



Scaphoideus titanus up-to-the-minute: biology, ecology, and role as a vector

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With 3 figures and 1 table

Abstract: Native to the Nearctic region, *Scaphoideus titanus* Ball (Hemiptera: Cicadellidae) has become a major threat for grapevine production after being unintentionally introduced into Europe, where it became the main vector of flavescence dorée phytoplasma, being mainly associated with the genus *Vitis*. *Scaphoideus titanus* is a highly efficient vector of the most important phytoplasma affecting grapevine. For this reason, compulsory insecticide treatments have been introduced against this pest in many European countries. Moreover, the continuous expansion of its geographical distribution makes this leafhopper a serious threat for several non-European Countries. In this article, we review the current knowledge about its taxonomy, morphology, biology, ecology, and its role as a vector. Finally, we point out the main challenges for research aimed at reducing *S. titanus* and flavescence dorée expansion across Europe and avoiding spread of the disease outside the Old World.

Keywords: vector distribution; flavescence dorée; Cicadellidae; life cycle; morphology and taxonomy; feeding behaviour

1 Introduction

The Nearctic leafhopper *Scaphoideus titanus* Ball (Hemiptera: Cicadellidae: Deltocephalinae) became a major pest for wine-producing countries after its introduction in Europe, due to its role as the main vector of flavescence dorée phytoplasma (FDp) to grapevine (EFSA 2020). In view of its high efficiency in sustaining epidemic spread of the disease, *S. titanus* has been subject to compulsory insecticide treatments in several European Countries for more than 20 years (Boudon-Padiou 2003; Chuche & Thiéry 2014). Moreover, its geographical distribution is continuously expanding (Mirutenko et al. 2018; Aguin-Pombo et al. 2020) and its unintentional introduction into other areas, e.g., South America and China (Quiroga et al. 2017; Pierro et al. 2019), is regarded as a major threat for global viticulture, particularly considering the effects of climate change that may shift the area of distribution toward higher latitudes (EFSA 2016).

Considering the economic impact of this insect, major research efforts have been recently conducted regarding several aspects of its biology, ecology, invasiveness, vector competence, monitoring, and management. However, in the last few years, research advances have not yet been summarized, as the last review article on *S. titanus* was published ten years ago (Chuche & Thiéry 2014). More recent research on this insect shed light on key issues including insights on its biology and behaviour (particularly life cycle duration, fecundity, feeding behaviour and preferences) (Chuche et al. 2015, 2017a; Bocca et al. 2020; Ripamonti et al. 2022b), its interactions with FDp and implications for disease spread (Alma et al. 2018; Trivellone et al. 2019; Malembic-Maher et al. 2020; Arricau-Bouvery et al. 2021; Galetto et al. 2023), and its microbiome (Gonella et al. 2015; López-Fernández et al. 2017; Ottati et al. 2020).

Herein we provide a comprehensive and updated review on the biology, ecology, population dynamics, and vector competence of *S. titanus*. We also discuss the emerging issues to be addressed by research to prevent the continuous spread of this vector and the transmitted phytoplasma across European grapevine-growing areas.

2 Morphology, biology, and life cycle

2.1 Life stages

In Europe, *S. titanus* is primarily associated with the genus *Vitis*, on which it completes its entire life cycle (Chuche & Thiéry 2014). A few other broad-leaved plants (e.g., *Vicia faba* L., *Trifolium repens* L., *Ranunculus repens* L.) can sustain feeding activity of nymphs and adults, both under field and semi-field (Trivellone et al. 2013), and laboratory conditions (Caudwell et al. 1970). *Scaphoideus titanus* undergoes a typical heterometabolic development, with a succession of five pre-adult (nymphal) life stages (N1–N5) after egg hatching, followed by emergence of adult males

and females. The egg has a reniform shape, with a tapered cephalic pole and a rounded caudal pole, is whitish in colour and has a length of 1.3–1.5 mm. Nymphs are 1.5–1.8 (N1) to 5.2–5.3 (N5) mm long, whitish coloured through N3, after which they develop ochre to brown coloured spots in N4 and N5 (Vidano 1964; Della Giustina et al. 1992). In N5, a remarkable differentiation of size can be recorded according to the sex, with females being bigger (4.92–6.15 mm long) than males (4.67–5.41 mm long) (Della Giustina et al. 1992). A common trait in all instars is the presence of two black, rhomboid-like spots on the last abdominal segment (Vidano 1964; Della Giustina et al. 1992). Adults are 5–6 mm long and have ochre to brown colour, with white and dark spots on the wings. They are recognizable by the head shape and by the presence of red-brown transverse bands on the dorsum of the head and thorax (Vidano 1964).

2.2 Voltinism

Scaphoideus titanus undergoes a single generation per year, with a winter diapause at the egg stage (Fig. 1). Eggs are laid from August to October, hatching after 6–8 months (Chuche & Thiéry 2014; Bocca et al. 2020). Despite being well adapted to cold winters, which support faster egg development in spring, *S. titanus* does not require cold temperatures to break its diapause (Chuche & Thiéry 2012), although the lower the post-winter temperatures, the longer the post-dormancy required to allow egg hatching (Falzoi et al. 2014). However, egg hatch is synchronized with grapevine bud break, irrespective of winter temperatures (Chuche et al. 2015). Accordingly, distinct hatching periods are observed in vineyards located in areas with different climatic conditions (Chuche & Thiéry 2014). The overall post-embryonic development takes from 21 to 53 days, depending on the temperature, with later nymphal instars taking longer to complete than earlier ones (Falzoi et al. 2014). Also nymphal mortality increases in later instars (Chuche & Thiéry 2014; Falzoi et al. 2014). The first adults appear from late June to July and while they were previously believed to live about one month, recent studies demonstrated that (under laboratory and semi-field conditions) their longevity can exceed two months, and females usually outlive males (Bocca et al. 2020). Greater female longevity, combined with protandrous development, results in prolonged occurrence of a high proportion of fecund females at the end of the season. Oviposition begins approximately 12–14 days after eclosion. A single female can lay on average more than 60 eggs during her whole life, sometimes exceeding 130 eggs (Bocca et al. 2020). Oviposition rate tends to decrease with female age rather than seasonal progress, and oviposition may be frequent even in late October (Bocca et al. 2020).

Despite only univoltine individuals having been recorded so far, the possible emergence of a second generation has been hypothesized (Bernard et al. 1988). The recently reported expansion of the geographical range of *S. titanus* to regions with warmer climates (Aguin-Pombo et al. 2020)

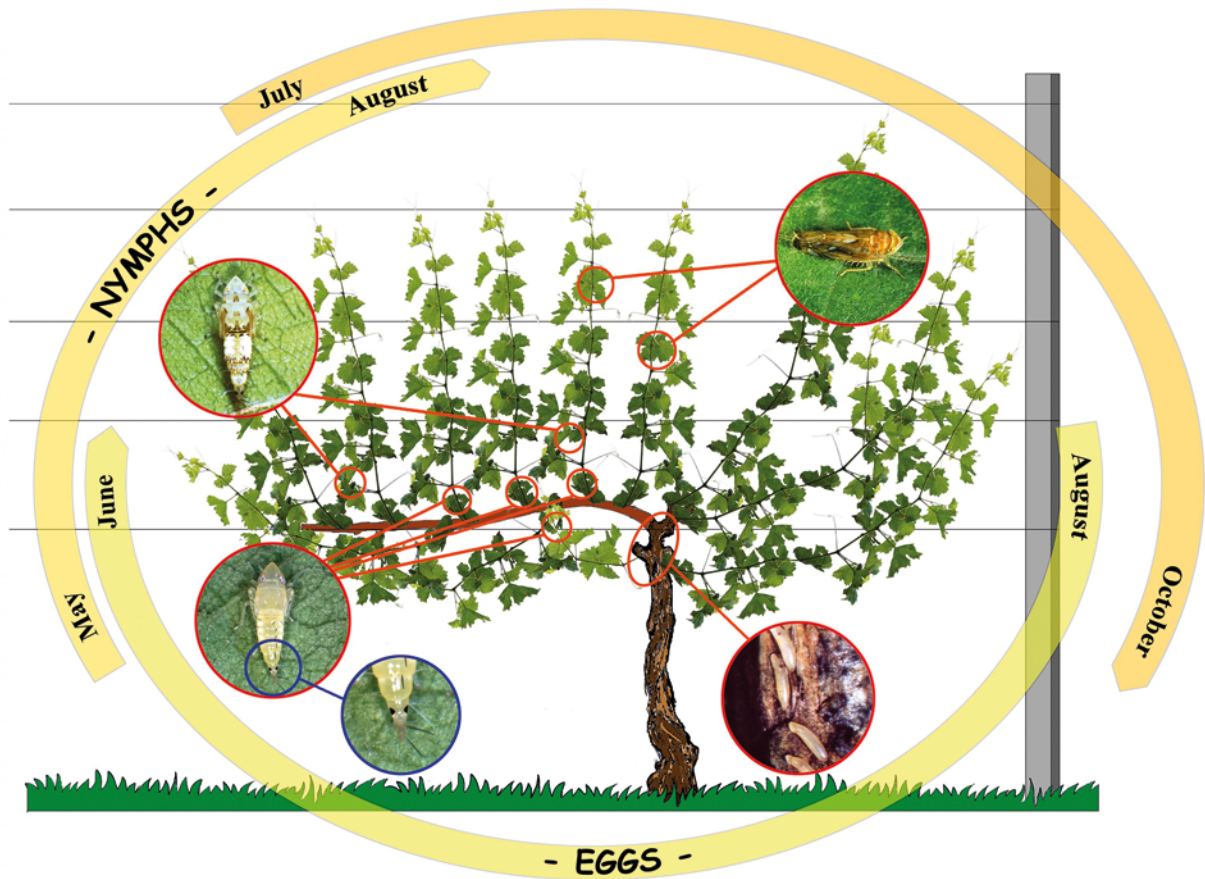


Fig. 1. Life cycle of *Scaphoideus titanus*; showing location of different life stages on grapevine throughout the year.

than in its typical European distribution between 35 and 50 ° north latitude (Chuche & Thiéry 2014) may support an increase in voltinism and deserves further investigation.

3 Behavioural ecology and population dynamics

3.1 Mating behaviour

The mating behaviour of *S. titanus* is primarily mediated by substrate-borne vibrational signals mediating supporting communication between males and females on the same plant. Comprising four distinct phases – (1) calling, (2) identification, (3) location, and (4) courtship – this process showcases a fascinating “call-fly” strategy employed by males. Males alternate between calling and flights to locate receptive females in the vineyard vegetation (Mazzoni et al. 2009a; Polajnar et al. 2014).

The male calling song (MCS) comprises pulses (MP1) emitted at regular intervals (~0.3 s) accompanied by a fragmented noise known as “rumbling”. A female’s response involves emitting pulses (FP) between two consecutive

MP1s, avoiding overlap. The male then searches her on the plant, alternating short trains of MP1s with quick movements towards the female. Notably, the signal’s active space, defined as the total surface area of the plant from which the signal can potentially elicit a response in the receiver, includes adjacent leaves on the same vine shoot where the signal is emitted (Mazzoni et al. 2014). Moreover, it can even travel up to 7 cm through the air, underscoring its relatively wide range (Eriksson et al. 2011).

Once the male arrives at the female’s leaf, the courtship phase initiates with the Male Courtship Phrase (MCrP). This complex signal includes a second pulse (MP2) paired with MP1 and a high-frequency signal (900–1200 Hz) called the “buzz.” The courtship duet continues until copulation, with the transition from location to courtship influenced by the amplitude of FP perceived by the male. Additionally, *S. titanus* males exhibit strong rivalry behaviour, emitting disturbance noise (DN) or eavesdropping on FP when competing for a female (Mazzoni et al. 2009a).

Mating behaviour predominantly occurs in the late afternoon to early evening (approximately 5 PM to 10 PM) (Mazzoni et al. 2009a; Akassou et al. 2022), which is also

corroborated by field trials in which more males are captured around twilight hours (Lessio & Alma 2004a; Lessio et al. 2009; Pavan et al. 2023). Environmental factors like high temperatures ($> 25\text{ }^{\circ}\text{C}$) and wind speed ($> 3.5\text{ m/s}$) strongly reduce courtship activity, due to cessation of MCS emissions (Akassou et al. 2022).

3.2 Other sensory modalities

The roles of other sensory modalities, namely vision and olfaction, seem to be mostly associated with the search for host plants and the ability to target a landing site while flying and jumping. *S. titanus* can detect colours, with a preference for red and yellow demonstrated by field trials using coloured sticky panels (Lessio & Alma 2004b; Mazzoni et al. 2011; Pavan et al. 2023). Similar results were observed in laboratory two-choice tests with a glass vertical Y-tube, which indicated a preference for red (females) and yellow (males) over green and blue (Mazzoni et al. 2011).

Regarding olfaction, *S. titanus* antennae have a few olfactory sensilla and small antennal lobes, even compared to closely related Auchenorrhyncha (i.e., planthoppers) (Rossi Stacconi et al. 2014). Four main types of sensilla have been described on the antenna: hair-shaped and campaniform sensilla present on the pedicel and flagellum, and two types of sensory cavities visible on the dorsal side of the flagellum. Despite the weak response to *Vitis* volatiles measured by electroantennography (EAG), nymphs showed effective positive orientation when exposed to volatile compounds from apical grapevine shoots. Conversely, their accuracy was lower when leaves were the sole source, indicating a probable preference for plant apices for feeding (Mazzoni et al. 2009b).

3.3 Feeding behaviour

Scaphoideus titanus is primarily a phloem feeder. However, as shown by the electropetrography (EPG) technique, prolonged xylem ingestion also occurs (Chuche et al. 2017a). The duration of the phloem feeding phase can be related to the sex, as males exhibit longer phloem ingestion events than females (Chuche et al. 2017a). Significant differences were also recorded depending on the grapevine variety: for example, phloem ingestion is significantly longer on ‘Barbera’ than on ‘Brachetto’ and ‘Moscato’ (Ripamonti et al. 2022c). Interestingly, in different cultivars the frequency of phloem ingestion correlates with insect longevity and fecundity (Ripamonti et al. 2022a, b). *S. titanus* showed enhanced fitness on a preferred variety (with longer feeding and higher number of salivation events in the phloem) compared to a non-preferred variety (with reduced phloem-feeding phases), on which very high nymphal mortality, as well as a prolonged development time, were recorded. In the cultivar where the *S. titanus* fitness was reduced, the production of aromatic compounds in the phloem was suggested to repel the insect, disturbing phloem feeding (Ripamonti et al. 2022b). A particular trait of *S. titanus* feeding behaviour is

the high frequency of mixed phloem and xylem ingestion. Such a feeding behaviour is likely a way to obtain micronutrients missing from phloem sap and rehydrate in response to osmotic stress (Chuche et al. 2017a). The nutrition obtained from xylem vessels is not negligible, especially in females (Chuche et al. 2017a, b). However, sex-related divergence in feeding behaviour may vary according to the vine cultivar. Males fed on phloem of ‘Cabernet-Sauvignon’ plants for a longer time than females (Chuche et al. 2017a); whereas experimental trials conducted on several Italian cultivars showed either a reduced frequency of non-feeding events or no differences between sexes (Ripamonti et al. 2022b). Due to the difficulties of direct behavioural observations and the constraints limiting the possibility to perform extensive EPG studies on this insect, the knowledge of *S. titanus* feeding behaviour is still limited, and will require more detailed studies on different grape cultivars at different phenological stages and with insects of both sexes at different ages.

Notably, *S. titanus* has been utilized as a model to study the role of sap feeders in transferring endophytes between grapevines. In the work of López-Fernández et al. (2017), nymphs of *S. titanus* were found to be responsible for transferring large sets of microorganisms to in vitro micro-propagated grapevines, thus shaping their endophyte community. This result supports the hypothesis that even insects commonly considered pests of a certain crop can play an important ecological role in spreading potentially beneficial microorganisms from plant to plant.

3.4 Landscape ecology and dynamics within vineyards

The effects of landscape ecology on *S. titanus* presence and spatial distribution have not been thoroughly studied. In Switzerland, topographical factors like orientation and slope significantly affected *S. titanus* density in vineyards of the canton of Geneva (Linder & Jermini 2007; Bilotta et al. 2019). Gentle slopes with a south-easterly exposure harbour more individuals, while steeper slopes had fewer. The Ticino plain showed higher abundance than hillsides, and large contiguous vineyards had more individuals than fragmented ones, suggesting an association with vineyard size. Microclimatic conditions, influenced by site topography, played a crucial role in *S. titanus* occurrence (Bilotta et al. 2019). Monitoring recommendations suggest sampling in sunny vineyards and the middle areas of large vineyards. Grass cover in the inter-rows did not directly influence *S. titanus* abundance (Bilotta et al. 2019).

Studies on wild or semi-natural vegetation near vineyards have explored their role as habitats for *S. titanus*. Abandoned or untreated vineyards, with vegetation originating from rootstocks, and natural vegetation with naturalised or wild *Vitis* spp. served as reservoirs for FDP and *S. titanus* (Lessio & Alma 2006; Pavan et al. 2012; Zanettin et al. 2018; Rossi et al. 2019; Ripamonti et al. 2020; Oggier et al. 2023). American *Vitis* spp., mostly symptomless but susceptible to

FDp, are attractive hosts for *S. titanus*, consistent with the Nearctic origin of this leafhopper (Eveillard et al. 2016). Wild and naturalised *Vitis* spp. host large *S. titanus* populations, and the lack of proper insecticide treatments makes them significant sources for nearby vineyards. Wild and feral *Vitis* are widespread in Europe and, apart for *V. vinifera* subsp. *sylvestris*, which is of European origin, they derive from imported American rootstocks, hybrids of *V. riparia*, *V. rupestris* and *V. berlandieri*.

Mathematical modelling of pathogen dispersal and epidemiological dynamics of FD at the landscape level (Adrakey et al. 2023), aligned with *S. titanus* flying capacity estimates (Lessio et al. 2014), indicate the role of feral grapevines in FD epidemiology. Zanettin et al. (2018) studied *S. titanus* abundance in semi-natural areas and in managed vineyards. Larger populations were found in organic vineyards within complex landscapes, increasing over the season; in these environments insecticides were poorly effective even at low densities of *S. titanus*. Wild and feral grapevines in semi-natural habitats near vineyards could provide a refuge for *S. titanus* during insecticide applications within managed vineyards, allowing the leafhoppers to re-colonize. Factors affecting increased FD infection rates (Adrakey et al. 2022) suggested that the presence of surrounding woods and urban areas increased *S. titanus* occurrence at the landscape level.

4 Geographical distribution, biological traits in the native area and history of the invasion with respect to phytoplasma interaction

The leafhopper genus *Scaphoideus* Uhler comprises 230 valid species and is distributed throughout the temperate and tropical regions of the world except in Central and South America (Dmitriev et al. 2022 onward). Species of the genus are mostly associated with perennial woody host plants in forests (Barnett 1977) but some Afrotropical and Asian species appear to be associated with grasses (Nusillard 2007; Webb & Viraktamath 2007). Little is known about the ecology of most *Scaphoideus* species. The phylogeny and biogeography of the genus also remain poorly studied and it is not known whether the genus as a whole is monophyletic, although species of the genus share a unique set of morphological traits including presence of 4–6 branches on forewing vein R (radius) and dissociation of the male connective from the aedeagus (Barnett 1977) and, therefore, may represent a lineage distinct from other Deltocephalinae leafhoppers.

Scaphoideus titanus is native to the deciduous forests of temperate North America and its native range apparently includes the entire continental USA and southern Canada although it is most common east of the Rocky Mountains (Barnett 1977) (Fig. 2). This species generally had never aroused much interest and had no known economic relevance until it was recorded in Europe in 1958 (Bonfils & Schvester

1960) and its role in spreading FDp from grapevine to grapevine was confirmed (Caudwell 1957; Schvester et al. 1962a). Since then, many studies documenting the spread of this species across Europe and the ecological and epidemiological features of the European population have been published (e.g., Schvester et al. 1962b; Chuche & Thiéry 2014; Trivellone et al. 2013). In Europe, the preferred host plant of *S. titanus* appears to be *Vitis vinifera* L., but alternative non-crop temporary hosts have also been identified (Trivellone et al. 2013).

In Europe, *S. titanus* is one of only two *Scaphoideus* species recorded, the other being *S. dellagiustinai* Webb & Viraktamath (Mazzoni et al. 2017), which occurs in Africa and southern Europe on *Tripidium ravennae* (L.) H. Scholz and other grasses typical of sand dune systems and has a distinct colour pattern (Webb & Viraktamath 2007). Another Nearctic species of Scaphoideini recently introduced into Europe, *Osbornellus auronitens* (Provancher), is similar to *S. titanus* in size and colour but is easily distinguishable by the forewing venation, elongate male subgenital plates, and details of the colour pattern (Trivellone et al. 2017). In 2016, one specimen of *O. auronitens* collected in Switzerland tested positive for a 16SrV-C related strain of phytoplasma (Trivellone et al. 2022). However, so far, neither of these other two introduced European Scaphoideini species have been implicated as competent vectors of phytoplasmas in the field. This accentuates the need for correct taxonomic identification in programs aimed at controlling the spread of plant pathogens.

4.1 Ecology of Nearctic populations

Little is known about the ecology of *S. titanus* within its native range. This may be partly because, in the Nearctic region, this species often co-occurs in the same habitats with several other species of *Scaphoideus*, many of which are difficult to distinguish except by examining the male genitalia (Barnett 1977; Cwikla 1987). Thus, use of common sampling methods such as sweeping, Malaise and light trapping in the USA and Canada, usually yield specimens of multiple *Scaphoideus* species (Barnett 1977 and unpublished observations). According to published records, in North America, *S. titanus* has been recorded from various woody and herbaceous plant species including *Crataegus* sp., *Juniperus virginiana* L., *Onoclea sensibilis* L., *Polygonum* sp., *Prunus* sp., *Salix* sp., *Solidago* sp., *Ulmus* spp. and *Vitis* spp. (DeLong 1948; Barnett 1977). Unfortunately, it is not clear whether such records document actual food plants or only incidental occurrences because of the lack of systematic collection on single plant species and experiments of host plant preferences. Gibson (1973) collected and, in some cases, reared specimens identified as several taxa currently treated as synonyms of *S. titanus* (*S. diutius*, *S. littoralis*, *S. nigrellus*, and *S. scelestus*) on American Elm and associated understory plants but the reliability of these identifications is uncertain. Despite these uncertainties, the wide range of

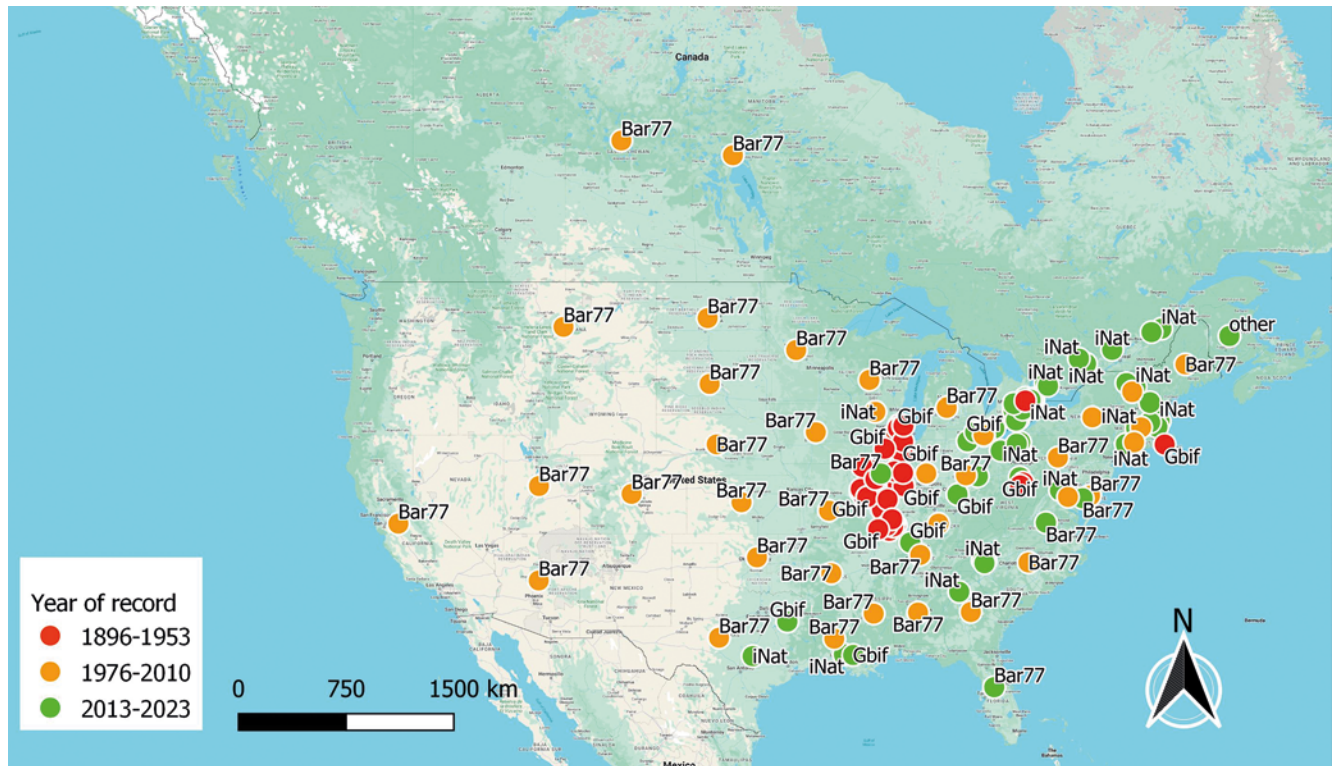


Fig. 2. Distribution of *Scaphoideus titanus* in North America. The data were collected from three main sources: Bar77 (Barnett 1977); iNat (iNaturalist database, <https://www.inaturalist.org/>); Gbif (GBIF database, <https://www.gbif.org/>). Other sources (other) include various published literature. For information from published literature coordinates represent the centroid of the State (Bar77 and other). All the other points are the coordinate of the collecting event provided in the databases GBIF and iNaturalist. Map created with QGIS v 3.10.0 (Open Source Geospatial Foundation Project) using a dataset generated by the authors at the Illinois Natural History Survey (USA).

recorded hosts in its native range suggests the possibility that Nearctic “*S. titanus*” may comprise multiple, ecologically distinct species, possibly requiring revalidation of some taxa now treated as junior synonyms.

4.2 Taxonomic and phylogenetic status of *S. titanus*

In his morphology-based taxonomic revision of Nearctic *Scaphoideus*, Barnett (1977) adopted a broad definition of the species, treating as junior synonyms eight taxa described from different geographic areas and considered by previous authors to represent distinct species (Table 1). *Scaphoideus titanus*, as defined by this author, is readily distinguishable from most other Nearctic *Scaphoideus* by the relatively short, poorly sclerotized male connective processes (elongate in other species except *S. opalinus*, which differs markedly in coloration). However, as acknowledged, his broad concept of *S. titanus* encompasses morphological variants that exhibit considerable differences in both coloration and male genitalia (Barnett 1977). Unfortunately, few attempts have been made to assess the extent of genetic variation or phylogenetic relationships among populations of *S. titanus* within the native range of the species (Papura et al. 2012).

Published analyses of molecular data suggest that extant European populations of *S. titanus* are largely homogeneous genetically and originated from a single introduction (Bertin et al. 2007; Papura et al. 2012). However, the geographic source of the introduction is unclear partly because populations sampled so far from the north-eastern USA and Canada are genetically divergent from the European population (Papura et al. 2012). The exact timing of the introduction of *S. titanus* into Europe also remains unknown. The first record of this species in Europe was published in 1958 (Bonfils & Schvester 1960) but its introduction probably occurred much earlier, either during the importation of American vines into France following the powdery mildew crisis of the 1850s (Gale 2002), or during the resulting *Phylloxera* crisis, when dormant American vines and, subsequently, American rootstocks were imported in large numbers beginning around 1872.

Preliminary phylogenetic analysis of mitochondrial COI DNA barcode sequence data from NCBI groups of North American *Scaphoideus* identified them as either *S. titanus*, one of the taxa treated as synonyms of *S. titanus* by Barnett (1977), or *S. opalinus*, a species with similar male genitalia but different coloration, into a single clade (Clade A, Fig. 3)

Table 1. List of eight species in the genus *Scaphoideus* synonymized with *S. titanus* by Barnett (1977) and voucher type material.

Species name	Reference	Voucher type	Location
<i>Scaphoideus immistus</i> var. <i>titanus</i>	Ball (1932)	Holotype, paratype	US, West Virginia
		Allotype	CA, Ontario
<i>Scaphoideus littoralis</i>	Ball (1932)	Holotype, allotype, paratype	US, Massachusetts
<i>Scaphoideus cyprius</i>	Ball (1932)	Holotype, paratype	US, Iowa
<i>Scaphoideus amplus</i>	DeLong & Mohr (1936)	Holotype, allotype	US, Pennsylvania
<i>Scaphoideus brevidens</i>	DeLong & Mohr (1936)	Holotype, allotype, paratype	US, Tennessee
<i>Scaphoideus diutius</i>	DeLong & Mohr (1936)	Holotype, allotype, paratype	US, Illinois
<i>Scaphoideus nigrellus</i>	DeLong & Mohr (1936)	Holotype, allotype	US, Illinois
<i>Scaphoideus scelestus</i>	DeLong & Mohr (1936)	Holotype, allotype	US, Pennsylvania
<i>Scaphoideus aduncus</i>	DeLong & Knull (1971)	Holotype, paratype	US, Texas
	DeLong & Knull (1971)	Paratype	US, California

sister to other North American *Scaphoideus* species (Clade B, Fig. 3). This clade includes several genetically divergent lineages, one of which includes unpublished sequence data from several specimens of European *S. titanus* collected in several different countries (Czech Republic, Italy, Serbia, Switzerland; blue clade, Fig. 3) as well as specimens identified (in NCBI) as *S. nigrellus* or *S. cyprius* (both treated as synonyms of *S. titanus* by Barnett 1977). Three other genetically divergent clades of *S. titanus* (*sensu* Barnett) include additional North American specimens identified as *S. nigrellus*, *S. cyprius* and *S. titanus*. The currently valid species *S. opalinus* is nested within this larger lineage. Further studies incorporating additional specimens and genetic loci are needed but these preliminary phylogenetic results strongly suggest that *S. titanus*, as defined by Barnett (1977), comprises multiple genetically distinct lineages possibly corresponding to different biological species.

4.3 Vector status in the native area and role in European FD outbreaks

In North America, *S. titanus* is a suspected vector of North American grapevine yellows (NAGY, associated with two distantly related phytoplasma strains, 16SrI-B – ‘*Candidatus* (*Ca.*) Phytoplasma (*P.*) asteris’ and 16SrIII – ‘*Ca.* *P. pruni*’ related strains) because of its seasonal movement in and out of vineyards (Maixner et al. 1993; Beanland et al. 2006; Stoepler & Wolf 2013). However, it failed to inoculate NAGY (‘*Ca.* *P. pruni*’ related strains) in an experiment using sucrose feeding medium (Lenzi et al. 2019). The FD phytoplasmas belong to the 16SrV subgroups -C and -D that have, so far, not been recorded in the Western Hemisphere, except for 16SrV-C detected in the USA in wild plants such as *Apocynum cannabinum* L. and *Parthenocissus quinquefolia* (L.) Planch. (Harrison et al. 2001), and 16SrV-C phytoplasma associated with Alder Yellows (AldY) in *Alnus rubra* Bong. in Washington state, USA (Cai et al. 2022). Moreover, NAGY was never reported in Europe.

The introduction of *S. titanus* into Europe apparently facilitated the divergence of FD phytoplasmas from an ancestral AldY strain indigenous to Europe but infecting *Alnus* spp. (Malembic-Maher et al. 2020). Transmission of AldY phytoplasmas to grapevine probably resulted from occasional feeding by leafhoppers occurring on *Alnus* spp. (e.g., *Allygus* spp.) on grapevine, with an alternative epidemiological cycle, occurring in Italy, Balkans and eastern Europe, involving transmission by the European lanternfly *Dictyophara europaea* L. from *Clematis vitalba* L. to vines (Filippin et al. 2009; Malembic-Maher et al. 2020). However, because these insects did not prefer grapevine as a host, vine-to-vine transmission of the phytoplasma did not occur before the introduction of *S. titanus*, which feeds preferentially on grapevine in Europe (Nickel & Remane 2002; Nickel 2003). This leafhopper was, therefore, capable of transmitting the phytoplasma strains among *Vitis* plants, resulting in ecological and genetic divergence of FDp from its parent strain and the emergence of various FD-related phytoplasmas outbreaks in grapevine in Europe.

Two other North American *Scaphoideus* species, *S. carinatus* and *S. luteolus*, have also been shown to be competent vectors of phytoplasmas, specifically X-disease phytoplasmas (Rosenberger & Jones 1978) and Elm yellows phytoplasmas (Baker 1948) respectively. No species of this genus indigenous to the Old World are known as phytoplasma vectors although some species of related genera (tribe Scaphoideini) are associated with phytoplasmas in East Asia (Trivellone et al. 2022).

5 Relation with FDp and vector competence

Phytoplasmas are phloem-limited bacteria that colonize all parts of their host plants and are transmitted from plant to plant by insect vectors in which they exhibit a persistent cir-

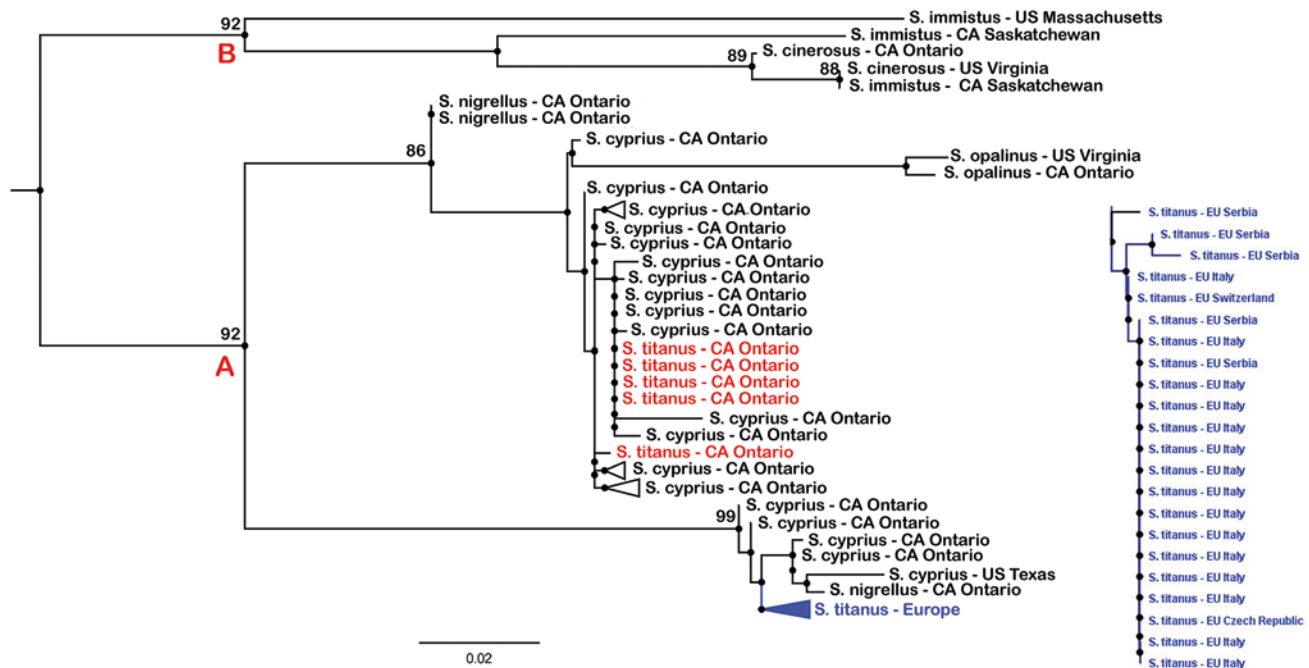


Fig. 3. Maximum-likelihood tree of the of the mitochondrial DNA *Cytochrome c oxidase I* (COI) gene for 60 specimens of *Scaphoideus*, 38 representing North American specimens from BOLD database (<https://www.boldsystems.org/>) and 22 unpublished sequences from European specimens (in blue). Clade A contains taxa that have been synonymized with *Scaphoideus titanus*, except *S. opalinus*. Clade B includes two more distantly related species, *S. immistus* and *S. cinerosus*. Specimens in red have been identified as *S. titanus*.

culative propagative cycle. Transmission of phytoplasmas by insects involves, at several levels, elements of host–pathogen specificity including host-range, feeding preference, and feeding behaviour, interactions between phytoplasma membrane proteins and insect receptors, and phytoplasma colonization and multiplication within the insect body, including salivary glands (Bosco & D’Amelio 2009).

5.1 Implication of feeding preference and behaviour for FDp transmission

Given the restricted host range of *S. titanus* that feeds mainly on *Vitis* spp. (Chuche & Thiéry 2014), this leafhopper is an efficient vector of FDp between grapevines. The preference of *S. titanus* for American *Vitis* spp. facilitates continuous FDp transmission. American grapevines are susceptible to FD infection but they generally do not show disease symptoms (Eveillard et al. 2016), often resulting in higher proportions of infected *S. titanus* in natural or naturalized vegetation than within vineyards (Ripamonti et al. 2020). Leafhoppers acquire FDp on feral *Vitis* (Lessio et al. 2007) and then move to vineyards where they transmit the pathogen (Lessio et al. 2014).

Feeding behaviour is one of the determinants of plant pathogen transmission ability by insect vectors and phytoplasmas are introduced into the phloem probably via watery saliva as the leafhopper stylets penetrate sieve element membranes (Weintraub & Beanland 2006). The complex

pattern of nutrition greatly influences the plant pathogen transmission process (Carpane et al. 2011; Backus et al. 2020; Cornara et al. 2024). Electrical Penetration Graph (EPG) studies identified two patterns that are possibly related to FDp transmission: (1) active phloem ingestion, and (2) inoculation, concurrent ingestion and salivation in the phloem (Chuche et al. 2017b). Longer phloem ingestion was reported on a FD-susceptible variety compared to tolerant varieties, suggesting that longer phloem feeding phases correlate with higher FDp inoculation efficiency (Ripamonti et al. 2022c). Consistently, acquisition of phytoplasmas by *S. titanus* is much more efficient when the insects feed on highly susceptible grapevine cultivars than when they feed on poorly susceptible ones (Bressan et al. 2005; Galetto et al. 2014; Eveillard et al. 2016; Galetto et al. 2016). Since poorly susceptible varieties are a poor source of infection for *S. titanus*, susceptibility is likely to have a major impact on the infection pressure and on FD spread at the vineyard level. This effect is confirmed at the landscape level as, in a study conducted in South-Western France, the probability of FD infection increased with the proportion of land covered by susceptible cultivars (Adrakey et al. 2022).

5.2 Dispersal capability in relation to FD spread

Primary phytoplasma spread due to infected leafhoppers arriving from outside the vineyard is strongly influenced by the dispersal ability of the insect. Adults of *S. titanus* are

not very mobile and, indeed, in a study of the spatial distribution pattern of this species conducted with a geostatistical and neural network approach, the adult catches appears moderately correlated within a short distance (≤ 210 m) and decays at a longer distance (Lessio et al. 2011). However, a study investigating the movement of the leafhopper using the mark–capture technique demonstrated that many individuals collected inside the vineyards were actually coming from woodlands with feral *Vitis* into a vineyard (Lessio et al. 2014). Marked adults decreased exponentially with distance from these feral grapevines with up to 80% of them captured within 30 m, but few over 200 m. This mode of FDp spread by *S. titanus* has been confirmed by Rossi et al. (2019) who showed that FDp genotypes identified in (i) feral grapevines, (ii) *S. titanus* collected outside and inside the vineyards, and (iii) infected grapevines inside the vineyards largely overlap, suggesting flow of phytoplasmas from nearby wild vegetation into cultivated vines. All this information, together with the clear and repeatedly reported edge effect in infected grapevines within the vineyard (Martini et al. 2019), suggest the importance of infected *S. titanus* adults migrating from outside the vineyard in transmission of FDp. However, the extent to which feral grapevines are present in the viticultural landscape varies a lot, being lower in highly intensive viticultural areas and higher in fragmented landscapes with vineyards interspersed within woodlands, other crops, or urban areas (Ripamonti et al. 2020; Drakey et al. 2022; Oggier et al. 2023).

5.3 *Scaphoideus titanus*-FDp interactions

Scaphoideus titanus acquires FDp when it feeds in the phloem of infected grapevine. Phytoplasmas then cross the epithelial barrier of the midgut, colonize the muscle surrounding epithelial cells, enter the haemolymph and colonize various organs including salivary gland cells during the latency access period (LAP). No vertical transmission has been observed so far, due to the inability of FDp to colonize reproductive organs, as has been found for the experimental vector *Euscelidius variegatus* Kirschbaum (Lefol et al. 1994). Once the phytoplasmas have multiplied in salivary gland cells, they enter the saliva allowing *S. titanus* to inoculate them into a plant during the inoculation access period (IAP). *Scaphoideus titanus* can acquire both in nymphal and adult stages (Bressan et al. 2006b; Alma et al. 2018). Once *S. titanus* is infected, it becomes an efficient vector in the adult stage and remains infected until death. The minimal duration between the acquisition of phytoplasmas and the ability of *S. titanus* to inoculate them into a plant is 28 days (21 days of AAP and LAP, and 7 days of IAP) (Caudwell et al. 1970) although shorter LAPs have been observed in laboratory conditions on broad beans (Alma et al. 2018). As the AAP increases, the percentage of infected insects increases due to 1) the higher probability to feed on phytoplasma-infected sieve elements of the grapevine, which is not homogeneously infected (Morone et al. 2004; Eveillard et al. 2016), and

2) the higher probability of efficient crossing by phytoplasmas of the midgut barrier protected by the perimicrovillar membrane.

The main two barriers to phytoplasma movement within the vector are the midgut epithelial cells and the salivary gland cells that act as independent barriers (Bosco & D'Amelio 2009). These two barriers are implicated, with the immune response, in the specificity of insect transmission. Indeed, crossing these insect cells is an active process that requires recognition between the phytoplasma adhesins and corresponding insect receptors before the phytoplasmas enter insect cells by endocytosis (Hogenhout et al. 2008). On one hand, vector competency of FDp seems to be highest in leafhopper species that belong to the family Cicadellidae, subfamily Deltocephalinae (Bressan et al. 2006a; Malembic-Maher et al. 2020). On the other hand, the sequence of the surface exposed membrane proteins VmpA and VmpB of the phytoplasmas belonging to the 16SrV group is correlated with vector competency (Malembic-Maher et al. 2020), and the interaction of the surface protein Imp of FDp with both midgut and salivary gland proteins is required for the insect to transmit FDp (Trivellone et al. 2019). Few data are available regarding the invasion of insect cells by phytoplasmas at the molecular level, and no data presently exist describing the invasion process of *S. titanus* cells by FDp. The closest model consists of an infection of the experimental vector *E. variegatus* by FDp (Caudwell et al. 1972). Use of this model showed that the variable membrane protein VmpA is an adhesin that binds glycoconjugates present at the insect cell surface (Arricau-Bouvery et al. 2018, 2021) and most likely the insect surface protein uk1_LRR containing leucine rich repeat domains (Canuto et al. 2023). VmpA also binds the perimicrovillar membrane surrounding the intestinal epithelium, and probably is implicated in crossing of the midgut barrier by phytoplasmas. As the surface glycosylation of midgut and salivary gland cells are very similar between *E. variegatus* and *S. titanus* (Arricau-Bouvery et al. 2021), it is expected that similar processes occur in the cells of these two species following ingestion of phytoplasmas. When phytoplasmas attach to the insect cells, they are endocytosed by clathrin-mediated endocytosis (Arricau-Bouvery et al. 2023) and probably then escape from endocytosis vesicles to reach the cytosol of insect cells as shown by electron microscopy (Hirumi & Maramorosch 1969). Once in the cell cytosol, FDp may interact with cell cytoskeleton as in the case of the protein Imp of lime witches' broom and wheat blue dwarf phytoplasmas, which interacts with actin, myosin, and α -tubulin (Siampour et al. 2011; Ding et al. 2022). This may allow phytoplasmas to move through the cells before exocytosis.

Several other FDp genes are differentially expressed in plant and insect hosts, and could therefore play important roles in multiplication and colonization of the insect vector leading to efficient transmission (Jollard et al. 2020; Galetto et al. 2023). On the insect side, the protein ATP synthase β ,

which caused alteration of developing egg morphology in *S. titanus* ovaries when its expression was down regulated by RNA interference (Ripamonti et al. 2022a), seems to be important for the multiplication of FDp in *E. variegatus* (Galetto et al. 2021), probably through its interaction with the phytoplasma Imp protein (Siampour et al. 2011).

6 Microbiome

The microbial community associated with *S. titanus* has been extensively studied over the last two decades. The microbiome of *S. titanus* is dominated by the primary bacterial symbiont ‘*Candidatus Sulcia muelleri*’, which is strictly required by the hosts due to its nutritional provisioning (Gil & Latorre 2019). *Sulcia* is usually accompanied by additional obligate symbionts that differ according to the host lineage. In most species of the subfamily Deltocephalinae, the supplementary obligate symbiont is the Beta-proetobacterium ‘*Candidatus Nasuia deltocephalinicola*’ (Bennett & Moran 2013), although in some species it has been replaced by other microbial partners, including *Sodalis* bacteria (Kobialka et al. 2018a) and a yeast-like fungus in the genus *Ophiocordyceps* (Kobialka et al. 2018b). This is the case in *S. titanus*, where a yeast-like symbiont was detected in specialized cells of the fat bodies and showed transovarial transmission (Sacchi et al. 2008). This fungal associate was subsequently recognized as the *Ophiocordyceps* co-dominant symbiont of *S. titanus* together with *Sulcia* (Abbà et al. 2022). Additional bacterial symbionts that have been extensively found in the FD vector belong to the genus *Cardinium* (Marzorati et al. 2006), however they have been detected only in European populations, and they are suspected to have been acquired by *S. titanus* after its introduction into Europe. This hypothesis is corroborated by evidence of horizontal transmission of *Cardinium* by *S. titanus* via the plant (Gonella et al. 2015); nonetheless the interaction between *V. vinifera*, *S. titanus* and *Cardinium* requires further elucidation.

Secondary symbionts associated with *S. titanus* include Proteobacteria known to be widespread in insects, such as *Wolbachia*, *Rickettsia*, and *Asaia* (Crotti et al. 2009; Abbà et al. 2022). *Asaia* was extensively studied as it was proposed as a candidate control agent against FD (Gonella et al. 2018). Although its effect on host fitness is still unknown, *Asaia* is vertically transmitted by egg smearing (Crotti et al. 2009), and is horizontally transferred among specimens sharing the same feeding source (co-feeding) (Gonella et al. 2012), suggesting that the insect tends to retain this symbiont due to a beneficial activity. Strikingly, the *Asaia* strain affiliated to *S. titanus* differentiated from closely related strains infecting other insects, as it was not cultivable in axenic media, probably because it requires specific factors produced by the host or by the gut microbiome (Crotti et al. 2009).

The viral community associated with *S. titanus* has been recently described (Ottati et al. 2020). The study showed a striking difference in the diversity and abundance of the viral species identified in the native area, North America, and in Europe. Indeed, seven viral species were discovered from three individuals collected in the USA, whereas only two viral species, *Scaphoideus titanus* iflavivirus 1 and *Scaphoideus titanus* toti-like virus 1, were collectively identified following the analyses of 214 samples, coming from various European sites (where most of the specimen were virus-free). Nothing is known about the pathogenicity or fitness cost induced by these viruses, but further studies should explore the possibility to exploit these naturally occurring viruses as specific and targeted biocontrol agents.

7 Conclusions and future research challenges

The biology, behavioural traits, and high vector competence of *S. titanus* make it a serious threat for grapevine production in view of its crucial role in the spread of FDp across European territories. Several issues are presently challenging the management of *S. titanus* to control FD. These relate to the past, present and the future of the leafhopper’s spread into and across Europe.

A first important issue regards the epidemiological history of the *S. titanus* – FDp association. Genetic studies indicate a single introduction of *S. titanus* populations from North America (Papura et al. 2012), with the leafhopper presumed to have entered Europe via France as a result of importation of American vines and rootstocks to address the sequential crises of grapevine production due to powdery mildew and phylloxera, during the 19th century (Cao et al. 2020). On the other hand, the 1927 inventory of the family Jassidae (now Cicadellidae) in southwest France (in the area of introduction) (Ribaut 1952) did not mention *S. titanus*. Therefore, we may assume that during its initial establishment *S. titanus* was uncommon, similarly to another pest, *Lobesia botrana* (Denis & Schiffermüller) (Lepidoptera: Tortricidae), until 1900 (Benelli et al. 2023). In the case of *S. titanus*, the lack of early detection may be related to the almost complete lack of direct feeding damage to grapevines by this species as well as the relative paucity of entomological research in Europe during the first half of the 20th century, as a result of the World Wars. Due to the potentially long period of cryptic presence of *S. titanus* in many European grape-growing regions following its initial establishment, it is difficult to determine when exactly the association with FDp started. However, at the end of the 20th century a sudden acceleration in spread of the pathogen was observed with several FD outbreaks especially occurring in France and Italy. The spread of *S. titanus* may have been facilitated by trade of vines among wine-growing regions, whereas the recent change

of climatic conditions (i.e., temperature increase and water limitation) is likely to have taken little part, since the areas of initial invasion already provided the climate preferred by *S. titanus*. Unveiling the reason for an initial slow expansion followed by a dramatic acceleration of FD outbreaks is certainly a key point that needs to be addressed to inform future control measures. These efforts may be also supported by additional studies to stabilize *S. titanus* taxonomy, clarify the relationship of introduced European populations to their native North American counterparts, and obtain supplementary ecological and life-history data on the species within its native range. Providing the correct taxon names for an economically important species has important implications for understanding its relationship with its environment (Hoberg et al. 2022).

The most recent research has highlighted some bio-ethological and environmental factors that may modulate the role of *S. titanus* in FDP transmission. The novel evidence of mixed and differential feeding behaviour according to the plant source underlines a correlation between FD susceptibility and *S. titanus* feeding preference, highlighting that the less susceptible varieties may sustain lower transmission levels along with lower symptom appearance. This should be carefully considered within selection of grape varieties for new plantings in FD-infested areas. Only a small number of grapevine cultivars have already been tested for their suitability as hosts for *S. titanus*; this number should be increased especially considering local varieties grown in areas that are currently still FD-free. Moreover, the ability of *S. titanus* to transmit additional/multiple pathogens should be further explored.

Finally, additional important aspects that should be taken into consideration for future management of *S. titanus* are climate scenarios that may change the pest voltinism, distribution and abundance, with important implications on FD epidemiology. Global warming may support a northward extension of *S. titanus* spread across Europe, as well as the colonization of higher altitudes, potentially increasing the threatened regions throughout all European countries (Sneiders et al. 2019). On the other hand, recent pest records at lower latitudes point out how little we know about the real range of climatic variation tolerated by this species. In this context, a deeper knowledge about life-history traits of *S. titanus* at the field level, under different climatic conditions, is needed to disentangle the actual variability of many relevant parameters of its life cycle, such as cold requirements, diapause, instar durations, and adult lifespan. Improved knowledge of such traits will help address the ongoing and future changes needed for the management of this pest.

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