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Performance of the tree-killing bark beetles *Ips typographus* and *Pityogenes chalcographus* in non-indigenous lodgepole pine and their historical host Norway spruce

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Abstract

1 The North American lodgepole pine *Pinus contorta* has been planted on 660 000 ha in Sweden.
2 We compared the performance of *Ips typographus* and *Pityogenes chalcographus* in storm-felled and standing pheromone-baited trees of the historical host species Norway spruce (*Picea abies*) and lodgepole pine.
3 In the first summer after a storm, *I. typographus* colonized 0.2% and *P. chalcographus* colonized 2.4% of the storm-felled lodgepole pines compared with 31% and 25%, respectively, of the storm-felled Norway spruces. In the second summer 1.6% and 41.5% of the lodgepole pines were colonized by *I. typographus* and *P. chalcographus*, respectively. The reproductive success of *I. typographus* was five-fold higher in Norway spruce than in lodgepole pine. Other species colonizing lodgepole pine were *Ips duplicatus*, *Orthotomicus proximus*, *Orthotomicus laricis*, *Monochamus sutor* and *Pissodes pini*.
4 The male attack densities of both bark beetle species required to overcome defences of standing pheromone-baited trees were much higher in lodgepole pine than in Norway spruce. The reproductive success of *I. typographus* and *P. chalcographus* was approximately five- and 14-fold higher, respectively, in Norway spruce than in lodgepole pine.
5 Larvae of the most important groups of bark beetle enemies were present in both storm-felled and standing pheromone-baited lodgepole pines colonized by *I. typographus* and *P. chalcographus*. In the standing trees, the densities of enemy larvae were lower in lodgepole pine than in Norway spruce, whereas the opposite was true for storm-felled trees.

Keywords Bark- and wood-boring beetles, critical threshold of attack density, enemy-free space, *Ips typographus*, novel host, *Picea abies*, *Pinus contorta*, *Pityogenes chalcographus*, spruce bark beetle, storm-felled trees.

Introduction

Non-indigenous tree species have been used for a long time in forestry to increase biomass production. The Food and Agriculture Organization estimates that approximately 25% of all tree plantations world-wide use exotic tree species (Food and Agriculture Organization of the United Nations, 2010). In Scandinavia, interest in using new tree species has further increased in recent years as a way of increasing the sustainability of forestry under climate change by diversifying forest production (Felton *et al.*, 2013; Kjær *et al.*, 2014). For example, lodgepole pine (*Pinus contorta* Douglas var. *latifolia*), native to north-western U.S.A. and western Canada, has been used from the 1970s onwards in Swedish forestry because it grows considerably more rapidly than the native Scots pine (*Pinus sylvestris* L.) (Elfving *et al.*, 2001). So far, it has been planted on approximately 660 000 ha in central and northern Sweden (Skogsstyrelsen, 2014).

However, replacing native trees with non-indigenous species is associated with various types of ecological risk. Thus, introductions should be supported by research quantifying these

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risks (Felton *et al*., 2013). One such risk is damage caused by native bark beetles (Coleoptera, Curculionidae). Tree-killing bark beetles are severe disturbance factors in conifer forests. For example, bark beetles have killed trees with volumes exceeding 150 million m^3 in Europe during the last 50 years, and have also caused increasing damage in recent decades in both Europe and North America (Schelhaas *et al*., 2003; Raffa *et al*., 2008; Seidl *et al*., 2011; Meddens *et al*., 2012). Tree-killing bark beetles may also colonize and reproduce in novel host tree species. Reported examples include the Eurasian spruce bark beetle *Ips typographus* (L.) in the North American Engelmann spruce, white spruce, Sitka spruce, Lutz spruce, black spruce and red spruce (Økland *et al*., 2011); the mountain pine beetle *Dendroctonus ponderosae* in jack pine, red pine and interior hybrid spruce (McKee *et al*., 2013; Erbilgin *et al*., 2014; Cale *et al*., 2015); and the red turpentine beetle *Dendroctonus valens* in Chinese red pine (Yan *et al*., 2005; Liu *et al*., 2014).

Ips typographus is the most destructive insect pest of mature Norway spruce [*Picea abies* (L.) Karst] in Europe, and may kill millions of trees during outbreaks (Seidl *et al*., 2011; Marini *et al*., 2017), which may be triggered by storm disturbances, warm summers or precipitation deficits (Marini *et al*., 2013, 2017). Storm is the most frequent disturbance factor in Swedish forests, felling large volumes of trees, and Norway spruce is an especially vulnerable tree species (Nilsson *et al*., 2004; Mason & Valinger, 2013). Thus, major storms leave large numbers of storm-felled Norway spruce trees with weak defences, thereby creating abundant ideal breeding material for *I. typographus*, in which reproductive success is high (Komonen *et al*., 2011). Hence, in the second summer after a storm, population densities may be sufficiently high to enable the beetles to kill standing trees (Schroeder & Lindelöw, 2002; Kärvemo *et al*., 2014). Similar to Norway spruce, lodgepole pine is also vulnerable to storm disturbances (Mason & Valinger, 2013; Österberg & Näsman, 2015) and thus could potentially offer large volumes of suitable breeding material for *I. typographus*. However, no previous studies have examined how extensively *I. typographus*, as well as other bark- and wood-boring insects, may colonize and reproduce in storm-felled lodgepole pines.

When bark beetles attack living trees, the beetles and their associated microorganisms are confronted with diverse tree defence mechanisms (Franceschi *et al*., 2005; Krokene, 2015). Thus, to overcome defences of healthy trees, a coordinated mass attack of many beetles is required (Berryman, 1982; Mulock & Christiansen, 1986). Bark beetles boring into trees produce aggregation pheromones from precursors in the tree or *de novo*, which coordinates beetle mass attacks (Blomquist *et al*., 2010; Tittiger & Blomquist, 2016). A certain number of attacking beetles is required to overcome tree defences, often denoted as the critical threshold of attack density, which is essential for successful reproduction (Berryman, 1982; Raffa & Berryman, 1983; Mulock & Christiansen, 1986). The critical threshold of attack density is likely to vary among tree species as a result of differences in their defence traits and the ability of the bark beetle to produce pheromones in them. In Scandinavia, *I. typographus* may reportedly kill some trees in mature lodgepole pine stands (Löyttyniemi *et al*., 1979; Austarå *et al*., 1983). Another bark beetle species that may attack lodgepole pine is *Pityogenes chalcographus* L., which readily colonized cut lodgepole pines in a field experiment and has reportedly killed lodgepole pines in younger stands (Ehnström, 1985; Lindelöw & Iacobaeus, 1985). Nevertheless, the capacity of these bark beetle species to overcome host defences and reproduce in living lodgepole pines compared with that occurring in Norway spruces has not previously been tested experimentally.

Besides the beetles ability to overcome tree defences, enemy pressure also influences the reproductive success of bark beetles. Insect herbivores colonizing new host plants may benefit from a lower enemy pressure or efficiency of their natural enemies (Lill *et al*., 2002; Singer *et al*., 2004). This may trigger a switch to a new host plant because it offers an 'enemy-free space' (or, more strictly, substrate where pressure from enemies are lower than in previous hosts), in which the fitness of herbivores may be higher (Jeffries & Lawton, 1984). Many species of insect enemies prey on various bark beetle developmental stages (Erbilgin & Raffa, 2001; Kenis *et al*., 2004). Moreover, exclosure experiments (comparing the performance of beetles in caged and uncaged stem sections) have clearly demonstrated that enemies can strongly impair the reproductive success of bark beetles (Weslien, 1992; Weslien & Schroeder, 1999; Schroeder, 2007). However, few previous studies have addressed effects of a shift to a new host tree species on bark beetle enemy densities.

On 12 December 2013, storm Ivar felled 8 million m^3 of forest in northern Sweden, including approximately 1 million m^3 of lodgepole pine (M. Andersson & E. Normark, personal communication). This offered the first opportunity to compare the occurrence of *I. typographus*, *P. chalcographus* and other bark- and wood-boring beetles in storm-felled lodgepole pines and Norway spruces after extensive storm disturbance. In addition, the capacities of *I. typographus* and *P. chalcographus* to colonize and reproduce in standing lodgepole pines and Norway spruces were explored by baiting trees with their aggregation pheromones. The specific questions addressed were: (i) do proportions of storm-felled trees colonized by *I. typographus* and *P. chalcographus*, and the reproductive success of *I. typographus*, differ between lodgepole pine and Norway spruce; (ii) do the critical thresholds of attack density, and the reproductive success of the beetles, differ between pheromone-baited healthy lodgepole pines and Norway spruces; and (iii) do the densities of the beetles' enemies differ between the tree species?

Materials and methods

Study region

The present study was conducted in northern Sweden in the provinces of Ångermanland, Medelpad, Hälsingland and Jämtland. The populations of *I. typographus* in the region were high during the study period because there was a continuous supply of suitable breeding material in the form of storm-felled trees during the summers of 2012–2014 (after storms Dagmar in December 2011 and Ivar in December 2013). The high populations resulted in approximately 550 000 m^3sk of *I. typographus*-killed Norway spruces in 2015 and 2016 in the study region (Wulff, 2016).

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Field surveys and experiments

The study had two parts: (i) surveys of the occurrence of bark- and wood-boring beetles in storm-felled lodgepole pines and Norway spruces after storm Ivar and (ii) field experiments in which standing lodgepole pines and Norway spruces were baited with bark beetle pheromones to compare the bark beetles' capacities to overcome defences of the two tree species.

Surveys of storm-felled trees. The main aims of the survey were to determine which species of bark- and wood-boring beetles colonized lodgepole pines felled by storm Ivar and to record the reproductive success of *I. typographus* in them. The inspections were conducted in 2015 (the second year after the storm). In the spring (5–19 May), storm gaps were selected and the storm-felled trees were checked for signs of attacks in the previous year (i.e. the first summer after the storm). In the autumn (24 August to 3 September), the storm gaps were re-inspected for evidence of attacks during the summer of 2015 (the second summer after the storm). Data obtained from a similar survey in gaps created by storm Ivar in Norway spruce stands, in the same region, were included to compare colonization frequencies in the non-indigenous and native tree species. However, the storm-felled Norway spruces were only inspected after the first summer (15 September to 13 October 2014) because they were all cleared before the second summer.

Fifty trees were examined in each of 11 storm gaps in lodgepole pine stands and 13–50 (mean 35) trees in 18 gaps in Norway spruce stands. The diameter at breast height (DBH) (1.3 m) of each tree was recorded and its trunk was carefully searched for signs of activity of bark- and wood-boring beetles, such as entrance and exit holes, boring dust or loss of bark. When such signs were found, the bark was removed and the species were identified from the appearance of galleries or the insects themselves, if present. Bark samples (15 × 45 cm) were taken from all lodgepole pines colonized by *I. typographus* and from 1–5 colonized trees (average 3.7) per Norway spruce gap and then analyzed in the laboratory (see below). The minimum distances between lodgepole pine gaps and between Norway spruce gaps were 4900 and 700 m, respectively.

Field experiments with pheromone-baited standing trees. From 5 to 8 May 2015, pairs of trees, 50 m apart, in edges of six lodgepole pine stands with uncleared storm gaps were baited at 1.8 m height with *I. typographus* pheromone (Ipslure®; Kjemikonsult, Norway). At the end of August, the trees were checked for attacks by *I. typographus* and bark samples (15 × 45 cm) were taken from successfully colonized (resulting in offspring production) trees.

In 2016, 10 pairs of edges of lodgepole pine and Norway spruce stands beside forest roads were chosen. The distance between paired stands ranged from 282 to 1840 (mean 801 m), whereas the minimum distances between Norway spruce stand edges and between lodgepole pine stand edges were 264 and 469 m, respectively. In each selected stand edge, four living trees were baited during 25–30 May: two with *I. typographus* pheromone (Ipslure®) dispensers and two with *P. chalcographus* pheromone (Chalcosan®; PheroNova AG, Switzerland) dispensers. An Ipslure dispenser contains 1500 mg of methylbutenol, 70 mg of *cis*-verbenol and 15 mg of ipsdienol (Kjemikonsult no. 2016), whereas no compositional data are available for Chalcosan. The minimum distance between baited trees was 50 m and the two types of baits were placed alternately along each stand edge. The dispensers were attached to tree trunks at 1.8 m height and on sides of the trees facing the interior of the stand. The mean ± SE DBH for Ipslure-baited Norway spruce and lodgepole pine trees was 26.0 ± 0.53 cm and 25.4 ± 0.45 cm, respectively, and the corresponding records for Chalcosan-baited trees were 15.8 ± 0.28 cm and 16.4 ± 0.41 cm, respectively. There was no significant difference in DBH between the tree species subjected to the same baiting treatment (*t*-test; Ipslure-baited trees $P = 0.39$, Chalcosan-baited trees $P = 0.28$). Somewhat smaller trees were selected for the *P. chalcographus* experiment because this species is known to kill trees in younger stands (Ehnström *et al*., 1974; Hedgren, 2004). From 22 to 25 August 2016, the lower 2.5 m of each baited tree was inspected for bark beetle attacks. If successfully attacked, a bark sample (15 × 45 cm) was taken just above the pheromone bait. For unsuccessful attacks, when not possible to remove bark sample, the number of entrance holes and maternal galleries was counted in a 15 × 45 cm area just above the bait.

Bark sample analysis

The bark samples were stored at +5 °C until analyzed in the laboratory. The variables recorded were: maternal gallery lengths, numbers of male entrance holes, maternal galleries, maternal galleries per attacking male, live adults, pupae and larvae, and emergence holes. The number of male entrance holes per m^2 bark and number of maternal galleries per m^2 bark represents the density of attacking males and density of colonizing females, respectively. The lengths of maternal galleries are generally correlated with number of eggs laid by each female. The number of maternal galleries per attacking male was recorded to test whether female choice to accompany a male into a mating chamber is influenced by host tree characteristics. In addition, the thickness of the bark samples was measured.

The sum of live adults remaining in the bark sample and exit holes gives an estimate of the total number of beetles produced per m^2. Reproductive success was defined as the number of daughters per mother beetle (number of beetles produced × 0.5)/(number of maternal galleries) (Hedgren & Schroeder, 2004). Larvae and pupae were not included in estimates of production and reproductive success of *I. typographus* because they have low probabilities of surviving hibernation (Koštál *et al*., 2011; Dworschak *et al*., 2014). However, they were included in corresponding estimates for *P. chalcographus* because all of its life stages may successfully hibernate (Hedgren, 2004). A 25% portion of each bark sample (11.25 × 15 cm) was examined to record the *P. chalcographus* variables. It was not possible to estimate the number of *P. chalcographus* male entrance holes in three Norway spruce trees baited with the *P. chalcographus* pheromone because their bark was very dry, stuck to the wood and came away in small pieces.

The only variable of other bark beetle species recorded was coverage of their gallery systems in the bark samples. Densities

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of bark beetle enemy larvae (no adults were detected) were estimated by counting the larvae present in the bark samples. They were not identified to species level but were grouped into three categories: parasitoids, predatory flies of the genus *Medetera* and predatory beetles of the genus *Thanasimus*. These three groups include the most common insect enemies of *I. typographus* (Weslien, 1992; Hedgren & Schroeder, 2004; Kenis *et al*., 2004). *Thanasimus* could include two species, *Thanasimus formicarius* and *Thanasimus femoralis*, whereas the parasitoids and *Medetera* groups include several species. At the time of sampling, most *Thanasimus* larvae should have already left the samples, whereas considerable proportions of parasitoids, and most *Medetera*, hibernate under bark (Weslien, 1992; Schroeder, 1999; Hedgren & Schroeder, 2004). Thus, our density estimates should be accurate for *Medetera*, somewhat underestimated for parasitoids, and strongly underestimated for *Thanasimus*.

Statstical analysis

For storm-felled trees densities of *I. typographus* maternal galleries, offspring production, reproductive success and enemy densities were compared between lodgepole pines colonized in the second summer and Norway spruces colonized in the first summer after the storm. For the tree-baiting experiment conducted in 2016, the variables mentioned above and, in addition, densities of male entrance holes and maternal gallery length, were compared between the two tree species for both *I. typographus* and *P. chalcographus*. Analyses were conducted including all baited trees and only including trees in which the beetles reproduced. Differences were tested with *t*-tests or, if there were many zero-values, with Mann–Whitney test. The test used, as well as the number of replicates for each test, is provided where appropriate. $P < 0.05$ was considered statistically significant. Data are present as the mean ± SE.

Results

Storm gaps

Almost all of the examined storm-felled trees (96% of Norway spruces and 97% of lodgepole pines) had root contact. Among the storm-felled trees, the Norway spruces had a significantly higher mean DBH than the lodgepole pines (27.3 ± 0.3 cm versus 19.4 ± 0.4 cm; *t*-test, $P < 0.001$). Thirty-eight percent of the Norway spruces were attacked by beetles during the first summer after the storm disturbance, whereas just 4% of the lodgepole pines were attacked. *Ips typographus* and *P. chalcographus* were the most frequent species in Norway spruce, whereas *P. chalcographus* and *Pissodes* sp. were most common in lodgepole pine (Table 1). Ninety-two percent of the lodgepole pines colonized by *P. chalcographus* in the first summer were broken (i.e. had no root contact).

In the second summer, 44 ± 9% of the lodgepole pines were colonized by bark- and wood-boring beetles. *Pityogenes chalcographus* was the most common species, whereas *I. typographus* only attacked a few trees (Table 1). The presence of new-generation adults demonstrated that *I. typographus*, *Ips duplicatus*, *P. chalcographus*, *Orthotomicus proximus* and *Orthotomicus laricis* had been able to reproduce in the storm-felled lodgepole pines. Stem sections from lodgepole pines colonized by *Pissodes* and *Monochamus* were put in emergence boxes in the laboratory and, from these, *Pissodes pini* and *Monochamus sutor* adults emerged.

The density of *I. typographus* maternal galleries was similar in colonized storm-felled lodgepole pine and Norway spruce trees (Table 2). However, the mean offspring production was approximately 12-fold higher and the mean reproductive success was approximately five-fold higher in Norway spruce than in lodgepole pine, with both these differences being significant. All of the storm-felled lodgepole pines colonized by *I. typographus* were also attacked by *P. chalcographus* (mean coverage of gallery systems, 71%), whereas the two species co-occurred in 48% of the Norway spruces (mean coverage of *P. chalcographus*, 37%). Larvae of the bark beetle enemies *Medetera* sp., *Thanasimus* sp. and parasitoids were present in both tree species, and the mean density of *Medetera* was significantly higher in lodgepole pine than in Norway spruce (Table 2).

Pheromone-baited trees

Eleven of the 12 standing lodgepole pines baited with the *I. typographus* pheromone in 2015 were attacked and, in three of them, the attacks resulted in production of new-generation beetles. In these three trees, the mean maternal gallery density was 116 ± 2 per m^2 bark, offspring production was 122 ± 47 per m^2 bark, and reproductive success was 0.53 ± 0.21 daughters per mother beetle.

All standing Norway spruces and lodgepole pines baited with the *I. typographus* pheromone in 2016 were attacked by *I. typographus*. The mean bark thickness was significantly higher in samples from colonized Norway spruces than in samples from colonized lodgepole pines (5.8 ± 0.3 mm, $n = 18$, versus 3.3 ± 0.3 mm, $n = 9$, respectively; $P < 0.001$, *t*-test). The mean density of male entrance holes (used as a proxy of male attack density) was similar in the two tree species, whereas maternal gallery density was approximately four-fold higher, on average, in Norway spruce than in lodgepole pine, with this difference being significant (Table 3). New-generation beetles were produced in 95% of the Norway spruces, although only 30% of the lodgepole pines. The mean maternal gallery length and number of maternal galleries per attacking male did not significantly differ between the two tree species (Table 4). The mean production of new-generation beetles, as well as reproductive success, was 17–18-fold higher in baited Norway spruces than in baited lodgepole pines (including trees in which no reproduction was detected), with both these differences being significant (Table 3). Excluding trees in which no reproduction occurred, these variables were approximately five-fold higher in Norway spruce than in lodgepole pine, with the difference being significant for production of new-generation beetles and close to significant for reproductive success (Table 4).

There was a linear relationship between *I. typographus* male attack density and density of maternal galleries in Norway spruce ($y = -44 + 1.5x$, $r^2 = 0.64$, $n = 20$, $P < 0.001$) (Fig. 1A), whereas female reproductive success peaked between 200–400 entrance holes per m^2 (Fig. 1B). In lodgepole pine, *I. typographus* maternal galleries mainly occurred in trees with male attack densities

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Table 1 Proportions of storm-felled trees, as well as storm gaps, colonized by bark- and wood-boring beetles in lodgepole pine and Norway spruce stands

Species	Lodgepole pine		Norway spruce	Native host
	First summer Colonized trees (gaps) (%)	Second summer Colonized trees (gaps) (%)	First summer Colonized trees (gaps) (%)	
Curculionidae				
Scolytinae				
Pityogenes chalcographus	2.4 (82)	41.5 (100)	25.4 (100)	S, (P)
Ips typographus	0.2 (9)	1.6 (36)	31.3 (94)	S
Ips duplicatus		0.4 (18)	1.6 (33)	S
Orthotomicus proximus		0.4 (18)		S, P
Orthotomicus laricis		0.4 (9)	0.5 (11)	S, P
Polygraphus sp.		0.2 (9)	0.5 (11)	S
Crypturgus sp.		0.2 (9)	0.2 (6)	S,P
Dryocoetes autographus			0.5 (6)	S
Curculioninae				
Pissodes sp.	1.3 (36)	1.8 (27)	0.5 (17)	S, P
Cerambycidae				
Lamiinae				
Monochamus sp.	0.2 (9)	3.1 (55)	1.4 (22)	S, P
Rhagium sp.			0.8 (11)	S, P

In total, 550 storm-felled lodgepole pines in 11 storm gaps and 630 Norway spruces in 18 storm gaps were inspected. Native host tree species: S, Norway spruce; P, Scots pine.

of > 500 entrance holes per m^2 and reproduction mainly in trees of > 600 male entrance holes per m^2. Two of the lodgepole pines and three of the Norway spruces that were baited with the *I. typographus* pheromone were also attacked by *P. chalcographus*.

Pityogenes chalcographus attacked 95% of the Norway spruces and all lodgepole pines baited with its pheromone. The mean bark thickness was significantly higher in samples from colonized Norway spruces than in samples from lodgepole pines (3.8 ± 0.2 mm, $n = 17$, versus 2.1 ± 0.1 mm, $n = 8$; $P < 0.001$, *t*-test). The mean male attack density was two-fold higher in lodgepole pine than in Norway spruce, with this difference being close to significant, whereas the maternal gallery density was similar in the two tree species (Table 3). Offspring (larvae, pupae, beetles) were produced in 30% of the lodgepole pines and 75% of the Norway spruces. The mean maternal gallery length and number of maternal galleries per attacking male did not significantly differ between the two tree species (Table 4). The mean offspring production was approximately 10-fold higher, and reproductive success approximately 29-fold higher, in baited Norway spruces than in baited lodgepole pines, when also including trees in which no reproduction was detected, with both these differences being significant (Table 3). Excluding trees in which no reproduction occurred, mean offspring production was close to significantly (approximately five-fold) higher, and reproductive success significantly (approximately 14-fold) higher in Norway spruce than in lodgepole pine (Table 4).

There was a linear relationship between *P. chalcographus* male attack density and densities of maternal galleries in Norway spruce ($y = -16 + 16.3x$, $r^2 = 0.41$, $n = 16$, $P < 0.01$) (Fig. 2A), although there was no significant relationship between male attack density and female reproductive success (Fig. 2B). In lodgepole pine, *P. chalcographus* maternal galleries and reproduction only occurred in trees with male attack densities of > 1500 entrance holes per m^2.

Fourteen of the lodgepole pines and all Norway spruces that were baited with the *P. chalcographus* pheromone were also attacked by *I. typographus* and five of the six lodgepole pine trees in which *P. chalcographus* reproduced were also attacked by *I. typographus*. There was no significant relationship between *I. typographus* attack density and *P. chalcographus* maternal gallery density ($r^2 = 0.03$) in lodgepole pine. The mean number of *I. typographus* entrance holes per m^2 bark (male attack density), in attacked trees, was 62 ± 11 in lodgepole pine and 296 ± 31 in Norway spruce.

Bark beetle enemy densities were generally higher in Norway spruce than in lodgepole pine (Table 5). The mean densities of *Medetera* sp., *Thanasimus* sp. and parasitoids were approximately 3.5-, 2.4- and 16-fold higher, respectively, in Norway spruce than in lodgepole pine. Of these the differences for *Medetera* sp. and parasitoids were significant.

Discussion

The results of the present study show that *I. typographus* can colonize and reproduce in storm-felled lodgepole pines, although they were colonized much less frequently than storm-felled Norway spruces. In the first summer after the storm, only 0.2% of the storm-felled lodgepole pines were colonized compared with 31% of the Norway spruces. In the second summer, the proportion of attacked lodgepole pines increased somewhat to 1.6%. By then, all Norway spruce gaps had been cleared (as required by the Swedish Forestry Act) and so no comparable data were available for Norway spruce. However, earlier studies have demonstrated that large numbers of Norway spruces that are

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Table 2 *Ips typographus* maternal gallery density, offspring production, reproductive success and density of natural enemies in storm-felled lodgepole pines and Norway spruces

Variable	Lodgepole pine	Norway spruce	*P*-value
Ips typographus			
Maternal galleries per m^2			
Mean	173	172	0.98
SE	84	10	
Offspring production per m^2			
Mean	118	1422	**0.001**
SE	40	94	
Reproductive success			
Mean	1.07	5.10	**0.03**
SE	0.34	0.45	
Enemies			
Medetera sp.			
Mean	193	59	**0.001**
SE	46	7	
Thanasimus sp.			
Mean	15	0.2	
Range	0–51	0–14	
Parasitoids			
Mean	11	3	
Range	0–78	0–77	

The lodgepole pines were colonized in the second summer (2015) and the Norway spruces in the first summer (2014) after the storm. Only trees with offspring production were included: seven lodgepole pines and 67 Norway spruces. *P*-values obtained from *t*-tests; significant values are indicated in bold.

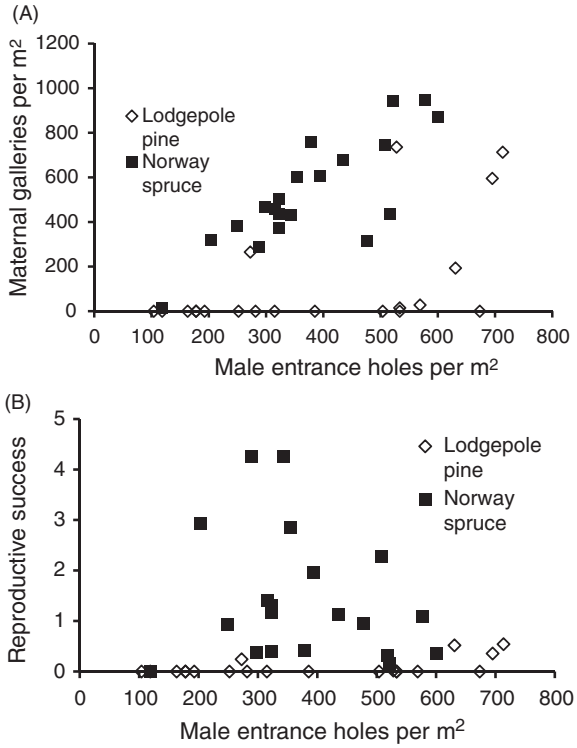


Figure 1 Relationship between densities of (A) *Ips typographus* male entrance holes and maternal galleries and (B) *Ips typographus* male entrance holes and female reproductive success in lodgepole pine and Norway spruce. Each symbol represents one living tree baited with the pheromone of *I. typographus*. Twenty replicates for each tree species.

not attacked in the first summer are colonized by *I. typographus* in the second summer after a major storm disturbance (Göthlin *et al*., 2000; Schroeder, 2010; Komonen *et al*., 2011). Because *I. typographus* prefers large-diameter storm-felled trees (Göthlin *et al*., 2000; Schroeder, 2010), the significantly higher mean diameter of Norway spruce may have contributed to the higher proportion of colonized spruces. However, if only including Norway spruces with a diameter ≤ 24 cm (resulting in mean dimeter of 19.9 ± 0.2 cm, which is very similar to the mean diameter of lodgepole pine 19.4 ± 0.4 cm), 18.9% of the Norway spruces were still colonized by *I. typographus*. Altogether, these observations indicate that storm-felled lodgepole pines are not a preferred breeding substrate for *I. typographus*.

The most common species colonizing the storm-felled lodgepole pines was *P. chalcographus*. Similar to *I. typographus*, this species colonized a much lower proportion of storm-felled lodgepole pines than Norway spruces in the first summer after the storm: 3% and 25%, respectively. However, in the second summer, the proportion of colonized lodgepole pines increased to 42%. The low proportion of colonized lodgepole pines in the first summer may have been a result of the defences of storm-felled lodgepole pines (most of which had root contact) still being too strong. In accordance with this hypothesis, most of the trees colonized in the first summer were broken (i.e. had no root contact) and, in a previous study with cut lodgepole pines (i.e. no root contact), 63% of the trees were colonized by *P. chalcographus* in the first summer (Lindelöw & Iacobaeus, 1985).

The much higher colonization frequency on lodgepole pine of *P. chalcographus* than of *I. typographus* may be an effect of the former species having broader host species preferences. *Pityogenes chalcographus* also commonly colonize cut trees or parts of trees of the native Scots pine (Foit, 2012, 2015), whereas attacks by *I. typographus* on Scots pine are rare and often a result of switching from nearby attacked Norway spruces (Komonen *et al*., 2011). Thus, *P. chalcographus* may be more able than *I. trypographus* to colonize also other pine species such as lodgepole pine. One important component of bark beetle colonization is the ability to produce aggregation pheromones. Thus, differences in the ability to produce pheromones in pines between the two bark beetle species may be one explanation contributing to the observed difference in colonization. Of the two main *I. typographus* pheromone components, 2-methyl-3-buten-2-ol is produced *de novo* (i.e. no specific precursor required), whereas *cis*-verbenol is produced from the precursor (−)-α-pinene (Lanne *et al*., 1989; Lindström *et al*., 1989). This precursor is present in lodgepole pine but accounts for only 5% on average of total monoterpene content (Pureswaran *et al*., 2004), which is a much lower proportion than in Norway spruce (Schiebe *et al*., 2012). Thus, both proportions and amounts of pheromones produced in lodgepole may differ from Norway spruce as demonstrated for the mountain pine beetle in historical and naïve host trees (Erbilgin *et al*., 2014; Cale *et al*., 2015). The origins of *P. chalcographus* pheromone components are unclear but, obviously, the species is also able to produce pheromones in pines.

The capacities of *I. typographus* and *P. chalcographus* to colonize and reproduce were much lower in pheromone-baited

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Table 3 Densities of male entrance holes and maternal galleries, offspring production and reproductive success of the bark beetles *Ips typographus* and *Pityogenes chalcographus* in pheromone-baited Norway spruces and lodgepole pines

	Ips typographus			*Pityogenes chalcographus*		
Variable	Norway spruce	Lodgepole pine	*P*-value	Norway spruce	Lodgepole pine	*P*-value
Male entrance holes per m^2						
Mean	377	391	0.81	536	1052	0.06
SE	28	47		82	228	
Maternal galleries per m^2						
Mean	529	127	**< 0.001**	932	964	> 0.10
Range	15–948	0–736		0–1878	0–4405	
Offspring production per m^2						
Mean	1411	79	**< 0.001**	2741	245	**< 0.002**
Range	0–3445	0–774		0–10 667	0–2391	
Reproductive success						
Mean	1.43	0.08	**< 0.001**	2.07	0.06	**< 0.001**
Range	0–4.26	0–0.54		0–5.68	0–0.56	

Twenty trees were included in each bark beetle-tree species combination, except for *P. chalcographus* in spruce in which 17 trees were included (because the variables could not be measured in three unsuccessfully attacked trees as a result of very dry bark). *P*-values obtained from *t*-tests (for numbers of male entrance holes) or Mann–Whitney tests (other variables); significant values are indicated in bold.

Table 4 Densities of maternal galleries, maternal gallery length, number of maternal galleries per attacking male, offspring production and reproductive success of the bark beetles *Ips typographus* and *Pityogenes chalcographus* in pheromone-baited standing Norway spruces and lodgepole pines only including trees in which the variable occurred

	Ips typographus			*Pityogenes chalcographus*		
Variable	Norway spruce	Lodgepole pine	*P*-value	Norway spruce	Lodgepole pine	*P*-value
Maternal galleries per m^2						
Mean	529	364	0.159	1147	3214	**< 0.001**
SE	54	118		248	514	
n	20	7		13	6	
Maternal gallery length (cm)						
Mean	7.02	7.14	0.858	2.17	2.31	0.470
SE	0.33	0.54		0.12	0.09	
n	18	5		12	6	
Maternal galleries per male						
Mean	1.69	1.82	0.362	2.72	2.48	0.477
SE	0.06	0.16		0.19	0.26	
n	18	5		12	6	
Offspring production per m^2						
Mean	1485	264	**0.017**	3655	818	0.070
SE	261	118		992	461	
n	19	6		12	6	
Reproductive success						
Mean	1.51	0.34	0.056	2.76	0.19	**0.002**
SE	0.10	0.10		0.48	0.10	
n	19	5		12	6	

P-values obtained from *t*-tests; significant values are indicated in bold. *n*, number of included trees.

healthy lodgepole pines than in baited Norway spruces. *Ips typographus* reproduced in 25% and 30% of these lodgepole pines in 2015 and 2016, respectively, compared with 95% of the Norway spruces in 2016. *Pityogenes chalcographus* reproduced in 30% of the baited lodgepole pines compared with 75% of the Norway spruces. These differences were not a result of the males choosing not to bore into the baited lodgepole pines because the average density of male entrance holes did not differ between the tree species (*I. typographus*) or was close to significantly higher in the baited lodgepole pine (*P. chalcographus*). Instead, the critical attack density required for maternal gallery establishment and brood production appears to be much higher in lodgepole pine than in Norway spruce for both bark beetle species: > 500 male entrance holes per m^2 for *I. typographus* and > 1500 male entrance holes per m^2 for *P. chalcographus* in lodgepole pine. By contrast, in Norway spruce, the critical threshold for establishment of maternal galleries appeared to be approximately 100–200 entrance holes per m^2 for both bark beetle species and, above this, there was a linear relationship between densities of entrance holes and maternal galleries. These findings demonstrate that the two bark beetle species have less ability to overcome lodgepole pine

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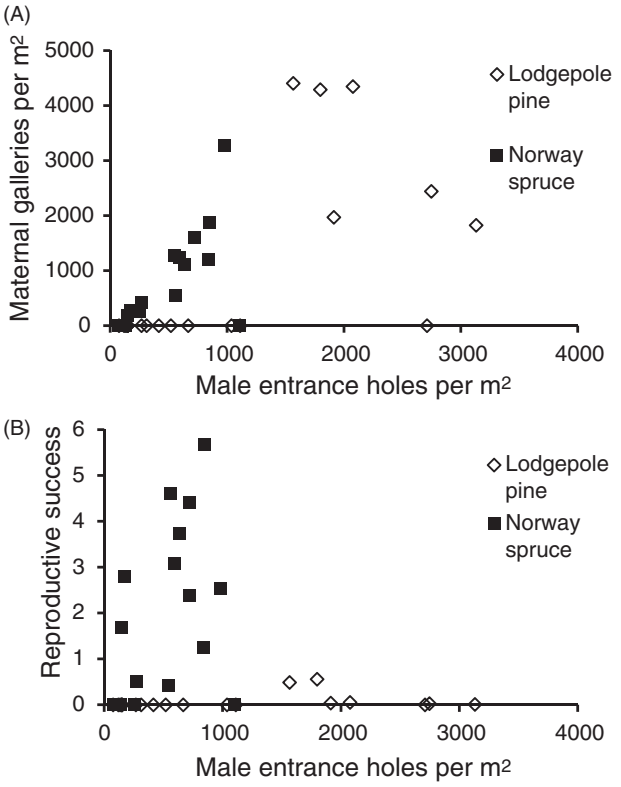


Figure 2 Relationship between densities of (A) *Pityogenes chalcographus* male entrance holes and maternal galleries and (B) *Pityogenes chalcographus* male entrance holes and female reproductive success in lodgepole pine and Norway spruce. Each symbol represents one living tree baited with the pheromone of *P. chalcographus*. Twenty replicates for lodgepole pine and 16 for Norway spruce. Note that some observations are stacked on top of each other in the diagram (at *x*-values below 400 entrance holes per m^2 and *y*-values of zero) and thus are not visible.

defences than Norway spruce defences. Even though the tree genera spruce and pine are both in the Pinaceae, they may still be quite different regarding physical and chemical defence traits because of their different evolutionary histories, which may explain the results. In accordance with this, there was no difference in the capacity of *I. typographus* to colonize (measured as length of maternal galleries) pheromone-baited live Norway spruces and the much more closely-related exotic red spruce, Engelmann spruce and Lutz spruce (Økland *et al*., 2011), whereas a tree-baiting experiment with the mountain pine beetle demonstrated a low capacity to colonize live interior hybrid spruce compared with its host lodgepole pine (Huber *et al*., 2009).

The offspring production and reproductive success of *I. typographus* were much lower in both storm-felled and standing healthy lodgepole pine trees than in the corresponding Norway spruce trees. Similarly, offspring production and reproductive success of *P. chalcographus* were much lower in standing healthy lodgepole pine trees than in corresponding Norway spruces, in accordance with previous findings indicating that it produces less offspring in lodgepole pine than in its native host Norway spruce among cut trees in the field (Lindelöw & Iacobaeus, 1985) and in rearing experiments (Bertheau *et al*., 2009). For *I. typographus*, there is no previously published information about reproductive success in lodgepole pine. The lower reproductive success in pheromone-baited trees was not an effect (for either of the two bark beetle species) of females establishing shorter maternal galleries in lodgepole pine. Differences in both physical and chemical traits between the tree species may have contributed to the observed differences in reproductive variables. One such trait is bark thickness, which appears to be considerably lower (among trees with similar diameters) in lodgepole pine than in Norway spruce. The correspondingly smaller amounts of phloem feeding substrate for the bark beetle larvae in lodgepole pine may reduce offspring production per unit area of bark, and there will be higher intraspecific competition for food among the offspring (which reduces reproductive success) as a result of the higher attack densities required for overcoming its defences (Anderbrant *et al*., 1985; Anderbrant, 1990; Schroeder, 2007; Komonen *et al*., 2011). Visual inspections of the bark samples from the killed trees showed that, in lodgepole pine, larger areas of the phloem were not utilized by the bark beetles and also that there were fewer larval galleries compared with those in Norway spruce. This indicates that the chemical properties of the lodgepole pine bark were unfavorable for brood production. By contrast, the reproduction of *I. typographus* in stem sections of the exotic red spruce, Engelmann spruce and Lutz spruce was comparable with the reproduction in Norway spruce (Økland *et al*., 2011), which may be a result of these tree species being more closely related to the historical host Norway spruce as discussed above. In accordance with this, the reproductive success of the mountain pine beetle in the naïve host tree species jack pine and red pine is similar to the success in its historical host, lodgepole pine, whereas it was lower in interior hybrid spruce (McKee *et al*., 2013; Erbilgin *et al*., 2014; Cale *et al*., 2015). One factor that should be addressed in future studies is the ability of fungal associates of bark beetles to colonize non-indigenous tree species. Fungi play an important role in the capacity of bark beetles to overcome tree defences and may also be involved in pheromone production (Krokene, 2015; Zhao *et al*., 2015; Kandasamy *et al*., 2016).

Table 5 Densities of larvae of the bark beetle enemies *Medetera* sp., *Thanasimus* sp. and parasitoids in pheromone-baited standing Norway spruces and lodgepole pines

Variable	Norway spruce	Lodgepole pine	*P*-value
Medetera sp.			
Mean	58.1	16.6	**< 0.05**
Range	0–203	0–43	
Thanasimus sp.			
Mean	17.1	7.1	< 0.10
Range	0–73	0–72	
Parasitoids			
Mean	74.2	4.7	**< 0.001**
Range	0–166	0–29	

Data relating to trees baited with the pheromone of *Ips typographus* and *Pityogenes chalcographus* were pooled. Only trees in which bark beetles reproduced were included in the comparison: 35 Norway spruces and 12 lodgepole pines. *P*-values obtained from Mann–Whitney tests; significant values are indicated in bold.

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The fact that *I. typographus* also attacked several of the trees baited with the *P. chalcographus* pheromone may have facilitated the colonization by *P. chalcographus*, particularly as *I. typographus* is considered to be a more efficient tree killer than *P. chalcographus* as a result of its association with tree-killing fungi (Krokene & Solheim, 1996; Krokene, 2015). Such an effect cannot be excluded, especially for Norway spruce, because all baited trees of the species were attacked by *I. typographus* with a male attack density of similar magnitude to trees baited with the species' own pheromone. In lodgepole pine, such an effect is less likely, partly because of the markedly lower attack density and partly because there was no correlation between *I. typographus* attack density and *P. chalcographus* maternal gallery density. The two bark beetle species have also previously been reported to commonly occur together in storm-felled and killed Norway spruces (Göthlin *et al*., 2000; Hedgren & Schroeder, 2004; Komonen *et al*., 2011).

Reductions in enemy pressure after shifts to new host plants may increase the fitness of herbivores. In the present study, larvae of the most important groups of bark beetle enemies were present in both storm-felled and standing lodgepole pines colonized by *I. typographus* and *P. chalcographus*. However, the densities compared with those in the native Norway spruce differed between storm-felled and standing trees. In the pheromone-baited standing trees, the densities of enemy larvae were lower in lodgepole pine than in Norway spruce, whereas the opposite was true for storm-felled trees. The presence of enemies in the non-indigenous lodgepole pine may be a result of most bark beetle enemies being generalists that utilize several bark beetle species reproducing in different tree species and, generally, they do not appear to rely on species-specific host tree cues when locating bark beetle-attacked trees. Instead, they may be attracted by bark beetle pheromones, host tree volatiles such as α-pinene that are present in many tree species, or volatiles from host-associated fungi (Kenis *et al*., 2004; Kandasamy *et al*., 2016).

The results of the present study have implications for the protection of North American forests because the recorded species included some of the most frequently intercepted insect pests in imported wood at ports in U.S.A. from 1985 to 2000 (Haack, 2006). *Pityogenes chalcographus* was the most frequently intercepted, and *I. typographus* the fourth most frequently intercepted, bark beetle species (517 and 253 interceptions, accounting for 10% and 5% of intercepted Scolytinae, respectively), whereas *Monochamus* was the most frequently intercepted cerambycid beetle genus (432 interceptions, accounting for 26% of intercepted Cerambycidae). The results indicate that risks of colonization of weakened and healthy lodgepole pines by *I. typographus* after an introduction are low. For this species, establishment in North American spruce species is much more probable (Økland *et al*., 2011). By contrast, both *P. chalcographus* and *M. sutor* (and some of the other species recorded) appear to pose higher risks of establishment in weakened lodgepole pines if they are introduced. Risks of damage by invasive species when interacting with North American beetles and fungi are difficult to predict. Thus, it is important to reduce the risks of introduction by means of strong legislative requirements for appropriate measures, such as heat treatment of wood exported from Europe to North America, and to ensure that treatments are conducted in a correct way.

After large-scale storm disturbances, considerable volumes of storm-felled trees may remain in forests during the first summer as a result of limited logging resources (Schroeder *et al*., 2006). Thus, the foresters must decide which storm gaps to salvage first. This decision should be based on both the risk for degradation of the quality of the fallen trees by attacks by bark- and wood-boring beetles and risks for subsequent tree mortality caused by bark beetles in areas that are not salvaged. Because of the low proportions of lodgepole pines colonized by bark- and wood-boring beetles in the first summer, as well as the poor performance of *I. typographus* in storm-felled and standing trees, storm gaps in Norway spruce and Scots pine stands should be salvaged first. The high critical threshold of attack density in lodgepole pine strongly indicates that outbreaks of *I. typographus* and *P. chalcographus* in stands of this tree species are unlikely, at least as long as tree vitality is not compromised.

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