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Tree species preference and impact on native species community by the bark beetle *Ips amitinus* in a recently invaded region

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Abstract

Non-native bark beetle species represent a major threat to forest ecosystems. The bark beetle *Ips amitinus* has recently expanded its range from Finland into northern Sweden. In the present study, we asked the following questions: (i) What is the distribution status in Sweden? (ii) Is there a difference in preference and reproductive success between Norway spruce and Scots pine? (iii) How common is the species after range expansion and does it influence the native community of bark- and wood-boring beetle species?

We established the presence of *I. amitinus* and co-existence with the native community through checks of logging residues at 382 localities in northern Sweden. In addition, attack densities and reproductive success were compared between spruce and pine through investigating field material and by a no-choice rearing experiment.

We found that *I. amitinus* is distributed over large parts of northern Sweden. Within its distribution area, it was found in 58% of all checked localities. It is one of the most common bark beetle species in logging residues and a higher proportion of Norway spruce objects compared to Scots pine were colonised. Attack density and reproductive success were higher in Norway spruce in field material and in the rearing experiment. There was no significant difference in the number of native bark- and wood-boring beetle taxa between localities where *I. amitinus* was present or absent.

Keywords

community ecology, ecological impact, invasion range, small spruce bark beetle, species interactions

Introduction

Non-native forest pests present a major threat to forest ecosystems globally (Brockerhoff et al. 2006; Aukema et al. 2011). In recent decades, establishments of alien species have steadily increased over time (Roques et al. 2009; Brockerhoff and Liebhold 2017; Seebens et al. 2017). Biological invasions can broadly be divided into two types: (1) human-mediated long-distance transportation of propagules into regions that could not be reached by natural dispersal (often inter-continental) and (2) range expansion caused by human-induced environmental changes allowing a species to disperse and establish in adjacent areas previously not colonised (Pyšek et al. 2012; Essl et al. 2019). In the latter case, species first establish in regions adjacent to the historic native range and subsequently colonise regions further away from the historic range as the expansion progresses (Essl et al. 2019). Additionally, in this case, human-mediated transportation may contribute to range expansion. Even though the second type of range expansions seem to have become more common (Lenoir and Svenning 2015), they have been given less attention in research than human-mediated long-distance establishments (Essl et al. 2019). However, there are important differences between these two modes of expansions. During long-distance human-mediated establishments, species encounter naïve hosts and very different ecological communities compared with those in their native areas. In the case of range expansions adjacent to native areas, species often encounter hosts and ecological communities that are similar to those in their native range.

One example of the second type of range expansion is the bark beetle *Ips amitinus* (Eichhoff, 1872). The distribution of *I. amitinus* ranges from the mountainous regions of central and south-eastern Europe to France, Belgium and The Netherlands to the West (Jurc and Bojović 2004; Holuša et al. 2012; Mazur and Kuźmiński 2013). In the last century, the species has expanded its range northwards. *Ips amitinus* was first observed in Estonia around the 1930s (Zolk 1932), in southern Finland in early 1950s (Koponen 1975) and is now established throughout Finland (Økland et al. 2019). In 2012, *I. amitinus* was recorded for the first time in Sweden, close to the Finish border in the most northern part of the country (Lindelöw 2013). However, the finding was a random encounter and not a result of a systematic search after the species then or previously. Thus, most probably the species was present in Sweden already before 2012.

In the present study, we assessed the distribution range of *I. amitinus* in Sweden, its performance in Norway spruce (*Picea abies* L. Karst) and Scots pine (*Pinus sylvestris* L.) and its influence on the native community of bark- and wood-boring beetles. *Ips amitinus* reproduces in both Norway spruce and Scots pine (Økland and Skarpaas 2008; EPPO 2022). Most studies of *I. amitinus* report attacks on spruce in Central Europe (Jakuš 1998; Witrylak 2008; Grodzki 2009; Holuša et al. 2012) and during the northern range expansion (Annila and Nuorteva 1976; Martikainen et al. 1996; Mandelshtam 1999) while a few studies from Russia report attacks on pine (Mandelshtam 1999; Kerchev and Krivets 2021). We are unaware of earlier studies comparing the preference and the reproductive success of *I. amitinus* between the two tree species. Understanding the connection between preference and reproduction success may improve predictions of extend and speed of further range expansion by *I. amitinus* in landscapes with different proportions of these two host trees.

Although range expansions have been documented for several bark beetle species (Dodds et al. 2018; Wermelinger et al. 2020), the effect on native communities of bark- and wood-boring beetles in the invaded regions has, to our knowledge, not yet received attention in scientific literature. We hypothesise that similarities between the communities associated with Norway spruce and Scots pine in the native and expanded range might result in a smooth invasion by *I. amitinus* without large consequences for the native community in the invaded range.

We asked the following questions for *I. amitinus*: (i) What is the current distribution in Sweden? (ii) Is there a difference in preference and reproductive success between Norway spruce and Scots pine? (iii) How does the presence of the invading species influence the native community of bark- and wood-boring beetle species?

Material and methods

Data collection

The study consists of: (1) a survey of *I. amitinus* in northern Sweden to assess its current distribution, commonness, host tree preferences and potential impact on native bark- and wood-boring beetle species, (2) investigation of naturally colonised material for assessing colonisation density and reproductive success and (3) a rearing experiment comparing *I. amitinus* reproductive success in Norway spruce and Scots pine (hereafter spruce and pine).

Surveys of occurrence, tree species and object type preferences

To assess the current distribution of *I. amitinus* in Sweden, we conducted two surveys in the counties of Norrbotten and Västerbotten in northern Sweden. Norrbotten is bordering Finland from where the species is expected to have spread. When the species were found in large parts of Norrbotten, we continued the survey further south in Västerbotten to find the southern range limit (Fig. 1). The first survey was carried out in the summers of 2016 and 2017. Five types of localities were inspected: clear-cuts, thinnings, cuttings along roads, cuttings under power lines and wind-felled trees in forest stands (Table 1). Five types of objects were checked: tops, branches, logs, cut small trees (trees with diameter up to 15 cm) and large trees (cut or wind-felled trees with diameter larger than 15 cm) (Table 2). All objects were cut or wind-felled during the previous winter. The presence of *I. amitinus* colonisation was determined by visual inspection after strips of bark were removed from the whole length of each object. If signs of beetle attack were present, more bark was removed to determine which species were present. The identification of *I. amitinus* was based on adults (when present) and/or the characteristics of the gallery system (Suppl. material 1: *Ips amitinus* description).

Table 1. Numbers of the five types of locations surveyed for presence of *Ips amitinus*. The first survey was conducted in 2016–2017 and the second in 2018–2019.

Year	Total no. localities	Location type				
		Clear-cut	Along Road	Stand	Thinning	Power lines
2016	12	–	10	–	1	1
2017	153	45	63	12	20	13
2018	118	100	–	–	18	–
2019	99	92	–	–	7	–

Table 2. Numbers of spruce and pine objects and of each of the five types of objects, surveyed in the first (2016–2017) and second (2018–2019) survey.

Year	Tree species		Type of objects					Total no. objects
	Spruce	Pine	Tops	Branches	Logs	Small trees	Large trees	
2016	11	10	–	–	2	5	14	**21**
2017	831	873	499	23	100	988	95	**1705**
2018	2255	1216	1470	31	114	1815	42	**3472**
2019	2981	2301	3407	–	–	1875	–	**5281**

In 2016, the survey focused on confirming the establishment of *I. amitinus* in Sweden. Trap logs of spruce and pine were cut close to the location of the first discovery in Sweden in 2012. Material such as wind-felled trees, found while driving between the trap log locations, was inspected as well. In 2017, the survey focused on establishing the presence of *I. amitinus* along the Finnish border, the assumed entry of the species to Sweden (Økland et al. 2019) and to determine how far south the species had spread in Sweden. In both years, inspection sites were located by driving along roads. In both 2016 and 2017, a maximum of 30 objects were checked in each locality when available. However, inspections ended when an *I. amitinus*-colonised object was found, even if it was the first checked object.

In the second survey (conducted in the summers of 2018–2019), we adjusted the survey methodology, based on experience gained in the first survey and only included clear-cuts and thinnings harvested during previous winter (between October and March) (Table 1). Spruce and pine forest stands were not surveyed (except recently thinned stands) because of a very low probability of finding suitable breeding material (i.e. dying or newly-dead conifers or parts of trees) inside stands that had not been thinned recently. We decided to focus on clear-cuts as these constituted most of all cuttings and information was available about their locations from the Swedish Forest Agency and forest companies. In addition, in the spring of 2019, clear-cuts from winter 2017–2018 were checked for colonisation by *I. amitinus* during the previous summer (2018), to increase the number of surveyed localities along the distribution limit (these clear-cuts were not inspected during 2018). In 2018, the same five types of objects were inspected as in the previous years. In 2019, we only inspected tops and small trees, as those objects had the highest probability of attack (see results). In 2018, at each location, 30 objects were randomly selected and inspected for the presence of *I. amitinus* (i.e. even if the species were found in the first object, all 30 objects were checked). In 2019, the protocol was adjusted to ensure a more accurate estimate of absence. Initially, 30 objects would be inspected. If *I. amitinus* were not detected in those 30 objects, we continued until 100 objects had been inspected. For each object, we recorded tree species (spruce or pine), type of object, diameter, length and the presence of *I. amitinus*.

For each inspected object during the second survey, we also recorded the presence of other (native) bark beetle species and other bark- and wood-boring beetles. Species identification was based on adults and gallery systems (Ehnström and Axelsson 2002). As there are two species of the bark beetle genus *Pityogenes* that commonly reproduce in logging residues of pine (*P. bidentatus* and *P. quadridens*) and because species identification is not possible, based on their gallery systems, their identification was only done to *genus* level (referred to as *Pityogenes* spp.). Only one *Pityogenes* species, (*P. chalcographus* Linnaeus, 1761*)*, is known to commonly colonise spruce in Sweden (Ehnström and Axelsson 2002; Jonsell et al. 2007). In Central Europe, *P. chalcographus* can often be found in pine as well (Foit 2012, 2015). However, that does not seem to be the case in Scandinavia (Ehnström and Axelsson 2002; Åke Lindelöw, personal communication, but see Lekander et al. 1977).

Performance in naturally colonised material

Field-collected colonised material was used to assess *I. amitinus* performance in spruce and pine. The material was collected between 21 and 26 May 2018, prior to emergence of offspring resulting from colonisation earlier in spring (no exit holes present), from seven clear-cuts harvested during the previous winter. Most of the collected material were spruce tops and small spruce trees (60 objects from 7 clear-cuts), but also some small pine trees were collected (11 objects from 2 clear-cuts) (Table 3).

The objects were grouped by tree species and location before being placed in separate emergence cages (seven cages with spruce and two cages with pine) in a climate chamber (20 °C, 20 hours day length). When adult emergence had ceased, we recorded for each object, diameter, length, *I. amitinus* attack density (number of male entrance holes and maternal galleries per mantel area) and number of maternal galleries per mating chamber. Emerging *I. amitinus* were collected daily from cages and stored in boxes with moist paper at 5 °C to be used later in the rearing experiment (see below).

Table 3. Number, mean length and diameter of naturally colonised objects used for evaluating the performance of *Ips amitinus* in Norway spruce and Scots pine.

Tree species	No. objects	Length (cm) Mean ± SE	Range	Diameter (cm) Mean ± SE	Range
Norway spruce	60	61.67 ± 0.51	48–70	8.9 ± 0.4	4–15.5
Scots pine	11	56.54 ± 1.95	41–61	12.4 ± 0.41	11–15.5

Performance in rearing experiment

We used the *I. amitinus* adults reared from the naturally colonised spruce and pine for a no-choice experiment with stem sections of spruce and pine. From seven spruce and five pine trees, a 60 cm long stem section was cut (at 3 m from the base of the trees) between 9 and 10 July near Uppsala. The diameter of the stem sections was 17.6 ± 0.4 cm (mean ± SE) and they were stored at room temperature for 48 hours after which cut surfaces were waxed to prevent desiccation. Subsequently, the stem sections were stored at room temperature for another 24 hours before being moved to a climate chamber (20 °C, 20 hours day length). Each section was placed standing in a separate cage (70 × 53 × 50 cm). The following day, 90 *I. amitinus* adults were released into each cage. All reared beetles were mixed together prior to release. As colonisation success was deemed insufficient (based on amount of boring dust), an additional 70 adults were released into each cage after three days. Low vitality adults (slow in movement) were discarded prior to release.

All dead beetles were collected from each cage prior to the emergence of the new generation. These dead beetles were parent beetles that left the stem section after mating and egg laying, in addition to beetles that never entered the logs. The emerging offspring were collected daily and colour-classified during the first weeks to ensure that they were not parent beetles (darker). After emergence ended, density and length of *I. amitinus* maternal galleries, number of maternal galleries per mating chamber and number of male entrance holes were recorded. We also noted the success or failure of maternal galleries, based on presence (success) and absence (failure) of larval galleries.

Statistical analyses

All statistical analyses were performed in R, version 2021.09.2 (R Core Team 2019).

Surveys of occurrence

All data collected during the surveys from 2016 to 2019 were used to calculate the distribution area. The speed of range expansion was calculated using the latitudinal difference between the most southern record for each survey year, from 2017 to 2019. During the 2018 and 2019 survey, we checked 13.5% and 13%, respectively, of all fresh clear-cuts along the yearly southern distribution limit (on an approximate 66 × 10 and 65 × 12 km area).

Tree species and object type preference

For analysis of observational data from the second survey, we used generalised linear mixed models with a binomial error distribution (glmer, lme4 package; Bates et al. 2015), to estimate the relationship between colonisation (i.e. the presence/absence of *I. amitinus*), using the explanatory variables tree species (two levels: spruce and pine), object type (two levels: tops and small trees), diameter and total number of other bark beetle taxa as covariates. Interactions between explanatory variables tree species and object type and between object type and the number of other species were also included in the model. Object diameter was included to control for potential effects on the response variable. Year and clear-cut identity were included as random factors. We encountered some problems with model convergence. Hence, we set adaptive Gauss-Hermite quadrature points (nAGQ) to zero (Olver et al. 2010), to calculate the log-likelihood, even though the accuracy of the method in parameter estimation decreased.

Performance in naturally colonised material

To assess *I. amitinus* performance in the field-collected material, we used attack density per m^2 of bark (two measures: male entrance holes and maternal galleries), reproductive success (number of daughters per maternal gallery) and the number of offspring produced per m^2 bark area as the response variables. Cage was the level of replication for the reproductive success. The attack densities were recorded for each object (level of replication). We used a linear model with the explanatory variable tree species (two levels: spruce or pine). We used Levene's test to check for homogeneity of variance in the residuals (LeveneTest; car-package). When the model assumption of homogeneity of variance was violated, the response variable was log-transformed (natural logarithm), to comply with model assumptions.

Performance in rearing experiment

We performed the same analyses for the no-choice rearing experiment. One spruce log was excluded from the analysis because of lack of reproductive activity. We used the same response variables, which we calculated in the same way, as for the field-collected material.

Co-occurrence with native species

To assess the co-occurrence of *I. amitinus* with the native species, we used manyglm model (mvabund package; Wang et al. 2012), fitted with a negative binomial distribution, with the number of other bark-and wood-boring beetle species present in each locality as the multivariate response variable and presence/absence of *I. amitinus* as the explanatory variable. The data were pooled by locality and split by tree species; the model was run separately for spruce and pine. We also performed a series of Non-Metric Multidimensional Scaling (NMDS), using metaMDS function (Vegan package; Oksanen et al. 2013) to allow for better visualisation of our data. NMDS is a method that allows for a better visualisation of patterns in community abundance, in a reduced number of dimensions (Dexter et al. 2018). We looked at the presence/

absence of other species versus presence/absence of *I. amitinus* at locality level in both spruce and pine. We set the distance metric to "bray", number of dimensions (K) set to 3, max. number of iterations set to 999 and the number of random starts was set at 300. For both the manyglm model and for the NMDS analysis, only bark- and wood-boring beetle species known to attack each one of the tree species were included in the analyses. Only localities colonised by at least one species were included in the model.

Results

Surveys of occurrence

Ips amitinus was found in 184 out of 382 inspected localities in the years 2016–2019. North of its southern distribution limit, the species was recorded in 57.9% of all checked localities during the four-year study. Our observations show that the species is presently distributed from the border of Finland in the north-eastern part of the Province of Norrbotten (67°29.915'N, 23°17.330'E) and south to the northern part of the Province of Västerbotten (65°11.628'N, 20°46.218'E) (Fig. 1A).

Based on the yearly surveys, we found that the estimated speed of expansion varied yearly from 17 km from 2017 to 2018 and 11 km from 2018 to 2019, suggesting an average range expansion of 14 km per year (Fig. 1B).

The average proportion of objects colonised by *I. amitinus* per occupied locality was 16.6 ± 1.9% in 2018, ranging from 3% to 57% and 11.6 ± 1.2% in 2019, ranging from 3% to 37%. *Ips amitinus* was not detected in any of the 64 localities checked south of the 2019 distribution limit. No overwintering adults were found under bark in colonised substrates in any of the 33 clear-cuts (79 attacked objects) that were colonised in 2018 and checked in early spring 2019.

Tree species and object type preference

Ips amitinus was present in 23.4% (376 colonised objects) of sampled spruce tops and small trees in 2018 and 16.2% (236 colonised objects) in 2019, within its distribution limit. The colonisation rate in pine was lower in both 2018 (3.0%, 25 colonised objects) and 2019 (0.2%, two colonised objects). The interaction between tree species and object type indicated that, for pine, *I. amitinus* prefers small trees compared to tops, whereas for spruce, no clear difference was detected (Fig. 2, Table 4).

The interaction between object type and the number of other bark beetle taxa present indicates that, in small trees, the presence of more species is associated with a higher probability of colonisation by *I. amitinus*. We found a positive significant relationship with object diameter independent of object type (0.31 ± 0.03; $X^2 = 127.39$, $p < 0.0001$) and this relationship is also independent from other explanatory variables (Table 4).

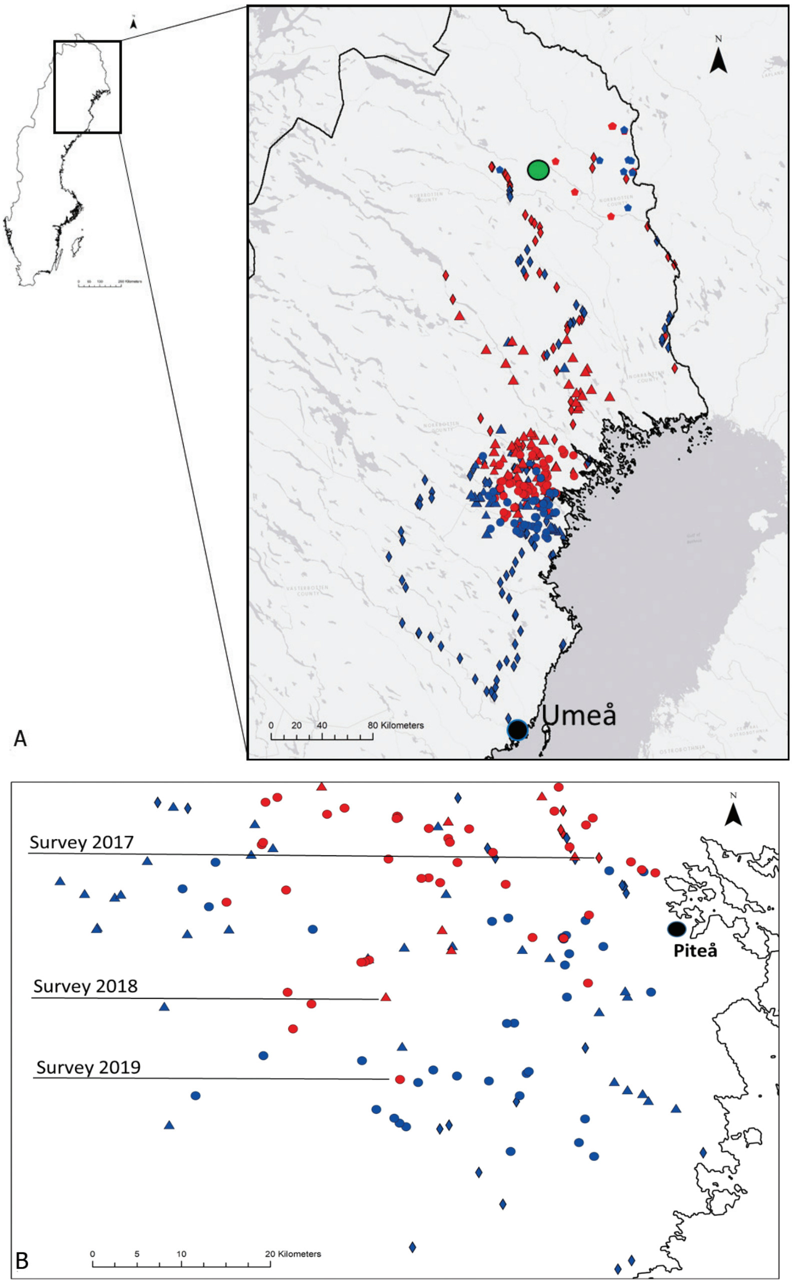

Figure 1. A locations checked for presence of *Ips amitinus* in northern Sweden in 2016 – 2019. Red symbols = presence and blue symbols = absence. Green symbol = first record in 2012. 2016 = pentagon, 2017 = diamond, 2018 = triangle and 2019 = circle. Umeå (63°49.877'N, 20°15.651'E) **B** *Ips amitinus* southern distribution limit in 2017, 2018 and 2019 in northern Sweden. Localities are with (red symbols) and without (blue symbols) findings of *I. amitinus* in the surveys. Diamond symbols represent the 2017 survey, triangle – 2018 and circle - 2019 survey. Black horizontal lines denote the most southern location with *I. amitinus* for each year. The distance from the first find in 2012 (green circle in Fig. 1A) to the distribution limit in 2017 is 250 km.

Figure 2. The probability of attack between the two different tree species and object types, based on the results from the 2018 and 2019 survey. The central lines of the box plot represent the median, the box indicates lower and upper quartiles and the whiskers represent the largest and smallest observations that fall within 1.5 times the box size from the nearest quartile. Black circles represent outliers.

Table 4. Anova (type III test; Anova; car-package) and estimates for the generalised linear mixed effects model testing the effect of tree species, object type, number of other bark beetle taxa and diameter on *I. amitinus* colonisation probability. The Table shows the final model with the chi-squared value, degrees of freedom (df), estimates and the standard error of the mean (SE). The standard deviation for intercept (for the random effects) is given as well. The variables printed in bold are significant at $p < 0.05$. The intercept represents the overall mean. Values were obtained by using sum contrasts, as we wanted to compare the intercept to the overall mean.

Response	**Explanatory**	**X^2**	**df**	**Est**	**SE**	**P**	**Random effects: Site, Year**	
							Std. dev.	**Intercept**
							Site	**Year**
I. amitinus	Intercept	**312.88**	**1**	**-6.20**	**0.35**	**<0.0001**	0.96	0.10
colonisation	Tree species (pine)	**164.45**	**1**	**-1.74**	**0.14**	**<0.0001**		
	Object type (small tree)	0.12	1	0.06	0.18	–		
	Other bark beetle taxa	0.76	1	-0.10	0.12	–		
	Diameter	**127.39**	**1**	**0.31**	**0.03**	**<0.0001**		
	Tree species (pine) × Object type (small tree)	**25.02**	**1**	**0.66**	**0.13**	**0.0001**		
	Object type (small tree) × Other bark beetles	**10.21**	**1**	**0.36**	**0.11**	**0.001**		

Performance in naturally colonised material

Attack density, expressed as density of male entrance holes per m^2 of bark ($F_{1,69} = 8.261$, $p = 0.005$; Fig. 3A), as well as the density of maternal galleries ($F_{1,69} = 8.238$, $p = 0.005$; Fig. 3B) were significantly higher in spruce objects compared to pine, independent of object type.

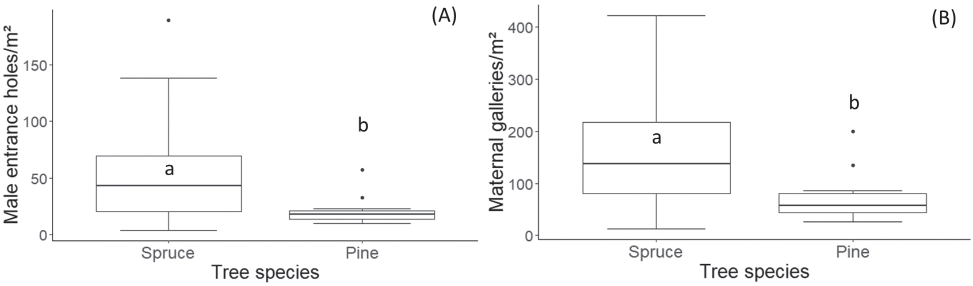

Figure 3. Male attack and female gallery density in host material naturally colonised by *Ips amitinus*. (**A**) Male entrance holes per m^2 bark and (**B**) maternal galleries per m^2 bark.

However, there was no significant difference in the number of maternal galleries per mating chamber between spruce (3.08 ± 0.08) and pine (3.27 ± 0.26; $F_{1,69}$ = 0.267, p = 0.61). Reproductive success, expressed as number of daughters per mother (i.e. per maternal gallery), was significantly higher in spruce (4.53 ± 0.70), compared to pine (1.90 ± 0.06; $F_{1,7}$ = 5.369, p = 0.05). In addition, the number of offspring produced per m^2 was significantly higher in spruce (1447 ± 469) compared to pine (328 ± 96), ($F_{1,7}$ = 5.056, p = 0.05). Maternal gallery length was significantly longer in pine (11.97 ± 0.78 cm) compared to spruce (8.92 ± 0.28 cm; $F_{1,69}$ = 16.88, p = 0.0001). The density of *I. amitinus* male entrance holes did not differ between the pine objects with and without the bark beetle *Tomicus piniperda* (L.) ($F_{1,9}$ = 3.006, p = 0.11). However, the density of *I. amitinus* maternal galleries per m^2 was more than two-fold higher within pine when *T. piniperda* was absent (108 ± 27), compared to when both species were present in the same object (47 ± 7.6; $F_{1,9}$ = 5.379, p = 0.04). No living adult *I. amitinus* beetles were found under the bark at the end of the rearing of naturally colonised material though a few dead individuals were found.

Performance in rearing experiment

The density of male entrance holes per m^2 of bark was significantly higher in spruce compared to pine ($F_{1,9}$ = 5.155, p = 0.05; Fig. 4A). The density of maternal galleries, on the other hand, only showed an indication of being higher in spruce ($F_{1,9}$ = 3.849, p = 0.08; Fig. 4B). The reproductive success was significantly higher in spruce compared to pine ($F_{1,9}$ =5.407, p = 0.05; Fig. 4C). In addition, the number of offspring produced per m^2 was significantly higher in spruce compared to pine ($F_{1,9}$ = 19.1, p = 0.002; Fig. 4D).

Maternal gallery length did not differ between the pine and spruce (13.8 ± 5.6 cm for spruce and 10.6 ± 4.7 cm for pine, $F_{1,9}$ = 1.93, p = 0.19). We did not find a difference in the number of maternal galleries per mating chamber, between spruce and pine (2.4 ± 0.2 and 2.1 ± 0.3 respectively, $F_{1,9}$ = 1.291, p = 0.28). The emergence time of the new generation did not differ between the two tree species. No adult beetles remained under the bark at the end of the experiment.

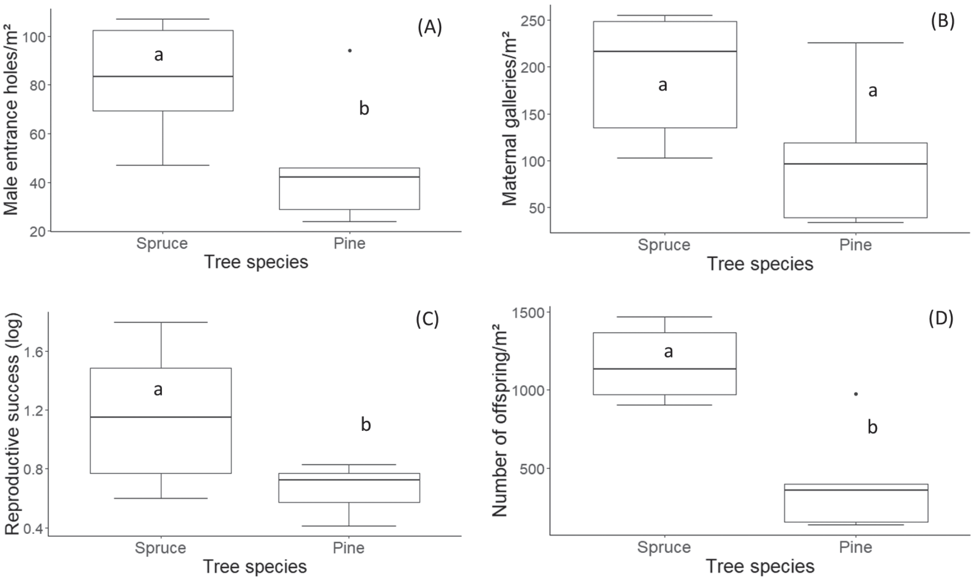

Figure 4. The results from the no-choice rearing experiment with *Ips amitinus*. Male entrance holes per m^2 bark (**A**), maternal galleries per m^2 bark (**B**), reproductive success (log transformed), (**C**) and number of offspring produced per m^2 bark (**D**). Means with different lowercase letters are significantly different at $p < 0.05$. There were six replicates for Norway spruce and five for Scots pine.

Co-occurrence with native species

A total of 16 native bark beetle, weevil and long horn beetle species/taxa were recorded in the study (Suppl. material 1: table S1). The results from manyglm ANOVA show that, for spruce, there was no significant difference in the number of native bark- and wood-boring beetle species between localities where *I. amitinus* was present or absent (LRT = 14, p = 0.09). The result of our NMDS analysis shows also a similar pattern in the number of native bark- and wood-boring beetle species between localities when *I. amitinus* is present or absent (Fig. 5A). For the pine, we did find a significant difference between the total number of other bark- and wood-boring beetle species and locations with and without *I. amitinus* (LRT = 20, p = 0.002). Amongst the species, a significant negative relationship with the presence of *I. amitinus* was found for *T. piniperda* (LTR = 5.7, p = 0.04). This is also confirmed by the reduced overlap in the NMDS analysis between the area when *I. amitinus* is present and absent (Fig 5B).

Ips amitinus was the third most common species colonising the inspected wood objects within its distribution limit. When looking at only spruce objects, *I. amitinus* was the second most common species and, on only pine objects, the fourth most common species (Suppl. material 1: table S1.) Spruce accounted for 57.5% of all objects inspected within the distribution area for *I. amitinus*, the remaining 42.5% being pine. On average 5.2% of all the objects checked during the four years were not colonised by any species. From all the colonised objects, only 0.07% were colonised by *I. amitinus*

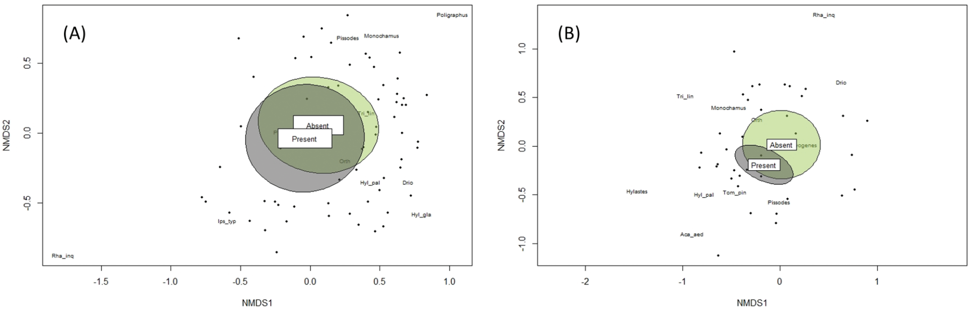

Figure 5. NMDS visualisation of the relationship between the other species found in spruce (**A**) and pine (**B**) in relation to the presence/absence of *I. amitinus*. Stress: 0.1868 (spruce) and 0.1173 (pine).

alone. There was no marked difference in the average number of other bark beetle taxa that colonised either spruce or pine north of the distribution limit compared to south (1.2 – 1.1 for spruce and 1.0 – 1.1 for pine). Only objects colonised by at least one species were included in this calculation.

Discussion

In this study, we set out to establish the range distribution of *I. amitinus* in Sweden and the preferred tree species and host material used in the new range. We found that *I. amitinus* has expanded its range south approximately 200 km over land from the Finnish border (Fig. 1A). In addition, we observed a preference for spruce as a host on which the species also achieves the highest reproduction success. We did not find an indication that the arrival of *I. amitinus* has a transformative effect on the native bark beetle community despite being one of the most common species.

Due to the lack of *I. amitinus* records around Umeå (Fig. 1A), we argue that our observations support the conclusion that this species spread over land into Sweden from Finland. The continuous presence of *I. amitinus* from the northern Finnish border with Sweden to the southern limit of observations in Sweden is additional support for range expansion over land. The first observation of *I. amitinus* in Sweden in 2012 was a chance observation; it is unclear what the distribution limit of the species was at that time. When the targeted surveys started in 2017, our observations indicate that, from the southern range limit observed in 2017 to the range limit observed in 2019, *I. amitinus* expanded south with an estimated average speed of 14 km per year, which is similar to the average rate of spread through Finland observed in previous studies (Økland et al. 2019; Fig. 1B).

In earlier studies, spruce has been recorded as breeding material more often than pine (Annila and Nuorteva 1976; Witrylak 2008; Grodzki 2009; Holuša et al. 2012; Mazur and Kuźmiński 2013), but without quantitative comparisons. Our study shows that the brood of this species is most frequently found in spruce and male attack density is higher in spruce compared to pine in both field and laboratory studies, indicating a male preference for spruce. Competition with *T. piniperda* in pine (which colonises hosts earlier in spring than *I. amitinus*) might be one factor that has contributed to higher preference and higher male and female attack density in spruce. The higher reproductive success in spruce, for both the field and experimental material, could be another contributing factor for the preference for spruce (Fig. 4). Neither of the rearing experiments showed a significant difference between the number of maternal galleries per nuptial chamber between the tree species, which indicates that once males manage to colonise an object, they are equally attractive to females regardless of the tree species they chose.

To our knowledge, this is the first study to show that both *I. amitinus* preference and performance are highest in spruce within its invaded range. In the native range, Stauffer and Zuber (1998) compared *I. amitinus* performance between Norway spruce and the Swiss stone pine (*Pinus cembra*, Linnaeus). They showed that *I. amitinus* can breed successfully in both tree species, both in a dual choice (where spruce was preferred) and a no-choice experiment. However, the offspring production was lower in stone pine. Apart from the above-mentioned study, most other studies on *I. amitinus* performance (such as abundance, attack and emergence rates) only considered spruce (Annila and Nuorteva 1976; Witrylak 2008; Grodzki 2009; Holuša et al. 2012; Mazur and Kuźmiński 2013).

Our surveys show that *I. amitinus* is one of the most common bark- and wood-boring species in fresh logging residues, even though the species has most probably only been present for a rather short time (See Økland et al. 2019; Fig. 1A; Suppl. material 1: table S1). *Ips amitinus* was the second most common bark beetle taxon in spruce and the fourth in pine logging residues. In studies conducted in Central Europe, *I. amitinus* is also reported to be one of the most common bark beetle species, together with *P. chalcographus* and *I. typographus*, although quantitative comparisons are lacking (Grodzki 1997, 2009; Witrylak 2008; Holuša et al. 2012; Mazur and Kuźmiński 2013). This begs the question, how did *I. amitinus* become so abundant in northern Sweden in a relatively short time? One explanation might be that the host tree species are the same and the community of bark- and wood-living beetles is similar to the native range. An additional explanation may be the species' ability to successfully reproduce in logging residues. At the landscape level, harvesting of forest stands are conducted each year in many locations, thereby creating a relatively continuous supply of breeding material. The use of logging residuals by *I. amitinus* was also observed in Finland, a country with similar forestry practices as Sweden (Annila and Nuorteva 1976; Martikainen et al. 1996) and where the rate of spread was similar to our results.

We find that the community of bark boring insects in spruce is not different when *I. amitinus* is present or absent (Fig. 5A), indicating that the species found in the spruce manage to attack and reproduce regardless of *I. amitinus* presence. In other words, our results for spruce could indicate a vacant niche for *I. amitinus* in the invaded community. However, the results for pine (Fig. 5B) show a smaller overlap, which could indicate that more species are associated with objects not colonised by *I. amitinus*, compared to objects colonised by *I. amitinus*, with the strongest negative relationship between *T. piniperda* presence and *I. amitinus* presence. Based on these results, we propose that the invasion of *I. amitinus* did not have strong negative consequences for the native community associated with spruce in the invaded areas.

The significant difference observed for *T. piniperda*, in relation to the presence of *I. amitinus*, might be explained by the earlier flight period for *T. piniperda* than for *I. amitinus*. The earlier flight period will give *T. piniperda* the opportunity to colonise breeding material before *I. amitinus*, potentially leading to competitive exclusion of *I. amitinus*.

As our study merely scratches the surface of potential ecological effects of *I. amitinus* invasion, we see a need for more detailed studies into the effects on reproductive success and enemy pressure on *I. amitinus* and its community. We expect that the space available for brood production on logging residues by native species have been reduced to some extent, especially since only a small proportion of the inspected objects were not colonised and some of these may have been too dry or in some other way unsuitable for native bark beetle colonisation. Our observations strongly suggest that *I. amitinus* will continue expanding its range south in Sweden.

In conclusion, the range expansion of *I. amitinus* in Sweden does not appear to markedly affect the native community of bark- and wood-boring insects. In areas where pine is dominating, the invasion success of *I. amitinus* might be slowed down because of its lower reproduction success and stronger competition with *T. piniperda*. The low impact of *I. amitinus* in its invaded range might be related to the similarities with the community in its native range. Future studies of and comparisons with other species expanding into a naïve range and potential host switching will be needed to understand the importance of this similarity.

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Supplementary material 1

***Ips amitinus* description, table S1**

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Data type: pdf file

Explanation note: *Ips amitinus* adults were collected for identification in the laboratory when possible. *Ips amitinus* differ from other *Ips* species present in Sweden by a shiny declivity at the back of the elytra (Knižek 2001; Nierhaus-Wunderwald and Forster 2004; Åke Lindelöw, pers. communication). The gallery system is highly characteristic for the species. It has a very large nuptial chamber in the late stages, as the male usually attracts between two and seven females. The mother galleries often start away from the direction of the wood fibre, then turn after about one centimetre and continue along the wood fibre in a rather windy way. The gallery system could be confused to other bark beetles in the early stages (like Orthotomicus spp.), but it is rather specific in the later stages (for a visual comparison, see Knižek 2001); **table S1.** Percentages of localities and wood objects colonised by bark- and wood-boring beetle taxa north and south of the *Ips amitinus* 2019 southern distribution limit. The number of colonised localities and objects is given within parenthesis. Species were ordered, based on the percentage (and number) of colonised localities north of *Ips amitinus* distribution limit. Taxonomic group: B = bark beetle; L = longhorn beetle; W = weevil (except bark beetles). Host tree: S = Norway spruce; P = Scots pine. The percentage of colonised objects is calculated, based on the number of objects from their host tree species.

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