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# Biotic resistance and the spatiotemporal distribution of an invading woodwasp, *Sirex noctilio*

Christopher J. Foelker · Dylan Parry · Melissa K. Fierke

**Abstract** Quantifying the strength of interactions among introduced and native species across space and time is critical in understanding biological invasions as they can attenuate or amplify the magnitude of impact. The European woodwasp, *Sirex noctilio* F., a global threat to pines, is a recent invader to North America. It attacks and kills primarily *Pinus resinosa* and *Pinus sylvestris*, and encounters a diverse assemblage of potential competitors for this resource. We quantified spatial colonization patterns of this woodwasp and resident competitors including scolytine bark beetles, woodboring cerambycid and buprestid beetles, and the fungal root rot diseases *Armillaria* and *Heterobasidion* across an 80 year old pine plantation over 4 years. All xylophages were spatially aggregated, but only on a localized scale of 15–20 m. Colonizers occurred non-randomly within trees, with *S. noctilio* negatively or neutrally associated with all other colonizing agents, whereas all other insect and root rot colonizers were mostly positively co-associated. An autologistic regression with spatially-weighted variables indicated the probability of a dead tree exhibiting symptoms of *S. noctilio* attack was positively associated with tree density, host species (*P. sylvestris*), and density of *S. noctilio*-attacked trees from the current and previous year. Interspecific stand patterns were weaker; probability of attack was negatively associated only with root rot pathogens. Across spatial scales, there were mixed (woodborers) and neutral (bark beetles) associations between *S. noctilio* and other co-colonizing insects. Our results suggest that competitive interactions with resident species may be contributing to the limited success of *S. noctilio* in North America, but are unlikely to be driving it by themselves.

**Keywords** Aggregation · Auto- and cross-correlation · Autologistic regression · Non native insect · *Pinus*

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## Introduction

A poorly understood component of invasion biology is the interaction among invaders and native biota, particularly across space and time (Denno et al. 1995; Niemelä and Mattson 1996; Keane and Crawley 2002; Parker and Hay 2005; Carlsson et al. 2009). Collectively, the role native species play in impeding establishment and spread of an invasive species is

termed biotic resistance (Elton 1958). While extensive research has focused on biotic resistance of native plants to invaders in plant communities, relatively few studies have looked at other organisms. Competitive biotic resistance, in particular, is poorly represented in studies of non-plant invasions.

Among bark and woodboring insects, direct or indirect interspecific competition can drive distribution, abundance, and population dynamics (Graham 1925; Coulson et al. 1976; Light et al. 1983; Miller 1986; Rankin and Borden 1991; Hofstetter et al. 2005; Davis and Hofstetter 2009). These interactions are often asymmetrical and can be mediated by biotic and abiotic factors, such as plant host, microbial associates, natural enemies, disturbance, and climate (Price et al. 1980, 1986; Paine et al. 1981; McClure 1984; Denno et al. 2000; Erbilgin and Raffa 2000; Aukema et al. 2004). For primary tree-attacking insects, co-colonization with heterospecifics can exert negative feedback via competition for resources or intraguild predation (Coulson et al. 1976; Rankin and Borden 1991; Schlyter and Anderbrant 1993; Schroeder and Weslien 1994; Dodds et al. 2001; Aukema et al. 2010).

In 2005, *Sirex noctilio* F. (Hymenoptera: Siricidae), the European woodwasp, was identified from a 2004 survey trap in central New York State, USA (Hoebeke et al. 2005). Discovery of this non-native insect was of particular concern because of its history as a devastating introduced pest in plantations of North American pine across the Southern Hemisphere (Madden 1988; Slippers et al. 2015). Female *S. noctilio* inoculate hosts with phytotoxic mucus and a mutualist fungus, *Amylostereum areolatum*, both of which aid in weakening and killing trees (Coutts 1969a, b). Developing larvae are dependent upon *A. areolatum* as a nutritional substrate, extracting nutrients from colonized tissue and cellulases produced by the fungus that facilitate xylem digestion (Francke-Grosman 1939; Parkin 1941; Buchner 1965; Thompson et al. 2012).

Confounding early predictions, *S. noctilio* has caused limited tree mortality in North America, with successful attacks restricted primarily to suppressed *Pinus resinosa*, a native pine, and *Pinus sylvestris*, a naturalized pine from Europe (Dodds et al. 2010; Ayres et al. 2014). A diverse guild of native parasitoids have readily adopted *S. noctilio* as a host since its advent in North America (Long et al. 2009; Eager et al. 2011; Standley et al. 2012; Ryan et al. 2012b; Foelker et al. 2016a). However, levels of

parasitism exhibit large spatial and temporal variations, as do the component members of this guild attacking *S. noctilio* (Foelker et al. 2016b; Haavik et al. 2016). While not definitive, inconsistent and often relatively low levels of overall parasitism suggest that by themselves, parasitoids are not acting as a strong regulating force limiting the success of this invader.

In North America, unlike anywhere else in its invaded range, *S. noctilio* has encountered a large assemblage of native co-colonizing insects associated with *Pinus* spp. (Graham 1925; Savely 1939; Erbilgin et al. 2002; Dodds et al. 2012). Unfortunately, relationships between *S. noctilio* and competing insects are largely uninvestigated in its native range in Europe due to its lack of economic importance, whereas these interactions are absent entirely in the Southern Hemisphere. Thus, an understanding of these multipartite species interactions is lacking, even though they may be a significant driver of the invasion ecology of *S. noctilio* in North America.

The suite of pine colonizers is extensive in eastern North America. *Ips pini* (Coleoptera: Curculionidae) is the most prevalent of a large contingent of scolytines that colonize all portions of the tree (Ayres et al. 2001) and are active across a wide temporal window that extends into early fall (Aukema et al. 2004). In addition, multiple woodboring beetles (Cerambycidae) feed deep in the xylem tissue (Erbilgin and Raffa 2002; Erbilgin et al. 2002) and can even facultatively feed on *S. noctilio* as larvae (Thompson 2013). Adding to the complexity, interactions among *S. noctilio*, bark beetles, and woodborers are likely indirect, mediated through their respective fungal associates (Hurley et al. 2012; Ryan et al. 2012a; Yousuf et al. 2014a). This array of competitors may be more analogous to what *S. noctilio* encounters in its native range in Eurasia and North Africa where it is largely a secondary mortality agent (Chrystal and Myers 1928; Spradbery and Kirk 1978; Ayres et al. 2014).

While spatiotemporal attack patterns of *S. noctilio* have been described for some invaded regions of the Southern Hemisphere (Tribe and Cillié 2004; Corley et al. 2007; Corley and Villacide 2012; Lantschner and Corley 2015), analysis of dispersal and colonization is lacking for North American populations. Though *S. noctilio* is a large robust insect, it is suggested that long distance dispersal is fairly limited, as these events present a substantial risk for these insects (Corley et al.

2007; Corley and Villacide 2012). Generally, dispersal by insects in forest settings is influenced by predation risk, parasites, energetic reserves, and abundance/quality of host material (Capinera and Barbosa 1976; Barbosa et al. 1981; Villacide and Corley 2008). Empirical and theoretical work indicate a majority of bark and woodboring insects are located in close proximity to their emergence site and only a small proportion actually fulfill their full dispersal potential (Raffa and Berryman 1980; Safranyik et al. 1992; Turchin and Thoeny 1993; Cronin et al. 2000; Smith et al. 2001; Corley et al. 2007).

Here, we investigate stand-level colonization patterns of *S. noctilio*, co-occurring bark and woodboring insects, and root rot disease fungi at a *P. resinosa* and *P. sylvestris* plantation in New York State from 2011 to 2014. Planted stands of similar composition and age are ubiquitous across the Northeastern USA and indeed, appear to represent the majority of habitat occupied by *S. noctilio* since its arrival (Dodds et al. 2010). We specifically investigated the independent distributions and aggregation patterns of five typical and prominent colonizing agents to pine mortality in the region: bark beetles (Coleoptera: Curculionidae: Scolytinae), woodborers (Coleoptera: Cerambycidae and Coleoptera: Buprestidae), Armillaria root disease, Annosum root disease, and *S. noctilio*. Our main objectives were to explore: (a) patterns of aggregation, (b) co-occurrence within trees, and (c) spatiotemporal patterns of *S. noctilio* attack in relation to density of co-colonists (both current and previous year) and to other stand-level factors.

## Methods

Pack Demonstration Forest (43.549753°N, − 73.821885°W), near Warrensburg, NY in the southeastern corner of the Adirondack Park, is comprised primarily of 80–90 year old *P. resinosa*, *P. sylvestris*, and *P. strobus* plantations. The 48.5 ha site was historically used for soil nutrients and silviculture research in the 1940–1950s, but has not been thinned for over 30 yr (Buxbaum et al. 2005). We conducted a full stand census of all *P. resinosa* and *P. sylvestris* compartments in late summer from 2012 to 2014 (15 Aug–30 Aug 2012, 25 Aug–5 Sep 2013, and 25 Aug–5 Sep 2014). We marked all dead/dying trees from the previous summer using a handheld GPS (Garmin Rino

520HCx; accuracy < 3 m), recorded DBH and species (*P. resinosa* or *P. sylvestris*), and established boundaries for all compartments using GPS coordinates (Fig. 1).

Chronology of *S. noctilio* colonization can be reconstructed reliably for the current and previous attack year based on two diagnostic features: resin beads and exit holes. Siricid exit holes are distinguishable from other woodborers as they are circular, angled perpendicular to the direction of the main bole, and are usually clustered together in groups of 10–20 (Ayres et al. 2014). *Sirex noctilio* exit holes and resin beads are indistinguishable from those of native siricids. However, native siricids are much less abundant than *S. noctilio* in attacked trees (Eager et al. 2011; Ryan et al. 2012b; Foelker et al. 2016b).

We recorded visual evidence (exit holes and frass) of insect co-colonizers along the lower 3 m of the tree as either being from woodborers and/or bark beetles and confirmed observations by removing the outer bark. Prevalent bark beetles were *I. pini*, *Tomicus piniperda* (a non-native European species), and *Dendroctonus valens*.

We also inspected the root collar for presence of two ecologically and economically important root rot diseases, Armillaria and Annosum. There is a lack of taxonomic consensus on the causal agents of these diseases in North America, at least at the species level (Ross-Davis et al. 2011; Garbelotto and Gonthier 2013), so we hereafter refer to each as *Armillaria* sp. (Basidiomycota: Agaricales) and *Heterobasidion irregulare* sensu lato (s.l.) (Basidiomycota: Russulales). Bark was peeled at three equidistant points along the perimeter of the root collar to a depth of ∼ 30 cm. *Armillaria* sp. was identified via presence of thick white mycelial fans or black rhizomorphs (Omdal et al. 2004; Bendel and Rigling 2008). *Heterbasidion irregulare* s.l. was diagnosed using fruiting bodies, but also by the presence of a paper-thin mycelium with pustules, lamination (separation of the growth rings), and pitting (spotted bleaching of the wood caused by oxidation) (Omdal et al. 2004; Bendel and Rigling 2008; Garbelotto and Gonthier 2013). Dead trees in known areas of root rot disease, particularly *H. irregulare* s.l., were checked the following year for signs because fruiting bodies are often not present during the year of mortality (Woodard et al. 1998). We collected binary data (yes/no) for each dead tree on the presence of each of

**Fig. 1** All stand compartments containing *P. sylvestris* or *P. resinosa* dead trees (*n* = 992) recorded from 2011 to 2014 at Pack Demonstration Forest in the Adirondack Park of New York State
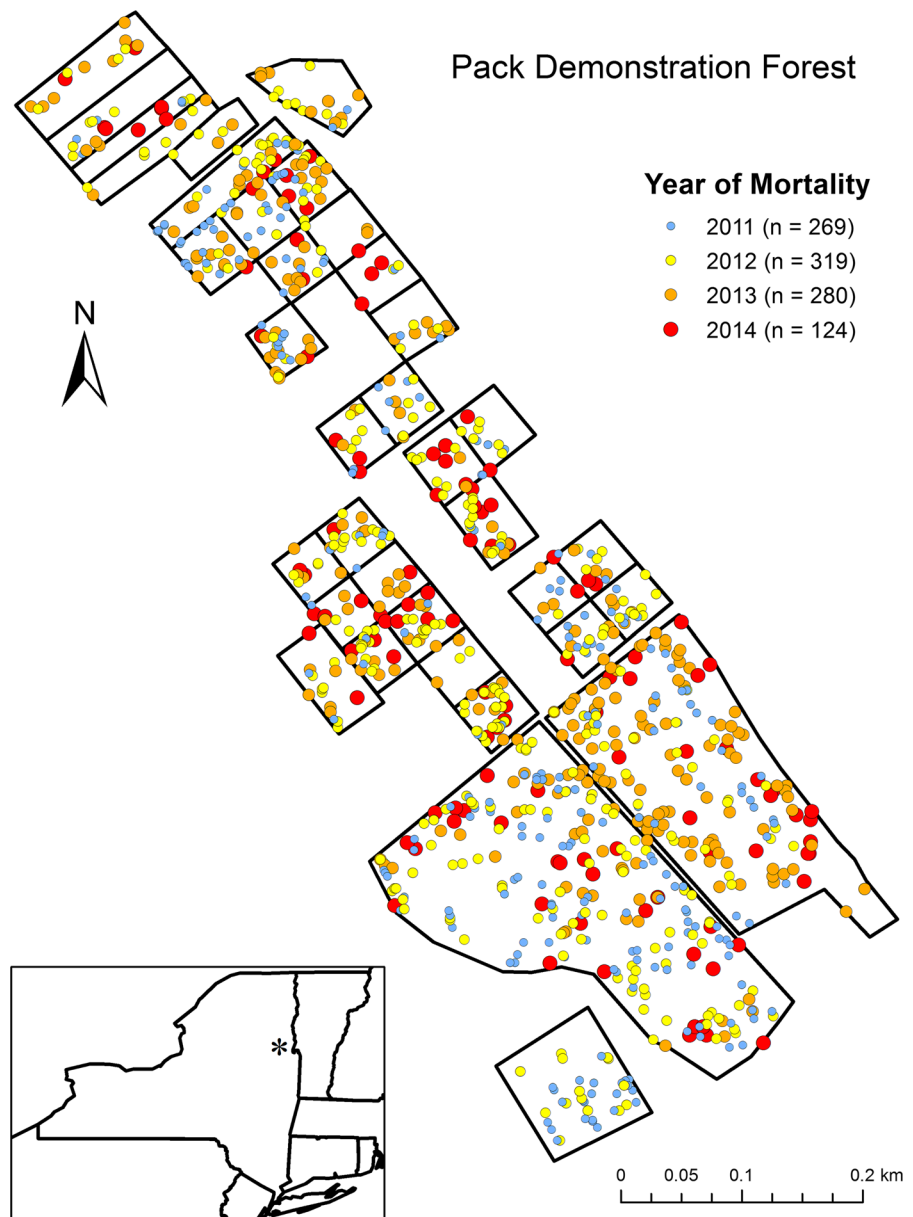


these five colonizing agents and allowed for multiple agents simultaneously in the same tree.

Site variable measurements included a modified version of Morisita's ordered distance protocol (Nielson et al. 2004) where each compartment was sampled with two, randomly placed, 50 m transects. We ran three transects in the two largest compartments in the southeastern portion of the site. At 10 m intervals along the transects, the third nearest tree was located, its distance measured to the transect point, and

diameter at breast height (DBH) recorded. We used these data to estimate stand density (trees/ha) by Morisita's equation. At three points along the transect (10, 30, and 50 m), we measured basal area (m²/ha) with an English BAF 10X prism.

Statistical analysis

We analyzed within-tree correlations of presence/absence of colonizing agents using phi ($\varphi$) coefficients

(a derivative of Pearson's correlation used for binary data). Ten dying/dead trees exhibited no symptoms of the investigated colonizing agents and were removed from the analysis.

We tested the individual aggregative pattern of each colonizing agent using Ripley's inhomogeneous *K* function with border correction (Ripley 1976). This function tests the null hypothesis of complete spatial randomness using an expanding search radius centered on each event. The inhomogeneous component of the model allows for scaling based on the intensity of points (i.e. stand density). We set a maximum search radius of 50 m to test if the density of events occurring inside the circle was significantly different from the global density of events using 2500 bootstrap replicates.

The spatial autocorrelation for *S. noctilio* and cross-correlation for pairwise comparisons of *S. noctilio* and all other colonizing agents was estimated using a non-parametric covariance function with 1000 iterations of bootstrap resampling (Bjørnstad and Falck 2001). We used this pairwise comparison method on data pooled from all years to establish a region of influence for *S. noctilio* specifically (autocorrelation) and between *S. noctilio* and each individual colonizing agent (cross-correlation).

To investigate spatial and temporal patterns of *S. noctilio* and colonizing agents, we conducted an autologistic regression on all dead trees using symptoms of *S. noctilio* (resinosis) as the response variable and separate spatially lagged variables for each co-colonizer: density of trees killed in the current year ($t$) and in the previous year ($t − 1$). The spatially lagged variable was calculated as the density of trees attacked by an individual co-colonizer within a fixed radius of each tree. Unique radii ($r$) were calculated for each colonizing agent based on the spatial autocorrelation (for *S. noctilio*) and cross-correlation function (see above). Extent of spatial cross-correlations (radii) was calculated based on the maximum distance over which covariance was detectable (range) (i.e. covariance $>$ or $< 0$). Density of trees was standardized based on established boundaries that only included sampled stands (Fig. 1). A parameter for bark beetles was not included in the model as the covariance function indicated an absence of spatial association between this factor and *S. noctilio*.

Stand-level variables of trees species (*P. resinosa* or *P. sylvestris*), density (stems/ha), and basal area

($m^2$/ha) were included in the model. Analysis was conducted only on dead trees sampled from 2012 to 2014 ($n = 723$) to include both colonization from the current ($t$) and previous year ($t − 1$). Data from 2011 ($n = 269$) were omitted as response variables and only used as previous year ($t − 1$) variables for 2012. We constructed one full model with all spatially-lagged and stand-level variables. All input variables were standardized ($x_i/2\sigma_i$) to facilitate comparison among predictors (Gelman 2008). We calculated log odds ratios on untransformed parameter coefficients to present a magnitude of effect. All data were managed in ArcGIS (v10.2.2 ESRI) and analyses were conducted in R using the packages 'ncf', 'spatstat', 'MBA', and 'lme4.'

## Results

Over the duration of this study, 992 dead trees were identified (Fig. 1). The most prevalent colonizing agents were *S. noctilio* and bark beetles, collectively associated with 88.7% of all dead trees (Fig. 2). The root rot diseases *Armillaria* sp. and *H. irregulare* s.l. were recorded in 24.2% of dead trees, however, they were never found in the same tree. All colonizing agents, independent of each other, exhibited a degree of spatial aggregation, but it was limited to a moderate spatial scale, exhibiting significant aggregation only within a radius of 15–20 m (Fig. 3). *Heterobasidion irregulare* s.l. differed in that it was strongly aggregated, but there was considerable variability with this species given its limited abundance at the site (Fig. 2).

*Sirex noctilio* exhibited strong negative interspecific associations for within-tree colonization patterns. It was negatively associated with all other colonizing agents except bark beetles, with which it was neutral (Table 1). *Armillaria* sp. and *H. irregulare* s.l. had a weak but significant negative correlation and these two agents were never identified in the same dead tree. All other colonizing agents had significant positive associations, except for bark beetles, which had a negative association with *Armillaria* sp. and a neutral association with *H. irregulare* s.l.

The degree of spatial autocorrelation and cross correlation was variable for all pairwise comparisons against *S. noctilio* (Fig. 4). Positive spatial autocorrelations of *S. noctilio* and negative cross correlation of *S. noctilio* and woodborers exhibited the greatest
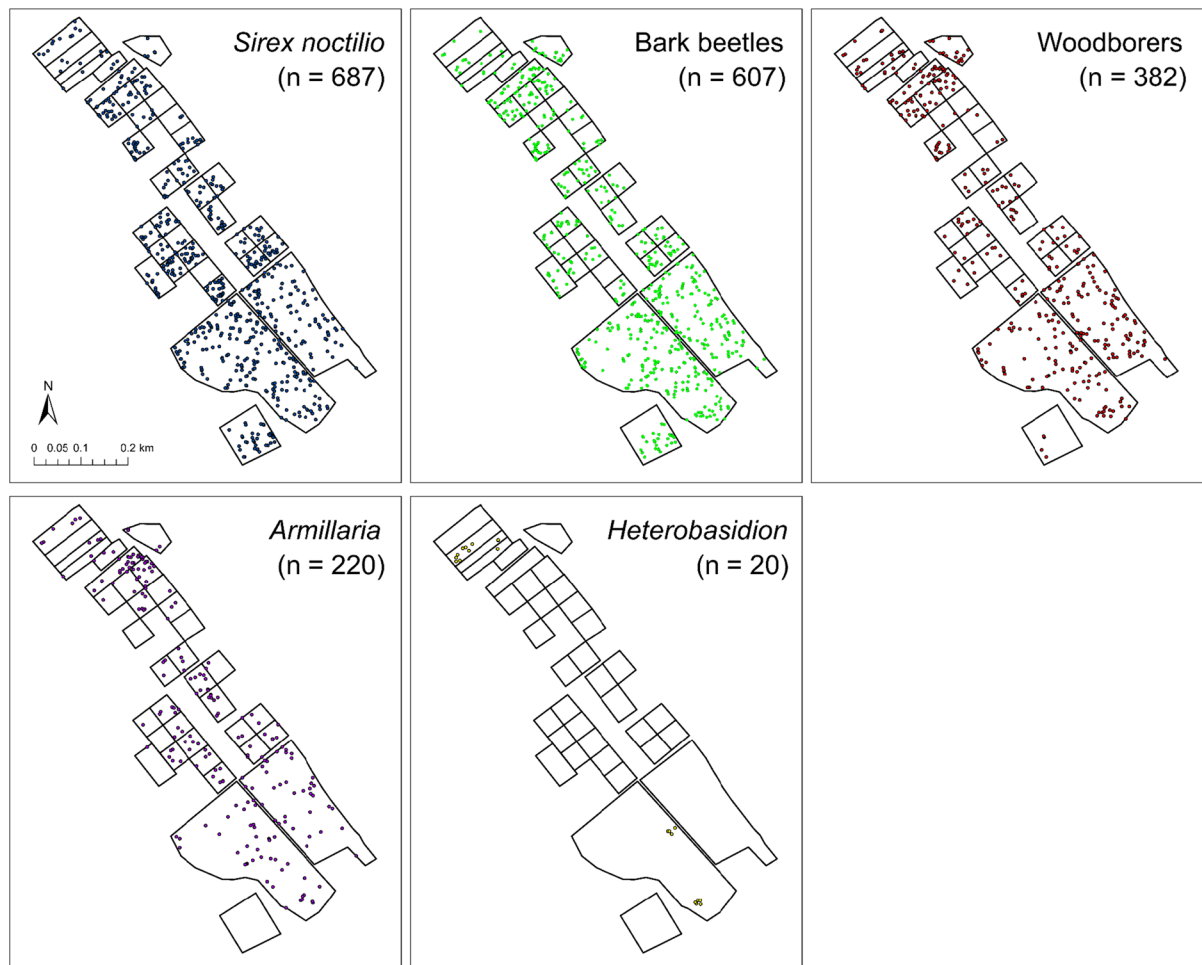
**Fig. 2** Distributions of five pine colonizing agents across Pack Demonstration Forest, NY. Counts represent the total number of trees from 2011 to 2014 colonized by each agent. Multiple agents could be present in the same tree

distance of correlation ($r = 185.7$ and $r = 188.7$, respectively). Similar to within-tree correlations, *S. noctilio* exhibited negative interspecific associations in stand-level colonization patterns, again with the exception of bark beetles (neutral). Subsequently, we did not include bark beetles as a factor in the autologistic regression model as there were no within-tree correlations and the spatial cross correlation was not significantly different from zero.

The autologistic regression model indicated probability of *S. noctilio* attack increased significantly with *S. noctilio* attack density from the current and previous year, density of woodborer attack from the previous year, stem density, and if the pine host was *P. sylvestris* (Table 2). Presence of root rot disease (both *Armillaria* sp. and *H. irregulare* s.l.) from the current

year were significantly negatively associated with evidence of *S. noctilio* attack. Comparisons among standardized variables indicate the three strongest factors were density of current year *S. noctilio* attack (positive effect), host species (*P. sylvestris*) (positive effect), and density of current year *Armillaria* sp. attack (negative effect). The strongest factor, current year *S. noctilio* attack, had almost a fourfold greater impact than the two weakest significant factors (density of previous year woodborer attack and density of current year *H. irregulare* s.l. attack).

Patterns of *S. noctilio* attack were highly aggregated both in space and through time, with an increase of one attacked tree within the range (i.e. radius when spatial autocorrelation = 0) in the current and previous year increasing the probability of attack by *S.*
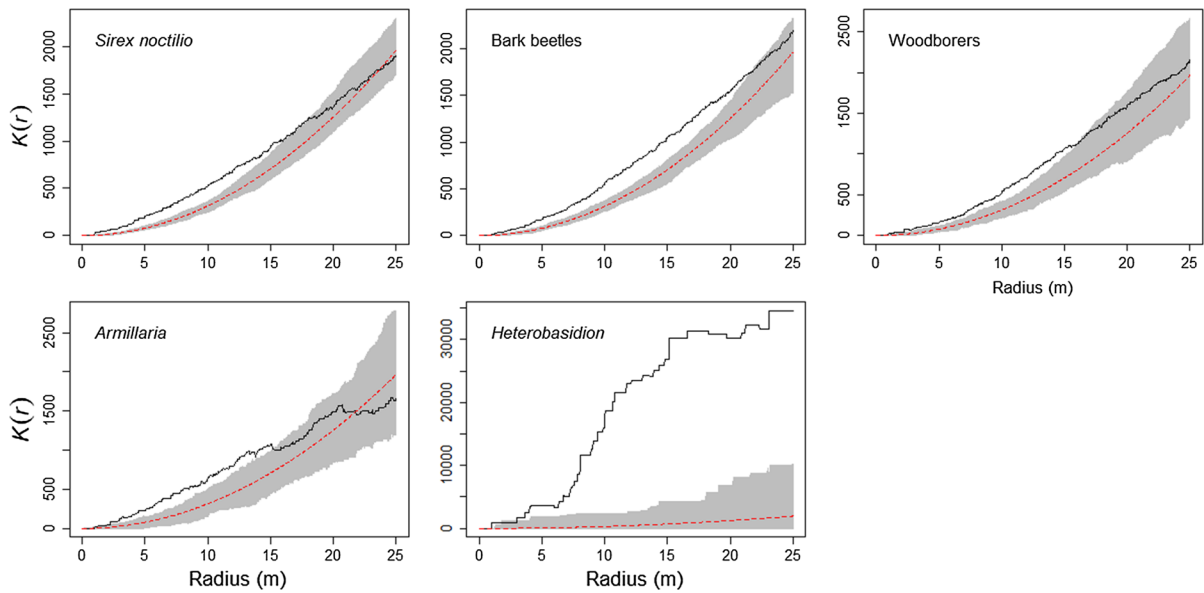
**Fig. 3** Spatial aggregation of colonizing agents at Pack Demonstration Forest, NY using Ripley's inhomogeneous *K* function with borders correction. The red dashed line indicates complete spatial randomness and the grey envelope indicates a 95% confidence envelope calculated from 2500 bootstrapping replications. The black line indicates the degree of aggregation for each colonizing agent. The space above the grey envelope indicates aggregation and the space below indicates regularity

**Table 1** Phi ($\varphi$) coefficients for within-tree associations for all pine colonizing agents in 992 dead trees identified at Pack Demonstration Forest in northeastern New York State in 2011–2014

|                   | Scolytinae | Cer/Bup[a] | *Armillaria* sp. | *H. irregulare* s.l. |
|-------------------|-----------|-----------|------------------|----------------------|
| *Sirex noctilio*  | − 0.03    | − 0.35**  | − 0.42**         | − 0.14**             |
| Scolytinae        |           | 0.35**    | − 0.12**         | 0.01                 |
| Cer/Bup[a]        |           |           | 0.24**           | 0.06*                |
| *Armillaria* sp.  |           |           |                  | − 0.08*              |

*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$

[a]Cerambycidae/Buprestidae

*noctilio* by 13.4 and 9.7%, respectfully (Table 2). Log odds indicated an increase of 100 stems/ha translated to a 15.1% increase in probability of a dead tree being symptomatic for *S. noctilio*. A density increase of one tree attacked by either root rot diseases in the current year decreased probability of *S. noctilio* attack by ~ 18%. However, the log odds confidence interval ranges for density of current year *H. irregulare* s.l. attack as well as previous year woodborer attack were almost twice as wide as that of other significant variables with both intervals nearly encompassing 1, indicating they were more variable and less predictive than other significant factors.

## Discussion

This study is the first to investigate the spatial dynamics of *S. noctilio* in North America and one of the first on spatial pattern of *S. noctilio* mortality in a stand through multiple years (Corley et al. 2007). Aggregation of this insect appears to operate across space and through time, with different factors driving distributions at different spatial scales (Levin 1992). A strong aggregative pattern by *S. noctilio* at broad spatial scales has been shown in South America (Corley et al. 2007), but this dissipates as *S. noctilio* populations become epidemic (Lantschner and Corley
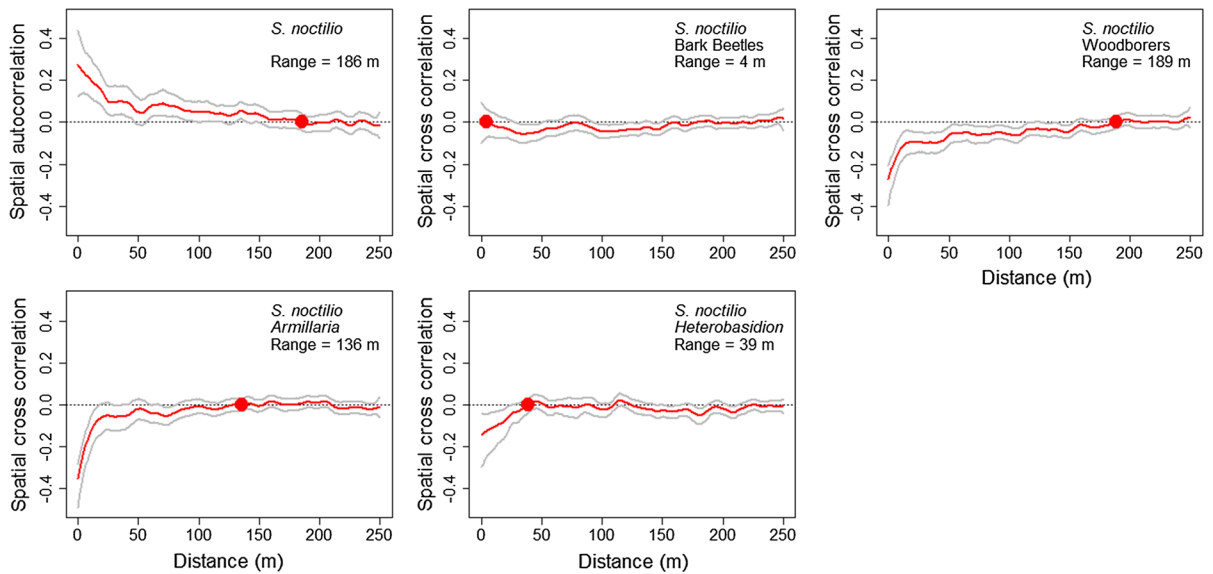
**Fig. 4** Spatial nonparametric covariance function estimates of autocorrelation of *S. noctilio* attack and cross correlation of *S. noctilio* and other colonizing agents at Pack Demonstration Forest. Red lines indicate the true data and the grey lines indicate a 95% confidence envelope based on 1000 bootstrapping replicates. The red point is the range (covariance = 0) or the maximum distance over which a spatial relationship is detectable. The range was used to calculate spatially lagged variables

**Table 2** Full autologistic regression models testing effects of spatially lagged colonizing agents from the current ($t$) year and previous year ($t − 1$) and stand-level variables

| Factor | Estimate (SE) | $z$-value | $P$ value | Log odds | 95% CI |
|---|---|---|---|---|---|
| Intercept | − 2.26 (0.78) | − 2.89 | 0.004 | 0.104 | 0.022, 0.474 |
| *S. noctilio*$_t$ | 1.51 (0.28) | 5.49 | < 0.001 | 1.134 | 1.085, 1.187 |
| *S. noctilio*$_{t−1}$ | 0.81 (0.22) | 3.70 | < 0.001 | 1.097 | 1.045, 1.153 |
| Woodborers$_t$ | 0.45 (0.28) | 1.59 | 0.113 | 1.083 | 0.982, 1.196 |
| Woodborers$_{t−1}$ | 0.38 (0.19) | 2.02 | 0.044 | 1.092 | 1.003, 1.191 |
| *Armillaria* sp.$_t$ | − 1.05 (0.27) | − 3.83 | < 0.001 | 0.852 | 0.784, 0.924 |
| *Armillaria* sp.$_{t−1}$ | − 0.24 (0.23) | − 1.03 | 0.305 | 0.964 | 0.898, 1.034 |
| *H. irregulare* s.l.$_t$ | − 0.38 (0.19) | − 2.00 | 0.046 | 0.844 | 0.709, 0.991 |
| *H. irregulare* s.l.$_{t−1}$ | − 0.13 (0.18) | − 0.71 | 0.475 | 0.957 | 0.848, 1.078 |
| Density (stems/ha) | 0.46 (0.23) | 1.99 | 0.047 | 1.000 | 1.000, 1.002 |
| Basal area (m²/ha) | − 0.29 (0.23) | − 1.23 | 0.220 | 0.995 | 0.987, 1.003 |
| Species (*P. sylvestris*) | 1.15 (0.27) | 4.20 | < 0.001 | 3.154 | 1.866, 5.470 |

Log odds ratios and 95% CI are calculated on unstandardized coefficient variables

2015). It is notable that *S. noctilio* displays a high degree of aggregation at small spatial scales even though this insect is a large, effective flier as indicated by flight mill studies showing potential dispersal of healthy females can exceed 30 km (Villacide and Corley 2008). Abiotic factors can also impact *S. noctilio* aggregation at larger spatial scales, such as aspect and elevation (Lantschner and Corley 2015); all of which can be compounded by acute or chronic stressors like drought (Madden 1988).

Co-colonizing insects play a role in patterns of *S. noctilio* mortality, but these effects are strongest at the tree level rather than the stand. Stand-level interactions were important for root rot diseases though, with *S. noctilio* exhibiting negative associations with both *Armillaria* sp. and *H. irregulare* s.l. This may stem from the relative immobility and strong aggregative nature of root rot diseases due to their below-ground vegetative spread. Hanson (1939) and Parkin (1942) suggest interactions between these two agents hinges

on fungal colonization of xylem tissue, with developing siricid larvae avoiding or failing to develop on wood tissue infected or altered by *Armillaria* or *Heterobasidion* sp. The negative association documented in our study may be driven by avoidance, with ovipositing *S. noctilio* avoiding these trees during host selection. Siricid ovipositors have complex sensory structures (Fukuda and Hijii 1996; Hayes et al. 2015), which facilitate precise host selection by females as they are able to distinguish subtle changes in tree moisture content and plant secondary chemistry.

There are surprisingly mixed co-colonization patterns for *S. noctilio* and bark and woodboring beetles at the tree and stand level. All insects in this study (*S. noctilio*, bark beetles, and woodborers) are effective fliers in pine stands at the scale analyzed in this study and limitations due to dispersal were likely minimal. The negative or neutral associations with these insects suggest *S. noctilio* may be targeting a different subset of trees for colonization. Because of its unique ability to weaken or condition a tree by injecting phytotoxic mucus and fungal arthrospores, *S. noctilio* may be avoiding co-colonization by attacking trees healthier than those targeted by most bark and woodboring beetles. Whether these insects then attack trees weakened by *S. noctilio* may be contingent upon local populations, timing of initial attack, tree condition, and attack intensity. This could explain the neutral association between *S. noctilio* and bark beetles, with some *S. noctilio* attacked trees appearing early enough in the season to incite colonization by late summer generations of bark beetles (e.g., *I. pini*), but some being attacked so late in the fall that they enter winter with only *S. noctilio* colonization and are then unsuitable for bark beetles in the early spring due to their deteriorated condition.

Indirect interactions with bark beetles are hypothesized to negatively affect *S. noctilio* (Dodds and de Groot 2012; Ryan et al. 2012c; Yousuf et al. 2014a). The results of our research provide no evidence that these two agents strongly co-occur or partition resources though; as there was a lack of association between *S. noctilio* and bark beetles as indicated by the whole-tree (Table 1) and stand-level analyses (Fig. 4). Meaningful interactions with bark beetles (and their associated fungi) are likely contingent on the spatial scale of analysis. Within-tree patterns may yield more representative outcomes for these relationships. This could have implications for *S. noctilio*'s population

dynamics though, as negative associations at the individual insect level do not appear to translate to patterns at the broader spatial scales addressed in this study. This is important because it could function as a negative feedback mechanism if *S. noctilio* attacked trees are in close proximity to bark beetle attacked trees.

Interestingly, Ayres et al. (2014) found similar patterns in host colonization associations for *S. noctilio* and insect assemblages in Galicia, Spain, with *S. noctilio* having neutral relationships with scolytines, excluding *T. piniperda* (with which it has a positive association). Unfortunately, fall surveys for this project occurred long after *T. piniperda* colonization and reasonable species level identifications could not be determined via gallery systems. Ayres et al. (2014) also found similar patterns of association among all species (Scolytinae, Buprestidae, Cerambycidae, *Armillaria* sp.) when compared to this study (Table 1), suggesting major insect and root pathogen assemblages in North America are a suitable analog to its native habitat in Eurasia.

Recent studies in North America present evidence that biotic resistance from native insect assemblages may hamper the success of *S. noctilio* (Ryan et al. 2012c; Haavik et al. 2015) and that these assemblages are similar to those present in Europe, where it is a non-pest (Ayres et al. 2014). The strongest mechanistic explanation for this hypothesis is that competition for xylem tissue between *A. areolatum* and bark beetle-vectored fungi (*Ophiostoma* and *Leptographium* spp.) does not favor *S. noctilio*'s symbiont and can compromise development. This has support from emergence studies (Ryan et al. 2012c), in vitro competition assays between these fungi (Ryan et al. 2011; Hurley et al. 2012; Yousuf et al. 2014b), exclusion manipulations (Haavik et al. 2015), and in situ comparisons of survivorship (Foelker 2016). However, it is unknown if this mechanism is acting alone or in concert with other factors.

Biotic resistance is multifaceted and may be operating through multiple mechanisms across spatial scales. A possible additional limitation is that native insects are removing potential host trees early in the season before *S. noctilio* emergence—over 30% of dead trees in this study showed no evidence of *S. noctilio* attack. When *S. noctilio* does emerge, it likely rejects trees already colonized by woodborers and bark beetles due to an aversion to host infected with

bluestain fungi (Ryan et al. 2012a), a pattern noted in the Southern Hemisphere (Clarke et al. 2016). These native insects thus narrow the pool of potential hosts across a stand. This scenario is not present in the Southern Hemisphere, where trees may persist in a weakened state for an extended time since there are very few mortality agents.

Bottom-up factors also can influence patterns of mortality attributed to *S. noctilio*. More attacks occurred on *P. sylvestris*, an ancestral Eurasian host naturalized to North America, as has been found in other studies of *S. noctilio* (Dodds et al. 2010; Zylstra et al. 2010; Ayres et al. 2014). The basis for this pattern is unclear and could involve several factors, including preference for a familiar host, variation in defensive responses, or environmental stressors. There is considerable interspecific variation in secondary chemistry and the composition of co-colonizing insects among pine species (Thoss et al. 2007; Zylstra et al. 2010; Böröczky et al. 2012; Dodds et al. 2012), but it is uncertain if this is biologically meaningful for *S. noctilio*. Additionally, *P. sylvestris* stands across northeastern North America are largely unmanaged and often overstocked, senescing, and located at sites with poor growing conditions (Dodds and de Groot 2012).

Due to its size and high vagility, *S. noctilio* may function over larger spatial scales than other forest insects. This is particularly important in comparisons between the invaded regions of North America and the Southern Hemisphere, as one of the key differences is the extent, distribution, and homogeneity of host across the landscape (Dodds and de Groot 2012). Increasingly homogeneous landscapes in terms of host composition have intrinsic properties that can positively affect insect population dynamics, such as increasing patch size and decreasing distance among patches (Dunning et al. 1992). Each patch can subsequently support a larger population and dispersants have a higher likelihood of encountering a host and a shorter distance to travel. The distribution and amount of suitable pine for *S. noctilio* across northeastern North America is dispersed and limited, which may be an underlying factor limiting its population growth in the region. This, in concert with parasitoids and competition from native insects, is likely exerting a strong degree of biotic resistance. It is uncertain how this scenario could be altered as *S. noctilio* invades southern forests, where climate and host composition

and homogeneity are more closely aligned with Southern Hemisphere conditions.

### Compliance with ethical standards

**Conflict of interest** The authors declare that they have no conflict of interest.

## References

Aukema BH, Richards GR, Krauth SJ, Raffa KF (2004) Species assemblage arriving at and emerging from trees colonized by *Ips pini* in the Great Lakes region: partitioning by time since colonization, season, and host species. Ann Entomol Soc Am 97:117–129. https://doi.org/10.1603/0013-8746(2004)097[0117:SAAAAE]2.0.CO;2

Aukema BH, Zhu J, Møller J et al (2010) Predisposition to bark beetle attack by root herbivores and associated pathogens: roles in forest decline, gap formation, and persistence of endemic bark beetle populations. For Ecol Manage 259:374–382. https://doi.org/10.1016/j.foreco.2009.10.032

Ayres BD, Ayres MP, Abrahamson MD, Teale SA (2001) Resource partitioning and overlap in three sympatric species of *Ips* bark beetles (Coleoptera: Scolytidae). Oecologia 128:443–453. https://doi.org/10.1007/s004420100665

Ayres MP, Pena R, Lombardo JA, Lombardero MJ (2014) Host use patterns by the European woodwasp, *Sirex noctilio*, in its native and invaded range. PLoS ONE 9:e90321. https://doi.org/10.1371/journal.pone.0090321

Barbosa P, Cranshaw W, Greenblatt JA (1981) Influence of food quantity and quality on polymorphic dispersal behaviors in the gypsy moth, *Lymantria dispar*. Can J Zool 59:293–296. https://doi.org/10.1139/z81-044

Bendel M, Rigling D (2008) Signs and symptoms associated with *Heterobasidion annosum* and *Armillaria ostoyae* infection in dead and dying mountain pine (*Pinus mugo* ssp. *uncinata*). For Pathol 38:61–72. https://doi.org/10.1111/j.1439-0329.2007.00530.x

Bjørnstad ON, Falck W (2001) Nonparametric spatial covariance functions: estimation and testing. Environ Ecol Stat 8:53–70. https://doi.org/10.1023/A:1009601932481

Böröczky K, Zylstra KE, McCartney NB et al (2012) Volatile profile differences and the associated *Sirex noctilio* activity in two host tree species in the northeastern United States. J Chem Ecol 38:213–221. https://doi.org/10.1007/s10886-012-0077-y

Buchner P (1965) Endosymbiosis of animals with plant microorganims. Wiley, Hoboken

Buxbaum CA, Nowak CA, White EH (2005) Deep subsoil nutrient uptake in potassium-deficient, aggrading *Pinus resinosa* plantation. Can J For Res 35:1978–1983. https://doi.org/10.1139/x05-102

Capinera JL, Barbosa P (1976) Dispersal of first-instar gypsy moth larvae in relation to population quality. Oecologia 26:53–60. https://doi.org/10.1007/BF00345652

Carlsson NO, Sarnelle O, Strayer DL (2009) Native predators and exotic prey—an acquired taste? Front Ecol Environ 7:525–532. https://doi.org/10.1890/080093

Chrystal RN, Myers JG (1928) The *Sirex* woodwasps and their parasites. Emp For J 7:145–154

Clarke CW, Carnegie AJ, Yousuf F et al (2016) Minimizing the disruptive effect of *Ips grandicollis* (Coleoptera: Scolytinae) on biocontrol of *Sirex noctilio* (Hymenoptera: Siricidae). For Ecol Manage 381:134–143. https://doi.org/10.1016/j.foreco.2016.09.023

Corley JC, Villacide JM (2012) Population dynamics of *Sirex noctilio*: influence of diapause, spatial aggregation and flight potential on outbreaks and spread. In: Slippers B, de Groot P, Wingfield MJ (eds) The *Sirex* woodwasp and its fungal symbiont. Springer, Dordrecht, pp 51–64

Corley JC, Villacide JM, Bruzzone OA (2007) Spatial dynamics of a *Sirex noctilio* woodwasp population within a pine plantation in Patagonia, Argentina. Entomol Exp Appl 125:231–236. https://doi.org/10.1111/j.1570-7458.2007.00623.x

Coulson RN, Mayyasi AM, Foltz JL, Hain FP (1976) Interspecific competition between *Monochamus titillator* and *Dendroctonus frontalis*. Environ Entomol 5:235–247. https://doi.org/10.1093/ee/5.2.235

Coutts MP (1969a) The mechanism of pathogenicity of *Sirex noctilio* on *Pinus radiata* L. effects of the symbiotic fungus *Amylostereum* sp. (Thelophoraceae). Aust J Biol Sci 22:915–924

Coutts MP (1969b) The mechanism of pathogenicity of *Sirex noctilio* on *Pinus radiata* II. Effects of *S. noctilio* mucus. Aust J Biol Sci 22:1153–1162

Cronin JT, Reeve JD, Wilkens R, Turchin P (2000) The pattern and range of movement of a checkered beetle predator relative to its bark beetle prey. Oikos 90:127–138

Davis TS, Hofstetter RW (2009) Effects of gallery density and species ratio on the fitness and fecundity of two sympatric bark beetles (Coleoptera: Curculionidae). Environ Entomol 38:639–650. https://doi.org/10.1603/022.038.0315

Denno RF, McClure MS, Ott JR (1995) Interspecific interactions in phytophagous insects: competition reexamined and resurrected. Annu Rev Entomol 40:297–331. https://doi.org/10.1146/annurev.en.40.010195.001501

Denno RF, Peterson MA, Gratton C et al (2000) Feeding-induced changes in plant quality mediate interspecific competition between sap-feeding herbivores. Ecology 81:1814–1827

Dodds KJ, de Groot P (2012) *Sirex*, surveys and management: challenges of having *Sirex noctilio* in North America. In: Slippers B, de Groot P, Wingfield MJ (eds) The *Sirex* woodwasp and its fungal symbiont. Springer, Dordrecht, pp 265–286

Dodds KJ, Graber C, Stephen FM (2001) Facultative intraguild predation by larval Cerambycidae (Coleoptera) on bark beetle larvae (Coleoptera: Scolytidae). Environ Entomol 30:17–22. https://doi.org/10.1603/0046-225X-30.1.17

Dodds KJ, de Groot P, Orwig DA (2010) The impact of *Sirex noctilio* in *Pinus resinosa* and *Pinus sylvestris* stands in New York and Ontario. Can J For Res 40:212–223. https://doi.org/10.1139/X09-181

Dodds KJ, Zylstra KE, Dubois GD, Hoebeke ER (2012) Arboreal insects associated with herbicide-stressed *Pinus resinosa* and *Pinus sylvestris* used as *Sirex noctilio* trap trees in New York. Environ Entomol 41:1350–1363. https://doi.org/10.1603/EN12180

Dunning JB, Danielson BJ, Pulliam HR (1992) Ecological processes that affect populations in complex landscapes. Oikos 65:169–175. https://doi.org/10.2307/3544901

Eager PT, Allen DC, Frair JL, Fierke MK (2011) Within-tree distributions of the *Sirex noctilio* Fabricius (Hymenoptera: Siricidae)—parasitoid complex and development of an optimal sampling scheme. Environ Entomol 40:1266–1275. https://doi.org/10.1603/EN10322

Elton CS (1958) The ecology of invasions by animals and plants. University of Chicago Press, Chicago

Erbilgin N, Raffa KF (2000) Effects of host tree species on attractiveness of tunneling pine engravers, *Ips pini*, to conspecifics and insect predators. J Chem Ecol 26:823–840. https://doi.org/10.1023/A:1005495806100

Erbilgin N, Raffa KF (2002) Association of declining red pine stands with reduced populations of bark beetle predators, seasonal increases in root colonizing insects, and incidence of root pathogens. For Ecol Manage 164:221–236. https://doi.org/10.1016/S0378-1127(01)00596-5

Erbilgin N, Nordheim EV, Aukema BH, Raffa KF (2002) Population dynamics of *Ips pini* and *Ips grandicollis* in red pine plantations in Wisconsin: within- and between-year associations with predators, competitors, and habitat quality. Environ Entomol 31:1043–1051. https://doi.org/10.1603/0046-225X-31.6.1043

Foelker CJ (2016) Beneath the bark: associations among *Sirex noctilio* development, bluestain fungi, and pine host species in North America. Ecol Entomol 41:676–684. https://doi.org/10.1111/een.12342

Foelker CJ, Standley CR, Fierke MK et al (2016a) Host tissue identification for cryptic hymenopteran parasitoids associated with *Sirex noctilio*. Agric For Entomol 18:91–94. https://doi.org/10.1111/afe.12137

Foelker CJ, Standley CR, Parry D, Fierke MK (2016b) Complex ecological relationships among an assemblage of indigenous hymenopteran parasitoids, the exotic European woodwasp (*Sirex noctilio*; Hymenoptera: Siricidae), and a native congener. Can Entomol 148:532–542

Francke-Grosman H (1939) On the symbiosis of woodwasps (Siricinae) with fungi. Z Angew Entomol 25:647–679

Fukuda H, Hijii N (1996) Host-tree conditions affecting the oviposition activities of the woodwasp, *Sirex nitobei* Matsumura (Hymenoptera: Siricidae). J For Res 1:177–181

Garbelotto M, Gonthier P (2013) Biology, epidemiology, and control of *Heterobasidion* species worldwide. Annu Rev Phytopathol 51:39–59

Gelman A (2008) Scaling regression inputs by dividing by two standard deviations. Stat Med 27:2865–2873

Graham SA (1925) The felled tree trunk as an ecological unit. Ecology 6:397–411. https://doi.org/10.2307/1929106

Haavik LJ, Dodds KJ, Allison JD (2015) Do native insects and associated fungi limit non-native woodwasp, *Sirex noctilio*, survival in a newly invaded environment? PLoS ONE 10:e0138516. https://doi.org/10.1371/journal.pone.0138516

Haavik LJ, Dodds KJ, Ryan K, Allison JD (2016) Evidence that the availability of suitable pine limits non-native *Sirex noctilio* in Ontario. Agric For Entomol 18:357–366. https://doi.org/10.1111/afe.12167

Hanson HS (1939) Ecological notes on the *Sirex* wood wasps and their parasites. Bull Entomol Res 30:27–65

Hayes RA, Griffiths MW, Nahrung HF (2015) Electrophysiological activity of the *Sirex noctilio* ovipositor: you know the drill? J Asia-Pac Entomol 8:165–168. https://doi.org/10.1016/j.aspen.2015.01.003

Hoebeke ER, Haugen DA, Haack RA (2005) *Sirex noctilio*: discovery of a Palearctic siricid woodwasp in New York. Newsl Mich Entomol Soc 50:24–25

Hofstetter RW, Cronin JT, Klepzig KD et al (2005) Antagonisms, mutualisms and commensalisms affect outbreak dynamics of the southern pine beetle. Oecologia 147:679–691. https://doi.org/10.1007/s00442-005-0312-0

Hurley BP, Hatting HJ, Wingfield MJ et al (2012) The influence of *Amylostereum areolatum* diversity and competitive interactions on the fitness of the *Sirex* parasitic nematode *Deladenus siricidicola*. Biol Control 61:207–214. https://doi.org/10.1016/j.biocontrol.2012.02.006

Keane RM, Crawley MJ (2002) Exotic plant invasions and the enemy release hypothesis. Trends Ecol Evol 17:164–170. https://doi.org/10.1016/S0169-5347(02)02499-0

Lantschner MV, Corley JC (2015) Spatial pattern of attacks of the invasive woodwasp *Sirex noctilio*, at landscape and stand scales. PLoS ONE 10:e0127099. https://doi.org/10.1371/journal.pone.0127099

Levin SA (1992) The problem of pattern and scale in ecology: the Robert H. MacArthur award lecture. Ecology 73:1943–1967

Light DM, Birch MC, Paine TD (1983) Laboratory study of intraspecific and interspecific competition within and between two sympatric bark beetle species, *Ips pini* and *I. paraconfusus*. Z Für Angew Entomol 96:233–241. https://doi.org/10.1111/j.1439-0418.1983.tb03664.x

Long SJ, Williams DW, Hajek AE (2009) *Sirex* species (Hymenoptera: Siricidae) and their parasitoids in *Pinus sylvestris* in eastern North America. Can Entomol 141:153–157. https://doi.org/10.4039/n08-068

Madden JL (1988) *Sirex* in Australia. In: Berryman AA (ed) Dynamics of forest insect populations. Springer, New York, pp 407–429

McClure MS (1984) Influence of cohabitation and resinosis on site selection and survival of *Pineus boerneri* Annand and *P. coloradensis* (Gillette) (Homoptera: Adelgidae) on red pine. Environ Entomol 13:657–663

Miller MC (1986) Within-tree effects of bark beetle insect associates on the emergence of *Ips calligraphus* (Coleoptera: Scolytidae). Environ Entomol 15:1104–1108. https://doi.org/10.1093/ee/15.5.1104

Nielson RM, Sugihara RT, Boardman TJ, Engeman RM (2004) Optimization of ordered distance sampling. Environmetrics 15:119–128. https://doi.org/10.1002/env.627

Niemelä P, Mattson WJ (1996) Invasion of North American forests by European phytophagous insects. Bioscience 46:741–753. https://doi.org/10.2307/1312850

Omdal DW, Shaw CG III, Jacobi WR (2004) Symptom expression in conifers infected with *Armillaria ostoyae* and *Heterobasidion annosum*. Can J For Res 34:1210–1219. https://doi.org/10.1139/x04-007

Paine TD, Birch MC, Švihra P (1981) Niche breadth and resource partitioning by four sympatric species of bark beetles (Coleoptera: Scolytidae). Oecologia 48:1–6

Parker JD, Hay ME (2005) Biotic resistance to plant invasions? Native herbivores prefer non-native plants. Ecol Lett 8:959–967

Parkin EA (1941) Symbiosis in larval Siricidæ (Hymenoptera). Nature 147:329. https://doi.org/10.1038/147329a0

Parkin EA (1942) Symbiosis and siricid woodwasps. Ann Appl Biol 29:268–274. https://doi.org/10.1111/j.1744-7348.1942.tb07593.x

Price PW, Bouton CE, Gross P et al (1980) Interactions among three trophic levels: influence of plants on interactions between insect herbivores and natural enemies. Annu Rev Ecol Syst 11:41–65

Price PW, Westoby M, Rice B et al (1986) Parasite mediation in ecological interactions. Annu Rev Ecol Syst 17:487–505

R Core Team (2017) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/

Raffa KF, Berryman AA (1980) Flight responses and host selection by bark beetles. In: Proceedings of the second IUFRO conference on dispersal of forest insects: evaluation, theory, and management implications. Conference Office, Cooperative Extension Service, Washington State University, Pullman Washington, pp 213–233

Rankin LJ, Borden JH (1991) Competitive interactions between the mountain pine beetle and the pine engraver in lodgepole pine. Can J For Res 21:1029–1036. https://doi.org/10.1139/x91-141

Ripley BD (1976) The second-order analysis of stationary point processes. J Appl Probab 13:255–266. https://doi.org/10.2307/3212829

Ross-Davis AL, Hanna JW, Kim M-S, Klopfenstein NB (2011) Advances toward DNA-based identification and phylogeny of North American *Armillaria* species using elongation factor-1 alpha gene. Mycoscience 53:161–165. https://doi.org/10.1007/s10267-011-0148-x

Ryan K, Moncalvo J-M, de Groot P, Smith SM (2011) Interactions between the fungal symbiont of *Sirex noctilio* (Hymenoptera: Siricidae) and two bark beetle-vectored fungi. Can Entomol 143:224–235. https://doi.org/10.4039/n11-001

Ryan K, de Groot P, Davis C, Smith SM (2012a) Effect of two bark beetle-vectored fungi on the on-host search and oviposition behavior of the introduced woodwasp *Sirex noctilio* (Hymenoptera: Siricidae) on *Pinus sylvestris* trees and logs. J Insect Behav 25:453–466. https://doi.org/10.1007/s10905-011-9313-5

Ryan K, De Groot P, Nott RW et al (2012b) Natural enemies associated with *Sirex noctilio* (Hymenoptera: Siricidae) and *S. nigricornis* in Ontario, Canada. Environ Entomol 41:289–297. https://doi.org/10.1603/EN11275

Ryan K, de Groot P, Smith SM (2012c) Evidence of interaction between *Sirex noctilio* and other species inhabiting the bole of *Pinus*. Agric For Entomol 14:187–195. https://doi.org/10.1111/j.1461-9563.2011.00558.x

Safranyik L, Linton DA, Silversides R, McMullen LH (1992) Dispersal of released mountain pine beetles under the canopy of a mature lodgepole pine stand. J Appl Entomol 113:441–450. https://doi.org/10.1111/j.1439-0418.1992.tb00687.x

Savely HE (1939) Ecological relations of certain animals in dead pine and oak logs. Ecol Monogr 9:321–385. https://doi.org/10.2307/1943233

Schlyter F, Anderbrant O (1993) Competition and niche separation between two bark beetles: existence and mechanisms. Oikos 68:437–447. https://doi.org/10.2307/3544911

Schroeder LM, Weslien J (1994) Reduced offspring production in bark beetle *Tomicus piniperda* in pine bolts baited with ethanol and α-pinene, which attract antagonistic insects. J Chem Ecol 20:1429–1444. https://doi.org/10.1007/BF02059871

Slippers B, Hurley BP, Wingfield MJ (2015) *Sirex* woodwasp: a model for evolving management paradigms of invasive forest pests. Annu Rev Entomol 60:601–619. https://doi.org/10.1146/annurev-ento-010814-021118

Smith MT, Bancroft J, Li G et al (2001) Dispersal of *Anoplophora glabripennis* (Cerambycidae). Environ Entomol 30:1036–1040

Spradbery JP, Kirk AA (1978) Aspects of the ecology of siricid woodwasps (Hymenoptera: Siricidae) in Europe, North Africa and Turkey with special reference to the biological control of *Sirex noctilio* F. in Australia. Bull Entomol Res 68:341–359. https://doi.org/10.1017/S0007485300009330

Standley CR, Hoebeke ER, Parry D et al (2012) Detection and identification of two new native hymenopteran parasitoids associated with the exotic *Sirex noctilio* in North America. Proc Entomol Soc Wash 114:238–249. https://doi.org/10.4289/0013-8797.114.2.238

Thompson BM (2013) Community ecology and *Sirex noctilio*: interactions with microbial symbionts and native insects. Ph.D. dissertation, Department of Entomology, The University of Maryland, College Park, MD, USA

Thompson BM, Grebenok RJ, Behmer ST, Gruner DS (2012) Microbial symbionts shape the sterol profile of the xylem-feeding woodwasp, *Sirex noctilio*. J Chem Ecol 39:129–139. https://doi.org/10.1007/s10886-012-0222-7

Thoss V, O'Reilly-Wapstra J, Iason GR (2007) Assessment and implications of intraspecific and phenological variability in monoterpenes of Scots pine (*Pinus sylvestris*) foliage. J Chem Ecol 33:477–491. https://doi.org/10.1007/s10886-006-9244-3

Tribe GD, Cillié JJ (2004) The spread of *Sirex noctilio* Fabricius (Hymenoptera: Siricidae) in South African pine plantations and the introduction and establishment of its biological control agents. Afr Entomol 12:9–17

Turchin P, Thoeny WT (1993) Quantifying dispersal of southern pine beetles with mark-recapture experiments and a diffusion model. Ecol Appl 3:187–198

Villacide JM, Corley JC (2008) Parasitism and dispersal potential of *Sirex noctilio*: implications for biological control. Agric For Entomol 10:341–345. https://doi.org/10.1111/j.1461-9563.2008.00395.x

Woodard S, Stenlid J, Karjalainen R, Hüttermann A (1998) *Heterobasidion annosum*: biology, ecology, impact and control. CAB International, Wallingford

Yousuf F, Carnegie AJ, Bashford R et al (2014a) Bark beetle (*Ips grandicollis*) disruption of woodwasp (*Sirex noctilio*) biocontrol: direct and indirect mechanisms. For Ecol Manage 323:98–104. https://doi.org/10.1016/j.foreco.2014.03.009

Yousuf F, Gurr GM, Carnegie AJ et al (2014b) The bark beetle, *Ips grandicollis*, disrupts biological control of the woodwasp, *Sirex noctilio*, via fungal symbiont interactions. FEMS Microbiol Ecol 88:38–47. https://doi.org/10.1111/1574-6941.12267

Zylstra KE, Dodds KJ, Francese JA, Mastro V (2010) *Sirex noctilio* in North America: the effect of stem-injection timing on the attractiveness and suitability of trap trees. Agric For Entomol 12:243–250. https://doi.org/10.1111/j.1461-9563.2010.00476.x