Ecological Role of Entomopathogenic Nematodes in Suppressing Insect Pests in Maize (*Zea mays* L.)

Gitanjali Devi

Maize (*Zea mays* L.) is an annual crop mainly grown for food in tropical and subtropical regions of the world. Among various abiotic and biotic factors, infestation of pest is one of the factors in low production of maize. Although chemical insecticides are the main means of pest suppression, various agro-ecological approaches have been suggested for pest management through the actions of natural enemies. Among the natural enemies of insect pests of maize, entomopathogenic nematodes (EPNs) are one of the important natural enemies that have several positive attributes as biocontrol agent. EPNs, *Steinernema* spp. and *Heterorhabditis* spp. are obligate parasites of insect pests attacking agricultural crops including maize. They carry pathogenic bacterial symbionts which are responsible for killing the insect host within 24 - 48 hrs. However, the efficacy of EPNs to control insect pests is adversely affected by various ecological factors. Differences in virulence, application techniques, resource competitors as well as environmental conditions have been cited as possible reasons for variable field performance. Technological advances in EPN mass production and application methods with changing agricultural practices will provide further opportunities to include the use of EPNs in pest management programs in maize crop. Therefore, knowledge about the EPN population dynamics and their behavioral ecology is essential for optimizing their use as sustainable pest management approaches. By combining traditional insights with new innovative methods, with better formulation and application practices we can expand EPN applications in agroecosystems, fostering eco-friendly maize cultivation.

Keywords: *Maize, Insect pests, Entomopathogenic nematodes (EPNs), Natural enemies, Ecology*

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Introduction

Maize or corn (*Zea mays* L.), the 'queen of cereals' is cultivated in wide range of climatic conditions throughout the world. It is used as food, poultry feed and fodder crops. Moreover, there is an increasing importance of grain for ethanol production (Baker & Zahniser, 2006). In India, maize is cultivated predominantly as a Kharif crop on 108.87 lakh hectares with productivity of 3 metric ton per hectare and has a modest share of 2.7 percent in global maize production during 2023-24 (Reddy, 2024). Heavy lodging, competition with weed, infestation of disease and pests etc. are some of the obstructions in production of maize. Among all, incidence of diseases and insect pests are main problem. As many as 141 insect pests cause a varying degree of damage right from sowing to harvest or storage (Singh & Jaglan, 2018). The total economic loss of in India due to insect pest attack in maize has been estimated to be 5-15% (Patel & Rajput, 2024). Though chemical insecticides are recommended practices against these insect pests, indiscriminate use of chemical insecticides leads to pesticide resistance, health and environmental concerns. Moreover, chemical insecticides destroy beneficial natural enemies in the agro-ecosystem. Therefore, biological management is the effective and sustainable alternative management method where natural enemies are manipulated for a long-term sustainability of the ecosystem (Zhou et al.,2024). Natural enemies would include insect parasitoids, predaceous arthropods, nematodes, and microbial pathogen such as bacteria, fungi and virus (Babendreier et al., 2020). Among the natural enemies of insect pests, Entomopathogenic nematodes (EPNs) have been recognized as a major natural enemy in agricultural, horticultural, and forestry ecosystem (Koppenhofer et al., 2020). EPNs, *Steinernema* spp. from the Steinernematidae and *Heterorhabditis* spp. from the Heterorhabditidae families under the order Rhabditida are obligate parasites of insects in agricultural crops including maize.

Mode of action of EPNs

The free-living third stage juvenile is a non-feeding stage present in the soil. The infective juvenile (IJ) carry symbiotic bacteria and search for insect host and penetrate into the hemocoel by invading through the natural openings and become parasitic by releasing their symbiont bacteria, *Xenorhabdus* spp. in Steinernematids and *Photorhabdus* spp. in heterorhabditids, respectively (Tarasco et al., 2023). The bacterial symbionts, are responsible for killing the host usually within 24 to 48 h, defending against secondary invaders, and providing the nematodes with nutrition

Ecological role of EPNs

Environment, host and innate characteristics of the nematodes, all influence the potentials of EPNs. For biocontrol efficacy, ecology of the target pest should match with the behavior and action of EPNs. In the agro-ecosystem there should be manipulation of agricultural habitats to optimize environmental conditions to be less favorable for insect pest and more favorable to beneficial organisms and facilitate their persistence. Soil is the natural habitat of EPNs and 90% of insect pest species spend at least part of their life cycle in soil. Therefore, greater understanding of the fundamental ecology of these organisms in the natural environment and post-application would be of immense value in the development of more ecologically sound management approaches (Barbercheck, 2024). EPNs have a broad host range with diverse species. The prevalence of infective juveniles (IJs) of EPNs in different habitats is affected by both intrinsic and extrinsic factors (Stuart et al., 2015). Knowledge about these factors in determining their distribution in agro-ecosystems is essential to enhance the ecosystem service that EPN provide.

In a survey for natural control agents of the fall armyworm (FAW) in corn fields of southern Mexico, demonstrated larval mortality due to entomopathogens was 12.99%, which were prevalent as natural control agents and affected later stages of the larvae (Ruiz-Nájera et al.,2013). Raulston et al., (1992) showed that natural infection of FAW by EPNs with 4% of infection of FAW pupae in maize fields. Plant roots often attract root herbivores that serve as hosts for EPNs, while root architecture can impact EPN movement and host searching ability, thus plants indirectly affect EPN activity and natural occurrence in soil ecosystems (Hazir et al., 2016). Rasmann et al., (2005) and Robert et al., (2017) demonstrated that EPNs were found to orient towards (strongly attracts *H. megidis* and less attracts *H. bacteriophora*) the western corn rootworm (WCR) (*Diabrotica virgifera virgifera*) - damaged maize roots using the root-emitted organic volatile compound sesquiterpene, (E)-β-caryophyllene. WCR larvae are able to sequester benzoxazinoids. This sequestration provides them with resistance against certain strains of *H. bacteriophora* and their symbiotic bacteria (Bruno et al., 2020).

Beneficial behavior of EPNs

EPNs appear to be opportunists rather than biocides (Kaya and Gaugler, 1993). The behavior may be different for different species and even strains or known to change over time under laboratory culture (Ishibashi & Kondo, 1990). The beneficial behavior can be checked in the laboratory before field application (Blanco-P´erez et al., 2024). The ability of IJs to persist and disperse until host location, and infection is a good behavioral mechanism of EPNs. The principle biotic components like soil microorganisms, plants, and invertebrates have a major role on nematode persistence. Persistence in soil in the absence of a host depends upon temperature, humidity, natural enemies, and soil type. Most experiments proved that applied nematodes can persist in field soils long enough to control *D. v. virgifera* larvae (Pilz et al., 2012). Similarly, the EPNs dispersal depends on numerous inherent and extrinsic factors. Active movement increases chances in finding a host and survival. Soil porosity also affects nematode dispersal.

Nematodes disperse passively by rain, wind, soil, insects and human activity. Once the habitat has been selected, some species appear to prefer to search for hosts at or near the soil surface (ambusher) like *S. carpocapsae, S. scapterisci*, and *S. fabii* whereas others are adapted to search deeper in the soil profile (cruiser) like *H. indica*, *H.bacteriophora*, *S. feltiae*, *S. glaseri* , *H. noenieputensis*, *H. safricana*, *S. jeffreyense*, and *S. yirgalemense* (Campbell & Lewis, 2002; Rakubu et al., 2024). Lewis et al., (2015) have demonstrated that cruiser nematodes may shift from ranging to localized search, by decreasing their search area and rate of locomotion. After selection of host, attachment to the host is a requirement to infection. Nictation is a behavior related to nematode orientation to host insects and attachment (Campbell & Gaugler, 1993). When unable to nictate, EPN activity to find host or mobile insects decreases. Penetration or invasion into the host is an important behavior in the infection process. EPNs penetrate through spiracles, oral, anal region or sometimes smooth cuticle. Penetration rates may be species-specific or may vary within populations of the same species, e.g. *S. carpocapsae* and *S. feltiae* (Alonso et al.,2018).

Infective juvenile (IJs) age has a significant effect on host-seeking behavior, penetration and activation. Infection by EPNs is the result of a complex process through releasing the symbiotic bacteria they carry along with excreted / secreted nematode proteins (Alonso et al., 2018). EPN IJ infection is a species-specific and host-specific process and that nematode host preferences coincide. Certain EPN symbionts have shown strong virulence with number of bacterial cells carried by each individual IJ. The virulence of EPNs depends on the host species as well as their developmental stage (Fuxa et al., 1988; Glazer et al., 2025).

When the nematodes become established and reproduce, their progeny continue to infect the target insect (Griffin, 2012). EPN densities are another factor, as lower numbers of IJs needed more time to infect and reproduced inside the insect's body. EPNs are usually applied in high numbers; up to billions of IJs (25 IJs/cm2) is required to increase the chances of finding host insects. EPNs applied with sowing of maize at relatively low rates in the soil persist long enough to potentially control all three larval instars of *D. v. virgifera* (Pilz et al.,2012). Spraying of *H. bacteriophora* HbSD suspension on maize leaves exhibited high lethal effects on FAW larvae at concentrations of 2000 IJs per 3rd stage larva (Chen et al., 2023). Scavenging is another alternative pathway for EPNs. Blanco-Perez et al., (2019) observed that *H.bacteriophora* did not reproduce as a scavenger. Studies have revealed that EPN-infected rootworms release specific volatiles, such as butylated hydroxytoluene, that attracted new rootworms and increased nematode reproductive success (Zhang et al., 2019).

Performance or efficacy of EPNs is the ability to infect host insect, and multiply inside them or to persist in the pest's environment (Shapiro-Ilan et al., 2012). As EPNs are generally isolated from soil habitats, they have been extensively exploited to suppress soil-dwelling insect pests in agricultural fields (Table.1). Better environmental tolerance in EPN strains can be related to geographic origin because EPNs are expected to adapt to native conditions (Glazer, 2002). The effectiveness of EPNs for aboveground applications has been limited due to desiccation and ultraviolet radiation.

Successful parasitism of corn earworm by *S. riobravis* under field conditions may be attributed to its subtropical origin and adaptation to high temperatures (>38℃) (Raulston et al.,1992). Three Turkish strains *viz., S. carpocapsae, S. feltiae* and *H. bacteriophora*, at 30°C on the last instar larvae of the corn stalk borer, *Sesamia cretica* cause mortality of 82, 92 and 94%, respectively (Gozel & Guneş,2013). The osmotic pressure of the spray solution also influences as it increases during evaporative loss of water from the leaf (Glazer & Salame 2000). As *D. v. virgifera* larvae are usually most damaging in clay soils, control efficacies of nematodes are higher in clay soils than in sandy soils. However, the impact of temperature or moisture on EPN efficacy can be nullified by choosing the right EPN strain and application at the right time, with proper application technology (Shapiro-Ilan et al., 2006).

Wright et al., (1993) observed effectiveness of *S. riobravis* when applied to moist soils after irrigation or via in-furrow irrigation against soil-inhabiting stages of corn earworm. After being sprayed by using adjuvants or anti-desiccants on maize leaves against FAW, IJs of *H.bacteriophora* HbSD reduced the risk of desiccation (Chen et al., 2023). The direct application of *S.carpocapsae* and *H. indica,* to the whorl with sand as carrier material may provide better results against FAW.

Conclusion and future perspectives

EPNs are potential natural enemies of insect pests which can reduce pest populations of maize plantation in an ecofriendly way. More works are needed in the interactions of EPNs with other biotic agents or antagonists or the impact of soil habitat complexity. To widen the utilization of EPN, isolation and screening of EPN species/strains that meet the efficacy requirements is also important.

Therefore, there is a need to implement more powerful molecular tools with a finer taxonomic resolution, such as high-throughput sequencing (Depuydt et al., 2024). EPN adaptations and parasitism strategies have widespread ecological implications, from influencing insect populations in natural ecosystems to providing sustainable solutions for pest management in agriculture.

Table 1. Entomopathogenic Nematodes against Insect-Pests of Maize

Pests	Entomopathogenic nematodes	Experimental condition	Mortality (%)	References
Corn borer (*Chilo partellus*)	*Steinernema innovationi*	Lab	60% @ 500 IJ/Pupa	Ramakuwela et al., (2018)
Corn borer (*Chilo agamemnon*)	*Heterorhabditis bacteriophora* (BA1) *S. carpocapsae* (BA2)	Field	Significant reduction of larvae	El-Wakeil & Hussein (2009)
Cutworm (*Agrotis ipsilon*)	*H.indica*+ *Metarhizium anisopliae*	Field	22.18 % decrease in plant mortality @ 0.5 b IJs /ha + 5 X 10^{11} spores/ ha.	Bhagat et al., (2008)
	S.feltiae, Mexican and Kapow *S. bibionis* *H.heliothidis*	Field	50% reduction in plant damage by *S. feltiae*@ 5 × 10^5/ m^2	Capinera et al., (1988)
	H. megidis *H. bacteriophora* *S. carpocapsae* *S. riobrave*	Lab, Pot	Fourth and/or fifth instars were the most susceptible stages to most EPN species, and pupae were the least susceptible	Ebssa & Koppenhofer (2012)
European corn borer (*Ostrinia nubilalis*)	*S. carpocapsae* All and 'Mexican' strains *H. bacteriophora* HP88	Field	Reduced the rate of ear damage from 20% - 5% by *S.carpocapsae* @50,000 IJ / plant	Ben-Yakir et al., (1998)
	H. bacteriophora (BA1) *S. carpocapsae* (BA2)	Field	Significant reduction of larvae	El-Wakeil & Hussein (2009)
	S. feltiae *S. glaseri*	Lab, Greenhouse, Microplot	Effectively controlled damage	Riga et al., (2001)
Asian corn borer (*Ostrinia furnacalis*)	*S. carpocapsae*	Lab	100% pupae mortality	Cheng et al., (1999); Chao et al., (2025)
	S. feltiae	Field	90.5% larval mortality @200 IJs/plant	He et al., (1991)
Fall armyworm (FAW) (*Spodoptera frugiperda*)	*H. indica* *S. carpocapsae*	Semi-field conditions. @ 500 IJs	86.67% by *H.indica*, 83.33% by *S.carcocapsea*	Ratnakala et al., (2023)
	H. bacteriophora HbSD	Lab Pot	3 IJs/ 3rd stage larvae cause 54.39% mortality 78.33% -100% of 5th instar larvae 2000:1 per larva, with a mortality of 51.56% - 68.72%	Chen et al., (2023)

		Field	@10,000IJs/plant, 51.20% @25,000 IJs/plant	
	H. indica *Steinernema* sp. (IBCB-n6)	Lab	100% third-instar larvae @ 280 IJs	Garcia et al., (2008)
	S.carpocapsae	Lab	*S. carpocapsae* + chlorantraniliprole or spinetoram caused larvae mortality of over 90%	Viteri et al., (2018)
	S. feltiae	Field	71% infection, up to 53% reduction of a mixed population of *H. zea* and *S. frugiperda*	Richter & Fuxa (1990)
	H. indica CICR-HI-MN CICR-HI-CL	Lab	High mortality of 3rd, 4th, 5th instar larvae	Shinde et al., (2022)
	S. feltiae *S. glaseri*	Lab, Greenhouse, Microplot	Effectively controlled	Riga et al., (2001)
	S. carpocapsae (All) *H.bacteriophora* (HP88)		100% for the 3rd and 5th larval instars by *S. carpocapsae* @80 IJs/ml 88.9% mortality by *H. bacteriophora*	Sayed et al., (2022)
	H. indica 1 NBAIIH38 *S. carpocapsae* NBAIRS59	Lab Field	100% in third- and fourth-instar larvae. *H. indica* reduced number of larvae and leaf damage scores.	Patil et al., (2022)
	H. indica *H. bacteriophora*, *Heterorhabditis* sp. *S.carpocapsae* *S. arenarium* *S. longicaudum* *S. kushidai*	Lab	*H. indica*, *S. carpocapsae*, *S. longicaudum* highly virulent against late larval and pupal stages	Acharya et al., (2020)
	S.carpocapsae (EGAZ10) *H. indica* (EGAZ5)	Field	Decrease of larvae by 93.3 ± 2.7% by *S.carpocapsae*	Azazy et al., (2025)
	S. arenarium *Heterorhabditis* sp. RSC02	Lab Greenhouse	At 200 IJ/, *S. arenarium*, *Heterorhabditis* sp. caused 100 and 97.6% mortality respectively, 77.5 and 87.5% mortality	Andaló et al., (2010)
Fall armyworm (FAW) (*Spodoptera frugiperda*)	*S.carpocapsae*	Lab, Field	100% of second- and third-instar larvae	Fallet et al., (2022;2024)
	S. feltiae, *S.feltiae* hybrid *S. bibionis*	Lab	*S. feltiae* cause 100% mortality of first-instar @ 30 to 60 IJs /0.7 ml	Fuxa et al., (1988)

			Pupae mortality 7-20%	
	S.carpocapsae *H. bacteriophora*	Lab	100%	Rashed et al., (2024)
	S. carpocapsae *H. indica* (EGAZ2)	Lab	2nd to 6th instars *S. carpocapsae* 100% 150–2400 IJs *H. indica* caused 100% mortality in early instars	Mohamed & Shairra (2023)
	S. diaprepesi	Lab	100% @ 100 IJs	Caccia et al., (2014)
	H. indica *S. siamkayai*	Lab Greenhouse conditions (pot)	83% of 2nd instar larvae with *H. indica* at 250 IJs/ ml 68% mortality with *S. siamkayai* at 300 IJs /ml. 58% by *H. indica* 45% by *S.siamkayai* at 50,000 IJs/ ml	Wattanachaiy ingcharoen et al., (2021)
Western corn rootworm, *Diabrotica virgifera virgifera*	*H. bacteriophora*	Field Field	At 2 billion nematodes / ha reduced *D. v. virgifera.* Reduced *D. v. virgifera* by 65 ± 34%	Toepfer & Zellner (2017); Pilz et al., (2009)
	H. bacteriophora, *H. megidis,* *S. feltiae,* *S. arenarium,* *S. kraussei* *S. carpocapsae* *S.glaseri*	Lab Field	All larval instars and even pupae are effectively killed; Adults appeared less susceptible; *S abassi* was found intermediate; *S carpocapsae* and *S glaseri* less virulent; *H. bacteriophora*, *H. megidis* are highly effective	Jackson, (1996); Jackson & Brooks, (1989;1995); Jackson & Hesler (1995); Journey& Ostlie (2000); Toepfer et al., (2005,2008); Kurtz et al., (2009); Hiltpold et al., (2009,2012); Pilz et al., (2011); Modic et al., (2020); Jaffuel et al., (2019;2020); Toth et al., (2022)

	H. bacteriophora	Field	Root damage was less	Kim et al., (2021)
	S. carpocapsae 'Mexican' and 'All' strains	Field	Significantly lower root injury	Ellsbury et al., (1996)
	H. bacteriophora, *H. megidis* *S.feltiae* *S. carpocapsae* *S. diaprepesi* *S.riobrave* *H. bacteriophora* (Missouri wild-type) *S. rarum*	Lab	Third-instar larva @60-120 IJs/larva Except *S. rarum* All were highly effective in mortality	Geisert et al., (2018)
	S. feltiae *S. glaseri*	Lab, Greenhouse , Microplot	Effectively controlled	Riga et al., (2001)
Northern corn rootworm (NCR), (*Diabrotica barberi*)	*S. feltiae* Mexican *S. bibionis*	Lab	First instar NCR @10,000 IJs/ linear meter of corn row. Reduction of larvae	Thurston & Yule (1990)
Stem borer (*Sesamia calamistis*)	*Heterorhabdidtis* sp.	Field	Laval mortalities 4-57%	Claudius-Cole (2018)
	S. innovationi	Lab	100% larval mortality	Ramakuwela et al., (2018)
Corn borers (*Sesamia cretica*)	*H. bacteriophora* (BA1) *S. carpocapsae* (BA2)	Lab	97% and 100% mortality of larvae	El-Wakeil & Hussein (2009)
	H. bacteriophora *H.taysearae*	Lab, Field	1000 IJs / ml 40.62% - 67.86% mortality	Saleh et al., (2000)
	S.carpocapsae, *S.feltiae* , *H. bacteriophora*	Lab	82, 92 and 94% mortality of last instar larva	Gözel & Güneş (2013)
	S. carpocapsae All, *H. bacterionphora* HP88	Lab, Field	100,200 and 400 IJs of *S.carpocapsae* /ml) cause 20.0 - 33.3 % mortality ; 28 % reduction of dead heart plants.	Halawa et al., (2007)
Corn earworm, (*Helicoverpa zea*)	*H.bacteriophora* (HP88 and VS strains), *H.floridensis* (K22 strain), Hgkesha (Kesha strain), *S. carpocapsae* (All and Cxrd strains), *S. feltiae* (SN strain), *S. rarum* (17c+e strain), *S. riobrave* (355 and 7–12 strains	Lab Field at 20 IJs/cm2 and 2 ml/plant	98.3% - 100.0% on first to fourth instars, fifth instars, and pupae *S. riobrave* 355 cause larval mortality 78.2%	Zhang et al., (2024)

	S. riobravis *S. carpocapsae*	Field	200,000 IJs/m^2 *S. riobrave* cause 95% parasitism	Cabanillas & Raulston (1995;1996)
	Neoaplectana carpocapsae DD136	Field	4×10^4 IJs / ml sprayed twice at 3 days interval showed 55% control	Bong & Sikorowski (1983); Bong (1986)
	S. carpocapsae	Field	40,000 IJs /ml 74.5 % mortality	Purcell et al., (1992)
	S. riobravis	Field	1.2×10^7 IJs/m^2 of soil cause 91.3% mortality	Feaster & Steinkraus (1996)
	S. riobravis *S. carpocapsae*	Field	*S. riobravis* @ 200,000 IJ/m² cause 97% parasitism	Cabanillas & Raulston (1996)
	Steinernema sp.	Field	Prepupae and pupae 11.6% were parasitized	Raulston et al., (1992)
	S.adamsi	Lab	74.2% - 100% 1st to 4th instars mortality, Pupae were not killed; *S. adamsi* with 0.05% sodium alginate and 0.02% Congo red 98% larval mortality	Glover et al., (2025)
Corn earworm, (*Helicoverpa armigera*)	*H. amazonensis* MC01 *H. amazonensis* JPM4 *S. carpocapsae*	Lab, greenhouse	80% mortality @400 IJs/ pupa	Andalo et al., (2021)
Grey maize weevil (*Tanymecus dilaticollis*)	*S.carpocapsae* *H.bacteriophora*	Lab	*S.carpocapsae* @ 83-333 IJs /adult caused > 94% mortality; *H. bacteriophora* caused 27-61% mortality	Toshova et al., (2024)
Seedcorn maggot (*Delia platura*)	*S. feltiae* *S. glaseri*	Lab, Greenhouse , Microplot	Significant larval mortality	Riga et al., (2001)

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