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## Forest Stand Preference of *Sirex Nigricornis*, and *Sirex Noctilio* Hazard in the Southeastern United States

Kevin D. Chase

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Forest stand preference of *Sirex nigricornis*, and *Sirex noctilio* hazard in the Southeastern  
United States

By

Kevin D. Chase

A Thesis  
Submitted to the Faculty of  
Mississippi State University  
in Partial Fulfillment of the Requirements  
for the Degree of Master of Science  
in Agricultural Life Sciences  
in the Department of Biochemistry, Molecular Biology, Entomology & Plant Pathology

Mississippi State, Mississippi

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Kevin D. Chase  
2013

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United States

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The Eurasian wood wasp, *Sirex noctilio*, is considered a secondary pest in its native range; however, it has caused significant economic damage when introduced to pine plantations in the Southern Hemisphere. *Sirex noctilio* was recently introduced to the northeastern U.S., which has raised concerns about its potential impact on Southeastern pine plantations. This research was conducted to understand how silvicultural management affects populations of a native wood wasp, *Sirex nigricornis*, a wood wasp with similar ecosystem functions as *S. noctilio*. *Sirex nigricornis* abundance was higher in un-managed pine plantations than in managed plantations, mixed, and old growth forests. Additionally, geospatial models were built displaying *S. noctilio* hazard for the Southeastern U.S. based on oviposition host preference assays and historical outbreak information. *Sirex noctilio* hazard models will inform land managers about areas of greatest concern under various scenarios and should be used to decrease susceptibility of pine forests to this pest.

## DEDICATION

To my wife, Lindsey Chase, whose love and support is not taken for granted.

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# CHAPTER I

## INTRODUCTION

The ecology of siricid wood wasps (Hymenoptera: Symphyta: Siricidae) native to North America is poorly understood because of their status as non-economic pests (Schiff et al. 2012). However, with the arrival of *Sirex noctilio* F. to North America (Hoebeke et al. 2005, de Groot et al. 2006), research regarding wood wasps has risen. *Sirex noctilio* is an invasive wood wasp that has devastated non-native pine plantations in the Southern Hemisphere (Rawlings 1955, Carnegie et al. 2005). In its native range of Eurasia, *S. noctilio* is considered a secondary pest, utilizing stressed or dead trees (Hall 1968, Spradbery and Kirk 1978). Native wood wasps in Eurasia and North America are kept in check by a complex of Hymenopteran parasitoids and nematode parasites (Spradbery and Kirk 1978, Coyle and Gandhi 2012). The question remains whether *S. noctilio* will devastate North American pine forests as it did in the Southern Hemisphere, or act as a secondary pest as it does in its native range (Spradbery and Kirk 1981, Dodds et al. 2010, Ryan et al. 2012). One way of addressing this issue is to investigate the factors that prevent outbreaks of native wood wasps. This thesis is an investigation of: 1) the effects of forest stand management and structure on the abundance of native wood wasps, and by association the possible abundance of the introduced European wood wasp should it reach forests of the Southeastern U.S.A. 2) the phenology of native siricid and siricid parasitoids across plant hardiness zones in the United States 3) construction of a

hazard map of *S. noctilio* for the Southeastern U.S. based on oviposition host preference data.

## CHAPTER II

### LITERATURE REVIEW

#### **Siricidae: Siricidae Taxonomy and Life-History**

Wood wasps (Hymenoptera: Siricidae) are woodboring insects commonly known as horntails. Siricids include  $\approx 125$  species worldwide, of which 33 species occur in the New World (Schiff et al. 2012). Currently, no endemic extant species have been found in the Southern Hemisphere (Schiff et al. 2012). Siricidae are composed of two sub-families based on morphology that also reflects their host preferences: Tremicinae and Siricinae. In North America the Tremicinae includes three genera in North America that feed within angiosperms: *Tremex* Jurine, *Xeris* A. Costa, and *Eriotremex* Benson, and the Siricinae includes two genera that feed within gymnosperms: *Sirex* (L.) and *Urocerus* Geoffroy (Smith and Schiff 2002). Horntails are generally considered secondary pests of stressed, mature, or dying trees and aid in forest succession by decomposing woody material (Hall 1968).

The life cycle of a wood wasp typically requires 1 to 3 years, depending on the species and latitude (Stillwell 1966, Schiff et al. 2006, Schiff et al. 2012). Larvae hatch from eggs 8-12 days after oviposition, depending on ambient temperature (Madden 1981). The larval stage is the longest stage of the life cycle, lasting one to three years and undergoing 6-12 instars (Madden 1981). Larvae feed on symbiotic fungus in the oviposition chamber (Madden 1981). The pupal period is about three weeks (Madden

1981), after which the adult siricid emerges from the tree. Males emerge before the females and form mass aggregations at the tops of trees where they wait for females to emerge (Madden 1982, Schiff et al. 2012). Once the females emerge, the males release a pheromone that attracts both males and females (Cooperband et al. 2011). Once mated, females will search out an appropriate host (stressed or weakened) with proper moisture content and inject the eggs, phytotoxic mucus, and a fungal symbiont (Coutts and Dolezal 1965, Madden 1968, Schiff et al. 2012). Wood wasps are arrhenotokous, meaning that mated females will produce both male and female offspring while unmated females will produce only male offspring (Taylor 1981, Borchert et al. 2007).

Siricid wood wasps carry symbiotic basidiomycete wood decaying fungi (Stillwell 1966, Gaut 1969, Slippers et al. 2003). Female adult wood wasps carry oidia, hyphal fragments or fungal arthrospores in mycangia that are paired intersegmental pouches called mycangia (Smith and Schiff 2002, Slippers et al. 2003). Horntails in *Tremex* harbor *Cerrena* (Bull.) fungi. *Tremex columba*, native to North America, is associated with *Cerrena unicolor* (Fr.) and mainly utilizes hickories (*Carya*), maples (*Acer*), and elms (*Ulmus*). *Xeris* spp. do not carry symbiotic fungus and oviposit at sites that have been previously inoculated by other siricids. Horntails in Siricinae (*Sirex* and *Urocerus*) carry *Amylostereum* Boidin fungus (Tabata & Abe 1995, Slippers et al. 2003). *Amylostereum* fungus (commonly known as white rot fungus), along with  $\gamma$ -Proteobacteria and *Streptomyces* spp., aid in breaking down cellulose that are eaten by siricid larvae (Talbot 1977, Adams et al. 2011). Native *Sirex* species carry *Amylostereum chailletii* (Fr.) and *S. noctilio* carries *Amylostereum areolatum* (Fr.) (Bedding and Akhurst 1974, Slippers 2002). Female horntails also inject a phytotoxic mucus that acts

synergistically with the fungus to stress or kill the tree, thereby creating a suitable habitat within the host tree (Bedding 2009, Nielsen et al. 2009).

### ***Sirex noctilio* Invasion and Current Status in the United States**

*Sirex noctilio*, or the European wood wasp, is a wood-boring forest insect that has caused extensive mortality in the Southern Hemisphere in non-native pines within monoculture plantations. *Sirex noctilio* was first detected in New Zealand in the early 1900's as an introduction from its native range of Eurasia and northern Africa (Rawlings and Wilson 1949, Hall 1968). Over the past century, *S. noctilio* has spread through the Southern Hemisphere [Australia (1952), South Africa (1994) and South America (1980)], most likely arriving in wooden crates and pallets (Tribe and Cillie 2004, Nielson et al. 2009). Economic losses induced by *S. noctilio* reached \$10-12 million in Australian *Pinus radiata* (Monterey pine) stands (Haugen et al. 1990). In Brazil, ≈300,000 hectares of pine plantations have been infested by *S. noctilio*, which continues to spread through Uruguay, Argentina, and Chile (Carnegie et al. 2005).

In the fall of 2004, *Sirex noctilio* was detected in North America (Oswego County, New York) and is thought to have been introduced via solid wood packing materials (SWPM) (Hoebeke 2005, de Groot et al. 2006). *Sirex noctilio* is considered to create a high risk for pine plantations in the United States, meaning that it is predicted to cause substantial economic damage to the forestry industry (Borchert et al. 2007). The areas of greatest concern are the western and southern states where large stands of unmanaged pine plantations subsist (Haugen 1999, Hoebeke et al. 2005). The southern U.S. contains the largest softwood timber industry in the world valued at \$8 billion/year. Loblolly pine, *Pinus taeda* L., is the most economically important species in the South



and is a known host of *S. noctilio* (Carnegie et al. 2006, Borchert et al. 2007). Estimates for potential damage from *S. noctilio* in the western U.S. range from \$24 to \$131 million. Since its introduction, *S. noctilio* has spread to six states in the northeast and is behaving as an intermediate pest, colonizing stressed and overtopped trees (Dodds et al. 2010).

*Sirex noctilio* is not the only non-native wood wasp that has been introduced to North America. *Eriotremex formosanus* Matsumura (commonly known as the Asian horntail) is native to Asia and was first detected from counties in Florida and Georgia in 1974 (Smith 1975). Since its introduction, *E. formosanus* has spread to the following states: AL, AR, FL, GA, LA, MS, NC, SC, TX and VA (Smith 1996, Warriner 2008). *Eriotremex formosanus* is not an economically important pest, as it appears to attack only dead or dying angiosperms (Schiff et al. 2006, Ulyshen and Hanula 2010). A second species, *Urocerus sah* Mocsáry, was found among specimens loaned to Dr. David Smith by the University of New Hampshire and is currently adventive in the same state (Smith 1987, Schiff et al. 2006). This species is native to North Africa, Asia Minor and eastward to Afghanistan, and is commonly known as the Asian horntail (Schiff et al. 2012). Hosts of *U. sah* are fir (*Abies* spp.), spruce (*Picea* spp.) and pine (*Pinus* spp.) (Schiff et al. 2006). Two other Siricids, *S. juvencus* (L.) and *Xeris spectrum* (L.), are consistently discovered at ports of entry on incoming solid wood packing materials, but are not believed to have established populations in the United States or Canada (Schiff et al. 2012).

The introduction of *S. noctilio* to the United States provides a unique opportunity to study an invasive forest insect with an account unlike any other. *Sirex noctilio* has a 100 year record as an eruptive outbreak pest throughout the Southern Hemisphere and

now subsists in an environment that resembles the wood wasp's native range (Berryman 1987, Morgan 1989, Slippers and Wingfield 2012). The forest stand conditions (mixed pine-hardwood temperate forest) and parasite/parasitoid complex (*Megarhyssa* spp., *Rhyssa* spp., *Ibalia* spp., *Deladenus* spp.) of North America are similar to those in Eurasia and it has been hypothesized (Dodds et al. 2010, Coyle and Gandhi 2012) that these factors could potentially limit the extent of *S. noctilio*'s invasion. *Sirex noctilio* is currently behaving as an intermediate pest in New York and central Ontario within high basal area pine plantations with smaller diameter trees (Dodds et al. 2010).

### **Siricid Inhibitory Factors: Allee Effects**

Biological factors that inhibit the establishment of invasive species can lead to founder (Allee) effects. Founder populations are generally very small and therefore more susceptible to eventual extinction (MacArthur & Wilson 1967, Liebhold & Tobin 2008). This phenomenon is explained by the Allee effect, which states that the overall fitness of a population decreases as the size of the population decreases (Allee et al. 1949, Stephens et al. 1999). One example of an Allee effect is the presence (or introduction) of natural enemies and strong competitive forces (Owen & Lewis 2001, Fagan et al. 2002, Case et al. 2005). Another mechanism that can limit the fitness of a population is the ability to find a mate in a new environment, which is a density dependent process, and the distance the species can disperse through the environment (South & Kenward 2001, Dennis 2002, Stepien et al. 2005). Finally, the availability, quality and density of a suitable host as a food source for development can deter the establishment of invasive species (Bartell & Nair 2003). The following sub-sections discuss what factors may (or may not) limit the

overall fitness of native siricid populations and could potentially limit founder populations of the invasive *Sirex noctilio*.

### **Siricid Inhibitory Factors: Hymenopteran Parasitoids**

A complex of siricid-specific hymenopteran obligate parasitoids (*Ibalia* Latreille, *Rhyssa* Gravenhorst, *Megarhyssa* Ashmead, and *Schlettererius* Ashmead) exists in North America. *Ibalia* spp. (Hymenoptera: Ibalidae) have short ovipositors and parasitize eggs and first- or second-instar larvae (Taylor 1978, Liu and Nordlander 1994). Ryan et al. (2012) recently reported that *Ibalia leucospoides* Hockenwarth is the dominant parasitoid of *S. noctilio* in North America. *Rhyssa* and *Megarhyssa* spp. (Hymenoptera: Ichneumonidae) have long ovipositors that are used to parasitize late stage larvae that have bored deeper into the bole (Middlekauf 1960, Spradbery 1970). *Schlettererius cinctipes* Cresson (Hymenoptera: Stephanidae) is the only North American species in this genus, and it has a long ovipositor that can parasitize siricid larvae up to 3.4 cm into the tree (Taylor 1967, Coyle & Gandhi 2012). Additionally, the cleptoparasite *Pseudorhyssa nigricornis* Ratzeburg is a parasitoid of *Rhyssa* larva, developing on the remaining Siricid larvae after eliminating the *Rhyssa* larva (Schiff et al. 2012, Standley et al. 2012). Hymenopteran parasitoids are hypothesized to play an important role in keeping native siricids from reaching outbreak levels and may contribute to the biological control of *S. noctilio* in North America.

### **Siricid Inhibitory Factors: Nematode Parasites**

Nematodes of the genus *Deladenus* (*Beddingia*) Bedding (Neotylenchidae) are also important parasites of siricids (Bedding 2009). Seven species of *Deladenus* have

been described from 29 countries (Bedding and Akhurst 1978). *Deladenus* nematodes have a complex life cycle and unique morphology based on two possible cycles: mycetophagous (fungus feeding) and parasitic on siricids (Bedding and Akhurst 1978). *Deladenus* nematodes are mycetophagous if there is available fungus in the surrounding area and will continue this cycle until environmental conditions change (high CO<sub>2</sub> or low pH) or the resource is depleted (Keeler 2012). If a juvenile *Deladenus* nematode encounters a siricid larva or an egg comes into contact with the larva, the nematode will enter the parasitic cycle. In this cycle, fertilized females penetrate the cuticle of the siricid larvae and enter the haemocoel (Bedding 1972, Keeler 2012). An average range of five to 20 nematodes has been recorded within a single siricid host, the highest recorded infestation is 100 (Bedding 1972). Juvenile nematodes enter the ovaries of the developing female siricid host and infest the eggs, causing them to be infertile. After siricid development is complete, parasitized adult female siricids emerge and oviposit infected eggs to a new host source, where nematodes continue their life cycle on siricid hosts. Male hosts are considered dead-end hosts because the nematodes are not disseminated after infestation (Bedding 2009).

*Deladenus siricidicola* Bedding was the main control agent of the European wood wasp and has been very successful. In Australia and Brazil, a strain of the nematode (termed the Kamona strain after the region in Tasmania where it was isolated) was inoculated into trees infested with *S. noctilio* and parasitism rates were observed at 90% (Hocking 1967, Bedding and Akhurst 1974, Leal et al. 2012). Unfortunately, the Kamona strain has not been as successful in other areas of *S. noctilio*'s introduced range. Local biotic factors (i.e. wood moisture content and fungal competition) have been

hypothesized to limit the nematodes efficacy (Hurley et al. 2007). Williams et al. (2012) are currently investigating the effectiveness of the Kamona strain in North America and what, if any, ecological effects may be incurred to native *Deladenus* and siricid populations.

### **Siricid Inhibitory Factors: Native Insect Assembly Competition**

Competition from native and previously established exotic woodboring insects are hypothesized to have an important role in preventing a *Sirex noctilio* outbreak and may also be what keeps native siricids from reaching outbreak levels. Ryan et al. (2012) reported that *S. noctilio* was found unaccompanied only 10% of the time from the bole of 60 infested pine trees in Ontario, Canada. The most common species inhabiting the bole of the trees with *S. noctilio* were *Gnathotrichus materiarius* Fitch, *Ips grandicollis* Eichhoff, *Monochamus carolinensis* Olivier, *Pissodes nemorensis* Germar, and *Tomicus pinperda* L., and reduced emergence rates were displayed when these species were present. de Groot & Turgeon (1998) reported that they found 260 species inhabiting the bole of *Pinus* spp. and that up to 1,100 species utilize pine as a host. In the Southeastern U.S., *S. noctilio* would have to directly compete against the bark beetle guild [*Dendroctonus frontalis* (southern pine beetle), *D. terebrans* (black turpentine beetle), *Ips avulsus* (four-spined engraver), *I. grandicollis* (five-spined engraver), and *I. calligraphus* (six-spined engraver)], scolytines known to quickly detect and infest stressed pine hosts (Nebeker 2011). Pressures from competition can contribute to smaller body size, reduced progeny and potentially limit the rate at which a population grows (Schlyter and Anderbrandt 1993).

A large number of wood wasps in North America utilize *Pinus* spp. as hosts and will compete for the same resource as *S. noctilio* (Ryan 2011, Schiff et al. 2012). In the eastern U.S. *Sirex nigricornis* F. is the most abundant native horntail that utilizes various *Pinus* spp. and this species ranges from Ontario south to Florida and west to Texas and Alberta. Schiff et al. (2012) reports that the phenology of *S. nigricornis* is late July through early October, with the peak flight periods being in the latter half of July and the end of August. Climatic factors have been shown to influence and even change phenology of species from different populations (Pozo et al. 2008, Dukes et al. 2009). The introduced *S. noctilio* is recorded to emerge in early July and fly through mid October (Schiff et al. 2012). Because the phenology of *S. nigricornis* and *S. noctilio* overlap and oviposit on the same host, it is reasonable to hypothesize that they may directly compete for the same resource. The potential impacts and associations of North American wood wasps on *S. noctilio* are still unknown and require further investigation. One objective of this study is to investigate the mean phenology of *S. nigricornis* in the forests of Mississippi (see Chapter 3).

Bark beetle-vectored fungi may also be playing an important role in reducing siricid outbreak potential including that of *Sirex noctilio* in the U.S. The Southeastern United States has a rich fauna of scolytine bark beetles (Coleoptera: Curculionidae) that vector an assortment of fungi, the most common species of fungi being those in the genera *Ophiostoma* and *Leptographium*. The fungal symbiont of *Sirex noctilio* and *S. nigricornis* (*Amylosterum* spp.) is a weak competitor against *Leptographium* and *Ophiostoma* fungus in lab and field tests (King 1966, Ryan 2011). *Sirex noctilio* also displayed oviposition behavior that preferred sites away from portions of the tree

inoculated with *L. wingfieldii* and *O. minus* (Kirisits 2004, Ryan et al. 2011). The beetle *Tomicus piniperda* carries both *L. wingfieldii* and *O. minus* in *S. noctilio*'s native range, and it is proposed that *S. noctilio* has the ability to detect both fungal species since they co-evolved together (Ryan et al. 2011).

### **Siricid Inhibitory Factors: *Sirex noctilio* Dispersal Potential and Host Availability**

Dispersal potential is not hypothesized to inhibit the fitness of *S. noctilio*. The European woodwasp is considered a strong flier, capable of moving up to 18-31 miles/year (Haugen et al. 1990), depending on the size of the wood wasp and the degree of parasitism by *Deladenus* nematodes (Taylor 1981, Madden 1988). In a study conducted recently by Bruzzone et al. (2009) using flight mills, *S. noctilio* females flew between 0.68 and 29.4 miles over a 24 hour period. Also, it is possible that *S. noctilio* could disperse through the United States via infested materials such as untreated timber and SWPM.

In regard to host availability and suitability, *S. noctilio* is not limited by the abundance and range of host material (*Pinus* spp.). In the United States, there are more than 58 million hectares of susceptible pine forests in the U.S., with the largest tracts of pine in the southern and western states (Borchert 2007, Schneeberger 2007). In areas of previous invasion, *S. noctilio* was able to successfully colonize North America *Pinus* spp. that it had not encountered in its native range including: Monterey pine (*Pinus radiata* D. Don) in Australia, loblolly pine (*Pinus taeda* L.) and slash pine (*Pinus elliottii* Engelm) in Uruguay, and Mexican weeping pine (*Pinus patula* Schiede) in South Africa (Tribe and Cillie 2004). Dinkins (2011) recently conducted choice and no-choice oviposition host preference tests for North American *Pinus* spp. and found that *S. noctilio* females were

able to successfully utilize *P.echinata* Mill, *P. elliotii*, *P. palustris* Mill, *P. strobus* L., *P. taeda*, *P. virginiana* Mill, and *P. sylvestris* L.. *Pinus* spp. are continuous along the eastern seaboard and would allow for natural dispersal of *S. noctilio* from northern Canada to the Southeastern United States.

### **Forestry Management Practices and *Sirex noctilio* Outbreaks**

*Sirex noctilio* outbreaks occur in areas where non-native monoculture pine plantations exist. In the wood wasp native range of Eurasia, *S. noctilio* is considered a secondary pest of pines, attacking only stressed or dying trees and playing a natural role in forest succession (Hall 1968). The forest stand structure within the native range of this wood wasp resembles the mixed temperate forests of North America, displaying a wide range of species diversity and a heterogenous landscape. The trees that *S. noctilio* encountered in the Southern Hemisphere (i.e. *Pinus ponderosa*, *Pinus radiata*, *Pinus taeda*) were extremely overstocked, non-native plantations (Rawlings 1952, Haugen 1990). Tree vigor within these stands was exceptionally low during and after periods of drought, and this condition is associated with outbreaks of *S. noctilio* (Gilmour 1965, Morgan 1989).

Tree vigor is a gauge of individual tree health (Voelker 2008). The definition of tree vigor is “stem growth production per unit leaf area” (Waring et al. 1980, Larsson et al. 1983). Indicators of tree vigor include crown health, bark characteristics, and starch content (Miller and Keen 1960, Smith et al. 1997, Wargo et al. 2002). Greater tree vigor is correlated with healthier trees that are less prone to insect attack (Larsson 1983, Allen et al. 2010, Haavik et al. 2010) and disease (Filip et al. 2009). Reduced tree vigor has been associated with outbreaks of insects [i.e. mountain pine beetle (*Dendroctonus*



*ponderosae* Hopkins)] and reduced profit for land managers (Waring and Pitman 1985, Romme et al. 1986). Tree vigor within a plantation setting can be increased by reducing basal area (therefore reducing competition of resources) and proper fire regimes (Mitchell et al. 1983, Brown et al. 1987, Stevenson et al. 2008, Allen et al. 2010). Measurement of tree vigor is useful in determining the susceptibility of a stand to population outbreaks and the value of a stand.

The overall vigor of a forest stand can be measured using standard forestry measurement techniques. One common technique that measures the total basal area of a forest stand is fixed-area circular plots (FACP) (Williams et al. 2001). FACP are measured by calculating the basal area (cross-sectional area of tree trunk measured at breast height) of individual trees within a fixed circular area. The size of the fixed circular area is determined by the total acreage of the forest stand sampled. Other common attributes that are measured within these plots are tree height of the dominant or co-dominant trees, tree species, living or dead, and live crown ratio. Mean diameters of the plots are extrapolated to give the total basal area of the stand (Williams et al. 2001). Management decisions then can be made based on the basal area of the stand based on the overall management objective. In this study, we assessed the impact of forest management practices on native siricid wood wasp abundance (see chapter 3). With this information we hope to better predict and assess what stands could be the most hazardous for *S. noctilio*. The overall objective is to give land managers a plan that could reduce susceptibility of attack by modeling basal areas that suppress siricid populations.

## ***Sirex noctilio* Monitoring and Control**

The ability to detect the presence of an invasive pest in a landscape is an important but sometimes difficult task for those monitoring introduction of invasive species. Some invasive species slip into a new territory unseen and are not noticed until they reach pest status (Crooks & Soule 1999, Lux et al. 2003, Delaney et al. 2008). This can be especially true when one stage of the life cycle is "hidden" (i.e. woodborers that may not be seen until they emerge). Additionally, some invasive species are misidentified upon arrival or appear so similar to native species that they go unnoticed until an outbreak occurs (Martin 2001, Ahern et al. 2008). It is important to develop survey programs that quickly and accurately detect the presence and distribution of an invasive species and is cost efficient. The following discussion covers detection, monitoring, and control techniques that have been used throughout the Southern Hemisphere. Most of the discussion is based on the report made by Haugen et al. (1990) that describe strategies used in the *Sirex noctilio* program in Australia.

Detection of *S. noctilio* in its initial infestation stages allows managers to implement management and control efforts more effectively. A *S. noctilio* detection program should include an education program that informs land managers, timber mill personnel, and the general public about the general biology and signs/symptoms of *S. noctilio*. If the wood wasp is found within an area, quarantine should be considered that prohibits the transportation of pine host material (Haugen et al. 1990).

Risk and hazard maps are useful tools for detecting the areas of greatest susceptibility to an outbreak. Hazard and risk rating systems have inherent differences. Risk maps are based on existing stand hazard and presence of pest populations. Hazard

maps are used to predict the infestation potential if the pest were to arrive in the area of concern (Dodds et al. 2004). One goal of this research is to create a hazard map for *S. noctilio* based on recent oviposition host preference data and stand density index (stand condition). This map will provide government agencies and land managers information on the areas of greatest concern if *S. noctilio* were to invade the Southeastern U.S.

If *S. noctilio* becomes established in an area, there are two main strategies that have been used to detect wood wasp populations in areas of eruptive outbreaks. 1) Plots of trap-trees are selected to detect populations of *S. noctilio* before they reach outbreak status. A plot consists of 5 chemically stressed trees [basal stem injection of Dicamba (3,6-dichloro-2-methoxybenzoic acid)] and are placed in susceptible stands (>10 years old and having not received proper thinning treatments). The number of plots in a stand is dependent on the distance of the wood wasp to the stand and the size of the stand. If *S. noctilio* is within 100 hectares of the stand of concern, it is advisable to put one trap tree plot for every 100 hectares of susceptible pine material (Haugen et al. 1990). Zylstra et al. (2010) found that the effectiveness of trap trees for *S. noctilio* in North America was dependent upon timing (one month prior to *S. noctilio* emergence) and host species. 2) Aerial detections should not be used primarily to detect initial infestations but rather to observe forest stands that are beginning to display foliage symptoms. These areas can then be ground checked for signs of a *S. noctilio* attack. Forests that have recently been subjected to wind, fire, hail, and lightning damage should be monitored more closely for a *S. noctilio* outbreak (Haugen et al. 1990).

Monitoring for *S. noctilio* outbreaks utilizes the following strategies: repeatable transects, aerial surveys, aerial photography, and remote sensing. Repeatable transects

measure new tree mortality on an annual basis. A sample size of >500 trees per stand is recommended and these same trees should be checked every year to record new tree deaths (Haugen et al. 1990). Aerial surveys are conducted using either fixed wing aircrafts or helicopters, with the latter being the vehicle of choice. Aerial surveys are a poor technique for spotting new outbreaks and should only be used to calculate mortality once the stand mortality is >5%. Aerial photography has been one technique that has been used to evaluate *P. radiata* stands in Australia. Photographs are taken at time intervals and compared to see the movement and spread of a *S. noctilio* outbreak. All of these techniques are time consuming and expensive, and continued research on *S. noctilio* needs to focus on cost-effective, accurate, and pre-outbreak monitoring. North America has not been subjected to a *S. noctilio* outbreak to date; therefore, it is unknown how effective these monitoring techniques will work if an outbreak were to occur.

Control of *S. noctilio* can be broken into two categories: silvicultural and biological control. Silvicultural control reduces the risk of a *S. noctilio* outbreak from occurring by reducing the basal area in a stand and promoting stand vigor (Haugen et al. 1990). Silvicultural control should be enforced before an outbreak occurs and strictly follow recommended thinning practices. Dodds et al. (2010) reports *S. noctilio* attacking small diameter trees within high basal area stands in the northeastern U.S. and recommends that “silvicultural treatments should be a key component of integrated plans for *S. noctilio*”. Biological control refers to the purposeful introduction of parasites and parasitoids from Eurasia and North America that attack *S. noctilio*. Biological control is typically implemented in areas where a large outbreak is occurring and *S. noctilio* populations are substantial. The United States has a well established suite of parasitoids

(some of which were used in the biocontrol program in Australia) that are hypothesized to limit the potential of a *S. noctilio* outbreak (Coyle and Gandhi 2012). Research regarding the use of *D. siricidicola* as a biocontrol agent is currently being investigated. A concern exists that release of *D. siricidicola* could have detrimental effects on native wood wasps in North America. Additionally, a strain of *D. siricidicola* has already been found to exist in North America that could hybridize with the Kamona strain and reduce the impact of the parasite (Williams et al. 2012). Pre-emptive control measures such as silvicultural control is a far superior technique because valuable timber is not lost and the costs/risks associated with a biocontrol program can be substantial.

The detection of *S. noctilio* initiated efforts by federal, state and local authorities to assess what ecological and economical impacts the wood wasp would have in North America and what control strategies could be implemented to reduce these potential impacts. Borchert (2007) rated *S. noctilio* as having a high overall risk to the United States based on cumulative risk, habitat suitability, dispersal potential and economic impact in a risk assessment report. However, this assessment is based on ecological aspects of the wood wasp's behavior in the Southern Hemisphere where it attacked non-native plantations and encountered zero forces that might have led to an Allee effect (Yemshanov et al. 2010). Currently, biological knowledge gaps (i.e. host preference, parasitoid communities, phenology, fungal associates etc.) that exist for *S. noctilio* and native siricids in North America are being investigated to increase the robustness of future assessments (Coyle and Gandhi et al 2012, Dinkins 2012, Ryan et al. 2012, Standley et al. 2012).

## Summary

*Sirex noctilio* has an extensive history as an eruptive outbreak pest in *Pinus radiata* plantations in the Southern Hemisphere and raises concerns with its introduction to North America (Berryman 1987, Hoebeke 2005, Borchert 2007). Mortality of individual pine plantations in Australia reached 90% (Morgan 1989), but were typically reported at 30-40% (Madden 1975, Neumann et al. 1987). Factors that led to extensive outbreaks in the Southern Hemisphere included: 1) high basal area non-native plantations (Morgan 1989, Haugen 1990), 2) a non-existent parasite/parasitoid complex, 3) very few larval or fungal competitors, 4) years of consecutive drought that decreased tree vigor (Rawlings 1948, Morgan 1989), and 5) a larger mucus reservoir in *S. noctilio* than other siricids (Spradberry 1977, Dodds 2010). A major outbreak of *S. noctilio* in Australia has not occurred since the 1950's and 1960's, but *S. noctilio* is still considered an economic pest in this country, causing low levels of mortality and damaging timber products (Bashford 2007).

*Sirex noctilio* was introduced into North America recently and received a risk analysis ranking of high based on potential to cause economic and ecological damage (Borchert 2007). Some studies have been conducted to better understand these risks: 1) forestry management options to reduce pine susceptibility to *S. noctilio* attack (Dodds et al. 2007, Dodds et al. 2010), 2) use of nematode trap trees for controlling *S. noctilio* in North America (Francese et al. 2009, Zylstra et al. 2010), 3) siricid parasitoid complex (Coyle and Gandhi 2012, Ryan et al. 2012, Standley et al. 2012), and 4) competition between the wood wasp and native insects and fungal associates (Ryan 2011, Ryan et al. 2012). *Sirex noctilio* is currently behaving somewhere between a secondary and a

primary pest in the northeastern United States, attacking small diameter pine trees in high basal area stands (Dodds et al. 2010). Concerns still exist that *S. noctilio* could become an eruptive outbreak pest if it invaded the Southeastern or western U.S. These areas have large tracts of poorly managed pine plantations and are more prone to drought, which has been a pre-cursor to outbreaks in the Southern Hemisphere.

The role that structure and management of forest stands have on native siricid abundance and how these dynamics affect *S. noctilio* in its native range has not been studied. Therefore, research on this topic needs to be conducted to understand what factors limit *S. noctilio* from reaching epidemic levels and how to better manage valuable timber stands so they are less susceptible to attack. The objectives of this thesis is to investigate: 1) the effects of forest stand management and structure on the abundance of native wood wasps, and by association the possible abundance of the introduced European wood wasp should it reach forests of the Southeastern U.S.A. and 2) construct a hazard map of *S. noctilio* for the Southeastern U.S. based on oviposition host preference data.

## References Cited

- Adams, A. S., M. S. Jordan, S. M. Adams, G. Suen, L. A. Goodwin, K. W. Davenport, C. R. Currie, and K. F. Raffa. 2011. Cellulose-degrading bacteria associated with the invasive wood wasp *Sirex noctilio*. *The ISME journal* 5: 1323-1331.
- Ahern, R. G., D. J. Hawthorne, and M. J. Raupp. 2009. Founder effects and phenotypic variation in *Adelges cooleyi*, an insect pest introduced to the eastern United States. *Biological Invasions* 11: 959-971.
- Allee, W. C., O. Park, A. E. Emerson, T. Park, and K. P. Schmidt. 1949. *Principles of Animal Ecology*. W. B. Saunders, Philadelphia, PA.
- Allen, C. D., M. Savage, D. A. Falk, K. F. Suckling, T. W. Swetnam, T. Schulke, P. B. Stacey, P. Morgan, M. Hoffman, and J. T. Klingel. 2002. Ecological restoration of southwestern ponderosa pine ecosystems: a broad perspective. *Ecological Applications* 12: 1418-1433.
- Allen, C. D., A. K. Macalady, H. Chenchouni, D. Bachelet, N. McDowell, M. Vennetier, T. Kitzberger, A. Rigling, D. D. Breshears, and E. Hogg. 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *Forest Ecology and Management* 259: 660-684.
- Ameden, H. A., S. B. Cash, and D. Zilberman. 2007. Border enforcement and firm response in the management of invasive species. *Journal of Agricultural and Applied Economics* 39: 35-46.
- Andersen, M. C., H. Adams, B. Hope, and M. Powell. 2004. Risk analysis for invasive species: general framework and research needs. *Risk Analysis* 24: 893-900.
- Animal Plant Health Inspection Service, U.S. Department of Agriculture. 2005. Asian longhorned beetle (*Anoplophora glabripennis*) fact sheet. January 2005 version. [http://www.aphis.gov/lpa/pubs/fact\\_fa\\_notice/fs\\_phalb.html](http://www.aphis.gov/lpa/pubs/fact_fa_notice/fs_phalb.html).
- Armstrong, S. 1995. Rare plants protect Cape's water supplies. *New Scientist* 145: 8.
- Arntzen, J., and P. Sá-Sousa. 2007. Morphological and Genetical Differentiation of Lizards (*Podarcis bocagei* and *P. hispanica*) in the Ria de Arosa Archipelago (Galicia, Spain) Resulting From Vicariance and Occasional Dispersal, pp. 365-401. *In* Renema E., ed. *Biogeography, Time, and Place: Distributions, Barriers, and Islands*. Springer, Dordrecht.
- Avery, M. L., R. M. Engeman, K. L. Keacher, J. S. Humphrey, W. E. Bruce, T. C. Mathies, and R. E. Mauldin. 2010. Cold weather and the potential range of invasive Burmese pythons. *Biological Invasions* 12: 3649-3652.



- Ayres, M. P., and M. J. Lombardero. 2000. Assessing the consequences of global change for forest disturbance from herbivores and pathogens. *Sci Total Environ* 262: 263-286.
- Bartell, S. M., and S. K. Nair. 2004. Establishment risks for invasive species. *Risk Analysis* 24: 833-845.
- Bashford, D. 2007. The current status of *S. noctilio* distribution, impact and management control development in Australia, pp. 11. *In Proceedings, International Sirex Symposium and Workshop*, pp. 1-64. *In, International Sirex Symposium and Workshop*, 9-16 May 2007, Pretoria & Pietermaritzburg, South Africa.
- Basset, Y., G. A. Samuelson, A. Allison, and S. E. Miller. 1996. How many species of host-specific insects feed on a species of tropical tree? *Biological Journal of the Linnean Society* 59: 201-216.
- Bedding, R. 1972. Biology of *Deladenus siricidicola* (Neotylenchidae) an entomophagous-mycetophagous nematode parasitic in siricid wood wasps. *Nematologica* 18: 482-493.
- Bedding, R., and R. Akhurst. 1974. Use of the nematode *Deladenus siricidicola* in the biological control of *Sirex noctilio* in Australia. *Australian Journal of Entomology* 13: 129-135.
- Bedding, R. A. 2009. Controlling the pine-killing wood wasp, *Sirex noctilio*, with nematodes. *Use of Microbes for Control and Eradication of Invasive Arthropods*: 213-235.
- Bernays, E., and M. Graham. 1988. On the evolution of host specificity in phytophagous arthropods. *Ecology*: 886-892.
- Berryman, A. 1982. Mountain pine beetle outbreaks in Rocky Mountain lodgepole pine forests. *Journal of Forestry* 80: 410-419.
- Berryman, A., and R. Stark. 1985. Assessing the risk of forest insect outbreaks. *Zeitschrift für angewandte Entomologie* 99: 199-208.
- Berryman, A. A. 1986. *Forest Insects: Principles and Practice of Population Management*, Plenum Press, New York, NY/London.
- Berryman, A. 1987. The theory and classification of outbreaks, pp. 3-30. *In P. Barbosa and J.C. Schultz (eds.), Insect Outbreaks*. Academic Press San Diego, CA.
- Bjørnstad, O. N., M. Peltonen, A. M. Liebhold, and W. Baltensweiler. 2002. Waves of larch budmoth outbreaks in the European Alps. *Science* 298: 1020-1023.

- Bolen, E. G., and W. L. Robinson. 2003. Wildlife ecology and management, Prentice Hall Upper Saddle River, NJ, USA.
- Borchert, D., G. Fowler, and L. Jackson. 2007. Organism Pest Risk Analysis: risks to the Conterminous United States Associated with the Wood wasp, *Sirex noctilio* Fabricius, and the Symbiotic Fungus, *Amylostereum areolatum*, (Fries: Fries) Boidin. [http://www.aphis.usda.gov/plant\\_health/ea/downloads/Sirexnoctilio-0307.pdf](http://www.aphis.usda.gov/plant_health/ea/downloads/Sirexnoctilio-0307.pdf).
- Brockway, D. G., K. W. Outcalt, D. J. Tomczak, and E. E. Johnson. 2005. Restoring longleaf pine forest ecosystems in the southern US. Restoration of boreal and temperate forests. CRC Press. New York, New York, USA: 501-522.
- Brown, M., T. Nebeker, and C. Honea. 1987. Thinning increases loblolly pine vigor and resistance to bark beetles. Southern Journal of Applied Forestry 11: 28-31.
- Carnegie, A., M. Matsuki, D. Haugen, B. Hurley, R. Ahumada, P. Klasmer, J. Sun, and E. Iede. 2006. Predicting the potential distribution of *Sirex noctilio* (Hymenoptera: Siricidae), a significant exotic pest of *Pinus* plantations. Annals of Forest Science 63: 119-128.
- Carnegie, A. J., R. H. Eldridge, and D. G. Waterson. 2005. History and management of *Sirex* wood wasp in pine plantations in New South Wales, Australia. New Zealand Journal of Forestry Science 35: 3-24.
- Carrasco, L., R. Baker, A. MacLeod, J. Knight, and J. Mumford. 2010. Optimal and robust control of invasive alien species spreading in homogeneous landscapes. Journal of the Royal Society Interface 7: 529-540.
- Carriere, N. 2010. Distribution patterns and general biology of woodland caribou based on collection of local and traditional knowledge in north-central Saskatchewan. M.S. thesis, University of Saskatchewan, Saskatoon, SK.
- Forest stand preference of *Sirex nigricornis*, and *Sirex noctilio* hazard in the Southeastern United States Castello, J. D., and S. A. Teale. 2011. Forest Health: an Integrated Perspective. Cambridge University Press, New York, NY.
- Chase, K.D., Schiefer, T.L., and Riggins, J.J. 2012. First incidence of *Sinoxylon indicum* and *Sinoxylon sudanicum* (Coleoptera: Bostrichidae) in Mississippi. Florida Entomologist 95: 767-770.
- Forest stand preference of *Sirex nigricornis*, and *Sirex noctilio* hazard in the Southeastern United States Chitty, D. 1967. Natural selection of self-regulatory behaviour in animal populations. Proceedings of the Ecological Society of Australia. 2:51-78.
- Cohen, A. N., and J. T. Carlton. 1998. Accelerating invasion rate in a highly invaded estuary. Science 279: 555-558.

- Conner, W. H., I. Mihalja, and J. Wolfe. 2002. Tree community structure and changes from 1987 to 1999 in three Louisiana and three South Carolina forested wetlands. *Wetlands* 22: 58-70.
- Cooperband, M. F., K. Böröczky, A. Hartness, T. H. Jones, K. E. Zylstra, J. H. Tumlinson, and V. C. Mastro. 2012. Male-produced pheromone in the European wood wasp, *Sirex noctilio*. *Journal of Chemical Ecology* 38:52-62.
- Coulson, R., and F. Stephen. 2006. Impacts of insects in forest landscapes: implications for forest health management, pp. 101-125. *In* Payne, T.D. (eds.), *Invasive Forest Insects, Introduced Forest Trees, and Altered Ecosystems: Ecological Pest Management in Global Forests of a Changing World*. Springer-Verlag, New York, NY.
- Coutts, M., and J. Dolezal. 1965. *Sirex noctilio*, its associated fungus, and some aspects of wood moisture content. *Australian Forest Research* 1:3-13.
- Coyle, D. R., and K. J. K. Gandhi. 2012. The ecology, behavior, and biological control potential of hymenopteran parasitoids of wood wasps (Hymenoptera: Siricidae) in North America. *Environmental Entomology* 41: 731-749.
- Coyle, D. R., J. A. Pfammatter, A. M. Journey, T. L. Pahs, V. J. Cervenka, and R. L. Koch. 2012. Community composition and phenology of native siricidae (Hymenoptera) attracted to semiochemicals in Minnesota. *Environmental Entomology* 41: 91-97.
- Crooks, J. A., M. E. Soulé, and O. Sandlund. 1999. Lag times in population explosions of invasive species: causes and implications. *In* Sandlund, O.T. et al. (eds.), *Invasive species and biodiversity management*. Kluwer Academic Publishers, Norwell, MA.
- Cubbage, F., P. Mac Donagh, J. Sawinski Junior, R. Rubilar, P. Donoso, A. Ferreira, V. Hoeflich, V. M. Olmos, G. Ferreira, and G. Balmelli. 2007. Timber investment returns for selected plantations and native forests in South America and the Southern United States. *New Forests* 33: 237-255.
- De Groot, P., and J. Turgeon. 1998. Insect-pine interactions. ecology and biogeography of *Pinus*. Cambridge University Press, Cambridge, UK: 354-380.
- de Groot, P., K. Nystrom, and T. Scarr. 2006. Discovery of *Sirex noctilio* (Hymenoptera: Siricidae) in Ontario, Canada. *Great Lakes Entomologist* 39: 49-53.
- Delaney, D. G., C. D. Sperling, C. S. Adams, and B. Leung. 2008. Marine invasive species: validation of citizen science and implications for national monitoring networks. *Biological Invasions* 10: 117-128.
- Dennis, B. 2002. Allee effects in stochastic populations. *Oikos* 96: 389-401.

- Dinkins, J. 2011. *Sirex noctilio* host choice and no-choice bioassays: wood wasp preferences for Southeastern U.S. Pines. M.S. Thesis, University of Georgia, Athens, GA.
- Dodds, K., P. de Groot, and D. Orwig. 2010. The impact of *Sirex noctilio* in *Pinus resinosa* and *Pinus sylvestris* stands in New York and Ontario. *Canadian Journal of Forest Research* 40: 212-223.
- Dodds, K., R. Cooke, and D. Gilmore. 2007. Silvicultural options to reduce pine susceptibility to attack by a newly detected invasive species, *Sirex noctilio*. *Northern Journal of Applied Forestry* 24: 165-167.
- Dodds, K., S. L. Garman, D.W. Ross. 2004. Landscape analysis of Douglas-fir beetle populations in northern Idaho. *Forest Ecology and Management* 231: 119-130.
- Doody, J., B. Green, R. Sims, D. Rhind, P. West, and D. Steer. 2006. Indirect impacts of invasive cane toads (*Bufo marinus*) on nest predation in pig-nosed turtles (*Carettochelys insculpta*). *Wildlife Research* 33: 349-354.
- Dukes, J. S., Pontius, J., Orwig, D., Garnas, J.R., Rodgers, V.L., Brazee, N., Cooke, B., Theoharides, K.A., Stange, E.E., Harrington, r., Ehrenfeld, J., Gurevitch, J., Lerda, M., Stinson, K., Wick, R., and Ayres, M. 2009. Responses of insect pests, pathogens, and invasive plant species to climate change in the forests of northeastern North America: What can we predict? *Canadian Journal of Forest Research* 39: 231-248.
- Dullinger, S., T. Dirnböck, and G. Grabherr. 2004. Modelling climate change-driven treeline shifts: relative effects of temperature increase, dispersal and invasibility. *Journal of Ecology* 92: 241-252.
- Erwin, T. 1982. Tropical forests: Their richness in Coleoptera and other arthropod species. *Coleopterists Bulletin* 36: 74-75.
- Evans, A. M., and T. G. Gregoire. 2007. A geographically variable model of hemlock woolly adelgid spread. *Biological Invasions* 9: 369-382.
- Fagan, W. F., M. A. Lewis, M. G. Neubert, and P. Van den Driessche. 2002. Invasion theory and biological control. *Ecology Letters* 5: 148-157.
- Filip, G. M., S. A. Fitzgerald, K. L. Chadwick, and T. A. Max. 2009. Thinning ponderosa pine affected by armillaria root disease: 40 years of growth and mortality on an infected site in central Oregon. *Western Journal of Applied Forestry* 24: 88-94.
- Finch, M. 2009. Life history and population dynamics of Eastern Sand Darter (*Ammocrypta pellucida*) in the lower Thames River, Ontario. M.S. thesis, University of Waterloo, Waterloo, ON.

- Finegan, B. 1984. Forest succession. *Nature* 312: 109-114
- Francese, J. A., K. E. Zylstra, and V. C. Mastro. 2009. Published. Creating trap trees for detection and control of *Sirex noctilio*, p. 24-25. *In* Proceedings, 20<sup>th</sup> U.S. Department of Agriculture Interagency Research Forum on Invasive Species, 13-16 January 2009, Annapolis, MD. USDA Forest Service, Newtown Square, Pennsylvania.
- Gandhi, K. J. K., and D. A. Herms. 2010. Direct and indirect effects of alien insect herbivores on ecological processes and interactions in forests of eastern North America. *Biological Invasions* 12: 389-405.
- Gaut, I. P. C. 1969. Identity of the fungal symbiont of *Sirex noctilio*. *Australian Journal of Biological Sciences* 22: 905-914.
- Gilbert, M., J. C. Grégoire, J. Freise, and W. Heitland. 2004. Long-distance dispersal and human population density allow the prediction of invasive patterns in the horse chestnut leafminer *Cameraria ohridella*. *Journal of Animal Ecology* 73: 459-468.
- Gilliam, F. S. 2007. The ecological significance of the herbaceous layer in temperate forest ecosystems. *BioScience* 57: 845-858.
- Gilmour, J. 1965. The life cycle of the fungal symbiont of *Sirex noctilio*. *New Zealand Journal of Forestry* 10: 80-89.
- Gordon, D. R. 1998. Effects of invasive, non-indigenous plant species on ecosystem processes: lessons from Florida. *Ecological Applications* 8: 975-989.
- Greenbank, D. 1957. The role of climate and dispersal in the initiation of outbreaks of the spruce budworm in New Brunswick: II. The role of dispersal. *Canadian Journal of Zoology* 35: 385-403.
- Gurevitch, J., and D. K. Padilla. 2004. Are invasive species a major cause of extinctions? *Trends in Ecology & Evolution* 19: 470-474.
- Haack, R. A. 2001. Intercepted Scolytidae (Coleoptera) at US ports of entry: 1985-2000. *Integrated Pest Management Reviews* 6: 253-282.
- Haack, R. A. 2006. Exotic bark- and wood-boring Coleoptera in the United States: recent establishments and interceptions. *Canadian Journal of Forest Research* 36: 269-288.
- Haavik, L., M. Fierke, and F. Stephen. 2010. Factors affecting suitability of *Quercus rubra* as hosts for *Enaphalodes rufulus* (Coleoptera: Cerambycidae). *Environmental Entomology* 39: 520-527.

- Hall, M. 1968. A survey of siricid attack on radiata pine in Europe. *Aust. For* 32: 155-162.
- Hartley, M. J. 2002. Rationale and methods for conserving biodiversity in plantation forests. *Forest Ecology and Management* 155: 81-95.
- Haugen, D., S. Taxon, and E. P. I. H. Risk. 1999. Record in the exotic forest pest informatoin system published by the North American forest commision. <http://src.fabinet.up.ac.za/Sirex/Sirexlit/Haugen1999-ExFor.pdf>.
- Haugen, D., R. Bedding, M. Underdown, and F. Neumann. 1990. National strategy for control of *Sirex noctilio* in Australia. *Australian Forest Grower* 13: 7.
- Heisey, R. M., and Heisey T.K. 2003. Herbicidal effects under field conditions of *Ailanthus altissima* bark extract, which contains ailanthone. *Plant and Soil* 256: 85-99.
- Hellmann, J. J., J. E. Byers, B. G. Bierwagen, and J. S. Dukes. 2008. Five potential consequences of climate change for invasive species. *Conservation Biology* 22: 534-543.
- Hirai, K. 1988. Sudden outbreaks of the armyworm, *Pseudaletia separata* Walker and its monitoring systems in Japan. *Japan Agricultural Research Quarterly* 22: 166-174.
- Hocking, H. 1967. A nematode (*Deladenus* sp.: Neotylenchidae) associated with *Rhyssa* spp.(Hymenoptera: Ichneumonidae), parasites of siricid wood wasps. *Australian Journal of Entomology* 6: 52-56.
- Hoebeke, E., D. Haugen, and R. A. Haack. 2005. *Sirex noctilio*: Discovery of a Palearctic Siricid Wood wasp in New York. *Newsletter of the Michigan Entomological Society* 50: 24-25.
- Horsley, S. B., R. P. Long, S. W. Bailey, R. A. Hallett, and P. M. Wargo. 2002. Health of eastern North American sugar maple forests and factors affecting decline. *Northern Journal of Applied Forestry* 19: 34-44.
- Hu, S. 1979. *Ailanthus*. *Arnoldia* 39: 29-50.
- Hulme, P. E. 2009. Trade, transport and trouble: managing invasive species pathways in an era of globalization. *Journal of Applied Ecology* 46: 10-18.
- Hurley, B., B. Slippers, and M. Wingfield. 2007. A comparison of control results for the alien invasive wood wasp, *Sirex noctilio*, in the Southern Hemisphere. *Agricultural and Forest Entomology* 9: 159-171.
- Huxel, G. R. 1999. Rapid displacement of native species by invasive species: effects of hybridization. *Biological Conservation* 89: 143-152.

- Iede, E.T., S.R.C. Penteado, D.C. Machado. 1989. Primeiro registro de ataque de *Sirex noctilio* em *Pinus taeda* no Brasil. EMBRAPA-CNPQ, Circular Técnica, Colombo.
- Kausrud, K., B. Økland, O. Skarpaas, J. C. Grégoire, N. Erbilgin, and N. C. Stenseth. 2012. Population dynamics in changing environments: the case of an eruptive forest pest species. *Biological Reviews* DOI: 10.1111/j.1469-185X.2011.00183.x
- Keeler, D.M. 2012. Flight period and species composition of *Sirex* (Hymenoptera: Siricidae) and associated *Deladenus* (Nematoda: Neotylenchidae) within Arkansas pine forests. M.S. thesis, University of Arkansas, Fayetteville, AR.
- King, J. M. 1966. Some aspects of the biology of the fungal symbiont of *Sirex noctilio*. *Australian Journal of Botany* 14: 25-30.
- Kirisits, T. 2004. Fungal associates of European bark beetles with special emphasis on the ophiostomatoid fungi, pp. 181-236. *In* Lieutier, F., Day, K.R., Battisti, A. Gregoire, J.-C., and Evans, H.F. *Bark and wood boring insects in living trees in Europe: a synthesis*. Kluwer Academic Publishers, Dordrecht, Netherlands.
- Kolb, T., M. Wagner, and W. W. Covington. 1994. Concepts of forest health. *Journal of Forestry* 92:10-15.
- Kovacs, K. F., R. G. Haight, D. G. McCullough, R. J. Mercader, N. W. Siegert, and A. M. Liebhold. 2010. Cost of potential emerald ash borer damage in US communities, 2009–2019. *Ecological Economics* 69: 569-578.
- Larsson, S., R. Oren, R. Waring, and J. Barrett. 1983. Attacks of mountain pine beetle as related to tree vigor of ponderosa pine. *Forest Science* 29: 395-402.
- Leal, I., B. Foord, C. Davis, P. de Groot, X. Mlonyeni, and B. Slippers. 2012. Distinguishing isolates of *Deladenus siricidicola*, a biological control agent of *Sirex noctilio*, from North America and the Southern Hemisphere using PCR–RFLP. *Canadian Journal of Forest Research* 42: 1173-1177.
- Lee, C. E. 2002. Evolutionary genetics of invasive species. *Trends in Ecology & Evolution* 17: 386-391.
- Liebhold, A. M., and P. C. Tobin. 2008. Population ecology of insect invasions and their management. *Annual Review of Entomology* 53: 387-408.
- Liu, Z., and G. Nordlander. 1994. Review of the family Ibalidae (Hymenoptera: Cynipoidea) with keys to genera and species of the World. *Entomology Scandinavian* 25: 377-392.
- Lotka, A. J. 1925. *Elements of physical biology*. Williams & Wilkins, Baltimore, MD.

- Lugo, A. E. 1997. The apparent paradox of reestablishing species richness on degraded lands with tree monocultures. *Forest Ecology and Management* 99: 9-19.
- Lux, S. A., R. S. Copeland, I. M. White, A. Manrakhan, and M. Billah. 2003. A new invasive fruit fly species from the *Bactrocera dorsalis* (Hendel) group detected in East Africa. *Insect Science and its Application* 23: 355-361.
- MacArthur, R. H., and E. O. Wilson. 1967. *The Theory of Island Biogeography*, Princeton University Press, Princeton, NJ.
- MacLellan, P., and J. Stewart. 1986. Latitudinal gradients in vegetation along a disturbed transmission line right-of-way in Manitoba. *Canadian Journal of Botany* 64: 1311-1320.
- Madden, J. 1968. Physiological aspects of host tree favourability for the wood wasp, *Sirex noctilio* F. *Proceedings of the Ecological Society of Australia* 3: 147-149.
- Madden, J. 1975. An analysis of an outbreak of the wood wasp, *Sirex noctilio* F. (Hymenoptera, Siricidae), in *Pinus radiata*. *Bulletin of Entomological Research* 65: 491-500.
- Madden, J. 1981. Egg and Larval Development in the Wood wasp, *Sirex noctilio* F. *Australian Journal of Zoology* 29: 493-506.
- Madden, J. L. 1982. Avian predation of the wood wasp, *Sirex noctilio* F., and its parasitoid complex in Tasmania. *Australian Wildlife Research* 9: 135-144.
- Madden, J. L. 1988. *Sirex* in Australasia. Dynamics of forest insect populations: patterns, causes, implications, pp. 407-429. *In* Berryman, A.A. (eds.), *Dynamics of Forest Insect Populations: Patterns, Causes, Implications*. Plenum Press, New York, NY/London.
- Martin, J. 2001. Description of an invasive new species of Neotropical aleurodicine whitefly (Hemiptera: Aleyrodidae)-a case of complete or partial misidentification? *Bulletin of Entomological Research* 91: 101-108.
- Marzluff, J. M., R. Bowman, and R. Donnelly. 2001. *Avian ecology and conservation in an urbanizing world*. Kluwer Academic Publishers, New York, NY.
- Mattson, W. J., and N. D. Addy. 1975. Phytophagous insects as regulators of forest primary production. *Science* 190: 515-522.
- Mattson, W. J., and R. A. Haack. 1987. The role of drought in outbreaks of plant-eating insects. *BioScience* 37: 110-118.



- McCarthy, S. A., and F. M. Khambaty. 1994. International dissemination of epidemic *Vibrio cholerae* by cargo ship ballast and other nonpotable waters. *Applied and Environmental Microbiology* 60: 2597-2601.
- Middlekauff, W. W. 1960. The siricid wood wasps of California. *Bulletin of the California Insect Survey* 6: 59-77.
- Miller, D., and A. Clark. 1935. *Sirex noctilio* (Hym.) and its Parasite in New Zealand. Cambridge Univ Press, New York, NY.
- Miller, J. M., and F. P. Keen. 1960. Biology and control of the western pine beetle: a summary of the first fifty years of research. USDA Miscellaneous Publication 800.
- Mitchell, R., R. H. Waring, and G. Pitman. 1983. Thinning lodgepole pine increases tree vigor and resistance to mountain pine beetle. *Forest Science* 29: 204-211.
- Mooney, H., and E. Cleland. 2001. The evolutionary impact of invasive species. *National Academy of Sciences* 98: 5446-5451.
- Morgan, F. D. 1989. Forty years of *Sirex noctilio* and *Ips grandicollis* in Australia. *New Zealand Journal of Forestry Science* 19: 198-209.
- Morris, R. F. 1963. The dynamics of epidemic spruce budworm populations. *Memoirs of the Entomological Society of Canada* 95:1-12.
- Morse, L. E., J. M. Randall, N. Benton, R. Hiebert, and S. Lu. 2004. An invasive species assessment protocol: Evaluating non-native plants for their impact on biodiversity. Version 1. NatureServe, Arlington, Virginia.
- Nebeker, T.E. 2011. Southern Pine Bark Beetle Guild, pp. 199-209. *In* R.N. Coulson and K.D. Klepzig (eds.), *Southern Pine Beetle II*. United States Department of Agriculture Forest Service, Southern Research Station, Asheville, NC.
- Neumann, F. G., J. Morey, and R. McKimm. 1987. The *Sirex* wasp in Victoria. Department of Conservation, Forest and Lands, Victoria, Australia.
- Neumann, F., and G. Minko. 1981. The *Sirex* wood wasp in Australian radiata pine plantations. *Australian Forestry* 44: 46-63.
- Nielsen, C., D. Williams, and A. Hajek. 2009. Putative source of the invasive *Sirex noctilio* fungal symbiont, *Amylostereum areolatum*, in the eastern United States and its association with native siricid wood wasps. *Mycological research* 113: 1242-1253.
- Olson, L. J. 2006. The economics of terrestrial invasive species: a review of the literature. *Agricultural and Resource Economics Review* 35: 178.

- Olson, M. G. 2012. Remote Sensing of Forest Health Trends in the Northern Green Mountains of Vermont. MS thesis, The University of Vermont Burlington, VT.
- Otuka, A., M. Matsumura, S. Sanada-Morimura, H. Takeuchi, T. Watanabe, R. Ohtsu, and H. Inoue. 2010. The 2008 overseas mass migration of the small brown planthopper, *Laodelphax striatellus*, and subsequent outbreak of rice stripe disease in western Japan. *Applied Entomology and Zoology* 45: 259-266.
- Owen, M., and M. Lewis. 2001. How predation can slow, stop or reverse a prey invasion. *Bulletin of Mathematical Biology* 63: 655-684.
- Peterson, A. T., and D. A. Vieglais. 2001. Predicting species invasions using ecological niche modeling: new approaches from bioinformatics attack a pressing problem. *BioScience* 51: 363-371.
- Pickett, S. T. A., S. Collins, and J. Armesto. 1987. Models, mechanisms and pathways of succession. *The Botanical Review* 53: 335-371.
- Pimentel, D., S. McNair, J. Janecka, J. Wightman, C. Simmonds, C. O'connell, E. Wong, L. Russel, J. Zern, and T. Aquino. 2001. Economic and environmental threats of alien plant, animal, and microbe invasions. *Agriculture, Ecosystems & Environment* 84: 1-20.
- Pimentel, D., R. Zuniga, and D. Morrison. 2005. Update on the environmental and economic costs associated with alien-invasive species in the United States. *Ecological Economics* 52: 273-288.
- Poland, T. M., and D. G. McCullough. 2006. Emerald ash borer: invasion of the urban forest and the threat to North Americas ash resource. *Journal of Forestry* 104: 118-124.
- Pozo, C., A. Luis-Martínez, J. Llorente-Bousquets, N. Salas-Suárez, A. Maya-Martínez, I. Vargas-Fernández, and A. D. Warren. 2008. Seasonality and phenology of the butterflies (Lepidoptera: Papilionoidea and Hesperioidea) of Mexico's Calakmul region. *Florida Entomologist* 91: 407-422.
- Price, T., K. A. Brownell, M. Raines, C. L. Smith, and K. J. K. Gandhi. 2011. Multiple detections of two exotic auger beetles of the genus *Sinoxylon* (Coleoptera: Bostrichidae) in Georgia, USA. *Florida Entomologist* 94: 354-355.
- Prokopy, R. J., and E. D. Owens. 1983. Visual detection of plants by herbivorous insects. *Annual Review of Entomology* 28: 337-364
- Raffa, K. F., and E. B. Smalley. 1995. Interaction of pre-attack and induced monoterpene concentrations in host conifer defense against bark beetle-fungal complexes. *Oecologia* 102: 285-295.

- Raffa, K. F., B. Aukema, B. J. Bentz, A. Carroll, N. Erbilgin, D. A. Herms, J. A. Hicke, R. W. Hofstetter, S. Katovich, and B. S. Lindgren. 2009. A literal use of forest health' safeguards against misuse and misapplication. *Journal of Forestry* 107: 276-277.
- Rawlings, G. 1952. Progress in establishment of *Ibalia leucospoides*, a parasite of *Sirex noctilio*, the horntail borer of pine. *New Zealand Science Review* 10: 107-108.
- Rawlings, G. 1955. Epidemics in *Pinus radiata* forests in New Zealand. *New Zealand Journal of Forestry* 7: 53-55.
- Rawlings, G. B. 1948. Recent observations on the *Sirex noctilio* population in *Pinus radiata* forests in New Zealand. *New Zealand Journal of Forestry* 5: 411.
- Rawlings, G. B., and N. M. Wilson. 1949. *Sirex noctilio* as a beneficial and destructive insect to *Pinus radiata* in New Zealand. *New Zealand Journal of Forestry* 6: 1-11.
- Raymond, B., A. Vanbergen, A. Watt, S. Hartley, J. Cory, and R. Hails. 2002. Escape from pupal predation as a potential cause of outbreaks of the winter moth, *Operophtera brumata*. *Oikos* 98: 219-228.
- Reaser, J. K., L. A. Meyerson, Q. Cronk, M. De Poorter, L. Eldrege, E. Green, M. Kairo, P. Latasi, R. N. Mack, and J. Mauremootoo. 2007. Ecological and socioeconomic impacts of invasive alien species in island ecosystems. *Environmental Conservation* 34: 98-111.
- Ricciardi, A., R. J. Neves, and J. B. Rasmussen. 1998. Impending extinctions of North American freshwater mussels (Unionoida) following the zebra mussel (*Dreissena polymorpha*) invasion. *Journal of Animal Ecology* 67: 613-619.
- Romme, W. H., D. H. Knight, and J. B. Yavitt. 1986. Mountain pine beetle outbreaks in the Rocky Mountains: regulators of primary productivity? *American Naturalist*: 484-494.
- Roy, H., E. Wajnberg, and E. Wilson. 2008. From biological control to invasion: the ladybird *Harmonia axyridis* as a model species. *BioControl* 53: 1-4.
- Royo, A. A., and W. P. Carson. 2006. On the formation of dense understory layers in forests worldwide: consequences and implications for forest dynamics, biodiversity, and succession. *Canadian Journal of Forest Research* 36: 1345-1362.
- Ryan, K., P. De Groot, R. Nott, S. Drabble, I. Ochoa, C. Davis, S. Smith, and J. Turgeon. 2012. Natural enemies associated with *Sirex noctilio* (Hymenoptera: Siricidae) and *S. nigricornis* in Ontario, Canada. *Environmental Entomology* 41: 289-297.

- Ryan, K. 2011. Interactions between the Wood wasp *Sirex noctilio* and Co-habiting Phloem-and Woodboring Beetles, and their Fungal Associates in southern Ontario. PHD dissertation, University of Toronto, Toronto, ON.
- Ryan, K., P. de Groot, and S. M. Smith. 2011. Evidence of interaction between *Sirex noctilio* and other species inhabiting the bole of *Pinus*. *Agricultural and Forest Entomology* 14:187-195.
- Ryan, K., P. de Groot, C. Davis, and S. Smith. 2011. Effect of two bark beetle-vectored fungi on the on-host search and oviposition behavior of the introduced wood wasp *Sirex noctilio* (Hymenoptera: Siricidae) on *Pinus sylvestris* trees and logs. *Journal of Insect Behavior*: 1-14.
- Saccheri, I., and I. Hanski. 2006. Natural selection and population dynamics. *Trends in Ecology & Evolution* 21: 341-347.
- Sakai, A. K., F. W. Allendorf, J. S. Holt, D. M. Lodge, J. Molofsky, K. A. With, S. Baughman, R. J. Cabin, J. E. Cohen, and N. C. Ellstrand. 2001. The population biology of invasive species. *Annual Review of Ecology and Systematics*: 305-332.
- Sanders, N. J., N. J. Gotelli, N. E. Heller, and D. M. Gordon. 2003. Community disassembly by an invasive species. *Proceedings of the National Academy of Sciences* 100: 2474-2477.
- Sanderson, L., J. Mclaughlin, and P. Antunes. 2012. The last great forest: a review of the status of invasive species in the North American boreal forest. *Forestry* 85: 329-340.
- Schiff, N., A. Goulet, D. Smith, C. Boudreault, A. Wilson, and B. Scheffler. 2012. Siricidae (Hymenoptera: Symphyta: Siricoidea) of the Western Hemisphere. *Canadian Journal of Arthropod Identification* 21:1-305.
- Schiff, N. M., S. A. Valley, J. R. LaBonte, and D. R. Smith. 2006. Guide to the siricid wood wasps of North America. USDA Forest Service, Forest Health Technology Enterprise Team, Morgantown, WV.
- Schlyter, F., and O. Anderbrant. 1993. Competition and niche separation between two bark beetles: existence and mechanisms. *Oikos*: 437-447.
- Schneeberger, N. F. 2007. Response to the recent find of *Sirex noctilio* in the United States, pp. 20. *In* Proceedings, International *Sirex* Symposium, 9-16 May 2007, Pretoria, South Africa.
- Singh, T., and J. Satyanarayana. 2009. Insect Outbreaks and Their Management, pp. 331-350. *In* Peshin, R., and Dhawan, A. K. (eds.), *Integrated Pest Management: Innovation-Development Process*. Springer, New York, NY.

- Six, D. L., M. Poulsen, A. K. Hansen, M. J. Wingfield, J. Roux, P. Eggleton, B. Slippers, and T. D. Paine. 2011. Anthropogenic effects on interaction outcomes: examples from insect-microbial symbioses in forest and savanna ecosystems. *Symbiosis* 53: 101-121.
- Slippers, B., T. Coutinho, B. Wingfield, and M. Wingfield. 2003. A review of the genus *Amylostereum* and its association with wood wasps. *South African Journal of Science* 99: 70-74.
- Slippers, B and M.J. Wingfield. 2012. *Sirex* Research and Management: Future Prospects, pp. 287-295. In B. Slippers, P. de Groot, and M.J. Wingfield (eds.), *The Sirex wood wasp and its fungal symbiont: research and management of a worldwide pest*. Springer, New York, NY.
- Smith, D. R., and N. M. Schiff. 2002. A review of the siricid wood wasps and their ibaliid parasitoids (Hymenoptera: Siricidae, Ibaliidae) in the eastern United States, with emphasis on the mid-Atlantic region. *Proceedings of the Entomological Society of Washington* 104: 174-194.
- Smith, D. R. 1996. Discovery and Spread of the Asian Horntail, *Eriotremex formosanus* (Matsumura)(Hymenoptera: Siricidae), in the United States. *Journal of Entomological Science* 31: 166-171.
- Smith, D. 1987. *Urocerus sah* (mocsary)(Hymenoptera: Siricidae) new to North America and key to North American species of *Urocerus*. *Proceedings of the Entomological Society of Washington* 89: 834-835.
- Smith, D. 1975. *Eriotremex formosanus* (Matsumura), an Asian horntail in North America (Hymenoptera: Siricidae). US Department of Agriculture, Cooperative Economic Insect Report 25: 851-854.
- Smith, D. M., B. C. Larson, M. J. Kelty, and P. M. S. Ashton. 1997. *The practice of silviculture: applied forest ecology*. John Wiley and Sons Inc., Hoboken, NJ.
- South, A., and R. Kenward. 2001. Mate finding, dispersal distances and population growth in invading species: a spatially explicit model. *Oikos* 95: 53-58.
- Spradbery, J. 1970. Host finding by *Rhyssa persuasoria* (L.), an ichneumonid parasite of siricid wood wasps. *Animal Behaviour* 18: 103-114.
- Spradbery, J. 1977. The oviposition biology of siricid wood wasps in Europe. *Ecological Entomology* 2: 225-230.
- Spradbery, J., and A. Kirk. 1978. Aspects of the ecology of siricid wood wasps (Hymenoptera: Siricidae) in Europe, North Africa and Turkey with special reference to the biological control of *Sirex noctilio* F. in Australia. *Bulletin of Entomological Research* 68: 341-359.

- Spradbery, J., and A. Kirk. 1981. Experimental studies on the responses of European siricid wood wasps to host trees. *Annals of Applied Biology* 98: 179-185.
- Standley, C. R., E. R. Hoebeke, D. Parry, D. C. Allen, and M. K. Fierke. 2012. Detection and Identification of Two New Native Hymenopteran Parasitoids Associated with the Exotic *Sirex noctilio* in North America. *Proceedings of the Entomological Society of Washington* 114: 238-249.
- Stanturf, J. A., C. Van Oosten, D. A. Netzer, M. D. Coleman, and C. J. Portwood. 2001. Ecology and silviculture of poplar plantations. *Poplar Culture in North America*: 153-206.
- Stephens, P., W. Sutherland, and R. Freckleton. 1999. What is the Allee effect? *Oikos*: 185-190.
- Stepien, C. A., J. E. Brown, M. E. Neilson, and M. A. Tumeo. 2005. Genetic diversity of invasive species in the Great Lakes versus their Eurasian source populations: insights for risk analysis. *Risk Analysis* 25: 1043-1060.
- Stevenson, A. P., R. M. Muzika, and R. P. Guyette. 2008. Fire scars and tree vigor following prescribed fires in Missouri Ozark upland forests, pp. 525-534. *In* Proceedings, 16th Central Hardwoods Forest Conference, 7-10 April 2008, Newton Square, PA, U.S.D.A., Forest Service, Northern Research Station.
- Stillwell, M. 1966. Wood wasps (Siricidae) in conifers and the associated fungus, *Stereum chailletii*, in eastern Canada. *Forest Science* 12: 121-128.
- Stohlgren, T. J., and J. L. Schnase. 2006. Risk analysis for biological hazards: what we need to know about invasive species. *Risk Analysis* 26: 163-173.
- Strayer, D. L., V. T. Eviner, J. M. Jeschke, and M. L. Pace. 2006. Understanding the long-term effects of species invasions. *Trends in Ecology & Evolution* 21: 645-651.
- Swanson, M. E., J. F. Franklin, R. L. Beschta, C. M. Crisafulli, D. A. DellaSala, R. L. Hutto, D. B. Lindenmayer, and F. J. Swanson. 2010. The forgotten stage of forest succession: early-successional ecosystems on forest sites. *Frontiers in Ecology and the Environment* 9: 117-125.
- Tabata, M., and Y. Abe. 1995. *Cerreana unicolor* isolated from the mycangia of a horntail, *Tremex longicollis*, in Kochi Prefecture, Japan. *Mycoscience* 36: 447-450.
- Talbot, P. 1977. The *Sirex-Amylostereum-Pinus* association. *Annual Review of Phytopathology* 15: 41-54.

- Taylor, K. 1967. Parasitism of *Sirex noctilio* F. by *Schlettererius cinctipes* (Cresson)(Hymenoptera: Stephanidae). Australian Journal of Entomology 6: 13-19.
- Taylor, K. 1978. Evaluation of the insect parasitoids of *Sirex noctilio* (Hymenoptera: Siricidae) in Tasmania. Oecologia 32: 1-10.
- Taylor, K. 1981. The *Sirex* wood wasp: ecology and control of an introduced forest insect. The Ecology of Pests, CSIRO, Australia: 231–248.
- Thomsen, I., and S. Harding. 2011. Fungal symbionts of siricid wood wasps: isolation techniques and identification. Forest Pathology 41: 325-333.
- Tobin, P. C., S. L. Whitmire, D. M. Johnson, O. N. Bjørnstad, and A. M. Liebhold. 2007. Invasion speed is affected by geographical variation in the strength of Allee effects. Ecology Letters 10: 36-43.
- Tribe, G., and J. Cillie. 2004. The spread of *Sirex noctilio* Fabricius (Hymenoptera: Siricidae) in South African pine plantations and the introduction and establishment of its biological control agents. African entomology 12: 9-17.
- Tsutsui, N. D., A. V. Suarez, D. A. Holway, and T. J. Case. 2000. Reduced genetic variation and the success of an invasive species. Proceedings of the National Academy of Sciences 97: 5948.
- Ulyshen, M. D., and J. L. Hanula. 2010. Host-use Patterns of *Eriotremex formosanus* (Hymenoptera: Siricidae) in South Carolina, USA. Entomological News 121: 97-101.
- Van der Maarel, E. 2005. Vegetation ecology—an overview. Vegetation ecology: 1-51.
- Veblen, T. T. 1992. 4 Regeneration dynamics. Plant succession: Theory and prediction 11: 152.
- Voelker, S. L., R. M. Muzika, and R. P. Guyette. 2008. Individual tree and stand level influences on the growth, vigor, and decline of red oaks in the Ozarks. Forest Science 54: 8-20.
- Volterra, V. 1926. Fluctuations in the abundance of a species considered mathematically. Nature 118: 558-560.
- Wargo, P. M., R. Minocha, B. L. Wong, R. P. Long, S. B. Horsley, and T. J. Hall. 2002. Measuring changes in stress and vitality indicators in limed sugar maple on the Allegheny Plateau in north-central Pennsylvania. Canadian Journal of Forest Research 32: 629-641.

- Waring, R., and G. Pitman. 1985. Modifying lodgepole pine stands to change susceptibility to mountain pine beetle attack. *Ecology*: 889-897.
- Waring, R., W. Thies, and D. Muscato. 1980. Stem growth per unit of leaf area: a measure of tree vigor. *Forest Science* 26: 112-117.
- Warriner, M. D. 2008. First Record of the Asian Horntail, *Eriotremex formosanus* (Hymenoptera: Siricidae), in Arkansas, USA. *Entomological News* 119: 212-213.
- Webster, C. R., M. A. Jenkins, and S. Jose. 2006. Woody invaders and the challenges they pose to forest ecosystems in the eastern United States. *Journal of Forestry* 104: 366-374.
- Wilcove, D. S., D. Rothstein, J. Dubow, A. Phillips, and E. Losos. 1998. Quantifying threats to imperiled species in the United States. *BioScience* 48: 607-615.
- Williams, M.S., M.T. Williams, and H.T. Mowrer. 2001. A boundary reconstruction method for circular fixed-area plots in environmental survey. *Journal of Agricultural, Biological, and Environmental Statistics* 6:479-494.
- Williams, M. C., and G. M. Wardle. 2007. *Pinus radiata* invasion in Australia: identifying key knowledge gaps and research directions. *Austral Ecology* 32: 721-739.
- Williams, D.W., Zylstra, K.E., and Mastro, V.C. 2012. Ecological considerations in using *Deladenus* (Beddingia) *siricidicola* for the biological control of *Sirex noctilio* in North America, pp. 135-148. *In* B. Slippers, P. de Groot, and M.J. Wingfield (eds.), *The Sirex wood wasp and its fungal symbiont: research and management of a worldwide invasive pest*. Springer, New York, NY.
- Wilson, E. O. 2002. *The future of life*. Knopf, New York, NY.
- Wilson, E. O., and W. H. Bossert. 1971. *A primer of population biology*. Sinauer Associates, Sunderland, MA.
- Wu, Z. L., H. M. Liu, and L. Y. Liu. 2001. Rubber cultivation and sustainable development in Xishuangbanna, China. *The International Journal of Sustainable Development & World Ecology* 8: 337-345.
- Yemshanov, D., F. Koch, Y. Ben Haim, and W. Smith. 2010. Robustness of risk maps and survey networks to knowledge gaps about a new invasive pest. *Risk Analysis* 30: 261-276.
- Yemshanov, D., F. Koch, D. McKenney, M. Downing, and F. Sapio. 2009. Mapping invasive species risks with stochastic models: A cross border United States Canada application for *Sirex noctilio* Fabricius. *Risk Analysis* 29: 868-884.



Zylstra, K. E., K. J. Dodds, J. A. Francese, and V. Mastro. 2010. *Sirex noctilio* in North America: the effect of stem injection timing on the attractiveness and suitability of trap trees. *Agricultural and Forest Entomology* 12: 243-250.

## CHAPTER III

# NATIVE WOOD WASP (HYMENOPTERA: SIRICIDAE) ABUNDANCE AND *SIREX NOCTILIO* FABRICIUS PREVENTION IN THE SOUTHEASTERN UNITED STATES

### **Abstract**

In 2005, a non-native woodboring pest, *Sirex noctilio* F., was found established in North America. *Sirex noctilio* has an extensive history as an economically important pest in pine plantations throughout the Southern Hemisphere. The United States has a rich fauna of native Siricidae and associated parasitoids, but they are rarely studied due to their status as economically inconsequential organisms. With the introduction of *S. noctilio*, interest in the ecology of native siricid populations has increased. A study was conducted in Fall 2011 to investigate the effects of forest stand characteristics and stand types on native Siricidae abundance, and the flight phenology of Siricidae. A newly developed method was used to collect wood wasps; the pairing of Lindgren funnels with fresh pine material. A total of 609 native Siricidae were captured, consisting of 608 *Sirex nigricornis* F. and 1 *Urocerus cressoni* Norton. The flight period of Siricidae captured in our study was similar to that of studies from Arkansas, (October - December) but differed other studies across the U.S (June or July - October). Unthinned pine plantations had significantly more Siricidae than thinned pine plantations, mixed pine-hardwood and old growth forests. It appears that proper silvicultural management of pine plantations may

reduce stand hazard to native Siricidae in the southeastern U.S. as it does to *S. noctilio* in the Southern Hemisphere. We propose that silvicultural models used for the southern pine beetle be implemented and encouraged for prevention of infestations from *S. noctilio* and other pine pests.

### **Introduction**

Siricids, commonly called wood wasps or horntails (Hymenoptera: Siricidae), are xylophagous insects that help decompose woody material in temperate forest ecosystems (Hall 1968, Spradberry & Kirk 1978). Worldwide there are 122 species of Siricidae in 10 extant genera; the Americas contain 33 species in 7 genera (Schiff et al. 2012). The family Siricidae is composed of two subfamilies. The subfamily Siricinae oviposit into gymnosperms and harbor fungus in the genus *Amylostereum*, whereas the subfamily Tremicinae utilize angiosperms as hosts and harbor *Cerrena* fungus (Tabata & Abe 1995, Schiff et al. 2006). Siricids are rarely studied in their natural habitat because of their economically inconsequential status. However, global interest in Siricidae have increased as the European woodwasp, *Sirex noctilio* Fabricius, has been introduced throughout the Southern Hemisphere and most recently in North America (Hoebeke et al. 2005, Carnegie et al. 2006).

*Sirex noctilio* was detected in Oswego County, New York (2004) and the following summer in Ontario, Canada (2005) (Hoebeke et al. 2005, de Groot 2006). *Sirex noctilio* has caused significant damage (up to 90% mortality) to pine plantations throughout the Southern Hemisphere, travelling via solid wood packing materials (Neumann et al. 1987, Morgan 1989, Tribe & Cillie 2004). In North America, *Sirex noctilio* is not currently a serious pest (Dodds et al. 2010). However, *S. noctilio* is

predicted to cause economical loss if it becomes established in Southeastern and northwestern North America (Haugen 1990, Hoebeke et al. 2005, Yemshanov et al. 2009, Ryan et al. 2012). One way of improving our predictions of how *S. noctilio* will behave in North America is to better understand the ecology and biology of the native siricid fauna and what factors prevent these populations from reaching outbreak status.

The introduction of *S. noctilio* has spurred a great deal of research in North America concerning taxonomy (Schiff et al. 2006, Schiff et al. 2012), the native siricid parasitoid complex (Eager et al. 2011, Coyle & Gandhi 2012, Standley et al. 2012), silvicultural control efforts (Dodds et al. 2007, Dodds et al. 2010, Zylstra et al. 2010) and the composition of native Siricidae and woodboring insect competitors in North America (Ryan et al. 2011, Coyle et al. 2012, Ryan et al. 2012, Dodds et al. 2012). The effect of management schemes on *S. noctilio* or native Siricidae abundance has yet to be determined in North America. Because *S. noctilio* is not currently present in the Southeast, it is unknown how stand characteristics and management practices might impact its distribution, abundance, and behavior. However, *S. nigricornis* F. is a species whose ecosystem function is very similar to that of *S. noctilio* in its native range. By understanding how *S. nigricornis* populations are affected by management practices, better inferences can be made on how *S. noctilio* might behave if introduced into the Southeastern U.S. forests.

The objectives of this study were three-fold: 1) to examine siricid flight activity in northern Mississippi and compare results to other studies performed throughout the United States (Coyle et al. 2012, Keeler 2012, Schiff et al. 2012); 2) to investigate what affect forest stand type and management practice have on native Siricidae abundance; and

3) to determine what forest stand characteristics (i.e. tree diameter, age and height) are correlated with native Siricidae abundance.

## **Methods**

### **Forest Stand Types**

This study was conducted in four forest stand types: unthinned pine plantation, thinned pine plantation, mixed hardwood-pine forest, and old growth forest (Table 3.1). The age of each forest was determined from known planting dates for each forest stand except for the mixed stand at Longview Road, which was unknown (estimated to be 45 years of age in analysis). Sixteen stands (each stand type having four locations) were selected in northern Mississippi (Figure 3.1) based on the definitions in Table 3.1. Pine plantations consisted of *Pinus taeda* L. (loblolly pine), which was also the dominant pine species found in mixed and old growth forests. *Pinus echinata* Mill. (shortleaf pine) was sparsely found throughout mixed and old growth forests.

### **Insect Trapping**

Three Lindgren<sup>®</sup> funnel traps with wet collection cups (Lindgren 1983) (Synergy Semiochemical Corp., Burnaby, BC, Canada) were dispersed at each of the 16 sites (48 traps total). Each trap location was arbitrarily selected within the stand and traps were hung at breast height ( $\approx 1.7$  m). Traps were separated by a distance of at least 150 m. Traps were placed on the week of 28 September 2011 and removed the week of 21 December 2011. Collection cups contained a mixture of 50/50 Prestone<sup>®</sup> Low Tox<sup>®</sup> Antifreeze/Coolant and water. A recent study found that standard *Sirex* lures (comprised of a 70:30  $\alpha/\beta$ -pinene blend) were relatively ineffective attractants for native Siricidae in

the Southeastern U.S. (Barnes 2012), thus a recently developed trapping method was utilized for this study. A polypropylene mesh bag (55.9 cm X 45.7 cm) (U-Line product # S-14435) was filled with small diameter (> 7.62 cm) pine slash partially stripped of its bark (using a Stihl® FS 550 clearing saw) and hung parallel to the funnel trap. This will be referred to as "pine lure" for the remainder of the study. Insects were collected weekly, and pine lures were replaced bi-weekly at every trap.

Weekly samples were stored in Whirl-Pak® (SKS Science, Watervliet, NY ) bags and placed in a -20°C freezer. Captured Siricidae with a Leica® MZ 12.5 microscope and identified using Schiff et al. (2006), with the only exception being that *Sirex edwardsii* Brulle was treated as *Sirex nigricornis* Fabricius according to recent changes in siricid taxonomy (Schiff et al. 2012). Voucher specimens from the study were deposited into the Entomological Museum at Mississippi State University.

### **Forest Stand Measurements**

Fixed-radius circular plots (1/25 or 1/50 ha based on total acreage) were conducted at all 16 locations and geographically referenced using a Garmin GPSmap® 60CSx (Garmin, Olathe, Kansas) (Avery and Burkhart 2002). Diameter at breast height (cm) (dbh), height of two dominant or co-dominant pines (to the nearest 0.1 m), and species were recorded for all trees greater than 7.62 cm (3 in.) dbh within plots. A TruPulse® 200 rangefinder (Laser Technology Inc., Centennial, CO) was used to record tree heights. Number of standing dead pines was also recorded within plots.

### **Data Analyses: Siricid Capture Analyses**

Total number of *S. nigricornis* captured per week in each trap within each stand type was analyzed using a generalized mixed linear model (PROC GLIMMIX, SAS Institute 2008). This procedure was used to determine the effect of treatment (stand type), week, and week x week interaction on *S. nigricornis* capture. A high proportion of traps captured zero *S. nigricornis* throughout the study, therefore the response distribution was set to POISSON and the link function was set to LOG. Degrees of freedom were calculated using the Kenward- Roger method for fixed effects on all variables (Kenward and Roger 1997). Least square means (lsmeans) calculated from the GLIMMIX model were used to compare treatment means [T grouping for lsmeans (Alpha = 0.05)].

### **Data Analyses: Forest Stand Characteristic Analyses**

Linear and multiple regression analyses were performed using InStat 3 (Graphpad Software, Inc., San Diego, CA) to determine the relationship between forest stand characteristics and numbers of captured Siricidae. The fixed effect model included the mean number of wood wasps caught per week. Stand variables analyzed were: 1) mean tree height, 2) pine basal area (PBA), 3) total basal area (TBA), 4) age of stand, 5) mean number of dead pines, and 6) mean pine dbh. TBA encompasses PBA and were modeled separately.

## **Results**

### **Siricidae Abundance, Composition, and Flight Activity**

A total of 609 wood wasps were captured throughout the 12 week study, of which all were female (Figure 3.3). Collected species included 608 *Sirex nigricornis* and 1

*Urocerus cressoni* Norton. No exotic Siricidae (i.e. *Sirex noctilio* or *Eriotremex formosanus* Matsumura) were captured in this survey. One siricid parasitoid, *Ibalia leucospoides ensiger* Norton (Hymenoptera: Ibalidae), was captured in traps.

Significantly more ( $F=7.34$ ;  $df = 3, 139.7$ ;  $P < 0.0001$ ) wood wasps were captured each week in unthinned pine plantations ( $1.78 \pm 0.29$ ) (Mean  $\pm$ SE) than thinned pine plantations ( $0.95 \pm 0.19$ ), mixed pine-hardwood forests ( $0.81 \pm 0.15$ ), or old growth forests ( $0.68 \pm 0.14$ ). There was no significant difference in wood wasps captured between thinned pine plantations, mixed pine-hardwood forests, or old growth forests (Figure 3.2).

*Sirex nigricornis* was captured from 5 October – 17 December, 2011. Peak flight period (Figure 3.3) occurred during weeks 5, 6, and 7 (late October through mid November) with 170, 157, and 108 wood wasps caught (71% of total wood wasps captured) between all forest stand types, respectively. A single specimen of *Urocerus cressoni* was collected during the week of 15 October – 22 October at the Holly Springs National Forest unthinned pine plantation. A single specimen of *I. l. ensiger*, a siricid parasitoid, was collected during the week of 29 October – 5 November at the Holly Springs National Forest mixed stand. There was no evidence that stand type had an effect on siricid flight period ( $P < 0.34$ ).

### **Forest Stand Characteristics**

Forest stand composition was calculated from all trees measured within fixed-radius plots (Table 3.2). The mixed stand at the Jess Lyons road location had the lowest coniferous composition (10%). The thinned stand at the St. Mark road location had the greatest coniferous composition (96%). PBA was highest in unthinned plantations, with



all locations  $> 23.0 \text{ m}^2/\text{ha}$ . Two of the old growth stands had moderately high PBA ( $19.4 \text{ m}^2/\text{ha}$  and  $24.4 \text{ m}^2/\text{ha}$ ), however, this level can be attributed to larger (greater DBH) pine trees as opposed to total number of trees within the stand (Table 3.2).

Multiple and linear regression analysis for all 16 stands provided no significant correlations between the number of mean wood wasps captured and forest stand characteristics (Table 3.3). Among the 16 stands, the only significant correlation between stand variables was the interaction between the mean number of dead pines and pine basal area ( $F = 14.277$ ;  $df = 15$ ;  $P = 0.002$ ). This was expected since lower tree vigor is associated with dense stocking.

All sites in the Holly Springs National Forest (HSNF) had greater total woodwasp capture across stand types than all other stands (Table 3.2). The HSNF is more northerly than the rest of the stands and it is possible that latitudinal, climatic, or regional differences may have had an effect on woodwasp abundance. Therefore, the HSNF stands were separated from the other 12 stands and re-analyzed (Table 3.3). Since there were only 4 locations in the HSNF, models between mean wood wasps captured and all other variables could not be analyzed together.

## Discussion

This experiment with *Sirex nigricornis* was conducted to determine its flight activity, composition, and abundance within various forest stand types. The overall goal of this study was to make inferences about how *S. noctilio* might behave, were it to arrive in the Southeastern U.S. The following section is a discussion of our findings and what preemptive management strategies should be considered to reduce stand susceptibility for *S. noctilio*.

## **Flight Activity**

Peak flight period for *S. nigricornis* in northeastern Mississippi occurred from late October - mid November; however, wood wasps were captured from 5 October – 17 December. Our findings were consistent with data reported from Arkansas (Keeler 2012) and Georgia (Barnes 2012) but differs from other prior studies. Coyle et al. (2012) reported that *S. nigricornis* flight activity occurred between late June to late-October in Minnesota. Schiff et al. (2012) report the flight activity of *S. nigricornis* ranges from late July to early October based on 893 field-collected specimens from across the eastern U.S. The flight activity differences between these studies may be due to differences in latitude, but also may be due to a lack of complete information synthesis and/or trapping period of siricid wood wasps (e.g. we may not have installed traps early enough in the season or other studies may have removed traps too soon).

Currently, the flight period of *S. noctilio* in the northeastern U.S. is from early July through September (Zylstra et al. 2010). The effect of latitudinal climatic variability in North America on *S. noctilio* flight activity or development in the southern and western portions of the continent are unknown. In South Africa, where seasons are reversed, *S. noctilio* flight phenology ranges from mid-November through April and peaks in March, in agreement with findings from Australia (Tribe and Cillie 2004). Monitoring the flight activity of *S. noctilio* is important to know when to employ management techniques such as trap trees (Zylstra et al. 2010) and to understand which competitive interactions may be occurring (Ryan et al. 2011).

## **Trapping Method**

The use of pine lures was successful in attracting *Sirex nigricornis* females in northern Mississippi. A total of 608 *S. nigricornis* females were captured using this technique in the fall of 2011. Apart from rearing specimens from infested host material (Barnes 2012), collecting methods for Siricidae are poor, especially for male specimens (Smith and Schiff 2002, Schiff et al. 2012). Pine lures may be a tool that could be used to monitor siricid populations and potential presence of the invasive *S. noctilio*. This technique is not recommended for large scale monitoring programs due to the investment of labor, time, and resources it takes to make and maintain multiple pine lures. In fact, the costs were so high that we were only able to complete only one season of trapping. Pairing synthetic lures with multiple funnel traps remains to be the most time and cost effective method for collecting Siricidae. Coyle et al. (2012) was able to catch 609 Siricidae over a three year period in Minnesota using the standard *Sirex* lure. A male-produced pheromone has recently been detected that attracts both males and females, which may have applications in future field studies (Cooperband et al. 2012).

## **Forest Stand Characteristics and Management**

Similar to *S. noctilio* in the Southern Hemisphere, the abundance of *S. nigricornis* was greater in densely stocked pine plantations. Pine basal area in all unthinned stands exceed the recommended stocking density for *Pinus taeda* (<23.0 m<sup>2</sup>/ha), and generally (in 3 of 4 stands) contained higher quantities of standing dead pines (Burkhart et al. 1986). All thinned stands were > 75% pine, and all unthinned stands were > 40% pine. Two of the unthinned stands contained numerous small DBH (7.62 cm to 10.16 cm) for deciduous trees (e.g. *Liquidambar styraciflua* and *Carya* spp.) that greatly decreased pine

basal area. All old growth and mixed stands were composed of  $\leq 40\%$  pine and a mean pine DBH  $> 30$  cm. Dodds et al. (2010) found that *S. noctilio* abundance was scarce in *P. resinosa* Ait. stands with a mean DBH  $\geq 30$  cm in New York and Ontario. Stand composition and stocking density influenced the abundance of *S. nigricornis* in a manner similar to that reported for *S. noctilio*.

Although not measured in this study, we observed that Siricidae capture may have been influenced by adjacent stands and pine slash left on the forest floor after pre-commercial thinning. Composition of adjacent forest stands has been correlated with severity of attack and abundance of pest species in other studies (i.e. Kouki et al. 1997, Jactel et al. 2002). In this study, we observed that funnel traps in mixed and old growth stands that were closer to adjacent stands, consisting of pine monocultures, had increased captures of *S. nigricornis*. Perkins and Matlack (2002) suggest that human mediated landscape transformation has created larger and more continuous pathways for pests to spread and recommend that plantations be separated with non-host barriers. It was also noted that high volumes of pine slash, left after a pre-commercial thinning, comprised much of the forest floor in the thinned stand at Holly Springs National Forest, this may be one reason why *S. nigricornis* abundance was three times higher than other thinned stands. Siricids are xylophagous; so if large volumes of slash remain after a thinning treatment, conditions may be conducive to population increases.

Management of pine plantations should focus on removing stressed trees, proper planting sites, and reducing basal area to recommended stocking (i.e. *P. taeda*  $< 23.0$  m<sup>2</sup>/ha), therefore increasing stand vigor and reducing *S. noctilio* hazard (Burkhart et al. 1986, Dodds et al. 2007). Fortunately, a silvicultural system that is widely practiced and

understood is already in place for the southern pine beetle (*Dendroctonus frontalis* Zimmerman) and may serve as a surrogate management plan for *S. noctilio*.

The southern pine beetle is a cyclical outbreak insect that has devastated pine plantations across the Southeastern U.S. Southern pine beetle outbreaks, like *S. noctilio*, are associated with high stand density and reduced radial growth, both characteristics associated with poorly managed plantations (Coulson et al. 1974, Morgan 1989, Fettig et al. 2007). Silvicultural guidelines for reducing southern pine beetle hazard recommend thinning stands at a basal area between 16.1 m<sup>2</sup>/ha (70 ft<sup>2</sup>/acre) and 23.0 m<sup>2</sup>/ha (100 ft<sup>2</sup>/acre) in loblolly pine plantations (Brown et al. 1987, Belanger et al. 1993). Lower stand basal area increases individual tree vigor by reducing competition for resources (i.e. sunlight, water, nutrients, etc.). Preventing off-site planting, and proper burning practices also reduce susceptibility of stands to insect attack (Guldin 2011). Guidelines for reducing SPB hazard are very similar to recommendations for *S. noctilio* management for northeastern U.S. pine plantations and plantations across the Southern Hemisphere (Haugen et al. 1990, Dodds et al. 2007). Land managers, large and small, in the southeastern U.S. should consider using silvicultural practices associated with southern pine beetle prevention to reduce *S. noctilio* hazard and susceptibility in pine plantations.

### Summary

*Sirex nigricornis* is an abundant woodwasp in Mississippi forests that are attracted to freshly killed pine trees. In northern Mississippi and Arkansas, *S. nigricornis* adults are active from early October to mid-December. *Sirex nigricornis* abundance was higher in unthinned pine plantations with basal areas > 23.0 m<sup>2</sup>/ha. We recommend that the current southern pine beetle management system be used as a surrogate system if *S. noctilio* were

to arrive in the southeastern U.S. We encourage land owners to utilize this pre-existing system to reduce stand susceptibility for both the southern pine beetle, *S. noctilio*, and other pine plantation pest's.

Table 3.1 Definitions of treatments used in study

Forest Stand Type	Definition
Unthinned loblolly pine plantation	A stand that is at least 10 years old and has not received any silvicultural thinning.
Thinned loblolly pine plantation	A stand that is at least 10 years old and has received at least one silvicultural thinning.
Old Growth (mature) forest	Mature forests contain these structural components: supercanopy trees, canopy trees, understory trees, shrubs and saplings, decaying wood, ground cover, organic litter, pits and mounds, cavity trees, and snags. Stands will be greater than 60 years of age.
Mixed pine-hardwood forest	Pine-hardwood stands contain 30-50% hardwood and 51-69% pine in the main canopy. Stands will be no more than 50 years old.

Table 3.2 Forest stand characteristics

Stand type	Stand name	# Sirecids caught	Stand age	$\mu$ pine DBH (cm)	% pine / % hardwood	PBA (m <sup>2</sup> )	TBA (m <sup>2</sup> )	$\mu$ tree height (m)	$\mu$ # Dead Pine
Thinned	St. Mark Road	13	20	20.38	96% / 4%	11.62	12.06	19.55	0.33
Thinned	McGee Road	10	20	22.68	97% / 3%	11.82	12.14	19.57	0.43
Thinned	Dickerson Road	28	21	23.40	83% / 17%	22.70	23.57	17.91	0.95
Thinned	Holly Springs Thinned	86	25	27.07	76% / 24%	15.80	18.34	20.01	2.44
Unthinned	Holly Springs Unthinned	119	18	22.94	82% / 18%	31.02	32.42	18.07	0.22
Unthinned	Virginia Pine	30	11	17.31	88% / 12%	40.93	42.86	16.16	7.17
Unthinned	Storage Units	62	11	25.32	42% / 58%	30.77	40.89	19.18	2.33
Unthinned	Dummy Line Road	46	21	17.98	62% / 38%	29.20	34.95	19.15	4
Mature	Dorman Lake Road	8	84	53.06	22% / 78%	24.40	36.32	38.90	0.13
Mature	Holly Springs Mature	63	129	41.70	9% / 91%	4.66	27.34	28.39	0.05
Mature	Ennis Road	12	66	38.91	40% / 60%	19.40	28.84	31.51	0
Mature	B-ville-L-ville Road	15	68	54.58	19% / 81%	8.29	27.97	34.04	0
Mixed	Noxubee River	14	50	46.84	25% / 75%	8.61	11.99	36.08	0.57
Mixed	Holly Springs Mixed	56	51	35.03	23% / 77%	12.76	28.70	27.25	0.33
Mixed	Longview Road	42	Unknown	32.96	34% / 66%	16.019	30.18	31.06	0
Mixed	Jess Lyons Road	5	41	33.88	10% / 90%	7.20	22.79	29.86	0.23

$\mu$  = mean of the characteristic

Note: Measurements recorded Fall, 2011



Table 3.3 Regression analysis results showing affect of variables on wood wasp capture

Sites	Variable(s)	F	d.f.	P	R <sup>2</sup>
All stands	PBA, DBH, age, mean height, mean dead pine	1.5363	10	0.259	0.36
All stands	TBA, DBH, age, mean height, mean dead pine	1.7054	10	0.219	0.38
All stands	PBA	1.508	15	0.24	0.1
All stands	TBA	1.18	15	0.296	0.08
All stands	DBH	1.7	15	0.213	0.11
All stands	Age	0.3228	15	0.579	0.02
All stands	Mean height	3.355	15	0.088	0.19
All stands	Mean dead pine	0.2121	15	0.652	0.01
Excluding Holly Springs	PBA, DBH, age, mean height, mean dead pine	3.2803	6	0.082	0.65
Excluding Holly Springs	TBA, DBH, age, mean height, mean dead pine	4.5078	6	<b>0.047</b>	0.79
Excluding Holly Springs	PBA	5.875	11	<b>0.036</b>	0.37
Excluding Holly Springs	TBA	5.218	11	<b>0.046</b>	0.34
Excluding Holly Springs	DBH	2.654	11	0.134	0.21
Excluding Holly Springs	Age	3.848	11	0.078	0.28
Excluding Holly Springs	Mean height	2.737	11	0.129	0.21
Excluding Holly Springs	Mean dead pine	2.904	11	0.119	0.23
Holly Springs only	PBA	9.684	3	0.09	0.83
Holly Springs only	TBA	0.01058	3	0.776	0.05
Holly Springs only	DBH	6.264	3	0.129	0.76
Holly Springs only	Age	1.415	3	0.356	0.41
Holly Springs only	Mean height	11.755	3	0.076	0.86
Holly Springs only	Mean dead pine	0.02872	3	0.881	0.01

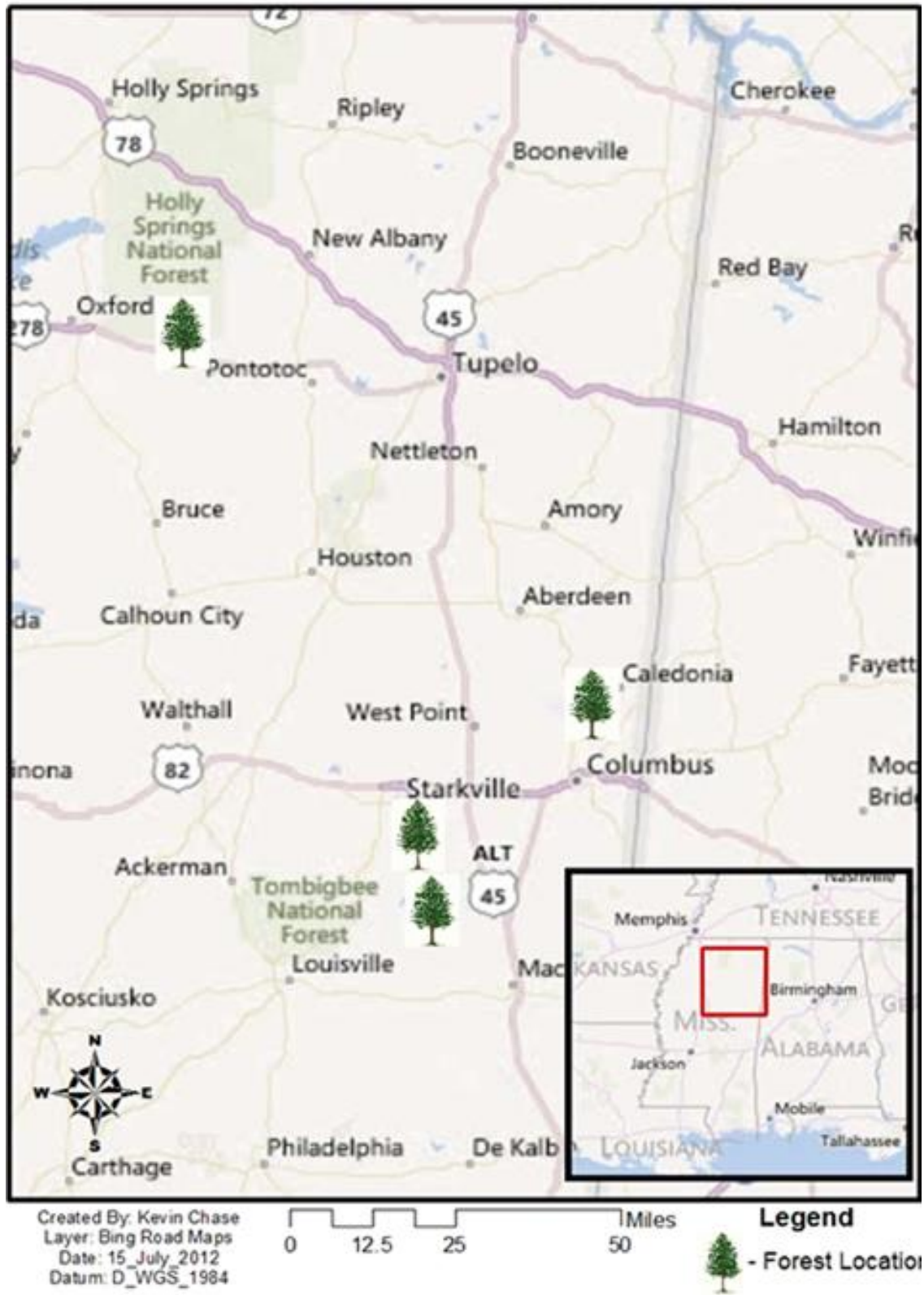


Figure 3.1 Map displaying locations of Siricidae trapping, Fall 2011

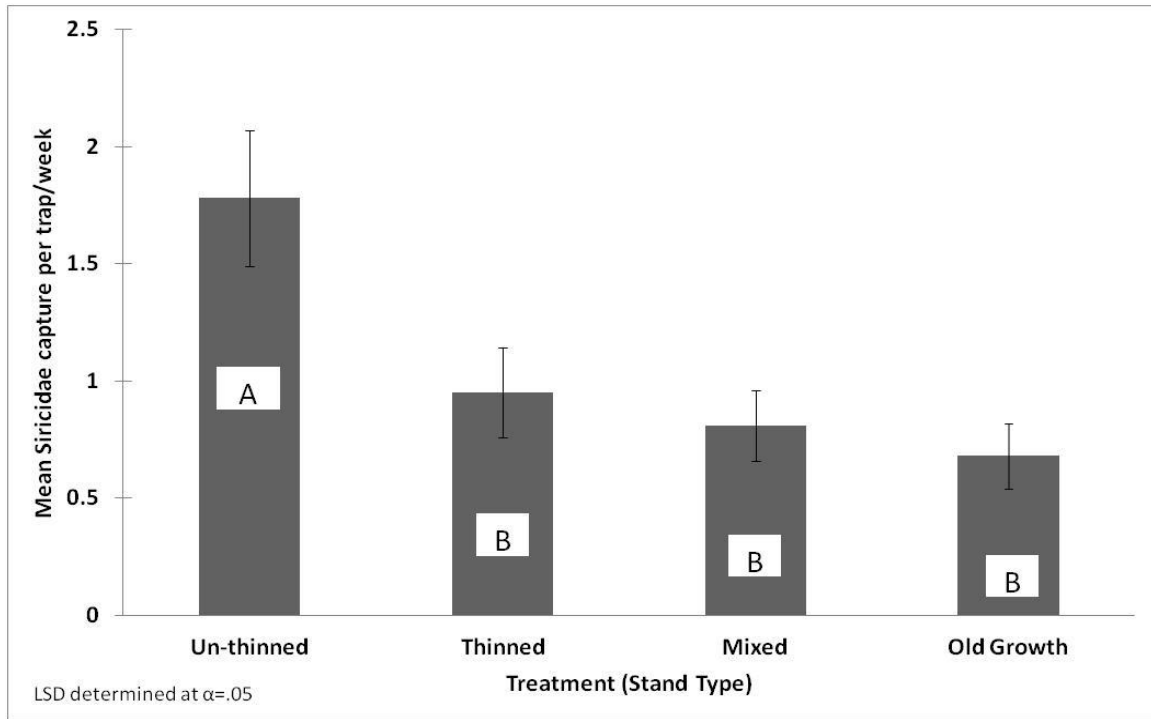


Figure 3.2 Mean Sirex nigricornis Capture

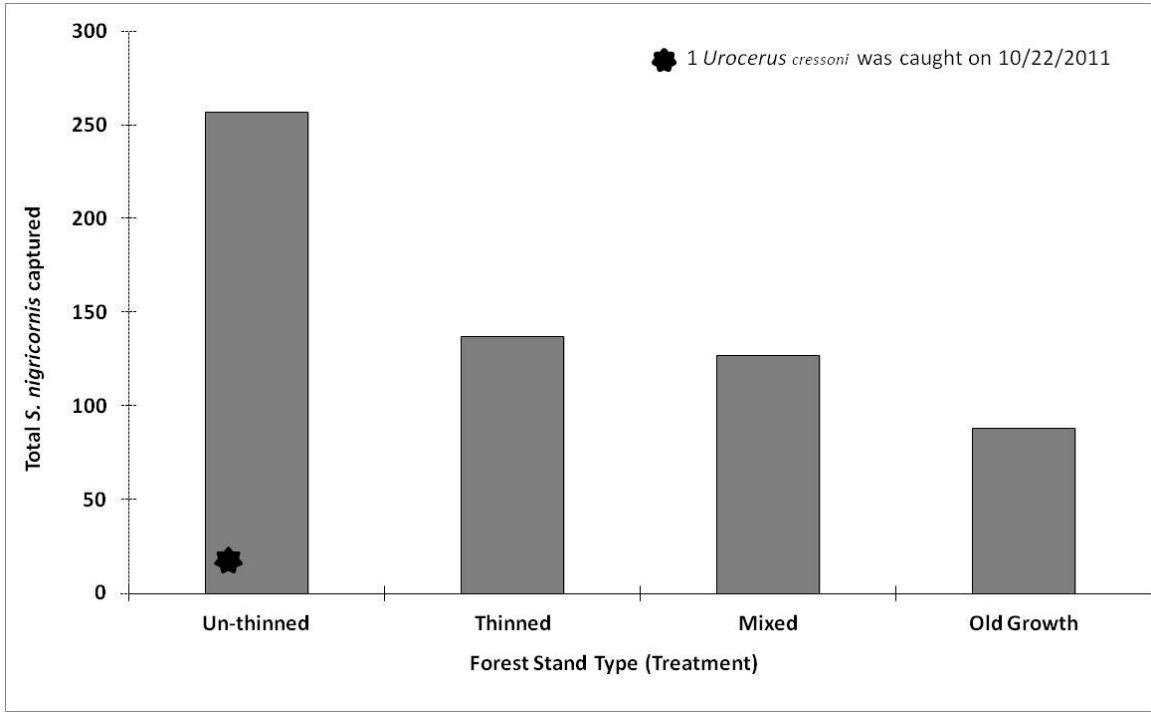


Figure 3.3 Total *Sirex nigricornis* captured among treatments

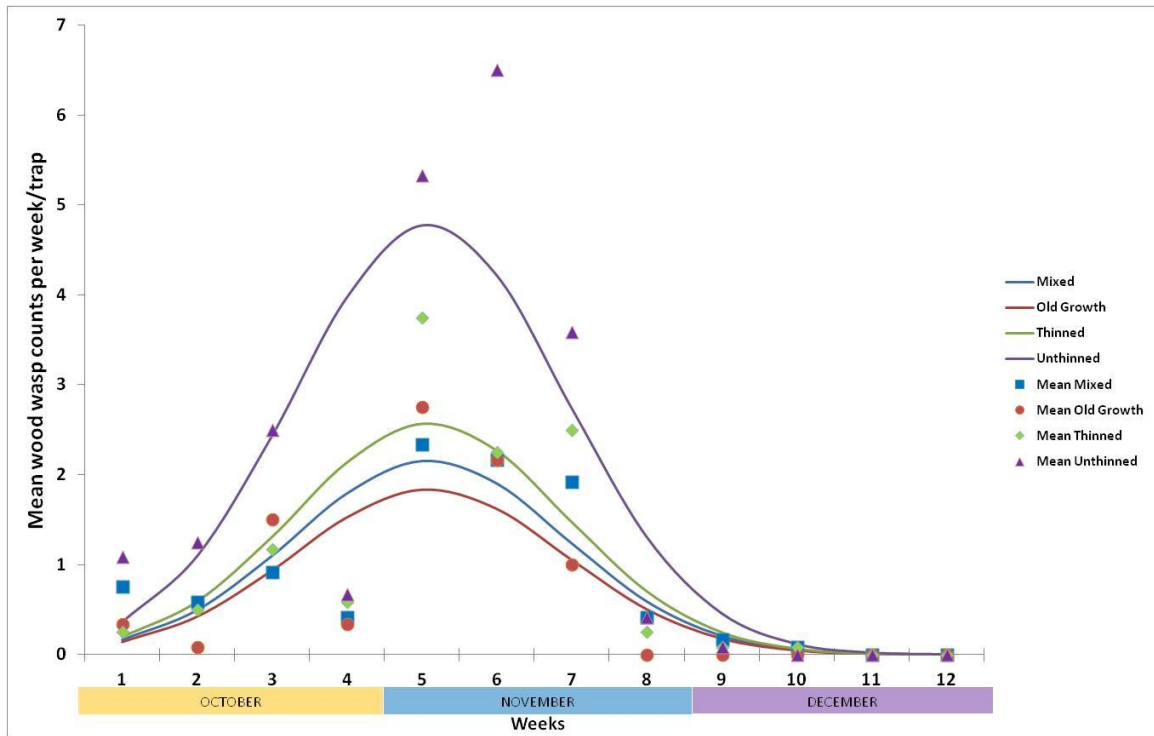


Figure 3.4 Model based estimate phenology curve of *S. nigricornis*

## References Cited

- Avery, T. E. and H. E. Burkhart. 2002. Forest Measurement. 5th ed. McGraw-Hill, New York.
- Barnes, B. F. 2012. Trapping method for large woodboring insects in southeastern U.S. forests. M.S. thesis, University of Georgia, Athens, GA.
- Belanger, R. P., R. L. Hedden, and P. L. Lorio Jr. 1993. Management strategies to reduce losses from the southern pine beetle. Southern Journal of Applied Forestry 17: 150-154.
- Brown, M.W., T. E. Nebeker, and C. R. Honea. 1987. Thinning increases loblolly pine vigor and resistnace to bark beetles. Southern Journal of Applied Forestry 11: 28-31.
- Burkhart, H. E., H. L. Haney Jr., J. D. Newberry, W. A. Leuschner, C. L. Morris, and D. D. Reed. 1986. Evaluation of thinning for reduction of losses from southern pine beetle attack in lobolly pine stands. Southern Journal of Applied Forestry. 10: 105-108.
- Carnegie, A., M. Matsuki, D. Haugen, B. Hurley, R. Ahumada, P. Klasmer, J. Sun, and E. Iede. 2006. Predicting the potential distribution of *Sirex noctilio* (Hymenoptera: Siricidae), a significant exotic pest of *Pinus* plantations. Annals of Forest Science 63: 119-128.
- Cooperband, M. F., K. Böröczky, A. Hartness, T. H. Jones, K. E. Zylstra, J. H. Tumlinson, and V. C. Mastro. 2012. Male-produced pheromone in the European wood wasp, *Sirex noctilio*. Journal of Chemical Ecology 38:52-62.
- Coulson, R. N., F. P. Hain, T. L. Payne. 1974. Radial growth characteristics and stand density of loblolly pine in relation to the occurence of the southern pine beetle. Environmental Entomology 3: 425-428.
- Coyle, D. R., and K. J. K. Gandhi. 2012. The ecology, behavior, and biological control potential of hymenopteran parasitoids of wood wasps (Hymenoptera: Siricidae) in North America. Environmental Entomology 41: 731-749.
- de Groot, P., K. Nystrom, and T. Scarr. 2006. Discovery of *Sirex noctilio* (Hymenoptera: Siricidae) in Ontario, Canada. Great Lakes Entomologist 39: 49-53.
- Dodds, K. J., K. E. Zylstra, G. D. Dubois, and E. R. Hoebeke. Arboreal insects associated with herbicide-stressed *Pinus resinosa* and *Pinus sylvestris* used as *Sirex noctilio* trap tree in New York. Environmental Entomology 41: 1350-1363.

- Dodds, K., P. de Groot, and D. Orwig. 2010. The impact of *Sirex noctilio* in *Pinus resinosa* and *Pinus sylvestris* stands in New York and Ontario. *Canadian Journal of Forest Research* 40: 212-223.
- Dodds, K., R. Cooke, and D. Gilmore. 2007. Silvicultural options to reduce pine susceptibility to attack by a newly detected invasive species, *Sirex noctilio*. *Northern Journal of Applied Forestry* 24: 165-167.
- Eager, P.T., D. C. Aleen, J. L. Frair, and M. K. Fierke. 2011. Within-tree distributions of the *Sirex noctilio* Fabricius (Hymenoptera: Siricidae) - parastoid complex and development of an optimal sampling scheme. *Environmental Entomology* 40: 1266-1275.
- Fettig, C. J., K. D. Klepzig, R. F. Billings, A. S. Munson, T. E. Nebeker, J. F. Negrón, and J. T. Nowak. 2007. The effectiveness of vegetation management practices for prevention and control of bark beetle infestations in coniferous forests of the western and southern United States. *Forest Ecology and Management* 238: 24-53.
- Guldin, J. M. 2011. Silvicultural Considerations in Managing Southern Pine Stands in the Context of Southern Pine Beetle. *In: Southern Pine Beetle II, General Technical Report-SRS-140*. U.S. Department of Agriculture, Forest Service, Southern Research Station, Asheville, NC, pp. 317-352.
- Hall, M. 1968. A survey of siricid attack on radiata pine in Europe. *Aust. For* 32: 155-162.
- Haugen, D., R. Bedding, M. Underdown, and F. Neumann. 1990. National strategy for control of *Sirex noctilio* in Australia. *Australian Forest Grower* 13: 7.
- Hoebeke, E., D. Haugen, and R. A. Haack. 2005. *Sirex noctilio*: Discovery of a Palearctic Siricid Wood wasp in New York. *Newsletter of the Michigan Entomological Society* 50: 24-25.
- Jactel, H., M. Goulard, P. Menassieu, and G. Goujon. 2002. Habitat diversity in forest plantations reduces infestations of the pine stem borer *Dioryctria sylvestrella*. *Journal of Applied Ecology* 39: 618-628.
- Keeler, D.M. 2012. Flight period and species composition of *Sirex* (Hymenoptera: Siricidae) and associated *Deladenus* (Nematoda: Neotylenchidae) within Arkansas pine forests. M.S. thesis, University of Arkansas, Fayetteville, AR.
- Kenward, M. G. and J. H. Roger. 1997. Small sample inference for fixed effects estimators from restricted maximum likelihood. *Biometrics* 53: 983-997.

- Kouki, J., D. G. McCullough, and L. D. Marshall. 1997. Effect of forest stand and edge characteristics on the vulnerability of jack pine stands to jack pine budworm (*Choristoneura pinus pinus*) damage. *Canadian Journal of Forest Resources* 27: 1765-1772.
- Lindgren, B. S. 1983. A multiple funnel trap for scolytid beetles (Coleoptera). *Canadian Entomology* 115: 299-302.
- Morgan, F. D. 1989. Forty years of *Sirex noctilio* and *Ips grandicollis* in Australia. *New Zealand Journal of Forestry Science* 19: 198-209.
- Neumann, F. G., J. Morey, and R. McKimm. 1987. The *Sirex* wasp in Victoria. Department of Conservation, Forest and Lands, Victoria, Australia.
- Perkins, T. E. and G. R. Matlack. 2002. Human-generated pattern in commercial forests of southern Mississippi and consequences for the spread of pests and pathogens. *Forest Ecology and Management* 157: 143-154.
- Ryan, K., P. De Groot, R. Nott, S. Drabble, I. Ochoa, C. Davis, S. Smith, and J. Turgeon. 2012. Natural enemies associated with *Sirex noctilio* (Hymenoptera: Siricidae) and *S. nigricornis* in Ontario, Canada. *Environmental Entomology* 41: 289-297.
- Ryan, K., P. de Groot, and S. M. Smith. 2011. Evidence of interaction between *Sirex noctilio* and other species inhabiting the bole of *Pinus*. *Agricultural and Forest Entomology* 14:187-195.
- Schiff, N., A. Goulet, D. Smith, C. Boudreault, A. Wilson, and B. Scheffler. 2012. Siricidae (Hymenoptera: Symphyta: Siricoidea) of the Western Hemisphere. *Canadian Journal of Arthropod Identification* 21:1-305.
- Schiff, N. M., S. A. Valley, J. R. LaBonte, and D. R. Smith. 2006. Guide to the siricid wood wasps of North America. USDA Forest Service, Forest Health Technology Enterprise Team, Morgantown, WV.
- Smith, D. R., and N. M. Schiff. 2002. A review of the siricid wood wasps and their ibaliid parasitoids (Hymenoptera: Siricidae, Ibalidae) in the eastern United States, with emphasis on the mid-Atlantic region. *Proceedings of the Entomological Society of Washington* 104: 174-194.
- Spradbery, J., and A. Kirk. 1978. Aspects of the ecology of siricid wood wasps (Hymenoptera: Siricidae) in Europe, North Africa and Turkey with special reference to the biological control of *Sirex noctilio* F. in Australia. *Bulletin of Entomological Research* 68: 341-359.



- Standley, C. R., E. R. Hoebeke, D. Parry, D. C. Allen, and M. K. Fierke. 2012. Detection and Identification of Two New Native Hymenopteran Parasitoids Associated with the Exotic *Sirex noctilio* in North America. *Proceedings of the Entomological Society of Washington* 114: 238-249.
- Tabata, M., and Y. Abe. 1995. *Cerrena unicolor* isolated from the mycangia of a horntail, *Tremex longicollis*, in Kochi Prefecture, Japan. *Mycoscience* 36: 447-450.
- Tribe, G., and J. Cillie. 2004. The spread of *Sirex noctilio* Fabricius (Hymenoptera: Siricidae) in South African pine plantations and the introduction and establishment of its biological control agents. *African entomology* 12: 9-17.
- Yemshanov, D., F. Koch, D. McKenney, M. Downing, and F. Sapio. 2009. Mapping invasive species risks with stochastic models: A cross border United States Canada application for *Sirex noctilio* Fabricius. *Risk Analysis* 29: 868-884.
- Zylstra, K. E., K. J. Dodds, J. A. Francese, and V. Mastro. 2010. *Sirex noctilio* in North America: the effect of stem injection timing on the attractiveness and suitability of trap trees. *Agricultural and Forest Entomology* 12: 243-250.

CHAPTER IV  
A HOST-PREFERENCE BASED HAZARD MAP FOR *SIREX NOCTILIO*  
(HYMENOPTERA: SRICIDAE) IN THE SOUTHEASTERN  
UNITED STATES

**Abstract**

*Sirex noctilio* F., an invasive pest of pine (*Pinus* spp.) plantations in the Southern Hemisphere, was introduced to North America in 2004. Risk maps were made for *S. noctilio* in 2006 displaying infestation potential in North America; however, these maps were based on biological information from the Southern Hemisphere. Recent oviposition host preference assays were used to create hazard models for *S. noctilio* in pine forests of the Southeastern United States. Stand density index and soil dryness index spatial data were also included in the models because both factors are correlated with *S. noctilio* outbreaks in the Southern Hemisphere. A suite of models were investigated to emphasize areas of the southeastern U.S. that require immediate silvicultural attention to reduce *S. noctilio* hazard. The corridor of *Pinus strobus* L. and *P. virginiana* Mill. from northern Virginia to central Alabama were areas identified as having high *S. noctilio* hazard. Densely stocked loblolly plantations in the Gulf Coastal Plain and the Ouachita mountain range were areas identified as having medium high *S. noctilio* hazard. Silvicultural management techniques that increase individual tree vigor within plantations should be considered to reduce *S. noctilio* hazard throughout the southeastern U.S. Fortunately, a

system that reduces risk of southern pine beetle infestations already exists and should be considered to also reduce *S. noctilio* hazard.

## **Introduction**

### **Background**

Invasive species are pests that become established in a foreign ecosystem and are capable of causing economic and/or ecological damage (Mooney and Cleland 2001). Approximately 50,000 invasive species that are currently established in the U.S. are estimated to cause \$120 billion/year in damages (Pimentel et al. 2005). Invasive species have also been linked to regional extirpations of species and altering food webs (Ricciardi et al. 1998, Baxter et al. 2004). Currently, 42% of the endangered or threatened species in the United States (U.S.) are at risk because of the presence of invasive species (Wilcove et al. 1998, Pimentel et al. 2005). Importation of invasive species is strongly correlated with global trade, arriving in ballast water, wood packaging material, and/or host material (Cohen and Carlton 1998, Brockerhoff et al. 2006, Haack 2006, Hulme 2009, Price et al. 2011). As international commerce increases, the number and overall impact of invasive species are predicted to increase (Mooney and Cleland 2001, Bax et al. 2003, Molnar et al. 2008, Hulme 2009).

When invasive species arrive in a new environment, the ability to assess their potential for invasion is a critical component of initiating a management plan (Koch et al. 2009). Assessments of invasion potential usually consider areas of greatest concern based on known susceptible habitats/hosts, pathways of movement (i.e. wind, human mediation, etc.), climate compatibility, and the potential economic or ecological impacts (Yemshanov et al. 2010). One problem that scientists encounter when making these

assessments is a lack of knowledge about the pest in its native environment and how it will behave in a new ecosystem (Venette et al. 2010). The biology of invasive species are rarely studied in their native range because a complex of coevolved parasites, predators, and competitors, along with host resistance, exist that restrict them from reaching pest status (Tsutsui 2003). Hence, even the most basic biology of these organisms may not be known before they exploit a new environment. These knowledge gaps can reduce the robustness of a pest assessment and lead to poor decision making (Yemshanov et al. 2010).

Risk and hazard models have become popular means of spatially displaying the predicted threat posed by a pest and what actions need to be taken to prevent or limit ecological/economic damage (Worner et al. 2006, Koch et al. 2009, Yemshanov et al. 2010). Inherent differences exist between the terms risk and hazard; unfortunately, these terms are often misused (Logan et al. 2007). We agree with Dodds et al. (2004) who state that hazard rating systems are "used to determine insect infestation potential and where the heaviest damage is expected to occur given certain biotic/abiotic conditions." Risk rating systems are "the likelihood that an insect infestation will occur in a given area and depends on both stand hazard and insect population densities" (Dodds et al. 2004). Risk and hazard maps have been essential tools for government officials to make management decisions and are easily interpreted by the general public (Venette et al. 2010).

### **Species of Concern: *Sirex noctilio***

The Eurasian wood wasp, *Sirex noctilio* F. (Hymenoptera: Siricidae), is an invasive species that has an extensive history as an outbreak pest in pine plantations of the Southern Hemisphere (Rawlings 1955, Morgan 1989). Native to Eurasia and northern

Africa, *S. noctilio* was introduced to New Zealand in the early 1900's and later spread to Australia where it caused widespread mortality (up to 90%) of non-native pine (*Pinus radiata* D. Don) plantations (Miler and Clark 1935, Rawlings 1949, Morgan 1989).

Factors that contribute to *S. noctilio* outbreak are drought and overstocking in pine plantations (Madden 1975, Morgan 1989). *Sirex noctilio* continues to spread throughout the Southern Hemisphere via solid wood packing materials (SWPM), and is currently a pest in pine plantations in Argentina, Brazil, Chile, Uruguay, and South Africa (Ciesla 2003, Tribe 2004, Carnegie 2006, Corley 2007, Hurley 2007).

*Sirex noctilio* was detected in North America in 2004, having arrived in SWPM, and is now established in Michigan, New York, Ohio, Pennsylvania, Vermont, and Ontario and Quebec, Canada (Schiff et al. 2012). In the U.S., the Eurasian wood wasp received a cumulative risk assessment score of high (12 of 15 criteria points) based on habitat suitability, host range, dispersal potential, economic impact, and environmental impact (Borchert 2007). Pine plantations in the southern and western U.S. are expected to receive the greatest loss from a *S. noctilio* invasion. *Sirex noctilio* is predicted to eventually colonize southern pine stands by natural dispersal (Haugen et al. 1990, Borchert 2007). However, *S. noctilio* could arrive earlier through movement of infested materials or from a separate introduction via the numerous ports of entry in the South.

Forests in the Southeastern U.S. are comprised of 46% pine plantation or mixed pine-hardwood forests compared to the northeastern U.S., which is made up of a sparse 6% pine plantation or mixed pine-hardwood forests (Smith et al. 2001). Fox et al. (2006) reported that Southeastern states contain 32 million acres of pine plantations, consisting mostly of loblolly pine (*Pinus taeda* L.), and are worth approximately \$8 billion

(Borchert 2007). Loblolly pine is a known host of *S. noctilio* in South America (Iede et al. 1988). The impacts of *S. noctilio* to Southeastern U.S. pine plantations are only speculative at this point, however, if outbreaks of *S. noctilio* mimic those in the Southern Hemisphere, large economic losses could occur to timber on public and private lands.

Risk models have been developed by the United States Department of Agriculture - Forest Service - Forest Health Technology Enterprise Team (FHTET) depicting introduction potential (Figure 4.1), establishment potential (Figure 4.2), and susceptibility potential (Figure 4.3) of *S. noctilio*. However, these models were based on biological information from the Southern Hemisphere where native predators, parasitoids, and competitive interactions are absent and the trees are non-native species. The next step in modeling *S. noctilio* hazard is to include biological data from studies conducted within the U.S.

The objective of this study was to utilize *S. noctilio* oviposition host preference assays (Dinkins 2011) to build more robust *S. noctilio* hazard models (using a GIS) of the Southeastern U.S. This is the first time biological information acquired from the North America has been incorporated into hazard maps for *S. noctilio* in the U.S. These models are intended to provide land managers with a more robust representation of forested areas that should be targeted for *S. noctilio* prevention by prescribing proper silvicultural efforts (such as those described in Dodds et al. 2007). A range of scenarios were modeled displaying *S. noctilio* stand hazard under various abiotic stressors and at different levels of preference for host species.

## Materials and Methods

### Study area

*Sirex noctilio* hazard was modeled in pine plantations across the Southeastern region of the U.S. (Figure 4.4). This region was selected because of the high density of susceptible hosts (*Pinus* spp.) to *S. noctilio* and the commercial value of softwood timber within these states.

### Imagery acquisition and supplemental information

All spatial data were provided by the United States Department of Agriculture Forest Service [USDA-FS-Forest Inventory and Analysis (FIA) and Forest Health Technology Enterprise Team (FHTET)]. All spatial data were obtained as a raster file [cell size (X, Y) 240m, 240m] in GRID format. Spatial data were imported into ArcGIS 10 (ESRI, Redlands, CA) and maintained in Albers Conical Equal Area projection (NAD\_1983\_Albers, meters, Parallels: 29.5°N, 45.5°N, Central Meridian: 96°W, Origin: 23°N).

Input spatial data included three primary classes of rasters: individual pine species (IPS) (Table 4.1) that were used in oviposition host preference assays (except for *Pinus sylvestris* L. because it does not extend into the area of concern), Stand Density Index (SDI), and the Natural Soil Drainage Index (DI). IPS inputs are based on forest surveys conducted by the USFS-FIA. SDI, also measured by USFS-FIA surveys, is a measure of stand density that takes into account quadratic mean diameter, tree stocking, and stand basal area (Reineke 1933). In general, a greater SDI value equates to greater individual tree stress within plantations (Barnes et al. 1998). The DI is a measure of soil moisture throughout the ground strata and is determined by slope, drainage, soil textural family,

and soil taxonomic subgroup (Schaetzl et al. 2009). The DI was used to quantify drought in relation to *S. noctilio* hazard. Values of the DI ranged from 0 to 100 with a value of 0 equaling total saturation (e.g., a lake) and a value of 100 equaling extremely dry conditions. Climatic layers were not included in hazard models; Carnegie et al. (2006) used a climatic mapping system (CLIMEX) to display predicted areas of distribution for *S. noctilio* in the U.S. and found that climate was not a limiting factor.

The spatial extent of DI and SDI were limited exclusively to the spatial extent of the IPS investigated in the model. This was accomplished by the following: 1) combining the 6 IPS layers into one raster file ("raster 1") using the weighted sum tool and applying an even weight of 1 so that pixel values did not change; 2) reclassifying (Spatial Analyst) the "raster 1" raster with 2 classes such that pixels with a value of 0=NoData and all other pixel values=1; and 3) using the raster calculator tool to multiply the DI and SDI layers by the reclassified "raster 1" layer. The final step transformed all pixels in the DI and SDI that did not correspond with pixels in the "raster 1" output into having values of "NoData", which would not represent any value. This does not mean that only *Pinus* spp. are represented in the SDI input however. Each pixel in the SDI input represents 5.76 ha of forested land, which may consist of a heterogeneous landscape within that hectare. Heterogeneous landscapes are not as susceptible to outbreaks of *S. noctilio* and pixels with these features may not accurately portray true *S. noctilio* hazard. However, because the spatial extent of the SDI was limited to the IPS, only pixels containing pine are present. Also, values of SDI (0-100) correspond to the density of pine stocking, therefore a high value would indicate a plantation setting and correspond with high *S. noctilio*



hazard. SDI was used as a multiplier in this study to better predict *S. noctilio* hazard in overstocked pine plantations.

### **Hazard weightings**

Results from assays of *S. noctilio* oviposition host preference (Dinkins 2011) were used as decision making criteria for weighting IPS in the development of hazard maps (Table 4.1). A maximum weight threshold of 0.5 (on a scale of 0.1- 0.99) was applied to IPS by a panel (John J. Riggins, Kamal J.K. Gandhi, and the author) (Hessburg et al. 2007) in relation to their historical importance of drought and overstocked plantations during a *S. noctilio* outbreak. In order to systematically assign weights to IPS, parameters were established using the oviposition host preference data. This was done by dividing the species (*Pinus strobus*) with the highest mean oviposition preference (1.7657059) by 5 (maximum weight threshold of IPS) to create 5 weight classes. *Pinus* spp. were then assigned a weight according to the upper and lower class boundaries established (Table 4.2). Weighting of SDI and SWDI were decided by the panel based on historical outbreak information and the scenario that was modeled.

### **Weighted Sum Tool**

The weighted sum tool allows multiple inputs to be individually weighted and combines the inputs into a single integrated layer. The cell values of each raster layer are multiplied by their assigned weight and summed together to create the output raster. The pixels of the output layer from the weighted sum function are assigned as floating point data and attribute tables cannot be created in this format. Therefore, each model created was reclassified using the reclassify (spatial analyst) tool which converts floating point

data to integer data. Once converted, an attribute table was created and the number of pixels within each hazard class could be counted and compared between models. Pixels were converted to number of hectares that were in each hazard class.

### **Model scenarios**

Models investigated the following hypothetical scenarios of *S. noctilio* hazard in the southeastern U.S.:

1) Southeastern pine model - *Sirex noctilio* oviposition host preference for Southeastern *Pinus* spp. without regard to stocking density or soil moisture conditions.

2) Southeastern pine, SDI, and DI model - *S. noctilio* oviposition host preference for Southeastern trees with regard to stocking density of soil moisture conditions. DI and SDI were weighted in accordance with the *S. noctilio* establishment map created by the USFS-FHTET in 2006 such that SDI accounted for double the weight of DI in models where DI was not intentionally modified (the epidemic drought model). The output of this model was classified according to natural breaks (Jenks) which are separated based on large jumps in the inherent data (Jenks 1963). Natural break values from this model were used as baseline breaks for the remaining models to accurately compare outputs.

3) Virginia and eastern white pine model - *S. noctilio* is able to reach outbreak status in *Pinus strobus* and *P. virginiana* forests. Therefore, *P. strobus* and *P. virginiana* were weighted maximally (0.99).

4) Epidemic drought model - *S. noctilio* hazard in the midst of an epidemic drought (DI weighted 0.99). Historically, large outbreaks of *S. noctilio* in the Southern Hemisphere have occurred after extended periods of drought (Morgan 1989).

5) Loblolly pine models - *S. noctilio* preference for *P. taeda* is different than that observed in oviposition host preference assays. A series of models were created to display varying levels of *S. noctilio* hazard to different weightings of *P. taeda*. In oviposition host preference assays, *P. taeda* was not a favored host of *S. noctilio*. However, loblolly pine plantations are known to be attacked by *S. noctilio* in South America (Iede et al. 1989).

## **Results and Discussion**

### **Southeastern pine model**

The Southeastern pine model (SPM) (Figure 4.5) depicts *S. noctilio* hazard solely on the six pine species tested in oviposition host preference assays (Dinkins 2011) without consideration of soil moisture or overstocking as a multiplier. The model output displays medium-high to high *S. noctilio* hazard in the distribution of *P. strobus* and *P. virginiana* from the western edge of mid-Virginia through central Alabama. The Great Smoky Mountains National Park, Nantahala National Forest, and Chattahoochee National Forest are public lands predicted to have areas of high *S. noctilio* hazard by this model. However, under the criteria and assumptions of this model, less than 1% (529,788 hectares, Table 4.3) of the total pine forested areas of the Southeastern U.S. had a high *S. noctilio* hazard rating. Yellow pine (*P. taeda*, *P. elliotii*, *P. echinata* Mill., and *P. palustris* Mill.) plantations in southern Mississippi, Alabama, the western panhandle of Florida, and the Ouachita mountains in eastern Oklahoma and western Arkansas are areas this model indicated might exhibit low to medium low hazard. Forested areas containing low *S. noctilio* hazard rating account for more than half (54%) of the southeastern U.S. (Table 4.3).

The SPM displays which Southeastern pine species should be targeted for management if *S. noctilio* were to arrive in this region based on oviposition host preference assays. Fortunately *P. strobus* and *P. virginiana*, the two pine species favored in the assays, are not common plantation species (except as Christmas trees) and are typically found in heterogeneous landscapes. However, both species are common along highway corridors and may act as a pathway for *S. noctilio* to enter plantation species in the Southeastern U.S. Therefore, it is recommended that future *S. noctilio* survey programs target highway corridors (e.g. Interstate-81, I-75, and I-59) containing *P. strobus* and *P. virginiana* and monitor transportation of softwood commodities that are potentially infested.

#### **Southeastern pine, SDI, and DI model (SSSM)**

The SSSM (Figure 4.6) illustrates the closest estimate of *S. noctilio* hazard for the Southeastern U.S. based on historical outbreak information (Morgan 1989) and oviposition host preference assays (Dinkins 2011). The main difference between the SSSM and the SPM is a large portion of forests increased one *S. noctilio* hazard class. This jump is due to the presence of overstocked stands and areas that are prone to drought. A total of 3% (2,419,937 ha) of the SSSM was ranked as high hazard and 35 % (31,202,899 ha) was ranked as low hazard (Table 4.4); areas of high hazard were the same as the SPM. *Pinus echinata* and *P. taeda* forests in the Ouachita mountain range of OK and AR in addition to *P. taeda* plantations in the coastal plains of AL and MS were classified as medium high *S. noctilio* hazard stands (7,373,692 ha).

### **Virginia and eastern white pine model (VEM)**

The VEM (Figure 4.7) was constructed to show *S. noctilio* hazard in a worst case scenario that *P. strobus* and *P. virginiana* is highly conducive to *S. noctilio* hazard. A more defined high hazard corridor of *S. noctilio* hazard is displayed in this model from northern VA to the heart of Alabama. Fragmented patches of high *S. noctilio* hazard areas are also expressed in KY. High hazard areas made up 8% (6,708,833 hectares) of the model output (Table 4.4).

In 2006, when the FHTET created a *S. noctilio* susceptibility potential map (Figure 4.3), *P. strobus* was ranked as having low (on a scale of low, medium, high, and very high) potential for establishment; *Pinus virginiana* was ranked as having high potential. The Virginia and eastern white pine model greatly differs from the susceptibility potential map because of the difference in weights (ranks) assigned in the model building process. The southeastern pine model shows very little associated risk in western VA and eastern KY; areas in the southeastern U.S. that contain *P. strobus*. In the northeastern U.S., where *S. noctilio* is currently established, the wood wasp has attacked *P. strobus* (Dodds et al. 2007) but has not been reported from *P. virginiana* in field conditions. It is important to monitor if *S. noctilio* populations are able to move into *P. virginiana* stands and how populations fluctuate in stands of *P. strobus*.

### **Epidemic drought model (EDM)**

The epidemic drought model (EDM) (Figure 4.8) represents a "worst case" scenario in which the entire Southeastern U.S. is in a state of extreme drought. DI was maximally weighted (0.99) to include all pine forested areas that are susceptible to extreme drought. High *S. noctilio* hazard accounted for 50% of the total hectares in the

southeastern U.S. in the model (Table 4.4). Drought will probably never be this severe in the southeastern U.S. However, longer and more excessive droughts are occurring globally, possibly due to changes in the global climate (Easterling et al. 2000). Specifically in the southeastern U.S., more severe droughts and irregular rainfall has occurred in a recent 30 year period (1978-2007) than in the previous 30 years (1948-77) (Wang et al. 2010). In 2011, Texas forests lost an estimated 10-20 million pine trees to drought (Chris Edgar, personal communication, Texas A&M Forest Service, College Station). The purpose of the EDM is to display the intensity of *S. noctilio* hazard in the event of an epidemic drought, and to provide a map that displays the vastness of pine forests that could be affected across the Southeastern U.S.

### **Loblolly pine models**

*Pinus taeda* is the most important timber plantation species in the Southeastern U.S. (Antony et al. 2012). During oviposition host preference assays (Dinkins 2011), *P. taeda* was not a "favored" host of *S. noctilio* in the presence of other *Pinus* spp. However, *P. taeda* is a known host of *S. noctilio* in South American plantations. In fact, up to 60% mortality has occurred in *P. taeda* and *P. elliottii* Engelm. plantations in Argentina (Hurley et al. 2007). *Sirex noctilio* is currently established outside the range of *P. taeda* in North America and we do not know how this insect will interact with loblolly plantations in forested settings. We therefore, thought it necessary to model *S. noctilio* hazard across a range of "preferences" (weights) of the wood wasp to *P. taeda*. These models are purely pre-cautionary in nature and represent theoretical "worst case" scenarios.

The loblolly pine models (LPM) (Figures 4.9-4.13) display how *S. noctilio* hazard changes across the Southeastern U.S. if *S. noctilio* preference for *P. taeda* differed from

that of the oviposition host preference assays (Table 4.5). As the relative weight of loblolly pine is adjusted from 0.2 – 0.6 in the LPM's, the high *S. noctilio* hazard category encompassed 4% (LPM-A), 7% (LPM-B), 19% (LPM-C), 31% (LPM-D), and 38% (LPM-E) of the total area across the Southeastern U.S., respectively. Generally, as *P. taeda* weight increased, the number of hectares susceptible to high *S. noctilio* hazard drastically increased (Figure 4.14). LPM's indicate that *S. noctilio* preference for loblolly pines will be the primary factor determining *S. noctilio* severity in the SOUTHEASTERN U.S. It is vital to monitor how *S. noctilio* populations fluctuate in *Pinus* spp. not previously encountered in the U.S. Model outputs clearly define the extent and density of *P. taeda* in this region and display areas that should be targeted for silvicultural management (Dodds et al. 2007) in the event of a *S. noctilio* outbreak.

### **Sirex noctilio model summary**

*Sirex noctilio* hazard models represent infestation susceptibility based on abiotic (drought) and biotic (pine species and overstocking of plantations) factors. We stress that certain scenarios were modeled to intentionally display worst case scenarios, thereby showing extreme events, which may not represent reality. Although these scenarios are highly unlikely, it is our intention to provide land managers with easily interpretable displays of *S. noctilio* hazard under various extreme biotic and abiotic stressors.

### **Reducing Sirex noctilio hazard**

Silvicultural thinning is an effective method of reducing *S. noctilio* hazard in the Southern Hemisphere and is also recommended in North America (Haugen 1990, Dodds et al. 2010). Thinning in the Southeastern U.S. is also recommended to reduce southern

pine beetle (*Dendroctonus frontalis* Zimmerman) (SPB) risk in pine plantations. A thinning regiment with a lower limit of residual at 16.1 m<sup>2</sup>/ha (70 ft<sup>2</sup>/acre) and an upper limit of residual at 23.0m<sup>2</sup>/ha (100 ft<sup>2</sup>/acre) is recommended to reduce stand risk for the SPB (Guldin 2011). Regular fire return intervals, managing pine-hardwood mixed forests, and selecting site appropriate species are also attributes that can reduce SPB risk and should be considered to reduce *S. noctilio* hazard (Belanger et al. 1993, Clarke 2001, Guldin 2011). Hazard rating systems have been developed for the SPB (i.e. Mason et al. 1985, Stephen and Lih 1985) and could possibly be used to rate stands for *S. noctilio* hazard as these systems identify factors that affect both species (see chapter 2).

In North America, *S. noctilio* is attacking suppressed trees with low crown classes in overstocked stands of *P. sylvestris* and *P. resinosa* Ait. (red pine) (Dodds et al. 2010). A complex of factors exist that may be limiting *S. noctilio* potential in North America, such as known siricid parasitoids (Coyle and Gandhi 2012, Standley 2012), native woodboring insects that compete for the same host resource (Ryan et al. 2011A), and fungal pathogen (i.e. *Ophiostoma* spp. and *Leptographium* spp.) competition (Ryan et al. 2011B). It is still unknown how *S. noctilio* will behave in Southeastern pine plantations, if it were to arrive. However, we do know there are extensive stretches of overstocked pine plantations in drought prone areas that are potentially hazardous to *S. noctilio* invasion. The best way to reduce stand hazard is reduce basal area and increase tree vigor in these plantations. Enforcing protocols that restrict the movement of infested materials will also reduce the likelihood of *S. noctilio* establishment in the southeastern U.S.



## Conclusion

The suite of maps depicting *S. noctilio* hazard are the first to consider host preference data (biological information) from native host species (*Pinus* spp.) in the U.S. It is clear that the southeastern U.S. has an abundance of host material that could harbor large populations of the wood wasp. *Sirex noctilio* hazard models presented here display areas of greatest concern for invasion potential, however, caution must be taken regarding the robustness of these maps. The weights assigned to IPS are based on a single study performed in a laboratory setting on sections of dead trees. Actual oviposition host preference of *S. noctilio* may differ in natural forests or plantations. Nonetheless, oviposition host preference data allows decision makers to more accurately assess the potential threat of *S. noctilio* as the information is based on empirical evidence. Silvicultural management that aims to increase stand vigor is currently the best strategy to prepare for a *S. noctilio* outbreak. Southern pine beetle management models, whose very goal is to increase pine plantation stand vigor, are already in place in the Southeastern U.S. and should be encouraged to reduce *S. noctilio* hazard as well.

Table 4.1 *Sirex noctilio* mean oviposition host preference (Dinkins 2011)

Tree Species	Mean Oviposition Host Preference
<i>Pinus elliottii</i> (slash pine)	0.0784314 ± 0.0472219
<i>Pinus taeda</i> (loblolly pine)	0.1764706 ± 0.0607527
<i>Pinus echinata</i> (shortleaf leaf)	0.2156863 ± 0.0703700
<i>Pinus palustris</i> (longleaf pine)	0.3333333 ± 0.0824463
<i>Pinus virginiana</i> (Virginia pine)	0.9411765 ± 0.1134547
<i>Pinus strobus</i> (white pine)	1.7647059 ± 0.3493279

Table 4.2 Class boundaries used to establish pine species weights

<b>Weight</b>	<b>Upper and Lower Class Boundaries</b>
0.1	0 - 0.35294118
0.2	0.35294118 - 0.70588236
0.3	0.70588236 - 1.05882354
0.4	1.05882354 - 1.41176472
0.5	1.41176472 - 1.7647059

Table 4.3 Weights used and area in each *S. noctilio* hazard class for the Southeastern pine model

<b>Layer</b>	<b>Weight</b>
Slash	0.1
Loblolly	0.1
Shortleaf	0.1
Longleaf	0.1
Virginia	0.3
White	0.5

<b>Hazard Class</b>	<b>Hectares</b>
Extremely Low	17640956
Low	47765428
Medium Low	9508936
Medium High	3320680
High	529788

Table 4.4 Weights used and area in each *S. noctilio* hazard class for the SSSM, VEM, and EDM

Layer	SSSM	VEM	EDM
	Weight	Weight	Weight
<i>Pinus elliottii</i> (Slash Pine)	0.1	0.1	0.1
<i>Pinus taeda</i> (Loblolly Pine)	0.1	0.1	0.1
<i>Pinus echinata</i> (Shortleaf Pine)	0.1	0.1	0.1
<i>Pinus palustris</i> (Longleaf Pine)	0.1	0.1	0.1
<i>Pinus virginiana</i> (Virginia Pine)	0.3	0.99	0.3
<i>Pinus strobus</i> (E. White Pine)	0.5	0.99	0.5
Natural Soil Drainage Index (DI)	0.4	0.4	0.99
Stand Density Index (SDI)	0.6	0.6	0.6
Hazard Class	Hectares	Hectares	Hectares
Extremely Low	18593591	18198035	3089785
Low	31202899	29647532	6168931
Medium Low	28752831	27559423	8733139
Medium High	7373693	6229129	24366338
High	2419937	6708833	45984758

Table 4.5 Weights used and area in each *S. noctilio* hazard class for the LPM

Layer	Lob A	Lob B	Lob C	Lob D	Lob E
	Weight	Weight	Weight	Weight	Weight
<i>Pinus elliottii</i> (Slash Pine)	0.1	0.1	0.1	0.1	0.1
<i>Pinus taeda</i> (Loblolly Pine)	0.2	0.3	0.4	0.5	0.6
<i>Pinus echinata</i> (Shortleaf Pine)	0.1	0.1	0.1	0.1	0.1
<i>Pinus palustris</i> (Longleaf Pine)	0.1	0.1	0.1	0.1	0.1
<i>Pinus virginiana</i> (Virginia Pine)	0.3	0.3	0.3	0.3	0.3
<i>Pinus strobus</i> (E. White Pine)	0.5	0.5	0.5	0.5	0.5
Natural Soil Drainage Index (DI)	0.4	0.4	0.4	0.4	0.4
Stand Density Index (SDI)	0.6	0.6	0.6	0.6	0.6
Hazard Class	Hectares	Hectares	Hectares	Hectares	Hectares
Extremely Low	14398675	12337972	11046010	10156130	9469855
Low	23296101	19553725	17572372	16275738	15339427
Medium Low	27126847	20696826	17166661	15425516	14278660
Medium High	20362314	29987649	25905329	18983232	15276298
High	3429014	5766780	16652581	27502335	33978712

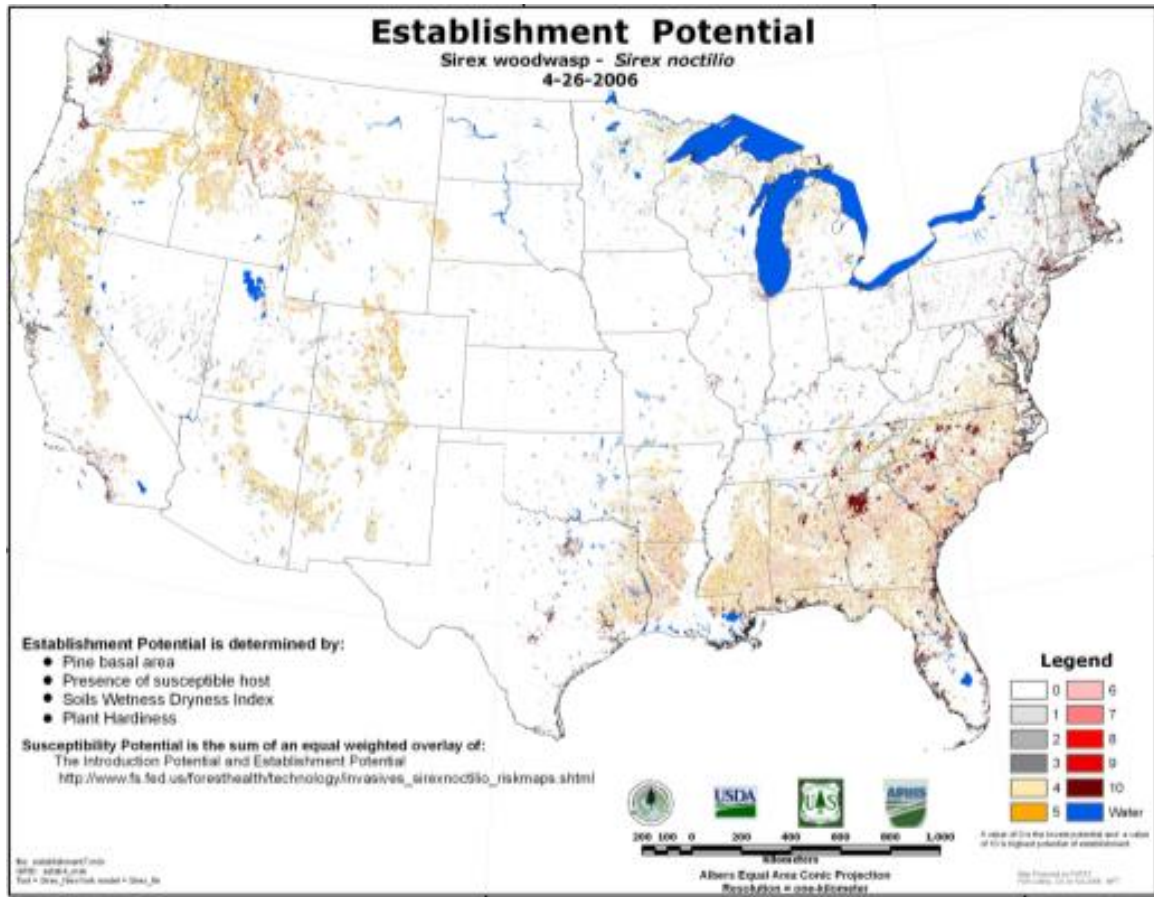


Figure 4.1 Establishment potential of *Sirex noctilio* in the United States.

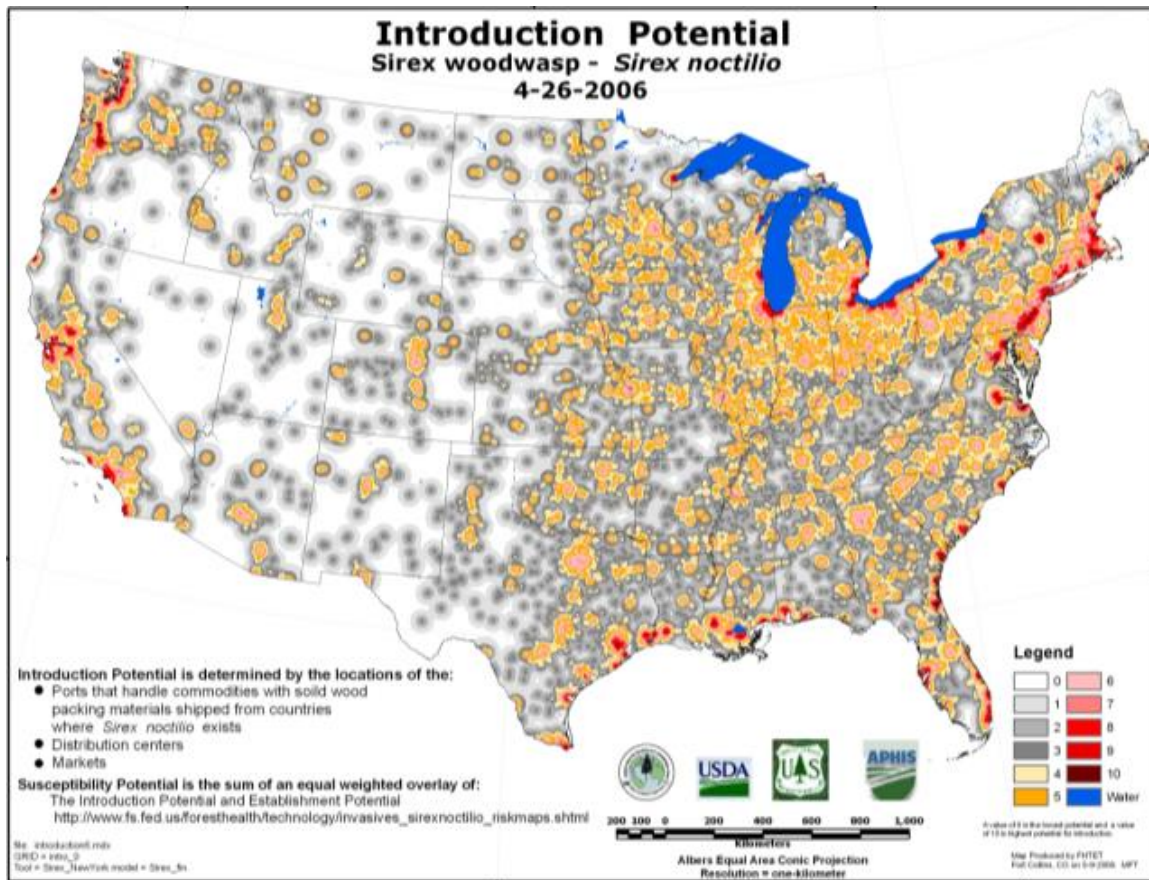


Figure 4.2 Introduction potential of *Sirex noctilio* in the United States

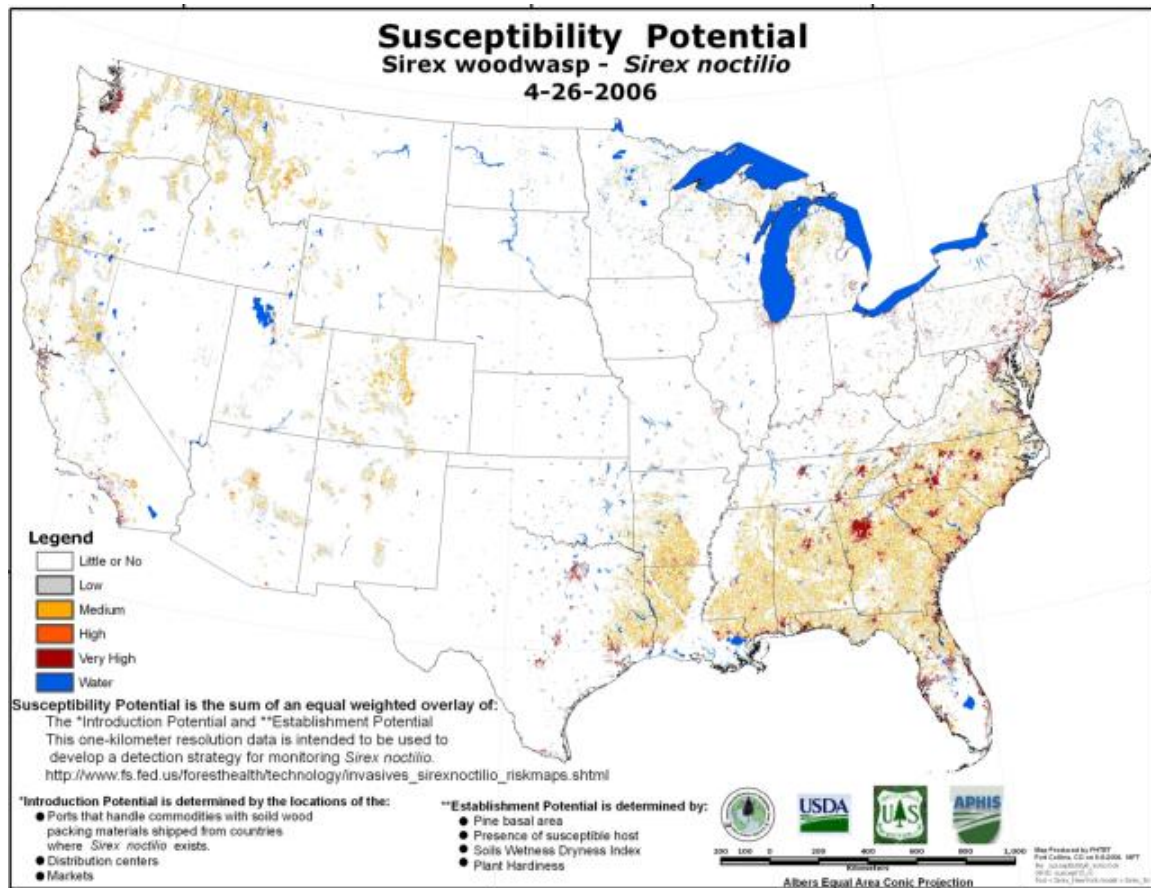


Figure 4.3 Susceptibility potential of *Sirex noctilio* in the United States

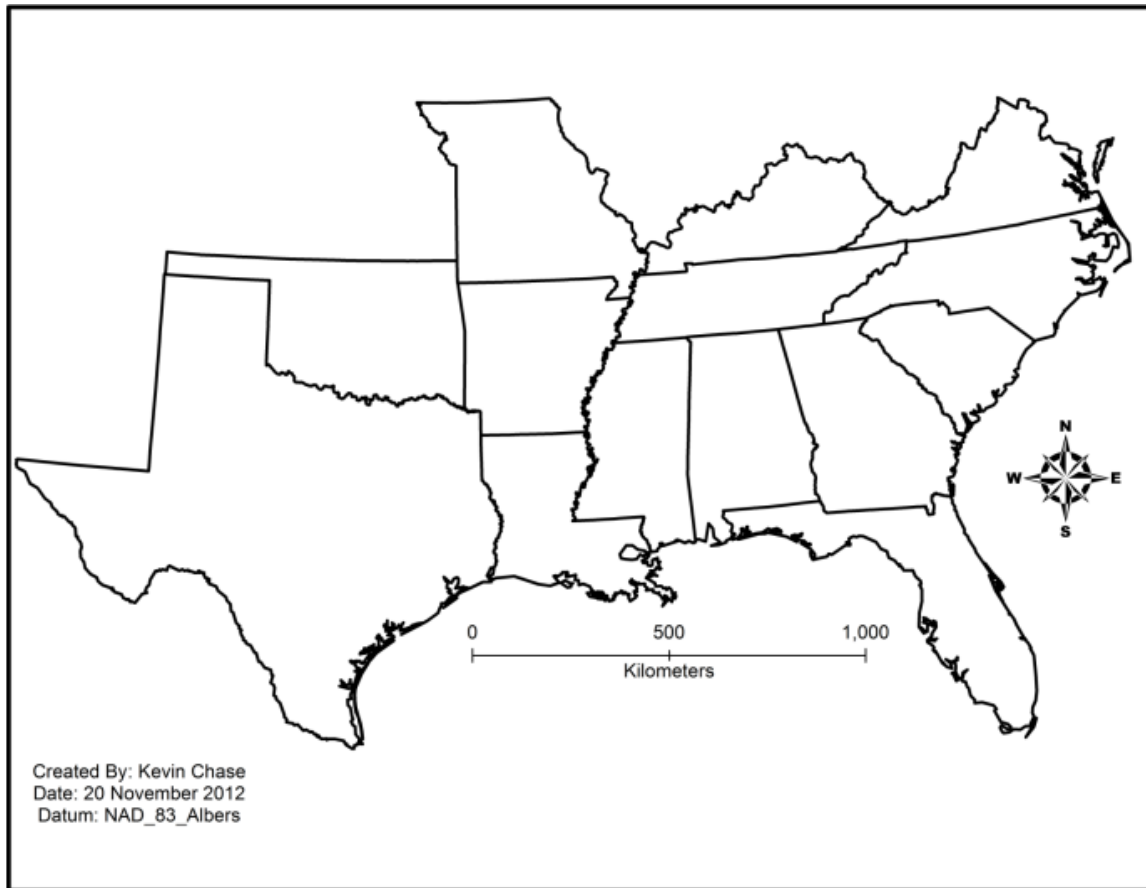


Figure 4.4 The Southeastern states of America

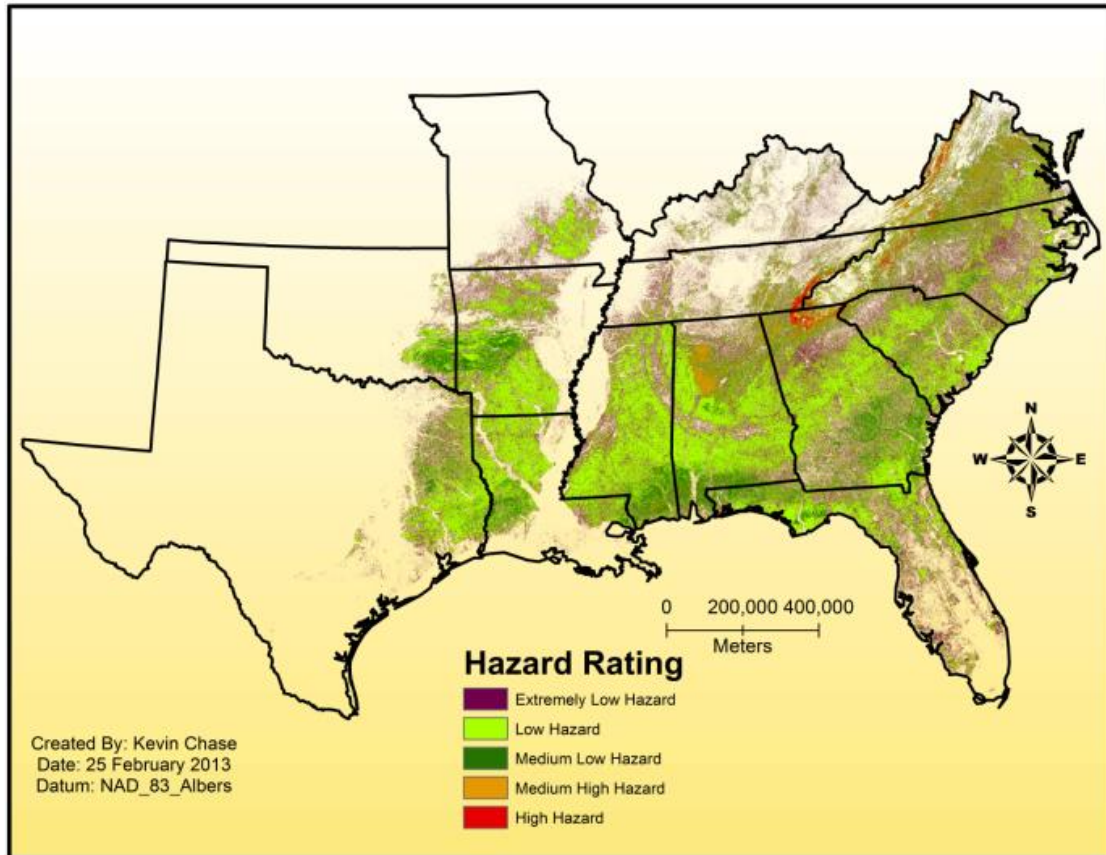


Figure 4.5 Southeastern pine model (SPM) depicting *Sirex noctilio* hazard

Layers and weights used: *Pinus elliottii* (0.1), *P. taeda* (0.1), *P. echinata* (0.1), *P. palustris* (0.1), *P. virginiana* (0.3), *P. strobus* (0.5).



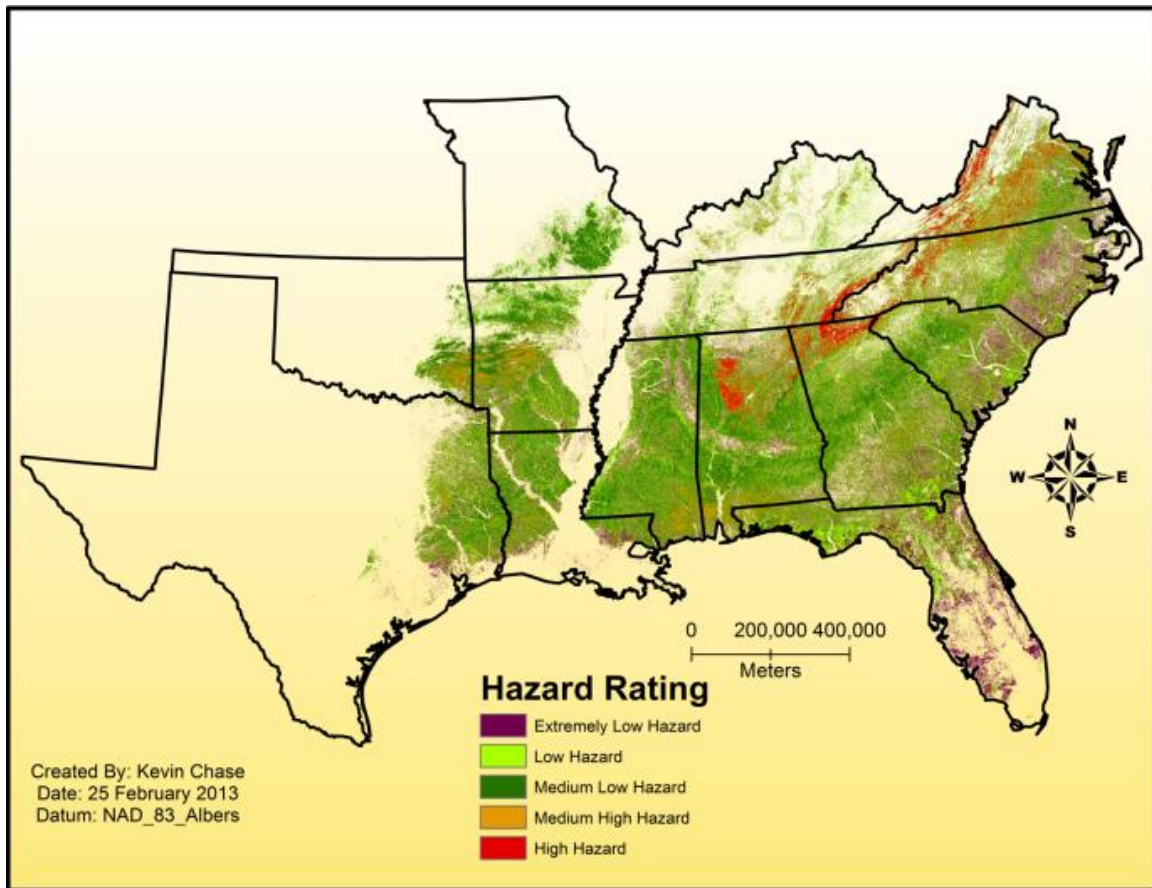


Figure 4.6 Southeastern pine species, stand density index, and dryness index model (SSSM) depicting *Sirex noctilio* hazard

Layers and weights used: *Pinus elliottii* (0.1), *P. taeda* (0.1), *P. echinata* (0.1), *P. palustris* (0.1), *P. virginiana* (0.3), *P. strobus* (0.5), drainage index (0.4), stand density index (0.6).

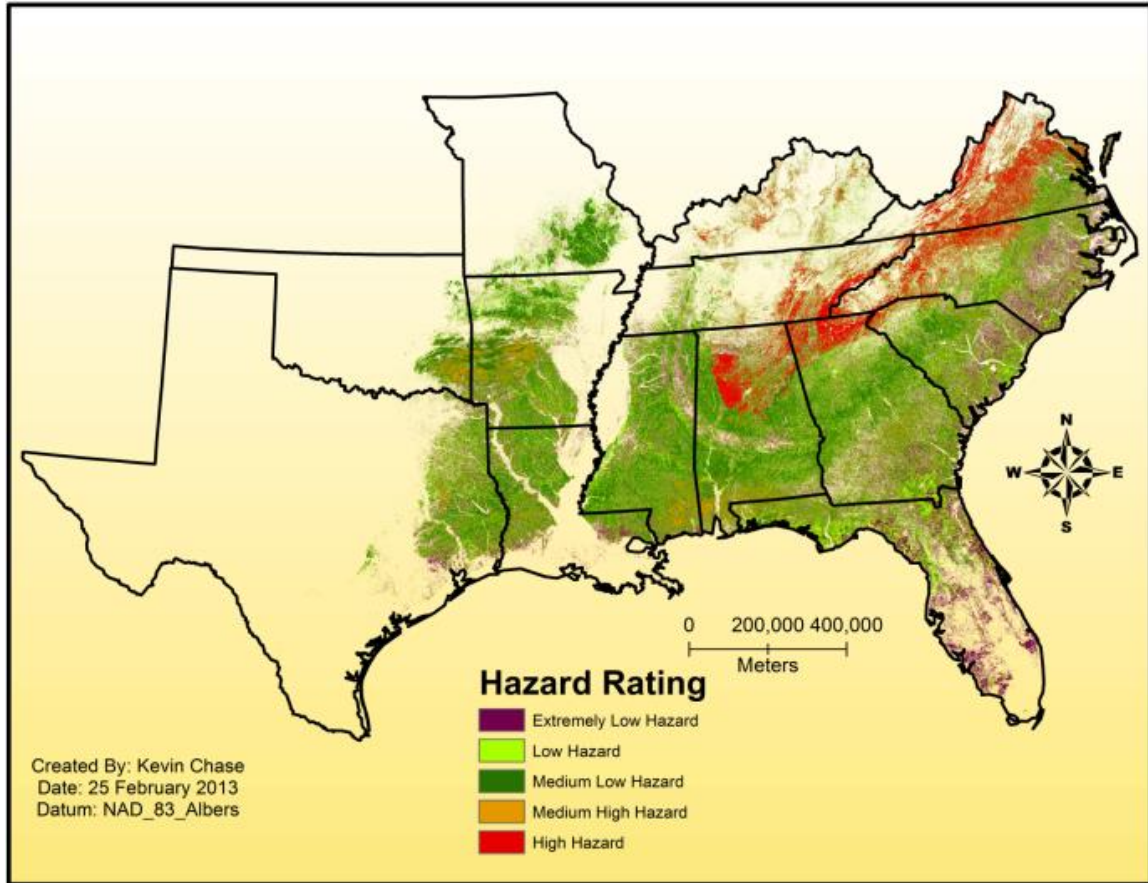


Figure 4.7 Virginia and eastern white pine model (VEM) depicting *Sirex noctilio* hazard

Layers and weights used: *Pinus elliottii* (0.1), *P. taeda* (0.1), *P. echinata* (0.1), *P. palustris* (0.1), *P. virginiana* (0.99), *P. strobus* (0.99), drainage index (0.4), stand density index (0.6).

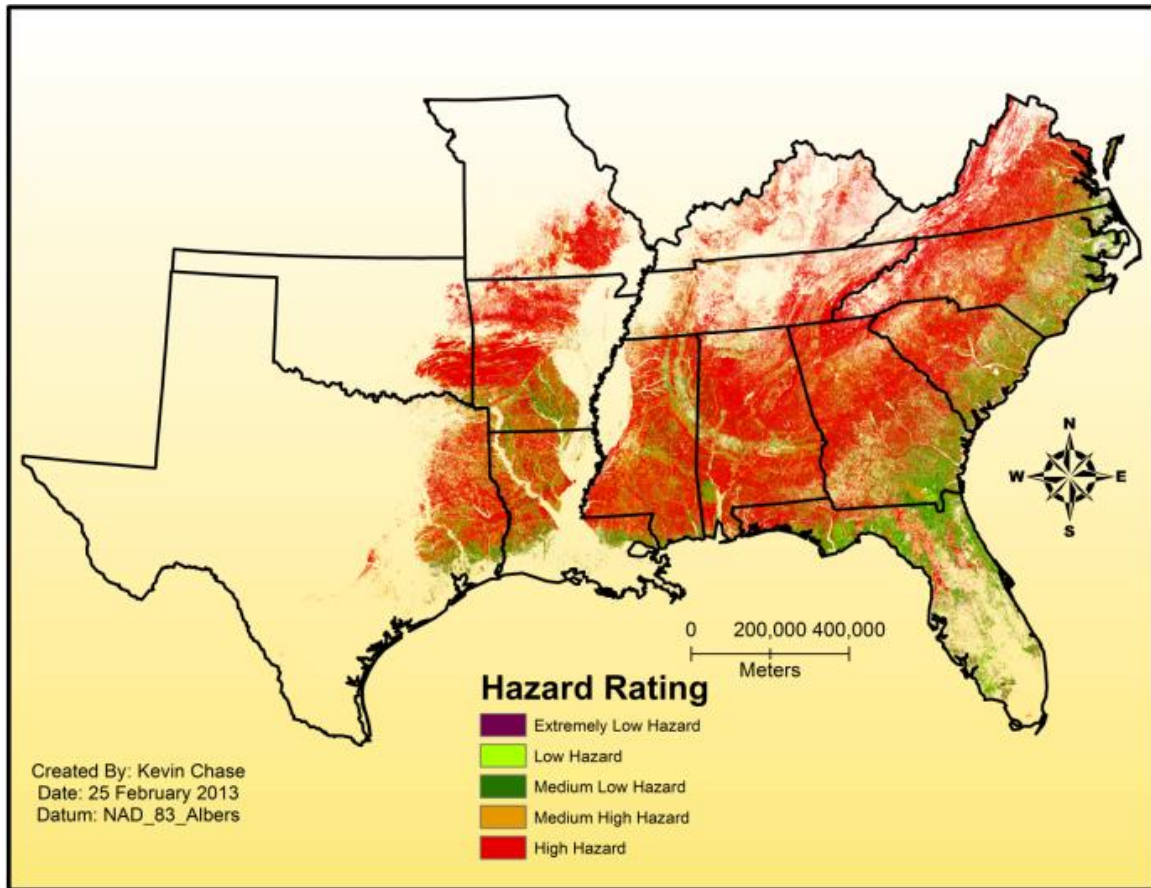


Figure 4.8 Epidemic drought model (EDM) depicting *Sirex noctilio* hazard

Layers and weights used: *Pinus elliottii* (0.1), *P. taeda* (0.1), *P. echinata* (0.1), *P. palustris* (0.1), *P. virginiana* (0.3), *P. strobus* (0.5), drainage index (0.99), stand density index (0.6).

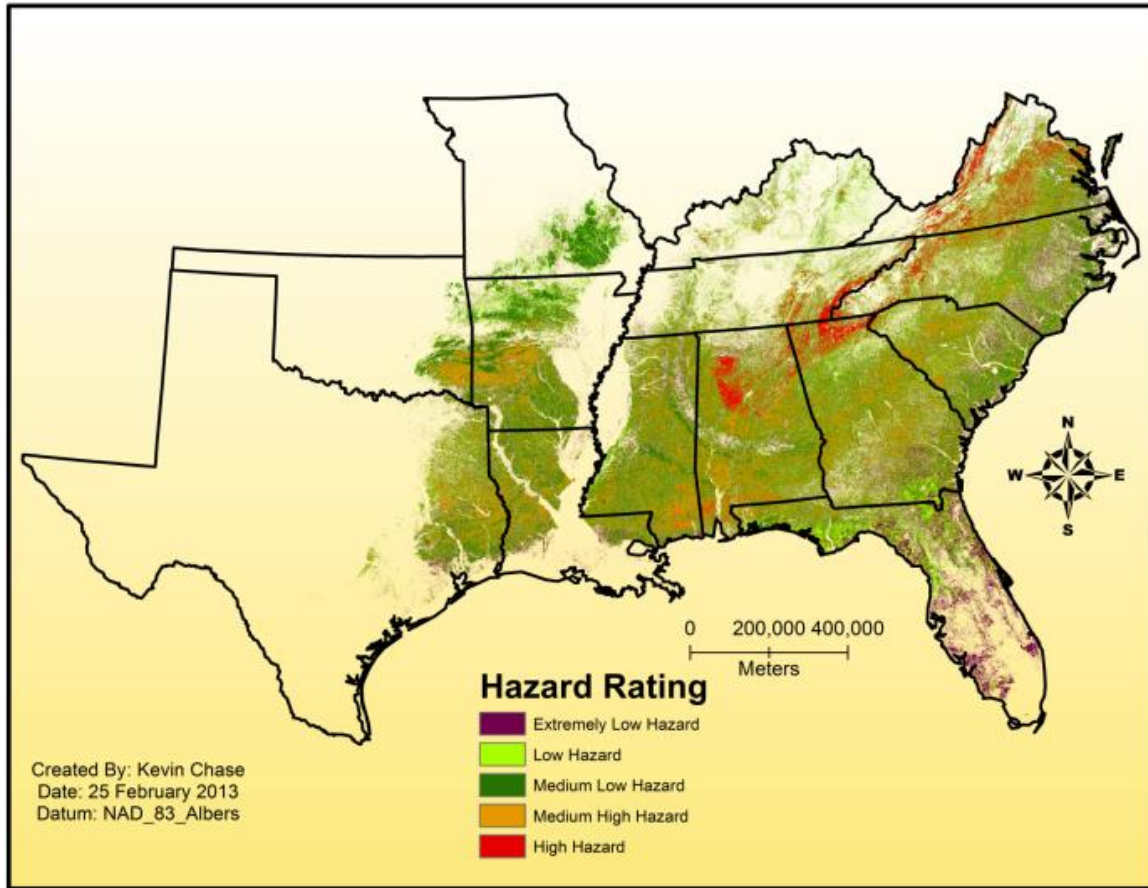


Figure 4.9 Loblolly pine model A (LPM-A) depicting *Sirex noctilio* hazard

Layers and weights used: *Pinus elliottii* (0.1), *P. taeda* (0.2), *P. echinata* (0.1), *P. palustris* (0.1), *P. virginiana* (0.3), *P. strobus* (0.5), drainage index (0.4), stand density index (0.6).

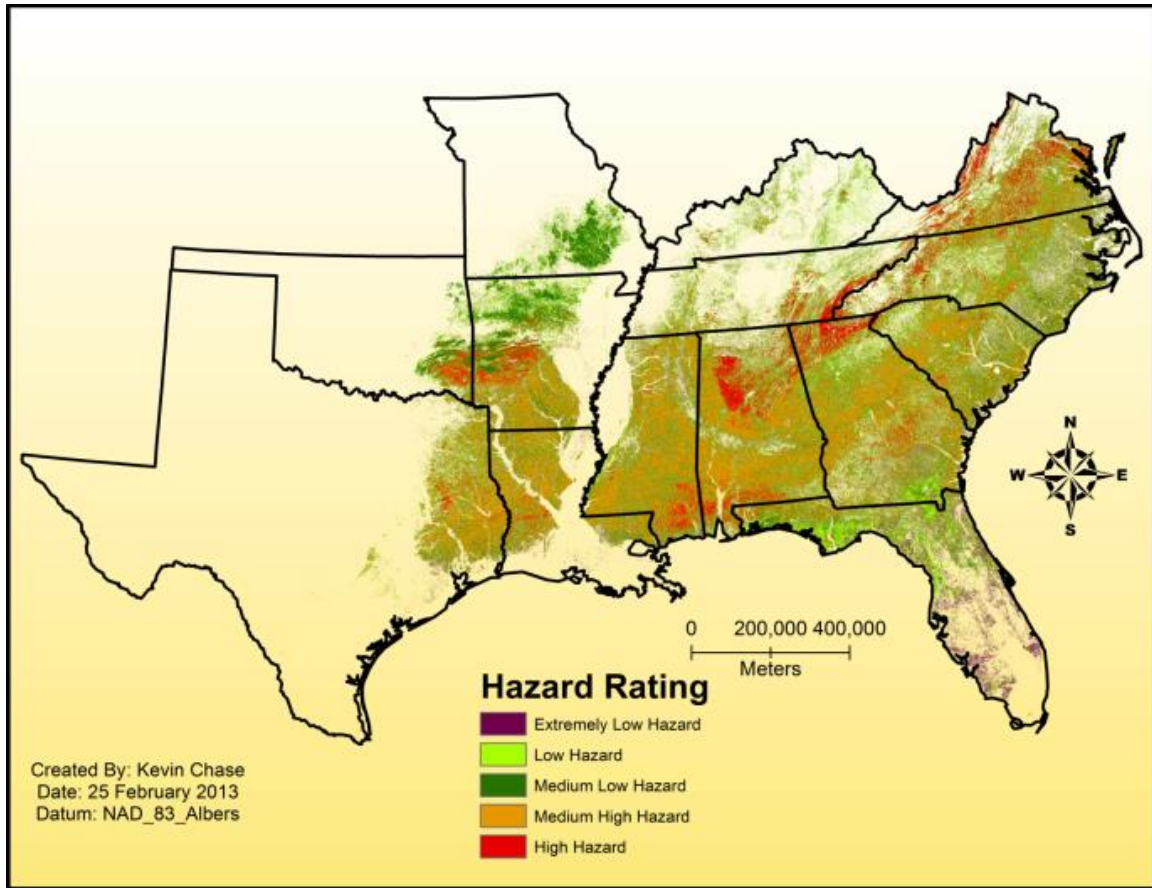


Figure 4.10 Loblolly pine model B (LPM-B) depicting *Sirex noctilio* hazard

Layers and weights used: *Pinus elliottii* (0.1), *P. taeda* (0.3), *P. echinata* (0.1), *P. palustris* (0.1), *P. virginiana* (0.3), *P. strobus* (0.5), drainage index (0.4), stand density index (0.6).

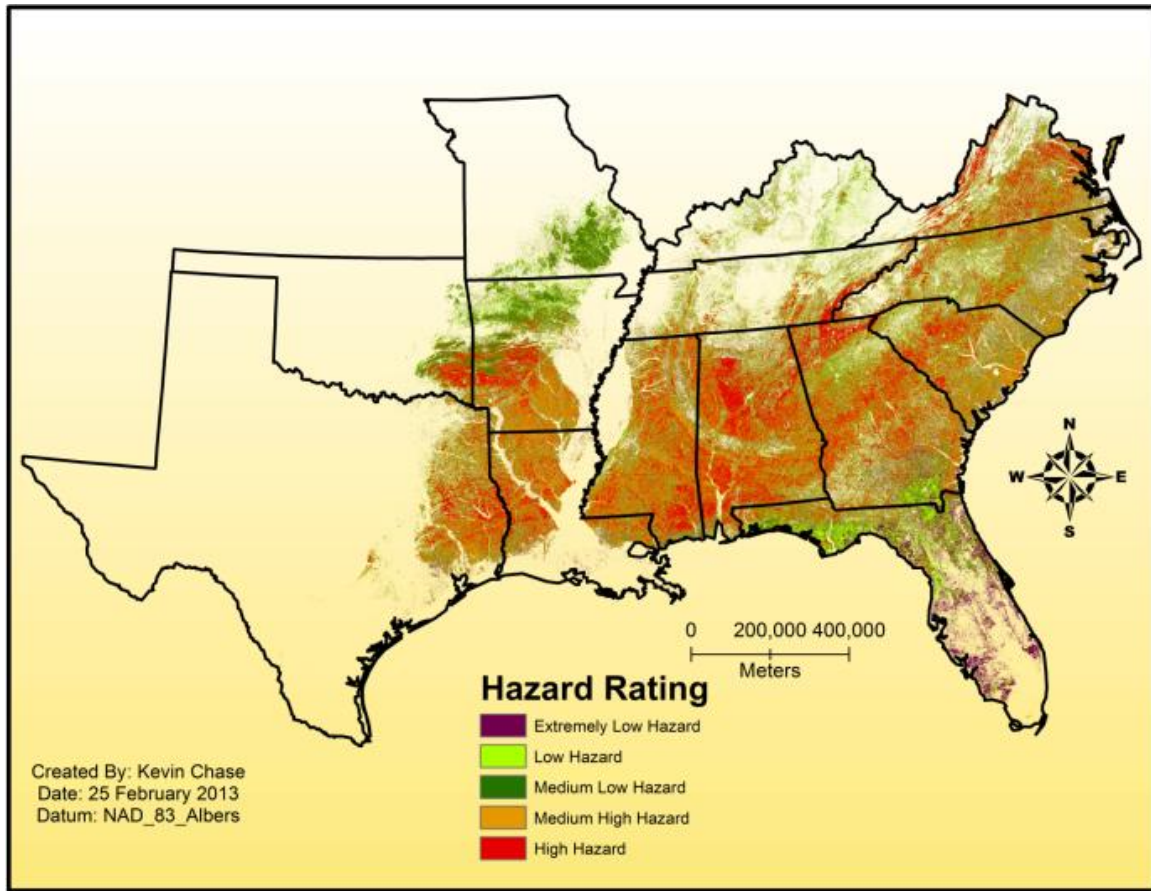


Figure 4.11 Loblolly pine model C (LPM-C) depicting *Sirex noctilio* hazard

Layers and weights used: *Pinus elliottii* (0.1), *P. taeda* (0.4), *P. echinata* (0.1), *P. palustris* (0.1), *P. virginiana* (0.3), *P. strobus* (0.5), drainage index (0.4), stand density index (0.6).

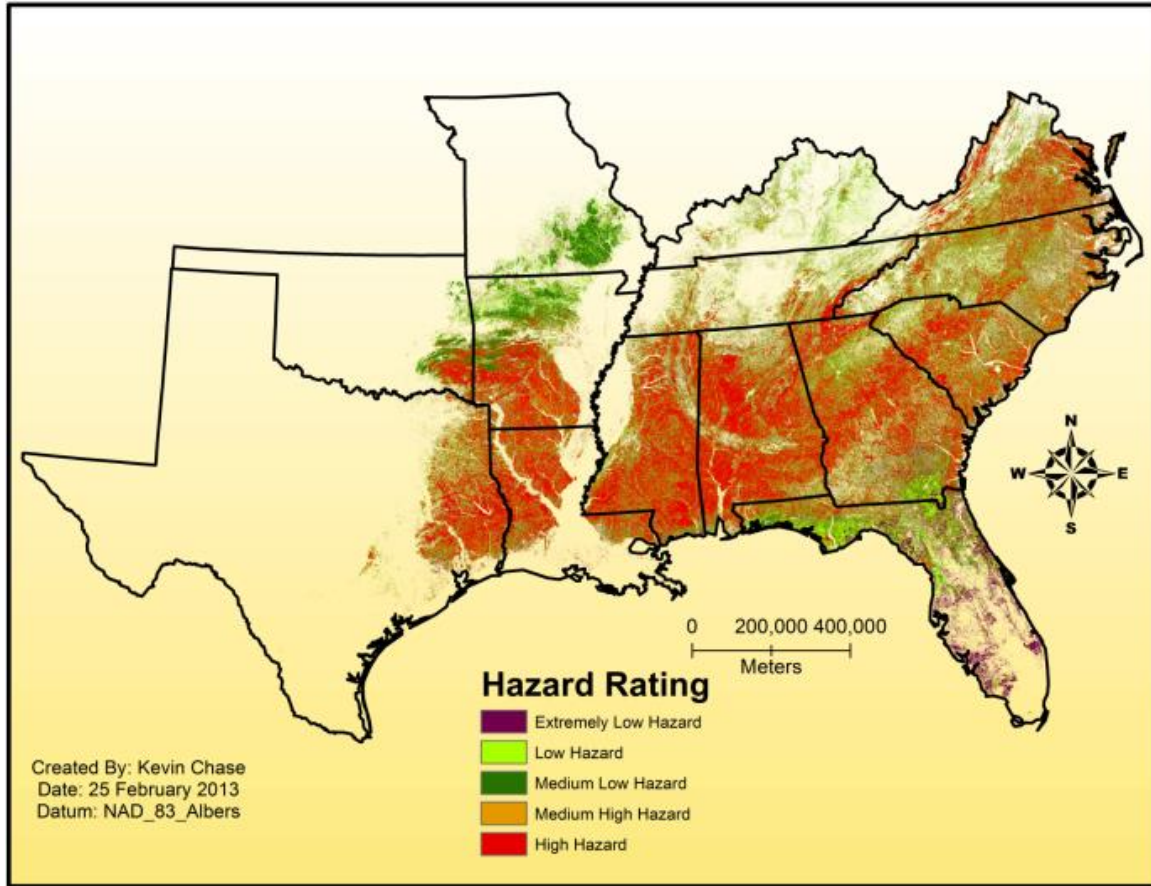


Figure 4.12 Loblolly pine model D (LPM-D) depicting *Sirex noctilio* hazard

Layers and weights used: *Pinus elliottii* (0.1), *P. taeda* (0.5), *P. echinata* (0.1), *P. palustris* (0.1), *P. virginiana* (0.3), *P. strobus* (0.5), drainage index (0.4), stand density index (0.6).

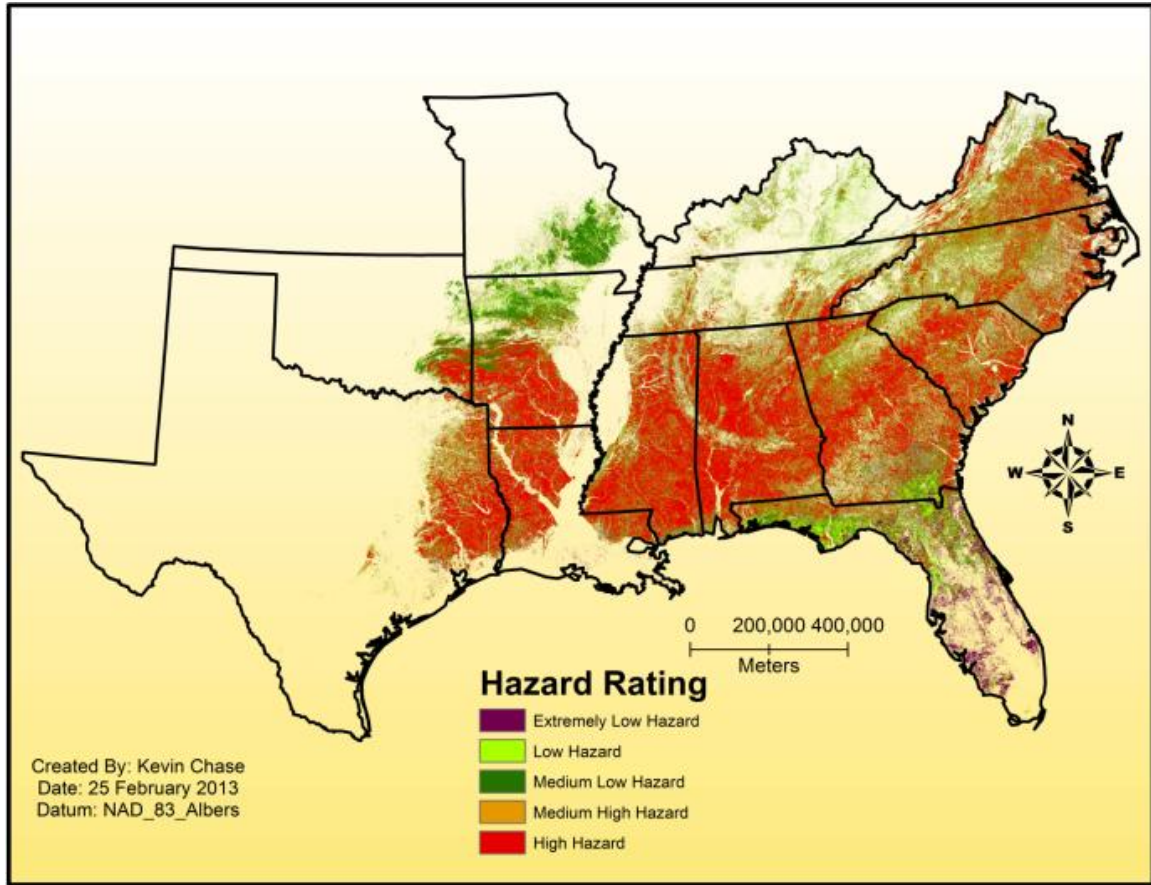


Figure 4.13 Loblolly pine model E (LPM-E) depicting *Sirex noctilio* hazard

Layers and weights used: *Pinus elliottii* (0.1), *P. taeda* (0.6), *P. echinata* (0.1), *P. palustris* (0.1), *P. virginiana* (0.3), *P. strobus* (0.5), drainage index (0.4), stand density index (0.6).



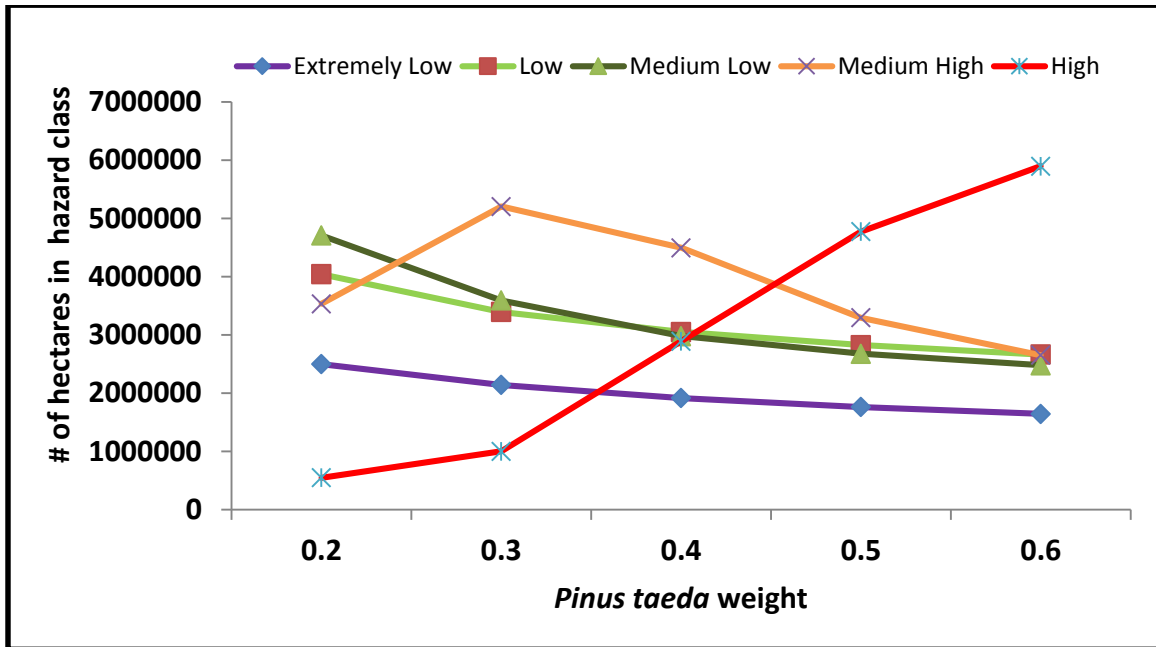


Figure 4.14 Total area in each *Sirex noctilio* hazard class across the five loblolly pine models (LPM) (Figures 4.9-4.13)

## References Cited

- Antony, F., L. R. Schimleck, and R. F. Daniles. 2012. Identification of representative sampling heights for specific gravity and moisture content in plantation-grown loblolly pine (*Pinus taeda*). *Canadian Journal of Forest Resources* 42: 574-584.
- Barnes, B. V., D. R. Zak, S. R. Denton, and S. H. Spurr. 1998. *Forest Ecology*. 4th ed. Wiley, New York.
- Bax, N., A. Williamson, M. Aguero, E. Gonzalez, and W. Geeves. 2003. Marine invasive alien species: a threat to global biodiversity. *Marine Policy* 27: 313-323.
- Baxter, C. V., K. D. Fausch, M. Murakami, and P. L. Chapman. 2004. Fish invasion restructures stream and forest food webs by interrupting reciprocal prey subsidies. *Ecology* 85: 2656-2663.
- Belanger, R. P., R. L. Hedden, and P. L. Lorio Jr. 1993. Management strategies to reduce losses from the southern pine beetle. *Southern Journal of Applied Forestry* 17: 150-154.
- Boissin, E., B. Hurley, M.J. Wingfield, R. Vasaitis, J. Stenlid, C. Davis, P. De Groot, R. Ahumada, A. Carnegie, A. Goldarazena, P. Klasmer, B. Wermelinger, and B. Slippers. 2012. Retracting the routes of introduction of invasive species: the case of *Sirex noctilio* woodwasp. *Molecular Ecology* 21: 5728-5744.
- Borchert, D., G. Fowler, and L. Jackson. 2007. Organism Pest Risk Analysis: risks to the Conterminous United States Associated with the Wood wasp, *Sirex noctilio* Fabricius, and the Symbiotic Fungus, *Amylostereum areolatum*, (Fries: Fries) Boidin. [http://www.aphis.usda.gov/plant\\_health/ea/downloads/Sirexnoctilio-0307.pdf](http://www.aphis.usda.gov/plant_health/ea/downloads/Sirexnoctilio-0307.pdf).
- Brockerhoff, E. G., J. Bain, M. Kimberley, and M. Knížek. 2006. Interception frequency of exotic bark and ambrosia beetles (Coleoptera: Scolytinae) and relationship with establishment in New Zealand and worldwide. *Canadian Journal of Forest Research* 36: 289-298.
- Carnegie, A., M. Matsuki, D. Haugen, B. Hurley, R. Ahumada, P. Klasmer, J. Sun, and E. Iede. 2006. Predicting the potential distribution of *Sirex noctilio* (Hymenoptera: Siricidae), a significant exotic pest of *Pinus* plantations. *Annals of Forest Science* 63: 119-128.
- Ciesla, W.M. 2003. European Woodwasp: a potential threat to North America's conifer forests. *Journal of Forestry* March: 18-23.
- Clarke, S.R. 2001. Review of the operationa IPM program for the southern pine beetle. *Integrated Pest Management Review*. 6: 293-301.

- Cohen, A. N., and J. T. Carlton. 1998. Accelerating invasion rate in a highly invaded estuary. *Science* 279: 555-558.
- Corley, J.C., J.M. Villacide, and O.A. Bruzzone. 2007. Spatial dynamics of a *Sirex noctilio* woodwasp population within a pine plantation in Patagonia, Argentina. *Entomologia Experimentalis et Applicata* 125: 231-236.
- Coyle, D. R., and K. J. K. Gandhi. 2012. The ecology, behavior, and biological control potential of hymenopteran parasitoids of wood wasps (Hymenoptera: Siricidae) in North America. *Environmental Entomology* 41: 731-749.
- Dinkins, J. 2011. *Sirex noctilio* host choice and no-choice bioassays: wood wasp preferences for Southeastern U.S. Pines. M.S. Thesis, University of Georgia, Athens, GA.
- Dodds, K., S.L. Garman, D.W. Ross. 2004. Landscape analysis of Douglas-fir beetle populations in northern Idaho. *Forest Ecology and Management* 231: 119-130.
- Dodds, K., R. Cooke, and D. Gilmore. 2007. Silvicultural options to reduce pine susceptibility to attack by a newly detected invasive species, *Sirex noctilio*. *Northern Journal of Applied Forestry* 24: 165-167.
- Dodds, K., P. de Groot, and D. Orwig. 2010. The impact of *Sirex noctilio* in *Pinus resinosa* and *Pinus sylvestris* stands in New York and Ontario. *Canadian Journal of Forest Research* 40: 212-223.
- Easterling, D. R., G. A. Meehl, C. Parmesan, S. A. Changnon, T. R. Karl, and L. O. Mearns. 2000. Climate extremes: observations, modeling, and impacts. *Science* 289: 2068-2074.
- Fox, T. R., H. L. Allen, T. J. Albaugh, R. Rubilar, and C. A. Carlson. 2006. Forest fertilization in southern pine plantations. *Better Crops* 90: 12-15.
- Guldin, J.M. 2011. Silvicultural Considerations in Managing Southern Pine Stands in the Context of Southern Pine Beetle. *In: Southern Pine Beetle II, General Technical Report-SRS-140*. U.S. Department of Agriculture, Forest Service, Southern Research Station, Asheville, NC, pp. 317-352.
- Haack, R. A. 2006. Exotic bark-and wood-boring Coleoptera in the United States: recent establishments and interceptions. *Canadian Journal of Forest Research* 36: 269-288.
- Haugen, D., R. Bedding, M. Underdown, and F. Neumann. 1990. National strategy for control of *Sirex noctilio* in Australia. *Australian Forest Grower* 13: 7.

- Hessburg, P. F., K. M. Reynolds, R. E. Keane, K. M. James, and R. B. Salter. 2007. Evaluating wildland fire danger and prioritizing vegetation and fuels treatment. *Forest Ecology and Management* 247: 1-17.
- Hulme, P. E. 2009. Trade, transport and trouble: managing invasive species pathways in an era of globalization. *Journal of Applied Ecology* 46: 10-18.
- Hurley, B., B. Slippers, and M. Wingfield. 2007. A comparison of control results for the alien invasive wood wasp, *Sirex noctilio*, in the Southern Hemisphere. *Agricultural and Forest Entomology* 9: 159-171.
- Iede, E.T., S.R.C. Pentead, D.C. Machado. 1989. Primeiro registro de ataque de *Sirex noctilio* em *Pinus taeda* no Brasil. EMBRAPA-CNPq, Circular Técnica, Colombo.
- Jenks, G. F. 1963. Generalization in statistical mapping. *Annals of the Association of American Geographers* 53: 15-26.
- Koch, F. H., D. Yemshanov, D.W. McKenney, and W.D. Smith. 2009. Evaluating critical uncertainty thresholds in a spatial model of forest pest invasion risk. *Risk Analysis* 29: 1227-1241.
- Logan, J.A., J. Régnière, D.R. Gray, and A.S. Munson. 2007. Risk assessment in the face of a changing environment: gypsy moth and climate change in Utah. *Ecological Applications* 17: 101-117.
- Madden, J. 1975. An analysis of an outbreak of the wood wasp, *Sirex noctilio* F. (Hymenoptera, Siricidae), in *Pinus radiata*. *Bulletin of Entomological Research* 65: 491-500.
- Mason, G. N., P. L. Lorio Jr., R. P. Belanger, and W. A. Nettleton. 1985. Rating the susceptibility of stands to southern pine beetle attack. *Agric. Handb.* 645. Washington, DC: U.S. Department of Agriculture Forest Service, Cooperative State Research Service: 31 pp.
- Miller, D., and A. Clark. 1935. *Sirex noctilio* (Hym.) and its Parasite in New Zealand. Cambridge Univ Press, New York, NY.
- Molnar, J. L., R. L. Gamboa, C. Revenga, and M. D. Spalding. 2008. Assessing the global threat of invasive species to marine biodiversity. *Frontiers in Ecology and the Environment* 6: 485-492.
- Mooney, H., and E. Cleland. 2001. The evolutionary impact of invasive species. *Proceedings of the National Academy of Sciences* 98: 5446-5451.
- Morgan, F. D. 1989. Forty years of *Sirex noctilio* and *Ips grandicollis* in Australia. *New Zealand Journal of Forestry Science* 19: 198-209.

- Pimentel, D., R. Zuniga, and D. Morrison. 2005. Update on the environmental and economic costs associated with alien-invasive species in the United States. *Ecological Economics* 52: 273-288.
- Price, T., K. A. Brownell, M. Raines, C. L. Smith, and K. J. K. Gandhi. 2011. Multiple detections of two exotic auger beetles of the genus *Sinoxylon* (Coleoptera: Bostrichidae) in Georgia, USA. *Florida Entomologist* 94: 354-355.
- Rawlings, G. 1955. Epidemics in *Pinus radiata* forests in New Zealand. *New Zealand Journal of Forestry* 7: 53-55.
- Rawlings, G. B., and N. M. Wilson. 1949. *Sirex noctilio* as a beneficial and destructive insect to *Pinus radiata* in New Zealand. *New Zealand Journal of Forestry* 6: 1-11.
- Reineke, L.H. 1933. Perfecting a stand-density index for even-aged forests. *Journal of Agricultural Research* 46:627-638.
- Ricciardi, A., R. J. Neves, and J. B. Rasmussen. 1998. Impending extinctions of North American freshwater mussels (Unionoida) following the zebra mussel (*Dreissena polymorpha*) invasion. *Journal of Animal Ecology* 67: 613-619.
- Ryan, K., P. de Groot, and S. M. Smith. 2011a. Evidence of interaction between *Sirex noctilio* and other species inhabiting the bole of *Pinus*. *Agricultural and Forest Entomology* 14:187-195.
- Ryan, K., P. de Groot, C. Davis, and S. Smith. 2011b. Effect of two bark beetle-vectored fungi on the on-host search and oviposition behavior of the introduced wood wasp *Sirex noctilio* (Hymenoptera: Siricidae) on *Pinus sylvestris* trees and logs. *Journal of Insect Behavior*: 1-14.
- Schaetzl, R.J., F.J. Krist, K. Stanley, and C.M. Hupy. 2009. The natural soil drainage index: an ordinal index of long-term soil wetness. *Physical Geography* 30: 383-409.
- Schiff, N., A. Goulet, D. Smith, C. Boudreault, A. Wilson, and B. Scheffler. 2012. Siricidae (Hymenoptera: Symphyta: Siricoidea) of the Western Hemisphere. *Canadian Journal of Arthropod Identification* 21:1-305.
- Smith, W. B., J. S. Vissage, D. R. Darr and, R. M. Sheffield. 2001. Forest Resources of the United States, 1997. General Technical Report NC-219. St. Paul, MN: U.S. Dept. of Agriculture, Forest Service, North Central Research Station.
- Standley, C. R., E. R. Hoebeke, D. Parry, D. C. Allen, and M. K. Fierke. 2012. Detection and Identification of Two New Native Hymenopteran Parasitoids Associated with the Exotic *Sirex noctilio* in North America. *Proceedings of the Entomological Society of Washington* 114: 238-249.

- Stephen, F. M. and M. P. Lih. 1985. A *Dendroctonus frontalis* infestation growth model: organization, refinement, and utilization. In: Branham, S.J.; Thatcher, R.C., eds. Integrated Pest Management research symposium: the proceedings. Gen. Tech. Rep. S056. New Orleans, LA: U.S. Department of Agriculture Forest Service, Southern Forest Experiment Station: 186-194.
- Tribe, G., and J. Cillie. 2004. The spread of *Sirex noctilio* Fabricius (Hymenoptera: Siricidae) in South African pine plantations and the introduction and establishment of its biological control agents. African entomology 12: 9-17.
- Tsutsui, .D., A.V. Suarez, and R.K. Grosberg. 2003. Genetic diversity, asymmetrical aggression, and recognition in a widespread invasive species. PNAS 100:10778 - 1083.
- Venette, R. S., D. J. Kriticos, R. D. Magarey, F. H. Koch, R. H. A. Baker, S. P. Worner, N. N. G. Raboteaux, D. W. McKenney, E. J. Dobesberger, D. Yemshanov, P. J. De Barro, W. D. Hutchison, G. Fowler, T. M. Kalaris, and J. Pedlar. 2010. Pest risk maps for invasive alien species: a roadmap for improvement. Bioscience 60: 349 -362.
- Wang, H., R. Fu., A. Kumar, and W. Li. 2010. Intensification of summer rainfall variability in the Southeastern United States during recent decades. Journal of Hydrometeorology 11:1007-1018.
- Wilcove, D. S., D. Rothstein, J. Dubow, A. Phillips, and E. Losos. 1998. Quantifying threats to imperiled species in the United States. BioScience 48: 607-615.
- Worner, S.P. and M. Gevrey. 2006. Modelling global insect pest species assemblages to determine risk of invasion. Journal of Applied Ecology 43: 858-867.
- Yemshanov, D., F. Koch, Y. Ben Haim, and W. Smith. 2010. Robustness of risk maps and survey networks to knowledge gaps about a new invasive pest. Risk Analysis 30: 261-276.