



Management of *Sirex noctilio* populations in exotic pine plantations: critical issues explaining invasion success and damage levels in South America

Juan C. Corley^{1,2} · María Victoria Lantschner¹ · Andrés S. Martínez¹ · Deborah Fischbein¹ · José M. Villacide¹

Received: 17 January 2018 / Revised: 1 October 2018 / Accepted: 27 October 2018
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Abstract

Plantation forestry with non-native trees is steadily increasing in the southern hemisphere and alien pest problems are also accumulating, as a consequence of the growing international movement of people and goods. Here, we present an overview of studies on the ecology and on the control practices deployed against the European woodboring wasp *Sirex noctilio*, in South America. Management actions have been largely adopted from other southern hemisphere countries, although generally with very little local adaptation or critical evaluation of successes and failures. The knowledge acquired in South America allows us to look retrospectively at critical issues that explain woodwasp invasion success and damage levels, and to identify specific research areas that warrant further work. We emphasize the need of population ecology studies in both the invaded and native ranges, the development of specific sampling protocols, and detailed studies aimed at evaluating the role played by natural enemies in preventing large-scale population outbreaks. These demands may be generalized to the management of other invasive pests in plantation forestry with non-native trees in the southern hemisphere.

Keywords Woodwasp · Forest insect monitoring · Pine plantations · Population ecology · Biological control

Key message

- The woodwasp *Sirex noctilio* is currently a widespread invasive forest insect pest of pine plantations throughout the southern hemisphere.
- In South America, and unlike what happens in its native range, populations show a pulse-like eruptive behavior that may cause massive tree killings.
- Several management actions have been deployed in the region, largely adopted from other southern hemisphere countries, lacking local adaptation and a critical evaluation of local successes and failures.
- Our review identifies several specific research areas for further work. These highlight the need for studies on the population dynamics of *S. noctilio*, with protocols that allow comparison among regions.

Communicated by N. Meurisse.

Special Issue on Invasive Pests of Forests and Urban Trees.

✉ Juan C. Corley
elmallin@gmail.com

¹ Grupo de Ecología de Poblaciones de Insectos, Instituto de Investigaciones Forestales y Agropecuarias Bariloche, INTA-CONICET, Modesta Victoria 4450, Bariloche, Argentina

² Departamento de Ecología, Centro Regional Universitario Bariloche, Universidad Nacional del Comahue, Bariloche, Argentina

Introduction

Plantation forestry with non-native trees is substantially increasing in many developing countries of the southern hemisphere (Brockerhoff et al. 2008; Wingfield et al. 2015). In South America, more than 12 million hectares are planted with fast-growing exotic species, essentially pine (*Pinus* spp.) and eucalypt (*Eucalyptus* spp.) (Payn et al. 2015). Plantations are established for the production of timber, pulp and fuel, and largely consist of intensively managed, even aged, and regularly spaced stands of single species, usually with low levels of genetic variation (FAO 2015).

Disease and insect outbreaks affect a significant proportion of forest worldwide, especially natural and planted native tree forests in the temperate northern hemisphere (Payn et al. 2015; van Lierop et al. 2015). In contrast, plantations with non-native species in the Southern Hemisphere are generally considered to be less impacted (Keane and Crawley 2002). This is mostly because they are being kept free of coevolved pests and diseases, which are usually associates in their native range, until they are eventually reunited (the “enemy releases hypothesis”). This enemy-free period, during which substantial stand losses can be avoided, can be variable, but is expected to be reduced in the current context of increasing accidental transportation of alien forest organisms (Brockhoff and Liebhold 2017). Global change, and in particular the unprecedented movement of goods and people, can therefore arguably be considered the most important threat to plantation forestry with non-native species (Walther et al. 2009; Wingfield et al. 2015).

In forest plantations in South America, the detection of established non-native pests has increased in recent years. In Argentina, Botto (2008) has shown an exponential increase in the annual detection rates of non-native insect pests on *Eucalyptus* spp. between 1991 and 2005. A recent report jointly produced by FAO and the quarantine agencies of several South American countries (Argentina, Bolivia, Brazil, Chile, Paraguay and Uruguay) states that by 2008 there were at least 58 non-native insects established (FAO 2008). Argentina reported the largest number of species (37), followed by Brazil (24) and Chile (14), and *Eucalyptus* spp. were the most affected tree species. About a quarter of the alien pests and pathogens in this list were found in more than one country (Corley and Villacide 2014).

Among the non-native forest insects shared by many countries and regions of South America in pines, the wood-wasp *Sirex noctilio* F. (Hymenoptera: Siricidae) is probably the most notorious, because of its widespread distribution and impact (Fig. 1; Villacide and Corley 2012; Corley and Villacide 2014; Lantschner et al. 2014). The species is native to Eurasia and northern Africa and has successfully invaded several countries of the southern hemisphere in the last century. It was first reported in New Zealand around 1900 (Miller and Clark 1935), in Australia in 1951, and arrived in South America by 1980 and in South Africa in 1994 (Gilbert and Miller 1952; Tribe 1995; Maderni 1998; Boissin et al. 2012).

Sirex noctilio is a woodboring wasp that has a solitary, cryptic lifestyle. Females lay eggs directly into the wood by drilling holes in stems of stressed pines. The successful egg hatching and development of *S. noctilio* larvae relies on the disruption of tree physiology caused by the combined effect of a symbiotic fungus (*Amylostereum areolatum*) and a phytotoxic venom introduced into the tree at the time of drilling by the female (Madden 1988; Slippers et al. 2015). After

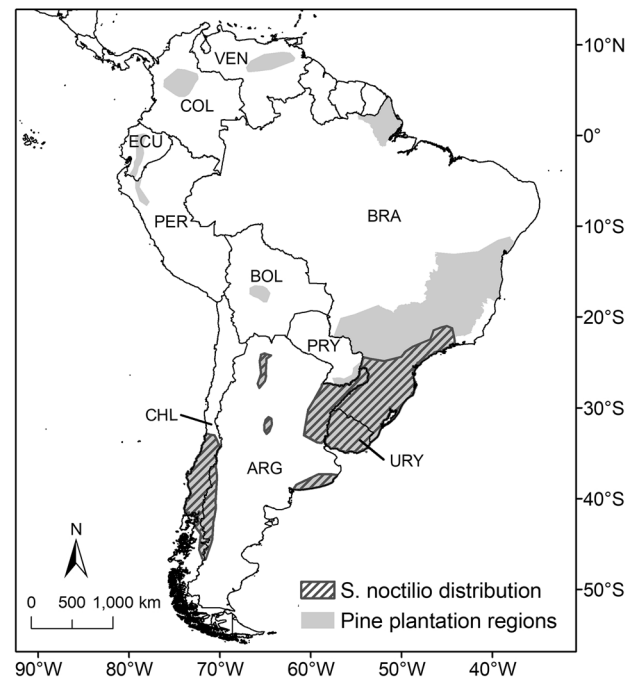


Fig. 1 Distribution of pine plantations and *Sirex noctilio* in South America. ARG: Argentina, BOL: Bolivia, BRA: Brazil, CHL: Chile, COL: Colombia, ECU: Ecuador, PRY: Paraguay, PER: Peru, URY: Uruguay, VEN: Venezuela

1–3 years development period inside the wood (depending on the climatic region), adults emerge, mate and attack new trees (Morgan and Stewart 1966; Madden and Coutts 1979). A list of specific life history traits of *S. noctilio* recorded in South America is provided in Table 1.

Our aim is to provide an overview of the ecology of *Sirex noctilio* in South America. We also devote attention on the successes and failures of the management strategies for the pest in the continent, to identify future research needs. We expect this synopsis will support further understanding of the risks and impacts posed by alien insects to plantation forest in South America and elsewhere in the world.

Distribution in South America

The historical spread of *S. noctilio* across South America is shown in Fig. 2, with emphasis on the two most important regions in terms of pine plantations surface: the south of Brazil, Uruguay and northeastern Argentina (about 2.4 million ha); and Chile and southwestern Argentina (about 2 million ha; for details see Table 2).

Sirex noctilio was recorded for the first time in South America in Cerro Largo Department, Uruguay in 1980 (Maderni 1998). The wasp then rapidly colonized all regions with pines in this country, reaching Argentina in

Table 1 Life history traits of *Sirex noctilio* woodwasp recorded in South America

Traits	Characteristics	References
Adult longevity	Field conditions: 4–5 days. Laboratory conditions (median): ♂: 11, ♀: 14 days	Carvalho et al. (1993), Villacide (2015)
Egg load	Related to female body size: 69–502 eggs	Villacide (unpub. data)
Mating behavior	Protandry. Generally, females mate multiple times. Mating occurs before dispersal	Villacide (2015), Caetano and Hajek (2017)
Life cycle	4–12 month cycles in warm regions; extended cycles (for up to 36 months) in cold and temperate regions	Corley and Villacide (2012), Iede et al. (2012)
Adult emergence patterns	October–April with a peak in November–December in warmer regions; December–May, with two peaks in January and March in temperate regions	Eskiviski et al. (2004), Corley and Villacide (2012), Iede et al. (2012), Rojas and Beèche (2010)
Flight potential capacity and patterns (laboratory conditions)	Related to adult body size: ♂: 0.8–37.3 km (mean: 11.3 km); ♀: 1.1–49.7 km (mean: 17.4 km). Large females are capable of longer and faster flights, while smaller females only perform short flights with long pauses	Bruzzone et al. (2009), Villacide and Corley (2008), Corley and Villacide (2012)
Long distance dispersal	Frequently, by adult flight and human-mediated infested logs movement	Villacide (2015)
Sex-ratio	Highly variable: from 0:1 to 32:1 ♂:♀	Eskiviski et al. (2004), Lopez et al. (2002), Gepi unpub data., Ruiz (2006), Iede et al. (1998)
Adult body size	Thorax width: ♂: mean: 3.1 (range 1.7–6.9 mm); ♀: mean: 3.9 (range 2.1–6.8 mm)	Villacide (unpub. data)
Population dynamics	Pulse-like eruptive outbreaks	Corley et al. (2007), Aparicio et al. (2013), Lantschner and Corley (2015)
Spatial aggregation	Yes, occurrence at different spatial scales	Corley et al. (2007), Aparicio et al. (2013), Lantschner and Corley (2015)
Main host tree species	<i>Pinus taeda</i> ; <i>P. elliotti</i> ; <i>P. patula</i> ; <i>P. oocarpa</i> ; <i>P. caribea</i> ; <i>P. strobus</i> ; <i>P. kesiya</i> ; <i>P. ponderosa</i> ; <i>P. contorta</i> ; <i>P. radiata</i>	Iede et al. (2012), Beèche et al. (2012), Corley and Villacide (2012)

1985 and Brazil in 1988 (Iede et al. 1998). Within Brazil, it was first detected in the state of Rio Grande do Sul, from where it spread northwards, rapidly colonizing the states of Santa Catarina in 1989, Paraná in 1996, São Paulo in 2004 and Minas Gerais in 2005 (Iede and Zanetti 2007). In Argentina, the first report in 1985 was in the province of Entre Ríos, and over a ten-year period, it spread toward the north, reaching the provinces of Corrientes and Misiones, which border with Brazil. Later, accidental introductions into the other parts of Argentina took place: the province of Buenos Aires in 1988, the province of Río Negro (Patagonia) in 1993, the north-western province of Jujuy in 1994 and the central region of the country (Cordoba province) in 1995 (Klasmer and Botto 2012). In 2001, a few female wasps were caught in funnel traps located in the Valparaíso and distant Los Lagos regions of Chile (SAG 2004). There were no captures of *S. noctilio* in Valparaíso after 2004, suggesting local extinction (Beèche 2012). In contrast, in Los Lagos, the species became established and spread during the following years, toward the north and south of that country. Establishments were first recorded in 2002 in Los Ríos and La Araucanía and then in 2009 in Bio-Bio, in 2011 in Maule, in 2012 in Aysén

and in 2016 in O'Higgins and Valparaíso (Beèche et al. 2012; SAG 2017).

Over the last 50 years, *S. noctilio* has shown an extraordinary capacity to reach most areas where pines are grown in South America. The northernmost location known to date is the Minas Gerais province in Brazil (21° S; Iede and Zanetti 2007), and the southernmost location is The Aysén region in Chile (46° S; SAG 2017). This broad distribution within South America includes contrasting eco-climatic regions with mean annual temperatures that range from 5.1 to 20.5 °C and rainfall regimes from 450 to 2300 mm annually (Hijmans et al. 2005). Likewise, *S. noctilio* has adapted and succeeded in locations with different forest composition, growth rates and management practices.

Populations of *S. noctilio* in South America appear to originate from two major sources or lineages; one most likely from Europe, and the other of an unknown origin (Boissin et al. 2012). Despite some national, regional and local efforts deployed to prevent the geographical spread of *S. noctilio* in South America (e.g., quarantine programs; Iede et al. 1998; Villacide and Corley 2012; SAG 2017), spread rates shown by this insect were high along all invaded districts (Table 2; Lantschner et al.

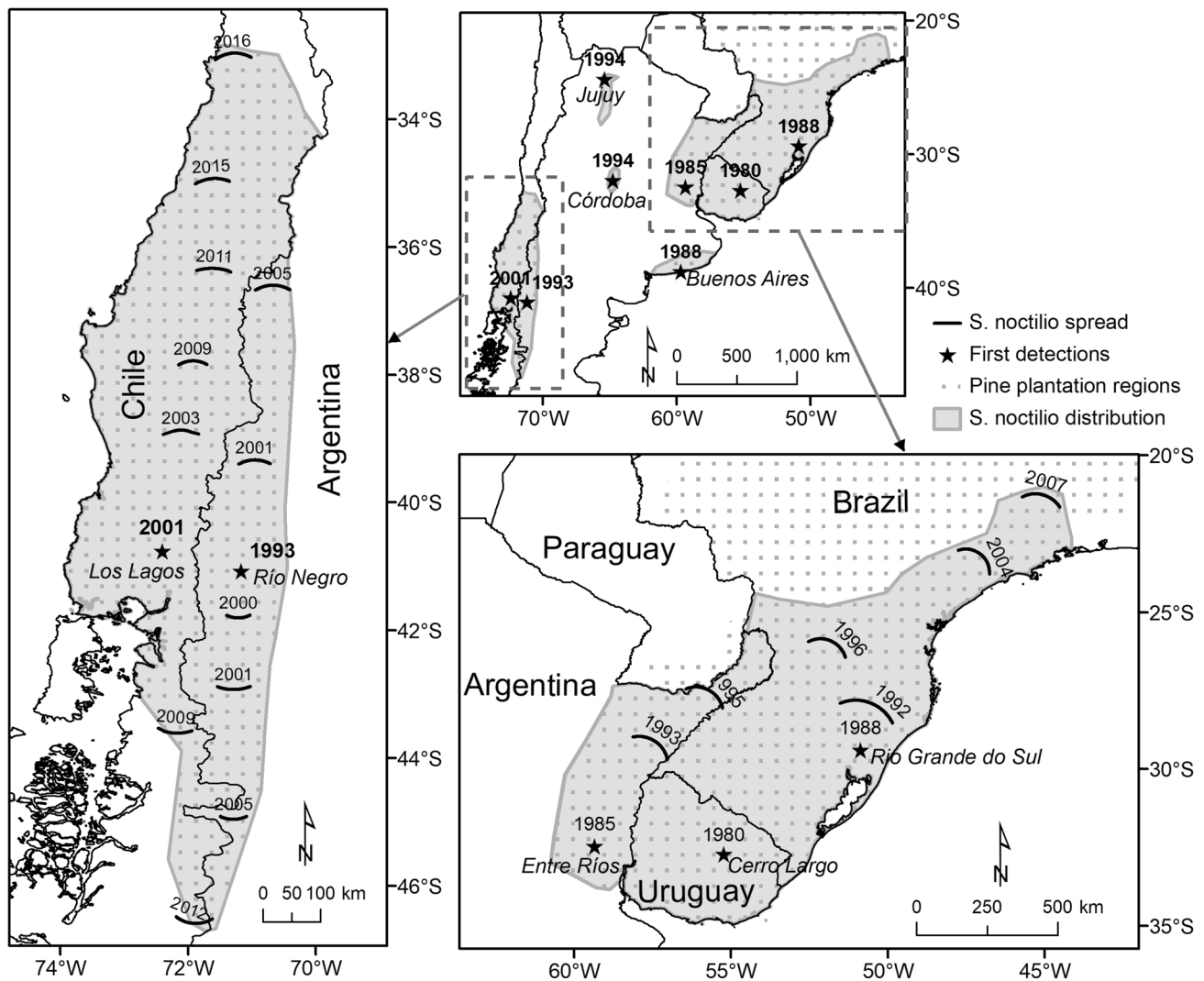


Fig. 2 Distribution and spread history of *Sirex noctilio* in South America, detailing the two most important regions in terms of pine plantations surface: the south of Brazil, Uruguay and northeastern Argentina (right); and Chile and southwestern Argentina (left)

2014), being even higher than most of those observed for other invasive forest insect species in different parts of the world (see examples in Evans 2016). For *S. noctilio*, it has been shown that spread rates increase with increasing mean annual temperature and isothermality, ranging from 17 km/year in SW Argentina, to 32.6 km/year in Chile, and 46.3 km/year in Brazil (Table 1; Lantschner et al. 2014). Climatic models have predicted that *S. noctilio* could establish further north from its current distribution—i.e., northern Brazil, Bolivia, Peru, Ecuador, Colombia and Venezuela (Carnegie et al. 2006; Ireland et al. 2018). However, there is no evidence to date that the species has established in any of these areas (see Fig. 1). Furthermore, the northern edge of current distribution, at latitude 21°S (Minas Gerais, Brazil), does not correspond to an eco-climatic rupture (Lantschner et al. 2014; Ireland et al. 2018).

Population dynamics and impact

In most regions within the invaded range, the *S. noctilio* displays a pulse-like eruptive population behavior (Berryman 1987). The species population dynamics is characterized by long periods during which populations remain at relatively low densities and rapidly increase to outbreak levels in an unpredictable fashion (Berryman 1987; Villacide and Corley 2012; Lantschner et al. under review). The occurrence of *S. noctilio* population outbreaks in South America and the resulting damage has been described for most areas where the woodwasp has established, such as Uruguay (Maderni 1998), southern Brazil (Rodigheri et al. 2006), southern Argentina (Lantschner and Corley 2015) and central Chile (Poisson et al. 2016) (Table 2).

Table 2 Comparison of pine plantation and *Sirex noctilio* status, monitoring methods and management current practices in South America. *Sources:* Beèche et al. (2012), Eskiviski et al. (2004), FAO (2015), Fischbein and Corley (2015), Iede et al. (1988, 2012), Klas-

mer and Botto (2012), Lantschner and Corley (2015), Lantschner et al. (2014), Maderni (1998), Poisson et al. (2016), Rodigheri et al. (2006), SAG (2004)

Description	Argentina		Brazil	Chile	Uruguay
	(North-east)	(South-west)			
Pine plantations					
Surface (ha)	590,035	96,000	1,562,782	1,951,600	256,900
Main planted species	<i>P. taeda</i> , <i>P. elliotii</i>	<i>P. ponderosa</i> , <i>P. contorta</i>	<i>P. taeda</i> , <i>P. elliotii</i>	<i>P. radiata</i>	<i>P. radiata</i>
<i>Sirex noctilio</i>					
1st detection date	1985	1993	1988	2001	1980
Spread rate (km/year)	Unknown	17	46.3	32.6	Unknown
Currently present throughout the country or region	Yes	Yes	No	Yes	Yes
Highest damage level detected (% attacked trees/stand)	30	75	60	50	70
Monitoring methods					
Aerial surveys	No	No	No	Yes (by private foresters)	–
Ground surveys	Yes	Yes	Yes	Yes	–
Trap trees	Yes	Yes	Yes	Yes	–
Traps + kairomones	State level	State level	–	Country-wide	–
Biological control agents					
<i>Beddingia siricidicola</i>					
Introduction	Deliberate	Deliberate	Deliberate	Deliberate	–
Parasitism (%)	24	14–90	above 70	10–65	–
<i>Ibalia leucospoides</i>					
Introduction	Accidental	Accidental	Accidental	Accidental and deliberate	Accidental
Parasitism (%)	Up to 35	25	Up to 29	25–30	24
<i>Megarhyssa nortoni</i>					
Introduction	No	Deliberate	Deliberate	Deliberate	No
Parasitism (%)	–	7.5–91.7	Not established	1.6–3.3	–
<i>Rhyssa persuasoria</i>					
Introduction	No	Deliberate	Deliberate	Deliberate	No
Parasitism (%)	–	Not established	Not established	Not established	–

– Information is lacking or irrelevant

Sirex noctilio outbreaks in South America, as well as in other parts of the southern hemisphere, have been found to be commonly triggered by increased disposal of stressed trees, suggesting that resource availability plays a key role in regulating local population abundance. Outbreaks have been found to be more likely in pine stands that are overstocked, damaged and unmanaged (Beèche et al. 2012; Iede et al. 2012; Lantschner and Corley 2015), as well as in plantations set on slopes at locations with drier conditions (Lantschner and Corley 2015). For southern Argentina, Lantschner and Corley (2015) suggest that the forest composition may also be an important factor determining outbreak probability: lodgepole pine (*P. contorta*) is remarkably more attacked than other pines planted there (i.e., *P. ponderosa*). This

has also been noted in Uruguay and Brazil where *P. taeda* is reportedly more susceptible than *P. elliotii* (Iede et al. 2012).

The “intermittent drought hypothesis” proposed by Madden (1988) for Australia proposes that tree stress factors, usually rapid changes in the physiological status of trees associated with drought stresses, are predisposing particular stands or occasionally entire forest regions to *S. noctilio* attacks. Once a population has initially established in a susceptible area, the spatial aggregation of attacks becomes stronger as the woodwasp population grows. This indicates positive density-dependent processes are certainly a key factor for the onset of outbreaks at the landscape scale (Corley et al. 2007; Aparicio et al. 2013). At this scale, another

feature associated with the probability of wasp populations reaching outbreak levels is their proximity to stands bearing outbreaks concurrently or recently (Lantschner and Corley 2015). Female dispersal may have a significant effect both on the onset and in expanding outbreaks throughout the landscape (Aparicio et al. 2013; Lantschner and Corley 2015; Lantschner et al. under review). Consequently, under the influence of an abrupt drought, *S. noctilio* populations rise and disperse from epicenters to create more widespread epidemics (Table 1; Fig. 3).

The termination of the epidemics appears to result from intra-specific competition due to widespread food depletion caused by the massive tree killings, or because of increased mortality due to natural enemies, as it has been suggested for other parts of the world (i.e., Australia and New Zealand; Madden 1988). Although in South America extensive biocontrol programs have been deployed (see below “Management strategies”), the role played by natural enemies in preventing and/or terminating outbreaks remains an open question. Information about the success of natural enemies at different phases of *S. noctilio* population dynamics is still very limited.

Monitoring *Sirex noctilio* populations in South America

Damage due to established *S. noctilio* populations may be reduced through adequate silvicultural practices and biological control. However, damage levels can be important upon the arrival of woodwasps into new afforested areas, related to the absence of natural enemies and possibly a local high abundance of susceptible trees. This has resulted in the need of detection methods for new establishments and to monitor established populations.

Historically, *S. noctilio* early detection has been carried out in many countries through indirect methods (i.e., looking for attack symptoms, rather than the insect itself). Such

methods rely on the identification of attacked pines (i.e., crown chlorosis and resin droplets on the main stem, produced after wasp drilling during oviposition), which are carried out through ground surveys (e.g., sequential sampling) or aerial surveys. However, these methods lack sensitivity during the early phases of establishment due to the small number of affected trees (Carnegie et al. 2005).

An additional method widely deployed throughout affected areas is the “trap-tree” technique. This method is based on the attraction shown by female *S. noctilio* wasps toward stressed trees (Madden and Irvine 1971; Bordeaux and Dean 2012) and consists of treating a small group of trees (e.g., 4–10 trees) with herbicide or through other methods such as girdling, a few months prior to the wasp flight season. In South America, after the flight season ends, treated trees are felled and cut into billets that are caged to check for adult emergence. The density of trap-tree plots is variable, ranging from 1 plot/25 ha in areas with known presence of *S. noctilio*, to 1 plot/10,000 ha in border areas or sites located more than 50 km away from established *S. noctilio* populations (COSAVE 2002). Trap trees also can be used in biological control practices, by using the felled trees as substrate for the release of the nematode *D. siricidicola*, and to estimate the presence and parasitism rates achieved by nematode and parasitoid releases.

More recently, developments have been made toward cost-effective methods based on the direct detection of adult wasps. This is generally implemented by means of static trapping systems baited with semiochemicals (Bashford 2008; Crook et al. 2008). A typical capture unit consists of an intercept panel trap or Lindgren multiple funnel trap in combination with a blend of kairomones, usually terpenes (different combinations of α and β pinene). These volatiles are those released by stressed trees (Simpson 1976; Simpson and Mc Quilkin 1976; Bashford and Madden 2012). Kairomone traps have already been implemented by nationwide programs in many countries affected by *S. noctilio* (i.e., Australia, South Africa, Canada and the United States), and

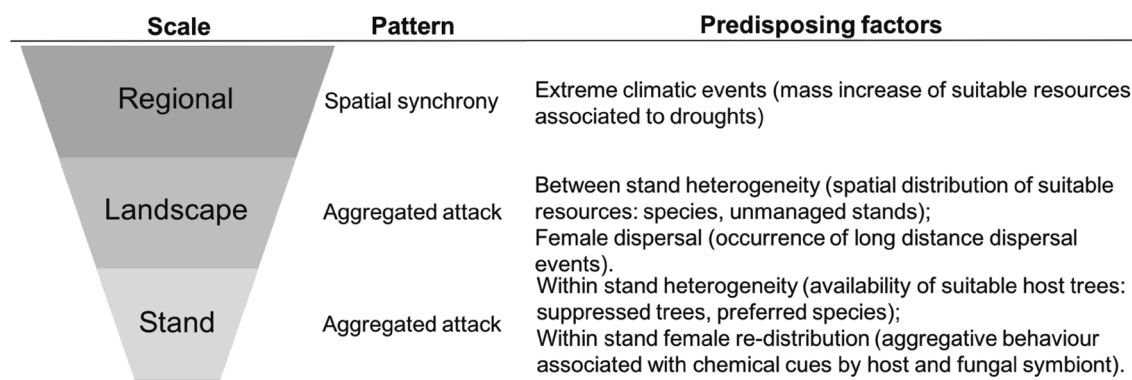


Fig. 3 Observed patterns of *Sirex noctilio* population outbreaks in South America, and proposed predisposing factors as affected by spatial scale

their use seems to be slowly taking off in South America (Table 2). Despite the fact that the benefits of kairomone-baited traps methods are clear, their effectiveness has been questioned when *S. noctilio* populations are low. This is because kairomones from traps compete with volatiles released by trees that are stressed naturally (i.e., in drought conditions) or artificially (i.e., trap trees) (Bashford and Madden 2012).

The challenge presented for effective monitoring and hence management is the limited ability of cost-effective methods in detecting low-density populations in forests (Bashford and Madden 2012; Hurley et al. 2015) or in high-risk areas such as ports and sawmills. In this sense, pheromone-baited traps may prove an important addition, since this type of traps can be highly specific and work at low population densities (Witzgall et al. 2010). *Sirex noctilio* chemical communication, especially the compounds involved in mate location, has been generally understudied, probably because of the elusive mating behavior displayed by this insect (i.e., copulation generally occurs at the top of tall trees). Some recent work shows that a male produced pheromone attracts both females and males in laboratory assays but not in the field (Böröczky et al. 2009; Cooperband et al. 2012; Hurley et al. 2015). It has also been shown that *S. noctilio* females as well as its parasitoids can discriminate previously attacked trees from other, by specific blends of chemicals they release (Martínez et al. 2006; Fischbein et al. 2012; Fernández Ajó et al. 2015; Jofré et al. 2016). Understanding the orientation response of foraging *S. noctilio* females, notably the volatiles that are elicited by the development of the fungal symbiont *A. areolatum*, represents another prospect for early detection.

Management strategies

The management of *S. noctilio* in South America is primarily set on reducing tree mortality associated with outbreaks. It is mainly comprised by two components: silviculture and the introduction of natural enemies for biological control (Klasmer and Botto 2012; Beèche et al. 2012; Iede et al. 2012).

Silvicultural management can be of preventive nature when it is aimed at reducing tree susceptibility to *S. noctilio* new attacks, essentially through pruning and thinning of stands. Sanitary thinning is also a common practice to reduce woodwasp populations. In this case, stands are carefully ground surveyed, and all trees found with symptoms of woodwasp attacks are felled and either chipped, burned or buried in trenches (Klasmer and Botto 2012; Beèche et al. 2012; Iede et al. 2012).

The parasitic nematode *D. siricidicola* is considered the primary biological control agent for *S. noctilio* in the

southern hemisphere (Slippers et al. 2015). In South America, the release of nematodes was performed from 1989 in Brazil and Northern Argentina (Iede et al. 2012), from 1999 in Southern Argentina (Klasmer and Botto 2012), and from 2006 in Chile (Beèche et al. 2012). The released nematodes were mass produced in laboratories in Chile, Brazil, and Argentina, from original Kamona strains from Australia, and occasionally supplemented by nematodes re-isolated from initial release sites in Brazil and Chile (SAG 2004; Beèche et al. 2012; Iede et al. 2012). In 2004, a new strain obtained from infested *S. noctilio* adults brought to Chile from New Zealand was isolated for mass production (the “Tangoio strain”; SAG 2004; Beèche et al. 2012). Nematode populations have become well established in most release sites, although parasitism levels reported are highly variable across areas and with time, ranging from 14 to 90% in some locations (Table 2).

Variability in parasitism success by *D. siricidicola* in different regions has been proposed to be associated with the wood moisture of pine trees, the development of local resistance by *S. noctilio*, loss of nematode virulence and/or the presence of competing micro-organisms or fungi (Hurley et al. 2008; Slippers et al. 2012). A study carried out in Southern Argentina suggested that the spatial arrangement of the releases can also affect the local abundance of parasitism achieved at the landscape scale, during the first years (Corley et al. 2014). However, the reduction of diversity in nematode populations due to the selection process and inbreeding as a consequence of intensive laboratory rearing, may be the key factor affecting parasite success (Bedding and Iede 2005; Mlonyeni et al. 2011). Likely, the lack of diversity in nematode populations may reduce their capacity to adapt and establish in climatically different environments, on different *Pinus* spp., and to parasitize different populations of *S. noctilio* (Slippers et al. 2012).

In addition, three species of parasitoid wasps, native to Europe and North America have been released into the invaded range of *S. noctilio* in South America (Cameron 2012). The hymenopteran species *Ibalia leucospoides* (Hochenwarth), *Megarhyssa nortoni* (Cresson) and *Rhyssa persuasoria* (Linnaeus) were introduced and established successfully in many, though not all, *Sirex*-infested pine-growing areas of South America (Iede et al. 2012; Beèche et al. 2012; Fischbein and Corley 2015). Interestingly, and in contrast with other regions of the Southern Hemisphere where similar biological control programs have been carried out (e.g., South Africa), *I. leucospoides* arrived in Argentina, Brazil and Uruguay accidentally, presumably in pest-infested wood from unknown origins [refer to Boissin et al. (2012) for description of possible origins of *S. noctilio* in South America]. This parasitoid has effectively established viable populations in these countries (Fischbein and Corley 2015). In other countries, notably Chile, females of *I.*

leucospoides were collected in the field, to rear and locally augment populations (Beèche et al. 2012). *M. nortoni* from Tasmania were released for the first time in 1996 in Brazil (Iede et al. 2012), and since 2005 individuals from New Zealand and Tasmania were repeatedly imported in southern Argentina and Chile (Beèche et al. 2012). However, these releases have been associated with variable establishment success (see Table 2 for details). For instance, this parasitoid has never been recovered from the field in Brazil (Iede et al. 2012). *R. persuasoria* was introduced in Brazil from Tasmania and to Chile and Argentina (via Chile) from New Zealand. This species has apparently not established in Argentina [F. Azzaro (SENASA), personal communication and personal observation], nor in Chile (Beèche et al. 2012) or Brazil (Iede et al. 2012). A general observation is that while *I. leucospoides* has established well and may perform better in warmer and drier climatic regimes (Spradbery and Kirk 1978; Taylor 1978; Corley and Bruzzone 2009), *M. nortoni* may do better in temperate to cold climates (Collett and Elms 2009; Cameron 2012).

The mortality on *S. noctilio* populations in South America assigned to *Ibalia leucospoides*, *Megarhyssa nortoni* and *Rhyssa persuasoria* is largely variable, ranging from an estimated 13–90% (Table 2). Although, in broad terms, parasitism rates are not negligible allowing us to consider these species as effective mortality agents of *S. noctilio* in a number of regions (Cameron 2012; Fischbein and Corley 2015), they may not contribute to prevent woodwasp outbreaks (Lantschner et al. under review). Their impact as non-regulating mortality factors depends on the environmental conditions in which they have established (Taylor 1978; Corley and Bruzzone 2009), their different life history traits such as reproductive mode, host stage attacked, attack rate, host searching strategy and dispersal abilities (Spradbery 1970; Fischbein et al. 2011, 2018; Fischbein and Corley 2015). Some data on host-parasitoid population interactions among these parasitoids collected in other Southern Hemisphere regions, suggesting that the populations of *M. nortoni* and *R. persuasoria* respond to delayed density-dependent factors, whereas *I. leucospoides* populations primarily respond to density-independent factors (e.g., Taylor 1978).

Conclusions and future prospects

Sirex noctilio is currently one of the most important threats to plantation forestry throughout South America (Villacide and Corley 2012). The pest is present in most *Pinus* spp. plantations in the region, and in some localities, may cause remarkably high levels of tree mortality. Such impact has led to national efforts in the pine-growing countries, to prevent pest spread and manage populations where these have established. These practices have been largely adopted from

management programs developed in other regions of the world, with limited local adaptation and lacking comparative evaluation of success and failures. Nonetheless, recent studies of *S. noctilio* in South America provide further insight of the general ecology and behavior in that species. These may contribute more widely to improved management of damaging populations throughout the invaded range.

In South America, *S. noctilio* has reached most areas where pine are grown above the 21° latitude south, largely favored by human activities such as the movement of infested wood (Fig. 1; Carnegie et al. 2006; Boissin et al. 2012). However, inside each area, the spread has also been suggested to be strongly determined by the wasps' natural dispersal capacity (Table 2; Bruzzone et al. 2009; Villacide et al. 2014; Villacide 2015), and spread rates have been found to be particularly influenced by temperature (i.e., higher spread rates in warmer climates; Lantschner et al. 2014).

Sirex noctilio population across South America, unlike what possibly happens in its native range, have been found consistently to show pulse-like eruptive population behavior, although there are some particular areas where outbreaks seem to be more sustained (e.g., Southern Argentina). The onset of *S. noctilio* outbreaks in South America appears to be triggered by density-independent factors, such as abrupt increase in the drought severity, which in inappropriately managed stands (e.g., overcrowded), increase the availability of susceptible host trees. Dispersal, on the other hand, may also have a significant effect in expanding outbreaks at more local scales, while the role of biological control in regulating populations is still unclear (see Fig. 3 for observed outbreak patterns and predisposing factors as affected by spatial scale). Long-term studies to understand the drivers of these population eruptions have been very scarce in South America (Corley et al. 2007; Aparicio et al. 2013; Lantschner and Corley 2015).

Classical biocontrol has been a key component of integrated pest management practices deployed against invasive *S. noctilio* populations in the southern hemisphere. In South America, three insect parasitoids and a parasitic nematode have been introduced in all affected countries. The historical data available about their releases suggests generally a 'haphazard approach', lacking quantitative follow-up surveys. Few if any quantitative recommendations or lessons may be drawn from the available data, to improve current and future biocontrol practices with parasitic insects in the region. For instance, we are unable to determine appropriate release strategies that consider the spatial and temporal organization of releases, and the optimal number of individuals to release. It is known that the number of individuals released serves to overcome demographic stochasticity and the negative effects of inverse density-dependent processes (Grevstad 1999a; Fauvergue and Hopper 2009) and the number of

release events helps to reduce the influence of environmental stochasticity (Grevstad 1999b).

Given that bottom-up effects are important drivers of woodwasp population dynamics, management practices that contribute to tree vigor will help prevent outbreaks. Thus, efforts aimed at reducing the availability of susceptible host trees, such as silviculture and landscape design, should be prioritized, especially during years in which a rapid increase in drought severity is expected. Alternative proposed control measures, such as breeding programs to select varieties of *Pinus* spp. resistant to *S. noctilio* attacks, will also help (Slippers et al. 2015).

Early detection is a key factor contributing to the success of non-native pest management programs (Liebhold and Tobin 2008). For forest insects in general, the use of monitoring methods that employ semiochemicals has increased in the last decades, becoming a key component of many Integrates pest management (IPM) programs (Nadel et al. 2012). In South America, kairomone traps currently available for *S. noctilio* have a limited availability to detect small populations, and for this reason early detection still in many cases still rely on labor-intensive survey types such as visual surveys or trap trees.

The knowledge acquired on the ecology and management for the *Sirex* woodwasp in South America identifies five specific research areas for further work on this forest pest worldwide:

1. The establishment of effective and standardized sampling protocols that allow for the collection of quantitative *S. noctilio* population data, including early detection in sites with high risk of initial introductions such as ports and urban areas. These include efficient trap and lure designs and statistically valid sampling efforts, which should provide data for populations during endemic phases and in diverse environmental conditions. Such protocols are needed to replace current population size estimates based on tree damage or designed for other purposes such as the implementation of control measures (i.e., trap trees, sequential sampling protocols).
2. The collection of cross-border comparative data on woodwasp phenology, distribution and damage levels. This information is important to establish common management practices and to map pest incidence. This is also baseline information needed to interpret the success of the control practices deployed.
3. Long-term studies of focal populations and field experiments based on tree/stand droughting for a better understanding of *S. noctilio* population dynamics in the invaded range, especially focused on outbreak behavior. Population studies developed to date where a set of predictive variables are analyzed against observed past population eruptions, and no mechanisms are put to test.

Moreover, much of this research has been carried out in one region, in the presence of biocontrol practices, and there is little information for other regions of South America or for other countries in which *S. noctilio* is present.

4. Spatio-temporal and life-table studies of host-parasitoid and host-pathogen interactions of *S. noctilio* in its natural range, with the aim of completing past work (e.g., Taylor 1978) to fully understand the role played by the natural enemies in woodwasp population regulation. Such studies, enriched by modern niche modeling techniques and genetic tools, could also allow for the identification of new, better climatically matched or more efficient biological control agents.
5. Treatment-control studies on the efficacy of given IPM methods in preventing populations outbreaks, slowing geographical spread or even driving local populations to extinction. These should include comparisons of different silvicultural regimes (timing and intensity of pruning and thinning), and comparisons of methods to release biocontrol agents (timing, number and spatial distribution of releases, number of individuals).

Many of the ideas listed above, may be generally relevant for the management of invasive alien species in plantation forestry with non-native tree species.

Author contributions

JC conceived and wrote the manuscript. All other authors discussed ideas and wrote, read and approved the manuscript. VL and JV prepared the figures.

Acknowledgements This work was partially supported by Grants: PICT 2013-557, PICT-2014-419, PICT 2014-527, PICT StarUp-2015-3864 (Agencia Nacional para la Promoción Científica y Tecnológica, Argentina) INTA PNFOR-1104072 (Instituto Nacional de Tecnología Agropecuaria, Argentina) and IcoS, FS- USDA International Programmes.

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