

Review

Nematodes Versus White Grubs: Long But Challenging Association

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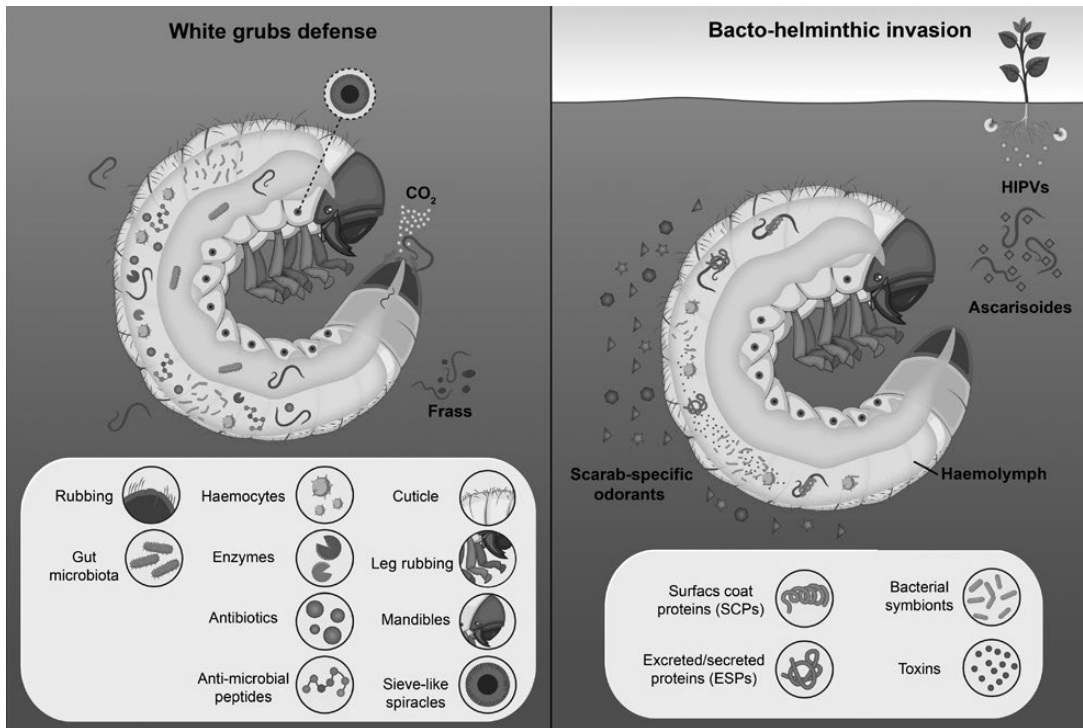
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Abstract

Soil as a shared habitat of white grubs and entomopathogenic nematodes (EPNs) is a double-edged sword from the biological control point of view. Soil encompasses a diverse array of EPNs that could be exploited in grub microbial control; on the other hand, soil promotes the natural resistance of grubs to EPNs via the battle between both sides within the soil matrix. White grubs and EPNs have been armed in this battle by a multifaceted range of mechanisms, namely grub structural and physiological barriers, antagonism of grub gut microbiota toward the nematode bacterial symbionts, EPN excreted/secreted proteins, surface coat proteins, ascaroside pheromones produced by EPNs, and evolution of EPN resistance to herbivore self-defense. From the evolutionary point of view, EPN–grub interactions, the most advanced (sophisticated) association among others, could have evolved from other types of associations. Entomophilic nematode (e.g., *Pristionchus* spp.), the cognate bacterium and scarab associations along with the formation of dauer juveniles, are proof of pre-adaptation to entomopathogeny in a continual evolution. Here, we delve into the salient features of each component of EPN–white grub–host plant tripartite interactions as well as hints to improved exploitation of EPNs for grub management. Also, evolutionary associations between nematodes and scarabs will be reviewed, in short.

Graphical Abstract



Key words: nematode, scarab, interaction, plant, association

White grubs, the larvae of root-feeding scarab beetles (Coleoptera: Scarabaeidae), contain numerous important pests of agriculture and forestry in different geographical regions owing to the diversity of species and the consequent variety of niches and feeding preferences. Achieving efficient grub control has been difficult due to the cryptic nature of grubs and their occurrence in diverse ecosystems. Grubs have evolved efficient defense mechanisms like midgut juice rich in proteinases which results in low efficiency of some grub control methods, e.g., chemical control (Wagner et al. 2002). Interestingly, a diverse group of natural enemies, including entomopathogenic nematodes (EPNs), are associated with white grubs (Potter 1998, Karimi et al. 2019). Among natural enemies of grubs, EPNs, sharing the same habitat, have received considerable interest in control of grubs (Grewal et al. 2005) and EPN success in grub control can be equal to the conventional insecticides in some circumstances (Grewal et al. 2004, Guo et al. 2013, Patil et al. 2020). Nevertheless, their unpredictability and inconsistency under natural conditions, along with ecological and commercial challenges (Grewal et al. 2005, Elmowitz et al. 2013, Del Valle et al. 2017), could damage their approval and decline the public demand for them. Therefore, deep insight into EPN-grub-host plant interactions would be conducive to a more efficient and sensible management of scarabs. This review highlights the effect of different components in the tripartite interactions and clarifies the significant factors involved in the success or failure of EPNs as biological control agents against white grubs.

Notably, all types of nematode–arthropod associations (phoresy, necromeny, facultative parasitism, and obligate parasitism) have been discovered in case of scarab–nematode interactions. The evidences and examples that consolidate the concept of transition from free-living nematodes to obligate parasites of scarabs during evolutionary history will be discussed in the next section.

Scarab–Nematode Associations: Evolutionary Perspective

Scarab–nematode associations compose a wide range including phoresy, necromeny (embarking on the live host and waiting for the cadaver colonisation), ecto-, endo-parasitism, and entomopathogeny. *Rhabditis adenobia* Poinar (Rhabditida: Rhabditidae), *Mesorhabditis irregularis* (Körner) (Rhabditida: Rhabditidae), and *M. quercophila* Rühm were found in a phoretic relationship with *Oryctes monoceros* L. (Coleoptera: Scarabaeidae) and *Melolontha afflicta* (Coleoptera: Scarabaeidae), respectively (Azizoglu et al. 2016). Necromenic nematodes of Diplogastridae and Diplogasteroididae viz. *Pristionchus pacificus*, *P. maupasi*, *Diplogaster* spp., and *Diplogasteriodes* spp., were recovered from different species within Scarabaeidae (Chamberlin 1944, Kiontke et al. 2001, Manegold and Kiontke 2001, Herrmann et al. 2006, Darsouei et al. 2014). According to Hong et al. (2008), these nematodes even co-occur on the same beetle individual and scarabs represent a microcosm for nematodes.

The parasitism of *Cephalobellus* spp. (Oxyurida: Thelastomatidae) in different species of grubs stands somewhere in the middle of this spectrum. *Cephalobellus papilliger* Cobb. (syn. *Scarabanema cylindricum*), *C. leukarti* Hammerschmidt, *C. brevicaudatum* (Leidy), *C. galliardi* Basir, and *C. lobulata* Camino & Reboledo, were recovered from a wide range of scarabs across the world (Christie 1933, Camino and Reboledo 2000, Karimi et al. 2019). Among the ecto-parasitic nematodes of scarabs, *Cephalobus* (*Acrobeloides*) *persegnis* Bastian and *Mesorhabditis spiculigera* Steiner have been reported from *Scarabaeus sacer* L. (Coleoptera: Scarabaeidae) (Azizoglu et al. 2016).

Steinernema scarabaei Stock & Köppenhofer (Rhabditida: Steinernematidae), *S. kushidai* Mamiya (Rhabditida:

Steinernematidae), and *Heterorhabditis* spp. (Rhabditida: Heterorhabditidae) appear to be associated with scarabs in an obligate entomopathogenic relationship and *Oscheius rugoensis* Zhang (Rhabditida: Rhabditidae) (Darsouei et al. 2014) and *Rhabditis regina* (Rhabditida: Rhabditidae) (Schulte and Poinar 1991, Jimenez-Cortés et al. 2016) in a facultative entomopathogeny. Either of the entomopathogenic and necromenic relationships involve specific bacteria (Shi and Bode 2018), and the conservation of some scarab–nematode associations indicate a link between scarab bacterial communities and their associated nematodes (Koneru et al. 2016). Interestingly, necromenic nematodes are in competition with EPNs and can feed on scarabs killed by EPNs (Blanco-Perez et al. 2017).

It has been postulated that insect parasitism evolves by transition from free-living insect associates to parasites, providing the formation of a dauer juvenile (J3) and special adaptations in the ancestral lineage as bacterial feeding inhabitants of decaying materials (Sudhaus 2008, 2010), similar to grub habitats. The transformed dauer juveniles and association with the cognate bacteria (*Pseudomonas*, *Serratia*, *Bacillus*, and *Enterobacter*) (Enterobacteriales: Enterobacteriaceae) are evidenced in *Pristionchus* and *Diplogasteriodes*, two closely scarab-associated nematodes. Even within one nematode genus, i.e., *Caenorhabditis elegans* Maupas (Rhabditida: Rhabditidae) and *C. briggsae* Dougherty & Nigon, both free-living and entomopathogeny have been witnessed.

The transitional phases are also observed in the bacteria ranged from trophism and simply vectored by free-living nematodes to mutualism with entomopathogenic nematodes (Dillman et al. 2012) and insect-pathogenic on their own. The genus *Serratia* is symbiont of *Oscheius* spp. while *Serratia entomophila* Grimont is an entomopathogenic bacteria of the grass grub *Costelytra zealandica* (White) (Coleoptera: Scarabaeidae).

White Grub Management

Due to the white grub terrestrial habitats, a wide range of soil-borne entomopathogens, e.g., entomopathogenic nematodes have been isolated from grubs. *Steinernema arenarium* (Artyukhovsky), *S. glaseri* Glaser, *S. kushidai*, *S. scarabaei*, *Heterorhabditis megidis* Poinar, Jackson & Klein were originally collected from naturally infected white grubs and several species like *Steinernema carpocapsae* Weiser and *Heterorhabditis bacteriophora* use grubs as natural hosts (Poinar 1990, Karimi and Salari 2015). Conventionally, many of the early studies use original generic names of EPNs, i.e. *Neoaplectana* for *Steinernema*. The first attempt to use EPNs for white grub control started when Glaser et al. (1935) tried to release *Neoaplectana* (now *Steinernema*) *glaseri* Steiner, discovered from *Popillia japonica* Newman, against the grubs; although they could not get much success mainly due to the unawareness of the bacterial symbiont role in infection along with climatic conditions (Gaugler et al. 1992). Subsequently, *Heterorhabditis* (*Neoaplectana*) *hopta* (Turco) and *Steinernema* (*Neoaplectana*) *glaseri* were isolated from *P. japonica* and *Strigoderma arboricola* F. (Coleoptera: Scarabaeidae) grubs, respectively (Turco 1970, Poinar 1978).

EPNs are considered effective biocontrol agents for terrestrial pests; however, their application for grubs has not always been successful except for some species. Grubs of *P. japonica*, *Cyclocephala* spp. Dejean, *Rhizotrogus majalis* Razoumowsky, *Anomala orientalis* Waterhouse, *Maladera castanea* (Arrow), *Phyllophaga* spp. Harris, *Polyphylla* spp., *Ectimohoplia rufipes* Motschulsky, *Phyllognathus dionysius* Fabricius, *Brahmina coriacea* (Hope), *Holotrichia parallela* Motschulsky, *Hoplia philanthus* Fuessly, and *C. zealandica*

have been inconsistently controlled by EPNs under field conditions with variable degrees of control (Table 1).

To date, *S. scarabaei*, *S. glaseri*, *S. kushidai*, *Heterorhabditis marelata* Liu and Berry, *Heterorhabditis zealandica* Poinar, and *H. bacteriophora* have been commercialized for grub control (Grewal et al. 2005, Koppenhöfer et al. 2020). In general terms, *S. scarabaei* and *S. kushidai* work well for most grub species especially Melolonthinae and Rutelinae subfamilies while some strains of *H. bacteriophora* and *H. zealandica* are advantageous choice for control of Dynastinae (Koppenhöfer et al. 2004).

Tripartite Interactions

Bacto-helminthic Complex

Nematode

Selection of EPNs for a target pest species depends on factors such as nematode host range, foraging strategy, and role of environmental factors on survival and efficacy of EPNs (Hajek and Shapiro-Ilan 2018). Both virulence and persistence are important factors in EPN success for grub control (Koppenhöfer and Fuzy 2009). Poor field efficacy could be explained by low EPN persistence (Georgis et al. 2006). Poor adaptation of a nematode species to the target host (host unsuitability) could be the causal factor of low efficacy.

EPNs can evade, suppress, or modulate the immune response of white grubs. Screening for nematode species/strain with an ability to overcome or evade the host resistance/defense response is the first step to select the most effective nematode species/strain for a particular host (Wang et al. 1994). Koppenhöfer et al. (2007) reported that parameters of incurred mortality, establishment, and lethal time in EPNs could be influenced by white grub species. Moreover, they showed no two nematode species correspond well in terms of the aforementioned factors for all tested white grub species, but one particular EPN shows very similar penetration sites for various grub species.

Each nematode species has some dispersal and foraging traits that are suitable to infect grubs and others that fail to work for scarab infection (Table 2).

Improved host finding is one of the favorable traits of EPNs as biocontrol agents against white grubs (Gaugler et al. 1994a, Hiltbold et al. 2010, Salame et al. 2010). Previous studies emphasized on selection pressure involved in detecting sedentary host chemical cues by EPNs, thereby allowing us to select for ambusher populations sensitive to long-range cues (Gaugler 1988, Gaugler et al. 1990). Lewis et al. (1992, 1993) support the cruise seeker reliance on volatile host cues, preferably CO₂ to alter their behavior and find immobile subterranean hosts. The classification of EPNs as discrete (real) cruiser, ambushers and intermediate, has been replaced by the concept that many EPNs can take either ambushing/sprinting or cruising strategy depending on the environment and insect hosts (Wilson et al. 2012, Bal et al. 2014, Gang and Hallem 2016). EPNs are often able to cruise toward host-emitted sensory cues. EPN ecological host range could be affected by various factors, including spatial and temporal factors, e.g., asynchronous life cycles and habitat preference with the target pest (Grewal et al. 2005). EPNs are confined in small geographic areas (Tarasco et al. 2015, Tumialis et al. 2016, Abate et al. 2017). This confinement exerts sufficient pressure on each population to adapt to local hosts and deal with their defense mechanisms through different approaches (Bruno et al. 2020).

On the other hand, EPNs show group movement and aggregate distribution (Stuart and Gaugler 1994, Shapiro-Ilan et al. 2014);

Table 1. Efficacy of entomopathogenic nematodes against white grub species under field conditions

Scarab species	Nematode species/strain	% Control	System
<i>Popillia japonica</i>	<i>H. bacteriophora</i> GPS11	34–97 (Grewal et al. 2004)	Lawn
	<i>H. bacteriophora</i> TF	65–92 (Koppenhöfer and Fuzy 2003a, b)	Ryegrass field
	<i>H. bacteriophora</i> ItH-LU1	44–93	Hayfield
	<i>H. bacteriophora</i> (Larvanem)	46 (Marianelli et al. 2018)	Lawn
	<i>H. zealandica</i> X1	73–98 (Grewal et al. 2004)	Ryegrass field
	<i>S. scarabaei</i>	100 (Koppenhöfer and Fuzy 2003a)	Lawn
	<i>S. kushidai</i>	88 (Cappaert and Koppenhöfer 2003)	Golf course
	<i>S. carpocapsae</i>	70–80 (Koppenhöfer et al. 2000a)	Golf course
<i>Cyclocephala borealis</i> <i>Cyclocephala hirta</i>	<i>H. bacteriophora</i> GPS11	53 (Shetlar et al. 1988)	Lawn
	<i>H. bacteriophora</i> TF	47–83 (Grewal et al. 2004)	Ryegrass field
	<i>H. zealandica</i> X1	6–20 (Koppenhöfer and Fuzy 2003a)	Lawn
	<i>S. kraussei</i> UK	72–96	Ryegrass field
	<i>S. glaseri</i> MB	50	Bluegrass
	<i>S. scarabaei</i>	0 (Grewal et al. 2004)	Golf course
	<i>H. bacteriophora</i> NC1	58–84 (Koppenhöfer and Fuzy 2003a)	
	<i>S. kushidai</i>	<20 (Koppenhöfer et al. 2000a)	
<i>Rhizotrogus majalis</i>	<i>S. glaseri</i> NC	50 (Koppenhöfer et al. 2000a)	
	<i>S. kushidai</i>	~30 (Koppenhöfer et al. 2000b)	
<i>Anomala orientalis</i>	<i>H. bacteriophora</i> TF	38	Lawn
	<i>S. scarabaei</i>	88 (Cappaert and Koppenhöfer 2003)	
<i>Maladera castanea</i>	<i>H. bacteriophora</i> TF	0–53 (Koppenhöfer and Fuzy 2003a, 2003b)	Ryegrass
	<i>S. glaseri</i> Dongrae	49 (Koppenhöfer et al. 1999)	Turfgrass
	<i>S. scarabaei</i>	77–100 (Koppenhöfer and Fuzy 2009)	Blueberries
<i>Phyllophaga</i> sp. <i>Polyphylla comes</i>	<i>S. scarabaei</i>	50–95 (Polavarapu et al. 2007)	Ryegrass
	<i>H. bacteriophora</i> TF	12–33	
<i>Polyphylla olivieri</i> <i>Ectinohoplia rufipes</i>	<i>S. scarabaei</i>	71–86 (Koppenhöfer and Fuzy 2003c)	
	<i>S. feltiae</i> DD-136	43	Tree plantations
<i>Phyllognathus dionysius</i>	<i>Heterorhabditis heliothidis</i>	69 (Kard et al. 1988)	
	<i>H. bacteriophora</i> (Larvanem)	6.25–11.52 (Haji Allahverdipour and Sheikhi Garjan, 2019)	Turfgrass
<i>Brahmina coriacea</i>	<i>S. carpocapsae</i> (BioSafe)	70.2–80	Golf course
	<i>S. glaseri</i> Dongrae	79.4 (Choo et al. 2002)	
<i>Holotrichia parallela</i>	<i>H. indica</i>	77.80–83.98	Turmeric
	<i>S. carpocapsae</i>	55.50–56.65 (Patil et al. 2020)	
<i>Hoplia philanthis</i>	<i>H. indica</i>	66–80	Potato Fields
	<i>S. carpocapsae</i>	83 (Sharma et al. 2009)	
<i>Costelytra zealandica</i>	<i>Steinernema longicaudum</i> X-7	96.8	Peanut Fields
	<i>H. bacteriophora</i> H06	94.1	
<i>Costelytra zealandica</i>	<i>S. carpocapsae</i> All	35.1 (Guo et al. 2013)	
	<i>Heterorhabditis bacteriophora</i> (Nema-green)	39–66 (Ansari et al. 2006)	Lawn
<i>Costelytra zealandica</i>	<i>Steinernema</i> (<i>Neoaplectana</i>) <i>glaseri</i>	66 (Kain et al. 1982)	Pasture

presumably, patchiness in EPN distributions does not contribute much to infection of hosts with an aggregated distribution like white grubs (Campbell et al. 1998). The vertical and horizontal stratification of EPNs and scarabs in the soil could be an impediment in the success of EPNs against sessile grubs. Conversely, it is also believed that patchily distributed hosts are a causal factor in aggregation of EPNs (Stuart et al. 2006).

There are several traits in endemic EPNs in terms of host seeking and infectivity which are essential for this natural association. Understanding the differences in infection routes and optimum soil parameters has conferred enhanced effectiveness of EPNs against white grubs (Lacey et al. 2015).

Both nematodes and their bacterial symbionts have inhibitory activity against the host immune system. *Steinernema glaseri* employs anti-immune proteins like surface coat protein (SCP3a) to suppress immune system of *P. japonica* through hemocyte lysing activity and reduction in melanotic encapsulation phagocytosis (Wang and Gaugler 1999). The SCPs from different nematode species show intra- and inter-species variation and host specificity but do not

convey host susceptibility (Li et al. 2007). Although some virulent EPN species/strains might lack these types of proteins, it is possible to confer this trait by crossing the EPNs with feral field populations featuring SCPs (Rivera et al. 2016).

It has been postulated that root herbivores can utilize plant secondary metabolites for self-defense against their own enemies and EPNs can evolve resistance to these defenses (Zhang et al. 2019). Bruno et al. (2020) isolated several strains of *H. bacteriophora* from corn fields with long history of *Diabrotica virgifera virgifera* LeConte (Coleoptera: Chrysomelidae) infestation. Some of the strains were able to overcome the benzoxazinoid-based resistance of *D. virgifera virgifera*. They implied that EPNs belonging to an environment rich in plant defense metabolites, e.g., benzoxazinoids, might have shared an evolutionary history with benzoxazinoid containing root herbivores and have an enhanced capacity to resist the benzoxazinoid-dependent defenses of herbivores. It has been concluded that exploiting this counteraction through breeding or engineering of EPNs likely enhances EPN efficacy against root-feeding pests (Hiltpold et al. 2010, Bruno et al. 2020).

Table 2. EPNs strengths and drawbacks in white grub control (Gaugler et al. 1997, Potter 1998, Koppenhöfer and Fuzy 2003a, Jackson and Klein 2006, Bal and Grewal 2015)

Nematode species	Pros	Cons
<i>H. bacteriophora</i>	Virulent and grub-active strains; Appropriate foraging strategy; Quick orientation toward non-mobile hosts; Good persistence	Inconsistent virulence to grubs; Differential infectiousness of individuals; Challenge in production
<i>S. scarabaei</i>	Specificity; High virulence; Evolved to overcome grubs immunity; Outstanding persistence; Recycling in grubs	Absence of widespread commercialization; Not adapted for in vitro culture; patchy distribution
<i>S. kushidai</i>	Grub-active strains; Significant searching ability and penetration rate	Absence of widespread commercialization
<i>S. glaseri</i>	Great recovery at farthest distance;	Inconsistent virulence to grubs; Challenge in production
<i>S. carpocapsae</i>		Lack of appropriate foraging strategy, scarab recognition, evasion and weak invasion; limited mobility; wide host range; sexual reproduction

Grewal et al. (2004) refer to nematode strain as one of the key variables in EPN efficacy. Different strains of a particular nematode species have different host specificity and even in the same host, they show varying degrees of penetration efficiency and elicit various intensities of immune responses (Grewal et al. 2002, Li et al. 2007). An et al. (2012) even detected difference in virulence of inbred lines of *H. bacteriophora* and attributed this to EPN evasion of encapsulation.

Other variants such as the concentration of penetrated infective juveniles (IJs), age of IJs, and laboratory propagation, i.e., the number of EPN generations and infection rate could have an impact on EPN virulence (Kenney et al. 2019, Eliáš et al. 2020).

Ascarosides as self-cue

EPNs pheromones, ascarosides blends, play a major role with various effects in IJ behaviors at emergence from insect cadavers, dispersal and foraging stages under natural conditions. Cadaver-derived ascarosides shorten IJ quiescence and promote IJ dispersal, leading to improved EPN efficacy and downgrading the negative effect of low field temperatures (Oliveira-Hofman et al. 2019, Kaplan et al. 2020). Nematode pheromones could be employed in biocontrol of pests, and the pheromone-based products for instance, Nemastim have been patented as a nematode conditioner. Presumably, infection of grubs relatively resistant to EPNs could be promoted by the use of nematode pheromone (Shapiro-Ilan et al. 2019). EPN response to these pheromones is known to be highly conserved across species (Choe et al. 2012, Kaplan et al. 2012); nevertheless, enhanced infectivity of grub-active EPNs, i.a., *S. scarabaei* exposed to the pheromone under field conditions needs to be explored further.

Symbiont bacterium

The role of bacterial symbionts during nematode infection could be highlighted by its functionality in release of proteases and other virulence factors and expression of corresponded genes that can trigger or suppress the insect immune response independently (Kenney et al. 2019); for example, *Photorhabdus* spp. Boemare (Enterobacterales: Morganellaceae) possess toxin complex (TC) which is orally active against Coleoptera and Lepidoptera (Ffrench-constant and Bowen 2000). In return, the symbionts require nematodes for dissemination and protection against environment and host antibacterial proteins (Stock and Goodrich-Blair 2008).

An and Grewal (2007) reported different virulence mechanisms for various species of bacterial symbionts in spite of similar growth rates/trend inside *R. majalis*. They pointed out although virulence of the bacteria is a requirement for pathogenicity but is not enough. In fact, symbiotic bacteria, showing comparable virulence against a particular grub, induced different pathogenicity due to the way the nematodes transferred bacteria. However, they underestimated the impact of white grub hosts in the infection process and attributed the incurred virulence mainly to the bacterium–nematode interactions.

The low number of bacterial cells carried by a specific nematode (Heryanto and Eleftherianos 2020) and low virulence of its associated symbiotic bacteria have been noticed in EPN low rate of success. For instance, *Steinernema scapterisci* Nguyen & Smart carry fewer bacterial cells than *S. carpocapsae* and its symbiont has relatively low virulence; thereby, *S. scapterisci* cannot kill *P. japonica*, but the latter can (Kim et al. 2017).

Employment of engineered bacterial symbiont resistant to plant secondary metabolites to manage the resistance of bacto-helminthic complex could improve the ability of EPNs to kill root-feeding pests (Machado et al. 2020). Due to the shift from monoxenic paradigm

to pathobiome, manipulation of the bacterial partners should not only be focused on core symbionts but also exploitation of the frequently associated microbiota (FAM) in the virulence and efficacy of EPNs (Ogier et al. 2020). The FAM is not only exclusive to EPNs; they have even been detected from *Pristionchus*, a parasite of scarab beetles (Rae et al. 2008) with little known about their functions.

White Grubs

Unsuccessful host infection by EPNs could be the result of (1) host morphological barriers to EPN invasion, (2) host behavioral traits including evading or excluding, (3) host physiological resistance, and (4) host inhabiting habitats hostile to EPNs (Georgis et al. 2006); the first three explanations have been confirmed in case of white grubs.

Innate resistance has been observed in some white grub species (Gaugler et al. 1994a). Grub tolerance to EPNs has been observed in case of *Polyphylla olivieri* Cast. (Coleoptera: Scarabaeidae) and *P. fullo* L. larvae to *H. bacteriophora* and *S. glaseri* (Parvizi 2001; Karimi et al. 2010a, 2010b; Demir et al. 2015; Haji Allahverdi-pour and Sheikh Garjan 2019). This resistance may partially stem from morphological or behavioral barriers of grubs (Klein et al. 2007, Karimi et al. 2010a); while the best strategy employed by grubs against EPNs is avoidance facilitated by soil as a buffer. The earthen cells of grub pupae in soil acts like a shelter against nematode attack (Gaugler et al. 1994b, Koppenhöfer and Fuzy 2004).

Specialized, host-specific set of excreted/secreted proteins (ESPs) by nematodes are involved in varied virulence of EPNs toward different scarab hosts (Chang et al. 2019, Kenney et al. 2019, Eliáš et al. 2020). Utilization of specific ESPs in improvement of EPN efficacy against grubs through isolation, identification, and characterization of these molecules from various species of EPNs should be taken into account.

Moreover, the susceptibility of host may vary among different populations of the same species of grubs. For instance, *H. bacteriophora* and *S. scarabaei* caused different mortalities in several populations of *C. borealis* (Koppenhöfer et al. 2006).

In addition, different stages of grubs vary in their susceptibility to EPNs (Koppenhöfer and Fuzy 2004, Khatri-Chhetri et al. 2011, Del Valle et al. 2017), which might result from fluctuation in enzymatic activity of different instars as seen in the second and third instar larvae of *Polyphylla adspersa* Motsch. (Karimi et al. 2010a, Alvandi et al. 2017). Infection of scarab adults by EPNs has been confirmed in the case of *P. japonica* (Lacey et al. 1995, Morris and Grewal 2011) and *Papuauna unindis* (Theunis 1998). The artificially infected adults can be employed in passive dispersal of EPNs; nevertheless their mass production requires modification. Life cycle duration of grubs varies along 1–7 yr depending on species and climate/temperature. These intervals are determinant factors in persistence of EPNs for grub control; while annual life cycle results in absence of susceptible hosts, perennial life cycle facilitates perpetuation of nematode populations (Koppenhöfer et al. 2008).

Morphological barriers

The cribriform spiracles of white grubs equipped with sieve plates covered with small size aeropyles and tuft-like hairs could prevent the penetration of EPNs (Forschler and Gardner 1991) and grub legs, raster and mandibles can deter or kill EPNs as well (Gaugler et al. 1994b). The chitinous, dense peritrophic membrane (PE) of grubs with small pore size and multi-laminate structure obstructs immediate gut penetration of EPNs (Forschler and Gardner 1991). Cui et al. (1993) mentioned penetration through PE as an essential step mainly in Steinernematid parasitism.

Physiological barriers

Immune responses

Immune reactions of coleopteran hosts in general and scarabs in particular to EPNs are understudied. Cellular responses of grubs usually include the fluctuation of hemocyte types and counts and cellular encapsulation, while humoral responses are mainly composed of prophenol oxidase cascade activity, antimicrobial peptides (AMPs) involvement, and melanization. Different white grub species show various immune responses against EPNs (Li et al. 2007) and the immune suppression mediated by one species of nematode may only apply to a white grub species or ecologically related species (Wang and Gaugler 1999). Immune responses of the insects against EPNs mainly correspond to host suitability for nematode reproduction. With respect to the white grub immune response to EPNs, *Cyclocephala borealis* Arrow was resistant to *S. glaseri* and *H. bacteriophora*. *A. orientalis*, and *Popillia japonica* were semi-refractory hosts for *H. bacteriophora*, while *S. glaseri* reproduces in large numbers in these susceptible hosts (Li et al. 2007).

Popillia japonica shows various responses to nematode invasion from none to strong encapsulation and melanization in a relatively short period of time depending on nematode species. EPNs have been shown to evade encapsulation in *P. japonica* and *C. borealis* (An et al. 2012). Relatively weak cellular and humoral reactions of *P. adspersa* to *S. glaseri* and *H. bacteriophora* were suppressed by the EPNs (Alvandi et al. 2017).

Escape from encapsulation following recognition is a mechanism that discriminates between resistant and susceptible hosts and determines the virulence of different inbred lines (Li et al. 2007, An et al. 2012).

Another physiological barrier of grubs against EPNs is grub gut fluid, characterized by high pH value (~9). The content and high pH of the gut fluid could inactivate, cause anoxia, or kill EPN species such as *H. bacteriophora* while *S. glaseri* is more tolerant (Wang et al. 1995).

Antagonistic bacteria

There is a mutual antagonism between insect midgut microbiota and EPN bacterial symbionts. Bonifassi et al. (1999) witnessed non-symbiont microbes attenuate *S. scapterisci* virulence. Among the scarab-associated microbiota, several bacteria protect *Melolontha melolontha* (L.) (Coleoptera: Scarabaeidae) from EPNs and might play a key role in insect resistance to EPN pressure and/or involve in defense responses to various EPNs (Skowronek et al. 2020). This bacterial community, e.g., *Pseudomonas*, *Serratia*, *Bacillus* and *Enterobacter* could be transmitted between the aboveground adults and the underground larvae by necromenic nematodes like *Pristionchus* (Rae et al. 2008, Koneru et al. 2016 Skowronek et al. 2020). Apart from the transfer of this line of defense (i.e., bacteria) to scarabs, this represents an important step in the evolutionary development and radicalization of EPN-grub associations. Koneru et al. (2016) delineated distinct association between specific scarab taxa and certain bacterial composition and the cognate necromenic nematodes. They introduced these interactions as prerequisite for transition of entomophilic to entomopathogenic associations under preadaptation concept.

Insect host cues

Attraction of nematodes to scarab pheromone, e.g., sex pheromone has been confirmed in case of *Pristionchus* orientation to scarab adults in scarab-nematode associations. These scarab-specialist parasites benefit from scarab-specific odorants (such as phenol) and plant volatiles for finding the host. They exploit species-specific

scarab-derived compounds in host attraction and recognition (Hong and Sommer 2006, Hong et al. 2008).

A further instance of EPN attraction to host cues is use of *Diaprepes abbreviatus* L. (Coleoptera: Curculionidae) sex pheromone [(E)-3-(2-Hydroxyethyl)-4-methyl-2-pentenoate] by the EPN for host location, thus increasing feral EPN responsiveness and the consequent higher host mortality (Rivera et al. 2017). There is still a dearth of knowledge on deployment of these infochemicals in different agroecosystems.

Having been inhabited in the soil and exposed to many terrestrial natural enemies including EPNs, grubs generally evolved to downgrade their attraction signals and compounds, i.e., scarab-specific odorants, to deceive EPNs (Gaugler et al. 1994a).

Behavioral barriers

Aggression

Defensive behaviors of white grubs like grooming (brushing and rubbing) by legs, mouthparts and raster can lead to injury, death, and removal of a considerable percentage of attacking EPNs (Gaugler et al. 1994b, Wang et al. 1995, Koppenhöfer et al. 2000c). Even one IJ of a nematode can provoke defensive behavior from grubs (Gaugler et al. 1994b). Grubs can also smash penetrated EPNs through chewing by their strong mandibles (Prasad et al. 2012).

CO₂ has been reported as a key host location cue for EPNs (Gaugler et al. 1980, Wang and Gaugler 1998), but abrupt release of CO₂ compared to a continuous flow provides white grubs with an ability to deter nematodes (Gaugler 1988).

Evasion

Grubs are able to detect EPN attack and move away from the point of EPN introduction. According to Gaugler et al. (1994b) grub evasion represents a more effective defense than aggression after reaching a EPN density threshold. Evasive movements including crawling, digging, and rearing are frequently induced following exposure to EPNs resulting in reduced nematode attack and parasitism.

Frequent defecation could help white grubs elude some EPNs depending on their penetration routes (Gaugler 1988, Cui et al. 1993). Additionally, it is argued that feeding enhances grub infection by some EPNs through facilitating nematode penetration (Wang and Gaugler 1998); concurrently, third-instar grubs that have purged their intestines and stopped feeding, are significantly less susceptible to EPN infection compared with actively feeding third instars (Koppenhöfer and Fuzy 2004, Koppenhöfer et al. 2008).

The intensity of evasive migration and aggressive responses vary among different EPN-grub combinations (Koppenhöfer et al. 2000c).

Host Plants as Mediators

EPNs are attracted to both intact and wounded grass roots with more attraction to damaged roots as a way to maximize their contact with insect host (Wang and Gaugler 1998). This gives the plants a chance to protect their roots against pests while EPNs benefit from herbivore-induced and SOS signals, not specifically volatile chemicals (van Toll et al. 2001, Degenhardt et al. 2009). Some plant varieties and lines, lacking attractive signals and attractants (e.g., (E)- β -caryophyllene) to EPNs, yield to inconsistent results of EPN efficacy. Conversely, reintroduction of SOS signal in plant varieties and/or selection for EPN strains that are more responsive to the attractant, could enhance EPN efficacy (Rasmann et al. 2005, Hiltbold et al. 2010, Robert et al. 2013). However, Rivera et al. (2016) found that induced defensive plant chemistries, i.e., (E)- β -caryophyllene and

pregeijerene (1,5-dimethylcyclodeca-1,5,7-triene) are not attractive to local population of *S. glaseri* and had no significant effect on infection of *A. orientalis* in blueberry agroecosystem. There was also, to some extent, repellency to EPNs in cages containing *A. orientalis*, indicating harsh defensive mechanisms of this pest. This result was not in agreement with Polavarapu et al. (2007) that reported the herbivore-induced plant volatile (HIPV) aka. pregeijerene, isolated from weevil-damaged citrus roots, attracted naturally occurring EPNs and increased mortality of *A. orientalis* and *Galleria mellonella* L. (Lepidoptera: Pyralidae) in citrus and blueberry agroecosystems. Rivera et al. (2016) attributed this inconsistency to the avirulent strain of *S. glaseri* and resistance of the white grub host to this strain.

Due to the system specificity of HIPVs, the exact relationships between the components of plant-herbivore-EPN tritrophic interactions should be investigated under laboratory and field conditions in advance to deploy a suitable HIPV in a specific agroecosystem for belowground pests like white grubs. Additionally, Hiltbold et al. (2015) observed the positive effect of pea root-cap exudates on the qualitative traits (infectiousness, mobility, lipid content, and persistence) of stored EPNs and they suggest application of specific root exudates for increasing efficiency of EPNs.

Conversely, negative host plant effects on EPN virulence have been observed. Hazir et al. (2016) indicated that *Steinernema riobrave* Cabanillas, Poinar, and Raulston had reduced infectivity toward tobacco-fed, *Helicoverpa zea* Boddie (Lepidoptera: Noctuidae) compared to tomato and eggplant fed larvae due to the effect of herbivore diet on foraging and reproduction of EPN; however, this negative impact could be resolved through genetic selection. Furthermore, it is assumed that deep root system of host plant and subsequent deep distribution of grubs could play a role in low effectiveness of EPNs (Koppenhöfer et al. 2008).

Environmental Factors

Environmental conditions and particularly soil conditions could influence behavior of IJs, white grub hosts as well as their spatial and temporal distributions. Temperature and humidity specifically have an impact on physiological activity, the amount of body lipids and the rate at which energy reserves are depleted (Abate et al. 2019). Environmental conditions such as soil moisture and temperature, thatch depth, soil type, and seasonal temperature can directly or indirectly influence performance of EPNs (Georgis and Gaugler 1991).

Tolerance to temperature extremes varies among the nematode species/strains. Overall, *S. glaseri* is considered a heat-tolerant species, while *H. megidis* and *H. marelata* are adapted to cold temperatures (Shapiro-Ilan et al. 2017). The main drawback of EPNs is that their effectiveness is often limited by the low soil temperatures where grubs are still active (Jackson and Klein 2006).

Torres and Aponte (2013) inferred that movement of cruiser EPNs in process of host location was limited by humidity, composition and granulometry of the substrate, temperature, and so on; therefore, the characteristics of soil play a paramount role principally in the efficacy of cruisers. Georgis and Gaugler (1991) pointed out that smaller soil particles provide improved EPN efficacy, whereas mixed effects of soil texture in managed systems have been observed (Campos-Herrera et al. 2012). The effect of soil type on EPN efficacy is somehow variable due to its impact on nematode movements and soil moisture content depending on each EPN requirement. For some cruisers, fine-textured soil restricts downward movements of IJs and keeps them more populated in the area where the grubs are active, plus its more stable

water content has beneficial impacts on the longevity and activity of EPNs. On the other hand, while some EPNs prefer coarse-textured soils, others are not affected by soil texture. Generally, sandy soils provide a better matrix for EPN movement and survival than fine-textured, but at the same time they lose their moisture content more quickly and obstruct EPN activity. The gradual loss of soil moisture favors IJ persistence (Koppenhöfer et al. 2020).

Concluding Remarks

Even though biocontrol tactics are hard to implement in soil substrate, entomopathogenic nematodes and fungi can easily adapt to this ecological niche. The rule of the right person, the right place, the right time should be considered in microbial control of scarabs by EPNs. That is, choosing the right nematode in a specific agroecosystem and its application at the appropriate time in the season.

Subterranean habitats of white grubs act like a double-edged sword in biocontrol of grubs by EPNs. On one hand, it increases the diversity of natural entomopathogens collected from grubs that could be exploited in their biological control, but it also raises the natural tolerance/resistance to soil-borne entomopathogens, including EPNs, due to the evolutionary battle between these microorganisms and grubs. Some grub species have evolved some level of tolerance to invasion by EPNs in an evolutionary ‘arms race’ with their coevolved EPNs. This evolutionary success might originate from gut microbiota activity of the grubs (Zimmermann 1992, Skowronek et al. 2020). It has been evidenced that insect gut microbiota acts as an early line of defense inside the scarab larvae against EPN infection. However, some EPNs have acquired counter-adaptation to grubs defensive measures in a shared evolutionary history. Investigation into the plant metabolite-based defense of grubs and survey for EPN isolates that can overcome this kind of defense need to be carried out. The bottom line is that there are unexplored opportunities in the manipulation of nematode–scarab–plant relationships that will need to be exploited in efficient control of grubs.

Presence of association between scarabs and entomophilic nematode (*Pristionchus* spp., *Diplogasteroides*), and the cognate bacteria and formation of dauer juveniles in *Pristionchus* spp. are proof of preadaptation; beginning from a phoretic association and reaching an entomopathogenic one in a continual evolution (Sudhaus 2008, Weller et al. 2010, Dillman et al. 2012, Koneru et al. 2016). In addition to finding scarab-specific and virulent species/strains of EPNs, isolation of free-living nematodes associated with scarabs provides an opportunity for pathogenicity and potential assessment of these understudied groups in white grub management as well as nematode conservation.

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