form of KBV was detected in Spanish individuals of *L. humile* (VILJAKAINEN & al. 2023). Clinical symptoms of ABPV were observed in artificially infected ants of *L. niger*, confirming the virus' ability to replicate in the ant host (SCHLÄPPI & al. 2020). At the individual level, infected ants displayed a reduction in their movements, along with shaky and uncontrolled motions. Conversely, at the colony level, ABPV infection led to a decrease in the number of newly emerged workers and fewer pupae, thereby weakening the overall colony fitness (SCHLÄPPI & al. 2020).

Black queen cell virus (BQCV): BQCV is classified as a *Cripavirus* genus within the Distriviridae family (GISDER & GENERSCH 2017). It can be detected in honey bee

queen pupae and / or pre-pupae, being the most common cause of queen pupae death, leading to decomposition in irregular and black cells (GISDER & GENERSCH 2017). BQCV has a broad host range, affecting various species such as hymenopterans, hoverflies, beetles, roaches, and spiders (NANETTI & al. 2021). Although this virus was found in eight ant species (i.e., *Anoplolepis gracilipes*, *Brachymyrmex* sp., *Camponotus* sp., *Crematogaster* sp., *Formica* sp., *Linepithema humile*, *Nylanderia* sp., and *Pheidole* sp.), the replicative form was not reported in any of them (LEVITT & al. 2013, COOLING & al. 2017, GRUBER & al. 2017, LESTER & al. 2019, DOBELMANN & al. 2020, PAYNE & al. 2020, FELDEN & al. 2022, DOBELMANN & al. 2023). However, studies investigating the presence of this virus in ants were limited to the USA, New Zealand, and Australia. Queens of *A. gracilipes* were found to be positive for BQCV in declining wild ant populations (COOLING & al. 2017). In all other studies, the hypothesis of interspecific transmission between honey bees and ants was tested by collecting ants in the presence or absence of hives (LEVITT & al. 2013, GRUBER & al. 2017, LESTER & al. 2019, DOBELMANN & al. 2020, PAYNE & al. 2020, FELDEN & al. 2022, DOBELMANN & al. 2023). Comparisons between these sites indicated significantly higher BQCV loads in invasive *L. humile* when they interacted with honey bees (GRUBER & al. 2017, LESTER & al. 2019). In contrast, a recent survey reported a higher BQCV load in honey bees when this ant species was present (DOBELMANN & al. 2023). The increase in BQCV titers in honey bees could suggest a spillback of pathogens from ants, as previous studies have demonstrated the capacity of ants to vector pathogens (MOREIRA & al. 2005, ALHARBI & al. 2019, DOBELMANN & al. 2023). Despite this, the routes of transmission and dynamics remain unknown and uncertain, necessitating further studies.

Chronic bee paralysis virus (CBPV): CBPV was one of the first honey bee viruses to be isolated and described, although it remains an unclassified ssRNA (+) virus (RIBIÈRE & al. 2002, OLIVIER & al. 2008). In infected honey bees, CBPV displays neurotropism, leading to symptoms of paralysis that manifest as an inability to fly and trembling. Additionally, infected bees exhibit hair loss on the abdomen, resulting in a dark appearance (RIBIÈRE & al. 2010, GISDER & GENERSCH 2017). CBPV has been observed in wild bee species as well as in wasps, and flies (NANETTI & al. 2021, CILIA & al. 2022). A single survey conducted in France confirmed the presence of CBPV in two ant species (*Camponotus vagus* and *Formica rufa*) collected from three apiaries (CELLE & al. 2008). Replication of CBPV was detected in both workers and pupae of *C. vagus*. The CBPV load varied among individuals, ranging from 2.3×10^3 to 1.8×10^7 copies in *F. rufa* workers, from 1.1×10^8 to 1.3×10^{11} copies in *C. vagus* workers, and reaching 1.3×10^6 CBPV copies in *C. vagus* pupae. In addition, sequence analysis revealed a close to 100% homology between sequences obtained from honey bees, ants, and mite *Varroa destructor* (CELLE & al. 2008). CBPV spreads among honey bees through contact within the colony or contact with infected faeces (BAILEY & al. 1983, RIBIÈRE & al. 2007),

suggesting that ants may act as vectors, contributing to the circulation of the pathogen within the hive and the environment. However, further investigations are needed to define the specific role of ants in the spread of infection.

Lake Sinai viruses (LSVs): LSVs are classified within the *Sinivirus* genus group of viruses and are most closely related to CBPV (RUNCKEL & al. 2011). Presently, the LSVs group comprises more than six lineages, namely LSV1, LSV2, LSV3, LSV4, LSV5, and LSV6 (DAUGHENBAUGH & al. 2015). While the pathogenicity of LSVs is not fully understood, some cases of CCD have been linked to higher LSVs load in colonies (CORNMAN & al. 2012). Specifically, it has been observed that an increased abundance of LSV2 is associated with weaker or deceased colonies (DAUGHENBAUGH & al. 2015, FAUROT-DANIELS & al. 2020). This virus group has been detected exclusively in the Mediterranean area, in particular in the ant species *Messor barbarus*, *Messor capitatus*, and *Messor concolor* from France, Spain, Morocco, and Greece (BIGOT & al. 2017). In addition, an individual of *M. concolor* sampled in Greece was found to be co-infected with two variants of LSV: LSV1 and LSV2 (BIGOT & al. 2017).

Sacbrood virus (SBV): SBV is a widespread and common virus in honey bees, belonging to the *Iflavirus* genus in the Dicistroviridae family (BAILEY & al. 1964, CHEN & SIEDE 2007, NIELSEN & al. 2008). This pathogen can infect both larvae and adults. Signs of the disease become apparent when the larva undergoes a colour change, turning pale yellow, leading to larva death and assuming a brown sac-like appearance (GRABENSTEINER & al. 2001, CHEN & SIEDE 2007). SBV also infects different hosts, including wild bees, wasps, flies, roaches, earwigs, butterflies, moths, and even spiders (NANETTI & al. 2021, CILIA & al. 2022). Only two studies have investigated the presence of this pathogen in ants, both conducted in the USA (LEVITT & al. 2013, PAYNE & al. 2020). However, SBV was found only in *Solenopsis* spp. workers and its replicative form has not been detected (PAYNE & al. 2020).

Moku virus: Moku virus is a recently discovered virus, classified within the *Iflavirus* genus. The virus was first described in *Vespula pensylvanica* in Hawaii, and it has also been detected in honey bees and *Varroa destructor* mites sampled in the same locality (MORDECAI & al. 2016). Despite the unknown and unclear symptoms and effects on honey bee and wasp populations, the presence of the Moku virus in other hymenopterans and spider species is increasing (BRETTELL & al. 2019, DOBELMANN & al. 2020). In New Zealand, *Linepithema humile* workers sampled near apiaries were found to be infected with the Moku virus, and its replicative form was also detected (DOBELMANN & al. 2020).

Microsporidia and trypanosomatids

Honey bees can be affected by other pathogens and parasites, that is, fungi, including microsporidia, and trypanosomatids (GENERSCH & al. 2010, EVANS & SCHWARZ 2011, STROBL & al. 2019). *Nosema* spp. (microsporidia fungi) are obligate unicellular parasites that can affect

honey bee gastrointestinal epithelial cells, leading to a disease called nosemosis (APPLEGATE & PETRITZ 2020, MARÍN-GARCÍA & al. 2022). Symptoms can range from dysentery in *Nosema apis* infection to alterations in honey bee physiology and behaviour in *Nosema ceranae* infection (GÓMEZ-MORACHO & al. 2021, CILIA & al. 2022, MARÍN-GARCÍA & al. 2022). *Nosema ceranae* has been detected in several hymenopteran species and other pests' hives (i.e. *Aethina tumida* and *Vespa velutina*; CILIA & al. 2018, NANETTI & al. 2021). Trypanosomatids, a family of unicellular protozoan flagellate parasites, can colonize the gut of honey bees in *Crithidia mellificae* infection or the hindgut of *Bombus* spp. in *Crithidia bombi* infection (STROBL & al. 2019, DAVIS & al. 2021, BARTOLOMÉ & al. 2022). They are found in a wide variety of wild solitary and social bees (NANETTI & al. 2021). Infected bees exhibit symptoms affecting both behaviour and lifespan (STROBL & al. 2019, DAVIS & al. 2021, BARTOLOMÉ & al. 2022). Microsporidia *Nosema* spp. and trypanosomatids have also been observed in other insects, including, wasps, flies and the coleopteran *Aethina tumida* (NANETTI & al. 2021, CILIA & al. 2022).

Both *Nosema* spp. and *Crithidia* spp. were investigated in honey bees, wild bees, and ants during a six-month monitoring period in the USA (ALLEN & RANKIN 2022). Two ant species were sampled (*Forelius mccooki*, *Solenopsis xyloni*), and both tested positive for *Nosema* spp. and *Crithidia* spp. Additionally, ants exhibited a peak in the prevalence of *Nosema* spp. and *Crithidia* spp. in the late summer (ALLEN & RANKIN 2022). The prevalence of pathogens among honey bees, native bees, and ants showed an interaction between sampling location and period, suggesting potential interspecific transmission of pathogens through species interactions (ALLEN & RANKIN 2022).

Co-infections: The simultaneous presence of multiple pathogens infecting a host can occur in nature, and its role can be decisive in the epidemiology of each pathogen (ALIZON & al. 2013). However, the interactions between pathogens within the same host are not yet well understood (TELFER & al. 2010, ARMITAGE & al. 2022). In honey bees, multiple infections may reduce the virulence of the pathogen (COSTA & al. 2011, DOUBLET & al. 2015, MORDECAI & al. 2016, TRITSCHLER & al. 2017). However, in other cases, the interaction between pathogens may have a synergistic effect, leading to an increase in virulence and negative effects (CHEN & al. 2004, DOUBLET & al. 2015, CHAGAS & al. 2021, GAJDA & al. 2021, BORDIN & al. 2022, CILIA & al. 2022). The simultaneous presence of two or more honey bee pathogens has also been found in ants, demonstrating that co-infections can occur in these organisms as well (BIGOT & al. 2017, DOBELMANN & al. 2020, PAYNE & al. 2020, ALLEN & RANKIN 2022). In addition, in one study, the presence of one or more pathogens was detected in 89% of different ant species sampled within apiaries, whereas only in 15% of ants sampled in sites without hives (PAYNE & al. 2020). Further studies are needed to understand the role of bee-ant interactions and the effects of multiple infections in these hosts.

Conclusion

Recent interest in the interspecific transmission of honey bee pathogens has led to the detection of an increasing number of new hosts (LEVITT & al. 2013, BURNHAM & al. 2021, DALMON & al. 2021, NANETTI & al. 2021, CILIA & al. 2022). Ants have also been found to harbour several honey bee viruses as well as *Nosema* spp. and trypanosomatids. The infection could be facilitated by interactions between honey bees and ants within apiaries as well as through shared flowers, other plant parts, other insects, and environmental elements. However, further studies are needed to confirm these potential routes of transmission. Many studies have focused on invasive species and their role in spreading diseases, exploring the possibility of using pathogens as a biocontrol method for invasive species (MAZZEI & al. 2018, LESTER & al. 2019, MAZZEI & al. 2019, FELDEN & al. 2022). The possible involvement of ants in vectoring pathogens raises additional concerns for the health of bees as well as other hymenopterans and insects, including the possibility of spillback events to honey bees.

Numerous questions persist regarding whether these pathogens impact ant populations in field conditions, their potential transmission between different ant species, the adaptation, and the consequent effect of viruses on new hosts. Future research should investigate the replicability of pathogens in ants to elucidate their potential role as primary hosts in infections, their role as disease vectors for other insects, and the potential symptoms exhibited by ants. Understanding the impacts and effects of novel EIDs' transmission is essential to safeguard the health of bees, ants, and other insects.

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