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Local antagonism and resource partitioning between two invasive pine plantation pests

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Abstract

1 The woodwasp *Sirex noctilio* Fabricius, native to Eurasia and North Africa, regularly co-occurs with a North American origin *Pissodes* sp. on *Pinus* trees in South Africa. The nature of this co-occurrence and potential impacts on either of the species is unknown.

2 Using structured sampling, we investigated the pattern and degree of co-occurrence of *S. noctilio* and *Pissodes* sp. in six sites in *P. patula* plantations in South Africa aiming to better understand the potential for interactions and population-level feedbacks. We compared density, adult body size and within-tree distribution of both insect species in trees where they co-occurred or occurred singly.

3 *Sirex noctilio* and *Pissodes* sp. co-occurred on 68.0 ± 3.8% of infested trees (range 55–80%). Both insect species were more abundant in trees where they occurred alone relative to co-inhabited trees.

4 The within-tree distribution of *S. noctilio* did not differ in the presence of *Pissodes* sp.; however, in the presence of *S. noctilio*, *Pissodes* sp. were more frequent in the bottom than the middle tree section where *S. noctilio* was at higher density and this could be an indication of resource partitioning. Body size of *S. noctilio* and *Pissodes* sp. was not influenced by co-occurrence.

5 The results obtained in the present study suggest a broad overlap for both insects in preference for stressed trees in similar states of decline, as well as moderate antagonism between the species leading to lower emergence of both species in shared trees. The influence of *S. noctilio* on *Pissodes* sp. population densities may still be a net positive at a landscape scale because *Pissodes* sp. prefers declining or recently dead trees that are readily created by *S. noctilio* via attacks on healthy trees.

Keywords Facilitation, phloem-feeding insect, *Pinus*, *Pissodes*, plantation pests, *Sirex noctilio*, wood borer, woodwasp.

Introduction

Biological invasion is occurring at an unprecedented rate as a result of increasing global trade and transport, threatening native biota and community integrity in invaded regions (Mack *et al.*, 2000; Sala *et al.*, 2000; Stein *et al.*, 2000; Simberloff, 2011; Schaffner *et al.*, 2013). The likelihood of interaction among sympatric invaders increases with introduced species richness, with potential consequences for their ecology and evolution, as well as for invasive impacts (Garnas *et al.*, 2016). These interactions may be direct or indirect, symmetric or asymmetric, strong or weak, pairwise or diffuse and novel or co-evolved in the native range (Denno *et al.*, 1995; Wingfield *et al.*, 2016). Additionally, species interactions may result in positive or negative feedbacks dependening in part on whether they are fundamentally antagonistic (e.g. predatory, parasitic, or competitive), mutualistic or facilitative (Hawkins, 2005; Heimpel *et al.*, 2010; Hajek *et al.*, 2016).

Both facilitative and antagonistic interactions are well known in forest insect systems (Dewey *et al.*, 1974; Barbosa & Wagner, 1988). For example, primary tree-killing bark beetles such as the Southern pine beetle *Dendroctonus frontalis* Zimmermann

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facilitate a suite of secondary colonizers that take advantage of weakened tree defences subsequent to mass attack (Hofstetter *et al.*, 2006). Similarly, co-occurrence with other native bark beetles facilitates persistence of low-density endemic populations in the Mountain pine beetle *Dendroctonus ponderosae* Hopkins (Smith *et al.*, 2011). Facilitation of certain species via interactions with shared hosts may be particularly dramatic where invasive species are concerned (Rodriguez, 2006). For example, invaders such as the Emerald ash borer *Agrilus planipennis* Fairmaire provide a short-term pulse in resource availability for saproxylic insects, as well as native predators, including woodpeckers (Klooster *et al.*, 2018), and may have facilitated range expansion in at least one other buprestid beetle in Europe (Orlova-Bienkowskaja, 2015). In some cases, the cascade of facilitative interactions among invaders can be quite large (e.g. up to eleven species) (Heimpel *et al.* (2010). Antagonistic interactions among invasive insects are also common. For example, in the eastern U.S.A., introduced Hemlock woolly adelgid *Adelges tsugae* (Annand) and Elongate hemlock scale *Fiorinia externa* Ferris limit each other's populations on eastern hemlock by approximately 30% in mixed versus single species treatments (Preisser *et al.*, 2008; Preisser & Elkinton, 2008). Negative interactions between *F. externa* and the introduced circular hemlock scale *Nuculapsis tsugae* (Marlatt) have also been reported, where the density of the latter was reduced by 74% in the presence of the former (McClure, 1981).

In some cases, an aggressive invader may arrive that alters ecological conditions and/or feedbacks for already-established invaders. Such is the case with the weevil *Pissodes* sp. (Curculionidae, Coleoptera) and the European woodwasp *Sirex noctilio* Fabricius (Siricidae, Hymenoptera), which have both become established in *Pinus* plantations in South Africa, as well as in other parts of the world (Webb, 1974; Hurley *et al.*, 2007; Slippers *et al.*, 2015). *Pissodes* sp. was first detected in South Africa in 1942 and identified as the deodar weevil *Pissodes nemorensis* Germar, a native to North America (Webb, 1974; EPPO, 1999). Recent research, however, has shown that it is not the deodar weevil but rather an unrecognized species of the *P. strobi* complex of North American origin (Wondafrash *et al.*, 2016). As with other members of the genus, *Pissodes* sp. often breeds on the bole of declining or recently dead trees, although it has also been observed attacking terminal leaders of young healthy trees (Gebeyehu & Wingfield, 2003). Published research on flight phenology and voltinism is lacking for this weevil in South Africa. Adults and larvae of the weevil are present throughout the year, however, suggesting multiple, overlapping generations per year. The weevil has also been shown to at least incidentally carry the pitch canker fungus *Fusarium circinatum* Nirenberg & O'Donnell (Coutinho *et al.*, 2007; Mitchell *et al.*, 2011), which causes a disease of major importance in South Africa and other parts of the world.

Sirex noctilio is native to Eurasia and North Africa and was first detected in South Africa in 1994 (Tribe, 1995). The woodwasp has become one of the most damaging insect pests of *Pinus* in South Africa and other Southern Hemisphere countries (Hurley *et al.*, 2007; Slippers *et al.*, 2015). Female *S. noctilio* drills into the sapwood and oviposits at the same time as inoculating trees with spores of an obligate symbiotic fungus *Amylostereum areolatum* (Chaillet ex Fries) Boidin and a phytotoxic mucus/venom. The *A. areolatum* and the phytotoxic mucus act synergistically to suppress the resistance of infested trees and provide suitable hosts for the larvae (Gaut, 1969; Bordeaux *et al.*, 2014). *Amylostereum areolatum* serves as important source of nutrition for the larvae and is also involved in xylem digestion during larval development, probably by contributing cellulolytic enzymes and acting as an external gut (Thompson *et al.*, 2014). The woodwasp completes its larval development within the xylem of coniferous trees. Eggs are placed within the sapwood where larvae form tunnels and later pupate and emerge as adults. In general, the woodwasp develops in 1–3 years, although, in most regions, the majority of the emergence occurs after 1 year (Morgan, 1968). In South Africa, adults emerge from October to January within the summer rainfall area, including KwaZulu Natal. Most trees start declining and die by late summer (February). Flight period and tree decline phenology are approximately 1 month later in the winter rainfall areas of the Eastern and Western Cape (Ryan & Hurley, 2012). Extensive tree mortality as a result of *S. noctilio* occurs in parts of the invasive range, especially where trees have been exposed to other biotic and abiotic stress factors (Neumann & Minko, 1981).

In South Africa, *Pissodes* sp. and *S. noctilio* are often observed co-occurring on trees. Trees attacked by *S. noctilio* are generally suitable hosts of *Pissodes* sp. because both the woodwasps and the weevils prefer stressed or declining trees (Gebeyehu & Wingfield, 2003; Ryan & Hurley, 2012). Although preferences for the exact stage of decline are not currently known for either *S. noctilio* or *Pissodes* sp., there are some indications that the woodwasp attacks trees in earlier stages of decline relative to the weevil. Based on literature and field observations, the woodwasp appears to prefer moderately stressed trees that are alive and standing at the time of attack (Bordeaux & Dean, 2012; Ryan & Hurley, 2012). By contrast, the weevil larvae and pupae are primarily found in severely declining or recently dead trees, including downed trees (Gebeyehu & Wingfield, 2003; Wondafrash *et al.*, 2016). The degree to which the attack behaviour of *S. noctilio* provides a breeding habitat that would have otherwise been unavailble to *Pissodes* sp. is not known. Facilitation of *Pissodes* sp. by *S. noctilio* appears likely, however, given that woodwasps attack healthy trees that are later co-colonized by weevils as the trees decline and die. The presence of *Pissodes* sp. and *S. noctilio* in South Africa provides an opportunity to study patterns of co-occurrence and possible consequences of direct or indirect interactions therein.

Direct interaction via competition for resources is not expected between *S. noctilio* and *Pissodes* sp. because they utilize different parts/tissues of the tree. *Sirex noctilio* develops in the sapwood (Ryan & Hurley, 2012), whereas most members of the genus *Pissodes*, including the weevil, in South Africa are limited to the inner bark and the phloem, and only excavate superficial galleries in the outer surface of the xylem. These species could interact indirectly, however, via the induction of tree defences (e.g. traumatic resin duct formation or change in resin quantity or quality), tree physiological state (e.g. xylem water content, tree vigour) and/or rate of tree decline/death with effects on nutritional quality or suitability of the resource. For example, primary bark beetles exhaust resin via mass attack, which make trees more accessible to subsequent bark or phloem feeders (Ryan *et al.*, 2015).

Table 1 Study sites, GPS coordinates and infestation levels of *Sirex noctilio* and *Pissodes* sp. in *Pinus patula* plantations in Mpumalanga, March to May 2015

Site	Latitude	Longitude	Age of trees (year)	*Sirex* infestation (%)	*Pissodes* infestation (%)
Rooihoogte C3	26° 44.005′S	30° 18.041′E	16	12.2	11.6
Rooihoogte N56	26° 38.031′S	30° 20.046′E	17	16.8	11.2
Lothair U27	26° 23.079′S	30° 37.437′E	16	13.1	11.1
Lothair W17	26° 25.521′S	30° 37.628′E	16	9.3	11.0
Lothair H2	26° 32.452′S	30° 41.492′E	16	7.7	6.9
Torburnlea T6a	26° 12.215′S	30° 35.054′E	17	14.2	11.0
Average				12.2 ± 1.4	10.5 ± 0.7

The co-occurrence of *S. noctilio* and *Pissodes* sp. could influence the growth and survival of *A. areolatum*, the obligate fungal symbiont of *S. noctilio*. Previous studies have reported on possible outcomes of interactions between *A. areolatum* and ophiostomatoid fungi associated with bark- and wood-boring insects such as *P. nemorensis* (Hurley *et al.*, 2007; Ryan *et al.*, 2011; Ryan *et al.*, 2012; Yousuf *et al.*, 2014; Haavik *et al.*, 2015). However, the outcome of the interaction between *A. areolatum* and other insect-associated fungi could depend on their respective growth rates and phenologies, as well as microhabitat, nutritive and microclimatic optima. Disruption of the growth and survival of *A. areolatum* could impact the development of *S. noctilio* with potential consequences for survival or fecundity.

In the present study, we have examined the patterns and consequences of co-occurrence of the two forest insect pests, *Pissodes* sp. and *S. noctilio* in their invasive range in South Africa. The study aimed to (i) determine the degree and pattern of co-occurrence of *S. noctilio* and *Pissodes* sp.; (ii) assess positive or negative consequences of co-occurrence on body size and emergence; and (iii) examine evidence for resource partitioning in co-colonized trees in the form of differential emergence as a function of bole height.

Materials and methods

Study sites and host plant

The present study was conducted in pine plantations in the central South African province of Mpumalanga (Table 1). Plantations in Mpumalanga were selected because of the high incidence of *S. noctilio* and *Pissodes* sp. in this region in recent years. Six sites across three *Pinus patula* plantations (in Lothair, Rooihoogte and Torburnlea) were selected based on their history of higher *S. noctilio* and *Pissodes* sp. infestations in the previous years. The study was conducted in 16–17-year-old stands. Only trees with adult emergence holes and pupal chambers were included in the study because these are clear indicators of infestation and easier to identify. Standing trees infested with *Sirex* and/or *Pissodes* sp., including those attacked in previous years, were included in the present study. In cases where emergence holes were not visible on the lower bole, resin droplets were used as indicators of *Sirex* infestation higher up in the trees. Such trees were felled and closely checked for emergence holes. Considering older trees raises the possibility of measuring consecutive rather than concurrent colonization (i.e. that *Pissodes* sp. may have arrived after *S. noctilio* had left, or vice versa). It is highly unlikely that *S. noctilio* could have arrived after *Pissodes* sp. had come and gone, given the strong preference of the former for live trees (Bordeaux & Dean, 2012; Ryan & Hurley, 2012). There may be some cases where *Pissodes* sp. arrived too late to influence *S. noctilio* development or, in some cases, even after woodwasps have emerged. Based on preference of *Pissodes* sp. for stressed or recently dead trees (Gebeyehu & Wingfield, 2003) and the rapid rate of decline of woodwasp-infested trees, serial utilization of the resource is likely to be rare.

Degree and pattern of co-occurrence

In each of the sites, two transects were sampled along two randomly selected rows of trees. *Pissodes* sp. and/or *S. noctilio*-infested trees were noted and each transect was continued until obtaining 100 infested trees. Here, infested trees include all infestation types [*Pissodes* sp. only (P), *Sirex noctilio* only (S), and *Sirex noctilio* and *Pissodes* sp. (S + P)]. Diameter at breast height (DBH) of each of the infested trees was measured. Emergence holes for the two species are quite similar, and so bark was removed with a drawknife to confirm species identity by assessing the presence or absence of *Pissodes* sp. pupal chambers, diagnostic for the insect (Fig. 1A,B). At the time of our assessment, most insects had already emerged from the tree, with only a few cases where (typically dead) insects remained. In cases where pupal chambers and emergence holes were absent from the bottom section of dead trees and identification of infestation types were difficult, trees were felled and thoroughly examined for pupal chambers of *Pissodes* sp. (Fig. 1A) and/or emergence holes of *S. noctilio* (Fig. 1B).

Effect of co-occurrence on insect density and body size

Five trees per site of each infestation type (P, S and S + P) were randomly selected from the transects. In total, 90 trees (i.e. 30 per infestation type) were felled and each of them was divided into three equal sections (bottom, middle and top) based on the total tree height. Two logs per tree (80 cm each), one from the bottom and the other from the middle tree section, where symptoms of infestation were observed, were sampled (Fig. 1C). We selected only the bottom and middle tree sections because *Pissodes* sp. is rarely found in top sections (M. Wondafrash, personal observations). The length and circumference of each log were measured for the purpose of standardizing estimates of insect density by wood volume. Bark was removed from

Figure 1 (A) *Pissodes* sp. pupal chambers, (B) *Sirex noctilio* emergence holes, (C) Logs from mature *Pinus patula* trees infested with *Pissodes* sp. and/or *S. noctilio* and (D) *Pissodes* sp. pupal chamber and *S. noctilio* emergence holes co-occurring on the same tree. [Colour figure can be viewed at wileyonlinelibrary.com].

logs with a drawknife to differentiate between *Pissodes* sp. and *S. noctilio* infestations. Pupal chambers of *Pissodes* sp. (Fig 1A,D) and/or emergence holes of *S. noctilio* (Fig. 1B,D) were then counted with the objectives of comparing emergence densities and within-tree spatial distribution of each species in co-inhabited (S + P) versus *S. noctilio* (S) or *Pissodes* sp. (P) trees.

Emergence hole diameter correlates strongly with body size in *S. noctilio* (Madden, 1981) and was used as a proxy for body size in the present study. We measured the diameters of 10 randomly selected *S. noctilio* emergence holes from each log sample collected from S and S + P trees. Prior literature on the correlation between emergence hole or pupal chamber size and body size is lacking for *Pissodes* sp. To establish the strength of this relationship, we determined the Pearson correlation coefficient (*r*) between adult body size, the width and length of the pupal chamber, and the diameter of the adult emergence hole in a preliminary rearing study using stata, version 13 (StataCorp, 2013). Logs from *Pissodes*-infested trees were kept in emergence cages and frequently monitored for the emerging adults. Fifty adults were each stored in a separate vial in 96% ethanol and were given unique codes that matched them to each pupal chamber. In some cases, multiple adults emerged between checks of the emergence cage and could not be definitively matched to a single new emergence hole. These adults/holes were excluded from further analysis. Width and length of the corresponding pupal chambers, as well the diameter of emergence holes, were measured and measurements were made on five adult morphological characters (Williams & Langor, 2002). All five characters were found to be strongly correlated with adult emergence hole diameter and the length and width of pupal chambers (*r* ranged from 0.73 to 0.97) (for details and a list of characters assessed, see Table 2). Ultimately, pupal chamber width was selected as the sole proxy for adult size as a result of ease of measurement and high correlation coefficient (*r* ranged from 0.87 to 0.97). We then measured the width of 10 pupal chambers from each P and S + P logs only in the bottom tree section. Measurements of *Pissodes* sp. size were not obtained from the middle tree section because of the limited number of pupal chambers, particularly in S + P trees.

Table 2 Correlation coefficient among five morphometric characters and diameter of emergence hole and width and length of pupal chamber of *Pissodes* sp. in South Africa

	EL	EB	PL	PW	SL	EH	WPC	LPC
EL	1.000							
EB	0.973	1.000						
PL	0.904	0.926	1.000					
PW	0.911	0.945	0.803	1.000				
SL	0.884	0.847	0.771	0.770	1.000			
EH	0.945	0.912	0.843	0.860	0.822	1.000		
WPC	0.965	0.933	0.874	0.872	0.879	0.936	1.000	
LPC	0.861	0.822	0.807	0.731	0.811	0.818	0.872	1.000

EL, length of elytra along mid line; EB, width of elytra at base; PL, length of pronotum on midline; PW, width of pronotum at widest point; SL, length of snout between apex and eye margin at mid-height; EH, adult emergence hole; WPC, width of pupal chamber; LPC, length of pupal chamber.

Statistical analysis

Co-occurrence of *S. noctilio* and *Pissodes* sp. was compared with random using a Monte Carlo randomization procedure where expected frequencies of co-occurrence were calculated given the observed densities of *S. noctilio* and *Pissodes* sp. trees at each site. The Monte Carlo procedure was necessary because we did not collect data on uncolonized trees and therefore did not have a full contingency table to work with, in which case a chi-squared or Fisher's exact test would have been appropriate. The model was run for 10 000 iterations per site and coded in R (R Core Team, 2016). The density of each insect species in trees of different infestation types (infestation types being S and S + P for *Sirex*, and P and S + P for *Pissodes* sp.) was standardized and expressed as the number of insects per unit volume (insects dm^{-3}) of the log. With *Pissodes* sp. being a phloem feeder, phloem surface area estimates could be considered to be a more appropriate denominator in the estimation of weevil density. However, wood volume estimate was preferred to maintain consistency across the two species and make comparisons on their within-tree distribution. Furthermore, the relevant comparisons (Figs 3 and 4) are not across but rather within species (i.e. the co-occurring versus the occurring-singly comparison for *Sirex* and *Pissodes*). Additionally, scaling by surface area did not qualitatively influence our results within the range of tree sizes that we considered (data not shown). Wood volume was calculated using the equation $V = \pi r^2 h$ assuming the boles as perfect cylinders, where V is wood volume, r is radius and h is length of the log. The effect of co-occurrence on density and adult body size of *S. noctilio* and *Pissodes* sp. was determined using a general linear models approach using SAS, version 9.3 (SAS Institute Inc, 2011). We performed separate models using density and size of *S. noctilio* and *Pissodes* sp. as the response variables. Response variables were square-root transformed to meet model assumptions of normality and homogeneity of variance.

Analyses were conducted separately for the bottom and middle tree section because there were no interactions detected between tree section and infestation type. To examine changes in within-tree colonization patterns across trees with different densities of insects, we compared the slopes corresponding to the proportion of insects in the middle section (where a slope of 0.5 corresponds to equal distribution in the middle versus the bottom, < 0.5 to higher densities in the bottom; > 0.5 to higher densities in the middle). The 95% confidence intervals (CIs) of linear regression slopes were calculated for all the infestation categories based on the density of insects in middle versus middle plus bottom tree section. The confidence intervals were then checked with respect to whether or not they encompassed 0.5.

Results

Degree and pattern of co-occurrence

The degree of *S. noctilio* and *Pissodes* sp. co-occurrence ranged from 55–80% depending on study site. Overall, *S. noctilio* and *Pissodes* sp. were found co-occurring on 68.0 ± 3.8% (mean ± SE) of the infested trees. The remaining 32.0 ± 3.8% of trees were infested by a single species, 21.8 ± 4.6% by *S. noctilio* and the remaining 10.2 ± 3.2% by *Pissodes* sp. This degree of co-occurrence was indistinguishable from random based on the relative frequencies of each species in each study site, with P-values ranging from 0.08 to 0.35 (Fig. 2). A mean ± SE DBH of 12.8 ± 0.3 cm was recorded from all infested trees. The DBH of S trees (11.9 ± 0.6 cm) was significantly smaller than S + P trees (13.8 ± 0.5 cm), whereas that of P trees (12.7 ± 0.5 cm) was not different from either (based on Tukey's honestly significant difference, full model: $F_{2,135} = 3.4$, $P = 0.04$).

Insect density

In total, 90 trees were felled (i.e. 180 logs: 90 each from the bottom and middle tree sections) to determine the density of *S. noctilio* and/or *Pissodes* sp. In total, we counted 4196 *S. noctilio* and 3354 *Pissodes* sp. emergence holes across the bottom and middle sections of the 90 trees. A mean ± SE of 24.6 ± 3.7 and 45.3 ± 4.8 *S. noctilio* emergence holes and 38.5 ± 4.4 and 20.8 ± 4.4 *Pissodes* sp. emergence holes were counted in bottom versus middle tree sections.

Sirex noctilio density was significantly lower in S + P trees compared with the density in S trees both in bottom $F_{1,48} = 13.3$, $P = 0.0007$) and middle ($F_{1,48} = 21.4$, $P < 0.0001$) tree sections (Fig. 3A). This effect was considerable, with 63.2% and 57.1% fewer emergence holes in the bottom and middle tree sections, respectively. There was a significant but moderate site effect on *S. noctilio* density in the middle ($F_{5,48} = 2.6$; $P = 0.03$) but not bottom ($F_{5,48} = 0.9$; $P = 0.31$) tree sections. No site × infestation type interactions were observed in either log section.

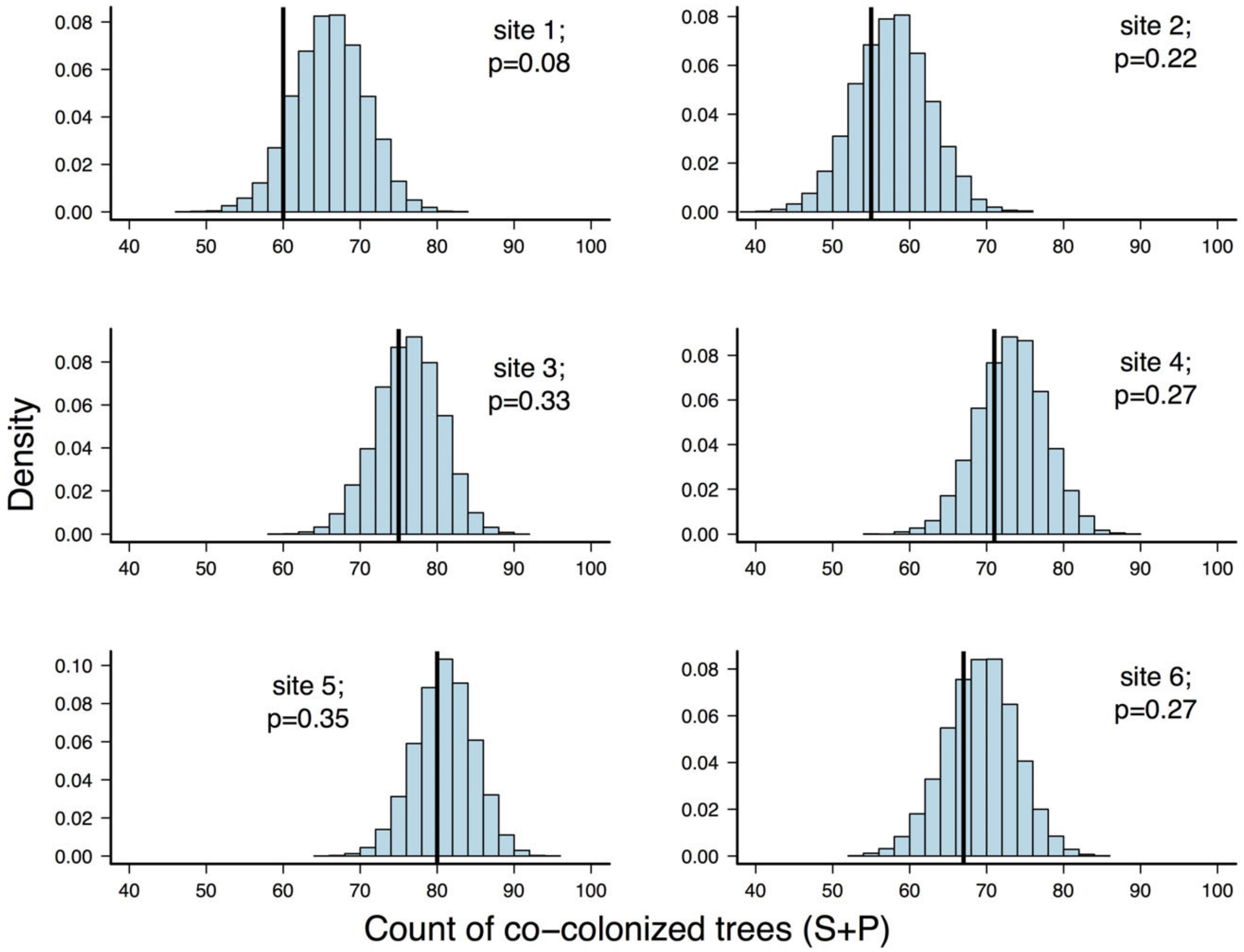

Figure 2 Observed and expected frequencies of *Sirex noctilio* and *Pissodes* sp. co-occurrence on *Pinus patula* trees in Mpumalanga, South Africa. The histograms indicate the expected number of trees that would host both *S. noctilio* and *Pissodes* sp. within the subset of 100 attacked trees (within each site) under the assumption of randomness. The vertical black lines are the observed count of *S. noctilio* and *Pissodes* sp. (S + P) trees. The *P*-value is the proportion of expected values (of 10 000) that were lower than the observed. Because all vertical lines fall near the middle of the random distribution, no divergence from random was detected. [Colour figure can be viewed at wileyonlinelibrary.com].

The density of *Pissodes* sp. in S + P trees was significantly lower compared with its density in P trees in middle tree section ($F_{1,48} = 18.6$, $P < 0.0001$) (Fig. 3B). Density of *Pissodes* sp. in the middle section of S + P trees was 62.9% lower than the corresponding density in P trees. The density in bottom tree section was not affected significantly ($F_{1,48} = 1.8$, $P = 0.18$) (Fig. 3B). There was significant though moderate site effect on *Pissodes* sp. density in the bottom ($F_{5,48} = 3.1$, $P = 0.02$) but not middle ($F_{5,48} = 0.6$, $P = 0.71$) tree sections. No site × infestation type interactions were observed in either log section.

Insect body size

Body size of *Sirex noctilio* in S + P trees did not differ significantly from the size in S trees either in the bottom ($F_{1,43} = 0.5$, $P = 0.47$) or the middle ($F_{1,46} = 0.7$, $P = 0.39$) tree sections. However, there was a general trend of larger *S. noctilio* in S + P trees compared with S trees. Size of *S. noctilio* in S + P trees was 13.8% and 13.5% greater in middle and bottom tree section, respectively, compared with the size in S trees. The effect of infestation type (S and S + P) on *S. noctilio* size remained consistent across sites both in the bottom (infestation type × site: $F_{5,43} = 2.0$, $P = 0.09$) and middle (infestation type × site: $F_{5,46} = 1.8$, $P = 0.13$) tree sections. There was no significant difference in *Pissodes* sp. body size in S + P versus P trees ($F_{1,43} = 0.3$, $P = 0.58$) in the bottom tree section. The effect of infestation type on body size of *Pissodes* sp. remained consistent throughout the study sites (infestation type × site: $F_{5,43} = 0.7$, $P = 0.61$).

Within-tree distribution of insects

The within tree spatial distribution of *Pissodes* sp. varied between S + P and P trees (Fig. 4). In P trees, *Pissodes* sp. was equally abundant in bottom versus middle tree section, relative to the total insect density in each section (slope = 0.50; 95% CI = 0.44–0.55), whereas, in S + P trees, it was more abundant in the bottom tree section than in the middle (slope = 0.24; 95%

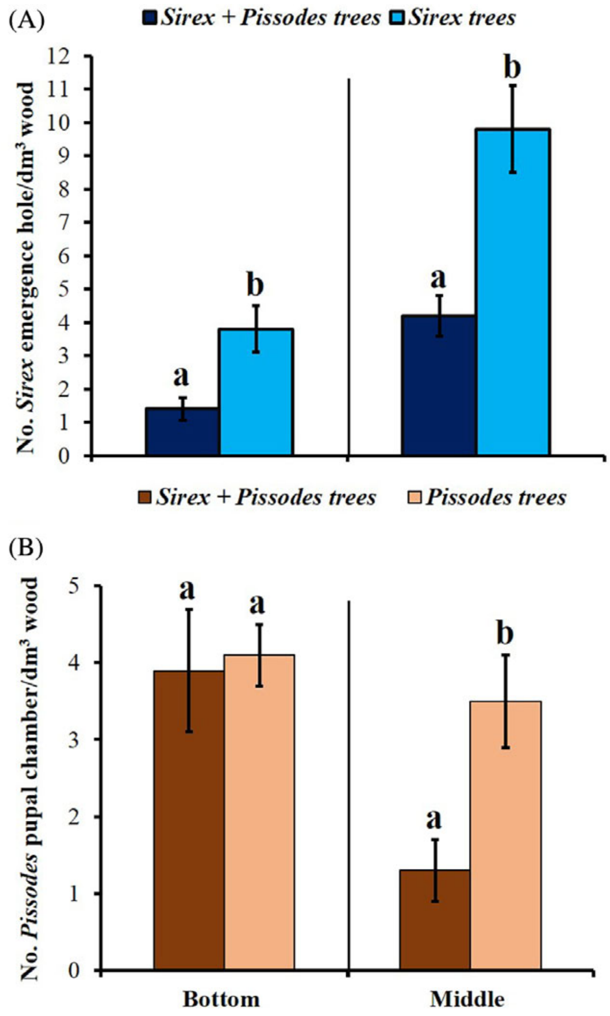

Figure 3 Mean density of (A) *Sirex noctilio* emergence holes and (B) *Pissodes* sp. pupal chambers in bottom and middle tree sections of co-inhabited *versus S. noctilio* or *Pissodes* sp. only trees. Error bars indicate the mean ± SE and different lowercase letters indicate significant differences at $P \leq 0.05$. The means were not compared between the bottom and middle tree sections, as indicated by the faint vertical lines. [Colour figure can be viewed at wileyonlinelibrary.com].

CI = 0.14–0.34). By contrast, the within tree spatial distribution of *S. noctilio* did not vary between S + P and S trees. *Sirex noctilio* was more abundant in middle tree section both in S + P (slope = 0.74; 95% CI = 0.66–0.83) and S (slope = 0.71; 95% CI = 0.65–0.76) trees compared with the bottom tree section.

Discussion

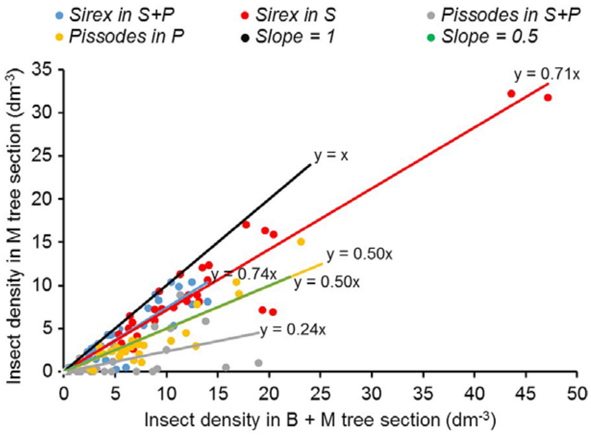

Figure 4 Within tree spatial distribution of *Sirex noctilio* and *Pissodes* sp. in *Pinus patula* trees in South Africa. Distribution of *S. noctilio* in *S. noctilio* and *Pissodes* sp. (S + P) trees (light blue line); *S. noctilio* in *Sirex noctilio* only (S) tress (orange line); *Pissodes* sp. in S + P trees (grey line); and *Pissodes* sp. in *Pissodes* sp. only (P) trees (yellow line); slope = 0.5 (green line) and slope = 1.0 (black line). A slope of 0.5 corresponds to equal distribution of insects in the middle versus the bottom tree section, < 0.5 to higher densities in the bottom, > 0.5 to higher densities in the middle, and 1.0 to all insects in the middle. M, middle; B, bottom. [Colour figure can be viewed at wileyonlinelibrary.com].

The present study is the first to investigate the pattern of co-occurrence and potential interactions between *S. noctilio* and *Pissodes* sp. in their invasive range. Largely by virtue of their preference for the same host trees in similar physiological conditions, *S. noctilio* and *Pissodes* sp. co-occur together on over two-thirds (68.0 ± 3.8%) of dead trees. In this sense, it can be said that these species are strongly aggregated on similar resources. When comparing actual co-occurrence rates with expectations (i.e. under the simplifying assumption that tree preferences are equivalent), we found no evidence for a departure from a random pattern of co-utilization of trees within the region we assessed (mid-bole or below). In other words, given the total number of trees that were attacked by each species and assuming that their preferences for trees overlap completely, the predicted number of shared and unshared trees does not differ significantly from random chance. This does not preclude facilitation or antagonism, however, and it is possible that both are occurring at different spatiotemporal scales. This may appear counter-intuitive, although it is perfectly plausible to hypothesize that, for example, many or all of the wasp-killed trees with weevil emergence holes would have been unavailable to *Pissodes* sp. in the absence of *S. noctilio*; indeed, this is highly likely. Thus, it stands to reason that populations of *Pissodes* sp. have likely been augmented (facilitated) by the presence of *S. noctilio* at a landscape scale, even if they are not preferentially selecting or avoiding *Sirex*-colonized trees within stands that contain suitable trees with and without the woodwasps.

Distinguishing patterns arising from positive or negative interactions between species from those that emerge as a consequence of sometimes subtle variation in preference or suitability of host trees is not a trivial task and would require manipulative experiments, which are highly challenging in this system. However, the examination of within-tree spatial patterns for evidence of resource partitioning can shed some light on its existence, direction or strength. Interestingly, the density and the within-tree spatial distribution of *S. noctilio* and *Pissodes* sp. in S + P trees were significantly different from S or P trees, respectively. Vertical colonization patterns for *Pissodes* sp. appeared to shift lower in the tree in the presence of *S. noctilio* when total insect density per section was accounted for (Fig. 4), whereas 70–75% of *S. noctilio* colonization was in the mid-bole, irrespective of co-occurrence with *Pissodes* sp. This is an indication of resource partitioning where the within-tree distribution of *Pissodes* sp. is influenced by the occurrence of *S. noctilio*.

The results of the present study with respect to body size contrast with the results obtained by Ryan *et al.* (2012) who reported larger body size of *S. noctilio* (particularly for males) in beetle-infested trees in Canada, whereas we found no impact of *Pissodes* sp. on *S. noctilio* body size. Ryan *et al.* (2012) suggested that this was a result of the possible accelerated drying of sapwood in the presence of Ophiostomatoid fungi (fungal associates of many bark beetles and other wood-inhabiting insects; Chow & Obermajer, 2007) and the faster growth of *A. areolatum* in drier wood (Coutts & Dolezal, 1969), which might have ultimately improved larval nutrition in beetle-positive trees. The incongruence between the result of the present study and those reported by Ryan *et al.* (2012) could be because of differences in the identity and diversity of insect species co-occurring with *S. noctilio* in Canada and South Africa. In South Africa, *Pissodes* sp. is the most frequently co-occurring species with *S. noctilio*. *Orthotomicus erosus*, *Hylastes angustatus* and *Hylurges ligniperda* are also introduced pine-feeding insects (Garnas *et al.*, 2016), although they are rare in mature *P. patula* plantations and were not detected in the present study. However, in Canada, Ryan *et al.* (2012) reported that five subcortical beetles species (*Tomicus piniperda*, *Ips grandicollis*, *Gnathotricus materiarius*, *Monochamus carolinensis* and *P. nemorensis*) commonly co-occur with *S. noctilio*.

The invasion of *S. noctilio* in South Africa has significantly increased *Pinus* tree mortality, particularly under outbreak conditions (Hurley *et al.*, 2007; Hurley *et al.*, 2012). Ninety percent of dead trees included in the present study were found to be infested with *S. noctilio*. The majority (> 75%) of these *S. noctilio* infested trees were found to be co-inhabited by *Pissodes* sp., suggesting a high degree of overlap in preference and/or performance of *Pissodes* sp. on declining trees in a similar physiological condition to that utilized by *S. noctilio*. This could also be a result of facilitation of one insect species by the other. Preference of *Pissodes* sp. and *S. noctilio* for declining/recently dead trees is well documented (Hopkins, 1911; Gebeyehu & Wingfield, 2003; Wermelinger & Thomsen, 2012), although the precise physiological state of trees preferred for oviposition or that are optimal for larval development may differ among insects specializing on declining or stressed trees. Accordingly, mixed (negative or neutral) co-colonization patterns were observed between *S. noctilio* and bark and wood boring beetles at tree and stand level in North America, which was attributed to differences in tree preferences by different insect species (Foelker *et al.*, 2018). Interestingly, *S. noctilio* co-occurred nonrandomly with *Tomicus* sp. and with cerambycids in Spanish pine, although not with *Pissodes* sp. (Ayres *et al.*, 2014).

Although patterns of co-occurrence cannot strictly be interpreted as proof of competition or facilitation, it appears likely that *S. noctilio* in South Africa has increased the availability of suitable trees for *Pissodes* sp. by attacking and weakening trees that would otherwise be too vigorous and therefore unavailable to the weevil. This is based on other evidence such as apparently lower densities of *Pissodes* sp. observed in areas where the density of *S. noctilio* is low and where far fewer dead and dying trees are available. This feedback is likely complex and variable in time and space. For example, in sites/years where *S. noctilio* is at ‘endemic’ or low levels and is principally utilizing stressed and declining trees that would have been available to *Pissodes* sp. anyway, the direction of its effect on *Pissodes* sp. may be slightly negative because of competition for resources. At higher densities, however, *S. noctilio* is capable of killing healthier trees (Spradbery, 1973; Ryan & Hurley, 2012; Lantschner & Corley, 2015), which almost certainly creates additional habitat for *Pissodes* sp. This would imply that, although the influence of *S. noctilio* on *Pissodes* sp. populations is negative at the tree scale, the influence at the landscape level could be positive or negative depending on population or density of the woodwasp. Overall, we suspect that there may be a net positive effect of *S. noctilio* on *Pissodes* sp., although more research is needed to explore this question further. Based on the results of the present study, it appears that the effect of *Pissodes* sp. on *S. noctilio* may be negligible in the bole. Nevertheless, in pine plantations where *Pissodes* sp. feeds on terminal leaders of young trees resulting in double leaders, this could represent a positive feedback if these double leader trees are more susceptible to *S. noctilio*.

The lower density of *S. noctilio* and *Pissodes* sp. in the sampled sections of S + P trees compared with the density in the sampled sections of S or P trees is a potential indicator of negative interactions. This pattern could emerge from reduced preference for attacked trees by *S. noctilio* and *Pissodes* sp., although this appears to be unlikely for *S. noctilio* given the observation that wasps typically arrive first. Alternatively, larval mortality, perhaps as a function of excessive bole drying or poor performance of fungal symbiont of *S. noctilio*, could be elevated in the presence of *Pissodes* sp. Previous studies have reported potential interactions between *S. noctilio* and the co-occurring community of insects, where co-occurring insects and their associated fungi in North America were suggested as possible factors that regulate *S. noctilio* populations (Ryan *et al.*, 2012; Haavik *et al.*, 2015). These studies were conducted in the Northern Hemisphere where *Pinus* species are native and support a diverse, potentially co-evolved community of insects, including numerous other subcortical phytophagous insects (wood borers and bark beetles) (Ryan *et al.*, 2012; Haavik *et al.*, 2015). Although body size appears to be unaffected, *S. noctilio* density in South Africa does appear to respond in a similar way to *Pissodes* sp. compared with co-occurring beetles in the Northern Hemisphere.

Differences in the within-tree spatial distribution of *Pissodes* sp. in S + P versus P trees are another potential indicator of interactions between *S. noctilio* and *Pissodes* sp. A higher proportion of *Pissodes* sp. were present in the bottom tree section of S + P trees compared with P trees, indicating that *Pissodes* sp. shifts away from the middle tree section (i.e. the preferred habitat of *S. noctilio*) (Morgan & Stewart, 1966; Neumann *et al.*, 1982; Ryan *et al.*, 2012) when co-occurring with *S. noctilio*. This suggests the partitioning of a common resource among these two co-occurring insects. Previous studies have suggested partitioning of a common resource as a mechanism that minimizes interspecific competition among bark beetle species (Paine *et al.*, 1981; Grunwald, 1986; Flamm *et al.*, 1987). For example, avoidance of oviposition site was observed among four co-occurring insect species on grapevine, namely the European grapevine moth *Lobesia botrana*, the grape berry moth *Eupoecilia ambiguella*, the codling moth *Cydia pomonella* and the oriental fruit moth *C. molesta* (Thiéry & Gabel, 1993). By contrast to *Pissodes* sp., the within-tree spatial distribution of *S. noctilio* was not influenced by the presence of *Pissodes* sp. The majority of *S. noctilio* emergence holes were in the middle tree section, both in S + P trees and S trees. This is consistent with previous reports from Canada (Ryan *et al.*, 2012), South Africa (Hurley *et al.*, 2008), and New Zealand, Australia and Brazil (Morgan & Stewart, 1966; Neumann *et al.*, 1982; Ryan *et al.*, 2012).

Studies on patterns of co-occurrence of invasive species can shed light on the nature and potential interaction among them, which can drive dynamics and also change over time as the environments or management regimes change, or as new species arrive. In the present study, we detected high levels of co-occurrence of *S. noctilio* and *Pissodes* sp. and potential indications of both positive (landscape scale) and negative (tree scale) interactions between the two species, in their invasive range in South Africa. These interactions will need to be confirmed via manipulative experiments, although, if present, this could have potential implications for the management of these species.

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