Sirex noctilio (Hymenoptera: Siricidae) in Ontario (Canada) pine forests: observations over five years

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Abstract—More than a decade after its discovery in North America, the European woodwasp, *Sirex noctilio* Fabricius (Hymenoptera: Siricidae), has not been an aggressive tree killer in northeastern North American pine (*Pinus* Linnaeus; Pinaceae) forests. Concern that *S. noctilio* has potential to become a more aggressive pest as it spreads south, or as environmental conditions change, is warranted, because it has caused extensive pine losses on other continents that it has invaded. We observed *S. noctilio* impact and attack behaviour in eight pine stands throughout Ontario, Canada annually for a five-year period (2012–2016). *Sirex noctilio* impact was variable in unmanaged pine forests; it killed 3–48% of pine stems, and 3–36% of pine basal area. Most *S. noctilio*-caused mortality was limited to suppressed and intermediate trees. Of the 17% of pines in the entire study that were affected by *S. noctilio*, many (44%) were attacked in multiple years. Depending on the year, between 46% and 79% of trees remained alive in the year immediately after attack, which suggests that many study trees were at least initially resistant to attack by *S. noctilio*. Though its impact appears to be limited in most forests for now, we recommend that observations continue in future years.

Introduction

Invasive forest pests can alter the structure, composition, and function of forest ecosystems. The severity of these impacts varies among pests and forest types. For example, the hemlock woolly adelgid, *Adelges tsugae* (Annand) (Hemiptera: Adelgidae), has changed the structure and function of eastern hemlock (*Tsuga canadensis* (Linnaeus) Carrière and *T. caroliniana* Engelmann; Pinaceae) forests in eastern North America (Orwig and Foster 1998; Orwig *et al.* 2008). This has had cascading effects on hydrology, nutrient cycling, and biodiversity because hemlock is a foundation species that functionally supports many other species in these forests (Ellison *et al.* 2005). Emerald ash borer, *Agrilus planipennis* Fairmaire (Coleoptera: Buprestidae), has already killed nearly all ash (*Fraxinus* Linnaeus; Oleaceae) it has encountered in areas it

has invaded in North America (Knight *et al.* 2013; Klooster *et al.* 2014). This invasion has changed forest composition, and threatens the community of specialists that inhabit and/or feed upon ash (Wagner and Todd 2015). In contrast, some exotic insects never reach a threshold where economic or ecological damage is widespread or intense. For example, the pine shoot beetle, *Tomicus piniperda* (Linnaeus) (Coleoptera: Curculionidae: Scolytinae), predicted to be a high-risk pest, has become only a minor pest of pine (*Pinus* Linnaeus; Pinaceae) in North America, partly because it is not a very aggressive tree killer (Morgan *et al.* 2004). The pine shoot beetle, essentially a naturalised resident, is now part of a species-rich community of insects that feed on pines in the Great Lakes Region. Several species of exotic ambrosia beetles are also established in North America where they cause damage in nursery settings (Ranger *et al.* 2016), but no

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noticeable impacts in natural forests have been recorded. Some of these species have become so common that they now are dominant Scolytinae captured in bark beetle surveys in some environments (Coyle *et al.* 2005; Reed and Muzika 2010).

Predicting the impact of a new invasive pest can be difficult. An invading insect faces many challenges, including interactions with host trees, other invertebrates and microorganisms, and abiotic factors such as climate. For these reasons, the impact of a pest can vary in different places. This has been the case with the European woodwasp, *Sirex noctilio* Fabricius (Hymenoptera: Siricidae), which is native to Europe and Asia, and introduced in North America and many countries throughout the Southern Hemisphere (Hurley *et al.* 2007; Slippers *et al.* 2015). In some areas, *S. noctilio* is a major pest of pine, especially in exotic pine monocultures with limited herbivore (and associated natural enemy) communities found throughout the Southern Hemisphere (Madden 1988; Haugen 1990; Hurley *et al.* 2007). Poor management practices and drought have also exacerbated the impact of *S. noctilio* in the Southern Hemisphere (Madden 1988; Haugen 1990; Hurley *et al.* 2007). Since it was detected in 2004 (Hoebeke *et al.* 2005; de Groot *et al.* 2006), *S. noctilio* has not been a major pest in North America. This is probably because forests in North America are similar to those in the native range of the pest; they are more heterogeneous and patchy on the landscape, and support a rich community of natural enemies and potential competitors of *S. noctilio* (Dodds and de Groot 2012).

Though established and likely spreading in North America, *S. noctilio* has primarily been found in unmanaged stands, particularly in scots pine, *P. sylvestris* Linnaeus, and red pine, *P. resinosa* Torrey (Dodds *et al.* 2010; Ayres *et al.* 2014), less often in jack pine, *P. banksiana* Lambert (Ryan *et al.* 2012b), and rarely in white pine, *P. strobus* (Zylstra and Mastro 2012). Natural enemies and competitors may play a role in limiting *S. noctilio* in North America, but pine resistance appears to be the most important limiting factor (Haavik *et al.* 2015). The most suitable hosts for S. *noctilio* are intermediate and suppressed pines (Ayres *et al.* 2014; Dodds *et al.* 2010, 2014; Haavik *et al.* 2016) that are likely stressed and not well defended against herbivores.

There is some evidence that availability of pine, especially suppressed pine, has limited *S. noctilio* in Ontario, Canada (Haavik *et al.* 2016). In areas with more suppressed trees, more co-dominant trees were attacked, but not killed by *S. noctilio*, which suggests it has potential to become a pest (Haavik *et al.* 2016), perhaps under stressful environmental conditions. To date, there has been no effort to quantify the short-term impact of *S. noctilio* over time in North American pine forests.

Periodic reporting and analysis (*i.e.*, short-term impact) of *S. noctilio* activity from a long-term study will help to identify variables that drive temporal changes in *S. noctilio* population dynamics in North America that may be missed with longer sampling intervals. We sought to better understand and describe *S. noctilio* impact on forests and attack behaviour in Ontario over a five-year period. Using eight pine stands, our specific objectives were to examine general patterns in *S. noctilio* activity annually between 2012 and 2016, and ascertain the fate of trees attacked by *S. noctilio* over time.

Materials and methods

Site selection

We used locations with positive trap captures from the 2006 and 2007 Ontario Ministry of Natural Resources delimitation surveys for *S. noctilio* in southern Ontario as a guide to select study sites. We also selected sites in northern Ontario where *S. noctilio* was likely to have established (*P. sylvestris*, *P. resinosa,* or *P. banksiana* stands with little or no indication of recent forest management). We examined 50 potential sites, and chose eight for this study (Fig. 1). We selected sites with differing levels of *S. noctilio* activity to represent forests that varied in apparent favourability for and/or success of *S. noctilio*. Stand sizes, along with pine density and basal area (in 2012 and 2016) are listed in Table 1.

Stands located in southern Ontario included Beagle Club, Thames, Old Church, Little Lake, Kendal, and Guelph. Beagle Club was a topographically flat, unmanaged *P. sylvestris* plantation. Thames was a topographically flat, unmanaged mixed *P. sylvestris*, *Abies balsamea* (Linnaeus) Miller (Pinaceae), and hardwood forest. Old Church was a small, unmanaged forest

Fig. 1. Map showing names, locations, and level of *Sirex* impact in eight pine stands in Ontario. Low impact stands are represented by circles; high impact stands by triangles, and stands in northern Ontario by squares.

patch located on the ridge-top of a slope, populated by *P. sylvestris* and *P. banksiana*. Little Lake was a topographically flat, unmanaged *P. sylvestris* plantation. Kendal was a topographically flat *P. resinosa* plantation that had not yet been thinned. Guelph was a *P. sylvestris* forest on slightly hilly terrain that had not been managed.

Two stands, Iron Bridge and Patton, were located in northern Ontario. We assumed *S. noctilio* spread to northern Ontario after its introduction to southern Ontario, probably arriving years later. Iron Bridge was a topographically flat, unmanaged *P. sylvestris* plantation. Patton was a topographically flat, mixed *P. resinosa*, *P. sylvestris*, and hardwood forest; it may have been thinned, but not recently.

Pine surveys

We obtained forest measurements and quantified *Sirex* activity in three, circular fixed-radius (7 m) plots at each site, spaced at least 25 m apart and 15 m from the forest edge. Sites ranged in size from 0.80 to 2.27 ha (Table 1). Kendal (low activity, southern Ontario) was larger (5.13 ha) than the others, but was homogeneous in pine density and *Sirex* activity throughout.

To establish permanent plots, in the winter of 2012 we affixed unique metal identification tags to each standing pine that was within a plot. We surveyed these trees through visual assessment and assigned possible mortality factors (dead or alive; attacked or colonised by *Sirex*, bark beetles, and/or wood borers); assigned crown class (suppressed, intermediate, or co-dominant); and collected stand-level forest measurements. To assess pine health, we visually surveyed each tree with binoculars from the base of the bole to the top of the crown for fresh resin beading, *i.e.*, resinosis, indicative of *Sirex* attack (Ryan *et al.* 2013), and adult emergence holes from *Sirex*, bark beetles, or other wood borers (*Monochamus* Dejean;

Coleoptera: Cerambycidae) to confirm successful colonisation (Ayres *et al.* 2009). Although it was not possible to distinguish between evidence of *S. noctilio* and the native pine woodwasp, *S. nigricornis* Fabricius, in most cases evidence was probably attributable to *S. noctilio*, because many more *S. noctilio* than *S. nigricornis* adults emerged from trees identified as attacked by *Sirex* in these stands (Haavik *et al.* 2016). We defined *Sirex* activity as the collective amount of pine attacked or killed by either *S. noctilio* or *S. nigricornis*.

For the entire study, a total of 493 pines were surveyed annually over a five-year period from 2012 to 2016. We surveyed pine health at all sites after the adult flight periods of *S. noctilio* and *S. nigricornis* had ceased (Ryan *et al.* 2012a), in the winter of 2012, and late fall of 2013–2016. In 2012 and again in 2016, we measured diameter at breast height (1.4 m from the ground) for all pines $\geqslant 5$ cm diameter at breast height in order to estimate pine basal area (in $m^2\ ha^{-1}$). Forest measurements (stem density and basal area) from the three plots at each site were summed, converted to a

Table 1. Summary of size, location, and composition of stands surveyed for *Sirex noctilio* activity in Ontario.

Site	Approximate size (ha)	UTM location*	Tree species present	Live pine (trees ha⁻¹) 2012	Live pine (trees ha⁻¹) 2016	Basal area live pine 2012 (m² ha⁻¹)	Basal area live pine 2016 (m² ha⁻¹)
Beagle Club	0.80	731512, 4886806	Ps	628	411	19.91	15.24
Thames	0.93	432126, 4722320	Ps, Ab	455	238	15.71	9.59
Old Church	1.10	595741, 4863969	Ps, Pb	758	628	30.84	28.00
Little Lake	2.27	272916, 4880520	Ps	1385	1234	37.59	38.87
Kendal	5.13	697491, 4875925	Pr	1753	1602	48.78	45.81
Guelph	1.02	571202, 4825912	Ps	1104	931	39.37	35.80
Iron Bridge	1.72	327021, 5127498	Ps	1861	1537	48.01	48.73
Patton[†]	1.05	327709, 5130768	Ps, Pr	1385	1169	51.95	50.35

* All sites located in Zone 17 T, except Little Lake (Zone 18 T).
[†] Stand not measured in 2012 (2013 density reported).
Ab, *Abies balsamea*; Pb, *Pinus banksiana*; Ps, *P. sylvestris*; Pr, *P. resinosa*; UTM, Universal Transverse Mercator.

Table 2. Stem density and basal area of pine killed by *Sirex* at sites in Ontario between 2012 and 2016.

Site	Location	Pine killed by *Sirex* (trees ha⁻¹)	%2012 pine density killed by *Sirex*	Basal area of pine killed by *Sirex* (m² ha⁻¹)	%2012 pine basal area killed by *Sirex*
Beagle Club	S	303	48	7.20	36
Thames	S	174	38	5.58	36
Old Church	S	218	29	5.59	18
Little Lake	S	152	11	2.25	6
Kendal	S	66	4	1.05	2
Guelph	S	66	6	1.23	3
Iron Bridge	N	87	5	2.13	4
Patton*	N	44	3	1.47	3

* Stand not measured in 2012 (change from 2013 to 2016 reported).
S, southern Ontario; N, northern Ontario.

per ha basis, and used as an estimate for each site. For each pine that was standing and dead in 2012, we included it in the survey only if it had died recently (1–3 years ago: branch structure and bark intact, no decay fungus visible). In 2013 and 2014, between one and five *Sirex*-infested trees were removed from each site, though well outside of survey plots used for this study. A few *Sirex* emerged from the removed trees (mean = 8 ± 2 (standard error), range = 0–28 females per tree), except one tree from Thames that produced 150 females. It is possible that these tree removals had some influence in mitigating the impact of *S. noctilio* at the survey sites, especially at Thames, although we expect that this influence is minimal over time.

Table 3. Percentage of pine killed by *Sirex* in Ontario by site and year.

| Site	2012	2013	2014	2015	2016
Beagle Club	28	4	13	4	5
Thames	29	0	6	15	0
Old Church	11	9	0	3	0
Little Lake	0	2	5	2	0
Kendal	0	0	1	4	1
Guelph	2	0	3	0	0
Iron Bridge	0	1	4	1	1
Patton*		2	3	4	0

* Stand not surveyed in 2012.

Results and discussion

Forest impact

Among the eight sites surveyed in 2012, density of live pine susceptible to *Sirex* (*P. resinosa*,

Fig. 2. *Sirex* activity at Beagle Club. Proportion of pine alive in 2012 that was (**A**; all years) attacked (grey) and killed (black) by crown position; number of pines that were not attacked, attacked, and also killed by (**B**; all years) crown position; and size class in (**C**) 2012 and (**D**) 2016. The killed portion of bars in (**C**) and (**D**) represents trees that were both attacked and killed that year, and the attacked portion represents trees that were attacked but did not die that year, whereas in (**A**) and (**B**) trees that were attacked and killed are represented in both the attacked bar and the killed bar. DBH, diameter at breast height.
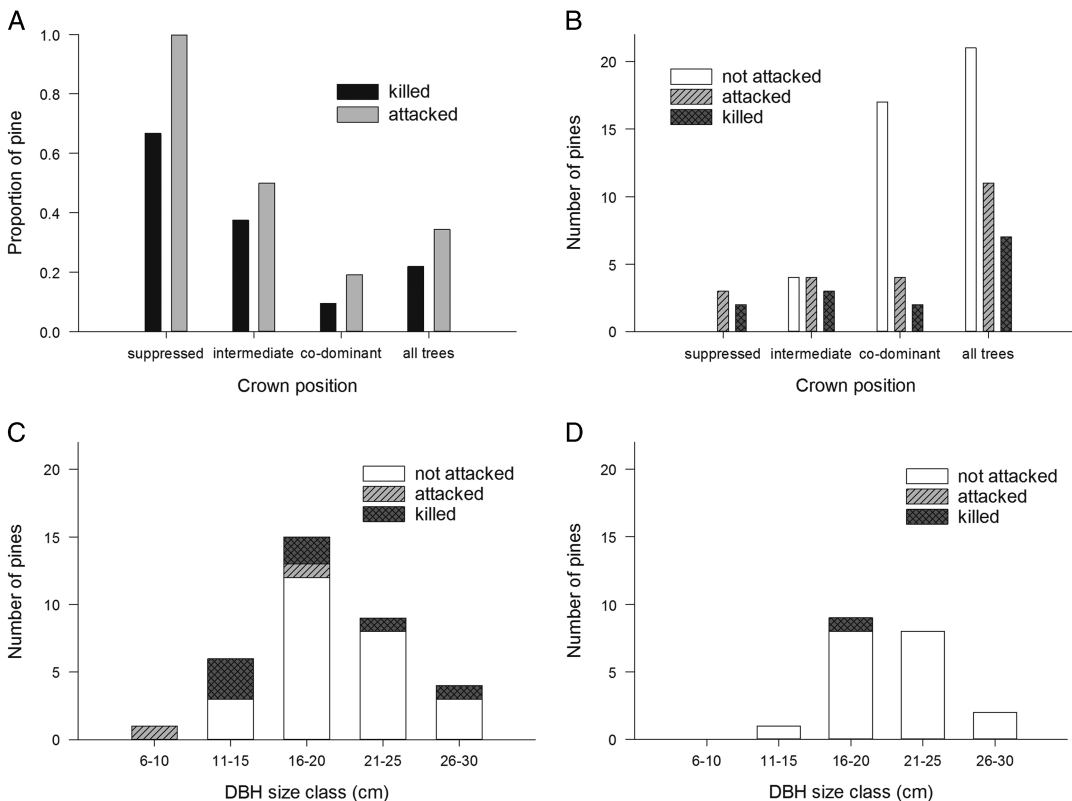
P. sylvestris, *P. banksiana*) varied from 455 to 1861 stems per ha, and declined by 130 to 324 stems per ha to between 411 and 1602 stems per ha in 2016 (Table 1). The average decline in pine density between 2012 and 2016 was 197 ± 58 (standard error) stems per ha. *Sirex* killed between 44 and 303 stems per ha (29–48%, 4–11%, and 3–5% of stem density at high activity, low activity, and northern Ontario sites, respectively) between 2012 and 2016 (Table 2), an average of 139 ± 84 stems per ha.

In 2012, the basal area of live pine susceptible to *Sirex* varied from 15.71 to 51.95 m^2/ha, and in 2016, it varied from 9.59 to 50.35 m^2/ha (Table 1). Six sites experienced a decrease, and two sites experienced an increase in live pine basal area

between 2012 and 2016. The change in basal area among all sites ranged from a 1.28 m^2/ha increase to a 6.12 m^2/ha decrease; average change in basal area was a decrease of 2.47 ± 2.36 m^2/ha. Basal area of pine killed by *Sirex* between 2012 and 2016 varied from 1.05 to 7.20 m^2/ha (18–36%, 2–6%, and 3–4% of basal area at high activity, low activity, and northern Ontario sites, respectively, Table 2), an average of 3.31 ± 2.26 m^2/ha.

In 2008, *S. noctilio* had already killed 3–18% of trees in several *P. resinosa* and *P. sylvestris* stands in New York (United States of America) and Ontario (Dodds *et al.* 2010). Another study in New York reported that between 5% and 17% of pines were recently dead or dying in 2009, about half of which were affected (attacked and/or

Fig. 3. *Sirex* activity at Thames. Proportion of pine alive in 2012 that was (**A**; all years) attacked (grey) and killed (black) by crown position; number of pines that were not attacked, attacked, and also killed by (**B**; all years) crown position; and size class in (**C**) 2012 and (**D**) 2016. The killed portion of bars in (**C**) and (**D**) represents trees that were both attacked and killed that year, and the attacked portion represents trees that were attacked but did not die that year, whereas in (**A**) and (**B**) trees that were attacked and killed are represented in both the attacked bar and the killed bar. DBH, diameter at breast height.
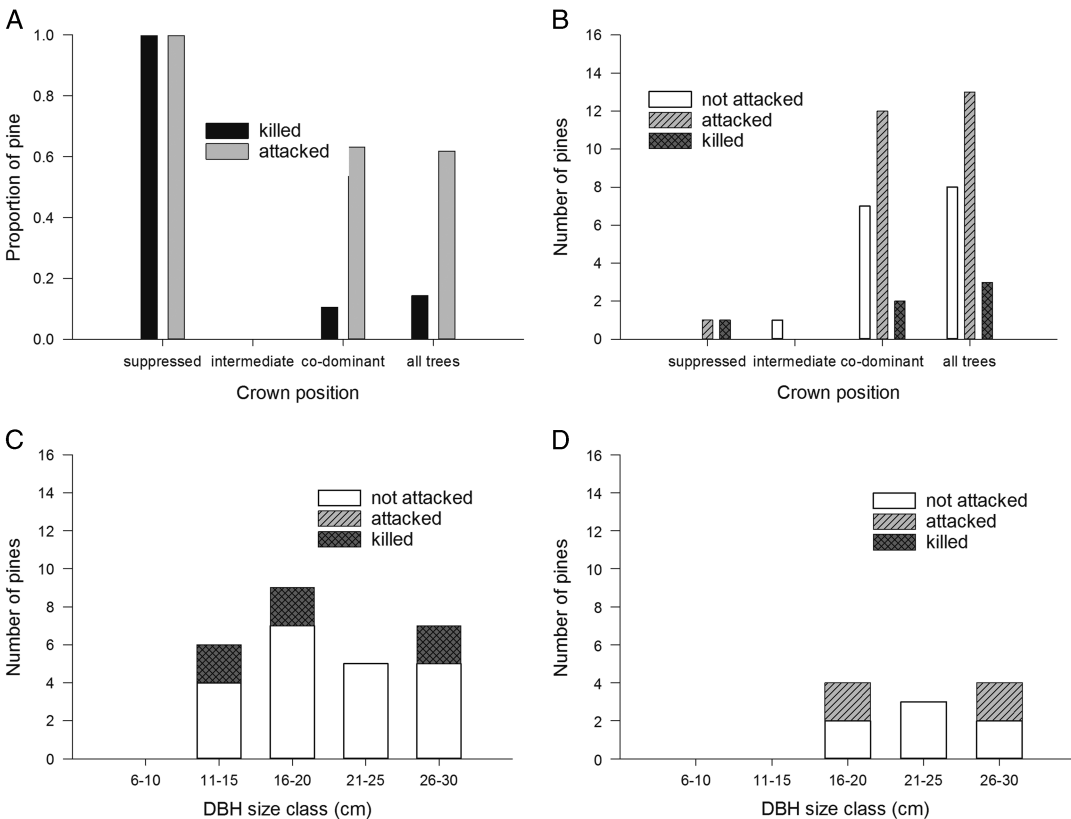
Fig. 4. *Sirex* activity at Old Church. Proportion of pine alive in 2012 that was (**A**; all years) attacked (grey) and killed (black) by crown position; number of pines that were not attacked, attacked, and also killed by (**B**; all years) crown position; and size class in (**C**) 2012 and (**D**) 2016. The killed portion of bars in (**C**) and (**D**) represents trees that were both attacked and killed that year, and the attacked portion represents trees that were attacked but did not die that year, whereas in (**A**) and (**B**) trees that were attacked and killed are represented in both the attacked bar and the killed bar. DBH, diameter at breast height.
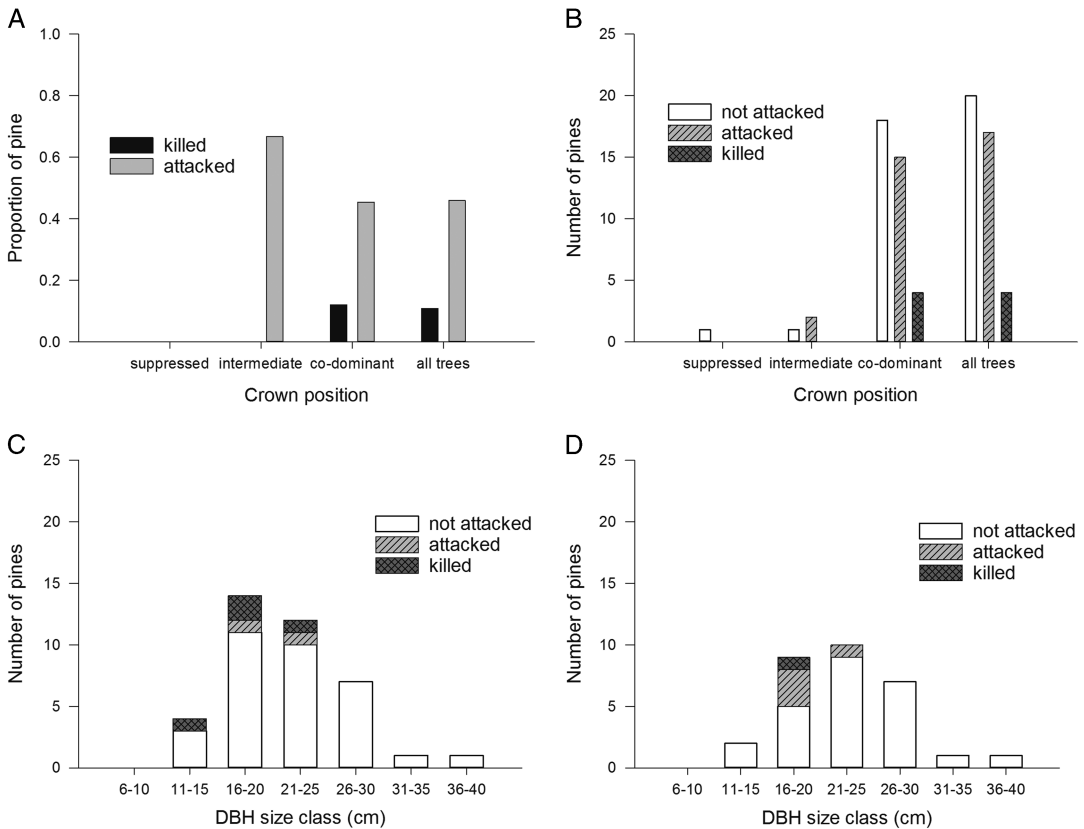
killed) by *S. noctilio* (Ayres *et al.* 2014). It appears that since 2009, in areas where *S. noctilio* is present (*i.e.*, unmanaged pine forests), it has acted somewhere between a primary and secondary pest. It is unclear whether this difference is due to time since invasion, since it was first detected at most of these sites in 2006 or 2007 (2014 by us in the northern Ontario sites, although delimitation efforts in Ontario had ceased after 2009). Continued monitoring of *S. noctilio* activity at our study sites will likely reveal sources of variability in the aggressiveness of the woodwasp.

Comparatively, during outbreaks in Australia and New Zealand, where it behaves as a primary pest, *S. noctilio* has killed 35–90% and 5–30% of pine in high and low impact areas, respectively (Rawlings 1948; Madden 1975; Neumann *et al.* 1987; Morgan 1989; Haugen 1990). In its native range, *S. noctilio* is present in dying pine, but is not considered an aggressive, primary tree killer. For example, in Galica, Spain, 3–71% of dying pines at affected sites were attacked and/or killed by *S. noctilio* (Ayres *et al.* 2014). In the Rhone Valley, Switzerland, *S. noctilio* was found in roughly 8% of *P. sylvestris* suffering from decline (Wermelinger *et al.* 2008). Clearly, *S. noctilio* has not yet had the impact in North America that it has in other invaded areas in the Southern Hemisphere, and its impact is more similar to that within its native range.

Fig. 5. *Sirex* activity at Little Lake. Proportion of pine alive in 2012 that was (**A**; all years) attacked (grey) and killed (black) by crown position; number of pines that were not attacked, attacked, and also killed by (**B**; all years) crown position; and size class in (**C**) 2012 and (**D**) 2016. The killed portion of bars in (**C**) and (**D**) represents trees that were both attacked and killed that year, and the attacked portion represents trees that were attacked but did not die that year, whereas in (**A**) and (**B**) trees that were attacked and killed are represented in both the attacked bar and the killed bar. DBH, diameter at breast height.
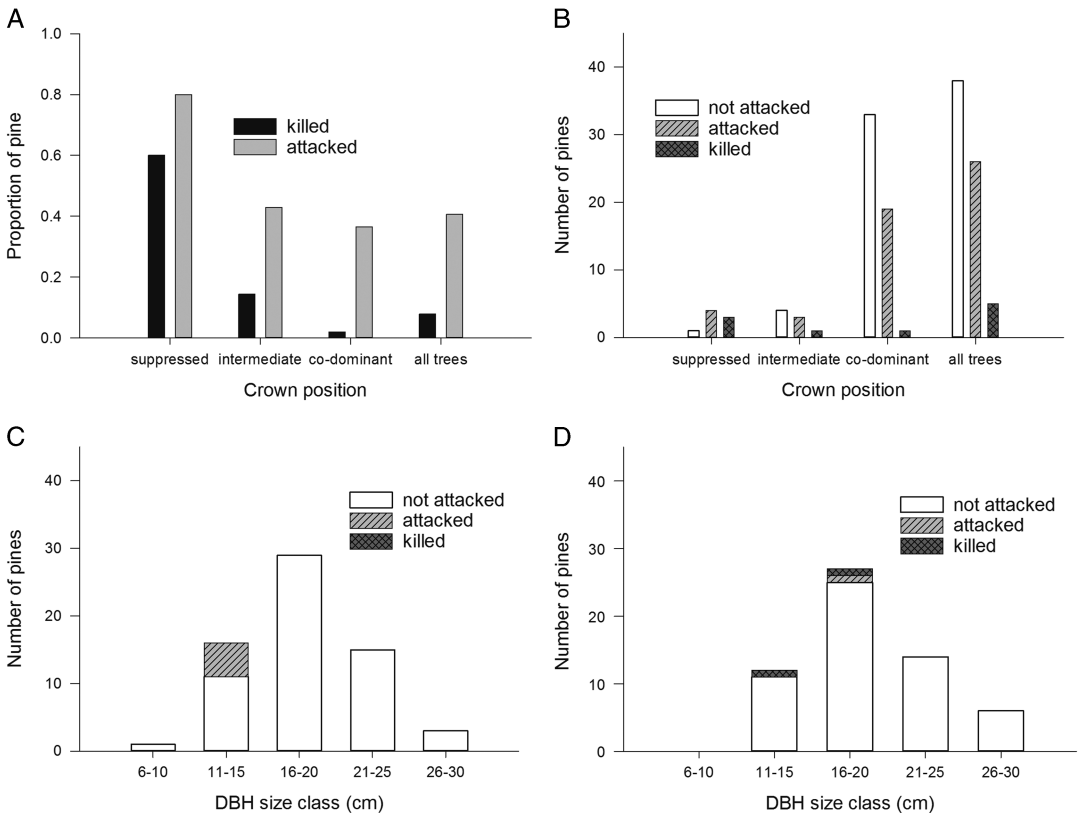
In our study, there were minor fluctuations from year to year in the percentage of pines killed by *Sirex*, with an overall mean among sites and years of $4 \pm 6\%$ (Table 3). No year stood out among all sites as experiencing more *Sirex*-caused tree mortality than other years. At all sites, relatively more intermediate and suppressed than co-dominant pines were attacked and/or killed by *Sirex* (Figs. 2–9A, 9B), a continuation of the pattern observed previously (Dodds *et al.* 2010; Ayres *et al.* 2014). Also, a greater proportion of pine was attacked than actually killed by *Sirex*, a pattern that was particularly strong among co-dominant relative to intermediate and suppressed pine (Figs. 2A–9A). Although co-dominant pines represent the majority of trees at all sites, trees in

intermediate and/or suppressed canopy positions remain at most sites; this indicates that at least some host material that is presumably suitable for *Sirex* is still available at these sites. With respect to site, size classes affected by *Sirex* in 2012 were the same size classes affected in 2016 (Figs. 2–9C–D). Collectively, these observations suggest that *S. noctilio* populations remained stable at these sites between 2012 and 2016, and have not progressed to killing trees in the main canopy.

Fate of attacked trees

Only 17% (86) of trees surveyed during the five years of the study were affected by *Sirex* (attacked or attacked and killed). One-third (29) of trees attacked by *Sirex* died within the year following

Fig. 6. *Sirex* activity at Kendal. Proportion of pine alive in 2012 that was (**A**; all years) attacked (grey) and killed (black) by crown position; number of pines that were not attacked, attacked, and also killed by (**B**; all years) crown position; and size class in (**C**) 2012 and (**D**) 2016. The killed portion of bars in (**C**) and (**D**) represents trees that were both attacked and killed that year, and the attacked portion represents trees that were attacked but did not die that year, whereas in (**A**) and (**B**) trees that were attacked and killed are represented in both the attacked bar and the killed bar. DBH, diameter at breast height.
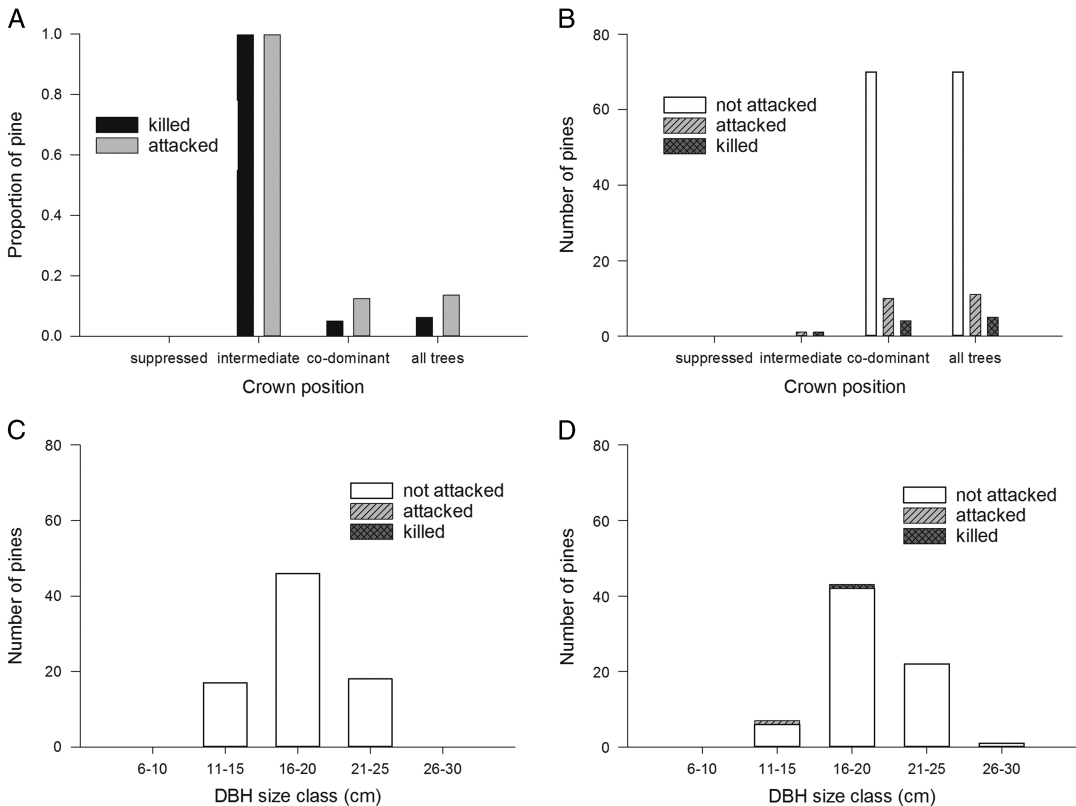

attack, which was synonymous with successful colonisation, *i.e.*, brood (F1 generation) production as evidenced by exit holes (Table 4). Of trees that died within the year following attack, some did not produce *Sirex* brood and were re-attacked in the same year that they died (Fig. 10). These trees may have lived long enough after re-attack by *Sirex* to be colonised and killed by bark beetles (which either out-competed or co-existed with a two-year *Sirex* brood), or the initial *Sirex* brood did not survive and trees were successfully killed very quickly after re-attack (between cessation of adult flight in summer and our tree survey in fall). More trees (nine of 11) exhibited evidence of bark beetle attacks than of *Sirex* brood failure and rapid mortality after re-attack. In Ontario,

Ips grandicollis (Eichhoff) typically attacks trees later in the season than *S. noctilio* (Ryan *et al.* 2012b), and may be multivoltine. In addition, bark beetles are likely more aggressive colonisers of weakened pines than *S. noctilio*, given their ability to concentrate attacks through aggregation pheromones, and their fungal associates are known to out-compete *Sirex* fungal associates (Ryan *et al.* 2011; Yousuf *et al.* 2014). *Sirex noctilio* can have a two-year and even three-year generation time (Morgan and Stewart 1966), which can have major consequences for population growth if a large enough portion (25%) of the population has an extended generation time (Corley and Villacide 2012); however, it has been estimated that $< 5\%$ of the *S. noctilio* population in Ontario requires

Fig. 7. *Sirex* activity at Guelph. Proportion of pine alive in 2012 that was (**A**; all years) attacked (grey) and killed (black) by crown position; number of pines that were not attacked, attacked, and also killed by (**B**; all years) crown position; and size class in (**C**) 2012 and (**D**) 2016. The killed portion of bars in (**C**) and (**D**) represents trees that were both attacked and killed that year, and the attacked portion represents trees that were attacked but did not die that year, whereas in (**A**) and (**B**) trees that were attacked and killed are represented in both the attacked bar and the killed bar. DBH, diameter at breast height.
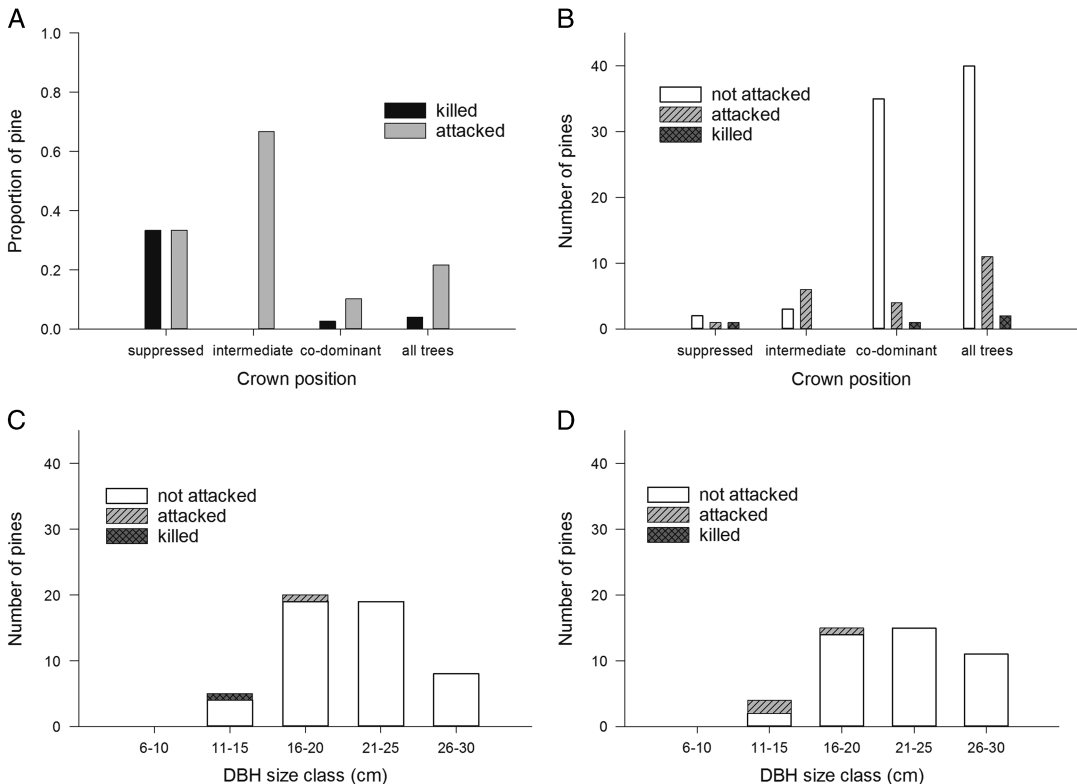

two or more years to complete development (Ryan *et al.* 2012a).

Depending on the year, between 46% and 79% of trees remained alive in the year immediately after *Sirex* attack (Fig. 10). No trees that remained alive in the year following *Sirex* attack successfully produced brood (*i.e.*, an absence of exit holes), which provides evidence that pines in Ontario die before *S. noctilio* completes development. Others have reported that trees may remain alive, or only portions of the tree die, after successful *S. noctilio* colonisation (Morgan and Stewart 1966), but this has rarely been observed in North America. Among trees that survived one year of *Sirex* attack, between 15% and 51% were re-attacked by *Sirex* the following year; the remaining survivors were not revisited by *Sirex* in

the following year (Fig. 10). Of the trees attacked by *Sirex* that remained alive in 2016 (57), 46% of them had been attacked in multiple years (not necessarily in sequential years, though) (Table 4); 41% (12) of trees that died from *Sirex* infestation survived multiple years of attack before mortality (Table 4). In trees that were attacked multiple times, *Sirex* likely injected a toxic venom and its fungal partner, *Amylostereum* Boidin (Amylostereaceae) (*A. areolatum* (Chaillet ex Fries) Boidin or *A. chialletii* (Persoon) Boidin) (Gaut 1969; Wooding *et al.* 2013), which would weaken trees over time. This provides further evidence that many pines in North American forests are resistant to *S. noctilio*, at least when initially attacked, and especially if *S. noctilio* population levels remain low.

Fig. 8. *Sirex* activity at Iron Bridge. Proportion of pine alive in 2012 that was (**A**; all years) attacked (grey) and killed (black) by crown position; number of pines that were not attacked, attacked, and also killed by (**B**; all years) crown position; and size class in (**C**) 2012 and (**D**) 2016. The killed portion of bars in (**C**) and (**D**) represents trees that were both attacked and killed that year, and the attacked portion represents trees that were attacked but did not die that year, whereas in (**A**) and (**B**) trees that were attacked and killed are represented in both the attacked bar and the killed bar. DBH, diameter at breast height.
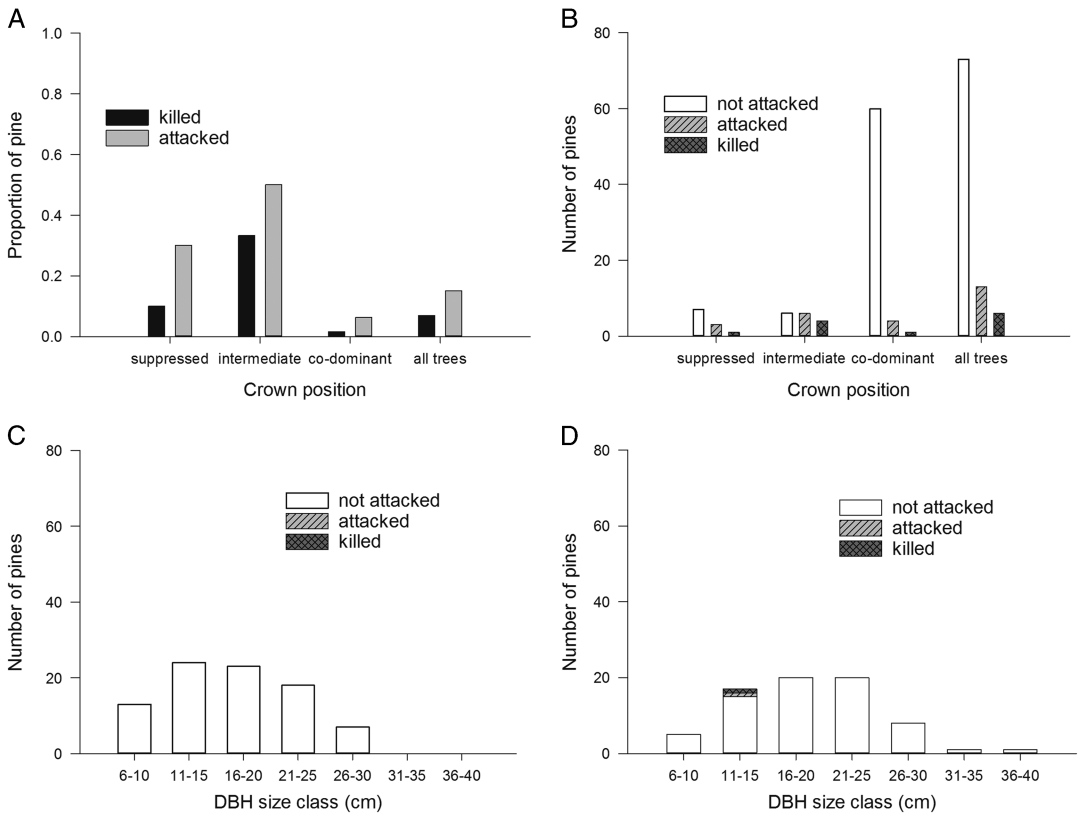

Conclusions

Several studies have investigated the effects of *S. noctilio* in pine stands in North America (Dodds *et al.* 2010; Ayres *et al.* 2014; Haavik *et al.* 2016). Those studies generally relied on one year of forest health survey information and the ability to track *S. noctilio* effects in stands for one or two years previous to sampling through tree damage. Our study is the first in North America that revisited susceptible and *Sirex*-infested stands for multiple years and tracked the survival of individual trees. Like other studies, our data suggest that in Ontario, *S. noctilio* has thus far largely been limited to suppressed or otherwise stressed pines; and in most areas, has not caused appreciable

reductions in pine basal area. We found no evidence that *S. noctilio* has had a significant impact on general pine forest health after being present in Ontario forests for a decade or more.

As *S. noctilio* has demonstrated the capacity to outbreak and cause extensive economic damage on other continents, and it behaved more like a primary pest in some unmanaged pine forests in this study, temporal observations of its activity are important for describing its long-term threat to North American pine forests. Revisiting plots in these eight stands and following the fate of individual pines in future years will allow us to generate a dataset to evaluate whether or not *S. noctilio* will become a major pest in North America. We will be able to determine if

Fig. 9. *Sirex* activity at Patton. Proportion of pine alive in 2012 that was (**A**; all years) attacked (grey) and killed (black) by crown position; number of pines that were not attacked, attacked, and also killed by (**B**; all years) crown position; and size class in (**C**) 2012 and (**D**) 2016. The killed portion of bars in (**C**) and (**D**) represents trees that were both attacked and killed that year, and the attacked portion represents trees that were attacked but did not die that year, whereas in (**A**) and (**B**) trees that were attacked and killed are represented in both the attacked bar and the killed bar. DBH, diameter at breast height.
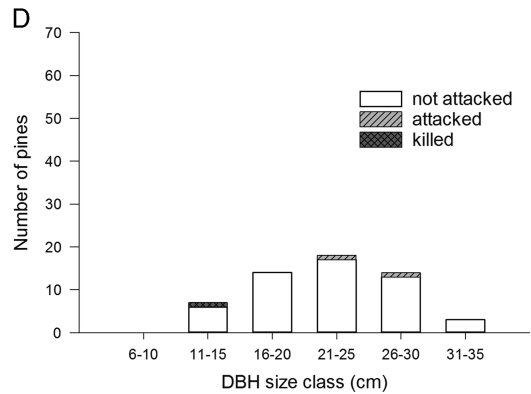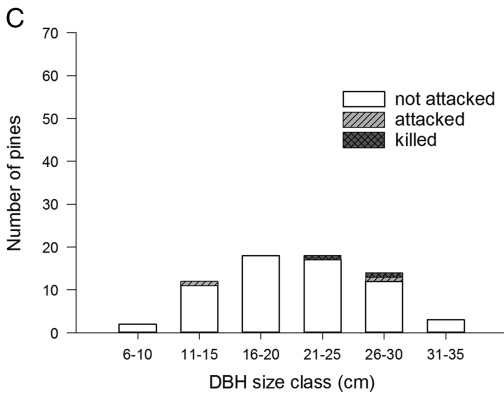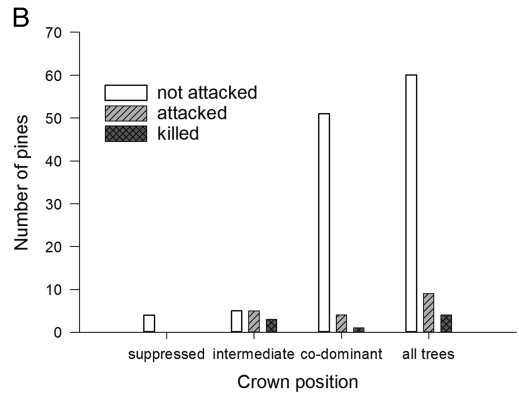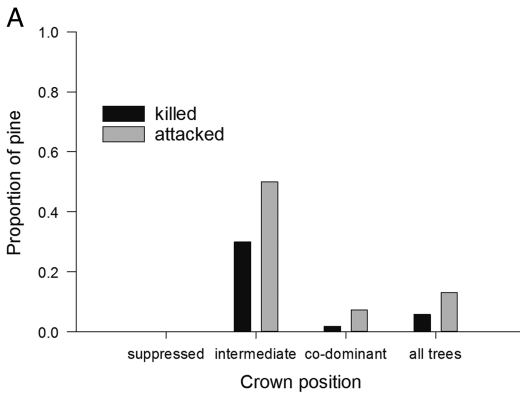

Table 4. Among trees attacked by *Sirex* (all sites combined), number of years in which trees were attacked or re-attacked by *Sirex*.

	Condition in 2016	
Years attacked	Alive	Dead
One	31	17
Two	17	10
Three	8	2
Four	1	0

S. noctilio populations can escape low, non-harmful levels on their own by building slowly over time, or if changing environmental conditions (increased frequency and intensity of droughts, increasing temperatures, longer

Fig. 10. Fate and infestation status of pines attacked by *Sirex* (**A–D**: 2012–2015) in the year following attack (2013 status–2016 status). Pines were either re-attacked (attacks), successful as hosts for the F1 generation (exits), or showed no further signs of *Sirex* infestation (none).
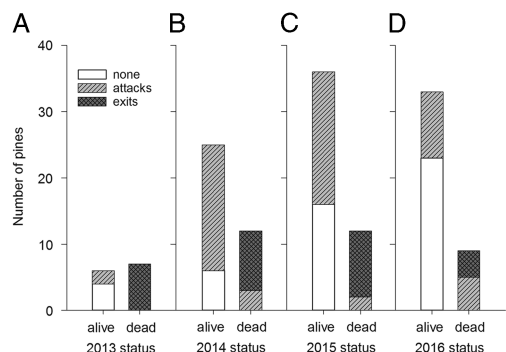
growing seasons), or forest management strategies (thinning versus do nothing) will allow *S. noctilio* populations to reach damaging levels.

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