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Entomopathogenic nematology in Latin America: A brief history, current research and future prospects

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ABSTRACT

Since the 1980s, research into entomopathogenic nematodes (EPNs) in Latin America has produced many remarkable discoveries. In fact, 16 out of the 117 recognized species of EPNs have been recovered and described in the subcontinent, with many more endemic species and/or strains remaining to be discovered and identified. In addition, from an applied perspective, numerous technological innovations have been accomplished in relation to their implementation in biocontrol. EPNs have been evaluated against over 170 species of agricultural and urban insects, mites, and plant-parasitic nematodes under laboratory and field conditions. While much success has been recorded, many accomplishments remain obscure, due to their publication in non-English journals, thesis dissertations, conference proceedings, and other non-readily available sources. The present review provides a brief history of EPNs in Latin America, including current findings and future perspectives.

1. Introduction

Biological control practices in Latin America have increased during recent decades. Some authors estimate that almost 25% of the total global area under biological control is located in the Central and South-American sub-continent (van Lenteren and Bueno, 2003). Records of biological control methods date from the early 1900s. For example, in 1903, coccinellids were introduced in Chile to control scale insects

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Table 1
Entomopathogenic nematodes described from Latin-America.

Nematode species	Localization	Vegetation	Reference
Steinernema australe	Isla Magdalena, Chile	Mixed grasses	Edgington et al. (2009a)
Steinernema brazilense	Near Porto Murtinho city, Mato Grosso state, Brazil	Natural vegetation	Nguyen et al. (2010)
Steinernema colombiense	Maracay Experimental Station, Western slopes of the Central Andes, Colombia	Coffee plantation	López-Núñez et al. (2008)
Steinernema costariscence	Conservation area of Guanacaste. Costa Rica	Rainforest transition.	Uribe-Lorío et al. (2007)
Steinernema cubanum	Pinar del Rio, Cuba	Citrus plantation	Mráček et al. (1994)
Steinernema goweni	El Venado, Zulia State, Venezuela	Natural grassland	San-Blas et al. (2016)
Steinernema papillatum	Finca el Tigre, Zulia State, Venezuela	Cultivated grassland	San-Blas et al. (2015a)
Steinernema puertoriscense	North eastern area of Puerto Rico	Coconut plantation	Román and Figueroa (1994)
Steinernema puntauvense	Gandoca-Manzanillo. Close to Punta Uva, Costa Rica	Sand dunes	Uribe-Lorío et al. (2007)
Steinernema relatorei	Veracruz State, Mexico	Sugar cane	Grifaldo-Alcántara et al. (2017)
Steinernema scapterisci	Near Rivera, Uruguay (but brought and described at the USA)	Isolated in mole cricket *Scapteriscus vicinus* cadavers	Nguyen and Smart (1990)
Steinernema unicornium	Archipielago of Tierra del Fuego, Chile	Natural vegetation	Edgington et al. (2009b)
Heterorhabditis amazonensis	Northern part of the state of Amazonas, near the city of Benjamin Constant, Brazil.	Rain forest	Andaló et al. (2006)
Heterorhabditis atacamensis	San Pedro de Atacama, Chile	Soil samples	Edgington et al. (2011)
Heterorhabditis mexicana	Northern part of the state of Tamaulipas. Mexico	Sorghum field	Nguyen et al. (2004)
Heterorhabditis sonorensis	Caborca, Sonora State, Mexico	Asparagus field	Stock et al. (2009)

attacking various crops. In 1904, in Peru, the natural enemies of cotton scales were released, and in 1908, Argentina started a program to control peach scales using parasitoid wasps (Altieri et al., 1989). However, the availability of chemical pesticides, along with few biological control research programs and the lack of commercial biocontrol companies, have limited biological control practices in many countries (Bueno and van Lenteren, 2003).

With respect to entomopathogenic nematodes (EPNs) (Steinernematidae and Heterorhabditidae), research in Latin America dates from the 1920s. In Brazil, the species currently known as *Steinernema glaseri* was isolated and characterized (Travassos, 1927). To date, 16 out of 117 currently described species (12 *Steinernema* and 4 *Heterorhabditis*) (Shapiro-Ilan et al., 2018) were first discovered in Latin America, including *Steinernema colombiense* (López-Núñez et al., 2008), *S. goweni* (San-Blas et al., 2016), *S. papillatum* (San-Blas et al., 2015a), *S. puntauvense* (Uribe-Lorío et al., 2007), *Heterorhabditis atacamensis* (Edgington et al., 2011) and *H. sonorensis* (Stock et al., 2009) being considered endemic (Table 1). Additional isolates and species remain undescribed.

Since the 1980s, studies on the biology, ecology and biological control potential of EPNs, has increased exponentially (San-Blas, 2013). However, much information is limited to local journals, published in Spanish or Portuguese, or are restricted to theses, dissertations or congress proceedings. Furthermore, many reviews contain a limited amount of information in terms of biodiversity, research scope and the use of EPNs in different Latin American countries (Wassink and Poinar, 1984; Georgis and Hom, 1992; Grewal et al., 2001; Kaya et al., 2006).

The current review summarizes EPN research in Latin America, and provides a perspective for future work. Data are grouped within geographical regions, namely North America, Central America, the Caribbean islands, and South America. Before the standardization of EPN identification (including molecular tools) (Hominick et al., 1998), the nematodes were identified based on their morphology and morphometrical measurements. This review used the data provided by the literature content as such. We assume that the identifications before 2000 were done in good manners; but there is a chance of misidentifications of the species/strains reported through history.

2. North America

2.1. History

Studies on EPN diversity in Mexico are restricted to a few regions (Fig. 1), with surveys from both cultivated and non-cultivated soils (Molina-Ochoa et al., 2003a, 2003b; Montores-Ramirez et al., 2016). Alatorre-Rosas, was a pioneer in the study of these nematodes in Mexico. Early studies focused on the evaluation of a non-native strain *Steinernema carpocapsae* Weiser (Rhabitida: Steinernematidae), to control *Zadiprion falsus* Smith (Hymenoptera: Diprionidae) and *Dendroctonus adjunctus* Blandford (Coleoptera; Curculionidae) in pine trees (Alatorre-Rosas, 1971). Later, a native *S. carpocapsae* was recovered from *Cydia pomonella* L. (Lepidoptera: Tortricidae) in Chihuahua (Poinar, 1979, 1986). EPNs were also evaluated as biocontrol agents for vector pests. For example, *S. carpocapsae* was tested against triatomid bugs, vectors of the Chagas disease (Wassink and Poinar, 1984), and *S. feltiae* Filipjev was tested against blackflies, *Simulium* spp., to control onchocerciasis; although its success was limited (Gaugler et al., 1983).

2.2. Surveys

Since 1998, surveys have been conducted in different Mexican states, and several *Steinernema* and *Heterorhabditis* populations were recovered (Lezama-Gutiérrez et al., 2001; Molina-Ochoa et al., 2003a,b; Zepeda-Jazo et al., 2014). Yet many isolates remain unidentified due to the lack of expertise in systematics and taxonomy (Fig. 1; Table 1; supplementary). In a later study, *Heterorhabditis indica* Poinar and a new species, *S. mexicana* (Nguyen et al., 2004), were isolated from soil samples from sorghum fields [*Sorghum* spp. (Poales: Poaceae)] in the state of Tamaulipas. Three additional species, *S. feltiae*, and two unidentified *Steinernema* and *Heterorhabditis* strains were recovered from an agave fields in Oaxaca state (Ruiz-Vega et al., 2003). In 2009, a new *Hetereorhabditis species, H. sonorensis* Stock, Rivera-Ordiuo & Flores-Lara was recovered from nymphs of the seasonal cicada *Diceroprocta ornea* Walker (Homoptera: Cicadidae) (Stock et al., 2009), in asparagus in Caborca, Sonora State. More recently, *H. mexicana*, *S. carpocapsae* and *S. feltiae* were isolated from the Central Valley of Oaxaca, and tested in aqueous suspension against *Phyllophaga vetula* white grubs killing 75% of larvae (Girón et al., 2015). In 1917 *Steinernema ralatorei* was described. This nematode was isolated from sugarcane areas at Veracruz (Grifaldo-Alcántara et al., 2017).

2.3. Laboratory and greenhouse assays

Different EPN species (native and non-native strains) were evaluated against the fall armyworm, *S. frugiperda* (Table 2). Additional studies have tested pathogen combinations. For example, Lezama-

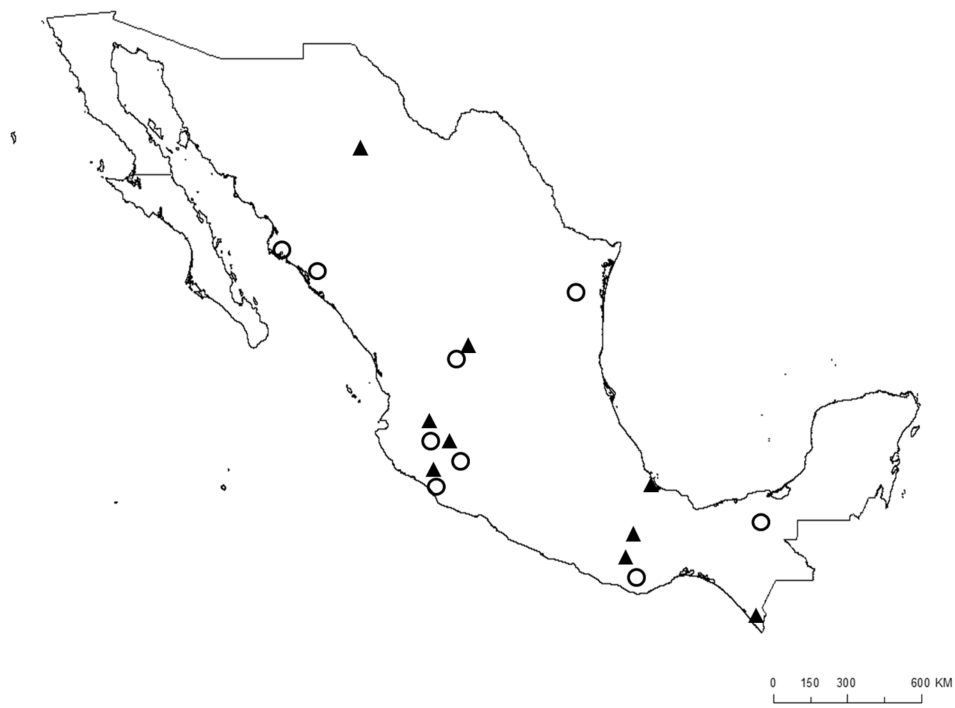

Fig. 1. Sampling sites (approximation) in Mexico (North America) where entomopathogenic nematodes have been isolated. ▲ = *Steinernema*; O = *Heterorhabditis*.

Gutiérrez et al. (1996a) tested *Heterorhabditis bacteriophora* Poinar with the entomopathogenic fungus (EPF) *Nomuraea rileyi* Farlow (Hypocreales: Clavicipitaceae) under laboratory conditions. Both organisms were pathogenic to larvae, but not pupae, and no synergy was observed when they were applied together.

Ruiz-Vega et al (2000) tested combinations of a native *Heterorhabditis* strain and non-native *H. bacteriophora* (NC strain) with two EPF, *Beauveria bassiana* Bals-Criv. (Hypocreales: Clavicipitaceae), and *Metarhizium anisopliae* Metchnikoff (Hypocreales: Clavicipitaceae), against *Phyllophaga* larvae in greenhouse trials. The study revealed that both EPN species were virulent and caused 75% mortality, while the fungi alone required six days to kill 50% of the larva. Furthermore, synergistic effects were observed with the combined application of *M. anisopliae* and *Heterorhabditis;* with an observed LT_{50} at day 4 post inoculation (Ruiz-Vega et al 2000).

Heterorhabditis bacteriophora was also assessed against several fruit flies species including *Anastrepha obliqua* Macquart, *A. serpentina* Wiedemann, and *A. ludens* Loew (Diptera: Tephritidae) under laboratory conditions (Lezama et al., 1996b; Toledo et al., 2001, 2006b) (Table 2). These studies showed that early instars and pupae were susceptible to this nematode species. Larvae mortality was temperature, achieving the highest mortality between 26 °C and 27 °C (Toledo et al., 2005a,b).

2.4. Field trials

Field trial studies have been limited in Mexico Ruiz-Vega et al. (2012), evaluated a combination of *S. carpocapsae* and *M. anisopliae* against white grubs in corn field trials in Oxaca State. Results from this study showed 70% control of the white grub population and an increase of corn yields by 17% (Ruiz-Vega et al., 2012). Also Toledo et al (2006a) evaluated the infection of *Anastrepha ludens* following soil applications of *Heterorhabditis bacteriophora* in a mango orchard, reaching 74% of larvae mortality.

2.5. Mass production

In vitro production of infective juveniles (IJs) of EPNs has succeeded through artificial media. For example, the use of inexpensive local by-products such as agave juice (aguamiel) and whey (a waste product discarded into rivers) were used as liquid basal media to produce *S. carpocapsae* (249,000 IJs/ml with aguamiel medium and 126,000 using whey medium) (Islas-López et al., 2005; Chavarría-Hernández et al., 2006). In addition, improvements in the design of fermenters such as the configuration of internal reactor loops and geometry promoted the mating of *S. carpocapsae* (Chavarría-Hernández et al., 2007, 2011) and enhanced the production IJs in submerged cultures (Chavarría-Hernández and de la Torre, 2001; Chavarría-Hernández et al., 2003, 2014).

3. Central America

3.1. History

Various institutions in Central American have focused their research efforts on the study of EPNs. For example, in 1989, the Center for Biological Control of Central America (currently known as the Laboratory for Biological Control), which is part of the Integrated Pest Management Program at Zamorano University, was founded by the US Agency for International Development (USAID), with the goal of promoting teaching, research and implementation of biological control practices in the region. Currently, this laboratory focuses on the mass production and commercialization of biological control agents, including EPNs.

In Panama, research into EPNs at the Instituto de Investigación Agropecuaria of Panamá (IDIAP) (http://www.idiap.gob.pa/) started in the early 1990s. The studies have mostly focused on evaluating EPNs against white grubs (*Phyllophaga* sp. and *Anomala* sp.) and the Guatemalan potato moth [*Tecia solanivora* Povolný (Lepidoptera: Gelechiidae)]. In 2005, Cuban specialists from the National Center for Plant and Animal Health (CENSA) trained Salvadorian researchers on the *in vivo* mass production, formulation and application of EPNs, to control lepidopteran pests (Mayra Rodríguez pers. comm.). As a result, a *H. amazonensis* strain (from Cuba) is currently mass-produced for the control of *Plutella xylostella* L. (Lepidoptera: Plutellidae) in brassica crops at Chalatenango region. The use of EPNs in some Salvadorian

Table 2
Target organisms and their control using entomopathogenic nematodes tested in Mexico (North America).

Common name	Scientific name	Crop	Nematode species	Experimental location	Mortality	Reference
Fall armyworm	*Spodoptera frugiperda*	Maize	*H. bacteriophora* *H. megidis* *S. carpocapsae* *S. riobrave*	Laboratory	65–81%	Molina-Ochoa et al. (1999)Lezama-Gutiérrez et al. (1996a)
Mexican fruit fly	*Anastrepha ludens*	Mango *Mangifera indica* (Sapindales: Anacardiaceae)	*H. bacteriophora* *S. carpocapsae* *S. felitae* *S. riobrave*	Laboratory Field	70–90%	Toledo et al. (2001)Lezama-Gutiérrez et al. (1996b)Toledo et al. (2005a, 2006a)
West Indian fruit fly	*Anastrepha obliqua*		*H. bacteriophora*	Laboratory	8–82%	Toledo et al. (2005b)
Sapote fruit fly	*Anastrepha serpentina*			Laboratory	55%	Toledo et al. (2006b)
Striped grass lopper	*Mocis latipes* Guenée (Lepidoptera:Noctuide)	Grasses		Semi-field	41–100%	González-Ramírez et al. (2000)
White grubs	*Phyllophaga vetula* *Phyllophaga polyphylla* *Phyllophaga* spp.	Maize	*H. bacteriophora* *H. indica* *Heterorhabditis* sp. *S. carpocapsae* *S. glaseri*	Laboratory Semi-field Field	16–93%	Alatorre-Rosas (1971)Ruiz-Vega et al. (2012)Sánchez-Saavedra (2012a)Girón et al., (2015)Martínez-Hernández et al. (2015)
Horn fly	*Haematobia irritans* L. (Diptera: Muscidae)		*H. bacteriophora* *S. arenarium* *S. carpocapsae* *S. glaseri* *S. longicaudatum* *S. riobrave*	Laboratory	50–90%	Rodríguez-Solano et al. (2004)
Mexican bean beetle	*Epilachna varivestis* Mulsant (Coleoptera: Coccinellidae)		*S. carpocapsae*	Laboratory	S	Alatorre-Rosas (1971)
	Dendroctonus adjunctus Blandford (Coleoptera: Curculionidae)				70%	
	Zadiprion falsus Smith (Hymenoptera: Diprionidae)				S	
	Copturus aguacatae Kissinger (Coleoptera: Curculionidae)	Avocado	*H. indica*	Laboratory	93%	Sánchez-Saavedra et al. (2012b)
Coffee berry borer	*Hypothenemus hampei*	Coffee	*Heterorhabditis* sp. *S. carpocapsae* *Steinernema* sp.	Laboratory	32–61%	Castillo and Marbán-Mendoza (1996)
Agave weevil	*Scyphophorus acupunctatus* Gyllenhal (Coleoptera: Curculionidae)	*Agave* sp.	*H. bacteriophora* *S. carpocapsae* *S. feltiae*	Laboratory Field	72–100%	Aquino et al. (2006)Delgado-Gamboa et al. (2015)
Sweet potato whitefly	*Bemisia tabaci*	Tomato	*H. bacteriophora* *H. indica* *S. feltiae*	Laboratory	70%	Meza-García et al. (2014)
Central America black fly	*Simulium* sp.		*S. feltiae*	Field	NS	Gaugler et al. (1983)
Bite bugs	*Rhodinus prolixus* Stal (Hemiptera: Reduviidae)		*S. carpocapsae*	Laboratory	VS	Wassink and Poinar (1984)
	Triatoma barberi Usiger (Hemiptera: Reduviidae)				S	
	Triatoma mazzotti Usiger (Hemiptera: Reduviidae)				S	
House fly	*Musca domestica* L. (Diptera: Muscidae)		*H. indica* *Heterorhabditis* sp. *Steinernema* sp.	Laboratory	3–54%	Arriaga and Cortez-Madrigal (2018)
Cattle ticks	*Rhipicephalus microplus*		*S. diaprepresi*	Laboratory	40.0	Molina-Ochoa et al. (2009)

S = Susceptible.
VS = Very susceptible.
NS = Non susceptible.

fields, led to a series of extension activities, including seminars and workshops for more than 300 farmers and their families. More than 70 extension specialists have been trained using demonstration plots in different schools at La Palma Municipality

3.2. Surveys

In 2005, Costa Rica started research on EPNs (Fig. 2, Table 3, supplementary). Uribe-Lorío et al. (2005), conducted a survey on the Pacific coast and south-eastern region. Both *H. indica* and two new *Steinernema* species [*S. puntauvense* (Uribe-Lorío et al., 2007) and *S. costariscence* (Uribe-Lorío et al., 2007)] were described. In 2009, surveys in rainforest soil samples using *Galleria mellonella* L. (Lepidoptera: Pyralidae) and *Tenebrio molitor* L. (Coleoptera: Curculionidae) baiting isolated six EPN species (Powers et al., 2009). These were *H. bacteriophora*, *H. indica*, an undescribed *Heterorhabditis* (isolated from forest litter), and *S. puntauvense*, *S. feltiae*, and *S. carpocapsae.* Melo-Molina et al. (2004), in Panama, attempted to isolate native EPNs from agricultural soil samples in Coclé, Veraguas and Chiriquí provinces; however, only saprophytic nematodes were recovered. In recent years, surveys have resulted in the isolation of several *Heteorhabditis* spp. which remain undescribed (Muñoz et al, 2015).

3.3. Laboratory and greenhouse assays

Several bioassays have been conducted in Costa Rica to evaluate the

Fig. 2. Sampling sites (approximation) in Central America and the Caribbean where entomopathogenic nematodes have been isolated. ▲ = *Steinernema*; O = *Heterorhabditis*.

efficacy of EPNs against white grubs and banana weevils. For example, Rodríguez et al. (2009) tested a native *Heterorhabditis* sp. (strain CIA-NE-07) against larvae of *Phyllophaga elenans* Saylor (Coleoptera: Melolonthidae). Results of this study showed that the nematodes were more effective in killing second instar larvae than third instar larvae, with an observed percent mortality of 68% vs 24%. Amador et al. (2015) assessed the virulence of *Heterorhabditis atacamensis* (strain CIA-NE07) against the weevil *Cosmopolites sordidus* Gemar (Coleoptera: Curculionidae) (Table 3). The achieved mortality of weevils was 80% at 10 days post inoculation.

In Guatemala, Oliva and Bonilla (2004) evaluated a non-native isolate of *S. carpocapsae* to control the palm oil rootworm *Sagalassa valida* Walker (Lepidoptera: Brachodidae). Their study showed that a single application of 1.5 million IJs per plant was effective at killing the rootworms. Moreover, the observed levels of control were similar to those achieved with endosulfan. Rivera (2014) assessed the virulence of a non-native strain of *Heterorhabditis bacteriophora* (=*H. heliothidis*) alone, and in combination with the EPF *B. bassiana* against *Phyllophaga* larvae in coffee. Results from this study showed that when *H. bacteriophora* and *B. bassiana were* combined, they exhibited an additive effect, resulting in over 70% mortality. Meléndrez (2016) tested a Dutch isolate of *H. bacteriophora*, against the spittlebug *Aeneolamia postica* Walker (Homoptera: Cercopidae) in sugar cane (Table 3). Two doses were tested, 50 and 100 million IJs/ha. Their results showed 71–75% mortality, 72 h post inoculation.

In Honduras, *H. bacteriophora* applied via two drip irrigation systems (pump vs gravity) was investigated. No significant differences were found between the irrigation systems and the nematodes were equally dispersed in the soil (Mata and Rodríguez, 2013). In another experiment, the movement of IJs and their infectivity to *G. mellonella* was tested under different conditions of soil moisture and texture. The results showed highest *G. mellonella* infection occurred in sandy loam soils at field capacity (Turcios et al., 2009).

3.4. Field trials

Honduras has been the leader in field application trials of EPN in Central America. For example, Juárez (2007) demonstrated that *H. bacteriophora* was more efficient than the EPF, *B. bassiana* and *M. anisopliae*, in controlling the dung beetle, *Alphitobius diaperinus* Panzer (Coleoptera: Tenebrionidae). This is an important pest in poultry facilities, that vectors of human pathogens including *Salmonella typhimurium* Kauffmann and Edwards and *Escherichia coli* Escherich (Enterobacteriales: Enterobacteriaceae). Results from this study showed some level of control (47%) of this beetle at a dose of 75,000 IJ/m^2 and via direct irrigation into the poultry beds.

Research in Honduras also focused on the control of *Phyllophaga* spp. For example, Perrera (2009) considered mixed applications of *H. bacteriophora* and chemical insecticides, applied via drip systems to control white grubs in field-grown lettuce. At an application rate of 2×10^8 IJ/ha, an 81% mortality was achieved. These results were similar to those observed with the application of carbofuran (Perrera, 2009). In a similar study, Espinoza and Toledo, (2008) tested *H. bacteriophora* against *P. obsoleta* in strawberry fields; however a low mortality (~30%) was observed. Chicas and Mojica (2016) evaluated different application methods for *H. bacteriophora* and *S. carpocapsae* against the banana weevil *C. sordidus* using a backpack-type sprayer to control larvae in the root system, and pseudo-stem traps inoculated with EPNs to attract adult weevils. This study demonstrated that spraying EPNs directly into the base of the banana plants was a better strategy to reduce weevil larvae populations, achieving 67% mortality. Contrastingly, 19% of adult weevils mortality was observed with the pseudo-stem traps.

Ávila (2010) tested the application of *H. bacteriophora* at 4×10^8 IJ/ha directly on the aerial part of coffee plants to control the coffee berry borer *Hypothenemus hampei* Ferrari (Coleoptera: Curculionidae) in El Paraiso Province. Results from this experiment provided that 86% mortality of adult beetles. Similarly, Bauer (2016) demonstrated that soil surface applications of *H. bacteriophora* and *S. carpocapsae* at a concentration of 4×10^8 IJs/ha achieved 60% and 33% mortality for each species, respectively. Chávez and Hurtado (2010) compared foliar applications of *H. bacteriophora* with chemical pesticides to control *P. xylostella* in brassica crops. The results indicated that the nematodes reduced the larvae by 18% compared to 80% reduction using the insecticide chlorantraniliprole.

In Nicaragua, research on EPNs has been limited. A single study by Méndez, (1997) compared the virulence of two non-native EPN strains, *H. bacteriophora*, *S. carpocapsae*, against *Phyllophaga* larvae under field

Table 3
Target insects and their control using entomopathogenic nematodes tested in Central America and the Caribbean islands.

Country	Common name	Scientific name	Crop	Nematode species	Experimental location	Mortality	Reference
Costa Rica	White grubs	*Phyllophaga elenans*		*Heterorhabditis* sp.	Laboratory	24–68%	Rodríguez et al. (2009)
	Banana weevil	*Cosmopolites sordidus*	*Musa* sp. (Zingiberales: Musaceae)	*H. atacamensis* (Non native)	Laboratory	88–100%	Amador et al. (2015)
Cuba	Citrus green-blue weevil (larvae)	*Pachnaeus litus* Germar (Coleoptera: Curculionidae)	*Citrus* sp. L. (Sapindales: Rutaceae)	*H. indica*	Laboratory Nurseries	70–95%	Montejo and Montes (1990)
	Sweet potato weevil (larvae)	*Cylas formicarius* F (Coleoptera: Curculionidae)	Sweet potato	*H. amazonensis* *H. indica* *Heterorhabditis* sp.	Laboratory Field	82–90%	Rodríguez (2015)
	Coffee mealy bugs	*Planococcus minor* Maskell (Hemiptera: Pseudococcidae)	Coffee	*H. amazonensis*	Laboratory Semi controlled Field	84–88%	Rodríguez et al. (1997, 1998)
	Fall army worm	*Spodoptera frugiperda*		*H. amazonensis* *H. indica* *Heterorhabditis* sp. *S. cubanum*	Laboratory	72–100%	Marrero (2006)Rodríguez (2015)
	Green scale	*Coccus viridis* Green (Hemiptera: Coccidae)		*H. amazonensis* *Steinernema* sp.	Laboratory	83–93%	Castellanos (2000)
	Melon aphid	*Aphis gossypii* (Hemiptera: Aphididae)		*H. amazonensis* *Steinernema* sp.	Laboratory	86–65%	Castellanos (2000)
	Whitefly	*Aleuroglandulus malangae* *Bemisia tabaci* (Hemiptera: Aleyrodidae)		*H. amazonensis* *Steinernema* sp.	Laboratory	67–82% 23–39%	Castellanos (2000)
	Banana aphids	*Pentalonia nigronervosa* Cql. (Hemiptera: Afididae)		*Heterorhabditis* sp.	Laboratory	69%	Castellanos et al. (2000)
	Coffee berry borer Larvae, pupae, adults	*Hypotenemus hampei*	Coffee	*H. amazonensis* *H. indica* *S. cubanum*	Laboratory Semi controlled Field	80–100% 50–93% 40–70%	Valdés and Escobar (2006) Sánchez and Rodríguez (2007)Rodríguez (2015) Valdés et al. (2016)
	Melon worm	*Diaphania hialinata* L. Lepidoptera: Pyralidae	Cucumber *Cucumis sativus* L. (Cucurbitales: Cucurbitaceae)	*H. amazonensis* *H. indica* *Heterorhabditis* sp.	Laboratory Field	62–68%	Valdés et al. (2005)
	Diamondback moth	*Plutella xylostella* L. (Lepidoptera: Plutellidae)	Cabbage	*H. amazonensis* *H. indica* *Heterorhabditis* sp.	Laboratory Field	72–100%	Marrero (2006)Rodríguez et al. (2013a)
	Tobacco budworm Larvae instars	*Heliothis virescens* F. Lepidoptera: Noctuidae	Tobacco *Nicotiana tabacum* (Solanales: Solanaceae)	*H. amazonensis* *H. indica* *Heterorhabditis* sp.	Laboratory Nurseries	100%	Marrero (2006)Pozo et al. (2007)
			Chickpea (*Cicer arietinum* L.) (Leguminosae: Fabaceae)	*H. amazonensis*	Field	90%	Rodríguez (2015)
	White grubs	*Phyllophaga* sp. *Cyclocephala* sp. (Coleoptera: Scarabaeidae)		*S. cubanum* *H. indica* *Heterorhabditis* sp.	Laboratory	VS	Pozo et al. (2006a,b)
	Citrus snow scale	*Unaspis citri* Comst (Hemiptera: Coccoidea)		*H. indica*	Laboratory	14–74%	Gómez et al. (2007)
	Hemispherical scale	*Saissetia coffeae* Walker (Hemiptera: Coccidae)		*H. indica*	Laboratory	89–91%	Gómez et al. (2007)
	Silky cane weevil (adults)	*Metamasius hemipterus* L. (Coleoptera: Curculionidae)	.	*Heterorhabditis* sp.	Laboratory	100%	Evans et al. (2009)
	Small green stink bugs (nymphs and adults)	*Piezodorus guildinii* W (Hemiptera: Pentatomidae)		*H. amazonensis*	Laboratory	100%	Suárez et al. (2011)
	Southern green stink bugs (nymphs and adults)	*Nezara viridula* L. (Hemiptera: Pentatomidae)				100%	
	Termites (workers and soldiers)	*Nasutitermes* sp. (Hexapoda: Isoptera)		*H. indica*	Laboratory	70–100%	Cuevas et al. (2013)
	Pineapple mealybug	*Dysmicoccus brevipes* Cockerell (Hemiptera: Pseudococcidae)	White ginger lily *Hedychium coronarium* K (Zingiberales: Zingiberaceae)	*H. amazonensis*	Laboratory Semi controlled Field	80–95%	Rodríguez et al. (2013b)
	Tomato pinworm	*Keiferia lycopersicella* (Walsingham) (Lepidoptera: Gelechiidae)	Tomato	*H. bacteriophora*	Field	80%	Sierra et al. (2014)

(*continued on next page*)

Table 3 (*continued*)

Country	Common name	Scientific name	Crop	Nematode species	Experimental location	Mortality	Reference
	Sweet potato leaf beetle	*Typophorus nigritus* F. Crotch (Coleoptera: Chrysomelidae)	Sweet potato	*H. indica*	Laboratory Field	90%	Castellón et al. (2014)
	American sunflower moth	*Homeosoma electellum* (Hulst) (Lepidoptera; Pyralidae)	Sunflower *Helianthus annuus* L. (Asterales: Asteraceae)	*H. indica*	Field	S	Limonte et al. (2010)
	Papaya webworm moth	*Davara caricae* Dyar (Lepidoptera: Pyralidae)	Papaya *Carica papaya* L. (Brassicales: Caricaceae)	*H. indica*	Field	93%	Ventura et al. (2017)
Guatemala	White grubs	*Phyllophaga* sp.	Coffee	*H. bacteriophora* (Non native)	Field	5.5%	Rivera (2014)
	Termites	Termites (Isoptera: Rhinotermitidae)	Sugar cane	*Heterorhabditis* sp.	Field	S	Márquez (2014)
Honduras	Lesser mealworm Diamondback moths Fall armyworm Melonworm moth White grubs	*Alphitobius diaperinus* *Plutella xylostella,* *Spodoptera frugiperda* *Diaohania hyalinata* *Phyllophaga* sp *Phyllophaga obsoleta*	 Lettuce *Letuca* sp. Strawberry *Fragaria × ananassa* Sweet potato	*H. bacteriophora* *Heterorhabditis* sp. *Heterorhabditis* sp. *Heterorhabditis* sp. *H. bacteriophora*	Laboratory Laboratory Laboratory Laboratory Laboratory Field	47.1% 50–90% 50–90% 50–90% 10–97%	Juárez (2007) Molina (2007) Molina (2007) Molina (2007) Perrera (2009)Espinoza and Toledo (2008)Nuñez (2011)
	Banana weevil	*Cosmopolites sordidus*	*Musa* sp.	*H. bacteriophora S. carpocapsae*	Laboratory Field	67%	Chicas and Mojica (2016)
	Diamondback moths Coffee berry borer	*Plutella xylostella* *Hypothenemus hampei*	Brassicaceae Coffee	*H. bacteriophora* *H. bacteriophora* *S. carpocapsae* (Non natives)	Field experiment Laboratory Field	18% 29–96% 30%	Chávez and Hurtado (2010) Ávila (2010)Bauer (2016)
Nicaragua	White grubs	*Phyllophaga* sp	Potato and cabbage	*H. bacteriophora* *S. carpocapsae*	Laboratory Field	95%	Méndez (1997)
Panama	Dark sword-grass, or black cutworm	*Agrotis ipsilon*	Lettuce	*Heterorhabditis* sp.	Laboratory	100%	Muñoz et al. (2015)
	Sugarcane giant borer	*Telchin licus*	Sugarcane	*Heterorhabditis* sp.	Laboratory Field	75%	Guerra-Moreno (unpublished)
	Sugarcane stem borer	*Diatraea* sp.			Laboratory	75%	
	Spittlebug	*Aeneolamia* sp.			Laboratory Field	75%	
	Fall armyworm	*Spodoptera frugiperda*			Laboratory	75%	
Puerto Rico	Banana weevil Sugarcane rootstalk borer	*Cosmopolites sordidus* *Diaprepes abbreviatus*	*Musa* sp. *Citrus* sp.	*Steinernema* sp.	Field	13–60% 13–93%	Figueroa (1990) Figueroa and Román (1990)
	Mole cricket	*Scapteriscus didactylus* *Scapteriscus abbreviatus*	*Grasses* (golf courses) Vegetables	*S. scapterisci*	Field	S	Leppla et al. (2007)

S = Susceptible.
VS = Very susceptible.
NS = Non susceptible.

conditions showing over 90% mortality of larvae (Méndez, 1997) (Table 3).

3.5. Mass production

In Honduras, Zamorano University produces *H. bacteriophora in vivo*, and distributes them to local farmers (Cave et al., 2011). Additional attempts have been made to establish *in vitro* mass production by using published protocols (Udo-Ehlers, 2001). EPN yields of 132,000 IJs/ml in 10 days, out of an initial inoculum of 1000 IJs/ml were achieved (Grijalva, 2014).

In Panama, *Heterorhabditis* sp. has been produced *in vivo* using *G. mellonella*, since 2011 by a private company (Compañia Azucarera La Estrella S.A. (CALESA)). EPN have been applied at a rate of 50 billion of IJs/Ha to 12 ha in sugar cane fields infested with *Telchin licus* Drury (Lepidoptera: Castniidae), and *Aeneolamia* spp. yielding 90% mortality. Pest damage levels were under 10% five years after the original application (Abby Guerra-Moreno pers. comm).

4. Caribbean islands

4.1. History

Research with EPNs has been conducted in the Caribbean since the 1980s. Two steinernematids, *Steinernema cubanum* Mráček, Hernández and Boemare and *Steinernema puertoricense* Román and Figueroa, have been described (Mráček et al., 1994; Román and Figueroa, 1994) (Fig. 2, Table 3, supplementary). In the late 1980s, the Cuban Ministry of Agriculture started the National Program of Biological Control Agents. This initiative created a network of laboratories known as CREE (Centers for the Mass Production of Entomophagous and Entomopathogenic Organisms), and other facilities to make EPNs available to local farmers, which is still operating to date. In a review, Rodríguez (2015) noted that after 20 years of intensive use in augmentative applications, EPNs have become one of the most popular biological control agents among Cuban farmers. One reason for this success is that the EPNs do not require legal registration for their commercialization (Fernández-Larrea, 2012). Consequently, the production has increased steadily year after year (Rodríguez, 2015).

In Puerto Rico, research into EPNs advanced significantly in the 1980s and early 1990s. Initial studies focused on the control of *Diaprepes abbreviatus* L. (Coleoptera: Curculionidae) in citrus. The first EPNs isolated were obtained from a *D. abbreviatus* larvae parasitized with *Heterorhabditis* sp., *S. glaseri* and *S. feltiae* (Román and Beavers, 1983; Figueroa and Román, 1990).

4.2. Surveys

In the early 1980s two undescribed *Heterorhabditis* and *Steinernema cubanum* (Arteaga-Hernandez and Mráček, 1984; Mráček et al., 1994) were isolated from Cuban soils. Later, in a more complete survey between 1992 and 1994, 251 samples from 27 different crops in 9 provinces (64% of Cuban provinces) were collected and examined. The results showed that *Heterorhabditis* was the most predominant genus in the island (Rodríguez, 2015) (Fig. 2, supplementary). In 1992, another *Heterorhabditis* was isolated, in Puerto Rico. Although undescribed it was determined this species was closely related to *H. bacteriophora* and *H. indica* (Román and Figueroa, 1995). In 1994, *Steinernema puertoricense* was isolated from a coconut [*Cocos nucifera* L. (Arecales: Arecaceae)] plantation in the north-eastern region of the island (Román and Figueroa, 1994) (Fig. 2, supplementary). Orbe et al. (1998) isolated three *Heterorhabditis* spp. from plantain (*Musa* sp.) fields (Table 3) in the Dominican Republic, but the isolates remain unidentified.

4.3. Laboratory and greenhouse assays

In Cuba, several laboratory and greenhouse studies were carried out to determine the virulence of different EPN strains against 32 insect pests (Table 4). In Puerto Rico, Román and Figueroa, (1985) tested a Mexican strain of *S. carpocapsae* to control the weevil *D. abbreviatus.* However, their results revealed a limited larvae mortality. Subsequently, Figueroa and Román (1990) tested *S. feltiae* and *S. glaseri* (from Biosis Laboratories, California) to control the same pest under greenhouse conditions. Their study showed that the nematodes were effective in controlling 12- to 16-week-old grubs in pots at rates of 1000–3000 IJ/pot with a mortality above 50%. The same species were also tested against sixth and the seventh instar larvae of *C. sordidus* at doses from 400 to 40,000 IJs/plant in pot trials. Results from these studies showed low (13%) to moderate mortality (60%) (Román et al., 1993) (Table 3). Jenkins et al., (2008) assessed the efficacy of *Steinernema riobrave* and *Heterorhabditis megidis* against *D. abbreviatus* larvae in a high clay-content oxisol soil with potted *Litchi chinensis* (Sapindales: Sapindaceae). This study revealed that both EPN species tested significantly reduced (70%) the population of *D. abbreviatus* larvae (Jenkins et al., 2008).

4.4. Field trials

The ability of EPNs to manage root-knot nematodes in field trials was reported by Águila et al. (2008). IJs of *H. bacteriophora* reduced infestation of *Meloidogyne* nematodes in guava [*Psidium guajava* L. (Myrtales: Myrtaceae)], cabbage [*Brassica oleracea* L. (Brassicales: Brassicaceae)] and *Musa* spp. Other field studies conducted in the western region, included EPN applications against insects and root-knot nematodes (*Meloidogyn*e sp.) in plantations of guava, avocado [*Persea americana* L. (Laurales: Lauraceae)], grapes [*Vitis vinifera* L. (Vitales: Vitaceae)], *Xanthosoma* sp. (Alismatales: Araceae), sweet potato [*Ipomea batatas* L. (Solanales: Convolvulaceae)], *Musa* spp., and different vegetables (Hernández et al., 2015) (Table 3).

In Puerto Rico, an introduced *S. feltiae* strain was applied to the soil to control *D. abbreviatus* larvae. Infection rates were higher in soils with relatively high sand content, suggesting that infectivity was positively correlated with soil porosity (Román and Beavers, 1983). *Steinernema scapterisci* (Nguyen and Smart, 1990) was also introduced (a Uruguayan strain reproduced in the US, see Section 5.2) to control the mole cricket *Scapteriscus didactylus* Latreille. Nematode applications were made in experimental plots in Puerto Rico from 2001 to 2004, using 2.5 billion IJs/ha. Nematodes were applied in November 2001, and August 2003, on an irrigated golf course with clay loam soil, and on an organic vegetable farm. Mole crickets captured at the golf course were infected by *S. scapterisci*, but those from the vegetable farm were not infected. The persistence of infected crickets at the golf course remained for more than 7 months which indicated that *S. scapterisci* became established (Leppla et al., 2007) (Table 3).

4.5. Mass production

Cuba has pioneered the *in vivo* production of EPNs since 1994 suing *G. mellonella* larvae (Rodríguez, 2015). A combination of cereals and by-products from the sugar cane industry, such as molasses and fibers (bagasse sugarcane), has been used as substitute diet for the rearing of *G. mellonella* (Enrique et al., 2006). Currently, the CREE network (see Section 4.1) is implementing this methodology in 10 out of 14 provinces around the country for the production and commercialization of EPNs. In 2016, more than 812 billion IJs were produced by CREE (Jiménez, 2017). Different substrates have been considered for the *in vitro* formulation of EPNs, including sponges that are soaked with the nematodes and placed in polyethylene bags (Sánchez et al., 2001). These bags are able to maintain 80% of IJs viable for 72 days when stored at room temperature (25 °C).

5. South America

South America has led research on EPNs in Latin America. Several scientists, including Pizano and Arrigoni (Brazil), de Doucet (Argentina), and Wassnik (Venezuela), were pioneers in the area. Research in South America has achieved many milestones, including developing technology for the field application of EPNs, and the establishment of several companies to produce and commercialize EPNs. Extensive laboratory and field experiments are also reported (Tables 4 and 5). However, in most cases, markets remain local and with limited volumes of production.

5.1. History

The first description of EPNs was reported by Steiner in 1923. He described an unknown nematode as *Aplectana kraussei.* In 1927, Travassos in Brazil, revised Steiner's description and erected the new genus, *Steineria*. Later, the name was changed to *Steinernema* (Wouts et al., 1982). In 1954, *S. carpocapsae* (DD-136) was introduced from US to Chile by Dutky (1957) for tests against white grubs. EPNs were also sent to Leopoldo Caltagirone (La Cruz Research Station, central Region of Chile), who tested them against *Aegorhinus phaleratus* Erichson (Coleoptera; Curculionidae), with encouraging results. Dutky tested EPNs against other pests in Chile, including *Dalaca* sp. and *Agrotis* sp. (both Lepidoptera: Noctuidae), *Pantomorus* sp. (Coleoptera: Curculionidae), and a tabanid larva, confirming their susceptibility to the EPNs

In Peru, Tang (1958) was the first one to test *S. carpocapsae* against different cotton pests (Table 5). In Colombia, Landazabal et al. (1973) tested *S. carpocapsae* against *S. frugiperda* and other common pests of several crops including corn, rice, sorghum, wheat, sugarcane, and other grasses. Meanwhile, Bustillo (1976) experimented with the same nematode against larvae, prepupae and pupae of *Oxydia trychiata* Guenée (Lepidoptera: Geometridae) in cypress, pine and coffee. Amaya and Bustamante (1975) tested the virulence of *S. carpocapsae* against three coleopteran larvae. Prada and Gutiérrez (1976) evaluated the susceptibility of *Tuta absoluta* Meyrick (Lepidoptera: Gelechiidae) to *S. carpocapsae* and *Bacillus thuringiensis* Berl. (Bacillales: Bacillaceae). Later, Benjumea et al. (1978) initiated the experimental mass production of *S. carpocapsae* to control *S. frugiperda* in field trials.

Table 4
Target pest organisms and their control using entomopathogenic nematodes tested in Argentina.

Common name	Scientific name	Crop	Nematode species	Experimental location	Mortality	Reference
Grasshoppers	*Dichroplus punctulatus* Thunberg (Acrididae)		*H. bacteriophora*	Laboratory	NS	de Doucet and Giayetto (1994)
	Undetermined (Acrididae)		*H. bacteriophora* *S. feltiae* *S. rarum*	Laboratory	S	de Doucet et al. (1999)
Leaf miners	*Liriomyza huidobrensis* Blanchard (Agromyzidae)		*H. bacteriophora*	Laboratory	NS	de Doucet and Giayetto (1994)
Blue alfalfa aphid	*Acyrthosiphon kondoi* Shinji (Aphididae)		*H. bacteriophora* *S. feltiae* *S. rarum*	Laboratory	S	de Doucet et al. (1999)
Melon aphid	*Aphis gossypii* Glover (Aphididae)		*H. bacteriophora* *S. feltiae* *S. rarum*	Laboratory	NS	de Doucet et al. (1999)
Aphids	*Macrosiphum rosae* L. (Aphididae)		*H. bacteriophora*	Laboratory	NS	de Doucet and Giayetto (1994)
Honey bees	*Apis mellifera* L. (Apidae)	Alfalfa	*H. bacteriophora* *S. feltiae* *S. rarum*	Laboratory	12% S S	de Doucet and Giayetto (1994)Stock (1996)de Doucet et al. (1999)[†]
Bumble bees	*Bombus* sp. Latreille (Apidae)		*H. bacteriophora*	Laboratory	NS	de Doucet and Giayetto (1994)
Pill-bug	*Armadillium vulgare* Latreille (Armadillidiidae)		*S. rarum*	Laboratory	30.4%	Picca et al. (2008)
Oriental cockroach	*Blatta orientalis* L. (Blattidae)		*H. bacteriophora*	Laboratory	S	de Doucet and Giayetto (1994)
American cockroach	*Periplaneta americana* L. (Blattidae)		*H. bacteriophora*	Laboratory	S	de Doucet and Giayetto (1994)
Ground Beetles	*Anisodactylus* sp. Dejean (Carabidae)		*Steinernema* sp.	Laboratory	40%	Caccia et al. (2011)
	Calosoma argentinense Csiki (Carabidae)		*H. bacteriophora* *Steinernema* sp.	Laboratory	NS 40%	de Doucet and Giayetto (1994)Caccia et al. (2011)
Longhorn beetles	*Stenodontes spinibarbis* L. (Cerambycidae)		*H. bacteriophora*	Laboratory	NS	de Doucet and Giayetto (1994)
Spittlebug	*Notozulia entrerriana* Berg (Cercopidae)		*H. bacteriophora*	Laboratory	S	de Doucet and Giayetto (1994)
Leaf beetles	*Botanochara angulata* Germ. (Chrysomelidae)		*H. bacteriophora*	Laboratory	NS	de Doucet and Giayetto (1994)
	Chrysodina sp. (Chrysomelidae)		*H. bacteriophora* *S. feltiae* *S. rarum*	Laboratory	S	de Doucet et al. (1999)
	Diabrotica speciosa Germ. (Chrysomelidae)	Alfalfa	*H. bacteriophora*	Laboratory	16%	de Doucet and Giayetto (1994)Stock (1996)[†]
	Plagiodera erithroptera Blanchard (Chrysomelidae)		*H. bacteriophora*	Laboratory	S	de Doucet and Giayetto (1994)
Elm leaf beetle	*Xanthogaleruca luteola* Müller (Chrysomelidae)		*H. bacteriophora* *S. diaprepesi*	Laboratory	NS/S 93–100%	de Doucet and Giayetto (1994)Giayetto and Cichón (2006)Lax et al. (2012)
Leafhopper	*Empoasca* sp. Walsh (Cicadellidae)		*H. bacteriophora*	Laboratory	S	de Doucet and Giayetto (1994)
	Edwardsiana crataegi Douglas (Cicadellidae)		*H. bacteriophora*	Laboratory	S	Giayetto and Cichón (2006)
Ladybugs	*Ceratomegilla* sp.Crotch (Coccinelidae)		*H. bacteriophora*	Laboratory	NS	de Doucet and Giayetto (1994)
	Epilachna paenulata Germar (Coccinelidae)		*H. bacteriophora*	Laboratory	NS	de Doucet and Giayetto (1994)
	Eriopis connexa Germar (Coccinellidae)		*H. bacteriophora* *S. feltiae* *S. rarum*	Laboratory	S	de Doucet et al. (1999)
	Hippodamia convergens Guérin-Méneville (Coccinellidae)		*H. bacteriophora* *S. feltiae* *S. rarum*	Laboratory	NS/S S S	de Doucet and Giayetto (1994)de Doucet et al. (1999)Giayetto and Cichón (2006)
Bugs	*Pachylis argentinus* Berg (Coreidae)		*H. bacteriophora* *S. feltiae* *S. rarum*	Laboratory	S	de Doucet et al. (1999)
	Achyra bifidalis F. (Crambidae)		*H. bacteriophora* *S. feltiae* *S. rarum*	Laboratory	S	de Doucet et al. (1999)
Sugarcane Borer				Laboratory	S	de Doucet et al. (1999)

(continued on next page)

Table 4 (*continued*)

Common name	Scientific name	Crop	Nematode species	Experimental location	Mortality	Reference
	Diatraea saccharalis (Fabricius) (Crambidae)		*H. bacteriophora* *S. feltiae* *S. rarum*			
Mosquitoes	*Aedes aegypti* L. (Culicidae)		*H. bacteriophora*	Laboratory	0–92.5%	Ulvedal et al. (2017)
	Culex apicinus Philippi (Culicidae)		*S. rarum*	Laboratory	5–75%	Cagnolo and Almirón (2010)
	Culex pipiens L. (Culicidae)		*H. bacteriophora* *S. feltiae* *S. rarum*	Laboratory	S S NS	de Doucet et al. (1999)
	Culex quinquefasciatus Say (Culicidae)		*H. bacteriophora* *S. rarum*	Laboratory	2.5–80% 89.2%	Cagnolo and Almirón (2007)Ulvedal et al. (2017)
	Culex saltanensis Dyar (Culicidae)		*H. bacteriophora*	Laboratory	NS	de Doucet and Giayetto (1994)
Weevils	*Naupactus* sp. (Curculinidae)	Alfalfa	*H. bacteriophora*	Laboratory	58%	Stock (1996)[†]
	Naupactus cinereidorsum Hustache (Curculinidae)		*H. bacteriophora* *S. feltiae* *S. rarum*	Laboratory	NS S S	de Doucet et al. (1999)
	Naupactus leucoloma Boheman (Curculinidae)		*H. bacteriophora*	Laboratory	S	de Doucet and Giayetto (1994)
	Naupactus xanthographus Dejean (Curculionidae)		*H. bacteriophora*	Laboratory	S	de Doucet and Giayetto (1994)Giayetto and Cichón (2006)
	Rhigopsidius piercei Heller (Curculionidae)	Potato	*Heterorhabditis* sp. *S. rarum*	Laboratory	50% 50%	Doucet et al. (2005)
Ants	*Acromyrmex lundii* Guérin-Méneville (Formicidae)		*H. bacteriophora* *S. feltiae* *S. rarum*	Laboratory	NS/S S S	de Doucet and Giayetto (1994)de Doucet et al. (1999)Giayetto and Cichón (2006)
	Solenopsis saevissima Smith (Formicidae)		*H. bacteriophora*	Laboratory	NS	de Doucet and Giayetto (1994)
	Undetermined[*] (Formicidae)		*H. bacteriophora*	Laboratory	NS	de Doucet and Giayetto (1994)
	Neocurtilla claraziana Saussure (Gryllotalpidae)		*S. riobrave* (Non native)	Garden	42–83%	Reboredo and Camino (2014)
	Photinus fuscus Germ. (Lampyridae)		*H. bacteriophora*	Laboratory	NS	de Doucet and Giayetto (1994)
Wax scales	*Ceroplastes grandis* Hempel (Lecaniidae)		*H. bacteriophora* *S. feltiae* *S. rarum*	Laboratory	S	de Doucet et al. (1999)
Cottony cushion scale	*Icerya* sp. (Margarodidae)		*H. bacteriophora*	Laboratory	S	de Doucet and Giayetto (1994)
	Icerya purchasi Maskell (Margarodidae)		*H. bacteriophora*	Laboratory	NS	de Doucet and Giayetto (1994)
	Epicauta adspersa Klug (Meloidae)		*H. bacteriophora* *S. feltiae* *S. rarum*	Laboratory	NS/S S S	de Doucet and Giayetto (1994)de Doucet et al. (1999)
Root-knot nematode	*Meloidogyne incognita* (Kofoid and White) (Meloidogynidae)	Sweet pepper Summer squash	*H. bacteriophora*	Greenhouse	37–37.6%	Del Valle et al. (2013)
	Meloidogyne javanica (Treub) (Meloidogynidae)	Sweet pepper	*H. bacteriophora* *S. rarum*	Laboratory	43.6–57.4%	Del Valle and Doucet (2014)
Spotted maize beetle	*Astylus atromaculatus* Blanchard (Melyridae)		*H. bacteriophora* *S. feltiae* *S. rarum*	Laboratory	S/NS S S	de Doucet and Giayetto (1994)de Doucet et al. (1999)
Buffalo treehopper	*Ceresa* sp. Amyot and Serville (Membracidae)		*H. bacteriophora*	Laboratory	S	de Doucet and Giayetto (1994)
House fly	*Musca domestica* L. (Muscidae)		*H. bacteriophora* *S. feltiae* *S. rarum*	Laboratory	S	de Doucet et al. (1999)
Bugs	*Nabis* sp. (Nabidae)		*H. bacteriophora* *S. feltiae* *S. rarum*	Laboratory	S	de Doucet et al. (1999)
	Lobiopa insularis (Castelnau) (Nitidulidae)	Strawberry	*H. bacteriophora*	Field	23%	Eliceche et al. (2016)
Black cutworm	*Agrotis ipsilon* (Hufnagel) (Noctuidae)	Alfalfa	*H. bacteriophora*	Laboratory	36%	Stock (1996)[†]
Velvetbean caterpillar		Soybean		Laboratory		

(*continued on next page*)

Table 4 (*continued*)

Common name	Scientific name	Crop	Nematode species	Experimental location	Mortality	Reference
	Anticarsia gemmatalis Hübne (Noctuidae)		*H. bacteriophora* *S. feltiae* *S. rarum*		S 76–96% 60–100%	de Doucet and Giayetto (1994)de Doucet et al. (1999)Cagnolo et al. (2011)Gianfelici et al. (2014)
Bollworm	*Helicoverpa gelotopoeon* (Dyar) (Noctuidae)	Soybean	*S. diaprepesi*	Laboratory	87–93%	Caccia et al. (2014)
	Heliothis sp. (Noctuidae)		*H. bacteriophora* *S. feltiae* *S. rarum*	Laboratory	S	de Doucet et al. (1999)
Soybean looper	*Pseudoplusia includens* Walker (Noctuidae)		*Steinernema* sp.	Laboratory	100%	Caccia et al. (2012)
Caterpillars	*Rachiplusia nu* Guenée (Noctuidae)		*H. bacteriophora* *S. feltiae* *S. rarum*	Laboratory	S	de Doucet et al. (1999)
Fall armyworm	*Spodoptera frugiperda* Smith (Noctuidae)	Maize	*H. bacteriophora* *S. diaprepesi* *S. feltiae* *S. rarum*	Laboratory	S 93–100% S S	de Doucet and Giayetto (1994)de Doucet et al. (1999)Caccia et al. (2014)
Western yellow-striped armyworm	*Spodoptera praefica* Grote (Noctuidae)		*H. bacteriophora*	Laboratory	S	de Doucet and Giayetto (1994)
Caterpillars	*Agraulis vanillae* L. (Nymphalidae)		*H. bacteriophora*	Laboratory	S	de Doucet and Giayetto (1994)
	Diogas erippus Cramer (Nymphalidae)		*H. bacteriophora*	Laboratory	S	de Doucet and Giayetto 1994)
Stink bug	*Dichelops furcatus* F. (Pentatomidae)		*H. bacteriophora* *S. feltiae* *S. rarum*	Laboratory	S S S	de Doucet et al. (1999)
Head louse	*Pediculus humanus* Haeckel (Pediculidae)		*H. bacteriophora* *S. feltiae* *S. rarum*	Laboratory	25–100% NS 5–64.5%	de Doucet et al. (1998, 1999)
Southern green stink bug	*Nezara viridula* L. (Pentatomidae)		*H. bacteriophora* *S. rarum*	Laboratory	NS 35.7%	de Doucet and Giayetto (1994)Picca et al. (2008)
Small green stink bug	*Piezodorus guildinii* Westwood (Pentatomidae)		*H. bacteriophora* *S. feltiae* *S. rarum*	Laboratory	S NS S	de Doucet and Giayetto (1994)de Doucet et al. (1999)
Pentatomid bugs	Undetermined (Pentatomidae)		*H. bacteriophora* *S. feltiae* *S. rarum*	Laboratory	S S S	de Doucet et al. (1999)
Caterpillars	*Colias lesbia* (Pieridae)		*H. bacteriophora* *S. diaprepesi* *S. feltiae* *S. rarum*	Laboratory	S 82% S S	de Doucet and Giayetto (1994)de Doucet et al. (1999)Del Valle et al. (2014)
	Platypus sulcatus Chapuis (Platypodidae)		*H. bacteriophora*	Laboratory	S	Giayetto and Cichón (2006)
False root-knot nematode	*Nacobbus aberrans* (Thorne and Allen) (Pratylenchidae)	Tomato	*H. bacteriophora* *S. rarum*	Greenhouse	53% 57%	Caccia et al. (2013)
	Oiketicus platensis Berg (Psychidae)		*H. bacteriophora*	Laboratory	S	de Doucet and Giayetto (1994)Giayetto and Cichón (2006)
Pear psylla	*Cacopsylla pyricola* Förster (Psyllidae)		*H. bacteriophora*	Laboratory	S	Giayetto and Cichón (2006)
Greater wax moth	*Galleria mellonella* L. (Pyralidae)		*H. bacteriophora* *Steinernema* sp. *S. carpocapsae* *S. feltiae* *S. rarum*	Laboratory	1–100% 100% 25–100% S 24–85%	de Doucet et al. (1999)Stock (1996)Caccia et al. (2011)†
Kissing bug	*Dipetalogaster maximus* Uhler (Reduviidae)		*H. bacteriophora* *S. feltiae* *S. rarum*	Laboratory	NS S S	de Doucet et al. (1999)
	Triatoma infestans Klug (Reduviidae)		*H. bacteriophora* *S. feltiae* *S. rarum*	Laboratory	S NS NS	de Doucet and Giayetto (1994)de Doucet et al. (1999)
	Automeris coresus Boisduval (Saturniidae)		*H. bacteriophora*	Laboratory	S	de Doucet and Giayetto (1994)
	Rothschildia jacobaeae Walker (Saturniidae)		*H. bacteriophora*	Laboratory	S	de Doucet and Giayetto (1994)
White grubs	*Diloboderus abderus* Sturm (Scarabaeidae)	Alfalfa Wheat	*H. bacteriophora* *S. rarum*	Laboratory Greenhouse Field	42–95% 30	Stock (1996)Del Valle et al. (2017)†
Tobacco hornworm	*Manduca sexta* L. (Sphingidae)		*H. bacteriophora*	Laboratory	S	de Doucet and Giayetto (1994)
Lesser mealworm				Poultry facilities		Del Valle et al. (2016)

(*continued on next page*)

Table 4 (*continued*)

Common name	Scientific name	Crop	Nematode species	Experimental location	Mortality	Reference
	Alphitobius diaperinus (Panzer) (Tenebrionidae)		*H. bacteriophora* *S. rarum*		50.4% 40.8%	
Mealworm	*Tenebrio molitor* L. (Tenebrionidae)		*H. bacteriophora* *Steinernema* sp. *S. diaprepesi* *S. feltiae* *S. rarum*	Laboratory	S 40–100% 22.5% S 12.5–62%	de Doucet and Giayetto (1994)de Doucet et al. (1999)Doucet and Bertolotti (2006)Caccia et al. (2011, 2012) Del Valle et al. (2014)
Confused flour beetle	*Tribolium confusum* Jacquelin du Val (Tenebrionidae)		*H. bacteriophora*	Laboratory	S	de Doucet and Giayetto (1994)
Mediterranean fruit fly	*Ceratitis capitata* Wiedermann (Tephritidae)		*Heterorhabditis* sp. *H. bacteriophora* *S. feltiae* *S. rarum*	Laboratory	15–20% S S S	de Doucet et al. (1999)Bertolotti et al. (2007)
European red mite	*Panonychus ulmi* Koch (Tetranychidae)		*H. bacteriophora*	Laboratory	S	Giayetto and Cichón (2006)
Western flower thrips	*Frankliniella occidentalis* Pergande (Thripidae)		*H. bacteriophora*	Laboratory	S	Giayetto and Cichón (2006)
	Crocidosema aporema Walsingham (Tortricidae)		*H. bacteriophora* *S. rarum*	Laboratory	80–90% 90%	Gianfelici et al. (2014)
Codling moth	*Cydia pomonella* L. (Tortricidae)		*H. bacteriophora*	Laboratory	S	de Doucet and Giayetto (1994)Giayetto and Cichón (2006)
Oriental fruit moth	*Grapholita molesta* (Busck) (Tortricidae)		*H. bacteriophora*	Laboratory	S	Giayetto and Cichón (2006)
Wasps	Undetermined (Vespidae)		*H. bacteriophora* *S. feltiae* *S. rarum*	Laboratory	S	de Doucet et al. (1999)

S = susceptible.
VS = very susceptible.
NS = non susceptible.
† Reported as *H. argentinensis* by Stock (1996).

Ahmad (1974a,b) reported for the first time *Steinernema* and *Heterorhabditis* spp. in the Pampean region of Argentina. He isolated these nematodes from several naturally infected weevils, including *Graphognatus*, *Pantomorus* and *Naupactus*, in alfalfa [*Medicago sativa* L. (Fabales: Fabaceae)] fields (Ahmad, 1974a,b). In the 1980s, de Doucet and collaborators (Universidad Nacional de Córdoba) studied the biology, ecology and biocontrol potential of several EPN spp.

In Venezuela, research on EPNs was initiated between 1980 and 1990 at the Instituto de Zoología Agrícola, Facultad de Agronomía, Universidad Central de Venezuela. The main goal was to develop culture media for their mass production. However, the research was discontinued a few years later in the mid 80s (Wassink and Poinar, 1984) but resumed in the late 1990s by other scientists.

5.2. Surveys

In Argentina, several studies were carried out in the Pampean region, mostly in the provinces of Córdoba and Santa Fe between the 1970s and 1980s, (Fig. 3, supplementary). As a result, two native species, *Steinernema rarum* (de Doucet 1986) and *Steinernema ritteri* (de Doucet and Doucet, 1990) were described. In 1993, Stock isolated *H. bacteriophora* from naturally parasitized larvae of *Graphognathus* sp. (Coleoptera: Curculionidae) in the province of Santa Fe (Stock, 1993). In other surveys, *H. bacteriophora* was isolated in several places; showing to be the most ubiquitous species in this country and the one with the southern distribution (Giayetto and Cichón, 2006). Other EPNs including *S. feltiae, S. carpocapsae, S. scapterisci, S. glaseri,* and *S. diaprepesi* Nguyen and Duncan have been reported in this region (Fig. 3, supplementary). EPNs were also isolated in the Patagonia region of Argentina, in particular in the provinces of Rio Negro and Neuquén (de Doucet and Bertolotti, 1996; de Doucet and Giayetto, 1999). Giayetto et al. (1998) and de Doucet et al. (2001) also reported an unidentified *Steinernema* sp. in Península de Valdés (Chubut province). The second most widespread species recovered is *S. rarum* (Table 5). Bertolotti (2002), Cagnolo and Campos (2008) and Del Valle et al. (2014) also investigated the life cycle and other ecological aspects of several native isolates.

In Brazil, several surveys have been conducted in different regions over the past decades. Fowler (1988) collected soil samples from 1532 locations, using mole crickets (*Scapteriscus* and *Neocurtilla* spp.) (Orthoptera: Gryllotalpidae) as baits. Overall, 18 isolates of *Steinernema* and 13 isolates of *Heterorhabditis* spp. were recovered. Among the described species are *S. scapterisci* (Nguyen and Smart, 1990). Fowler and Garcia (1988) isolated *S. feltiae* from mole crickets in the state of São Paulo. Machado et al. (2005) also recovered *H. indica* in Itapetininga, São Paulo (Fig. 3, supplementary). Andaló et al. (2006) isolated and identified a new species, *H. amazonensis,* in the Amazonian region. Dolinski et al. (2008) conducted a survey in Monte Negro, Rondônia, and identified five strains of *H. indica* and four of *Heterorhabditis baujardi* Phan, Subbotin, Nguyen and Moens. Nguyen et al. (2010) also conducted a survey in the state of Mato Grosso do Sul, and isolated a novel species, Steinernema *brazilense* Nguyen, Ginarte, Leite, Santos, Harakava (Fig. 3, Table 1). In a survey in Lavras, Minas Gerais, Andaló et al. (2009) recovered two *H. amazonensis* strains from cultivated sorghum and garlic fields. Barbosa-Negrisoli et al. (2010a) isolated EPNs in the state of Rio Grande do Sul, reporting the presence of *S. rarum* and *S. riobrave*. Dell'Acqua et al. (2013) studied EPNs from São Paulo and Mato Grosso do Sul and identified *H. indica* and *H. amazonensis*, *S. riobrave*, *S. glaseri*, *S. australe*, *S. puertoricense* and *S. brazilense* (Fig. 3, supplementary). Rosa et al. (2013), reported the occurrence of *S. brazilense*, *S. diaprepesi*, *S. glaseri*, *S. rarum*, *H. amazonensis* and *H. indica* in agricultural areas and natural habitats in different Brazilian

Table 5
Target pest organisms and their control using entomopathogenic nematodes tested in South America (excluding Argentina).

Country	Common name	Scientific name	Crop	Nematode species	Experimental location	Mortality	Reference
Brazil	Oriental fruit moth	*Grapholita molesta* Busck (Lepidoptera: Tortricidae)	Peach	*H. bacteriophora* *S. rarum*	Laboratory Field	94–97%	Barbosa-Negrisoli et al. (2013)
	Brazilian apple leaf roller	*Bonagota salubricola*	Apple	*H. bacteriophora*	Field	61–70%	Barbosa-Negrisoli et al. (2010b)
	Sugarcane borer	*Diatraea saccharalis*	Sugarcane	*H. baujardi* *S. carpocapsae*	Greenhouse	S	Bellini and Dolinski (2012)
	Fall armyworm	*Spodoptera frugiperda*	Corn	*H. amazonensis*	Greenhouse	80–100%	Andaló et al. (2012)
	Guava weevil	*Conotrachelus psidii*	Guava	*H. baujardi* *H. indica*	Laboratory Greenhouse Field	34–85% 30–58% 33–50%	Dolinski et al., (2006) Silva et al. (2010)
	Sugarcane billbug	*Sphenophorus levis*	Sugarcane	*H. indica* *S. brazilense* *Steinernema* sp.	Laboratory Greenhouse	31–95% 42–85%	Gionetti et al. (2011)Tavares et al. (2007)
	Scarab beetle	*Leucothyreus* sp.		*S. brazilense*	Field	50%	Leite et al. (2012)
	Corn rootworm	*Diabrotica speciosa*	Maize	*H. amazonensis* *S. glaseri*	Laboratory Greenhouse	78–94%	Santos et al. (2011)
	South American fruit fly	*Anastrepha fraterculus*	Peach	*H. bacteriophora* *S. riobrave*	Field	28–51% 20–24%	Barbosa-Negrisoli et al. (2009)
	Mediterranean fruit fly	*Ceratitis capitata*		*H. bacteriophora* *S. carpocapsae*	Laboratory	35–85%	Rohde et al. (2012)
			Guava	*H. baujardi*	Laboratory Field	90–100% 66–93%	Minas et al. (2016)Silva et al. (2010)
	Fungus gnat	*Bradysia mabiusi* Lane (Diptera: Sciaridae)	Nursery plants	*H. indica* *S. glaseri* *S. carpocapsae* *S. brazilense* *S. feltiae*	Laboratory Greenhouse	67–100% 50–70%	Leite et al. (2007)Tavares et al. (2012)
	Coffee root mealybug	*Dysmicoccus texensis*	Coffee	*H. amazonensis*	Laboratory Greenhouse Field	82–100% 70% 65%	Alves et al. (2009a, b)
	Sugarcane spittlebug	*Mahanarva fimbriolata* (Hemiptera: Cercopidae)	Sugarcane	*H. indica* *S. carpocapsae* *S. glaseri*	Laboratory Field	96–100% 54–74%	Leite et al. (2003)Leite et al. (2005)
	Spittlebug	*Mahanarva spectabilis*	Elephant grass *Pennisetum purpureum* Schumacher (Poales: Poacaeae)	*S. carpocapsae* *S. feltiae* *S. riobrave* *H. amazonensis*	Laboratory Greenhouse	40–90% 14–71%	Batista et al. (2014)
	Mound-forming termites	*Cornitermes cumulans* K. (Isoptera: Termitidae)	–	*S. carpocapsae*	Laboratory	80–100%	Rosa et al. (2008)
	Pink pineapple mealybug	*Dysmicoccus brevipes* Cockerell (Hemiptera: Pseudococcidae)	Pineapple *Ananas comosus* L. (Poales: Bromeliaceae)	Different native isolates	Laboratory	24–100%	Ferreira et al. (2015)
	Lesser mealworm	*Alphitobius diaperinus*		Different strains	Laboratory	100%	Costa et al. (2007)Alves et al. (2012)
	Cattle tick	*Rhipicephalus microplus*		Different strains	Laboratory Greenhouse	90% 90%	Monteiro and Prata (2013)
	Cayenne tick	*Amblyomma sculptum*		*S. glaseri*	Laboratory	3–13%	Cardoso et al. (2013)
	Tropical horse tick	*Dermacentor nitens* Neumann (Acari: Ixodidae)		Different strains	Laboratory	56–96%	Monteiro et al. (2014)
	Yellow fever mosquito	*Aedes aegypti*		Different strains	Laboratory	50–100%	Cardoso et al. (2015)
	Stable fly	*Stomoxys calcitrans* L. (Diptera: Muscidae)		*H. bacteriophora* *H. baujardi*	Laboratory	33–100%	Leal et al. (2017)
	Asian trampsnail	*Bradybaena similaris* (Stylommatophora: Bradybaenidae)		*H. indica*	Laboratory	55%	Tunholi et al. (2014)
	American ribbed fluke snail	*Lymnaea columella* Say (Stylommatophora: Bradybaenidae)		*H. baujardi*	Laboratory	67%	Tunholi et al. (2017)
	Root-knot Nematode	*Meloidogyne mayaguensis* Rammah and Hirschmann (Tylenchida: Meloidogynidae)	Tomato	*H. baujardi* *S. feltiae*	Laboratory Greenhouse	Significant reduction in galls formation	Molina et al. (2007)
Chile		*Lophotus phaleratus* Schoenherr (Coleoptera: Curculionidae)		*S. carpocapsae*	Laboratory	VS	Dutky (1957)Wassink and Poinar, 1984
		Hylamorpha elegans				VS	

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Table 5 (*continued*)

Country	Common name	Scientific name	Crop	Nematode species	Experimental location	Mortality	Reference
		Agrotis sp				S	
		Maculella noctuides Pfitz (Lepidoptera: Hepialidae)				VS	
		Tipula sp. (Diptera: Tipulidae)				NS	
		Phthorimaea operculella Zeller (Lepidoptera: Gelechiidae)				VS	
		Margarodes vitium Giard (Hemiptera: Margarodidae)				S	
		Crocidosema aporema (Lepidoptera: Noctuidae)				S	
		Langsdorfia sp. (Lepidoptera: Pyraustidae)				VS	
		Pantomorus sp.				VS	
		Asynonychus cervinus Boheman (Coleoptera: Curculionidae)		*Steinernema* spp. *Heterorhabditis* spp.	Laboratory Field	VS	France (2013)Merino and France (2009)
	Black vine weevil	*Otiorhynchus sulcatus* F. (Coleoptera: Curculionidae)	Blueberry			75%	
	Codling moth	*Cydia pomonella*	Apple	*S. austral*		S	Devotto et al. (2010)
	Fruit tree weevil	*Naupactus xanthographus*	Vineyards and fruits trees	*S. unicornium* *S. feltiae*	Laboratory Field	62–70%	Luppichini et al. (2013)
	Black cutworms	*Dalaca pallens*	Pastures	*S. australe* *S. unicornium*	Laboratory Field	95%	Maldonado et al. (2012)
	Raspberry weevil	*Aegorhinus superciliosus*	Raspberry, blueberry, strawberry and others	*S. australe* *S. diaprepesi*		72–87%	France (2013) Maldonado et al. (2012)
Colombia	Sugar froghopper	*Aeneolaimia varia*	Grasses	*S. colombiense* *S. carpocapsae* *H. bacteriophora*	Laboratory Field	75% 100%	Aristizábal et al (2015)
	Tomato leafminer	*Tuta absoluta*	Tomato	*S. carpocapsae*	Field	16–50%	Prada and Gutiérrez, (1976)
	Colombian defoliator	*Oxydia trychiata*	Cypress Pine Coffee		Laboratory	60%	Bustillo (1976)
	Potato white grub	*Premnotrypes vorax*	Potato	*S. carpocapsae* *Steinernema* sp.	Laboratory	30%	Amaya and Bustamante (1975)
	Root borer	*Sagalassa valida*	Oil palm *Elaeis guineensis* Jacq. (Arecales: Arecaceae)	*Steinernema* sp, *Heterorhabditis* sp.	Laboratory Field	45.5–72.7% 64%	Sáenz-Aponte et al. (2005)Sáenz-Aponte and Olivares (2008)
	Diamond back moth	*Plutella xylostella*	Cruciferae	*H. indica* *H. bacteriophora*	Laboratory Field	95.6% 80%	Sáenz-Aponte (2012)Correa-Cuadros et al. (2016)
	Pasture bedbug	*Collaria scenica*	Grass	*Steinernema* sp. *Heterorhabditis* sp.	Field Laboratory	60–80% 100%	Naranjo et al. (2011)
	Ox beetle	*Strategus aloeus*	Oil palm	Different native isolates	Laboratory	2–45%	Gómez and Sáenz-Aponte (2015)
	Giant borer of African palm	*Cyparissius Daedalus*	Oil palm	*Steinernema* sp. *Heterorhabditis* sp	Field	48–61.67%	Ayala et al. (2004)
	Bean seed fly	*Delia platura*	Spinach *Spinacia oleracea* L. (Caryophyllales: Amaranthaceae)	Different native isolates *Steinernema* sp. *H. bacteriophora*	Laboratory Field	20–85% 50%	Jaramillo and Sáenz-Aponte (2013)Jaramillo et al. (2013)
	Guava weevil	*Conotrachelus psidii*	Guava	Different native isolates	Laboratory Field	20–82% 40–85%	Delgado and Sáenz-Aponte (2016)
	Ground pearl scale	*Eurhizococcus colombianus* Jakubski (Hemiptera: Margarodidae)	Blackberry *Rubus glaucus* Benth (Rosales: Rosaceae)	*S. colombiense* *H. bacteriophora*	Laboratory	75–100%	Aristizábal et al. (2015)
	Silky cane weevil	*Metamasius hemipterus* Sericeus (Coleoptera: Curculionidae)		*S. carpocapsae* *H. bacteriophora*	Laboratory	38% 45%	Jiménez et al. (2012)
	Guatemalan potato moth	*Tecia solanivora*	Potato	*S. feltiae* *H. indica*	Laboratory	100%	Sáenz-Aponte (2003)
	White grub	*Clavipalpus ursinus* Blanchard (Coleoptera: Melolonthidae)	Grass, Potato	*S. feltiae*	Laboratory	88%	Sáenz-Aponte (2003)

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Table 5 (*continued*)

Country	Common name	Scientific name	Crop	Nematode species	Experimental location	Mortality	Reference
	Fall armyworm	*Spodoptera frugiperda*	Maize	*S. glaseri* *S. anomali* *S. carpocapsae*	Laboratory Field	70–100% 50%	Landazabal et al. (1973) Benjumea et al. (1978)
	Coffee berry borer	*Hypothenemus hampei*	Coffee	Different native isolates	Laboratory	49.6–50.9%	Molina and López (2003)
	American palm cixii	*Haplaxius crudus* Van Duzee (Homoptera: Cixiidae)	Oil palm	Different native isolates	Laboratory	20–40%	Bustillo (1976)
	Burrowing bugs	*Cyrtomenus bergi*	Cassava	Different native isolates	Laboratory	5–30%	Caicedo and Bellotti (1996)
Ecuador	Andean weevil	*Premnotrypes vorax*	Potato	Different native isolates	Laboratory	68%	Hernández (2006)
	Guatemalan potato moth	*Tecia solanivora*				69%	
	Moths	*Symmetrischema tangolias*				74%	
	White grubs	*Phyllophaga* sp.			Laboratory Field	70%	Asaquibay et al. (2011) Báez and Oña (2015)
Peru	Silkworm	*Bombyx mori* L. (Lepidoptera: Bombycidae)		*S. carpocapsae*	Laboratory	100%	Tang (1958)
	Lesser wax moth	*Achroia grisella* F. (Lepidoptera: Pyralidae)				100%	
		Mescinia peruella Schaus (Lepidoptera: Pyralidae)	Cotton *Gossypium* sp L. (Malvales: Malvaceae)		Laboratory	100%	
		Anthonomus vestitus Bohm (Coleoptera: Curculionidae)				100%	
		Dysdercus peruvianus Guerin (Hemiptera: Pyrrhocoridae)				100%	
	Tobacco budworm	*Heliothis virescens* F. (Lepidoptera: Noctuidae)				VS	
	Cycads	*Proarna bergi* Distant (Homoptera: Cicadidae)	Asparagus	*Heterorhabditis* sp.	Commercial	43%	Cedano (pers. comm.)
	White grubs	*Cyclocephala* sp. *Anomala* sp. *Gymnetis* sp. (Coleptera: Scarabaeidae)	Blueberry	*Heterorhabditis* sp.	Commercial Laboratory	60% 100%	Cedano et al. (2015) Narrea-Cango et al. (2013)
	Mediterranean fruit fly	*Ceratitis capitata*	Citrus spp.	*Heterorhabditis* sp.	Laboratory	68%	Vílchez (2014)
	Lesser cornstalk borer	*Elasmopalpus lignosellus*	Asparagus	*Heterorhabditis sp.*	Field	50%	Jaramillo and García (2007)
Venezuela	Bite bugs	*Rhodinus prolixus*		*S. carpocapsae*	Field	VS	Wassink and Poinar (1984)
	Guatemalan potato moth	*Tecia solanivora*	Potato	*H. bacteriphora* *Heterorhabditis* sp.	Laboratory	70–100%	Fan et al, (2000)
	Fall armyworm	*Spodoptera frugiperda*	Maize	Different native isolates	Laboratory	42–100%	San-Blas et al. (2015b)
	West Indian sweet potato weevil	*Eucespes postfasciatus*	Sweet potato	Different native isolates	Laboratory	36–94%	San-Blas et al. (2015b)
	Coffee berry borer (larvae and adults)	*Hypothenemus hampei*	Coffee	*Heterorhabditis* sp.	Field experiment	30–44%	Pacheco and Torres (2005)
	Pinneaple weevil	*Metamasius dimidiatipennis*	Pineapple	Different native isolates	Laboratory	50–95%	García-Caicedo et al. (2013)
	White grubs	*Phyllophaga* spp.	Grass	Different native isolates	Laboratory	3–16%	San-Blas et al. (2015b)
	Mangoes fruit fly	*Anastrepha obliqua*	Mango	Different native isolates	Laboratory	44–96%	San-Blas et al. (2015b)
	Guava fruit fly	*Anastrepha striata*	Guava	Different native isolates *H. indica*	Laboratory Field	24–100% 75–79%	San-Blas et al. (2015b)
	Sapodilla fruit fly	*Anastrepha serpentine*	Sapodilla	Different native isolates *H. indica*	Laboratory Field	33–100% 50–78%	San-Blas et al. (2015b)
	Sugar froghopper	*A. varia*	Sugar cane	*H. bacteriophora*	Commercial	71–75%	Ferrer et al. (2004)
	Fungus gnat	*Bradysia* spp.	Sweet pepper seedlings *Capsicum annum* L. (Solanales: Solanaceae)	Different native isolates *H. amazonensis* *S. papillatum*	Laboratory Field	80–85%	San-Blas et al. (2015b)

(*continued on next page*)

Table 5 (*continued*)

Country	Common name	Scientific name	Crop	Nematode species	Experimental location	Mortality	Reference
			Mushrooms *Agaricus bicolor* Pers. (Agaricales: Agaricaceae)	Different native isolates *H. amazonensis* *S. papillatum*	Laboratory Field Laboratory	45–85%	San-Blas et al. (2015b, 2017a,b)
			Tomatoes (Cherry)			75%	
			Daisy gerbera flowers			79%	
	Wireworms	*Agriotes* sp.	Sweet corn	*H. amazonensis*	Laboratory	80–100%	San-Blas et al. (2015b)
	Western flower thrips	*Frankliniella occidentalis*	Roses *Rosa* sp. L. (Rosales: Rosaceae)	*H. amazonensis*	Laboratory	18–85%	San-Blas et al. (2015b)

S = susceptible.
VS = very susceptible.
NS = non susceptible.

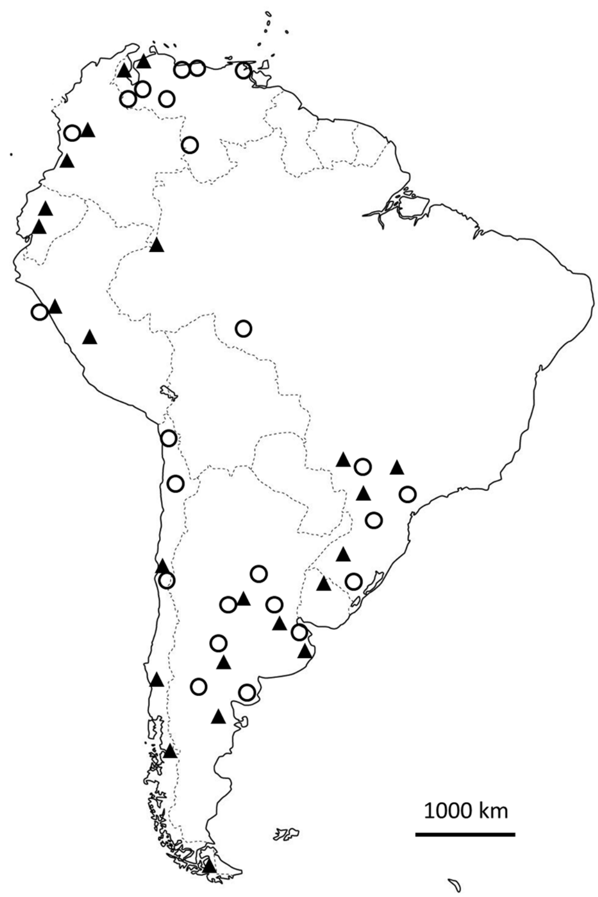

Fig. 3. Sampling sites (approximation) in South America where entomopathogenic nematodes have been isolated. ▲ = *Steinernema*; O = *Heterorhabditis*.

regions. Brida et al. (2017) also isolated *H. amazonensis* and *S. rarum* from soils samples of several fruit and forest crop fields (Fig. 3, supplementary).

Before 2000, the biodiversity of EPNs in Chile was largely unexplored. However, in 2006, Edgington et al (2010) conducted a countrywide survey, ranging from the Atacama Desert and the high Andean Altiplano in the north, to Patagonia and Tierra del Fuego in the south. This was a Darwin Initiative Project funded project that followed Charles Darwin's route during the Beagle expedition in the 19th century. Several EPN species were reported including *Heterorhabditis safricana* s.f., *Steinernema feltiae*, and three new species, *S. australe*, *S. unicornium* Edgington, Buddie, Tymo, France, Merino, Hunt and *H. atacamensis* Edgington, Buddie, Moore, France, Merino, Tymo, (Fig. 3, Table 1, supplementary). *Steinernema unicornum* was isolated from the archipelago of Tierra del Fuego, but it is widely distributed throughout the country (Edgington et al., 2009b). *Steinernema australe* was isolated from humid, loamy sand soil close to the sea on Isla Magdalena (Edgington et al., 2009a). *Heterorhabditis atacamensis* was recovered from the Atacama Desert, which is one of the driest deserts in the world, from a sandy bank located 2499 m above sea level (Edgington et al., 2011) (Fig. 3, Table 1, supplementary).

In Colombia, EPN discovery has been based on isolating nematodes for the control of specific crop pests (Table 5). López-Núñez et al. (2007) found that 92% of the isolates from the central Andean region were *Steinernema*, with only 7.2% *Heterorhabditis*. Detailed studies on the morphology and molecular characteristics of *Steinernema* isolates revealed the presence of *S. websteri*, and of four other undescribed species. In 2008, one of the isolates was described as *S. colombiense* (López-Núñez et al., 2008) (Table 1).

In Ecuador, Argotti et al. (2011) investigated 357 soil samples from the provinces of Carchi, Cotopaxi y Chimborazo. Their survey of a variety of habitats, including agricultural fields and native vegetation, isolated 28 nematode strains. The EPN diversity was associated with different ecological habitats. For example, Argotti et al. (2011) showed that all EPN isolates were located at altitudes between 2640 and 3573 masl. Among the soil properties associated with the isolates, all of the steinernematid isolates were retrieved from loam soils with pH ranging from 5.5 to 6.4, and being comprised of between 7% and 16% organic matter, while the heterorhabdtids were isolated from loam and sandy loan soils, with pH ranging from 6.5 to 8.1, and an average of 7.5% organic matter. Molecular and phylogenetic studies revealed that the *Steinernema* species isolated in that survey belong to *S. feltiae* (Pallo, 2017) (Fig. 3, supplementary).

In Peru, Ecuador and Bolivia, Alcázar et al. (2007) and Kaya et al. (2009) isolated and evaluated new native EPNs to control Andean potato weevil and other tuber pests. A total of 37 native EPN isolates were found, with 13 in Ecuador, 5 in Bolivia, and 19 in Peru, comprising 20 *Heterorhabditis* spp., and 17 *Steinernema* spp. (Fig. 3, Table 5).

There has been no formal study of EPN diversity in Uruguay. However, a survey for mole cricket (*Scapteriscus* spp.) natural enemies was initiated by the University of Florida to achieve classical biological control of invasive crickets in Florida and Puerto Rico. Surveys in Brazil and Uruguay (Nguyen and Smart, 1991) recovered crickets infected by EPNs in both countries. In 1985 some isolates were brought from Uruguay to USA where it was determined that the nematode was a new species, described as *Steinernema scapterisci* (Nguyen and Smart, 1990). The *S. scapterisci* was subsequently cultured, released and established in the USA and Puerto Rico, where it has helped suppress several invasive *Scapteriscus* spp. (Leppla et al., 2007).

Many regions of Venezuela were sampled for EPNs during the past two decades. About 50 *Steinernema* and *Heterorhabditis* isolates have been retrieved. *Heterorhabditis amazonensis* and *H. indica*, comprise almost 70% of the nematodes isolated (San-Blas et al., 2015b; Morales et al., 2016) including some isolates that remain unidentified. A few *steinernematids* have been found, of which four belong to the recently described *S. papillatum* (San-Blas et al., 2015a) and *S. goweni* (San-Blas et al., 2016), whereas the rest remain unidentified (Fig. 3, Table 1, supplementary).

5.3. Laboratory and greenhouse assays

In Argentina, native EPNs have been targeted against many insect hosts (Table 4). Research also concentrated on the morphology of native EPNs (de Doucet et al., 1990, 1992, 1996), and the effects of temperature on virulence (de Doucet et al., 1991). Del Valle et al. (2017) assessed *H. bacteriophora* against the first (L1) and second instars (L2) of *Diloboderus abderus* (Coleoptera: Scarabaeidae) Sturm. Results of greenhouse trials showed 95% and 45% mortality to L1 and L2, respectively, and the insect population was reduced in subsequent field trials by applying 2.5×10^9 IJs/ha into the soil (Table 4). EPNs have also been tested against the root knot nematodes (RKN) *Meloidogyne incognita* Kofoid and White (Tylenchida: Heteroderidae) and *Meloidogyne javanica* Treub (Tylenchida: Heteroderidae) (Del Valle et al. 2013; Del Valle and Doucet, 2014). The application of *G. mellonella* cadavers infected by either *H. bacteriophora* or *S. diaprepesi* into the soil, reduced the number of galls and egg masses produced by both RKN species in sweet pepper [*Capsicum annuum* L. (Solanales: Solananceae)] and summer squash [*Cucurbita* sp. L. (Cucurbitales: Cucurbitaceae)] plants. In tomato [*Solanum lycopersicum* L. (Solanales: Solananceae)], the inoculation of *S. rarum* and *H. bacteriophora* IJs into the soil reduced the reproduction rate of the false root-knot nematode *Nacobbus aberrans* Thorne (Tylenchida: Pratylenchidae) (Caccia et al., 2013) (Table 4).

In Brazil, EPNs have shown promise in many greenhouse experiments (Table 5). The application of a suspension of *H. baujardi* and *S. glaseri* to tick-infested cattle was ineffective (Carvalho, 2008). However, in a simulated field study, *H. bacteriophora* HP88 and *H. baujardi* LPP7, applied via insect cadavers to grass grown in pots, infected 98% and 92% of *R. microplus* ticks, respectively (Monteiro et al., 2014). In another set of experiments, the authors also found mortality levels of 60% and 43% for ticks using *H. bacteriophora* HP88 and for *H. baujardi* LPP7 respectively, when EPN-insect cadavers were applied 60 days prior to the ticks being placed in the pots (Monteiro and Prata, 2013). Molluscicidal potential of EPNs has been also tested in Brazil. In the laboratory, application of *H. indica* (LPP1 strain) caused 55% mortality of the snail *Bradybaena similaris* Férussac (Stylommatophora: Bradybaenidae) (Tunholi et al., 2014), while *H. bauardi* (strain LPP7) produced 67% mortality in *Lymnaea columella* (Gastropoda: Pulmonata) (Tunholi et al., 2017) (Table 5).

Argotti et al. (2010b) screened 11 isolates of Ecuadorian EPNs (seven steinernematids and four heterorhabditids), which all attained > 90% mortality against *G. mellonella* larvae. Thereafter, they explored their virulence against fourth instar of *T. solanivora* and *P. vorax*, obtaining promising results using *Heterorhabditis* H01T and CC01. Argotti et al. (2010a) evaluated ecological characteristics of the two isolates, including reproductive potential, dispersion in different substrates and the impact of water content in the soil. *H. bacteriophora* (H04-D strain) was evaluated in two-month-old raspberry plants that were infested with five scarabaeid larvae. Ten IJs/g of soil were inoculated onto the soil under greenhouse conditions. A reduction of 70% of the larvae was recorded after 14 days (Báez et al., 2014).

The coffee borer, *H. hampei,* was detected in Venezuela in 2005 (Montilla et al., 2006), having presumably emigrated from Colombian fields. The evaluation of native *Heterorhabditis* and *Steinernema* isolates to control *H. hampei* larvae in Petri dishes resulted in 23.7% and 44.4% larval mortality, respectively (Pacheco and Torres, 2005) (Table 5). The effect of EPNs on *A. serpentina* (which attacks Sapodilla [*Manilkara zapota* Royen (Ericales: Sapotaceae)], *A. striata* (found in guava) and *A. obliqua* (which is a pest of mango *Mangifera indica* L. [Sapindales: Anacardiaceae]) provided control rates from 45% to 100%, depending on the species/strains concerned (San-Blas et al., 2015b) (Table 5).

5.4. Field trials

In Argentina, Eliceche et al. (2016) applied *H. bacteriophora* in strawberry fields to control *Lobiopa insularis* Castelnau (Coleoptera: Nitidulidae) and reported 46–23% reduced fruit damage in EPN plots. Del Valle et al. (2016) also showed that the application of *S. rarum* and *H. bacteriophora* to rice hull, serving as bedding for poultry production, reduced populations of *A. diaperinus* as high as 40.8% and 50.4%, respectively.

In Brazilian field trials (Table 5), good results were obtained against *M. fimbriolata* (sugar cane root spittlebug) (Leite et al., 2005), *C. psidii* (Dolinski et al., 2006), *Ceratitis capitata* Wiedemann (Diptera: Tephritidae), *Anastrepha fraterculus* Wied (Diptera: Tephritidae), and *D. texensis* (Alves et al., 2009b). In a field study, *Leucothyreus* sp. and *S. levis* on sugar cane were treated with *S. brazilense*, insecticides (fipronil or thiamethoxam), and mixtures of *S. brazilense* and insecticides. The best result against *Leucothyreus* sp was obtained with the mixture of *S. brazilense* combined with thiamethoxam, which provided 83% control. For *S. levis*, no significant mortality was observed (Leite et al., 2012). Another experiment conducted in Brazil with *H. baujardi* (strain LPP7) applied via an irrigation system, showed that the nematodes can tolerate 35 °C for 2 h, and high pressure (2344 kPa) for 30 min (Lara et al., 2008a). Furthermore, the infectivity and mobility of *H. baujardi* was not affected after passage through the low-pressure irrigation sprays which typically operate at a pressure between 103 and 307 kPa (Lara et al., 2008b). Similarly, IJs of another species, *S. glaseri* remained viable at pressures of 1379 KPa (Garcia et al., 2005). Moreira et al. (2013) also investigated the pressure of different spray nozzles and reported that *S. feltiae* IJs were undamaged at a pressure of 620 kPa, and also reported the compatibility of this nematode with vegetable and mineral oils as adjuvants. The authors also observed that agitation in a motorized backpack sprayer for 30 min did not affect *S. feltiae* IJs (Garcia et al., 2008) (Table 5).

The use of nematodes against foliar pests has also been investigated in Brazil. For example, Barbosa-Negrisoli et al. (2010b) assessed different EPN isolates, in apple orchards applied with or without adjuvants. The authors reported that *H. bacteriophora* + sorbitol was the most effective treatment against *Bonagota salubricola* Meyrick (Lepidoptera: Tortricidae), achieving 71% of larval mortality. Bellini and Dolinski (2012) also reported the leaf application of *Heterohabditis baujard* LPP7 and *Steinernema carpocapse* (All strain) with different adjuvants to control the sugar cane borer, *D. saccharalis*. A 50% reduction of plant damage was observed for the nematode treatments.

Del Valle et al. (2009) also tested coating methods of insect cadavers (*G. mellonella* infected by *H. baujardi*) for field applications and investigated the behavior of *Ectatomma* ants (Hymenoptera: Formicidae) towards the coated EPN-infected cadavers. Their study showed that talc and gelatin capsules did not affect the emergence of IJs from the cadavers. When the talc formulated cadavers were placed close to the openings of ant nests, the ants carried the cadavers up to 20 cm, but were unable to move gelatin capsules with the infected cadavers.

In Ecuador, Asaquibay et al. (2011) evaluated EPN-infected *G. mellonella* cadavers on compost in potato fields. This study was conducted in three locations of Chimborazo province, tested EPN-infected *G. mellonella* larvae against white grubs. The compost was kept at field capacity and distributed at a rate of 0.5 kg per plant in the field different post planting intervals. Results of this study showed levels of control, with only 12.2% of the potato tubers showing signs of damage when compared with 31.2% in control plots.

The Chavimochic irrigation project, located on the northern coast of

Peru, has allowed desert areas to be cultivated with export crops. Since 2006, asparagus cultivation has been affected by the cicada *Proarna bergi* Distant (Homoptera: Cicadidae), whose nymphs damage the root system and reach densities of 500 individuals per m^3 soil (Leal, 2007). Preliminary tests were performed on asparagus plantations, applying *Heterorhabditis* sp. to the soil at 2.5×10^3 and 5×10^4 IJs per plant by drenching. In another treatment, EPN were applied by burying one to three infected *G. mellonella* cadavers per linear m. Insect reduction exceeding 70% was achieved by all treatments (Malqui, 2015) (Table 5). A subsequent trial was conducted on a three-year-old, heavily insect-infested asparagus plantation. Infective juvenile *Heterorhaditis* sp. were extracted by manually grinding EPN-infected *G. mellonella* cadavers (3000 per ha). Immediately after filtration, the nematodes were brought to a volume of 200 L and introduced into a drip irrigation system. Results from pitfall traps demonstrated 26% control 30 days post-EPN application, and 42% after 60 days (Carolina Cedano pers. comm) (Table 5).

In Venezuela, Ferrer et al. (2004) performed trials against the sugar froghopper (*Aenolamia varia*) in commercial sugar cane fields. A Cuban isolate of *H. amazonensis*, applied at 50–100 million IJs/ha resulted in 75% control. On a commercial button mushroom [*Agaricus bisiporus* Lange (Agaricales: Agaricaceae)] farm, *H. amazonensis* proved to be effective against fungus gnats [*Bradysia difformis* Frey (Diptera: Sciaridae)], using 1.5×10^6 nematodes/m^2 in the casing layer of production bags. The mushroom yield was enhanced by 20% over the chemical control (San-Blas et al., 2017a). Another experiment in El Jarillo (Miranda State), showed that 50,000 IJs of *H. amazonensis* per plant, applied to flower pots containing gerbera daisies [*Gerbera* sp. (Asterales: Asteraceae)], provided similar control of *B. difformis* as did cyromazine. Moreover, based on the dose and frequency of application, *H. amazonensis* was significantly more effective than the chemical product, when used in the field (San-Blas et al., 2017b) (Table 5).

5.5. Mass production

EPN mass production in Brazil originally focused on *in vivo* rearing methods using mainly larvae of *G. mellonella* but also *Diatraea saccharalis* F. (Lepidoptera: Crambidae) and *T. molitor* (Folegatti et al., 1988). Due to the cost in the production of *G. mellonella*, Molina et al. (2004) used alternative hosts including *T. molitor, S. frugiperda,* and *Bombyx mori* L. (Lepidoptera: Bombycidae) to rear *S. carpocapsae* and *S. glaseri*. Leite (2006) developed an *in vitro* medium based on beef liver soaked in sponges that yielded up to 1.8×10^5 IJs/ml of *Heterorhabditis* sp. More recently, Leite et al. (2016a, 2016b, 2016c) tested another medium based on egg yolk, egg white, yeast extract, glucose and peanut oil, obtaining over 10^5 IJs/ml of medium

In Peru, commercial application of EPNs was undertaken by Camposol, a private company producing asparagus and avocado on 3000 ha of land. Since 2008, Camposol has produced its own EPNs (*Heterorhabditis* sp.) to control white grubs in blueberry orchards (Carolina Cedanao pers. comm).

6. Latin American perspectives for the future

Many studies considering EPN have been conducted in Latin America for the control of endemic or introduced insect species. However, most studies have been conducted in the laboratory, and comprehensive and well-designed filed studies are lacking in many countries including Ecuador, Chile, Peru, and most oft the Central American countries. It is critical that more studies are conducted in demonstration plots and in collaboration with farmers. There is no doubt that EPNs have great potential in IPM practices in many agricultural systems. Unfortunately, the lack of funding both from private and federal funding agencies is one of the many impediments for moving forward into this direction. Furtheremore, the lack lof commitment from policymakers, the untimely interruption of EPN research projects due to funding and other unexpected reasons have limited the development of new ideas and mass production of EPN. Educational programs in agricultural sustainability are needed to encourage an understanding of the benefits of using biological control agents when compared to chemical pesticides. While the majority of farmers recognize some microbial control agents, such as fungi or bacteria, most have no idea of the existence of EPNs (Dolinski et al., 2012; San-Blas et al 2015b). Investing in educational programs for farmers, school teachers and consumers while releasing EPNs in the fields may help promote their use. Researchers should educate the next generation of agronomists, biologists and scientists about entomopathogenic nematology into course curricula that go beyond thesis or dissertation projects or the sporadic mentioning of EPNs in the content of lectures.

The unparalleled diversity of EPNs in the South American subcontinent should also be considered as a goldmine for advancing research in entomopathogenic nematology (San Blas, 2013). Carefully designed surveys should be expanded, to expand the discovery of novel species that will lead to improved opportunities for biological control, especially in countries that have not yet initiated surveys, such as Bolivia, Uruguay and most of Central American countries. The study of the EPN symbiotic bacteria should also be done in parallel to enhance mass production methods. The EPN bacterial symbionts may also prove by themselves their potential in controlling plant pests and pathogens (San-Blas et al., 2012, 2013).

Additionally, cooperation among Latin American countries needs to be improved. Scientists need to stop working in isolation and share experiences by teaming up with multidisciplinary expertise. Private initiatives to mass-produce EPNs are likely to continue, but growth may also come from cottage-scale producers who use *in vivo* and *in vitro* techniques. A few international companies (i.e. Koppert, e-nema) have prompted the commercialization of EPNs in different Latin American countries but use of their products remains restricted to a few users. The growth rate of the EPN industry will depend on legislation, consumer education, and technological innovation. However, in all cases, growth will be favored by awareness of the critical importance of improving agricultural methods, by reducing chemical inputs, and overcoming the challenges of poverty and hunger.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jip.2019.03.010.

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