The impact of *Sirex noctilio* in *Pinus resinosa* and *Pinus sylvestris* stands in New York and Ontario

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Abstract: *Sirex noctilio* Fabricius has a long history as an invasive insect species in pine plantations throughout the Southern Hemisphere and has been recently discovered in North America, where it is uncertain how this insect will behave in pine ecosystems. To assess the impact and attack behavior of *S. noctilio*, forest surveys and measurements from attacked and unattacked trees were taken in nine *Pinus resinosa* Ait. and *Pinus sylvestris* L. plantations in New York, USA, and Ontario, Canada. There was a trend of *S. noctilio* attacking suppressed trees with smaller live crowns and reduced growth. Some *S. noctilio* attacks were also found in dominant crown classes but at a lower rate than overtopped or intermediate classes. *Sirex noctilio* appeared to have more of an impact in *P. sylvestris* forests, as they attacked more stems (9%–18%) and higher basal area (1.6–5.5 m^2/ha) than *P. resinosa* stands (3%–8% of stems and 0.4–2.4 m^2/ha). Dead trees with signs of Siricidae and dead from other causes were also quantified, and in some *P. resinosa* stands, levels were greater in magnitude than *S. noctilio* losses. Data from this study suggest that silvicultural treatments should be a key component of integrated pest management plans for *S. noctilio*.

Résumé : *Sirex noctilio* Fabricius est connu depuis longtemps comme une espèce invasive d’insecte dans les plantations de pin partout dans l’hémisphère Sud et a récemment été découvert en Amérique du Nord où l’on ignore le comportement qu’aura cet insecte dans les écosystèmes où le pin est présent. Afin d’évaluer l’impact et le comportement d’attaque de *S. noctilio*, des inventaires forestiers et des mesures sur des arbres attaqués et intacts ont été prises dans neuf plantations de *Pinus resinosa* Ait. et de *Pinus sylvestris* L. dans l’État de New York, aux États-Unis, et en Ontario, au Canada. L’insecte avait tendance à attaquer les arbres supprimés dont la croissance était faible et la cime vivante plus petite. Certaines attaques de *S. noctilio* ont été observées dans les classes de cime dominantes mais avec une fréquence plus faible que dans les classes intermédiaire ou supprimée. L’insecte a semblé avoir plus d’impact dans les forêts de *P. sylvestris* où il a attaqué plus de tiges (9 %–18 %) et une plus grande surface terrière (1,6–5,5 m^2/ha) que dans les peuplements de *P. resinosa* (3 %–8 % des tiges et 0,4–2,4 m^2/ha). Les arbres morts portant des signes de Siricidae et les arbres dont la mort était due à d’autres causes ont aussi été quantifiés et leurs niveaux étaient plus élevés que les pertes causées par *S. noctilio* dans certains peuplements de *P. resinosa*. Les données provenant de cette étude indiquent que des traitements sylvicoles devraient être une composante essentielle des programmes de lutte antiparasitaire intégrée dans le cas de *S. noctilio*.

[Traduit par la Rédaction]

Introduction

North America has a lengthy history of invasive species introductions that have changed the composition, structure, and functionality of forested ecosystems (Liebhold et al. 1995; Orwig 2002; Haack 2006). Exotic species have been arriving at an increased rate over the past 100 years (Sailer 1983; Hendrickson 2002) and are a threat to the future integrity of native, commercial, and urban forests. At least 585 exotic and invasive phytophagous species have established in the forests of the United States and Canada (Mattson et al. 1994; Langor et al. 2009), but little is known about the impacts of many species (Kenis et al. 2009). Impacts can be severe, such is the case of emerald ash borer (*Agrilus planipennis* Fairmaire) and redbay ambrosia beetle (*Xyleborus glabratus* Eichhoff), which both demonstrate the extreme of invasive introductions and threaten to extirpate several tree species from North America (Poland and McCullough 2006; Mayfield 2007). In many introductions, however, ecological impacts are hard to define or accurately assess, as little apparent damage is observed.

In 2004, *Sirex noctilio* Fabricius (Hymenoptera: Siricidae) joined the growing list of invasive forest pests detected in North America (Hoebeke et al. 2005; de Groot et al. 2007). *Sirex noctilio* has been a successful invader of commercial plantations of North American pine species throughout the Southern Hemisphere where it has caused considerable economic damage (Madden 1988; Tribe 1995; Iede et al. 1998). Prior to being found established in forests in 2005, *S. noctilio* had periodically been detected at North American ports of entry (Ciesla 2003). Host volatile based trapping surveys conducted from 2005 to 2008 over gradually larger portions

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of the northeastern and midwestern United States, Ontario, and portions of Quebec, New Brunswick, and Nova Scotia indicated that *S. noctilio* was established over a large area, including west-central New York, northern Pennsylvania, eastern Michigan, northern Vermont, southern Ontario, and western Quebec (Fig. 1). The large geographical extent of known *S. noctilio* detections suggests that this insect was present in North America prior to its detection in 2004.

While insight has been gained into factors contributing to epidemic populations of *S. noctilio* in Southern Hemisphere commercial forests (Neumann et al. 1987), little is known about how this insect behaves in its endemic habitat. Siricidae in Eurasia are generally considered secondary species colonizing trees in weakened condition or suffering from other biotic or abiotic disturbances (Hall 1968; Spradbery and Kirk 1978). However, *S. noctilio* appears to have an expanded niche compared with other Siricidae, successfully colonizing stressed trees in better physiological condition than available to other siricid species (Spradbery 1973; Spradbery and Kirk 1978; Spradbery and Kirk 1981). *Sirex noctilio* has been reported to have a larger reservoir of phytotoxic mucus than other siricids (Spradbery 1977) and this may be the mechanism that has led to an expanded niche of living, stressed trees. Even with the ability to colonize living trees, there are few reports of tree losses caused by *S. noctilio* in Eurasian forests (Spradbery and Kirk 1981).

Various factors can influence population levels of forest insects and the resultant damage from reproductive activities or feeding. For *S. noctilio* in the Southern Hemisphere, characteristics that have contributed to outbreaks and high levels of damage appear to be even-aged pure pine plantations covering large areas and containing overstocked stand conditions (McKimm and Walls 1980; Neumann et al. 1987). In these stands, smaller, weakened, and suppressed trees are generally the preferred host trees for *S. noctilio*, allowing populations to build locally (Madden 1975; McKimm and Walls 1980; Neumann and Minko 1981). North American forests where *S. noctilio* has been detected are generally more similar in structure to natural forests than commercial plantations where *S. noctilio* has thrived (Dodds et al. 2007; Dodds and de Groot 2010). Much of this region contains forests with relatively high tree diversity and heterogeneous landscapes compared with the homogenous landscapes of single-species plantations where this insect has been problematic. Because of the differences in landscapes and forest structure between where it has been invasive and where it is currently established in North America, it is unknown what ecological impacts *S. noctilio* may have on regional forests.

The introduction of *S. noctilio* into North America provides a unique opportunity to study an insect species that has been highly invasive on North American pine species but, to date, only where these species have been grown outside their range in commercial plantations in the Southern Hemisphere. While documented host species exist throughout North America, it is unknown how *S. noctilio* will respond to them when growing in their native ecosystems. Several confirmed host pine species grow naturally or are planted throughout the area currently inhabited by *S. noctilio*, including *Pinus resinosa* Ait., *Pinus strobus* L., and *Pinus banksiana* Lamb., and all have been confirmed as host species (Dodds et al. 2007). In addition to the North American pines present in this area, *Pinus sylvestris* L. also exists in managed and unmanaged plantations or Christmas tree farms and provides *S. noctilio* a host species from its native range.

To evaluate management options for *S. noctilio* in the currently infested area in North America, it is critical to assess the potential impacts that this insect might have in central North American pine forests. Insights gained from *S. noctilio* behavior in pine forests could provide important information for the development and implementation of integrated pest management plans similar to those created elsewhere (e.g., Haugen et al. 1990). The objectives of this study were to (*i*) describe *P. resinosa* and *P. sylvestris* stands recently colonized by *S. noctilio* and assess damage caused by this insect and (*ii*) describe previous growth patterns and tree characteristics of *P. resinosa* and *P. sylvestris* trees with and without *S. noctilio* attack.

Materials and methods

Study areas

Surveys to assess the impacts of *S. noctilio* on pine stands were concentrated in west-central New York and southern Ontario (Fig. 1). Surveys in New York were conducted in the summers of 2006 and 2007, while stands in southern Ontario were sampled in the fall of 2008. Six *P. resinosa* and three *P. sylvestris* stands were surveyed for this study (Table 1). Stands consisted of 70%–99% of total basal area in pine.

Determining the presence of *S. noctilio* in a stand

To determine the presence of *S. noctilio*, pine stands in the known infested area were surveyed for symptoms of attack including resin beads and exit holes. Initial large-scale surveys of pine stands suggested that *S. noctilio* was rarely found in managed stands. Consequently, forests that had received limited silvicultural treatments, were overstocked, or were in poor condition were the eventual focus of surveys. Trees in these stands were examined for small resin beading, a characteristic that has been confirmed as a strong indication of *S. noctilio* attack on pine trees in North America and elsewhere (Haugen and Hoebeke 2005). In terms of the Siricidae, this type of resin beading is unique to *S. noctilio* and occurs as a result of a living tree's resin defense responding to female oviposition attempts. Native siricids colonize dead trees that lack active resin defenses and therefore do not produce resin beads. Resin beading is also easily differentiated from symptoms of other bark beetles and woodborers. Round exit holes (approximately 2–6 mm in diameter), in combination with resin beads or drips, further support the presence of *S. noctilio* in a stand and were used to determine if *S. noctilio* was or had been present in a stand over the previous 1–2 years. If symptoms of *S. noctilio* presence were located, forest stand surveys were commenced.

Forest stand surveys

Once *S. noctilio* infested trees were located, walk-through surveys were conducted to determine the spatial extent of each stand. The size and shape of selected stands varied, but in all cases, approximately 10% of the total stand area was sampled with between four and nine plots. Fixed-radius

Fig. 1. The currently known distribution of *Sirex noctilio*, as of 2008, in North America and location of study sites in New York and southern Ontario. Darkened counties are positive for *S. noctilio.*

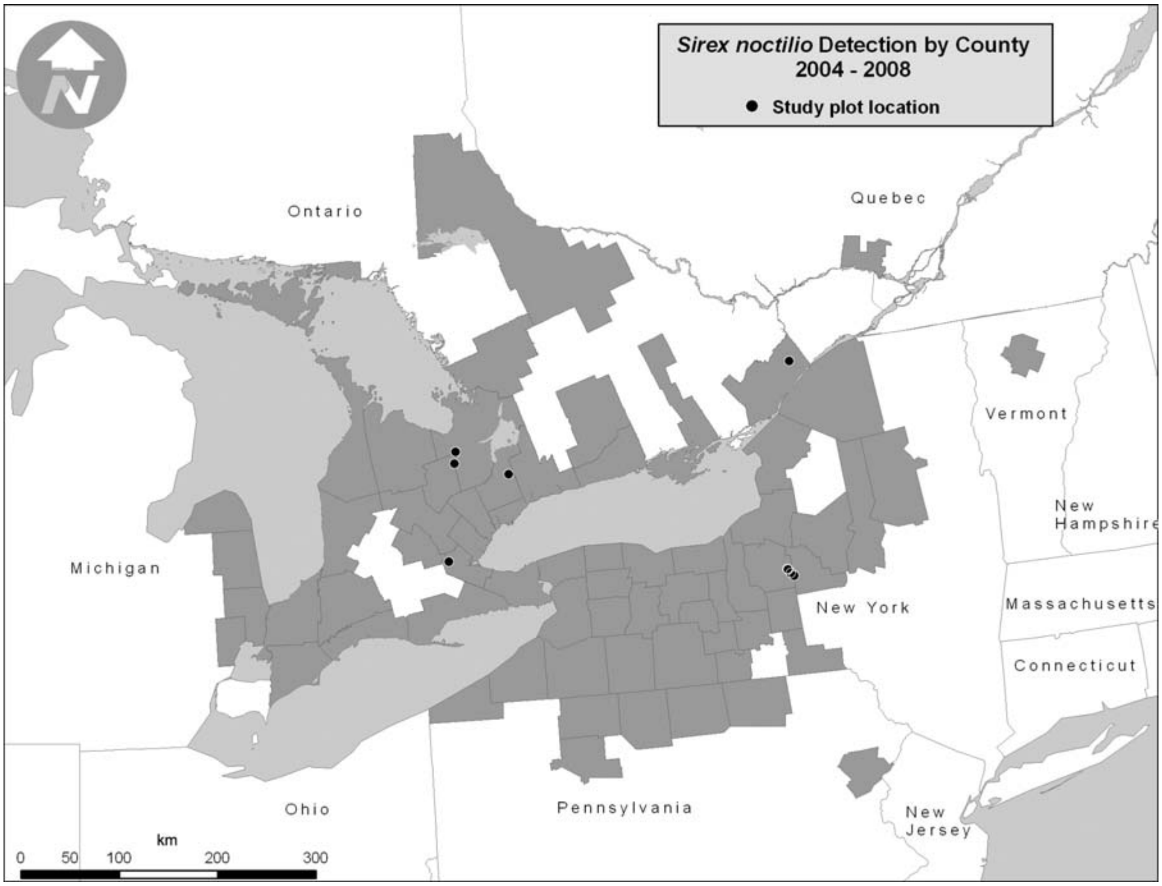


Table 1. Stand type, size, ownership, and forest origin of pine stands surveyed for *Sirex noctilio* in west-central New York and southern Ontario.

Stand location	Dominant pine	Approximate size (ha)	Land ownership	Forest origin
Brentwood (Ontario)	*P. resinosa*	1.1	County	Plantation
Cazenovia (New York)	*P. resinosa*	1.5	Private	Plantation
Limerick (Ontario)	*P. resinosa*	1.3	County	Plantation
North Tract (Ontario)	*P. resinosa*	0.6	County	Plantation
Simcoe (Ontario)	*P. resinosa*	1.4	County	Plantation
Westfield (Ontario)	*P. resinosa*	0.6	Private	Plantation
Indian Hills (New York)	*P. sylvestris*	1.2	Private	Plantation
Pompey (New York)	*P. sylvestris*	1.8	Private	Christmas tree farm
Windy Hill (New York)	*P. sylvestris*	1.6	Private	Christmas tree farm

(7 m) circular plots were randomly placed throughout each stand to estimate tree and stand parameters and *S. noctilio* activity at each site. Each plot was separated by at least 25 m and no data were taken from within 15 m of any stand edge. For every tree over 7.5 cm diameter at breast height (DBH) in each plot, tree species, DBH, crown class, living or dead, and presence or absence of *S. noctilio* indicators (resin beads, exit holes, none) were recorded. Binoculars were used to examine the tree for exit holes and resin beads. If a tree was dead or dying, it was classified as having either *S. noctilio* present, Siricidae exit holes present, or dead from other causes. The classification "dead from other causes" included trees showing signs of pathogens, bark beetles, or other undetermined causes. Crown classes were differentiated based on exposure to light, including overtopped, intermediate, codominant, and dominant (Smith 1986). Plot level data were expanded to a per hectare basis (Husch et al. 2003).

Determining the presence of *S. noctilio* in a tree

Because of the complexity of North American conifer ecosystems and the presence of numerous native insects, tree mortality could only be attributed to *S. noctilio* within a 2-year period following attack. Trees with resin beads, no round exit holes, and some crown still present (green, fading, or brown) were considered attacked during the survey year. Trees with round exit holes and resin beads present were considered attacked during the previous year, with adults emerging during the survey year. Trees with round exit holes and no resin beads were often present in the stands and may have been colonized by *S. noctilio*, but it was not possible to conclusively classify these as attacked by the invasive insect and therefore, they were classified as colonized by a siricid. Round exit holes are more problematic for diagnostic use in North America compared with the Southern Hemisphere because native woodborers (e.g., Cerambycidae, Siricidae) make similar type holes when leaving a brood tree. While it is possible to determine what genera or species created some of these exit holes (e.g., *Monochamus* spp. and other phloem/xylem feeders) by the shape and presence of larval galleries on the surface of the phloem and xylem and by insect frass, there is currently no way of separating native Siricidae exit holes from those created by *S. noctilio*. If round exit holes indicative of a siricid were present, crown condition, presence of resin beading, and timing during the year of the survey were all evaluated to determine if a tree had been colonized by *S. noctilio*. If no siricid exit holes were located on dead or dying trees, then these were classified as dead from other causes.

Dendroecological sampling

Pine trees of similar diameter with and without *S. noctilio* attack were cored in each stand for age determinations and radial growth analyses. One increment core from each tree was taken at breast height (approximately 1.4 m). Whenever possible, cores were taken from trees within the 7 m fixed radius vegetation plots. In some cases, *S. noctilio* attacked trees were not found within vegetation plots and trees from outside plot boundaries were sampled. All increment cores were air dried, sanded, and aged with a dissecting microscope, and annual rings were measured to the nearest 0.01 mm using a Velmex measuring system (Velmex, East Bloomfield, New York). Tree age was considered as the number of rings measured, with no additional estimation for cores that missed the pith. Average growth over the lifespan of the tree, over the previous 10 years, and over the previous 5 years was determined for both *S. noctilio* attacked and unattacked trees at each site. At the time when increment cores were taken, crown class, DBH, total tree height, and height to the base of the live crown were measured for every tree that was cored. A Haglöf Vertex IV Hypsometer or a clinometer was used to estimate tree height measurements.

Statistics

Average diameters of trees that were alive at the time of sampling, had *S. noctilio* present, had Siricidae exit holes present, or were dead from unknown causes were analyzed with a one-way ANOVA and mean differences were separated with Tukey's HSD pairwise comparisons. Normality and heteroscedasticity were checked during each test, but transformations were not needed. Average growth rates determined from increment cores and live crown ratios of attacked and unattacked trees were tested for differences using *t* tests. Analyses were conducted in JMP version 6.0.3 (SAS Institute Inc., Cary, North Carolina).

Results

Sirex noctilio infested *P. resinosa*

Pinus resinosa stands infested with *S. noctilio* varied in the level of management and disturbance that had occurred since stand initiation. Two privately owned stands (Cazenovia and Westfield) experienced no management activity since planting approximately 30–45 years ago, while others had evidence of thinning. Basal area of living trees ranged from 16.3 to 36.1 m^2/ha, with pine accounting for over 90% of the basal area in all stands but one. Live pine tree density ranged from 292 to 1191 stems/ha, with most stands in the 700–900 stems/ha range (Table 2). In all but one stand (Cazenovia), over 90% of stems were *P. resinosa*. Other trees found in stands included *Acer saccharum* Marsh., *Acer rubrum* L., *Fraxinus americana* L., *Picea abies* (L.) Karst., *P. sylvestris*, *P. strobus*, and *Prunus serotina* Ehrh.

Mortality in *P. resinosa* stands resulting from *S. noctilio* attack ranged from 3.2% to 8.2% of stems (Fig. 2). There was a strong association between total basal area and number of *S. noctilio* killed trees (R^2 = 0.70). The highest amount of basal area attacked by *S. noctilio* was found at Westfield (2.4 m^2/ha), with the lowest levels at Brentwood (0.4 m^2/ha) (Table 2). In all but Westfield, definitive *S. noctilio* attacks only occurred during the year of stand surveys. In four of the six stands, trees attacked by *S. noctilio* had significantly smaller diameters than unattacked trees (Table 3).

There was a large range in the percentage of trees showing signs of Siricidae exit holes present or dying from other causes, and in several cases, the levels were higher than trees showing *S. noctilio* signs (Fig. 2). Between 2.8% and 22.4% of sampled trees had Siricidae exit holes present, while trees dead from other causes ranged from 3.4% to 19.4%. Basal area of trees with Siricidae exit holes ranged from 0.5 to 5.5 m^2/ha, while dead basal area from other causes ranged from 0.3 to 4.3 m^2/ha (Table 2). As was the case for trees attacked by *S. noctilio*, trees with Siricidae exit holes or dead from unknown causes had significantly smaller diameters than living trees in four of the six *P. resinosa* stands (Table 3).

Crown class distributions with signs of *S. noctilio* present, Siricidae exit holes, or dead from other causes are shown in Fig. 3. In most *P. resinosa* stands, there were few overtopped and intermediate crown class trees available. When these trees were present in a stand, most were killed or attacked by *S. noctilio*, had signs of Siricidae exit holes, or had signs of other mortality agents. Mortality varied in each stand, but *S. noctilio* attacked all canopy classes. Trees classified as having Siricidae exit holes present or dying from other causes were frequent in stands and in most cases followed a similar pattern as trees with signs of *S. noctilio*.

Pinus resinosa growth rates and tree characteristics

There was a trend in all stands that *P. resinosa* attacked by *S. noctilio* were growing slower prior to attack than trees without the insect (Table 4). However, in only three of the six stands were these differences statistically significant (Table 4). Average live crown ratio for *S. noctilio* attacked trees ranged from 20% to 32%, while that for unattacked trees ranged from 30% to 47% (Table 5). Of the six *P. res-*

Table 2. Stand-level variables and estimates of tree mortality for *Pinus resinosa* stands surveyed for *Sirex noctilio* in west-central New York and southern Ontario.

	Stand					
Variable	Brentwood	Cazenovia	Limerick	North Tract	Simcoe	Westfield
No. of living trees/ha	796	719	804	292	1191	893
Living basal area (m^2/ha)	24.9	31.8	36.1	16.3	34.9	34.7
Live pine basal area (m^2/ha)	24.2	22.1	32.9	15.5	34.7	34.0
Basal area attacked by *S. noctilio* (m^2/ha)	0.4	1.4	0.9	0.6	0.8	2.4
Basal area with Siricidae exit holes (m^2/ha)	0.6	0.7	0.5	3.2	3.3	5.5
Basal area dead from unknown causes (m^2/ha)	0.5	3.6	0.3	4.3	2.5	1.6
Average stand age (years ± SE)	28 ± 1	28 ± 1	31 ± 1	63 ± 2	34 ± 1	46 ± 1

Fig. 2. Percent mortality of tree stems with signs of *Sirex noctilio*, Siricidae exit holes, or dead from other causes in six *Pinus resinosa* dominated stands.

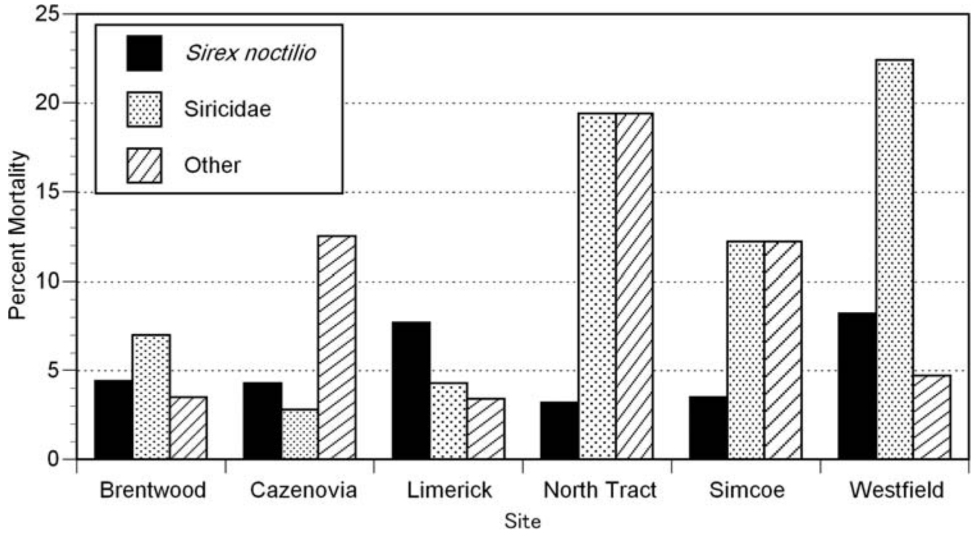


Table 3. Average diameter (cm ± SE) at breast height (1.4 m) of trees classified as unattacked, attacked by *Sirex noctilio*, having Siricidae exit holes present, or dead from unknown causes in *Pinus resinosa* and *Pinus sylvestris* stands.

	Alive		*Sirex noctilio*		Siricidae		Unknown		
Stand	*N*	Diameter	*N*	Diameter	*N*	Diameter	*N*	Diameter	*P*
Pinus resinosa									
Brentwood	97	19.4 ± 0.4a	7	11.8 ± 1.4b	7	10.9 ± 1.4b	4	13.2 ± 1.8b	**<0.0001**
Cazenovia	58	19.7 ± 0.3a	3	21.6 ± 1.3a	2	19.3 ± 1.5a	9	20.3 ± 0.7a	0.4248
Limerick	99	22.0 ± 0.6a	9	12.3 ± 1.9b	5	12.3 ± 2.6b	4	11.0 ± 2.9b	**<0.0001**
North Tract	18	25.5 ± 1.1a	1	21.2a	3	18.8 ± 2.8a	9	22.8 ± 1.6a	0.135
Simcoe	164	18.8 ± 0.3a	8	12.9 ± 1.4b	29	14.1 ± 0.7b	28	12.2 ± 0.8b	**<0.0001**
Westfield	55	21.6 ± 0.5a	7	16.0 ± 1.5b	19	14.8 ± 0.9b	4	17.3 ± 2.0ab	**<0.0001**
Pinus sylvestris									
Indian Hills	113	16.4 ± 0.4a	6	11.5 ± 1.5b	0	na	3	11.0 ± 2.2b	**0.0008**
Windy Hill	91	20.2 ± 0.4a	15	14.7 ± 1.0b	5	15.1 ± 1.7b	3	18.8 ± 2.2ab	**<0.0001**
Pompey	73	22.9 ± 0.5a	20	20.1 ± 1.0ab	8	18.2 ± 1.6b	9	15.5 ± 1.5b	**<0.0001**

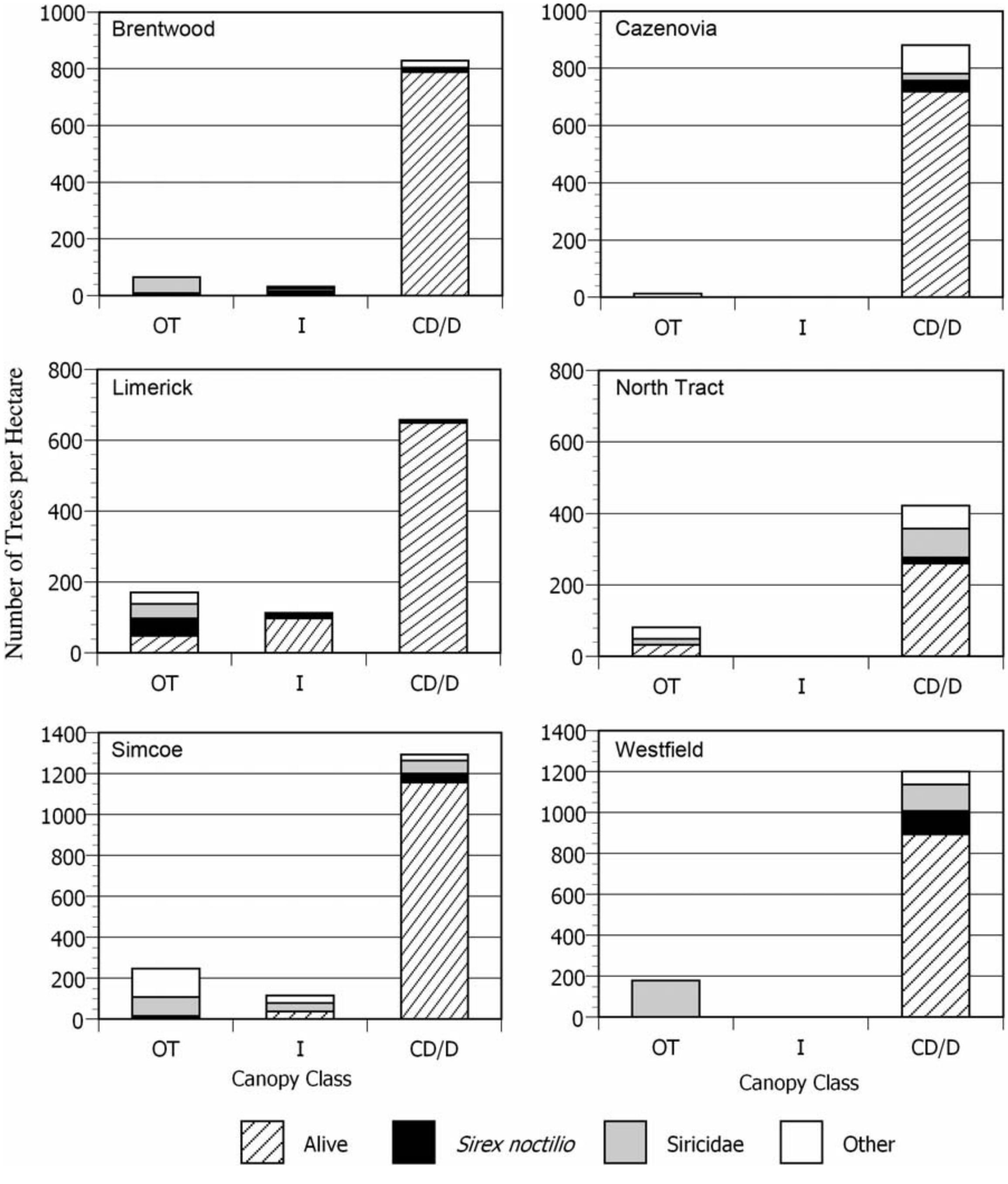
Note: Average diameters were compared with a one-way ANOVA. Means followed by the same letter within a row are not significantly different (Tukey's HSD, $P > 0.05$). na, not applicable.

inosa stands sampled, live crown ratios were significantly smaller on trees attacked by *S. noctilio* in four stands.

Sirex noctilio infested *P. sylvestris*

Pinus sylvestris stands attacked by *S. noctilio* originated from either Christmas tree farms or plantations that received little to no management since initiation. Number of living pine trees ranged from 613 to 1411 stems/ha, and basal area of living trees ranged from 31.9 m^2/ha at Indian Hills and Pompey to 33.6 m^2/ha in Windy Hills (Table 6). The three

Fig. 3. Mortality factors by crown class in *Pinus resinosa* stands in New York and Ontario. Note that the scale of the *y*-axis varies among graphs.



stands had at least 80% of basal area in *P. sylvestris*. Other trees present in stands included *Robinia pseudoacacia* L., *A. rubrum*, *F. americana*, and *P. serotina*.

Sirex noctilio caused tree mortality ranged from 9% to 18% of trees in *P. sylvestris* stands (Fig. 4). There was a strong association between total basal area and number of *S. noctilio* killed trees (R^2 = 0.88). *Sirex noctilio* attacked the largest amount of basal area in Pompey and lower levels at Indian Hills (Table 6). Two years of *S. noctilio* activity was found in Pompey and Windy Hill, sites that were approximately 6 km apart. Average diameters of *S. noctilio* attacked trees ranged from 11.8 to 20.1 cm and were smaller than unattacked trees in each stand (Table 3).

In addition to having the highest percentage of trees with *S. noctilio*, Pompey also had the highest percentage of trees with Siricidae exit holes present or dead from other causes (Fig. 4). Between 0% and 7.3% of sampled *P. sylvestris* trees showed signs of Siricidae exit holes present, while trees dying from other causes ranged from 2.5% to 7.3% of trees. Basal area with Siricidae exit holes present ranged from 0 to 1.9 m^2/ha, while amounts classified as dead from other causes ranged from 0.4 to 1.3 m^2/ha (Table 6). As was

Table 4. Average overall, previous 10-year, and previous 5-year growth rates (mm ± SE) of *Pinus resinosa* and *Pinus sylvestris* attacked and unattacked by *Sirex noctilio*.

	Overall growth rate			10-year growth rate			5-year growth rate		
Stand	Attacked	Unattacked	*P*	Attacked	Unattacked	*P*	Attacked	Unattacked	*P*
Pinus resinosa									
Brentwood	1.85 ± 0.12	2.48 ± 0.13	**0.005**	0.55 ± 0.12	0.98 ± 0.14	**0.04**	0.27 ± 0.07	0.71 ± 0.10	**0.004**
Cazenovia	2.65 ± 0.14	2.81 ± 0.12	0.36	0.54 ± 0.08	0.57 ± 0.03	0.77	0.41 ± 0.09	0.47 ± 0.05	0.55
Limerick	1.72 ± 0.13	2.71 ± 0.24	**0.002**	0.37 ± 0.06	1.23 ± 0.17	**0.0001**	0.18 ± 0.03	1.13 ± 0.20	**0.0001**
North Tract	1.69 ± 0.14	2.03 ± 0.22	0.29	0.28 ± 0.03	0.34 ± 0.06	0.48	0.23 ± 0.04	0.24 ± 0.05	0.82
Simcoe	1.72 ± 0.13	2.23 ± 0.13	**0.015**	0.44 ± 0.10	0.93 ± 0.15	**0.016**	0.37 ± 0.11	0.81 ± 0.13	**0.019**
Westfield	1.57 ± 0.06	1.79 ± 0.14	0.183	0.27 ± 0.04	0.38 ± 0.08	0.25	0.18 ± 0.03	0.22 ± 0.05	0.50
Pinus sylvestris									
Indian Hills	1.80 ± 0.25	1.87 ± 0.22	0.49	0.42 ± 0.07	0.67 ± 0.10	**0.052**	0.26 ± 0.04	0.55 ± 0.09	**0.008**
Pompey	1.95 ± 0.09	2.25 ± 0.11	**0.047**	0.39 ± 0.07	0.88 ± 0.09	**0.0002**	0.35 ± 0.08	0.81 ± 0.10	**0.001**
Windy Hill	1.77 ± 0.05	1.87 ± 0.01	0.38	0.54 ± 0.05	0.49 ± 0.06	0.52	0.30 ± 0.04	0.43 ± 0.06	0.10

Table 5. Average live crown ratio estimates (±SE) of *Pinus resinosa* and *Pinus sylvestris* attacked and unattacked by *Sirex noctilio*.

Stand	df	Attacked	Unattacked	*P*
Pinus resinosa				
Brentwood	10	25.81 ± 3.31	46.83 ± 3.52	**0.0015**
Cazenovia	24	32.22 ± 2.45	39.92 ± 1.60	**0.0146**
Limerick	20	28.78 ± 4.57	39.05 ± 2.04	**0.0536**
North Tract	6	23.43 ± 3.94	37.30 ± 2.28	**0.0226**
Simcoe	16	31.19 ± 3.01	38.16 ± 2.69	0.1036
Westfield	10	19.82 ± 4.73	30.35 ± 1.74	0.0635
Pinus sylvestris				
Pompey	40	13.00 ± 1.18	20.65 ± 1.26	**<0.0001**
Windy Hill	30	8.54 ± 0.69	17.71 ± 0.93	**<0.0001**

the case for *S. noctilio* attacked trees, trees with Siricidae exit holes present or dying from other causes had significantly smaller diameters than living trees (Table 3).

As in *P. resinosa* stands, *S. noctilio* was found in all canopy classes in *P. sylvestris* stands (Fig. 5). However, *S. noctilio* more frequently attacked overtopped and intermediate trees than codominant/dominant trees. Trees with Siricidae exit holes were found only in the stands at Pompey and Windy Hill, where they were in all canopy classes. Trees dying from other causes were distributed throughout all canopy classes in the three stands.

Pinus sylvestris growth rates and tree characteristics

Pinus sylvestris trees attacked by *S. noctilio* were growing slower than unattacked trees, but these differences were not always statistically significant (Table 4). The overall average growth rate was significantly different only for Pompey ($P = 0.047$). However, the previous 10-year and previous 5-year growth rates were significantly lower in attacked trees compared with unattacked trees in Indian Hills and Pompey. Average live crown ratio for infested *P. sylvestris* ranged from 9% to 13%, while uninfested trees ranged from 18% to 21% (Table 5). Of the three *P. sylvestris* stands sampled, only two (Pompey and Windy Hill) had measurable live crowns present on infested trees. In both cases, attacked trees had significantly smaller live crown ratios when compared with unattacked trees (Table 5).

Discussion

Sirex noctilio has caused significant economic damage in Southern Hemisphere countries where it has been introduced (Madden 1988; Carnegie et al. 2005). Based primarily on its aggressive behavior in the Southern Hemisphere, *S. noctilio* was rated as a high-risk species if introduced into North America (Haugen 1999) and has the potential to influence future timber supplies (Yemshanov et al. 2009). However, much variation exists in North American pine ecosystems and it is unknown how this species will behave in the heterogeneous landscapes and diverse forests of the northeastern United States and southern Ontario where it has been detected. This study retrospectively investigated *S. noctilio* behavior in pine stands in this area, estimating stand and tree level mortality associated with this insect in a new environment to gain insights into its potential ecological impact.

Sirex noctilio infested pine stands

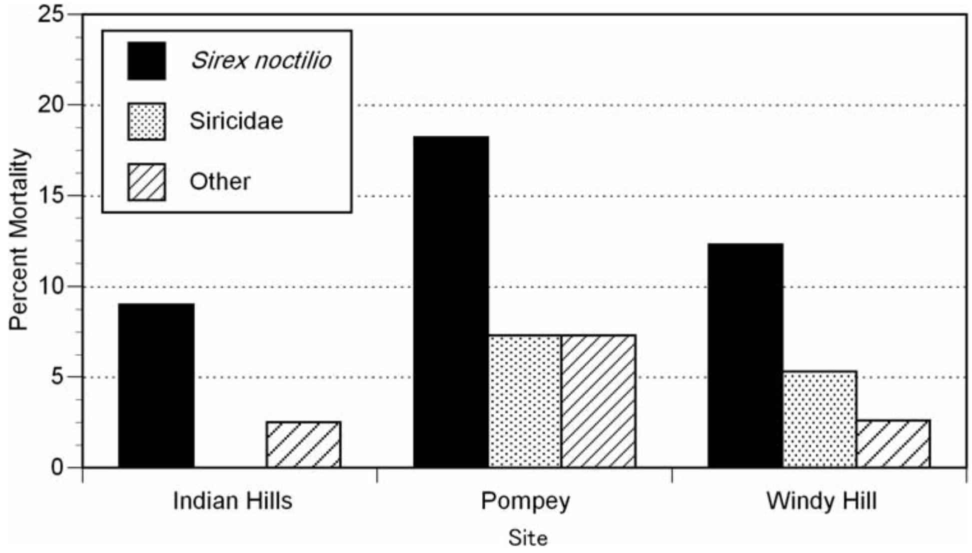
Pinus resinosa and *P. sylvestris* stands attacked by *S. noctilio* were generally in poor condition, suffering from numerous biotic and abiotic stressors. Almost all stands exceeded stocking levels recommended for effective management of *P. resinosa* (Ek et al. 2007), leaving many trees in a stressed condition and susceptible to an array of phytophagous organisms. Evidence of repeated ice and snow damage was present in the stands, including broken branches and tree crowns. In addition, many of these pine stands were planted on sites better suited for hardwood species. No management guidelines exist for *P. sylvestris* in North America; however, it likely responds to competition in a similar manner as *P. resinosa* on these sites.

With the exception of one stand, all others consisted of over 80% pine with the remaining trees made up of various hardwoods or conifers that naturally seeded in since planting. While stands were generally overstocked and in most cases almost pure plantations, a relatively low percentage of basal area was lost to *S. noctilio* colonization. *Pinus resinosa* stands had lower percent losses (1.7%–5.4%) of pine basal area compared with *P. sylvestris* stands where losses

Table 6. Stand-level variables and estimates of tree mortality from *Pinus sylvestris* stands surveyed for *Sirex noctilio* in New York.

	Stand		
Variable	Indian Hills	Pompey	Windy Hill
No. of living trees/ha	1411	613	986
Living basal area (m^2/ha)	31.9	31.9	33.6
Live pine basal area (m^2/ha)	28.1	25.8	32.6
Basal area attacked by *S. noctilio* (m^2/ha)	1.6	5.5	2.8
Basal area with Siricidae exit holes (m^2/ha)	0	1.9	1.2
Basal area dead from unknown causes (m^2/ha)	0.4	1.3	0.97
Average stand age (years ± SE)	25 ± 1	38 ± 1	33 ± 1

Fig. 4. Percent mortality of tree stems with signs of *Sirex noctilio*, Siricidae exit holes, or dead from other causes in three *Pinus sylvestris* dominated stands.



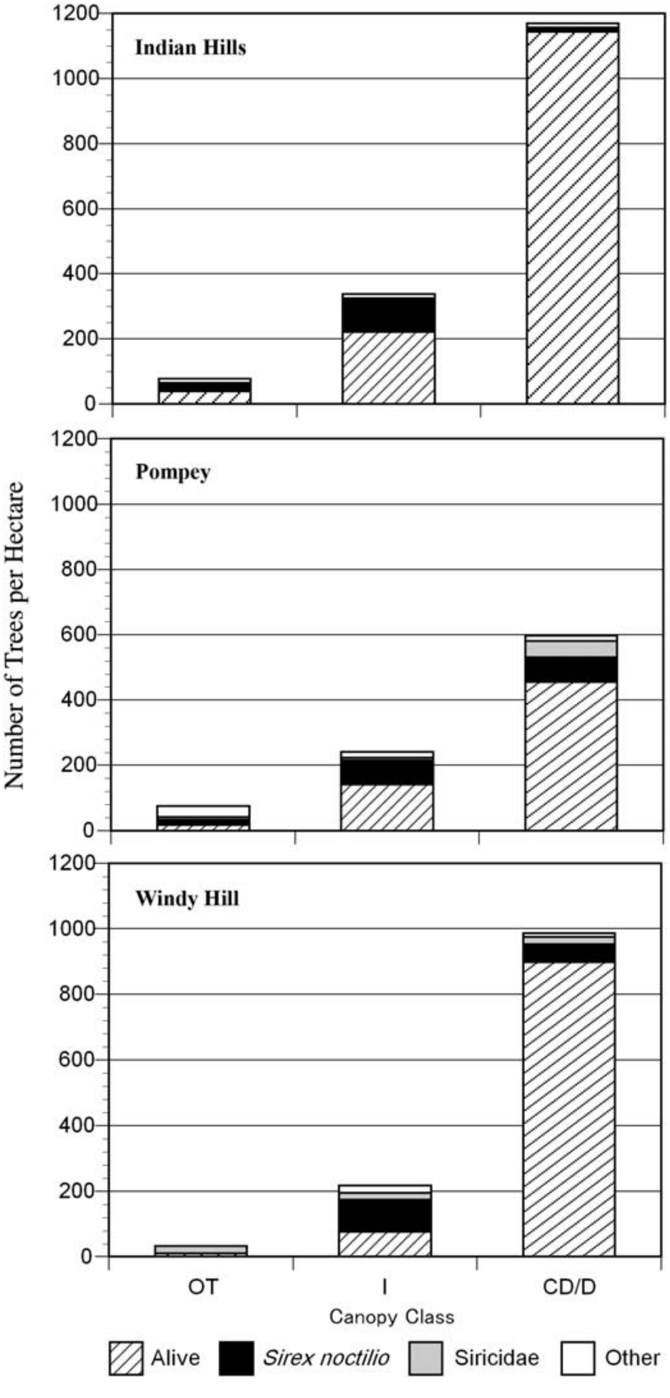
were higher (5.4%–16.0%). However, there were only three *P. sylvestris* stands surveyed and caution must be taken in drawing broader conclusions based on this small sample. Highest basal area losses were found from the stand at Pompey, which was a stand with several biotic and abiotic disturbances (e.g., gall rust, storm damage) occurring simultaneously and the majority of trees in relatively poor condition. If this trend of *P. sylvestris* being colonized more frequently is true, the higher levels of basal area loss may simply be explained by *P. sylvestris* being a more apparent host to *S. noctilio*. *Pinus sylvestris* has an evolutionary history with *S. noctilio*, and there is some evidence that this species is a more attractive resource than *P. resinosa* in the region (Zylstra et al. 2010)

Well-managed *P. resinosa* stands, or stands with larger average DBH (approximately 30 cm or greater), exist in the area but it was difficult to find *S. noctilio* in these stands. Neumann and Minko (1981) found that more trees over 26 cm DBH survived an outbreak and trees over 29 cm DBH were not attacked by *S. noctilio*, even when populations were high. *Pinus resinosa* often exists in plantations that receive some intermediate silvicultural treatments and then are eventually clearcut at maturity (Ek et al. 2007), so mature stands have very few smaller susceptible trees present, a structural characteristic that seems important for *S. noctilio* establishment. Even in the unmanaged *P. resinosa* and *P. sylvestris* stands that were sampled in this study, small-diameter (<12 cm) overtopped trees were often scarce and the lack of this stand structural characteristic may help regulate local populations. *Sirex noctilio* densities are reported to increase in smaller trees and then move into larger trees as local populations build (McKimm and Walls 1980). From our crown class distributions, it is apparent that much of this material is either already dead, inhabited by other organisms, or not present in the stands. It is also possible that *S. noctilio* has already killed all smaller trees in these stands and has moved into larger size classes. If larger numbers of overtopped, smaller diameter trees were present, higher levels of *S. noctilio* activity may have been observed in stands. This observation also suggests that regenerating stands near their first crown closure may be at a higher risk than the mature stands common on the landscape.

Characteristics of *S. noctilio* infested trees

For both *P. resinosa* and *P. sylvestris* trees, *S. noctilio* was found more often in smaller suppressed trees (both diameter and crown class) than in larger trees. In a few stands, *S. noctilio* or other factors accounted for 100% mortality of the overtopped crown class, although it should be noted that there were few trees present in some of the smaller size

Fig. 5. Mortality factors by crown class in three *Pinus sylvestris* stands in New York.



classes. Attacks concentrated on smaller trees are consistent with *S. noctilio* behavior in other *Pinus* systems (McKimm and Walls 1980). *Sirex noctilio* was found infesting larger codominant/dominant crown classes but less frequently than in the suppressed crown classes. While Neumann and Minko (1981) reported that trees above 29 cm had not been attacked by *S. noctilio* in an unthinned *P. radiata* plantation, we observed several *P. sylvestris* trees of greater than 30 cm DBH in the dominant crown class attacked by *S. noctilio*. It may be that variables associated more directly with conifer vigor, defenses, or volatile release may be more important to attraction, assessment, and colonization (Raffa and Berryman 1982, 1983).

Suppressed trees and trees with low growth rates are known to attract *S. noctilio* in the Southern Hemisphere (Madden 1975) and it appears that similar behavior is occurring in North America. Increment cores from all trees showed declining exponential growth regardless of attack history, and crown development was poor for most trees in the stands. However, there was an overall trend that *S. noctilio* attacked trees were growing slower and had smaller live crown ratios than unattacked trees. While growth and live crown ratio differences between attacked and unattacked trees were sometimes small, these differences may make some trees less attractive to *S. noctilio* or enable resistance to colonization attempts. The continued overcrowded conditions in *Pinus* stands will likely facilitate *S. noctilio* populations until intertree competition is reduced and vigor of residual trees is increased. Fortunately, these conditions can be mitigated by silvicultural treatments. Preliminary data from *P. resinosa* and *P. sylvestris* stands in New York suggest that thinning even high-hazard stands can substantially reduce the impact of *S. noctilio* (K.J. Dodds, unpublished data).

Crown condition has important implications for tree growth and vigor (Waring et al. 1980; Zarnoch et al. 2004), but few studies have related live crown ratio directly to tree vigor, as other crown characteristics are important (i.e., leaf area). It is difficult to assess the biological relevance of the live crown ratio differences found in most stands. While it is unknown how a 10% increase in live crown ratio directly relates to vigor, in a stand of stressed trees, this small difference may be enough to avoid *S. noctilio* colonization at a given point in the invasion.

Insect communities and *S. noctilio*

Because of the poor condition of surveyed stands, it was difficult at times to assign mortality directly to *S. noctilio*. Bark beetles, native woodborers, and pathogens are common in *P. resinosa* and *P. sylvestris* stands in this region (Whitney 1988; Klepzig et al. 1991; Erbilgin and Raffa 2002) and their presence, along with abiotic disturbances such as an impermeable plow pan layer and severe winter storms, increased tree stress and provided opportunities for biotic organisms to colonize trees. The exact sequence of tree decay or stress is unknown in surveyed stands and assessing when *S. noctilio* first attacked given trees is impossible in a retrospective study where only a 2-year window exists to categorize mortality. In addition, some trees classified as attacked by *S. noctilio* also showed the presence of signs of colonization by native and other exotic insects (e.g., *Tomicus piniperda* (L.)). What is clear from the data is that *S. noctilio* contributed to increased tree mortality in these stands and colonized some trees that showed no other signs of insects or disease. Whether or not these trees would have been colonized or killed by other species is unknown and likely would have varied by local population levels of phytophagous insects and pathogens. Whatever the case, *S. noctilio* is increasing tree mortality in overstocked pine stands that are growing under poor conditions at this time.

Dead trees were classified as attacked by *S. noctilio*, having Siricidae exit holes present, or dead from other causes.

This classification was conservative and may have resulted in underestimating *S. noctilio* activity in these pine stands. While the dead from other causes classification incorporated other insects and pathogens, the trees classified as Siricidae exit holes present and not *S. noctilio* were more problematic. Round Siricidae exit holes without the presence of resin beads could not be differentiated between native species and *S. noctilio* further back than 2 years, so care must be taken in interpreting these results. A conservative interpretation would suggest that only the number of trees classified as having signs of *S. noctilio* present were the only trees that this insect actually inhabited and it only recently (i.e., 2 years) colonized these stands. Conversely, all trees classified as having Siricidae exit holes present could be added to the total of *S. noctilio* trees to provide a higher estimate of tree mortality caused by the invasive. Trees with Siricidae present were similar in diameters to those colonized by *S. noctilio* and this observation could lend support for the supposition that at least some of these were actually *S. noctilio* infested trees. Unfortunately, little is currently known about most native Siricidae present in North America to provide any insights into their oviposition behavior or host selection. The true level of *S. noctilio* activity remains unknown but probably lies somewhere between our estimates of *S. noctilio* colonized trees and the total of these and trees classified as having Siricidae exit holes present combined.

Management implications

Results from this work have important implications for managing *S. noctilio* in North America. Stand thinning is consistently recommended in Southern Hemisphere countries as a means to lower stand hazard and remove potential *S. noctilio* habitat (Neumann et al. 1987; Haugen 1990). Because *S. noctilio* was often found attacking suppressed trees at this point in the invasion in North America, silvicultural treatments such as thinning from below, targeting weakened, injured, and suppressed trees will simultaneously increase available resources for residual trees and remove potential *S. noctilio* habitat (Dodds et al. 2007). Silvicultural treatments that increase stand vigor would also reduce susceptibility to other pine-infesting species (Mitchell et al. 1983; Morgan et al. 2004).

While *S. noctilio* has not yet caused widespread tree losses in north-central North American pine stands, it is unknown how this insect will behave as it gradually spreads outward. The study area that we focused on has several attributes that may impede severe *S. noctilio* outbreaks. It is a highly fragmented heterogeneous landscape dominated by hardwoods with a low proportion of potential hosts, affording more resistance to pine-infesting insects like *S. noctilio*. In addition, young, densely spaced *P. resinosa and P. sylvestris* plantations are uncommon on the landscape, limiting potential *S. noctilio* resources. However, despite these deterrents, *S. noctilio* has overcome a seemingly hostile environment and integrated into several native ecosystems over a large geographical area (Fig. 1). This, coupled with its long history as an invasive, provides further evidence that *S. noctilio* is a strong invader and poses a serious threat to North American pine forests (Ciesla 2003).

As *S. noctilio* populations spread into the southern, northern, and western pine regions in the United States and Canada, the landscapes and forests may be more conducive to promoting and maintaining populations. Intensively grown commercial forests (e.g., *Pinus taeda* L., *Pinus elliotti* Engelm.) left unmanaged beyond their thinning cycle or natural stands that develop with dense stockings (e.g., *P. banksiana*, *Pinus contorta* Dougl. ex Loud.) appear particularly susceptible to *S. noctilio* attack. Furthermore, insect outbreaks such as jack pine budworm (*Choristoneura pinus pinus* Freeman) could lead to a greater availability of weakened hosts. Consequently, the low level of *S. noctilio* caused tree mortality observed to date in the study sites in New York and Ontario may not portend the impact of *S. noctilio* in other North American pine ecosystems.

Conclusions

In the northeastern United States and southern Ontario, *S. noctilio* appears to be behaving somewhere between a primary and secondary species interacting as a member of the insect community utilizing stressed and dead trees as reproductive habitat. Individual trees that were colonized by *S. noctilio* were often growing at slower rates and had reduced tree crowns, both indications of a weakened condition and likely compromised defensive capabilities. In some cases, larger apparently healthy trees were also colonized but at a lower frequency than the smaller suppressed trees. Even with mortality occurring from other tree-killing agents, tree mortality in sampled stands was not extensive and *S. noctilio* does not appear to be causing excessive tree mortality at this point in the invasion. It is uncertain how long *S. noctilio* has been present in the region and therefore difficult to assess its potential for damage in this or other areas of North America. Interactions of population density with regional climatic conditions (e.g., increased temperatures, drought) and other stresses such as attack by defoliating insects could lead to this insect becoming a more important mortality agent in pine stands throughout the region.

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