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REVIEW

Use the insiders: could insect facultative symbionts control vector-borne plant diseases?

Julien Chuche[1,3] · Nathalie Auricau-Bouvery[2] · Jean-Luc Danet[2] · Denis Thiéry[1]

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Abstract Insect vector-borne plant diseases, particularly those whose causative agents are viral, or phloem- and xylem-restricted bacteria, greatly impact crop losses. Since plants are immobile, the epidemiology of vector-borne diseases greatly depends on insect vectors, which are the only means of dissemination for many pathogens. The effectiveness of a vector-borne pathogen relies upon the vectorial capacity, which is affected by vector density, feeding activity on hosts, longevity before and after pathogen ingestion, duration of the incubation period, and vector competence. During the last decade, research on human vector-borne epidemics has stimulated interest in novel control strategies targeting different parts of the vector cycle, and our purpose here is to draw parallels between this field of research and agronomy. We review the literature on insect vectors of crop diseases and their symbiotic microorganisms with the aim of suggesting future integrated management techniques based on current research on insect-vectored human diseases. Vector transmission is a complex process and different modes of transmission are encountered irrespective of the pathogen. Facultative symbionts have varied effects on life history traits that could be used for vector population control. Symbiont selection, transformation, and their manner of dissemination are important when developing an integrated vector management system based on symbiont manipulation. In the short term, progress on our knowledge of the microflora of insect vectors of plant diseases must be made. In the long term, symbiont manipulation, which has been successfully demonstrated against human insect-vectored diseases, could be adapted to insect-borne plant diseases to increase sustainable crop production.

Keywords Symbiont · Vector-borne disease · Insect · Hemiptera · Integrated pest management

Key message

- Insect vector-borne plant diseases have a great importance worldwide in crops, particularly those transmitting viruses or phloem- and xylem-restricted bacteria.
- Insect vectors harbor numerous facultative symbionts that could be used to control them.
- During the last decade, researches on human and animal vector-borne epidemics have stimulated interest to experience vector control through symbionts manipulation.
- We review potential candidates, advantages and limitations of the development of such techniques in vector-borne plant diseases management in agriculture.

Introduction

Since the beginning of agriculture, crops have suffered high losses due to pest injuries. Even now, the potential losses due to crop pests are estimated to range from 50 to 80 %

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✉ Denis Thiéry
thiery@bordeaux.inra.fr

[1] INRA, UMR 1065 Santé et Agroécologie du Vignoble, Bordeaux Sciences Agro, ISVV, 33882 Villenave d'Ornon Cedex, France

[2] INRA, UMR 1332 Biologie du Fruit et Pathologie, Université de Bordeaux, 33882 Villenave d'Ornon Cedex, France

[3] Present Address: Department of Biology, Maynooth University, Maynooth, County Kildare, Ireland

depending on the crops and the planting latitude. Pest control only limits the outbreaks by 25–40 % (Oerke 2006). Pesticides, including insecticides, have been extensively used for less than a century but with important ecological side effects on targeted agrosystems and non-targeted ecosystems: the emergence of animal and plant parasite resistance (Hazarika et al. 2009; Powles 2008; van den Bosch and Gilligan 2008), the resurgence or emergence of new pests (Hardman et al. 1991; Hazarika et al. 2009), and the destruction of natural enemies (Croft and Brown 1975; Desneux et al. 2007). The impact of pesticides on non-target species, including humans, has been corroborated (Coats 1994; Elbaz et al. 2009) since Rachel Carson's pioneering publication (Carson 1962). Additionally, the increased use of pesticides in agriculture over the last 40 years has not significantly decreased yield losses (Oerke 2006). Thus, alternative pest control approaches are urgently needed. The public's perception of the environmental impact of pesticides in agriculture intensifies the need to develop more sustainable agriculture and practical integrated pest management solutions that reduce the dependence on insecticides. Crop protection has to be based on a more rigorous and better-targeted use of chemicals and/or the development of alternative techniques.

Insect vector-borne diseases, particularly those with viral, or phloem- and xylem-restricted bacterial causative agents, have a great, and yet underestimated, role in crop losses. The epidemiology of vector-borne diseases greatly depends on their vectors, which are the only route of dissemination for many pathogens. The effectiveness of a vector-borne pathogen depends on the vectorial capacity, which is related to the vector's density, feeding activity on hosts, longevity before and after pathogen ingestion, duration of the incubation period, and vector competence (Cook et al. 2008). During the last decade, research on human vector-borne epidemics has stimulated interest in novel control strategies targeting different parts of the vector cycle. Recent research also highlighted the role of symbiotic microorganisms in the coevolution of hosts and their parasites (Dheilly et al. 2015), which stresses its potential importance in biological control programs. Our purpose is to draw a comprehensive parallel between this field of research and agronomy to increase our understanding of plant disease vectors and to present future control scenarios.

Many pest insects that feed on poor and unbalanced food sources, such as phloem and xylem, harbor symbiotic bacteria (endosymbionts) within specialized host cells, called bacteriocytes, which can group together to form the bacteriome (Buchner 1965). Symbionts supply the host with components lacking in the host's diets, thereby, improving the host's physiology and invasive power. Symbionts can be divided into two categories: (i) obligate symbionts, which contribute to the nutrition of the host and are essential for its survival, and (ii) facultative symbionts that are non-essential and have diverse effects on host fitness (Buchner 1965). Obligate and facultative symbionts differ in many respects, including their maintenance and transmission across host generations. Obligate symbionts are directly transmitted to a host from its parents (vertical transmission) and have essential functions in the host's biology, including its metabolism and reproduction (Heddi et al. 1999). Facultative symbionts usually have less specialized interactions but also have intimate relationships with their host. They are transmitted both vertically and horizontally, and seem to infect host populations repetitively depending on environmental stress conditions, including parasitism and high temperature (Moran et al. 2008).

Two control strategies against plant vector-borne diseases based on insect–symbiont manipulation could be developed: (1) vector eradication targeting the essential host-physiological functions in which obligate symbionts are involved, or (2) facultative symbiont-mediated manipulation of insect traits with the aim of suppressing the vector's transmission ability without the objective of vector eradication. Facultative symbionts appear to be the best candidates for manipulating symbiont control in insect vectors. In this review, after a brief overview of the insect vectors of pathogens causing crop diseases and the symbionts of these vectors, we attempt to identify how symbiont manipulation could contribute to an ecological engineering control approach and suggest research perspectives that should be developed.

Insect vectors of pathogens causing crop diseases

Most pathogenic viruses (>200) and tissue-associated bacteria are transmitted from plant to plant by insects and nematodes (Hogenhout et al. 2008). Vector-borne microorganisms, including viruses, bacteria, and phytoplasmas, are mostly associated with hemipteran insects that feed on plant vascular tissues. In the Sternorrhyncha sub-order, aphids (Aphididae) and whiteflies (Aleyrodidae) are the most important vectors of viruses (Hogenhout et al. 2008), while psyllids (*Psyllidae*) transmit bacteria and phytoplasmas (Haapalainen 2014). In the Auchenorrhyncha sub-order, leafhoppers (Cicadellidae*)*, froghoppers (Cercopidae), and planthoppers (Delphacidae, Cixiidae, and Dictyopharidae) are able to transmit both viruses, bacteria, and phytoplasmas (Hogenhout et al. 2008; Weintraub and Beanland 2006). Thrips (Thysanoptera) transmit only a few viruses but these have significant economic impacts (Hogenhout et al. 2008; Whitfield et al. 2005). All of the plant pathogens transmitted by these insects cause important diseases in crop plants, including grapes, citrus, coffee, fruit trees, rice, vegetables, and ornamentals. The rice-infecting viruses that are transmitted by planthoppers and leafhoppers have resulted in significant disease outbreaks in Asia (Hibino 1996). Severe yield losses caused by begomoviruses transmitted by whiteflies have been reported for several crop plants, including tomato, cassava, and cotton (Briddon and Markham 2000; Costa 1976; Czosnek and Laterrot 1997; Legg et al. 2014). Barley yellow dwarf virus, transmitted by aphids, causes considerable losses of small grain cereals worldwide, including yield losses of up to 46 % in *Triticum aestivum* (wheat), 25 % in *Hordeum vulgare* (barley), and 15 % in *Avena sativa* (oat) (Larkin et al. 2002; Ordon et al. 2009). Phytoplasmas, wall-less bacteria, are associated with more than 700 diseases in hundreds of plant species (Weintraub and Beanland 2006). The bacterium *Xylella fastidiosa* that causes Pierce's disease of grape and citrus variegated chlorosis, two economically important diseases, also affects many other plant species, such as alfalfa, peach, plum, almond, elm, coffee, sycamore, oak, maple, olive, and pear (Chatterjee et al. 2008).

Vector transmission is a complex process and, irrespective of the pathogen, different modes of transmission are encountered (Nault 1997 and Table 1): (1) non-persistent and semi-persistent, (2) persistent, circulative, and (3) persistent, circulative propagative. These systems of transmission imply several, narrow, and specific interactions between a plant pathogen and its insect vector. Indeed, some of these plant-pathogenic agents are considered symbionts of their insect vector, while also being plant pathogens (Caspi-Fluger and Zchori-Fein 2010). In some cases, the pathogen can invade the oocytes within the female vector insect and be transmitted to the offspring, which is the case for the rice stripe virus transmitted by the planthopper *Laodelphax striatellus* (Huo et al. 2014) and phytoplasmas (Hanboonsong et al. 2002; Kawakita et al. 2000; Tedeschi et al. 2006). The specificity of the transmission can be very strict or, alternatively, several viruses or bacteria can be transmitted from plant to plant by the same insect (Hogenhout et al. 2008; Lee et al. 2000). The latent period, the time between the vectors' acquisition of the pathogen and the moment when the vector is able to inoculate plants, may be considerably different among the vectors and the pathogens, ranging from no latent period to a long period of days or weeks.

Non-persistent transmission

Non-persistent transmission occurs through insects that can transmit the pathogen only during a short time after acquisition, i.e., up to 12 h. In general, the non-persistent transmission of viruses occurs after a brief period of acquisition and no latent period is required. This is the case for the potato virus Y and other potyviruses (Quenouille et al. 2013). In such cases, viruses are restricted and linked to the aphid's stylet tip and, more rarely, to the foregut. The interactions between viruses and insects is mediated by direct interactions between capsid and insect proteins, as with cucumber mosaic cucumovirus (Bricault and Perry 2013), or by "helper" proteins distinct from capsid proteins, which facilitate the transmission by aphids, as with tobacco vein mottling virus (Maia et al. 1996). Since aphids rapidly lose their infectivity, such viruses cannot be dispersed over a large geographical area. However, due to their feeding behavior and their capacity to probe different plants, including non-hosts, aphids can transmit viruses to many different plant species.

Bacteria of the genus *Xylella* are transmitted by xylem sap-feeding insects, such as sharpshooters, leafhoppers, and spittlebugs (Chatterjee et al. 2008). *Xylella* transmission does not require a latent period (Purcell 1979). The bacteria are localized in the vector foregut where they attach and multiply, and can be transmitted for several weeks or months by the insect depending on its lifespan, or on the occurrence of molting during which the insects become uninfected (Almeida and Purcell 2006; Fuente et al. 2007).

Table 1 Representative examples of pathogens transmitted by insect vectors to cultivated plants

Transmission type	LP	Transmission duration	E.g., of vectors	E.g., of pathogens
Non-persistent	No	<12 h	Aphid *Myzus persicae*	Turnip mosaic virus
Semi-persistent		Hours-days		
Persistent, non circulative	No	Days-life	Sharpshooter *Homalodisca vitripennis*	*Xylella fastidiosa*
Persistent, circulative	Hours	Days-life	Leafhopper *Circulifer tenellus*	Beet curly top virus
Persistent, circulative, propagative	Days to weeks	Days-life	Leafhopper *Scaphoideus titanus*	"*Candidatus* Phytoplasma vitis"
			Planthopper *Laodelphax striatellus*	Rice stripe virus

LP latent period

Persistent, circulative transmission

In persistent circulative transmission, vectors can transmit the pathogen for several days or weeks, depending on how long the insects feed on the infected plants, and thus, the amount of pathogen ingested. In this case, the plant-pathogenic agent is not able to multiply in its insect vector but has to circulate in it to be transferred to the plant. For example, the beet curly top virus can be transmitted by the leafhopper *Circulifer tenellus* after a latent period of few hours, but the transmission period can continue for several weeks (Carter 1973; Soto and Gilbertson 2003). Luteoviruses that cause barley yellow dwarf and potato leaf roll are other examples of viruses transmitted over a long period by aphids without multiplication in their vector (Harrison 1958; Miller and Rasochová 1997). The potato leaf roll virus specifically binds the symbionin, a symbiotic bacterial protein present in the hemolymph, allowing the virus to be carried to the accessory lobes of the aphid's salivary glands (van den Heuvel et al. 1999). Maize streak virus, which causes a serious disease of maize in many regions of Africa, is transmitted in a persistent manner by leafhoppers in the genus *Cicadulina* (Bosque-Pérez 2000).

Persistent, propagative transmission

In this type of transmission, microorganisms have to multiply in their insect host to complete their persistent, propagative transmission to the plant. They often multiply in several organs that are not directly linked to the acquisition/inoculation (gut and salivary glands), thus, they can also affect the physiology or behavior of the insect vector. The length of the latent period depends on the multiplication and colonization of the insect by the plant pathogen. It can be sensitive to temperature, such as in the case of phytoplasma multiplication (Salar et al. 2013). Bacteria using this mode of transmission belong to the Mollicutes (phytoplasmas and spiroplasmas), Alphaproteobacteria ("*Candidatus* Liberibacter sp."), and Gammaproteobacteria ("*Candidatus* Arsenophonus phytopathogenicus" and "*Candidatus* Phlomobacter fragariae") classes (Bressan 2014; Grafton-Cardwell et al. 2013; Weintraub and Beanland 2006). They are restricted to the phloem of the plant. Phytoplasmas are responsible for a wide array of diseases on many crops of great economic interest, whereas spiroplasmas cause the citrus stubborn (*Spiroplasma citri*) and corn stunt (*Spiroplasma kunkelii*) diseases (Garnier et al. 2001). Both phytoplasmas and spiroplasmas are transmitted by species of insects among the leafhoppers, planthoppers, and psyllids. The psyllids *Diaphorina citri* and *Trioza erytreae* are the vectors of *Liberibacter* that causes huanglongbing in *Citrus* (Grafton-Cardwell et al. 2013; Van den Berg 1990). Viruses are also transmitted using persistent, propagative transmission. At least 14 rice viruses transmitted by planthoppers and leafhoppers cause rice diseases. Vector-borne reoviruses replicate in several organs of their insect vectors and some can spread to the ovary and be transmitted to offspring. Viruses are also able to multiply in whitefly, such as tomato yellow leaf curl virus in *Bemisia tabaci* (Ghanim 2014).

Symbionts

Eukaryotes, from plants to mammals, maintain complex interactions with microorganisms. In insects, these microorganisms are most frequently bacteria living intracellularly, but viruses and yeast-like microorganisms can also occur (Heddi and Gross 2011). When those microorganisms form intimate associations with host species and form chronic infections, they are commonly called "symbionts" (Moran 2006). The effects of symbionts on the host can vary from mutualism to pathogenicity, depending on the symbiont–host association and may have beneficial and detrimental effects at the same time (Moran 2006; Zug and Hammerstein 2015). Symbionts play an important role in the evolution of their hosts. Two main interactions are encountered: obligate and facultative relationships. In obligate symbiosis, symbiont acquisition is ancient and co-diversification between symbionts and their hosts is reported (Baumann 2005). While obligate symbionts are essential for the host's survival, reproduction, and development, the facultative symbionts may instead play important roles in the ecology and adaptation of hosts in a given environment. The principal mode of symbiotic transmission is vertical, i.e., transmission through the maternal line, but horizontal transmission, i.e., intra or interspecific transmission from one insect to another, can occur and it permits colonization of insects by facultative symbionts. The lack of genetic divergence among some facultative symbionts within and between herbivorous insect species indicates that horizontal transmission is an important mode of dissemination (Russell et al. 2003; Sandström et al. 2001; Thao et al. 2000). Horizontal transmission has also been involved in the replacement of obligate symbionts (Conord et al. 2008; Lefèvre et al. 2004; Pérez-Brocal et al. 2006). This review focuses on facultative symbionts that are the easiest targets for vector control.

Facultative symbionts can be inherited vertically (Frydman et al. 2006; Sacchi et al. 2008) but are more often horizontally transmitted. For example, horizontal transmission can occur through food plants (Caspi-Fluger et al. 2012), parasitoid wasps (Ahmed et al. 2015; Gehrer and Vorburger 2012) or during mating (Moran and Dunbar 2006). This allows the symbionts to colonize diverse species as is the case for *Hamiltonella* and *Arsenophonus*, which are found in different species of aphids, psyllids, whiteflies, and planthoppers (Baumann 2005; Dale et al. 2006; Gherna et al. 1991; Russel et al. 2003; Sémétey et al. 2007). These symbionts are erratically distributed in the insect population as for example within the different putative species whitefly *Bemisia tabaci*, which harbor contrasting symbionts (Chiel et al. 2007; Gueguen et al. 2010; Gnankiné et al. 2012; Tajebe et al. 2015). They reside in the hemolymph and/or colonize a wide variety of organs, including reproductive organs (Moran et al. 2005). When localized inside the host cells, they were found either in a vacuole or free in the cytoplasm. Genomes of facultative symbionts often contain elements related to the type III secretion system (TTSS) that are implicated in the pathogenesis of many enteric bacteria. These genes may help the symbiont to invade insect cells by injecting effectors directly into the cytoplasm of host cells. The *Hamiltonella* genome contains homologs of *Salmonella enterica* Pathogenic Island 1 and 2 genes that code for TTSS proteins (Moran et al. 2005), and *Arsenophonus nasoniae* has two complete TTSSs that are very similar to that of *Yersinia* in terms of gene content and order (Wilkes et al. 2010). Facultative symbionts have a variety of biological characteristics, ranging from mutualism to parasitism. Facultative symbionts can be cultivated outside their natural hosts in insect cell lines, such as *Arsenophonus* and *Rickettsia* (Dale et al. 2006; Darby et al. 2005; Pontes and Dale 2006; Welburn et al. 1987).

Some symbionts can colonize a wide variety of arthropods. This includes *Arsenophonus*, which infects approximately ~5 % of arthropods, including arachnids, such as ticks, and insects, such as aphids, psyllids, whiteflies, planthoppers, cockroaches, true bugs, bees, wasps, lice, flies, and beetles (Duron et al. 2008). Acetic acid bacteria of the genus *Asaia* are symbionts of phylogenetically different insect species, including anopheline mosquitoes and the phytoplasma vector *Scaphoideus titanus* (Hemiptera: Cicadellidae) (Crotti et al. 2010). *Cardinium* has been found in leafhoppers, as well as in *S. titanus* (Marzorati et al. 2006) and whiteflies (Thierry et al. 2011; Weeks et al. 2003). *Wolbachia* is an important symbiont that infects most arthropod species (Hilgenboecker et al. 2008; Zug and Hammerstein 2012) and among them are insect vectors, including aphids (De Clerck et al. 2014; Wang et al. 2014). Additionally, one organism can host many different prokaryotes. Symbiont communities in aphids have been found to be diverse and dynamic, with up to eight facultative symbionts, *Serratia*, *Hamiltonella*, *Rickettsia*, *Spiroplasma*, *Wolbachia*, *Arsenophonus*, *Regiella*, and *Rickettsiella* (Oliver et al. 2010; Tsuchida et al. 2010). Seven facultative symbionts, *Arsenophonus* (Chiel et al. 2007; Thierry et al. 2011; Zchori-Fein and Brown 2002), *Hamiltonella* (Chiel et al. 2007; Thierry et al. 2011), *Wolbachia* (Chiel et al. 2007; Weeks et al. 2003; Zchori-Fein and Brown 2002), *Cardinium* (Thierry et al. 2011), *Fritschea* (Everett et al. 2005), *Rickettsia* (Chiel et al. 2007; Gottlieb et al. 2006; Thierry et al. 2011), and *Hemipteriphilus* (Bing et al. 2013), were found in the whitefly *B. tabaci*, depending on its genotype (Chiel et al. 2007; Thierry et al. 2011), and the symbiont community of Auchenorrhyncha includes *Asaia, Cardinium, Rickettsia*, and *Wolbachia* (Gonella et al. 2012, 2011).

Facultative symbionts and insect life history traits

Facultative symbionts can drive the development of their host by improving its survival, development rates, and/or influencing its sex ratio (Table 2). Symbiotic bacteria can also have huge effects on insect physiology, such as providing a better resistance to abiotic stresses, such as heat (Brumin et al. 2011; Montllor et al. 2002) or speeding up larval development (Chouaia et al. 2012). Interestingly, facultative symbionts also have roles in typical parameters, such as adaptation to the host plant, pathogen transmission, vector relations with natural enemies, and insecticide resistance that could be used in managing vectors of crop diseases (Table 2).

Sex-ratio disturbance

Insect population dynamics can be hugely distorted by symbiont strains that skew host offspring sex ratios. The sex-ratio disturbance is mainly due to the killing of males by symbionts that are maternally inherited through the egg cytoplasm (Engelstadter and Hurst 2009; Ma et al. 2014). Among them, diverse clades of bacteria, such as *Arsenophonus*, *Cardinium*, *Rickettsia*, *Spiroplasma*, and *Wolbachia*, are able to manipulate their host's reproductive system to increase the proportion of infected individuals in the female populations, and thus, their spread (Engelstadter and Hurst 2009; Himler et al. 2011, Ma et al. 2014). There are four main reproductive manipulations: (1) killing of male symbiont hosts (Hurst and Jiggins 2000), (2) cytoplasmic incompatibility, in which matings between infected and uninfected individuals, or between two individuals infected by different strains of the same bacterium, do not produce viable offspring (Perlman et al. 2006; Werren 1997), (3) feminization of males, in which infected males reproduce as females (Rousset et al. 1992), and (4) thelytokous parthenogenesis, in which non-fertilized eggs produce females (Groot and Breeuwer 2006; Pannebakker et al. 2004).

Table 2 Representative examples of facultative symbiont effects on insect vector life history traits

Symbiont	Hosts	Reproduction	Pathogen transmission	Exploitation of host plant	Susceptibility to natural enemies	Resistance to insecticide
Alcaligenes xylosoxidans denitrificans	Sharpshooter		x			
Arsenophonus	Aphids, planthoppers, psyllids, whiteflies	x	x			
Burkholderia	True bugs					x
Hamiltonella	Aphids, whiteflies			x	x	
Rickettsia	Aphids, planthoppers, psyllids, whiteflies	x		x	x	
Wolbachia	Aphids, planthoppers, psyllids, whiteflies	x		x		

Adaptation to the host plant

The role of symbionts in the affiliation of aphids with different host plants has been investigated and provided interesting results. The study of the relationships between *Acyrthosiphon pisum* populations collected from different plant species and their symbiotic microbiota showed a strong link between symbiont occurrence and pea aphid host plant specialization (Ferrari et al. 2004; Leonardo and Muiru 2003; Simon et al. 2003; Tsuchida et al. 2004). Thus, correlations between certain facultative symbionts and the use of particular host plants by aphid and psyllid species have been demonstrated (Ferrari et al. 2012; Russell et al. 2013). For example, genotypes of *A. pisum* harbored *Serratia symbiotica* and *Rickettsia* when sampled from pea or bean and they harbored *Hamiltonella defensa* when collected on alfalfa or lotus (Ferrari et al. 2004; Frantz et al. 2009; Simon et al. 2003). Interestingly, aphid interspecific *Regiella insecticola* transfer from *A. pisum* to the vetch aphid *Megoura crassicauda* confers to *M. crassicauda* the ability to develop on a non-host plant, i.e., a plant on which a phytophagous insect species cannot grow or reproduce (Tsuchida et al. 2011). Additionally, the host plant-symbiont association can have an effect on insect fitness (Chen et al. 2000). The presence of *R. insecticola* in pea aphid lines specialized on white clover provides a greater fecundity compared to *R. insecticola*-free clones. The experimental manipulation of an *R. insecticola* infection in a single aphid genotype indicated that this symbiont enhanced female fecundity on clover compared with on vetch, but induces a higher mortality when fed alfalfa (Tsuchida et al. 2004). The roles and relative importance of symbionts in plant specialization greatly depend on the genetic backgrounds of the insects and bacteria (Ferrari et al. 2007; Leonardo 2004).

Symbionts can also help their insect host to exploit a resource by regulating the plant's defense-related genes (Barr et al. 2010; Casteel et al. 2012), detoxifying plant allelochemicals (Dowd and Shen 1990; Karban and Agrawal 2002) and/or manipulating plant physiology to enhance the resource quality. For example, *Wolbachia* symbionts of the leaf-mining moth *Phyllonorycter blancardella* inhibit apple tree leaf senescence by increasing cytokinin production, which provides *P. blancardella* a longer feeding period (Kaiser et al. 2010). In another example, several resistance genes from some varieties and wild rice species have been identified and incorporated into high-yielding rice varieties to reduce planthopper and leafhopper damage to rice in Asia (Ferrater et al. 2013). However, insects quickly adapted to the resistant rice and virulent vector populations are now common. The implication of a symbiont is a probable explanation for such a quick adaptation (Ferrater et al. 2013).

Facultative and obligate symbionts can also improve host plant exploitation by providing nutrients that insect hosts alone cannot synthesize. Thus, yeast-like symbionts recycle uric acid synthesized by the planthopper *Nilaparvata lugens* (Hemiptera: Delphacidae) as an amino acid source (Sasaki et al. 1996). The same phenomenon was described with an *Erwinia*-like symbiont and its host *Parastrachia japonensis* (Hemiptera: Parastrachiidae; Kashima et al. 2006).

Transmission of pathogens

Facultative symbionts are not confined to bacteriocytes and can be found in various parts of their insect host. Thus, they can be co-localized with plant pathogens in some insect tissues, such as the midgut and salivary glands (Marzorati et al. 2006; Rana et al. 2012), and can affect the transmission of plant pathogens. For instance, in aphids and whiteflies, symbionts produce proteins that bind to virus particles and protect them in the insect hemolymph to allow a high transmission efficiency level (Gottlieb et al. 2010; Rana et al. 2012).

Breaking the life cycle of vector-borne human diseases by blocking the development of the pathogen in the mosquito is a promising research area (Riehle and Jacobs-Lorena 2005). A pathogen-blocking effect of symbionts present in the vector has been demonstrated for a wide variety of pathogenic organisms, such as nematodes, viruses and protozoans (Kambris et al. 2009; Moreira et al. 2009). The density and/or the distribution of the symbiont in the tissue of the vector can efficiently reduce the pathogen's success (Lu et al. 2012; Moreira et al. 2009). Several hypotheses have been proposed for this phenomenon, (i) stimulation by the symbiont of the vector's innate immunity (Kambris et al. 2009; Rancès et al. 2012), (ii) competition for key cellular locations or resources between the symbiont and the pathogen (McGraw and O'Neill 2013), and/or (iii) the production by the symbiont of toxins which inhibit the pathogen (Aksoy 2003; Carter et al. 2013). However, the successful use of mass release of engineered vectors depends upon how the toxin produced by symbiont affects the vector fitness and allow them to compete with wild populations of vectors (Carter et al. 2013).

Protection against natural enemies and pathogens

Facultative symbionts can also provide protection against insect pathogens and parasitoids. The efficiency of the resistance afforded by symbionts against natural enemies varies greatly depending on host and parasitoid genotypes (Ferrari et al. 2001; Vorburger et al. 2009). Symbionts belonging to the genera *Regiella*, *Rickettsia*, *Rickettsiella*, and *Spiroplasma* can directly reduce mortalities due to fungal infections, but also indirectly by decreasing sporulation on dead aphids (Łukasik et al. 2013). The presence of the symbiont *R. insecticola* allows a better resistance to the fungal pathogen *Pandora neoaphidis* in the aphid *A. pisum* (Scarborough et al. 2005). This symbiont is also associated with resistance in two other aphid species, *Myzus persicae* and *Aphis fabae*, to the parasitoid wasp *Aphidius colemani* (Vorburger et al. 2010). *H. defensa* is a symbiont that is well-known to offer protection against parasitoid wasps (Vorburger 2014). Although the mechanisms involved in the resistance to natural enemies are globally poorly known, the protection provided by *H. defensa* is due to a toxin-encoding bacteriophage carried by a symbiont (Oliver et al. 2009). The presence of this bacteriophage is essential in the protection provided by *H. defensa*, but it also provides a higher weight at adulthood and numerous offspring (Weldon et al. 2013). Protection by *Wolbachia* against viruses was also reported in dipterans (Chrostek et al. 2013; Hedges et al. 2008). This protection provided by symbionts, however, has a cost and the presence of such symbionts in insect populations decreases without parasitic pressure (Oliver et al. 2008).

Using symbionts to enhance predation and parasitism on insect vectors represents an interesting opportunity for crop protection. The susceptibility of aphids to parasitoids and predators is partly related to their color and some studies showed that green aphids suffer higher rates of parasitoid attacks while red ones were more susceptible to predation (Libbrecht et al. 2007; Losey et al. 1997). The body color of the pea aphid varies according to the amount of blue-green polycyclic quinones, which are modified by a *Rickettsiella* infection (Tsuchida et al. 2010). In addition to color, kairomonal prey odors are important for parasitoids and predators during their food search. Symbionts can make their host more or less attractive to their natural enemies. *Staphylococcus sciuri*, which inhabits some aphid guts, when present in honey dew, produces odors that attract and stimulate oviposition of females of the larval aphid predator *Episyrphus balteatus* (Diptera: Syrphidae) (Leroy et al. 2011).

Resistance to insecticides

The extensive use of chemical insecticides for decades has led to the development of insecticide resistance. The mechanisms involved in this resistance are diverse but are often linked to changes in pest genomes. They include the over-expression of detoxifying enzymes, alterations of pesticide target loci, reductions in the sensitivity of the sodium channels to insecticide binding, and/or the up-regulation of degrading esterases (Denholm and Rowland 1992; Hemingway and Ranson 2000). Insecticide resistance due to an insecticide-degrading bacterial symbiont was recently reported (Kikuchi et al. 2012). The pest and fungal vector *Riptortus pedestris* (Hemiptera: Alydidae) acquires gut symbiotic bacteria of the genus *Burkholderia* from soil during the nymphal instar stages. Some strains of this symbiont are able to degrade fenitrothion and confer resistance to the host insects that harbor it. *Burkholderia* symbionts can live in the absence of pest insects and their development is favored under fenitrothion applications. Thus, under insecticide pressure, the level of fenitrothion-degrading *Burkholderia* strains increases, which in return increases their probability of being acquired by the insect, increasing the proportion of insecticide resistance in the pest population. On the other hand, the insecticidal activity of *Bacillus thuringiensis* on *Lymantria dispar* (Lepidoptera: Erebidae) depends on the presence of midgut symbionts. In fact, individuals of *L. dispar* that harbor gut symbionts are not directly killed by *B. thuringiensis*, but the *B. thuringiensis* toxin enables the midgut bacteria to reach the hemocoel and cause septicemia by permeabilizing the gut epithelium (Broderick et al. 2006). In other systems, however, symbionts can have protective roles against *B. thuringiensis* and gut flora-cured mosquitoes have a high mortality rate when exposed to *B. thuringiensis* (Patil et al. 2013).

Symbiont manipulation in integrated vector management

In disease vectors, the vectorial capacity (*V*), i.e., the ability to spread a disease, has been related to five main variables (Chuche and Thiéry 2014; Cook et al. 2008):

$$V = \frac{ma^2p^nb}{-\ln p},$$

where *m* is the vector density, *a* is the probability of the vector feeding on a host, which can be extended to all behaviors related to feeding, such as leaf choice, plant choice, and spatial dispersion, *p* is the probability of vector survival, n is the duration of the latent period, *b* is the vector competence, and *1/(−lnp)* is the longevity of the vector's life after the latent period.

A higher vectorial capacity is thus attained when the insect vector has a wide range of host plants, is mobile to locate new host plants and new habitats, and has sufficient longevity to optimally acquire and transmit the pathogen. Feeding behaviors, like those of sucking insects with specialized mouthparts, allow for the efficient acquisition and transmission of pathogens. In vector-borne pathogens, the rate of transmission varies depending upon the vector or pathogens' life history traits and environmental ecosystem parameters, such as resource availability and distribution of main hosts, potential alternative hosts, natural enemies, and climatic conditions (Daugherty et al. 2010). Thus, the transmission rate of vector-borne pathogens is strongly correlated with the size and dynamics of the vector population (Jeger et al. 2004), as well as its biology and behavior.

By using symbionts to affect these parameters, it is possible to influence the vectorial capacity and propose alternatives to chemical controls (Fig. 1). Shortening vector lifespans would reduce the transmission of pathogens that require long latent periods. This period, between pathogen acquisition and the ability to inoculate plants, implies that older insects contribute disproportionately to pathogen transmission (Cook et al. 2008). Consequently, small changes in vector lifespan could have huge impacts on the transmission dynamics of a disease (Cook et al. 2008; Rasgon and Scott 2004). To succeed in insect vector population control using insect microflora, the choice of the symbiont species/strains is critical. The symbiont's features will determine its ability to be modified, its manner of dissemination and the limits of its efficiency (Table 3).

Paratransgenic control

Selecting or modifying a symbiont that is able to produce a molecule to inhibit or kill the vector-borne pathogen or the vector itself is probably the easiest part of the process using the paratransgenic approach. Paratransgenesis consists of genetically modifying a symbiotic microorganism of an arthropod to express an anti-plant pathogen effector and then re-introducing it into the vector to generate a pathogen-resistant phenotype (Caljon et al. 2013). According to Beard et al. (2002), a successful paratransgenic control strategy has six requirements that could be extended to other symbiont-associated control approaches: (1) a symbiotic relationship between bacteria and vector, (2) bacterial cultivation, (3) a feasible and stable genetic modification, (4) maintenance of modified bacterial fitness, (5) production of an anti-parasitic molecule by the bacteria, and (6) an efficient dispersion system for the bacteria. Thus, best candidate microorganisms are free-living and acquired by arthropods from their environment, such as from water or plant surfaces. Symbionts that are dependent on the arthropod's environment need to use insect host cells as cultivating media (Welburn et al. 1987), which is more complicated. Because *Wolbachia* is present in a high number of insect species (Hilgenboecker et al. 2008; Zug and Hammerstein 2012) and has been well studied (reviewed in Stouthamer et al. 1999; Werren 1997), it is probably the best candidate for vector-borne disease control. Symbiont paratransgenesis is based on the use of episomal plasmids that can express the anti-pathogen effector in an autonomous way, or integrative plasmids that allow for the insertion of genes into the symbiont's chromosomal DNA (Caljon et al. 2013). Another good control candidate would be *Asaia* sp. that were suggested as potential targets for the paratransgenic control of anopheline mosquitoes (Riehle and Jacobs-Lorena 2005) and that are found in plant disease vectors, which acquire them during feeding (Crotti et al. 2009). Paratransgenic control is now being considered for vector-borne plant diseases. Thus, genetically modified yeast may be used against the planthopper vector of Fiji disease virus, *Perkinsiella saccharicida*, in sugarcane in Australia (Hughes et al. 2011). A *Candida* yeast was isolated from *P. saccharicida*, cultured and transformed. The transformation was accomplished by electroporation of *Candida albicans* codon-optimized plasmids, designed to integrate into the genome via homologous recombination. Transgenic lines were observed but no stably transformed yeast lines could be isolated. Overcome the obstacles to the production of stable engineered yeast lines will be necessary before considering the transformation of yeast symbionts of vector to produce a molecule to inhibit or kill the vector-borne

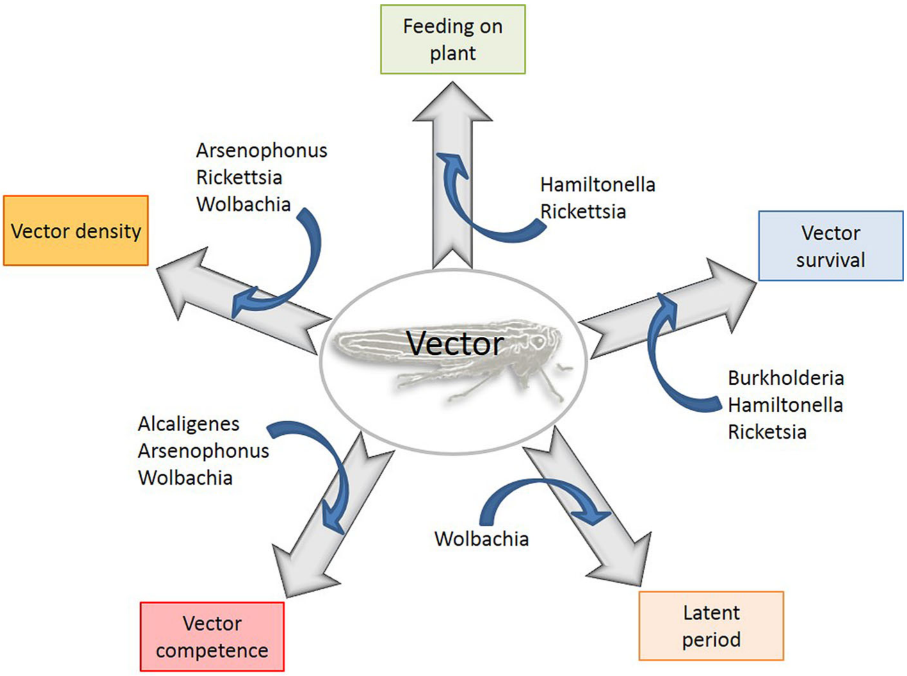

Fig. 1 Example of symbionts able to influence the insect vectorial capacity. The five variables, related to the vectorial capacity, are effective drivers of action in the reduction of the transmission of pathogens by insect vectors. Useful symbionts can act on a vector species by modifying its feeding behavior (feeding on plant), shortening its lifespan (vector survival), increasing the latent period (latent period), blocking the pathogen transmission (vector competence), affecting its reproduction, and increasing its susceptibility to natural enemies (vector density). The arrows show published effects on each variable (see Table 2 and text for details)

Table 3 Most promising facultative symbionts for vector-borne disease control

Symbiont	Hosts	Acquirable from environment	Cultivable	Easily transformable	Vertical transmission	Widely distributed	Other
Alcaligenes xylosoxidans denitrificans	Sharpshooter	In plant	x	x			
Arsenophonus	Aphids, planthoppers, psyllids, whiteflies		x		x	x	
Asaia	Leafhoppers, planthoppers	x		x	x	x	
Hamiltonella	Aphids, whiteflies	By parasitoids					
Rickettsia	Aphids, planthoppers, psyllids, whiteflies	In plant	x				
Wolbachia	Aphids, planthoppers, psyllids, whiteflies				x	x	Gene transfer to insect genome

pathogen as a potential way to control vector-borne diseases.

Symbiont dissemination

The most challenging step in the control of plant vector-borne diseases based on host–symbiont manipulation is successfully distributing the selected or modified symbiont in the vector's population. The selected symbiont must survive in the environment prior to vector acquisition, and then spread and survive in the vector's body. To ensure a better spread, symbionts should be horizontally and vertically transmitted. But, even if horizontal transmission enhances the symbiont spread in the vector population, this way of transmission allows in some cases the transfer from one species to another. Thus, vertical transmission should be avoided in cases of risk towards non-targeted species. The ability of the symbiont to be transmitted, and the manner of transmission, vertical and/or horizontal, depend on the biology of the symbiont.

Much of the research into the use of symbiotic bacteria to control human vector-borne epidemics was performed on malaria and its mosquito vector. The non-biting aquatic larval stage in the life cycles of some insects, such as mosquitoes, raised the possibility of bacterial acquisition by spraying the selected bacteria in water, even though more than 99 % of mosquito bacteria are lost between the last larval and the adult instar (Moll et al. 2001). Similarly, some *Enterobacter* species are being used to block *Plasmodium* sp. in *Anopheles* sp. vectors (Riehle and Jacobs-Lorena 2005). The goal is to prevent the pathogen from passing through the intestinal barrier after acquisition during feeding. Thus, the symbiont chosen for pathogen blocking should be localized in the midgut. Even though it appears promising, this approach is limited because midgut bacteria are not transovarially transmitted to the offspring. This method may also increase target specificity since the bacteria's adaptation to the mosquito gut could restrict the bacteria's ability to colonize non-target organisms. Additionally, the symbiont acquisition by feeding during larval life is critical in most plant pathogen vectors that are hemimetabolous, with nymphs and adults having the same feeding habits or ecological niche. Thus, it is more difficult to transfer symbionts to hemipteran than to dipteran because all of the instars feed on plant sap. Choosing the best manner to disseminate a symbiont in a species requires a good knowledge of the vector's behavior. Some hemipteran, vectors of human and plant pathogens, can acquire facultative symbionts during feeding. For example, *Rhodnius prolixus* (Hemiptera: Reduviidae), a vector of *Trypanosoma cruzi*, which causes Chagas disease, acquires *Rhodococcus* symbionts by ingesting fecal deposits (Durvasula et al. 2003). The newly emerging first-instars are aposymbiotic and acquire their symbionts through coprophagy on fecal droplets deposited by adults. Trials aimed to infect *R. prolixus* first instar nymphs using simulated fecal paste containing modified *Rhodococcus* were successful (Durvasula et al. 2003). Since aphids can acquire bacteria from the plant surfaces or from the honeydew of infected aphids (Stavrinides et al. 2009), infecting vectors by spraying cultures containing a symbiont able to survive until ingestion could be tested. Attempts to establish horizontal transmission between infected and uninfected aphid feeding on the same plant have been unsuccessful (Chen et al. 2000), while laboratory techniques, such as rearing vectors on artificial diets and microinjection, have been, to date, more successful (Pontes and Dale 2006).

Symbiont dissemination could occur by parasitoids transferring them horizontally when sequentially stabbing infected and uninfected insects. In this way, *H. defensa* and *R. insecticola* were experimentally transferred among aphids (Gehrer and Vorburger 2012), and *Wolbachia* among *B. tabaci* individuals, which resulted in stably infected *B. tabaci* lines (Ahmed et al. 2015). The use of parasitoids as vaccine agents to transfer selected symbionts to vector populations should be considered even if the rate of transmission and symbiont establishment in the prey population is affected by the mortality induced by the parasitoids.

The best source of symbionts for acquisition could be the crop targeted for protection from the vector-borne disease. Thus, endophytic bacteria could be used as insect symbionts. Some bacteria living in plants are highly genetically similar to hemipteran symbionts, and vector-borne plant pathogens are good examples of microorganisms that can live both in plants and insects (Caspi-Fluger and Zchori-Fein 2010). Thus, the production of plants harboring target symbionts that act as an inoculum source for insect vector infections is possible. This plant-mediated transmission was achieved in the lab with the acquisition of *Rickettsia* by the whitefly *B. tabaci* that had fed on *Rickettsia*-containing plants previously infected by *Rickettsia* infected *B. tabaci* (Caspi-Fluger et al. 2012). Exploiting the abilities of some bacteria to live in plants and animals for vector control was investigated. The cultivable bacterium *Alcaligenes xylosoxidans denitrificans*, which can be found in grapes, was isolated from the sharpshooter *Homalodisca vitripennis*, a vector of *X. fastidiosa* (Bextine et al. 2004). This bacterium seems to be a good candidate to control Pierce's disease because it can easily be modified to produce anti-*X. fastidiosa* factors, and colonizes both host plants and insect vectors, allowing for its potential employment in driving anti-pathogenic factors. In theory, according to the microbial ecological data available, such factors could operate within the insect or directly inside the plant, to cure infected grapevines by neutralizing or eliminating existing *X. fastidiosa* colonies (Bextine et al. 2005, 2004). This could reduce economic costs due to the removal and replacement of diseased grapevines and reducing costs associated with lost yields in subsequent seasons.

Advantages and limitations

A great advantage of using engineered symbionts is the easiness of producing large amounts of bacteria or yeasts as compared with producing equivalent amounts of insect vectors that would be required to ensure population replacement. Furthermore, the release of a weak population of vectors carrying selected symbionts into the wild can be sufficient to settle an engineered symbiont in wild vector population. Rapid spread in natural populations was hence obtained with a limited number of vectors carrying engineered *Wolbachia* in mosquito vector population (McGraw and O'Neill 2013). Bacteria can also be rather easily genetically modified to express several different effector molecules against vectors and/or pathogens (Riehle and Jacobs-Lorena 2005).

Another great advantage of using symbionts is their sustainability, except when their use leads to local population eradication followed by re-colonization. Indeed, well selected symbionts should be able to spread and maintain themselves in the vector population. For example, the life-shortening symbiont *Wolbachia w*Mel, which was discovered in *Drosophila melanogaster*, has been successfully introduced into Australian mosquito populations, 100 % of individuals being infected 1.5 years after their initial release (McGraw and O'Neill 2013). The sustainability of this method could be reinforced by using symbionts as gene vectors to modify the life history traits of insects. Indeed, lateral gene transfer from symbionts to host has been demonstrated in four insect species and suspected in three others (Dunning Hotopp et al. 2007). *Wolbachia* is an intracellular symbiont that can colonize germinal cells, transfer up to their entire genome (>1 megabase) into the insect genome and provide new heritable traits to the insect host. Because bacterial sequences are usually considered as contamination during eukaryote genome sequencing, the importance of gene transfers from symbionts to eukaryote hosts is probably underestimated and could be a promising way to modify insect vectors traits (Dunning Hotopp et al. 2007). Selected or engineered strains of *Wolbachia* could be used to disseminate interesting traits, such as pathogen transmission-blocking patterns, in insect vector populations. With this technique, even if the *Wolbachia* infection is not stable over time, selected traits may persist and spread. The complexity of the pathogen-blocking mechanism could also be an advantage in avoiding or delaying the emergence of insect resistance against this trait. If insect hosts take advantage of colonization by symbiont-mediated pathogen blocking, a co-evolutionary process maintaining the blocking trait could be expected (McGraw and O'Neill 2013).

Even though symbiont infection often has a fitness cost for the vector, it is not necessarily an obstacle to the success of control strategies against plant vector-borne diseases based on host–symbiont manipulation. Models showed that *Wolbachia* causing cytoplasmic incompatibility was able to spread in uninfected insect populations even with a 50 % reduction in host fitness, although the dissemination rate was affected (Turelli 2010). The success of such techniques depends on the effectiveness of the selected symbionts and their ability to be spread in the vector population. This success can also be under environmental control. The temperature hinders the efficacy of the *w*AlbB strain of *Wolbachia* which reduced *Plasmodium falciparum* prevalence and oocyst intensity at 28 °C, had no effect on prevalence and increased oocyst intensity at 24 °C, and had no effect on prevalence or intensity at 20 °C in *Anopheles stephensi* even though the vector was stably transinfected with the *w*AlbB strain (Murdock et al. 2014). Another factor that can limit the successful use of symbiont-modified vectors is the existence of reproductively isolated strains. Reproductive isolation prevents the members of two different populations that cross or mate from producing offspring, and thus, prevents the spread of the modified symbiont in vector population through vertical and horizontal transfer. In *Anopheles gambiae* sensu stricto, the most important vector of the malaria parasite in sub-Saharan Africa, there are two populations with different molecular forms of ribosomal DNA that coexist without cross-breeding (della Torre et al. 2002). Thus, the infection of individuals from one molecular form with a target symbiont will impact only this form and not lead to the infection of all *A. gambiae s.s.* The existence of such reproductively isolated strains is also known in plant vectors, such as the sympatric host-race evolution in *Hyalesthes obsoletus* (Hemiptera: Cixiidae) populations, a vector of the Stolbur phytoplasma in Germany (Imo 2013). The existence of *H. obsoletus* host plant races (bindweed and nettle) causes different disease epidemics (Imo 2013). The stinging nettle-specific phytoplasma strain leads to outbreaks of the grapevine disease Bois Noir and, in this case, it would be preferable to infect *H. obsoletus*–nettle populations with selected symbionts.

Potential risks associated to symbiont uses

Even though application perspectives could reduce the use of pesticides in crop protection, using symbionts could bear some ecological risks. While the potential of controlling plant diseases using vector or pest symbionts seems promising, the risk of create stronger vector insects may arise for example in case of fitness benefits conferred to them. Resistance to predators is one of the risks, as recently demonstrated in aphids (Polin et al. 2015). Another obvious risk is changing the *a* variable in the vectorial capacity model presented above (Cook et al. 2008). This probability of the vector feeding on a host, which can be extended to all behaviors related to feeding, such as leaf choice, plant choice, and spatial dispersion Insect harboring selected symbiont could be better adapted to their host plant crop or attack new crop species by becoming more specialized or reversely more generalist (Leonardo and Muiru 2003; Tsuchida et al. 2004). Vector feeding behavior, a key point in pathogen transmission, could also be affected and make the insect more efficient in disease spread. Such feeding behavior modification was observed for *Wolbachia*-infected mosquitoes *A. aegypti* that are less able to obtain blood meals in old age than uninfected ones due to a defect in the insect's proboscis (Turley et al. 2009).

Recent findings (Bressan 2014; Salar et al. 2010) support the hypothesis that some plant-pathogenic bacteria transmitted by insect vectors originating from insect symbionts (Bové and Garnier 2002; Caspi-Fluger and Zchori-Fein 2010). Such a symbiotic origin of plant pathogens concerns mainly Mollicutes (*Phytoplasma* and *Spiroplasma*), γ-(*Arsenophonus* and *Phlomobacter*) and α-

Proteobacteria (*Liberibacter* and *Rickettsia*). Hence a symbiont engineered decreasing the vectrorial capacity of the vector could potentially become a new plant pathogen and be responsible of new epidemics. Moreover, the existence of symbionts transferred horizontally through the plant from one vector species to another (Gonella et al. 2015) increases the risk of dissemination of a “plant-pathogenic insect-symbiont”. Indeed, other species than the targeted vector could spread the pathogen to different host plant species and create new uncontrolled epidemies in other crops. To minimize such risk, the engineered symbionts should not be chosen in clades where plant pathogens occur.

The main objective of control strategies against plant vector-borne diseases based on insect–symbiont manipulation is to have a sustainable alternative to the widely use of chemical spraying. But, in some cases, symbiont manipulation could have an antagonism effect on existing integrated pest management (IPM) approaches as it is observed between chemical pesticide use and IPM (Guesdes et al. 2016; Desneux et al. 2007). In this way, well established IPM, such as biological control, could be negatively impacted by the use of symbionts.

Hamiltonella sp. is a good symbiont candidate because it have genes coding for effectors helping it to invade insect cells (Moran et al. 2005), can be horizontally transferred, e.g., during feeding (Darby and Douglas 2003), mating (Moran and Dunbar 2006) and by parasitoid (Gehrer and Vorburger 2012). Thus, their spread in nature after the release of insect vectors harboring engineered *Hamiltonella* would be efficient and allow a stable establishment of this symbiont. This symbiont is also involved in plant adaptation (Frantz et al. 2009) and could be used in order to divert the insect vector from the crop to another plant. But *Hamiltonella* also offer protection to aphids against parasitoid wasps (Vorburger 2014) that are the main biological control agents against aphid (Boivin et al. 2012). This protection is not negligible and can reduce parasitism rate by 41.5 % in pea aphids exposed to *Aphidius ervi* (Oliver et al. 2003) and provide almost complete resistance against *Lysiphlebus fabarum* (Vorburger et al. 2009). Because, insect vector protection against parasitoids by symbionts occurs naturally in the field, the use of biological control agents would be act as a selection pressure and increase the proportion of insect vector harboring defensive symbionts. Biological control using parasitoid should be lead to the outbreak of resistance, as for insecticides (Vorburger et al., 2009). The mechanisms involved in the protection provided by *H. defensa* begin to be understood and are due to a toxin-encoding bacteriophage (Oliver et al. 2009). Because the presence of this bacteriophage is essential in the protection provided by *H. defensa*, inactivating it in engineered *Hamiltonella* could be a way to avoid providing parasitoid protection to insect vector. The most challenging issue will be to confer desired traits to insect vectors while avoiding traits allowing them to counter existing pest management techniques.

Conclusion

The use of symbionts to control vector-borne diseases appears to be within reach. The first success was not recent: the eradication of local populations of the filariasis vector by cytoplasmic incompatibility induced by *Wolbachia* in the 1960’s (Laven 1967). The further, stable introductions of such symbionts in vector populations against different species of mosquito (Hoffmann et al. 2011; O’Connor et al. 2012) confirmed the practicality of this strategy. Due to technical progress, understanding the basis of molecular and biochemical mechanisms that drive insect–symbiont interactions, and their consequences on host ecology, has improved. Thus, the use of symbionts in insect control is becoming realistic. Such promising techniques, which have sometimes demonstrated their success against human diseases, could be adapted to insect-borne diseases of plants. This, however, requires, as a first step, progress in our knowledge of insect vector microflora. Many plant pathogen vectors have similar habits, such as feeding on the same tissues. Therefore, using a single symbiont strain could affect many vector species. In addition to scientific and technical progress, such innovative techniques would need the approval of the public and the authorities. Because the use of emerging technologies can be rejected by the public, even when they aim at controlling human pandemics (McGraw and O’Neill 2013), it will be essential to anticipate possible public concerns.

Author contribution

All authors collected and analyzed the literature and wrote the manuscript. All authors reviewed and approved the final manuscript.

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References

Ahmed MZ, Li SJ, Xue X, Yin XJ, Ren SX, Jiggins FM, Greeff JM, Qiu BL (2015) The intracellular bacterium *Wolbachia* uses parasitoid wasps as phoretic vectors for efficient horizontal transmission. PLoS Pathog 11:19. doi:10.1371/journal.ppat.1004672

Aksoy S (2003) Control of tsetse flies and trypanosomes using molecular genetics. Vet Parasitol 115:125–145. doi:10.1016/s0304-4017(03)00203-6

Almeida RPP, Purcell AH (2006) Patterns of *Xylella fastidiosa* colonization on the precibarium of sharpshooter vectors relative to transmission to plants. Ann Entomol Soc Am 99:884–890. doi:10.1603/0013-8746(2006)99[884:POXFCO]2.0.CO;2

Barr KL, Hearne LB, Briesacher S, Clark TL, Davis GE (2010) Microbial symbionts in insects influence down-regulation of defense genes in maize. PLoS One 5:e11339. doi:10.1371/journal.pone.0011339

Baumann P (2005) Biology of bacteriocyte-associated endosymbionts of plant sap-sucking insects. Annu Rev Microbiol 59:155–189. doi:10.1146/annurev.micro.59.030804.121041

Beard CB, Cordon-Rosales C, Durvasula RV (2002) Bacterial symbionts of the triatominae and their potential use in control of Chagas disease transmission. Annu Rev Entomol 47:123–141. doi:10.1146/annurev.ento.47.091201.145144

Bextine B, Lauzon C, Potter S, Lampe D, Miller TA (2004) Delivery of a genetically marked *Alcaligenes sp.* to the glassy-winged sharpshooter for use in a paratransgenic control strategy. Curr Microbiol 48:327–331. doi:10.1007/s00284-003-4178-2

Bextine B, Lampe D, Lauzon C, Jackson B, Miller T (2005) Establishment of a genetically marked insect-derived symbiont in multiple host plants. Curr Microbiol 50:1–7. doi:10.1007/s00284-004-4390-8

Bing XL, Yang J, Zchori-Fein E, Wang XW, Liu SS (2013) Characterization of a newly discovered symbiont in the whitefly *Bemisia tabaci* (Hemiptera: Aleyrodidae). Appl Environ Microbiol 79:569–575. doi:10.1128/AEM.03030-12

Boivin G, Hance T, Brodeur J (2012) Aphid parasitoids in biological control. Can J Plant Sci 92:1–12. doi:10.4141/cjps2011-045

Bosque-Pérez NA (2000) Eight decades of maize streak virus research. Virus Res 71:107–121. doi:10.1016/s0168-1702(00)00192-1

Bové JM, Garnier M (2002) Phloem-and xylem-restricted plant pathogenic bacteria. Plant Sci 163:1083–1098. doi:10.1016/S0168-9452(03)00033-5

Bressan A (2014) Emergence and evolution of *Arsenophonus* bacteria as insect-vectored plant pathogens. Infect Genet Evol 22:81–90. doi:10.1016/j.meegid.2014.01.004

Bricault CA, Perry KL (2013) Alteration of intersubunit acid–base pair interactions at the quasi-threefold axis of symmetry of *Cucumber mosaic virus* disrupts aphid vector transmission. Virology 440:160–170. doi:10.1016/j.virol.2013.02.020

Briddon RW, Markham PG (2000) Cotton leaf curl virus disease. Virus Res 71:151–159. doi:10.1016/S0168-1702(00)00195-7

Broderick NA, Raffa KF, Handelsman J (2006) Midgut bacteria required for *Bacillus thuringiensis* insecticidal activity. Proc Natl Acad Sci USA 103:15196–15199. doi:10.1073/pnas.0604865103

Brumin M, Kontsedalov S, Ghanim M (2011) *Rickettsia* influences thermotolerance in the whitefly *Bemisia tabaci* B biotype. Insect Sci 18:57–66. doi:10.1111/j.1744-7917.2010.01396.x

Buchner P (1965) Endosymbiosis of animals with plant microorganisms. Wiley, New York

Caljon G, De Vooght L, Van den Abbeele J (2013) Options for the delivery of anti-pathogen molecules in arthropod vectors. J Invertebr Pathol 112:S75–S82. doi:10.1016/j.jip.2012.07.013

Carson R (1962) Silent Spring. Houghton Mifflin Co, Boston

Carter W (1973) Insects in relation to plant disease. Wiley, New York

Carter V, Underhill A, Baber I, Sylla L, Baby M, Larget-Thiery I, Zettor A, Bourgouin C, Langel U, Faye I, Otvos L, Wade JD, Coulibaly MB, Traore SF, Tripet F, Eggleston P, Hurd H (2013) Killer bee molecules: antimicrobial peptides as effector molecules to target sporogonic stages of *Plasmodium*. PLoS Pathog. doi:10.1371/journal.ppat.1003790

Caspi-Fluger A, Zchori-Fein E (2010) Do plants and insects share the same symbionts? Isr J Plant Sci 58:113–119. doi:10.1560/ijps.58.2.113

Caspi-Fluger A, Inbar M, Mozes-Daube N, Katzir N, Portnoy V, Belausov E, Hunter MS, Zchori-Fein E (2012) Horizontal transmission of the insect symbiont *Rickettsia* is plant-mediated. Proc R Soc Biol Sci Ser B 279:1791–1796. doi:10.1098/rspb.2011.2095

Casteel CL, Hansen AK, Walling LL, Paine TD (2012) Manipulation of plant defense responses by the tomato psyllid (*Bactericera cockerelli*) and its associated endosymbiont *Candidatus Liberibacter psyllaurous*. PLoS One 7:e35191. doi:10.1371/journal.pone.0035191

Chatterjee S, Almeida RPP, Lindow S (2008) Living in two worlds: the plant and insect lifestyles of *Xylella fastidiosa*. Annu Rev Phytopathol 46:243–271. doi:10.1146/annurev.phyto.45.062806.094342

Chen DQ, Montllor CB, Purcell AH (2000) Fitness effects of two facultative endosymbiotic bacteria on the pea aphid, *Acyrthosiphon pisum*, and the blue alfalfa aphid, *A. kondoi*. Entomol Exp Appl 95:315–323. doi:10.1046/j.1570-7458.2000.00670.x

Chiel E, Gottlieb Y, Zchori-Fein E, Mozes-Daube N, Katzir N, Inbar M, Ghanim M (2007) Biotype-dependent secondary symbiont communities in sympatric populations of *Bemisia tabaci*. Bull Entomol Res 97:407–413. doi:10.1017/s0007485307005159

Chouaia B, Rossi P, Epis S, Mosca M, Ricci I, Damiani C, Ulissi U, Crotti E, Daffonchio D, Bandi C, Favia G (2012) Delayed larval development in *Anopheles* mosquitoes deprived of *Asaia* bacterial symbionts. BMC Microbiol 12:S2. doi:10.1186/1471-2180-12-s1-s2

Chrostek E, Marialva MSP, Esteves SS, Weinert LA, Martinez J, Jiggins FM, Teixeira L (2013) *Wolbachia* variants induce differential protection to viruses in *Drosophila melanogaster*: a phenotypic and phylogenomic analysis. PLoS Genet 9:22. doi:10.1371/journal.pgen.1003896

Chuche J, Thiéry D (2014) Biology and ecology of the Flavescence dorée vector *Scaphoideus titanus*: a review. Agron Sustain Dev 34:381–403. doi:10.1007/s13593-014-0208-7

Coats JR (1994) Risks from natural versus synthetic insecticides. Ann Rev Entomol 39:489–515. doi:10.1146/annurev.en.39.010194.002421

Conord C, Despres L, Vallier A, Balmand S, Miquel C, Zundel S, Lemperiere G, Heddi A (2008) Long-term evolutionary stability of bacterial endosymbiosis in curculionoidea: additional evidence of symbiont replacement in the dryophthoridae family. Mol Biol Evol 25:859–868. doi:10.1093/molbev/msn027

Cook PE, McMeniman CJ, O'Neill SL (2008) Modifying insect population age structure to control vector-borne disease. In: Aksoy S (ed) Transgenesis and the management of vector-borne disease, vol 627., Advances in experimental medicine and biologySpringer, New York, pp 126–140. doi:10.1007/978-0-387-78225-6_11

Costa AS (1976) Whitefly-transmitted plant diseases. Annu Rev Phytopathol 14:429–449. doi:10.1146/annurev.py.14.090176.002241

Croft BA, Brown AWA (1975) Responses of arthropod natural enemies to insecticides. Ann Rev Entomol 20:285–335. doi:10.1146/annurev.en.20.010175.001441

Crotti E, Damiani C, Pajoro M, Gonella E, Rizzi A, Ricci I, Negri I, Scuppa P, Rossi P, Ballarini P, Raddadi N, Marzorati M, Sacchi L, Clementi E, Genchi M, Mandrioli M, Bandi C, Favia G, Alma A, Daffonchio D (2009) *Asaia*, a versatile acetic acid bacterial symbiont, capable of cross-colonizing insects of phylogenetically distant genera and orders. Environ Microbiol 11:3252–3264. doi:10.1111/j.1462-2920.2009.02048.x

Crotti E, Rizzi A, Chouaia B, Ricci I, Favia G, Alma A, Sacchi L, Bourtzis K, Mandrioli M, Cherif A, Bandi C, Daffonchio D (2010) Acetic acid bacteria, newly emerging symbionts of insects. Appl Environ Microbiol 76:6963–6970. doi:10.1128/aem.01336-10

Czosnek H, Laterrot H (1997) A worldwide survey of tomato yellow leaf curl viruses. Arch Virol 142:1391–1406. doi:10.1007/s007050050168

Dale C, Beeton M, Harbison C, Jones T, Pontes M (2006) Isolation, pure culture, and characterization of "*Candidatus* Arsenophonus arthropodicus," an intracellular secondary endosymbiont from the hippoboscid louse fly *Pseudolynchia canariensis*. Appl Environ Microbiol 72:2997–3004. doi:10.1128/aem.72.4.2997-3004.2006

Darby AC, Douglas AE (2003) Elucidation of the transmission patterns of an insect-borne bacterium. Appl Environ Microbiol 69:4403–4407. doi:10.1128/AEM.69.8.4403-4407.2003

Darby AC, Chandler SM, Welburn SC, Douglas AE (2005) Aphid-symbiotic bacteria cultured in insect cell lines. Appl Environ Microbiol 71:4833–4839. doi:10.1128/aem.71.8.4833-4839.2005

Daugherty MP, Lopes JRS, Almeida RPP (2010) Vector within-host feeding preference mediates transmission of a heterogeneously distributed pathogen. Ecol Entomol 35:350–366. doi:10.1111/j.1365-2311.2010.01189.x

De Clerck C, Tsuchida T, Massart S, Lepoivre P, Francis F, Jijakli MH (2014) Combination of genomic and proteomic approaches to characterize the symbiotic population of the banana aphid (Hemiptera: Aphididae). Environ Entomol 43:29–36. doi:10.1603/en13107

della Torre A, Costantini C, Besansky NJ, Caccone A, Petrarca V, Powell JR, Coluzzi M (2002) Speciation within *Anopheles gambiae*: the glass is half full. Science 298:115–117. doi:10.1126/science.1078170

Denholm I, Rowland MW (1992) Tactics for managing pesticide resistance in arthropods: theory and practice. Ann Rev Entomol 37:91–112. doi:10.1146/annurev.en.37.010192.000515

Desneux N, Decourtye A, Delpuech J-M (2007) The sublethal effects of pesticides on beneficial arthropods. Ann Rev Entomol 52:81–106. doi:10.1146/annurev.ento.52.110405.091440

Dheilly NM, Poulin R, Thomas F (2015) Biological warfare: microorganisms as drivers of host-parasite interactions. Infect Genet Evol. doi:10.1016/j.meegid.2015.05.027

Dowd PF, Shen SK (1990) The contribution of symbiotic yeast to toxin resistance of the cigarette beetle (*Lasioderma serricorne*). Entomol Exp Appl 56:241–248. doi:10.1111/j.1570-7458.1990.tb01402.x

Dunning Hotopp JC, Clark ME, Oliveira DCSG, Foster JM, Fischer P, Munoz Torres MC, Giebel JD, Kumar N, Ishmael N, Wang S, Ingram J, Nene RV, Shepard J, Tomkins J, Richards S, Spiro DJ, Ghedin E, Slatko BE, Tettelin H, Werren JH (2007) Widespread lateral gene transfer from intracellular bacteria to multicellular eukaryotes. Science 317:1753–1756. doi:10.1126/science.1142490

Duron O, Bouchon D, Boutin S, Bellamy L, Zhou L, Engelstädter J, Hurst GD (2008) The diversity of reproductive parasites among arthropods: *Wolbachia* do not walk alone. BMC Biol 6:27. doi:10.1186/1741-7007-6-27

Durvasula RV, Sundaram R, Beard CB (2003) *Rhodnius prolixus* and its symbiont, *Rhodococcus rhodnii*, a model for paratransgenic control of disease transmission. In: Bourtzis K, Miller TA (eds) Insect Symbiosis. CRC Press, Boca Raton, pp 85–97

Elbaz A, Clavel J, Rathouz PJ, Moisan F, Galanaud JP, Delemotte B, Alperovitch A, Tzourio C (2009) Professional exposure to pesticides and parkinson disease. Ann Neurol 66:494–504. doi:10.1002/ana.21717

Engelstadter J, Hurst GDD (2009) The ecology and evolution of microbes that manipulate host reproduction. Annu Rev Ecol Evol Syst 40:127–149. doi:10.1146/annurev.ecolsys.110308.120206

Everett KDE, Thao ML, Horn M, Dyszynski GE, Baumann P (2005) Novel chlamydiae in whiteflies and scale insects: endosymbionts '*Candidatus* Fritschea bemisiae' strain Falk and '*Candidatus* Fritschea eriococci' strain Elm. Int J Syst Evol Microbiol 55:1581–1587. doi:10.1099/ijs.0.63454-0

Ferrari J, Muller CB, Kraaijeveld AR, Godfray HCJ (2001) Clonal variation and covariation in aphid resistance to parasitoids and a pathogen. Evolution 55:1805–1814. doi:10.1554/0014-3820(2001)055[1805:CVACIA]2.0.CO;2

Ferrari J, Darby AC, Daniell TJ, Godfray HCJ, Douglas AE (2004) Linking the bacterial community in pea aphids with host-plant use and natural enemy resistance. Ecol Entomol 29:60–65. doi:10.1111/j.1365-2311.2004.00574.x

Ferrari J, Scarborough CL, Godfray HCJ (2007) Genetic variation in the effect of a facultative symbiont on host-plant use by pea aphids. Oecologia 153:323–329. doi:10.1007/s00442-007-0730-2

Ferrari J, West JA, Via S, Godfray HCJ (2012) Population genetic structure and secondary symbionts in host-associated populations of the pea aphid complex. Evolution 66:375–390. doi:10.1111/j.1558-5646.2011.01436.x

Ferrater J, Jong P, Dicke M, Chen Y, Horgan F (2013) Symbiont-mediated adaptation by planthoppers and leafhoppers to resistant rice varieties. Arthropod Plant Interact 7:591–605. doi:10.1007/s11829-013-9277-9

Frantz A, Calcagno V, Mieuzet L, Plantegenest M, Simon J-C (2009) Complex trait differentiation between host-populations of the pea aphid *Acyrthosiphon pisum* (Harris): implications for the evolution of ecological specialisation. Biol J Linn Soc 97:718–727. doi:10.1111/j.1095-8312.2009.01221.x

Frydman HM, Li JM, Robson DN, Wieschaus E (2006) Somatic stem cell niche tropism in *Wolbachia*. Nature 441:509–512. doi:10.1038/nature04756

Fuente LDL, Burr TJ, Hoch HC (2007) Mutations in type I and type IV pilus biosynthetic genes affect twitching motility rates in *Xylella fastidiosa*. J Bacteriol 189:7507–7510. doi:10.1128/jb.00934-07

Garnier M, Foissac X, Gaurivaud P, Laigret F, Renaudin J, Saillard C, Bové JM (2001) Mycoplasmas, plants, insect vectors: a matrimonial triangle. Cr Acad Sci III-Vie 324:923–928. doi:10.1016/S0764-4469(01)01372-5

Gehrer L, Vorburger C (2012) Parasitoids as vectors of facultative bacterial endosymbionts in aphids. Biol Lett 8:613–615. doi:10.1098/rsbl.2012.0144

Ghanim M (2014) A review of the mechanisms and components that determine the transmission efficiency of Tomato yellow leaf curl virus (Geminiviridae; Begomovirus) by its whitefly vector. Virus Res 186:47–54. doi:10.1016/j.virusres.2014.01.022

Gherna RL, Werren JH, Weisburg W, Cote R, Woese CR, Mandelco L, Brenner DJ (1991) *Arsenophonus nasoniae* gen. nov., sp. nov., the causative agent of the son-killer trait in the parasitic wasp *Nasonia vitripennis*. Int J Syst Bacteriol 41:563–565. doi:10.1099/00207713-41-4-563

Gnankiné O, Mouton L, Henri H, Terraz G, Houndeté T, Martin T, Vavre F, Fleury F (2012) Distribution of *Bemisia tabaci* (Homoptera: Aleyrodidae) biotypes and their associated symbiotic bacteria on host plants in West Africa. Insect Conserv Diver 6:411–421. doi:10.1111/j.1752-4598.2012.00206.x

Gonella E, Negri I, Marzorati M, Mandrioli M, Sacchi L, Pajoro M, Crotti E, Rizzi A, Clementi E, Tedeschi R, Bandi C, Alma A, Daffonchio D (2011) Bacterial endosymbiont localization in *Hyalesthes obsoletus*, the insect vector of Bois Noir in *Vitis* *vinifera*. Appl Environ Microbiol 77:1423–1435. doi:10.1128/aem.02121-10

Gonella E, Crotti E, Rizzi A, Mandrioli M, Favia G, Daffonchio D, Alma A (2012) Horizontal transmission of the symbiotic bacterium Asaia sp. in the leafhopper *Scaphoideus titanus* Ball (Hemiptera: Cicadellidae). BMC Microbiol 12:S4. doi:10.1186/1471-2180-12-S1-S4

Gonella E, Pajoro M, Marzorati M, Crotti E, Mandrioli M, Pontini M, Bulgari D, Negri I, Sacchi L, Chouaia B, Daffonchio D, Alma A (2015) Plant-mediated interspecific horizontal transmission of an intracellular symbiont in insects. Sci Rep 5:15811. doi:10.1038/srep15811

Gottlieb Y, Ghanim M, Chiel E, Gerling D, Portnoy V, Steinberg S, Tzuri G, Horowitz AR, Belausov E, Mozes-Daube N, Kontsedalov S, Gershon M, Gal S, Katzir N, Zchori-Fein E (2006) Identification and localization of a *Rickettsia* sp. in *Bemisia tabaci* (Homoptera: Aleyrodidae). Appl Environ Microbiol 72:3646–3652. doi:10.1128/AEM.72.5.3646-3652.2006

Gottlieb Y, Zchori-Fein E, Mozes-Daube N, Kontsedalov S, Skaljac M, Brumin M, Sobol I, Czosnek H, Vavre F, Fleury F, Ghanim M (2010) The transmission efficiency of tomato yellow leaf curl virus by the whitefly *Bemisia tabaci* is correlated with the presence of a specific symbiotic bacterium species. J Virol 84:9310–9317. doi:10.1128/jvi.00423-10

Grafton-Cardwell EE, Stelinski LL, Stansly PA (2013) Biology and management of Asian citrus psyllid, vector of the huanglongbing pathogens. Ann Rev Entomol 58:413–432. doi:10.1146/annurev-ento-120811-153542

Groot TVM, Breeuwer JAJ (2006) *Cardinium* symbionts induce haploid thelytoky in most clones of three closely related *Brevipalpus* species. Exp Appl Acarol 39:257–271. doi:10.1007/s10493-006-9019-0

Guedes RNC, Smagghe G, Stark JD, Desneux N (2016) Pesticide-induced stress in arthropod pests for optimized integrated pest management programs. Ann Rev Entomol 61:43–62. doi:10.1146/annurev-ento-010715-023646

Gueguen G, Vavre F, Gnankiné O, Peterschmitt M, Charif D, Chiel E, Gottlieb Y, Ghanim M, Zchori-Fein E, Fleury F (2010) Endosymbiont metacommunities, mtDNA diversity and the evolution of the *Bemisia tabaci* (Hemiptera: Aleyrodidae) species complex. Mol Ecol 19:4365–4378. doi:10.1111/j.1365-294X.2010.04775.x

Haapalainen M (2014) Biology and epidemics of *Candidatus* Liberibacter species, psyllid-transmitted plant-pathogenic bacteria. Ann Appl Biol 165:172–198. doi:10.1111/aab.12149

Hanboonsong Y, Choosai C, Panyim S, Damak S (2002) Transovarial transmission of sugarcane white leaf phytoplasma in the insect vector *Matsumuratettix hiroglyphicus* (Matsumura). Insect Mol Biol 11:97–103. doi:10.1046/j.0962-1075.2001.00314.x

Hardman JM, Rogers REL, Nyrop JP, Frisch T (1991) Effect of pesticide applications on abundance of European red mite (Acari: tetranychidae) and *Tryphlodromus pyri* (Acari: phytoseiidae) in Nova Scotian apple orchards. J Econ Entomol 84:570–580

Harrison BD (1958) Studies on the behavior of potato leaf roll and other viruses in the body of their aphid vector *Myzus persicae* (Sulz.). Virology 6:265–277. doi:10.1016/0042-6822(58)90074-6

Hazarika LK, Bhuyan M, Hazarika BN (2009) Insect pests of tea and their management. Ann Rev Entomol 54:267–284. doi:10.1146/annurev.ento.53.103106.093359

Heddi A, Gross R (2011) Proteobacteria as primary endosymbionts of Arthropods. In: Zchori-Fein E, Bourtzis K (eds) Manipulative tenants, Bacteria associated with Arthropods. CRC Press, Boca Raton, pp 1–27

Heddi A, Grenier AM, Khatchadourian C, Charles H, Nardon P (1999) Four intracellular genomes direct weevil biology: nuclear, mitochondrial, principal endosymbiont, and *Wolbachia*. Proc Natl Acad Sci USA 96:6814–6819. doi:10.1073/pnas.96.12.6814

Hedges LM, Brownlie JC, O'Neill SL, Johnson KN (2008) *Wolbachia* and virus protection in insects. Science 322:702. doi:10.1126/science.1162418

Hemingway J, Ranson H (2000) Insecticide resistance in insect vectors of human disease. Ann Rev Entomol 45:371–391. doi:10.1146/annurev.ento.45.1.371

Hibino H (1996) Biology and epidemiology of rice viruses. Annu Rev Phytopathol 34:249–274. doi:10.1146/annurev.phyto.34.1.249

Hilgenboecker K, Hammerstein P, Schlattmann P, Telschow A, Werren JH (2008) How many species are infected with *Wolbachia*?—A statistical analysis of current data. FEMS Microbiol Lett 281:215–220. doi:10.1111/j.1574-6968.2008.01110.x

Himler AG, Adachi-Hagimori T, Bergen JE, Kozuch A, Kelly SE, Tabashnik BE, Chiel E, Duckworth VE, Dennehy TJ, Zchori-Fein E, Hunter MS (2011) Rapid spread of a bacterial symbiont in an invasive whitefly is driven by fitness benefits and female bias. Science 332:254–256. doi:10.1126/science.1199410

Hoffmann AA, Montgomery BL, Popovici J, Iturbe-Ormaetxe I, Johnson PH, Muzzi F, Greenfield M, Durkan M, Leong YS, Dong Y, Cook H, Axford J, Callahan AG, Kenny N, Omodei C, McGraw EA, Ryan PA, Ritchie SA, Turelli M, O'Neill SL (2011) Successful establishment of *Wolbachia* in *Aedes* populations to suppress dengue transmission. Nature 476:454–457. doi:10.1038/nature10356

Hogenhout SA, Ammar E-D, Whitfield AE, Redinbaugh MG (2008) Insect vector interactions with persistently transmitted viruses. Annu Rev Phytopathol 46:327–359. doi:10.1146/annurev.phyto.022508.092135

Hughes GL, Allsopp PG, Webb RI, Ri Yamada, Iturbe-Ormaetxe I, Brumbley SM, O'Neill SL (2011) Identification of yeast associated with the planthopper, *Perkinsiella saccharicida*: potential applications for Fiji leaf gall control. Curr Microbiol 63:392–401. doi:10.1007/s00284-011-9990-5

Huo Y, Liu W, Zhang F, Chen X, Li L, Liu Q, Zhou Y, Wei T, Fang R, Wang X (2014) Transovarial transmission of a plant virus is mediated by vitellogenin of its insect vector. PLoS Pathog. doi:10.1371/journal.ppat.1003949

Hurst GDD, Jiggins FM (2000) Male-killing bacteria in insects: mechanisms, incidence, and implications. Emerg Infect Dis 6:329–336. doi:10.3201/eid0604.000402

Imo M (2013) Host race formation in *Hyalesthes obsoletus* (Signoret 1865). Johannes Gutenberg-Universität, Mainz

Jeger MJ, Holt J, Bosch FVD, Madden LV (2004) Epidemiology of insect-transmitted plant viruses: modelling disease dynamics and control interventions. Physiol Entomol 29:291–304. doi:10.1111/j.0307-6962.2004.00394.x

Kaiser W, Huguet E, Casas J, Commin C, Giron D (2010) Plant green-island phenotype induced by leaf-miners is mediated by bacterial symbionts. Proc R Soc Biol Sci Ser B 277:2311–2319. doi:10.1098/rspb.2010.0214

Kambris Z, Cook PE, Phuc HK, Sinkins SP (2009) Immune activation by life-shortening *Wolbachia* and reduced filarial competence in mosquitoes. Science 326:134–136. doi:10.1126/science.1177531

Karban R, Agrawal AA (2002) Herbivore offense. Annu Rev Ecol Syst 33:641–664. doi:10.1146/annurev.ecolsys.33.010802.150443

Kashima T, Nakamura T, Tojo S (2006) Uric acid recycling in the shield bug, *Parastrachia japonensis* (Hemiptera: Parastrachiidae), during diapause. J Insect Physiol 52:816–825. doi:10.1016/j.jinsphys.2006.05.003

Kawakita H, Saiki T, Wei W, Mitsuhashi W, Watanabe K, Sato M (2000) Identification of mulberry dwarf phytoplasmas in the genital organs and eggs of leafhopper *Hishimonoides* *sellatiformis*. Phytopathology 90:909–914. doi:10.1094/PHYTO.2000.90.8.909

Kikuchi Y, Hayatsu M, Hosokawa T, Nagayama A, Tago K, Fukatsu T (2012) Symbiont-mediated insecticide resistance. Proc Natl Acad Sci USA 109:8618–8622. doi:10.1073/pnas.1200231109

Larkin P, Kleven S, Banks P (2002) Utilizing Bdv2, the *Thinopyrum intermedium* source of BYDV resistance, to develop wheat cultivars. In: Henry M, McNab A (eds) Barley yellow dwarf disease: recent advances and future strategies. Proceedings International Symposium Mexico, 1–5 September, 2002 CIMMYT, pp 60–63

Laven H (1967) Eradication of *Culex pipiens fatigans* through cytoplasmic incompatibility. Nature 216:383–384. doi:10.1038/216383a0

Lee IM, Davis RE, Gundersen-Rindal DE (2000) Phytoplasma: Phytopathogenic mollicutes. Annu Rev Microbiol 54:221–255. doi:10.1146/annurev.micro.54.1.221

Lefèvre C, Charles H, Vallier A, Delobel B, Farrell B, Heddi A (2004) Endosymbiont phylogenesis in the Dryophthoridae weevils: evidence for bacterial replacement. Mol Biol Evol 21:965–973. doi:10.1093/molbev/msh063

Legg JP, Shirima R, Tajebe LS, Guastella D, Boniface S, Jeremiah S, Nsami E, Chikoti P, Rapisarda C (2014) Biology and management of *Bemisia* whitefly vectors of cassava virus pandemics in Africa. Pest Manag Sci 70:1446–1453. doi:10.1002/ps.3793

Leonardo TE (2004) Removal of a specialization-associated symbiont does not affect aphid fitness. Ecol Lett 7:461–468. doi:10.1111/j.1461-0248.2004.00602.x

Leonardo TE, Muiru GT (2003) Facultative symbionts are associated with host plant specialization in pea aphid populations. Proc R Soc Biol Sci Ser B 270:S209–S212. doi:10.1098/rsbl.2003.0064

Leroy PD, Sabri A, Heuskin S, Thonart P, Lognay G, Verheggen FJ, Francis F, Brostaux Y, Felton GW, Haubruge E (2011) Microorganisms from aphid honeydew attract and enhance the efficacy of natural enemies. Nat Commun 2:348. doi:10.1038/ncomms1347

Libbrecht R, Gwynn DM, Fellowes MDE (2007) *Aphidius ervi* preferentially attacks the green morph of the pea aphid, *Acyrthosiphon pisum*. J Insect Behav 20:25–32. doi:10.1007/s10905-006-9055-y

Losey JE, Harmon J, Ballantyne F, Brown C (1997) A polymorphism maintained by opposite patterns of parasitism and predation. Nature 388:269–272. doi:10.1038/40849

Lu P, Bian G, Pan X, Xi Z (2012) *Wolbachia* induces density-dependent inhibition to dengue virus in mosquito cells. PLoS Negl Trop Dis 6:e1754. doi:10.1371/journal.pntd.0001754

Łukasik P, van Asch M, Guo H, Ferrari J, Godfray CJ (2013) Unrelated facultative endosymbionts protect aphids against a fungal pathogen. Ecol Lett 16:214–218. doi:10.1111/ele.12031

Ma WJ, Vavre F, Beukeboom LW (2014) Manipulation of arthropod sex determination by endosymbionts: diversity and molecular mechanisms. Sex Dev 8:59–73. doi:10.1159/000357024

Maia IG, Haenni A-L, Bernardi F (1996) Potyviral HC-Pro: a multifunctional protein. J Gen Virol 77:1335–1341. doi:10.1099/0022-1317-77-7-1335

Marzorati M, Alma A, Sacchi L, Pajoro M, Palermo S, Brusetti L, Raddadi N, Balloi A, Tedeschi R, Clementi E, Corona S, Quaglino F, Bianco PA, Beninati T, Bandi C, Daffonchio D (2006) A novel bacteroidetes symbiont is localized in *Scaphoideus titanus*, the insect vector of flavescence dorée in *Vitis vinifera*. Appl Environ Microbiol 72:1467–1475. doi:10.1128/AEM.72.2.1467-1475.2006

McGraw EA, O'Neill SL (2013) Beyond insecticides: new thinking on an ancient problem. Nat Rev Microbiol 11:181–193. doi:10.1038/nrmicro2968

Miller WA, Rasochová L (1997) Barley yellow dwarf viruses. Annu Rev Phytopathol 35:167–190. doi:10.1146/annurev.phyto.35.1.167

Moll RM, Romoser WS, Modrakowski MC, Moncayo AC, Lerdthusnee K (2001) Meconial peritrophic membranes and the fate of midgut bacteria during mosquito (Diptera: Culicidae) metamorphosis. J Med Entomol 38:29–32. doi:10.1603/0022-2585-38.1.29

Montllor CB, Maxmen A, Purcell AH (2002) Facultative bacterial endosymbionts benefit pea aphids *Acyrthosiphon pisum* under heat stress. Ecol Entomol 27:189–195. doi:10.1046/j.1365-2311.2002.00393.x

Moran NA (2006) Symbiosis. Curr Biol 16:R866–871. doi:10.1016/j.cub.2006.09.019

Moran NA, Dunbar HE (2006) Sexual acquisition of beneficial symbionts in aphids. Proc Natl Acad Sci USA 103:12803–12806. doi:10.1073/pnas.0605772103

Moran NA, Degnan PH, Santos SR, Dunbar HE, Ochman H (2005) The players in a mutualistic symbiosis: Insects, bacteria, viruses, and virulence genes. Proc Natl Acad Sci USA 102:16919–16926. doi:10.1073/pnas.0507029102

Moran NA, McCutcheon JP, Nakabachi A (2008) Genomics and evolution of heritable bacterial symbionts. Annu Rev Genet 42:165–190. doi:10.1146/annurev.genet.41.110306.130119

Moreira LA, Iturbe-Ormaetxe I, Jeffery JA, Lu G, Pyke AT, Hedges LM, Rocha BC, Hall-Mendelin S, Day A, Riegler M, Hugo LE, Johnson KN, Kay BH, McGraw EA, van den Hurk AF, Ryan PA, O'Neill SL (2009) A *Wolbachia* symbiont in *Aedes aegypti* limits infection with dengue, Chikungunya, and *Plasmodium*. Cell 139:1268–1278. doi:10.1016/j.cell.2009.11.042

Murdock CC, Blanford S, Hughes GL, Rasgon JL, Thomas MB (2014) Temperature alters *Plasmodium* blocking by *Wolbachia*. Sci Rep. doi:10.1038/srep03932

Nault LR (1997) Arthropod transmission of plant viruses: a new synthesis. Ann Entomol Soc Am 90:522–541. doi:10.1093/aesa/90.5.521

O'Connor L, Plichart C, Sang AC, Brelsfoard CL, Bossin HC, Dobson SL (2012) Open release of male mosquitoes infected with a *Wolbachia* biopesticide: field performance and infection containment. PLoS Negl Trop Dis 6:e1797. doi:10.1371/journal.pntd.0001797

Oerke EC (2006) Crop losses to pests. J Agric Sci 144:31–43. doi:10.1017/s0021859605005708

Oliver KM, Russell JA, Moran NA, Hunter MS (2003) Facultative bacterial symbionts in aphids confer resistance to parasitic wasps. Proc Natl Acad Sci USA 100:1803–1807. doi:10.1073/pnas.0335320100

Oliver KM, Campos J, Moran NA, Hunter MS (2008) Population dynamics of defensive symbionts in aphids. Proc R Soc Biol Sci Ser B 275:293–299. doi:10.1098/rspb.2007.1192

Oliver KM, Degnan PH, Hunter MS, Moran NA (2009) Bacteriophages encode factors required for protection in a symbiotic mutualism. Science 325:992–994. doi:10.1126/science.1174463

Oliver KM, Degnan PH, Burke GR, Moran NA (2010) Facultative symbionts in aphids and the horizontal transfer of ecologically important traits. Ann Rev Entomol 55:247–266. doi:10.1146/annurev-ento-112408-085305

Ordon F, Habekuss A, Kastirr U, Rabenstein F, Kühne T (2009) Virus resistance in cereals: sources of resistance, genetics and breeding. J Phytopathol 157:535–545. doi:10.1111/j.1439-0434.2009.01540.x

Pannebakker BA, Pijnacker LP, Zwaan BJ, Beukeboom LW (2004) Cytology of *Wolbachia*-induced parthenogenesis in *Leptopilina clavipes* (Hymenoptera: Figitidae). Genome 47:299–303. doi:10.1139/G03-137

Patil CD, Borase HP, Salunke BK, Patil SV (2013) Alteration in *Bacillus thuringiensis* toxicity by curing gut flora: novel approach for mosquito resistance management. Parasitol Res 112:3283–3288. doi:10.1007/s00436-013-3507-z

Pérez-Brocal V, Gil R, Ramos S, Lamelas A, Postigo M, Michelena JM, Silva FJ, Moya A, Latorre A (2006) A small microbial genome: the end of a long symbiotic relationship? Science 314:312–313. doi:10.1126/science.1130441

Perlman SJ, Hunter MS, Zchori-Fein E (2006) The emerging diversity of *Rickettsia*. Proc R Soc Biol Sci Ser B 273:2097–2106. doi:10.1098/rspb.2006.3541

Polin S, Le Gallic J-Fo, Simon J-C, Tsuchida T, Outreman Y (2015) Conditional reduction of predation risk associated with a facultative symbiont in an insect. PLoS One 10:e0143728. doi:10.1371/journal.pone.0143728

Pontes MH, Dale C (2006) Culture and manipulation of insect facultative symbionts. Trends Microbiol 14:406–412. doi:10.1016/j.tim.2006.07.004

Powles SB (2008) Evolved glyphosate-resistant weeds around the world: lessons to be learnt. Pest Manag Sci 64:360–365. doi:10.1002/ps.1525

Purcell AH (1979) Evidence for noncirculative transmission of Pierce's disease bacterium by sharpshooter leafhoppers. Phytopathology. doi:10.1094/Phyto-69-393

Quenouille J, Vassilakos N, Moury B (2013) Potato virus Y: a major crop pathogen that has provided major insights into the evolution of viral pathogenicity. Mol Plant Pathol 14:439–452. doi:10.1111/mpp.12024

Rana VS, Singh ST, Priya NG, Kumar J, Rajagopal R (2012) *Arsenophonus* GroEL interacts with CLCuV and is localized in midgut and salivary gland of whitefly *B. tabaci*. PLoS One 7:e42168. doi:10.1371/journal.pone.0042168

Rancès E, Ye YH, Woolfit M, McGraw EA, O'Neill SL (2012) The relative importance of innate immune priming in *Wolbachia*-mediated dengue interference. PLoS Pathog 8:e1002548. doi:10.1371/journal.ppat.1002548

Rasgon JL, Scott TW (2004) Impact of population age structure on *Wolbachia* transgene driver efficacy: ecologically complex factors and release of genetically modified mosquitoes. Insect Biochem Mol Biol 34:707–713. doi:10.1016/j.ibmb.2004.03.023

Riehle MA, Jacobs-Lorena M (2005) Using bacteria to express and display anti-parasite molecules in mosquitoes: current and future strategies. Insect Biochem Mol Biol 35:699–707. doi:10.1016/j.ibmb.2005.02.008

Rousset F, Bouchon D, Pintureau B, Juchault P, Solignac M (1992) *Wolbachia* endosymbionts responsible for various alterations of sexuality in arthropods. Proc R Soc Biol Sci Ser B 250:91–98. doi:10.1098/rspb.1992.0135

Russell JA, Latorre A, Sabater-Munoz B, Moya A, Moran NA (2003) Side-stepping secondary symbionts: widespread horizontal transfer across and beyond the Aphidoidea. Mol Ecol 12:1061–1075. doi:10.1046/j.1365-294X.2003.01780.x

Russell JA, Weldon S, Smith AH, Kim KL, Hu Y, Lukasik P, Doll S, Anastopoulos I, Novin M, Oliver KM (2013) Uncovering symbiont-driven genetic diversity across North American pea aphids. Mol Ecol 22:2045–2059. doi:10.1111/mec.12211

Sacchi L, Genchi M, Clementi E, Bighardi E, Avanzati AM, Pajoro M, Negri I, Marzorati M, Gonella E, Alma A, Daffonchio D, Bandi C (2008) Multiple symbiosis in the leafhopper *Scaphoideus titanus* (Hemiptera : Cicadellidae): details of transovarial transmission of *Cardinium sp* and yeast-like endosymbionts. Tissue Cell 40:231–242. doi:10.1016/j.tice.2007.12.005

Salar P, Sémétey O, Danet J-L, Boudon-Padieu E, Foissac X (2010) '*Candidatus* Phlomobacter fragariae' and the proteobacterium associated with the low sugar content syndrome of sugar beet are related to bacteria of the arsenophonus clade detected in hemipteran insects. Eur J Plant Pathol 126:123–127. doi:10.1007/s10658-009-9520-5

Salar P, Charenton C, Foissac X, Malembic-Maher S (2013) Multiplication kinetics of Flavescence dorée phytoplasma in broad bean. Effect of phytoplasma strain and temperature. Eur J Plant Pathol 135:371–381. doi:10.1007/s10658-012-0093-3

Sandström JP, Russell JA, White JP, Moran NA (2001) Independent origins and horizontal transfer of bacterial symbionts of aphids. Mol Ecol 10:217–228. doi:10.1046/j.1365-294X.2001.01189.x

Sasaki T, Kawamura M, Ishikawa H (1996) Nitrogen recycling in the brown planthopper, *Nilaparvata lugens*: involvement of yeast-like endosymbionts in uric acid metabolism. J Insect Physiol 42:125–129. doi:10.1016/0022-1910(95)00086-0

Scarborough CL, Ferrari J, Godfray HCJ (2005) Aphid protected from pathogen by endosymbiont. Science 310:1781. doi:10.1126/science.1120180

Sémétey O, Gatineau F, Bressan A, Boudon-Padieu E (2007) Characterization of a γ-3 proteobacteria responsible for the syndrome "Basses Richesses" of sugar beet transmitted by *Pentastiridius* sp. (Hemiptera, Cixiidae). Phytopathology 97:72–78. doi:10.1094/phyto-97-0072

Simon JC, Carre S, Boutin M, Prunier-Leterme N, Sabater-Munoz B, Latorre A, Bournoville R (2003) Host-based divergence in populations of the pea aphid: insights from nuclear markers and the prevalence of facultative symbionts. Proc R Soc Biol Sci Ser B 270:1703–1712. doi:10.1098/rspb.2003.2430

Soto MJ, Gilbertson RL (2003) Distribution and rate of lovement of the Curtovirus *Beet mild curly top virus* (Family *Geminiviridae*) in the beet leafhopper. Phytopathology 93:478–484. doi:10.1094/phyto.2003.93.4.478

Stavrinides J, McCloskey JK, Ochman H (2009) Pea aphid as both host and vector for the phytopathogenic bacterium *Pseudomonas syringae*. Appl Environ Microbiol 75:2230–2235. doi:10.1128/aem.02860-08

Stouthamer R, Breeuwer JAJ, Hurst GDD (1999) *Wolbachia pipientis*: Microbial manipulator of arthropod reproduction. Annu Rev Microbiol 53:71–102. doi:10.1146/annurev.micro.53.1.71

Tajebe LS, Guastella D, Cavalieri V, Kelly SE, Hunter MS, Lund OS, Legg JP, Rapisarda C (2015) Diversity of symbiotic bacteria associated with *Bemisia tabaci* (Homoptera: Aleyrodidae) in cassava mosaic disease pandemic areas of Tanzania. Ann Appl Biol 166:297–310. doi:10.1111/aab.12183

Tedeschi R, Ferrato V, Rossi J, Alma A (2006) Possible phytoplasma transovarial transmission in the psyllids *Cacopsylla melanoneura* and *Cacopsylla pruni*. Plant Pathol 55:18–24. doi:10.1111/j.1365-3059.2005.01292.x

Thao ML, Clark MA, Baumann L, Brennan EB, Moran NA, Baumann P (2000) Secondary endosymbionts of psyllids have been acquired multiple times. Curr Microbiol 41:300–304. doi:10.1007/s002840010138

Thierry M, Becker N, Hajri A, Reynaud B, Lett JM, Delatte H (2011) Symbiont diversity and non-random hybridization among indigenous (Ms) and invasive (B) biotypes of *Bemisia tabaci*. Mol Ecol 20:2172–2187. doi:10.1111/j.1365-294X.2011.05087.x

Tsuchida T, Koga R, Fukatsu T (2004) Host plant specialization governed by facultative symbiont. Science 303:1989. doi:10.1126/science.1094611

Tsuchida T, Koga R, Horikawa M, Tsunoda T, Maoka T, Matsumoto S, Simon J-C, Fukatsu T (2010) Symbiotic bacterium modifies aphid body color. Science 330:1102–1104. doi:10.1126/science.1195463

Tsuchida T, Koga R, Matsumoto S, Fukatsu T (2011) Interspecific symbiont transfection confers a novel ecological trait to the recipient insect. Biol Lett 7:245–248. doi:10.1098/rsbl.2010.0699

Turelli M (2010) Cytoplasmic incompatibility in populations with overlapping generations. Evolution 64:232–241. doi:10.1111/j.1558-5646.2009.00822.x

Turley AP, Moreira LA, O'Neill SL, McGraw EA (2009) *Wolbachia* infection reduces blood-feeding success in the dengue fever mosquito, *Aedes aegypti*. PLoS Negl Trop Dis 3:e516. doi:10.1371/journal.pntd.0000516

van den Berg MA (1990) The citrus psylla, *Trioza erytreae* (Del Guercio) (Hemiptera: Triozidae): a review. Agric Ecosyst Environ 30:171–194. doi:10.1016/0167-8809(90)90104-L

van den Bosch F, Gilligan CA (2008) Models of fungicide resistance dynamics. Annu Rev Phytopathol 46:123–147. doi:10.1146/annurev.phyto.011108.135838

van den Heuvel JFJM, Hogenhout SA, van der Wilk F (1999) Recognition and receptors in virus transmission by arthropods. Trends Microbiol 7:71–76. doi:10.1016/s0966-842x(98)01434-6

Vorburger C (2014) The evolutionary ecology of symbiont-conferred resistance to parasitoids in aphids. Insect Sci 21:251–264. doi:10.1111/1744-7917.12067

Vorburger C, Sandrock C, Gouskov A, Castaneda LE, Ferrari J (2009) Genotypic variation and the role of defensive endosymbionts in an all-parthenogenetic host–parasitoid interaction. Evolution 63:1439–1450. doi:10.1111/j.1558-5646.2009.00660.x

Vorburger C, Gehrer L, Rodriguez P (2010) A strain of the bacterial symbiont *Regiella insecticola* protects aphids against parasitoids. Biol Lett 6:109–111. doi:10.1098/rsbl.2009.0642

Wang Z, Su X-M, Wen J, Jiang L-Y, Qiao G-X (2014) Widespread infection and diverse infection patterns of *Wolbachia* in Chinese aphids. Insect Sci 21:313–325. doi:10.1111/1744-7917.12102

Weeks AR, Velten R, Stouthamer R (2003) Incidence of a new sex-ratio-distorting endosymbiotic bacterium among arthropods. Proc R Soc Lond B 270:1857–1865. doi:10.1098/rspb.2003.2425

Weintraub PG, Beanland L (2006) Insect vectors of phytoplasmas. Ann Rev Entomol 51:91–111. doi:10.1146/annurev.ento.51.110104.151039

Welburn SC, Maudlin I, Ellis DS (1987) *In vitro* cultivation of rickettsia-like-organisms from *Glossina* spp. Ann Trop Med Parasitol 81:331–335

Weldon SR, Strand MR, Oliver KM (2013) Phage loss and the breakdown of a defensive symbiosis in aphids. Proc R Soc Biol Sci Ser B 280:20122103. doi:10.1098/rspb.2012.2103

Werren JH (1997) Biology of *Wolbachia*. Ann Rev Entomol 42:587–609. doi:10.1146/annurev.ento.42.1.587

Whitfield AE, Ullman DE, German TL (2005) Tospovirus-thrips interactions. Annu Rev Phytopathol 43:459–489. doi:10.1146/annurev.phyto.43.040204.140017

Wilkes TE, Darby AC, Choi JH, Colbourne JK, Werren JH, Hurst GDD (2010) The draft genome sequence of *Arsenophonus nasoniae*, son-killer bacterium of *Nasonia vitripennis*, reveals genes associated with virulence and symbiosis. Insect Mol Biol 19:59–73. doi:10.1111/j.1365-2583.2009.00963.x

Zchori-Fein E, Brown JK (2002) Diversity of prokaryotes associated with *Bemisia tabaci* (Gennadius) (Hemiptera: Aleyrodidae). Ann Entomol Soc Am 95:711–718. doi:10.1603/0013-8746(2002)095[0711:DOPAWB]2.0.CO;2

Zug R, Hammerstein P (2012) Still a host of hosts for *Wolbachia*: analysis of recent data suggests that 40 % of terrestrial arthropod species are infected. PLoS One 7:3. doi:10.1371/journal.pone.0038544

Zug R, Hammerstein P (2015) Bad guys turned nice? A critical assessment of *Wolbachia* mutualisms in arthropod hosts. Biol Rev 90:89–111. doi:10.1111/brv.12098