

Sirex Woodwasp: A Model for Evolving Management Paradigms of Invasive Forest Pests

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Abstract

The *Sirex* woodwasp, *Sirex noctilio*, and its fungal mutualist, *Amylostereum areolatum*, together constitute one of the most damaging invasive pests of pine. Despite a century of research and well-established management programs, control remains unpredictable and spread continues to new areas. Variable success in managing this pest has been influenced by complex invasion patterns, the multilayered nature of biological interactions, the varying local ecologies, and microevolutionary population processes in both the bio-control organisms and in the wasps. Recent research findings are challenging the historical perspectives on methods to manage the *Sirex* woodwasp, calling for management programs to incorporate the variable local dynamics affecting this pest complex. In this regard, the *Sirex* woodwasp provides a superb model to illustrate the need for a different approach to develop efficient and sustainable management tools to deal with the growing and global nature of pest invasions in forests and plantations.

Sirex system: refers to the wasp and its symbionts and natural enemies

▶ Supplemental Material

INTRODUCTION

The woodwasp *Sirex noctilio* together with its fungal symbiont *Amylostereum areolatum* and a fascinating array of biological control agents, including the parasitic nematode *Deladenus siricidicola*, which feeds on *A. areolatum*, compose one of the most intriguing forest pest problems (99) (**Supplemental Figures 1** and **2**; for all **Supplemental Material**, follow the link from the Annual Reviews home page at <http://www.annualreviews.org>). By the 1990s, researchers thought *S. noctilio* and its many associates were well understood, and management of this pest in its invasive range was considered sufficient. Understanding of the *Sirex* system at that point had benefited from decades of intensive and fruitful research, mostly in Australasia (8, 70, 74, 79, 108). However, in the subsequent two decades, *S. noctilio* continued to spread within Australia, South America, and Southern Africa, eventually reaching North America (50, 56). Despite the extensive body of knowledge regarding the management of *Sirex*, its spread has been characterized by variable levels of control and some devastating outbreaks (56).

The invasion history and impact of *S. noctilio* in different regions of the world can be clearly seen when examining the patterns of research output linked to it (a search using the term “*Sirex*” in the ISI Web of Science yielded 728 papers since 1913; accessed April 2014). A clear peak of activity is evident from 1960 to 1980 (217 papers), spanning the period of most intensive research in Australia and New Zealand (reviewed in 74, 108). The most significant peak in research activity, however, came after the first report of *S. noctilio* in North America in 2005 (50). Responding to the potential threat to plantations and native forest ecosystems in North America, coupled with the continuing outbreaks in new areas of Australia, South Africa, and countries of South America, research since 2005 has been the most productive to date (producing 207 papers).

This review does not repeat the details of the life history and biology of the *Sirex* system, which have been more than adequately treated elsewhere (see 99) (also see **Supplemental Figures 1** and **2**). Instead, it focuses on how recent advances in our understanding of the invasion history and the biology of the wasp, its symbionts, and its natural enemies can contribute to improved management programs. We also consider how the unique body of knowledge, the global distribution of the wasp, and the tools developed to study the *Sirex* system provide an outstanding model to study processes that affect the spread, colonization, and management of invasive forest pests and of symbioses in general (see sidebar, A Model to Study Microevolution of Invasive Pests and Biological Control).

A MODEL TO STUDY MICROEVOLUTION OF INVASIVE PESTS AND BIOLOGICAL CONTROL

Rius & Darling (84) highlighted the need for systems to experimentally test hypotheses regarding the role of microevolutionary processes in invasive populations. *S. noctilio* and *A. areolatum*, as well as their biological control, provide excellent opportunities for developing an experimental system (121). Such a system would offer depth of background knowledge, numerous collections spanning vast areas and decades of collection, an active global community working on the system, extensive laboratory protocols, as well as molecular and other tools to manipulate and study all the organisms involved. It would also offer the opportunity to manipulate experimental and control populations in the laboratory or the field to address questions such as the influence of genetic diversity and phenotypic plasticity on adaptability and the evolution of virulence or resistance. In terms of evolution of symbioses, the *Sirex* system also provides opportunities to study fidelity and specificity in host-mutualist and host-parasite interactions. The consequences of long-term asexual transmission (e.g., 22) of basidiomycete symbionts and aspects of the evolution of sexual reproduction and ploidy in fungi can also be studied in this system. Such studies will be enhanced by the expected release of the genomes of the wasp, fungus, and parasitic nematode.

THE INVASION HISTORY OF *S. NOCTILIO*, *A. AREOLATUM*, AND *D. SIRICIDICOLA*

The vertical mode of transmission of the asexual spores (arthrospores or oidia) of *A. areolatum* by *S. noctilio* results in clonality in the fungal populations. Studies using vegetative compatibility groups first revealed that siricids in Scandinavia were associated with clones of *A. areolatum* and *A. chaillatii* and that they had spread these clones over vast areas (110, 116). This discovery made it possible to investigate the global spread of *S. noctilio*, as reflected by the fungal symbiont (101, 103, 114). Subsequent studies using vegetative compatibility groups, together with data from DNA sequences and PCR restriction fragment length polymorphisms, showed that a clone of the fungus had spread across three continents, presenting arguably the largest geographic spread of a single fungal individual ever recorded (**Figure 1a**). Studies to determine the possible origin of the North American introduction of *S. noctilio* combined data for six mitochondrial and nuclear loci of the fungus (9, 80) and showed that the introduction had most likely occurred more than once and from different sources. Some of these North American fungal genotypes are shared with those from the Southern Hemisphere and Europe, but others are apparently unique (**Figure 1a**).

The possibility that some strains of *A. areolatum* could be native to North America was first suggested when *A. areolatum* was identified from *S. "nitidus"* outside the invasive range of *S. noctilio* (80). This possibility has been further supported following the isolation of *A. areolatum* from *S. nigricornis* at relatively high levels of frequency in Louisiana, which is well outside the known distribution of *S. noctilio* (81). However, *A. areolatum* could also have been introduced with other invasive siricid species such as *S. juvencus* (e.g., see interceptions discussed in References 18, 50), but evidence for this supposition is poor.

The most comprehensive study of the global spread of *S. noctilio* to date was based on mitochondrial COI (cytochrome oxidase I) sequence data and simple sequence repeat markers applied to the wasp (10) (**Figure 1a**). The data revealed a much more complex pattern of global invasion than had previously been considered. Thus, most populations of the wasp appear to be admixtures from independent introductions. These would originally have been from native regions (possibly Europe), with subsequent secondary spread among invaded regions. Importantly, two major sources or lineages were identified: one most likely from Europe, with a second of unknown origin. The source of unknown origin (outside Europe) has apparently contributed to populations in South Africa, Chile, and Switzerland. South African and South American populations also received genetic diversity from the first lineage, apparently multiple times and from multiple sources. Together with fungal data, these results reveal a complex history of introduction and reintroduction around the world, leading to admixed populations with substantial and often unique mixtures of diversity.

The parasitic nematode *Deladenus siricidicola* was first discovered in populations of *S. noctilio* located in New Zealand, where it arrived without human intervention (127). In all other regions of the Southern Hemisphere, the nematode has been introduced deliberately as part of biological control programs and following extensive rearing in laboratories (**Figure 1b**). During the 1960s and 1970s, a number of *D. siricidicola* strains were collected from the natural range of *S. noctilio*, but ultimately only one (the Sopron strain, later reisolated as the Kamona strain) was selected for mass rearing and release in Australia, South America, and South Africa (8, 100). Mlonyeni et al. (78) showed that this has resulted in highly homozygous nematode populations across these disparate areas, most likely as a result of the repeated bottleneck and inbreeding events resulting from the transfer of relatively small numbers of genetically related nematodes during subculturing. The nematode has also recently been reported in North America (61, 64, 77, 126), where two distinct "types" have been identified on the basis of internal transcribed spacer rDNA and COI sequence data (**Figure 1b**).

Arthrospores or oidia: small mycelial fragments that detach from the mycelial body

Vegetative compatibility groups: mycelium of two isolates of a fungus will fuse in culture when the alleles at incompatible loci are identical

Admixture: interbreeding between previously isolated populations

Sopron and Kamona strains: refer to the locations in Hungary and Tasmania where *D. siricidicola* strains were isolated

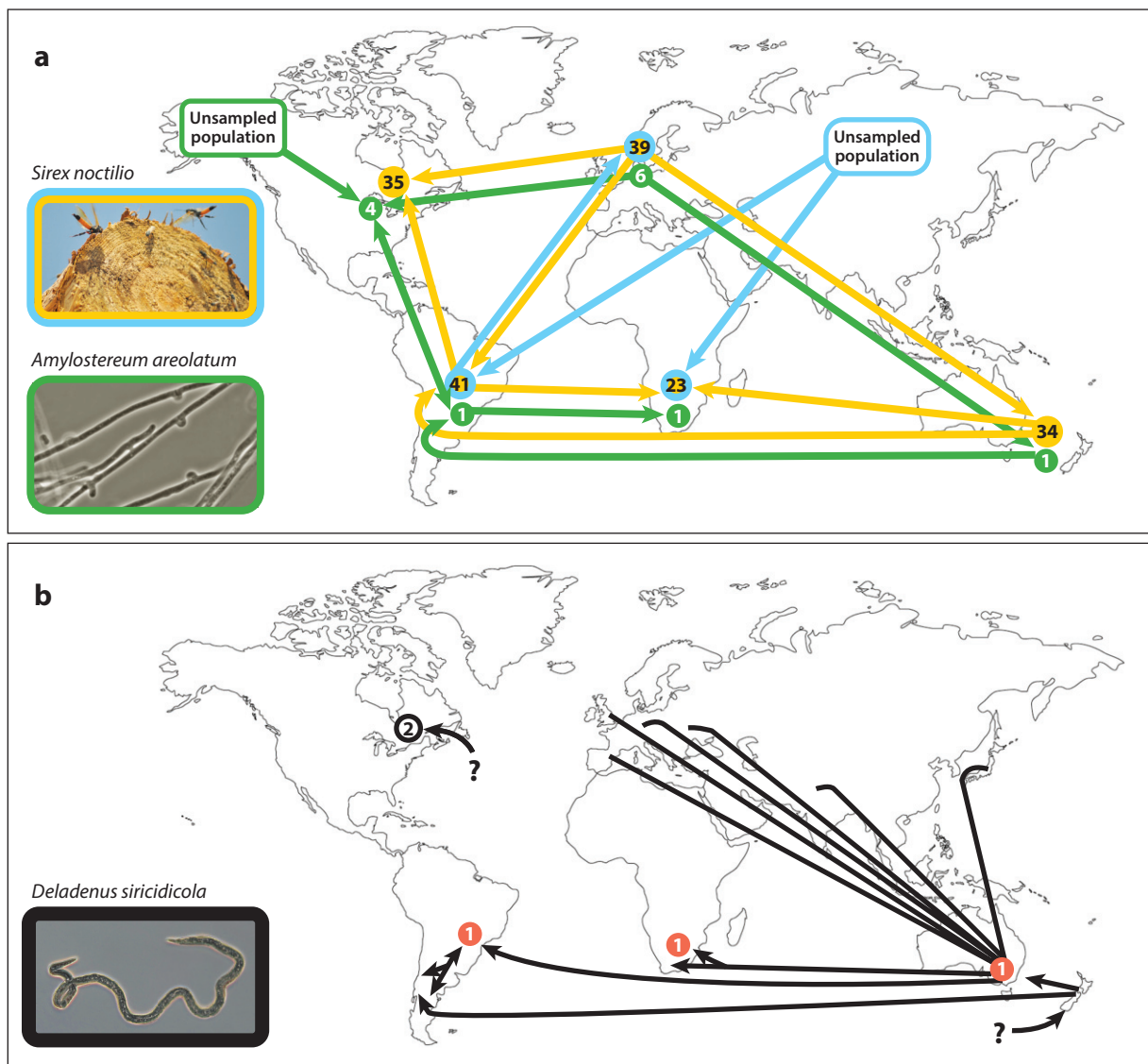


Figure 1

Patterns of spread of (a) *Sirex noctilio* (blue and yellow lines) and *Amylostereum areolatum* (green lines) and (b) *Deladenus siricidicola*, inferred from population genetics analyses, recorded collections, and distribution of the nematode for biocontrol efforts. Numbers of genotypes are indicated in circles: The diversity of *S. noctilio* (yellow and blue circles) reflects multilocus microsatellite genotypes from 40 resampled samples from a larger collection from each region, whereas the diversity of *A. areolatum* (green circles) is based on multilocus sequence and related genotypes using restriction fragment length polymorphisms. The diversity of (b) *D. siricidicola* is based on genotypes from data using internal transcribed spacer rDNA and COI (cytochrome oxidase I) loci sequences as well as microsatellite markers. One strain (red circles), known as the Kamona strain, has been spread throughout the Southern Hemisphere as a biological control agent. The source of the introduction of the nematode into New Zealand and North America (where two different strains have been identified) is currently unknown.

CHANGING PERSPECTIVES OF THE BIOLOGY OF THE *SIREX* SYSTEM

Recent research considering the invasion of new areas has significantly advanced our understanding of the biology of the *Sirex* system. Here we consider three main areas in which such changes have occurred: (a) the specificity of the symbiotic interactions, (b) the diversity and roles of mutualistic and parasitic organisms, and (c) the chemical ecology of host and mate detection (**Figure 2**).

Fidelity and Specificity

Partner uniformity, fidelity, and transmission are important when considering the evolution and stability of mutualisms (49, 60). In recent years, our understanding of the mutualism between *Amylostereum* spp. and siricids has changed dramatically in this regard. Earlier literature describes the relationship as species specific, with uniparental (female), vertical transmission of (asexual) genotypes between wasp generations (reviewed in 98, 114). The fact that there is little evidence for cospeciation between siricids and *Amylostereum* spp. (*Amylostereum* spp. are shared among siricid genera and species), however, suggests that horizontal transmission occurs, at least at longer evolutionary timescales (98, 107, 114, 115). A similar process occurs in the related wood-wasp *Xiphydria* and its associated xylariaceous fungi, whose genotypes are exchanged frequently (82).

Direct evidence for horizontal transmission of symbionts between siricid individuals and species has been lacking until very recently. Independent studies have now shown that *S. nigricornis*, a native North American species that is normally associated with *A. chailletii*, can acquire *A. areolatum* in its mycangia (48, 81, 120). One clone (determined through analysis of vegetative compatibility groups) was found in *S. noctilio* and *S. nigricornis* individuals emerging from the same tree (120) (**Figure 2**). A reciprocal, albeit apparently less common, acquisition of *A. chailletii* by *S. noctilio* has also been found (120). Accordingly, specificity for *Amylostereum* spp. is not an evolved trait in these siricid species. The dominance of one fungal species associated with a wasp species has likely been influenced by either geographic ranges or differences in host tree preferences.

Early work on the distribution and ability of *Deladenus* spp. to feed on different *Amylostereum* spp. suggested that this relationship is species specific (7). Therefore, the infection of siricid species, believed to have specific associations with *Amylostereum* spp., was also assumed to be species specific. Morris et al. (77), however, showed that *D. siricidicola* could infect *S. nigricornis*, even when it carries *A. chailletii*. They further showed that *D. proximus* is able to infest *S. noctilio* that normally carries *A. areolatum*. However, despite lack of specificity, phylogenetic analysis showed cospeciation over longer time periods between the North American wasps and nematodes sampled (77). Nonnative *S. noctilio* apparently disrupts these coevolutionary relationships.

Bedding (6) reported that egg parasitism is specific to wasp and nematode populations. For example, a Belgian strain of the nematode did not sterilize Belgian *S. noctilio* but did sterilize Australian *S. noctilio*. Though long ignored, population-level wasp-nematode interaction specificity is reemerging as important in the context of *S. noctilio* control. In North America, for example, recent studies show that *D. siricidicola* does not enter and sterilize the eggs of *S. noctilio* (61, 77, 126) (**Figure 2**). Apart from killing the host, the nematode also has indirect impacts on the fitness of the wasp population, such as female size, fecundity, and energy reserves, which are likely strain specific (8, 24, 61).

Deladenus spp. appear to be specific to *Amylostereum* (7). For practitioners working with these nematodes in culture, anecdotal evidence suggested that *D. siricidicola* might even prefer certain strains of *A. areolatum*. Relative to a strain isolated from *S. noctilio* in South Africa, however,

Fidelity: a process wherein a genetically identical symbiont is transmitted directly or vertically between generations of the host

Vertical transmission of symbionts: direct sharing of a symbiont in the symbiont and host, evident in congruent molecular phylogenies

Cospeciation: parallel speciation in the symbiont and host, evident in congruent molecular phylogenies

Horizontal transmission of symbionts: genotypes of the symbiont are exchanged between unrelated individuals or species of the host

Mycangia: two specialized, internal sac-like structures at the base of the ovipositor in *Sirex* females that contain propagules of an *Amylostereum* species

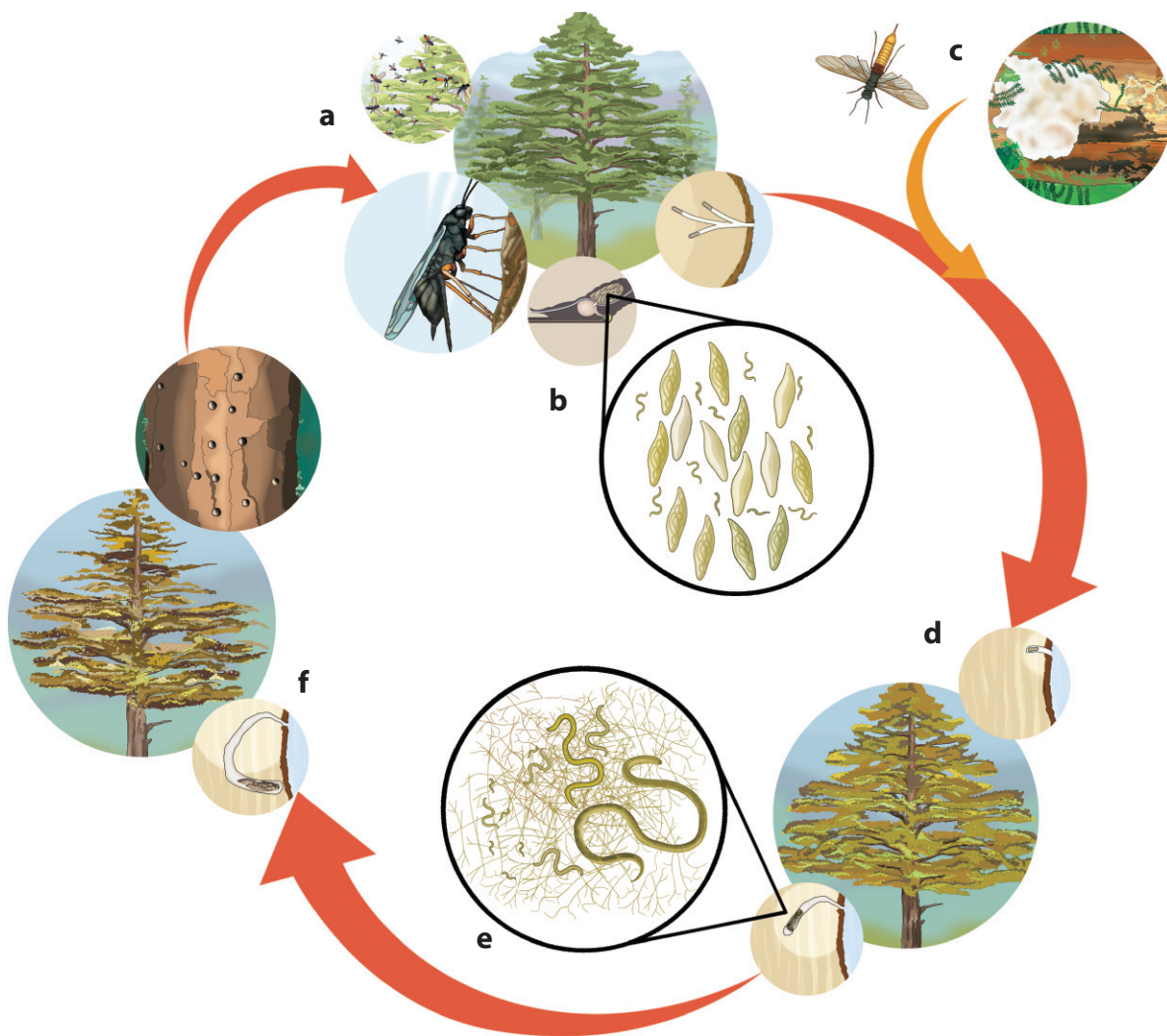



Figure 2

Recent insights into the biology of the *Sirex* system (also see **Supplemental Figures 1 and 2**; follow the **Supplemental Materials** link from the Annual Reviews home page at <http://www.annualreviews.org>). (a) Research into the visual and olfactory cues involved with *Sirex noctilio* mating and host location has confirmed the strong phototactic response of emerging wasps and identified putative pheromones, both of which might contribute to the mating swarms observed above the tree canopy. This understanding, together with optimization of plant volatile (kairomone) lures, will enable researchers to develop more effective monitoring tools. (b) Possible evolution of resistance in *S. noctilio* populations or evolution of reduced virulence in nematode populations can result in incompatibility between wasp and nematode strains whereby not all eggs are penetrated by the nematode. This needs to be interpreted in terms of the introduction history and genetic diversity of the wasp and nematode populations (**Figure 1**). (c) Horizontal acquisition of fungal genotypes and nematode parasites could be achieved via coinfections of the pine host by other wasps or sexually produced genotypes by the fungus. (d) The fungus *Amylostereum areolatum* decays lignin and cellulose in wood, releasing carbohydrates that are pressed as a liquid from the wood and ingested by developing larvae. Bacteria could contribute to cellulose digestion and most likely fix nitrogen for the larvae. (e) Nitrogen is also limiting for the fungus but could be obtained from bacteria or through parasitism of the nematode. Such parasitism can potentially affect nematode population levels in the tree. (f) The larvae leave the fungal colonized area during pupation, possibly to avoid parasitism.

 **Supplemental Material**

Hurley et al. (54) showed equivalent developmental rates and reproduction of *D. siricidicola* on a laboratory strain of *A. areolatum* that originated from *S. juvencus* in Hungary and had been used to rear the nematode for the past three decades. In contrast, Morris et al. (76) found very significant (100-fold) differences between development on *D. siricidicola* on the same laboratory strain and four strains of the fungus from the United States.

Mycetophagy:
deriving the majority
of nutrition from
feeding on fungi

Nutrition and Modes of Interaction

Siricid symbioses have long been seen as bipartite mutualistic associations with *Amylostereum* fungi that enable developing larvae to access nutrients in wood, particularly through cellulose digestion (62, 69, 71, 108) (**Figure 2**). Although other microbes are also present in galleries of siricids (68), their role in the biology of the wasp was unclear. Researchers have yet to determine the extent to which the fungus serves as a nutrient source for the larvae (mycetophagy) (as has been postulated since 1942) and how it contributes to wood digestion.

Thompson et al. (112) have shown that phytosterols (from pine) and not ergosterol (from *Amylostereum*) dominate *S. noctilio* tissues, suggesting that the woody substrate makes up the majority of the larval diet. A follow-up study showed that *S. noctilio* mandibles are adapted to extract liquid from wood fragments scraped from the walls of the larval tunnels (113). Wood fragments are then discarded and moved underneath the body to be packed behind the larvae, rather than through the digestive tract. The larvae concentrate their feedings at the edges of the fungus-colonized wood, where enzymatic degradation would be most active, leaving the fungus-colonized area for pupation after the eighth instar (**Figure 2**). These studies favor an “external rumen hypothesis” in which plant molecules are digested externally by the fungus, after which the larvae feed on released starch and sugars in the extracted liquid. *S. noctilio* may also contribute either externally or internally to this cellulose digestion, as has been found in other insects (36).

Recent work has shown that bacteria may also play a role in cellulose digestion in *Sirex* galleries (2, 109). Adams et al. (2) identified six clades of cellulose-degrading *Streptomyces* and Gammaproteobacteria associated with *S. noctilio* in the United States, although they were not found consistently together with all larvae. These studies suggest that these highly efficient lignocellulose-degrading bacteria may complement the cellulose-degrading ability of the fungus. In addition, some of the sterols obtained by *S. noctilio* could be bacterial derived (113).

Apart from having a possible role in cellulose digestion and providing certain sterols, bacteria could be involved in fixing nitrogen. Dead wood is a very poor source of available nitrogen, and microbes are commonly involved in fixing nitrogen in symbioses with insects and fungi that rely on this substrate (e.g., 36, 46, 51). Contemporary analyses suggest that such associates are involved in the *Sirex* life cycle (111; B. Thompson, personal communication). Understanding this crucial aspect of the nutrition of *S. noctilio* will be important in gaining a more comprehensive understanding of the ecology of the *Sirex* system.

A recent and important advance in our understanding of the biology of *Sirex* symbionts has been the unexpected discovery of the apparent parasitism of *D. siricidicola* by *A. areolatum* (75) (**Figure 2**). Morris & Hajek (75) showed that nematode reproduction in both *D. siricidicola* and *D. proximus* can be negatively affected by a unique mechanism of parasitism of adults and eggs by *Amylostereum*. This discovery provides a possible explanation why *Deladenus* does not survive in culture when *Amylostereum* is fast growing or when the ratio of nematodes to fungus is inordinately biased toward the fungus (8). The emergence of this form of parasitism makes evolutionary sense, given that it could positively affect the fitness of both the fungus and the wasp (through possible reduction in parasitism). This factor will be important to consider in biological control programs.

Pheromone:

chemical produced by an individual organism that affects the behavior of other members of its species

Chemical Ecology

It is a long-recognized fact that *S. noctilio* is attracted to the stems of stressed pine trees (95, 96) (**Figure 2**). A large number of volatile compounds (>60) are associated with such pine stems, with the bulk of these made up of monoterpene hydrocarbons (>95%) such as α - and β -pinene (29, 95, 96). Until 2004, researchers in Australia had exploited this knowledge for lure-based trapping of *S. noctilio* (5). Much work has recently been expended to refine these lures, and complex blends of up to six different compounds are now used (29, 52). A two-component lure of α - and β -pinene is, however, most widely used in the United States and Canada to monitor *S. noctilio* populations (32) as well as to study native wasps (e.g., seven native siricids in Minnesota) (28). Böröczky et al. (15) further examined the role of host volatiles and found that trees that produced greater amounts of volatiles, specifically careen, trapped more wasps.

Investigators are beginning to acquire promising knowledge regarding pheromones linked to *S. noctilio* biology. Soon after emergence, both wasp sexes fly up to the forest canopy, where they aggregate in male-dominated swarms (70) (**Figure 2**). Research has determined that the original signal after emergence is phototactic (see 94), after which either visual (light, structure above the canopy, other wasps and their coloration) or olfactory cues (pheromones) could direct wasp behavior. The male and female antennal sensilla have many contact chemoreceptors (30). Consistent with this fact, Böröczky et al. (14) isolated three nonvolatile cuticular hydrocarbon compounds from female wasps that elicited a mating response from males at short (contact) range. More recently, researchers have isolated from around groups of male wasps three unsaturated alcohol compounds, which could act as longer-range volatile pheromones (23). Although these compounds showed promise in experiments using gas chromatography electroantennal detection as well as Y tubes, they failed to catch wasps in field trials (53), perhaps because of the wasps' strong phototactic response (94).

The detection of *Amylostereum* volatiles by *S. noctilio* has been poorly studied. The ability to detect *Amylostereum* volatiles appears to have evolved in parallel in *Xeris* species (Siricidae) (42) and two parasitoid lineages (*Ibalia leucospoides*, *I. drewseni*, and *Rhyssa* spp.) (17, 66, 72, 104, 105). Because *Amylostereum* volatiles would indicate a substrate that is suitable for larval development, their detection by other siricids makes evolutionary sense. Such detection would also serve to enhance horizontal acquisition of fungal strains (**Figure 2**). Despite the above-mentioned recent efforts, details of the kairomone and pheromone cues that influence host-finding and mating behavior of the siricid woodwasp remain obscure; this field presents exciting opportunities.

POPULATION DYNAMICS AND MANAGEMENT

Subsequent to the first outbreaks of *S. noctilio* more than 60 years ago, a major focus of research is the factors that influence population dynamics and that might provide the keys to managing population outbreaks. The bulk of this work has been done in Australasia, and the simplistic notion that management tools could be easily transferred to other regions has slowed down local adaptation of management programs and has also led to variable control results in various parts of the world (55, 56, 102, 117). In this section, we consider the emerging challenges and opportunities linked to four main factors affecting *S. noctilio* population fluctuations: its natural enemies, the pine host, the wasp, and co-occurring organisms (**Figure 3**).

Natural Enemies

Top-down control of *S. noctilio* populations by its natural enemies is considered to be one of the most important tools for active management of this pest in invaded nonnative pine plantations

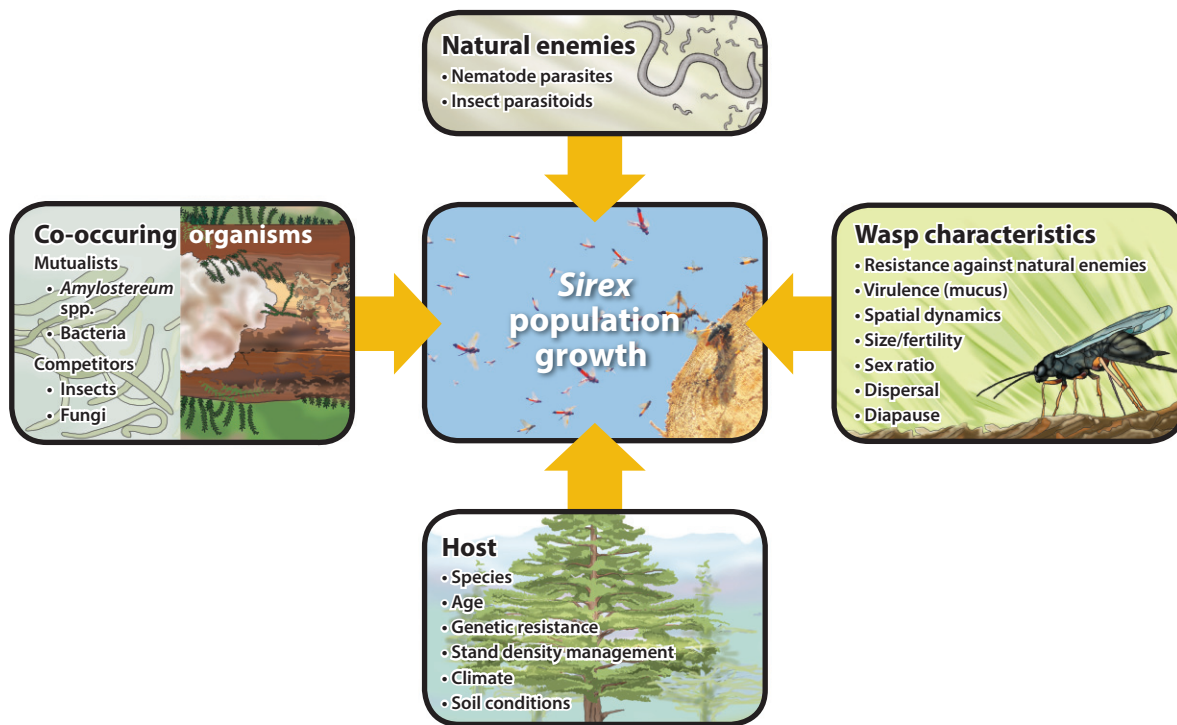


Figure 3

Factors that do or may influence *Sirex noctilio* population dynamics and that have implications for the development of management strategies.

(8, 20, 56, 70). This also plays an important role in populations in natural woody ecosystems (4, 27, 37, 65, 90, 106, 129). Despite the existence of a large body of literature, substantial gaps in our knowledge remain to be filled to improve management systems using natural enemies in many invaded regions of the world.

Numerous parasitic wasp species (*Ibalia*, *Megarhyssa*, *Rhyssa*, and *Schlettererius* species) have been introduced into Australasia for the biological control of *S. noctilio* (19, 20, 56). These insects, however, remain patchily distributed in other areas of the world. This is unfortunate, as these parasitoid species are important at different densities of *S. noctilio* and in different environments (19, 20). *Ibalia leucospoides* has been the most widely used of these parasitoids. Yet, even for this species, recent data on dispersal ability (which is half that of *S. noctilio*), feeding, the cost of long-distance dispersal, and constraints on host location suggest that a reevaluation of methods of rearing, spread, and the potential of augmentative releases is required (26, 38, 39, 40, 83). Furthermore, the diversity of these parasitoids is poorly understood, despite its potential importance for understanding and managing adaptability of parasitoid populations (e.g., see 85, 86).

Reduction of diversity through human selection and inbreeding in serial culture has had a substantial influence on populations of *D. siricidicola* (78), which is widely considered to be the most important natural enemy of the wasp. The threat of such a narrow genetic base became abundantly evident during the Australian “Green Triangle” outbreak, when the nematodes used in biocontrol programs lost their virulence in culture (8). Other consequences of extreme selection processes

Virulence: in the *Sirex* system, reflects reduced or an absence of sterilization of eggs

Resistance: in the *Sirex* system, includes the ability to resist initial infection or the infection of eggs

► Supplemental Material

and the lack of nematode diversity have, however, rarely been considered (e.g., 85, 86). In light of emerging knowledge regarding diversity of global *S. noctilio* populations and the specificity of nematode-wasp and nematode-fungus interactions (discussed above), such factors can significantly affect the success of biological control. For example, Slippers et al. (100) speculated that variation in infection levels could reflect a possible evolution of resistance in *S. noctilio* populations or, alternatively, the evolution of reduced virulence in the nematode. The latter option would be influenced by a trade-off between transmission efficiency inside and outside the eggs and host availability in the next generation (**Supplemental Table 1**).

The Southern Hemisphere (Kamona) strain of *D. siricidicola* has been considered for management of the *S. noctilio* invasion in North America (119). The recent discovery of *A. areolatum* associated with native siricid species, as well as the occurrence of other strains of this nematode species in North America, appears to make this an unnecessary risk (61, 64, 77, 126). A suite of other natural enemies associated with native siricids is also attacking *S. noctilio* in North America (4, 27, 37, 65, 129). Thus, additional biological control, at least given the current distribution of the wasp, seems unnecessary (32). A renewed focus on the natural enemies of *S. noctilio* in North America promises to reverse a long period when this subject received little attention. In addition, researchers now have access to these enemies in their native range and may be able to use them in other regions of the world.

Pine Host

S. noctilio is a secondary pest that attacks only stressed or dying trees (4, 12, 67, 106). Managing stress is thus important in efforts to manage *Sirex* (20, 31, 70). However, the economics of plantation management and unpredictability of stresses arising from variable climate, fire, and biotic factors result in damaging outbreaks of the pest that often cannot be predicted (52). For this reason, it is important to monitor vulnerable plantations and to maintain an understanding of developing outbreaks. A suite of recent studies has pursued these objectives through the use of remote sensing tools, which have become increasingly accurate (1, 57, 58). These studies have also made it possible to identify local stress factors such as sites with rapid soil moisture evapotranspiration as well as intermittent rainfall that influence *S. noctilio* susceptibility (59).

S. noctilio infests a wide range of *Pinus* species across its global distribution (12, 91). The comparative susceptibility of these *Pinus* spp. is poorly understood, possibly because large areas in the Southern Hemisphere are typically dominated by monocultures of a particular *Pinus* species. In Europe and North America, however, where mixed stands of native *Pinus* spp. are more common, European *Pinus* species are generally preferred to North American species (4, 33). Ayres et al. (4) observed that *P. radiata*, which is commonly attacked in the Southern Hemisphere, is not a preferred species in the native range of *S. noctilio*. Thus, when there is no or limited choice of host, wasp populations can reach very high population levels on *Pinus* species that are less favored.

Resistance to *S. noctilio* infestation in *Pinus* spp. and the response of these trees to infection by *A. areolatum* have never been directly considered in breeding programs, even though researchers know that mechanisms that contribute to resistance have a genetic basis (e.g., resin production, ethylene, and polyphenol production) (11–13). Owing to the availability of alternative control measures, resistance breeding has been given low priority. An improved understanding of the volatile and resin profiles of susceptible hosts (e.g., 13), the genetics and biochemistry linked to the interactions between *Pinus* and *Sirex* mucus (venom) injected into trees at the time of egg laying (11), and the clonality of *A. areolatum* associated with some invasive populations (101) could provide better targets for resistance breeding in the future.

Wasp

Various aspects of the life history of *S. noctilio* can dramatically influence its population dynamics (reviewed in 24, 91, 117) (**Figure 3**). These factors include fecundity, reproductive potential, adult size, sex ratio, and the influence of diapause on the length of the larval period (1–3 years). All these factors vary significantly within and between wasp populations, yet the extent of variation and the mechanisms controlling them remain very poorly understood. Aparacio et al. (3) suggest these factors alone may explain wasp outbreaks, independent of environmental factors.

Sex ratios in *S. noctilio* vary dramatically among populations, ranging from one or two males per female to more than 20 males per female (91, 106). Very high male to female ratios are often attributed to the haplodiploid reproductive system and Allee effects such as mate finding in invading or expanding populations. But many of these skewed ratios persist despite high population numbers (e.g., greater than ~10:1 in eastern parts of South Africa over many years) (55). The importance of sex ratio on reproductive potential, ability to overcome host defenses, and dispersal has begun to drive research initiatives to explore possible influencing factors, including, for example, endosymbionts, resource quality variation, and genetic mechanisms such as a reduced diversity at sex determining loci.

The spatial dynamics, including both aggregation and flight potential, of *S. noctilio* populations represent important issues in understanding the development and spread of outbreaks (16, 24, 25, 63, 117). Such studies showed increasing spatial aggregation under preoutbreak and outbreak conditions, which became less evident as the outbreak developed (25, 117) (**Supplemental Table 1**). The aggressiveness of *S. noctilio* increases with density: It primarily attacks stressed trees (4) but then can overcome the defenses of healthy trees under outbreak conditions (25). Beyond the stand level, spatial dynamics are significantly affected by flight potential (16, 24, 25). Lantschner et al. (63) calculated that *S. noctilio* spreads between 12 km (Argentina) and 78 km (eastern part of South Africa) per year; the spread rate best correlates with mean annual temperature and isothermality. Temperature also has a major impact on phenology and, consequently, on the management of *Sirex* in different environments (47, 91).


Resistance to infection by specific nematode strains exists in some *S. noctilio* populations (6, 61, 100, 126) (also see above discussion). Because various factors may have been involved in the steady decline in nematode parasitism in some parts of Australia (20), development of resistance in the wasp should be investigated in this region as well as in other parts of the world. Understanding which factors may influence the development of such resistance relates directly to the evolution of invasive species and biological control more broadly (see 85, 86) (**Supplemental Table 1**).

Co-Occurring Organisms

Other than the mutualistic interactions between *S. noctilio* and various microorganisms, many xylophagous insects can be found in the trunks of *S. noctilio*-infested trees. Such insects may interact with *S. noctilio* either directly or indirectly by introducing competing fungi (4, 88, 92, 118, 125). *A. areolatum* is a weak competitor against certain fungi that occur as endophytes in *Pinus* (e.g., *Diplodia sapinea* in South Africa) or that are introduced by bark beetles in North America and Australia (e.g., *Ophiostoma ips* introduced by *Ips grandicollis* and *Leptographium wingfieldii* by *Tomicus piniperda*) (54, 92, 125, 128). These fungi can affect the rate at which trees die and the wood moisture levels in infested trees, which has indirect negative effects on *A. areolatum* (125) and on the oviposition behavior of the wasp (89). Apart from their competition with *A. areolatum*, competing insects can also interfere with management programs (28, 34, 35, 44, 45, 125, 128). In Australia, for example, colonization of dying trees by *I. grandicollis* reduces the number of *S. noctilio* oviposition events, the size of *S. noctilio* individuals in trap trees, and the level of

Haplodiploid: most hymenoptera produce haploid males from unfertilized eggs and diploid females from fertilized eggs

Allee effects: effects that reduce individual fitness at low population densities

 Supplemental Material

parasitism of the wasp by *D. siricidicola* (125). Despite these potential influences on *S. noctilio* infestations, especially in the case of trap trees, data collected by Ayres et al. (4) suggest competing organisms were not a major limiting factor in host use by *S. noctilio* in Spain and the United States.

CONCLUSIONS

The history of the global spread of *S. noctilio* reflects a complex pattern of introductions that have occurred multiple times and from numerous different sources. The likelihood that these introductions will continue represents a significant threat for currently unaffected *Pinus* forests and plantations in Africa, Australia, South America, parts of Asia (e.g., Japan), and North America (for potential distribution and risk analysis, see 21, 122). Continued accidental introductions of *S. noctilio* are also likely to further contribute to admixture and the potential for evolution and spread of resistance to the nematode in these populations. For these reasons, quarantine remains critically important even in countries where the wasp is well established. Importantly, this calls for the development of more effective monitoring and detection tools as well as for the enhancement of risk analyses (53, 59, 73, 123, 124).

The appearance of *S. noctilio* in North America has mobilized research capacity and investment on a pest that had been relatively poorly studied. Its appearance has also provided a fascinating opportunity to study an alien invasive pest in an environment very similar to its native habitat. Furthermore, renewed research provides an opportunity to challenge as well as to transform our understanding of the *Sirex* system. Much remains to be learned about the ecology of the multiple components of mutualistic and parasitic interactions that either facilitate or restrict the development of *S. noctilio* populations. Substantial new insights are likely to arise from comparative studies across systems in different parts of the world, as has been well illustrated in recent studies on the spread, biology, and ecology of the wasp (4, 10, 21, 63). Such information will be invaluable in the quest to refine and sustain management programs around the world.

The patterns of continued, complex, and increasingly rapid rates of introduction are not unique to *S. noctilio* but, unfortunately, represent a general trend for many invasive species (41, 84, 87, 93, 97). All findings indicate that we face a future with much greater pressure due to a diversity of pests in natural woody ecosystems and in planted forests. As a result, to maintain the sustainability of forests and plantations, management programs will be under significantly greater pressure to develop more rapidly and yield greater impact. On the basis of our experience with the *Sirex* system, we suggest two areas in particular need of change. First, more robust international cooperative networks are needed to share information, experience, and tools, including biological control agents, for pest management (see 43). Moreover, these networks will need to be implemented more rapidly than they have in the past. Second, management programs will need to be refined to ensure their stability and impact, thus requiring a deeper understanding of the mechanisms that influence the success of both the invader pests and biological control agents at local levels. In this regard, the *S. noctilio* system serves as an outstanding model of a globally important and biologically complex invasive system. The lessons learned from understanding and dealing with it will contribute substantially to managing the health of future forests and plantations.

SUMMARY POINTS AND FUTURE DIRECTIONS

1. *S. noctilio* has continued to spread despite quarantine systems. Thus, we must prepare for further introductions, and reintroductions, of the wasp, including those from nonnative to native areas.

2. There is an urgent need to refine chemical and remote sensing tools to monitor and quantify populations of *S. noctilio*.
3. Complex patterns of interaction at varying levels of specificity among *S. noctilio*, *A. areolatum*, bacteria, competing insects and fungi, and the tree host and its natural enemies facilitate or restrict population growth of *S. noctilio*.
4. Classical biological programs such as those applied to *S. noctilio* need continuous monitoring and refinement. They are likely to require knowledge of local ecology, diversity, and microevolution for successful transfer between regions.
5. There are both an opportunity and a need for international comparative studies, including in native and various nonnative habitats, to characterize factors that influence invasion and local population ecology.
6. More refined knowledge of the genetics, biochemistry, and chemical ecology of *S. noctilio* and the many organisms associated with this wasp will contribute to opportunities to breed and select trees with resistance to this pest.
7. The *Sirex* system reflects similar processes in other invasive pests and thus represents an outstanding model to study the evolution of an invasive forest pest, its biological control, and the many fascinating aspects of the ecology and evolution of symbioses.

DISCLOSURE STATEMENT

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4. Gives a powerful example of a cross-continental comparative study of the *Sirex* system.

10. Provides the most comprehensive study of the global spread of *Sirex noctilio*.

11. Discusses landmark studies on the biochemistry and host response to the phytotoxic *Sirex noctilio* “mucus”/venom.

21. Discusses ways in which many currently uninfested areas would be suitable for *S. noctilio* invasion.

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RELATED RESOURCES

Comprehensive list of *Sirex*-related literature: <http://fabinet.up.ac.za/index.php/sirex-literature>

Sirex listserver connecting the global community working on this pest complex: sirex@kendi.up.ac.za

Sirex working group website: <http://www.woodwasps.com/>