Microscopic Hunters in the Soil: Entomopathogenic Nematodes as Allies in Crop Protection

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Introduction:

Insect pests take a heavy toll on crops, and many of the worst offenders spend a hidden part of their lives underground. White grubs chew roots, weevil larvae tunnel into stems and tubers, and cutworms hide in the soil by day, all beyond the reach of most foliar sprays. Chemical insecticides applied to soil are costly, can harm beneficial organisms, and with repeated use they select for resistant pest populations.

Nature offers a different tool: parasites of insects that live in the soil itself. Among the most successful are **entomopathogenic nematodes** (EPNs), microscopic roundworms whose infective stage is roughly a millimetre long or less. The name simply means "insect-disease-causing". EPNs seek out insects, kill them within days and multiply inside the dead body. They have been used in biological control for decades and are sold commercially in many countries (Lacey and Georgis, 2012).

Nematode and Bacterium: A Lethal Partnership

Two families matter for plant protection: Steinernematidae, with the genus *Steinernema*, and Heterorhabditidae, with the genus *Heterorhabditis*. Each carries a bacterial partner in its gut: *Steinernema* with bacteria of the genus *Xenorhabdus*, and *Heterorhabditis* with *Photorhabdus*. The worm is the delivery vehicle; the bacterium is the killer (Dillman et al., 2012). Neither does well alone. The bacteria depend on the nematode to reach new hosts, and the nematode depends on the bacteria to overcome the insect's defences and to turn its body into food.

Life Cycle: From Infective Juvenile to Next Generation

The only stage that lives freely in soil is the third-stage infective juvenile, a non-feeding larva that serves as the nematode's travelling form. It searches for a host and enters through natural openings such as the mouth, anus and breathing pores (spiracles); *Heterorhabditis* can also pierce thin areas of the cuticle with a small tooth (Kaya and Gaugler, 1993). Inside the insect's

body cavity the juvenile releases its bacteria, which multiply and produce toxins and enzymes. The insect typically dies within one to three days (Kaya and Gaugler, 1993).

The nematodes then feed on the bacteria and the softened tissues, mature and reproduce for one to several generations. When the food runs out, a new generation of infective juveniles leaves the cadaver and returns to the soil, often after one to two weeks, ready to hunt again. A single dead caterpillar or grub can release many thousands of them.

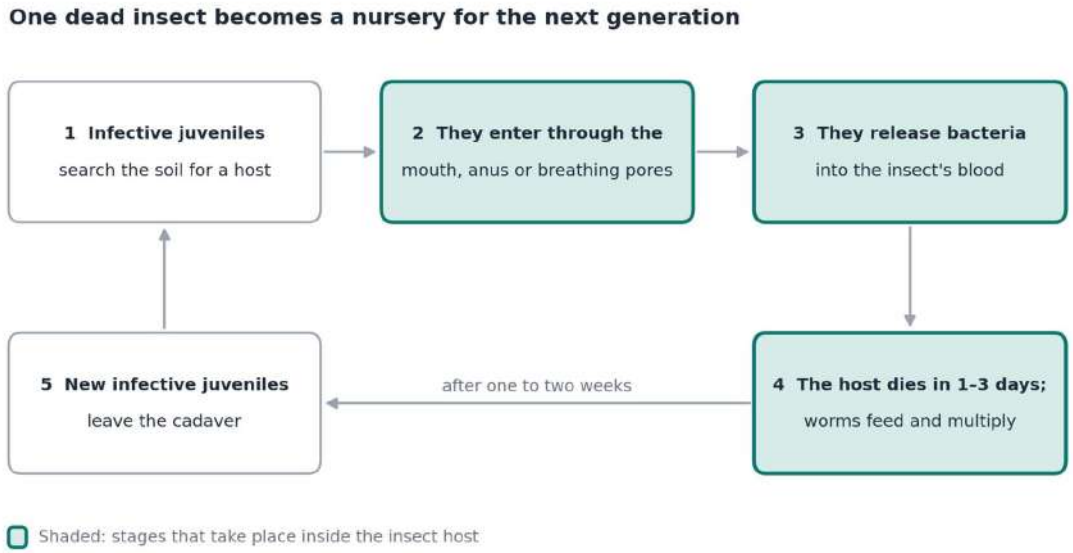


Figure 1. Life cycle of an entomopathogenic nematode inside its insect host (Kaya and Gaugler, 1993; Dillman et al., 2012).

Hunting Strategies: Ambushers and Cruisers

EPNs differ in how they hunt. Ambushers, such as *Steinernema carpocapsae*, stand on their tails near the soil surface and wait, sometimes leaping, to attach to a passing insect. Cruisers, such as *Heterorhabditis bacteriophora* and *Steinernema glaseri*, move through the soil following carbon dioxide and other chemical cues from roots and hosts. Many species fall between the two (Lewis et al., 2006).

The strategy matters when choosing a nematode. Ambushers suit mobile pests that move near the surface, such as cutworms, while cruisers suit sedentary hosts deeper in the soil, such as white grubs. Table 1 summarises the species most often used.

Table 1. Commonly used entomopathogenic nematodes (compiled from Kaya and Gaugler, 1993; Lewis et al., 2006; Lacey and Georgis, 2012).

Nematode	Bacterial partner	Hunting style	Temperature tendency	Typical targets
Steinernema carpocapsae	*Xenorhabdus nematophila*	Ambusher	Moderate to warm	Cutworms, armyworms, webworms and other surface-active larvae

S. feltiae	*X. bovienii*	Intermediate	Cool to moderate	Fungus gnats, thrips pupae in soil, leaf miners
S. glaseri	*X. poinarii*	Cruiser	Warm	White grubs (scarab larvae)
Heterorhabditis bacteriophora	*Photorhabdus luminescens*	Cruiser	Moderate to warm	White grubs, weevils
H. indica	*P. luminescens*	Cruiser	Warm to hot (tropical)	Soil pests of tropical and subtropical crops

Target Pests and Cropping Systems

The strongest results come against insects that live in or pass through the soil. Commercial products target scarab grubs in turf and field crops, vine weevil in nurseries and berries, fungus gnats in greenhouses and cutworms in vegetables. EPNs can also reach insects hidden in tunnels, such as the larvae of some boring moths and weevils, because the juveniles travel along galleries in films of water where sprays cannot follow (Georgis et al., 2006).

Above ground, results are less consistent. Sunlight and dry air kill infective juveniles quickly, so foliar applications work best in humid, shaded conditions, in the evening, with protective additives, and against pests sheltered in leaf mines, buds or plant crevices (Arthurs et al., 2004).

Greenhouses are a particular success story. The enclosed, humid environment and the absence of drying sun favour nematodes, and *Steinernema feltiae* applied to the growing medium is widely used against fungus gnat larvae, which damage the roots of young seedlings and cuttings (Lacey and Georgis, 2012).

Plant Signals: Roots That Call for Help

Plants are not passive victims. In a well-known study, maize roots attacked by western corn rootworm larvae released a volatile compound, (E)-β-caryophyllene, which attracted the nematode *Heterorhabditis megidis* through the soil to the damaged roots (Rasmann et al., 2005). Plants thus recruit nematodes as bodyguards. This opens the possibility of breeding crops, or applying signals, that make the partnership between roots and nematodes even stronger.

Mass Production and Formulation

Commercial supply depends on mass production. Small producers rear nematodes in live insect larvae, commonly the greater wax moth, and harvest the juveniles as they emerge from the cadavers. Large companies grow them in liquid culture in fermenters, feeding the bacteria and nematodes on a nutrient medium (Ehlers, 2001). The harvested juveniles are then formulated, for example on sponges or clay or in water-dispersible granules, so that they survive transport and storage (Georgis et al., 2006).

Field Application: Practical Guidelines

EPNs are living organisms, so handling decides success. A few practical rules recur in the literature (Georgis et al., 2006; Lacey and Georgis, 2012):

- **Match the species to the pest and the climate.** Use a cruiser for white grubs and an ambusher for surface-active caterpillars, and prefer a heat-tolerant species in the tropics.
- **Apply in water.** Nematodes are mixed into water and sprayed, drenched or sent through drip lines. Fine screens and high pressures can block or damage them.
- **Use a sound dose.** A commonly cited rate is about 2.5 billion infective juveniles per hectare for soil pests.
- **Protect them from sun and drying.** Apply in the evening or on overcast days, and irrigate before and after so that the soil stays moist.
- **Keep them fresh.** Store them cool, use them before the expiry date and check that the juveniles are moving and alive.

Integration with Pest Management and Safety

EPNs combine well with other tools. Many chemical insecticides and fungicides can be used alongside them, and some combinations, notably certain neonicotinoids with nematodes against white grubs, work better together than either alone, although a few nematicides and other chemicals are harmful and should be checked before mixing (Koppenhöfer and Grewal, 2005).

They are also remarkably safe. EPNs do not infect people, livestock or plants, and many countries exempt them from the registration normally required for pesticides (Akhurst and Smith, 2002). That makes them attractive for organic farming, for greenhouses where workers are present, and for fields where pollinators and natural enemies must be protected. Some non-target insects can be infected under laboratory conditions, but field effects are generally small. For growers aiming at residue-free produce for organic or export markets, EPNs leave no pesticide residue on the harvest.

Experience from India and the Tropics

Tropical conditions call for nematodes that tolerate heat. *Heterorhabditis indica* was first described from India (Poinar et al., 1992), and *Steinernema thermophilum*, a heat-tolerant species, was described from Indian soil (Ganguly and Singh, 2000). Indian research institutions maintain native isolates and have tested them against a range of soil and hidden pests (Divya and Sankar, 2009). Local isolates are often the best choice because they are already adapted to local soils and temperatures.

Limitations and Challenges

EPNs are not a cure-all, and the record includes failures as well as successes (Georgis et al., 2006). The main hurdles are:

- **Environmental sensitivity.** Heat, drought, ultraviolet light and some soil types, especially heavy clays that restrict movement, reduce performance.
- **Cost and shelf life.** Living products are more expensive and less durable than chemical insecticides, so careful logistics and timing matter.
- **Variable field results.** Success depends on matching the right nematode to the right pest stage under suitable conditions.
- **Production.** Rearing nematodes in live insects is labour-intensive, while fermenter-based production scales better but is more demanding (Ehlers, 2001).

Future Prospects

Research is tackling these limits on several fronts: formulations that keep juveniles alive longer, strains selected or improved for heat and drought tolerance, and cheaper mass production. Another promising idea is to release nematodes inside infected insect cadavers, which can improve their survival and dispersal in the field (Shapiro-Ilan et al., 2017). Reviews of ecology and applied technology suggest that the role of EPNs in sustainable crop protection will keep growing (Campos-Herrera, 2015).

Conclusion

Entomopathogenic nematodes are living insecticides that find their targets on their own, act quickly and leave no residue. They work best against soil-dwelling and hidden pests, when the right species is applied with care to moist soil, and they sit comfortably inside integrated pest management.

For farmers and students of plant protection alike, they are a reminder that some of the best solutions already live in the soil. Understanding them well is the first step to putting them to work.

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