Systematic Review

Pathogens Spillover from Honey Bees to Other Arthropods

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Abstract: Honey bees, and pollinators in general, play a major role in the health of ecosystems. There is a consensus about the steady decrease in pollinator populations, which raises global ecological concern. Several drivers are implicated in this threat. Among them, honey bee pathogens are transmitted to other arthropods populations, including wild and managed pollinators. The western honey bee, *Apis mellifera*, is quasi-globally spread. This successful species acted as and, in some cases, became a maintenance host for pathogens. This systematic review collects and summarizes spillover cases having in common *Apis mellifera* as the maintenance host and some of its pathogens. The reports are grouped by final host species and condition, year, and geographic area of detection and the co-occurrence in the same host. A total of eighty-one articles in the time frame 1960–2021 were included. The reported spillover cases cover a wide range of hymenopteran host species, generally living in close contact with or sharing the same environmental resources as the honey bees. They also involve non-hymenopteran arthropods, like spiders and roaches, which are either likely or unlikely to live in close proximity to honey bees. Specific studies should consider host-dependent pathogen modifications and effects on involved host species. Both the plasticity of bee pathogens and the ecological consequences of spillover suggest a holistic approach to bee health and the implementation of a One Health approach.

Keywords: spillover; inter-species transmission; honey bee diseases; pathogens; virus; bacteria; microsporidia; *Nosema*; trypanosomatids; wild bees; arthropods; Hymenoptera

1. Introduction

Interspecific transmission may occur from a definite maintenance host (aka “reservoir”) to an incidental or non-maintenance species (aka “spillover host”). Spillover cases are crucial to pathogen dynamics [1,2].

In a single-host scenario, reservoirs are sufficient and pathogen replication does not need other host species [3]. The basic reproduction number (R0) defines the frequency of new cases originating from each primary event, where R0 = 1 is the threshold between declining infections (R0 < 1) and pathogen persistence within the population by intraspecific transmission (R0 > 1) [4]. When multiple host species are involved, the presence of new maintenance or incidental hosts may result in an increased pathogen transmission [1]. In this case, R0 >> 0 denotes multi-host pathogen scenarios that may be respectively true or apparent, depending on the high or low interspecies transmission. When the R0 is between 0 and 1, the event is called “apparent multi-host pathogen”, while “true multi-host pathogen” indicates an event in which there are two different maintenance hosts and the occurrence of interspecies transmission is higher than 1 [5].

Strictly speaking, spillover only occurs when the recipient species is characterized by R0 ≈ 0 [5]. However, in this review, we follow the use of the term *sensu lato*, commonly indicating a multifaceted range of host shift events [2].

Pollinators are crucial to the generation of crops contributing to the human diet [6]. These agroecosystem service is provided by a range of different species, including honey
bees, wild bees, wasps, hoverflies, and butterflies [7–10]. However, different factors contribute to a decline of pollinating entomofauna, in terms of population size, biodiversity, abundance and distribution [11–19].

Pathogens and parasites are deemed drivers of this decline, together with other factors including pesticides and global warming. Nonetheless, the global picture is certainly far from complete, since data may misrepresent the actual distribution and gaps remain in our understanding of both epidemiological features and invasion dynamics of many pathogens [12,20–25]. Apis mellifera is known to share pathogens with bumblebee species, including viruses, bacteria, fungi and protozoa [26–34]. After acting as incidental hosts, western honey bees may become the primary maintenance host, as occurred in the cases of Nosema ceranae, Crithidia bombi, and Apicystis bombi [35]. Pathogens may also genetically adapt to a range of new species [12,13,23,30,36], acting as incidental or maintenance hosts [37–39].

Interspecific transmission to arthropods sharing the same environment as honey bees may occur orofecally, via direct contact and by pollen contamination [38]. Besides, infected foragers may contaminate pollen, nectar and floral organs with pathogens [40–44]. Spillover could also involve species not expected to come into direct contact with the bees. Wasps predate infected bees [45–48] and cannibalizing their carcasses [49–51] are likely to become contaminated with pathogens.

Honey bees and other insects have natural immune defense systems against bacteria, protozoa, mites, and viruses. They include antimicrobial peptides like apidaecin, defensin, abaecin, hymenoptaecin, and lysozyme, which are regulated by the immune pathways Toll, IMD, JAK/STAT and JNK [52]. Those defenses are challenged by insecticides and other pesticides used in modern agriculture [53].

Spillover events are difficult to prove. Indeed, viral infection and replication in new hosts, which may not develop under artificial conditions, can occur in nature [36,54,55]. The increasing number of reports about honey bee pathogens found in new hosts contributes to depict a scenario including one reservoir species and multiple spillover events. Indeed, population studies might elucidate those aspects [56] which, in the specific case of wild bees, are complicated by the peculiar characteristics of those species [17,57,58]. This makes spillover routes generally unknown and undetermined [59], albeit each report deserves further research to illustrate thoroughly their respective epidemiological scenarios.

This systematic review is intended to collect, group, and summarize the spillover cases sensu lato reported by the literature and involving honey bee pathogens. Other arthropods were also considered as alternative hosts. The spillover cases are grouped by: (i) host species, condition and stage, (ii) geographical region and year of the report, and (iii) co-occurrence in the same host.

2. Results

In total, from 1960 to 2021, 81 studies investigated spillover cases of honey bee pathogens to wild and/or managed arthropods (Figure 1). Some of the studies considered more than one species. In detail, they considered the spillover to other bee species (Supplementary Table S1), other Hymenoptera (Supplementary Table S1) and other arthropods (Supplementary Table S2).
Figure 1. Cumulative number of spillover studies of honey bee pathogens available in the literature between 1960 and 2021 involving other bees (A), non-bee Hymenoptera (B), and other arthropods (C).
As shown in Figure 1A, the first article about spillover of honey bee pathogens to other bees was published in 1964, but the number of articles on this topic steadily increased from the year 2020, likely due to the quick development of molecular genetic tools for pathogen detection. Considering other hymenopteran species, the first detection of spillover cases dates back to 2008, with a rapid increase of cases in the following years (Figure 1B). The first spillover case to other arthropods was assessed in 2009, but later the frequency increased, covering a wide range of species (Figure 1C).

The geographical distribution of spillover studies present in the literature (Figure 2) shows a high number of studies in both North and South America, Europe and New Zealand, whereas the reports from other countries were less frequent.

Figures 3 and 4 summarize the spillover cases for each honey bee pathogen in relation to arthropods groups. In events encompassing at least 20 spillover cases, DWV was the most frequently detected (158 cases). BQCV, SBV, IAPV, ABPV, KBV, N. ceranae, SBPV and LSV resulted implicated with progressively decreasing frequency.

The chord graph (Figure 3) shows all spillover cases described in this review, evaluating the relationship to the investigated arthropod genus. Additionally, Figure 4 highlights the reported frequency of honey bee pathogens in the investigated arthropod communities, to emphasize their plasticity to the host.

Some individuals were found infected with multiple honey bee pathogens (Figure 5). The highest incidence of co-infections was found in bumblebees, followed by mason bees, mining bees and the honey bee pest Aethina tumida. A high number of co-infections was reported for Eucera nigrescens, Osmia bicornis and Osmia cornuta, for which 6 pathogens were found in the same individuals. Besides, the most abundant co-infecting pathogens able to co-infect the arthropods hosts were DWV, BQCV, SBV, ABPV and N. ceranae.
Figure 3. Visual schematization of honey bee pathogen spillover to alternative host arthropods reported in the literature. Different colors denote distinct pathogens or host genera. Legend: ABPV: Acute Bee Paralysis Virus; IAPV: Israeli Acute Paralysis Virus; BQCV: Black Queen Cell Virus; SBV: Sacbrood Virus; DWV: Deforming Wing Virus; LSV; Lake Sinai Virus; AmFV: Apis mellifera Filamentous Virus; KBV: Kashmir Bee Virus; SBPV: Slow Bee Paralysis Virus; CBPV: Chronic Bee Paralysis Virus; VdMLV: Varroa destructor Macula-like Virus.
Figure 4. Frequency of spillover events involving single honey bee pathogens and the range of arthropods found infected with them. Different colors denote distinct host groups. Legend: ABPV: Acute Bee Paralysis Virus; IAPV: Israeli Acute Paralysis Virus; BQCV: Black Queen Cell Virus; SBV: Sacbrood Virus; DWV: Deforming Wing Virus; LSV: Lake Sinai Virus; AmFV: Apis mellifera Filamentous Virus; KBV: Kashmir Bee Virus; SBPV: Slow Bee Paralysis Virus; CBPV: Chronic Bee Paralysis Virus; VdMLV: Varroa destructor Macula-like Virus.
Figure 5. Co-occurrence of honey bee pathogens in individual hosts. These are grouped as bees, beetles, and wasps. Box size is indicative of the frequency. Legend: ABPV: Acute Bee Paralysis Virus; IAPV: Israeli Acute Paralysis Virus; BQCV: Black Queen Cell Virus; SBV: Sacbrood Virus; DWV: Deforming Wing Virus; LSV: Lake Sinai Virus; AmFV: Apis mellifera Filamentous Virus; KBV: Kashmir Bee Virus; SBPV: Slow Bee Paralysis Virus; CBPV: Chronic Bee Paralysis Virus; VdMLV: Varroa destructor Macula-like Virus.
3. Discussion

The results of this systematic review highlights that the case history of spillover events involving honey bee pathogens increased over the past six decades. This is consistent with the growing interest of the scientific community in understanding the underlying factors [12,20,22,54]. The higher incidence of spillover cases recorded in Europe, New Zealand, and the Americas may reflect their advances in research and apiculture compared to other regions [60–67].

Viruses vectored by *V. destructor* (DWV, KBV, and IAPV) and quasi-ubiquitous pathogens (BQCV, SBV and *N. ceranae*) were among the most frequently reported cases.

Bumblebees, mason bees and leafcutter bees were the species in which the spillover was studied more intensely, possibly because of their use in crops and fruit pollination. The fact that some of the surveys were carried out on arthropods ranging freely in the same environment as the managed honey bees is indicative of a pathogen circulation in their common environment. Despite honey bee pathogens were detected in other arthropods, symptoms and other effects on the alternative host populations remain unknown—except for some publications reporting individual bumblebees with crippled wings and scoring positive to DWV [68,69].

The importance of investigating the spillover of honey bee pathogens is also indicated by the discovery of active coinfections in wild hymenopteran individuals. As for the honey bees [30,70,71], multiple infections were found in wild bees, wasps and *Aethina tumida* individuals, which shows the importance of other arthropods as incidental hosts. The multiple infections that were identified (Figure 5 and Supplementary Table S1) have both the effect to increase the circulation of pathogens within the arthropod communities, and to recirculate them to the managed honey bee colonies, so generating damage at individual and colony levels.

All of these aspects, including their modifications and effects encompass the implementation of a One Health approach to bee health [72,73]. The health of managed honey bees is dependent on the health of wild bees and other arthropods, and vice versa. This approach is essential to provide suitable ecosystems to pollinators and other arthropods contributing to human livelihoods and environmental health, and for understanding the eco-immunology to prevent the transmission of pathogens and pests, thereby limiting damages in managed and wild insect populations [73–75]. Therefore, the circulation/recirculation and the possible impact of honey bee pathogens to the arthropod communities are crucial to build the basis for the One Health approach to the bee health. Here we provide a brief discussion of each of the honey bee pathogens reported in Supplementary Tables S1 and S2, in relation to their spillover hosts.

3.1. Viruses

3.1.1. Deformed Wing Virus (DWV)

DWV is a non-enveloped ssRNA (+) virus belonging to *Iflavirus* genus within the *Picornaviridae* family [76]. The DWV is a pathogen including three distinct genomotypes: A, B and C [77,78].

The DWV is probably the most known, spread, prevalent, and studied honey bee pathogen, often associated to *V. destructor* [79]. The DWV can be asymptomatically replicated in *V. destructor* mites [80].

The impact of DWV on honey bees leads to increased interspecific transmission, reaching several species of hymenopterans and other arthropods (Supplementary Tables S1 and S2). The virus was identified not only in species living in close contact with the honey bees, like *A. tumida*, *G. mellonella*, *Vespa* spp. [39,45,47,81,82], but also in *Apis* and non-*Apis* species that may act as incidental hosts [38,39]. DWV was found in naturally and artificially infected asymptomatic arthropods [38,39,54,59,79], although some commercial and wild *B. terrestris* and *B. pascuorum* individuals were found with crippled wings [68,69]. Besides, artificial infection experiments highlighted that DWV reduced the individual lifespan in some *Bombus* species [40,83–85] or generate reinfection in the honey bees [38,39,81,82,86].
3.1.2. Kashmir Bee Virus (KBV)

KBV is a non-enveloped ssRNA (+) virus belonging to the Cripavirus genus within the Dicistroviridae family [28,81,87]. The genome of KBV is strictly related to ABPV (Acute Bee Paralysis Virus) and IAPV (Israeli Acute Paralysis Virus) [88–90].

Although the virus is considered endemic in America and New Zealand, it has been rarely reported in other regions, both in honey bees and other arthropods (Supplementary Tables S1 and S2).

KBV was found in various Hymenoptera species, like Bombus spp. [38,91–93], Eucera spp., Anthophora spp., Osmia spp. [38], wasps, hornets [46,91,94,95], and ants [49,91]. It was also detected in A. tumida [39,81], Galleria melonella, earwigs, roaches and crickets [39,91].

3.1.3. Acute Bee Paralysis Virus (ABPV)

ABPV is a non-enveloped virus and widespread ssRNA (+) virus belonging to Apavirus genus within the Dicistroviridae family [28,96]. As reported above, ABPV is genetically linked to KBV and IAPV [88]. ABPV was detected in V. destructor, where is is reported incapable to replicate [97,98]. ABPV spillover is not recent (Figure 1 and Supplementary Table S1) as in 1964 various Bombus species were found infected in the United Kingdom [99].

The list of bees in which ABPV was found increases constantly, including many Bombus species as well as a wide range of other bee species [54,100,101]. In non-bee Hymenoptera, ABPV was detected in Ancistrocerus auctus, Polistes spp., V. germanica, Scolia flavifrons and Linepithema humile [49,54,94].

3.1.4. Israeli Acute Paralysis Virus (IAPV)

Israeli acute paralysis virus (IAPV) is a non-enveloped ssRNA (+) virus belonging to Apavirus genus within the Dicistroviridae family [28,96]. The virus has been isolated in Israel, but there are several known strains [102]. In honey bees, it induces disorientation, shivering wings, crawling, progressive paralysis and death within or outside the nest [104].

The IAPV is widespread [102] and spillover cases were studied in a wide range of non-Apis bee species (Supplementary Table S1). Furthermore, the virus was found in the wasps, V. germanica and V. vulgaris [38,94] and in the ants, Camponatus spp. and L. humile [39,49]. Outside Hymenoptera, earwigs, spiders, moths, small hive beetles [39], and V. velutina [48] showed to act as IAPV incidental hosts.

3.1.5. Slow Bee Paralysis Virus (SBPV)

Slow bee paralysis virus (SBPV) is an icosahedral non-enveloped ssRNA(+) virus from the Iflaviridae family [105,106]. The infection is responsible for paralysis of the first and second pairs of legs in roughly 12-day old honey bees and their sudden death [107,108].

Recently, it was found in wild Bombus spp., E. nigriscens and O. bicornis in Kyrgyzstan, Germany and Georgia [109], in the United Kingdom [110,111] and Belgium [112]. Furthermore, E. nigriscens and O. bicornis species in Kyrgyzstan, Germany and Georgia scored positive for SBPV infection [109] (Supplementary Table S1). No further spillover events have been reported so far in other arthropods.

3.1.6. Chronic Bee Paralysis Virus (CBPV)

Chronic bee paralysis virus (CBPV) is an unclassified enveloped ssRNA (+) virus characterized by articulate genome and association to a satellite virus (CBPSV) [113,114]. The infection causes a multifaceted disease encompassing different combinations of symptoms evidencing neurotropism like ataxia, incapability to fly, and trembling, as well as hairlessness and dark colour in the infected bees [114,115].

CBPV is capable to infect other insects. Spillover was reported in the wild in individuals of B. dalhombii [92], B. impatiens and B. ruderatus [116], B. pauloensis [117], B. terrestris [92,116],
X. augusti and X. nigrocinta [117], X. dissimilis [109], H. amplilobus [117] and H. parallelum [109]. Replicative CBPV was found in two ant species, C. vagus and F. rufa also [118].

3.1.7. Sacbrood Virus (SBV)

SBV is a non-enveloped ssRNA (+) virus belonging to Iflaviridae genus and Dicistroviridae family [27,28,119]. It is very common in honey bees, that exhibit symptoms in pre-imaginal stages coming into contact with the virus during the brood tending [27]. The virus is spread worldwide and genetic variants were identified in Korea (K-SBV), China (C-SBV), Thailand (T-SBV), Europe (E-SBV) and New Guinea (G-SBV) [120–124]. SBV was detected in a wide range of non-\textit{Apis} bees (Supplementary Table S1) and other hymenopteran species (Supplementary Table S2) [38,39,54,110,116,125–128]. CBPV was detected in hoverflies, small hive beetles, spiders and lepidopterans also [39,82,129,130].

3.1.8. Black Queen Cell Virus (BQCV)

BQCV belongs to the Cripavirus genus within Dicistroviridae family. As the other Dicistroviridae, BQCV is non-enveloped and ssRNA (+) virus [22,131,132]. Despite a high prevalence in adult honey bees [28,97,133–135], symptomatic infections occur in queen pupae and/or pre-pupae, that decompose in irregular, black cells [133,136]. BQCV is spread worldwide and affects several honey bee species and subspecies, like \textit{A. mellifera}, \textit{A. cerana indica}, \textit{A. cerana japonica}, \textit{A. dorsata} and \textit{A. florea} [137]. The range of possible hosts is very wide and includes several wild hymenopteran species [37–39,46,54,109,110,125,136,139]. Small hive beetles, hoverflies, roaches, spiders and wax moths scored positive to BQCV also [39,129,130].

3.1.9. Lake Sinai Virus (LSV)

LSV is an ssRNA(+) belonging to the Sinhaliviridae family and \textit{Sinaivirus} genus, of which two strains have been identified so far: LSV-1 and LSV-2 [140]. The virus was discovered in honey bees sampled during a colony transhumance near the Lake Sinai, South Dakota, USA. LSV was reported as involved in the colony collapse disorder, despite both pathogenicity and epidemiology have not been clarified yet [70,141]. Cases of LSV spillover have been reported in \textit{Andrena} spp. [37,127], \textit{Bombus} spp., [85,112,127], and species belonging to the families of \textit{Halictidae} and \textit{Megachilidae} [127]. LSV has never been detected outside the Apoidea superfamily so far.

3.1.10. \textit{Apis mellifera} Filamentous Virus (\textit{Am}FV)

\textit{Am}FV is an unclassified dsDNA isolated from honey bees, whose relationship with the host and epidemiology are poorly studied. Originally, the pathogen was described as a rickettsia disease, but recently it has been recognized as a virus [142,143]. Severe infections of adult honey bees are associated to milk white hemolymph as a consequence of the high virion concentration. The infected bees show signs of weakness and tend to gather at the hive entrance. Nevertheless, the virus is weakly pathogenic and has low impact on bee lifespan [143–146]. Few spillover cases have been reported so far. They involved as alternative hosts \textit{Andrena} spp. [37], \textit{Bombus} spp. [147], \textit{Osmia} spp. [37] and in \textit{A. tumida} [148] (Supplementary Table S1).

3.1.11. \textit{Varroa destructor} Macula-like Virus (\textit{Vd}MLV)

\textit{Vd}MLV is an unclassified ssRNA (+) virus of the Tymoviridae family. The mite \textit{V. destructor} is its primary host and the virus was found in the honey bees as a likely result of the trophic activity of the parasite [149]. Little knowledge is available for this virus. Few spillover cases have been reported so far about \textit{Vd}MLV (Supplementary Table S1), all of them in the wild. Those involved \textit{B. lapidarius}, \textit{B. pascuorum} and \textit{B. pratorum} as host species [112].
3.1.12. Moku Virus

Moku virus is an unclassified ssRNA (+) *Iflaviridae*. The virus was first discovered in *Vespula pensylvanica* in Hawaii, but it spread in honey bees too, often associated to *V. destructor* [150]. Since its discovery, Moku virus findings increased rapidly until the detection in a wide range of Hymenoptera species (Supplementary Table S1), that includes *Polistes* spp. [91], *Vespa* spp. [91,95,130,150], *V. velutina* [151] and *L. humile* [91]. Besides, Moku virus was found capable to infect the spiders *H. minitabunda* and *S. capensis* [91] (Supplementary Table S2).

3.2. Fungi

3.2.1. *Nosema ceranae*

*Nosema ceranae* is a microsporidium that causes nosemosis type C in western honey bees [152,153]. It is an intracellular obligate parasite, infecting the ventricular epithelial cells [154,155]. The effects of *N. ceranae* infections can be recognized both at individual and colony levels, impacting the bee lifespan, inducing lethargic behaviour, reducing the pollen and honey harvest, and causing colony dwindling [156–159].

The main known spillover event occurred when the pathogen jumped from the Asian honey bee *A. ceranae*, which is deemed as the original host, to the western honey bee *A. mellifera* [152,153].

In addition to *A. cerana* and *A. mellifera*, the microsporidium was reported in several other Hymenoptera (Supplementary Table S1), including *A. ventralis*, *H. truncorum* and *Osmia* spp. [37], commercial and wild Bombus species [36,37,83,125,147,160–162], stingless bees, and *Polybua* spp. [163]. Besides, it was detected in the small hive beetle as well as in *A. tumida* [148,164]. Finally, the microsporidium was found in the regurgitated pellets of the European bee-eater *Merops apiaster* [165].

3.2.2. *Nosema apis*

*Nosema apis* is the classic microsporidium infecting *A. mellifera*, which is responsible for the nosemosis Type A [166]. Like the other microsporidians, it is an intracellular obligate parasite. It causes, in contrast to *N. ceranae*, severe dysentery that impacts mainly the colony foragers [166–168]. Presently, its spread is limited to specific ecological niches as a possible consequence of the competition with the predominant *N. ceranae* [71,157]. *N. apis* was detected in commercial *B. terrestris* colonies [20], but the transmission route remained unclarified.

3.2.3. *Ascosphaera apis*

The fungus *Ascosphaera apis* is a honey bee pathogen responsible for the mycosis called chalkbrood disease [169,170]. The infection occurs by spore ingestion in bee larvae, especially in those of the fifth instar, that reduces food consumption and prevents eating [169,170]. The proliferating mycelium invades the larval body, which is transformed into a chalk-like “mummy”, so the disease name [169,171,172].

Despite the disease is typical to the honey bees, artificial infections showed the pathogen capability to colonize the intestine of *B. terrestris* adults and larvae [20].

3.3. Bacteria

3.3.1. *Melissococcus plutonius*

The bacterium *M. plutonius* is the Gram-negative coccus representing the etiological agent of the European foulbrood disease [173,174].

The pathogen is spread worldwide and infects the brood, which dies by under-nutrition [175,176]. The infected larvae become flaccid and yellowish by 5 days after infection [173,175,176].

In the United Kingdom, *M. plutonius* was found to impair the development of *B. terrestris* colonies [20].
3.3.2. Spiroplasma apis

*Spiroplasma apis* is a small, helical and motile Gram-positive *Eubacterium* deprived of a cell wall \([177,178]\). The bacterium was isolated in France from colonies showing symptoms of “May disease” \([179]\). *S. apis* is lethal to the honey bees when ingested, and the infection may spread by faecal contamination \([179]\).

Strains of *S. apis* were isolated and detected in wild specimens belonging to *B. atratus* \([125]\) and *O. bicornis* \([37]\), with unknown effects.

3.3.3. Spiroplasma melliferum

*Spiroplasma melliferum* is another *Eubacterium* isolated from the honey bees \([180]\). The *S. melliferum* infection has similar symptoms and transmission route as *S. apis*, although less virulent \([179,180]\). As for *S. apis*, *S. melliferum* spillover was observed occasionally (Supplementary Table S1). This is the case of *O. bicornis* individuals, that were found infected in Belgium \([37]\).

3.3.4. Wolbachia spp.

*Wolbachia* spp. are Gram-negative intracellular bacterial symbionts, which can infect the cells of both female honey bees and drones \([181,182]\). *Wolbachia* spp. impacts the host reproduction. The vertical transmission via the eggs represents the main transmission route to persist in honey bee populations \([183,184]\).

During a national survey in the U.S.A. (Supplementary Tables S1 and S2), several arthropods scored positive to *Wolbachia* spp.: *Andrena* spp., several *Bombus* species, *Lasiglossum* spp., *Halictus* spp., *D. sylvestris*, *V. germanica* and *V. vulgaris*, and two hoverflies \([128]\).

3.4. Trypanosomatidae

3.4.1. Lotmaria passim

*Lotmaria passim* is a trypanosomatid with a single flagellum, capable to colonize the digestive tract of *A. mellifera* \([185,186]\). The parasite spreads within the colony by fecal contact, and the transmission occur via the oro-faecal route \([187,188]\). The infection impacts the colony by altering behaviour and lifespan of the infected bees \([141,189]\). *L. passim* is spread worldwide. The colonization implied the replacing of the other honey bee trypanosomatids *Crithidia mellificae* \([190,191]\).

Besides, *L. passim* is present in bumblebee species (Supplementary Table S1) namely the South American *B. funebris*, *B. dalhobii*, *B. opifex*, *B. ruderatus* and *B. terrestris* \([92,147]\).

*L. passim* was found also in the small hive beetle, *A. tumida*, as a possible result of the feeding behaviour of this scavenger \([81,148]\).

3.4.2. Crithidia mellificae

*Crithidia mellificae* is another trypanosomatid which can replicate in the honey bee intestine to survive \([185,186]\). Transmission route and impact on bees are very similar to the other parasite *L. passim* \([187,188,192]\). *C. mellificae* was almost completely replaced by *L. passim* and its infection has been rarely observed \([185,193,194]\). Despite that, one spillover case was observed in *A. tumida*, that live in contact with bee colony debris \([81]\).

3.4.3. Crithidia bombi

*Crithidia bombi* is a trypanosomatid infecting *B. terrestris* colonies \([195,196]\). The infection occurs during the external activity of the forager bumblebees \([197,198]\) and, back to the nest, it spreads by fecal contamination to the other workers \([199,200]\). *C. bombi* may harm the bumblebee populations as hibernating queens may reduce the success in founding the colonies and remarkably lower their fitness \([201]\). On queen emergence from the diapause, *C. bombi* infections grow together with the colony that is being established \([200]\).

*C. bombi* is transmitted during the foraging activity. The pathogen was detected in the wild on *A. vaga* and *O. bicornis* individuals \([37]\) and in small hive beetles collected from the
nest of honey bee colonies [148]. Artificial infections showed that C. bombi can replicate in O. lignaria, M. rotundata and H. ligatus [202,203].

3.5. Neogregarine

Apicystis bombi

Apicystis bombi is a parasite found primarily in bumblebees. It was found to occur also in honey bees from Europe and North America [204–206]. Upon the ingestion of the oocytes by the bee, the sporozoites develop and migrate to the fat body, where they develop, multiply and disrupt the adipose tissue. The infection increases the worker mortality rate and, due to the fat body disruption, both queen survival to hibernation and colony foundation success are impaired [84,207,208]. Likely, the infection occurs via contact on contaminated flowers [208]. Indeed, A. bombi was found in wild species also, namely A. vaga, A. ventralis, H. truncorum, O. bicornis and O. cornuta [37].

4. Materials 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 [209]. The research question to be reviewed was: “Which honey bee pathogens may generate spillover to managed and wild Hymenoptera species and, more in general, to the arthropofauna?” The search intentionally excluded arthropods living in close contact with the honey bees that, like V. destructor, are obligate parasites.

The article search was carried out in PubMed, Web of Science, Science Direct, Google Scholar, and Scopus scientific databases for studies aimed to assess the detection of spillover cases of honey bee pathogens. Filters were used to select articles published from January 1960 to April 2021. The last search date was 31 May 2021.

The following search strategy was designed and utilized: “Honey Bee Pathogens” OR “Bumblebee Pathogens” OR “Spillover” OR “Spill-over” OR “Inter species transmission” OR “Inter taxa transmission” OR “Host species transmission” OR “Apis mellifera” OR “Honey Bee Diseases” OR “Honey Bee Virus” OR “Honey Bee Bacteria” OR “Honey Bee Microsporidia” OR “Honey Bee Protozoa” OR “Managed Bees” OR “Wild Bees” OR “Commercial Bees” OR “Artificial Infection” OR “Replicative Virus” OR “Bumblebees” 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 “Ascosphaera” OR “Apicystis” OR “Arthropods” OR “Entomofauna” OR “Hive Hosts” OR “Hive” OR “Free-Ranging Insect” OR “Bee Interaction” OR “Varroa destructor”. The logical operator “OR” was used to combine the descriptors.

Studies carried out both in field and laboratory conditions were selected. Besides, studies that did not assess whether the presence of the honey bee pathogens could be related to external contamination were not included. The detected active replication of honey bee viruses was also reported in the Supplementary Materials with an asterisk.

Duplicate studies were excluded. The search and screening for titles, abstracts and results were carried out independently by the authors, including all articles, letters, notes, scientific notes and communications aimed to assess a spillover case of honey bee pathogens and excluding reviews, books, book chapters and theses.

The potentially eligible research articles were read and reviewed independently by the authors and the data were compared to ensure integrity and reliability.

For each article included in this review, relevant information related to the authors, publication year, host species, host conditions, host stage, pathogens and prevalence were extracted. The data from the eligible studies are expressed in the Supplementary Materials.
and Figures. The authors provided a narrative synthesis of the results for each pathogen capable to generate a spillover case, according to the main characteristics and results related to the topic addressed.

5. Conclusions

This review shows that, in recent years, the frequency of recorded spillover cases of honey bee pathogens to other arthropods, including wild bees, has dramatically increased. Certainly, human movements and globalization have fostered the inflow of novel pathogenic microorganisms, often with detrimental consequences. However, it should also be considered that the analytical methods currently available give impulse to the research on bee pathology, increasing the chance to identify interspecific transmission events.

The host plasticity shown by some honey bee pathogens raises ecological concern for the potential negative consequences on the pollinating entomofauna and ecosystems in general. Despite the fact that research on these pathogens has significantly improved, we have limited knowledge of their potential impact on other bees, insects, and arthropods in general and the cascade of environmental effects. Laboratory studies are not sufficient to cover this gap, for the intricate interaction of the involved biotic and abiotic factors. For the same reasons, the exploitation of these pathogens in the control of arthropods considered as pests (e.g., A. tumida, G. melonella, V. velutina, L. humile) should be considered with extreme carefulness.

The tight interaction between honey bees and the other environmental components suggests a holistic approach to the study of bee diseases, including their control. Indeed, pathogens may survive in alternate hosts, generating spillback events and possibly jeopardizing the efficacy of the treatments. This emphasizes the beekeeper’s responsibility to maintain healthy colonies to benefit both their production and the environment.

Spillover of honey bee pathogens may have undetected yet important repercussions on the health and functioning of an ecosystem. Health management of honey bee colonies is of high importance in this context. Honey bees and the beekeeping industry should, therefore, undertake an essential role in the One Health concept. This requires the adoption of dedicated research actions.

Supplementary Materials: The following are available online at https://www.mdpi.com/article/10.3390/pathogens10081044/s1, Table S1: Bee pathogen spillover and prevalence identified in hymenopteran hosts, of which are reported condition, stage, geographical area and year, Table S2: Bee pathogen spillover and prevalence identified in arthropod hosts, of which are reported condition, stage, geographical area and year [210–232].

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31. Cilia, G.; Sagona, S.; Giusti, M.; Jarmela dos Santos, P.E.; Nanetti, A.; Felicioli, A. Nosema ceranae infection in honeybee samples from Tuscanian Archipelago (Central Italy) investigated by two qPCR methods. *Studia J. Biol. Sci.* 2019, 26, 1553–1556. [CrossRef]

32. Beaurepaire, A.; Piot, N.; Doublet, V.; Antunez, K.; Campbell, E.; Chantawannakul, P.; Cheyanovsky, N.; Gajda, A.; Heerman, M.; Panziera, D.; et al. Diversity and Global Distribution of Viruses of the Western Honey Bee, *Apis mellifera*. *Insects* 2020, 11, 239. [CrossRef]

33. Laomettachit, T.; Liangruksa, M.; Termsaithong, T.; Tangthanawatsakul, A.; Duangphakdee, O. A model of infection in honeybee colonies with social immunity. *PLoS ONE* 2021, 16, e0247294. [CrossRef]

34. Hinshaw, C.; Evans, K.C.; Rosa, C.; López-UrIBE, M.M. The Role of Pathogen Dynamics and Immune Gene Expression in the Survival of Feral Honey Bees. *Front. Ecol. Evol.* 2019, 8, 505. [CrossRef]

35. Evans, J.D.; Schwarz, R.S. Bees brought to their knees: Microbes affecting honey bee health. *Trends Microbiol.* 2011, 19, 614–620. [CrossRef]

36. Manley, R.; Temperton, B.; Doyle, T.; Gates, D.; Hedges, S.; Wilfert, L. Knock-on community impacts of a novel vector: Spillover of emerging DWV-B from *Varroa*-infested honeybees to wild bumblebees. *Ecol. Lett.* 2019, 22, el01323. [CrossRef]

37. Ravoet, J.; De Smet, L.; Meeus, I.; Smagglie, G.; Wenseleers, T.; de Graaf, D.C. Widespread occurrence of honey bee pathogens in solitary bees. *J. Invertebr. Pathol.* 2014, 122, 55–58. [CrossRef]

38. Singh, R.; Levitt, A.L.; Rajotte, E.G.; Holmes, E.C.; Ostiguy, N.; vanEngelsdorp, D.; Lipkin, W.I.; dePamphilis, C.W.; Toth, A.L.; Cox-Foster, D.L. RNA Viruses in Hymenopteran Pollinators: Evidence of Inter-Varroa Virus Transmission via Pollen and Potential Impact on Non-Apis Hymenopteran Species. *PLoS ONE* 2010, 5, e14357. [CrossRef]

39. Levitt, A.L.; Singh, R.; Cox-Foster, D.L.; Rajotte, E.; Hoover, K.; Ostiguy, N.; Holmes, E.C. Cross-species transmission of honey bee viruses in associated arthropods. *Viruses* 2013, 176, 232–240. [CrossRef]

40. Mazzei, M.; Carrozza, M.L.; Luisi, E.; Forzan, M.; Giusti, M.; Sagona, S.; Tolari, F.; Felicioli, A. Infectivity of DWV Associated to *Vespa* for Plant Species. *PLoS ONE* 2014, 9, e113448. [CrossRef]

41. Chen, Y.; Evans, J.; Feldlaufer, M. Horizontal and vertical transmission of viruses in the honey bee, *Apis mellifera*. *J. Invertebr. Pathol.* 2010, 96, 152–159. [CrossRef]

42. Graystock, P.; Goulson, D.; Hughes, W.O.H. Parasites in bloom: Flowers aid dispersal and transmission of pollinator parasites within and between bee species. *Proc. R. Soc. B Biol. Sci.* 2015, 282. [CrossRef][PubMed]

43. Schittny, D.; Yañez, O.; Neumann, P. Honey Bee Virus Transmission via Hive Products. *Vet. Sci.* 2020, 7, 96. [CrossRef]

44. Alger, S.A.; Burnham, P.A.; Brody, A.K. Flowers as viral hot spots: Honey bees (*Apis mellifera*) unevenly deposit viruses across plant species. *PLoS ONE* 2019, 14, e0221800. [CrossRef]

45. Forzan, M.; Sagona, S.; Mazzei, M.; Felicioli, A. Detection of deformed wing virus in *Vespa crabro*. *Bull. Insectology* 2017, 70, 261–265.

46. Mazzei, M.; Cilia, G.; Forzan, M.; Lavazza, A.; Mutinelli, F.; Felicioli, A. Detection of replicative Kashmir Bee Virus and Black Queen Cell Virus in Asian hornet *Vespa velutina* (Lepelvier 1836) in Italy. *Sci. Rep.* 2019, 9, 1–9. [CrossRef]

47. Mazzei, M.; Forzan, M.; Cilia, G.; Sagona, S.; Bortolotti, L.; Felicioli, A. First detection of replicative deformed wing virus (DWV) in *Vespa velutina* nigrithorax. *Bull. Insectology* 2018, 71, 211–216.

48. Yañez, O.; Zheng, H.-Q.; Hu, F.-L.; Neumann, P.; Dietemann, V. A scientific note on Israeli acute paralysis virus infection of Eastern honeybee *Apis cerana* and vespine predator *Vespa velutina*. *Apidologie* 2012, 43, 587–589. [CrossRef]

49. Gruber, M.A.M.; Cooling, M.; Baty, J.W.; Buckley, K.; Friedlander, A.; Quinn, O.; Russell, J.E.E.; Sébastien, A.; Lester, P.J. Single-stranded RNA viruses infecting the invasive Argentine ant, *Linepithema humile*. *Sci. Rep.* 2017, 7, 1–10. [CrossRef][PubMed]

50. Sébastien, A.; Lester, P.J.; Hall, R.J.; Wang, J.; Moore, N.E.; Gruber, M.A.M. Invasive ants carry novel viruses in their new range and form reservoirs for a honeybee pathogen. *Biol. Lett.* 2015, 11, 20150610. [CrossRef]

51. Cooling, M.; Gruber, M.A.M.; Hoffmann, B.D.; Sébastien, A.; Lester, P.J. A metatranscriptomic survey of the invasive yellow crazy ant, *Anoplolepis gracilipes*, identifies several potential viral and bacterial pathogens and mutualists. *Insectes Soc.* 2017, 64, 197–207. [CrossRef]

52. Ilyasov, R.A.; Gaifullina, L.R.; Saltkova, E.S.; Poskryakov, A.V.; Nikolenko, A.G. Review of the expression of antimicrobial peptide defensin in honey bees *Apis mellifera* L. *Apic. Sci.* 2012, 56, 115–124. [CrossRef]

53. Collison, E.J.; Hird, H.; Tyler, C.R.; Cresswell, J.E. Effects of neonicotinoid exposure on molecular and physiological indicators of honey bee immunocompetence. *Apidologie* 2018, 49, 196–208. [CrossRef]

54. Dallon, A.; Diévat, V.; Thomasson, M.; Fouque, R.; Vaissière, B.E.; Guibaud, L.; Le Conte, Y.; Henry, M. Possible Spillover of Pathogens between Bee Communities Foraging on the Same Floral Resource. *Insects* 2021, 12, 122. [CrossRef]

55. Gusachenko, O.N.; Woodford, L.; Balbirnie-Cumming, K.; Ryabov, E.V.; Evans, D.J. Evidence for and against deformed wing virus spillover from honey bees to bumble bees: A reverse genetic analysis. *Sci. Rep.* 2020, 10, 16847. [CrossRef]

56. Benjamin-Chung, J.; Arnold, B.F.; Berger, D.; Luby, S.P.; Miguel, E.; Colford, J.M.; Hubbard, A.E. Spillover effects in epidemiology: Parameters, study designs and methodological considerations. *Int. J. Epidemiol.* 2018, 47, 332–347. [CrossRef]

57. Drossart, M.; Gérard, M. Beyond the decline of wild bees: Optimizing conservation measures and bringing together the actors. *Insects* 2020, 11, 649. [CrossRef]

58. Prendergast, K.S.; Menz, M.H.M.; Dixon, K.W.; Bateman, P.W. The relative performance of sampling methods for native bees: An empirical test and review of the literature. *Ecosphere* 2020, 11, e03076. [CrossRef]
90. Evans, J.D. Genetic Evidence for Coinfection of Honey Bees by Acute Bee Paralysis and Kashmir Bee Viruses. J. Invertebr. Pathol. 2001, 78, 189–193. [CrossRef]
91. Dobelmann, J.; Felden, A.; Lester, P.J. Genetic strain diversity of multi-host RNA viruses that infect a wide range of pollinators and associates is shaped by geographic origins. Viruses 2020, 12, 358. [CrossRef]
92. Arismendi, N.; Riveros, G.; Zapata, N.; Smagghe, G.; Gonzalez, C.; Vargas, M. Occurrence of bee viruses and pathogens associated with emerging infectious diseases in native and non-native bumble bees in southern Chile. Biol. Invasions 2021, 1–15. [CrossRef]
93. Sachman-Ruiz, B.; Narváez-Padilla, V.; Reynaud, E. Commercial Bombus impatiens as reservoirs of emerging infectious diseases in central México. Biol. Invasions 2015, 17, 2043–2053. [CrossRef]
94. Brenton-Rule, E.C.; Dobelmann, J.; Baty, J.W.; Brown, R.L.; Dvorak, L.; Grangier, J.; Masiocchi, M.; McGrannachan, C.; Shortall, C.R.; Schmack, J.; et al. The origins of global invasions of the German wasp (Vespula germanica) and its infection with four honey bee viruses. Biol. Invasions 2018, 20, 3445–3460. [CrossRef]
95. Quinn, O.; Gruber, M.A.M.; Brown, R.L.; Baty, J.W.; Bulgarella, M.; Lester, P.J. A metatranscriptomic analysis of diseased social wasps (Vespula vulgaris) for pathogens, with an experimental infection of larvae and nests. PLoS ONE 2018, 13, e0209589. [CrossRef] [PubMed]
96. Benjeddou, M.; Leat, N.; Allsopp, M.; Davison, S. Detection of Acute Bee Paralysis Virus and Black Queen Cell Virus from Honeybees by Reverse Transcriptase PCR. Appl. Environ. Microbiol. 2001, 67, 2384–2387. [CrossRef] [PubMed]
97. Berenyi, O.; Bakonyi, T.; Derakhshifar, I.; Koglberger, H.; Nowotny, N. Occurrence of Six Honeybee Viruses in Diseased Austrian Apiaries. Appl. Environ. Microbiol. 2006, 72, 2414–2420. [CrossRef]
98. Genersch, E.; Evans, J.D.; Fries, I. Honey bee disease overview. J. Invertebr. Pathol. 2016, 64, 395–407.
99. Bailey, L.; Gibbs, A.J. Acute infection of bees with paralysis virus. J. Insect Pathol. 1964, 6, 103–106. [CrossRef]
100. Melathopoulos, A.; Ovinge, L.; Veiga, P.W.; Castillo, C.; Ostermann, D.; Hoover, S. Viruses of managed alfalfa leafcutting bees (Megachile rotundata Fabricius) and honey bees (Apis mellifera L.) in Western Canada: Incidence, impacts, and prospects of cross-species viral transmission. J. Invertebr. Pathol. 2017, 146, 24–30. [CrossRef] [PubMed]
101. Alvarez, L.J.; Reynolds, F.J.; Rambello, P.; Garcia, M.L.G.; Gusaaza, G.H.; Abrhamovich, A.H.; Lucia, M. Detection of honey bee viruses in Argentinian stingless bees (Hymenoptera: Apidae). Insectes Soc. 2018, 65, 191–197. [CrossRef]
102. Chen, Y.P.; Pettis, J.S.; Corona, M.; Chen, W.P.; Li, C.J.; Visscher, P.K.; DeGrandi-Hoffman, G.; Boncristiani, H.; Zhao, Y.; et al. Israeli Acute Paralysis Virus: Epidemiology, Pathogenesis and Implications for Honey Bee Health. PLoS Pathog. 2014, 10, e1004261. [CrossRef]
103. Palacios, G.; Hui, J.; Quan, P.L.; Kalkstein, A.; Honkavuori, K.S.; Bussetti, A.V.; Conlan, S.; Evans, J.; Chen, Y.P.; van Engelsdorp, D.; et al. Genetic Analysis of Israel Acute Paralysis Virus: Distinct Clusters Are Circulating in the United States. J. Virol. 2008, 82, 6209–6217. [CrossRef] [PubMed]
104. Hou, C.; Rivkin, H.; Slabzeki, Y.; Chejanovsky, N. Dynamics of the Presence of Israeli Acute Paralysis Virus in Honey Bee Colonies with Colony Collapse Disorder. Viruses 2014, 6, 2012–2027. [CrossRef]
105. Kalynych, S.; Pridor, A.; Páliková, L.; Levdanys, Y.; de Miranda, J.R.; Plevka, P. Virion Structure of IFLavirus Slow Bee Paralysis Virus at 2.6-Angstrom Resolution. J. Virol. 2016, 90, 7444–7455. [CrossRef] [PubMed]
106. Santillán-Galicia, M.T.; Ball, B.V.; Clark, S.J.; Alderson, P.G. Slow bee paralysis virus and its transmission in honey bee pupae by varroa destructor. J. Apic. Res. 2014, 53, 146–154. [CrossRef]
107. De Miranda, J.R.; Dainat, B.; Locke, B.; Cordoni, G.; Berthoud, H.; Gauthier, L.; Neumann, P.; Budge, G.E.; Ball, B.V.; Stoltz, D.B. Genetic characterization of slow bee paralysis virus of the honeybee (Apis mellifera L.). J. Gen. Virol. 2010, 91, 2524–2530. [CrossRef]
108. Bailey, L.; Woods, R.D. Three previously undescribed viruses from the honey bee. J. Gen. Virol. 1974, 25, 175–186. [CrossRef]
109. Radzveviūtė, R.; Theodorou, P.; Husemann, M.; Japoshvili, G.; Krikiatdze, G.; Zhusupbaeva, A.; Paxton, R.J. Replication of honey bee-associated RNA viruses across multiple bee species in apple orchards of Georgia, Germany and Kyrgyzstan. J. Invertebr. Pathol. 2017, 146, 14–23. [CrossRef] [PubMed]
110. McMahon, D.P.; Fürst, M.A.; Caspar, J.; Theodorou, P.; Brown, M.J.F.; Paxton, R.J. A sting in the spit: Widespread cross-infection of multiple RNA viruses across wild and managed bees. J. Anim. Ecol. 2015, 84, 615–624. [CrossRef]
111. Manley, R.; Boots, M.; Wilfert, L. Condition-dependent virulence of slow bee paralysis virus in Bombus terrestris: Are the impacts of honeybee viruses in wild pollinators underestimated? Oecologia 2017, 184, 305–315. [CrossRef]
112. Parmentier, L.; Smagghe, G.; de Graaf, D.C.; Meeus, I. Varroa destructor Macula-like virus, Lake Sinai virus and other new RNA viruses in wild bumblebee hosts (Bombus pascuorum, Bombus lapidarius and Bombus pratorum). J. Invertebr. Pathol. 2016, 134, 6–11. [CrossRef]
113. Ribiére, M.; Triboulot, C.; Mathieu, L.; Aurieres, C.; Faucon, J.-P.; Pepin, M. Molecular diagnosis of chronic bee paralysis virus infection. Apidologie 2002, 33, 339–351. [CrossRef]
114. Ribiére, M.; Olivier, V.; Blanchard, P. Chronic bee paralysis: A disease and a virus like no other? J. Invertebr. Pathol. 2010, 103, S120–S131. [CrossRef]
115. Olivier, V.; Massou, I.; Celle, O.; Blanchard, P.; Schurr, F.; Ribiére, M.; Gauthier, M. In situ hybridization assays for localization of the chronic bee paralysis virus in the honey bee (Apis mellifera) brain. J. Virol. Methods 2008, 153, 232–237. [CrossRef]
116. Choi, Y.S.; Lee, M.Y.; Hong, I.P.; Kim, N.S.; Byeon, K.H.; Yoon, H. Detection of Honeybee Virus from Bumblebee (Bombus terrestris L. and Bombus ignitus). Korean J. Apic. 2010, 25, 259–266.
117. Fernandez de Landa, G.; Revainera, P.; Brasesco, C.; di Gerónimo, V.; Plischuk, S.; Merio, F.; Maggi, M.; Eguaras, M.; Quintana, S. Chronic bee paralysis virus (CBPV) in South American non-Apis bees. Arch. Virol. 2020, 165, 2053–2056. [CrossRef]

118. Celle, O.; Blanchard, P.; Olivier, V.; Schurr, F.; Cougoule, N.; Faucon, J.P.; Ribiére, M. Detection of Chronic bee paralysis virus (CBPV) genome and its replicative RNA form in various hosts and possible ways of spread. Virus Res. 2008, 133, 280–284. [CrossRef] [PubMed]

119. Bailey, L.; Gibbs, A.J.; Woods, R.D. Sacbrood virus of the larval honey bee (Apis mellifera linnaeus). Virology 1964, 23, 425–429. [CrossRef]

120. Evison, S.E.F.; Roberts, K.E.; Laurenson, L.; Pietravalle, S.; Hui, J.; Biesmeijer, J.C.; Smith, J.E.; Budge, G.; Hughes, W.O.H. Dynamics of Varroa destructor in France: a case study. J. Invertebr. Pathol. 2015, 129, 36–39. [CrossRef] [PubMed]

121. Reddy, K.E.; Yoo, M.S.; Kim, Y.H.; Kim, N.H.; Ramya, M.; Jung, H.N.; Thao, L.T.B.; Lee, H.S.; Kang, S.W. Homology differences between complete Sacbrood virus genomes from infected Apis mellifera and Apis cerana honeybees in Korea. Virus Genes 2016, 52, 281–289. [CrossRef] [PubMed]

122. Rana, R.; Bana, B.S.; Kaushal, N.; Kaundal, P.; Rana, K.; Khan, M.A.; Gwande, S.J.; Sharma, H.K. Identification of sacbrood virus infection in honey bee, Apis mellifera L. by using ELISA and RT-PCR techniques. Indian J. Biotechnol. 2011, 10, 274–284.

123. Roberts, J.M.K.; Anderson, D.L. A novel strain of sacbrood virus of interest to world apiculture. J. Invertebr. Pathol. 2014, 118, 71–74. [CrossRef]

124. Zhang, Y.; Huang, X.; Xu, Z.; Han, R.; Chen, J. Differential Gene Transcription in Honeybee (Apis cerana) Larvae Challenged by Chinese Sacbrood Virus (CBSV). Sociobiology 2013, 60, 413–420. [CrossRef]

125. Gamboa, V.; Ravoet, J.; Brunain, M.; Smaghe, G.; Meeus, I.; Figueroa, J.; Riaño, D.; de Graaf, D.C. Bee pathogens found in Bombus terrestris from Colombia. Arch. Virol. 2019, 164, 129–136. [CrossRef]

126. Reynaldi, F.; Sguazza, G.; Albicoro, F.; Pecoraro, M.; Galosi, C. First molecular detection of co-infection of honey bee viruses in Apis mellifera. Arch. Virol. 2016, 201, 759–765. [CrossRef]

127. Dolezal, A.G.; Hendrix, S.D.; Scavo, N.A.; Carrillo-Tripp, J.; Harris, M.A.; Wheelock, M.J.; O’Neal, M.E.; Toth, A.L. Honey Bee Viruses in Wild Bees: Viral Prevalence, Loads, and Experimental Inoculation. PLoS ONE 2016, 11, e0161940. [CrossRef] [PubMed]

128. Evison, S.E.F.; Roberts, K.E.; Laurenson, L.; Pietravelle, S.; Hui, J.; Biessemeier, J.C.; Smith, J.E.; Budge, G.; Hughes, W.O.H. Pervasiveness of Parasites in Pollinators. PLoS ONE 2012, 7, e36041. [CrossRef] [PubMed]

129. Bailes, E.J.; Deutsch, K.R.; Bagi, J.; Rondissone, L.; Brown, M.J.F.; Lewis, O.T. First detection of bee viruses in hoverfly (syrphid) pollinators. Biol. Lett. 2018, 14, 20180001. [CrossRef]

130. Brettell, L.E.; Schroeder, D.C.; Martin, S.J. RNAseq analysis reveals virus diversity within hawaiian apiary insect communities. Viruses 2019, 11, 397. [CrossRef]

131. Mayo, M.A. A summary of taxonomic changes recently approved by ICTV. Arch. Virol. 2002, 147, 1655–1656. [CrossRef] [PubMed]

132. Mayo, M.A. Virology Division News. Arch. Virol. 2002, 147, 1071–1076. [CrossRef]

133. Leat, N.; Ball, B.; Govan, V.; Davison, S. Analysis of the complete genome sequence of black queen-cell virus, a picorna-like virus of honey bees. J. Gen. Virol. 2000, 81, 2111–2119. [CrossRef] [PubMed]

134. Leat, N.; Ball, B.; Govan, V.; Davison, S. Analysis of the complete genome sequence of black queen-cell virus, a picorna-like virus of honey bees. J. Gen. Virol. 2000, 81, 2111–2119. [CrossRef] [PubMed]

135. Tentcheva, D.; Gauthier, L.; Zappulla, N.; Dainat, B.; Cousserans, F.; Colin, M.E.; Bergoin, M. Prevalence and seasonal variations of six bee viruses in Apis mellifera L. and Varroa destructor mite populations in France. Appl. Environ. Microbiol. 2004, 70, 7185–7191. [CrossRef] [PubMed]

136. Kajobe, R.; Marris, G.; Budge, G.; Laurensen, L.; Cordoni, G.; Jones, B.; Wilkins, S.; Cuthbertson, A.G.S.; Brown, M.A. First molecular detection of a viral pathogen in Ugandan honey bees. J. Invertebr. Pathol. 2010, 104, 153–156. [CrossRef] [PubMed]

137. Siede, R.; Büchner, R. Symptomatic Black Queen Cell Virus infection of drone brood in Hessian apiaries. Berl. Munch. Tierarztl. Wochenchr. 2003, 116, 130–133. [PubMed]

138. Mookhploy, W.; Kimura, K.; Disayathanoowat, T.; Yoshiyama, M.; Hondo, K.; Chantawannakul, P. Capsid Gene Divergence of Black Queen Cell Virus Isolates in Thailand and Japan Honey Bee Species. J. Econ. Entomol. 2015, 108, 1460–1464. [CrossRef] [PubMed]

139. Choi, N.R.; Jung, C.; Lee, D.-W. Optimization of detection of black queen cell virus from Bombus terrestris via real-time PCR. J. Asia. Pac. Entomol. 2015, 18, 9–12. [CrossRef]

140. Algner, S.A.; Burnham, P.A.; Boncristiani, H.F.; Brody, A.K. RNA virus spillover from managed honeybees (Apis mellifera) to wild bumblebees (Bombus spp.). PLoS ONE 2019, 14, e0217822. [CrossRef]

141. Altemeier, W.A.; Martin, M.; Brutscher, L.M.; Cavigli, I.; Garcia, E.; Lavin, M.; Flenningen, M.L. Honey bee infecting Lake Sinai viruses. Viruses 2015, 7, 3285–3309. [CrossRef] [PubMed]

142. Runckel, C.; Flenningen, M.L.; Engel, J.C.; Ruby, J.G.; Ganem, D.; Andino, R.; DeRisi, J.L. Temporal analysis of the honey bee microbiome reveals four novel viruses and seasonal prevalence of known viruses, Nosema, and Crithidia. PLoS ONE 2011, 6. [CrossRef] [PubMed]

143. Gauthier, L.; Cormon, S.; Hartmann, U.; Cousserans, F.; Evans, J.; de Miranda, J.; Neumann, P. The Apis mellifera Filamentous Virus Genome. Viruses 2015, 7, 3798–3815. [CrossRef] [PubMed]

144. Hartmann, U.; Forsgren, E.; Charrère, J.D.; Neumann, P.; Gauthier, L. Dynamics of Apis mellifera filamentous virus (AmFV) infections in honey bees and relationships with other parasites. Viruses 2015, 7, 2654–2667. [CrossRef]

145. Varis, A.L.; Ball, B.V.; Allen, M. The incidence of pathogens in honey bee (Apis mellifera L.) colonies in Finland and Great Britain. Apidologie 1992, 23, 133–137. [CrossRef]
145. Quintana, S.; Brasesco, C.; Porrini, L.P.; Di Gerónimo, V.; Eguras, M.J.; Maggi, M. First molecular detection of *Apis mellifera* filamentous virus (AmFV) in honey bees (*Apis mellifera*) in Argentina. *J. Api. Res.* 2021, 60, 111–114. [CrossRef]

146. Hou, C.; Li, B.; Luo, Y.; Deng, S.; Diao, Q. First detection of *Apis mellifera* filamentous virus in *Apis cerana cerana* in China. *J. Invertebr. Pathol.* 2016, 138, 112–115. [CrossRef] [PubMed]

147. Plischuk, S.; Fernández de Landa, G.; Revainera, P.; Quintana, S.; Pocco, M.E.; Cigliano, M.M.; Lange, C.E. Parasites and pathogens associated with native bumble bees (Hymenoptera: Apidae: *Bombus* spp.) from highlands in Bolivia and Peru. *Stud. Neotrop. Fauna Environ.* 2020. [CrossRef]

148. de Landa, G.F.; Porrini, M.P.; Revainera, P.; Porrini, D.P.; Farina, J.; Correa-Benítez, A.; Maggi, M.D.; Eguaras, M.J.; Quintana, S. Pathogens Detection in the Small Hive Beetle (*Aethina tumida* (Coleoptera: Nitidulidae)). *Neotrop. Entomol.* 2020, 1–5. [CrossRef] [PubMed]

149. De Miranda, J.R.; Scott Cornwall, R.; Evans, J.D.; Sembeg, E.; Haddad, N.; Neumann, P.; Gauthier, L. Genome characterization, prevalence and distribution of a macula-like virus from *Nosema apis* in honey bees and Varroa. *Sci. Rep.* 2016, 6, 34983. [CrossRef] [PubMed]

150. Gariglione, M.; Taminiau, B.; Al Agrei, N.; Cedar, D.; Gilliaux, G.; Hue, M.; Desmecht, D.; Daube, G.; Linden, A.; Famin, F.; et al. Moku Virus in Invasive Asian Hornets, Belgium, 2016. *Emerg. Infect. Dis.* 2017, 23, 2109–2112. [CrossRef]

151. Fries, I.; Feng, F.; da Silva, A.; Slemenda, S.B.; Pieniazek, N.J. First detection of *Ascosphaera apis* in European honey bees (*Apis mellifera*). *Vet. Sci.* 2020, 7, 34983. [CrossRef] [PubMed]

152. Cilia, G.; Cabbri, R.; Maiorana, G.; Cardaio, I.; Dall’Olio, R.; Nanetti, A. A novel TaqMan® assay for *Nosema ceranae* quantification in honey bee, based on the protein coding gene Hsp70. *Apic. Res. 2018, 63, 44–50. [CrossRef]

153. Michalczyk, M.; Sokol, R. Estimation of the influence of selected products on co-infection with *N. apis/N. ceranae* in *Apis mellifera* using real-time PCR. *Invertebr. Reprod. Dev.* 2018, 62, 92–97. [CrossRef]

154. Botías, C.; Martín-Hernández, R.; Meana, A.; Higes, M. Screening alternative therapies to control Nosemosis type C in honey bee (*Apis mellifera* iberiensis) colonies. *Res. Vet. Sci.* 2013, 95, 1041–1045. [CrossRef] [PubMed]

155. Cilia, G.; Garrido, C.; Bonetto, M.; Tesoriero, D.; Nanetti, A. Effect of Api-Bioxal® and ApiHerb® Treatments against *Nosema ceranae* Infection in *Apis mellifera* Investigated by Two qPCR Methods. *Vet. Sci.* 2020, 7, 125. [CrossRef] [PubMed]

156. Plischuk, S.; Martín-Hernández, R.; Prieto, L.; Lucia, M.; Botías, C.; Meana, A.; Abrahamovich, A.H.; Lange, C.; Higes, M. South American native bumblebees (Hymenoptera: Apidae) infected by *Nosema ceranae* (Microsporidia), an emerging pathogen of honeybees (*Apis mellifera*). *Environ. Microbiol. Rep.* 2009, 1, 131–135. [CrossRef] [PubMed]

157. Plischuk, S.; Lange, C.E. *Bombus brasiliensis* Lepeletier (Hymenoptera, Apidae) infected with *Nosema ceranae* (Microsporidia). *Rev. Bras. Entomol.* 2016, 60, 347–351. [CrossRef]

158. Graystock, P.; Yates, K.; Darvill, B.; Goulson, D.; Hughes, W.O.H. Emerging dangers: Deadly effects of an emergent parasite in a new pollinator host. *J. Invertebr. Pathol.* 2013, 114, 114–119. [CrossRef] [PubMed]

159. Porrini, M.P.; Porrini, L.P.; Garrido, P.M.; de Melo e Silva Neto, C.; Porrini, D.P.; Muller, F.; Nuñez, L.A.; Alvarez, L.; Iriarte, P.F.; Eguaras, M.J. *Nosema ceranae* in South American Native Stingless Bees and Social Wasp. *Microb. Ecol.* 2017, 74, 761–764. [CrossRef] [PubMed]

160. Cilia, G.; Cardaio, I.; dos Santos, P.E.J.; Ellis, J.D.; Nanetti, A. The first detection of *Nosema ceranae* (Microsporidia) in the small hive bee, *Aethina tumida* Murray (Coleoptera: Nitidulidae). *Apidologie* 2018, 49, 619–624. [CrossRef]

161. Higes, M.; Martín-Hernández, R.; Garrido-Bailón, E.; Botías, C.; Garcia-Palencia, P.; Meana, A. Regurgitated pellets of *Melops apias* as fomites of infective *Nosema ceranae* (Microsporidia) spores. *Environ. Microbiol.* 2008, 10, 1374–1379. [CrossRef]

162. Fries, I. *Nosea apis*—A Parasite in the Honey Bee Colony. *Bee World* 1993, 74, 5–19. [CrossRef]

163. Fries, I. Infectivity ans multiplication of *Nosema apis* Z. in the ventriculus of the honey bee. *Apidologie* 1988, 19, 319–328. [CrossRef]

164. Forsgren, E.; Fries, I. Comparative virulence of *Nosema ceranae* and *Nosema apis* in individual European honey bees. *Vet. Parasitol.* 2010, 170, 212–217. [CrossRef]

165. Heath, L.A.F. Chalk Brood Pathogens: A Review. *Bee World* 1982, 63, 130–135. [CrossRef]

166. Spiltoir, C.F. Life Cycle of *Ascosphaera apis* (*Pericystis apis*). *Ann. J. Bot.* 1955, 42, 501. [CrossRef]

167. Heath, L.A.F.; Gaze, B.M. Carbon dioxide activation of spores of the chalkbrood fungus *Ascosphaera apis*. *J. Api. Res.* 1987, 26, 243–246. [CrossRef]

168. Flores, J.M.; Spivak, M.; Gutiérrez, I. Spores of *Ascosphaera apis* contained in wax foundation can infect honeybee brood. *Vet. Microbiol.* 2005, 108, 141–144. [CrossRef]
173. Grossar, D.; Kilchenmann, V.; Forsgren, E.; Charrière, J.D.; Gauthier, L.; Chapuisat, M.; Dietemann, V. Putative determinants of virulence in *Melissococcus plutonius*, the bacterial agent causing European foulbrood in honey bees. *Virulence* 2020, 11, 554–567. [CrossRef]

174. Forsgren, E. European foulbrood in honey bees. *J. Invertebr. Pathol.* 2010, 103, S5–S9. [CrossRef]

175. Budgè, G.E.; Shirley, M.D.F.; Jones, B.; Quill, E.; Tomkies, V.; Feil, E.J.; Brown, M.A.; Haynes, E.G. Molecular epidemiology and population structure of the honey bee brood pathogen *Melissococcus plutonius*. *ISME J.* 2014, 8, 1588–1597. [CrossRef]

176. Arai, R.; Tominaga, K.; Wu, M.; Okura, M.; Ito, K.; Okamura, M.; Sugimura, Y.; Yoshiyama, M.; et al. Diversity of *Melissococcus plutonius* from honeybee larvae in Japan and experimental reproduction of European foulbrood with cultured atypical isolates. *PLoS ONE* 2012, 7. [CrossRef]

177. Regassa, L.B.; Gasparich, G.E. Spiroplasmas: Evolutionary relationships and biodiversity. *Front. Biosci.* 2006, 11, 2983–3002. [CrossRef] [PubMed]

178. Mouches, C.; Kilchenmann, V.; Forsgren, E. Single and mixed-species trypanosome and microsporidia infections elicit distinct, ephemeral cellular responses in honey bees. *Syst. Biodivers.* 2011, 9, 319–327. [CrossRef] [PubMed]

179. Arismendi, N.; Bruna, A.; Kleine, M.; Rovasio, C.; Bartolomé, C.; Higes, M. Epidemiological study of honeybee mass mortalities in Castilla-La Mancha (Spain). *Span. J. Agric. Res.* 2013, 166, 408–416. [CrossRef]

180. Arismendi, N.; Bruna, A.; Kleine, M.; Strohmeier, C.; Higes, M.; Boix, J.; Tscharntke, T.; Voss, H.; et al. *Melissococcus plutonius* population structure of the honey bee brood pathogen *Melissococcus plutonius* in Southwestern France. *Microb. Ecol.* 1982, 8, 387–399. [CrossRef] [PubMed]

181. Mouches, C.; Kilchenmann, V.; Forsgren, E.; Charrié, M.; Petit, M.; et al. European foulbrood in honey bees. *J. Invertebr. Pathol.* 2010, 103, S5–S9. [CrossRef]

182. Gerth, M.; Geibler, A.; Bleidorn, C. *Melissococcus plutonius* virulence in *Melissococcus plutonius* population structure of the honey bee brood pathogen *Melissococcus plutonius* in Southwestern France. *Microb. Ecol.* 1982, 8, 387–399. [CrossRef] [PubMed]

183. Ruiz-Gonzalez, M.X.; Bryden, J.; Moret, Y.; Reber-Funk, C.; Schmid-Hempel, P.; Brown, M.J.F. Larvae act as a transient transmission hub for the prevalent bumblebee parasite *Crithidia bombi*. *J. Invertebr. Pathol.* 2017, 148, 81–85. [CrossRef] [PubMed]
200. Popp, M.; Erler, S.; Lattorff, H.M.G. Seasonal variability of prevalence and occurrence of multiple infections shape the population structure of *Crithidia bombi*, an intestinal parasite of bumblebees (*Bombus* spp.). *Microbiologia* 2012, 1, 362–372. [CrossRef]

201. Brown, M.J.F.; Schmid-Hempel, R.; Schmid-Hempel, P. Strong context-dependent virulence in a host-parasite system: Reconciling genetic evidence with theory. *J. Anim. Ecol.* 2003, 72, 994–1002. [CrossRef]

202. Figueroa, L.L.; Grincavitch, C.; McArt, S.H. *Crithidia bombi* can infect two solitary bee species while host survivorship depends on diet. *Parasitology* 2021, 148, 435–442. [CrossRef]

203. Ngor, L.; Palmer-Young, E.C.; Burciaga Nevarez, R.; Russell, K.A.; Leger, L.; Giacomini, S.J.; Pinilla-Gallego, M.S.; Irwin, R.E.; McFrederick, Q.S. Cross-infectivity of honey and bumble bee-associated parasites across three bee families. *Parasitology* 2020, 147, 1290–1304. [CrossRef]

204. Murray, E.A.; Burand, J.; Trikoz, N.; Schnabel, J.; Grab, H.; Danforth, B.N. Viral transmission in honey bees and native bees, *Bombus* and *Melipona* spp. *Invertebr. Pathol.* 2011, 104, 732–739. [CrossRef] [PubMed]

205. Colla, S.R.; Otterstatter, M.C.; Gegear, R.J.; Thomson, J.D. Plight of the bumble bee: Pathogen spillover from commercial to wild populations. *Biol. Conserv.* 2006, 129, 461–467. [CrossRef]

206. Piot, N.; Snoeck, S.; Vanlede, M.; Smagghe, G.; Meeus, I. In vivo study of Dicer-2-mediated immune response of the microsporidian *Nosema bombi* in invasive bumble bees. *Environ. Microbiol. Rep.* 2017, 9, 169–173. [CrossRef]

207. Plischuk, S.; Meeus, I.; Smagghe, G.; Lange, C.E. *Apicystis bombi* gen nov and *Apicystis bombi* (Liu, Macfarlane & Pengelly) comb nov (Protozoa: Neogregarinida), a cosmopolitan parasite of *Bombus* and *Apis* (Hymenoptera: Apidae). *Apidologie* 1996, 27, 29–34. [CrossRef]

208. Plischuk, S.; Meeus, I.; Smagghe, G.; Lange, C.E. *Apicystis bombi* (Apicomplexa: Neogregarinorida) parasitizing *Apis mellifera* and *Bombus terrestris* (Hymenoptera: Apidae) in Argentina. *Environ. Microbiol. Rep.* 2011, 3, 565–568. [CrossRef]

209. Colla, S.R.; Otterstatter, M.C.; Gegear, R.J.; Thomson, J.D. Plight of the bumble bee: Pathogen spillover from commercial to wild populations. *Biol. Conserv.* 2006, 129, 461–467. [CrossRef]

210. Murray, E.A.; Burand, J.; Trikoz, N.; Schnabel, J.; Grab, H.; Danforth, B.N. Viral transmission in honey bees and native bees, *Bombus* and *Melipona* spp. *Invertebr. Pathol.* 2011, 104, 732–739. [CrossRef] [PubMed]

211. Lipa, J.J.; Trigiani, G. *Apicystis* gen nov and *Apicystis bombi* (Liu, Macfarlane & Pengelly) comb nov (Protozoa: Neogregarinida), a cosmopolitan parasite of *Bombus* and *Apis* (Hymenoptera: Apidae). *Apidologie* 1996, 27, 29–34. [CrossRef]

212. Li, J.; Peng, W.; Wu, J.; Strange, J.; Boncristiani, H.; Chen, Y. Cross-Species Infection of Deformed Wing Virus Poses a New Threat to Pollinator Conservation. *J. Invertebr. Pathol.* 2016, 131, 1–9. [CrossRef]

213. Toplak, I.; Šimenc, L.; Ocepek, M.P.; Bevk, D. Determination of Genetically Identical Strains of Four Honeybee Viruses in **Bombus terrestris** through feeding and injection. *J. Invertebr. Pathol.* 2015, 121, 64–69. [CrossRef]

214. Colla, S.R.; Otterstatter, M.C.; Gegear, R.J.; Thomson, J.D. Plight of the bumble bee: Pathogen spillover from commercial to wild populations. *Biol. Conserv.* 2006, 129, 461–467. [CrossRef]

215. Murray, E.A.; Burand, J.; Trikoz, N.; Schnabel, J.; Grab, H.; Danforth, B.N. Viral transmission in honey bees and native bees, supported by a global black queen cell virus phylogeny. *Environ. Microbiol.* 2018, 21, 972–983. [CrossRef]

216. Plischuk, S.; Meeus, I.; Smagghe, G.; Lange, C.E. *Apicystis bombi* (Apicomplexa: Neogregarinorida) parasitizing *Apis mellifera* and *Bombus terrestris* (Hymenoptera: Apidae) in Argentina. *Environ. Microbiol. Rep.* 2011, 3, 565–568. [CrossRef]

217. Li, J.; Peng, W.; Wu, J.; Strange, J.; Boncristiani, H.; Chen, Y. Cross-Species Infection of Deformed Wing Virus Poses a New Threat to Pollinator Conservation. *J. Invertebr. Pathol.* 2016, 131, 1–9. [CrossRef]

218. Santamaria, J.; Villalobos, E.M.; Brettell, L.; Nikaido, S.; Graham, J.R.; Martin, S. Evidence of Varroa-mediated deformed wing virus spillover in Hawaii. *J. Invertebr. Pathol.* 2018, 151, 126–130. [CrossRef]

219. Wawrzeniuk, P.; Taczek, P.; Piot, N.; Smagghe, G.; Meeus, I. Honey bee-collected pollen is a potential source of *Ascosphaera apis* infection in managed bumble bees. *PloS ONE* 2021, 16, e0249842. [CrossRef] [PubMed]

220. Pereira, K.D.S.; Meeus, I.; Smagghe, G.; Meeus, I.; Smagghe, G. Honey bee-collected pollen is a potential source of *Ascosphaera apis* infection in managed bumble bees. *Sci. Rep.* 2019, 9, 1–9. [CrossRef]

221. Tapia-González, J.M.; Morfin, N.; Macías-Macías, J.O.; De La Mora, A.; Tapia-Rivera, J.C.; Ayala, R.; Contreras-Escañero, F.; Gashou, H.A.; Guzman-Novoa, E. Evidence of presence and replication of honey bee viruses among wild bee pollinators in subtropical environments. *J. Invertebr. Pathol.* 2019, 168, 107256. [CrossRef]

222. Santamaria, J.; Villalobos, E.M.; Brettell, L.; Nikaido, S.; Graham, J.R.; Martin, S. Evidence of Varroa-mediated deformed wing virus spillover in Hawaii. *J. Invertebr. Pathol.* 2018, 151, 126–130. [CrossRef]

223. Ueira-Vieira, C.; Almeida, L.O.; De Almeida, F.C.; Amaral, I.M.R.; Brandebugro, M.A.M.; Bonetti, A.M. Scientific note on the first molecular detection of the acute bee paralysis virus in Brazilian stingless bees. *Apidologie* 2015, 46, 628–630. [CrossRef]

224. Morfin, N.; Gashou, H.A.; Macías-Macías, J.O.; De la Mora, A.; Tapia-Rivera, J.C.; Tapia-González, J.M.; Contreras-Escañero, F.; Guzman-Novoa, E. Detection, replication and quantification of deformed wing virus-A, deformed wing virus-B, and black queen cell virus in the endemic stingless bee, *Melipona colimana*, from Jalisco, Mexico. *Int. J. Trop. Insect Sci.* 2020, 41, 1285–1292. [CrossRef]
225. Guzman-Novoa, E.; Hamiduzzaman, M.M.; Anguiano-Baez, R.; Correa-Benítez, A.; Castañeda-Cervantes, E.; Arnold, N.I. First detection of honey bee viruses in stingless bees in North America. *J. Apic. Res.* **2015**, *54*, 93–95. [CrossRef]

226. Purkiss, T.; Lach, L. Pathogen spillover from *Apis mellifera* to a stingless bee. *Proc. R. Soc. B Biol. Sci.* **2019**, *286*, 20191071. [CrossRef] [PubMed]

227. Ravoet, J.; De Smet, L.; Wenseleers, T.; de Graaf, D.C. Genome sequence heterogeneity of Lake Sinai Virus found in honey bees and Orf1/RdRP-based polymorphisms in a single host. *Virus Res.* **2015**, *201*, 67–72. [CrossRef]

228. Gabín-García, L.B.; Bartolomé, C.; Guerra-Tort, C.; Rojas-Nossa, S.V.; Llvo, J.; Maside, X. Identification of pathogens in the invasive hornet *Vespa velutina* and in native Hymenoptera (Apidae, Vespidae) from SW-Europe. *Sci. Rep.* **2021**, *11*, 1–12. [CrossRef] [PubMed]

229. Marzoli, F.; Forzan, M.; Bortolotti, L.; Pacini, M.I.; Rodríguez-Flores, M.S.; Felicioli, A.; Mazzei, M. Next generation sequencing study on RNA viruses of *Vespa velutina* and *Apis mellifera* sharing the same foraging area. *Transbound. Emerg. Dis.* **2020**. [CrossRef] [PubMed]

230. Lin, C.-Y.; Lee, C.-C.; Nai, Y.-S.; Hsu, H.-W.; Lee, C.-Y.; Tsuji, K.; Yang, C.-C.S. Deformed Wing Virus in Two Widespread Invasive Ants: Geographical Distribution, Prevalence, and Phylogeny. *Viruses* **2020**, *12*, 1309. [CrossRef]

231. Schläppi, D.; Lattrell, P.; Yanez, O.; Chejanovsky, N.; Neumann, P. Foodborne Transmission of Deformed Wing Virus to Ants (*Myrmica rubra*). *Insects* **2019**, *10*, 394. [CrossRef] [PubMed]

232. Eyer, M.; Chen, Y.P.; Schäfer, M.; Pettis, J.; Neuman, P. Honey bee sacbrood virus infects adult small hive beetles, *Aethina tumida* (Coleoptera: Nitidulidae). *J. Apic. Res.* **2009**, *48*, 296–297. [CrossRef]