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RAPID COMMUNICATION

# Can entomophagous nematodes slow the spread of invasive pest populations? The case study of *Beddingia siricidicola* released for the management of *Sirex noctilio*

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**Abstract** Though rarely used in this way, biological control could potentially be exploited for managing spread of invasive species. Because spread of invasive species emerges from the combined action of population growth and dispersal, natural enemies that affect either of these processes should also affect spread. Dispersal of parasitoid species plays a key role in determining their impact on population growth of an invading host species along their expanding population front. In contrast, dispersal of most true parasites only occurs via movement of hosts so any impact that parasites may have on host dispersal may limit the parasite's own capacity to keep up with an expanding host population. We test this premise by examining field data from what is probably the best example of the successful use of true parasites in biological control: the nematode *Beddingia* (=*Deladenus*) *siricidicola,* which is released for management of *Sirex noctilio* populations. We analyze the historical impact of nematode releases on the rate of spread of invasive *S. noctilio* populations in Southern Argentina. Our findings suggest that, nematode releases did not discernibly slow the spread of *S. noctilio* populations. We conclude that although entomophagous parasites could be effective at reducing the growth and dispersal of localized host populations, they are unlikely, unless widely released through the leading edges, to slow the spread of invading hosts.

**Keywords** Macroparasites · Forest insects · Biological control · Patagonia

## Key message

- Biological control using parasitoids or pathogens could be exploited for managing the spread of invasive insect species.
- We analyzed the historical impact of nematode releases on the rate of spread of *Sirex noctilio* in Patagonia and note that these did not discernibly slow its spread.
- We suggest that although parasites could be effective at reducing the growth and dispersal of localized host populations, they are unlikely, unless widely released through the leading edges, to slow the spread of invading hosts.

## Introduction

The geographical spread of invading species arises from the combination of population growth and dispersal (Liebhold and Tobin 2008). Invasive species are typically highly fecund and may grow exponentially at the leading edge where intra-specific competition is minimal. In turn, dispersal can take several forms, but is essentially driven by the individual capacities for movement (e.g., flight potential) or through passive anthropogenic movement (e.g., "hitchhiking"). In combination, these processes result in continuous spread over short distances coupled with highly discontinuous, stochastic spread over long

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distances; this phenomenon, referred to as 'stratified dispersal' results in much higher rates of spread than would occur via short distance dispersal alone (Shigesada and Kawasaki 1997). Reducing the rate at which a species spreads, involves either disturbing population growth by, for instance, enhancing mate finding Allee effects, or by altering dispersal, either reducing short-range or long-range movement.

Biological control, the use of natural enemies to suppress or regulate pest population growth, is a key component of modern pest management. For classical biocontrol of non-indigenous insects, natural enemies are selected from the native range of pests and introduced into the new, invaded habitat (Eilenberg et al. 2001). While there is a long record of successful application of classical biological control utilizing parasitoids and predators (Kidd and Jervis 2007), there have been fewer attempts made using true parasites or pathogens (Hajek 2004; Hajek et al. 2007).

Entomopathogenic nematodes are important biological control agents for a variety of economically serious pests (Grewal et al. 2005; Hajek et al. 2007; Batalla-Carrera et al. 2010). Nematodes belonging to the families Steinernematidae and Heterorhabditidae have been used with variable success against insects occupying different habitats. Most success has been achieved targeting soil dwelling pests or pests in cryptic habitats such as inside galleries in plants (Hajek et al. 2007; Hajek 2009).

The first successful, and probably best known, example of the use of nematodes to control an insect pest was the introduction of *Beddingia* (=*Deladenus*) *siricidicola* (Tylenchida: Neotylenchidae) to manage invasive populations of the woodwasp *Sirex noctilio* Fabricius (Hymenoptera: Siricidae) in Australia (Bedding 1993; Hajek et al. 2007; Hajek 2009). Though native to Eurasia, *S. noctilio* is only a pest in its invaded range, particularly in the southern hemisphere where it frequently kills large numbers of pines planted in commercial plantations; the species has recently invaded North America but so far has caused little damage (Villacide and Corley 2012).

The biology of *B. siricidicola* includes female dimorphism: a free-living mycetophagus form feeds on the host's fungal symbiotic fungus and a parasitic life form feeds on woodwasp tissue (Bedding 1967). During oviposition, *S. noctilio* females inject spores of the fungus from which mycelia develop and this supports feeding by juvenile and adult nematodes. However, some fertilized juvenile females may switch to a parasitic cycle and locate and penetrate host larvae. Within *S. noctilio* females, juvenile nematodes can suppress ovarian development, reducing wasp fecundity (Bedding 1972, 1984). Parasitized *S. noctilio* females may still display oviposition behaviors. Thus, infected wasps will lay eggs filled with nematodes into new susceptible trees (Bedding 1984; Bedding and Iede 2005). Nematodes spreading within the tree may parasitize the larvae hatched from eggs laid by uninfected females in the same tree, thus ensuring the natural transmission of the infection among woodwasps.

The nematode *B. siricidicola* has been released for woodwasp control and has become established in several countries in the Southern Hemisphere (Hajek et al. 2007; Hurley et al. 2007; Bedding 2009). It has been shown that the nematode sterilization of woodwasp females affects population growth and hence its prime use as a biocontrol agent (Bedding 1972, 1984). In turn, *B. siricidicola* may affect other wasp traits such as adult body size or body reserves (Bedding and Iede 2005) or even flight capacity (Villacide and Corley 2008) which may also contribute to pest control through diminished longevity and dispersal of female woodwasps.

Because entomopathogenic nematodes may reduce female fecundity and may indirectly alter dispersal behavior, we hypothesize that these parasites, aside from limiting pest populations locally, should also contribute to stopping or slowing the spread of invasive insect pests (Fagan et al. 2002; Hilker et al. 2005). We test this premise by examining the releases of *B. siricidicola* for the biological control of *S. noctilio* populations. We focus on historical field data on the impact nematode releases have had on the invasion spread of *S. noctilio* populations in Southern Argentina. While woodwasp geographical spread among pine plantations in the region has been analyzed elsewhere (Lantschner et al. 2014) here we compare spread, both directly following first detection and the introduction of *B. siricidicola*.

## Methods

Spread of *S. noctilio* was quantified using woodwasp detection data collected as part of surveys conducted in northwestern Patagonia, from the period 1993 to 2006. These data consist of records of *S. noctilio* presence/absence in individual pine plantations; the period 1993–2006 spans the interval between first detection in the region to the establishment of the species in most of the region (Lantschner et al. 2014; Fig. 1). Data on the date and location of nematode releases was reconstructed from reports submitted by *Servicio Nacional Sanidad Agroalimentaria* (SENASA), the Argentine national authority responsible for animal and plant protection of Argentina, and by provincial forestry authorities.

In Patagonia, released nematodes were obtained from INTA Monte Carlo (Argentina) and SAG (Chile) mass rearing laboratories. These *B. siricidola* populations were comprised of several strains: "Encruzhilada do Sul" imported from Brazil and produced in Argentina and Chile,

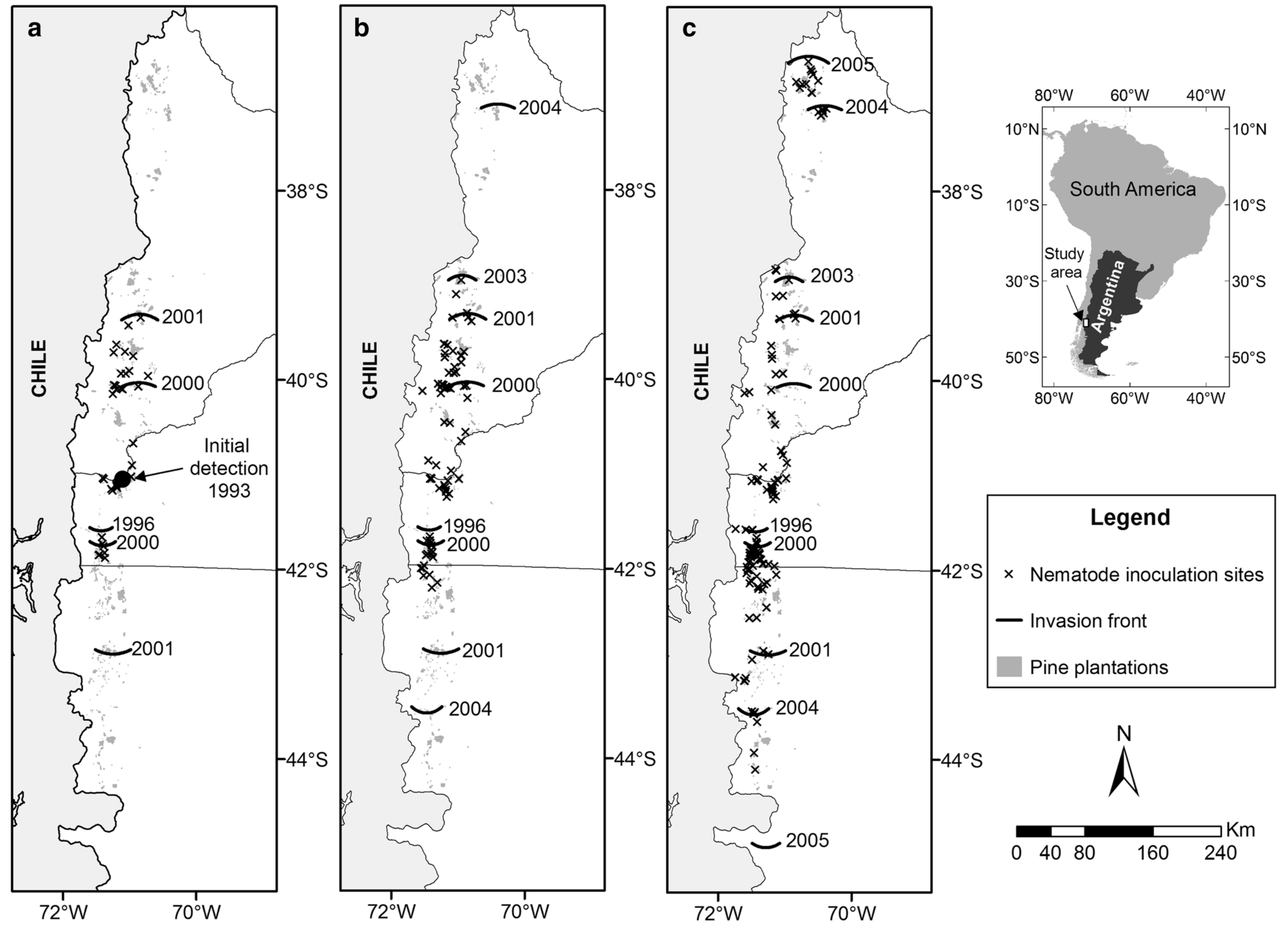

**Fig. 1** Temporal sequence and geographical distribution of nematode inoculation sites and *Sirex noctilio* spread among pine plantations in northwestern Patagonia. Dates indicate the leading edge of spread at that time (invasion front) and crosses show inoculation sites. **a** 2001–2002 period, corresponding to initial inoculation campaign, **b** 2003–2004 period inoculation campaign and **c** 2006, inoculations when wasps had spread throughout the distribution of pine plantations in the region. Note that *S. noctilio* was first detected in Patagonia in 1993

and “Tangoio” produced in Chile and originating from New Zealand. Nematodes were mass reared and inoculated into selected, felled woodwasp-infested trees in the field (Bedding and Iede 2005). Inoculations were carried out during the months of October and November. Sirex-attacked trees suitable for inoculation were identified through visual inspections, marked, and felled immediately prior to inoculation. Nematodes were suspended in a gelatin solution and introduced into trees through several holes made with a specialized hammer device (Bedding and Iede 2005).

By splitting the survey data obtained in two groups (before and after nematode inoculations began), and through simple linear modeling of distance as a function of time (Gilbert and Liebhold 2010; Lantschner et al. 2014), we quantified historical spread rates of woodwasp populations prior to and following *B. siricidicola* release. Infection status was corroborated by dissecting wasps captured at different times during the invasion process. In this way, we were able to confirm firstly, that no nematodes were present before inoculation programs began and secondly that nematode introductions had been successful.

## Results

Table 1 summarizes woodwasp infection status following nematode releases into Patagonian pine plantations. No infection was detected before 2001, the year in which inoculations began, eliminating the possibility of natural invasion from other woodwasp/nematode populations (e.g., Northern Argentina). Also nematode infections grew rapidly within inoculated stands (as indicated by increasing rates of parasitism) indicating that, in contrast to what has been observed in some world regions (e.g., South Africa, Hurley et al. 2007, 2008), the inoculation process was

**Table 1** Nematode release history and percent parasitism in Patagonia, for the period 2001–2006

| Year | Number of nematode packs released[a] | Number of inoculated trees | Number of *S. noctilio* females disected | Parasitism percent[b] |
|---|---|---|---|---|
| 2001 | 208 | 700 | – | – |
| 2002 | 513 | 1,976 | 93 | 22.6 |
| 2003 | 215 | 1,851 | 94 | 43.6 |
| 2004 | 997 | 2,805 | 53 | 41.5 |
| 2005 | 1,200 | 2,965 | 105 | 66.7 |
| 2006 | 785 | 3,580 | 60 | 73.3 |

Infection rates were determined through dissections of random samples of specimens carried out the year after nematode releases

[a] A pack of nematodes consists of a 20 ml inoculum of approximately 1-millon of living nematodes

[b] Average regional parasitism. Sources SENASA-SAG (2002); Corfone (2003) and Echeverría (2005)

– indicates no available data. Refer to Fig. 1 for details of geographical and temporal distribution and of inoculation sites

highly successful and widely dispersed throughout the attacked pine plantations of Patagonia (see also Klasmer et al. 1998; Hurley et al. 2007; Fig. 1).

A contrasting result is observed in Fig. 2. Here, *S. noctilio* spread rates did not decrease following nematode introductions. The rate of woodwasp spread before nematode release (1993–2000) was 10.39 km/year ($y = 3.67 + 10.39x$; $p = 0.0105$). During the period of active nematode release (2001–2006) woodwasp spread was 20.11 km/year ($y = -39.63 + 20.11x$; $p = 0.0339$) despite the steadily increasing nematode infection rate (Table 1). Spread rates during these two periods were not significantly different ($t(2,44) = 0.98$; $p = 0.333$). Nevertheless, spread rates to the north of first detection (note that pine plantations are generally distributed along a North-South axis) are comparable to or slightly greater than those southward; and that in the southerly direction, nematode inoculations generally occurred later (Fig. 1c). Spread to the north reached 20.0 km/year; inoculations began in 2001 (Fig. 1a) and were conducted across the entire area infested by *S. noctilio* at the time and across all northern pine plantations by 2004. In contrast, spread of *S. noctilio* to the south reached 15.6 km/year and inoculations were always conducted well behind the woodwasp invasion front (Fig. 1b, c).

## Discussion

The woodwasp *S. noctilio* has spread throughout Patagonian pine plantations since it was first detected in the area in 1993. Despite a highly fragmented landscape—pines are planted in patches of variable size on the scrublands of the Patagonian steppe—populations have spread at an average rate of 17.7 km/year. A more detailed analysis of woodwasp spread rates in the Southern Hemisphere is provided elsewhere (Lantschner et al. 2014). Following initial detection, management objectives have transitioned in the region from an initial unsuccessful eradication attempt, then to slowing the spread, and reducing outbreak intensities. Management has also included implementation of improved silviculture practices, augmentation of populations of the parasitoid *Ibalia leucospoides* (which

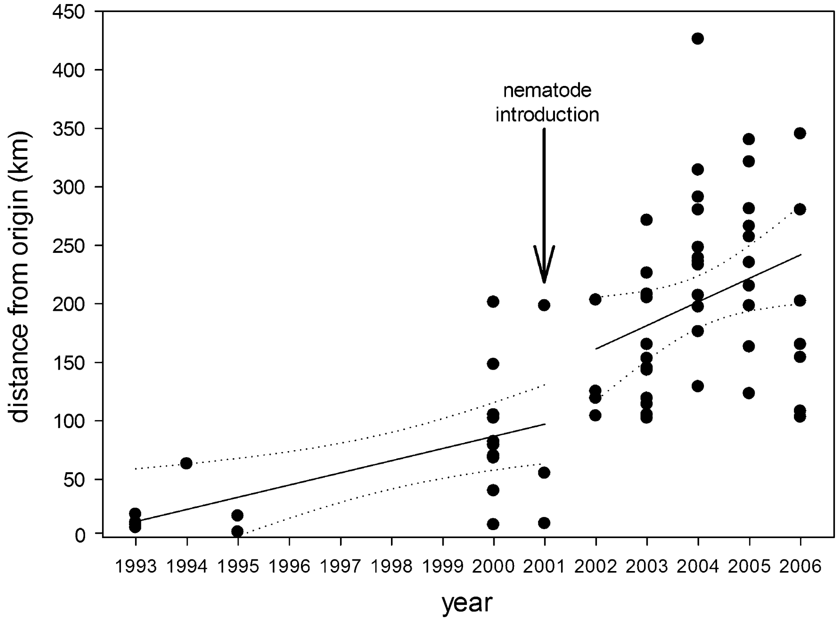

**Fig. 2** Records of newly established *Sirex noctilio* populations with radial distance (from the site of initial discovery near Bariloche in Patagonia, Argentina, in 1993) plotted vs. year. Separate linear regression lines are shown. Slopes of regression equations provide estimates of radial spread rates (Gilbert and Liebhold 2010) during the initial stage of invasion and after nematode introductions. *Dashed lines* indicate 95 % CI. The introduction of the nematode *Beddingia siricidicola* began in 2001 (indicated by an *arrow*) and has been continuously released since, across most areas with pines in the region

apparently arrived in the area together with the founding woodwasp population), the release of *B. siricidicola* and more recently, the introduction of *Megarhyssa nortoni* (Hurley et al. 2007; Villacide and Corley 2012).

Releases of *Deladenus siricidicola* in NW Patagonia have been highly successful. As expected, nematodes rapidly established among woodwasp populations and infection rates increased through time (Table 1). Six years following initial introduction and with increasing inoculation effort, parasitism exceeded 70 %. While not quantified to date, the presence of nematodes is believed to have contributed to dampening of the impact *S. noctilio* populations on pines in this region as a result of the direct density-dependent influence they have on woodwasp population growth (Bedding and Iede 2005; Bedding 1984). Despite this apparent success, geographical spread of *S. noctilio* did not slow following the introduction of *B. siricidicola* into infested stands in NW Patagonia (Fig. 1).

The observed spread rates of *S. noctilio* woodwasps in Patagonia are slower than those recorded for other regions (see Lantschner et al. 2014 for data for Patagonia and other regions). Lantschner et al. (2014) proposed that differences in spread among regions are related to the effects of temperature on wasp development. While it is possible that in northwestern Patagonia and in the absence of nematodes woodwasp spread rates from 2001 to 2006 could have been faster, we lack specific controls to test for this.

There are several possible explanations why nematodes may not have contributed to slowing the spread of invasive *S. noctilio* populations in Patagonia. First, *B. siricidicola* parasitism rates may have been both too variable among sites, well behind the advancing population front, or else insufficient. Second, nematodes could have evolved into non-pathogenic strains, which have little or no effect on woodwasp reproduction. This may occur in part as a result of quality deterioration during colony propagation, as was found in Australia (Bedding 2009). While at least two different strains have been released in Patagonia and samples from populations collected in the field have been used extensively to maintain genetic diversity in the laboratory (E. Eskiviski, INTA Monte Carlo pers.com.), there have been observations of a small number of wasps that while bearing parasites in the body cavity, had an intact reproductive system (J. Villacide, unpub. data). Consequently, through any of these reasons, the impact of nematodes on woodwasp population growth may be smaller than that estimated from total infection rates.

Differential dispersal among healthy and infected females may also limit the capacity of nematodes to slow geographical spread (Villacide and Corley 2008, 2012). In order for nematode populations to increase within the host population, healthy and infected wasps must meet on the same tree. Nematodes are then transmitted when infected wasps lay nematode-filled eggs; these multiply within the sapwood and finally attack healthy larvae. Thus, the nematode can only spread to new trees when infected female wasps fly out in search of trees. Females *S. noctilio* are remarkably good fliers, but recent work has shown that body size is a critical aspect of flight potential (Bruzzone et al. 2009). While nematode infected *S. noctilio* woodwasps are in many ways identical in behavior with healthy individuals, a heavy parasite burden results in a smaller adult body size. Because they are smaller, parasite-infected wasps fly less than healthy individuals and for shorter distances (Villacide and Corley 2008). Therefore, it is likely that infected wasps may primarily spread the nematode among trees in a localized area, such as within a plantation or compartment, while larger, highly fecund uninfected females fly further away, and spread the *S. noctilio* population into new areas or plantations without transporting nematodes.

In contrast with what may occur with other natural enemies such as pathogens or parasitoids, nematode dispersal is tightly linked to host dispersal. Because the parasite has no free-living life stage capable of dispersal, host individuals bearing the nematodes are the vectors of the infection and as such must either directly encounter healthy hosts, or else share common feeding, breeding, or oviposition sites. Nevertheless, any negative effects that parasitism may have on the dispersal ability of hosts could alter the host's rate of invasion spread. The leading edge of the invasive species may be largely composed of healthy individuals unless infection is able to keep up and is widespread (Hilker et al. 2005). A consequence of this model is that, the combined effects nematodes may have on pest population growth and individual dispersal does not result in a reduced pattern of host invasion spread.

Biological control, using predators or pathogens has been addressed in the light of invasion biology (Fagan et al. 2002; Hilker et al. 2005). Theoretical population models confirm that infections by natural enemies can affect host invasion spread and spread of hosts may be slowed down or even reversed by the introduction of an infectious disease or other agent. Yet, the effects of pathogens on spread depend on the strength of Allee effects in the host population, the virulence of the introduced disease, as well as on the pathogen's dispersal ability, which determines its ability to keep up with the movement of the host invasion front (Hilker et al. 2005).

While the ecological significance of the dispersal abilities of introduced biocontrol agents is well known, partly because of the risks associated with the intentional introduction of species into new habitats (Simberloff and Stiling 1996), the spread of natural enemies is also central to its success in impacting host spread (Fagan et al. 2002). A key factor here is the pattern of spread displayed by the invading pest. Invasions in host species with increasing spread speeds over time, as often occurs in those species driven by long-distance dispersal events, are unlikely to be adequately controlled by natural enemies that are incapable of long-distance dispersal (Fagan et al. 2002).

While the impact of entomophagous parasites in suppressing insect pest populations is unquestioned, these natural enemies may have less impact on the invasion spread. More in-depth knowledge of the dispersal behavior of potential hosts and their natural enemies, as well as the design of appropriate strategies of natural enemy releases, that take into account host and natural enemy dispersal are essential components of success of pest management using true parasites. While our data do not allow us to determine why *B. siricidicola* has not limited the spread of invasive *S. noctilio* populations in Patagonia, because of its retrospective nature, we suggest that parasite dispersal—vector transmitted via infected hosts—is lower than that of healthy woodwasps affecting the natural spread of the nematodes. This information may be useful in planning future nematode releases aimed at managing expanding *S. noctilio* populations.

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