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Positioning entomopathogenic nematodes for the future viticulture: exploring their use against biotic threats and as bioindicators of soil health

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Abstract: Vineyards face several biotic threats that compromise the grape quality and quantity. Among those that cause relevant economic impact and have worldwide distribution are the oomycete *Plasmopara vitícola*, the fungi *Erysiphe necator* and *Botrytis cinerea*, and the arthropods *Lobesia botrana*, *Tetranychus urticae*, and *Phylaenus spumarius* (principal vector of the bacterial disease *Xylella fastidiosa* in Europe). Their management relies primarily on agrochemicals with short persistence; widespread use of these chemicals causes environmental and human health problems. The challenge of sustainable viticulture is to provide ecologically sound alternatives. In this regard, the application of entomopathogenic nematodes (EPNs) and natural products derived from their symbionts can be an alternative. EPNs are well-known biocontrol agents for soil-dwelling insects. However, current research demonstrates the great potential of both EPN and their derivates as direct bio-tools against some of the key fungal and arthropods pests present aboveground. In addition, recent evidence shows that detecting EPN presence and activity and their relation with other soil organisms associated with them can help us to understand the impact of different agricultural practices on vineyard management. Altogether, this review illustrates the great potential of EPN to enhance pest and disease management in the next generation of viticulture.

Key words: Vineyards, *Steinernema, Heterorhabditis, Photorhabdus, Xenorhabdus*, natural products

1. Introduction

Grapevine (*Vitis vinifera* L.) is a widely cultivated plant species across arid and semi-arid ecosystems. Indeed, according to the International Organization of Vine and Wine (OIV), the total area dedicated to vineyards worldwide was around 7.5 million hectares in 2018, which yielded 77.8 million tons of grapes.[1] Therefore, viticulture is considered a key sector with a significant impact on the socioeconomic and cultural aspects, especially relevant in the principal wine-producing regions e.g., France, Spain, Italy, China, and the USA.

Vineyards are one of the most intensely managed crops (Nicholls et al., 2008). Grapevine management often uses conventional production practices, such as the widespread use of agrochemical and soil tillage practices responsible for environmental impact, including soil and water pollution (Pose-Juan et al., 2015; Herrero-Hernández et al., 2017). In the Mediterranean region, vineyards are also one of the land areas with the highest erosion rates (Rodrigo-Comino et al., 2018). During the last decade, the implementation of integrated production rules is strongly encouraged and regulated. One of the keys to integrated production is the pests and diseases management (called Integrated Pest and Disease Management, IPDM), with the general aim to keep the population density of potential pests, diseases, and "weeds" below economic damage thresholds. Strategies are implemented that combine legal, biological, cultural, biotechnological (including plant improvement), and, ultimately, chemical measures. Therefore, advancing towards vineyard protection following sustainable viticulture, providing efficient management tools with low ecological impact, is a key challenge for the maintenance of this sector. In this review, we will place in context the main biotic threats that face the vineyards, the potential

[1] IOV (2019). Statistics. www.oiv.int/en/databases-and-statistics/statistics.

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use of the entomopathogenic nematodes (EPNs) or their derivates as a direct tool of control of pests, and how we can use EPN presence and their association with other soil members in the context of soil health to allow selecting more ecologically-friendly management strategies to be implemented in the vineyards of the future.

2. Persistent and emergent biotic stress associated with grapevine production

The vineyard faces numerous biotic threats (viruses, viroids, phytoplasmas, bacteria, oomycetes, fungi, mites, insects, and nematodes). There are 65 virus species, five viroids, and eight phytoplasmas described as threats to the vineyard (Martinelli, 2014). However, in terms of economic impact, the short internode virus (GFLV), the Arabis mosaic virus (ArMV), the viruses associated with the rolling of the vine leaf (GLRaV), and viruses linked to the rough wood disease (GRWD) stand out (Perrone et al., 2017). Among the bacteria, it is worth highlighting the tumors of the vine (*Agrobacterium* spp./*Rhizobium* spp. Rhizobiales: Rhizobiaceae, according to the new nomenclature, Flores-Félix et al., 2020), and the bacterial necrosis of the vine (*Xylophilus ampelinus*, Proteobacteria: Pseudomonadaceae) both of which are of wide distribution and economic impact (Armijo et al., 2016). Furthermore, Pierce's disease (*Xylella fastidiosa*, Proteobacteria: Xanthomonadaceae) is nowadays an emerging disease of impact in the Mediterranean basin affecting several crops, including the vineyard.[2,3] Among the oomycetes, the downy mildew *Plasmopara vitícola* (Peronosporales: Peronosporaceae) stands out, which, together with the fungi powdery mildew of the vine, *Erysiphe necator* (Erysiphales: Erysiphaceae) and the gray mold of the clusters, *Botrytis cinerea* (Helotiales: Sclerotiniaceae), is responsible for most of the phytosanitary treatments applied in vineyards (Pertot et al., 2017). Also noteworthy are the black rot of the vine *Phyllosticta ampelicida* (Botryosphaeriales: Phyllostictaceae) and the species complex associated with wood diseases (Gramaje et al., 2018). On the other hand, there are more than 100 phytophagous arthropods described as causative agents of damage in the vineyard (Marco et al., 2008). However, the most worldwide persistent are the insects *Lobesia botrana* (Lepidoptera: Tortricidae) (European Grapevine moth) and *Sparganothis pilleriana* (Lepidoptera: Tortricidae) (the piral of the vine), and the mites *Eotetranychus carpini* (yellow spider) and *Tetranychus urticae* (two-spotted spider mite) (Prostigmata: Tetranychidae) (Marco et al., 2008). However, other arthropods are gaining great international relevance. For example, *Philaenus spumarius* (Hemiptera: Aphrophoridae) is the principal vector of the bacterium *X. fastidiosa* in Europe.[2,3] Also, cottony mealybugs (Hemiptera: Pseudococcidae) and green mosquitoes (Hemiptera: Cicadellidae), in some cases disease vectors, are making a strong resurgence in large areas in South Europe (Cabaleiro et al., 2020). Other pests such as phylloxera, *Dactylosphaera vitifoliae* (Hemiptera: Phylloxeridae), although at present are less critical thanks to integrated pest and disease management (IPDM) measures, yet the impact of climate change and the possibility of overcoming genetic resistance by the phylloxera, add uncertainty. The species *Xylotrechus arvicola* (Coleoptera: Cerambycidae) is considered an emerging pest still practically unknown and with high potential for damage (Marco et al., 2008). Regarding nematodes, the ectoparasitic nematode *Xiphinema index* (Dorylaimida: Longidoridae), known to be a vector of GFLV, and several species of the genus *Meloidogyne* (Tylenchida: Meloidogynidae), with *M. incognita*, *M. arenaria*, and *M. javanica*, stand out among the most prevalent (Saucet et al., 2016; Aballay et al., 2020).

The management of these biotic threats is complex because they are not individually present in the vineyards but co-occurring and, in some cases, interacting, such as GFLV-*X. index*, *L. botrana*-*B. cinerea*, and *P. spumarius*-*X. fastidiosa*. Hence, management will depend on the population/virulence of the species/strain, its relationship with the specific grape variety present in the field, and the interactions of all these with the environment. Finally, it is expected that climate change may impact the development of pests and diseases, increasing the number of cycles per year (multivoltine species) or the number of individuals generated, so it is estimated that it is necessary to increase the number of doses/treatments with agrochemicals (Delcour et al., 2015). This scenario might also promote the resurgence of previously considered secondary pests and diseases to key problems, and even the emergence of new threats such as the complex *P. spumarius*-*X. fastidiosa*. Hence, the new viticulture should fight against persistent and emergent problems by using as much as possible the rational and specific tools available.

3. Challenges for the pest and pathogen management in sustainable viticulture

Overall, IPDM prioritizes preventive or indirect control measures, such as actions to favor the biodiversity of agro-ecosystems. At the same time, IPDM tends to limit the use of direct control measures, in particular, chemical control strategies based on synthetic compounds, restricting them only when the economic threshold is exceeded and exceptional situations. However, the current situation accounts for intense phytosanitary treatments throughout the productive cycle of the vine,

[2] EFSA (2018a). Scientific opinion on the updated pest categorisation of *Xylella fastidiosa*. EFSA Journal 16:5357. 10.2903/j.efsa.2018.5357.

[3] MAPA (2019). https://www.mapa.gob.es/images/es/ xylellafastidiosa_contingencia _febrero2019_tcm30-501581.pdf

corresponding on average about 12–15 treatments/year with fungicides (25–30 treatments depending on the year), between 1-4 insecticide/acaricide treatments (rising to 8 in the case of table grapes) and 1-2 herbicide applications or tillage management (Pertot et al., 2017). In general, the management of pests and diseases is often based on the use of short-lived agrochemicals whose widespread use compromises their effectiveness (mainly due to the appearance of resistance) and poses serious environmental and human health problems. Therefore, the vineyard, like most agroecosystems, is also governed by an IPDM with inertia towards "intelligent pesticide management" (Nicholls, 2010). This intense management promotes the presence of pesticide residues in the soils. In this regard, Silva et al. (2019) noticed that more than 80% of European agricultural soils contain pesticides residues, and, in more than 50% of them, there were mixtures of several compounds. The combined effect of various pesticides residues is unknown and, therefore, difficult to assess in terms of health risk and environmental issues concerned (Silva et al., 2019). The current situation is that vineyards suffer intense management with agrochemical, and their availability is revised and, in some cases, not renewed, such as the well-known synthesis fungicides Mancozeb and Quinoxyfem[4,5] (and the insecticides Chlorpyrifos methyl and Propargite.[6,7] In contrast, in the last years, there is an increase in new products compatible with organic agriculture (Figure 1). This swift illustrates the urgent need to provide efficient and non-polluting tools for the management of biotic threats such as the use of beneficial organisms (entomopathogens, growth promoters, etc.), biopesticides (defined as chemical mixture derived from biological sources such as plants, bacteria, fungi) and specific elicitor-triggered immunity to enhance the grapevine plant defense (Pertot et al., 2017; Daane et al., 2018; Damalas and Koutroubas, 2018; Thiéry et al., 2018; Héloir et al., 2019).

4. Exploring the possible contribution of entomopathogenic nematodes to future viticulture

Entomopathogenic nematodes (EPNs) in the genera *Steinernema* and *Heterorhabditis* are well-known biological control agents (Campos-Herrera, 2015). EPNs are naturally occurring in the soil in their resistance stage called "infective juvenile" (IJ), with the ability to actively locate their host by recognizing different signals that reveal their presence (vibrations, significant increase in the concentration of CO_2, volatile specific produced by plants damaged by herbivore, etc.) (Griffin, 2015). After penetrating through their natural orifices (mouth, anus, spiracles), they reach the hemocele and release the symbiont bacteria that they carry inside, *Xenorhabdus* in the case of *Steinernema* and *Photorhabdus* for the *Heterorhbditis* species (Dillman et al., 2012; Lacey et al., 2015; Stock, 2015). The joint action of both organisms makes it possible to avoid the host's immune response and kill it by septicemia within 24–48 h post-infection. Both the bacteria and the nematode reproduce within the dead host for 7-15 days, depending on the species and environmental conditions, until a new generation of IJs massively emerge to start the cycle again.

EPNs are distributed in soils throughout the world (Adams et al., 2006), including in commercial vineyards (Belair et al., 2001; Mracek et al., 2005; Campos-Herrera et al., 2008; Blanco-Pérez et al., 2020). EPN infectivity and survival ability are mediated by abiotic (type of soil, humidity, temperature, etc.), and biotic factors (inter and intraspecific competition, natural enemies, predators, etc.) (Stuart et al., 2015). Many agricultural practices, such as traditional tillage, expose EPNs to extreme conditions (temperature, ultraviolet light, etc.) that significantly reduce their biocontrol potential, even reaching the extinction of the natural populations in our crops. Hence, there is increasing interest in identifying the factors that define EPN population dynamics in agroecosystems (Griffin, 2015; Lewis et al., 2015). Their identification can allow us establishing the best practices to favor suitable ecological scenarios to enhance their activity.

The availability of commercial products based on IJs of various species (Lacey et al., 2015) makes them excellent products in IPDM programs and even in organic production (Campos-Herrera, 2015). Most products consist of formulations of IJs in artificial substrates that increase the storage period (which can range from 1 to 3 months in refrigerated conditions) at the cost of reducing their activity (Hiltpold, 2015). Then, their application is based on a first simple suspension of the product in water and a subsequent release by different methods. One of the most widespread application is spraying using motorized tanks, recommended for large areas of fruit trees and other perennial crops, although they can also be applied directly to irrigation lines (Shapiro-Ilan & Dolinski 2015). Recently, an indirect application system uses insect larvae

[4] EFSA (2018b). Peer review of the targeted hazard assessment of the pesticide active substance quinoxyfen. EFSA Journal 16: 5085. 10.2903/j.efsa.2018.5085.

[5] EFSA (2020). Peer review of the pesticide risk assessment of the active substance mancozeb. EFSA Journal 18:5755. 10.2903/j.efsa.2020.5755.

[6] EFSA (2011). Conclusion on the peer review of the pesticide risk assessment of the active substance propargite. EFSA Journal 9:2087. 10.2903/j.efsa.2011.2087.

[7] EFSA (2019). Updated statement on the available outcomes of the human health assessment in the context of the pesticides peer review of the active substance chlorpyrifos-methyl. EFSA Journal 17:5908. 10.2903/j.efsa.2019.5908

previously infected with EPNs, which increase the control in the treatments (for example, with joint applications with the sowing of seeds). This approach can keep the IJs protected from the harassing conditions from the environment, thus increasing its persistence in the soil (Gumus et al., 2015). In addition, the recent advances in the application technology by using specific formulations, adjuvants, and release systems have allowed the successful

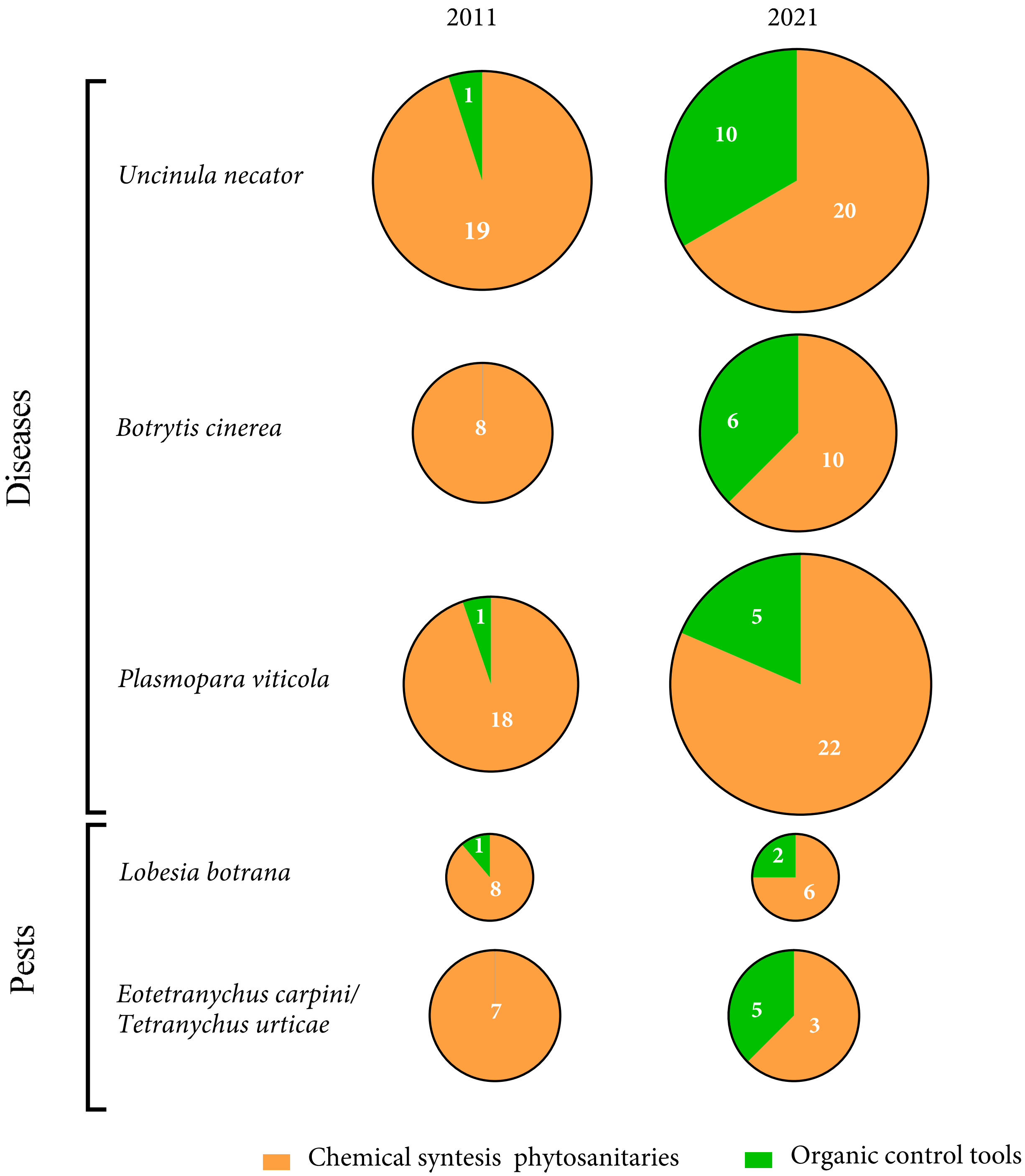

Figure 1. Example of the progression of authorized phytosanitary product usage in Spain against the most important diseases and pests of vineyards during the last decade. The size of each circle is proportional to the total number of phytosanitary authorized against each biotic threat.[1]

[1] MAPA (2021). https://www.mapa.gob.es/es/agricultura/temas/sanidad-vegetal/productos- fitosanitarios/ registro/menu.asp

implementation of certain EPNs against aerial pests (Shapiro-Ilan & Dolinski, 2015).

Despite the huge potential of the EPN to manage numerous pests, vineyards as target agroecosystem have been poorly investigated. One of the reasons could be the lack of serious soil-dwelling pests or the fact that the real impact of these soil pests is often hidden (Marin et al., 2020). In this regard, one of the most threatening pests, the phylloxera *D. vitifoliae,* is normally successfully managed by using the appropriate rootstock (Ollat et al. 2016) although some studies report some regional high infestation rates on aerial parts (Granett et al. 2001; Fahrentrapp et al. 2015). English-Loeb et al. (1999) reported certain control potential in laboratory studies when using EPN under high moisture scenarios, but further studies were not performed against this pest. However, nowadays, the use of EPN is not restricted to the belowground application either to their use just as a biological control agent. Recent studies are providing evidence that the natural presence of EPN can be an indicator of the impact of soil management (Campos-Herrera et al., 2008; 2014; Valadas et al., 2014; Majic et al., 2019; Blanco-Pérez et al., 2020). Hence, the framework of the use of EPN is now expanded to all components of the IPDM in a direct or indirect approach (Figure 2). On the one hand, EPN action can be explored as biocontrol agents (classical, augmentation, or conservation) but also in a more technological perspective by the search of new active materials derived from their symbionts to be used as biopesticides. In particular, the secondary metabolites produced during fermentation of these bacteria have a broad-spectrum activity, i.e. insecticidal, fungicidal, bactericidal, acaricidal and nematicidal capacity (Bode, 2009; Eroglu et al., 2019; da Silva et al., 2020). On the other hand, the impact of soil management, cultural practices, and application of conventional pesticides can be explored using EPN as a model organism. Herein, we illustrate both approaches in the use of EPN in viticulture and highlight the gap of knowledge that requires further research for their full integration in IPM associated with vineyards.

5. Application of entomopathogenic nematodes and their derivates to protect grapevine against the main biotic threats

The efficacy of EPN against various arthropod pests associated with vineyards has been elucidated mainly in the laboratory and semi-field experiments, with limited success. The study by English-Loeb et al. (1999) targeting phylloxera showed the complexity of EPN use in the vineyard agroecosystems, obtaining moderate control only in highly moistened soils in laboratory conditions. Similarly, relatively low control has been evidenced by other studies against certain pests of local or regional

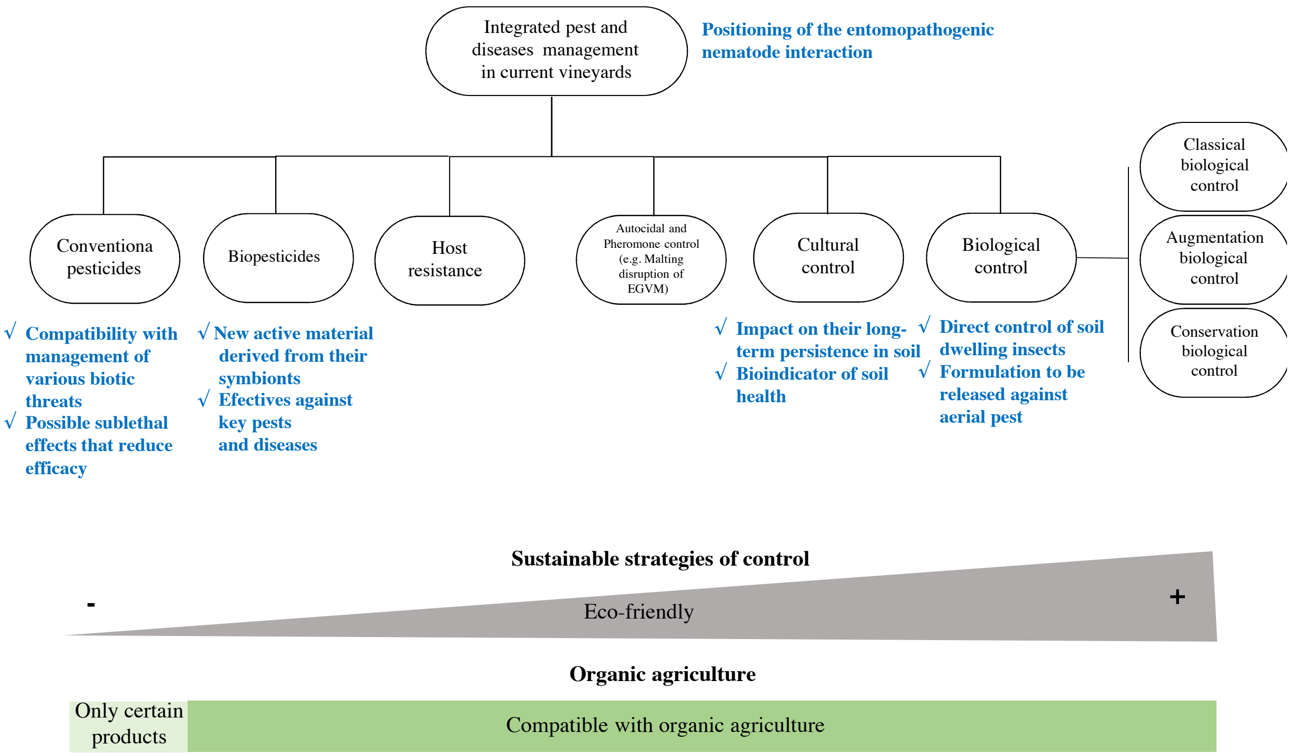

Figure 2. Integrated pest and disease management (IPDM) in viticulture and the possible interaction with entomopathogenic nematodes studies (in blue) (Modified from Eilenberg et al., 2001, and Provost and Pedneault, 2016).

relevance. For example, Vieux and Malan (2015) investigated the use of EPN against the vine mealybug, *Planococcus ficus* (Hemiptera: Pseudococcidae) in South African vineyards, reaching mortalities around 50% in the best scenarios and under laboratory conditions. Similarly, Steyn et al. (2021) investigated the efficacy of EPN against *Thaumatotibia leucotreta* (Lepidoptera: Tortricidae) under laboratory conditions, registering low mortality against the pupae. Some field experiments of augmenting EPN to fight against the grape root borer *Vitacea polistimorfis* (Lepidoptera: Sessidae) are more promising (Williams et al., 2010). This study registered a mean percentage control of 55%–74%, and the applied nematodes survived from 1 year up to 21 months, depending on the species, which opened the possibility of a conservation biological control approach to managing the grape root borer.

The development of new application approaches to release the EPN to fight against above-ground pests, which is linked to the potential use of the natural products generated by the symbiotic bacteria (Bode, 2009; Tobias et al., 2017), is expanding the possible use of EPN or their derivates as biocontrol agents or biopesticides (Figure 2). Hence, now it is plausible to target some of the worldwide threats for the future viticulture such as the arthropods *T. urticae, L. botrana* and *P. spumarius*, the oomycete *P. viticola*, and the fungi *E. necator* and *B. cinerea* (Gutiérrez et al., 2017; Pertot et al., 2017; Daane et al., 2018). For example, Eroglu et al. (2019) recently demonstrated that the secondary metabolites produced by the bacterial symbiont of certain EPN species show a huge potential of biocontrol against various stages of *T. urticae*. In particular, metabolites produced by *Xenorhabdus szentirmaii* (symbiont of *S. rarum*) caused 80% mortality after just two days' post-exposure against larvae and adult males. Subsequent studies demonstrated that these new natural products are compatible with natural enemies of *T. urticae*, the predatory mites *Phytoseiulus persimilis* and *Neoseiulus californicus* (Acari: Phytoseiidae) (Cevizci et al., 2020). Current research has allowed the identification of the specific compounds responsible for that acaricidal activity (Incedayi et al., 2021). Presumably, this new active material will show efficiency with other mites, such as *E. carpini*, frequently present in vineyards in warm areas. However, their real implementation as bioproduct still requires additional studies and scale up to industrial development.

Concerning the two main insects that threaten vineyards, *L. botrana* and *P. spumarius* (vector of *X. fastidiosa*), ongoing studies demonstrate the potential use of EPN of their derivates. In detail, a recent study has probed the efficacy of EPN and the natural products derived from cell-free supernatant obtained from the symbionts against nymphs of *P. spumarius* (Vicente-Díez et al., 2021). This study proved that the IJs survived and were able to kill after 72 h exposure to the foam produced by the *P. spumarius* nymphs. Because locating nymphs in the foam is easily recognized, the application of the EPN could be in a site-specific application approach (the foam) that might protect the EPN against the harassed effect of temperature, humidity, and UV (Lacey and Georgis, 2012). In addition, the efficacy of the EPN application ranged from 50%–90% nymphal mortality after five days post-exposure when using steinernematids. Interestingly, the application of the cell-free supernatant from *P. laumondii*, the symbiont of *H. bacteriophora*, resulted in nymphal mortalities of 64%, higher than any natural product derived from *Xenorhabdus* spp. after five days of exposure (Vicente-Díez et al., 2021). Finally, ongoing studies demonstrate the efficacy of EPN and the natural products derived from their symbionts against different larval instars of *L. botrana*.[8] This study registered 100% mortality in the 5th instar after five days of exposure to IJs of *S. carpocapsae* and > 90% mortality to the 1st and 3rd instar when the cell-free supernatant was applied to the artificial diet. In any case, as for the control of mites, the stage of development is on the initial steps, and further investigation is required for the implementation as novel bioproducts.

Similarly, a promising area to search for new active materials to fight against the oomycete *P. vitícola*, and the fungus *E. necator* and *B. cinerea* are the natural compounds generated during the fermentation of the EPN symbionts (Bode, 2009; Tobias et al., 2017). Overall, there is a wide range of effects against plant pathogenic oomycetes and fungi, including therapeutic and protective effects. For example, Fran et al. (2011, 2014) reported mycelial *B. cinerea* growth inhibition on tomato fruits produced after exposure to the natural products derived from the EPN symbionts produced in artificial fermentation. Similarly, ongoing studies have proved the inhibition growth of *B. cinerea* when exposed to *Xenorhabdus* spp. derivates in grapevine leaves (Figure 3), confirming their possible efficacy in this crop [8] although additional research is needed focusing on the grapevine cluster and determining the possible non-target effect in the plant. Finally, recent studies evaluated the deterring effect of volatile organic compounds (VOCs) produced by *Xhenorhabdus* and *Photorhabdus* species, which can cause an antifungal effect

[8] Vicente-Díez I et al. (2021), Blanco-Pérez R, Chelkha M, Puelles M, Pou A, et al. (2021). *Steinernema carpocapsae* and *Xenorhabdus nematophila* based products for the control of the grapevine moth and the grey mold in vineyards. Abstract in 2021 International Congress on Invertebrate Pathology and Microbial Control & 53rd Annual Meeting of the Society for Invertebrate Pathology, Virtual Meeting, June 28th-july 2nd 2021. www.lestudium-ias.com/event/2021-international-congress-invertebrate-pathology-and-microbial-control-53rd-annual-meeting.

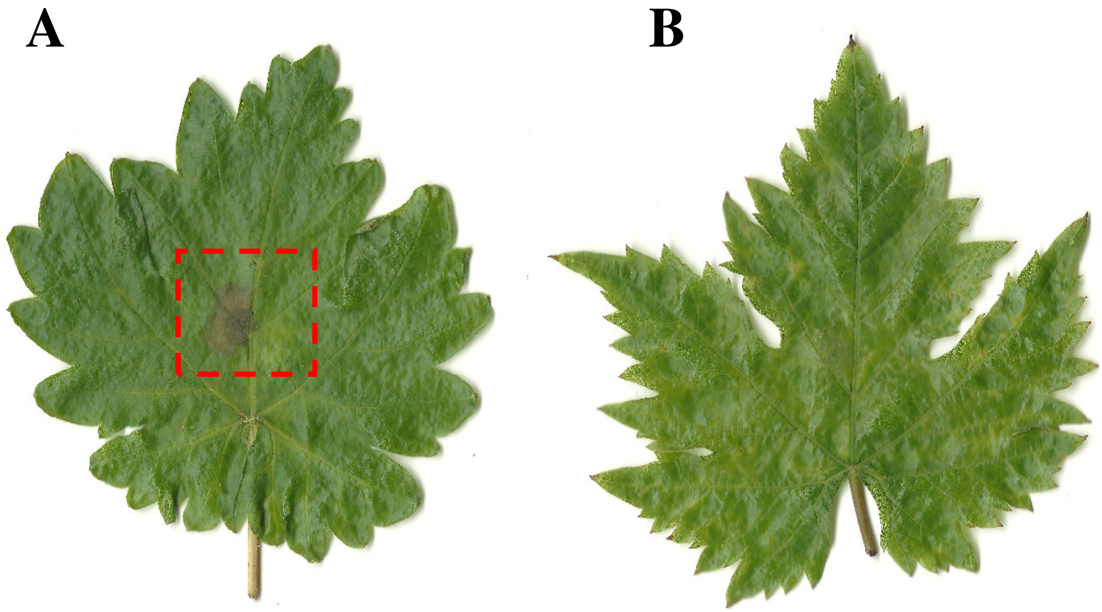

Figure 3. Preventive inhibition growth effect against *Botrytis cinerea* over grapevine leaves three days after the infection. A. Destilled water (control treatment). B. *Xenorhabdus nematophilus* natural products treatment.

against the fungi development (Chacón-Orozco et al., 2020).

Overall, the studies on EPN and natural products derived from their bacteria are promising. However, additional research is needed to make these new bio-tools available to growers. For example, in the IJs application, co-formulation with adjuvants (antidesiccants, brighteners, etc.) will be required to enhance their survival in the aerial part (Shapiro-Ilan & Dolinski, 2015). To date, the evaluation of certified adjuvants to be released in vineyards is limited but has shown good potential and margin to improvement in laboratory and greenhouse approaches[9] (Platt et al., 2019). Similarly, the temperature can modulate the activity of the EPNs, in particular, if applied for targeting overwintering stages. In this regard, species such as *S. feltiae* with a broad spectrum of activity at low temperatures (Grewal et al., 2006) should be carefully considered. Moreover, it is critical to determine the efficacy of these new biocontrol agents released aboveground compared with current biological control agents designated for these pests (Cevizci et al., 2020). Similarly, it is important to establish the compatibility of IJs application with other management measures typically implemented in a vineyard, such as those performed to control oomycetes and fungi as well as other biotic threats, by using chemical insecticides acaricides, herbicides, fungicides (Figure 2). Previous studies have shown compatibility of the IJs with various current active materials with different functions (Yan et al., 2019; Ozdemir et al., 2020; Jean-Baptiste et al., 2021) although also some sub-lethal effects were reported (Gutiérrez et al., 2008). Interestingly, the IJs are capable to use insect cadavers that were killed by insecticides (Nalinci et al., 2021). Hence, exploring the compatibility of EPN with the current chemical compounds approved in viticulture (Figure 1) will contribute to coordinate and compatibilized the agricultural practices management.

6. Evaluating the impact of vineyard management using entomopathogenic nematodes

The maintenance of functional biodiversity is key to the sustainability of viticulture[10] (Gliessman, 2007). In a general meta-analysis, Karimi et al. (2021) showed that organic viticulture practices promote soil biodiversity, resulting in 3 and 4-fold higher than the biodiversity observed in conventional viticulture. So, the use of pesticides—especially herbicides, tillage, the absence of soil cover, and mineral fertilization are significantly deleterious to the whole soil biodiversity. In contrast, practices such as the use of cover crops, organic fertilizers, and the addition of grapevine pruning wood have been proposed to produce

[9] González-Trujillo MM, Čepulyte R, Vicente-Díez I, Blanco-Pérez R, Chelkha M, et al. (2021). Screening of adjuvants to enhance the entomopathogenic nematode survival and adherence after aerial application on grapevine leaves. Abstract in 2021 International Congress on Invertebrate Pathology and Microbial Control & 53rd Annual Meeting of the Society for Invertebrate Pathology, Virtual Meeting, June 28th-july 2nd 2021. www.lestudium-ias.com/event/2021-international-congress-invertebrate-pathology-and-microbial-control-53rd-annual-meeting.

[10] IOV (2016). Resolución OIV-CST 518-2016. Principios generales de la OIV para una vitivinicultura sostenible. Aspectos medioambientales, sociales, económicos y culturales. www.oiv.int/js/lib/pdfjs/web/viewer.html?file=/public/medias/ 4957/oiv-cst-518-2016-es.pdf.

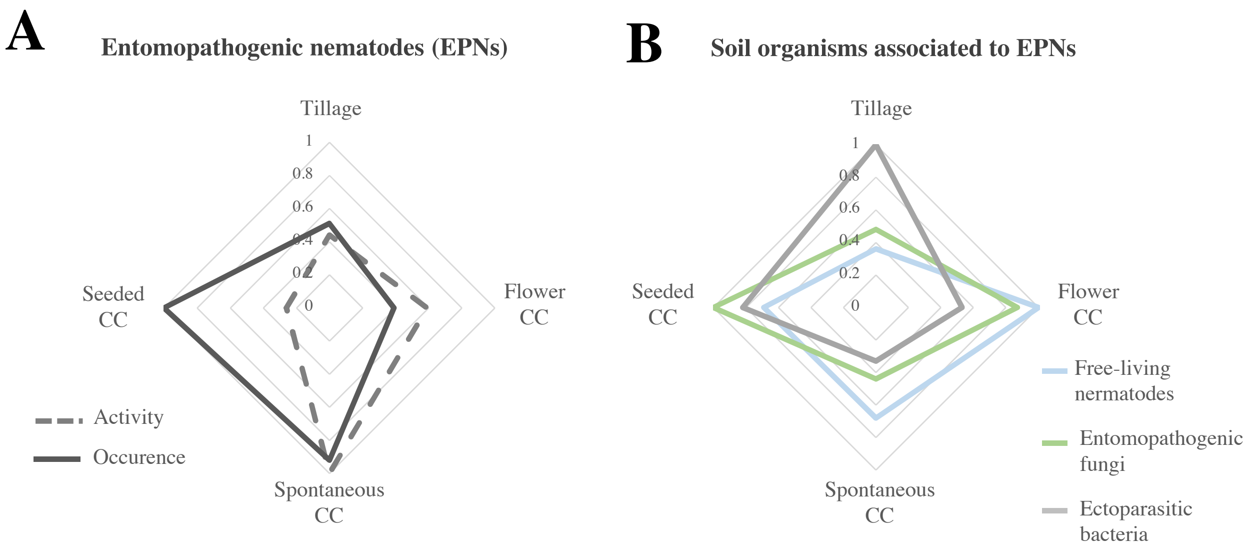

Figure 4. Evaluation of the impact of cover crops (CC) in the entomopathogenic nematode (EPN) soil food web in a Spanish vineyard. A. Impact in the presence and activity of native EPNs. B. Presence of natural enemies (nematophagous fungi and ectoparasitic bacteria) and competitors for the resource (Free-living nematodes) (Data from Blanco-Pérez et al., 2020, modified for this figure).

a beneficial effect on biodiversity (Karimi et al., 2021). In this study, it was shown that the nematodes as a group suffered losses of up to two-thirds of individuals. It is now well established that soil nematodes are an excellent model group to investigate soil health (Bonger and Ferris, 1999). Nematodes form complex trophic food webs (Ettema, 1998), which allows estimating maturity indices and ecological footprints to investigate the state of degradation of the agroecosystem (Bonger, 1990; Ferris, 2010; Ferris et al. 2012).

In addition, despite EPNs are primarily used as a direct biological control agent (Lacey et al., 2015), recent studies also show their potential as model to measure the impact of soil management practices in agriculture (Campos-Herrera et al., 2008; 2014; Blanco-Pérez et al., 2020) (Figure 2). To unravel the impact of agricultural practices (tillage, pest-disease management, presence of cover crops, etc.), it is required to consider the multitrophic interactions affecting their presence, such as the presence of natural enemies (acari, collembolan, nematophagous fungi, ectoparasitic bacteria) and competitors for the cadaver as a resource (free-living nematodes, other entomopathogens, etc.) (Duncan et al., 2003, 2007; Campos-Herrera et al., 2011, 2012, 2013, 2019; Bueno-Pallero et al., 2018; Blanco-Pérez et al., 2019, 2020). In this context, a recent study that evaluated the impact of the implementation of plant covers on the EPN soil food web revealed that the spontaneous covers favored the presence of EPNs while reducing the presence of their natural enemies (Blanco-Pérez et al., 2020) (Figure 4). These results are consistent with those observed in aerial and epigeal entomofauna (Sáenz-Romo et al., 2019) pointing to spontaneous covers as management structures that can provide benefits to the biological control. Ongoing studies investigate whether the pest/disease management (integrated versus organic) and soil alteration (tillage versus no-tillage) can affect the EPN soil food web in the vineyards from the specific wine production region (denominated in Spanish "Denominación de Origen Calificada Rioja", DOCa Rioja). The preliminary results indicate that, in vineyards with organic management, there was a greater suppressive capacity of the soil by EPNs when compared with the soils under IPDM production. However, this activity was not influenced by soil management.[11] These results need to be complemented with the evaluation of the soil food web associated with EPN to elucidate to which extend the natural enemies and competitors might be responsible for this natural distribution. In any case, these studies illustrate the potential use of EPN as an indicator of the impact of agricultural management in soil biodiversity and can serve as valuable data to select the best cultural practices that support the biodiversity and resilience of the vineyards.

7. Concluding remarks and future directions

Future viticulture requires us to face various challenges, including the reduction of the use of chemical control

[11] Blanco-Pérez R, Vicente-Díez I, Ramos-Sáez de Ojer JL, Marco-Mancebón VS, Pérez-Moreno I, et al. (2021). Impact of differentiated vineyard management on the activity of entomopathogenic nematodes in La Rioja (Spain). Abstract in 2021 International Congress on Invertebrate Pathology and Microbial Control & 53rd Annual Meeting of the Society for Invertebrate Pathology, Virtual Meeting, June 28th-july 2nd 2021. www.lestudium-ias.com/event/2021-international-congress-invertebrate-pathology-and-microbial-control-53rd-annual-meeting.

to manage pests and diseases. It is critical to encourage alternative strategies (Figure 2) and reinforce the use of beneficial organisms, new bio-pesticides based on natural products, and the release of certain elicitors that can enhance the immune response of the plant and provide sufficient defense mechanisms (Pertot et al., 2017; Damalas and Koutroubas, 2018; Thiéry et al., 2018; Héloir et al., 2019). This review has demonstrated the enormous potential of EPN to contribute to the achievement of real sustainable viticulture. In this sense, the compatibility of EPN and the natural products derived from their symbionts against aerial pests of relevance in vineyards is probed under laboratory conditions (Eroglu et al., 2019; Cevizci et al., 2020; Incedayi et al., 2021; Vicente-díez et al., 2021), but further research is required to ensure the good performance in field applications. Concerning EPN aerial application, more research in the formulation with adjuvants is required.[9] Also, the efficacy of the EPN to target overwintering stages that could be in the grapevine bark or even in the soil could provide a further alternative of management that prevents a high starting population for the next production season. The fact that IJs are already formulated and available as commercial products (Lacey et al., 2015), can accelerate the implementation of this tool once optimized. Regarding the new biopesticides, further research is required to reach the stage of commercial product available for growers, but we envision a very successful future. Moreover, recent evidence has shown that, by investigating the EPN soil food web, it is possible to discriminate agricultural practices that can contribute to the maintenance of soil biodiversity and possible conservation biological control, as an indirect indicator of the resilience of the vineyards (Blanco-Pérez et al., 2020). By combining both approaches, EPN can contribute to the understanding of the vineyard as agroecosystems and protect them for future generations.

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