Evidence of interaction between *Sirex noctilio* and other species inhabiting the bole of *Pinus*

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Abstract

1 *Sirex noctilio* is a woodwasp native to Eurasia and Northern Africa and has recently been found infesting pines in eastern North America. Its pest status in this new range is not yet known, although it is an important pest in other areas where it has been introduced. *Pinus* spp. in North America are hosts to several native and alien species of subcortical insects. Interactions between the woodwasp and these species may influence its distribution or the characteristics of its life history, thus affecting its population dynamics over time.

2 Sixty *S. noctilio*-infested *Pinus* spp. were felled in Ontario, Canada, and all phloem-feeding and woodboring insects were collected and identified from each 1-m section of the tree.

3 *Sirex noctilio* was in a tree alone 10% of the time but commonly shared the tree with subcortical beetles, such as *Tomicus piniperda*, *Pissodes nemorensis*, *Ips grandicollis*, *Gnathotrichus materiarius* and *Monochamus carolinensis*. The woodwasp was distributed throughout the tree stem and this distribution overlapped with that of the beetles.

4 Fewer but larger *S. noctilio* males emerged from trees with beetles compared with those without, although there was no statistical difference in females.

5 These findings suggest that co-habiting beetles could negatively affect *S. noctilio* population dynamics over time. The potential mechanisms for this interaction are discussed.

Keywords Bark beetles, distribution, interaction, *Sirex noctilio*, woodboring beetles.

Introduction

The woodwasp *Sirex noctilio* Fabricius was recently detected in eastern North America (Hoebeke *et al*., 2005; de Groot *et al*., 2006). In its native range in Eurasia and North Africa, it is a secondary pest of *Pinus* spp. (Spradbery & Kirk, 1978) and is of little economic or ecological concern. Before its discovery in North America, the wasp had established in parts of the southern hemisphere (Ciesla, 2003), where, at times, it caused extensive tree mortality in plantations of introduced pines (Neumann & Minko, 1981). The extent to which this species will become a problem in North America has yet to be determined (Dodds *et al*., 2010; but see also Yemshanov *et al*., 2009).

Pinus spp. in Canada and the U.S.A. host in excess of 1100 species of insects, with approximately 260 species inhabiting

the bole (de Groot & Turgeon, 1998). Thus, the woodwasp is expected to share its host tree with other phloem-feeding and woodboring insects, although the degree to which interactions with them could influence *S. noctilio* survival and development, and subsequently its population size, remains unknown. We hypothesized that these interactions help to limit its impact in Eurasia where there is a well-developed community of insects sharing the tree with the wasp (Wermelinger *et al*., 2008), in contrast to its introduced range in the southern hemisphere where *Pinus* spp. are all exotic and therefore host fewer insect species. There are many Curculionidae and Cerambycidae that colonize declining and newly-dead *Pinus* spp. trees in eastern North America. Insects such as the introduced bark beetle *Tomicus piniperda* (L.) prefer pine hosts with similar characteristics to that favoured by *S. noctilio* (Schroeder, 1987; Paine *et al*., 1997). Other beetles, such as *Monochamus* spp. and *Pissodes* spp., are also expected to share host trees with the woodwasp (USDA, 1985). Therefore, there is a high

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likelihood for interactions to occur between these beetles and the woodwasp, either directly via predation (Dodds *et al.*, 2001) or indirectly via the fungal associates of one or both species.

Sirex noctilio has a complex biology and this may influence the way in which indirect interactions with other subcortical insects could occur. The woodwasp has an obligate relationship with its fungal symbiont *Amylostereum areolatum* (Fr.) Boidin (Gaut, 1969). After oviposition by *S. noctilio* into the sapwood, females deposit the fungus as well as a phytotoxic mucus in an adjacent drill tunnel (Coutts & Dolezal, 1969). When the growth of *A. areolatum* is inhibited, woodwasp development is impeded (Coutts & Dolezal, 1965; King, 1966; Madden, 1981). Most of the woodboring beetle species found in North America that are expected to share the tree with *S. noctilio* are known vectors of ophiostomatoid (blue stain) fungi (Nevill & Alexander, 1992; Hausner *et al.*, 2005). These beetle-associated fungi are primary colonists of dying or recently dead trees (Kirisits, 2004) and such pioneer species are characteristically fast-growing and effective at exploiting a new resource (Boddy, 2000). *Amylostereum areolatum* is a weak competitor compared with some of these fungi and cannot establish in sapwood that is already colonized by these species (Ryan *et al.*, 2011). Therefore, the woodwasp must compete with woodboring beetles for an ephemeral resource for its symbiont and this exploitative competition for substrate could act as a bottom-up factor influencing *S. noctilio* populations.

Evidence of interspecific interactions between *S. noctilio* and woodboring beetles could include inter-tree partitioning, altered within-tree distribution or different patterns in *S. noctilio* life-history traits (e.g. abundance, body size). Spatial partitioning of species in standing host trees is well documented in bark beetle communities where tree colonization by two or more beetle species affects distribution on the bole (Paine *et al.*, 1981; Schlyter & Anderbrant, 1993; Ayres *et al.*, 2001). The outcome of interspecific competition in these bark beetle communities can be a lower offspring body mass (Schlyter & Anderbrant, 1993; Amezaga & Garbisu 2000) or fewer progeny (Rankin & Borden, 1991; Schlyter & Anderbrant, 1993). An altered or biased sex ratio could also occur (Andersen, 1961).

The present study aimed to: (i) examine whether other woodboring insects are associated with *S. noctilio*-infested trees and, if so, how frequently; (ii) establish and compare the within-tree distribution of *S. noctilio* with or without other woodborers; and (iii) determine whether life-history traits (i.e. abundance, size and sex ratio) of *S. noctilio* would be affected by the presence of other woodborers.

Materials and methods

To meet these objectives, 60 *S. noctilio*-infested *Pinus* spp. from 17 stands located in southern and central Ontario, Canada, were felled in the early spring, before woodwasp emergence: 22 trees in May 2007 and 38 in May 2008. These forests were selected because *S. noctilio* females had been caught in survey traps within the preceding 2 years. In each stand, the entire bole of trees that had died since the onset of the previous year's *S. noctilio* flight season (i.e. those with red or brown foliage) was examined with binoculars to detect symptoms of *S. noctilio* attack (i.e. resin beads or drips resulting from

Table 1 Mean ± SE characteristics of *Pinus* spp. felled in 2007 and 2008 from stands located in Ontario, Canada, for study of *Sirex noctilio* and subcortical beetle emergence

Tree char-acteristic	2007		2008	
	Pinus banksiana (*n* = 5 trees)	*Pinus sylvestris* (*n* = 17)	*Pinus sylvestris* (*n* = 34)	*Pinus resinosa* (*n* = 4)
Height (m)	12.28 (0.86)	12.9 (0.72)	10.73 (0.61)	11.83 (0.53)
Diameter at breast height (cm)	12.58 (0.91)	13.78 (0.71)	14.08 (0.78)	14.43 (1.40)

oviposition activity) (Ryan, 2011). Only trees with at least five resin beads, and without woodwasp exit holes, were considered suitable for the present study. The number of trees selected per stand varied between one and nine, although the study objective was to collect a minimum of three trees per stand. Low numbers of infested trees dictated the tree selection in many of the forests sampled. A total of 51 *Pinus sylvestris* (17 in 2007, 34 in 2008), five *Pinus banksiana* and four *Pinus resinosa* were used in the present study. The location, species and other attributes of the selected trees are described in Ryan (2011). Mean attributes per tree species and year are provided in Table 1.

Trees were cut at the base (i.e. within 40 cm from ground), and the bole was sectioned into 1 m lengths (bolts) and numbered consecutively. Each bolt was stood apex side up in an individual cardboard cylinder (36 × 102 cm) with a tight-fitting, opaque plastic lid (Greif Lok-Rim Fibre drum, Greif Inc., Delaware, Ohio). A hole of approximately 9 cm in diameter was cut in the centre of each lid. A plastic cup (475 mL), with a small hole cut in its base, was inverted and glued over the 9-cm hole of the lid. A second, smaller, clear plastic cup (375 mL) was placed on top of the larger cup to collect emerging insects. A string with one end stapled to the apex of the bolt and the other glued outside the exit hole of the larger cup was installed in each cylinder to provide a means for insects to crawl out of the tube. Cylinders were stored upright in covered, unheated, translucent-sided sheds at Angus, Ontario (17T 589861 4908280).

Woodboring insects were removed regularly from each cylinder between May and October. The small plastic cups were emptied five times weekly between late June and early September, and three times a week otherwise. Each time, the bottom of cylinders was examined and insects that had not exited the cylinder were removed manually. Insects from each rearing cylinder were stored in a vial of 70% ethanol until they could be identified. The prothorax width of each woodwasp was measured and its sex was determined. Prothorax width was selected as a surrogate for woodwasp size because it showed good test, re-test reliability on preliminary testing. Bolts from trees collected in 2008 were left in rearing cylinders until October 2009 to assess whether some *S. noctilio* had a 2-year lifecycle in Ontario. Insects emerging in the second year were collected and processed as described above.

Siricids, curculionids and cerambycids were identified to species using keys and information available in Schiff *et al.* (2006), Bright (1976), Passoa and Cavey (2006), Downie and Arnett (1996) and Yanega (1996), along with supplementary

material provided by H. Goulet (unpublished data). Insects that required specialized taxonomic expertise (weevils and *Tetropium* spp.) were identified (or had identifications verified) by specialists in these taxa (D. Langor, Canadian Forest Service, Canada and S. LaPlante, Canadian National Collection of Insects, Agriculture & Agri-Foods Canada, Canada). Voucher specimens are deposited in the Forest Health insect collection maintained by the Canadian Forest Service, Natural Resources Canada, Sault Ste. Marie, Ontario.

Statistical analysis

To account for differences in unit size, insect abundance data were standardized and expressed as the number of insects per unit of surface area (m^2) of the bole (i.e. the area available for insect oviposition) using the equation for a tapered cylinder for between-tree analysis [surface area of sides $= \pi(r_1 + r_2) \times \sqrt{([r_1 - r_2]^2 + h^2)}$, where r is the radius and h is the height] or the equation for a cylinder for within-tree analysis [surface area $= 2(\pi r^2) + 2(\pi r)h$]. Standardized emergence data from the first season after felling were used in all analyses. For intra-tree distribution analysis, trees were categorized into three arbitrary height classes (total tree height <10 m, $10-15$ m and >15 m), and each group was analyzed separately.

Data were tested for normality and homoscedasticity before analysis, and were transformed using $\log_n + 1$. Nonparametric tests were used to analyze data that could not be adequately transformed. A two-sample pooled variance *t*-test was used to compare tree characteristics between trees with beetles and those without. An analysis of covariance (with tree diameter at breast height as a co-variate), or a Mann–Whitney *U*-test was used to compare insect parameters at tree level, and repeated measures analysis of variance or a Wilcoxon test was utilized to compare insect parameters by bolt. In these models, only the lower four bolts of each tree were analyzed, except in the tallest height class when the lower eight bolts were used, because sample sizes decreased at higher bolt positions. Statistical correlation between *S. noctilio* size and abundance per tree was measured with Spearman's rank correlation coefficient. Analyses were conducted in SYSTAT (Systat Software Inc., 2007).

To assess whether interactions between *S. noctilio* and co-habiting species existed, the data were organized and processed as follows: (i) all bark and woodboring beetles, regardless of species, were pooled because the effects of the beetles on the woodwasp were all expected to be similar and indirect; (ii) using a natural break in the data to guide categorization, trees with less than 10 co-habiting specimens were grouped with those with no co-habitants and categorized as 'beetle-negative' and trees with ≥ 17 beetles were considered beetle-positive; (iii) all tree species were pooled to increase sample size as an initial analysis of *P. sylvestris* only showed similar patterns; (iv) trees 7–15.5 m in height ($n = 45$) were used because, within this subset, trees in each category did not differ in height ($t_{43} = 0.29$, $P = 0.77$) or diameter at breast height ($t_{43} = -1.78$, $P = 0.08$), limiting the effect of tree size on insect community (for details, see Results).

To assess for the occurrence of larval or pupal mortality in the presence of ophiostomatoid fungi (Morgan & Stewart, 1966b), a subset of bolts was dissected to look for evidence of this interaction. Eighteen *S. noctilio*-positive bolts (nine each for beetle-positive and beetle-negative) were selected. These bolts were sawed lengthwise into 1-cm wide planks and examined for dead larvae or pupae.

Results

A total of 15 986 phloem-feeding- and woodboring insects representing 43 species emerged from the bolts in the first year after felling (6586 insects from trees cut in 2007 and 9400 from those cut in 2008). A list of all species collected is available from Ryan (2011). *Sirex noctilio* was the most common insect collected (7018 specimens: 1783 females, 5235 males) and emerged from all 60 trees. Other major species included *T. piniperda* ($n = 6242$), *Pissodes nemorensis* Germar ($n = 1111$), *Ips grandicollis* (Eichoff) ($n = 521$), *Gnathotrichus materiarius* (Fitch) ($n = 218$) and *Monochamus carolinensis* (Olivier) ($n = 191$). Two other siricid species, *Sirex nigricornis* Fabricius ($n = 204$) and *Sirex edwardsii* Brullé ($n = 20$) emerged from *S. noctilio*-infested trees. The emergence of *S. noctilio* can spread over two seasons: a total of 152 specimens (72 females, 80 males) emerged in 2009 from 16 of the 38 trees felled in May 2008 and reared until October 2009.

Both sexes of *S. noctilio* emerged from all three *Pinus* species and from both collection years (Table 2). *Sirex noctilio* emerged from each pine species between late June and the third week of September in each year. The number of *S. noctilio* per tree was highly variable (range 3–569 specimens), and so was the number per bolt (range 0–149). Sex ratios (M : F) over all 60 trees ranged between 0.3 and 41.0 (Table 2). Mean prothorax width ranged from 2.6 mm in *P. banksiana* to 4.6 mm in *P. resinosa* (Table 2).

The three most commonly collected co-habiting insects: *T. piniperda*, *P. nemorensis* and *I. grandicollis*, emerged from all three pine species, although few specimens emerged from *P. banksiana* (Table 2). *Gnathotrichus materiarius* and *M. carolinensis* emerged only from *P. sylvestris*. *Tomicus piniperda* emerged from the bolts before *S. noctilio* (Fig. 1) and *P. nemorensis* emerged during a similar period to the woodwasp in 2008. *Ips grandicollis*, *G. materiarius* and *M. carolinensis* began emerging before *S. noctilio* but emerged over an extended period of time; the emergence of the former two species concluded well after *S. noctilio* finished emerging (Fig. 1). Emergence data from 2007 are not presented as a result of high mortality (and therefore missing emergence dates) for a number of beetle specimens.
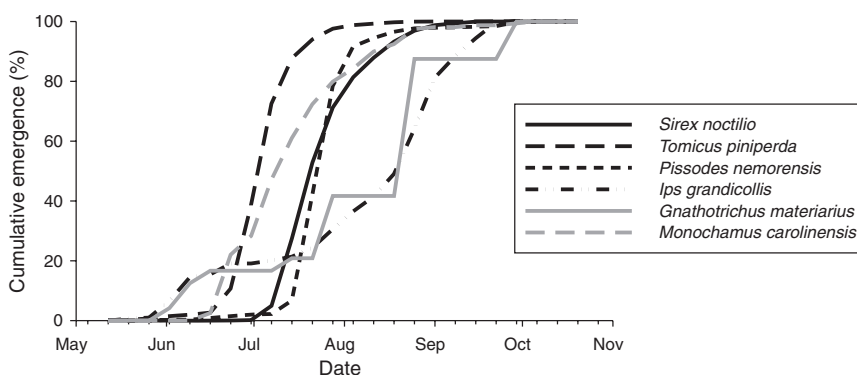
Within-tree distribution

In *P. sylvestris,* the number of males emerging was not uniform along the bole but the number of females emerging typically was (except in 10–15-m height class in 2007) (Table 3). Emergence of males tended to be higher in the mid-bole in the two largest height classes. In *P. banksiana*, both male and female emergence was statistically uniform along the bole. Female wasp emergence in *P. resinosa* differed significantly through the tree (Table 3). The number of males emerging from *P. resinosa* was low, thus precluding statistical analysis.

Table 2 Summary statistics on emergence of *Sirex noctilio* and the most common co-habiting species of beetles from *Pinus banksiana, Pinus resinosa* or *Pinus sylvestris* during the first year after felling

| | 2007 | | | | | | 2008 | | | | | |
| | *Pinus banksiana* (n = 5) | | | *Pinus sylvestris* (n = 17) | | | *Pinus sylvestris* (n = 34) | | | *Pinus resinosa* (n = 4) | | |
	n	Mean	Range	n	Mean	Range	n	Mean	Range	n	Mean	Range
Sirex noctilio												
Females	5	15	1–42	17	39	5–127	33	22	5–76	4	63	15–26
Males	5	39	12–104	17	144	5–452	34	71	1–414	4	39	4–84
Sex ratio (M : F)		4.67	0.54–13.0		3.90	0.83–5.04		3.65	0.50–41.0		0.53	0.27–0.95
Prothorax width (мм)	5	2.58	1.96–3.23	17	2.87	2.24–4.45	34	2.91	2.35–4.23	4	4.64	4.03–4.87
Tomicus piniperda	2	2	1–3	7	339	1–2375	15	208	1–1730	3	247	19–630
Pissodes nemorensis	2	3	2–3	11	10	1–29	17	20	1–161	4	163	6–377
Ips grandicollis	5	3	1–6	11	10	1–24	13	19	1–141	4	37	2–104
Gnathotrichus materiarius	–	–	–	6	31	3–120	7	5	1–12	–	–	–
Monochamus carolinensis	–	–	–	3	16	11–13	10	11	1–49	–	–	–

Trees were felled in 2007 and 2008 from stands located in Ontario, Canada. Emergence averaged over the number of trees with emergence records for that year.

Figure 1 Cumulative emergence over time of *Sirex noctilio* and the most common species of subcortical beetles collected from *S. noctilio*-infested *Pinus* spp. felled in Ontario, Canada, in 2008.

This was also the case for *T. piniperda. P. nemorensis, I. grandicollis, M. carolinensis* and *G. materiarius*, although the overall distribution of emergence as a function of bolt height above ground is provided for illustrative purposes (Fig. 2).

Sirex noctilio *life-history traits with and without beetles*

Sirex noctilio was the sole subcortical inhabitant of six trees (all *P. sylvestris*). Nineteen trees (14 *P. sylvestris*, one *P. resinosa* and four *P. banksiana*) had less than 10 co-habiting specimens: the remainder, 35 trees (31 *P. sylvestris*, three *P. resinosa* and one *P. banksiana*) had 17 or more specimens of beetles.

There was a significant difference in tree height between trees with less than 10 beetles (mean ± SE; 10.0 ± 0.6 m) and those with more than 16 beetles (12.6 ± 0.5 m) ($t = -3.31$, d.f. = 58, $P = 0.002$). *Sirex noctilio* was always alone in trees less than 7 m in height and always shared trees that were over 15.5 m with bark beetles.

Significantly fewer *S. noctilio* emerged from beetle-positive than beetle-negative trees. This difference between these categories of trees was the result of greater *S. noctilio* abundance throughout the tree (Fig. 3 and Table 4). Male

S. noctilio abundance patterns were similar to the pooled results. The abundance of female *S. noctilio* did not differ between the two categories (Table 4).

The average *S. noctilio* prothorax was wider in beetle-positive trees than in beetle-negative ones (Table 4). Male prothorax width was also greater in beetle-positive trees; there was no difference in female prothorax width (Table 4). There was a significant, negative correlation between male *S. noctilio* prothorax width and abundance within the tree ($r_s = 0.41$), although no such relationship existed in females ($r_s = 0.17$).

Sex ratio did not differ significantly between beetle-negative and positive trees (Table 4).

There were no dead larvae or pupae found in beetle-positive bolts, although seven dead larvae were found in beetle-negative bolts. Because there was no evidence of fungus-mediated larval or pupal mortality in this subset of beetle-positive bolts, the remaining bolts were not dissected.

Discussion

This is the first published description of the subcortical insect community sharing the tree with *S. noctilio* in North America.

Table 3 Mean ± SE number of female (F) and male (M) *Sirex noctilio* emerged per m^2 surface area per 1-m section of tree stem (bolt, numbered from the ground up) from dead *Pinus* spp. from three height classes in the first year after felling, and within-tree repeated measures analysis of variance by bolt

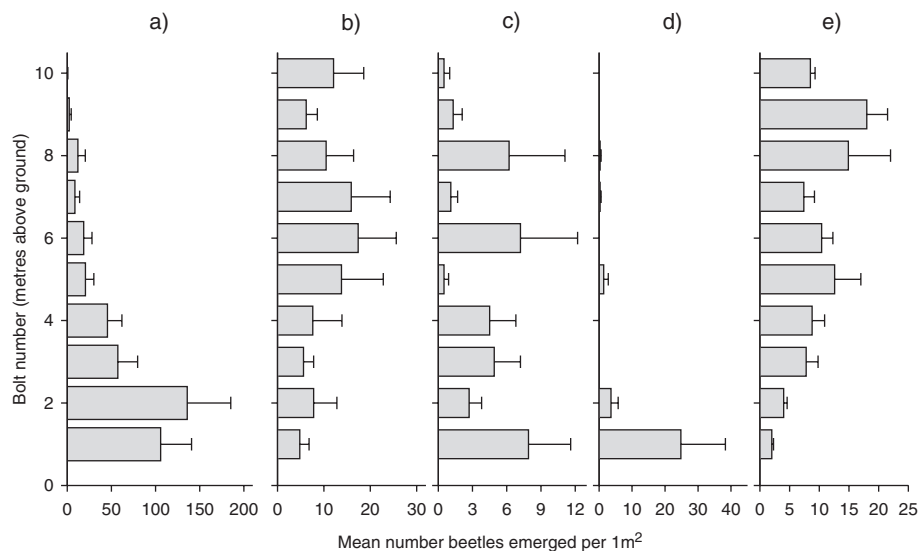| Bolt	<10 m *P. sylvestris* 2007 (n=3) F	M	<10 m *P. sylvestris* 2008 (n=11) F	M	10–15 m *P. sylvestris* 2007 (n=9) F	M	10–15 m *P. sylvestris* 2008 (n=18) F	M	10–15 m *P. resinosa* 2008 (n=4) F	M	10–15 m *P. banksiana* 2007 (n=4) F	M	>15 m *P. sylvestris* 2007 (n=5) F	M	>15 m *P. sylvestris* 2008 (n=5) F	M	>15 m *P. banksiana* 2008 (n=5) F	M	>15 m 2007 (n=1) F	M
1	24.0 ± 12.2	69.9 ± 32.2	9.4 ± 3.3	15.0 ± 4.2	8.4 ± 5.6	20.6 ± 9.8	4.3 ± 1.9	7.7 ± 3.9	2.4 ± 0.0	0 ± 0	10.2 ± 6.4	16.3 ± 10.6	1.1 ± 0.7	11.8 ± 11.8	7.7 ± 6.4	4.8 ± 3.3	–	–	8.2 ± 0	28.8 ± 0
2	20.3 ± 13.2	76.0 ± 31.0	17.4 ± 5.3	33.0 ± 8.4	13.0 ± 4.9	46.2 ± 24.1	5.1 ± 1.9	11.6 ± 5.3	15.9 ± 14.7	3.4 ± 3.4	8.6 ± 5.7	31.6 ± 18.2	6.5 ± 2.7	11.1 ± 6.6	4.1 ± 1.9	3.9 ± 2.1	–	–	11.4 ± 0	34.1 ± 0
3	19.4 ± 17.8	60.5 ± 39.9	12.2 ± 4.0	48.8 ± 14.7	21.0 ± 6.6	59.5 ± 24.4	6.7 ± 1.8	20.1 ± 6.1	16.3 ± 12.7	8.8 ± 7.5	2.5 ± 1.6	12.3 ± 7.5	20.9 ± 7.9	39.4 ± 16.7	6.6 ± 3.4	12.2 ± 8.2	–	–	18.9 ± 0	35.4 ± 0
4	13.8 ± 10.2	29.7 ± 22.3	10.3 ± 5.1	37.7 ± 13.3	17.5 ± 6.4	93.9 ± 26.0	7.5 ± 3.4	31.2 ± 8.2	31.2 ± 8.8	11.3 ± 4.7	1.6 ± 0.9	0.8 ± 0.8	22.9 ± 9.8	43.9 ± 10.3	13.5 ± 5.8	29.1 ± 21.4	–	–	12.9 ± 0	15.0 ± 0
5	15.6 ± 15.6	27.7 ± 27.7	11.9 ± 6.0	27.3 ± 16.7	15.0 ± 6.0	76.7 ± 28.0	10.7 ± 3.3	33.5 ± 8.5	24.8 ± 7.8	12.8 ± 5.7	0.8 ± 0.8	0.6 ± 0.6	12.9 ± 5.5	54.1 ± 15.4	15.7 ± 4.2	54.3 ± 27.2	–	–	17.4 ± 0	33.4 ± 0
6	9.7 ± 9.7	19.4 ± 19.4	6.9 ± 4.7	20.7 ± 13.4	17.4 ± 7.6	72.1 ± 22.7	6.0 ± 2.3	27.7 ± 6.7	26.7 ± 7.5	17.9 ± 8.9	1.1 ± 1.1	0 ± 0	12.7 ± 6.1	63.5 ± 25.1	10.9 ± 5.4	66.6 ± 43.4	–	–	12.9 ± 0	43.7 ± 0
7	–	–	0 ± 0	10.7 ± 4.1	15.4 ± 7.8	58.4 ± 21.8	3.7 ± 1.1	16.7 ± 3.9	18.6 ± 10.6	33.1 ± 15.1	0 ± 0	0 ± 0	8.1 ± 4.4	60.5 ± 21.6	14.2 ± 4.5	58.5 ± 27.8	–	–	8.2 ± 0	26.1 ± 0
8	–	–	–	–	8.0 ± 5.5	24.6 ± 13.6	3.1 ± 1.5	8.3 ± 2.2	28.8 ± 16.6	18.8 ± 15.1	0 ± 0	0 ± 0	9.6 ± 4.3	81.3 ± 44.0	4.9 ± 2.9	28.1 ± 13.9	–	–	8.7 ± 0	12.0 ± 0
9	–	–	–	–	14.1 ± 9.1	22.3 ± 10.3	2.6 ± 1.8	4.0 ± 1.7	43.1 ± 33.6	22.8 ± 10.1	0 ± 0	0 ± 0	5.8 ± 4.6	70.0 ± 38.3	1.5 ± 1.0	11.4 ± 6.7	–	–	6.0 ± 0	13.1 ± 0
10	–	–	–	–	7.6 ± 6.3	2.9 ± 2.9	0.4 ± 0.4	6.0 ± 2.7	0 ± 0	4.4 ± 0	–	–	3.4 ± 2.0	24.4 ± 13.1	0.5 ± 0.5	10.2 ± 6.5	–	–	9.8 ± 0	10.8 ± 0
11	–	–	–	–	0 ± 0	0 ± 0	1.1 ± 1.1	3.9 ± 2.3	–	–	–	–	4.7 ± 4.7	14.2 ± 14.2	0 ± 0	6.6 ± 5.8	–	–	3.6 ± 0	11.6 ± 0
12	–	–	–	–	–	–	–	–	–	–	–	–	2.2 ± 2.2	18.8 ± 18.8	1.4 ± 1.4	8.9 ± 6.5	–	–	3.9 ± 0	8.2 ± 0
13	–	–	–	–	–	–	–	–	–	–	–	–	9.6 ± 9.6	11.5 ± 11.5	0 ± 0	15.5 ± 15.5	–	–	0 ± 0	–
14	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0 ± 0	9.9 ± 9.9	–	–	–	–
15	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
16	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	Insufficient data	Insufficient data
	$F_{3,6}=1.22$	$F_{3,6}=5.09$	$F_{3,27}=2.21$	$F_{3,27}=3.73$	$F_{3,24}=3.85$	$F_{3,24}=4.08$	$F_{3,51}=1.35$	$F_{3,51}=8.50$	$F_{3,9}=8.16$	Insufficient data	$F_{3,9}=1.47$	$F_{3,9}=1.82$	$F_{7,28}=1.70$	$F_{7,28}=7.02$	$F_{7,28}=1.21$	$F_{7,28}=4.13$			Insufficient data	Insufficient data
	$P=0.38$	$P=0.04$	$P=0.11$	$P=0.02$	$P=0.02$	$P=0.02$	$P=0.27$	$P<0.001$	$P=0.006$		$P=0.29$	$P=0.21$	$P=0.15$	$P<0.001$	$P=0.33$	$P=0.003$				

All trees felled in Ontario, Canada, in 2007 and 2008.

Figure 2 Mean ± SE beetle emergence per 1-m² surface area of *Pinus* tree stem (tree species pooled). (a) *Tomicus piniperda* (*n* = 27 trees), (b) *Pissodes nemorensis* (*n* = 34), (c) *Ips grandicollis* (*n* = 33), (d) *Gnathotrichus materiarius* (*n* = 13), (e) *Monochamus carolinensis* (*n* = 13). Emergence averaged over number of trees each species emerged from (*n*). Tree felled in Ontario, Canada, in 2007 and 2008.
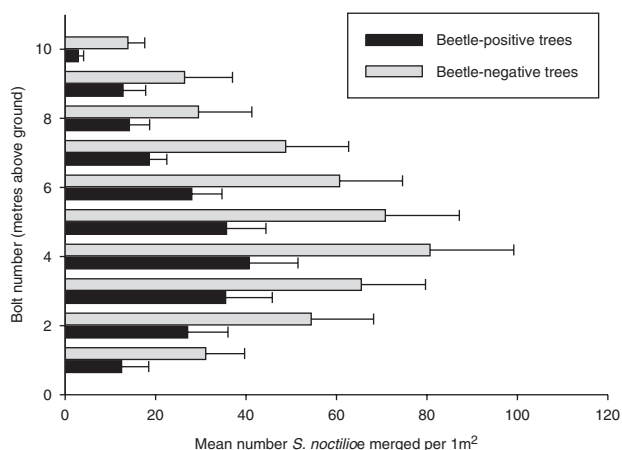

Figure 3 Mean ± SE *Sirex noctilio* emergence per 1-m² surface area of *Pinus* stem in beetle-positive (≥17 subcortical beetles per tree) and 'beetle-negative' (≤9 beetles per tree) *Pinus* trees felled in Ontario, Canada, in 2007 and 2008.

The findings of the study revealed the presence of many specimens of co-habiting beetles in more than 50% of the trees felled, comprising many species and guilds; *S. noctilio* was found alone in 10% of the trees. The identity of the most common species of co-habiting beetles was not unexpected; similar to *S. noctilio*, *T. piniperda* favours low vigour pines as a brood habitat (Schroeder, 1987) and the other common co-habiting species favour weakened, dying or recently dead pines (USDA, 1985).

The within-tree distribution of *S. noctilio* was similar to that found elsewhere in the insect's known range. In *P. sylvestris* (males) and *P. resinosa* (females), more of the woodwasp emergence was in the mid-tree, and this is similar to that described in *Pinus* spp. in New Zealand (*Pinus radiata*),

Australia (*P. radiata*) and Brazil (*Pinus taeda*) (Morgan & Stewart, 1966a; Neumann *et al.*, 1982; Penteado *et al.*, 1998). Regarding the woodboring beetles, the results of the present study show their within-tree distribution to be consistent to that reported in the literature. For example, *T. piniperda* is known to favour the rough-barked lower stem of the tree but is also found in thinner barked sections (Schroeder, 1997); *P. nemorensis* is usually found throughout the trunk (Atkinson *et al.*, 1988); and *Monochamus* species are typically found above 3 m from the ground (Walsh & Linit, 1985). Based on these findings, we can expect that *S. noctilio* will regularly interact with woodboring beetles throughout its distribution within the tree, notwithstanding tree size.

There was no evidence that *S. noctilio* was excluded from regions of the tree when woodboring beetles were present. The reduction in (but identical distribution of) *S. noctilio* emergence (pooled and males) in beetle-positive trees compared with beetle-negative ones was, however, a clear sign of interaction between them. The lack of significant differences in female woodwasp abundance between the two categories of trees may a result of the smaller sample size because trends were similar to that of males. Although the analysis was confined to a subset of trees of generally similar size, tree size did influence the community of subcortical insects in the full data set, and thus is likely to be a factor influencing interactions between these two groups.

The majority of co-habitants with *S. noctilio* were Curculionidae that feed in the phloem and were therefore unlikely to encounter the woodwasp directly. Thus, as hypothesized, interactions between *S. noctilio* and beetles are more likely to be indirect, and to be mediated by fungal associates. A reduced *S. noctilio* abundance in beetle-colonized trees could occur if woodwasp females are inhibited from ovipositing in trees where beetle-associated ophiostomatoid fungi are present (Ryan, 2011). Alternatively, the woodwasp's symbiont may be

Table 4 Mean ± SE emergence, analysis of covariance, Mann–Whitney U-test, repeated measures analysis of variance and Wilcoxon test (lower four 1-m bolts of tree stem are compared) results for life-history traits of *Sirex noctilio* emerging from beetle-positive dead *Pinus* spp. (co-habited by ≥17 individual subcortical beetles) compared with those from beetle-negative trees [few (≤9), or no beetles] (n = 45 trees)

			Analysis by tree				Analysis by bolt		
			Per tree mean *Sirex noctilio* emergence/m² without beetles	Per tree mean *Sirex noctilio* emergence/m² with beetles	Beetle effect tree level analysis	Diameter at breast height effect tree level analysis	Beetle effect by bolt	Bolt effect	Interaction beetle and bolt
Pooled *Pinus* spp.	Abundance	*Sirex noctilio* pooled	59 ± 12	32 ± 7	$F_{1,42} = 5.75\ P = 0.02$	$F_{1,42} = 1.21\ P = 0.28$		$F_{1,43} = 9.88\ P = 0.003$	$F_{3,129} = 10.53\ P < 0.001$
		Male *Sirex noctilio*	43 ± 9	23 ± 6	$F_{1,42} = 6.24\ P = 0.02$	$F_{1,42} = 1.26\ P = 0.27$		$F_{1,43} = 3.95\ P = 0.05$	$F_{3,129} = 7.38\ p < 0.001$
		Female *Sirex noctilio*	14 ± 3	9 ± 2	$F_{1,42} = 2.76\ P = 0.10$	$F_{1,42} = 0.78\ P = 0.38$		$F_{1,43} = 2.26\ P = 0.14$	$F_{3,129} = 3.00\ P < 0.03$
	Prothorax width (mm)	*Sirex noctilio* pooled	2.7 ± 0.1	3.2 ± 0.1	$U = 138.5\ P = 0.02$	–		$Z = -1.83\ P = 0.07$	–
		Male *Sirex noctilio*	2.6 ± 0.1	3.0 ± 0.1	$U = 130.0\ P < 0.001$	–		$Z = -1.83\ P = 0.07$	–
		Female *Sirex noctilio*	3.1 ± 0.1	3.4 ± 0.2	$U = 199.00\ P = 0.43$	–		$Z = -1.46\ P = 0.14$	–
	Sex ratio (M : F)	–	4.3 ± 0.7	5.3 ± 1.6	$U = 267.5\ P = 0.42$	–		–	–
Pinus sylvestris	Abundance	*Sirex noctilio* pooled	68 ± 15	34 ± 9	$F_{1,33} = 6.34\ P = 0.02$	$F_{1,33} = 2.07\ P = 0.16$		$F_{1,34} = 6.02\ P = 0.02$	$F_{3,102} = 9.51\ P < 0.001$
		Male *Sirex noctilio*	52 ± 12	25 ± 7	$F_{1,33} = 7.16\ P = 0.01$	$F_{1,33} = 2.42\ P = 0.13$		$F_{1,34} = 4.01\ P = 0.05$	$F_{3,102} = 8.95\ P < 0.001$
		Female *Sirex noctilio*	14 ± 3	9 ± 2	$F_{1,33} = 3.10\ P = 0.09$	$F_{1,33} = 1.34\ P = 0.26$		$F_{1,34} = 1.08\ P = 0.31$	$F_{3,102} = 2.41\ P = 0.07$
	Prothorax width (mm)	*Sirex noctilio* pooled	2.7 ± 0.1	3.0 ± 0.1	$U = 97.5\ P = 0.09$	–		$Z = -1.83\ P = 0.07$	–
		Male *Sirex noctilio*	2.6 ± 0.1	2.8 ± 0.1	$U = 93.0\ P = 0.06$	–		$Z = -1.83\ P = 0.07$	–
		Female *Sirex noctilio*	3.1 ± 0.1	3.2 ± 0.1	$U = 137.0\ P = 0.83$	–		$Z = -0.73\ P = 0.47$	–
	Sex ratio (M : F)	–	4.8 ± 0.8	5.6 ± 1.8	$U = 173.0\ P = 0.31$	–		–	–

Results for emergence from *P. sylvestris* trees alone are presented for comparison.

out-competed by beetle-associated-fungi, thereby causing mortality of the woodwasp's life stages (Hanson, 1939; King, 1966; Morgan & Stewart, 1966b; Titze & Stahl, 1970; Ryan *et al.*, 2011), resulting in fewer adults emerging. The mechanisms that would explain the interaction between these beetle-associated fungi and the woodwasp or its symbiont depends on the timing of entry into the tree. The most abundant co-habitant, *T. piniperda*, emerged earlier than the wasp, is reproductively active primarily in the early spring (Kennedy & McCullough, 2002), and appears to most often attack the tree the year after the woodwasp has done so (Ryan, 2011), therefore introducing its associated fungi into the tree when the woodwasp's development is well underway. Given this, the degree of reduced *S. noctilio* emergence in beetle-positive trees, in the absence of signs of increased larval mortality, was unexpected and suggests that this beetle species may not be an important a competitor to the wasp. We cannot, however, exclude the possibility that this beetle species' fungal associates induced woodwasp egg mortality if the egg eclosion was delayed by substrate or climate conditions: nothing is known of the woodwasp overwintering stage in this range. Beetles that emerge around the same time as *S. noctilio*, such as *P. nemorensis*, *I. grandicollis*, *G. materiarius* and *M. carolinensis*, could colonize the tree before or shortly after the woodwasp and plausibly interact with it through any of the suggested mechanisms. These species could be more important competitors with the woodwasp.

The larger male body size in beetle-positive trees was unexpected given that the *S. noctilio* symbiont is considered to be a poor competitor against beetle-associated fungi (King, 1966; Ryan *et al.*, 2011) and also that the woodwasp larvae depend on it for nutrition. Improved larval nutrition in beetle-positive trees could be expected if sapwood drying was accelerated within the tree as a result of the introduction of ophiostomatoid fungi (Chow & Obermajer, 2007), thus improving conditions for *A. areolatum* growth: the woodwasp symbiont grows more quickly in drier wood (Coutts & Dolezal, 1965). The negative correlation between male wasp prothorax size and abundance suggests an ecological trade-off between insect abundance and size.

The present study was not designed to investigate differences in *S. noctilio* characteristics and woodborer communities between *Pinus* species, although some patterns warrant further investigation because these factors may affect population dynamics in different stand types. The trend to larger *S. noctilio* and a lower male : female sex ratio in *P. resinosa* and, conversely, the trend to fewer and smaller woodwasps in *P. banksiana*, relative to other *Pinus* species, could affect the population dynamics of the woodwasp in these stands.

The present study describes the community of phloem-feeding and woodboring beetles sharing host trees with *S. noctilio* in northeastern North America. The reduction in *S. noctilio* emergence in trees with beetles shows evidence of competition between these two groups that could affect the population dynamics of this introduced insect. These signs of interactions are the first described for this system. Further experimental investigations are needed to provide a better understanding of the mechanisms of interaction between the various feeding guilds and the impact that they might have on *S. noctilio* populations and its pest status in its new range.

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