*Biopestic. Int.*13(2):79-112 (2017) ISSN 0973-483X / e-ISSN 0976-9412

Entomopathogenic Nematodes and their Mutualistic Bacteria: Their Ecology and Application as Microbial Control Agents

BARIS GULCU[1], HARUN CIMEN[2], RAMALINGAM KARTHIK RAJA[3] AND SELCUK HAZIR[2]*

[1]Department of Biology, Faculty of Arts and Science, Duzce University, Duzce, 81620, Turkey
[2]Department of Biology, Faculty of Arts and Science, Adnan Menderes University, Aydin, 09010, Turkey
[3]Department of Biotechnology, Periyar University, Salem, Tamil Nadu, India

KEY WORDS

Biological control

Heterorhabditis

Photorhabdus

Steinernema

Xenorhabdus

ABSTRACT Entomopathogenic nematodes (EPNs) belonging to the families heterorhabditidae (genus *Heterorhabditis*) and steinernematidae (genus *Steinernema*) are mutualistically associated with bacteria in the family Enterobacteriaceae (*Photorhabdus* spp. for *Heterorhabditis* and *Xenorhabdus* spp. for *Steinernema*). At present, there are 100 *Steinernema* and 17 *Heterorhabditis* species and 20 *Xenorhabdus* and 4 *Photorhabdus* species. In general, each EPN species has its own bacterial species, but a given bacterial species may be associated with more than one EPN species. The EPNs' natural habitat is the soil where the nematode-bacterium complex infects many different insect species killing them within 48 h. EPNs have been isolated from many different islands and from all continents except antarctica. Because EPNs and their associated bacteria are safe to humans, other vertebrates, and plants, can effectively kill soil insect pests in a short time, serve as an alternative to chemical pesticides, are easily massed produced *in vivo* and *in vitro*, and do not require registration in many countries, a number of EPN species have been produced commercially to target soil and plant-boring pests in high value crops. Moreover, the associated bacteria produce antibiotics and other compounds that have potential to be used against human, veterinary, and plant pathogens.

INTRODUCTION

Nematodes (often referred to as roundworms) are ubiquitous animals ranging in size from a few microns to more than 13 m in length, are found in marine, freshwater, and terrestrial environments, and occur from the polar to the tropical regions of the world (Viglierchio, 1991). They exist as free-living species that feed on bacteria, fungi, or detritus, whereas others are predators of other animals or are parasites of plants and animals including humans. Of those nematodes that parasitize animals, many are well-known such as the hookworms, pinworms, Guinea worm, dog heartworm, and filariasis (Viglierchio, 1991; Koppenhofer, 2007). On the other hand, a number of nematodes are beneficial to humans because they parasitize pestiferous mollusks and insects. For example, these beneficial nematodes include *Phasmarhabditis hermaphrodite* that is commercially available in Europe for controlling slugs in the garden (Ester and Wilson, 2005; Wilson and Grewal, 2005), *Romanomermis culicivorax* that parasitizes mosquito larvae (Shamseldean and

*Corresponding author: E-mail: selcuk.hazir@gmail.com

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Platzer, 1989; Platzer *et al.*, 2005), and *Deladenus siricidicola* that is mass produced and released for biological control of the *Sirex* woodwasp that attacks pines in several countries (Bedding, 2009; Bedding and Iede, 2005; Williams *et al.*, 2012). Numerous other nematode species provide natural biological control by parasitizing pestiferous insects (Bedding and Iede, 2005; Funderburk and Latsha, 2005; Platzer *et al.*, 2005) and are referred to as being entomogenous. Another group of nematode species is associated with symbiotic bacteria, and both nematode and bacterium are required for successful infection and killing of their insect hosts and subsequent nematode reproduction. Because these nematodes that belong to the genera *Steinernema* and *Heterorhabditis* are associated with bacteria for infection and host mortality, they are referred to as entomopathogenic nematodes (EPNs) and are the focus of this review.

Recently, the term "entomopathogeny" was defined by Dillman *et al.* (2012) as nematodes that: (1) Are carriers of the pathogenic bacteria by the infective third stage infective juveniles (IJs), (2) have host-seeking ability and infect by the IJs entering the hemocoel of their insect host, (3) efficiently release the bacteria into the insect hemolymph, (4) result in a fairly rapid death (i.e., 24–120 h) of the insect followed by nematode reproduction and bacterial proliferation driven by cadaver-nutrient utilization, (5) reassociates the pathogenic bacteria with new generations of IJs, and (6) finally, result in the emergence of the IJs from the nutrient depleted cadaver to initiate the search for new insect hosts (Fig. 1). Although entomopathogenic characterizes *Steinernema* and *Heterorhabditis* species,

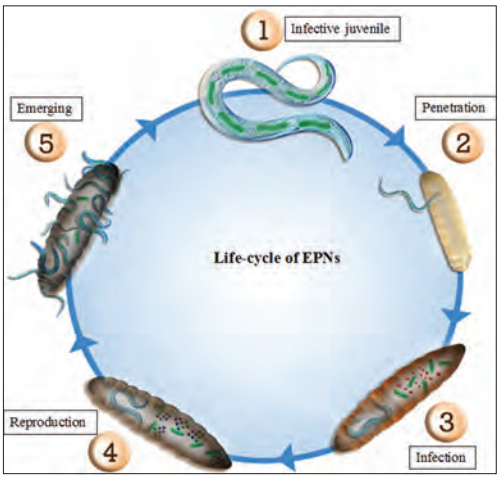

Fig. 1. General life cycle of entomopathogenic nematodes. The numbers on the figure show the order of stages in the life cycle of entomopathogenic nematodes. (Figure was modified from http://www.nosopharm.com).

other nematode species in the genera *Oscheius* and *Caenorhabditis* have been shown to use pathogenic bacteria to infect their insect hosts. For example, *Oscheius chongmingensis*, *O. carolinensis*, and *Caenorhabditis briggsae* have been isolated from soil using the bait insect technique described by Bedding and Akhurst (1975). These nematode species are associated with the bacterial species, *Serratia marcescens*, many strains of which are known insect pathogens (Schulenburg and Ewbank, 2004; Abebe *et al.*, 2011; Torres-Barragan *et al.*, 2011). Thus, *O. chongmingensis* and *C. briggsae* require their bacterial partners to cause host death, develop and reproduce within the killed insects, and emerge as dauer (German word for "endurance" or "duration" and often used synonymously with IJ) juveniles that are associated with *S. marcescens*. According to the standards proposed by Dillman *et al.* (2012), *C. briggsae* may not be an EPN species because the dauer juveniles recovered from dead insects can infect new hosts but are less virulent to the insect, *Galleria mellonella* (Lepidoptera: Pyralidae). Thus, *C. briggsae* appears to be between a necromenic and entomopathogenic species. However, at this time, *Oscheius* spp. should be considered as EPNs even though further research is required to determine the nature of their bacterial associations, and whether they are obligate or facultative EPNs (Dillman *et al.*, 2012). Nonetheless, only the nematodes in the genera *Heterorhabditis* and *Steinernema* have been commercially developed as microbial control agents (Shapiro-Ilan *et al.*, 2016).

EPNs are in the Families Steinernematidae (genus *Steinernema*) and Heterorhabditidae (genus *Heterorhabditis*), are obligate insect parasitic organisms, and occur in the soil environment in nature. Species of EPNs have mutualistic associations with bacteria in the family Enterobacteriaceae (*Xenorhabdus* spp. for *Steinernema* and *Photorhabdus* spp. for *Heterorhabditis*) that reside in the gut of the IJ. The IJs range in length from 400 to 1300 microns depending on species (Hazir *et al.*, 2003; Lewis and Clarke, 2012). Although the life cycle of nematodes in the genera, *Steinernema* and *Heterorhabditis*, are similar, they are not closely related (Blaxter *et al.*, 1998). Their similarities including mutualistic association with the EPN/bacterium complex are believed to have arisen through convergent evolution (Poinar, 1993). *Steinernema* spp. have a terrestrial rhabditid ancestor, whereas *Heterorhabditis* spp. have a marine rhabditid ancestor.

Most EPNs require their symbionts for growth and reproduction, but exceptions have been observed (Sicard *et al.*, 2005). There are also differences between biological characteristics of the two nematode taxa.

For example, *Heterorhabditis* maternally transmit symbionts by a sophisticated multistep process, whereas *Steinernema* have specialized host structures within which they carry their symbionts (biology of nematode/bacterium complex) (Enright and Griffin, 2004). Furthermore, although some *Steinernema* spp. can infect and kill insect hosts even in the absence of pathogenic bacteria under laboratory conditions, the *Heterorhabditis* spp. has not been reported to have this behavior (Han and Ehlers, 2000; Goodrich-Blair and Clarke, 2007).

The interest in EPNs as microbial control agents has occurred because of the need to find alternatives to chemical insecticides which can cause secondary pest resurgence, host resistance, and environmental contamination and pose a health concern to nontarget organisms including humans. EPNs occur naturally in many soils throughout the world, target primarily soils insect pests, do not contaminate the environment and are safe to most nontarget organisms and humans. Moreover, the use of EPNs is advantageous because they can actively seek their host, rapidly kill the insect, have high reproduction capacity within the insect cadaver resulting in the production of new IJs that may infect new hosts, and can be mass-produced *in vivo* and *in vitro*. In addition to the applied aspects, a vast database has been gained on basic aspects of EPNs such as the systematic and molecular studies, behavioral ecology, and the discovery of secondary metabolites from their mutualistic bacteria *Xenorhabdus* and *Photorhabdus* spp. (Webster *et al.*, 2002; Bode, 2009). For example, the secondary metabolites from the mutualistic bacteria have the potential to be used as control for plant, veterinary, and human pathogens (Fodor *et al.*, 2010; Fang *et al.*, 2014; Shapiro-Ilan *et al.*, 2014a; Nollman *et al.*, 2015; Bussaman and Rattanasena, 2016; Hazir *et al.*, 2016).

BIOLOGY OF NEMATODE/BACTERIUM COMPLEX

EPNs have six life stages: The egg, Juvenile 1, 2, 3, and 4 (referred to as J1, J2, J3, and J4), and adult. The non-feeding, free-living, third stage IJ infects the insect host in the soil environment (Fig. 1). The IJ, the only stage that occurs outside of an insect, is ensheathed in the second-stage cuticle that is easily lost in the steinernematids but is retained in the heterorhabditids until just before or shortly after host infection. In steinernematid IJs, *Xenorhabdus* bacterial cells are housed in the anterior intestinal caecum (a vesicle in the anterior part of the intestine), whereas in heterorhabditid IJs, *Photorhabdus* cells are found throughout in the intestinal tract. The IJs enter the host through natural openings (oral cavity, anus, and spiracles) and then penetrate into the hemocoel or in some cases by penetrating intersegmental membranes (Kaya and Gaugler, 1993). Dauer larvae of *H. bacteriophora* were observed using their proximal tooth for rupturing the insect body wall, and it was long believed that only *Heterorhabditis* could penetrate tissues like the insect's integument since dauer larvae of *Steinernema* lack the tooth. However, the penetration of *Steinernema feltiae* through the integument of leatherjackets challenged this perspective (Dowds and Peters, 2002). Inside the insect's hemocoel, the IJs release their mutualistic bacteria through the anus for steinernematids or through the mouth for heterorhabditids (Ciche and Ensign, 2003; Ciche *et al.*, 2006). Once the bacterial cells are released, they produce toxins and toxin complexes to suppress the insect's immune system. Subsequently, the insect dies due to septicemia or toxemia generally within 48 h. Insect cadavers with *Photorhabdus* become red because of the production of anthraquinone pigments and will luminescence in the dark because of the lux gene (Gupta *et al.*, 2003; Boemare and Akhurst, 2006). Insect cadavers with *Xenorhabdus* generally become ochre or black.

The IJs initiate their development, feeding on the multiplied bacterial cells and host tissues that have been metabolized by the mutualistic bacteria. *Xenorhabdus* and *Photorhabdus* also produce a large variety of antimicrobial compounds to prevent microbial contamination (Boemare and Akhurst, 2006; Lewis *et al.*, 2015) and a scavenger deterrent factor(s) that deters scavengers and omnivores from feeding on the nematode-killed insect (Baur *et al.*, 1998; Gulcu *et al.*, 2012; Jones *et al.*, 2017; Raja *et al.*, 2017).

Although only one IJ is needed to kill an insect, usually more than one will enter a host. Because the steinernematids are amphimictic, however, a male and female IJ must infect an insect host for successful reproduction to occur. On the other hand, the heterorhabditid IJs develop into hermaphroditic adults and only one IJ is needed for infection of the host for successful reproduction. In subsequent heterorhabditid generations, both hermaphroditic and amphimictic reproduction occurs (Koltai *et al.*, 1995). There are normally two to three nematode generations, although if nutrients are low, only one generation may result. Once nutrients are exhausted, the second stage nematodes develop into the IJs where they reinitiate the symbiosis by sequestering a group of their mutualistic bacterial cells. The IJs emerge from the insect cadaver to search for or wait for new hosts in the soil (Brown and Gaugler, 1997; Shapiro-Ilan *et al.*, 2016).

The release of the mutualistic bacteria by the IJs is not a random process. The IJs only have one

opportunity to release their mutualistic bacteria and have evolved mechanisms to prevent such early releases to occur except in an insect host. Ciche *et al.* (2006) demonstrated that heat- and protease-resistant, low-molecular-weight component from the insect's hemocoel activates the development of IJs and results in the release of the mutualistic bacteria. Thus, the IJs do not spontaneous release the bacteria except in an insect host. Even in *in vitro* production medium typically consisting of soybean protein, yeast extract, and vegetable oil, the IJs do not spontaneously release the bacteria (Peters *et al.*, 2017). In *in vitro* production of EPNs, usually axenic EPN eggs are used, and the corresponding bacterial species are added to the artificial medium which initiates IJ development. Other recent studies have shown that after entering the insect hemocoel, the EPNs do not immediately release the symbiotic bacteria in the host. For example, *S. glaseri* releases its symbiotic bacteria, *Xenorhabdus poinarii*, 4–6 h after its entry of the host hemocoel, while *H. bacteriophora* releases *Photorhabdus luminescens* 30 min later (Wang *et al.*, 1995; Bowen *et al.*, 1998). In cases where bacterial release is delayed, EPNs must evade or suppress the host immune responses to ensure the release of their mutualistic bacteria.

TAXONOMY OF NEMATODE/BACTERIUM COMPLEX

In the Steinernematidae, there are two genera represented by *Steinernema* with 100 species [Table 1] and *Neosteinernema* with only one species (*N. longicurvicauda*), whereas in the Heterorhabditidae, there is only the genus *Heterorhabditis* with 17 species [Table 2] (Nguyen and Hunt, 2007; Hunt and Subbotin, 2016; Abd-Elgawad *et al.*, 2017; Shapiro-Ilan *et al.*, 2017). The species for *Steinernema* and *Heterorhabditis* have been updated by Hunt and Subbotin (2016) [Tables 1 and 2] and a number of new synonymies have been proposed, mostly on a re-evaluate of their molecular data [Table 3]. The number of described *Steinernema* species is much higher than *Heterorhabditis*, and it has been speculated that hermaphroditism in *Heterorhabditis* is the reason for their lower biodiversity (Downes and Griffin, 1996; Hominick, 2002).

The mutualistic bacterial symbionts, *Xenorhabdus* and *Photorhabdus* species associated with a given *Steinernema* and *Heterorhabditis* species are listed in Tables 1 and 2, respectively. At present, 20 *Xenorhabdus* and 4 *Photorhabdus* species have been described [Tables 1 and 2].

With the increasing number of described species, traditional approaches such as comparative morphology have become of limited utility for EPN taxonomy and diagnosis. Thus, molecular techniques using DNA sequences along with basic local alignment search tool available in the National Center for Biotechnology Information GenBank are used to describe new EPN isolates. This approach is easier and saves time compared to using only morphological data (Altschul *et al.*, 1990). At present, nucleotide differences on the level of 4–5% of compared sequences are sufficient to identify new species (Spiridonov, 2017). Although molecular techniques have provided a tremendous amount of objective data toward EPN systematics, molecular taxonomy is not free from error (sequence length, mistakes in sequence reading, and alignment errors, etc.). Accordingly, new taxa should be supported by good quality sequences of both ITS (Internal Transcribed Spacer) and D2-D3 (28S rDNA) regions (Hunt, 2016) and to use both morphological and molecular data for the description of new species.

Comparison of 16S rRNA gene sequences is useful for determining molecular taxonomy among prokaryotic organisms (Woese, 1987) and has been used in the description of the genera *Xenorhabdus* and *Photorhabdus* (Rainey *et al.*, 1995). It has been confirmed that sequencing only a part of the 16S rRNA gene can be sufficient to establish phylogenetic relationships (Lane *et al.*, 1985). However, studying a single gene is not reliable because errors about sequences and misinterpretation are known to occur. At present, phylogenetic analysis of the genera *Xenorhabdus* and *Photorhabdus* is based on a multigene approach with the recombinase A (recA), DNA polymerase III beta chain (dnaN), glutamyl-tRNA synthetase catalytic subunit (gltX), DNA gyrase subunit B (gyrB,) and initiation factor B (infB) genes (Tailliez *et al.*, 2010; 2012). Furthermore, DNA-DNA hybridization analysis needs to be done if 16S rDNA similarity is over 97%. For this analysis, DNA-DNA relatedness should be below the 70% threshold for description as a new taxon (Wayne *et al.*, 1987). To provide a definitive taxonomy of the genera *Photorhabdus* and *Xenorhabdus*, molecular and phenotypic characterizations need to be done together.

MUTUALISM BETWEEN NEMATODE AND BACTERIA

In the nematode/bacterium complex, usually a given nematode species is specifically associated with one bacterial symbiotic species, but the bacterial species may be associated with more than one nematode species [Tables 1 and 2] (Hazir *et al.*, 2003; Shapiro-Ilan *et al.*, 2017). The relationship between the nematode and bacterium is truly mutualistic.

Table 1. *Steinernema* species with their known associated *Xenorhabdus* bacterial symbionts

Steinernema species	References	*Photorhabdus* symbiont
S. abbasi	Elawad *et al.* (1997)	*X. indica*
S. aciari	Qui *et al.* (2005a)	*X. ishibashii*
S. affine	(Bovien, 1937) Wouts *et al.* (1982)	*X. bovienii*
S. akhursti	Qui *et al.* (2005b)	Unknown
S. apuliae	Triggiani *et al.* (2004)	Unknown
S. arasbaranense	Nikdel *et al.* (2011)	Unknown
S. arenarium	(Artyukhovsky, 1967) Wouts *et al.* (1982)	*X. kozodoii*
S. ashiuense	Phan *et al.* (2006a)	Unknown
S. asiaticum	Anis *et al.* (2002)	Unknown
S. australe	Edgington *et al.* (2009a)	*X. magdalenensis*
S. backanense	Phan *et al.* (2006a)	Unknown
S. balochiense	Fayyaz *et al.* (2015)	Unknown
S. beddingi	Qui *et al.* (2005c)	Unknown
S. beitlechemi	Cimen *et al.* (2016a)	*X. khoisanae*
S. bicornutum	Tallosi (1995)	*X. budapestensis*
S. biddulphi	Cimen *et al.* (2016b)	Unknown
S. bifurcatum	Fayyaz *et al.* (2014)	*X. indica*
S. boemarei	Lee *et al.* (2009)	*X. kozodoii*
S. brazilense	Nguyen *et al.* (2010)	Unknown
S. cameroonense	Kanga *et al.* (2012a)	Unknown
S. carpocapsae	(Weiser, 1955) Wouts *et al.* (1982)	*X. nematophila*
S. caudatum	Xu *et al.* (1991)	Unknown
S. ceratophorum	Jian *et al.* (1997)	*X. budapestensis*
S. changbaiense	Ma *et al.* (2012a)	Unknown
S. cholashanense	Nguyen *et al.* (2008a)	Unknown
S. citrae	Stokwe *et al.* (2011)	Unknown
S. colombiense	López-Núñez *et al.* (2008)	Unknown
S. costaricense	Uribe *et al.* (2007)	*X. szentirmaii*
S. cubanum	Mrácek *et al.* (1994)	*X. poinarii*
S. cumgarense	Phan *et al.* (2006a)	Unknown
S. diaprepesi	Nguyen and Duncan (2002)	*X. doucetiae*
S. eapokense	Phan *et al.* (2006b)	Unknown
S. ethiopiense	Tamiru *et al.* (2012)	Unknown
S. fabii	Abate *et al.* (2016)	Unknown
S. feltiae	(Filipjev, 1934) Wouts *et al.* (1982)	*X. bovienii*
S. glaseri	(Steiner, 1929) Wouts *et al.* (1982)	*X. poinarii*
S. goweni	San-Blas *et al.* (2016)	Unknown
S. guangdongense	Qiu *et al.* (2004)	Unknown
S. hebeiense	Chen *et al.* (2006)	Unknown
S. hermaphroditum	Stock *et al.* (2004)	*X. griffiniae*
S. huense	Phan *et al.* (2014)	Unknown
S. ichnusae	Tarasco *et al.* (2008)	Unknown

(Contd...)

Table 1. ***(Continued)***

Steinernema species	References	*Photorhabdus* symbiont
S. innovationi	Cimen *et al.* (2015)	Unknown
S. intermedium	(Poinar, 1985) Mamiya (1988)	*X. bovienii*
S. jeffreyense	Malan *et al.* (2015)	Unknown
S. jollieti	Spiridonov *et al.* (2004)	*X. bovienii*
S. karii	Waturu *et al.* (1997)	*X. hominickii*
S. khoisanae	Nguyen *et al.* (2006a)	*X. khoisanae*
S. kraussei	(Steiner, 1923) Travassos (1927)	*X. bovienii*
S. kushidai	Mamiya (1988)	*X. japonica*
S. lamjungense	Khatri-Chhetri *et al.* (2011a)	Unknown
S. leizhouense	Nguyen *et al.* (2006b)	Unknown
S. litchii	Steyn *et al.* (2017)	Unknown
S. litorale	Yoshida (2004)	*X. bovienii*
S. loci	Phan *et al.* (2001a)	Unknown
S. longicaudum	Shen and Wang (1991)	*X. ehlersii*
S. minutum	Maneesakorn *et al.* (2010)	*X. stockiae*
S. monticolum	Stock *et al.* (1997)	*X. hominickii*
S. neocurtillae	Nguyen and Smart (1992)	Unknown
S. nepalense	Khatri-Chhetri *et al.* (2011b)	Unknown
S. nguyeni	Malan *et al.* (2016)	Unknown
S. nyetense	Kanga *et al.* (2012a)	Unknown
S. oregonense	Liu and Berry, 1996	*X. bovienii*
S. pakistanense	Shahina *et al.* (2001)	Unknown
S. papillatum	San-Blas *et al.* (2015)	Unknown
S. phyllophagae	Nguyen and Buss (2011)	Unknown
S. poinari	Mráček *et al.* (2014)	Unknown
S. puertoricense	Román and Figueroa (1994)	*X. romanii*
S. pui	Qiu *et al.* (2011)	Unknown
S. puntauvense	Uribe *et al.* (2007)	*X. bovienii*
S. pwaniense	Puža *et al.* (2016)	Unknown
S. ralatorei	Grifaldo-Alcantara *et al.* (2017)	Unknown
S. rarum	(de Doucet, 1986) Mamiya (1988)	*X. szentirmaii*
S. riobrave	Cabanillas *et al.* (1994)	*X. cabanillasii*
S. ritteri	de Doucet and Doucet (1990)	Unknown
S. robustispiculum	Phan *et al.* (2004)	Unknown
S. sacchari	Nthenga *et al.* (2014)	Unknown
S. sangi	Phan *et al.* (2001b)	Unknown
S. sasonense	Phan *et al.* (2006b)	Unknown
S. scapterisci	Nguyen and Smart (1990)	*X. innexi*
S. scarabei	Stock and Koppenhöfer (2003)	*X. koppenhoeferii*
S. schliemanni	Spiridonov *et al.* (2010)	Unknown
S. siamkayai	Stock *et al.* (1998)	*X. stockiae*
S. sichuanense	Mrácek *et al.* (2006)	Unknown

(Contd...)

Table 1. ***(Continued)***

Steinernema species	References	*Photorhabdus* symbiont
S. silvaticum	Sturhan *et al.* (2005)	*X. bovienii*
S. surkhetense	Khatri-Chhetri *et al.* (2011b)	Unknown
S. tami	Luc *et al.* (2000)	Unknown
S. texanum	Nguyen *et al.* (2007)	Unknown
S. thanhi	Phan *et al.* (2001a)	Unknown
S. thesami	(Gorgadze, 1988) Gorgadze *et al.* (2016)	Unknown
S. tielingense	Ma *et al.* (2012b)	Unknown
S. tophus	Cimen *et al.* (2014)	Unknown
S. unicornum	Edgington *et al.* (2009b)	Unknown
S. vulcanicum	Clausi *et al.* (2011)	Unknown
S. weiseri	Mrácek *et al.* (2003)	*X. bovienii*
S. xinbinense	Ma *et al.* (2012c)	Unknown
S. xueshanense	Mrácek *et al.* (2009)	Unknown
S. yirgalemense	Nguyen *et al.* (2005)	*X. indica*

S. abbasi: Steinernema abbasi, S. aciari: Steinernema aciari, S. affine: Stylidium affine, S. akhursti: Steinernema akhurstim, S. apuliae: Steinernema apulia, S. arasbaranense: Steinernema arasbaranense, S. arenarium: Steinernema arenarium, S. ashiuense: Steinernema ashiuense, S. asiaticum: Steinernema asiaticum, S. austral: Steinernema austral, S. backanense: Steinernema backanense, S. balochiense: Steinernema balochiense, S. bedding: Steinernema bedding, S. beitlechemi: Steinernema beitlechemi, S. bicornutum: Steinernema bicornutum, S. biddulphi: Steinernema biddulphi, S. bifurcatum: Steinernema bifurcatum, S. boemarei: Steinernema boemarei, S. brazilense: Steinernema brazilense, S. cameroonense: Steinernema cameroonense, S. carpocapsae: Steinernema carpocapsae, S. caudatum: Steinernema caudatum, S. ceratophorum: Steinernema ceratophorum, S. changbaiense: Steinernema changbaiense, S. cholashanense: Steinernema cholashanense, S. citrae: Steinernema citrae, S. colombiense: Steinernema colombiense, S. costaricense: Steinernema costaricense, S. cubanum: Steinernema cubanum, S. cumgarense: Steinernema cumgarense, S. diaprepesi: Steinernema diaprepesi, S. eapokense: Steinernema eapokense, S. ethiopiense: Steinernema ethiopiense, S. fabii: Steinernema fabii, S. feltiae: Steinernema feltiae, S. glaseri: Steinernema glaseri, S. goweni: Steinernema goweni, S. guangdongense: Steinernema guangdongense, S. hebeiense: Steinernema hebeiense, S. hermaphroditum: Steinernema hermaphroditum, S. huense: Steinernema huense, S. ichnusae: Steinernema ichnusae, S. innovationi: Steinernema innovationi, S. intermedium: Steinernema intermedium, S. jeffreyense: Steinernema jeffreyense, S. jollieti: Steinernema jollieti, S. karii: Steinernema karii, S. khoisanae: Steinernema khoisanae, S. kraussei: Steinernema kraussei, S. kushidai: Steinernema kushidai, S. lamjungense: Steinernema lamjungense, S. leizhouense: Steinernema leizhouense, S. litchii: Steinernema litchii, S. litorale: Steinernema litorale, S. loci: Steinernema loci, S. longicaudum: Steinernema longicaudum, S. minutum: Steinernema minutum, S. monticolum: Steinernema monticolum, S. neocurtillae: Steinernema neocurtillae, S. nepalense: Steinernema nepalense, S. nguyeni: Steinernema nguyeni, S. nyetense: Steinernema nyetense, S. oregonense: Steinernema oregonense, S. pakistanense: Steinernema pakistanense, S. papillatum: Steinernema papillatum, S. phyllophagae: Steinernema phyllophagae, S. poinari: Steinernema poinari, S. puertoricense: Steinernema puertoricense, S. pui: Steinernema pui, S. puntauvense: Steinernema puntauvense, S. pwaniense: Steinernema pwaniense, S. ralatorei: Steinernema ralatorei, S. rarum: Steinernema rarum, S. riobrave: Steinernema riobrave, S. ritteri: Steinernema ritteri, S. robustispiculum: Steinernema robustispiculum, S. sacchari: Steinernema sacchari, S. sangi: Steinernema sangi, S. sasonense: Steinernema sasonense, S. scapterisci: Steinernema scapterisci, S. scarabei: Steinernema scarabei, S. schliemanni: Steinernema schliemanni, S. siamkayai: Steinernema siamkayai, S. sichuanense: Steinernema sichuanense, S. silvaticum: Steinernema silvaticum, S. surkhetense: Steinernema surkhetense, S. tami: Steinernema tami, S. texanum: Steinernema texanum, S. thanhi: Steinernema thanhi, S. thesami: Steinernema thesami, S. tielingense: Steinernema tielingense, S. tophus: Steinernema tophus, S. unicornum: Steinernema unicornum, S. vulcanicum: Steinernema vulcanicum, S. weiseri: Steinernema weiseri, S. xinbinense: Steinernema xinbinense, S. xueshanense: Steinernema xueshanense, S. yirgalemense: Steinernema yirgalemense, X. indica: Xenorhabdus indica, X. ishibashii: Xenorhabdus ishibashii, X. bovienii: Xenorhabdus bovienii, X. kozodoii: Xenorhabdus kozodoii, X. magdalenensis: Xenorhabdus magdalenensis, X. khoisanae: Xenorhabdus khoisanae, X. budapestensis: Xenorhabdus budapestensis, X. nematophila: Xenorhabdus nematophila, X. szentirmaii: Xenorhabdus szentirmaii, X. poinarii: Xenorhabdus poinarii, X. doucetiae: Xenorhabdus doucetiae, X. griffiniae: Xenorhabdus griffiniae, X. hominickii: Xenorhabdus hominickii, X. japonica: Xenorhabdus japonica, X. ehlersii: Xenorhabdus ehlersii, X. stockiae: Xenorhabdus stockiae, X. romanii: Xenorhabdus romanii, X. cabanillasii: Xenorhabdus cabanillasii, X. innexi: Xenorhabdus innexi, X. koppenhoeferii: Xenorhabdus koppenhoeferii

Role of the Nematode

The bacteria rely on their nematode hosts for dispersal from one insect to another and protection from the external environment. Studies have shown that ca 200 colony forming units of *X. nematophila* will be sequestered in the receptacle (= anterior intestinal caecum) of a non-feeding IJ of *S. carpocapsae*, but this population is founded by only 1–2 individual bacterial cells (Martens *et al.*, 2003). This finding means that *X. nematophila* reproduces in the receptacle of *S. carpocapsae* IJ. Studies by Mitani *et al.* (2004) suggested that IJs may contribute energy reserves to feed the bacteria for ensuring future reproductive success within an insect host.

EPNs produce immune suppressive compounds to inhibit the insect host immune system to protect their mutualistic bacteria. Thus, EPNs have surface coat proteins and other surface components to suppress the host's immune response as well as destroy the host hemocytes (Maizels *et al.*, 2004; Li *et al.*, 2007). Other studies demonstrate that the cuticle of *S. feltiae* assists in the inactivation of the prophenoloxidase pathway

Table 2. *Heterorhabditis* species with their known associated *Photorhabdus* bacterial symbiont

Heterorhabditis species	References	*Photorhabdus* symbiont
H. amazonensis	Andalo *et al.* (2006)	Unknown
H. atacamensis	Edgington *et al.* (2010)	Unknown
H. bacteriophora	Poinar (1976)	*P. luminescens* subsp. *luminescens; P. luminescens* subsp. *laumondii; P. luminescens* subsp. *kayaii; P. luminescens* subsp. *thracensis*
H. baujardi	Phan *et al.* (2003)	*P. luminescens*
H. beicherriana	Xing-Yue *et al.* (2012)	Unknown
H. downesi	Stock *et al.* (2002)	*P. temperata*
H. floridensis	Nguyen *et al.* (2006c)	*P. luminescens* subsp. *luminescens*
H. georgiana	Nguyen *et al.* (2008b)	*P. luminescens* subsp. *akhurstii*
H. indica	Poinar *et al.* (1992)	*P. luminescens* subsp. *akhurstii; P. asymbiotica* (associated with *H. gerrardii* syn. of *H. indica*)
H. marelatus	Liu and Berry (1996)	Unknown
H. megidis	Poinar *et al.* (1987)	*P. temperata*
H. mexicana	Nguyen *et al.* (2004)	Unknown
H. noenieputensis	Malan *et al.* (2014)	Unknown
H. poinari	Kakulia and Mikaia	Unknown
H. safricana	Malan *et al.* (2008)	Unknown
H. taysearae	Shamseldean *et al.* (1996)	Unknown
H. zealandica	Poinar *et al.* (1990)	*P. heterorhabditis*

H. amazonensis: Heterorhabditis amazonensis, H. atacamensis: Heterorhabditis atacamensis, H. bacteriophora: Heterorhabditis bacteriophora, H. baujardi: Heterorhabditis baujardi, H. beicherriana: Heterorhabditis beicherriana, H. downesi: Heterorhabditis downesi, H. floridensis: Heterorhabditis floridensis, H. Georgiana: Heterorhabditis Georgiana, H. indica: Heterorhabditis indica, H. marelatus: Heterorhabditis marelatus, H. megidis Heterorhabditis megidi, H. Mexicana: Heterorhabditis Mexicana, H. noenieputensis: Heterorhabditis noenieputensis, H. poinari: Heterorhabditis poinari, H. safricana: Heterorhabditis safricana, H. taysearae: Heterorhabditis taysearae, H. zealandica: Heterorhabditis zealandica, P. luminescens: P. luminescens, P. temperate: P. temperate, P. asymbiotica: P. asymbiotica, P. heterorhabditis: P. heterorhabditis

which prevents the melanization process (Brivio *et al.*, 2002). Moreover, *S. feltiae* protects its associated bacteria by sequestering opsonization factors from the insect hemolymph resulting in reduced phagocytosis by the host hemocytes in *G. mellonella* (Brivio *et al.*, 2010). Finally, EPNs are known to produce paralyzing exotoxins and cytotoxic and proteolytic extracellular enzymes that adversely affect the host and enhances survival and reproduction of the nematode and bacteria. Hence, the EPNs may make major contributions to the successful infection of the host by the bacteria, but these contributions may be dependent on the insect host and nematode/bacterium complex (Dowds and Peters, 2002).

Role of Bacterium

Both *Xenorhabdus* and *Photorhabdus* symbionts make similar contributions by infecting the insect, quickly killing its insect host, maintaining suitable conditions for nematode reproduction, serving as a food source for the developing nematodes, and protecting the insect cadaver against scavengers and a wide range of opportunistic microorganisms through the production of antibiotics and other compounds (Akhurst and Boemare, 1990; Forst and Clarke, 2002; Hazir *et al.*, 2003; Goodrich-Blair and Clarke, 2007; Gulcu *et al.*, 2012). The bacterial symbiont limits or prevents the growth of competing microbes through the production of different types of antimicrobial compounds (Chaston *et al.*, 2011). Molecular studies have been conducted to demonstrate the source of the antimicrobial compounds. The genes involved in entomopathogenicity encoding the insecticidal toxins appear to be conserved among the bacterial species (Chaston *et al.*, 2011).

ECOLOGY OF EPNS

Biogeography

EPNs are widely distributed on every continent except Antarctica (Griffin *et al.*, 1990; Hominick, 2002), and in 2010, they have been reported to be isolated from 49 countries around the World (San-Blas, 2013; Stock, 2015). In addition to previous data, most of the new isolates and species have been recovered

Table 3. List of synonyms proposed for *Steinernema* and *Heterorhabditis* species on the basis of sequence analysis

Binomen	Junior synonym of
S. anatoliense	*S. carpocapsae*
S. dharanai	*S. hermaphroditum*
S. everestense	*S. akhursti*
S. maqbooli	*S. pakistanense*
S. meghalayense	*S. carpocapsae*
S. tbilisiense	*S. thesami*
S. websteri	*S. carpocapsae*
H. gerrardi	*H. indica*
H. pakistanensis	*H. indica*
H. somsookae	*H. baujardi*
H. sonorensis	*H. taysearae*

S. anatoliense: Steinernema anatoliense, S. dharanai: Steinernema dharanai, S. everestense: Steinernema everestense, S. maqbooli: Steinernema maqbooli, S. meghalayense: Steinernema meghalayense, S. tbilisiense: Steinernema tbilisiense, S. websteri: Steinernema websteri, H. gerrardi: Heterorhabditis gerrardi, H. pakistanensis: Heterorhabditis pakistanensis, H. somsookae: Heterorhabditis somsookae, H. sonorensis: Heterorhabditis sonorensis, S. carpocapsae: Steinernema carpocapsae, S. hermaphroditum: Steinernema hermaphroditum, S. akhursti: Steinernema akhursti, S. pakistanense: Steinernema pakistanense, S. thesami: Steinernema thesami, H. indica: Heterorhabditis indica, H. baujardi: Heterorhabditis baujardi, H. taysearae: Heterorhabditis taysearae

recently from Brazil (Nguyen *et al.*, 2010), Cameroon (Kanga *et al.*, 2012b), Chile (Edgington *et al.*, 2010), China (Ma *et al.*, 2013; Wang *et al.*, 2014), Georgia (Oleg *et al.*, 2015), Italy (Tarasco *et al.*, 2014), Lebanon (Noujeim *et al.*, 2011), Nepal (Khatri-Chhetri *et al.*, 2010), New Zealand (Ali and Wharton, 2017), Pakistan (Fayyaz *et al.*, 2015; Shahina *et al.*, 2016), Portugal (Valadas *et al.*, 2013), Syria (Jawish *et al.*, 2015), South Africa (Abate *et al.*, 2016; Cimen *et al.*, 2014, 2015, 2016a,b; Malan *et al.*, 2012; 2015; 2016; Nthenga *et al.*, 2014; Steyn *et al.*, 2017b), Tanzania (Puza *et al.*, 2016), United States (Ivanova *et al.*, 2013), and Venezuela (San-Blas *et al.*, 2016).

Host Range

EPNs can infect a wide range of insect species from different families and some arachnids under laboratory conditions (Georgis, 1992; Monteiro *et al.*, 2014; Butt *et al.*, 2016; Hussain *et al.*, 2015). Under these conditions, however, the environmental conditions are optimum, and there are no barriers for host contact. Under field conditions, EPNs kill significantly less insect species (Hazir *et al.*, 2003; Peters, 1996).

The most common method of isolating EPNs from the field is to take soil samples, bring soils back to the laboratory, and use the insect bait technique (Bedding and Akhurst, 1975). Researchers generally use *G. mellonella* larvae which do not live in soil but are very susceptible to nematode infection. Although this technique is very useful to isolate EPNs, it provides no information about the natural host range of the nematode (Hazir *et al.*, 2003). Thus, additional experiments with various soil insect species are needed to determine the host range of each EPN species that were isolated using the insect bait technique (Koppenhofer and Kaya, 1996; Koppenhofer and Fuzy, 2003; Gungor *et al.*, 2006; Bazman *et al.*, 2008). On the other hand, there are a number of examples where soil insects infected with EPNs have been isolated providing an indication of their natural host range. The most information about the host range is available on commonly studied and widespread EPN species such as *S. carpocapsae*, *S. feltiae*, *S. glaseri*, *H. bacteriophora*, and *H. megidis* (Peters, 1996).

Although many EPN species are considered to have a broad host range, some steinernematids are adapted to specific groups of insects. For example, *S. scapterisci* is adapted to orthopterans, especially mole crickets (Parkman and Smart, 1996). *S. kushidai* (Mamiya, 1989) and *S. scarabei* (Koppenhofer and Fuzy, 2003) appear to be specialized to scarabaeidae larvae. Therefore, correct matching of EPN species and target insect species plays a key role in a successful application.

Behavioral Ecology

When IJs emerged from a cadaver in the soil or are manually applied against a pest, they can begin to seek a host to infect. Active foraging increases the probability of finding an insect host, but it also enhances starvation of IJs and increases the risk of encountering a nematode pathogen. It has been hypothesized that if there is a seasonal abundance of hosts in the habitat, the local IJs regulate their metabolism according to the presence or absence of hosts like being inactivate until the preys appear (Griffin, 2015). During the host searching period, IJs exhibit different strategies to respond to volatiles (Lewis *et al.*, 2006; Dillman *et al.*, 2012), vibrations (Torr *et al.*, 2004), electromagnetic signals (Ilan *et al.*, 2013), and fine-scale temperature gradients (Byers and Poinar, 1982). In addition to these responses, Lewis *et al.* (2006) proposed three modes of foraging behaviors defined as cruiser, ambusher, and intermediate. Cruisers tend to occur deeper in the soil profile, actively search for a host and hone in on it using its volatiles, whereas ambushers tend to dwell near or at the soil surface and exhibit nictation and jumping behaviors to attach to a host. Intermediate strategists tend to occur just below the soil surface

and demonstrate behaviors that are between cruise and ambush (Campbell and Kaya, 1999; Campbell *et al.*, 2003). Heterorhabditids generally employ cruise foraging, while steinernematids, depending on species, exhibit one of the three foraging behaviors. For example, *S. feltiae* and *S. riobrave* forage for a host using an intermediate strategy and are most effective against insects just below the soil surface such as the larvae of the fungus gnats or lepidopterous prepupae (Campbell and Gaugler, 1997).On the other hand, *S. carpocapsae* and *S. scapterisci* are typical ambushers, and *S. glaseri* represents a typical cruiser. Ambush foragers respond to CO_2 or specific host odors (Dillman *et al.*, 2012) and are most successful attacking mobile, surface-dwelling insect hosts such as caterpillars and mole crickets (Gaugler *et al.*, 1997), but they can also kill immobile insects deeper in the soil profile away from the point of application (Dembilio *et al.*, 2010; Gumus *et al.*, 2015; Martinez de Altube *et al.*, 2008; Shapiro-Ilan *et al.*, 2016). In contrast, cruisers mainly infect immobile hosts deeper in the soil profile such as scarabaeidae larvae, but they can kill mobile insects closer to the surface as well.

Persistence

The survival of IJs is affected by various abiotic (temperature, moisture, soil texture, soil salinity, UV light, oxygen, and pH) and biotic (natural enemies, scavengers, competition, and plants) factors in the soil. A number of papers have been published on the persistence of EPNs (Shapiro and McCoy 2000; Shapiro-Ilan *et al.*, 2006a; Stuart *et al.*, 2015).

A-ABIOTIC FACTORS

Temperature

One of the key factors for survival of EPNs is temperature. Each EPN species has an optimum temperature for survival, infection, and reproduction (Grewal *et al.*, 1994; Hazir *et al.*, 2001). Temperature extremes (below 0°C or above 40°C) are lethal for most EPN species. In general, freezing temperatures can be tolerated better by the IJs than high temperatures (above 37°C) (Hazir *et al.*, 2003; Shapiro-Ilan *et al.*, 2014b). To survive at freezing temperatures, IJs use three mechanisms; (1) freeze-avoiding (Wharton and Surrey, 1994), (2) freezing tolerant (Brown and Gaugler, 1995), or (3) cryoprotective dehydration (Wharton *et al.*, 2003). *H. zealandica* is a typical example for freeze-avoiding strategy. The sheath of *H. zealandica* prevents the IJ from supercooling (−32°C) (Wharton and Surrey, 1994). On the other hand, *S. feltiae* and *H. bacteriophora* can exhibit freezing tolerant and cryoprotective dehydration; these two strategies were demonstrated by Brown and Gaugler (1995) and Wharton *et al.* (2003), respectively.

The heat survival by IJs is related to the presence of heat shock proteins (HSP). The HSP protein genes are conserved in many organisms and have also been reported from five heterorhabditid species and one steinernematid species. For example, *H. bacteriophora* (IS-5) which was isolated from the Negev Desert exhibits heat tolerance (Glazer, 2002), and Shapiro *et al.* (1997) improved a heat tolerant hybrid strain from *H. bacteriophora* (IS-5) and *H. bacteriophora* (Hp88) using classical genetic methods. The hybrid strain killed *G. mellonella* larvae as fast as IS-5 at 32°C. In addition, naturally, heat and cold tolerant EPN species/strains have been found. Thus, *S. siamkayai* Tiruchirappalli strain causes larval mortality and reproduces at 37.5°C and 35°C, respectively (Ramalingam *et al.*, 2011). *H. bacteriophora*, *S. feltiae*, *S. anomali* (= *S. arenarium*), *S. riobrave*, and *S. glaseri* have been isolated from cold regions, such as northern Europe, western Canada, and Russia, indicating they can tolerate sub-zero temperatures (Ali and Wharton, 2013). Moreover, EPN IJs enhance their survival at low temperatures within the cadavers of their insect hosts (Lewis and Shapiro-Ilan, 2002).

Soil Moisture

Moisture is the most important factor compared to other abiotic factors for terrestrial nematodes. The nematodes use the water films among soil particles for movement. If the soil is very wet or saturated, oxygen levels decrease, and movements of nematodes are restricted (Stuart *et al.*, 2015). Grant and Villani (2003) showed that infectivity of *H. bacteriophora*, *S. carpocapsae*, *S. feltiae*, and *S. glaseri* increased with soil moisture in sandy loam soils. Furthermore, in low moisture conditions, the virulence of EPNs usually decreases, but it can be increased by rehydrating the soil using irrigation or rainfall. Nematode infectivity is highest at moderate soil moistures (−10 to −100 kPa), and lower in wet (−1 kPa) and moderately dry (−1000 kPa) soil (Koppenhofer and Fuzy, 2007).

Soil Texture

In general, the most favorable soil type for nematode movement is sandy soils (Koppenhofer and Fuzy, 2006), whereas clay soils have poorest survival rates because of low oxygen levels in the small soil pores (Hazir *et al.*, 2003). Portillo-Aguilar *et al.* (1999) demonstrated the relationship of soil texture and survival and movement in the laboratory using *H. bacteriophora*, *S. carpocapsae*, and *S. glaseri*. The data showed that survival and movement of these

EPNs are related to soil texture and bulk density. All species moved more in sandy loam than silty clay loam or loamy soils. While survival of *H. bacteriophora* decreased, survival of *S. glaseri* increased with bulk density. Furthermore, the bulk density increased the infectivity of *S. carpocapsae*, but did not vary for *H. bacteriophora* and *S. glaseri*. Movement and infectivity of IJs are positively correlated if the space among soil particles are similar or greater than the diameter of an IJ (Stuart *et al.*, 2015), but there are exceptions as EPNs have been effective biological control agents of insects in heavy soils (Toepfer *et al.*, 2010).

Besides soil mineral component, the proportion of organic media in the soil affects nematode movement. The cruise forager, *H. megidis*, was not successful in pure peat for finding a host compared to the ambusher, *S. carpocapsae*. In addition, *S. carpocapsae* IJs dispersed better than *H. megidis* in pure peat (Kruitbos *et al.*, 2009). However, Ansari and Butt (2011) tested the effect of five commercial potting media peat, bark, coir (coconut husk), and peat blended with 10% and 20% compost green waste (CGW) on the virulence and dispersal of various EPN species. They reported that media type had no significant effect on EPN virulence. Rather, dispersal of *H. bacteriophora* was higher than *H. megidis*, *H. downesi*, and or *S. kraussei* in all media, whereas *S. feltiae* and *S. carpocapsae* dispersal were greatly reduced and restricted to peat blended with 20% CGW and coir, respectively. In another study, the cruiser, *H. downesi*, and the ambusher, *S. carpocapsae*, exhibited better performance in soils with peat than soils with mineral against the pine weevil (Williams *et al.*, 2013).

Salinity

EPNs appear to tolerate a wide range of salinities. For example, *H. bacteriophora* and *S. glaseri* tolerated exposure to salt solutions at concentrations found in soils with high salinity. Survival, virulence, and penetration efficiency of *S. glaseri* were not affected by NaCl, $CaCl_2$, and KCl. $CaCl_2$ and KCI had no effect on the survival, penetration efficiency, or movement through a soil column for *H. bacteriophora* but moderate concentrations of these salts enhanced the virulence. Although seawater has no negative effect on IJs (Griffin *et al.*, 1994), high concentrations of NaCl, $CaCl_2$, and KCl inhibit the infectivity and movement of *S. glaseri* (Thurston *et al.*, 1994; Grant and Villani, 2003).

Ultraviolet (UV)

The survival, virulence, or reproduction of EPNs can be affected by UV radiation (Gaugler *et al.*, 1992). Shapiro-Ilan *et al.* (2015a) investigated UV tolerance of nine different EPN species and 15 strains for survival and virulence. Their results showed that there was a significant variation in UV tolerance among EPN strains and species. In survival, steinernematids, mainly strains of *S. carpocapsae*, commonly displayed higher levels of UV tolerance compared with the heterorhabditids. Furthermore, it has been reported that shorter wavelengths (254 nm) had a negative effect on virulence compared to longer wavelengths (366 nm).

Oxygen and pH

Low oxygen level that can occur in water-saturated soils, clay soils (because of small pores) and soils with high organic matter content. Soil pH can also affect natural EPN distributions (Kanga *et al.*, 2012b). IJs can survive in a wide range of pH. Thus, soil pH between 4 and 8 did not have an adverse effect on IJ survival, but a pH of 10 or higher was harmful (Kung *et al.*, 1990).

B-BIOTIC FACTORS

Soil harbors a great number of different organisms such as bacteria, viruses, fungi, protozoans, turbellarians, collembolans, other nematodes, mites, tardigrades, oligochaetes, parasitoids, and vertebrate, and invertebrate scavengers (Kaya, 2002). Thus, EPNs interact with these organisms that can affect their survival and infectivity. Kaya (2002) reviewed the earlier studies on the interactions between EPNs and soil organisms, and our focus is primarily on the more recent studies.

Natural Enemies

Nematophagous fungi have received the most attention among the natural enemies of EPNs. For example, *Hirsutella rhossiliensis* causes a high mortality of IJs (Jaffee and Strong, 2005). El-Borai *et al.* (2009) reported that nematophagous fungi reduced the recovery of EPN by at least 82% in Florida. The other important natural enemies are some mite species which can be effective predators of EPNs (Epsky *et al.*, 1988; Karagoz *et al.*, 2007; Ekmen *et al.*, 2010a,b; Cakmak *et al.*, 2013).

Scavengers and Scavenger Deterrent Factors

Depending on EPN species or strains and temperature, nematode-killed insects remain in or on the surface of soil for 7–14 days before the new generation of IJs emerge from the host. During this period, the cadavers containing the nematode-bacterium complex are at risk of being consumed by scavengers such as ants, crickets, mites, cockroaches, wasps, predator

insects, and birds. Interestingly, these cadavers with the nematode-bacterium complex are protected from many scavengers because the symbiotic bacteria, *Xenorhabdus* and *Photorhabdus*, produce a deterrent factor (Baur *et al.*, 1998; Fenton *et al.*, 2011; Foltan and Puza, 2009; Gulcu *et al.*, 2012; Lewis *et al.*, 2015). The first experiments to demonstrate this phenomenon were conducted with ants, and therefore, the factor was called an Ant Deterrent Factor (ADF) (Baur *et al.*, 1998; Zhou *et al.*, 2002). Subsequently, it was reported that ADF not only repelled ants but also deterred other arthropod scavengers such as the beetle, *Pterostichus melanarius* (Foltan and Puza, 2009), the vespid wasps, *Vespa orientalis*, and *Paravespula* sp., the cricket *Gryllus bimaculatus* (Gulcu *et al.*, 2012), American cockroach, *Periplaneta americana* (Ulug *et al.*, 2014), the European robin, *Erithacus rubecula* (Fenton *et al.*, 2011) and freshwater omnivorous fish species, *Devario aequipinnatus*, and *Alburnoides bipunctatus* (Raja *et al.*, 2017). Hence, Gulcu *et al.* (2012) suggested to rename the ADF as the "Scavenger Deterrent Factor" (SDF). The main response of scavengers is to reject feeding on 2-day-old or older cadavers with *Photorhabdus* or *Xenorhabdus*. Moreover, the adults of vespid wasps and calliphoridae flies were deterred from feeding and/or ovipositing on meat treated with the supernatant of *Photorhabdus* or *Xenorhabdus* (Gulcu *et al.*, 2012).

The response of scavengers and omnivores to SDF is not an all or none response. For example, Ekmen *et al.* (2010a,b) demonstrated that the mite, *Sancassania polyphyllae*, and Gulcu *et al.* (unpublished data) showed that some ant species fed on cadavers with the nematode-bacterium complex. Moreover, Raja *et al.* (2017) showed that the omnivorous freshwater fish, *Squalius pursakensis*, did not feed on insect cadavers with heterorhabditids.

Competition

Insects are vulnerable food sources for many organisms. Thus, there is a competition among the organisms for having this food source. Competition can be intraspecific or interspecific. The outcome of the competition is often antagonistic, resulting in reduced fitness or species extinction. When the number of IJs penetrating into an insect host exceeded an optimal level, exploitative intraspecific competition occurred among the developing nematodes, which reduced the total number of progeny emerging from the cadaver (Alatorre-Rosas and Kaya, 1990; Sicard *et al.*, 2006). If the number of establishing IJs exceeded the carrying capacity of the host, no progeny was produced. At interspecific competition, two or more species of EPNs invade the same host, and they compete for the available food resource. Akhurst (1982) demonstrated that antibiotics produced by the bacterial symbiont of one EPN species differentially inhibited the bacterial symbionts of other EPN species. However, when inhibitory effects are lacking between the symbiotic bacteria of different nematode species, the nematodes have the potential to coexist in the same host (Koppenhofer *et al.*, 1995).

EPNs also compete with other organisms such as saprophytic and entomopathogenic fungi (i.e., *Beauveria bassiana, B. brogniartii*, *Metarhizium anisopliae*, and *Isaria fumosorosea*) (Barbercheck and Kaya, 1991; Zayed *et al.*, 2003; Shapiro-Ilan *et al.*, 2004), bacteria (i.e., *Bacillus thuringiensis* and *S. marcescens*), (Poinar *et al.*, 1990; Martin, 2002; Shapiro-Ilan *et al.*, 2004), and parasitoids (i.e., *Bracon hylobii, Hyposoter didymator, Mastrus ridibundus*, and *Liotryphon caudatus*) (Lacey *et al.*, 2003; Everard *et al.*, 2009). From a biological control standpoint, competitions may enhance efficacy by making the insect more susceptible to nematode infection, reducing the period of lethal infection, or having an additive or synergistic effect on mortality (Kaya and Koppenhofer, 1996).

Response to Plant Roots

Plant roots are not only have impact on the soil environment but also affect the dispersal and host-finding of EPNs. For example, there are reports of positive effects of citrus roots on survival of *S. diaprepesi* (Duncan and McCoy, 2001), facilitation of survival of *H. marelata* by the taproot of bush lupine (Preisser *et al.*, 2006), and enhancement in the lateral dispersal of *S. carpocapsae* and *H. bacteriophora* in the presence of vegetation (Bal *et al.*, 2014). When roots are attacked by insects, chemicals from the damaged roots can serve to attract EPNs (Boff *et al.*, 2001; Boff *et al.*, 2002; Rasmann *et al.*, 2005). Related to this interaction, a highly attractive volatile, β-caryophyllene, released by maize roots was also identified by (Rasmann *et al.*, 2005). Thus, *H. megidis* was highly attracted to maize roots damaged by the corn rootworm, *Diabrotica virgifera* due to β-caryophyllene. Additional studies have also showed that plant volatiles affected EPN dispersal and increased biocontrol activity in diverse environments (Ali *et al.*, 2012; Hiltpold and Turlings, 2012; Willett *et al.*, 2015).

MASS PRODUCTION

EPNs have proven particularly successful as biological control agents and are currently commercially mass-produced in six of the seven continents to treat pest

problems in agriculture, horticulture, and human husbandry. The ease of mass production, exemption from registration requirements in many countries, and good efficacy data against some key soil pests are major reasons for commercial developments of EPNs. From an efficacy standpoint, EPNs are effective when well matched with their insect hosts, but a major drawback to their wider use is their availability on demand.

The *in vivo* method is appropriate for a cottage industry, while the *in vitro* method has been successfully adopted for mass production. At present, EPNs are commercially produced by *in vivo* or *in vitro* (solid and liquid cultures) methods (Gaugler and Han 2002; Shapiro-Ilan and Gaugler, 2002). Each approach has advantages and disadvantages relative to the cost of production, capital outlay, technical expertise required, economy of scale, and product quality, and each approach has the potential to be improved. Small-scale farmers will benefit from *in vivo* production of EPNs using locally available insects. The hosts used *in vivo* methods must be susceptible, have high multiplication potential, not prone to become crop pests and reared easily using inexpensive materials. *In vivo* nematode production is labor intensive but produces good quality nematodes (Shapiro and McCoy 2000).On the other hand, large-scale commercial agricultural operations (orchards, large acreage farms, and nurseries) need to depend on *in vitro* production (see *in vitro* solid culture and *in vitro* liquid culture). *In vitro* production needs can be met through capital investment into the use of large fermentation chambers (Ehlers *et al.*, 1998). This approach has been successful in many countries (Ehlers and Shapiro-Ilan, 2005; Shapiro and McCoy, 2000). The startup costs for *in vitro* methods are beyond the scope of small-scale farmers, and *in vivo* production for large-scale agricultural operations is not practical. Following nematode production, a variety of formulation options are available (Peters *et al.*, 2016).

In Vivo Production

EPNs can be mass produced *in vivo* through mass inoculation where the insect serves as a small biological reactor. For laboratory use, small-scale field-testing and niche markets, *in vivo* EPN production is the appropriate method requiring the least capital outlay and the least amount of technical expertise for start-up but is hindered by the costs of labor and insect media (Shapiro-Ilan *et al.*, 2012). *In vivo* mass production depends on the availability of a highly reliable, highly susceptible and inexpensive supply of hosts (Gaugler and Han, 2002). *G. mellonella* is the conventional host for *in vivo* multiplication of EPNs, while other lepidopterous insects (e.g., *Chilo saccharipha*gus *indicus*) have also been used to study the infectivity and reproduction of *S. feltiae*, *S. glaseri*, and *H. bacteriophora* (Karunakar *et al.,* 1992; Ali *et al.*, 2008). The establishment of the alternative host for EPN reproduction is important, and the host should be easily raised or available inexpensively from a commercial source. The most efficient and cost-effective host would be promoted for use by farmers or by the cottage industry personnel. *In vivo* culture is a two-dimensional system that relies on production in trays and shelves. A White trap consists of a smaller dish with a piece of moist paper on which the cadavers rest surrounded by water which is contained in a larger dish or tray (White, 1927). The smaller dish (containing the cadavers) with the moist paper provides a substrate for the IJs to migrate into the water (e.g.,, inverted Petri dish lid lined with filter paper). As IJs emerge from the cadavers, they migrate to the surrounding water trap where they are harvested at regular intervals. The scale of the White trap in size and number can be expanded to commercial levels. IJ and inoculum size, host density, nematode infectivity, host susceptibility, host size, and environmental factors such as optimum temperature and maintaining adequate aeration and moisture can affect yield (Shapiro-Ilan *et al.*, 2012). Recent work has been done on automating *in vivo* production so that labor costs are decreased making the system more competitive. The LOTEK system of tools and procedures provides process technology for low-cost, high-efficiency mass production (Gaugler *et al.*, 2002).

In Vitro Solid Culture

The first *in vitro* method of EPN production was developed by Glaser (1932) using *S. glaseri* grown on axenic solid medium. Subsequently, it was realized that better EPN production increased by the presence of the natural symbiont bacteria (Poinar, 1966). Thereafter, the first successful commercial-scale monoxenic culture was developed by bedding and has known to be as the solid culture method (Bedding, 1981; 1984) using chicken offal or another protein-rich medium soaked in an inert carrier (sponge and polyurethane). In this method, nematodes are cultured on a crumbed polyether polyurethane sponge impregnated with emulsified beef fat and pig's kidney along with the appropriate symbiotic bacteria. The solid media process has successfully produced pathogenic steinernematids and heterorhabditids, but the high labor cost limits economics of scale (Bedding, 1990). However, large-scale production was further advanced through several measures including using bags with gas permeable Tyvac® strips for ventilation, automated mixing and autoclaving, simultaneous inoculation of nematodes

and bacteria, sterile room technology, and automated harvest through centrifugal sifters (Gaugler and Han, 2002).

In Vitro Liquid Culture

Glaser (1940) developed the first liquid medium, based on kidney extract, for axenic culture of *S. glaseri*. Stoll (1952) using an axenic liquid medium containing raw liver extract and incubating the cultures on a shaker was able to produce offspring reaching approximately 400 IJs/ml. A significant step forward was achieved in this direction by Buecher and Hansen (1971) by simply supplying sterile air through liquid media bottles. This modification showed that bubbling is an acceptable means of supplying aeration to the nematodes without affecting shear effect due to forced aeration. However, EPNs produced axenically could not be used for biocontrol purposes due to the low yields, high cost of the media, and most importantly, and the absence of symbiotic bacteria in the culture (Ehlers *et al.* 1997). At present, the *in vitro* liquid culture method is a commercially viable method wherever expertise, initial capital, and large bioreactors are available.

FORMULATIONS

For an effective application, EPN IJs have been applied in various formulations. For example, IJs have been applied formulated in water, desiccated cadavers, baits, and capsules (Grewal, 2002; Georgis, 1990). Water-dispersible granular formulation was found to be the most appropriate with longer shelf life, minimum space for storage, and ease of application (Grewal, 2000; 2002). Formulation is intended to improve activity, absorption, delivery, ease-of-use, or storage stability of an active ingredient. Typical examples of pesticide formulation ingredients (additives) include absorbents, adsorbents, antimicrobial agents, antioxidants, binders, carriers, dispersants, preservatives, solvents, surfactants, and UV absorbers (Grewal, 2002). To increase the efficacy, several considerations have been taken into account. IJs are applied to moist soil in the evening or early morning (Grewal and Georgis, 1988).

A nonviscous, nonadhesive and nontoxic liquid formulation was developed for EPN storage and transport based on neutral density colloidal *silica* suspensions (Wilson and Ivanova, 2004). Survival and virulence of stored IJs in this formulation without aeration were found superior than stored in aerated quarter strength Ringer's solution. Shapiro-Ilan *et al.* (2002) developed a method of formulating nematode-killed insects (often referred to as nematode-infected cadavers) to overcome the storage and application hindrances. Moreover, the formulated cadavers (starches, clays, etc.) were more resistant to rupturing and sticking during agitation than non-formulated cadavers. It was also shown that nematode-killed insects had better IJ survival and superior efficacy relative to aqueous applied nematodes when exposed to freezing temperatures (Lewis and Shapiro-Ilan, 2002; Shapiro-Ilan *et al.*, 2003). Live insects pre-infected with EPNs (living insect bombs) are the latest formulation and application approach to improve the efficacy of EPNs (Gumus *et al.*, 2015).

When IJs are placed into a tank mix of backpack sprayers, uneven distribution occurs, but this situation can be overcome with the addition of adjuvants. The function of the adjuvants is to not only prolong IJ survival but also to provide environmental conditions which enable rapid invasion of the IJs into a host. IJ performance was improved by selection of the best surfactant combination (Schroer *et al.*, 2005). However, the efficacy on foliage of soilborne nematodes is limited by abiotic factors such as UV-radiation (Gaugler *et al.*, 1992; Nickle and Shapiro, 1992), extreme temperature, or drought (Glazer, 2002). To prolong nematode survival on the leaf, several adjuvants have been evaluated (Glazer, 1992; Baur *et al.*, 1997; Mason *et al.*, 1998), but the improvements were not sufficient to increase the feasibility of nematode foliar application against the diamondback moth, *Plutella maculipennis* (Baur *et al.*, 1997). The addition of the surfactant/polymer formulation prevents nematodes from settling in the spray tank thus securing an even distribution; it deposits nematodes on the leaf reducing loss into the soil by runoff, produces optimal conditions for host invasion by reducing the mobility of the insect, and produces ideal conditions for the IJ host seeking and invasion. Another advantage of the formulation is the provision of humidity, which enables nematodes to survive, move, seek, and invade the host insect. Low humidity leads to rapid desiccation of IJs, and usually, survival is for no longer than a few hours (Glazer, 1992). Improving formulation technology may prolong IJ survival on the leaf (e.g., Baur *et al.*, 1995; Navon *et al.*, 1999).

IJs encapsulated in calcium alginate gels by means of external gel settings (Kaya and Nelson, 1985) and in other hydrophilic colloids (Patel and Vorlop, 1994). These gels and colloids were used to protect the IJs from desiccation and UV effects. An advanced formulation of alginate gel systems as a carrier for the IJs (Navon *et al.*, 1999) was based on an internal gel setting (King, 1982) in which they were evenly distributed in the gel matrix. Furthermore, the gel was made edible to lepidopterous larvae.

COMMERCIALIZATION

A key factor in the success of EPNs as bioinsecticides is their amenability toward mass production. Given the importance of efficient production and formulation to the commercial success of EPNs, 52 research papers were published on this topic in the years 2000–2010 (San-Blas, 2013). Low-cost mass production of EPNs is an important prerequisite toward their successful commercialization (Ramakuwela *et al.*, 2016). EPN products are generally more expensive than the primary alternative, chemical pesticides, in most markets (Gaugler and Han, 2002). Therefore, their use is on high-value crops, and when less expensive methods to produce EPNs are developed, there may be wider acceptance in other cropping systems.

MICROBIAL CONTROL

Regulation

EPNs and their symbiotic bacteria are considered exceptionally safe biological agents (Akhurst and Smith, 2002).They are safe to humans, other mammals and vertebrates as well as plants (Akhurst and Smith, 2002). Because their activity is specific to arthropods, their environmental risk is considerably lower than that of chemical agents for plant protection. Since the first use of EPNs for suppressing *Popillia japonica* in the USA (Glaser and Farrell, 1935) until now, no case of environmental damage due to these biological agents has been documented. Accordingly, native and/or indigenous EPNs have been exempted from registration process in many countries. For example, in the USA, the Environmental Protection Agency (EPA) does not require safety or efficacy data for EPNs that are already found there, but the Animal and Plant Health Inspection Service (APHIS) have restrictions on the importation and use of exotic or nonindigenous species/strains. Similarly, in the UK, the indigenous and genetically unmodified EPNs and their bacterial symbionts do not have obligations for registration regulations. In contrast, the European Commission is regulating and streamlining the procedures for the authorization of plant protection products including EPNs under the provision of Council Directive 91/414/EEC (Richardson, 1996). Other European countries either have the mandatory regulation based on Council Directive, whereas other countries do require registration.

Application Technology

To apply nematodes against soil insect pests, standard ground equipment including pressurized sprayers, mist blowers, and electrostatic sprayers can be used (Kaya and Gaugler, 1993). IJs may also be applied using aerial spray equipment and through the irrigation system. In each case, there is a variety of handling considerations including volume, agitation, nozzle type, pressure and recycling time, system environmental conditions, and spray distribution pattern (Fife *et al.*, 2003; 2005). IJs can passed through spray tubes with a diameter of at least 500 μm and are capable to withstand pressures up to 2000 kPa without harming them (Kaya and Gaugler, 1993; Grewal, 2002). Due to the sensitivity of IJs to UV radiation and desiccation, the recommendation is to apply IJs in the evening, early in the morning or on a cloudy day when the radiation and desiccation are minimal or nonexistent (Kaya and Gaugler, 1993).

EPNs have commonly been conserved, stored and applied in aqueous suspensions (Chen and Glazer, 2005). They can be applied with conventional liquid spraying technology such as manually activated sprinklers, electrostatic devices and electric, hydraulic, and pneumatic fluid pressure mechanisms (Shapiro-Ilan *et al.*, 2006b). However, refrigeration (storage technology), transportation and application (spraying technology) contribute to the elevated cost (Chen and Glazer, 2005). The encapsulation of EPN in pellets partially achieves these objectives because the pellet structure is designed to facilitate storage and transportation.

Applications of IJs formulated in pellets are still limited. This drawback is principally due to development of better formulations. The effectiveness of EPNs in the control of pest infestations can be affected by some of the pellet's characteristics, such as homogeneity (shape, size, quantity of nematodes, and weight), structure, mechanical resistance, and properties of the inert granular materials (Silver *et al.*, 1995; Hiltpold *et al.*, 2012). The encapsulation of EPNs in expansive clay materials has been developed by Bedding (1988), who developed a "sandwich" type formulation, so-called for its immobilization of the nematodes between two layers of attapulgite clay (AC). Silver *et al.* (1995) constructed granules with the following materials: Diatomaceous earth (DE), hydroxyethyl cellulose, amorphous silica, lignosulfonates, starch, and AC. Encapsulated *S. carpocapsae*, *S. feltiae*, *S. scapterisci,* and *S. riobrave* had over 90% survival for 6 weeks when stored at 25°C in these granules. A mechanized production process was also developed using continuous oscillatory granulation.

Target Insects

Most EPNs have a wide host range excluding a few species such as *S. scarabei*, *S. kushidai*, and *S.*

*scapter*isci. Many factors can influence the success of using EPNs, but matching the biology and ecology of both the nematode and the target insect pest is a crucial step for a successful application.

The list of economically important insect pests which are suppressed by EPNs is given in Table 4 (modified after Shapiro-Ilan *et al.*, 2016). Moreover, EPNs show good potential for the control of ticks (Monteiro *et al.*, 2014; Butt *et al.*, 2016).

Efficacy

Although EPNs are highly pathogenic against a large number of insect pest species under laboratory conditions, the success of EPNs in greenhouse or field varies from poor to excellent depending on a variety of biotic and abiotic factors that affect EPN survival and efficacy (Koppenhofer, 2000; Grewal *et al.*, 2005; Shapiro-Ilan *et al.*, 2006c). After matching the biology and ecology of both the nematode and the target pest, the presence of adequate moisture and temperature is another key factor to provide good results. EPNs usually show maximum efficacy against target insects living in soil or cryptic habitats. These habitats offer protection from environmental extremes. Nevertheless, in some cases, EPNs have effectively controlled above ground pests (Arthurs *et al.*, 2004; Grewal *et al.*, 2005). Due to cost considerations, most of the successful commercial applications have been limited to soil applications in relatively high-value crops.

A variety of tactics have been used to improve the efficacy of EPNs (Shapiro-Ilan and Dolinski 2015b). New approaches, formulations and adjuvants have been explored to improve efficacy of EPN applications in recent years. Mixing EPNs with a surfactant or a polymer (De Waal *et al.*, 2013; Schroer and Ehlers, 2005) and sprayable fire gel (Shapiro-Ilan *et al.*, 2010a) are some of the new approaches to improve the efficacy of EPN application.

Integration with Other Approaches

EPN IJs are amenable to integrated pest management approaches that include combinations with chemical compounds such as pesticides and fertilizers as well other biological control agents and cultural techniques (Duncan *et al.*, 2013). For example, substitution of sand for native soil in citrus planting sites in Florida created refugia characterized by increased richness and diversity of EPN species and greater efficacy in killing the root weevil, *Diaprepes abbreviatus*.

Another approach is to combine chemical pesticides and other microbe control agents for more effective pest suppression. The combination of two control agents can result in antagonistic, additive or synergistic effects on pest mortality. There is no interaction when the additive effect occurs because each agent acts independently of the other. If there is a more or less interaction between two agents, synergistic or antagonistic effects occur. Synergism is defined as the joint action of the two agents resulting in a greater effect than the sum of the two agents acting alone. The mortality caused by the individual agent should be low enough to allow for statistically significant improvements to occur to observe synergistic or antagonistic interactions (Koppenhofer and Grewal, 2005). Certain combinations of EPNs with other agents are synergistic and such combinations can be used to enhance pest control. Synergy can be obtained through combinations with chemical insecticides (e.g., carbaryl, chlorpyrifos, dimethoate, endosulfan, fonofos, tefluthrin, and imidacloprid) (Koppenhofer and Kaya, 1998; Nishimatsu and Jackson, 1998; Alumai and Grewal, 2004; Koppenhofer and Grewal, 2005; Koppenhofer and Fuzy, 2008; Shapiro-Ilan *et al.*, 2011). However, some chemicals used as inert ingredients or adjuvants in formulations can be toxic to nematodes as well as certain insecticides (e.g., abamectin, acephate, aldicarb, dodine, fenamiphos, methomyl, parathion, and Teflubenzuron) (Krishnayya and Grewal, 2002; Koppenhofer and Grewal, 2005). The relationship between chemical pesticides and EPNs varies based on the specific chemical and nematode species or strain, dosages, and timing of application (Benz, 1971; Koppenhofer and Grewal, 2005); thus, combinations should be tested on a case by case basis. Obviously, EPNs should not be combined with chemical nematicides.

Combinations of EPNs with other biocontrol agents such as other nematode species, fungi, and viruses generally result in additive effects on pest mortality, whereas nematodes combined with commercial bacterial agents such as *B. thuringiensis* results in interactions that range from antagonistic to synergistic (Koppenhofer *et al.*, 1995). When two organisms are coapplied against the same insect target, there will always be competition for resources even though under field conditions coinfections are less likely and avoidance is more likely (Koppenhofer and Kaya, 1996; Koppenhofer *et al.*, 1995). Often, using two different control agents are not economically feasible, and combined application of two agents is only useful if the target mortality is synergistically increased.

As a novel approach, earthworms may be used as phoretic agents to increase field population of EPNs. Biocontrol efficacy of the EPN, *S. carpocapsae*, against larvae of the pecan weevil, *Curculio caryae*, was

Table 4. Pest targeted commercially with entomopathogenic nematodes

Pest common name[a]	Pest scientific or family name	Key crop(s) targeted	Primary EPNs used
Lepidotera		Artichoke	Sc
Artichoke plume moth	*P. carduidactyla*	Vegetables	Sc, Sf, Sr
Armyworms	Various noctuid species	Ornamentals	Hb, Sc
Banana moth	*O. sachari*	Vegetables, corn	Sc
Black cutworm	*A. ipsilon*	Fruit trees and ornamentals	Hb, Sc, Sf
Borers (e.g.,, peach tree borer)	*Synanthedon* spp. and other sesiids	Pome fruit	Sc, Sf
Codling moth	*C. pomonella*	Vegetables, corn	Sc, Sf, Sr
Corn earworm	*H. zea*	Cranberries	Sc
Cranberry girdler	*C. topiaria*	Iris	Hb, Sc
Iris borer	*M. onusta*	Nut and fruit trees	Sc
Navel orange worm	*A. transitella*		
Coleoptera			
Banana root borer	*C. sordidus*	Banana	Sc, Sf, Sg
Billbug	*S.* spp.	Turf	Hb, Sc
Black vine weevil	*O. sulcatus*	Berries, ornamentals	Hb, Hd, Hm, Hmeg, Sc, Sg
Citrus root weevil	*Pachnaeus* spp.	Citrus, ornamentals	Sr, Hb
Corn rootworm	*Diabrotica* spp.	Vegetables	Hb, Sc
Diaprepes root weevil	*D. abbreviatus*	Citrus, ornamentals	Hb, Sr
Large pine weevil	*H. albietis*	Forest plantings	Hd, Sc
Plum curculio	*C. nenuphar*	Fruit trees	Sr, Sf
Scarab grubs	Scarabaeidae	Turf, ornamentals	Hb, Sc, Sg, Ss, Hz
Strawberry root weevil	*O. ovatus*	Berries	Hm, Sc
Sweet potato weevil	*C. formicarius*	Sweet potato	Hb, Sc, Sf
Diptera			
Crane fly	Tipulidae	Turf	Sc
Fungus gnats	Sciaridae	Mushrooms, greenhouse	Sf, Hb
Leafminers	*Liriomyza* spp.	Vegetables, ornamentals	Sc, Sf
Shore flies	*Scatella* spp.	Ornamentals	Sc, Sf
Thysanoptera			
Western ower thrips	*F. occidentalis*	Greenhouse, flowers	Sc, Sf
Orthoptera			
Mole crickets	*Scapteriscus* spp.	Turf	Sc, Sr, Sscap

[a]At least one scientific paper reported ≥75% suppression of these pests in the field; not meant to be an exhaustive list. Hb: Heterorhabditis bacteriophora, Hd: *Heterorhabditis downesi*, Hm: *Heterorhabditis marelata*, Hmeg: *Heterorhabditis megidis*, Hz: *Heterorhabditis zealandica*, Sc: *Steinernema carpocapsae*, Sf: *Steinernema feltiae*, Sg: *Steinernema glaseri*, Sr: *Steinernema riobrave*, Sscap: *Steinernema scapterisci*, Ss: *Steinernema scarabaei. Platyptilia carduidactyla: P. carduidactyla, Opogona sacchari: O. sacchari, Agrotis ipsilon: A. ipsilon, Cydia pomonella: C. pomonella, Helicoverpa zea: H. zea, Chrysoteuchia topiaria: C. topiaria, Macronoctua onusta: M. onusta, Amyelois transitella: A. transitella, Cosmopolites sordidus: C. sordidus, Otiorhynchus sulcatus: O. sulcatus, Diaprepes abbreviatus: D. abbreviatus, Hylobius albietis: H. albietis, Conotrachelus nenuphar: C. nenuphar, Otiorhynchus ovatus: O. ovatus, Cylas formicarius: C. formicarius, Frankliniella occidentalis: F. occidentalis,* EPNs: Entomopathogenic nematodes

significantly enhanced in the presence of earthworms based on increased nematode dispersal through the soil (Shapiro-Ilan and Brown, 2013). However, there are negative and positive reports about the role of earthworms. Boyer *et al.* (2013) reported that the earthworm, *Pontoscolex corethrurus*, reduces the population of certain plant-parasitic nematodes (*Heterodera sacchari* and *Pratylenchus zeae*), whereas Held *et al.* (2017) revealed that two earthworm species (*Eisenia foetida* and *Lumbricus terrestris*) are capable of dispersing plant-parasitic nematodes across golf greens, fields, and lawns.

EPNs have been combined with manure and urea in soil with mixed results. For instance, *S. carpocapsae* was combined with fresh cow manure, composted manure, or urea to determine if corn seedlings would benefit from these combinations against the black cutworm, *Agrotis ipsilon*. The results showed that black cutworm damage to the seedlings was greater in nematode-treated plots amended with fresh manure than in plots without manure or urea. Other amendments (urea and composted manure) did not have a detrimental effect on suppression of the black cutworm by *S. carpocapsae* (Shapiro-Ilan *et al.*, 1999). In another study, factorial treatments of EPNs and composted, manure mulches were evaluated for 2 years in a central Florida citrus orchard to study the post-application biology of EPN used to manage the root weevil *D. abbreviatus*. Manure mulch had variable effects on endoparasitic nematophagous fungi but consistently decreased the prevalence of trapping nematophagous fungi and increased the prevalence of EPNs and mortality of sentinel insect placed into the orchard (Duncan *et al.*, 2007; Dolinski *et al.*, 2012).

In terms of cultural approaches, Campos-Herrera *et al.* (2008) have shown that some EPNs are more abundant in undisturbed compared to intensively farmed habitats. Thus, Stuart *et al.* (2008) state that conservation biological control such as habitat manipulation and inoculation strategies might be effective for conserving and enhancing EPN communities to achieve long-term control.

Innovative Approaches

Besides spraying aqueous suspension, other alternative application methods are available such as the use of microjets (Georgis, 1990; McCoy *et al.*, 2000a), subsurface injection (Grewal, 2002; McCoy *et al.*, 2000b), and nematode-killed hosts (Jansson *et al.*, 1993). Use of insect cadavers containing IJs has resulted in effective pest suppression in field trials (Jansson *et al.*, 1993; Parkman *et al.*, 1993; Raja *et al.*, 2015) and greater nematode dispersal (Shapiro and Glazer, 1996; Dolinski *et al.*, 2015), persistence (Grewal, 2002), survival (Perez *et al.*, 2003), and infectivity (Shapiro-Ilan and Lewis, 1999) compared to aqueous application in laboratory experiments. Efficacy of cadaver application can be improved by protecting the cadavers from rupturing which prevents the IJs from desiccation and improves the ease of handling (Shapiro-Ilan *et al.*, 2001; 2010b; Del Valle *et al.*, 2009) for application with mechanized equipment for field distribution (Zhu *et al.*, 2011). Recently, nematodes applied in host cadavers were effective when added to bags of potting media for subsequent distribution to target pest sites (Deol *et al.*, 2011).

In certain habitats, spraying IJs or using insect cadavers with nematodes is not an efficient method for insect control. One such habitat is where insect control by spraying EPNs may be difficult is the tree trunk or branches infested with borers. Therefore, as a new EPN application approach, the efficacy of releasing live insect hosts that were pre-infected with EPNs referred to as "living insect bombs" were tested against an insect pest in tree trunks (Gumus *et al.*, 2015). This approach was superior to spraying IJs to control the goat moth, *Cossus*, which bores deep into the trunks of sweet chestnut trees. In selecting an insect host for this new approach, the candidate must be (1) susceptible to nematode infection, (2) easily mass reared or easily obtained in great numbers from nature, and (3) capable of penetrating on their own into the cryptic habitats where the target insect lives.

FUTURE PROSPECTS

Crop protection is still based predominantly on the use of conventional (synthesized) chemical pesticides. However, there are continued concerns over the impact of some of these products on human health and the environment. In response, many of the more toxic chemically active ingredients have been withdrawn from use, and the development of alternative crop protection approaches such as Integrated Pest Management (IPM), including the use of biological control organisms and natural products, has received more attention. EPNs with their broad host range, high virulence, safety to nontarget organisms, and high efficacy in favorable habitats are excellent microbial for control of insect pests. Progress achieved in genetic improvement, strain stabilization, mass production, formulation application strategies let nematode-based products to become competitive with chemical insecticides in medium- and high-value crops.

Another avenue to wider utilization is to employ the symbiotic bacteria of EPNs or their metabolites or byproducts as control materials for arthropod pests (Bussaman *et al.*, 2006; Ffrench-Constant *et al.*, 2007; Da Silva *et al.*, 2013), plant pathogens (Isaacson and Webster, 2002; Boszormenyi *et al.*, 2009; Fang *et al.*, 2014; Shapiro-Ilan *et al.*, 2014a; Hazir *et al.*, 2016; 2017), or a variety of human pathogens (Fodor *et al.*, 2010; Grundmann *et al.*, 2014; Hazir *et al.* unpublished). With progress such as these, EPNs will remain to help reduce dependence on chemical involvements in agriculture and human and veterinary health and increase sustainability. New and further technological advancements toward lowering product costs, increasing product availability, and improving efficacy will expand the registration demands and

market opportunities of the nematode-based products in the future.

Acknowledgements. We thank Dr. Harry K. Kaya, University of California, Davis, for his encouragement to write this review and for editing the initial drafts of this manuscript and to Dr. David Shapiro-Ilan, USDA-ARS, Byron, Georgia, for his editorial comments on a penultimate draft of this manuscript.

REFERENCES

Abate, B.A., Malan, A.P., Tiedt, L.R., Wingfield, M.J., Slippers, B. and Hurley, B.P. (2016) *Steinernema fabii* n. sp. (*Rhabditida*: Steinernematidae), a new entomopathogenic nematode from South Africa. *Nematology*, **18**, 235–255.

Abebe, E., Akele, F.A., Morrison, J., Cooper, V. and Thomas, K.T. (2011) An insect pathogenic symbiosis between *Caenorhabditis* and *Serratia*. *Virulence*, **2**, 158–161.

Abd-Elgawad, M.M.M., Askary, T.A. and Coupland, J. (2017) *Entomopathogenic* and *Slug Parasitic Nematodes*. CAB International, Wallingford, UK.

Akhurst, R.J. (1982) Antibiotic activity of *Xenorhabdus* spp., bacteria symbiotically associated with insect pathogenic nematodes of the families steinernematidae and heterorhabditidae. *J. Gen. Microbiol*., **128**, 3061–3065.

Akhurst, R.J. and Boemare, N.E. (1990) Biology and taxonomy of *Xenorhabdus. In* R. Gaugler and H.K. Kaya (eds.), *Entomopathogenic Nematodes in Biological Control*. CRC Press, Boca Raton, Florida, USA, pp. 75–90.

Akhurst, R. and Smith, K. (2002) Regulation and Safety. *In* R. Gaugler (ed.), *Entomopathogenic Nematology*, CAB International, Wallingford, UK, 311–332 pp.

Alatorre-Rosas, R. and Kaya, H.K. (1990) Interspecific competition between entomopathogenic nematodes in the genera *Heterorhabditis* and *Steinernema* for an insect host in sand. *J. Invertebr. Pathol.*, **55**, 179–188.

Ali, F. and Wharton, D.A. (2013) Cold tolerance abilities of two entomopathogenic nematodes, *Steinernema feltiae* and *Heterorhabditis bacteriophora*. *Cryobiology*, **66**, 24–29.

Ali, F. and Wharton D.A. (2017) A survey of entomopathogenic nematodes from Otago, New Zealand, with the first record of *Steinernema kraussei* (Steiner, 1923) (*Rhabditida*: Steinernematidae) from the Southern Hemisphere. *N. Z. J. Zool*., **44**, 245–255.

Ali, S.S., Pervez, R., Abid Hussain, M. and Ahmad, R. (2008) Susceptibility of three lepidopteran pests to five entomopathogenic nematodes and *in vivo* mass production of these nematodes. *Arch. Phytopathol. Plant Protect.*, **41**, 300–304.

Ali, J.G., Alborn, H.T., Campos-Herrera, R., Kaplan, F., Duncan, L.W., Rodriguez-Saona, C., Koppenhöfer, A.M. and Stelinski, L.L. (2012) Subterranean, herbivore-induced plant volatile increases biological control activity of multiple beneficial nematode species in distinct habitats. *PLoS One*, **7**, e38146.

Altschul, S.F., Gish, W., Miller, W., Myers, E.W. and Lipman D.J. (1990) Basic local alignment search tool. *J. Mol. Biol.*, **215**, 403–410.

Alumai, A. and Grewal, P.S. (2004) Tankmix compatibility of the entomopathogenic nematodes, *Heterorhabditis bacteriophora* and *Steinernema carpocapsae*, with selected chemical pesticides used in turfgrass. *Biocontrol Sci. Technol*., **14**, 725–730.

Andalo, V., Nguyen, K.B. and Moino, A. (2007) *Heterorhabditis amazonensis* n. sp. (*Rhabditida*: Heterorhabditidae) from Amazonas, Brazil. *Nematology*, **8**, 853–867.

Anis, M., Shahina, F., Reid, A.P. and Rowe, J. (2002) *Steinernema asiaticum* sp. n. (Rhabditida: Steinernematidae) from Pakistan. *Int. J. Nematol*., **12**, 220–231.

Ansari, M.A. and Butt, T.M. (2011) Effect of potting media on the efficacy and dispersal of entomopathogenic nematodes for the control of black vine weevil, *Otiorhynchus sulcatus* (Coleoptera: Curculionidae). *Biol. Control*, **58**, 310–318.

Arthurs, S., Heinz, K.M. and Prasifka, J.R. (2004) An analysis of using entomopathogenic nematodes against above-ground pests. *Bull. Entomol. Res.*, **94**, 297–306.

Bal, H.K., Michael, A. and Grewal, P.S. (2014) Genetic selection of the ambush foraging entomopathogenic nematode *Steinernema carpocapsae* for enhanced dispersal and its associated trade-offs. *Evol. Ecol*., **28**, 923–939.

Barbercheck, M.E. and Kaya, H.K. (1991) Effect of host condition and soil texture on host finding by the entomogenous nematodes *Heterorhabditis bacteriophora* (Rhabditida: Heterorhabditidae) and *Steinernema carpocapsae* (Rhabditida: Steinernematidae). *Environ. Entomol.*, **20**, 582–589.

Baur, M.E., Kaya, H.K. and Thurston, G.S. (1995) Factors affecting entomopathogenic nematode infection of *Plutella xylostella* on a leaf surface. *Entomol. Exp. Appl*., **77**, 239–250.

Baur, M.E., Kaya, H.K. and Tabashnik, B.E. (1997) Efficacy of a dehydrated steinernematid nematode against black cutworm (Lepidoptera: Noctuidae) and diamondback moth (Lepidoptera: Plutellidae). *J. Econ. Entomol*., **90**, 1200–1206.

Baur, M.E., Kaya, H.K. and Strong, D.R. (1998) Foraging ants as scavengers on entomopathogenic nematode-killed insects. *Biol. Control*, **236**, 231–236.

Bazman, I., Ozer, N. and Hazir, S. (2008) Bionomics of the entomopathogenic nematode, *Steinernema weiseri* (Rhabditida: Steinernematidae). *Nematology*, **10**, 735–742.

Bedding, R.A. and Akhurst, R.J. (1975) A simple technique for the detection of insect parasitic rhabditid nematodes in soil. *Nematologica*, **21**, 109–110.

Bedding, R.A. (1981) Low cost *in vitro* mass production of *Neoaplectana* and *Heterorhabditis* species for field control of insect pests. *Nematologica*, **27**, 109–114.

Bedding, R.A. (1984) Large scale production, storage and transport of the insect parasitic nematodes *Neoaplectana* spp. and *Heterorhabditis* spp. *Ann. Appl. Biol*., **104**, 117–120.

Bedding, R.A. (1988) *Storage of Insecticidal Nematodes*. World Patent No. WO 88/08668.

Bedding, R.A. (1990) Logistics and strategies for introducing entomopathogenic nematodes into developing countries. *In* R. Gaugler and H.K. Kaya (eds.), *Entomopathogenic Nematodes in Biological Control*, CRC Press, Boca Raton, Florida, pp. 233–248.

Bedding, R.A. and Iede, E.T. (2005) Application of *Beddingia siricidicola* for sirex woodwasp control. *In* P.S. Grewal, R.U. Ehlers and D.I. Shapiro-llan (eds.), *Nematodes as Biocontrol Agents*, CAB International, Wallingford, UK, pp. 385–399.

Bedding, R.A. (2009) Controlling the pine-killing woodwasp, *Sirex noctilio*, with nematodes. *In* A.E. Hajek, T.R. Glare and M. O'Callaghan (eds.), *Use of Microbes for Control of Invasive Arthropods*, Springer, The Netherlands, pp. 213–235.

Benz, G. (1971) Synergism of micro-organisms and chemical insecticides. *In* H.D. Burgess and N.W. Hussey (eds.), *Microbial Control of Insects and Mites*, Academic, London, UK, pp. 327–355.

Blaxter, M.L., De Ley, P., Garey, J.R., Liu, L.X., Scheldeman, P., Vierstraete, A., Vanfleteren, J.R., Mackey, L.Y., Dorris, M., Frisse, L.M., Vida, J.T. and Thomas, W.K. (1998) A molecular evolutionary framework for the phylum *Nematoda*. *Nature*, **392**, 71–75.

Bode, H.B. (2009) Entomopathogenic bacteria as a source of secondary metabolites. *Curr. Opin. Chem. Biol.*, **13**, 1–7.

Boemare, N. and Akhurst, R. (2006) The Genera *Photorhabdus* and *Xenorhabdus*. *In* M. Dworkin, S. Falkow, E. Rosenberg, K.H. Schleifer and E. Stackebrandt (eds.), *The Prokaryotes: Volume 6: Proteobacteria: Gamma Subclass*, Springer, New York, USA, pp. 451–494.

Boff, M.I.C., Zoon, F.C. and Smits, P.H. (2001) Orientation of *Heterorhabditis megidis* to insect hosts and plant roots in a Y-tube sand olfactometer. *Entomol. Exp. Appl*., **98**, 329–337.

Boff, M.I.C., van Tol, R.H.W.M. and Smits, P.H. (2002) Behavioural response of *Heterorhabditis megidis* towards plant roots and insect larvae. *BioControl*, **47**, 67–83.

Bowen, D.J., Rocheleau, T.A., Blackburn, M., Andreev, O., Golubeva, E., Bhartia, R. and Ffrench-Constant, R.H. (1998) Insecticidal toxins from the bacterium *Photorhabdus luminescens*. *Science*, **280**, 2129–2132.

Boyer, J., Reversat, G., Lavelle, P. and Chabanne, A. (2013) Interactions between earthworms and plant-parasitic nematodes. *Eur. J. Soil. Biol.*, **59**, 43–47.

Boszormenyi, E., Ersek, T., Fodor, A., Fodor, A.M., Foldes, L.S., Hevesi, M., Hogan, J.S., Katona, Z., Klein, M.G., Kormany, A., Pekar, S., Szentirmai, A., Sztaricskai, F. and Taylor, R.A.J. (2009) Isolation and activity of *Xenorhabdus* antimicrobial compounds against the plant pathogens *Erwinia amylovora* and *Phytophthora nicotianae*. *J. Appl. Microbiol.*, **107**, 746–759.

Brivio, M.F., Pagani, M. and Restelli, S. (2002) Immune suppression of *Galleria mellonella* (*Insecta*, *Lepidoptera*) humoral defenses induced by *Steinernema feltiae* (*Nematoda*, *Rhabditida*): Involvement of the parasite cuticle. *Exp. Parasitol*., **101**, 149–156.

Brivio, M.F., Mastore, M. and Nappi, A. (2010) A pathogenic parasite interferes with phagocytosis of insect immunocompetent cells. *Dev. Comp. Immunol*., **34**, 991–998.

Brown, I.M. and Gaugler, R. (1995) Cold tolerance of steinernematid and heterorhabditid nematodes. *J. Therm. Biol*. **23**, 75–80.

Brown, I.M. and Gaugler, R. (1997) Temperature and humidity influence emergence and survival of entomopathogenic nematodes. *Nematologica*, **43**, 363–375.

Buecher, E.J. and Hansen, E.L. (1971) Mass culture of axenic nematodes using continuous aeration. *J. Nematol*., **3**, 199–200.

Bussaman, P., Sermswan, R.W. and Grewal, P.S. (2006) Toxicity of the entomopathogenic bacteria *Photorhabdus* and *Xenorhabdus* to the mushroom mite (*Luciaphorus* sp.: Acari: Pygmephoridae). *Biocontrol Sci. Technol.*, **16**, 245–256.

Bussaman, P. and Rattanasena, P. (2016) Additional property of *Xenorhabdus stockiae* for inhibiting cow Mastitis-causing bacteria. *Biosci. Biotech. Res. Asia*, **13**, 1871–1878.

Butt, T.M., Wood, M., Taylor, J.W.D., Bakirci, S., Hazir, C., Ulug, D. and Hazir S. (2016) Differential susceptibility

of *Hyalomma excavatum* adults and nymphs to the entomopathogens *Metarhizium anisopliae* ARSEF 4556 and *Steinernema carpocapsae*. *Int. J. Pest Manag*., **62**, 261–266.

Byers, J.A. and Poinar, G.O. (1982) Location of insect hosts by the nematode *Neoaplectana carpocapsae*, in response to temperature. *Behaviour*, **79**, 1–10.

Cabanillas, H.E., Poinar, G.O. and Raulston, J.R. (1994) *Steinernema riobravis* n. sp. (Rhabditida: Steinernematidae) from Texas. *Fund. Appl. Nematol.*, **17**, 123–131.

Cakmak, I., Hazir, S., Ulug, D. and Karagoz, M. (2013) Olfactory response of *Sancassania polyphyllae* (*Acari*: *Acaridae*) to its phoretic host larva killed by the entomopathogenic nematode, *Steinernema glaseri* (Rhabditida: Steinernematidae). *Biol. Control*, **65**, 212–217.

Campbell, J.F. and Kaya, H.K. (1999). How and why a parasitic nematode jumps. *Nature*, **397**, 485–486.

Campbell, J.F. and Gaugler, R. (1997) Inter-specific variation in entomopathogenic nematode. Foraging strategy: Dichotomy or variation along a continuum? *Fundam. Appl. Nematol*., **20**, 393–398.

Campbell, J.F., Lewis, E.E., Stock, S.P., Nadler, S. and Kaya, H.K. (2003). Evolution of host search strategies in entomopathogenic nematodes. *J. Nematol*., **35**, 142–145.

Campos-Herrera R., Manuel Gómez-Ros, J.M., Escuer, M., Cuadra, L., Barrios, L. and Gutierrez, C. (2008) Diversity, occurrence, and life characteristics of natural entomopathogenic nematode populations from La Rioja (Northern Spain) under different agricultural management and their relationships with soil factors. *Soil Biol. Biochem.*, **40**, 1474–1484.

Chaston, J.M., Suen, G., Tucker, S.L., Andersen, A.W., Bhasin, A., Bode, E., Bode, H.B., Brachmann, A.O., Cowles, C.E., Cowles, K.N., Darby, C., de Léon, L., Drace, K., Du, Z., Givaudan, A., Herbert Tran, E.E., Jewell, K.A., Knack, J.J., Krasomil-Osterfeld, K.C., Kukor, R., Lanois, A., Latreille, P., Leimgruber, N.K., Lipke, C.M., Liu, R., Lu, X., Martens, E.C., Marri, P.R., Médigue, C., Menard, M.L., Miller, N.M., Morales-Soto, N., Norton, S., Ogier, J.C., Orchard, S.S., Park, D., Park, Y., Qurollo, B.A., Sugar, D.R., Richards, G.R., Rouy, Z., Slominski, B., Slominski, K., Snyder, H., Tjaden, B.C., van der Hoeven, R., Welch, R.D., Wheeler, C., Xiang, B., Barbazuk, B., Gaudriault, S., Goodner, B., Slater, S.C., Forst, S., Goldman, B.S. and Goodrich-Blair, H. (2011) The entomopathogenic bacterial endosymbionts *Xenorhabdus* and *Photorhabdus*: Convergent lifestyles from divergent genomes. *PLoS One*, **6**, **11**, e27909.

Chen, S. and Glazer, I. (2005) A novel method for long-term storage of the entomopathogenic nematode *Steinernema feltiae* at room temperature. *Biol. Control*, **32**, 104–110.

Chen, S., Li, X., Yan, A., Spiridonov, S.E. and Moens, M. (2006). A new entomopathogenic nematode, *Steinernema hebeiense* sp. n. (*Rhabditida*: Steinernematidae), from North China. *Nematology*, **8**, 563–574.

Ciche, T.A. and Ensign, J.C. (2003) For the insect pathogen *Photorhabdus luminescens* which end of a nematode is out? *Appl. Environ. Microbiol*., **69**, 1890–1897.

Ciche, T.A., Darby, C., Ehlers, R.U., Forst, S. and Goodrich-Blair, H. (2006) Dangerous liaisons: The symbiosis of entomopathogenic nematodes and bacteria. *Biol. Control*, **38**, 22–46.

Cimen, H., Lee, M.M., Hatting, J., Hazir, S. and Stock, S.P. (2014) *Steinernema tophus* sp. n. (Nematoda: Steinernematidae), a new entomopathogenic nematode from South Africa. *Zootaxa*, **3821**, 337–353.

Cimen, H., Lee, M.M., Hatting, J., Hazir, S., and Stock, S.P. (2015) *Steinernema innovationi* n. sp. (Panagrolaimomorpha: Steinernematidae), a new entomopathogenic nematode species from South Africa. *J. Helminthol.*, **89**, 415–427.

Cimen, H., Puza, V., Nermu, J., Hatting, J., Ramakuwela, T., Faktorova, L. and Hazir, S. (2016a) *Steinernema beitlechemi* n. sp., a new entomopathogenic nematode (Nematoda: Steinernematidae) from South Africa. *Nematology*, **18**, 439–453.

Cimen, H., Puza, V., Nermut, J., Hatting, J., Ramakuwela, T. and Hazir, S. (2016b) *Steinernema biddulphi* n. sp., a new entomopathogenic nematode (Nematoda: Steinernematidae) from South Africa. *J. Nematol*., **48**, 148–158.

Clausi, M., Longo, A., Rappazzo, G., Tarasco, E. and Vinciguerra, M.T. (2011) *Steinernema vulcanicum* n. sp. (Rhabditida: Steinernematidae), a new entomopathogenic nematode species from Sicily (Italy). *Nematology*, **13**, 409–423.

Da Silva, O.S., Prado, G.R., Da Silva, J.L.R., Silva, C.E., Da Costa, M. and Heermann, R. (2013) Oral toxicity of *Photorhabdus luminescens* and *Xenorhabdus nematophila* (Enterobacteriaceae) against *Aedes aegypti* (Diptera: Culicidae). *Parasitol. Res.*, **112**, 2891–2896.

De Waal, J.Y., Malan, A.P. and Addison, M.F. (2013) Effect of humidity and a superabsorbent polymer formulation on the efficacy of *Heterorhabditis zealandica* (Rhabditida: Heterorhabditidae) to control codling moth, *Cydia pomonella* (L.) (Lepidoptera: Tortricidae). *Biocontrol Sci. Technol.*, **23**, 62–78.

Del Valle, E.E., Dolinksi, C., Barreto, E.L.S. and Souza, R.M. (2009) Effect of cadaver coatings on emergence and infectivity of the entomopathogenic

nematode *Heterorhabditis baujardi* LPP7 (Rhabditida: Heterorhabditidae) and the removal of cadavers by ants. *Biol. Control*, **50**, 21–24.

Dembilio, O., Llacer, E., de Altube, M.D.M. and Jacas, J.A. (2010) Field efficacy of imidacloprid and *Steinernema carpocapsae* in a chitosan formulation against the red palm weevil *Rhynchophorus ferrugineus* (Coleoptera: Curculionidae) in *Phoenix canariensis*. *Pest Manag. Sci.*, **66**, 365–370.

Deol, Y.S., Jagdale, G.B., Canas, L., and Grewal, P.S. (2011) Delivery of entomopathogenic nematodes directly through commercial growing media via the inclusion of infected host cadavers: A novel approach. *Biol. Control*, **58**, 60–67.

Dillman, A.R., Chaston, J.M., Adams, B.J., Ciche, T.A., Goodrich-Blair, H., Stock, S.P. and Sternberg, P.W. (2012) An entomopathogenic nematode by any other name. *PLoS Pathog*., **8**, 3, e1002527.

Dolinski, C., Choo, H.Y. and Duncan, L.W. (2012) Grower acceptance of entomopathogenic nematodes: Case studies on three continents. *J. Nematol.*, **44**, 226–235.

Dolinski, C., Shapiro-Ilan, D.I., and Lewis, E.E. (2015) Insect cadaver applications: Pros and cons. *In* R. Campos-Herrera (ed.), *Nematode Pathogenesis of Insects and Other Pests: Ecology and Applied Technologies for Sustainable Plant and Crop Protection*, Springer International Publishing, Switzerland, pp. 207–229.

Doucet, M.M.A. (1986). A new species of *Neoaplectana Steiner*, 1929 (Nematoda: Steinernematidae) from Cordoba, Argentina. *Rev. Nematol.*, **9**, 317–323.

Doucet, M.M.A. and Doucet, M.E. (1990) *Steinernema ritteri* n. sp. (Nematoda: Steinernematidae) with a key to the species of the genus. *Nematologica*, **36**, 257–265.

Dowds, B.C.A. and Peters, A. (2002) Virulence mechanisms. *In* R. Gaugler (ed.), *Entomopathogenic Nematology*, CAB International, Wallingford, UK, pp. 79–98.

Downes, M.J. and Griffin, C.T. (1996) Dispersal behaviour and transmission strategies of the entomopathogenic nematodes *Heterorhabditis* and *Steinernema*. *Biocontrol Sci. Technol.*, **6**, 347–356.

Duncan, L.W., and McCoy, C.W. (2001). Hydraulic lift increases herbivory by *Diaprepes abbreviatus* larvae and persistence of *Steinernema riobrave* in dry soil. *J. Nematol*, **33**, 142–146.

Duncan, L.W., Graham, J.H., Zellers, J., Bright, D., Dunn, D.C., El-Borai, F.E. and Porazinska, D.L. (2007) Food web responses to augmenting the entomopathogenic nematodes in bare and animal manure-mulched soil. *J. Nematol.*, **39**, 176–189.

Duncan, L.W., Stuart, R.J., El-Borai, F.E., Campos-Herrera, R., Pathak, E. and Graham, J.H. (2013) Modifying orchard planting sites conserves entomopathogenic nematodes, reduces weevil herbivory and increases citrus tree growth, survival and fruit yield. *Biol Control*, **64**, 26–36.

Edgington, S., Buddie, A.G., Tymo, L.M., Hunt, D.J., Nguyen, K., France, A., Merino, L. and Moore, D. (2009a) *Steinernema australe* n. sp. (Panagrolaimomorpha: Steinernematidae), a new entomopathogenic nematode from Isla Magdalena, Chile. *Nematology*, **11**, 699–717.

Edgington, S., Buddie, A.G., Tymo, L.M., France, A., Merino, L., Hunt, D.J. (2009b) *Steinernema unicornum* sp. n. (Panagrolaimomorpha: Steinernematidae), a new entomopathogenic nematode from Tierra del Fuego, Chile. *J. Nematode Morph. Syst.* **12**, 113–131.

Edgington, S., Buddie, A.G., Moore, D., France, A., Merino, L. and Hunt, D.J. (2010) *Heterorhabditis atacamensis* n. sp. (Nematoda: Heterorhabditidae), a new entomopathogenic nematode from the Atacama Desert, Chile, *J. Helminthol.*, **85**, 381–394.

Ehlers, R.U., Wulff, A. and Peters, A. (1997) Pathogenicity of axenic *Steinernema feltiae*, *Xenorhabdus bovienii*, and the bacto-helminthic complex to larvae of *Tipula oleracea* (Diptera) and *Galleria mellonella* (Lepidoptera). *J. Invertebr. Pathol*, **69**, 212–217.

Ehlers, R.U., Lunau, S., Krasomil-Osterfeld, K. and Osterfeld, K.H. (1998) Liquid culture of the entomopathogenic nematode-bacterium-complex *Heterorhabditis megidis/Photorhabdus luminescens*. *BioControl*, **43**, 77–86.

Ehlers, R.U. and Shapiro-Ilan, D.I. (2005) Mass production. *In* P.S. Grewal, R.U. Ehlers, R.U. and D.I. Shapiro-llan (eds.), *Nematodes as Biological Control Agents*, CAB International, Wallingford, UK, pp. 65–79.

Ekmen, Z.I., Cakmak, I., Karagoz, M., Hazir, S., Ozer, N. and Kaya, H.K. (2010a) Food preference of *Sancassania polyphyllae* (Acari: Acaridae): Living entomopathogenic nematodes or insect tissues? *Biocontrol Sci. Technol.*, **20**, 553–566.

Ekmen, Z.I., Hazir, S., Cakmak, I., Ozer, N., Karagoz, M. and Kaya, H.K. (2010b) Potential negative effects on biological control by *Sancassania polyphyllae* (Acari: Acaridae) on an entomopathogenic nematode species. *Biol. Control*, **54**, 166–171.

Elawad, S., Ahmad, W. and Reid, A.P. (1997) *Steinernema abbasi* sp. n. (Nematoda, Steinernematidae), from the Sultanate of Oman. *Fundam. Appl. Nematol*., **20**, 433–442.

El-Borai, F.E., Bright, D.B., Graham, J.H., Stuart, R.J., Cubero, J. and Duncan, L.W. (2009) Differential susceptibility of entomopathogenic nematodes to nematophagous fungi from Florida citrus orchards. *Nematology*, **11**, 233–243.

Enright, M.R. and Griffin, C.T. (2004) Specificity of association between *Paenibacillus* spp. and the entomopathogenic nematodes, *Heterorhabditis* spp. *Microb. Ecol*., **48**, 414–423.

Epsky, N.D., Walter, D.E. and Capinera J.L. (1988) Potential role of nematophagous microarthropods as biotic mortality factors of entomogenous nematodes (Rhabditida: Steinernematidae, Heterorhabditidae). *J. Econ. Entomol*., **81**, 821–825.

Ester, A. and Wilson, M.J. (2005) Application of slug parasitic nematodes. *In* P.S. Grewal, R.U. Ehlers, R.U. and D.I. Shapiro-llan (eds.), *Nematodes as Biocontrol Agents*, CABI Publishing, Wallingford, UK, pp. 431–444.

Everard, A., Griffin, C.T., Dillon, A.B. (2009) Competition and intraguild predation between the braconid parasitoid *Bracon hylobii* and the entomopathogenic nematode *Heterorhabditis downesi*, natural enemies of the large pine weevil, *Hylobius abietis*. *Bull. Entomol. Res*., **99**, 151–161.

Fang, X., Zhang, M., Tang, Q., Wang, Y. and Zhang, X. (2014) Inhibitory effect of *Xenorhabdus nematophila* TB on plant pathogens *Phytophthora capsici* and *Botrytis cinerea in vitro* and in planta. *Sci. Rep.*, **4**, 1–7.

Fayyaz, S., Yan, X., Qui, L., Han, R., Gulsher, M., Khanum, T.A. and Javed, S. (2014) A new entomopathogenic nematode, *Steinernema bifurcatum* n. sp. (Rhabditida: Steinernematidae) from Punjab, Pakistan. *Nematology*, **16**, 821–836.

Fayyaz, S., Khanum, T.A., Ali, S., Solangi, G.S., Gulsher, M. and Javed, S. (2015) *Steinernema balochiense* n. sp. (Rhabditida: Steinernematidae) a new entomopathogenic nematode from Pakistan. *Zootaxa*, **3904**, 387–402.

Fenton, A., Magoolagan, L., Kennedy, Z. and Spencer, K.A. (2011) Parasite-induced warning coloration: A novel form of host manipulation. *Anim. Behav.*, **81**, 417-422.

Ffrench-Constant, R.H., Dowling, A. and Watereld, N.R. (2007) Insecticidal toxins from *Photorhabdus* bacteria and their potential use in agriculture. *Toxicon*, **49**, 436–451.

Fife, J.P., Derksen, R.C., Ozkan, H.E. and Grewal, P.S. (2003) Effects of pressure differentials on the viability and infectivity of entomopathogenic nematodes. *Biol. Control*, **27**, 65–72.

Fife, J.P., Ozkan, H.E., Derksen, R.C., Grewal, P.S. and Krause, C.R. (2005) Viability of a biological pest control agent through hydraulic nozzles. *Trans. ASAE*, **48,** 45–54.

Fodor, A., Fodor, A.M., Forst, S., Hogan, J.S., Klein, M.G., Lengyel, K., Saringer, G., Stackebrandt, E., Taylor, R.A.J. and Lehoczky, E. (2010) Comparative analysis of antibacterial activities of *Xenorhabdus* species on related and nonrelated bacteria *in vivo*. *J. Microbiol. Antimicrob.*, **2**, 36–46.

Foltan, P. and Puza, V. (2009) To complete their life cycle, pathogenic nematode-bacteria complexes deter scavengers from feeding on their host cadaver. *Behav. Process*., **80**, 76–79.

Forst, S. and Clarke, D. (2002) Bacteria-nematode symbiosis. *In* R. Gaugler (ed.), *Entomopathogenic Nematology*, CAB International, New York, USA, pp. 57–77.

Funderburk, J. and Latsha, K.S. (2005) The entomophilic *Thripinema*. *In* P.S. Grewal, R.U. Ehlers, R.U. and D.I. Shapiro-llan (eds.), *Nematodes as Biocontrol Agents*, CAB International, Wallingford, UK, pp. 401–410.

Gaugler, R., Bednarek, A. and Campbell, J.F. (1992) Ultraviolet inactivation of heterorhabditid and steinernematid nematodes. *J. Invertebr. Pathol.*, **59**, 155–160.

Gaugler, R. and Han, R. (2002) Production technology. *In* R. Gaugler (ed.), *Entomopathogenic Nematology*. CAB Internaional, Wallingford, UK, pp. 289–310.

Gaugler, R., Lewis, E.E. and Stuart, R.J. (1997) Ecology in the service of biological control: The case of entomopathogenic nematodes. *Oecologia*, **109**, 483–489.

Gaugler, R., Brown, I., Shapiro-Ilan, D.I. and Atwa, A. (2002) Automated technology for *in vivo* mass production of entomopathogenic nematodes. *Biol. Control*, **24,** 199–206.

Georgis, R. (1990) Formulation and application technology. *In* R. Gaugler and H.K. Kaya (eds.), *Entomopathogenic Nematodes in Biological Control*, CRC Press, Boca Raton, Florida, pp. 173–191.

Georgis, R. (1992) Present and future prospects for entomopathogenic nematode products. *Biocontrol Sci. Technol.*, **2,** 83–99.

Glaser, R.W. (1932) Studies on *Neoaplectana glaseri*, a nematode parasite of the Japanese beetle. Circ. N.J. Dep. Agric. no. 211.

Glaser, R.W. and Farrell, C.C. (1935) Field experiments with the Japanese beetle and its nematode parasite. *J. NY. Entomol. Soc.*, **43**, 345–371.

Glaser, R.W. (1940) The bacteria-free culture of a nematode parasite. *Proc. Soc. Exp. Biol. Med.*, **43**, 512–514.

Glazer, I. (1992) Invasion rate as a measure of infectivity of steinernematid and heterorhabditid nematodes to insects. *J. Invertebr. Pathol.*, **59**, 90–94.

Glazer, I. (2002) Survival biology. *In* R. Gaugler (ed.), *Entomopathogenic Nematology*, CAB International, Wallingford, UK, pp. 169–188.

Goodrich-Blair, H. and Clarke, D.J. (2007) Mutualism and pathogenesis in *Xenorhabdus* and *Photorhabdus*: Two roads to the same destination. *Mol. Microbiol*., **64**, 260–268.

Gorgadze, O.A., Ivanova, E.S., Lortkhipanidze, M.G. and Spiridonov, S. (2016) Redescription of *Steinernema thesami* Gorgadze, 1988 (Rhabditida: Steinernematidae) from Georgia. *Russ. J. Nematol*., **24**, 17–31.

Grant, J.A. and Villani M.G. (2003) Soil moisture effects on entomopathogenic nematodes. *Environ. Entomol*., **32**, 80–87.

Grewal, P.S., Lewis, E.E., Gaugler, R. and Campbell, J.F. (1994) Host finding behaviour as a predictor of foraging strategy in entomopathogenic nematodes. *Parasitology*, **108**, 207–215.

Grewal, P.S. and Georgis, R. (1998) Entomopathogenic nematodes. *In* F.R. Hall and J.J. Menn (eds.), *Biopesticides: Use and Delivery*, Humana Press, Totowa, NJ, pp. 271–299.

Grewal, P.S. (2002) Formulation and application technology. *In* R. Gaugler (ed.), *Entomopathogenic Nematology,* CAB International, Wallingford, UK, pp. 265–288.

Grewal, P.S. (2000) Enhanced ambient storage stability of an entomopathogenic nematode through anhydrobiosis. *Pest Manag. Sci*., **56**, 401–406.

Grewal, P.S. (2002) Formulation and application technology. *In* R. Gaugler (ed.), *Entomopathogenic Nematology*, CABI Publishing, Wallingford, UK, pp. 265–288.

Grewal, P.S., Ehlers, R.U. and Shapiro-Ilan, D.I. (2005) *Nematodes as Biocontrol Agents*, CAB International, Wallingford, UK.

Grifaldo-Alcantara, P.F., Alatorre-Rosas, R., Segura-Leon, O. and Hernandez-Rosas, F. (2017) *Steinernema ralatorei* n. sp. Isolated from sugarcane areas at Veracruz, Mexico. *Southwest. Entomol.*, **42**, 171–190.

Griffin, C.T., Downes, M.J. and Block, W. (1990) Tests of antarctic soils for insect parasitic nematodes. *Antarctic Sci.,* **2**, 221–222.

Griffin, C.T., Joyce, S.A., Dix, I., Burnell, A.M. and Downes, M.J. (1994) Characterisation of the entomopathogenic nematode *Heterorhabditis* (*Nematoda*: Heterorhabditidae) from Ireland and Britain by molecular and cross-breeding techniques, and the occurrence of the genus in these islands. *Fundam. Appl. Nematol*., **17**, 245–254.

Griffin, C.T. (2015) Behaviour and population dynamics of entomopathogenic nematodes following application. *In* R. Campos-Herrera (ed.), *Nematode Pathogenesis of Insects and Other Pests: Ecology and Applied Technologies for Sustainable Plant and Crop Protection*, Springer International Publishing, Switzerland, pp. 57–95.

Grundmann, F., Kaiser, M., Schiell, M., Batzer, A., Kurz, M., Thanwisai, A., Chantratita, N. and Bode, H. (2014) Antiparasitic chaiyaphumines from entomopathogenic *Xenorhabdus* sp. PB61.4. *J. Nat. Prod.*, **77**, 779–783.

Gulcu, B., Hazir, S. and Kaya, H.K. (2012) Scavenger deterrent factor (SDF) from symbiotic bacteria of entomopathogenic nematodes. *J. Invertebr. Pathol.*, **110**, 326–333.

Gumus, A., Karagoz, M., Shapiro-Ilan, D.I. and Hazir, S. (2015) A novel approach to biocontrol: Release of live insect hosts pre-infected with entomopathogenic nematodes. *J. Invertebr. Pathol*., **130**, 56–60.

Gungor, D.S., Keskin, N. and Hazir S. (2006) Ecological characterization of *Steinernema anatoliense* (Rhabditida: Steinernematidae). *J. Invertebr. Pathol.*, **92**, 39–44.

Gupta, R.K., Patterson, S.S., Ripp, S. and Sayler, G.S. (2003) Expression of the *Photorhabdus luminescens lux* genes (*luxA*, *B*, *C*, *D*, and *E*) in *Saccharomyces cerevisiae*. *FEMS Yeast Res.*, **4,** 305–313.

Han, R. and Ehlers, R.U. (2000) Pathogenicity, development, and reproduction of *Heterorhabditis bacteriophora* and *Steinernema carpocapsae* under axenic *in vivo* conditions. *J. Invertebr. Pathol.*, **75**, 55–58.

Hazir, S., Stock, S.P., Kaya, H.K., Koppenhofer, A.M. and Keskin, N. (2001) Developmental temperature effects on five geographic isolates of *Steinernema feltiae* (Nematoda: Steinernematidae) *J. Invertebr. Pathol*., **77**, 243–250.

Hazir, S., Kaya, H.K., Stock, S.P. and Keskin, N. (2003) Entomopathogenic nematodes (Steinernematidae and Heterorhabditidae) for biological control of soil pests. *Turk. J. Biol.*, **27**, 181–202.

Hazir, S., Shapiro-Ilan, D.I., Bock, C.H., Hazir, C., Leite, L.G. and Hotchkiss, M.W. (2016) Relative potency of culture supernatants of *Xenorhabdus* and *Photorhabdus* spp. on growth of some fungal phytopathogens. *Eur. J. Plant Pathol.*, **146**, 369–381.

Hazir, S., Shapiro-Ilan, D.I., Bock, C.H. and Leite, L.G. (2017) Trans-cinnamic acid and *Xenorhabdus szentirmaii* metabolites synergize the potency of some commercial fungicides. *J. Invertebr. Pathol.*, **144**, 22–31.

Held, L.D., Xiang, N., Hall, M., Till, S., Groover, W. and Dyer, D. (2017) Are earthworms a catalyst for nematode infection on golf courses? *Society of Nematologist (SON) Meeting*, Williamsburg, Virginia, USA.

Hiltpold, I. and Turlings, T.C.J. (2012). Manipulation of chemically mediated interactions in agricultural soils to enhance the control of crop pests and to improve crop yield. *J. Chem. Ecol.*, **38**, 641–650.

Hiltpold, I., Hibbard, B.E., French, D.W. and Turlings, T.C.J. (2012) Capsules containing entomopathogenic nematodes as a Trojan horse approach to control the western corn rootworm. *Plant Soil*, **358**, 11–25.

Hominick, W.M. (2002) Biogeography. *In* R. Gaugler (ed.), *Entomopathogenic Nematology*, CAB International, Wallingford, UK, pp. 115–144.

Hunt, D.J. (2016) Introduction. *In* D.J. Hunt and K.B. Nguyen (eds.), *Advances in Entomopathogenic Nematode Taxonomy and Phylogeny*, Brill Publishing, Leiden, The Netherlands, pp. 1–11.

Hunt, D.J. and Subbotin, S.A. (2016) Taxonomy and systematics. *In* D.J. Hunt and K.B. Nguyen (eds.), *Advances in Entomopathogenic Nematode Taxonomy and Phylogeny*, Brill Publishing, Leiden, The Netherlands, pp. 13–58.

Hussain, Z., Souza, P.E. and Puttalakshmamma, G.C. (2015) *In vitro* efficacy of three species of entomopathogenic nematodes on biocontrol of cattle tick *Rhipicephalus haemaphysaloides* Neumann (Acarina: Ixodidae). *Biol. Control*, **29**, 223–226.

Ilan, T., Kim-Shapiro, D.B., Bock, C.H. and Shapiro-Ilan, D.I. (2013) The impact of magnetic fields, electric fields and current on the directional movement of *Steinernema carpocapsae*. *Int. J. Parasitol.*, **43**, 781–784.

Isaacson, P.J. and Webster, J.M. (2002) Antimicrobial activity of *Xenorhabdus* sp. RIO (Enterobacteriaceae) symbiont of the entomopathogenic nematode, *Steinernema riobrave* (Rhabditida: Steinernematidae). *J. Invertebr. Pathol.*, **79**, 146–153.

Ivanova, E.S., Shepeleva, N.S. and Spiridonov, S.E. (2013) Morphological and molecular characterisation of *Steinernema costaricense* Uribe-Lorío, Mora and Stock, 2007 (Panagrolaimorpha: Steinernematidae) isolate from Bush Augusta State Park, Missouri, USA. *Syst. Parasitol.*, **85**, 219–234.

Jaffee, B.A. and Strong, D.R. (2005) Strong bottom-up and weak top-down effects in soil: Nematode-parasitized insects and nematode-trapping fungi. *Soil Biol. Biochem.*, **37**, 1011–1021.

Jansson, R.K., Lecrone, S.H. and Gaugler R. (1993) Field efficacy and persistence of entomopathogenic nematodes (Rhabditida: Steinernematidae, Heterorhabditidae) for control of sweetpotato weevil (*Coleoptera*: *Apionidae*) in Southern Florida. *J. Econ. Entomol.*, **86**, 1055–1063.

Jawish, A., Al-assas, K. and Basheer, A. (2015) A survey of entomopathogenic nematodes of the families Steinernematidae and Heterorhabditidae (Nematoda: Rhabditida) in Damascus countryside of Syria, *EPPO Bulletin*, **45**, 81–89.

Jian, H., Reid, A.P. and Hunt, D.J. (1997) *Steinernema ceratophorum* n. sp. (Nematoda: Steinernematidae), a new entomopathogenic nematode from north-east China. *Syst. Parasitol.*, **37**, 115–125.

Jones, R.S., Fenton, A., Speed, M.P. and Mappes, J. (2017) Investment in multiple defences protects a nematode-bacterium symbiosis from predation. *Anim. Behav.*, **129**, 1–8.

Kakulia, G. and Mikaia, N. (1997) A new species of the nematode *Heterorhabditis poinari* sp. n. (Rhabditida: Heterorhabditidae). *Bull. Georg. Acad. Sci.*, **155**, 457–459.

Kanga, F.N., Trinh, P.Q., Waeyenberge, L., Spiridonov, S.E., Hauser, S. and Moens, M. (2012a) Two new species of *Steinernema* Travassos, 1927 from the humid forest of southern Cameroon. *Russ. J. Nematol.*, **20**, 15–36.

Kanga, F.N., Waeyenberge, L., Hauser, S. and Moens, M. (2012b) Distribution of entomopathogenic nematodes in Southern Cameroon. *J. Invertebr. Pathol*, **109**, 41–51.

Karagoz, M., Gulcu, B., Cakmak, I., Kaya, H.K. and Hazir, S. (2007) Predation of entomopathogenic nematodes by *Sancassania* sp. (Acari: Acaridae). *Exp. Appl. Acarol.*, **43**, 85–95.

Karunakar, G., David, H. and Easwaramoorthy, S. (1992) Influence of temperature on infectivity, penetration and multiplication of *Steinernema feltiae*, *S. glaseri* and *Heterorhabditis indicus* on mortality of the host and multiplication of infective juveniles in sugarcane inter node borer, *Chilo sacchariphagus indicus*. *Biol. Control*, **6**, 26–28.

Kaya, H.K. and Nelson, C.E. (1985) Encapsulation of steinernematid and heterorhabditid nematodes with calcium alginate: A new approach for insect control and other application. *Environ. Entomol.*, **14**, 572–574.

Kaya, H.K. and Gaugler, R. (1993) Entomopathogenic nematodes. *Ann. Rev. Entomol.*, **38**, 181–206.

Kaya, H.K. and Koppenhofer, A.M. (1996) Effects of microbial and other antagonistic organism and competition on entomopathogenic nematodes. *Biocontrol Sci. Technol.*, **6**, 357–371.

Kaya, H.K. (2002) Natural enemies and other antagonists. *In* R. Gaugler (ed.), *Entomopathogenic Nematology*, CAB International, Wallingford, UK, pp. 189–203.

Khatri-Chhetri, H.B., Waeyenberge, L., Manandhar, H.K. and Moens M. (2010) Natural occurrence and distribution of entomopathogenic nematodes

(Steinernematidae and Heterorhabditidae) in Nepal. *J. Invertebr. Pathol.*, **103**, 74–78.

Khatri-Chhetri, H.B., Waeyenberge, L., Spiridonov, S., Manandhar, H.K. and Moens, M. (2011a) *Steinernema lamjungense* n. sp. (Rhabditida: Steinernematidae), a new species of entomopathogenic nematode from Lamjung district, Nepal. *Nematology*, **13**, 589–605.

Khatri-Chhetri, H.B., Waeyenberge, L., Spiridonov, S., Manandhar, H.K. and Moens, M. (2011b) Two new species of *Steinernema* Travassos, 1927 with short infective juveniles from Nepal. *Russ. J. Nematol.*, **19**, 53–74.

King, H.A. (1982) Brown seaweed extracts (alginates). *In* M. Glicksman (ed.), *Food Hydrocolloids*, Vol. 2, CRC Press, Boca Raton, FL, USA, pp. 115–188.

Koltai, H., Glazer, I. and Segal, D. (1995) Reproduction of the entomopathogenic nematode *Heterorhabditis bacteriophora* Poinar, 1976: Hermaphroditism vs amphimixis. *Fundam. Appl. Nematol*., **18**, 57–63.

Koppenhofer, A.M., Kaya, H.K., Shanmugan, S. and Wood, G.L. (1995) Interspecific competition between steinernematid nematodes within an insect host. *J. Invertebr. Pathol*., **66**, 99–103.

Koppenhofer, A.M. and Kaya, H.K. (1996) Co-existence of two steinernematid nematode species (Rhabditida: Steinernematidae) in the presence of two host species. *Appl. Soil Ecol*., **4**, 221–230.

Koppenhofer, A.M. and Kaya, H.K. (1998) Synergism of imidacloprid and an entomopathogenic nematode: A novel approach to white grub (Coleoptera: Scarabaeidae) control in turfgrass. *J. Econ. Entomol*., **91**, 618–623.

Koppenhofer, A.M. (2000) Nematodes. *In* L.A. Lacey and H.K. Kaya (eds.), *Field Manual of Techniques in Invertebrate Pathology*, Kluwer, Dordrecht, The Netherlands, pp. 283–301.

Koppenhofer, A.M. and Fuzy, E.M. (2003) Ecological characterization of *Steinernema scarabaei*, a scarab-adapted entomopathogenic nematode from New Jersey. *J. Invertebr. Pathol.*, **83**, 139–148.

Koppenhofer, A.M. and Grewal, P.S. (2005) Compatibility and interactions with agrochemicals and other biocontrol agents. *In* P.S. Grewal, R.U. Ehlers and D.I. Shapiro-Ilan (eds.), *Nematodes as Biological Control Agents*, CAB International, Wallingford, UK, pp. 363–381.

Koppenhofer, A.M. and Fuzy, E.M. (2006) Effect of soil type on infectivity and persistence of the entomopathogenic nematodes *Steinernema scarabaei, Steinernema glaseri, Heterorhabditis zealandica*, and *Heterorhabditis bacteriophora*, *J. Invertebr. Pathol.*, **92**, 11–22.

Koppenhofer, A.M. (2007) Nematodes. *In* L.A. Lacey and H.K. Kaya(eds.), *Field Manual of Techniques in Invertebrate Pathology: Application and Evaluation of Pathogens for Control of Insects and other Invertebrate Pests*, second edition, Springer, Dordrecht, Germany, pp. 249–264.

Koppenhofer, A.M. and Fuzy, E.M. (2007) Long-term effects and persistence of nematodes for suppression of white grubs Albrecht M. *USGA Turfgrass Environ. Res. Online*, **7**, 1–14.

Koppenhofer, A.M. and Fuzy, E.M. (2008) Early timing and new combinations to increase the efficacy of neonicotinoid-entomopathogenic nematode (Rhabditida: Heterorhabditidae) combinations against white grubs (*Coleoptera*: *Scarabaeidae*). *Pest Manag. Sci*., **64**, 725–735.

Krishnayya, P.V. and Grewal, P.S. (2002) Effect of neem and selected fungicides on viability and virulence of the entomopathogenic nematode *Steinernema feltiae*. *Biocontrol Sci. Technol.*, **12**, 259–266.

Kruitbos, L., Heritage, S. and Wilson M. (2009) Phoretic dispersal of entomopathogenic nematodes by *Hylobius abietis*. *Nematology*, **11**, 419–427.

Kung, S.P., Gaugler, R. and Kaya, H.K. (1990) Influence of soil pH and oxygen on entomopathogenic nematode persistence. *J. Nematol*., **22**, 440–445.

Lacey, L.A., Unruh, T.R. and Headrick, H.L. (2003) Interactions of two parasitoids (Hymenoptera: Ichneumonidae) of codling moth (Lepidoptera: Tortricidae) with the entomopathogenic nematode *Steinernema carpocapsae* (Rhabditida: Steinernematidae). *J. Invertebr. Pathol*., **83**, 230–239.

Lane, D.J., Pace, B., Olsen, G.J., Stahl, D.A., Sogin, M.L. and Pace, N.R. (1985) Rapid determination of 16S ribosomal RNA sequences for phylogenetic analyses. *Proc. Natl. Acad. Sci.*, **82**, 6955–6959.

Lee, M.M., Sicard, M., Skeie, M. and Stock, S.P. (2009) *Steinernema boemarei* n. sp. (Nematoda: Steinernematidae), a new entomopathogenic nematode from southern France. *Syst. Parasitol.*, **72**, 127–141.

Lewis, E.E. and Shapiro-Ilan, D.I. (2002) Host cadavers protect entomopathogenic nematodes during freezing. *J. Invertebr. Pathol*., **81**, 25–32.

Lewis, E.E., Campbell, J., Griffin, C., Kaya, H.K. and Peters, A. (2006) Behavioral ecology of entomopathogenic nematodes. *Biol. Control*, **38**, 66–79.

Lewis, E.E. and Clarke D.J. (2012) Nematode parasites and entomopathogens. *In* F.E. Vega and H.K Kaya (eds.), *Insect Pathology*, 2nd ed, Academic Press, San Diego, CA, USA, pp. 395-424.

Lewis, E.E., Hazir, S., Hodson, A. and Gulcu, B. (2015) Trophic relationships of entomopathogenic nematodes in agricultural habitats. *In* R. Campos-Herrera (ed.), *Nematode Pathogenesis of Insects and Other Pests: Ecology and Applied Technologies for Sustainable Plant and Crop Protection*, Springer International Publishing, Switzerland, pp. 139–163.

Li, X.Y., Cowles, R.S., Cowles, E.A., Gaugler, R. and Cox-Foster, D.L. (2007) Relationship between the successful infection by entomopathogenic nematodes and the host immune response. *Int. J. Parasitol*., **37**, 365–374.

Liu, J. and Berry, R.E. (1996) *Steinernema oregonensis* n.sp. (Rhabditida: Steinernematidae) from Oregon, USA. *Fund. Appl. Nematol.*, **19**, 375–380.

Liu, J. and Berry, R.E. (1996) *Heterorhabditis marelatus* n. sp. (Rhabditida: Heterorhabditidae) from Oregon. *J. Invertebr. Pathol*., **67**, 48–54.

López-Núñez, J.C., Plichta, K., Gongora-Botero, C.E. and Stock, S.P. (2008) A new entomopathogenic nematode, *Steinernema colombiense* n. Sp. (Nematoda: Steinernematidae) from Colombia. *Nematology*, **10**, 561–574.

Luc, P.V., Nguyen, K.B., Reid, A.P. and Spiridonov, S.E. (2000) *Steinernema tami* sp. n. (Rhabditida: Steinernematidae) from Cat Tien Forest, Vietnam. *Russ. J. Nematol.*, **8**, 33–43.

Ma, J., Chen, S., De Clercq, P., Han, R. and Moens, M. (2012a) *Steinernema changbaiense* sp. n. (Rhabditida: Steinernematidae), a new species of entomopathogenic nematodes from Northeast China. *Russ. J. Nematol.*, **20**, 97–112.

Ma, J., Chen, S.L., Li, H.X., Han, R.C., Khatri-Chhetri, H.B., De Clercq, P. and Moens, M. (2012b) A new entomopathogenic nematode, *Steinernema tielingense* n. sp. (Rhabditida: Steinernematidae), from north China. *Nematology*, **14**, 321–338.

Ma, M., Chen, S., De Clercq, P., Waeyenberge, L., Han, R. and Moense, M. (2012c) A new entomopathogenic nematode, *Steinernema xinbinense* n. sp. (Nematoda: Steinernematidae), from north China. *Nematology*, **14**, 723–739.

Ma, J., Chen, S., Moens, M., De Clercq, P., Li, X. and Han, R. (2013) Characterization in biological traits of entomopathogenic nematodes isolated from North China. *J. Invertebr. Pathol.*, **114**, 268–276.

Maizels, R.M., Balic, A., Gomez-Escobar, N., Nair, M., Taylor, M.D. and Allen, J.E. (2004) Helminth parasites-masters of regulation. *Immunol. Rev*., **201**, 89–116.

Malan, A.P., Nguyen, K.B., de Waal, J.Y. and Tiedt, L. (2008) *Heterorhabditis safricana* n. sp. (Rhabditida: Heterorhabditidae), a new entomopathogenic nematode from South Africa. *Nematology*, **10**, 381–396.

Malan, A.P., Knoetze, R. and Tiedt, L. (2012) *Heterorhabditis noenieputensis* n. sp. (Rhabditida: Heterorhabditidae), a new entomopathogenic nematode from South Africa. *J. Helminthol*., **88**, 139–151.

Malan, A.P., Knoetze, R. and Tiedt, L. (2014) *Heterorhabditis noenieputensis* n. sp. (Rhabditida: Heterorhabditidae), a new entomopathogenic nematode from South Africa. *J. Helminthol*., **88**, 138–151.

Malan, A.P., Knoetze, R. and Tiedt, L. (2015) *Steinernema jeffreyense* n. sp. (Rhabditida: Steinernematidae), a new entomopathogenic nematode from South Africa. *J. Helminthol*., **90**, 262–278.

Malan, A.P., Knoetze, R. and Tiedt, L. (2016) *Steinernema nguyeni* n. sp. (Rhabditida: Steinernematidae), a new entomopathogenic nematode from South Africa. *Nematology*, **18**, 571–590.

Mamiya, Y. (1988) *Steinernema kushidai* n. sp. (Nematoda: Steinernematidae) associated with scarabaeid beetle larvae from Shizuoca, Japan. *Appl. Entomol. Zool.*, **23**, 313–320.

Mamiya, Y. (1989) Comparison of the infectivity of *Steinernema kushidai* (Nematoda: Steinernematidae) and other steinernematid and heterorhabditid nematodes for three different insects. *Appl. Entomol. Zool.*, **24**, 302–308.

Maneesakorn, P., Grewal, P.S. and Chandrapatya, A. (2010) *Steinernema minutum* sp. nov. (Rhabditida: Steinernematidae): A new entomopathogenic nematode from Thailand. *Int. J. Nematol.*, **20**, 27–42.

Martens, E.C., Heungens, K. and Goodrich-Blair, H. (2003) Early colonization events in the mutualistic association between *Steinernema carpocapsae* nematodes and *Xenorhabdus nematophila* bacteria. *J. Bacteriol.*, **185**, 3147–3154.

Martin, P.A.W. (2002) An *in vitro* inhibition test that predicts toxicity of bacterial pathogen combinations in the Colorado potato beetle. *Biocontrol Sci. Technol*., **12**, 643–647.

Martinez de Altube, M., Strauch, O., Fernandez De Castroand, G. and Martinez Pena, A. (2008) Control of the flat-headed root borer *Capnodis tenebrionis* (Linné) (Coleoptera: Buprestidae) with the entomopathogenic nematode *Steinernema carpocapsae* (Weiser) (Nematoda: Steinernematidae) in a chitosan formulation in apricot orchards. *BioControl*, **53**, 531–539.

Mason, J.M., Mathews, G.A. and Wright, D.J. (1998) Screening and selection of adjuvants for the spray

application of entomopathogenic nematodes against a foliar pest. *Crop Prot.*, **17**, 461–470.

McCoy, C.W., Shapiro, D.I. and Duncan, L.W. (2000a) Application and evaluation of entomopathogens for citrus pest control. *In* L.A. Lacey and H.K. Kaya (eds.), *Field Manual of Techniques in Insect Pathology*, Kluwer Academic Publishers, Dordrecht, The Netherlands, pp. 577–596.

McCoy, C.W., Shapiro, D.I., Duncan, L.W. and Nguyen, K. (2000b) Entomopathogenic nematodes and other natural enemies as mortality factors for larvae of *Diaprepes abbreviates* (Coleoptera: Curculionidae). *Biol. Control*, **19**, 182–190.

Mitani, D.K., Kaya, H.K. and Goodrich-Blair, H. (2004) Comparative study of the entomopathogenic nematode, *Steinernema carpocapsae*, reared on mutant and wild-type *Xenorhabdus nematophila*. *Biol. Control*, **29**, 382–391.

Monteiro, C.M.O., Matos, R.S, Araujo, L.X., Perinotto, W.M.S., Bittencourt, V.R.E.P., Dolinski, C. and Prata, M.C.A. (2014) First report of pathogenicity of entomopathogenic nematodes of the genus *Heterorhabditis* on partially engorged females of *Dermacentor nitens* (Acari: Ixodidae). *Biol. Control*, **69**, 78–81.

Mracek, Z., Hernandez, E.A. and Boemare, N.E. (1994) *Steinernema cubana* sp. (Nematoda: Steinernematidae) and the preliminary characterization of its associated bacterium. *J. Invertebr. Pathol*., **64**, 123–129.

Mracek, Z., Sturhan, D. and Redi, A. (2003) *Steinernema weiseri* sp. n. (Rhabditida: Steinernematidae), a new entomopathogenic nematode from Europe. *Syst. Parasitol.*, **56**, 37–47.

Mracek, Z., Nguyen, K.B., Tailliez, P., Boemare, N. and Chen, S. (2006) *Steinernema sichuanense* n. sp. (Rhabditida: Steinernematidae)-A new species of entomopathogenic nematode from the province of Sichuan, East Tibetan Mts., China. *J. Invertebr. Pathol.*, **93**, 157–169.

Mracek, Z., Liu, Q.Z. and Nguyen, K.B. (2009) *Steinernema xueshanense* n. sp. (Rhabditida, Steinernematidae), a new species of entomopathogenic nematode from the province of Yunnan, southeast Tibetan Mts., China. *J. Inverteb. Pathol*., **102**, 69–78.

Mracek, Z., Puza, V. and Nermut, J. (2014) *Steinernema poinari* sp. n. (Nematoda: Steinernematidae) a new entomopathogenic nematode from the Czech republic. *Zootaxa,* **3760**, 336–350.

Navon, A., Keren, S., Salame, L. and Glazer, I. (1999) An edible-to-insects calcium alginate gel as a carrier for entomopathogenic nematodes. *Biocontrol Sci. Technol.*, **8**, 429–437.

Nguyen, K.B. and Smart G.C. Jr. (1990) *Steinernema scapterisci* n. sp. (Steinernematidae: Nematoda). *J. Nematol.*, **22**, 187–199.

Nguyen, K.B. and Smart, G.C. Jr. (1992) *Steinernema neocurtillis* n. sp. (Rhabditida: Steinernematidae) and a key to species of the genus *Steinernema*. *J. Nematol.*, **24**, 463–477.

Nguyen, K.B. and Duncan, L.W. (2002) *Steinernema diaprepesi* n. sp (Rhabditida: Steinernematidae), a parasite of the citrus root weevil *Diaprepes abbreviates* (L) (Coleoptera: Curculionidae). *J. Nematol*., **34**, 159–170.

Nguyen, K.B., Shapiro-Ilan, D.I., Stuart, R.J., McCoy, C.W., James, R.J. and Adams, B.J. (2004) *Heterorhabditis mexicana* n. sp. (Rhabditida: Heterorhabditidae) from Tamaulipas, Mexico, and morphological studies of the bursa of *Heterorhabditis* spp. *Nematology*. **6**, 231–244.

Nguyen, K.B., Tesfamariam, M., Gozel, U., Gaugler, R. and Adams, B.J. (2005) *Steinernema yirgalemense* n. sp. (Rhabditida: Steinernematidae) from Ethiopia. *Nematology,* **6**, 839–856.

Nguyen, K.B., Malan, A.P. and Gozel, U. (2006a) *Steinernema khoisanae* n. sp. (Rhabditida: Steinernematidae), a new entomopathogenic nematode from South Africa. *Nematology,* **8**, 157–175.

Nguyen, K.B., Qiu, L., Zhou, Y. and Pang, Y. (2006b) *Steinernema leizhouense* sp. n. (Nematoda: Steinernematidae), a new entomopathogenic nematode from southern China. *Russ. J. Nematol.*, **14**, 101–118.

Nguyen, K.B., Gozel, U., Koppenhofer, H.S. and Adams, B.J. (2006c) *Heterorhabditis* floridensis (Heterorhabditidae: Rhabditida) from Florida. *Zootaxa*, **11**, 1–19.

Nguyen, K.B. and Hunt, D.J. (2007). *Entomopathogenic Nematodes: Systematics, Phylogeny and Bacterial Symbionts. Nematology Monographs and Perspectives, 5*. Brill Publishing, Leiden, The Netherlands.

Nguyen, K.B., Stuart, R.J., Andalo, V., Gozel, U. and Rogers, M.E. (2007) *Steinernema texanum* n. sp. (Rhabditida: Steinernematidae), a new entomopathogenic nematode from Texas, USA. *Nematology*, **9**, 379–396.

Nguyen, K.B., Puza, V. and Mracek, Z. (2008a) *Steinernema cholashanense* n. sp. (Rhabditida, Steinernematidae), a new species of entomopathogenic nematode from the province of Sichuan, Chola Shan Mountains, China. *J. Invertebr. Pathol*., **97**, 251–264.

Nguyen, K.B., Shapiro-Ilan, D.I. and Mbata, G.N.M. (2008b) *Heterorhabditis georgiana* n. sp. (Rhabditida: Heterorhabditidae) from Georgia, USA. *Nematology*, **10**, 433–448.

Nguyen, K.B., Ginarte, C.M.A., Leite, L.G., dos Santos, J.M. and Harakava, R. (2010) *Steinernema*

brazilense n. sp (Rhabditida: Steinernematidae), a new entomopathogenic nematode from Mato Grosso, Brazil. *J. Invertebr. Pathol.*, **103**, 8–20.

Nguyen, K.B. and Buss, E.A. (2011) *Steinernema phyllophagae* n. sp. (Rhabditida: Steinernematidae), a new entomopathogenic nematode from Florida, USA. *Nematology*, **13**, 425–442.

Nikdel, M., Niknam, G.R. and Ye, W. (2011). *Steinernema arasbaranense* n. sp. (Nematoda: Steinernematidae), a new entomopathogenic nematode from Arasbaran forests, Iran. *Nematol. Mediterr*., **39**, 17–28.

Nickle, W.R. and Shapiro, M. (1992) Use of stilbene brightener, Tinopal LPW, as solar radiation protectants for *Steinernema carpocapsae*. *J. Nematol*., **24**, 371–373.

Nishimatsu, T. and Jackson J.J. (1998) Interaction of insecticides, entomopathogenic nematodes, and larvae of the western corn rootworm (Coleoptera: Chrysomelidae). *J. Econ. Entomol*., **91**, 410–418.

Nollmann, F.I., Heinrich, A.K., Brachmann, A.O., Morisseau, C., Mukherjee, K., Casanova-Torres, A.M., Strobl, F., Kleinhans, D., Kinski, S., Schultz, K., Beeton, M.L., Kaiser, M., Chu, Y.Y., Phan Ke, L., Thanwisai, A., Bozhuyuk, K.A.J., Chantratita, N., Gotz, F., Waterfield, N.R., Vilcinskas, A., Stelzer, E.H.K., Goodrich-Blair, H., Hammock, B.D. and Bode H.B. (2015). A *Photorhabdus* natural product inhibits insect juvenile hormone epoxide hydrolase. *Chem. Bio.Chem.*, **16**, 766–771.

Noujeim, E., Khater, C., Pages, S., Ogier, J.C., Tailliez, P., Hamze, M. and Thaler O. (2011) The first record of entomopathogenic nematodes (Rhabiditiae: Steinernematidae and Heterorhabditidae) in natural ecosystems in Lebanon: A biogeographic approach in the Mediterranean region. *J. Invertebr. Pathol.*, **107**, 82–85.

Nthenga, I., Knoetze, R., Berry, S., Tiedt, L.R. and Malan, A.P. (2014) *Steinernema sacchari* n. sp. (Rhabditida: Steinernematidae), a new entomopathogenic nematode from South Africa. *Nematology*, **16**, 475–494.

Oleg, G., Lortkhipanidze, M., Ogier, J.C., Tailliez, P. and Burjanadze, M. (2015) *Steinernema tbilisiensis* sp. n. (Nematoda: Steinernematidae)-A new species of entomopathogenic nematode from Georgia, *JASTA*, **5**, 264–276.

Parkman, J.P., Frank, J.H., Nguyen, K.B. and Smart, G.C. Jr. (1993) Dispersal of *Steinernema scapterisci* (Rhabditida: Steinernematidae) after inoculative applications for mole cricket (Orthoptera: Gryllotalpidae) control in pastures. *Biol. Control*, **3**, 226–232.

Parkman, J.P. and Smart, G.C. Jr. (1996) Entomopathogenic nematodes, a case study: introduction of *Steinernema scapterisci* in Florida. *Biocontrol Sci. Technol.*, **6**, 413–419.

Patel, A.V. and Vorlop, K.D. (1994) Entrapment of biological control agents applied to entomopathogenic nematodes, *Biotechnol. Tech.*, **8**, 569–574.

Perez, E.E., Lewis, E.E. and Shapiro-Ilan, D.I. (2003) Impact of the host cadaver on survival and infectivity of entomopathogenic nematodes (Rhabditida: Steinernematidae and Heterorhabditidae) under desiccating conditions. *J. Invertebr. Pathol.*, **82**, 111–118.

Peters, A. (1996) The natural host range of *Steinernema* and *Heterorhabditis* spp. and their impact on insect populations. *Biocontrol Sci. Technol.*, **6**, 389–402.

Peters, A., Han, R., Yan, X. and Leite, L.G. (2017) Production of entomopathogenic nematodes A2. *In* L.A. Lacey (ed.), *Microbial Control of Insect and Mite Pests*, Academic Press, London, UK, pp. 157–170.

Phan, K.L., Nguyen, N.C. and Moens, M. (2001a) *Steinernema loci* sp. n. and *Steinernema thanhi* sp. n. (Rhabditida: Steinernematidae) from Vietnam. *Nematology*, **3**, 503–514.

Phan, K.L., Nguyen, N.C. and Moens, M. (2001b) *Steinernema sangi* sp. n. (Rhabditida: Steinernematidae) from Vietnam. *Russ. J. Nematol.*, **9**, 1–7.

Phan, K.L., Subbotin, S.A., Nguyen, N.C. and Moens, M. (2003) *Heterorhabditis baujardi* sp. n. (Rhabditida: Heterorhabditidae) from Vietnam and morphometric data for *H. indica* populations. *Nematology*, **5**, 367–382.

Phan, K.L., Subbotin, S.A., Waeyenberge, L. and Moens, M. (2004) A new entomopathogenic nematode, *Steinernema robustispiculum* n. sp. (Rhabditida: Steinernematidae), from chumomray national park in Vietnam. *Syst. Prasitol*., **60**, 23–32.

Phan, L.K., Takemoto, S. and Futai, K. (2006a) *Steinernema ashiuense* sp. n. (Nematoda: Steinernematidae), a new entomopathogenic nematode from Japan. *Nematology*, **8**, 681–690.

Phan, L.K., Spiridonov, S.E., Subbotin, S.A. and Moens, M. (2006b) Four new species of steinernema travassos, 1927 with short infective juvenile from Vietnam. *Russ. J. Nematol.*, **14,** 11–29.

Phan, K.L., Mracek, Z., Puza, V., Nermut, J. and Jarosova, A. (2014) *Steinernema huense* sp. n., a new entomopathogenic nematode (Nematoda: Steinernematidae) from Vietnam. *Nematology*, **16**, 761–775.

Platzer, E.G., Mullens, B.A. and Shamseldean, M.M. (2005) Mermithid nematodes. *In* P.S. Grewal,

R.U. Ehlers and D.I. Shapiro-llan (eds.), *Nematodes as Biocontrol Agents*, CAB International, Wallingford, UK, pp. 411–418.

Poinar, G.O. (1966) The presence of *Achromobacter nematophilus* Poinar and Thomas in the infective stage of a *Neoaplectan*a sp. (Steinernematidae: Nematoda). *Nematologica*, **12**, 105–108.

Poinar, G.O. Jr. (1976) Description and biology of a new insect parasitic rhabditoid, *Heterorhabditis bacteriophora* n. gen., n. sp. (Rhabditida: Heterorhabditidae n. fam.). *Nematologica*, **21**, 463–470.

Poinar, G.O. (1985) *Neoaplectana intermedia* n. sp. (Steinernematidae: Nematoda) from South Carolina. *Rev. Nematol.*, **8**, 321–327.

Poinar, G.O. Jr., Jackson, T. and Klein, M. (1987) *Heterorhabditis megidis* sp. n. (Heterorhabditidae: Rhabditida) parasitic in the Japanese beetle, *Popillia japonic*a (Scarabaeidae: Coleoptera), in Ohio. *Proc. Helminthol. Soc. Wash.*, **54**, 53–59.

Poinar, G.O. (1990) Taxonomy and biology of Steinernematidae and Heterorhabditidae. *In* R. Gaugler and H.K. Kaya (eds.), *Entomopathogenic Nematodes in Biological Control*, CRC Press, Boca Raton, Florida, pp. 23–60.

Poinar, G.O. Jr., Karunakar, G.K. and David, H. (1992) *Heterorhabditis indicus* n. sp. (Rhabditida: Nematoda) from India: Separation of *Heterorhabditis* spp. by infective juveniles. *Fundam. Appl. Nematol.*, **15**, 467–472.

Poinar, G.O. (1993) Origins and phylogenetic relationships of the entomophilic rhabditids, *Heterorhabditis* and *Steinernema*. *Fund. Appl. Nematol.*, **16**, 333–338.

Portillo-Aguilar, C., Villani, M.G., Tauber, M.J., Tauber, C.A. and Nyrop, J.P. (1999) Entomopathogenic nematode (Rhabditida: Heterorhabditidae and Steinernematidae) response to soil texture and bulk density. *Environ. Entomol.*, **28**, 1021–1035.

Preisser, E.L., Dugaw, C.J., Dennis, B. and Strong, D.R. (2006) Plant facilitation of a belowground predator. *Ecology*, **87**, 1116–1123.

Puza, V., Nermut, J., Mracek, Z., Gengler, S. and Haukeland, S. (2016) *Steinernema pwaniensis* n. sp., a new entomopathogenic nematode (Nematoda: Steinernematidae) from Tanzania, *J. Helminthol.*, **91**, 20–34.

Qiu, L.H., Fang, Y.Y., Zhou, Y., Pang, Y. and Nguyen, K.B. (2004) *Steinernema guangdongense* sp. n. (Nematoda: Steinernematidae), a new entomopathogenic nematode from southern China with a note on *S. serratum* (*Nomen nudum*). *Zootaxa*, **704**, 1–20.

Qiu, L., Van, X., Zhou, Y., Nguyen, K.B. and Pang, Y. (2005a) *Steinernema aciari* sp. n. (Nematoda: Steinernematidae), a new entomopathogenic nematode from Guangdong, China. *J. Invertebr. Pathol.*, **88**, 58–69.

Qiu, L., Hu, X., Zhou, Y., Mei, S., Nguyen, K.B. and Pang, Y. (2005b) *Steinernema akhursti* sp. n. (Nematoda: Steinernematidae) from Yunan, China. *J. Invertebr. Pathol.*, **90**, 151–160.

Qiu, L., Hu, X., Zhou, Y., Pang, Y. and Nguyen, K.B. (2005c) *Steinernema beddingi* n. sp. (Nematoda: Steinernematidae), a new entomopathogenic nematode from Yunnan, China. *Nematology*, **7**, 737–749.

Qiu, L., Zhao, J., Wu, Z., Lv, Z. and Pang, Y. (2011) *Steinernema pui* sp. n. (Rhabditida, Steinernematidae), a new entomopathogenic nematode from Yunnan, China. *Zootaxa*, **2767**, 1–13.

Rainey, F.A., Ehlers R.U. and Stackebrandt E. (1995) Inability of the polyphasic approach to systematics to determine the relatedness of the genera *Xenorhabdus* and *Photorhabdus*. *Int. J. Syst. Bacteriol.*, **45**, 379–381.

Ramakuwela, T., Hatting, J., Laing, M.D., Hazir, S. and Thiebaut, N. (2016) *In vitro* solid-state production of *Steinernema innovationi* with cost analysis, *Biocontrol Sci. Technol.*, **26**, 792–808.

Ramalingam, K.R., Sivaramakrishnan, S. and Hazir, S. (2011) Ecological characterisation of Steinernema siamkayai (Rhabditida: Steinernematidae), a warm-adapted entomopathogenic nematode isolate from India. *BioControl*, **56**, 789–798.

Raja, K.R., Hazır, C., Gumus, A., Asan, C., Karagoz, M. and Hazir, S. (2015) Efficacy of the entomopathogenic nematode, *Heterorhabditis bacteriophora*, using different application methods in the presence or absence of a natural enemy. *Turk. J. Agric. For.*, **39**, 277–285.

Raja, K.R., Aiswarya, D., Gulcu, B., Raja, M., Perumal, P., Sivaramakrishnan, S., Kaya, H.K. and Hazir, S. (2017). Response of three cyprinid fish species to the scavenger deterrent factor produced by the mutualistic bacteria associated with entomopathogenic nematodes. *J. Invertebr. Pathol.*, **143**, 40–49.

Rasmann, S., Kollner, T.O., Degenhardt, J., Hiltpold, I., Toepfer, S., Kuhlmann, U., Gershenzon, J. and Turlings, T.C.J. (2005) Recruitment of entomopathogenic nematodes by insect-damaged maize roots. *Nature*, **434**, 732–737.

Richardson, P.N. (1996) British and European legislation regulating rhabditid nematodes. *Biocontrol Sci. Technol.*, **6**, 449–463.

Roman, J. and Figueroa, W. (1994) *Steinernema puertoricensis* n. sp. (Rhabditida: Steinernematidae), a new entomopathogenic nematode from Puerto Rico. *J. Agric.*, **78**, 167–175.

San-Blas, E. (2013) Progress on entomopathogenic nematology research: A bibliometric study of the

last three decades: 1980-2010. *Biol. Control,* **66**, 102–124.

San-Blas, E., Portillo, E., Nermut, J., Puza, V. and Morales-Montero, P. (2015) *Steinernema papillatum* n. sp. (Rhabditida: Steinernematidae), a new entomopathogenic nematode from Venezuela. *Nematology,* **17**, 1081–1097.

San-Blas, E., Morales-Montero, P., Portillo, E., Nermut, J. and Puza V. (2016) *Steinernema goweni* n. sp. (Rhabditida: Steinernematidae), a new entomopathogenic nematode from Zulia State, Venezuela. *Zootaxa*, **4067**, 200–214.

Schulenburg, H. and Ewbank, J.J. (2004) Diversity and specificity in the interaction between *Caenorhabditis elegans* and the pathogen *Serratia marcescens*. *BMC Evol. Biol*., **4**, 49.

Schroer, S. and Ehlers, R.U. (2005) Foliar application of the entomopathogenic nematode *Steinernema carpocapsae* for biological control of diamondback moth larvae (*Plutella xylostella*). *Biol. Control*, **33**, 81–86.

Schroer, S., Ziermann, D. and Ehlers R.U. (2005) Mode of action of a surfactant-polymer formulation to support performance of the entomopathogenic nematode *Steinernema carpocapsae* for control of diamondback moth larvae (*Plutella xylostella*), *Biocontrol Sci. Techn.,* **15**, 601–613.

Shamseldean, M.M. and Platzer, E.G. (1989) *Romanomermis culicivorax:* Penetration of larval mosquitoes. *J. Invertebr. Pathol*., **54**, 191–199.

Shamseldean, M.M., El-Sooud, A.A.B., Abd-Elgawad, M.M. and Saleh, M.M. (1996) Identification of a new *Heterorhabditid* species from Egypt, *Heterorhabditis taysaerae* n. sp. (Rhabditida: Heterorhabditidae). *Egypt. J. Biol. Pest. Control,* **6**, 129–138.

Shahina, F., Anis, M., Reid, A.P., Rowe, J. and Maqbool, M.A. (2001) *Steinernema pakistanense* sp. n. (Rhabditida: Steinernematidae) from Pakistan. *J. Nematol.,* **11**, 124–133.

Shahina, F., Tabassum, K.A., Salma, J., Mehreen, G. and Knoetze R. (2016) *Heterorhabditis pakistanense* n. sp. (Nematoda: Heterorhabditidae) a new entomopathogenic nematode from Pakistan. *J. Helminthol*., **91**, 222–235.

Shapiro, D.I. and Glazer, I. (1996) Comparison of entomopathogenic nematode dispersal from infected hosts versus aqueous suspension. *Environ. Entomol*., **25**, 1455–1461.

Shapiro, D.I., Glazer, I. and Segal, D. (1997) Genetic improvement of heat tolerance in *Heterorhabditis bacteriophora* through hybridization. *Biol. Control*, **8,** 153–159.

Shapiro-Ilan, D.I. and Lewis, E.E. (1999) Comparison of entomopathogenic nematode infectivity from infected hosts versus aqueous suspension. *Environ Entomol.,* **28**, 907–911.

Shapiro-Ilan, D.I., Lewis, L.C., Obrycki, J.J. and Abbas, M. (1999) Effects of fertilizers on suppression of black cutworm (*Agrostis ipsilon*) damage with *Steinernema carpocapsae*. *J. Nematol*., **31**, 690–693.

Shapiro, D.I. and McCoy, C.W. (2000) Virulence of entomopathogenic nematodes to *Diaprepes abbreviatus* (Coleoptera: Curculionidae) in the laboratory. *J. Econ. Entomol*., **293**, 1090–1095.

Shapiro, D.I., McCoy, C.W., Fares, A., Obreza, T. and Dou, H. (2000) Effects of soil type on virulence and persistence of entomopathogenic nematodes. *Environ. Entomol*., **29**, 1083–1087.

Shapiro-Ilan, D.I., Lewis, E.E., Behle, R.W. and McGuire, M.R. (2001) Formulation of entomopathogenic nematode-infected cadavers. *J. Invertebr. Pathol.*, **78**, 17–23.

Shapiro-Ilan, D.I., Mizell, R.F. and Campbell, J.F. (2002) Susceptibility of the plum curculio, *Conotrachelus nenuphar* to entomopathogenic nematodes. *J. Nematol.*, **34**, 246–249.

Shapiro-Ilan, D.I. and Gaugler, R. (2002) Production technology for entomopathogenic nematodes and their bacterial symbionts. *J. Ind. Microbiol. Biotechnol*., **28**, 137–146.

Shapiro-Ilan, D.I., Lewis, E.E., Tedders, W.L. and Son, Y. (2003) Superior efficacy observed in entomopathogenic nematodes applied in infected-host cadavers compared with application in aqueous suspension. *J. Invertebr. Pathol*., **83**, 270–272.

Shapiro-Ilan, D.I., Jackson, M., Reilly, C.C. and Hotchkiss, M.W. (2004) Effects of combining an entomopathogenic fungi or bacterium with entomopathogenic nematodes on mortality of *Curculio caryae* (Coleoptera: Curculionidae). *Biol. Control*, **30**, 119–126.

Shapiro-Ilan, D.I., Stuart, R.J. and McCoy, C.W. (2006a) A comparison of entomopathogenic nematode longevity in soil under laboratory conditions. *J. Nematol*., **38**, 119–129.

Shapiro-Ilan, D.I., Gouge, D.H., Piggott, S.J. and Patterson Fife, J. (2006b) Application technology and environmental considerations for use of entomopathogenic nematodes in biological control. *Biol. Control*, **38**, 124–133.

Shapiro-Ilan, D.I., Cottrell, T.E., Brown, I., Gardner, W.A., Hubbard, R.K. and Wood, B.W. (2006c) Effect of soil moisture and a surfactant on entomopathogenic nematode suppression of the pecan weevil, *Curculio caryae*. *J. Nematol.*, **38**, 474–482.

Shapiro-Ilan, D.I., Cottrell, T.E., Mizell, R.F., Horton, D.L., Behle, B. and Dunlap, C. (2010a)

Efficacy of *Steinernema carpocapsae* for control of the lesser peach tree borer, *Synanthedon pictipes*: Improved aboveground suppression with a novel gel application. *Biol. Control*, **54**, 23–28.

Shapiro-Ilan, D.I., Morales-Ramos, J.A., Rojas, M.G. and Tedders, W.L. (2010b) Effects of a novel entomopathogenic nematode–infected host formulation on cadaver integrity, nematode yield, and suppression of *Diaprepes abbreviatus* and *Aethina tumida* under controlled conditions. *J. Invertebr. Pathol*., **103**, 103–108.

Shapiro-Ilan, D.I., Cottrell, T.E. and Wood, B.W. (2011) Effects of combining microbial and chemical insecticides on mortality of the pecan weevil (Coleoptera: Curculionidae) *J. Econ. Entomol*., **104**, 14–20.

Shapiro-Ilan, D.I., Han, R. and Dolinksi, C. (2012) Entomopathogenic nematode production and application technology. *J. Nematol*., **44**, 206–217.

Shapiro-Ilan, D.I. and Brown, I. (2013) Earthworms as phoretic hosts for *Steinernema carpocapsae* and *Beauveria bassiana*: Implications for enhanced biological control. *Biol. Control*, **66**, 41–48.

Shapiro-Ilan, D.I., Bock, C.H. and Hotchkiss, M.W. (2014a) Suppression of pecan and peach pathogens on different substrates using *Xenorhabdus bovienii* and *Photorhabdus luminescens*. *Biol. Control*, **77**, 1–6.

Shapiro-Ilan, D.I., Brown, I. and Lewis E.E. (2014b) Freezing and desiccation tolerance in entomopathogenic nematodes: Diversity and correlation of traits. *J. Nematol.*, **46**, 27–34.

Shapiro-Ilan, D.I., Hazir, S. and Lete, L. (2015a) Viability and virulence of entomopathogenic Nematodes exposed to ultraviolet radiation. *J. Nematol*., **47**, 184–189.

Shapiro-Ilan, D.I. and Dolinski C. (2015b) Entomopathogenic nematode application technology. *In* R. Campos-Herrera (ed.), *Nematode Pathogenesis of Insects and Other Pests: Ecology and Applied Technologies for Sustainable Plant and Crop Protection*, Springer International Publishing, Switzerland, pp. 231–254.

Shapiro-Ilan, D.I., Cottrell, T.E., Mizell, R.F. and Horton, D.L. (2016) Curative control of the peachtree borer using entomopathogenic nematodes. *J. Nematol*., **48**, 170–176.

Shapiro-Ilan, D.I., Hazir, S. and Glazer, I. (2017) Basic and applied research: Entomopathogenic nematodes. *In* L.A. Lacey (ed.), *Microbial Control of Insect and Mite Pests, From Theory to Practice*, Academic Press, San Diego, USA, pp. 91–108.

Shen, C.P. and Wang, G.H. (1991) Description and study of an entomopathogenic nematode, *Steinernema longicaudum* sp. nov. and its application. *In* Young and Middle Aged Science and Technology Works, Plant Protection. *Procedings of the First National Academy Association*, Chinese Science and Technology Press, Beijing, China, pp. 220–231.

Sicard, M., Ramone, H., Le Brun, N., Pages, S. and Moulia, C. (2005) Specialization of the entomo-pathogenic nematode *Steinernema scapterisci* with its mutualistic *Xenorhabdus* symbiont. *Naturwissenschaften*, **92**, 472–476.

Sicard, M., Hinsinger, J., Le Brun, N., Pages, S., Boemare, N.E. and Moulia, C. (2006) Inter-specific competition between entomopathogenic nematodes (*Steinernema*) is modified by their bacterial symbionts (*Xenorhabdus*). *BMC Evol. Biol*., **6**, 68.

Silver, S.C., Dunlop, D.B. and Grove, D.I. (1995) *Granular Formulations of Biological Entities with Improved Storage Stability.* World Patent No. WO 95/0577.

Spiridonov, S. E., Krasomil-Osterfeld, K. and Moens, M. (2004) *Steinernema jollieti* sp. n. (Rhabditida: Steinernematidae), a new entomopathogenic nematode from the American Midwest. *Russ. J. Nematol.*, **12**, 85–95.

Spiridonov, S.E., Waeyenberge, L. and Moens, M. (2010) *Steinernema schliemanni* sp. n. (Steinernematidae; Rhabditida) a new species of steinernematids of the 'monticolum' group from Europe. *Russ. J. Nematol.*, **12**, 175–190.

Spiridonov, S.E. (2017) Biocontrol agents: Entomopathogenic nematodes of the families Steinernematidae and heterorhabditidae: Morphology and taxonomy. *In* M.M.M. Abd-Elgawad, T.A. Askary and J. Coupland (eds.), *Entomopathogenic and Slug Parasitic Nematodes*, CAB International, Wallingford, UK, pp. 45–63.

Steiner, G. (1923) *Aplectana kraussei* n. sp. eine in der Blattwespe Lyda sp. parasitierende *Nematoden* form, nebst Bemerkugen uber das Seitenorgan der parasitischen *Nematoden* Zb. Bakt. Parasitenk. Infektionrank. *Hyg. Abt.*, **2**, 14–18.

Steyn, W.P., Knoetze, R., Tiedt, L.R. and Malan, A.P. (2017a) *Steinernema litchii* n. sp. (Rhabditida: Steinernematidae), a new entomopathogenic nematode from South Africa. *Nematology*, **19**, 1157–1177.

Steyn, W.P., Malan, A.P., Daneel, M.S. and Slabbert, R.M. (2017b) Entomopathogenic nematodes from north-eastern South Africa and their virulence against false codling moth, *Thaumatotibia leucotreta* (Lepidoptera: Tortricidae). *Biocontrol Sci. Technol.*, **27**, 1–14.

Stock, S.P., Choo, H.Y. and Kaya, H.K. (1997) An entomopathogenic nematode, *Steinernema monticolum* sp. n. (Rhabditida: Steinernematidae) from Korea with a key to other species. *Nematologica*, **43**, 15–29.

Stock, S.P., Somsook, V. and Reid, A. (1998) *Steinernema siamkayai* n. sp. (Rhabditida: Steinernematidae), an entomopathogenic nematode from Thailand. *Syst. Parasitol.*, **41**, 105–113.

Stock, S.P., Griffin, C.T. and Burnell, A.M. (2002) Morphological characterisation of three isolates of *Heterorhabditis* Poinar, 1976 from the 'Irish group' (Nematoda: Rhabditida: Heterorhabditidae) and additional evidence supporting their recognition as a distinct species, *H. downesi* n. sp. *Syst. Parasitol.*, **51**, 95–106.

Stock, S.P. and Koppenhofer, A.M. (2003) *Steinernema scarabaei* n. sp. (Rhabditida: Steinernematidae), a natural pathogen of scarab beetle larvae (Coleoptera: Scarabaeidae) from New Jersey, USA. *Nematology*, **5**, 191–204.

Stock, S.P., Griffin, C.T. and Chaerani, R. (2004) Morphological and molecular characterisation of *Steinernema hermaphroditum* n. sp (Nematoda: Steinernematidae), an entomopathogenic nematode from Indonesia, and its phylogenetic relationships with other members of the genus. *Nematology*, **6**, 401–412.

Stock, S.P. (2015) Diversity, biology and evolutionary relationships. *In* R. Campos-Herrera (ed.), *Nematode Pathogenesis of Insects and Other Pests: Ecology and Applied Technologies for Sustainable Plant and Crop Protection*, Springer International Publishing, Switzerland, pp. 3–27.

Stokwe, N., Malan, A., Nguyen, K., Knoetze, R. and Tiedt, L. (2011) *Steinernema citrae* n. sp. (Rhabditida: Steinernematidae), a new entomopathogenic nematode from South Africa. *Nematology*, **13**, 569–587.

Stoll, N.R. (1952) Axenic cultivation of the parasitic nematode, *Neoaplectana glaseri*, in a fluid medium containing raw liver extract. *J. Parasitol.*, **39**, 422–444.

Stuart, R.J., El-Borai, F.E. and Duncan, L.W. (2008) From augmentation to conservation of entomopathogenic nematodes: Trophic cascades, habitat manipulation and enhanced biological control of *Diaprepes abbreviates* root weevils in Florida citrus groves. *J. Nematol.*, **40**, 73–84.

Stuart, R.J., Barbercheck, M.E. and Grewal, P.S. (2015) Entomopathogenic nematodes in the soil environement: distributions, interactions and the influence of biotic and abiotic factors. *In* R. Campos- Herrera (ed.), *Nematode Pathogenesis of Insects and other Pests: Ecology and Applied Technologies for Sustainable Plant and Crop Protection*, Springer International Publishing, Switzerland, pp. 97–137.

Sturhan, D., Spiridonov, S. and Mracek, Z. (2005) *Steinernema silvaticum* sp. n. (Rhabditida: Steinernematidae), a new entomopathogenic nematode from Europe. *Nematology*, **7**, 227–241.

Tailliez, P., Laroui, C., Ginibre, N., Paule, A., Pages, S. and Boemare, N. (2010) Phylogeny of *Photorhabdus* and *Xenorhabdus* based on universally conserved protein-coding sequences and implications for the taxonomy of these two genera. Proposal of new taxa: *X. vietnamensis* sp. nov., *P. luminescens* subsp. *hainanensis* subsp. nov., *P. temperata* subsp. *tasmaniensis* subsp. nov., and the reclassification of *P. luminescens* subsp. *thracensis* as *P. temperata* subsp. *thracensis* comb. nov. *Int. J. Syst. Evol. Microbiol.*, **60,** 1921–1937.

Tailliez, P., Pages, S., Edgington, S., Tymo, L.M. and Buddie, A.G. (2012) Description of *Xenorhabdus magdalenensis* sp. nov., the symbiotic bacterium associated with *Steinernema australe*. *Int. J. Syst. Evol. Microbiol*., **62**, 1761–1765.

Tallosi, B., Peters, A. and Ehlers, R.U. (1995) *Steinernema bicornutum* sp. n. (Rhabditida: Steinernematidae) from Vojvodina, Yugoslavia. *Russ. J. Nematol*., **3**, 71–80.

Tamiru, T., Waeyenberge, L., Hailu, T., Ehlers, R.U., Puza, V. and Mracek, Z. (2012) *Steinernema ethiopiense* sp. N. (Rhabditida: Steinernematidae), a new entomopathogenic nematode from Ethiopia. *Nematology*, **14**, 741–757.

Tarasco, E., Mracek, Z., Nguyen, K.B. and Triggiani, O. (2008) *Steinernema ichnusae* sp. n. (Nematoda: Steinernematidae) a new entomopathogenic nematode from Sardinia Island (Italy). *J. Invertebr. Pathol*., **99**, 173–185.

Tarasco, E., Clausi, M., Rappazzo, G., Panzavolta, T., Curto, G., Sorino, R., Oreste, M., Longo, A., Leone, D., Tiberi, R., Vinciguerra, M.T. and Triggiani. O. (2014) Biodiversity of entomopathogenic nematodes in Italy. *J. Helminthol.*, **89**, 359–366.

Thurston, G.S., Ni, Y. and Kaya, H.K. (1994) Influence of salinity on survival and infectivity of entomopathogenic nematodes. *J. Nematol.*, **26**, 345–351.

Torr, P., Heritage, S. and Wilson, M.J. (2004) Vibrations as a novel signal for host location by parasitic nematodes. *Int. J. Parasitol.*, **34**, 997–999.

Toepfer, S., Kurtz, B. and Kuhlmann, U. (2010) Influence of soil on the efficacy of entomopathogenic nematodes in reducing *Diabrotica virgifera virgifera* in maize. *J. Pest Sci*., **83**, 257–264.

Torres-Barragan, A., Suazo, A., Buhler, W.G. and Cardoza, Y.J. (2011) Studies on the entomopathogenicity and bacterial associates of the nematode *Oscheius carolinensis*. *Biol Control*, **59**, 123–129.

Triggiani, O., Mracek, Z. and Reid, A. (2004) *Steinernema apuliae* sp. N. (Rhabditida: Steinernematiae): A new entomopathogenic nematode from southern Italy. *Zootaxa*, **460**, 1–12.

Ulug, D., Hazir, S., Kaya, H.K. and Lewis E.E. (2014) Natural enemies of natural enemies: The potential top-down impact of predators on entomopathogenic nematode populations. *Ecol. Entomol*., **39**, 462–469.

Uribe-Lorio, L., Mora, M., Stock, S.P. (2007) *Steinernema costaricense* n. sp. and *S. puntauvense*

n. sp. (Rhabditida: Steinernematidae), two new entomopathogenic nematodes from Costa Rica. *Syst. Parasitol.*, **68**, 167–182.

Valadas, V., Laranjo, M., Mota, M. and Oliveira S. (2013) A survey of entomopathogenic nematode species in continental Portugal. *J. Helminthol.*, **88**, 327–341.

Viglierchio, D.R. (1991) *The World of Nematodes*. University of California, Davis, Sacramento, USA.

Wang, Y., Campbell, J.F. and Gaugler, R. (1995) Infection of entomopathogenic nematodes *Steinernema glaseri* and *Heterorhabditis bacteriophora* against *Popillia japonica* (Coleoptera: Scarabaeidae) larvae. *J. Invertebr. Pathol.*, **66**, 178–184.

Wang, H., Luan, J., Dong, H., Qian, H. and Cong, B. (2014) Natural occurrence of entomopathogenic nematodes in Liaoning (Northeast China). *J. Asia Pac. Entomol.*, **17**, 399–406.

Waturu, C.N., Hunt, D.J. and Reid, A.P. (1997) *Steinernema karii* sp. n. (Nematoda: Steinernematidae), a new entomopathogenic nematode from Kenya. *Int. J. Nematol.*, **7**, 68–75.

Wayne, L.G., Brenner, D.J., Colwell, R.R., Grimont, P.A.D., Kandler, O., Krichevsky, M.I., Moore, L.H., Moore, W.E.C., Murray, R.G.E., Stackebrandt, E., Starr, M.P. and Truper, H.G. (1987) Report of the ad hoc committee on reconciliation of approaches to bacterial systematics. *Int. J. Syst. Bacteriol.*, **37**, 463–464.

Webster, J.M., Chen, G., Hu, K. and Li, J. (2002) Bacterial metabolites. *In* R. Gaugler (ed.), *Entomopathogenic Nematology*, CAB International, London, UK, pp. 99–114.

Wharton, D.A. and Surrey, M.R. (1994) Cold tolerance mechanisms of the infective larvae of the insect parasitic nematode, *Heterorhabditis zealandica* Poinar. *Cryo Letters*, **15**, 353–360.

Wharton, D.A., Goodall, G. and Marshall, C.J. (2003) Freezing survival and cryoprotective dehydration as cold tolerance mechanisms in the Antarctic nematode *Panagrolaimus davidi*. *J. Exp. Biol.*, **206**, 215–221.

White, G.F. (1927) A method for obtaining infective nematode larvae from culture. *Science*, **66**, 302–303.

Willett, D.S., Alborn, H.T., Duncan, L.W. and Stelinski, L.L. (2015) Social networks of educated nematodes. *Sci. Rep.*, **5**, 14388.

Williams, D.W., Zylstra, K.E. and Mastro, V. (2012) Ecological considerations in using *Deladenus* (= *Beddingia*) *siricidicola* for the biological control of *Sirex noctilio* in North America. *In* B. Slippers, P. de Groot and M.J. Wingfield (eds.), *The Sirex Woodwasp and its Fungal Symbiont: Research and Management of a Worldwide Invasive Pest*, Springer, New York, pp. 135–148.

Williams, C.D., Dillon, A.B., Girling, R.D. and Griffin, C.T. (2013) Organic soils promote the efficacy of entomopathogenic nematodes, with different foraging strategies, in the control of a major forest pest: A meta-analysis of field trial data. *Biol. Control*, **65**, 357–364.

Wilson, M. and Ivanova, E. (2004) Neutral density liquid formulations for nematode-based biopesticides. *Biotech. Lett.*, **26**, 1167–1171.

Wilson, M.J. and Grewal, P.S. (2005) Biology, production and formulation of slug-parasitic nematodes. *In* P.S. Grewal, R.U. Ehlers and D.I. Shapiro-Ilan (eds.), *Nematodes as Biocontrol Agents*, CAB International, Wallingford, UK, pp. 421–429.

Woese, C.R. (1987) Bacterial evolution. *Microbiol. Rev.*, **51**, 221–271.

Wouts, W.M., Mracek, Z., Gerdin, S. and Bedding, R.A. (1982) *Neoaplectana* Steiner, 1929 a junior synonym of *Steinernema* Travassos, 1927 (Nematoda; Rhabditida). *Syst. Parasitol.*, **4**, 147–154.

Xing-Yue, L., Liu, Q.Z., Nermu, J., Puza, V. and Mracek, Z. (2012) *Heterorhabditis beicherriana* n. sp. (Nematoda: Heterorhabditidae), a new entomopathogenic nematode from the Shunyi district of Beijing, China. *Zootaxa*, **3569**, 25–40.

Xu, F.Z., Wang, G.H. and Li, X.F. (1991) A new species of the genus *Steinernema* (Rhabditida: Steinernematidae). *Zool. Res.*, **12**, 17–20.

Yoshida, M. (2004) *Steinernema litorale* n. sp. (*Rhabditida*: Steinernematidae), a new entomopathogenic nematode from Japan. *Nematology*, **6**, 819–838.

Zayed, A., Shamseldean, M., Abd-El Aleem, K.M. and Fergany Y.A. (2003) *In vivo* effects on host preference of the nematode and on pathogen progeny production in the greater wax moth *Galleria mellonella* L. *Efflatounia*, **3**, 15–24.

Zhou, X., Kaya, H. K., Heungens K. and Goodrich-Blair, H. (2002) Response of ants to a deterrent factor(s) produced by the symbiotic bacteria of entomopathogenic nematodes. *Appl. Environ. Microbiol.*, **68**, 6202–6209.

Zhu, H., Grewal, P.S. and Reding, M.E. (2011) Development of a desiccated cadaver delivery system to apply entomopathogenic nematodes for control of soil pests. *Appl. Eng. Agric.*, **27**, 317–324.

Accepted: 17 December 2017