Virulence of Entomopathogenic Nematodes and their Symbiotic Bacteria against Insect Pests, with Special Reference to *Agrotis ipsilon* (Lepidoptera: Noctuidae): A Comprehensive Review.

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ABSTRACT
 The use of entomopathogenic nematodes (EPNs) is a safe and eco-friendly alternative tosynthetic pesticides for the control ofsoil and above-ground insect pests in the world. The major objective of this review was to summarize the available publications concerning the virulence of different EPNs and their bacterial symbionts on several insect pests leading to death. In this context, different criteria had been discussed, such as the correlation between insect mortality and EPN concentration and time of exposure, the sensitive stage of insects to EPN, variation of the pathogenicity of various EPNs, and significance of the insect mortality. The impact of EPNs on some biological and physiological processes of the insect host hasbeen reviewed. The present review, also, highlighted the key factors and environmental conditions interfering with the EPNs' virulence against insect pests, in addition to the application techniques of EPNs and important precautions. In view of this discussion, many insect pests, in the soil or above ground, may be successfully controlled by using effective EPNs under suitable biotic and abiotic environmental conditions, as well as with appropriate EPN concentration and formulation.

Contents:

INTRODUCTION

In several countries, pest control operations still rely exclusively onsynthetic insecticides (Jeschke *et al*., 2011; Meslin *et al*., 2021) although the intensive use of many currently marketed insecticides usually causes serious environmental problems (Ibarra *et al*., 2006; Tiryaki and Temur, 2010; Chowański*et al*., 2015) and adversely affect the important natural enemies, allowing an exponential increase of pest populations (Calvo-Agudo *et al*., 2019; Demok*et al*., 2019). In addition, the widespread use ofsynthetic chemical insecticides exhibits negative effects on thephysiology and behavior of non-target beneficial insects, like pollinators, and has dangerous effects on human health (Blacquière*et al*., 2012; Vattikonda and Sangam, 2017) and domestic animals (Shahzad *et al*., 2020)

The black cutworm *Agrotis ipsilon* (Lepidoptera: Noctuidae) is widely distributed in the world due to its long-distance migratory ability (Capinera, 2018; Zeng *et al*., 2020). This moth can fly thousands of kilometers under suitable conditions expanding its distribution range (Liu *et al*., 2015, 2016;Liu, 2015; Hayat *et al*., 2021; Lee *et al*., 2023), besides its considerable reproductive capacity (Santos and Shield, 1998, Mishra, 2020). It is a polyphagous insect known to feed on several vegetables and many economically important grains worldwide (Navarro *et al*., 2010;Fernandes *et al*., 2013;Picimbon, 2020; Rodingpuia and Lalthanzara, 2021; Ahmed *et al*., 2022).

Some control practices are usually applied for controlling *A. ipsilon*, such as cultural control (Bajwa and Kogan, 2004; Guedes and Picanço, 2012), mechanical control (Manishkumar*et al*., 2020), physical control (Abd El-Hamid, 2004; Ali, 2011; Mohamed, 2012), host-plant resistance (Richmond and Shetlar, 2001; Hussaini *et al*., 2003a, b) and biological control (Viji and Bhagat, 2001; Salehi et al., 2005). However, the control strategy of *A. ipsilon* depends mainly on the application of synthetic insecticides (Shakur *et al*., 2007; Abd El-Aziz *et al*., 2019; Veres *et al*., 2020; Ismail, 2021), to which this pest quickly develops resistance and cross-resistance (Fahmy, 2014; Mahmoud *et al*., 2016; Ahmed *et al*., 2022). Also, chemical insecticides are often not effective and remain inadequate for the control of *A. ipsilon* because of its larval hiding behavior during the daylight hours causing hidden damage in the fields (Capinera, 2001; Takeda, 2008).

Therefore, alternative approaches have been encouraged recently to avoid or minimize insecticidal hazards and introduce new effective and safer alternatives (Laznik and Trdan, 2012; Glare *et al*., 2016; Derbalah*et al*., 2014). One of the eco-friendly control strategies is biological control by natural enemies (parasitoids, predators and pathogens). It is highly promising because these agents are safe for humans and the environment including the non-targeted organisms (Jagodič *et al*., 2019; Amutha *et al*., 2021; Devi *et al*., 2021).

Among the promising biological control agentsthe entomopathogenic nematodes (EPNs) which have a potential rolein killing the cutworms in soil (Laznik and Trdan, 2012; Glare *et al*., 2016;Kumar *et al*., 2022) and above-ground insect pests (Lacey *et al*., 2015; Peçen and Kepenekci, 2022). The potential of EPNs as biocontrol agents depends on their adaptability to the environment (Campos-Herrera *et al*., 2012). It is important to mention that the infective juveniles (IJs) of EPNs have suppressed the immune responses of the insect hosts leading to death (Arthurs *et al*., 2004; Lewis and Clarke, 2012; Shapiro-Ilan and Brown, 2013; Kaliaskar*et al*., 2022). They may achieve this role alone and/or with their symbiotic bacteria(Lewis and Clarke, 2012; Shapiro-Ilan and Brown, 2013; Chaston *et al*., 2013; Kumar et al., 2015; Leonar *et al*., 2022; Kaliaskar*et al*., 2022). Also, EPNs can be used individually or in combination with other biocontrol agents, such as entomopathogenic bacteria and fungi, to improve their efficacy incontrolling insect pests (Laznik *et al*., 2012).

For these reasons, researchers and different pest control institutions in the world are interested in the use of EPNs as a bio-control agent against different insect pests due to their wide host range, eco-friendly nature, active host finding strategy, easy mass culturing and compatibility with standard irrigation equipment (Laznik and Trdan, 2011, Belien, 2018;Tomar *et al*., 2022a). At least, EPNs can serve as an effective supplementary control as part of an integrated pest management (IPM) strategy (Odendaal *et al*., 2016; Odendaal *et al*., 2015; Belien, 2018; Gulcu*et al*., 2017). For some reviews, see Sujatha and Jeyasankar, 2018; Jagodič *et al*., 2019; Trdan*et al*., 2020; Askary and Abd-Elgawad, 2021; Kumar *et al*., 2022; Tomar *et al*.,2022 a; Shaurub, 2023). In this context, the major objective of this review was to summarize the available publications concerning the virulence of EPNs and their bacterial symbionts on several insect pests leading to death. The purpose of thepresent review, also, was to highlight the key factors and environmental conditions interfering with the EPNs' virulence against insect pests. In addition, the potential of EPNs as effective biocontrol agents against insect pests was discussed.

I. Global Attention for EPNs as Effective Biocontrol Agents Against the Insect Pests:
I.1. Pathogenic efficacy of the EPNs against insects:

Depending on the currently available literature, many studies investigated the EPN pathogenicity against various lepidopterous pests. With regard to the black cutworm *Agrotisipsilon* (Lepidoptera: Noctuidae), many studies have been conducted to evaluate the virulence and control potential of different EPN species, or their local isolates, against larvae in different parts of the world (Mathasoliya*et al*., 2004; Fetoh*et al*., 2009; Seal *et al*., 2010; Ebssa and Koppenhöfer, 2011; Lemma and Albrecht, 2012; Khattab and Azazy, 2013; Yuksel and Canhilal, 2018; Sobhy *et al*., 2020; Devi *et al*., 2021; Nouh, 2022). Most of these studies only investigated one larval instar: 3rd instar (Shapiro-Ilan et al., 2005, 2009), 4th instar (Koppenhofer and Fuzy, 2003), 5th instar (Morris *et al*., 1990) or 7th instar (Capinera*et al*., 1988). Moreover, some studies used mixtures of consecutive instars: 2nd and 3rd instars (Kunkel and Grewal, 2003) or 4th and 5th instars (Kaya *et al*., 1993; Kunkel and Grewal, 2003) or 6th and 7th instars (Epsky and Capinera, 1994), even though instars may differ significantly in susceptibility to different EPN species may differ among instars (Koppenhofer and Fuzy, 2003). Also, many studies investigated the infectivity of only one EPN species (Baur *et al*., 1997). Comparisons between studies, even where the same instar or EPN species were used, are more complicated by the use of different techniques, substrates, nematode concentrations, and exposure time intervals (Koppenhofer and Fuzy, 2003). In addition, several of the previously mentioned studies used onlyPetri dishes lined with filter paper as experimental arenas (Kunkel and Grewal, 2003) although the EPN virulence against *A. ipsilon* can remarkably vary with substrate and the overall effect can vary with the nematode species (depending on foraging strategy) (Shapiro *et al*., 1999; Ebssa and Koppenhöfer, 2012; Hassan *et al*., 2016).

On the other hand, few studies investigated the EPN infectivity against *A. ipsilon* in field or semi-field conditions. In 3 L pots with grass, the EPN *Steinernema carpocapsae* (Rhabditida: Steinernematidae) provided 93-100% control of mixed 4th and 5th instars, and *Heterorhabditisbacteriophora* (Rhabditida: Heterorhabditidae) gave only 11–18% (Kaya *et al*., 1993). In field experiments in corn, the application of *S. carpocapsae* reduced the damage of *A. ipsilon* to corn seedlings (Shapiro *et al*., 1999). A study conducted in turfgrass against *A. ipsilon* reported average control rates of 95% for *S. carpocapsae* and 62% for *H. bacteriophora* at a concentration of $2.5×10^9$ IJsha^{-1} (Georgis and Poinar, 1994). Therefore, a more in-depth evaluation of EPNs for their potential for *A. ipsilon* management appeared to be very timely. Ebssa and Koppenhöfer (2012) evaluated the virulence of seven EPN species formulated in commercial products against 3rd - 6th-instar larvae and pupae of *A. ipsilon*, and concluded that several *in vitro*-produced commercial EPN strains were highly virulent to *A. ipsilon* and warrant further testing under field conditions, along with some *in vivo*-produced strains.   Within the same order Lepidoptera, apart from*A. ipsilon*, the efficacies of *S. monticolum* and *H. bacteriophora* against larvae of the Egyptian cotton leafworm *Spodoptera littoralis* (Noctuidae) had been studied under laboratory conditions. The mortality was 100% at 200 IJs/dish (Sobhy *et al*., 2020).Also, Abd El Azim (2022) assessed the virulence of *Heterorhabditistaysearae* isolate against *S. littoralis*. At 150 IJs/larvae, a 100% mortality rate was recorded, followed by 90% at 120 IJs/larvae and 60% at 60 IJs/larvae, 72 hr post-treatment. Regarding the tobacco cutworm *Spodoptera litura* (Noctuidae), the 4th instar larvae were infected with *S. carpocapsae*, the maximal mortality (100%) of larvae was recorded at 400 IJs/Petri dish and the minimal mortality (55%) was observed at 100 IJs, 96 hr post-infection (Yadav *et al*.,2017). Yan *et al*. (2020) also reported similar insecticidal effects of some EPNs against *S. litura* larvae. Similar observations were recorded, also, by Burana *et al*. (2022) and Javed *et al*. (2022) found 95, 78, 74, 90 and 87% mortality of *S. litura* larvae, respectively. According to a study by Supriya *et al*. (2022), using EPN *H. indica*, 100% mortality was obtained at 40 IJs/100µl in 3rd instar larvae, whereas, in the case of 4th and 5th instar larvae 100% mortality was recorded at 60 IJs/100µl and 80 IJs/100µl, respectively. Recently, Thakur *et al*. (2023) carried out a trial to eco-friendly manage *S.litura* in tomatoes under polyhouse and field conditions, using *H.bacteriophora*, its symbiotic bacteria (*Photorhabdusluminescens*), and *Bacillus thuringiensis* var. *kurstaki*. In all cases, they obtained lower tomato damage percentage and high larval mortality

Considering the fall armyworm *Spodoptera frugiperda*(Noctuidae), Acharya *et al*. (2020) reported *S. carpocapsae* as highly potential EPN against younger larvae (1st–3rd instars) only, while other EPN species, such as *S. arenarium* and *S. longicaudum*, were highly potential against older instars (4th–6th instars). Wattanachaiyingcharoen*et al*. (2021) investigated the efficiencies of two Thai indigenous EPNs isolates against 2nd and 5th larval instars. The greatest mortality rate of 2nd instar larvae was 83% when *H. indica* isolate was applied at 250 IJs ml^{-1} and 68% when *S. siamkayai*isolate was used at 300 IJs ml^{-1}. Fallet *et al*. (2022) reported that Rwandan *S. carpocapsae* strain (RW14-G-R3a-2) caused 100% mortality in 2nd and 3rd instars of *S. frugiperda*, but the rate decreased somewhat to 75% in 6th instar. Sayed *et al*. (2022) recorded the highest mortality rate (100%) in both 3rd and 5th instar larvae after 3–4 days of irradiated *S. carpocapsae* infection but the mortality rate was decreased after infection with un-irradiated *S. carpocapsae*. Recently, Mohamed and Shairra (2023) found that *S. carpocapsae* was more virulent against all larval instars, causing 100% mortality after 48–72 h post-exposure, while *H. indica* caused 100% mortality in the early larval instars only after 96 h, but later larval instars required a longer time extending to 120–188 h. With regard to the cotton bollworm*Helicoverpaarmigera* (Noctuidae), Srivastava *et al*. (2022) found *S. abbasi* isolate CS-39 with high virulence to larvae since it caused 100%

larval mortality at concentration 200 IJs/larva, 36 h post-infection, whereas 100 IJs / larva caused 100% mortality, at 60 h.

In Egypt, Khashaba *et al*. (2020) isolated *H. indica* in soil samples collected from cultivated orchards of olives and mangos and assessed its virulence against the greater wax moth *Galleria mellonella* (Pyralidae). Using 50 IJs/larva from *H. indica*Aborawash andtheisolates ERSAG2 showed 100 and 86% mortality rate after 48 h, respectively. According to Ali et al. (2022), 100% mortality of the last instar larvae of *G. mellonella* was achieved by 40 IJs/L of M.22 and M.313 isolates of *S. affine* from the Syrian coastal region, at 72 h of exposure. In addition, Steyn *et al*. (2019) determined the ability of EPNs *Heterorhabditisbaujardi*, *H. indica* and *H. noenieputensis* to penetrate the leaf-mining galleries, and infection of the Cape grapevine leafminer*Holocacista capensis* (Heliozelidae) larvae, in South Africa. High mortality of leaf-mining larvae was obtained with *H. baujardi* (92%), *H. noenieputensis* (85%) and *H. indica* (83%), respectively. Pervez and Rao (2020) isolated and identified six EPNs from western Uttar Pradesh (India) and assessed their infectivity against larvae of some lepidopterous insects. They found *Steinernema* sp., *Oscheius* sp. and *Heterorhabditis* sp. as promising biocontrol agents against the bean pod borer *Maruca vitrata* (Crambidae) causing 100% mortality within 48 h.The beet armyworm *Spodoptera exigua* (Noctuidae) larvae were sensitive to *S. ceratophorum*, with mortality rates of 100% for the 2nd and 3rd instar after treatment for 48 h. For the 4th and 5th instars, although mortality did not reach 100% after treatment for 48 h when the EPN was applied at lower concentrations of 25 and 50 IJ/larva, mortality reached 100% after treated for 72 h (Yan *et al*., 2021).Kumar *et al*. (2022) evaluated the infectivity of EPN *S. asiaticum* against the diamondback moth *Plutellaxylostella*(Plutellidae) as a foliar spray on cabbage plants in screen house with single, two or three applications. All the treatments resulted in high larval mortality. Split concentration application (15,000 + 15,000 IJs per plant) caused higher larval mortality (48.33%) compared to a single application (36.00%, at 30,000 IJs per plant). For more examples, see Table (1).

In addition to the order Lepidoptera, several studies revealed the infectivity of different EPNs against various insect pests of different orders, as concisely reviewed herein. In Diptera, the EPN *S. ceratophorum* caused high mortality of larvae of the chive gnat *Bradysiaodoriphaga* (Sciaridae)(Ma *et al*., 2013 b). In a study conducted by Mokrini*et al*. (2020), the efficacy of five Moroccan EPN strains was evaluated against 3rd instar larvae of the Mediterranean fruit fly *Ceratitiscapitata* (Tephritidae). Their results revealed the highest larval mortality rates for *S. feltiae*- strain (MOR9)(96%), followed by *H. bacteriophora*-MOR7 and *S. feltiae*-MOR10 strains, with 90 and 83% mortality rates, respectively. Yağcı*et al*. (2021b) recorded a high mortality rate oflast instar larvae of *C. capitata* (94%) by *H. bacteriophora* (11 KG), followed by *H. bacteriophora* (TOK-20)(91%), *S. carpocapsae* (85%) and *S. feltiae* (Tokat-Emir)(71%), at 200 IJ/larvae. Thanwisai*et al*. (2022) isolated some EPNs and their bacterial flora from soil samples in Thailand and evaluated their efficacies for controlling mosquitolarvae. Their bioassays demonstrated that isolates of the EPN-symbiotic bacteria *Photorhabdus* were effective on and caused high larval mortality of both yellow fever mosquito *Aedes aegypti* (Culicidae) and the southern house mosquito *Culex quinquefasciatus*(Culicidae).

In order Hemiptera, Peçen and Kepenekci (2022) used some of the native isolates of *S. carpocapsae*, *S. feltiae* and *H. bacteriophora* against adults of the wheat stink bug *Aelia rostrata* (Pentatomidae) in Turkey. They found the Black sea isolate as the strongest pathogenic isolate that caused the highest mortality of the bug adults. In Morocco, El Aalaoui*et al*. (2022) evaluated the efficacy of two native EPN isolates of *S. feltiae* and *H. bacteriophora* against the prickly pear cochineal *Dactylopiusopuntiae* (Dactylopiidae) nymphs and young adult females. Depending on their results, *S. feltiae* appeared more

effective, causing higher mortality of nymphs and adult females (98.8% and 97.5%, respectively) after 8 days of exposure. In Dermaptera, the EPN *S. carpocapsae*exhibited a high virulence against the nymphs and adults of the earwig *Labidura riparia* (Labiduridae)(Reyad, 2012).

Table 1: Pathogenic effects of some EPNs on various lepidopterous pests, other than *A. ipsilon*.

Insect	Nematode species	Results	Reference
Spodoptera littoralis (Noctuidae)	40 IJs/ml of *Steinernema carpocapsae* and *Heterorhabditisbacteriophora*	100% larval mortality	Reyad, **2001**
The 5th instar larvae of *S. littoralis*	*S. carpocapsae* and *H. bacteriophora*	*H. bacteriophora* was more effective than *S. carpocapsae* on larvae causing 100% mortality at 48 h post-treatment	Taha, **2021**
Last (6th) instar larvae of *S. littoralis*	*S.carpocapsae*and *S.feltiae*	larval mortality 95.24% and 90.47%, respectively	Yağcı et al., **2022**
The 5th instar larvae of *Spodoptera litura* (Noctuidae)	*Heterorhabditis* spp. and *Steinernema* spp.	90% larval mortality after 72 h	Sun et al., **2021**
The *S. litura* larvae	At the concentration 350 IJs/ml of *S. pakistanense*; *S. siamkayai*, *S. ceratophorum*, *S. bifurcatum* and *H. indica*	high larval mortality	Tomar et al., **2022c**
The 3rd and 4th instar larvae of *S. litura*	indigenous *H. bacteriophora*	higher mortality rates after 120 h of exposure	Thakur et al., **2022**
Last instar larvae of *Spodoptera frugiperda* (Noctuidae)	concentrations 50-100 IJs of *S. diaprepesi*	mortality rates 93-100% after 144 h	Caccia et al., **2014**
The *S. frugiperda* larvae	*S. riobrave*	poorly effective even at high concentrations	Andaló et al., **2010**
The 3rd instar larvae of *Helicoverpaarmigera* (Noctuidae)	*H.bacteriophora* (HRJ) and *H. indica*	73.3% and 80.0% mortality, respectively, at 96 h exposure time	Vashisth et al., **2019**
The 3rd and 4th instar larvae of *H. armigera*	*H. bacteriophora*	The highest mortality rate after 120 hs of exposure	Thakur et al., **2022**
The *Phthorimaea operculella* (Gelechiidae) larvae	*S. feltiae, S. biobionis* and *S. carpocapsae*	95.5, 93.4 and 93.1% mortality, respectively	Ivanova et al., **1994**
The*Agrotis segetum* (Noctuidae) larvae	*H. bacteriophora* and *S. carpocapsae*	the highest larval mortality at concentration 100 IJs/insect	Goudarzi et al., **2015**
The 3rd and 4th instar larvae of *A. segetum*	*H. bacteriophora*	the highest mortality rate after 120 h of exposure	Thakur et al., **2022**
The *Tuta absoluta* (Gelechiidae) 4th instar larvae	*S. yirgalemense* and *S. jeffreyense*	mortality rates of 93% and 58.8%, respectively	Dlamini et al., **2020**
The *Pieris brassicae* (Pieridae) larvae	*H. bacteriophora* (2000 IJs/ml)	the maximal larval mortality	Tomar et al., **2022b**
The *Lobesiabotrana* (Tortricidae) larval instars (L1, L3, and L5)	*S. carpocapsae*	mortalities of ~50% for L1 and >75% for 3rd and 5th instars in only two days	Vicente-Díez et al., **2021**

Regarding the order Orthoptera, EPN *S. glaseri* killed almost 65% of 5th instar nymphs of the desert locust *Schistocerca gregaria* (Acrididae) within 72 hs post-infection in Egypt (Shairra, 2009). In Egypt, also, Abd-El Wahed and Elhadidy (2018) alsotested*S. carpocapsae* against the 5th instar nymphs of the migratory locust *Locusta migratoria*

(Acrididae). According to their results, 100% mortality of nymphs was observed after 3rd day of infection. In Turkey, Şahin *et al*. (2018) used *H. bacteriophora* HBH hybrid strain against *L. migratoria*. They recorded the highest mortality of the locust on day 3 of the experiment with 50000 IJs per trap. Virulence of *H. amazonensis* RSC05, *H. amazonensis* MC01, *S. carpocapsae* All (Weiser) and *H. amazonensis*GL was assessed by Andaló*et al*. (2018) against the field crickets *Gryllus* spp.(Gryllidae) in Brazil. Depending on their results, all EPN isolates were found to cause mortality in these crickets, and an increasein the EPN concentration resulted in an increased insect mortality rate. In South Africa, Du Preez *et al*. (2022) evaluated the virulence of 12 EPN species against nymphs of the katydid *Plangiagraminea*(Tettigoniidae). EPNs *H. zealandica*, *H. indica*, *S. jeffreyense* and *S. yirgalemense* caused > 90% mortality of the katydid. For some examples of the pathogenic effects of EPNs on different insect species belonging to the order Coleoptera, see Table (2).

Table 2: Pathogenic effects of some EPNs on various insects belonging to order Coleoptera.

Insect	Nematode species	Results	Reference
Dendroctonusvalens (Curculionidae) larvae	*S. ceratophorum*	high larval mortality	Jian et al., **2002**
Leptinotarsa decemlineata (Chrysomelidae) larvae	*S. feltiae*, *S. carpocapsae* and *H. bacteriophora*	96% 75%, 36% larval mortality, respectively	Kepenekci et al., **2015**
Rhynchophorus ferrugineus (Curculionidae) larvae	*S. carpocapsae*, *H. bacteriophora*, and *S. feltiae*	Maximal larval mortality 96.5%, 85.75% and 38.68%, respectively	Manzoor et al., **2017**
Temnorhynchus baal (Glaphyridae) larvae	*S. glaseri* and *H. bacteriophora*(4000 IJs/larva)	96 and 88% larval mortality, respectively	Adly et al., **2022**
Larvae of *Triboliumconfusum* (Tenebrionidae) andlesser grain borer *Rhyzopertha dominica* (Bostrichidae)	*S. pakistanense* (150 IJs/beetle)	Maximal mortality (100%), at 30°C.	Javed et al., **2020**
Last instar larvae of *Zophobasmorio*(Tenebrionidae)	*H. indica* isolates	various larval mortalities	Navarez et al., **2021**
Dendroctonusvalens (Curculionidae) larvae	*S. ceratophorum*	high larval mortality	Jian et al., **2002**
Pentodonbispinosus (Scarabaeidae) larvae	*S. glaseri*, *H. bacteriophora* and *S. carpocapsae*	100, 92 and 92 % larval mortalities, respectively	El-Ashry and Ramadan, **2021**
Some tenebrionid beetles	local compared to commercial *S. feltiae* and *S. carpocapsae*	a high mortality rate (67%) among larvae at dose 100 IJ/cm^2 of local EPN AF29	Kaliaskar et al., **2022**

I.2. Correlation of the Insect Mortality with the EPN Concentration:

In this context, it is important to point out that insect mortality usually depends on the EPN concentration. Several studies on *A. ipsilon* revealed a predominant trend of positive correlation between the mortality rate and the concentration of different EPN species (Shoeb *et al*., 2006; Fetoh *et al*., 2009; Bélair*et al*., 2013; Mahmoud *et al*., 2016; Yuksel and Canhilal, 2018;Ghoneim *et al*., 2023a). The mortality rates of termites, also, tended to increase with an increase in the rate of EPN inoculation (El-Bassiouny and El-Rahman, 2011). The available literature contains several studies on different insects reporting the same trend. For instance, the mortality percentages of some lepidopterous larvae increased with the increasing infective juveniles (**IJs**) dose of *H. indicus* and *H. bacteriophora* (Shairra, 2000). The pathogenicity of *Heterorhabditis* spp. against larvae of the rice moth *Corcyra cephalonica* (Lepidoptera: Pyralidae) was dose-dependent (El-Bishry *et al*., 2002).

Also, the pathogenicity of *H. bacteriophora* and *S. glaseri* against *S. gregaria* nymphs was found depending upon the IJs concentration (Shairra, 2007, 2009). Depending on the results of Shairra*et al*. (2016), the mortalitypercentage of the pink bollworm *Pectinophoragossypiella*(Lepidoptera:Gelechiidae) larvaeincreased with the increasing concentration of*S. riobrave* and *H. bacteriophora*. In their study on *S. littoralis*, Ahmed,*et al*. (2014) found an increasing mortality percentage of larvae with the increase in concentrations of *S. feltiae*, *S. riobrave* and *H. bacteriophora*. Some years later, Shaurub*et al*. (2021) assessed the effects of some EPN strains on*C. capitata* and found that the mortality of 3rd instar larvae proportionally increased with the nematode density (infective juveniles per cm^2). In a study to assess the virulence of *H. bacteriophora* and *S. feltiae*, as biological control agents against the full-grown larvae of peach fruit fly *Bactrocerazonata* (Diptera: Tephritidae). Also, Abd El-Motaal*et al*. (2021) found that the mortality rate increased as the concentration of IJs increased. In Turkey, a recent study by Barış *et al*. (2023) indicated that the last instar larvae of *Ph. operculella*were highly susceptible to native EPN *H. bacteriophora* (isolate Z-1), as well as larvae and pupae mortalities increased with the increasing concentration of EPN.

Although different factors interfering with insect mortality will be discussed in some detail in a later section of the present review, the insect mortality rate in insects may be due to the effect of EPN-associated symbiotic bacteria. Thus, it can be suggested that the higher concentrations of EPNs may elaborate much more symbiotic bacteria which in turn multiply rapidly producing ahuge number of bacteria with their toxins and finally killing the insect larvae more rapidly (Salem *et al*., 2007; Shaurub*et al*., 2021;Ghoneim *et al*.,2023a).

I.3. Increasing Insect Mortality Rate with Prolonged Time of Exposure to EPNs:

As reported in the current literature, mortality rate of *A. ipsilon* larvae increased with the increasing time interval of exposure to different EPN species, such as *S. carpocapsae* and *H. bacteriophora* (Mahmoud *et al*., 2016), *S. glaseri* and *H. bacteriophora* (Hassan *et al*., 2016) as well as to the local isolates of *S. carpocapsae* and *H. bacteriophora* (Yuksel and Canhilal, 2018). Recently, Ghoneim *et al*. (2023a) infected the 4th and 5th instar larvae of *A. ipsilon* with five concentrations of *S. carpocapsae* or *H. bacteriophora*. The mortality rate of infected larvae did not increase with the increasing time interval of exposure to *S. carpocapsae*. Whereas, the infection of 4th or 5th instar larvae with *H. bacteriophora* resulted in an increasing mortality rate with the increasing time interval of exposure.

To a great extent, the results of *A. ipsilon* were in corroboration with several reported results of increasing mortality rates in other insects with increasing time interval of exposure to various EPN species, such as *Heterorhabditis* spp. against *S. litura* and*P. xylostella* (Salem *et al*., 2007); *H. indica* against larvae of the fungus gnat *Bradysiamabiusi* (Diptera: Sciaridae) (Leite *et al*., 2007); *H. indica* against the rice leaf folder *Cnaphalocrosis medinalis* (Lepidoptera: Crambidae) (Sankar, 2009); *S. carpocapsae* against 3rd and 5th instar nymphs and adults of *S. gregaria* (Youssef, 2014); *S. riobrave* and *H. bacteriophora* against *P. gossypiella* (Shairra*et al*., 2016); *H. bacteriophora* and *S. glaseri* against *S. litura* (Safdar *et al*., 2018); *H. bacteriophora*, individually or in combination with *Beauveria bassiana*, against *Rh. ferrugineus* (Mehdi *et al*., 2018); EPN *Oscheiusrugaoensis* against *G. mellonella* (George *et al*., 2019); Egyptian local isolates of *H. indica* against *G. mellonella* (Khashaba *et al*., 2020), *S. glaseri* against the 6th instar of *S. frugiperda* (Meka *et al*., 2020) and *S. feltiae* HR1 and *H. bacteriophora* HR2 against *P. brassicae* (Kasi *et al*., 2021).

Similar results had been reported for *S. littoralis* larvae after infection with *S. feltiae*, *S.carpocapsae*and *H. bacteriophora* (Yağcı*et al*., 2022), *H. armigera*larvae infected with *S. abbasi* isolate CS-39 (Srivastava *et al*., 2022), the coconut rhinoceros beetle *Oryctes rhinoceros* (Coleoptera: Scarabaeidae) larvae infected with *S.carpocapsae* (CPCRI-Sc1) and *S. abbasi* (CPCRI-Sa1)(Sujithra *et al*., 2022), M.22 and M.313 isolates of *S. affine* from the

Syrian coastal region against the last instar larvae of *G. mellonella* (Ali *et al*., 2022), some isolatesof *S. feltiae*, *S.carpocapsae*and *H. bacteriophora* against *S. littoralis* larvae (Yağcı*et al*., 2022) and *S. abbasi* isolate CS-39 against *H. armigera* larvae (Srivastava *et al*., 2022).

Increasing mortality rate with increasing exposure time to EPNs is suggestive of higher penetration ofIJs (Ebssa and Koppenhöfer, 2012). Also, it can be attributed to the smaller size of IJs, which facilitates penetration of IJs through natural openings of larvae, i.e. spiracles, mouth, and anus or membranous areas of the cuticle (Adams and Nguyen, 2002). For example, IJs of *H. bacteriophora* can use their dorsal teeth to penetrate through the host cuticle (Bedding and Molyneux, 1982). A similar suggestion has been provided by some authors (Lalramliana and Yadav, 2009; Gorgadze *et al*., 2018). In addition, other authors (Shairra and Nouh, 2014; Sobhy *et al*.,2020) reported that the higher concentrations of EPNs exhibit acute toxicity, while the latent or chronic toxic effect has been observed in the case of lower ones. Also, the time passed for the larval mortality was prolonged with the increase in the infection dose of IJs, but when the size of the larva increased, the time passed for the larval mortality also was prolonged (Mantoo and Zaki, 2014). On the other hand, the mortality rate of EPN-infected larvae of some insects did not increase with the increasing time interval of exposure. This may indicate a strong acute pathogenicity of this EPN species or its stronger initial killing power against larvae than other EPN species (Ghoneim *et al*, 2023a).

I.4. Variation of the Median Lethal Concentrations (LC$_{50}$) of Different EPNs against Different Insects:

In insects, the EPN concentration-insect mortality relationship was typically expressed as LC$_{50}$ (concentration required to kill 50% of the insect population). It is important to shed some light on the variation of LC$_{50}$values in insects after infection with different EPN species through the following examples. LC$_{50}$values of four local Turkish EPNs isolates against the 4th instar *A. ipsilon* larvae ranged from 52 to 142 IJs, in the Petri dish experiment, and from 17 IJs to 24 IJs in the plastic container experiment (Yuksel and Canhilal, 2018). LC$_{50}$ values of two strains of *Heterorhabditis* spp., TAN5 and PGN6, against *A. ipsilon* larvae, were 1285.527 and 1560.747 IJs/cup, respectively (Nouh, 2021). Ghoneim *et al*. (2023a) determined LC$_{50}$ values of *A. ipsilon* larvae as 16 IJs/ml and 48 IJs/ml, for *S. carpocapsae* and *H. bacteriophora*, respectively, after infection of 4th instar larvae. On the other hand, LC$_{50}$ values were21 IJs/ml and 62 IJs/ml, after infection of 5th instar larvae, for the same EPN species, respectively.

Apart from *A. ipsilon*, LC$_{50}$ values for *H. bacteriophora*, *S. riobrave* and *S. feltiae* against *S. littoralis* larvae were 5.01, 8.57 and 16 IJs/larva, respectively (Ahmed *et al*., 2014). Also, Gomaa *et al*. (2020) investigated the pathogenicity of *H. bacteriophora* and *S. carpocapsae* against 3rd instar larvae of *S. littoralis*. Their data showed LC$_{50}$ values as 53.3 and 81.41 IJs/ml, respectively, at 72 h post-treatment. As recorded by Nouh (2022), LC$_{50}$ values of *H. bacteriophora* and *S. carpocapsae* against the 3rd instar larvae of *S. littoralis* were 38.489 and 40.791 IJs/larva, respectively, as well as against 5th instar larvae were 42.149 and 51.932 IJs/larva, respectively.

In addition, LC$_{50}$ of local *H. indica* (PIGCD1), isolated from peanuts in the Philippines, against *S. litura* under laboratory conditions was 7.13±1 IJs/larva (Dichusa*et al*., 2021). Results of Supriya *et al*. (2022) revealed that LC$_{50}$ of *H. indica* (CICR-Guava) against 3rd, 4th and 5th instar larvae of *S. litura* were 1.47, 2.04 and 2.21 IJs/100µl, respectively. These results were in line with the findings of Radhakrishnan and Shanmugam (2017) for the same insect. LC$_{50}$= 83.21 IJs for the *S. abbasi* isolate CS-39 against *H. armigera* larvae after 24 h of exposure (Srivastava *et al*., 2022). As recorded by Thakur *et al*. (2022) for indigenous EPNs *H. bacteriophora*, LC$_{50}$ values for *H. armigera* 3rd and 4th instar larvae were 60.14 and 57.90 IJs/larvae, respectively.

In Indonesia, Hade *et al.* (2020) evaluated the virulence of some isolates of *Steinernema* sp. against *S. frugiperda*. LC_{50} was found 163.5 lJs/ml for Kepahiang isolates and 186.5 lJs/ml for the Bengkulu isolates. Against *S. frugiperda*, also, LC_{50} values of *H. indica*, at 72 h post-incubation, were 20.26 and 62.07 IJs/larva for the 3rd and 5th larval instars, respectively, and 913.34 IJs/pupa for the pupae (Lalramnghaki*et al.*, 2021). Moreover,LC_{50} values of M.22 and M.313 isolates of *S. affine* against the last instar larvae of *G. mellonella* were 11.7 IJs/L, at 33.47 min., and 11.5 IJs/L at 32.43 min. (Ali *et al.*, 2022). After infection of *H. indica* into larvae (of 3rd, 4th and 5th instars) and pupae of citrus fruit piercing moth *Eudocima materna* (Lepidoptera: Erebidae), LC_{50} for 3rd instar was 14.43 IJs larva^{-1}, for 4th instar was 17.08 IJs larva^{-1}, for 5th instar was 23.63 IJs larva^{-1}, and LC_{50} of pupae was 85.91 IJs pupa^{-1}, after 48 hr post-exposure, respectively (Kumar *et al.*, 2022).

In Egypt, Abdelmonem*et al.* (2018) studied the virulence of *S. carpocapsae* and *H. bacteriophora* against the 4th instar larvae of *Ph. operculella*. They found LC_{50} values for *S. carpocapsae* and *H. bacteriophora* as 105.96 and 121.78 IJs/larva, respectively.Also, LC_{50} values of two strains of *Heterorhabditis* spp., TAN5 and PGN6, against 4th instar larvae of the same insect were 127.15 and 148.5994 IJs/larva, respectively, while $LC_{50}$of *S. glaseri* was 247.27 IJs/larva (Nouh, 2022). According to the recent study of Mohamed and Shairra (2023), the application of *S. carpocapsae* against all larval instars of the same insect resulted in LC_{50} values as 170.415 IJs/larva for 3rd instar larvae, 318.252 IJs/larva for 4th instar, and 567.108 IJs/larva for 5th instar. In the same study, LC_{50} values after infection with *H. indica*, were 506.78, 713.776 and 2442.3 IJs/larva for the 2nd, 3rd and 4th instars, respectively, as well as 184.282 IJs/larva for 5th instar larvae and 164 IJs/larva for 6th instar larvae.

Apart from order Lepidoptera, LD_{50} of *H. bacteriophora* against the plum sawfly *Hoplocampa flava* (Hymenoptera: Tenthredinidae) was 6.51 IJs while $LD_{50}$of isolate *S. carpocapsae* Tur-S4 was 16.617 IJs (Ulu *et al.*, 2015). LC_{50} against larvae of the Elm leaf beetle *Xanthogaleruca luteola* (Coleoptera: Chrysomelidae) was 167.59 for*S. feltiae*, while LC_{50} values were 218.23 IJ·mL^{-1} for *S. carpocapsae*, and 338.66 IJ·mL^{-1} of *H. bacteriophora* (Fard *et al.*, 2020). LD_{50} values for *S. glaseri* against *S. gregaria* 5th instar nymphs were recorded as 1505.13, 393.16 and 812.63 IJs/ml over the exposure periods of 48, 72 and 96 h, respectively (Shairra, 2009). Later on, Archana *et al.* (2017) evaluated the efficacy of *S. feltiae*, *S. glaseri*, *S. abbasi* and *H. indica* against larvae of the house fly *Musca domestica* (Diptera: Muscidae) in Petri dishes using 7 concentrations (50–3000 IJs/larva). According to their results, LC_{50} values for 2nd instar larvae 3 days post-treatment were 203 IJs/larva of *S. feltiae*, 63 IJs/larva of *S. glaseri*, 309 of *S. abbasi* and 29 IJs/larva of *H. indica*.

Similarly, recent studies have shown that LC_{50} value varies with both the insect and EPN species. LC_{50} value of the South American fruit fly *Anastrepha fraterculus* (Diptera: Tephritidae) larvae was found 427.2 IJs/ml of the isolated *S. carpocapsae* IBCB 02 (Chaneiko*et al.*, 2021). In India, Bhairavi *et al.* (2021) isolated some local isolates of two EPN species and assessed their virulence against the subterranean termite *Odontotermes obesus* (Hymenoptera: Termitidae). Based on their data, LD_{50} of *H. bacteriophora* was 13.054 IJs/termite, and LD_{50} of *S. aciari* was 42.040 IJs/termite. Then, Adly *et al.* (2022) treated the larvae of *T. baal* with *S. glaseri* and *H. bacteriophora* and estimated LC_{50} values as 937.44 and 1026.58 IJs/larvae, respectively. According to Sujithra *et al.* (2022), LC_{50}values of *S. carpocapsae* Sc1, *S. abbasi* Sa1 and *H. indica* Hi1 strains were 1078, 1663 and 9780 IJs larva^{-1}, respectively, at 72 h of incubation of *O. rhinoceros* larvae. Against 2nd and 3rd instar larvae of *P. bispinosus*, Nouh, (2022) calculated the LC_{50} values of *S. glaseri* in 1073.640 and 1330.312IJs/larva, respectively. Finally, LC_{50} values usually depend on the susceptibility of the infected insect and its stage or size, virulence of the tested EPN and its concentration, time of exposure and different experimental factors affecting the penetration of EPN species. Recently, Sallam et al. (2024) evaluated the efficacy of *Steinernema*

carpocapsae (AII), *S. carpocapsae* (EGAZ10), *Heterorhabditisbacteriophora* (HP88) and *H. indica* (EGAZ2) against the full-grownlarvae of *Bactrocerazonata* (Diptera: Tephritidae) under laboratory, semi-field and field conditions. The LC_{50} values were 794.3, 1063.2, 1249.8 and 1446.8 IJs/ml, for *S. carpocapsae* (AII), *S. carpocapsae* (EGAZ10), *H. bacteriophora* (HP88) and *H. indica* (EGAZ2), respectively, at 3 days post treatments.

I.5. Variable Pathogenicity of Different EPNs against the Same Insect:

Based on many reported results in the current literature, the EPN *S. carpocapsae* was more virulent than other EPNs against certain insects. For instance, *S. carpocapsae* was found more pathogenic than *H. bacteriophora* against *A. ipsilon* with a high speed of kill after 4 days under golf course conditions (Ebssa and Koppenhofer, 2011). Using the Petri dish technique, *S. carpocapsae* was more virulent than *H. bacteriophora* against the *A. ipsilon* larvae (Bélair*et al*., 2013; Mahmoud *et al*., 2016).In a recentstudy,Ghoneim *et al*. (2023a) recorded that *S. carpocapsae* was more pathogenic than *H. bacteriophora* against both the 4th and 5thinstar larvae of *A. ipsilon*.

Apart from *A. ipsilon*, Shapiro-Ilan and Cottrell (2006) found both *S. feltiae* and *S. carpocapsae* more effective than *H. bacteriophora* against the lesser peach tree borer *Synanthedonpictipes* (Lepidoptera: Sesiidae). Also, *S. feltiae* was higher pathogenic than *H. bacteriophora* against the *B. oleae* larvae (Sirjani*et al*., 2009). The EPN *S. carpocapsae*exhibited higher virulence against the nymphs of *L. riparia*. Also, *S. scarptasci* caused a higher mortality rate in the adults of this insect (Reyad, 2012). The EPN *S. glaseri* was more pathogenic than *H. bacteriophora* against the 3rd larval instar of *T. baal* (Atwa and Hassan, 2014). In another study, *S. carpocapsae* (Black Sea isolate) exhibited the highest mortality rate of the alfalfa pest *Holotrichapionpullum* (Coleoptera: Apionidae), followed by *S. feltiae* (Aydin isolate) and then *H. bacteriophora* (Aydin isolate)(Atay and Kepenekci, 2015). Later on, full-grown larvae of *P. gossypiella* were more susceptible to *S. riobrave* than to *H. bacteriophora* (Shairra et al., 2016). The EPN *S. glaseri* was more pathogenic than *H. indica* against 3rd instar larvae of the brinjal ash weevil *Myllocerus subfasciatus* (Coleoptera: Curculionidae) (Nithiskarani *et al*., 2019).

In the present decade, considerable progress has been achieved in this area of research. For instance, Rohde *et al*. (2020) recorded a killing power of both EPNs *S. carpocapsae* ALL and *H. amazonensis* JPM4 against *C. capitata* larvae and pupae, but *S. carpocapsae* ALL was the most potent EPN. According to the results of Mazurkiewicz *et al*. (2020), the *Steinernema* strains were more pathogenic than *H. megidis* against the cabbage moth *Mamestra brassicae* (Lepidoptera: Noctuidae) larvae. In another study, Gözel *et al*. (2020) evaluated the pathogenicity of three EPN species from Turkey against adults of the sunn pest *Eurygaster integriceps* (Hemiptera: Scutelleridae). They observed that the efficiency of isolates belonging to the genus *Steinernema* was higher than the isolates belonging to the genus *Heterorhabditis*. Later on, Pratissoli*et al*. (2021) evaluated the pathogenicity of *H. indica* and *S. carpocapsae* on pre-pupae of the fruit borer moth *Neoleucinodes elegantalis* (Lepidoptera: Crambidae). They found that *S. carpocapsae* was morepathogenic than *H. indica*. Also, Yağci *et al*. (2021a) recorded *S. carpocapsae* as the most pathogenic against the codling moth *Cydia pomonella* (Lepidoptera: Tortricidae) with the highest concentration (100 IJs/larva), killing 82.63% of larvae, followed by other tested EPNs. In the same year, Kary *et al*. (2021) investigated the effectiveness of *H. bacteriophora* and *S. feltiae* against larvae, pre-pupa, and pupa of *Ph. operculella*. Their results showed that *S. feltiae* was more effective than *H. bacteriophora* against larvae. Also, Vicente-Díez*et al*. (2021) determined the infectivity of four EPN species against *L. botrana* larval instars and pupae. All EPN species showed the capability of killing larval and pupal stages, but *S. carpocapsae* was found as the most pathogenic EPN.

In addition, *S. glaseri* (Sgib strain), among seven EPN strains, had good potential in the management of the walnut pest *Atrijuglans hetaohei* (Lepidoptera: Gelechioidea) (NanGong *et al*., 2022). In a study conducted by Peçen and Kepenekci (2022) on adults of wheat stink bug *Aelia rostrata* (Hemiptera: Pentatomidae), *S. carpocapsae* (Black sea isolate) was the most pathogenic among three EPNs tested including *S. feltiae* and *H. bacteriophora* isolates. Also, larvae of *T. baal* were more susceptible to the infection with *S. glaseri* than *H. bacteriophora*, at the highest concentration (4000 IJs/larva) (Adly *et al*., 2022). In the study of Nouh (2022), *S. glaseri* showed the highest efficacy against the 2nd and 3rd instar larvae of *P. bispinosus* compared to *H. bacteriophora* and *S. carpocapsae*. In another study, Peçen and Kepenekci (2022) found that *S.carpocapsae* (Black sea isolate) was the most pathogenic among the three EPNs tested including *S. feltiae* and *H. bacteriophora* isolates against the wheat stink bug *Aelia rostrata* adults. Also, El Aalaoui*et al*. (2022) evaluated the virulence of two Moroccan EPN isolates; *S. feltiae* and *H. bacteriophora* against the prickly pear cochineal *Dactylopiusopuntiae* nymphs and young adult females. *S. feltiae* was more virulent, causing higher mortality of nymphs and adult females (98.8% and 97.5%, respectively) after 8 days of exposure.Peçen and Kepenekci (2022) used native EPNs [*S. carpocapsae* (Black sea isolate), *S. feltiae* (isolate 09-31) (Aydin isolate) and *H.bacteriophora* (isolate 09-43) (Aydin isolate)] in Turkey against adults of the wheat stink bug *Aelia rostrata*. Depending on their results, *S. carpocapsae* (Black sea isolate) was the most pathogenic among the three nematodes tested.Recently, Mohamed and Shairra (2023) found that *S. carpocapsae* was more virulent against all larval instars of *S .frugiperda*, causing 100% mortality at different concentrations, 48–72 h post-exposure. According to Fathy and Abd El-Rahman (2023), *Steinernema* species was more pathogenic than *H. bacteriophora* to both 5th instar nymphs and adults of the African migratory locust *Locusta migratoria migratorioides*.

On the other hand, several studies revealed that some *Heterorhabditis* spp. were more virulent than *Steinernema* spp. against various insects. For example, Hussaini *et al*. (2005) found that the isolates of *H. indica* were more virulent than the isolate of *S. carpocapsae* against the *A. ipsilon* larvae. Some years later, *H. bacteriophora* was more pathogenic than *S. riobrave* and *S. feltiae* to *S. littoralis* larvae (Ahmed *et al*., 2014). Some strains of *H. bacteriophora* were found more virulent than *S. carpocapsae* strains against late 3rd instar larvae of *C. capitata* (Shaurub *et al*., 2015). In the same year, Ulu *et al*. (2015) recorded *H. bacteriophora* as more virulent than *S. carpocapsae* against larvae of the yellow sawfly *Hoplocampa flava*. Al-Ghnam and Heikal (2017) studied the infectivity of the EPNs, *S. carpocapsae* and *H. bcteriophora* against *Ph. operculella* larvae and pupae. Their results revealed that *H. bacteriophora* was more pathogenic than *S. carpocapsae*, at all concentrations.

In the current decade, some surveys in the Egyptian soils revealed that species of the familyHeterorhabditidae were more prevalent than species of the familySteinernematidae for biological control of some insect pests (Aashaq*et al*., 2020; Nouh,2021). Depending on the results of Gomaa *et al*. (2020), *H. bacteriophora* was more virulent than*S. carpocapsae* against the 3rd instar larvae of *S. littoralis*. In a study to assess the virulence of *H. bacteriophora* and *S. feltiae* as biological control agents against the full-grown larvae of peach fruit fly *Bactrocerazonata*, Abd El-Motaal *et al*. (2021) found that *H. bacteriophora* was more pathogenic than *S. feltiae*. In their study, Bhairavi *et al*. (2021) concluded that *H. bacteriophora* exhibited more virulence than *S. aciari* toward *A. ipsilon* and *O. obesus*. Taha (2021) studied the susceptibility of 5th instar larvae of *S. littoralis* to *S. carpocapsae*, and *H. bacteriophora*. Their data revealed that *H. bacteriophora* was the higher effective than *S. carpocapsae* on larvae causing 100% mortality after 48 hr post-treatment. Among different EPNs, Yağcı*et al*. (2021a) indicated that *H. bacteriophora* (TOK-20) isolates in Turkey were

the most effective at 1000 IJs/ml concentration against last instar larvae of *C. pomonella*. Wattanachaiyingcharoen *et al*. (2021) investigated the efficiencies of two Thai indigenous EPNs isolates (*H. indica* isolate AUT 13.2 and *S. siamkayai* isolate APL 12.3) against *S. frugiperda* and recorded the *H. indica* isolate as more infective than *S. siamkayai* isolate. Kary *et al*. (2021) studied the effectiveness of *H. bacteriophora* and *S. feltiae* against larvae, pre-pupa, and pupa of *Ph. operculella*. Their results showed that *H. bacteriophora* was more effective than *S. feltiae* on pupae. Based on LC$_{50}$, *H. indica* was the most pathogenic species, followed by *S. sangi*, *H. baujardi* and *S. surkhetense* against larvae and pupae of *S. frugiperda* (Lalramnghaki *et al*., 2021). Also, Gümüssoy*et al*. (2022) found *H. bacteriophora* more pathogenic than *S. carpocapsae* on larvae of *C. pomonella*.

Pathogenicity of EPNs against insect hosts depends on different factors, hence some EPNs have been found to be more pathogenic than others due to the EPN traits (such as EPN species/stain, application methods, behavior, and type of the associated symbiotic bacteria), the host characters (such as species, development and immune system), the abiotic environmental factors (such as temperature, humidity, UV radiation, soil characteristics, and chemicals) and the biotic environmental factors (such as natural enemies)(Mráček*et al*., 2005; Labaude and Griffin, 2018). For example, *Steinernema* spp. may be more pathogenic than other EPNs because the symbiotic bacterium, *Xenorhabdusnematophila*, exists in a large number of nematode IJs. The toxins it produced after being released into the host insect's haemocoel traveled to the connective tissues around the mid-gut, muscle fibers, and tracheae, where they caused harm and served as a source of nutrients for bacterial and nematode development (Fathy and Abd El-Rahman, 2023).

In addition, mortality rates of the insect hosts may be affected by the foraging strategies of EPNs. Therefore, *Steinernema* spp. is considered to be more effective than other species in controlling moving insects due to its foraging behavior, and the Petri dish may have created an environment that is more favorable to *Steinernema* spp. (Shapiro et al., 1999; Ebssa and Koppenhöfer, 2012; Hassan *et al*., 2016). Also, smaller EPNs were more infective and induced mortality more quickly (Shannag*et al*., 1994). These results can be, also, explained by variations in strategies to penetrate the interior of the insects through the mouth, anus, blow holes and track cuticle and by the entrance of IJs in the insect body (Lewis *et al*., 2006; Chaneiko*et al*., 2021). On the other hand, Jones *et al*. (2022) reported that *Steinernema* spp. can rapidly infect and kill a wide range of insect hosts owing to the host immunosuppression during the initial stages of infection. The lethal nature of *S. carpocapsae* infections has previously been credited to its symbiotic bacteria; however, it has become evident that the nematodes are able to effectively kill their hosts independently through their excretion/secretion products. For more detail, see Hinchlife *et al*. (2010), da Silva *et al*. (2020), and Santhoshkumar *et al*. (2021).

It may be informative to say that the major difference between the two families is in the reproductive strategies. Heterorhabditid adults, as opposed to steinernematid adults, have IJs that are hermaphrodites; therefore, only one juvenile is needed to enter the host for progeny production (Tanada and Kaya, 1993). The IJs of *Steinernema* develop into amphimictic adults. Their offspring either develop into dauer (infective) juveniles or to an F1 adult generation (Ehlers, 1996). For more detail, see the section "Key factors and environmental conditions interfering with the EPNs' virulence against insect pests" in the present review.

1.6. Susceptibility of the Insect Developmental Stages, Other Than Larvae, to EPNs:

Not only the insect larvae susceptible to EPNs, but also some studies reported the susceptibility of egg stage, pupal stage and adult stage to these EPNs. However, the available results of this point of interest could be reviewed in the following paragraphs.

Susceptibility of Egg Stage:

Limited knowledge exists in the current literature on egg susceptibility to EPNs.Although EPNs, especially *S. carpocapsae*, did not exhibit any pathogenicity against eggs of *B. agrestis* (Kim *et al*., 2004), Amutha *et al*. (2021) isolated different strains of EPNs from the warm region in India and tested for pathogenicity against *S. litura*. They found AC strain had considerable egg pathogenicity, at a dose of 75 IJs/20 eggs.

Susceptibility of Pupal Stage:

There is a great body of research concerning the assessment of susceptibility of thepupal stage of different insects to various EPNs.Although the pupae, as the dormant developmental stage of lepidopterous insects, are not normally targeted for pestcontrol by EPNs, the pupal stage was reported to be less conductive for EPNs (Malan *et al*., 2011; Odendaal *et al*., 2016; du Preez *et al*., 2021; Steyn *et al*., 2021). Depending on the results of Coleman (2020), four native EPN species were assessed against *T. absoluta* in South Africa. All EPNs were found to be highly effective against larvae (100% larval morality) but pupae were less susceptible. In Egypt, the3[rd] instar larvaeof *A. ipsilon* and *S. littoralis* were more sensitive than the pupae to*Heterorhabditis* sp. strain (TAN5)(Nouh, 2021). Also, some authors (Azazy, 2001; El-Kholy, 2004) reported that the pupae of *A. ipsilon*were less susceptible to EPN infections than larvae because the number of portal entries is small. Pupae of *L. vanillana* were less susceptible than larvae to the infection with *S. yirgalemense* and *S. jeffreyense* (Du Preez *et al*., 2021). Recently, Barış *et al*. (2023) indicated that the last instar larvae of *Ph. operculella*in Turkey were highly susceptible to native *H. bacteriophora* (isolate Z-1). The highest EPN concentration (1000 IJs/ml) caused 92.5% mortality of last instar larvae and 25.6% mortality of pupae, at 25 °C., i.e., pupae were less susceptible than larvae. Moreover, Jacob and Mathew (2016) evaluated the pathogenicity of 3 EPN species against the serpentine leaf miner*Liriomyzatrifolii*(Lepidoptera: Agromyzidae) pupae in infested leaves, in Petri dishes, using 5 concentrations, 10–30 IJs/mine, and found no mortality of pupae.

With regard to the fruit flies (Diptera), many EPNs were found to be unable to cause infection during the pupal stage of different species (Karagoz *et al*., 2009; Yee and Lacey, 2003) because pupae of fruit flies in the soil were found to be totally resistant to the EPN infection (James *et al*., 2018). As to the fruit flies, also, many studies have found that larvaewere more susceptible than pupae to EPNs infection (Kepenekci*etal*., 2015; Minas *et al*., 2016; Heve *et al*., 2017; Godjo*et al*., 2018; Aatif *et al*., 2019; Torrini*et al*., 2020; Rohde *et al*., 2020). Higher susceptibility of larvae than that of pupae to EPNs may be due to their locomotor activity and higher release of CO_2 which attracts EPNs (Shapiro-Ilan *et al*., 2017). Moreover, larvae have less sclerotized integument and wide somatic openings, like spiracles, that facilitate the insect's infection with EPNs (Minas *et al*., 2016; Rohde *et al*., 2020). These factors could separately or collectively increase the susceptibility of larvae to EPNs. For some detail of EPNs infection of larvae and pupae of different species of fruit flies, see studies of Grewal *et al*. (2001), Dias *et al*. (2008), Godjo*et al*. (2018), Steyn *et al*. (2019), Chergui *et al*. (2019), Mokrini *et al*. (2020), Torrini*et al*. (2020), Jean-Baptiste *et al*. (2021), Shaurub*et al*., (2021), Chaneiko*et al*. (2021), and Yağcı*et al*. (2021b).

On the contrary, many studies reported the susceptibility of pupae of different lepidopterous insects to infection with EPNs. For instance, Fetoh*et al*. (2009) reported that both larvae and pupae of *A. ipsilon* were highly susceptible to *S. carpocapsae* and *H. bacteriophora*, under laboratory conditions. According to Andaló*et al*. (2010), the use of EPNs for the control of prepupae and pupae of *S. frugiperda* andthe corn earworm *Helicoverpazea* (Lepidoptera: Noctuidae), in maize, resulted in high mortality ratesof these stages. The efficacy of various EPN species against pupae of *C. pomonella*, at 50 IJs per host, resulted in 20–75% pupal mortality (Malan *et al*., 2011).

In the current decade, Yan *et al.* (2020) recorded three EPN species, *viz.*, *H. indica*, *S. carpocapsae*, and *S. longicaudum*, as highly pathogenic to *S. frugiperda* pupae, whereas *S. kushidai* was not effective. Both EPNs *H. amazonensis* JPM4 and *H. amazonensis* MC01 were virulent to pupae of *H. armigera* (Andaló*et al*., 2021).Two local EPN species; *S. feltiae* and *H. bacteriophora*, were collected from soil samples in India and assessed against *P. brassicae*. In the case of pupae, mortality rates were 62.12 & 58.58% for *H. bacteriophora* and *S. feltiae*, respectively, at 160 IJs/cm^2; as well as 74 & 12% for both the tested EPNs, respectively, at 80 IJs/cm^2 (Kasi et al., 2021). Also, Amutha *et al*. (2021) isolated different strains of EPNs from certain warm regions in India for pathogenicity against *S. litura*. The IJs-treated pupae were observed after 96 h exposure which showed the highest mortality in AC culture with anLC$_{50}$valueof9.199 IJs/pupae and LC$_{90}$valueof16.824 IJs/pupae after 96 h. After infection of *H. indica* to *E. maternal* pupae, LC$_{50}$ was 85.91 IJs pupa^{-1}, at 48 h post-exposure (Kumar *et al*., 2022). Results of Lalramnghaki *et al*. (2021) clearly indicated that all isolated EPN species showed a high rate of pupicidal activity against *S. frugiperda*, and pupal mortality ranged between 37.50–68.75% (at concentrations 200–1600 IJs /pupa).

In addition to Lepidoptera, pathogenicity ofthe mustard beetle *Phaedon cochlearia* (Coleoptera: Chrysomelidae) pupae was observed for EPNs (Mahar *et al*., 2012). Also, Safari *et al*. (2013) recorded a high mortality of prepupae and pupae of theonion thrips *Trips tabaci* (Thysanoptera: Thripidae) compared to 2nd instar larvae when applying *S. feltiae*, *H. bacteriophora*, and *S. carpocapsae*. According to Gulzar *et al*. (2021), pupae of the tobacco thrips *Frankliniellafusca* were found to be susceptible to eight EPN species. Treatment of pupae (8-day old) of the flesh fly *Parasarcophaga aegyptiaca* (Diptera: Sarcophagidae) with *S. riobrave* and *H. bacteriophora*, at the concentrations of 500–4000 IJs/dish/5 pupae, resulted in 42–86 and 30–70% mortality, respectively (El-Sadawy*et al*., 2006). Mahmoud *et al*. (2007) treated pupae of the blow fly *Calliphora vicina* (Diptera: Calliphoridae) and the common green bottle fly *Lucilia sericata* (Diptera: Calliphoridae) (1-2-day old) with *S. feltiae*. Their results showed that mortality rates in treated pupae of both fly species were 0–17 and 7–70%, respectively. Some years later, Noujeim, *et al*. (2015) treated pupae of the serpentine leafminer fly *Liriomyza huidobrensis* (Diptera: Agromyzidae) with a concentration of 1000 IJs/5 pupae of *H. indica*, in Petri dishes. An average of 53% of pupal mortality had been recorded. The highest susceptibility of pupae might be due to their lack of mobility (Safari *et al*., 2013).

Susceptibility of adult stage:

As reported in the current literature, adults of many insect species have exhibited susceptibility to different EPNs. For example, *S. carpocapsae* displayed a high virulence against the nymphs and adults of the earwig *Labidura riparia* (Dermaptera: Labiduridae) (Reyad, 2012). Different EPN species were inoculated to different larval instars and adults of the red palm weevil *Rhynchophorus ferrugineus* (Coleoptera: Curculionidae) at the concentration of 100 IJs/larva+adult, and various mortalities of larvae and adults were recorded by Manzoor *et al*. (2017). Gaber *et al*. (2018) evaluated the virulence of four EPN species against adult males and females of the desert locust *Schistocerca gregaria* (Orthoptera: Acrididae). They found thatadultfemales aremore susceptible than adult males.According to research by Saleh *et al*. (2018), applying two concentrations (5 and 15 IJs/cm^2 of soil surface) of *H. marelatus* D1 on sandy soil containing old pupae of *B. zonata*, resulted in different mortality percentages of adults, according to the rate of EPN application rather than the EPN species. In the same year, Arviga and Cortez-Madrigal (2018) evaluated the pathogenicity of *H. indica* against larvae and adults of the house fly *Musca domestica* (Diptera: Muscidae) at 1200 and 1600 IJs/ml. As to adults, the females were more susceptible to EPN infection than males, with an average mortality of79.2% for females and 35.5% for males (at 1600 IJs/ml).

In the present decade, Gözel *et al*. (2020) assessed the pathogenicity of some isolates of three EPN species from Turkey on adults of the Sunn pest *E. integriceps*. According to their results, the susceptibility of adults to *Steinernema* isolates was more than that to *Heterorhabditis* isolates. Among four species of EPNs assessed by Javed*et al*. (2020), *S. pakistanense* and *S. bifurcatum* were the most virulent at 30°C, while *S. affinae* and *S. cholashanense*, at 20°C, giving the maximal mortality rate of adults of the beetles *T. confusum* and *Rh. dominica*. In addition, LC_{50} value against adults of *X. luteola* was 6.73 $IJ \cdot mL^{-1}$ for *S. feltiae*, while the LC_{50} value was 204.09 $IJ \cdot mL^{-1}$ for *S. carpocapsae*, and 70.29 $IJ \cdot mL{-1}$ for *H. bacteriophora* (Fard *et al*., 2020). For more examples, see studies of Chaneiko *et al*. (2021), Yağcı *et al*. (2021b), Peçen and Kepenekci (2022), El Aalaoui *et al*. (2022), and Nawab and Javed (2023).

1.7. Significance of the Insect Mortality:

To explicate the mortalities of EPN-infected insects, it is important to point out that EPNs are lethal endoparasites of insects, due to the production and secretion of some active insecticidal substances including toxins and proteases. There toxic materials contribute to the lethal effect on the infected host insects (Brown *et al*., 2006; Ffrench-Constant *et al*., 2007a, b; Toubarro *et al*., 2009). Therefore, it is evident that the EPNs are able to effectively kill their hosts independently through their excretion/secretion products, linked to the host immunosuppression during the initial stages of the infection process (Jones *et al*., 2022).

For some detail, the infective juveniles (IJs) of EPNs enter into the body of thehost insect through some openings (like mouth, anus and spiracles). These IJs constitute the only non-feeding and free-living stage of EPNs. They penetrate through the gut wall of the insect and regurgitate their symbiotic bacteria into the insect haemocoel (Mastore*et al*., 2015). Both EPNs and their symbiotic bacteria contribute to host mortality (Dowds and Peters, 2003) usually within 24-72 hr resulting from toxemia or septicemia in the late phase of infection (Adams and Nguyen, 2002; Ffrench-Constant et al., 2007a,b; Shapiro-Ilan *et al*., 2018).

To understand this mechanism of insect death by EPN infection, it is important to clarify the relationship between the EPNs and their symbiotic bacteria. This relationship is truly mutualistic for the following reasons: (1) bacteria break down the host tissues, and provide food sources for the EPN, which feeds and multiplies on bacterial cells and degrades host tissues. In other words, EPNs act by feeding on the bacteria and the damaging host tissue, they multiply, develop and reproduce (Mahmoud, 2016; Kumar *et al*., 2022). (2) bacteria need the nematodes for protection from the external environment, penetration into the host's haemocoel, and inhibition of the host's antibacterial proteins (Hazir *et al*., 2003; Griffin, 2012; Shaurub, 2023). In this context, *S. carpocapsae* excretion/secretion products (ESPs) have been linked to host immunosuppression during the initial stages of invasion to promote a suitable growing environment for their symbiotic bacteria (Chang *et al*., 2019; Parks *et al*., 2022).

Recalling the first scenario, physiological interactions between the EPN and its insect host must be considered, since the life cycle of an endoparasite is strongly related to its ability to evade and/or suppress the host immune responses in the early phase of infection (Castillo *et al*., 2011; Toubarro*et al*., 2013). Both EPN and bacteria overcome the insect immune system causing the death of the insect (Adams and Nguyen, 2002). This is a distinctive criterion of the relation of EPN/bacteria complex with the host insect.

Although the EPN pathogenicity is typically attributed to toxins and virulence factors that are released in conjunction with their symbiotic bacteria, some investigations have shown that EPNs play an active role in the pathogenicity of the nematode-bacteria complex (Lu *et al*., 2017). EPNs themselves should be considered, because shortly after infection, and before the bacteria is released from the gut of the invading nematode, there is a significant reduction in the total count of insect hemocytes, suggesting that the nematode

itself is capable of suppressing the hostimmune system, to the benefit of its endosymbiotic bacteria. Some evidence of the action potential of EPN apart from its symbiotic bacteria can be provided by the following examples. The EPN *S. carpocapsae*was shown to be able to kill insects and partly degrade insect tissues in the absence of any bacteria; however, the pathogenicity of such axenic EPN (without its symbiotic bacteria) was weaker than that of monoxenic EPNs (Darsouei*et al*., 2017). While, axenic *H. bacteriophora* were unable to kill *G. mellonella* larvae, axenic *S. carpocapsae* could kill insect hosts but produce a very small number of offspring (Han and Ehlers, 2000). This together suggests an almost obligatory relationship between EPNs and their symbionts. Indeed, symbiotic bacteria are also able to suppress the immune system of the hosts (Darsouei*et al*., 2017), thus favouring nematode colonization of their host and successful propagation. For some details, see Bobardt*et al*. (2020), Dowds and Peters (2003) and Shapiro-Ilan *et al*. (2018).

In this context, another interesting point is the variation in mortalityrates of the host insects, as recorded by Ghoneim *et al*. (2023a) for *A. ipsilon* larvae after infection with *S. carpocapsae* and *H. bacteriophora*, and many studies on the same insect or other insect species. This variation may be attributed to the number of larvae used for each study, since some researchers (Shoeb *et al*., 2006; Fetoh*et al*., 2009; Mahmoud *et al*., 2016) used 15, 25, or 20 larvae in their studies, while Yuksel and Canhilal (2018) used 40 larvae for each concentration.

However, variation in the mortality rates of infected insects can be explained by the different toxin complexes produced by the symbiotic bacteria *Xenorhabdus* and *Photorhabdus* species/strains because the toxin complexes and secondary metabolites play a major role in the suppression of the host immune system as well as toxicity to the host intestine (Shawer *et al*., 2018; Vicente-Díez *et al*., 2021).

2. Some EPN-infected Larvae or Pupae Can Successfully develop into The Next Developmental Stage:

On various agricultural insect pests, a number of studies reported the capability of some EPN-infected pupae to metamorphose to adults indicating some resistance of the pupal stage to EPNs (Malan *et al*., 2011; Odendaal *et al*., 2016; Du Preez *et al*., 2021; Steyn *et al*., 2021). The infection of *F. fusca* pupae (the soil-dwelling stage) with *S. feltiae*, *S. riobrave,*or*S. rarum* resulted in a reduction of adult emergence (Gulzar *et al*., 2021). When employing the high IJ concentrations of four EPN species (*S. feltiae, S. carpocapsae, S. riojaense* and *H. bacteriophora*) against pupae of *L. botrana*, adult emergence was significantly blocked (Vicente-Díez *et al*., 2021). In a study by Filgueiras and Willett (2021), the presence of EPNs can affect the developmental durations and changes in the risk of death of the non-susceptible pupal stage of the onion fly *Delia antique* (Diptera: Anthomyiidae) indicating an insect resistance to infection during the pupal period. This resistance may be due to its immune system, which synthesizes genes encoding antimicrobial peptides that encapsulate and inactivate the invading EPN (Castillo *et al*., 2011; Strand, 2008). Inactivation of EPN during the pupal stage of an insect and reestablishment of its activity during the adult stage indicate the ability of these EPNs to overcome the insect's immune system. They secrete antibiotic molecules that inhibit the action of the encapsulation enzyme produced by the host, conferring resistance to the process of phagocytosis (Vallet-Geley *et al*., 2008).

As far as our literature survey could ascertain, no information was available on the successful metamorphosis of EPN-infected larvae into pupae, except the recent study of Ghoneim *et al*. (2023a)because a few EPN-infected 4th instar larvae of *A. ipsilon* could pupate at the lower two concentrations of *S. carpocapsae* and *H. bacteriophora*. In this study, also, a similar result was recorded after infection of 5th instar larvae with *S. carpocapsae*. Moreover, the infected larvae with *H. bacteriophora* successfully pupated at

all concentrations except the highest one. Unfortunately, there is no scientific explanation for this criterion right now!!

3. Impact of EPNs on Some Biological and Physiological Processes of The Insect Host:

As easily shown in the current literature, many authors (Shapiro-Ilan and Brown, 2013; Shaurub *et al*., 2014; Lacey *et al*., 2015; Leonar *et al*., 2022; Kaliaskar*et al*., 2022) reported that insect death within 24-72 h post-infection with EPNs, regardless the insect species and the EPN species. On the other hand, several authors (Peschiutta *et al*., 2014; Cardoso *et al*., 2015; Liu *et al*., 2020; Ansari and Hussain, 2020; Shah *et al*., 2021) described the success of some infected individuals inavoiding the lethal effects of both EPN and its symbiotic bacteria using some innate immune defences. These host individuals developmentally transform into the next stage, but usually unhealthy because certain biological and physiological processes have been adversely affected. In this context, there has been increasing evidence that some EPNs influenced certain metabolic processes in the insect host (Shaurub *et al*., 2020; Ghoneim *et al*., 2022) and some important enzymatic activities (Shaurub*et al*., 2015; Ibrahim *et al*., 2015; Shairra*et al*., 2016; Vidhya *et al*., 2016; Ghoneim *et al*., 2023b).

As previously reviewed, some studies indicated the capability of some EPN-infected pupae to metamorphose into adults owing to some resistance of the pupal stage to EPNs (Malan *et al*., 2011; Odendaal *et al*., 2016; du Preez *et al*., 2021; Steyn *et al*., 2021). Ghoneim *et al*. (2023a) observed a few EPN-infected 4th instar larvae of *A. ipsilon* could pupate at the lower two concentrations of *S. carpocapsae* and *H. bacteriophora*. In the same study, also, a similar result was recorded after infection of 5th instar larvae with *S. carpocapsae*. In another study, Filgueiras and Willett (2021) recorded the effect of EPNs to alter the developmental durations and changes in the risk of death of the non-susceptible pupal stage of the *D. antique*, indicating an insect resistance to infection during the pupal stage. The inactivation of EPN during the pupal stage of an insect and thereestablishment of its activity during the adult stage indicate the ability of this EPN to overcome the insect's immune system (Vallet-Geley *et al*., 2008). With regard to the adult performance of EPN-infected insects, infection of *F. fusca* pupae (the soil-dwelling stage) with *H. bacteriophora* (Fl1-1), *S. feltiae, S. riobrave* or *S. rarum* resulted in a reduction of the adult emergence (Gulzar *et al*., 2021). After treatment of *L. botrana* pupae with high IJ concentrations of four EPN species (*S. feltiae, S. carpocapsae, S. riojaense* and *H. bacteriophora*), adult emergence was significantly blocked (Vicente-Díez*et al*., 2021). For more detail, see the section "Susceptibility of insect developmental stages, other than larvae, to EPNs" in the present review.

4. Key Factors and Environmental Conditions Interfering with the EPNs' Virulence Against Insect Pests:

4.1. Fundamental knowledge:

Firstly, EPNs, which exist naturally in soils throughout the world, are able to control soil-borne, cryptic, and subterranean pests in diverse habitats (Georgis *et al*., 2006; Lacey and Georgis, 2012) with no secondary effects on non-target organisms (Wright *et al*., 2005). Over the few last decades, several studies indicated that EPNs also have the potential to suppress above-ground insect pests, but only under certain conditions (Hazir *et al*., 2003; Head *et al*., 2004; Laznik *et al*., 2010). However, the virulence of EPNs, as biological control agents against insects, varies greatly depending on their traits and characteristics, such as reproductive capacity, host-seeking behaviors, host specificity and adaptation capabilities (Yan *et al*., 2020; Acharya *et al*., 2020).

Besides the application technique and agrochemicals (Lacey and Georgis, 2012), several studies have indicated that the environmental conditions strongly affect both survival and efficacy of EPNs (Liu and Glazer, 2000; Piggott *et al*., 2002; Glazer, 2015; Levy *et al*.,

2020). In some detail, the environmental parameters (biotic and abiotic factors), application technique, and others affect the EPN virulence against insect pests (Lacey and Georgis, 2012). The Biotic factors, such as natural enemies, species of EPNs, age of targeted insects, nematophagous fungi, Collembola, mites, predatory nematodes and competition for resources may also be important factors (Hazir *et al*., 2003; Shapiro-Ilan *et al*., 2012). The abiotic factors, such as extreme temperatures, soil moisture, osmotic pressure, pH, UV radiation and aeration are important limiting factors of the EPN virulence (Gaugler *et al*., 1992; Kaya and Gaugler, 1993). For these reasons, EPNs may beless efficient against insect pests outdoors, although many laboratories and even greenhouse assays revealed a much higher efficiency (Laznik and Trdan, 2011; Majić *et al*., 2019).

Grewal *et al*. (2005) reported the four most important variables for the high virulence of EPN in pest control: moisture, temperature, susceptibility of the targeted insect, and foraging behavior of EPN. Some years later, Lacey and Georgis (2012) described fouressentialfactors affecting the ability of an EPN and its associated symbiotic bacteria to succeed as a control agent: moisture requirements (or desiccation tolerance, with ±85% relative humidity (RH) being required for optimum control); optimal temperature range; and foraging strategy. The biology and behavior of EPN and the target host and the environment in which the EPNs are to be applied should also be considered carefully when designing a control strategy (Georgis *et al*., 2006). For instance, Ma *et al*., (2013a) investigated the environmental conditions imposing adverse effects on the virulence, survival, and reproduction of *Heterorhabditis* and *Steinernema* spp. in North China. Also, Ben Husin and Porta (2021) discussed some factors affecting the survival and efficacy of EPNs against the tomato leafminer*Tuta absoluta* (Lepidoptera: Gelechiidae), such as the EPN species; RH, temperature range, time required by EPNs to enter a tomato leaf and number of applications in whole leaf bioassays. Therefore, it is important to study the environmental conditions of the areas where EPN exists to ensure its success as a biological control agent (Ulvedal *et al*., 2017; Toksoz and Saruhan, 2018).

Another point of interest is the accordance of EPN virulence to the susceptibility of thetarget insect (Ramos-Rodríguez *et al*., 2006) and its developmental stage (Acharya *et al*., 2019, 2020; Yan *et al*., 2020). Also, it should be kept in consideration that IJs of EPNs rely on their host behaviors, body size of different host developmental stages, and insect host immunity to maximize the chances of EPN successful infection (Peschiutta *et al*., 2014).

Additionally, other critical factors should be taken into consideration, such as the method of cover and placement of EPNs on open surfaces (like foliar habitats), in contrast to those that are experienced in soil environments (Wright *et al*., 2005; Dito *et al*., 2016). Also, the EPN concentration used and the exposure time to EPN are all important for improving the EPN performance for pest control (NanGong *et al*., 2022). However, many investigators have paid great attention to various characteristics of EPNs and their symbiotic bacteria as well as different environmental conditions influencing the biocontrol potential of EPNs. Selected aspects should be highlighted below.

4.2. Characteristics of EPNs as a Key Factor of Their Virulence:

It is well known that the EPNs with higher infectivity and reproductive potential within a specific target insect may be more effective in controlling this insect under field conditions (Rahoo *et al*., 2018; Kapranas *et al*., 2020). The virulence of EPNs varies greatly depending on their innate characteristics, such as host-seeking behavior, adaptation capability, host specificity and reproductive capacity (Kapranas *et al*., 2020; Yan *et al*., 2020; Acharya *et al*., 2020).

The reproduction potential of an EPN may also be related to its species and isolates, and the host susceptibility, number of bacteria per IJ, invasion rate, temperature and RH (Rahoo *et al*., 2016, 2017; Nabeel *et al*., 2018). One of the main differences between the two

major EPN families, Heterorhabditidae and Steinernematidae is in the reproductive strategies. Heterorhabditid adults, as opposed to steinernematid adults, have IJs that are hermaphrodites; therefore, only one IJ is needed to enter the host body for progeny production (Tanada and Kaya, 1993). The IJs of *Steinernema* develop into amphimictic adults. Their offspring either develop into dauers (IJs) or to an F1 adult generation (Ehlers, 1996). More than two decades later, several studies indicated that *Heterorhabditis* species produced more IJs, hence they can be widely used for insect pest control (Fateh *et al*., 2017; Kayani *et al*., 2017; Khan *et al*., 2017; Tariq-Khan *et al*., 2017; Kassi *et al*., 2018). For example, Rahoo *et al*. (2018) recorded a significant effect of EPN species on the production of IJs in *G. mellonella* larvae. Significantly higher numbers of IJs were produced by Heterorhabditid species than Steinernematid species in the larval cadaver of this insect. Moreover, the production of IJ was the maximum in the case of *H. bacteriophora* but the minimum in the case of *S. feltiae*.

4.3. Mutualistic Association of EPNs with Specialized Symbiotic Bacteria as A Key Factor of EPN Virulence:

It is important to highlight the mutualistic association of symbiotic bacteria and EPNs because the EPN/bacterium complex works together in many cases against insect pests (Lacey *et al*., 2001). This relationship is a type of symbiosis, where both benefit from this association. For example, IJs of EPNs provide protected shelter for the symbiotic bacteria and carry them into the host body. After entering the insect body, the IJ penetrates through the gut wall and regurgitates its symbiotic bacteria into the insect haemocoel cavity (Mastore *et al*., 2015). On the other side, the bacteria break down the host tissues and provide food sources for the EPN, which feeds and multiplies on bacterial cells and degrades host tissues. In other words, EPNs act by feeding on the bacteria and the damaging host tissue, they multiply, develop and reproduce (Griffin, 2012). However, the bacteria provide the EPN, and themselves a protected niche by producing antibiotics, that suppress the competition from other microorganisms (for review, see Mahmoud, 2016).

From the pest control point of view, the EPN/bacteria association is crucial, since Steinernematids are less pathogenic without their symbiotic bacteria (Ehlers *et al*., 1990) and Heterorhabditids are not able to kill an insect without their symbiotic bacteria (Adams and Nguyen, 2002). For instance,EPN genera *Steinernema/ Neosteinernema*, *Heterorhabditis* and *Rhabditis* have a symbiotic association with the insect pathogenic Entomopathogenic bacteria belonging to genera *Photorhabdus, Xenorhabdus* and *Serratia*, respectively (Sooraj *et al*., 2019) and form a mutually beneficial symbiotic complex which are able to kill and reproduce in many insect species (Mahar *et al*., 2005).

Depending on several authors (Mrácek and Becvár, 2000; Campbell and Lewis, 2002; Stock and Blair, 2008), the symbiotic association of IJs with the bacterial endosymbionts is one among factors influencing the EPN virulence, *i.e*., symbiotic bacteria of EPNs play a crucial role in the EPN pathogenicity by releasing a wide range of secondary metabolites into host haemolymph (Bode, 2009). For some detail, some authors (Martens *et al*., 2003; Trdan *et al*., 2009; Laznik *et al*., 2010) suggested that the primary cause of the host death has been usually due to the associating symbiotic bacteria carried in the intestines of IJs. For example, bacteria *Photorhabdus* spp. are associated with EPNs *Heterorhabditis* spp. and bacteria *Xenorhabdus* spp. are associated with EPNs *Steinernema* spp. (Lacey *et al*., 2001; Lewis and Clarke, 2012; Chaston *et al*., 2013).

On the contrary, some studies with axenic EPNs have demonstrated that excretion/secretion products (ESPs) retain their toxic effects causing insect death within the first two hours after infection, which suggests that the success of EPNs is independent of the action of their mutualistic bacterial partners (Kenney *et al*., 2021). These ESPs include

proteases and protease inhibitors involved in tissue degradation as well as other small molecules and toxins that promote immune suppression in the host (Lu *et al*., 2017).

4.4. Foraging Strategies of EPNs as a Key Factor of The Virulence:

In this regard, some special attention should be paid tothe foraging strategy since it has been reported to interfere with EPN virulence (Erdou, 2021). For instance, *S. carpocapsae* is considered to be more effective than other species for controlling moving insects due to its foraging behavior, and the Petri dishes in laboratory bioassays may have provided an environment that is more favorable to *S. carpocapsae* (Campbell and Gaugler, 1993). The heterorhabditid EPNs display a cruiser strategy (active search strategy) and are suited to infect insects living under the soil, while steinernematid EPNs are more effective to insects near the soil surface because of their ambusher strategy (sit and wait) (Mahmoud, 2017). Moreover, Shapiro-Ilan *et al*. (2018) reported that EPN foraging strategies consist of a continuum from ambusher to cruiser behaviors, yet a number of species display intermediate foraging strategies between the two extremes. For instance, *S. feltiae* exhibits an intermediate forage strategy (Griffin *et al*., 2005), whereas *H. bacteriophora* displays a cruise strategy (Bal and Grewal, 2015).

In addition, EPNforages for finding a host and infection. It is influenced by various factors inside and outside the host cadaver (Lewis *et al*., 2003; Kaplan *et al*., 2012; Shapiro-Ilan *et al*., 2019). For example, EPN dispersal to find hosts depends on sinusoidal locomotion on wet surfaces (e.g., soil), which is governed by certain physical properties under a gravitational field (Hunt*et al*., 2001; Shen *et al*., 2012). In addition, EPNs are thought to navigate in part based on electromagnetic fields (Ilan *et al*., 2013). These physical factors that impact the locomotion and navigation would be absent or altered under microgravity conditions. Thus, studying EPN movement and infectivity under microgravity conditions can shed some light on the relative importance of such factors as they contribute to EPN foraging success on Earth (Kaplan *et al*., 2020).

Therefore, differences of the foraging behavior of EPNs may be important determining factors of their virulence against insect pests added to variation of the ambient temperature, EPN species, IJs dose or concentration, developmental stage of the targeted insect (Barbosa-Negrisoli*et al*., 2009; Trdan *et al*., 2009), as well as application method and different environmental conditions (Bode and Müller, 2005; Stock and Blair, 2008).

4.5. Developmental Stage and Physiology of The Insect Host as KeyFactors of EPN virulence:

Developmental Stageof the Insect Host:

Another point of interest in this context is the accordance of EPNvirulence to the insect species (Ramos-Rodríguez *et al*., 2006). Although Patil *et al*. (2020) found no difference between the virulence of *S. carpocapsae* against 2nd and 4th instar larvae of the oriental armyworm *Mythimna separata* (Lepidoptera: Noctuidae), some authors (Acharya *et al*., 2019; Yan *et al*., 2020) reported the dependence of EPNvirulence on the developmental stage of the targeted insect. The EPN virulence varies significantly among the larval instars since Acharya *et al*. (2020) found that both EPNs *H. indica* and *S. carpocapsae* were highly virulent against the early larval instars (1st, 2nd and 3rd instar larvae) of *S. frugiperda*, whereas both EPNs *S. arenarium* and *S. longicaudum* were highly virulent against later instars (4th, 5th and 6th instar larvae). For some detail, Park *et al*. (2001) reported that larger EPNs are able to penetrate larger host insects (particularly the later larval instars). The virulence of *S. carpocapsae* and *H. indica* was higher against later larval instarsof the dark-winged fungus gnat *Bradysia impatiens* (Diptera: Sciaridae)(Acharya *et al*., 2019). Also, Yan *et al*. (2020) reported that *S. arenarium* was more virulent against 3rd and 4th instar larvae of *S. litura* than against 2nd instar larvae.

As clearly shown in the available literature, the 4th larval instar of different insects was found the most sensitive one to different EPNs, *i.e.*, EPN is more virulent against the 4th larval instar. The 4th larval instar of *A. ipsilon* was the most susceptible instar to some EPNs (Ebssa and Koppenhöfer, 2012). The same larval instar of *A. ipsilon* was found more sensitive than 2nd instar larvae to *S. carpocapsae* GSN1 strain (ScG) (Lee and Potter, 2015). In the recent study of Ghoneim *et al.* (2023a), LC_{50} data of *S. carpocapsae* and *H. bacteriophora* revealed that the 4th instar larvae of *A. ipsilon* were more susceptible than 5th instar larvae to the EPN pathogenicity.Also, the 4th larval instar of *A. segetum* was more susceptible to IJs of all tested Turkish native EPN isolates at the concentration of 100 IJs/cm^2 after 72 hr of exposure (Yüksel *et al.*, 2022). In the lepidopterous insects *H. armigera, S. litura* and *A. segetum*, the 4th instar larvae were more sensitive than 3rd instar larvae to the pathogenicity of *H. bacteriophora* (Thakur *et al.*, 2022). The 4th larval instar of the cigarette beetle *Lasiodermaserricorne*(Coleoptera: Ptinidae) was found more sensitive than 3rd instar to nine isolates of *H. bacteriophora* (Giannasi *et al.*, 2018).

In Colombia, 4th larval instar nymphsof the American palm planthopper *Haplaxius crudus* (Hemiptera: Cixiidae) were the most susceptible to some EPNs (Guerrero and Pardey, 2019). Mhatre *et al.* (2020) reported that the EPN *S. cholashanense* caused the highest mortality in 4th larval instar (100%) of *Ph. operculella*, *i.e.*, this instar was the most susceptible, or the EPN was more virulent against this instar. Also, Yan *et al.* (2020) tested different concentrations of *S. carpocapsae* against 2nd, 3rd and 4th larval instars of *Ph. operculella* under controlled conditions. They found the 4th larval instar larvae the most susceptible. The 4th instar larvae of *P. brassicae* were more susceptible than 2nd instar larvae to the two EPNs local strains; *S. feltiae* HR1 and *H. bacteriophora* HR2EPN strains (Kasi *et al.*, 2021). Moreover, the EPN pathogenicity varies depending on the age of the same larval instar of the same target insect. It has been shown that in the infection process, *Photorhabdus luminescens*, the bacterial symbiont of *H. bacteriophora*, proliferate more rapidly in older 5th instar larvae of the tobacco hornworm *Manduca sexta* (Lepidoptera: Sphingidae), relative to younger 5th instar larvae (Eleftherianos *et al.*, 2006).

Why the later larval instars are more susceptible than the earlier instars to EPN pathogenicity? The question in other words, why EPNs are more virulent against later instar larvae than earlier ones? Some scenarios can be provided to explain this widespread observation. The lower susceptibility of earlier instar larvae may be due to their small mouthparts or feeding behavior that excludes large particles (Bedding *et al.*, 1983). The IJs are difficult to penetrate directly through the cuticle or pores in the 1st and 2nd instar larvae with very small body sizes (Molta and Hominick, 1989; Ulvedal *et al.*, 2017). For some detail, large-sized hosts could more readily ingest IJs without damaging them, while small-sized early instar larvae rarely ingest IJs, more often crushing them with their mandibular teeth because of their smaller oral aperture. Once the cuticle was broken, the IJ perished(Zohdy*et al.*, 2013).

On the contrary, earlier larval instars of certain insects were found more susceptible than the later instars. In this respect, Rosa *et al.* (2000) found that older larvae of the armyworm *Pseudaletia unipuncta* (Lepidoptera: Noctuidae) are less susceptible to EPN parasitism. Why the earlier instar larvae of mosquitoes are more susceptible than the later instars to invading IJs? Authors who obtained such results (Achinelly *et al.*, 2004; Pérez-Pacheco *et al.*, 2004) have attributed this higher susceptibility to the fact that the thin cuticle of earlier larvae facilitates the invasion of IJs, which have more difficulty penetrating the thicker larval cuticle of later instars. In other words, the thicker cuticle of later larval instars has assisted them in preventing the IJs frominserting their stylets and penetrating the host body. Also, the insect larvae exhibit a special physiological action to combat EPNs that try to invade their haemocoel (Hillyer, 2010). After theinvasion of their haemocoel, insect larvae

have a diverse array of cellular and humoral immune defences. It is reasonable to suggest that the later larval instars have exerted a stronger immune defence than the early instars to combat EPN invasion (Shamseldean *et al*., 2006; Liu *et al*., 2020).

In addition, the sensitivity of certain larval instar (s) to the EPNs can be attributed to the variation in genetics (Gaugler *et al*., 1989), infectivity (Griffin and Downes, 1991), physiology (Fitters *et al*., 1999), climatic adaptation (Solomon *et al*., 1999), and morphology of different EPN species (Stock *et al*., 2000). However, the aforementioned examples of studies indicated that the developmental stage of the insect host may play an important role in the establishment and proliferation of EPN-bacterial symbionts. Miranda *et al*. (2013) studied the effect of insect host physiology on the fitness of both EPNs *S. carpocapsae* and *H. sonorensis*, together with their symbiotic bacteria, *X. nematophila* and *Ph. luminescens*, respectively. They used *M. sexta*, as the insect host. Depending on their results, the insect developmental stage was an effector that impacted EPNvirulence.

Insect Host Physiology:

The insect host physiology should be taken into consideration in the context of EPN virulence because EPN life cycle occurs within the insect body. Some factors, such as nutrition, age, and hormone titers, are known to affect insect host physiology (Eleftherianos *et al*., 2008). Miranda *et al*. (2013) evaluated the effect of insect host physiology on the fitness of both EPNs *S. carpocapsae* and *H. sonorensis*, together with their symbiotic bacteria, *Xenorhabdus nematophila* and *Photorhabdus luminescens*, respectively. They used *M. sexta* as the insect host. Depending on their results, the nutritional status of the host had an effect on the fitness of the two tested EPN species. Also, Reyad (2005) reported that the nutritional requirements of *H. bacteriophora* are larger than those of *S. riobrave*; thus the principal nutrients of larvae infected with *H. bacteriophora* are lower than those infected with *S. riobrave*. This finding may account for the superiority of the reproductive potential of *H. bacteriophora* over that of *S. riobrave*. Host diet, also, had an effect on the production of IJ progeny in the insect cadavers. Barbercheck *et al*. (2003) suggested that insects reared on a high-lipid diet are more susceptible to EPN infection relative to those reared on a low-lipid diet. However, the effect of host diet on the bacterial symbionts was not assessed until now!!

4.6. Temperature As a Principal Limiting Factor of the EPN Virulence:

The ambient temperature is one of the limiting factors of EPN virulence. Some research works investigated the effect of ambient temperature and the heat resistance of EPNs. Generally, the optimal temperature for the development, infection, and reproduction of the genus *Heterorhabditis* is around 25°C (Shaurub *et al*., 2015). The optimum range for *H. bacteriophora* is 22-26°C (Doucet *et al*., 1996) and 25°C for *S. feltiae* (Belair et al., 2003). The virulent EPN species, identified in the study of Shah *et al*. (2021), were known to work better at higher temperatures, i.e. 20–30 °C (Kim and Alston, 2008; Power *et al*., 2009). In the specific case of *Heterorhabditisbaujardi*LPP7, an optimal temperature of 28°C for replication and infection had been reported by Sobrinho *et al*. (2023), with emphasis on the origin of this EPN strain, the Amazon rainforest strain; hence, it is probably already adapted to tropical environments (Dolinski *et al*., 2007). The cold-active EPN species, like *S. kraussei*, provide an interesting potential for further developments into EPN-based pest control strategies in orchard environments (Willmott *et al*., 2002).

On the other hand, González (2006) reported the viability of *H. baujardi* LPP7 at temperatures of 35°C for two hours, with no loss in efficacy against *G. mellonella* larvae. Whereas, a studyby Sobrinho *et al*. (2023) revealed that *H. baujardi* LPP7 lost efficacy against larvae of the stable fly *Stomoxyscalcitrans* (Diptera:Muscidae), after 72 h at 35°C. Moreover, several studies reported the adaptation of different EPN species to temperatures around 35°C (Kusakabe *et al*., 2019). Similarly, the considerable efficacy of EPNs for pest

control has been confirmed even when exposed to high temperatures, and on a wide variety of hosts (Mendonça *et al*., 2019).

For some detail, the efficacies of *H. bacteriophora* (HP88), *H. bacteriophora* (EASD98), *S. riobrave* and *H. indicus* (EAS59) against *S. littoralis* were studied by Shamseldean *et al*. (2008). All the tested EPNs attained almost 100% larval mortality at 4, 10 and 25ºC, but at 35ºC *H. bacteriophora* (HP88) achieved the least mortality (64%). In their study to assess four EPNs for controlling *L. decemlineata*, Trdan *et al*. (2009) recorded the highest adult mortality by *S. feltiae* and *S. carpocapsae* at temperatures ranging between 20ºC and 25ºC. At a lower temperature (15ºC), the highest dose of *S. feltiae* applied to overwintering adults showed high efficacy. Also, *S. carpocapsae* was more effective at higher temperatures and is therefore recommended for control of first-generation adult *L. decemlineata*.

In the current decade, four species of EPNs have been assessed by Javed *et al*. (2020) against certain beetles. The EPNs *S. pakistanense* and *S. bifurcatum* had the most virulence at 30°C, while *S. affinae* and *S. cholashanense*, at 20°C, giving the maximal mortality rate of adults of the beetles *T. confusum* and *Rh. dominica*. In a study by Majić *et al*. (2021), the pathogenicity of two EPNs was assessed against larvae and adults of *T. castaneum*. Different EPN concentrations were applied under two temperatures (15 and 25°C). The EPN *S. feltiae* was pathogenic to *T. castaneum* at 15°C which is optimal for storing grains. In another study, the virulence of *H. bacteriophora* and *S. feltiae* was evaluated by Abd El-Motaal*et al*. (2021) against the full-grown larvae of *B. zonata*. They found that *H. bacteriophora* was more effective at 25 than at 30°C. Ben Husin and Porta (2021) conducted a study to control *T. absoluta* using some EPNs. In this study, two *Steinernema* species caused similar mortality at 25°C, but *S. feltiae* was more virulent at lower temperatures (15 and 20°C) while *S. carpocapsae* was more virulent at higher temperatures (30 and 35°C). In a study on adults of wheat stink bug *Aelia rostrata* (Hemiptera: Pentatomidae), the higher mortality rates (75 and 70%) had been recorded for *S. carpocapsae* isolate at 15 and 12°C, respectively (Peçen and Kepenekci, 2022).

4.7. Effect of Desiccation On The Virulence And Drought Tolerance of EPNs:

As previously mentioned in some parts of the present review, EPN infection occurs when IJs gain entry through the natural openings or cuticle of the host, and release their symbiotic bacteria in haemocoel thereby contributing to the killing of the host quickly and effectively (Dillman and Sternberg, 2012; Mastore *et al*., 2015). The bacteria utilize the host to develop and reproduce (Griffin, 2012), while the multiplying EPNs feed on the bacteria inside the host cadaver. The IJs exiting in the host cadaver, carry the symbiotic bacteria in their intestines, in search of new hosts (Shapiro-Ilan *et al*., 2017; Sajnaga and Kazimierczak, 2020). However, many foliar pests, such as phytophagous insects, are highly susceptible to EPNs under a controlled-environment (Shapiro-Ilan *et al*., 2017).

As reported by several authors (Arthurs *et al*., 2004; Glazer, 2015; Shapiro-Ilan *et al*., 2017), the EPN's sensitivity to environmental stresses, such as desiccation, inhibits its effectiveness as a biological control agent. Thedesiccation,as an abiotic stress, leads to water removal from the EPN body to occur slowly (within days) (Piggott *et al*., 2002; Gal *et al*., 2003, 2005). Subsequently, EPNs are described as slow dehydration strategists, and their adaptation process to slow desiccationis also well characterized (Erkut *et al*., 2012; Yaari *et al*., 2016). However, when exposed to the plant surfaces, EPNs encounter rapid desiccation (RD), where water is removed from EPN body within minutes or hours (Susurluk and Ehlers, 2008; Mazurkiewicz *et al*., 2021). This environmental process leads to a drastic reduction in EPNs activity and viability (Shapiro-Ilan et al., 2006). According to many authors (Schroer *et al*., 2005; Navaneethan *et al*., 2010; Perry *et al*., 2012), a requirement of a thin film of water,

high RH (> 90%) and IJ activity limited by time (about one hour) hampers EPN's natural ability to achieve control of the target pest on foliar surfaces.

Based on the available literature, the characterization of RD and its impact on IJs of EPNs has relatively limited knowledge although EPN species differ in their capability to withstand RD (O'leary *et al*., 2001; Tyson *et al*., 2007). Shortly, it is very important to study RD systematically and identify the trends of survival in EPN, characterize the rate of water loss, and infectivity patterns at RD to understand the requirements from formulation and identify the optimum microenvironment required for EPN viability and activity in foliar applications (Ramakrishnan *et al*., 2022). For instance, IJs of *S.carpocapsae* are a better adaptable and tolerant than *S. feltiae* or *H. bacteriophora* as an optimal RH of > 90% is required by *S. feltiae* and *H. bacteriophora* while maintaining RH equivalent to 74% could sustain survival of *S. carpocapsae* under RD (Ramakrishnan *et al*., 2022).

With regard to the effect of soil moisture on EPNs for controlling the soil-dwelling insects, Gouge *et al*. (2000) reported that the ideal moisture content was to be about 30%. In Egypt, Shaurub *et al*. (2015) evaluated the effect of soil moisture on the infectivity of four EPN species against the late 3rd instar larvae of *C. capitata*. The infectivity of the four tested EPNs was drastically affected by extreme soil moisture levels. These results were in agreement with those reported results for the late 3rd instar of *C. capitata* (Rohde *et al*., 2010) and the Queensland fruit fly *Bactrocera tryoni* (Diptera: Tephritidae) (Langford *et al*., 2014). The low infectivity of the tested EPN species at the highest moisture level (30%) could be explained by the fact that soil saturation with water reduces oxygen concentration and restricts EPN mobility, which is required to infect the host (Glazer, 2002). On the other hand, the low infectivity of the tested EPNs at the lowest moisture content (5%) is probably related to the lack of water between the pores, which is also limiting for the EPN locomotion (Rohde *et al*., 2010). In a study to control *T. absoluta*, Ben Husin and Porta (2021) found decreases in the efficacy and survival of EPNs as RH declined. Also, *S. feltiae* was the most effective species followed by *S. carpocapsae* then *H. bacteriophora*. The EPN *S. carpocapsae* survived better at low RH than *S. feltiae*.

4.8. Host Plant and Its Secondary Metabolites as An Affecting Parameter of EPN Virulence:

In addition to the previously reviewed factors and conditions, host plant or plant secondary metabolites, consumed by insects, can indirectly affect the virulence of EPNs against insect pests *via* the nematode progeny production. In a study conducted by Shaurub*et al*. (2016) in Egypt, the EPNs *S. riobrave* and *H. bacteriophora* were applied to the last instar larvae of *S. littoralis*. Depending on their results, larvae raised on cabbage (the most lipid-rich diet) were most resistant to both tested EPN species, *i.e*, very low virulence of EPNs. The increased resistance of *S. littoralis* larvae reared on cabbage and infected later with *S. riobrave* or *H. bacteriophora* seems likely to be due to the indirect effect of cabbage on the tested EPNs where caterpillars were reared for several generations on this host plant before infection. The exact mechanism of the increased resistance of the insect is unknown. However, this finding may account for the superiority of the reproductive potential of *H. bacteriophora* over that of *S. riobrave* as evident in the study of Shaurub *et al*. (2016).

Although the impact of plant primary metabolites of the host plants on nematode production is scarce in the available literature, some studies reported the effects of the host plant and its secondary metabolites on nematode production. As recorded by Epsky and Capinera (1994), significantly declined progeny production in *S. carpocapsae* followed the infection of *A. ipsilon* larvae which were previously fed on collard, compared to the same EPN species infecting caterpillars fed on an artificial diet. In contrast, Barbercheck *et al*. (1995) recorded high nematode production in the same EPN following the infection of the spotted cucumber beetle *Diabroticaundecim punctata* (Coleoptera: Chrysomelidae) larvae

fed first on corn. The later authors, however, recorded lower nematode progeny production when larvae of this beetle fed on squash variety containing the secondary metabolite cucurbitacin D, compared to larvae fed on squash variety lacking this secondary metabolite. More than a decade later, Gassmann *et al*. (2010) investigated the role of plant secondary metabolites, pyrrolizidine alkaloids, in reducing the development of *H. sonorensis* and *S. riobrave* infecting the wooly bear *Grammiain corrupta* (Lepidoptera: Erebidae), fed first on plants containing secondary metabolites.

4.9. Additional Factors Affecting the EPN Efficiency for Insect Pest Control:
The Target Insect's Habitat as An Affecting Parameter of EPN Virulence:

Arthurs *et al*. (2004) analyzed 136 published greenhouse and field work that used the EPN *S. carpocapsae* against above-ground insects, and concluded that EPN efficacy depended on the insect's habitat (bore holes> cryptic foliage > exposed foliage) and trial location (greenhouse > field studies). Also, soil types can differ in their suitability for the survival of IJs, thereby affecting EPN abundance and diversity (Kaya and Gaugler, 1993). Shaurub *et al*. (2015) evaluated the effect of soil type (texture) on the infectivity of four EPNs against late 3rd instar larvae of *C. capitata*. Depending on their results, the EPN infectivity increased in sandy soil but decreased in silt and clay soils which explained the sandy soil as a more suitable microhabitat to facilitate the EPN infection of late 3rd instar larvae of *C. capitata*. Also, their results were consistent with the results reported for other tephritid species (Lezama-Gutiérez *et al*., 2006; Toledo *et al*., 2009; Kamali *et al*., 2013). Decreased virulence of EPNs in fine-textured soil could be related to reduction of pore space or increased water content between soil particles (Barbercheck, 1992). In addition, other soil characteristics can influence EPN virulence against insect pests, since Kung *et al*. (1990) reported that a soil pH of 10 or higher is likely to be dangerous to EPN applications, while soil pH in the range of 4–8 is normally compatible for these applications.

Application Techniques of EPNs and Important Precautions:

One of the most important parameters affecting the pathogenicity and virulence of EPNs is the application method against insects. Although EPNs are initially applied as soil applications against pests, promising results have been obtained by foliage applications depending on the new formulation techniques (Trdan*et al*., 2007; Laznik *et al*., 2010; Ebssa and Koppenhöfer, 2011; Coleman, 2020). For some detail, EPNs are usually used in different formulations and with various methods, such as sawdust, talc, desiccated cadavers, alginate gel, water-dispersibleg ranules, compost: charcoal powder mixture and water (Tahir and Shaheen, 2019). George *et al*. (2019) tested the EPN *Oscheiusrugaoensis* in six different formulations *in vitro* at two temperatures to evaluate their storage and infectivity against *G. mellonella* larvae. Based on their results, sawdust and Alginate gel formulations enhanced the highest survival of IJs than other formulations and caused high larval mortality of *G. mellonella* larvae. On the other hand, various EPNs formulations may be applied in aqueous suspension and bait formulations can promote EPN persistence and reduce the EPN quantity required per unit area. Also, baits can be developed further for wide applications (Grewal *et al*., 2005). Another application approach that has gained much attention is the delivery of EPNs in their infected host cadavers (Shapiro-Ilan *et al*., 2010). In addition, an effective application method is the use of EPNs in capsules from which nematodes can easily break through, and successfully infect the insect pests (Hiltpold *et al*., 2012). Besides these formulations and application methods, EPNs can be applied with almost all agricultural or horticultural ground equipment (Shapiro-Ilan *et al*., 2006).

From the technical point of view, Lanzoni *et al*. (2014) evaluated the effect of a spray application with a conventional hydraulic sprayer on the viability of *S. carpocapsae* in spinach crops In Italy. Their results showed that a static pressure ofup to 14 bar causes no significant damage to *S. carpocapsae* and that the passage of IJs through the flat fan nozzles

does not affect their viability. In this context, also, Youssef (2014) also studied the efficiency of *S. carpocapsae* against 3rd instar nymphs and adults of *S. gregaria* by two different methods; spray and soil surface application. Results of the infection with *S. carpocapsae*, soil treatment caused complete mortality (100%) of nymphs after 3 days but spray treatment caused similar mortality after 5 days. Thus, EPN was found to be more effective against *S. gregaria* nymphs when applied on the soil surface rather than spray treatment. To understand this finding, the soil is the natural habitat of EPN which shares this habitat with many other microbiota, including antagonists and other pathogens (Kaya, 2002). The EPNs live in the water-filled spaces, or pores, between soil particles. They need water to move and successfully locate a host, and oxygen to survive. Therefore, *S. carpocapsae* seems to be more efficient when applied against highly mobile surface-adapted insects (Youssef, 2014).

Also, a successful application of EPNs requires some principal factors, including informationon their life cycles; matching the correct EPN species with the targeted insect pest, applying them under suitable environmental circumstances to survive in the soil after application (Gan-Mor and Matthews, 2003), and applying them only with compatible agrochemicals (Mahmoud *et al*., 2016; Sujatha and Jeyasankar, 2018). In addition, the application of EPNs in IPM program requires more information about the interaction of EPNs with the usually used chemical pesticides to predict the EPN viability and efficiency under pesticide stress on pest mortality (De Nardo and Grewal, 2003; Laznik *et al*., 2012). The knowledge about the compatibility between chemical pesticides and EPNs may play a role in the development and improvement of thefoliar application of EPNs. For more detail on the application technology, see reviews of Koppenhöfer *et al*. (2020) and El-Ashry *et al*. (2020).

Production and Formulation of EPNs:

According to Grewal (2002), the EPN formulation process means the transformation of living organisms into a product for use by practical methods. It is a very important process to facilitate EPN storage, transport and application. Nowadays, many EPN species are produced commercially and available for short-term storage, since IJs can be produced relatively cheaply in large amounts (Shapiro-Ilan *et al*., 2006). In other words, the EPN formulation is one of the most important factors for the successful application of EPNs as potential biocontrol agents against insect pests (Grewal, 2002).

Different factors that affect the application should be taken into consideration for using EPNs as a component of the IPM program, including markets, crops and target insects, formulation and shelf life, usage directions, technical support, cost and others (Georgis *et al*., 2006; Lacey and Georgis, 2012). Tahir and Shaheen (2019) described some new molecules acting as phagostimulant and UV retardants that have been incorporated, if used along with nematode, can extend their survival on leafage.

However, some reviews have been available in the last two decades focusing on the progress of EPN formulation and application technology (Grewal and Peters, 2005; Shapiro-Ilan *et al*., 2006, 2012). Grewal (2002) provided a valuable review of the EPN formulation. Cruz-Martínez *et al*. (2017) provided another review in which they focused on the progress and perspective of the EPN formulations during the last years, and emphasized a systemic approach to include disciplines, such as invertebrate physiology, materials science, and systems modeling. Recently, Koppenhöferet *al*. (2020) provided a review of the mass production of EPNs.

Summary Points:

* Many studies have reported various degrees of pathogenicity of different EPN species against insects of several orders, such as Lepidoptera, including *Agrotisipsilon*, Diptera, Hemiptera, Orthoptera and Coleoptera.

* Various studies revealed a positive correlation between the mortality rate of insects and the concentration of different EPN species, i.e., the mortality rate of EPN-infected insect larvaeincreased with the increasing concentration of the nematode IJs.

* Although different reasons for insect mortality will be discussed in some detail later in the present review, variation of the insect mortality rates may be due to the fact that the success of initial penetration of some IJs individuals of EPNs opens pathways for other IJs. Also, the death of EPN-infected larvae is caused mainly by the effect of the EPN-associated symbiotic bacteria.

* The insect mortality rate of different insects has been reported to increase with increasing time intervals of exposure to EPN. This may indicate the susceptibility of these larvae to this EPN species increased with the prolongation of exposure time. On the other hand, the mortality rate of EPN-infected larvae of some insects did not increase with the increasing time interval of exposure. This may indicate a strong acute pathogenicity of this EPN species or its stronger initial killing power against larvae than other EPN species.

* Variation of the median lethal concentrations depends on the susceptibility of the infected insect and its stage or size, the virulence of the tested EPN and its concentration, infective juvenile age, time of exposure and different experimental factors affecting penetration of EPN species.

* The 4th larval instar of different insects was found the most sensitive one to different EPNs.On the contrary, other larval instars of certain insects were found more susceptible than 4th instar. In general, the sensitivity of certain larval instar (s) to the EPNs can be attributed to the variation in genetics, infectivity, physiology, climatic adaptation and morphology of different EPN species.

* Some EPN species are found more pathogenic than other species against the same insect due to the EPN traits (such as EPN species/stain, application methods, behavior andforaging strategies, reproductive strategies and species of the associated symbiotic bacteria), the host characters, the abiotic and biotic environmental factors.

* Some EPN-infected larvae can successfully transform into the next developmental stage. This vital event was reported in many studies that recorded the transformation of some EPN-infected pupae into adults, with a reduction in adult emergence. It can be explained by some resistance of the pupal stage for EPNs. However, the metamorphosis of EPN-infected larvae into pupae was rarely reported.

* Not only the insect larvae are susceptible to EPNs, but also some studies reported the susceptibility of egg stage, pupal stage and adult stage to these nematodes. However, many studies reported that pupae are less susceptible to EPN than larvae. Also, the insect adults that have been reported as susceptible to EPNs belong to orders other than Lepidoptera, as shown in the available literature.

* Besides the significance of insect mortality in a previous point, EPNs can produce and secrete some active insecticidal substances, including toxins and proteases, which contribute to the lethal effect on the infected host insects. These EPNs are able to effectively kill their hosts independently by their products, linked to host immunosuppression during the initial stages of infection. In addition, there are associating symbiotic bacteria in the intestines of nematode infective juveniles (IJs). These mutualistic bacteria were reported to contribute to the killing of insect hosts by certain mechanisms.

* The virulence of EPN, as biological control agents of specific target insects, varies greatly depending on their innate characteristics, such as host-seeking behaviors, adaptation capabilities, host specificity and reproductive capacity.

* Symbiotic association of EPNs with specialized bacteria is a key factorin EPN virulence. The nematodes/bacterias association is crucial since steinernematid EPNs are less pathogenic without their symbiotic bacteria and heterorhabditids EPNs are not able to kill

an insect without their symbiotic bacteria. The symbiotic association of IJs with the bacterial endosymbionts is one of thefactors influencing EPN virulence since symbiotic bacteria release a wide range of secondary metabolites into host haemolymph.

* The EPN pathogenicity or virulence of different EPN species against insect host can be affected by their foraging strategies. The heterorhabditid EPNs display a cruiser strategy and suit to infect insects living under the soil, while steinernematid EPNs are more effective to insects near the soil surface because of their ambusher strategy.

* The developmental stage of theinsect host is an essential parameter of the EPN virulence because the EPN virulence varies significantly among the larval instars. In some insects, the later larval instars are more susceptible to EPNs than earlier ones and *vice versa*.

* The ambient temperature is one of the limiting factors of EPN virulence. The target insect's habitat is an affecting parameter of EPN virulence. Insect host physiology is a key factor in EPN virulence. The EPN's sensitivity to environmental stresses, such as desiccation, inhibits its effectiveness as a biological control agent. The host plant and its secondary metabolites are an affecting parameter of EPN virulence.

* One of the most important parameters affecting the pathogenicity and virulence of EPNs is the application method of EPN formulations against insects.

* Nowadays, many EPN species are produced commercially and available for short-term storage, since IJs can be produced relatively cheaply in large amounts.

Conclusions: Many studies have reported the pathogenicity of several EPN species against several insect pests of different orders, such as Lepidoptera, including *Agrotisipsilon*, Diptera, Hemiptera, Orthoptera and Coleoptera. In particular, EPNs have been reported to quickly kill the insect host, by their own toxic secretions and products or by the products of their symbiotic bacteria. Therefore, many insect pests, in the soil or above ground, may be successfully controlled by using effective EPNs under suitable biotic and abiotic conditions, as well as with appropriate EPN concentration under suitable environmental conditions.

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