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Review

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Review

Evolutionary Diversification in Insect Vector–Phytoplasma–Plant Associations

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Abstract

The association between insect herbivores and vascular plants represents one of the greatest success stories in terrestrial evolution. Specific mechanisms generating diversity in the association remain poorly understood, but it has become increasingly clear that microbes play important roles in mediating plant–insect interactions. Previous research on phytoplasmas (*Acholeplasmatales*: *Acholeplasmataceae*), a diverse group of plant-pathogenic bacteria, and their hemipteran insect vectors suggests that this system provides a new model for understanding how interactions among distantly related but ecologically associated groups of organisms can drive evolutionary diversification. Phytoplasma infections affect the phenotypes of both plants and vectors, altering functional traits (e.g., diet breadth) and mediating host shifts which may, in turn, alter genetic and phylogenetic patterns. This review highlights previous research on the functional ecology and phylogenetic components of phytoplasma-plant-vector (PPV) associations relevant to the evolutionary diversification of this system. Although phytoplasmas and their hosts occur in most terrestrial biomes and have evolved together over the past 300+ million years, major gaps in knowledge of PPV associations remain because most prior research on the system focused on strategies for mitigating effects of phytoplasma diseases in agroecosystems. Study of this system within a broader evolutionary context could help elucidate mechanisms by which interactions between insect herbivores, microbes, and plants drive biological diversification and also help predict the emergence of diseases affecting agriculture. Future research should more thoroughly document PPV associations in natural habitats, examine the relative prevalence of cospeciation versus host shifts in this system, and test possible macroevolutionary consequences of host manipulation by phytoplasmas.

Key words: biodiversity, coevolution, herbivore, plant pathogen, Hemiptera

Earth's biodiversity comprises approximately 8.7 million extant species (Mora et al. 2011). About half of these species are insects and half of all insect species are herbivores (Nakadai 2017). Thus, the 400 million-year association between insect herbivores and vascular plants represents one of the greatest success stories in evolutionary history (Schoonhoven et al. 2005). Despite extensive research on the ecology and evolutionary patterns of insect–plant associations, the underlying mechanisms that generated species diversity in this system remain poorly understood (Futuyma 1991, Futuyma and Agrawal 2009, Kergoat et al. 2017, Mayhew 2018, Hardy et al. 2020). Strict co-speciation of insects and their host plants appears to be quite rare although closely related insects often feed on related plant species (Ehrlich and Raven 1964, Agosta 2006, Nyman 2010). In contrast, host shifts among distantly related plants occurred frequently in many different insect herbivore lineages (Mitter et al. 1991, Hoberg and Brooks 2008, Agosta et al. 2010, Forbes et al. 2017, Kergoat et al. 2017). Such shifts have major potential evolutionary consequences because they can open up new adaptive landscapes that promote speciation, but the ecological and genetic mechanisms driving such shifts remain poorly understood (Janz et al. 2006, Hardy 2017).

Symbiotic associations between plant-feeding insects and microbes are ubiquitous and microbial associates play crucial roles in mediating plant–insect trophic interactions (Janson et al. 2008, Giron et al. 2017). Much recent research on such associations has focused on obligate endosymbionts that supply essential nutrients lacking from insect diets (Moran et al. 2005, 2008; Takiya et al. 2006; Joy 2013; Sudakaran et al. 2015; Bell-Roberts et al. 2019). The origins of such mutualisms remain poorly understood although it has been suggested that mutualists often evolve from parasites (Degnan et al. 2011, Sachs et al. 2011, Chomicki et al. 2020). Parasitic bacteria, including plant pathogens, often manipulate host behavior and physiology in ways that might be expected to drive evolutionary diversification (Thomas et al. 2012, Mauck et al. 2014, 2018), such as triggering of host shifts

(Heil 2016, De Fine Licht 2018). Here we focus on one tri-trophic association involving a group of parasitic bacteria, the phytoplasma s (*Acholeplasmatales*: *Acholeplasmataceae*), their vascular plant hosts and their hemipteran insect vectors (hereafter referred to as PPV). Improved understanding of the evolution of such associations may help explain the origins of a substantial portion of extant terrestrial biodiversity (Harvell 2004, Blitzer et al. 2012, Zhan et al. 2014) as well as provide improved methods for predicting the emergence of vector-borne diseases affecting agriculture.

The PPV System

Phytoplasmas

Phytoplasmas are a diverse lineage of bacteria (phylum *Tenericutes,* class *Mollicutes*) strictly associated with the phloem sieve elements of vascular plants and internal organs of phloem-feeding hemipteran insects. Phytoplasmas, as well as three vector-borne *Mollicutes* species in the genus *Spiroplasma* (e.g., Kwon et al. 1999) and the *Alphaproteobacteria* '*Candidatus* Liberibacter' taxa, are obligate inhabitants of hosts representing two distantly related Kingdoms, plants (Plantae) and insects (Animalia), and have a unique life cycle among known plant pathogenic bacteria. The life cycle involves acquisition of the bacteria from an infected plant by a hemipteran insect, movement across multiple barriers within the insect vector's body, replication over several days, and inoculation into other plants (i.e., a persistent-propagative transmission mode) in order for dissemination across the environment to occur (Hogenhout et al. 2008, Huang et al. 2020).

Although they are responsible for major economic loss in cultivated crops and other plants (Bertaccini et al. 2014), phytoplasmas are among the least known *Mollicutes*, having been first observed in 1967 (Doi et al. 1967). To date, 35 groups and >150 subgroups have been recognized based on a *16S rRNA* gene sequence-based restriction fragment length polymorphism profiling scheme (Lee et al. 1993), and 43 have the provisional taxonomic status '*Candidatus*,' denoting putative species of not-yet cultured bacteria (Lee et al. 2000, 2011; IRPCM 2004; Zhao et al. 2009; Davis et al. 2012; Nejat et al. 2013). Each 16Sr rRNA group is designated by a Roman numeral, and different strains within each group are given a separate letter designation (e.g., 16Sr II-A). Phytoplasmas inhabit and multiply within the cytoplasm of host cells, and have the smallest genomes of all known plant pathogenic bacteria (~530–1,350 kb). Although there are a few reported cases of vertical transmission of phytoplasmas in plants (via seeds; e.g., Cordova et al. 2003) and in insects (transovarial; e.g., Alma et al. 1997, Hanboonsong et al. 2002, Tedeschi et al. 2006), the primary mode by which phytoplasmas move from plant to plant is horizontal transmission, almost always via hemipteran (sap-sucking) insect vectors, which obtain them by feeding on the phloem of infected plants and transmit them to other plants through dispersal and additional feeding or, very rarely, via parasitic plants (Dale and Kim 1969).

Associations with Plants

Phytoplasmas are distributed worldwide and infect ~700 plant species (in 100 families; Supp Table 1A [online only]) but many groups appear to be restricted to particular biogeographic regions and/or plant families (Trivellone 2019). Network analysis of the co-occurrence of 16S rRNA phytoplasma groups with their plant hosts indicates that the associations are significantly modular and nested (Trivellone and Flores Garcia 2019). This suggests that the pathosystem is specialized, with each phytoplasma group infecting a specific array of plants. Only three groups of phytoplasmas (16SrI, II, and XII) are associated with relatively large numbers of plant families and species (75, 36, 44 families and 201, 106, 116 species, respectively) (Fig. 1 reprinted from Trivellone and Flores Garcia 2019; Supp Table 1A [online only]). However, because nearly all available data on phytoplasma–plant associations were gathered by testing plants showing disease symptoms, these results may be biased by a general lack of data on phytoplasma prevalence in asymptomatic plants (e.g., Silva et al. 2014, Soufi and Komor 2014 in agroecosystems) and plants occurring primarily in natural areas. One recent regional survey of the prevalence of phytoplasma-infected symptomless wild plants in grassland surrounding agroecosystems showed that more than half of the noncrop species sampled were naturally infected (Zwolińska et al. 2019). Unfortunately, such studies are rare and the general lack of data on phytoplasmas infecting noneconomically important plants hampers the accurate assessment of potential plant-to-plant dispersal, especially due to polyphagous vectors which may enable phytoplasmas to traverse buffer zones between managed (agroecosystems) and unmanaged areas.

Associations with Insects

Phytoplasmas have been detected (via PCR and microscopy) in many phloem-feeding hemipteran species that have fed on infected plants. However, many hemipterans capable of acquiring phytoplasma infections have been shown to be incapable of transmitting them from plant to plant, i.e., they are dead-end hosts for the phytoplasma (e.g., *Metcalfa pruinosa* (Say) (Hemiptera: Flatidae) and *Ricania speculum* (Walker) (Hemiptera: Ricaniidae) for 16SrV-D phytoplasma; Galetto et al. 2019, Trivellone et al. 2019). For plant-to-plant transmission to occur, phytoplasmas, once acquired by the vector, must cross the midgut membrane, enter the hemolymph, replicate in various insect tissues, migrate to and cross the salivary gland membrane, and enter the saliva prior to feeding by the vector on a different plant (Lherminier et al. 1990, Lefol et al. 1994, Nakashima and Hayashi 1995). When an insect is able to acquire a phytoplasma from one plant and successfully transmit it to the phloem tissue of another plant, it is considered a competent vector for that specific pathogen strain.

About 200 insect species (in 13 families of Hemiptera: Auchenorrhyncha, Fulgoromorpha and Cicadomorpha, and Psylloidea; Supp Table 1B [online only]) are reported to be associated with phytoplasmas but fewer than half of them are competent vectors. Known phytoplasma vectors are scattered among several distantly related lineages. Most known vectors are leafhoppers (Cicadellidae); fewer are known among the planthoppers (Fulgoroidea) and only two genera of jumping plant lice (Sternorrhyncha: Psyllidae) are known to include phytoplasma vectors (Weintraub et al. 2019). Different vector groups are associated with different lineages of phytoplasmas. Among leafhoppers, known vectors are clustered within a few subfamilies, tribes, and genera (Trivellone et al. 2017, Trivellone 2019) suggesting that vector competence is rare but has evolved independently multiple times (Dietrich 2013). Several hemipteran genera include multiple vector species (Dietrich 2013), suggesting that vector competence can be an evolutionarily conservative trait maintained through multiple speciation events. Although vectors still have not yet been identified for most phytoplasma strains, many of the better studied strains appear to be associated with a single competent vector species or genus. Only a few phytoplasmas (e.g., 16SrI and XII) have multiple reported potential and competent vectors (5, 9 families and 77, 65 species, respectively) (Fig. 2 adapted from Trivellone and Flores Garcia 2019; Supp Table 1B [online only]) (Trivellone 2018, 2019). Particular groups of phytoplasmas also exclusively interact with particular groups of

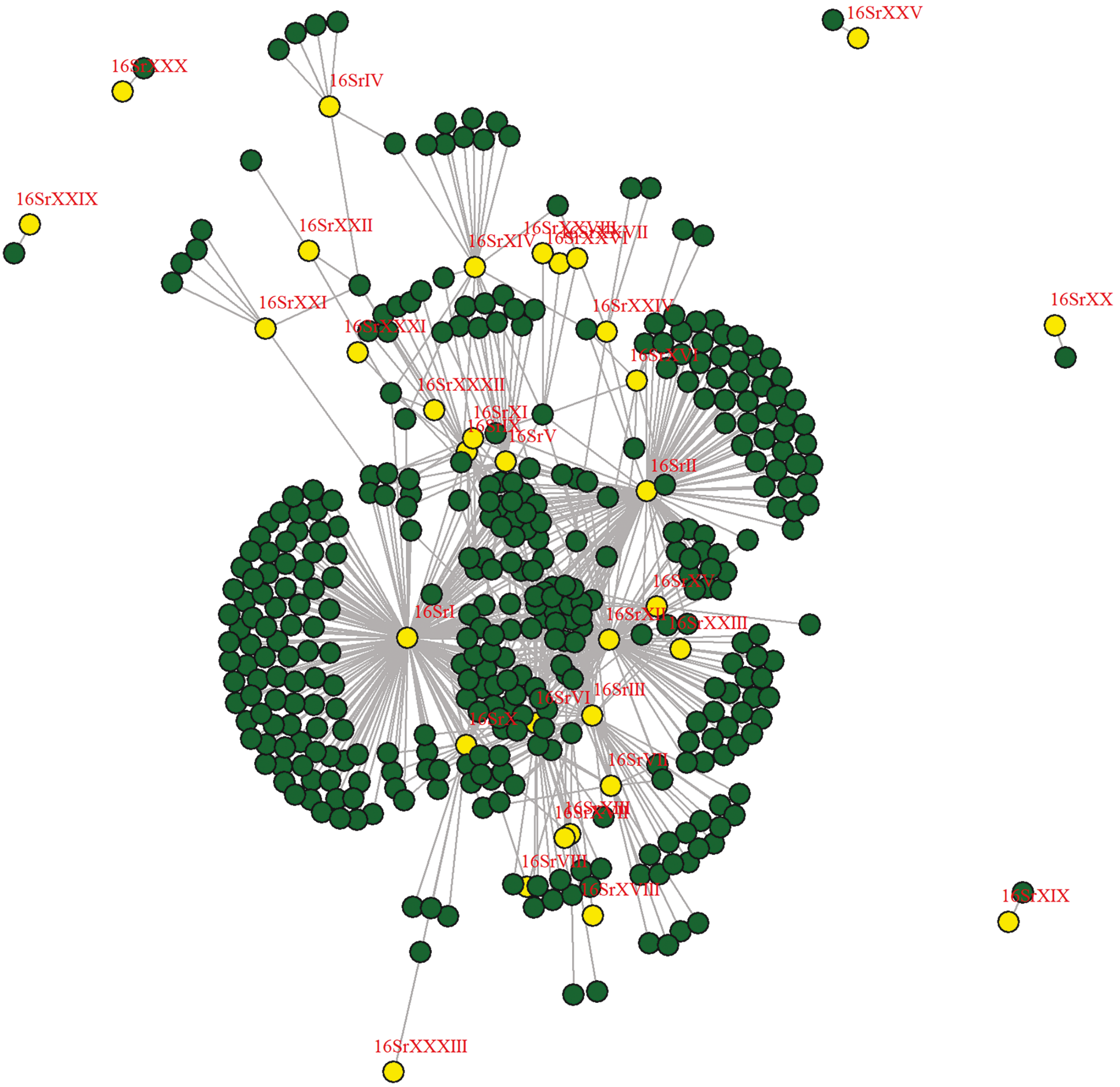

Fig. 1. Network graph of the interactions between phytoplasma groups (yellow/empty nodes identified by 16Sr followed by roman numeral number) and plant hosts (green/filled). The phytoplasma–plant dataset was analyzed and graphed using the *igraph* package (Csardi and Nepusz 2006) in R version 4.0.2 (R Core Team 2020). Reprinted from Trivellone and Flores Garcia (2019). Specific associations with plant taxa are summarized here: http://trivellone.speciesfile.org/tree.asp?key=trivellone.ins-phy-pla&b=Tracheophyta&t=List%20of%20Plants.

competent vectors (e.g., 16SrX group and Psylloidea). Unfortunately, there remain large gaps in knowledge of phytoplasma associations with insects, particularly in natural ecosystems.

A few recent investigations began elucidating molecular factors involved in the capacity of phytoplasmas to colonize insect tissues. The membrane proteins of several phytoplasmas have been sequenced and classified into three types: Immunodominant, Immunodominant A, and Antigenic membrane protein (Imp, IdpA and Amp, respectively) (Kakizawa et al. 2006). Phytoplasma Amp interacts with various insect proteins, e.g., actin, myosin, and ATP synthase, suggesting that the formation of an Amp-microfilament complex is correlated with ability of leafhopper vectors to transmit phytoplasmas from plant to plant (Suzuki et al. 2006, Kakizawa et al. 2009, Galetto et al. 2011). Rashidi et al. (2015) also provided indirect experimental evidence of the in vivo role of phytoplasma Amp in movement through the vector midgut epithelium and colonization of the salivary glands. Using an Imp-insect proteins model, Trivellone et al. (2019) provided evidence for a continuum in interaction capability with 16SrV-D phytoplasma among phylogenetically unrelated insect species, including nonvector hosts (2 species), potential vectors (2), and competent vectors (2), with the latter showing the strongest interactions. Several insect genes have been shown to facilitate movement of phytoplasmas within the body of the vector (Galetto et al. 2011) but genetic factors associated with vector capacity require more study. Specific mutations in several insect and phytoplasma protein-encoding genes that allow such protein–protein interactions suggest that persistent phytoplasma–vector associations involve a considerable amount of co-evolution.

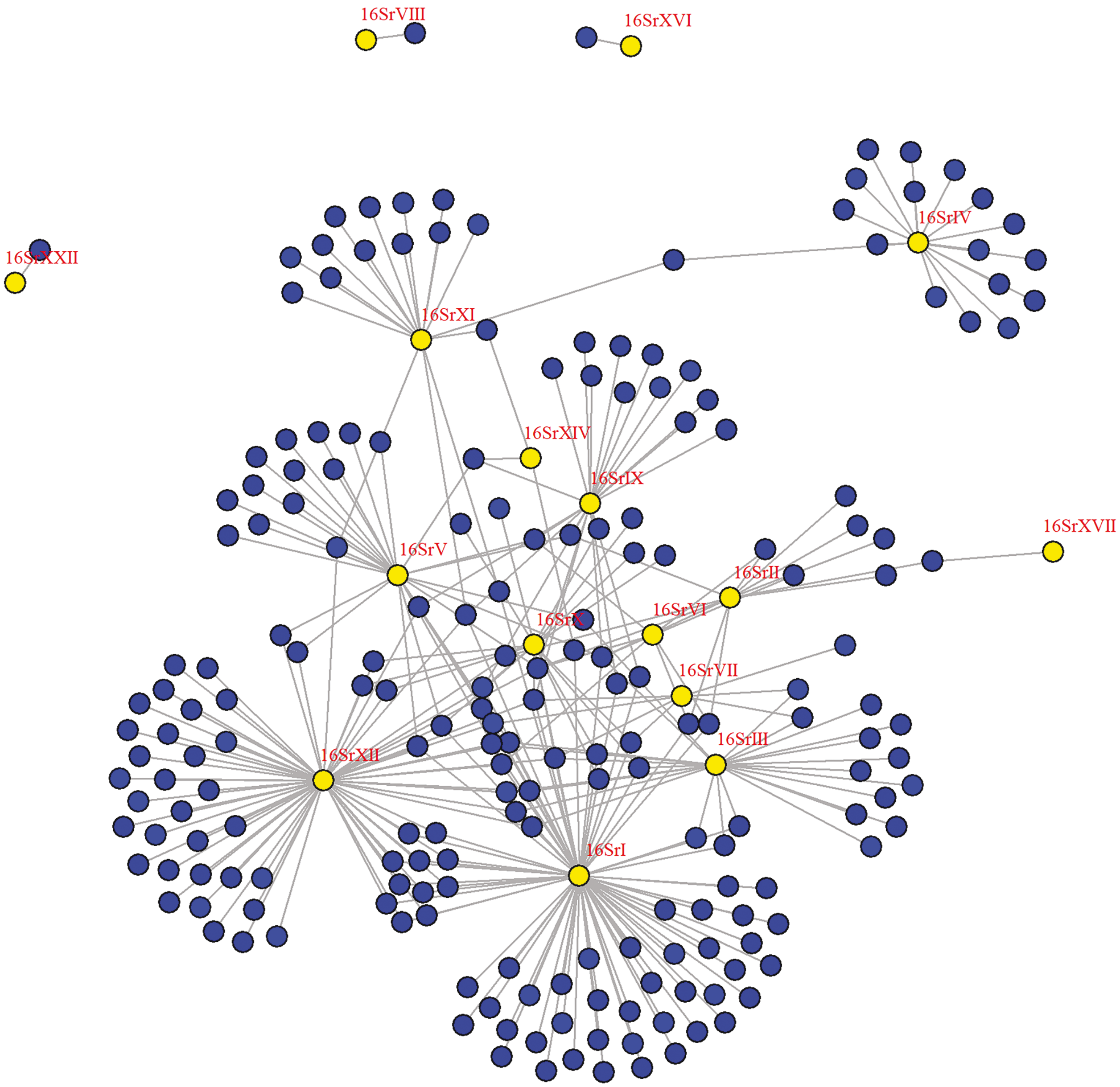

Fig. 2. Network graph of the interactions between phytoplasma groups (yellow/empty nodes identified by 16Sr followed by roman numeral number) and their potential and competent hemipteran vectors (blue/filled). The phytoplasma–insect dataset was analyzed and graphed using the *igraph* package (Csardi and Nepusz 2006) in R version 4.0.2 (R Core Team 2020). Adapted from Trivellone and Flores Garcia (2019). Specific associations with insect vector taxa are summarized here: http://trivellone.speciesfile.org/tree.asp?key=trivellone.ins-phy-pla&b=Homoptera&t=List%20of%20Hemiptera.

Effects of Phytoplasmas on Hosts

Vector-borne pathogenic bacteria often manipulate host functional traits (e.g., behavior, physiology, morphology) with cascading effects on biological communities; e.g., changes to plant phenotype that increase their attractiveness to vectors (Thompson 1998, Gandon et al. 2002, Friesen et al. 2011, Weinersmith and Faulkes 2014, Penczykowski et al. 2016, Ángeles-López et al. 2018). Available evidence strongly indicates that phytoplasmas manipulate their plant and insect hosts consistent with the Host-Manipulation Hypothesis (HMH, manipulation of the host in a manner that increases pathogen transmission and dispersal, Holmes and Bethel 1972). Experimental tests of the HMH on plant pathosystem models has shown how pathogen-host interactions can lead to phenotypic diversification and speciation (e.g., Mauck et al. 2014, Rajabaskar et al. 2014). Although it has been suggested that host manipulation is phylogenetically constrained (Poulin 1995, Longdon et al. 2014), few studies have investigated links between ecological and evolutionary mechanisms driving diversification in host–pathogen systems (Thomas et al. 2012, Heil 2016), and no such studies have been conducted on PPV associations.

Effects on Plants

Based on available evidence, phytoplasmas appear to have a strictly parasitic association with their vascular plant hosts. Unfortunately, the available data may be biased because nearly all surveys that have screened for the presence of phytoplasmas in plants have focused primarily on plants showing symptoms typical of phytoplasma diseases in agroecosystems. Phytoplasma disease symptoms prevalent in anthropogenic habitats may reflect the relative recency of such associations; in nature, such symptoms may be less common if plant–phytoplasma associations evolve toward commensalism over evolutionary timescales (e.g., as predicted by virulence-transmission trade-off theory; Alizon et al. 2009, Jansen et al. 2015).

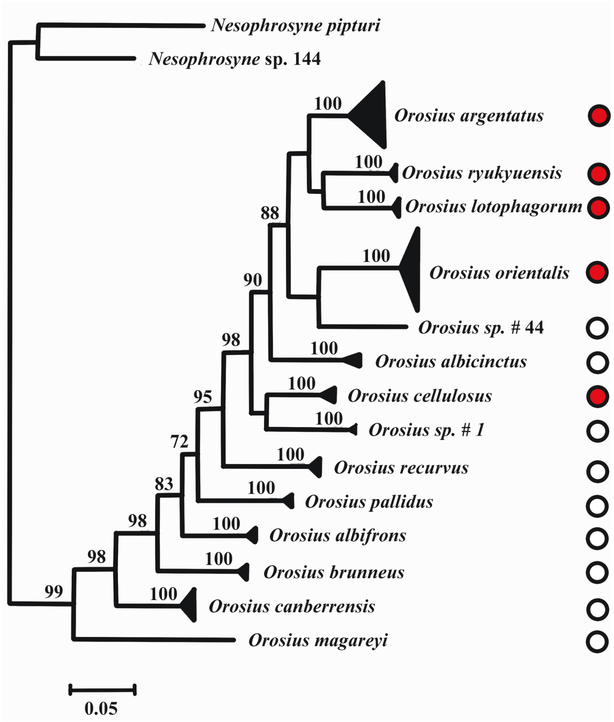

Fig. 3. Bayesian inference (BI) phylogram of 12 *Orosius* Distant species based on 103 COI *Orosius* haplotypes and two out-group *Nesophrosyne* Kirkaldy species. Known vector species are indicated by red/filled points; empty points indicate nonvectors or species for which vector competence is unknown. Adapted from Fletcher et al (2017).

Although agronomic research has extensively documented phytoplasma diseases causing yield reductions in crops, suggesting that these bacteria often negatively impact plant fitness (Bertaccini et al. 2014), a few studies have reported tolerance or resistance of certain plants to phytoplasma infections (Seemüller and Harries 2010, D'Amelio et al. 2011, Garcion et al. 2011). Severity of symptoms of phytoplasma infection may vary depending on climatic conditions, e.g., high ambient temperatures may enable plants to better tolerate infection (Soufi and Komor 2014, Al-Ghaithi et al. 2017). The few surveys that have examined prevalence of phytoplasmas in asymptomatic plants had the goal of identifying natural reservoirs of phytoplasmas in vegetation adjacent to agricultural fields (e.g., Jurga and Zwolińska 2020 for a review on Poaceae, Casati et al. 2016). Some such surveys have indicated that phytoplasmas are just as prevalent in plants showing no symptoms of disease as in those showing classic symptoms of infection (e.g., Tran-Nguyen et al. 2000, Zwolińska et al. 2019). This suggests that plants may acquire the ability to tolerate phytoplasma infection. No studies have investigated the possible fitness effects of phytoplasma infections on asymptomatic plants, although the potential importance of such plants as pathogen reservoirs that contribute to future outbreaks has been recognized (Donkersley et al. 2019). Recent comparative genomic studies of phytoplasmas indicate that, despite their reduced genomes, these bacteria are highly adapted to thrive within the tissues of two very different groups of hosts (plants and phloem-feeding hemipterans). A review of available phytoplasma genomes (Oshima et al. 2013) supports the hypothesis that the ancestral phytoplasma underwent a massive reduction in its genome with loss of many metabolic pathways such that these bacteria are dependent on their hosts for essential nutrients (Oshima et al. 2004). Although it was originally believed that plant disease symptoms associated with phytoplasma infections were side effects of the removal of nutrients from infected tissues, recent gene expression studies strongly indicate that most

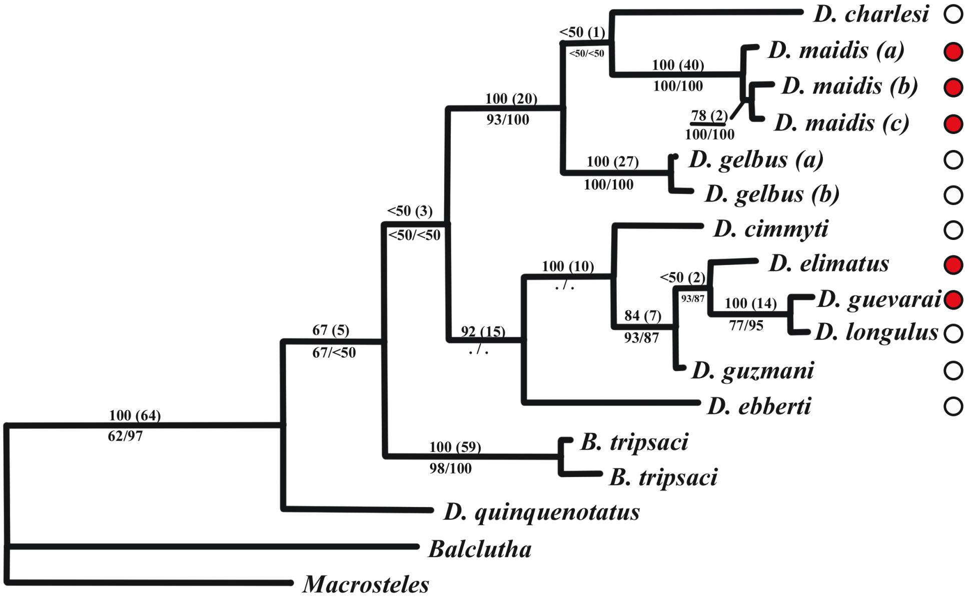

Fig. 4. Most parsimonious tree from maximum parsimony analyses of combined morphological and mtDNA sequence data of *Dalbulus* DeLong. Numbers above branches are maximum parsimony bootstrap scores and decay indices; below branches are neighbor joining boostrap scores and log determinant distances, respectively. Vector species are indicated by red/filled points; empty points indicate nonvectors or species for which vector competence is unknown. Adapted from Dietrich et al. (1998).

'classic' symptoms of phytoplasma disease are caused by expression of specific virulence 'effector' proteins (e.g., AY-WB Proteins, SAP), secreted by the phytoplasmas that target evolutionarily conserved proteins and processes in the plant genome and cause phenotypic changes in their hosts (Carella et al. 2018, Tomkins et al. 2018). Many such changes make the infected plant tissues more attractive to potential vectors and/or promote vector feeding (e.g., modulating plant defense responses), which may in turn promote growth, fecundity, and dispersal in vectors, thereby promoting phytoplasma spread (MacLean et al. 2011, 2014; Sugio et al. 2011a; Kallenbach et al. 2012; Maejima et al. 2014; Orlovskis and Hogenhout 2016; Wyckhuys et al. 2017; Chang et al. 2018; Rosa et al. 2018; Tomkins et al. 2018; Fernández et al. 2019).

Effects on Insects

Phytoplasma gene expression patterns change when phytoplasmas move from plants into their insect vectors but direct effects of phytoplasma infection on vectors are less well studied (Arismendi et al. 2015). The few studies that have examined effects of phytoplasma infection on hemipteran vectors have reported positive, negative, or no effects on vector fitness (Madden and Nault 1983, Arismendi and Carrillo 2015, Queiroz et al. 2016, Pradit et al. 2000). Nevertheless, feeding on phytoplasma-infected plants can increase longevity and fecundity (Sugio et al. 2011a, b) of both vector and nonvector leafhoppers (Queiroz et al. 2016) and acquisition of a phytoplasma by the vector may enable it to feed on healthy plants of the same species even if the plant is not its usual host (e.g., the corn leafhopper, *Dalbulus maidis* (DeLong) (Hemiptera: Cicadellidae) is usually a specialist on corn but individuals infected with the 16SrI-aster yellows phytoplasma can feed and survive on healthy asters) (Purcell 1988).

Some laboratory studies have shown that phytoplasma infection increases the fitness of vectors feeding on infected plants while reducing plant fitness, e.g., by inducing flower sterility, delayed seed production, and/or late flowering (MacLean et al. 2011, Maejima et al. 2014, Chang et al. 2018). For example, increased phyllody (development of leaf-like flowers) and virescence (greening of flower organs) caused by SAP54 gene expression (MacLean et al. 2011, Fernández et al. 2019) may make the plant more attractive to dispersing vectors. Witches broom (excessive shoot production) may increase the amount of phloem tissue available for feeding. Suppression of the jasmonic acid synthesis pathway may reduce plant resistance to feeding (Kallenbach et al. 2012, Rosa et al. 2018). Phytoplasmas also secrete carbohydrate-activated enzymes that degrade plant cell walls leading to additional disease symptoms (e.g., chlorosis) that may attract herbivores. Experimental studies suggest that visual rather than olfactory cues are important for attracting phytoplasma vectors to feed on infected plants (la Grange 2016). Nevertheless, some studies (e.g., Orlovskis and Hogenhout 2016) have shown that increased oviposition and feeding of leafhopper vectors on phytoplasma-infected plants is directly linked to the presence of a phytoplasma effector gene, regardless of whether or not disease symptoms are evident, suggesting that nonvisual cues may also occur. Phytoplasma infections may also make plants more attractive and/or palatable to generalist herbivores while disadvantaging specialists by increasing feeding competition with generalists (Wyckhuys et al. 2017). This may, in turn, increase chances for phytoplasmas to spread to new potential host plant species and diversify. The possible evolutionary implications of vector manipulation by phytoplasmas (e.g., by triggering host shifts) have not been investigated.

Evolution of the PPV System

Phytoplasma Phylogeny and Evolution

Phylogenetic analyses based on *16S rRNA* and *secY* (protein-coding gene) sequences (Zhao et al. 2015), as well as a recent large-scale phylogenomic analysis of the bacterial phylum *Tenericutes*, strongly support the monophyly of phytoplasmas, indicating that the group was derived from within a clade comprising facultative plant- and animal-associated intracellular bacteria within class *Mollicutes* (*Acholeplasma* Edward & Freundt; Martini et al. 2007, Gupta et al. 2018). Thus, extant phytoplasmas apparently evolved from a single common ancestor that acquired a specific association with phloem-feeding insects and their host plants (presumably a single ancestral host plant and vector species). Discovery of new phytoplasmas continues at a steady pace thanks to recent improvements in the use of molecular markers to characterize them (Zhao and Davis 2016).

A recent molecular timetree for phytoplasmas based on available *16S rRNA* sequence data (Cao et al. 2020) places the initial divergence of the phytoplasma lineage from *Acholeplasma*-like ancestors about 641 million years ago (Ma), predating the origin of terrestrial plants. Presumably the direct ancestors of modern phytoplasmas were similar to acholeplasmas, which are mostly either free living or commensal on various groups of animals. Wei et al. (2008) found evidence that phytoplasma divergence from *Acholeplasma*-like ancestors involved ancient phage attacks that led to formation of sequence-variable mosaics retained in modern phytoplasma genomes. Functional consequences of such changes remain poorly investigated but they could have facilitated horizontal acquisition of genes encoding proteins involved in phytoplasma–host interactions (Wei et al. 2008). Interestingly, although the phytoplasma lineage is much older than its vascular plant and hemipteran hosts, initial diversification of the phytoplasma crown clade did not occur until the Carboniferous (~316 Ma) (Cao et al. 2020), roughly coinciding with the early diversification of major vascular plant lineages (Morris et al. 2018) and the origin of phloem-feeding hemipterans (Johnson et al. 2018). This strongly suggests that diversification of phytoplasmas was facilitated by acquisition of the ability to parasitize the phloem sieve elements of vascular plants and utilize sap-feeding hemipteran insects as vectors. Molecular divergence time analysis strongly suggests that phytoplasmas, their hemipteran vectors, and vascular plants have been evolving together for hundreds of millions of years.

To date, phylogenies of phytoplasmas have been used almost exclusively as tools for taxonomic classification and pathogen diagnosis in support of epidemiological studies of agricultural diseases. However, a few recent studies demonstrate the potential of phylogenetic methods for elucidating overall evolutionary patterns in phytoplasmas as well as for understanding the evolution of particular strains important for agriculture. The best example of this approach is the *Flavescence dorée* (FD) disease system associated with two phytoplasmas subgroups (16SrV-C and 16SrV-D), which has been studied intensively in Europe for >70 yr. FD causes devasting decline in grapevines, hindering both quality and levels of production of one of the most important crops in Europe. As in other phytoplasma pathosystems, most research on FD has focused exclusively on disease mitigation. However, advances in molecular techniques have both accelerated the characterization and diagnosis of phytoplasmas associated with FD disease and helped elucidate the origins of pathogenic strains from wild ancestors. FD was originally thought to have been introduced into Europe from North America because the main vector of the strains pathogenic to grapevine is the introduced American leafhopper *Scaphoideus titanus*

Ball (Hemiptera: Cicadellidae). However, phylogenetic analyses of eight genetic markers demonstrated that FD-related phytoplasma strains have very high local diversity in Europe and appear to be derived from the indigenous phytoplasma strain associated with Alder yellows disease (Martini et al. 1999, 2002; Arnaud et al. 2007; Rossi et al. 2019; Malembic-Maher et al. 2020). The alder yellows phytoplasma (AldYp) is, in most cases, associated with asymptomatic *Alnus* Mill. spp. in Europe (Malembic et al. 2007). Presumably, occasional feeding by nongrape-specialist leafhopper vectors on grapevine resulted in transmission of AldYp from *Alnus* to grape but without vine-to-vine transmission (Malembic-Maher et al. 2020), probably due to the inability of nongrape-specialist leafhoppers to spend their entire life cycle on grapevine. However, once the introduced grape specialist, *S. titanus*, began transmitting the phytoplasma among grapevines, the stage was set for rapid genetic divergence of FD phytoplasma from AldYp. Not only did the phytoplasma colonize a new host, but the preference of the vector for grapevine reinforced its isolation from the parent population on *Alnus* and facilitated rapid evolution of the grape-*S. titanus*-FD pathosystem in Europe. This system is consistent with the predictions of the Stockholm Paradigm, a recently proposed framework for understanding the evolution of new diseases from wild ancestors following anthropogenic environmental change (Brooks et al. 2019).

Another historically important, diverse, and extensively studied phytoplasma group is 16SrI (Wei et al. 2007, Zhao et al. 2015) which includes phytoplasmas associated with Aster yellows (AY) disease. AY phytoplasmas are among the most diverse and widespread groups causing devastating diseases worldwide. AY phytoplasmas have been studied extensively but many aspects of this system remain poorly understood. In North America, recent research has focused on AY phytoplasma genetic diversity in agroecosystems (Clements et al. 2020) and patterns of migration of the vector species *Macrosteles quadrilineatus* Forbes (Hemiptera: Cicadellidae) from southern to northern agroecosystems (Chiykowski and Chapman 1965, Frost et al. 2013). A phylogeny based on *secY* gene sequences and in silico modeling of the SecY protein suggested that divergence in the AY group 16SrI-B is driven by host plants and vectors associated with different geographical areas (Davis et al. 2018). Unfortunately, only phytoplasmas isolated from cultivated host plants were included and further investigation on insect vectors only focused in agroecosystems (e.g., Lenzi et al. 2019 as a recent example). Thus, the possible roles of alternative plant and insect hosts in natural areas in the evolution of AY strains pathogenic to crops has been largely overlooked. A comprehensive phylogenetic reconstruction of this group is needed to elucidate its evolutionary origin, including associations in natural habitats. Further studies are also needed to elucidate the phylogeny and taxonomy of AY vectors. Earlier investigations reported more than 20 species of AY leafhopper vectors (Severin 1929, 1934, 1940, 1945, 1946, 1947a, 1947b, 1950; Severin and Frazier 1945; DeLong and Severin 1947, 1948) but inadequacies in the species-level taxonomy of the Aster leafhopper genus *Macrosteles* Fieber were highlighted more recently (Hamilton 1983) and the roles of the main vector, *M. quadrilineatus*, and alternative vectors in spreading the pathogens in agroecosystems need to be clarified.

Other important phytoplasma disease systems that have been extensively studied from an epidemiological perspective would benefit from using phylogenetic methods to trace the origins of the pathogenic phytoplasma strains and predict disease outbreaks. This is particularly important in areas struggling with food insecurity, e.g., in tropical regions such as Africa (Sasson 2012, Dodo 2020). The economy of several African provinces largely depends on coconut, which is also fundamental to local nutrition and customs. Beginning in 1992, the spread of lethal yellowing diseases (LYD) significantly affected the local genetic heritage and productivity of coconut palms (Gurr et al. 2016). A recent continent-wide (Ghana, Nigeria, Mozambique) phylogenetic study on genetic variants of two phytoplasma subgroups associated with LYD (16SrXXII-A and -B) showed a total of eight haplotypes. However, very low intracountry diversity suggested a possible bottleneck probably caused by the rapid death of diseased plants, with strongly clustered genetic diversity also indicating independent origins of LYD phytoplasmas in each nation (Pilet et al. 2019). A single study in Côte d'Ivoire tried to clarify the role of 'weed' species as source of inoculum of unknown strains of phytoplasmas associated with LYD (Arocha Rosete et al. 2016). Sampling remains limited and it is not possible to infer potential host switches from alternative hosts which remain broadly unknown. Insect vectors of LYD phytoplasmas also remain unknown, despite PCR detection in some palm-associated hemipterans (Kwadjo et al. 2018).

Host (Plant and Insect Vector) Phylogeny and Evolution

No phylogenetic studies of hemipteran genera comprising competent phytoplasma vectors have yet attempted to reconstruct the evolution of vector competence in those groups using phylogenetic ancestral trait reconstruction methods (e.g., Yu et al. 2020). Recent phylogenetic studies have provided well-supported estimates of relationships among major lineages of Hemiptera and within families comprising vector species (Dietrich et al. 2017, Johnson et al. 2018, Percy et al. 2018), but there have only been a few attempts to construct detailed species-level phylogenies of genera comprising known vectors. In a molecular phylogeny of the deltocephaline leafhopper genus *Orosius* Distant (Hemiptera: Cicadellidae) based on COI barcode sequence data (Fletcher et al. 2017), all five known vector species (mainly 16SrII phytoplasmas) (Fig. 3, red/filled points) grouped together in a single clade derived from within a paraphyletic grade comprising seven nonvector species (Fig. 3, empty points), suggesting that vector competence was acquired relatively recently in the genus and retained through multiple speciation events. A phylogeny of the maize leafhopper genus *Dalbulus* DeLong based on two mitochondrial genes (Dietrich et al. 1998) also suggests that phytoplasma vector competence for 16SrI phytoplasmas was derived recently but independently in *D. maidis* and the clade comprising *D. elimatus* (Ball) and *D. guevarai* DeLong (Fig. 4). The latter clade also comprises the nonvector species, *D. longulus* DeLong, which is sister species to *D. guevarai*; suggesting that a loss of vector competence may have coincided with the *D. guevarai*/*D. longulus* split. Only one molecular phylogeny of the Aster leafhopper genus *Macrosteles* (Le Roux and Rubinoff 2009), which includes several vectors of the AY phytoplasmas (16SrI), has been published but this study only included North American specimens, most of which were unidentified to species. Nevertheless, species of *Macrosteles* known to be vectors of phytoplasmas in the AY group (16SrI) are morphologically similar, suggesting that they are closely related (Hamilton 1983). Phylogenies of two other diverse genera of the leafhopper tribe Opsiini comprising phytoplasma vectors, *Hishimonus* Ishihara and *Neoaliturus* Distant (both Hemiptera: Cicadellidae), are not available but known vectors in these genera are also morphologically similar (Knight 1970, Young and Frazier 1954). Further studies are needed to provide explicit tests of these hypotheses within a robust phylogenetic context.

Because vectors of most known phytoplasmas remain undocumented, information on phylogenetic relationships of known vectors may be useful for narrowing the search for these still-unknown vectors. Some well-studied phytoplasmas are known to have multiple competent vectors, some of which are only distantly related (e.g., Cicadellidae and Flatidae include competent vectors of 16SrI-B; Supp Table 1B [online only]). Given the observation in several studies that phytoplasma infections often make plants more attractive to sap-sucking herbivores while also changing herbivore functional traits (diet breath and fecundity) (Sugio et al. 2011a, MacLean et al. 2014, Orlovskis and Hogenhout 2016), it is not surprising to find that there have been frequent host shifts among vector and potential vector species. In the FD phytoplasma system, for example, the ancestral strain apparently inhabited *Alnus* and its main vector appears to be the alder-specialist leafhopper *Oncopsis alni* (Schrank) (Hemipetra: Cicadellidae, Macropsini; Maixner and Reinert 1999), a species unrelated to *S. titanus* (Scaphoideini), the North American species that became the main vector of FD responsible for transmitting the phytoplasma among grape vines. Manipulation of the behaviors of the ancestral vector by the phytoplasma (i.e., increased tendency to disperse and possibly increased tolerance of nonancestral host plants) may have facilitated the shift from *Alnus* to *Vitis* L. Once the phytoplasma was present in *Vitis*, the introduced vector could propagate the phytoplasma from vine to vine, thus, facilitating genetic isolation from the parent strain. The planthopper *Hyalesthes obsoletus* Signoret (Hemiptera: Cixiidae) and its plant hosts provide an excellent example of insect vector genetic diversification associated with host plant shifts. Specifically, sympatric host race evolution, likely linked to allochronic reproductive isolation and climatic conditions (Imo et al. 2013), and cryptic speciation (Kosovac et al. 2018) of *H. obsoletus* have been uncovered by comparing populations associated with different host plants (*Convolvulus arvensis* L., *Urtica dioica* L., *Vitex agnus-castus* L., and *Crepis foetida* L.) from southeastern to western Europe. Although phytoplasmas have not been directly implicated in these host-shifts, the role of phytoplasmas in manipulating vector behavior was hypothesized because specific associations between phytoplasma strains, plant hosts and *H. obsoletus* host races have been continually observed in Europe. Nevertheless, survival experiments by Maixner et al. (2014) provided only weak evidence that phytoplasma infections has a positive effect on vector survival.

Although well-resolved, large-scale phylogenies of plants based on phylogenomic analyses have been published recently (Ran et al. 2018, Smith and Brown 2018, Leebens-Mack et al. 2019, Sousa et al. 2020), these have not yet been used as a framework for formal analyses of co-evolution among phytoplasmas and plant lineages. According to the recently published PPV database (Trivellone 2019), about 97% of plant genera hosting phytoplasmas are angiosperms, 2.8% are gymnosperms (excluding Gnetales), and 0.2% belong to the sole surviving genus in the family Equisetaceae, *Equisetum* L. In particular, the unique association between *Equisetum telmateia* Ehrh. and 16SrI-B was detected in a natural area near a plantation of ornamental trees affected by phytoplasma yellow decline disease (Sfalanga et al. 2002). Interestingly, a few species in Pinaceae and Cupressaceae are also associated almost exclusively with 16SrI (-A and -B phytoplasmas; Supp Table 1A [online only]), and both gymnosperms and horsetails arose about 325 Ma (Ran et al. 2018, Shen et al. 2018) roughly corresponding to the emergence of the clade including the 16SrI phytoplasma strain associated with this genus (Cao et al. 2020), suggesting an ancient association of phytoplasmas with Equisetaceae and gymnosperms. Several groups of phytoplasmas appear to be associated exclusively with particular groups of plants (e.g., 16SrIV phytoplasma group with Arecaceae and 16SrX phytoplasma group with Rosaceae; Trivellone 2018), suggesting that co-evolution may have occurred in some lineages, but there are also many instances of possible phytoplasma host shifts between distantly related plants (e.g., the shift from *Alnus* to *Vitis* in the FD system). Detailed phylogenies are available for several plant lineages (e.g., angiosperms; Yang et al. 2020) in which phytoplasma associations appear to be common but no attempts have been made to compare evolutionary patterns in PPV associations using methods designed to assess the degree of co-speciation among ecologically associated lineages. Nault and Delong (1980) hypothesized strict co-speciation between the maize genus *Zea* L. and its specialist *Dalbulus* leafhoppers but this hypothesis has not been rigorously tested using phylogenetic methods and no attempts have been made to examine the possible co-evolution of maize-associated phytoplasmas with their host plants.

Synthesis and Suggestions for Future Research

The wealth of available data and observations on the ecology and physiology of plant–phytoplasma–vector associations, as well as phylogenies showing the patterns of relationship among major lineages in each of these groups, provide numerous important clues regarding the evolutionary processes that gave rise to such associations and enabled them to persist and diversify over hundreds of millions of years. Unfortunately, nearly all of the research on this system still focuses too narrowly on traditional approaches to epidemiology and mitigation of phytoplasma diseases affecting ornamental plants and crops. Future research focusing on the broader evolutionary context of PPV associations might be expected to yield important insights into the evolutionary mechanisms that drive diversification in this system and the ecological and evolutionary contexts in which novel phytoplasma diseases might be expected to emerge (Brooks et al. 2019).

Evolution/Emergence of Infectious Disease

Since the germ-theory of disease was first proposed (Pasteur 1880), microbial pathogens have been the focus of intensive study from medical/veterinary perspectives as well as in agriculture. Plant diseases have been known since at least Biblical times (Genesis 41: 25–30) and have been responsible for major crop losses and famines throughout recorded human history (Strange and Scott 2005). The vast majority of modern plant disease research, including that focused on phytoplasmas, has continued to focus specifically on the identification and characterization of particular pathogens, their epidemiological effects and control (Rao et al. 2018, Topolovec-Pintarić 2020). Investigations of the roles of ecological and evolutionary processes in the emergence of particular pathogens have begun only recently (reviewed by Brooks et al. 2019) but have benefitted greatly from the wealth of data yielded by prior epidemiological research. Combined with such legacy data, studies of the broader ecological and evolutionary contexts in which certain microbes become pathogenic are not only useful for developing improved methods of disease management (Zhan et al. 2014), but may also contribute to a better understanding of how interactions between pathogenic microbes and their hosts can generate biodiversity (Harvell 2004).

Mechanisms of Diversification in Plant–Microbe–Herbivore Interactions

Prior theories on host–parasite evolution, mostly focused on animal pathosystems, have emphasized the role of trade-offs between transmissibility and virulence to explain why parasites evolve to fit their hosts (May and Anderson 1983, Alizon et al. 2009). Alternative standpoints consider parasites (Sensu *lato*) as drivers of their own evolution through ecological adaptations, such as host-switching, that transcend congruent host–pathogen phylogenies (Hoberg and Brooks 2008). While incorporating several complex theories, the recently proposed Stockholm Paradigm provides a unified framework to contextually test alternative hypotheses (Brooks et al. 2019) that explain the ecological and evolutionary processes that drive diversification in systems involving parasites and their hosts. A few recent studies have begun to use this framework to analyze evolutionary processes driving co-diversification (speciation) of pathogens and vectors (e.g., Apari et al. 2019, McKee et al. 2019). Such processes have scarcely been studied in plant pathosystems (Froissart et al. 2010), particularly those involving vector-borne microorganisms, and none of these approaches have been considered in the PPV pathosystem.

Results of previous research on phytoplasma taxonomy and epidemiological aspects of PPV associations have major, yet underappreciated potential significance for understanding how microbial associations may drive diversification in insect–plant interactions as well as for contributing to a more general understanding of the evolution of infectious disease. The availability of well-resolved phylogenies for all three groups of organisms and comparative methods for evolutionary analysis provide platforms for future studies that may elucidate the mechanisms by which phytoplasmas, their plant hosts, and hemipteran vectors may co-evolve and provide models useful for predicting the emergence of new phytoplasma diseases affecting agriculture. Nevertheless, improved understanding of the evolutionary history of host–phytoplasma associations is hindered by the still highly incomplete knowledge of vectors and plant hosts in wild habitats, which remain unknown for the vast majority of phytoplasmas.

Future Approaches to Study of PPV Associations

The importance of wildlife and natural habitats as reservoirs of actual or potential pathogens has gained prominence particularly in light of the current SARS-CoV-2 pandemic and other recent outbreaks of infectious diseases (Brooks et al. 2019, Morens and Fauci 2020). Such reservoirs give rise to pathogens directly affecting human health as well as plant diseases affecting agriculture with potential impacts on food security. The broader ecological and evolutionary contexts in which such pathogens emerge are best studied within a comprehensive phylogenetic and evolutionary framework. Most prior efforts to document phytoplasma diversity and identify phytoplasma vectors have been constrained by their almost exclusive focus on agroecosystems with screening for phytoplasmas largely limited to plants exhibiting classical symptoms of phytoplasma disease. More comprehensive approaches are needed. In particular future biodiversity inventories should focus on areas of native vegetation and screen both symptomatic and asymptomatic plants as well as all potential vectors (i.e., phloem-feeding hemipterans) for presence of phytoplasmas. The few previous studies that screened entire communities of sap-feeders in the field (e.g., Hill and Sinclair 2000, Trivellone et al. 2016) were extremely localized and were, thus, unable to provide the broader phylogenomic, biogeographic and evolutionary contexts needed. A coordinated, large-scale, global effort to screen for phytoplasmas in natural areas is needed to more fully document the diversity of phytoplasmas, their plant hosts, and actual or potential vectors. Such efforts are needed to mitigate the potentially biased nature of available data that have been compiled largely from human-managed systems and facilitate more informative comparative evolutionary analyses.

Detailed phylogenies of hemipteran lineages comprising known phytoplasma vectors are also needed to elucidate the degree to which vector competence is a conservative trait (acquired in a common ancestor and retained through multiple speciation events) and to determine the extent to which associations with phytoplasmas are correlated with evolution of various traits such as host plant preference and diet breadth. The extent to which vector competence reflects an existing capability of a phytoplasma to ‘fit’ novel host vectors (rapid host shift) without the emergence of novel genetic information also needs to be tested. Improved understanding of the relative importance of cospeciation versus host shifts and assessment of their possible ecological or biogeographic drivers will increase our ability to predict the emergence of new or previously undiscovered PPV associations. Due to the globalized nature of modern commerce, and the vagrant nature of vectors, most anthropogenic diversification of both vectors and pathogens should be driven by host-switching rather than cospeciation. Although such anthropogenic effects probably mimic natural processes that occurred periodically over the >300 million year history of the PPV system, phylogenetic evidence also suggests that some associations between lineages of phytoplasmas, plants and insects have persisted over millions of years.

Controlled laboratory experiments are needed to test hypotheses related to the role of host manipulation by phytoplasmas in ecological and evolutionary diversification, the degree to which PPV associations evolve from parasitism to mutualism over time and the ecological contexts in which virulence may increase or emerge. Such studies may ultimately identify variables and parameters most useful for development of evolutionary models that predict the emergence of new phytoplasma diseases, facilitating more pro-active and less reactive responses to phytoplasma disease management. Recent research on mutualistic associations between herbivorous insects and microbial symbionts has revealed the great diversity and ubiquity of such associations and their key roles in creating and maintaining biodiversity (Day and Young 2004, Pascual-García and Bastolla 2017). Although the PPV system has, so far, been studied primarily from the perspective of plant pathology and epidemiology, it may represent a useful model system not only for study of pathogen evolution but also to help elucidate the degree to which symbioses between bacteria and plant-feeding insects can drive evolutionary diversification.

Supplementary Data

Supplementary data are available at *Annals of the Entomological Society of America* online.

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