Chapter 1

Global biogeography of *Sirex noctilio* with emphasis on North America

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Abstract

Sirex noctilio is a Eurasian species in the woodwasp (Siricidae) insect family, a small and poorly understood group of insects. Several siricid species have invaded various world regions due to their frequent presence in wood moving in international trade. Like most other woodwasps, feeding by *S. noctilio* occurs in weakened or dying pines in its native range, and populations exist there at relatively low levels. But in non-native regions of the Southern Hemisphere, *S. noctilio* populations have thrived, colonizing hosts in plantations of non-native pines planted at high densities. Under such conditions, *S. noctilio* reproduction can drive populations to epidemic densities, causing considerable tree mortality. Invasions in the Southern Hemisphere started with colonization of New Zealand around 1900, then Australia in 1952, South America in 1980, and South Africa in 1994. Given the reputation of *S. noctilio* as a successful invader and its repeated interception from imported cargo at ports, invasion of North America by this species was greatly anticipated with caution. Those fears came true when it was detected in a trap placed in New York near Lake Ontario in 2004. Subsequent delimitation surveys, and discovery of larvae within trees, confirmed the presence of the species over a large 19-county area, indicating that populations had been present for many years and eradication was considered infeasible. Subsequently, *S. noctilio* has been found in nine northeastern US states and two eastern Canadian provinces and appears to be expanding its range. To date, however, populations in North America remain low and have caused little damage, similar to what is seen throughout most of its native range. Large regions of pine-dominated forests are still likely to be invaded, but it is not clear whether these regions are climatically suitable and whether populations will continue to remain at low densities as it spreads into regions with abundant pine forests.

Introduction

The species *Sirex noctilio* is a member of the Siricidae (woodwasp or horntail) family in the order Hymenoptera. The Hymenoptera exhibit considerable variation in life histories, including groups with species playing diverse ecosystem roles such as nectar/pollen-feeders, predators, parasitoids, and herbivores. The hymenopteran order is also characterized by major differences in the morphology and ecological niches of immature and mature forms; in some groups, adults provision immatures, and this is sometimes associated with varying levels of social behavior.

The Siricidae belong to the suborder Symphyta, which is considered the more evolutionarily primitive branch of the Hymenoptera and contains only herbivorous insects, including sawflies and woodwasps. The Siricidae is a relatively small family, with only about 100 known species that are almost entirely native to the Northern Hemisphere. All of these species exist most of their lives as larvae that bore in woody tissue of trees. Within the Siricidae, there are two subfamilies: the Tremicinae that mostly feed on hardwoods and the Siricinae that feed on conifers. A total of 23 species in the Siricidae are known to be native to North America (Schiff et al. 2012) (Table 1).

Table 1. Siricidae native to North America, north of Mexico (from Schiff et al. 2012).

SUBFAMILY	SPECIES	HOSTS[1]	NATIVE RANGE
Tremicinae	*Tremex columba*	Wide variety of hardwoods; main hosts are hickories, maples, and elms	Transcontinental N. America
	Xeris caudatus	**Fir**, spruce, pine, Douglas-fir	Western N. America
	Xeris chiricahua	Host tree not known	Western N. America
	Xeris indecisus	Wide host range in Pinaceae	Western N. America
	Xeris melancholicus	Wide host range in Pinaceae	Eastern and north-central N. America
	Xeris morrisoni	**Fir**, Douglas-fir, spruce	Western N. America
	Xeris tarsalis	Wide host range in Cupressaceae	Western N. America
Siricinae	*Sirex abietinus*	**Fir**, spruce, hemlock	Western N. America
	Sirex areolatus	Very wide host range with major hosts in Cupressaceae	Western N. America
	Sirex behrensii	**Pine**, Douglas-fir	Western N. America
	Sirex californicus	**Pine**, with a few other spp.	Western N. America
	Sirex cyaneus	**Fir**, larch, spruce, pine	Eastern and north-central N. America
	Sirex longicauda	**Fir**, pine, Douglas-fir	Western N. America
	Sirex nigricornis	**Pine**, spruce	Eastern and north-central N. America
	Sirex nitidus	**Spruce**, fir, larch, Douglas-fir, hemlock, pine, cypress	Transcontinental N. America
	Sirex obesus	**Pine**	Western N. America
	Sirex varipes	Very wide host range in Pinaceae	Western N. America
	Sirex xerophilus	**Pine**	Western N. America
	Urocerus albicornis	Very wide host range in Pinaceae, hemlock	Transcontinental N. America
	Urocerus californicus	Very wide host range in Pinaceae	Western N. America
	Urocerus cressoni	Wide host range in Pinaceae	Eastern and north-central N. America
	Urocerus flavicornis	Wide host range in Pinaceae, cedar	Transcontinental N. America
	Urocerus taxodii	Bald cypress	Eastern N. America

[1] Tree genera are in bold, when siricid species predominantly use that genus as a host.

All Siricidae share a common life history and exploit similar ecological niches. Adult females oviposit directly into tree xylem, and larvae spend their entire lives boring through woody tissue. This tissue is composed almost entirely of cellulose and lignin, neither of which can be directly digested by any insect species. Like other xylem-chewing insects (e.g., ambrosia beetles), siricids have co-evolved with mutualistic fungi that break down this material into compounds that can be readily assimilated. As described in chapters 4 and 5, the association of *S. noctilio* with its microbial symbionts is only partially understood, and even less is known about fungal symbionts of other species of Siricidae.

Most siricids colonize weakened and/or dying trees that lack physiological resistance to defend themselves. The degree to which hosts must be weakened prior to colonization varies considerably among siricid species. For example, in North America the native siricid *S. nigricornis* is only found colonizing severely weakened trees (see Chapter 6). These weakened trees may be dying as a result of wind damage, attack by other insects or diseases or suppression by larger trees. Invasive populations of *S. noctilio* in North America have behaved similarly, though in rare instances more vigorous trees have been colonized in addition to highly suppressed individuals in the same stand. *Sirex noctilio* is native across Eurasia (Fig. 1) but little is known about this species through most of this region. It is known that within the native range of *S. noctilio* in Europe, tree colonization is almost entirely limited to weakened and dying trees (Wermelinger and Thomsen 2012; Lombardero et al. 2016). However, within non-native *S. noctilio* populations in the Southern Hemisphere, colonization of seemingly vigorous trees is fairly common, particularly during outbreaks. It is not fully understood why outbreaks of *S. noctilio* occur in the Southern Hemisphere and why they sometimes colonize healthy trees there, while this generally does not happen in Europe and North America (see Chapter 10).

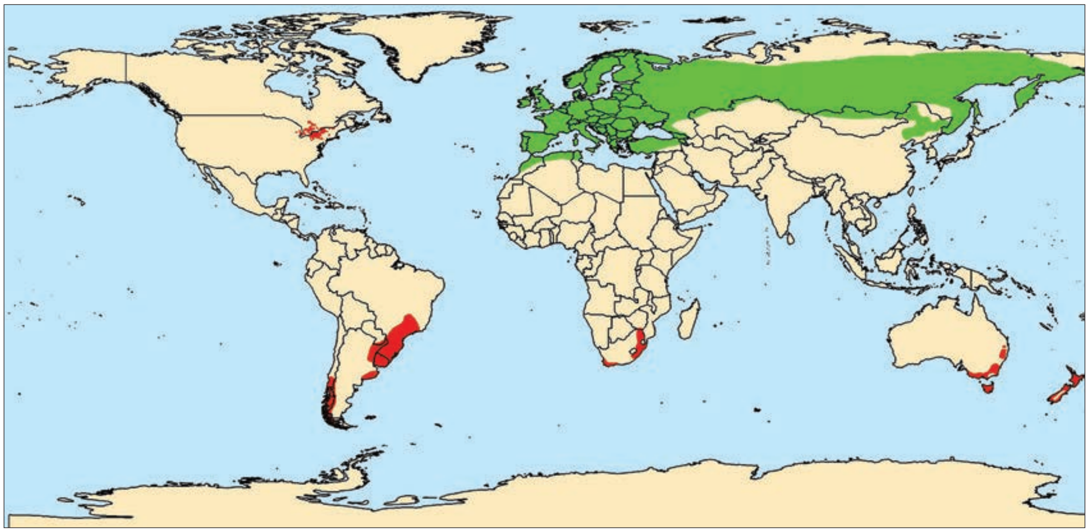

Figure 1. Global distribution of native and non-native *Sirex noctilio* populations. Native range is shown in green and invaded range in red.

History of *S. noctilio* global spread

Even though the Siricidae is a relatively small insect family, there are at least seven species that have successfully invaded new regions; three of these species have invaded North America (Table 2). Invasion success in this group can be attributed in part to their tendency to be accidentally transported with wood and wood packaging material, such as wooden pallets, crates, and dunnage. Burnip et al. (2010) reported

Table 2. Siricidae known to have invaded world regions outside their native ranges.

SUBFAMILY	SPECIES	HOSTS[1]	INVADED RANGE	NATIVE RANGE	CITATIONS
Siricinae[2]	*Sirex areolatus*	Very wide host range with major hosts in Cupressaceae	Europe	North America	Schiff et al. 2012
	Sirex noctilio	**Pine**, Douglas-fir	N. America, S. America, Australia, New Zealand, S. Africa	Europe, North Africa, Northeast Asia	Schiff et al. 2012
	Urocerus albicornis	Very wide host range in Pinaceae, hemlock	Europe	Transcontinental North America	CABI 2020a
	Urocerus gigas	Wide host range in Pinaceae, cypress	S. America	Europe, North Asia, North Africa	Schiff et al. 2012
	Urocerus sah	Pinaceae	N. America	Central Asia, Turkey, N. Africa	Schiff et al. 2012
Tremicinae	*Eriotremex formosanus*	**Oak**, **hickory**, sweetgum, pine	N. America	East Asia	Schiff et al. 2012
	Tremex fuscicornis	Poplar, black locust, maple	Australia, Chile	Europe, Asia	CABI 2020b; Schiff et al. 2012

[1] Tree genera are in bold, when siricid species predominantly use that genus as a host.
[2] There has been confusion for many years regarding *Sirex cyaneus* and species with similar appearances from North America and Europe. Schiff et al. (2012) state that misidentifications have occurred and there is confusion about names, but *S. cyaneus* is native to North America and the newly named *S. torvus* is native to Europe but is morphologically similar and has previously been called *S. cyaneus*.

that between 2001 and 2008, there were live siricid life stages discovered during inspections of 34 shipments arriving at New Zealand ports. Among these, the most common species intercepted were *S. noctilio*, *S. juvencus*, and *Urocerus gigas*. Two of these species have invaded the Americas (Table 2), illustrating their ubiquitous presence in the wood packaging pathway and its potential to drive invasions. In reaction to the growing realization of the risk associated with woodboring insects present in trade, from 2003 to 2005 the International Plant Protection Convention implemented the International Standard for Phytosanitary Measures-15 (ISPM-15). This phytosanitary standard requires all member countries of the World Trade Organization to enforce a system of mandatory heat treatment or fumigation of wood packaging used in international trade. Despite the partial success of ISPM-15 in reducing accidental pest introductions, there are several incidences of live *S. noctilio* emerging from ISPM-15-treated wood (Burnip et al. 2010). Thus, the risk of new introductions of *S. noctilio* and other species of Siricidae around the world has not been completely eliminated.

Sirex noctilio predominantly attacks pines (*Pinus* spp.). While pines are not native to the Southern Hemisphere, they have been planted there extensively for timber and pulp production. In several portions of the Southern Hemisphere, pines are planted at high densities in monocultures, a setting that is apparently ideal for *S. noctilio* population growth. Worldwide, the first invasion of *S. noctilio* occurred in the North Island of New Zealand around 1900 (Bain et al. 2012). But it wasn't until the late 1920's that it was identified as a pest, when it was found killing trees in overstocked plantations of radiata pine (*Pinus radiata*, also called Monterey pine) native to North America. During a period of drought between 1946 and 1951, intense outbreaks developed in this region, and tree mortality became very high in densely stocked stands (> 1,000 stems/ha or > 2,400 stems/ac). These outbreaks subsequently subsided during the 1950's as forestry practices were modified to include intermediate cuttings (thinning) to reduce stocking to 200–300 stems/ha (500–750 stems/ac). *Sirex noctilio* is now rarely observed in New Zealand and is not currently considered a significant forest pest. The reasons for this change in population behavior are not entirely known but may have resulted both from changes in forest management practices (thinning to lower stand densities) and biological control using imported natural enemies. Several hymenopteran parasitoid species were introduced, and the species *Rhyssa persuasoria persuasoria*, *Megarhyssa nortoni nortoni*, and *Ibalia leucospoides leucospoides* became well established, at times causing high levels of mortality. The parasitic nematode *Deladenus siricidicola* was apparently introduced along with founding *S. noctilio* populations and significantly contributes to control in New Zealand.

Following the massive outbreaks in New Zealand, *S. noctilio* was next discovered in Australia in 1952 (Carnegie et al. 2012). The initial invasion occurred in Tasmania, but by 1961 it was discovered in Victoria, near Melbourne. The insect continued to expand its range, arriving in South Australia and New South Wales in 1980 and in Queensland by 2009. The species has invaded most of the country's pine plantations, except those in Western Australia and coastal subtropical portions of New South Wales and Queensland.

Like New Zealand, large portions of Australia are planted with radiata pine for timber production. But typical site conditions in Australian pine stands are drier; consequently, these stands are more susceptible to *S. noctilio* outbreaks. The worst such outbreak occurred from 1987 to 1990 when over 5 million trees were killed during the "Green Triangle outbreak" in southeastern South Australia. Following this outbreak, the Australian Forestry Council developed a national strategy for managing *S. noctilio* populations (Haugen and Underwood 1990). Parasitoid populations had previously been introduced in the 1960's and 1970's but had not been effective at maintaining populations at low levels. The new national strategy outlined a system, still in place, that focuses on minimizing *S. noctilio* spread via quarantine and detection monitoring as well as population control using silviculture, population monitoring, and inoculative releases of the Kamona strain of the nematode *Deladenus siricidicola* (see Chapter 6). While these practices appear to have prevented the recurrence of another massive outbreak, *S. noctilio* remains a significant problem in Australian forestry, and research there continues to address this pest.

South America was the next continent to be invaded, with *S. noctilio* being discovered in Uruguay in 1980 (Maderni 1998). It subsequently spread and was discovered in Chile in 1981, in Argentina in 1985, and finally in Brazil in 1988. In New Zealand and Australia, the primary host of *S. noctilio* is radiata pine. This is also the principal host in certain parts of South America (e.g., northern Argentina and all of Chile), but elsewhere in South America the species has colonized other pine species, including loblolly (*P. taeda*) and slash (*P. elliottii*) pines in Brazil as well as lodgepole (*P. contorta*) and ponderosa (*P. ponderosa*) pines in Argentine Patagonia. As is the case elsewhere in the Southern Hemisphere, *S. noctilio* outbreaks develop in densely stocked stands. The onset of outbreaks is often related to drought conditions, and outbreaks result in extensive tree mortality (Lantschner et al. 2019). South American countries have largely adopted the same *S. noctilio* management tools used elsewhere in the Southern Hemisphere, namely silviculture, classical biological control using parasitoids, and inoculative biological control using the nematode *D. siricidicola*.

Africa is the last continent in the Southern Hemisphere to be invaded by *S. noctilio*. To date, the only country where the species is established is South Africa. *Sirex noctilio* was first discovered near Cape Town in 1994, and it subsequently spread through the majority of South African regions where pines are grown in plantations. The most common hosts for which *S. noctilio* is a problem in the country are radiata and patula (*P. patula*) pines, although loblolly, slash and slash-Caribbean (*P. caribaea*) hybrid pines are also colonized. Despite *S. noctilio* having been established the longest in the Western Cape region, outbreaks there are limited in extent. In contrast, extensive outbreaks and tree mortality have occurred in the Eastern Cape and KwaZulu-Natal regions, most likely due to the management of these stands at higher stocking levels for pulpwood production (Hurley et al. 2007). Similar to other areas in the Southern Hemisphere, biological control has been the principal approach to managing the pest. While damage still is extensive, it has subsided from levels experienced following the initial invasion (Hurley et al. 2007).

Following invasion of each continent, populations have expanded into climatically suitable regions with available hosts. Unfortunately, *S. noctilio* may frequently be present in harvested logs; when these logs are transported long distances, this facilitates spread. Lantschner et al. (2014) found that within a continent, the radial rate of invasive *S. noctilio* range expansion in various world regions varied from 12 to 82 km (7.5–51 mi) per year, with the highest spread rates occurring in the warmest climates, perhaps due to higher insect reproductive rates.

Invasion of North America by *S. noctilio*

Given its reputation as a destructive forest pest in other invaded areas, there has been considerable concern about potential damage that *S. noctilio* could cause should it invade North America. Ciesla (2003) argued that the large expanse of unmanaged pine forests in western and eastern North America would create ample resources for outbreaks of *S. noctilio*, and that these outbreaks could move into more intensively managed stands. Further evidence of risk included repeated historical interceptions of *S. noctilio* at North American ports; between 1993 and 2001, USDA inspectors found 103 shipments containing wood packaging contaminated with *S. noctilio* (Ciesla 2003).

This perception of invasion risk was proven true in September 2004 when a single *S. noctilio* adult was collected in a funnel trap deployed near Fulton, Oswego County, New York, as part of the USDA Cooperative Agricultural Pest Survey (CAPS) for exotic bark beetles (Hoebeke et al. 2005). The trap was baited with cis-verbenol, ipsdienol, and methyl butenol and deployed as part of CAPS detection monitoring at high-risk sites, such as near ports. The Fulton trap was deployed approximately 16 km (10 mi) from the port of Oswego (on Lake Ontario) and near the Oswego River, which is used for inland commercial barge passage.

In 2005, the presence of a reproducing population was confirmed by molecular analysis of *S. noctilio* larvae discovered in symptomatic trees in the vicinity of the initial trap capture. An attempt was made to delimit the population by deploying additional traps in an area in New York and adjoining Ontario within 100 km (62 mi) or more from the initial detection location. Several of these traps captured *S. noctilio* adults, indicating the presence of populations over a large area. By the end of 2005, detections were made in four Canadian and four US counties, and sites with trap captures were separated by hundreds of kilometers. Given this evidence of the large geographic extent of established populations, it was concluded that the population had most likely been established for several years and that eradication would not be feasible.

Additional delimitation surveys in 2006 confirmed *S. noctilio* presence in 19 Canadian counties across Ontario and in 24 US counties in New York and Pennsylvania. By 2020, *S. noctilio* was known from nine northeastern US states (New York, Pennsylvania, Vermont, Connecticut, Ohio, Michigan, New Jersey, Massachusetts, and New Hampshire) and from two Canadian provinces (Ontario and Quebec) (Fig. 2). Detection of spreading populations is difficult due to lack of highly active attractant lures (see Chapter 3) and the labor intensive challenge of searching for and finding infested host trees. While it is assumed that *S. noctilio* populations are continuing to spread slowly, there currently is no nationally coordinated survey program underway in the US or Canada, so there remains some uncertainty about the current geographical extent of established populations.

Across most of the area of northeastern North America currently invaded by *S. noctilio*, pine hosts comprise a relatively small proportion of forest composition (Fig. 3). While there are some areas of native pitch (*P. rigida*), red (*P. resinosa*), white (*P. strobus*), and jack (*P. banksiana*) pine, most forests in this region are dominated by broadleaf trees, and a large fraction of pines occur in widely scattered stands that were mostly planted 70 or more years ago. These plantations are often comprised of several different pine species, but *S. noctilio* is particularly common in non-native Scots pine (*P. sylvestris*) plantations. Many of these plantations are largely abandoned and not managed, resulting in high stocking levels with many suppressed trees that are ideal *S. noctilio* hosts. However, given the scattered distribution of these plantations, it appears that there are insufficient densities of host trees across the landscape to permit regional outbreaks to develop. Consequently, *S. noctilio* is presently an uncommon insect across most of its invaded range. This, along with

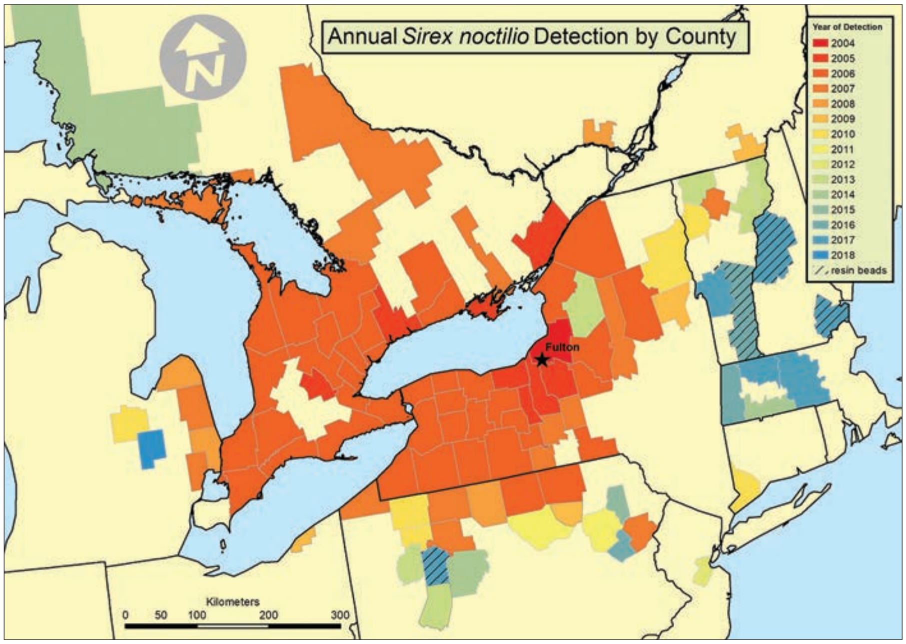

Figure 2. Historical records of first detections of *Sirex noctilio* in eastern North America (updated from Dodds and de Groot 2012). Site of initial detection in 2004 near Fulton, New York is shown with a "★".

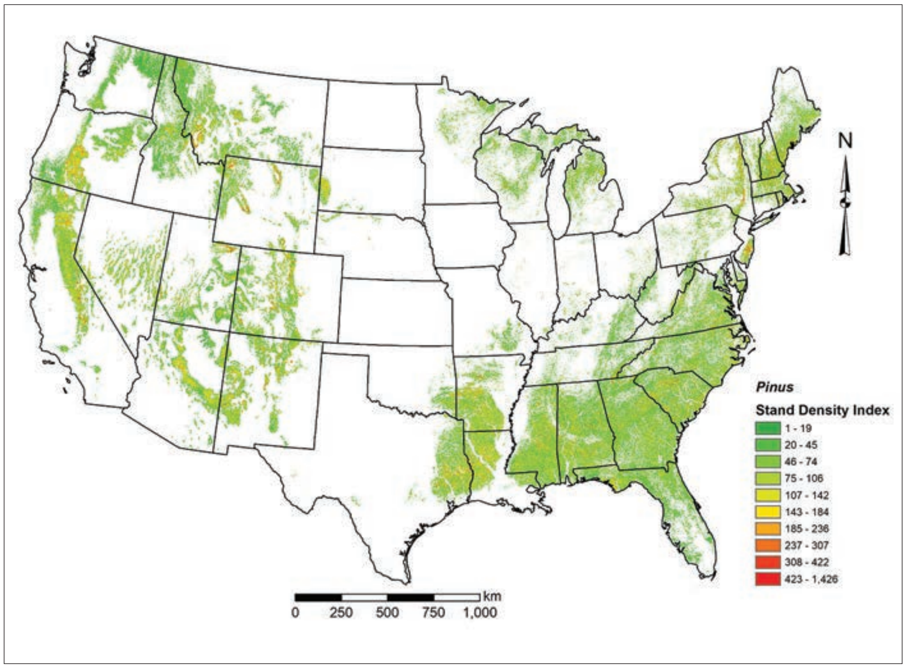

Figure 3. Density of pines (all species) across the conterminous US (data used to create map are from the USDA Forest Service Individual Tree Species Parameter Map database, https://www.fs.fed.us/foresthealth/applied-sciences/mapping-reporting/indiv-tree-parameter-maps.shtml).

the low level of surveillance currently conducted in the region, means that the current range of *S. noctilio* in North America is poorly defined. Most likely, the species has expanded well beyond areas shown in Figure 2, but additional survey data are lacking.

Researchers have used molecular methods to investigate the origin of *S. noctilio* that is now present in North America. *Sirex noctilio* has a large native distribution (Fig. 1), but data on the genomes are only available from a few native areas. Genetic samples are more easily available from invaded areas. Analyses from northeastern North America suggest that *S. noctilio* has been introduced at least twice to North America (Bittner et al. 2017). An evaluation conducted to hypothesize worldwide invasion patterns suggested that

S. noctilio populations in North America originated from an unknown location in Europe and from South America (Boissin et al. 2012).

Prospects for future invasions by *S. noctilio*

Sirex noctilio has already invaded every continent where pines exist (Fig. 1). Thus, there is limited potential for future long-distance invasion of new continents by this species. Nevertheless, there remain many areas within these continents that are still uninvaded. For example, the only portion of the African continent where *S. noctilio* is known to be established is South Africa, but there are several other countries (e.g., Mozambique, Tanzania, Kenya, Angola) with extensive pine plantations where *S. noctilio* invasion can be anticipated. Interestingly, there are also portions of Asia where *S. noctilio* is not native or currently present and may invade in the future, including large areas of native and exotic pine stands in southeastern Asia and the Indian subcontinent.

North America contains more suitable habitat that currently has not been invaded by *S. noctilio* than any other continent. Native and planted pine stands are extensive through western and southeastern North America (Fig. 3). In the Southern Hemisphere, many pine species native to North America are widely planted and have proven to be excellent hosts for *S. noctilio*, so there is reason for concern about the potential for damage when *S. noctilio* expands its North American range. However, climate-matching studies indicate that most of the pine region in the North American West may be only marginally suitable for *S. noctilio* (Ireland et al. 2018). This conclusion should be questioned and further investigated, however, since their maps also classify regions such as Argentine Patagonia as being climatically marginal for *S. noctilio*, even though the species has proven to be a serious pest in these regions.

There may be additional factors besides climate and host availability that may limit the future range of *S. noctilio*, or at least limit its outbreak range (see Chapter 10). While several of the most abundant pine species native to western North America are frequently attacked by *S. noctilio* in the insect's alien range, there is no guarantee this insect will increase to outbreak densities once it becomes established in the native range of these tree species. Thus, there is no certainty about whether the extensive damage caused by *S. noctilio* in the Southern Hemisphere will be replicated anywhere in North America once this species expands its range.

Acknowledgments

We thank Eugene Luzader for assistance in producing maps. AML acknowledges support from USDA Forest Service International Programs, National Science Foundation Macrosystems Biology Program (grant numbers 1241932, 1638702) and grant EVA4.0, No. CZ.02.1.01/0.0/0.0/16_019/0000803 financed by OP RDE. AR.

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