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Establishment and spread of non-native bark- and wood-boring beetles

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Cover: Illustration of the entry points in Sweden for the beetle species studies in this thesis.

Illustration: Dragos Cocos. Bark beetle silhouette: Kristina Gagalova (CC BY-SA 3.0). Longhorn beetle silhouette: Aracelia

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Abstract

One of the biggest threats to forest ecosystems globally is the introduction and establishment of non-native species. In Sweden alone, several bark- and wood-boring beetles have established populations in recent years. Three of the recently established species are the larch bark beetle *Ips cembrae* and the larch longhorn beetle *Tetropium gabrieli* in southern Sweden, as well as the small spruce bark beetle *I. amitinus* in northern Sweden. This thesis aims to assess their current distribution in Sweden and evaluate the factors that influence their local colonization and further spread.

Pheromone-baited traps were used to assess if *T. gabrieli* is attracted to congeneric pheromone. Subsequently such traps were also used to estimate the local population sizes of *I. cembrae* and *T. gabrieli*. A survey method was developed for delimiting the distribution of *I. amitinus* based on inspection of logging waste on fresh cuttings. The method was used for establishing the southern range limit and the inter-annual spread. Field and laboratory experiments were also used to assess factors that influence the species local colonization.

We found that *T. gabrieli* was attracted to the congeneric pheromone but not to the host volatiles. We found that local population sizes of both *I. cembrae* and *T. gabrieli* were related to the amount of suitable habitat in the landscape. We found that *I. amitinus* is already spread over large parts of northern Sweden and is one of the most common bark beetle species found in the region. Our results indicate that factors such as their reproductive strategy, forage for food and escape the enemy pressure influenced the probability of colonization. Allee effects, operating through the above mentioned components, might explain the low colonization probability for small local populations in the southern area and the abrupt range limit for *I. amitinus* in the north.

In conclusion, species life history traits should be considered when planning risk assessments and monitoring programs of non-native species as it is a strong indicator for establishment. At the same time, the use of a correct method for surveying non-native species is fundamental for an accurate conclusion of establishment and distribution.

Keywords: Allee effects, bark beetles, establishment, life history traits, longhorn beetles, non-native species

Etablering och spridning av icke inhemska bark- och vedinsekter

Abstract

Ett av de största globala hoten mot skogliga ekosystem är att främmande arter införs och etableras. Bara i Sverige har flera främmande bark- och vedlevande arter etablerat sig under de senaste åren. Exempel på tre arter som nyligen etablerat sig i Sverige är lärkborre *Ips cembrae* och lärkbock *Tetropium gabrieli* i södra Sverige, samt liten granbarkborre *I. amitinus* i norra Sverige. Avhandlingens syfte är att utvärdera dessa arters aktuella utbredning i Sverige och undersöka de faktorer som påverkar kolonisationer och spridning av dem. Feromonbetade fällor användes för att avgöra om *T. gabrieli* attraheras av feromonet till en annan art i samma släkte.

Feromonbetade fällor användes sedan för att uppskatta de lokala populationsstorlekarna för *I. cembrae* och *T. gabrieli*. En inventeringsmetod baserad på inspektioner av färskt avverkningsavfall utvecklades för I. amitinus. Metoden användes för att avgränsa artens södra utbredningsgräns och för att studera artens årliga expansion söderut. För att bedöma de faktorer som påverkar koloniseringarna gjordes också lab- och fältexperiment. Vi fann att *T. gabrieli* attraherades av kongeneriska feromoner men inte av värdträdsdofter.

Vi fann att lokala populationsstorelekar av både *I. cembrae* och *T. gabrieli* var relaterade till mängden lämpligt habitat i landskapet. Vi fann även att *I. amitinus* redan har etablerat sig över stora delar av norra Sverige och är en av de vanligaste barkborrearterna i regionen. Våra resultat indikerar att faktorer kopplade till deras reproduktionsstrategi, finna födoresurser och undvika predationstrycket påverkade chanser till kolonisationer. Ovan nämnda Allee-effekter kan förklara den låga kolonisationssannolikheten för små lokala populationsstorlekar i det sydliga studiesystemet och den abrupta utbredningsgränsen för *I. amitinus* i norr.

Slutsatsen är att skillnader i arters livshistoria bör beaktas när man gör riskbedömningar och planerar övervakningsprogram för främmande arter eftersom de påverkar sannolikheten för etablering. Samtidigt är val av rätt inventeringsmetod avgörande för att kunna dra korrekta slutsatser om etableringar och spridning av främmande arter.

Nyckelord: Allee-effekter, arters livshistoria, barkborrar, etablering, främmande arter, långhorningar

Dedication

To my family! For being there when I needed the most!

Contents

List of publications

This thesis is based on the work contained in the following papers, referred to by Roman numerals in the text:

I. Schroeder, M*., Cocos, D., Johansson, H. and Sweeney, J. (2020). Attraction of the cerambycid beetles *Tetropium gabrieli*, *T. castaneum* and *T. fuscum* to pheromones and host tree volatiles. Agricultural and Forest Entomology, 23 (issue), 203-211.

II. Cocos, D*., Klapwijk, MJ., Björkman, C., Ravn, H.P. and Schroeder, M. Population density and colonisation success of *Ips cembrae* and *Tetropium gabrieli* in relation to habitat availability at stand and landscape scale (submitted manuscript)

III. Cocos, D*., Klapwijk, MJ. and Schroeder, M. (2022). Tree species preference and impact on native species community by the bark beetle *Ips amitinus* in a recently invaded region. Neobiota (in press)

IV. Cocos, D*., Klapwijk, MJ., Björkman, C and Schroeder, M. A new sampling strategy for delimiting a bark beetle invasion – occupancy patterns of *Ips amitinus* when approaching the range limit (manuscript)

Papers I and III are open access publications (CC BY 4.0).
* Corresponding author

The contribution of Dragoș Cocoș to the papers included in this thesis was as follows:

I. Helped design the experiment, performed all the fieldwork, helped with the lab samples analysis, wrote the first draft for Materials and methods and contributed to the further writing.

II. Helped design the experiment, set up the field experiment, performed the field work, set up the rearing experiment, data analysis, wrote the first draft of the manuscript and contributed equally to the further writing

III. Helped design the experiment, performed the data collection, data analysis, wrote the first draft of the manuscript and contributed equally to the further writing.

IV. Helped design the experiment, performed the data collection, data analysis, wrote the first draft of the manuscript and contributed equally to the further writing.

1. Introduction

1.1 Invasive bark- and wood-boring beetles – a threat to global forestry

Invasive insect species represent one of the biggest threat to forest biodiversity (Hulme 2009; Bellard et al. 2016). The number of invasive forest insects establishing worldwide has dramatically increased in the last decades because of global trade (Brockerhoff and Liebhold, 2017; Meurisse et al. 2019) and climate change (Parmesan and Yohe 2003; Walther et al. 2009). Currently, more than 400 non-native insect species feeding on woody plants have been recorded in Europe alone (Liebhold et al. 2017a). The consequences can be devastating for the integrity of forests and the provision of their ecosystem services. Some of them cause substantial economic loses (Barbier, 2001; Aukema et al. 2011). Among intercepted non-native forest insects, bark- and wood-boring beetles are well represented and their establishment rates have increased strongly both around the globe and in Europe (Aukema et al. 2010; Sauvard et al. 2010; Brockerhoff & Liebhold 2017; Liebhold et al. 2017b).

1.2 Biological invasions

There are many ways in which non-native organisms invade new areas such as expansion of their natural range as a response to climatic changes (Travis and Dytham 2002; Parmesan and Yohe 2003; Walther et al. 2009), accidental introductions (Blackburn et al. 2014, Gollasch, 2008) and planned introductions as biological control agents (Brockerhoff et al. 2014; Brockerhoff & Liebhold 2017). The role of humans in the processes that lead to shifts in population ranges, between species accidentally introduced and species that expand their range naturally, is still debated. Hoffmann and Courchamp (2016) argue that the same mechanisms and processes, such as survival, reproduction, dispersal in the new environment and further range expansion apply to both categories. On the other hand, Wilson et al. (2016) believe that they are two different processes and argue that human dimension is a fundamental component that should not be neglected.

Regardless of the way in which a species colonizes new areas, all biological invasions can be considered as a sequence of phases (Fig. 1), including:
(1) arrival of a propagule of individuals to a new area (introduction), (2) establishment of an initial reproductive founder population, (3) population growth and spread and (4) impact on invaded ecosystem (Brockerhoff and Liebhold 2017). Because the exact arrival stage is often hard to detect (Liebhold and Kean 2018), detailed understanding of the second and third phase is critical as the success of eradication programs is much higher, and less costly, when populations are still small (Tobin et al. 2014; Liebhold et al. 2016).

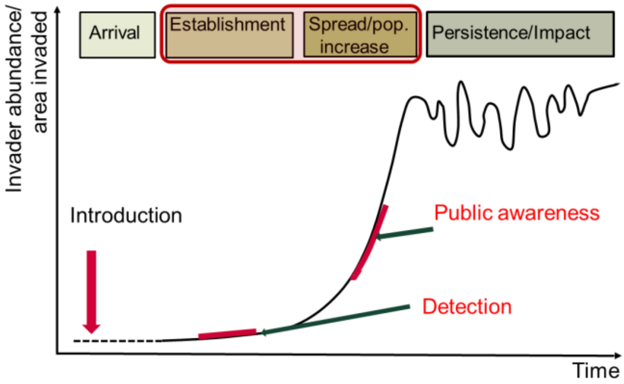

Figure 1. Theoretical invasion curve (black line) and the corresponding invasion phases (Adapted after Geburzi and McCarthy 2018).

Establishment is defined as ‘growth of a population to sufficient levels such that natural extinction is highly unlikely’ (Liebhold and Tobin 2008). A major task in invasion ecology is identifying the key factors that influence the risk of establishment of invasive species (Johnston et al. 2009). Some of the key factors that may influence establishment are propagule pressure (Simberloff 2009), habitat configuration (Musgrave et al. 2015; Walter et al. 2016), life history traits of the invading organism (Ducatez and Shine 2019; Davies and Britton 2021) and predation pressure (Roy et al. 2011; Tobin et al. 2011). Spread is defined as the range expansion of the invading species into new areas, where the arrival of new individuals and establishment are repeated across space and time. Spread is driven by population growth coupled with dispersal ability (Liebhold and Tobin 2008). However, invasion success or failure is determined by multiple factors at each stage (Blackburn et al. 2011).

1.3 The role of Allee effects in low density populations

Low-density populations are strongly affected by random effects, which include both environmental stochasticity (e.g., yearly variation in effects of weather) as well as demographic stochasticity (random variation in birth and death rates) which may result in extinctions (Palamara et al. 2016). In addition, demographic Allee effects, i.e. positive relationship between total individual fitness (usually quantified by the per capita population growth rate) and population size or density (Fig. 2), is believed to be a considerable constraint on the establishment and spread of low-density populations (Courchamp et al. 1999; Berec et al. 2006).

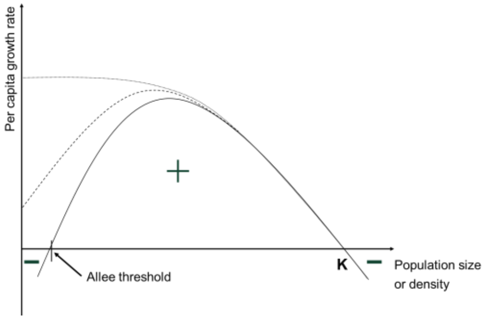

Figure 2. Illustration of the Allee effect or the positive density dependence. Dotted line illustrates the classical negative density dependence scenario. Dashed line illustrates a weak Allee effect and the full line illustrates a strong Allee effect. K represents the carrying capacity (Adapted after Courchamp et al. 1999).

Thus, Allee effects are of special interest in invasion biology (Liebhold & Tobin 2008; Simberloff 2009). Even though the role of Allee effects in population dynamics of invading populations is often considered, the majority of reports are theoretical (Courchamp et al. 2008), with relatively few empirical studies in the field (Grevstad 1999; Kramer et al. 2009; Chase 2016; Chase et al. 2023).

Component Allee effects designate a positive relationship between any measurable component of individual fitness and population size or density (in contrast to a demographic Allee effect that refers to the overall fitness level). The main mechanisms generating component Allee effects include mate finding (Fauvergue 2013; Walter et al. 2016), foraging efficiency (Courchamp and Macdonald 2001; Grünbaum and Veit 2003) and predator dilution (Tobin et al. 2011). Failure to locate a mate at low densities is believed to be one of the most important Allee effects, even though there are few empirical studies demonstrating it (but see Kuussaari et al. 1998; Rhainds et al. 2015). Foraging efficiency may decline in several ways at low densities. Tree-killing bark beetles are not able to overcome the defenses of living trees at low densities and even wind-felled trees may still have some defenses left that require that several beetles colonize simultaneously. The breeding material for bark- and wood-boring insects at endemic level is an ephemeral resource that is spread out in the forest landscape and in new locations each year. Thus, when population densities decrease, the probability that e.g. a wind-felled tree will be found by an individual that starts to produce aggregation pheromones (that attract other individuals) also decreases. Predation pressure may increase at low population densities of the prey while at high prey densities the predators may be satiated. But, on the other hand non-native species may escape from natural enemies when invading new areas.

The minimum density that must be present to sustain a viable reproducing population is denoted the Allee threshold (Fig. 2). Below this threshold the population will decrease and eventually go extinct, or in the case of introductions, a new population will not be able to establish. Thus, identification of Allee thresholds, and which component Allee effects that contributes to them, is important for survey and eradication strategies (Berec et al. 2006; Liebhold et al. 2016). Early detection surveys should be focused to areas where the probability is highest that propagule pressure will exceed the Allee threshold and eradication programs need only to reduce population densities below the threshold (and extinction should proceed without further actions). In addition, knowledge about important component Allee effects may be utilized in management of invasive species (Berec et al. 2006).

1.4 The relationship between population density and patch size

Establishment of a founder population requires that the individuals are able to locate habitat patches. The probability of initial detection of a habitat patch can be expected to be positively correlated with habitat patch size, because of a larger geographical extent and a higher release of host plant volatiles from larger patches (Bowman et al. 2002). After colonization, emigration and population growth can be expected to modulate the initial density/patch size relationship. Patch size determines whether migration rates or demography dominate the relationship, migration being more important in small and growth in large patches (Hambäck and Englund 2005). When demography and emigration are important, species population densities are positively correlated to patch size (Bowman et al. 2002). Thus, larger patches should increase the probability of populations exceeding the Allee threshold, but few studies have considered this for invasive species. However, for species utilizing short-lived habitat patches (only one generation), only immigration contribute to density and negative relationship with patch size may thus be expected (Ranius et al. 2017).

2. Aims

To increase the knowledge of processes/mechanisms influencing the establishment and spread of non-native forest insects, such as the small spruce bark beetle *Ips amitinus*, Eichoff (Curculionidae), the larch bark beetle *Ips cembrae*, Herr (Curculionidae) and the larch longhorn beetle *Tetropium gabrieli*, Weise (Cerambycidae). Such knowledge may provide the forest sector with more efficient tools for reducing the negative consequences of invasive forest pests.

To develop a new strategy for delimiting the distribution of *I. amitinus* based on colonization data.

2.1 Questions addressed

The main questions addressed are

- Is *Tetropium gabrieli* attracted by the pheromone of species of the same genera and do host tree volatiles increase the attraction? (**paper I**)

- Does habitat availability affect the local population size of *Ips cembrae* and *Tetropium gabrieli,* two species with different life history traits, and how is the colonization probability related to the local population size? (**paper II**)

- How far south has *Ips amitinus* already spread in Sweden, what host tree preference does it have and does it influence the local bark- and wood-boring community? (**paper III**)

- How does occupancy change for *Ips amitinus* when approaching the southern range limit, and how do size of habitat patches, and proportion of spruce objects in patches, influence occupancy? (**paper IV**)

2.2 Main hypotheses

This thesis is based on five main hypotheses

- There is a high probability that also *Tetropium gabrieli* is attracted to E-fuscumol, the pheromone of *T. fuscum* (**paper I**)
- A minimum population density is required for colonization of breeding material by *I. cembrae* and *T. gabrieli* in new localities and this threshold value is influenced by component Allee effects related to species reproductive strategies and predation pressure at different population densities (**paper II**)
- There is positive relationship for non-native species between habitat patch size and probability of establishment (**paper II**)
- No large impact on native species by *Ips amitinus* is expected because of similarity in species composition in the invaded area with the native area **(paper III)**
- The distribution and spread of already established species may be strongly affected by Allee effects resulting in abrupt range limits (**paper IV**)

3. Study systems

Two study systems were used for this thesis. The **first** system, from southern Sweden, consists of two recently established non-native bark- and wood-boring beetle species on European larch, *Larix decidua* Mill (Pinaceae): the larch bark beetle *I. cembrae* and the larch longhorn beetle *T. gabrieli*. The **second** system, from northern Sweden, is constituted by the non-native small spruce bark beetle *I. amitinus*.

3.1 The southern system

Both *I. cembrae* and *T. gabrieli* are native to the European Alps, and are considered pest species because they occasionally kill living trees (Evans et al. 2004; Grégoire and Evans 2004; Grodzki 2008). Both species expanded their range as a result of larch species being planted outside their native range (Ravn 2012; Lindelöw et al. 2015; Lynikiene et al. 2021). Also, both species could still be viewed as being in the first and second phase of biological invasion: arrival of propagules to new areas and establishment of reproductive founder populations, which made them a good study system for the project.

Reasons for choosing this as a study system:

(1) As a result of a monitoring project between SLU and the Swedish Forest Agency we had some information about the species current distribution in Sweden.

(2) Bark beetles (represented by *I. cembrae*) and cerambycid beetles (by *T. gabrieli*) constitute two of the most important groups of regulated forest pest

insects (Council Directive 2000/29/EC), which make the chosen species a proxy for important quarantine species.

(3) They also represent two groups of species with different life history traits regarding production of pheromones used for mate finding and regarding egg-laying. Bark beetles must bore into the inner bark of their host trees to produce pheromones, and for the females to lay their eggs, which means that they encounter host tree defenses and that both sexes must be present in each colonized substrate. In contrast, cerambycid beetles do not need to bore into trees to produce pheromones or to lay their eggs. Bark beetles lay all their eggs in one or two trees while the mated cerambycid females may distribute their eggs in many different objects. These differences should influence how sensitive the species are to Allee effects.

(4) For both species commercial baits were available that could be used to estimate population density by monitoring with baited traps (Sweeney et al. 2010; Lindelöw et al. 2015; Schroeder et al. 2020).

3.1.1 *Ips cembrae*

Ips cembrae was first detected in Sweden in 2011 (Lindelöw et al. 2015). Prior to our study *I. cembrae* had only been recorded from Southern Sweden in the provinces of Skåne, parts of Halland and Blekinge, with only a few places where the species seemed to have established populations (localities where beetles were caught every year) (Lindelöw et al 2015). *Ips cembrae* is also known to reproduce in Japanese larch (*L. kaempferi* Lamb. Carr) (CABI 2019), and hybrid larch (*L. x eurolepis* A Henry) (Eppo 2023b) (Fig. 3). Hybrid larch is the most planted larch species in both Denmark and Sweden. Outside its native area *I. cembrae* is already established in UK (Alexander 2007), the Netherlands (Luitjes 1974), up to Denmark and southern Sweden (Ravn 2012; Lindelöw et al. 2015).

In 2019, an attack from *I. cembrae* on a larch stand in southern Sweden (Duveke, Skåne), resulted in about 50 standing living trees being killed (Bo-Göran Vennström, personal communication). This small outbreak is the first known attack of *I. cembrae* on standing trees in Sweden. Bark samples taken from eight of the recently killed trees revealed a low attack density (Dragos Cocos, unpublished data), which indicates that other stress factors, such as the draught from the previous year, might have facilitated the attack.

Figure 3. *Ips cembrae* early gallery system on a larch branch (left panel) and a fully colonized standing tree (right panel), from Southern Sweden.

3.1.2 *Tetropium gabrieli*

Tetropium gabrieli was first recorded in Sweden in 2007 (Ericson 2010), in the province of Blekinge. Prior to this thesis *T. gabrieli* had a somewhat more widespread distribution than *I. cembrae*, as it also occurred in south-eastern Småland (Lindelöw et al. 2015). Outside its native range, *T. gabrieli* is already spread in several countries in Europe: in UK towards West (Crawshay 1907), Denmark and southern Sweden towards North (Hansen 1996, Ericson 2010, Lindelöw et al. 2015) and most recent Lithuania towards East (Lynikiene et al. 2021). Not much is known about other possible host trees for *T. gabrieli*. Lynikienė et al. (2021) mention *Larix* spp. However, in our attraction experiment performed in southern Sweden (paper I), *T. gabrieli* successfully colonized and reproduced in *L. x eurolepis* (Schroeder et al. 2020) (Fig. 4).

Figure 4. *Tetropium gabrieli* larvae and larval galleries in the phloem of a hybrid larch tree from Southern Sweden.

3.1.3 Planting of non-native larch

Siberian larch was present in Scandinavia after the last glaciation, but it disappeared along the way (Bergstedt and Lyck 2007). The planting of larch in Scandinavia started in the middle of the 18th century and the European larch has been planted in small areas, mostly in parks and avenues (Skogforsk 2016). During the last decades, the planting of larch has increased a lot with a high interest for *Larix x eurolepis*, which is a hybrid between the European and the Japanese larch (Ekö et al. 2004), as it grows faster and it is more resistant to drought. However, in our southern study area larch only amounts for 0.2% of the total growing stock (Anonymous 2022) and in Denmark larch constitutes 3.4% of total growing stock (Nord-Larsen et al. 2020). Thus, it represents a very patchy habitat for the studied beetle species.

3.2 The northern system

The second study system consists of a non-native bark beetle, *I. amitinus*, a species that colonizes and reproduces in both Norway spruce (Fig. 5) and Scots pine, hereafter referred to as spruce and pine. They are the two dominant native tree species in Sweden. Thus its habitat is not at all as fragmented as for the two species on larch. However, its main breeding habitat in Sweden consists of logging waste like tops, thick branches and small trees in fresh clear-cuts and thinnings. Thus, its main habitat is short-lived (one generation) and patchy. The species can be viewed as in the third phase on the invasion curve, the spread. *Ips amitinus* is also able to kill living trees and thus is considered a pest species (Jurc and Bojović 2004; Grodzki 2009; Kerchev and Krivets 2021).

Figure 5. *Ips amitinus* gallery system from a spruce top from northern Sweden. Specific characteristics of its gallery system that differs from the gallery system of the native spruce bark beetle *I. typographus* are the big mating chambers and rather windy mother galleries. Two adult parents and a pupae can also be seen in the picture.

The arguments for choosing this system were:

(1) *Ips amitinus* is already well established in northern Sweden and spreading south and is thus an excellent system to study the expansion of the distribution area.
(2) It represents a good system for studying the impact on the native bark- and wood-boring beetle species.
(3) The arrival of *I. amitinus* in Sweden might increase the risk of bark beetle outbreaks when approaching areas where outbreaks of *I. typographus* occur and, at the same time, it represent a challenge for the plantations of the non-native lodgepole pine (*Pinus contorta* Douglas).

3.2.1 *Ips amitinus* northern range expansion

Ips amitinus started expanding its range towards north about 100 years ago. It was first detected in Estonia in the early 1930s (Zolk 1932), around 1950s in southern Finland (Nuorteva, 1956) and is now spread all over the country (Økland et al. 2019). Based on the rate of spread through Finland, it was predicted to reach Sweden around 1987 (Koponen 1980). As it is so often the case with invasive species, the exact arrival time into Sweden is not known (no surveys were conducted). The first record is from 2012 close to the border of Finland in the most northern part of Sweden (Lindelöw 2013), although the species most probably arrived earlier. In the native range *Ips amitinus* also colonizes other species of *Pinus* such as Swiss pine (*P. cembra L.*) and mountain pine (*P. mugo* Turra) (EPPO 2023a), blue spruce (*Picea pungens* Engelmann) (Kula et al. 2011). In Finland, *I. amitinus* attacks were also recorded in lodgepole pine, both in standing trees, heavily defoliated by sawflies, and in logs and logging residues (Annila et al. 1983). In Sweden, the fist attack on standing lodgepole pines was recorded in 2022 (Skogssytrelsen 2023).

Since *P. contorta* is already planted over 660.000 ha in Sweden, the arrival of *I. amitinus* might represent a new threat to it, especially as most of the *P. contorta* plantations are located south of the current range limit for *I. amitinus*. In a small field experiment conducted in 2016, in northern Sweden, *I. amitinus* successfully colonized and reproduced in cut *P. contorta* trees. Early in the spring of 2016, 30 standing trees (six spruces, seven pines and 17 lodgepole pines), were felled at ten different locations, east of the location where *I. amitinus* was initially found in 2012. The aim of this study was first to assess if *I. amitinus* is spread over larger areas, especially close to the Finish border. The second aim was to assess *P. contorta* susceptibility to *I. amitinus* attacks (hence the higher number of replicates). The results showed that the initial find from 2012 (Lindelöw 2013) was not just a random find, but that *I. amitinus* was spread over a larger area, as it was found in four of the 10 locations. The results also showed that *I. amitinus* successfully colonized both *P. abies* and *P. contorta*. However, no attacks were seen on *P. sylvestris* (Fig. 6).

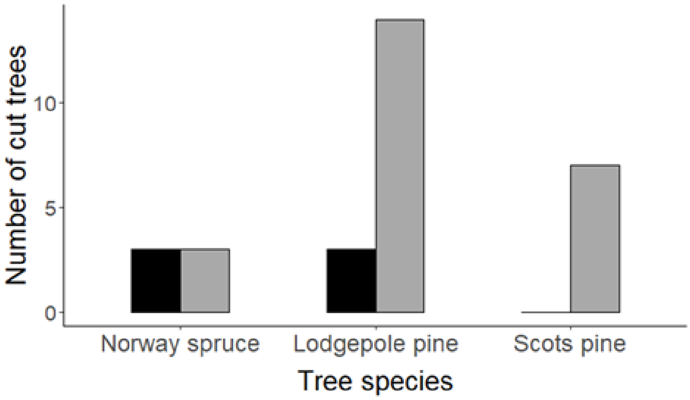

Fig 6. Comparison of different tree species susceptibility to attack and colonization from *Ips amitinus* field in a field experiment from 2016. Black bars = colonized trees, grey bars = uncolonized trees.

Lodgepole pine susceptibility to attacks from *I. amitinus* was also tested in a laboratory experiment from 2018, where 60 cm logs from *P. abies* (6 replicates), *P. contorta* (5 replicates) and *P. sylvestris* (5 replicates), were placed in rearing cages together with *I. amitinus* beetles. The results showed that *I. amitinus* successfully attacked and colonized logs from all three trees species and were able to complete a full life cycle (Fig. 7).

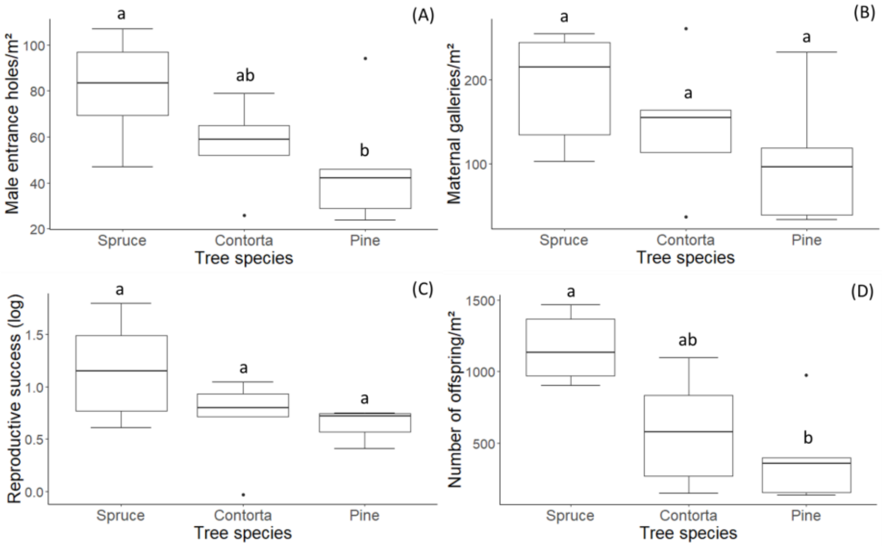

Figure 7. The results from the no-choice rearing experiment with *Ips amitinus*. Male entrance holes per m^2 bark (**A**), maternal galleries per m^2 bark (**B**), reproductive success (log transformed) (**C**), and number of offspring produced per m^2 bark (**D**). Means with different lowercase letters are significantly different at $p < 0.05$. Lodgepole pine seems to be intermediate between spruce and pine. The results for spruce and pine were already published in Cocos et al. 2023)

In 2022, the first standing lodgepole pines killed by *I. amitinus* was reported from northern Sweden. However, the attack was limited to six trees within the same forest stand (Skogsstyrelsen 2023). So far no standing spruces or pines killed by *I. amitinus* have been reported from Sweden.

4. Methods

The questions in this thesis were addressed by field experiments (**paper I and II**), laboratory experiments (rearing of beetles) (**paper I, II and III**), and field surveys (**papers III and IV**).

4.1 Field experiments

Pheromone baited traps (Fig. 9a) are often used for the early detection and surveillance of non-native beetles (Brockerhoff et al. 2006; Rassati et al. 2015). In **paper I,** we aimed at assessing the attraction of *T. gabrieli* to pheromone and host volatiles. Thus, a set of three different experiments were set up: In the first experiment, traps baited with *E*-fuscumol and host volatiles were compared to traps baited with host tree volatiles alone and unbaited traps. This was done to test whether *T. gabrieli* is attracted to *E*-fuscumol and host tree volatiles (ethanol and α-pinene), as demonstrated for other *Tetropium* species. In the second experiment, trap catches baited with E-fuscumol, to *E,Z*-fuscumol and *E,Z*-fuscumol acetate, all paired with host tree volatiles were compared. This was done to test the response of *T. gabrieli,* as well as the native *Tetropium* species, to *E,Z*-fuscumol and *E,Z*-fuscumol acetate. In the third experiment we wanted to determine whether the combination of *E*-fuscumol and host volatiles synergize attraction of *T. gabrieli.* This was done by comparing catches in traps baited with *E*-fuscumol alone, *E*-fuscumol plus host volatiles, and host volatiles alone.

The aim of **paper II** was to assess if habitat availability affects the local population size of *I. cembrae* and *T. gabrieli,* and also how the colonization probability is related to the local population size. Both pheromone baited traps and cut larch trees were included in a field experiment. The trapping experiment was conducted in 42 larch stands spread all over Denmark and southern Sweden (Fig. 8). In each locality two pheromone traps per species (Fig. 9a) were used to estimate local population size of *I. cembrae* and *T. gabrieli* respectively and the catches were later used in the analysis as a measure of the local population size. In 34 of the stands, colonization success of the two species was measured by felling five larch tree in each stand (Fig. 9b). All cut trees were debarked in the autumn and checked for presence and density of attacks of the two species.

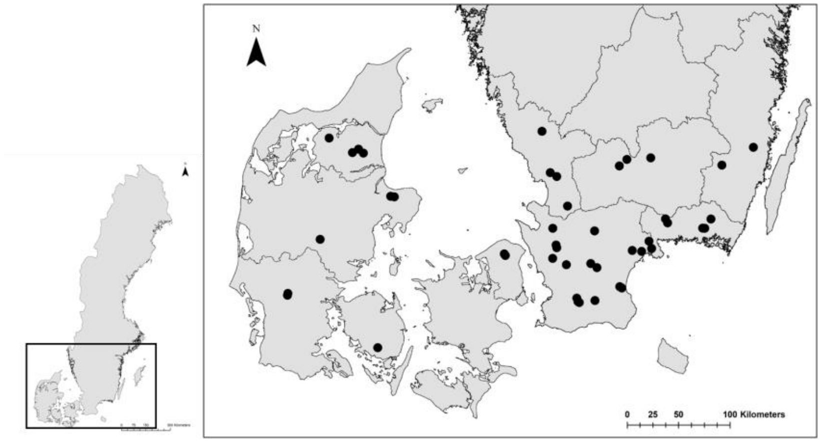

Figure 8. Map of Sweden and Denmark (left panel) with all the locations used for the pheromone trapping and colonization experiments in **paper II** (right panel). Each circle represents one location. (Figure adapted from **paper II**)

Figure 9. a) Pheromone trap type used for measuring the local population size and b) cut larch tree used for the colonization experiment from **paper I** and **II**.

4.1.1 Importance of habitat amount for the local population size of *Ips cembrae* and *Tetropium gabrieli*

To assess the relationship between the habitat amount and the local population size, for the localities included in **paper II,** all larch stands were mapped within two buffers with a radius of 500 m and 1 km around the focal larch stand. A maximum 1 km radius was used to avoid violating the independence of our observations. The mapping was based on forest owner stand registers, information from the Swedish Forest Agency and interpretation of aerial photographs. During summer the cut larch trees were inspected for colonization of *I. cembrae* and *T. gabrieli*. Dead standing trees, wind-felled trees or logging residues with a diameter > 5 cm were also inspected for presence, or absence of current year attacks in the focal stands.

4.1.2 Local population size and the probability of colonization

To assess the relationship between the local population size and the probability of colonization, five trees were cut in 34 of the 42 localities included in **paper II**. The trees were felled at a minimum distance of 30 m from each other and minimum 50 m away from the pheromone baited traps. All cut trees were checked for signs of attacks from *I. cembrae,* such as boring dust and entrance holes, both along the tree trunk and thick branches. The procedure was repeated at the end of each trap emptying. At the final inspection the bark from all trees without obvious signs of attack were peeled off with an axe, to check for possible larval galleries of *Tetropium* and *I. cembrae* attacks.

4.2 Field surveys

Field surveys (Fig.10) were used for both **paper III** and **paper IV**.

4.2.1 Field surveys as a method for assessing the species distribution area

In **paper III** we aimed at assessing the distribution range of *I. amitinus,* its host tree preference and potential impact on the native bark beetle community. We have developed a method for assessing if *I. amitinus* is present in a locality by checking conifer branches and tops on fresh clear-cuts for presence of the characteristic gallery system of the species. Based on the first field survey conducted in 2017 we know that the southern range limit of *I. amitinus* in Sweden was located close to Boden/Älvsbyn (**paper III**).

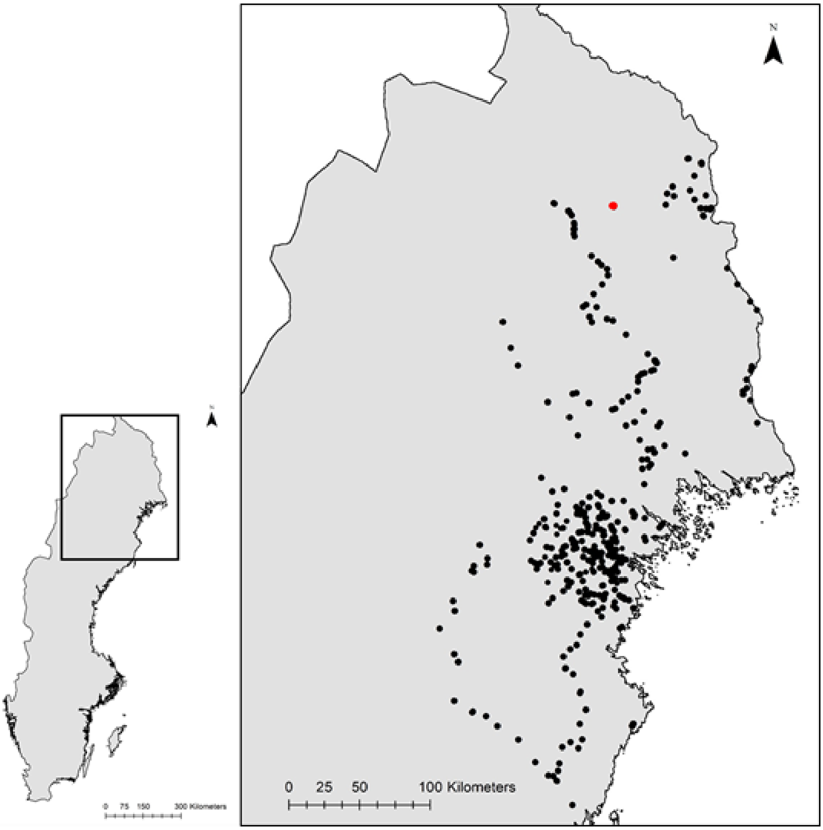

Figure 10. Map of Sweden showing the study area (left panel) and the locations used for the *Ips amitinus* field surveys from **paper III** and **IV**. Each circle represents a different location. Red circle represents the initial find from 2012

4.2.2 Delimiting survey for establishing the boundaries of the area in which a specific non-native species has established.

In **paper IV** the aim was to develop a delimiting survey of *I. amitinus* towards the range edge and how that is influences by the spatial distribution of habitat patches. Patch occupancy was measure at two different scales:

clear-cut level (larger scale) (Fig. 11) and wood object level (i.e. tops or branches) level (smaller scale) (Fig. 5). During 2018 and 2019, 217 fresh clear-cuts and thinnings (192 clear-cuts and 25 thinnings), located from the interior of the area of distribution towards the range limit (i.e. at different distances from the range limit), were inspected. During the 2018 survey, 30 objects were randomly selected and inspected for presence of *I. amitinus* in each locality. In 2019 we followed the same procedure but in case *I. amitinus* was not found in the first 30 objects a total 100 objects were inspected. In both years, for each of the inspected object, we recorded the tree species (spruce or pine) and presence/absence of *I. amitinus*.

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Figure 11. Example of location used for the field surveys for **paper III** and **IV**: fresh clear-cut from the 2018 survey.

4.3 Natural enemies

The effect of natural enemies on the non-native species were studied in **paper I** and **II.** The effect of parasitoid species on *T. gabrieli* was assessed through rearing experiments (**paper I** and **II**), by looking at the relationship between the number of emerging parasitoids and *T. gabrieli* from the colonized logs. The rate of parasitism was estimated for each log colonized by *T. gabrieli*. It was calculated as the number of emerging parasitoids divided by the sum of emerging *Tetropium* adults and parasitoids.

The effect of natural enemies on *I. cembrae* was assessed by looking at the relationship between *I. cembrae* and its predator *Thanasimus* spp. caught in the pheromone traps (**paper II**).

5. Results and discussion

The results comprised in this thesis show that all three studied non-native species have established in Sweden. The results also show that species specific life history traits influence their invasion process in different ways. In **paper I**, we show that *T. gabrieli* is attracted by fuscumol, a pheromone lure developed for the native *T. fuscum,* which then could be used for the field experiment in **paper II**. In **paper II,** I then looked at factors that influence the probability of colonization by comparing *I. cembrae* and *T. gabrieli,* two species with different life history traits. I show that the minimum population size required for colonization is influenced by both the amount of habitat in the landscape and the species life history traits. In **paper III,** I look at the spread of *I. amitinus*, a species that is already established. I show that it is already spread over large parts in northern Sweden, it has a preference for spruce and does not seem to have a strong negative impact on the native community of bark- and wood-boring beetles. In **paper IV** I first established the southern range limit and looked at factors that influence the probability of patch colonization and the proportion of colonized objects. I show that the distance to the range limit and proportion of spruce objects in habitat patches were positively related to both probability of patch colonization and proportion of colonized objects, while patch occupancy was negatively related to the patch size. We also show that the predation pressure is species specific, partly influenced by the species reproductive strategies (**paper I and II**). Below I examine these findings in more detail.

5.1 Pheromone trapping as a measure of the local population size

In **paper I,** we found that *T. gabrieli* is attracted to *E*-fuscumol, which makes it the fourth *Tetropium* species to be attracted by E-fuscumol (see Silk et al. 2007 and Sweeney et al. 2010 for the other species), and the first species that does not have spruce as the main host. This result enabled us to conduct the field experiment from **paper II** where we link the local population size to the colonization probability. In **paper I**, we also tested *T. gabrieli* attractiveness to two other variants of fuscumol, namely *E,Z*-fuscumol and *E,Z*-fuscumol acetate and the host volatiles α-pinene plus ethanol. As we expected catches from the two native *Tetropium* species (*T. fuscum* and *T. castaneum*), their results were compared with *T. gabrieli*. We found that traps baited with E-fuscumol plus host volatiles caught significantly higher number of beetles that traps baited only with host volatiles alone or the control traps. We found no difference in trap catches for any of the species when comparing traps baited with *E*-fuscumol and host volatiles versus traps baited with *E,Z*-fuscumol and host volatiles. However, *E,Z*-fuscumol and host volatiles caught higher number of native *Tetropium* species than traps baited with *E,Z*-fuscumol acetate and host volatiles. We also found that mean catches of *T. gabrieli* were significantly reduced when host volatiles were added to *E*-fuscumol, whereas mean catches of *T. castaneum* significantly increased. No effect on the mean catch was found for *T. fuscum*. The addition of host volatiles to pheromones seem the have a synergistic effect for the attraction of *T. castaneum* but not for *T. gabrieli* or *T. fuscum*. Thus, *T. gabrieli* and *T. fuscum* might respond to other more species specific host volatiles, like volatiles from *Larix* species for *T. gabrieli,* or more spruce specific volatiles for *T. fuscum* as shown by Sweeney et al. (2004). The knowledge gained from this study is an important asset. It will enable future projects and surveys to use pheromone traps to monitor and document the spread of *T. gabrieli* populations.

In **paper II,** I used trap catches as a measure of the local population size. I looked at factors that influence the size of the local population, and how the local population size influences the probability of colonization. I found that habitat availability influenced the local population size of both studied species. The size of the focal stand was the most important determinant for the local population size of *T. gabrieli* in both models including a 500 m and 1000 m buffer. On the other hand, the only important factor for the local population size of *I. cembrae* was the amount of larch within the 1000 m buffer zone. Other studies on bark beetles also showed a strong relationship between the amount of habitat and the local population size (Grodzki 2009; Schroeder 2013).

I found a positive relationship between the local population size and the probability of colonization of the cut trees for both *I. cembrae* and *T. gabrieli*. However, for *I. cembrae* a much higher local population size was required for colonization than for *T. gabrieli* and the difference might be explained by their different reproductive strategies. At low population densities the presence of component Allee effect for mate finding and foraging might influence the two studied species differently. Overall, the results from **paper I** and **II** show that both species are able to colonize and establish local populations in new areas with very fragmented habitat. This ability makes both species strong candidates for being included in early detection programs.

5.2 Delimiting the species distribution area

With these field surveys we aimed at finding how much *I. amitinus* has already spread, what is the preferred tree species and the effect it has on the native bark- and wood-boring beetles (**paper III**). Our aim was also to develop a method for recording species presence/absence based on colonized breeding material and find the current southern range limit and to study how occupancy was affected by the distance to the distribution limit (**paper IV**). We developed a fast and reliable method for recording the presence/absence, based on inspections of wood residues on clear-cuts and thinnings (**paper IV**). We also found that *I. amitinus* most probably has invaded Sweden from Finland (**paper IV**), is already well established in northern Sweden and has already spread over 200 km in Sweden. In **paper III,** I show that spruce is the preferred host tree when looking at the probability of attack (Fig. 12), which is in line with the results from **paper IV** where I show that both the probability of patch colonization and the proportion of colonized objects are higher is spruce dominated patches.

Figure 12. 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. (Figure reproduced from **paper III**).

I also show that the probability of patch colonization and the proportions of colonized objects are influenced by the distance to the distribution edge (**paper IV**). We show that both decrease when moving closer towards the distribution limit. This result was not due to either less spruce in the habitat patches or a decrease in the size of the patches, but rather a result of fewer dispersal sources close to the range limit.

I also show that the proportions of colonized habitat patches was still high at the range limit, which is an indication of an Allee effect that results in abrupt range limits. Lower probability of mate finding and the inability to forage for breeding material might contribute to this abrupt range limit. The result suggests that the species needs to build up its population levels over time, in order to spread further.

5.3 The effect of natural enemies on the non- native beetles' population density.

We found that the rate of parasitism on *T. gabrieli* from **paper I** was lower than the rate of parasitism reported in **paper II.** However, the rates of parasitism reported in both **paper I** and **II** were lower than the rate of parasitism reported in the natural range (Kenis and Hilszczanski 2004). Because we did not catch any parasitoid species in our traps (we did not expect that), we do not know their local population sizes. Such data could be a good indicator of how strong parasitoid pressure can be expected in our different study areas. However, our data tells us how the parasitoid species affect the reproductive success of *T. gabrieli*. The results show that there is no difference in the rate of parasitism between high and low population sizes of *T. gabrieli*. Hence, I would argue that we don't have an enemy pressure related Allee effect in this system.

When looking at the relationship between *I. cembrae* and its predator *Thanasimus* (**paper II**) I found no relationship between the local population densities of the two species, although the average catch was five times higher for *Thanasimus* compared to *I. cembrae*. This can be explained by *Thanasimus* being a generalist predator that preys on many other bark beetles (Schroeder 2001; Warzée and Grégoire 2006). Thus, a higher predation pressure can be expected at low population sizes of *I. cembrae* which might reduce colonization probability in locations with small *I. cembrae* populations. Thus, the component Allee effect of enemy pressure might influence colonization of *I. cembrae* negatively.

6. Conclusions

The results of this thesis show that non-native species can become a problem for the Swedish forests. I show that both *I. cembrae* and *T. gabrieli* have already established local population, but the rate of colonization of new areas was very different between them. *Ips cembrae* needs a much larger local population size to be able to colonize new areas compared to *T. gabrieli*. At the same time their further spread will also be limited by the availability of their host. On the other hand, *I. amitinus* is already well established and spread all over northern Sweden and has the potential to spread even further. It has almost unlimited host resources and their availability is only limited by the local forestry practices. It colonized both the native spruce and pine and the non-native lodgepole pine, with a preference for spruce. It will benefit in its expansion by the continuous creation of clear-cuts and thinnings and also by possibly reaching areas with more spruce. *Ips amitinus* is already the second most common species of bark beetles within its distribution range in Sweden in the conducted surveys.

In the southern system I also look at how the local population size is affected by the amount of habitat in the landscape. The results show that for *I. cembrae* the local population size is influenced only by the amount of larch within the 1000 m buffer zone. For *T. gabrieli*, the size of the focal stand was the most important determinant for the local population size in both models including the 500 m and 1000 m radius.

In the northern system we looked at how the colonization probability and the proportions of colonized objects differ when approaching the range limit. The results show that they both decrease with a decrease in distance towards the rage limit.

I also show that Allee effect, through components such as the ability to find mates, the ability to forage for food or the enemy pressure might have an effect on the probability of colonization especially in the areas with low population levels. At the same time this effect is species-specific.

Overall, this species-specific knowledge is very important when assessing the risk of invasions and should be integrated in risk assessments and monitoring programs. At the same time the use of an adequate method to quantify the distribution area of such species in fundamental.

References

Annila E, Heliövaara K, Puukko K, Rousi M (1983). Pests on lodgepole pine (*Pinus contorta*) in Finland. Communicationes Instituti Forestalis Fenniae, 115.

Anonymous (2022). Forest statistics 2022 - official statistics of Sweden, Swedish University of Agricultural Sciences, Umea 2022, 168 pp

Aukema JE, McCullough DG, Von Holle B, Liebhold AM, Britton K, Frankel SJ (2010). Historical Accumulation of Nonindigenous Forest Pests in the Continental United States, BioScience, 60(11): 886–897, https://doi.org/10.1525/bio.2010.60.11.5

Aukema, JE, Leung B, Kovacs K, Chivers C, Britton KO, Englin J, Frankel SJ, Haight RG, Holmes TP, Liebhold AM, McCullough DG, Von Holle B (2011). Economic impacts of non-native forest insects in the continental United States. PLoS One 6: e24587. https://doi.org/10.1371/journal.pone.0024587

Barbier, EB (2001). A note on the economics of biological invasions. Ecological Economics. 39: 197-202. https://doi.org/10.1016/S0921-8009(01)00239-7.

Bellard C, Cassey P, Blackburn TM (2016). Alien species as a driver of recent extinctions. Biological Letters 12(2): 20150623. https://doi.org/10.1098/rsbl.2015.0623

Berec L, Angulo E, Courchamp F (2006). Multiple Allee effects and population management. Trends in Ecology and Evolution 22: 185-191.

Bergstedt A, Lyck C (2007). Larch wood – a literature review. Forest & Landscape Working Papers no. 23-2007. Forest & Landscape Denmark

Blackburn, TM, Pyšek P, Bacher S, Carlton JT, Duncan RP, Jarošík V, Wilson JRU, Richardson DM (2011). A proposed unified framework for biological invasions. Trends in Ecology and Evolution, 26(7): 333–339, https://doi.org/10.1016/j.tree.2011.03.023

Blackburn TM, Essl F, Evans T, Hulme PE, Jeschke JM, Kühn I, et al. (2014). A Unified Classification of Alien Species Based on the Magnitude of their Environmental Impacts. PLoS Biol 12(5): e1001850. https://doi.org/10.1371/journal .pbio.1001850

Bowman J, Cappuccino N, Fahrig L (2002). Patch size and population density: The effect of immigration behavior. Conservation Ecology 6:9 https://doi.org/10. 5751/ES-00354-060109

Brockerhoff EG, Liebhold AM (2017). Ecology of forest insect invasions. Biological Invasions 19: 3141-3159. https://doi.org/10.1007/s10530-017-1514-1

Brockerhoff EG, Bain J, Kimberley M, Knižek M (2006). Interception frequency of exotic bark and ambrosia beetles (Coleoptera: Scolytinae) and relationship with establishment in New Zealand and worldwide. Canadian Journal of Forest Research, 36: 289-298. https://doi.org/10.1139/x05-250

Brockerhoff EG, Kimberley M, Liebhold AM, Haack RA, Cavey JF (2014). Predicting how altering propagule pressure changes establishment rates of biological invaders across species pools. Ecology. 95: 594–601. https://www.jstor.org/stable/43495182

CABI (2019). Ips cembrae (large larch bark beetle) datasheet. [Internet], Invasive Species Compendium. Wallingford, UK: CAB International, [https://www.cabi.org/isc/ datasheet/28820]. Accessed November 2022.

Chase KD (2016). Allee effects, host tree density and the establishment of invasive bark beetles. Thesis, University of Centerbury, New Zealand.

Chase KD, Kelly D, Liebhold AM, Brockerhoff EG (2023). The role of propagule pressure in experimental bark beetle invasions. Journal of Applied Ecology. 60: 342– 352. https://doi.org/10.1111/1365-2664.14326

Courchamp F, Macdonald DW (2001). Crucial importance of pack size in the African wild dog *Lycaon pictus*. Animal Conservation. 4: 169–174 https://doi.org/10.1017/S1367943001001196

Courchamp F, Clutton-Brock T, Grenfell B (1999). Inverse density dependence and the Allee effect. TREE 14: 405‑410. https://doi.org/10.1016/s0169-5347(99)01683-3

Courchamp F, Berec L, Gascoigne J (2008). Allee Effects in Ecology and Conservation. Oxford University Press, New York, USA.

Crawshay GA (1907). The life history of *Tetropium gabrieli*, Ws. – *T. fuscum*, Sharp – *T. crawshayi*, Sharp, etc. *Transactions of the Entomological Society of London*, Part II, 183–212.

Davies GD, Robert Britton J (2021). Consistency in the life history traits of four invasive *pseudorasbora parva* populations in Southern England. Journal of Applied Ichthyology. 37: 295– 302. https://doi.org/10.1111/jai.14175

Ducatez S, Shine R (2019). Life-history traits and the fate of translocated populations. Conservation Biology. 33: 853-860. https://doi.org/10.1111/cobi.13281

Ekö PM, Larsson-Stern M, Albrektson A (2004). Growth and yield of hybrid larch (Larix×eurolepis A. Henry) in Southern Sweden, Scandinavian Journal of Forest Research, 19: 320-328, https://doi.org/10.1080/02827580410024151

EPPO (2023a). *Ips amitinus*. EPPO datasheets on pests recommended for regulation. https://gd.eppo.int (accessed 2023-03-20)

EPPO (2023b). *Ips cembrae*. EPPO datasheets on pests recommended for regulation. https://gd.eppo.int (accessed 2023-03-22)

Ericson B (2010). Two species of beetles new to Sweden feeding on larch. (Två för Sverige nya skalbaggar (Coleoptera) som angriper lärk). Entomologisk Tidskrift 131: 131-136. (in Swedish, with English abstract).

Evans HF, Moraal LG, Pajares JA (2004). Biology, ecology and economic importance of Buprestidae and Cerambycidae. Bark and Wood Boring Insects in Living Trees in Europe, a Synthesis (ed. By F. Lieutier, K. R. Day, A. Battisti, J.-C. Grégoire and H. F. Evans). Kluwer Academic Publishers, Dordrecht.

Fauvergue X (2013). A review of mate-finding Allee effects in insects: From individual behavior to population management. Entomol. Exp. Appl. 146: 79–92. https://doi.org/10.1111/eea.12021

Gollasch, S. (2008). Is Ballast Water a Major Dispersal Mechanism for Marine Organisms? In: Nentwig, W. (eds) Biological Invasions. Ecological Studies, vol 193. Springer, Berlin, Heidelberg. https://doi.org/10.1007/978-3-540-36920-2_4

Grégoire J-C, Evans HF (2004) Damage and control of BAWBILT organisms – an overview. *Bark and Wood Boring Insects in Living Trees in Europe, a Synthesis* (ed. By F. Lieutier, K. R. Day, A. Battisti, J.-C. Grégoire and H. F. Evans). Kluwer Academic Publishers, Dordrecht.

Grevstad FS (1999). Experimental invasions using biological control introductions: the influence of release size on the chance of population establishment. Biological Invasion 1: 313-323. https://doi.org/10.1023/A:1010037912369

Grodzki W (2008). Ips cembrae Heer (Col.: Curculionidae, Scolytinae) in young larch stands - a new problem in Poland. Forstschutz Aktuell, 44: 8-9

Grodzki W (2009). Entomofauna of dying young spruces Picea abies (L.) Karst. in the area after forest decline in the Izerskie Mountains. Folia Forestalia Polonica 51: 161-170. https://doi.org/10.5281/zenodo.30731

Grünbaum D, Veit RR (2003). Black-browed albatrosses foraging on Antarctic krill: density-dependence through local enhancement? Ecology 84: 3265–3275. https://doi.org/10.1890/01-4098

Hambäck PA, and Englund G (2005). Patch area, population density and the scaling of migration rates: the resource concentration hypothesis revisited. Ecology Letters, 8: 1057-1065. https://doi.org/10.1111/j.1461-0248.2005.00811.x

Hansen M (1996). Katalog over Danmarks biller (Catalogue of the Coleoptera of Denmark). Entomologiske Meddelelser 64: 1-231

Hoffmann BD, Courchamp F (2016). Biological invasions and natural colonisations: are they that different? Neobiota. 29: 1–14. https://doi.org/10.3897/neobiota.29.6959

Hulme PE (2009). Trade, transport and trouble: managing invasive species pathways in an era of globalization. Journal of Applied Ecology. 46 (1): 10-8 https://doi.org/10.1111/j.1365-2664.2008.01600.x

Johnston EL, Piola RF, Clark GF (2009). The Role of Propagule Pressure in Invasion Success. In: Rilov G., Crooks J.A. (eds) Biological Invasions in Marine Ecosystems. Ecological Studies (Analysis and Synthesis), Vol 204. Springer, Berlin, Heidelberg.

Jurc M, Bojović S (2004). Bark beetle outbreaks during the last decade with special regard to the eight-toothed bark beetle (Ips amitinus Eichh.) outbreak in the Alpine region of Slovenia. In: Csóka, G, Hirka, A. and Koltay, A. (eds.) 2006: Biotic damage in forests. Proceedings of the IUFRO (WP7.03.10) Symposium held in Mátrafüred, Hungary, September 12-16, 2004.

Kenis M, Hilszczanski J (2004) Natural enemies of Cerambycidae and Buprestidae infesting living trees. *Bark and Wood Boring Insects in Living Trees in Europe, a Synthesis* (ed. by F. Lieutier, K. R. Day, A. Battisti, J.-C. Grégoire and H. F. Evans). Kluwer Academic Publishers, Dordrecht.

Kerchev IA, Krivets SA (2021). An attack of Ips amitinus (Coleoptera: Curculionidae: Scolytinae) on arboretum in West Siberia: new host of invasive bark beetle among exotic conifers. Journal of Asia-Pacific Entomology. 24: 148-152. https://doi.org/10.1016/j.aspen.2021.03.003

Koponen M (1980). Distribution of Ips amitinus (Eichhoff) (Coleoptera, Scolytidae) in Finland in 1974-1979. Notulae Entomologicae 60: 223-225.

Kramer AM, Dennis B, Liebhold AM, Drake JM (2009). The evidence for Allee effects. Population Ecology 51: 341-354. https://doi.org/10.1007/s10144-009-0152-6

Kula E, Kajfosz R, Polívka J (2011). Cambioxylophagous fauna developing on logging residues of blue spruce (*Picea pungens* Engelmann). Journal of Forest Science. 57: 24-33. https://doi.org/10.17221/3/2010-JFS

Kuussaari M, Saccheri IJ, Camara M, Hanski I (1998). Allee effect and population dynamics in the Glanville fritillary butterfly. Oikos, 82: 384-392.

Liebhold AM, Brockerhoff EG, Garrett LJ, Parke JL, Britton KO (2012). Live plant imports: the major pathway for forest insect and pathogen invasions of the US. Frontiers in Ecology and the Environment. 10: 135-143. https://doi.org/10.1890/110198

Liebhold AM, Berec L, Brockerhoff EG, Epanchin-Niell RS, Hastings A, Herms DA, Kean JM, McCullough DG, Suckling DM, Tobin PC, Yamanaka T (2016). Eradication of invading insect populations: from concepts to applications. Annual Review of Entomology 61: 335-352. https://doi.org/10.1146/annurev-ento-010715-023809

Liebhold AM, Brockerhoff EG, Kalisz S, Nunez MA, Wardle DA, Wingfield MJ (2017a). Biological invasions in forest ecosystems. Biological Invasions. 19: 3437-3458. https://doi.org/10.1007/s10530-017-1458-5

Liebhold AM, Brockerhoff EG, Kimberley M (2017). Depletion of heterogeneous source species pools predicts future invasion rates. Journal of Applied Ecology. 54: 1968-1977. https://doi.org/10.1111/1365-2664.12895

Liebhold AM, Kean JM (2018). Eradication and containment of non-native forest insects: successes and failures. Journal of Pest Sciences. 92(1): 83-91. https://doi.org/10.1007/s10340-018-1056-z.

Liebhold AM, Tobin P (2008). Population ecology of insect invasions and their management. Annual Review of Entomology 53: 387-408. https://doi.org/10.1146/annurev.ento.52.110405.091401

Lindelöw Å (2013). Väntad barkborre funnen i Sverige - fynd av *Ips amitinus* (Coleoptera, Scolytinae). [*Ips amitinus* (Coleoptera, Scolytinae) expected and found in Sweden.]. Entomologisk Tidskrift 134: 203-206.

Lindelöw Å, Isacsson G, Ravn HP, Schroeder M (2015). *Tetropium gabrieli* and *Ips cembrae* (Coleoptera; Cerambycidae and Curculionidae) – invasion of two potential pest species on larch in Sweden. Entomologisk Tidskrift 136:103-112.

Luitjes J (1974) *Ips cembrae*, a new noxious forest insect in the Netherlands. Nederlands Bosbouw Tijdschrift 46(11): 244-246

Lynikiene J, Tamutis V, Gedminas A, Marciulynas A, Menkis A (2021). First Report of the Larch Longhorn (*Tetropium gabrieli* Weise, Coleoptera: Cerambycidae: Spondylidinae) on *Larix spp*. in Lithuania. Insects. 12: 911. https://doi.org/10.3390/insects12100911

Meurisse N, Rassati D, Hurley BP, Brockerhoff EG, Haack RA (2019). Common pathways by which non-native forest insects move internationally and domestically. Journal of Pest Sciences. 92:13–27 https://doi.org/10.1007/s10340-018-0990-0

Musgrave J, Girard A, Lutscher F (2015). Population spread in patchy landscapes under a strong Allee effect. Theoretical Ecology, 8: 313-326. https://doi.org/10.1007/s12080-015-0252-1

Nord-Larsen T, Johannsen VK, Riis-Nielsen T, Thomsen IM, Jørgensen BB (2020). Skovstatistik 2019: Forest statistics (2019) Frederiksberg: Institut for Geovidenskab og Naturforvaltning, Københavns Universitet.

Nuorteva M (1956). *Ips amitinus* Eichh. kaarnakuoriaisen esiintymisesta Suomessa. Ref.: Uber das Auftreten des *Ips amitinus* Eichh. (Col., Scolytidae) in Finnland. Annales Entomologici Fennici, 22: 168–170.

Økland B, Flø D, Schroeder M, Zach P, Cocos D, Martikainen P, Siitonen J, Mandelshtam MY, Musolin DL, Neuvonen S, Vakula J, Nikolov C, Lindelöw Å, Voolma K (2019). Range expansion of the small spruce bark beetle *Ips amitinus*: a newcomer in northern Europe. Agricultural and Forest Entomology. 21: 286-298. https://doi.org/10.1111/afe.12331

Palamara GM, Carrara F, Smith MJ, Petchey OL (2016). The effects of demographic stochasticity and parameter uncertainty on predicting the establishment of introduced species. Ecology and Evolution. 6: 8440–8451 https://doi.org/10.1002/ece3.2495

Parmesan C, Yohe G (2003). A globally coherent fingerprint of climate change impacts across natural systems. Nature 421: 37-42. https://doi.org/10.1038/nature01286

Ranius T, Mestre L, Bouget C, Schroeder M (2017). Fragmentation effects on dead wood-dependent species associated with disturbed forest habitats: implications for stump harvesting, Scandinavian Journal of Forest Research. 32: 260-267. https://doi.org/10.1080/02827581.2016.1229021

Rassati D, Faccoli M, Petrucco Toffolo E, Battisti A, Marini L (2015). Improving the early detection of alien wood-boring beetles in ports and surrounding forests. Journal of Applied Ecology. 52: 50–58. https://doi.org/10.1111/1365-2664.12347

Ravn HP (2012). Stor laerkebarkbille I Danmark – opdatering af udbredelsen (in Danish) – Skoven 4: 194-196

Rhainds M, Heard SB, Hughes C, MacKinnon W, Porter K, Sweeney J, Silk P, DeMerchant I, Maclean S, Brodersen G (2015). Evidence for mate-encounter Allee effect in an invasive longhorn beetle (Coleoptera: Cerambycidae). Ecological. Entomology. 40: 829–832. https://doi.org/10.1111/een.12255

Roy HE, Lawson Handley LJ, Schönrogge K, Poland RL, Purse BV (2011). Can the enemy release hypothesis explain the success of invasive alien predators and parasitoids? BioControl 56: 451–468. https://doi.org/10.1007/s10526-011-9349-7

Sauvard D, Branco M, Lakatos F, Faccoli M, Kirkendall L (2010). Weevils and Bark Beetles (Coleoptera, Curculionoidea). Chapter 8.2. BioRisk 4: 219-266. https://doi.org/10.3897/biorisk.4.64

Schroeder LM (2001). Prolonged development time of the bark beetle predator *Thanasimus formicarius* (Col.: Cleridae) in relation to its prey species *Tomicus piniperda* (L.) and *Ips typographus* (L.) (Col.: Scolytidae). Agricultural and Forest Entomology. 1: 127-135. https://doi.org/10.1046/j.1461-9563.1999.00018.x

Schroeder LM (2013). Monitoring of *Ips typographus* and *Pityogenes chalcographus*: influence of trapping site and surrounding landscape on catches. Agricultural and Forest Entomology 15: 113-119. https://doi.org/10.1111/afe.12002

Schroeder M, Cocoş D, Johansson H, Sweeney J (2020). Attraction of the cerambycid beetles *Tetropium gabrieli*, *T. castaneum* and *T. fuscum* to pheromones and host tree volatiles. Agricultural and Forest Entomology 23: 203-211. https://doi.org/10.1111/afe.12422

Silk PJ, Sweeney J, Wu J, Price J, Gutowski JM, Kettela EG (2007). Evidence for a male-produced pheromone in Tetropium fuscum (F.) and Tetropium cinnamopterum (Kirby) (Coleoptera: Cerambycidae). Naturwissenschaften 94: 697–701. https://doi.org/10.1007/s00114-007-0244-0

Simberloff D (2009). The role of propagule pressure in biological invasions. Annual Review of Ecology, Evolution, and Systematics. 40: 81-102. https://doi.org/10.1146/annurev.ecolsys.110308.120304

Skogforsk (2016). Förädling av lärk i Sverige – Kunskapsläge och material. Genetic improvement of larch in Sweden – Knowledge status and seed materials. Arbetsrapport 895.

Skogsstyrelsen (2023). Skogsskador I Sverige 2022. Rapport 2023/04. (In Swedish with English abstract).

Sweeney JD, Groot P, Macdonald L, Smith S, Cocquempot C, Kenis M, Gutowski JM (2004). Host volatile attractants and traps for detection of *Tetropium fuscum* (F.), *Tetropium castaneum* L., and other longhorned beetles (Coleoptera: Cerambycidae). Environmental Entomology. 33: 844–854. https://doi.org/10.1603/0046-225X-33.4.844

Sweeney JD, Silk PJ, Gutowski JM, Wu J, Lemay MA, Mayo PD, Magee DI (2010). Effect of chirality, release rate, and host volatiles on response of *Tetropium fuscum* (F.), *Tetropium cinnamopterum* (Kirby), and *Tetropium castaneum* (L.) to the aggregation pheromone, fuscumol. Journal of chemical ecology. 36(12): 1309–1321. https://doi.org/10.1007/s10886-010-9876-1

Tobin PC, Berec L, Liebhold AM (2011). Exploiting Allee effects for managing biological invasions. Ecology Letters. 14: 615-624. https://doi.org/10.1111/j.1461-0248.2011.01614.x

Tobin PC, Kean JM, Suckling DM, McCullough DG, Herms DA, Stringer LD (2014). Determinants of successful arthropod eradication programs. Biological Invasions. 16(2): 401-414. https://doi.org/10.1007/s10530-013-0529-5

Travis JMJ, Dytham C. (2002). Dispersal evolution during invasions. Evolutionary Ecology Research. 4: 1119–1129.

Walter JA, Firebaugh AL, Tobin PC, Haynes KJ (2016). Invasion in patchy landscapes is affected by dispersal mortality and mate-finding failure. Ecology. 97(12): 3389–3401. https://www.jstor.org/stable/44082201

Walther GR, Roques A, Hulme PE, et al. (2009). Alien species in a warmer world: risks and opportunities. Trends in Ecology and Evolution. 24(12): 686-693 https://doi.org/10.1016/j.tree.2009.06.008

Warzée N and Grégoire JC (2006). *Thanasimus formicarius* (Coleoptera: Cleridae): Why a Large Range of Prey for a Specialized Predator? In Proceeding: IUFRO Kanazama 2003. Forest Insect Dynamics and Host Influence 16-18.

Wilson JRU, García-Díaz P, Cassey P, Richardson DM, Pyšek P, Blackburn TM (2016). Biological invasions and natural colonisations are different – the need for invasion science. NeoBiota. 31: 87-98. https://doi.org/10.3897/neobiota.31.9185

Zolk K (1932). Kodumaa ürasklased (Ipidae) ühes lühikese ülevaatega nende bionoomiast ja levimisest Eestis (Die Borkenkäfer (Ipidae) Estlands mit kurzer Berücksichtigung ihrer Bionomie und Verbreitung). – Eesti Metsanduse Aastaraamat (Estländisches forstwirtschaftliches Jahrbuch), VI. Tartu: 127-176 +36 Abbildungen.

Popular science summary

Forests provide many ecosystem services. According to Food and Agriculture Organization of the United Nations (FAO), forests cover 31 percent of the total land area. In the last decades the number of non-native species establishing worldwide has dramatically increased, which could be a threat the ecosystem services provided by forests.

The first part of this thesis focused on the establishment of two non-native beetle species in southern Sweden, the larch bark beetle (*Ips cembrae*) and the larch longhorn beetle (*Tetropium gabrieli*), both having the European larch (*Larix decidua*) as the main host. However, the type of larch most commonly planted in southern Sweden is hybrid larch, (*Larix x eurolepis*). The two species constitute an excellent system to study factors, such as colonization and reproduction, which affect the establishment phase.

The second part of the thesis focused on the small spruce bark beetle (*Ips amitinus*) that has invaded northern Sweden from Finland. It mainly attacks and colonizes wood residues from both Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*), both native tree species. *Ips amitinus* is considered a secondary species (species that do not have the ability to kill healthy trees under normal conditions), but that becomes possible when the trees are weakened by other factors such as severe drought. The species is already well established in northern Sweden and spreading south and is an excellent system to study the beetles spread in the landscape.

The aim of this thesis was to assess their current distribution in Sweden and evaluate the factors that influence their local colonization and further spread

I found that all three species have established local populations and are slowly spreading to new areas. Their ability to colonize and establish new populations is influenced by their life history characteristics. Overall my findings suggest that studying invasions of non-native species should be of prime importance and the species specific life history characteristics should be considered when planning national monitoring programs.

Populärvetenskaplig sammanfattning

Skogar förser oss med många ekosystemtjänster. Enligt Förenta nationernas fackorgan för jordbruk, skogsbruk och fiske (FAO), så består 31 procent av jordens totala landyta av skog. De senaste decennierna har antalet icke inhemska arter som etablerat sig på nya platser ökat dramatiskt. Spridning av icke inhemska arter kan ha förödande konsekvenser för våra skogars och därmed deras tillhandahållande av ekosystemtjänster och dessutom leda till ekonomiska förluster. För att minska risken för detta är det viktigt att studera hur icke inhemska arter sprider sig till och etablerar sig på nya platser.

Den första delen av denna avhandling handlar om på etablering av två icke inhemska skalbaggsarter i södra Sverige: lärkborre (*Ips cembrae*) och lärkbock (*Tetropium gabrieli*). Båda dessa arter lever på trädslaget lärk (*Larix* sp.), ett trädslag som blir allt vanligare inom skogsbruket i södra Sverige. Det är därför viktigt att studera vilka faktorer som påverkar etableringen av dessa skalbaggar.

Den andra delen av avhandlingen handlar om liten granbarkborre (Ips amitinus), en art som har spridit sig till Sverige österifrån via Finland. Den lilla granbarkborren lever främst på grenar och dylikt av tall och gran, och anses vara en så kallad sekundär skadegörare – d.v.s. en art som på egen hand inte kan döda friska träd. Den kan dock bli problematisk om träden är försvagade på grund av till exempel torka eller när den sprider sig till ett varmare klimat. Eftersom arten etablerat sig i norra Sverige och fortsätter sprida sig söderut är det viktigt att studera vilka faktorer som är viktiga för hur arter sprider sig

Jag kom fram till att alla tre arter är etablerade lokalt (i Sverige) och är på spridning. Arternas förmåga att sprida sig till och etablera sig till en ny plats påverkas av deras specifika egenskaper så som fortplantningsstrategi och förmåga att hitta föda. Mina resultat pekar på att det är viktigt att studera spridning och etablering av icke inhemska arter och att det är viktigt att ta hänsyn till deras specifika egenskaper när övervakningsprogram utformas.

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Attraction of the cerambycid beetles *Tetropium gabrieli*, *T. castaneum* and *T. fuscum* to pheromones and host tree volatiles

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Abstract

1 *Tetropium gabrieli* is native to the European Alps where it breeds in European larch and may be an important pest during drought periods by killing trees. It has spread to larch plantations in several European countries including Sweden.

2 In trapping studies conducted in Sweden, we tested whether *T. gabrieli* was attracted to *E*-fuscumol, *E,Z*-fuscumol, *E,Z*-fuscumol acetate and the host volatile combination of α-pinene plus ethanol. We also compared its response with those of the native congeners, *T. fuscum* and *T. castaneum*.

3 All three *Tetropium* species were caught in significantly higher numbers in traps baited with *E*-fuscumol plus host volatiles than in traps baited with host volatiles alone or in unbaited traps.

4 There was no difference in catch of any *Tetropium* species between traps baited with *E*-fuscumol plus host volatiles versus traps baited with *E,Z*-fuscumol plus host volatiles, but the latter treatment caught more *T. fuscum* and *T. castaneum* than did *E,Z*-fuscumol acetate plus host volatiles.

5 The addition of *E*-fuscumol to host volatile-baited traps significantly reduced mean catch of *T. gabrieli,* significantly increased mean catch of *T. castaneum,* and had no significant effect on catch of *T. fuscum.* Mean catch of all three species was significantly greater in traps baited with *E*-fuscumol alone than in traps baited with host volatiles alone.

6 All three species were caught from May to August. The median date of captures was about 2 weeks earlier for *T. fuscum* compared with the other two species.

Keywords ethanol, flight periods, fuscumol, fuscumol acetate, *Larix*, *Tetropium* emergence, *Tetropium* parasitoids, trapping, α-Pinene.

Introduction

The cerambycid beetle *Tetropium gabrieli* Weise (subfamily Spondylidinae) is native to the Alps in central Europe where it breeds in European larch, *Larix decidua* Mill. The species also reproduces in other larch species non-indigenous to Europe and is considered to be a secondary pest, breeding mainly in newly felled trees or weakened standing trees. However, in some regions in Europe *T. gabrieli* is classified as an important pest species during hot and dry summers (Gorius, 1955; Evans *et al.*, 2004). Thus, the economic importance of this species may increase in the future as a result of climate change increasing the frequency of prolonged droughts during summers.

The planting of larch outside the natural distribution of European larch has enabled *T. gabrieli* to expand its distribution and establish in many countries in Europe (Sama & Löbl, 2010). In Sweden, it has been reported several times from imported larch wood (Lundberg, 1986, 1988; Lundberg & Pettersson, 1997) and in 2007 *T. gabrieli* was detected infesting larch trees in a forest adjacent to a port in the province of Blekinge in southeastern Sweden (Ericsson, 2010). Surveys conducted from 2009 to 2011 using spring-felled larch trees demonstrated the beetle was present in several locations in southeastern Sweden but absent in more northern or western locations (Lindelöw *et al.*, 2015). Although this survey method worked, it is practical

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only in larch stands, requires permission to cut trees, is quite laborious, and requires either splitting of logs to remove larvae or incubation of logs to collect emerging adults for reliable species identification. A more cost-efficient method would be to capture adult *T. gabrieli* in attractant-baited traps. In recent years, a trap lure was developed for the congener *T. fuscum* (F.), a species native to Europe but which has established in Eastern Canada where it has caused considerable tree mortality among native spruce species (Silk *et al.*, 2007; Sweeney *et al.*, 2004, 2006, 2010). Traps are baited with three lures: racemic (*E*)-6,10-dimethyl-5,9-undecadien-2-ol (fuscumol), ethanol, and a blend of monoterpenes that approximates those sampled from bark of stressed spruce, i.e., racemic α-pinene, (−)-β-pinene, (+) 3-carene, (+) limonene and α-terpinolene. Male *T. fuscum* emit *S*-(*E*)-fuscumol but the synthetic racemic mixture of *R*- and *S*-(*E*)-fuscumol is as attractive as the pure *S*, and the combination of spruce host volatiles and racemic fuscumol synergizes attraction of both sexes of *T. fuscum* (Sweeney *et al.*, 2010). In addition to *T. fuscum*, *T. cinnamopterum* Kirby (native to North America) males also emit *S*-(*E*)-fuscumol and males and females of *T. cinnamopterum* and *T. castaneum* (L.) (native to Europe) are attracted to the combination of fuscumol and host volatiles (Silk *et al.*, 2007; Lemay *et al.*, 2010; Sweeney *et al.*, 2010). Thus, there is a high probability that additional *Tetropium* species may also be attracted to *E*-fuscumol and thus we wanted to test this for *T. gabrieli*.

We also wanted to test response of *T. gabrieli* to the structurally related (*E*)-6,10-dimethyl-5,9-undecadien-2-yl acetate (termed fuscumol acetate). Fuscumol, fuscumol acetate, and geranyl acetone [(*E*)-6,10-dimethyl-5,9-undecadien-2-one] are attractive to several species of longhorn beetles in the subfamily Spondylidinae (Silk *et al.*, 2007; Halloran *et al.*, 2018; Žunič-Kosi *et al.*, 2019) and Lamiinae (Mitchell *et al.*, 2011; Hughes *et al.*, 2013, 2016; Hanks & Millar 2016; Meier *et al.*, 2016, 2020; Halloran *et al.*, 2018). Because the fuscumol/fuscumol acetate motif appears to be common in Spondylidinae, we hypothesized that fuscumol acetate might be attractive to *T. gabrieli*. Finally, we wanted to compare the efficacy of racemic *E*-fuscumol to racemic *E,Z*-fuscumol and *E,Z*-fuscumol acetate, because the latter compounds are simpler and cheaper to synthesize than *E*-fuscumol, using *E,Z*-geranylacetone as the starting material (Mitchell *et al.*, 2011).

Although the main focus of the study was *T. gabrieli*, we also expected catches of *T. fuscum* and *T. castaneum* which both are common all over Sweden (Ehnström & Holmer, 2007). The following questions were addressed by the study: (i) Is *T. gabrieli* attracted to fuscumol or fuscumol acetate? (ii) Does addition of the host tree volatiles α-pinene and ethanol increase attraction of *T. gabrieli* compared with pheromone alone? (iii) Does the phenology of adult flight differ among the three species? (iv) How long is the emergence period of *T. gabrieli*? (v) What parasitoids species are associated with *T. gabrieli*? The host volatile α-pinene was chosen because it is one of the major monoterpenes in larch (Holm & Hiltunen, 1997; Ruuskanen *et al.*, 2007; Kajos *et al.*, 2013) while ethanol is released from stressed or decayed trees. Phenology of flight, emergence period and parasitoids are of interest for understanding the invasion biology of the species.

Materials and methods

Study area

The study was conducted in a 4.3 × 3.3 km (1440 ha) rectangular area in south-eastern Sweden (56°19′13.8"N 14°49′32.2″E, province of Blekinge) in 2017 in which *T. gabrieli* had been detected in earlier surveys using cut larch trees (Lindelöw *et al.*, 2015). Managed forest stands comprised 986 ha (72.6%) of the study area, including 60.5 ha (4.2% of study area) of hybrid larch stands, *Larix x eurolepis* A. Henry, (13 stands including one fresh clear-cut) and 925.5 ha (68.4% of study area) of Norway spruce, *Picea abies* (L.) H. Karst., and Scots pine, *Pinus sylvestris* L., dominated stands. The remainder of the study area included pastures and swamps (20.8%) and lakes (6.6%). In a 1.2 km buffer zone (2420 ha) around the study area, there was only one larch stand (4.6 ha, 0.2% of buffer area). The proportion of larch in the study area is much higher than the average for southern Sweden which is 0.1% of the total growing stock including all tree species (Anonymous, 2016).

Lures

Racemic *E*-fuscumol, racemic *E,Z*-fuscumol, and racemic *E,Z*-fuscumol acetate (99% purity) lures were purchased from Sylvar Technologies Inc. (Fredericton, New Brunswick, Canada). The lures were natural red rubber septa (sleeve stoppers), 5 × 11 mm (OD) (Wheaton, Millville, NJ) loaded with 50 mg of fuscumol or fuscumol acetate; release rates were 0.5–2.0 mg/day at 20 °C (measured indoors by weight loss). The host volatiles ethanol (95%) and (−)-α-pinene (98%, optical purity ee: ≥81%, GLC, Aldrich) were released from separate, sealed 50 ml PVC-containers filled with 30 ml of compound, with holes bored through the sides of the container just below the lid. Ethanol dispensers had four 0.5 mm-holes and (−)-α-pinene dispensers had eight 2 mm-holes. Release rates (determined by weight loss in the laboratory at 20 °C) were 140 mg/day for ethanol and 940 mg/day for (−)-α-pinene. We also measured host volatile release rates in the field as follows. At each trap check, the dispensers were refilled if more than half of the compound had been released and the amount that was added to each dispenser was recorded. By this method, we estimated average release rates in the field of 272 and 1605 mg/day for ethanol and (−)-α-pinene, respectively. However, this is an underestimate of the mean outdoor release rate of (−)-α-pinene because about half of the (−)-α-pinene dispensers were found empty during trap checks, i.e., all 30 ml dispensers had volatilized since the previous trap check 1–3 weeks earlier. This means that some traps were releasing no (−)-α-pinene for at least a portion of the experimental trapping period.

Field experiments

Three trapping experiments were conducted sequentially with the same traps, each with three treatments. In all three experiments, we used α-pinene and ethanol as host volatiles, released from the dispensers described above. The first experiment, conducted 8 May–13 June, compared catch of *T. gabrieli* in traps baited with *E*-fuscumol plus host volatiles, host volatiles alone, or left unbaited. The aim of this experiment was to test whether *T. gabrieli* was attracted by the combination of *E*-fuscumol and host tree volatiles as demonstrated for other *Tetropium* species. The second experiment, conducted 13 June–29 June, compared *E*-fuscumol, *E,Z*-fuscumol, and *E,Z*-fuscumol acetate, each paired with host volatiles. The objective here was to compare the response of *T. gabrieli*, as well as the native *Tetropium* species, to *E,Z*-fuscumol and *E,Z*-fuscumol acetate. The third experiment, conducted 29 June–12 September, compared catches in traps baited with *E*-fuscumol alone, *E*-fuscumol plus host volatiles, and host volatiles alone. Here, our objective was to determine whether the combination of fuscumol and host volatiles synergized attraction of *T. gabrieli* as has been observed with *T. fuscum* and *T. castaneum* (Sweeney *et al.*, 2010). In addition, because traps baited with *E*-fuscumol plus host volatiles were included in all three experiments, this allowed us to compare the seasonal phenology of adults of the three *Tetropium* species.

Treatments were replicated 12 times in a randomized complete block design, with re-randomization between experiments. The 12 blocks were distributed among 10 sites, 9 of which consisted of larch stands (each with one block) and one which was a fresh larch clear-cut (with three blocks). The average size of the larch stands was 4.6 ha (SE = 0.7 ha) while the clear-cut was 11.8 ha. Minimum distance between sites was 300 m and maximum distance 3700 m. Traps were spaced 50 m apart within blocks and at least 10 m from the edge of the stands.

Beetles were caught in 12-unit multiple funnel traps (ECONEX MULTIFUNNEL-12®, Econex SL) hung from 1.8 m wooden poles with 50% solution of ethylene glycol in the collecting cups. The traps were emptied seven times (exp. 1: twice; exp. 2: twice; exp. 3: three times) with intervals from 1 to 3 weeks (except for the last one with almost 5 weeks).

Tetropium adults were determined to species based on Pfeffer (1995) and Ehnström and Holmer (2007). The beetles were sexed by inspection of the tip of the abdomen. As is common in many Cerambycidae, a portion of the sixth abdominal tergite is visible beyond the pygidium of males (Yanega, 1996), whereas the female's pygidium is flatter and broader and the tip of the ovipositor is often visible.

On May 8–9 2017, we felled a larch tree in each of five larch stands in which we had traps and on September 11–14, we inspected them for colonization by *Tetropium* by debarking parts of the trunk every 3 m. In addition, 2 m logs were cut from the three trees that were colonized by *Tetropium* and also from a colonized wind-felled tree. The logs were stored outside the laboratory in Uppsala. On March 13, two 60 cm stem sections were cut from each of the logs and ends were waxed. Each stem section was placed in a separate cage in a climate chamber (20.4 °C, 18 h day-length) and checked each day (except weekends) for emerging insects for 78 days. On April 9, additional two 60 cm stem sections were cut from logs of the same four trees and handled in the same way as the first batch of stem sections. Mean diameter of the 16 stem sections was 21.3 cm (SE = 0.4). Emerging parasitoids were identified by Niklas Johansson at the Swedish Species Information Centre, Swedish University of Agricultural Sciences. Rate of parasitism was estimated for each tree by dividing the number of emerging parasitoids by the sum of emerging *Tetropium* beetles and parasitoids (assuming that each parasitoid killed one *Tetropium* larvae).

In addition, part of the colonized logs from three of the trees (40, 73 and 33 cm length stem sections respectively) were split on 15 March to count and collect *Tetropium* larvae. For each larva, the width of head-capsule was measured and it was noted if it occurred under the bark or in a gallery in the wood. The lengths of all galleries in wood, and of the plug blocking their entrances, were measured.

All nine larch stands used for trapping were inspected for occurrence of wind-felled larch trees which were checked for colonization by *Tetropium* by debarking. In addition to the cut and wind-felled trees, we also checked 30 stumps (30–40 cm in height) in the fresh clear-cut (cut winter 2016/2017) in early April 2018 for colonization by *Tetropium*.

Statistical analyses

For each species, catches were totalled for each treatment and block over the entire trapping period for each experiment and analysed using generalized linear models (SAS PROC GLIMMIX) with treatments fixed and blocks random. Blocks in which all three lure treatments had zero catch were deleted from analysis. The models were run with Gaussian, Poisson, and negative binomial distributions; results are reported for the distribution that best fit the data, according to the lowest value of the corrected Aikaike's Information Criterion (AIC_c). Post-hoc comparisons of least square means were done with Tukey–Kramer multiple comparisons which control the experiment-wise error rate ($P \leq 0.05$). We also analysed the raw data and data transformed by log $(y + 1)$ using standard ANOVA (SAS PROC GLM), testing residuals for normality using Shapiro-Wilks test, and compared results with those from the generalized linear mixed models. When results from the GLM and GLIMMIX analyses differed greatly, e.g., zero values for F in the generalized mixed model and significant F values in the GLM for the same data, we assumed the data were not suitable for analysis by the mixed models. This occurred in two cases (Experiment 3), possibly because the host volatile treatment caught zero *T. gabrieli* and *T. fuscum*. In these cases, count data were converted to ranks and analysed by Friedman's nonparametric ANOVA for randomized blocks, followed by the Ryan-Einot-Gabriel-Welsh multiple range test. For each *Tetropium* species, chi-square contingency tables (or Fischer's exact test in cases when expected values were below 5) were used to test whether sex ratio of trapped beetles was affected by lure treatment. Only treatments with at least four caught individuals were included in the sex ratio tests.

Results

Three *Tetropium* species were caught in the trapping experiments: the native *T. fuscum* (154 specimens) and *T. castaneum* (2230), and the exotic *T. gabrieli* (57). All three species were caught in all 12 blocks. Total catch per block (all experiments and treatments pooled per species) for *T. fuscum* was positively correlated with that of *T. castaneum* ($r = 0.81, N = 12, P = 0.001$) while there was no correlation between catches of *T. gabrieli* and

Table 1 Mean of total catch, SE and sex ratio (% males) of *T. gabrieli*, *T. fuscum* and *T. castaneum* in traps baited with *E*-fuscumol plus host volatiles (α-pinene and ethanol), host volatiles alone or in unbaited traps from 8 May to 13 June 2017

	T. gabrieli ($n = 10$)			*T. fuscum* ($n = 11$)			*T. castaneum* ($n = 12$)		
Treatment	Mean	SE	Males (%)	Mean	SE	Males (%)	Mean	SE	Males (%)
Host volatiles	0.50b	0.34	60	0.36b	0.20	75	6.67b	1.60	50
E-fuscumol + host volatiles	2.80a	0.80	39	10.20a	2.60	53	104.00a	21.20	58
Unbaited	0.10b	0.10		0.18b	0.12		1.67c	1.42	60
F	10.9			36.5			35.5		
df	2,27			2,30			2,33		
P	0.0003			<0.0001			<0.0001		
Distribution with best fit	Poisson			Poisson			Negative binomial		

For each species, blocks in which all three lure treatments had zero catches were deleted from analysis and n gives the number of remaining blocks. Data analysed by generalized linear models using distribution with best fit as measured by corrected Aikaike's information criterion. Means followed by different letters differed significantly, Tukey–Kramer multiple comparison test, $P \leq 0.05$. Sex ratio only given for treatments with ≥4 caught individuals.

T. fuscum ($r = -0.32$, $N = 12$, $P = 0.305$) or *T. gabrieli* and *T. castaneum* ($r = -0.22$, $N = 12$, $P = 0.492$).

Experiment 1. Catches of *T. gabrieli*, *T. fuscum* and *T. castaneum* were 28, 55 and 62 times higher in traps baited with *E*-fuscumol plus host volatiles than in unbaited traps and these differences were significant (Table 1). All three were also caught in significantly higher numbers in traps baited with *E*-fuscumol plus host volatiles than in traps baited with only host volatiles (Table 1). Traps baited with host volatiles alone caught 2–5 times more beetles than unbaited traps but the difference was significant only for *T. castaneum* (Table 1). Presence of *E*-fuscumol (i.e., *E*-fuscumol plus host volatiles vs. host volatiles alone) did not significantly affect sex ratio of *T. gabrieli* ($P = 0.63$) or *T. fuscum* ($P = 0.70$) (Fischer's exact test). (Table 1). Neither was there any significant difference in sex ratio between all three treatments for *T. castaneum* ($P = 0.38$, chi-square test).

Experiment 2. Mean catch of *T. gabrieli* did not differ significantly among traps baited with *E*-fuscumol plus host volatiles, *E,Z*-fuscumol plus host volatiles, or *E,Z*-fuscumol acetate plus host volatiles (Table 2). Catches of *T. fuscum* and *T. castaneum* were significantly higher (9 times and 6 times, respectively) in traps baited with *E,Z*-fuscumol plus host volatiles than in traps baited with *E,Z*-fuscumol acetate plus host volatiles (Table 2). In contrast, there was no significant difference in catch between *E*-fuscumol plus host volatiles and *E,Z*-fuscumol plus host volatiles for either *T. fuscum* or *T. castaneum* (Table 2). There was no significant difference in sex ratio between treatments for any of the species (*T. gabrieli*, $P = 0.91$, *T. fuscum*, $P = 0.84$, Fischer's exact test, *T. castaneum*, $P = 0.12$, chi-square test) (Table 2).

Experiment 3. Contrary to our expectations, adding α-pinene plus ethanol to traps baited with *E*-fuscumol significantly reduced mean catch of *T. gabrieli*; in fact mean catch in traps baited with *E*-fuscumol plus host volatiles was less than half of that in traps baited with *E*-fuscumol alone (Table 3). In contrast, traps baited with *E*-fuscumol plus host volatiles caught significantly more *T. castaneum* (5 times as many) than traps baited with *E*-fuscumol alone, which, in turn, caught significantly more *T. castaneum* (12 times as many) than traps baited with host volatiles alone (Table 3). Catches of *T. fuscum* were low. Mean catches in traps baited with *E*-fuscumol and *E*-fuscumol plus host volatiles did not differ, but both were significantly greater than

Table 2 Mean of total catch, range and sex ratio (% males) of *T. gabrieli*, *T. fuscum* and *T. castaneum* in traps baited with *E*-fuscumol plus host volatiles (α-pinene and ethanol), *E,Z*-fuscumol plus host volatiles or *E,Z*-fuscumol acetate plus host volatiles from 13 June to 29 June 2017

	T. gabrieli ($n = 9$)			*T. fuscum* ($n = 12$)			*T. castaneum* ($n = 12$)		
Treatment	Mean	SE	Males (%)	Mean	SE	Males (%)	Mean	SE	Males (%)
E-fuscumol + host volatiles	1.78a	0.72	56	2.50ab	0.93	43	65.08a	22.7	53
E,Z-fuscumol + host volatiles	2.11a	0.70	63	6.83a	2.25	41	71.83a	19.7	51
E,Z-fuscumol acetate + host volatiles	0.78a	0.36	71	0.75b	0.25	33	11.92b	2.96	60
F	2.6			7.89			22.5		
df	2,24			2,33			2,33		
P	0.0953			0.0016			<0.0001		
Distribution with best fit	Poisson			Negative binomial			Negative binomial		

For each species, blocks in which all three lure treatments had zero catches were deleted from analysis and n gives the number of remaining blocks. Data analysed by generalized linear models using distribution with best fit as measured by corrected Aikaike's information criterion. Means followed by different letters differed significantly, Tukey–Kramer multiple comparison test, $P \leq 0.05$. Sex ratio only given for treatments with ≥4 caught individuals.

Table 3 Mean of total catch, range and sex ratio (% males) of *T. gabrieli*, *T. fuscum* and *T. castaneum* in traps baited with *E*-fuscumol plus host volatiles (α-pinene and ethanol), E-fuscumol alone or host volatiles alone from 29 June to 13 September 2017

	T. gabrieli (*n* = 12)			*T. fuscum* (*n* = 8)			*T. castaneum* (n = 12)		
Treatment	Mean	SE	Males (%)	Mean	SE	Males (%)	Mean	SE	Males (%)
E-fuscumol + host volatiles	1.08b	0.60	62	1.50a	0.50	25	16.75a	3.53	37
E-fuscumol	2.75a	1.21	45	0.75a	0.25	17	3.08b	1.15	27
Host volatiles	0c	0		0b	0		0.25c	0.13	
F	11.59			5.93			23.7		
df	2,22			2,14			2,33		
P	0.0004			0.0136			<0.0001		
Distribution with best fit	NA			NA			Negative binomial		

For each species, blocks in which all three lure treatments had zero catches were deleted from analysis and n gives the number of remaining blocks. Data for *T. castaneum* analysed by generalized linear models using distribution with best fit as measured by corrected Aikaike's information criterion; means followed by different letters differed significantly, Tukey–Kramer multiple comparison test, *P* ≤ 0.05. Data for *T. gabrieli* and *T. fuscum* analysed by Friedman's test (ANOVA on ranks) followed by Ryan-Einot-Gabriel-welsh multiple range test (*P* ≤ 0.05). Sex ratio only given for treatments with ≥4 caught individuals.

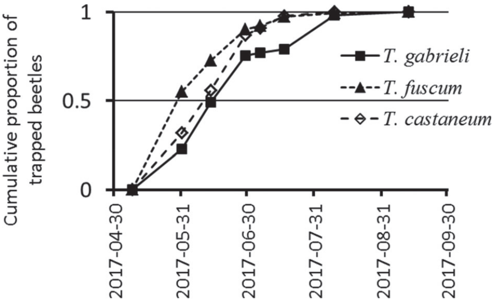

Figure 1 Seasonal patterns of catches of the exotic *T. gabrieli* and the native *T. fuscum* and *T. castaneum* in 12 multi-funnel traps baited with *E*-fuscumol, α-pinene and ethanol in larch stands. The total number of individuals caught was 57 *T. gabrieli*, 154 *T. fuscum* and 2230 *T. castaneum*.

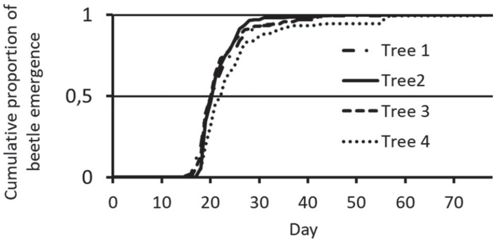

Figure 2 Emergence pattern of *T. gabrieli* from stem sections cut from four naturally infested cut and wind-felled larch trees in southern Sweden. From each tree, four 60-cm stem sections were cut in early spring and placed separately in cages in a climate room. The number of emerging adults were 276, 212, 142 and 152, respectively, from tree 1, 2, 3 and 4.

the zero catch in traps baited with host volatiles alone (Table 3). The addition of host volatiles to *E*-fuscumol did not affect the sex ratio for any of the three species (*T. gabrieli*, *P* = 0.33, chi-square test, *T. fuscum*, *P* = 1, Fischer's exact test, *T. castaneum*, *P* = 0.25, chi-square test) (Table 3).

Seasonal phenology of Tetropium spp. All three species were caught from May to August (Fig. 1). Most of the flight activity occurred in May and June. The median date of captures was about 2 weeks earlier for *T. fuscum* compared with the other two species. For both *T. fuscum* and *T. castaneum* (catches of *T. gabrieli* were too low for evaluation) a somewhat larger part of the flight activity of females than that of males occurred late in the season: 90% of the cumulative catches occurred about 10 days later for females than for males (data not shown).

Three of the five larch trees cut in the spring 2017 were colonized by *Tetropium*. About 75% of the tree stems were colonized. No other bark- and wood-boring beetle species were found on the stems. Wind-felled larch trees were found in two of the nine stands: six trees colonized in 2016 in one stand and one tree colonized in 2017 in another stand (same stand in which a cut tree was not colonized). There were no *Tetropium* emergence holes in the autumn in the colonized trees cut in the spring the same year. None of the 30 larch stumps inspected on the clear-cut were colonized by *Tetropium* spp.

Tetropium gabrieli was the only bark- and wood-boring insect species emerging from the 16 stem sections cut from four naturally infested cut and wind-felled larch trees except for four individuals of *Urocerus gigas* (L.) (Hymenoptera, Siricidae). A total of 782 individuals of *T. gabrieli* emerged: 276 (50% males), 212 (52% males), 142 (44% males) and 152 (50% males) individuals respectively from tree 1, 2, 3 and 4. The average production of *T. gabrieli* adults was 122 per m^2 bark (SE = 19, *N* = 4) and 2309 per m^3 wood (SE = 347) individuals. The emergence pattern was similar among trees: starting 14–17 days after stem sections were put in the climate chamber, 50% emergence after 19–21 days and 90% emergence after 25–32 days (Fig. 2). There was almost no difference in emergence pattern between sexes, 50% emergence of males occurred less than 1 day earlier than that for females (data not shown).

A total of 97 *Tetropium* larvae were found during the splitting of stem sections from three colonized trees. The *Tetropium* larvae were not determined to species but because only *T. gabrieli*

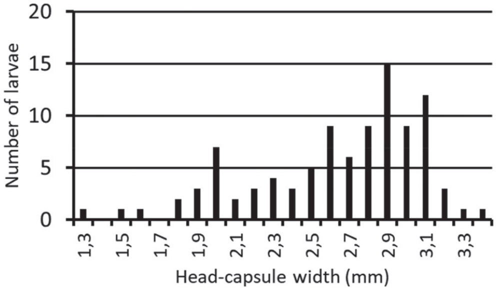

Figure 3 Size distribution of head-capsule widths among the 93 hibernating *Tetropium* larvae collected from the splitting of wood in early spring from three of the naturally infested larch trees.

adults emerged from the stem sections it is highly unlikely that the larvae were another species. All larvae were alive. About 34% of the larvae were found in galleries in the wood while the remaining 66% were found under the bark. Head-capsule width ranged from 1.3 to 3.4 mm with the majority (92%) >1.9 mm (Fig. 3). Head-capsule width was significantly larger for larvae in galleries in the wood than for larvae under bark: mean = 2.84 mm (SE = 0.06) and 2.53 mm (SE = 0.06) respectively ($P < 0.001$, *t*-test). Average length of galleries in the wood was 45 mm (SE = 2) and the entrance of all galleries were blocked with a plug (mean length = 7.4 mm, SE = 0.7 mm).

In addition to emergence of *T. gabrieli* adults, 110 parasitoid adults emerged from the stem sections: 28, 15, 38 and 29, respectively, from tree 1, 2, 3 and 4. They belonged to three species: *Rhimphoctona xoridiformis* Holmgren (Ichneumonoidea) (77 specimens, 60% males), *Helconidea dentator* (F.) (Braconidae) (31, 45% males) and *Neoxorides collaris* Gravenhorst (Ichneumonoidea) (2, 50% males). The average rate of parasitism was 13.2% (SE = 3.3%). Median emergence of *R. xoridiformis* occurred after 20 days while for *H. dentator* it occurred after 30 days.

Discussion

We present evidence from field-trapping experiments that *T. gabrieli* is attracted to racemic *E*-fuscumol. This is the fourth *Tetropium* species demonstrated to be attracted by *E*-fuscumol. *Tetropium castaneum*, *T. fuscum* and *T. cinnamopterum*, all with spruces as the main host tree species, are significantly attracted to the combination of *E*-fuscumol and host tree volatiles, and males of the latter two species emit *S*-fuscumol (Silk *et al.*, 2007; Sweeney *et al.*, 2010). These results suggest that *T. gabrieli* males may also emit fuscumol, but this must be confirmed by volatile collection and chemical analysis.

The effects of the host volatiles, α-pinene and ethanol, on trap catches varied among species. The addition of (−)-α-pinene plus ethanol to either unbaited traps or traps baited with *E*-fuscumol significantly increased catches of *T. castaneum*. The combination of *E*-fuscumol and host volatiles appeared to synergize attraction of *T. castaneum*, similar to what Sweeney *et al.* (2010) observed using a different blend of host volatiles that included α-pinene, ethanol, and four other monoterpenes. In contrast, neither *T. gabrieli* nor *T. fuscum* were attracted to (−)-α-pinene plus ethanol by themselves, and adding them to traps baited with *E*-fuscumol reduced catch of *T. gabrieli* and had no effect on catch of *T. fuscum*. These results suggest that *T. gabrieli* and *T. fuscum* respond to additional host-specific volatiles or volatile blends when searching for hosts. This was previously demonstrated for *T. fuscum* by Sweeney *et al.* (2004) who showed that trap catch of *T. fuscum* was significantly lower in traps baited with ethanol plus racemic α-pinene than in traps baited with ethanol plus a blend of five monoterpenes that approximated volatiles emitted from the boles of stressed spruce trees. Although there is variation among and within *Larix* species in the relative amounts of terpenes in leaves and twigs, common major components include (−)- and (+)-α-pinene, (−)-β-pinene, (+)-3-carene, and myrcene (Von Rudloff, 1987; Holm & Hiltunen, 1997; Ruuskanen *et al.*, 2007; Kajos *et al.*, 2013). Future research should compare the attraction of *T. gabrieli* to a synthetic blend of major monoterpenes emitted from larch trees (i.e., a larch blend) plus ethanol *versus* the (−)-α-pinene plus ethanol used in this study. These host volatile treatments should be also be tested with and without *E*-fuscumol and compared to *E*-fuscumol alone to determine whether the host volatiles synergize attraction of *T. gabrieli* to fuscumol.

Traps baited with host volatiles plus *E,Z*-fuscumol acetate caught significantly fewer individuals of *T. fuscum* and *T. castaneum* than did traps baited with host volatiles and *E,Z*-fuscumol, suggesting *E,Z*-fuscumol acetate is not attractive to these species. Lack of attraction of *T. fuscum* to fuscumol acetate is consistent with males not producing this compound (Silk *et al.*, 2007; Sweeney *et al.*, 2010); however, volatiles emitted by males of *T. castaneum* and *T. gabrieli* have not yet been determined. Catches of *T. gabrieli* in traps baited with host volatiles plus *E,Z*-fuscumol acetate were very low but did not differ significantly from catches in traps baited with host volatiles plus *E,Z*-fuscumol or *E*-fuscumol. However, to confirm whether or not *E,Z*-fuscumol is attractive to these species, one would have to compare catches in traps baited with *E,Z*-fuscumol acetate versus host volatiles versus *E,Z*-fuscumol acetate plus host volatiles versus unbaited traps.

There was no difference in catches of any of the *Tetropium* species between traps baited with *E,Z*-fuscumol plus host volatiles versus traps baited with *E*-fuscumol plus host volatiles, suggesting that the presence of *Z*-fuscumol did not inhibit response to *E*-fuscumol. This is further reinforced by the fact that the release rate of the attractive *E* isomer from the *E,Z* fuscumol lures was only about half of that from the *E*-fuscumol lures, because both lures were loaded with the same volume of *E,Z*-fuscumol or *E*-fuscumol. Flaherty *et al.* (2019) observed that traps baited with *E,Z*-fuscumol, *E,Z*-fuscumol acetate and ethanol captured significantly more *T. fuscum* and *T. cinnamopterum* than traps baited with monochamol, ipsenol, α-pinene and ethanol, whereas the converse was true for *T. castaneum*, suggesting the optimal combination of host volatiles and pheromone differs among these species.

The total catch (all experiments combined) of *T. gabrieli* was considerably lower than that of the other two *Tetropium* species. This is not surprising because *T. gabrieli* is monophagous on larch (Gorius, 1955) and larch stands constitute only 0.1%

(0.9 million m^3) of the total growing stock (i.e. all tree species) in southern Sweden compared with 48.5% (431 million m^3) for Norway spruce (Anonymous, 2016).

The positive correlation between *T. castaneum* and *T. fuscum* may be explained by the two species sharing the same host tree species Norway spruce. This result is in agreement with an earlier study conducted on these two species in Poland and on *T. fuscum* and *T. cinnamopterum* (also sharing the same host tree species) in Canada (Sweeney *et al.*, 2010). Because the experimental stands only included larch, all trapped *T. castaneum* and *T. fuscum* must have dispersed from colonized spruces in the surrounding landscape which means that the correlation in catches was not caused by the presence of previously colonized breeding substrates in the immediate vicinity of the traps. In contrast, there was no correlation between catches of *T. gabrieli* and those of *T. castaneum* and *T. fuscum*, and this was expected because of differences in host tree species.

An earlier study conducted in eastern Canada demonstrated that the exotic *T. fuscum* had a somewhat earlier flight period than the native *T. cinnamopterum* (Rhainds *et al.*, 2010). The median date of captures was >2 weeks earlier for *T. fuscum*. The present study demonstrates that also in its native range *T. fuscum* is an early occurring *Tetropium* species. In Sweden, the median date of captures was about 2 weeks earlier for *T. fuscum* compared with the native *T. castaneum* and the exotic *T. gabrieli*. Thus, *T. fuscum* should have an advantage compared with *T. castaneum* regarding colonization of the generally limited amounts of wind-felled or weakened standing spruce trees in the managed forests of Sweden.

The only *Tetropium* species emerging from the larch stem sections was *T. gabrieli*. This is in accordance with an earlier Swedish study, including stem sections from 17 trees in 6 stands, in which also only *T. gabrieli* emerged (Lindelöw *et al.*, 2015). Most *T. gabrieli* emerged during a relatively short time period after the breeding material was brought in to the climate room. Emergence started after about 2 weeks and after 4 weeks 90% of the beetles had already emerged. This is similar to what have been demonstrated for *T. fuscum* in Canada (Rhainds *et al.*, 2010). The synchronized emergence is in accordance with the fact that most of the flight activity occurred during May and June. *Tetropium gabrieli* most commonly overwinters as a mature pre-pupal larva, though a proportion of the population may overwinter as immature larvae (Crawshay, 1907; Schimitschek, 1929). This is in accordance with the variation in larval head-capsule width found in the present study for hibernating larvae of which the smaller ones may represent individuals emerging and flying later in the season.

The three species of parasitoids that emerged from the stem sections have all earlier been demonstrated to use *T. gabrieli* as a host (Kenis & Hilszczanski, 2004). They are also commonly associated with the native *T. castaneum* and *T. fuscum*. All three species have earlier been recorded from Sweden and are classified as native (www.dyntaxa.se). The rate of parasitism in the present study is low compared with earlier studies on *Tetropium* (see Kenis & Hilszczanski, 2004 for an overview). It is highly unlikely that this was a result of the methodology used because the *Tetropium* larvae in the cut larch trees were exposed to parasitoids during the whole summer before the stem sections were cut in September. The two most common parasitoids we collected, *R. xoridiformis* and *H. dentator*, are endoparasitic koinobionts, i.e., females oviposit in the early instar host larva which continues to develop to a mature larva or prepupa before the parasitoid consumes the host, emerges to spin a cocoon and pupates. Both *R. xoridiformis* and *H. dentator* overwinter as pupae and emerge as adults the following spring, shortly after emergence of *Tetropium* adults (Schimitschek, 1929). The median emergence of *R. xoridiformis* and *H. dentator* in our study was only 5 and 15 days, respectively, after median emergence of *T. gabrieli*, providing evidence that these species likely parasitize early instar larvae. The ectoparasite, *Neoxorides collaris*, develops externally on parasitized larvae and overwinters as a pupa between the bark and the wood (Kenis & Hilszczanski, 2004). Thus, exposure of fresh larch logs in May and removal of logs from the field in September would have provided ample opportunity for parasitism by these species.

Tetropium gabrieli seems to be able to establish, and continuously maintain populations, in forest landscapes with only a low proportion of larch stands (4.2% in the present study area) and with few wind-felled larch trees. In an earlier study, conducted during 2 years (2009 and 2010) in the same area as the present study, *T. gabrieli* colonized most cut larch trees (Lindelöw *et al.*, 2015). In the present study, it colonized wind-felled trees in 2016 (assuming the *Tetropium* larval galleries belonged to *T. gabrieli*, one adult found under bark in one of the trees) and cut and wind-felled trees in 2017. Factors explaining the ability to maintain populations in landscapes with low proportions of host trees may be a high production of adults per tree, a synchronized emergence and flight activity, and a strong attraction to their pheromones ensuring a high probability of mate finding. Low levels of interspecific competition and rate of parasitism should have contributed to the high production. No other bark- and wood-boring insects, except a few *U. gigas*, utilized the stems of the larch trees in this study and only a few in the earlier study (Lindelöw *et al.*, 2015).

The results demonstrate that *E*-fuscumol and *E,Z*-fuscumol can be used for early detection of *T. gabrieli* in areas where the species has not yet established. However, more research is needed to develop a synthetic blend of host volatiles that is more representative of those emitted by freshly felled larch trees than the α-pinene and ethanol used in this study, and to determine the enantiomer or enantiomers of fuscumol emitted by *T. gabrieli*. Combining *E*-fuscumol with an attractive 'larch blend' host volatile lure plus ethanol may result in even greater attraction of *T. gabrieli*, in much the same way as the combination of spruce blend, ethanol, and *E*-fuscumol synergizes attraction of *T. fuscum*. Trap catches would also likely be improved by coating trap surfaces with Fluon to reduce friction (Allison *et al.*, 2011; Graham & Poland, 2012; Allison *et al.*, 2016). Even though *T. gabrieli* is considered to be more of a secondary pest species in Europe, it may become more aggressive if encountering new host tree species, for example, different larch species in North America, as was the case with *T. fuscum* when it established in North America. Furthermore, the results of the present study demonstrate that the species is able to also establish in regions where its habitat is strongly fragmented and constitutes only a very small proportion of total forest cover which is a strong argument for including this species in early detection programs. In addition, the bait may also be useful for monitoring population levels in areas where it is already established and for documenting the spread in areas where it has recently established.

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Data availability statement

Data available on request from the authors

References

Allison, J.D., Johnson, C.W., Meeker, J.R., Strom, B.L. & Butler, S.M. (2011) Effect of aerosol surface lubricants on the abundance and richness of selected forest insects captured in multiple-funnel and panel traps. *Journal of Economic Entomology*, **104**, 1258–1264.

Allison, J.D., Graham, E.E., Poland, T.M. & Strom, B.L. (2016) Dilution of Fluon before trap surface treatment has no effect of longhorned beetle (Coleoptera: Cerambycidae) captures. *Journal of Economic Entomology*, **109**, 1215–1219.

Anonymous (2016) Forest statistics 2016 - official statistics of Sweden, Swedish University of Agricultural Sciences, Umeå 2016, 150 pp.

Crawshay, G.A. (1907) The life history of *Tetropium gabrieli*, Ws. – *T. fuscum*, Sharp – *T. crawshayi*, Sharp, etc. *Transactions of the Entomological Society of London*, **Part II**, 183–212.

Ehnström, B. & Holmer, M. (2007) *Nationalnyckeln till Sveriges flora och fauna*. Långhorningar, Skalbaggar Coleoptera: Cerambycidae. Artdatabanken, SLU, Uppsala. 302 pp.

Ericson, B. (2010) Two species of beetles new to Sweden feeding on larch. *Entomologisk Tidskrift*, **131**, 131–136 (in Swedish with English abstract).

Evans, H.F., Moraal, L.G. & Pajares, J.A. (2004) Biology, ecology and economic importance of Buprestidae and Cerambycidae. *Bark and Wood Boring Insects in Living Trees in Europe, a Synthesis* (ed. by F. Lieutier, K. R. Day, A. Battisti, J.-C. Grégoire and H. F. Evans). Kluwer Academic Publishers, Dordrecht.

Flaherty, L., Gutowski, J.M.G., Hughes, C. *et al.* (2019) Pheromone-enhanced lure blends and multiple trap heights improve detection of bark and wood-boring beetles potentially moved in solid wood packaging. *Journal of Pest Science*, **92**, 309–325.

Gorius, U. (1955) Unterzuchungen über den Lärchenbock, *Tertropium gabrieli* Weise mit besonderen Berücksichtigung seines Massenwechels. *Zeitschrift für Angewandte Entomologie*, **38**, 157–205.

Graham, E.E. & Poland, T.M. (2012) Efficacy of Fluon conditioning for capturing cerambycid beetles in different trap designs and persistence on panel traps over time. *Journal of Economic Entomology*, **105**, 395–401.

Halloran, S.T., Collignon, R.M., McElfresh, J.S. & Millar, J.G. (2018) Fuscumol and geranylacetone as pheromone components of Californian longhorn beetles (Coleoptera: Cerambycidae) in the subfamily Spondylidinae. *Environmental Entomology*, **47**, 1300–1305.

Hanks, L.M. & Millar, J.G. (2016) Sex and aggregation-sex pheromones of cerambycid beetles: basic science and practical applications. *Journal of Chemical Ecology*, **42**, 631–654.

Holm, Y. & Hiltunen, R. (1997) Variation and inheritance of monoterpenes in *Larix* species. *Flavour and Fragrance Journal*, **12**, 335–339.

Hughes, G.P., Zou, Y., Millar, J.G. & Ginzel, M.D. (2013) (*S*)-fuscumol and (*S*)-fuscumol acetate produced by a male *Astyleiopus variegatus* (Coleoptera: Cerambycidae). *The Canadian Entomologist*, **145**, 327–332.

Hughes, G.P., Meier, L.R., Zou, Y., Millar, J.G., Hanks, L.M. & Ginzel, M.D. (2016) Stereochemistry of fuscumol and fuscumol acetate influences attraction of longhorned beetles (Coleoptera: Cerambycidae) of the subfamily Lamiinae. *Environmental Entomology*, **45**, 1271–1275.

Kajos, M.K., Hakola, H., Holst, T. *et al.* (2013) Terpenoid emissions from fully grown east Siberian *Larix* cajanderi trees. *Biogeosciences*, **10**, 4705–4719.

Kenis, M. & Hilszczanski, J. (2004) Natural enemies of Cerambycidae and Buprestidae infesting living trees. *Bark and Wood Boring Insects in Living Trees in Europe, a Synthesis* (ed. by F. Lieutier, K. R. Day, A. Battisti, J.-C. Grégoire and H. F. Evans). Kluwer Academic Publishers, Dordrecht.

Lemay, M.A., Silk, P.J. & Sweeney, J. (2010) Calling behavior of *Tetropium fuscum* (Coleoptera: Cerambycidae: Spondylidinae). *Canadian Entomologist*, **142**, 256–260.

Lindelöw, Å., Isacsson, G., Ravn, H.P. & Schroeder, M. (2015) *Tetropium gabrieli* and *Ips cembrae* (Coleoptera; Cerambycidae and Curculionidae) – invasion of two potential pest species on larch in Sweden. *Entomologisk Tidskrift*, **136**, 103–112.

Lundberg, S. (1986) Några förklaringar till 1986 års skalbaggskatalog, med under 1984 och 1985 nytillkomna arter (notes to the 1986 Swedish Coleoptera catalogue, with species recorded for the first time during 1984 and 1985). *Entomologisk tidskrift*, **107**, 148–150 (in Swedish with English abstract).

Lundberg, S. (1988) Några intressanta skalbaggsfynd i till Norrbotten importerat barrvirke. (Records of Coleoptera from northern Sweden in timber imported from Central Europe). *Entomologisk Tidskrift*, **109**, 49–50 (in Swedish with English summary).

Lundberg, S. & Pettersson, R. (1997) Något om skalbaggsfaunan i ryskt virke vid en såg i Västerbotten. (Observations of the beetle fauna in Russian timber at a saw mill in Västerbotten, northern Sweden.). *Entomologisk Tidskrift*, **188**, 49–51 (in Swedish with English abstract).

Meier, L.R., Zou, Y., Millar, J.G., Mongold-Diers, J.A. & Hanks, L.M. (2016) Synergism between enantiomers creates species-specific pheromone blends and minimizes cross-attraction for two species of cerambycid beetles. *Journal of Chemical Ecology*, **42**, 1181–1192.

Meier, L.R., Zou, Y., Mongold-Diers, J.A., Millar, J.G. & Hanks, L.M. (2020) Pheromone composition and chemical ecology of six species of cerambycid beetles in the subfamily Lamiinae. *Journal of Chemical Ecology*, **46**, 30–39.

Mitchell, R.F., Graham, E.E., Wong, J.C.H. *et al.* (2011) Fuscumol and fuscumol acetate are general attractants for many species of cerambycid beetles in the subfamily Lamiinae. *Entomologia Experimentalis et Applicata*, **141**, 71–77.

Pfeffer, A. (1995) *Zentral- und westpaläarktische Borken und Kernkäfer*. Scolytidae, Platypodidae, Coleoptera Pro Entomologia, c/o Naturhistorisches Museum, Basel. 310 pp.

Rhainds, M., Heard, S.B., Sweeney, J.D., Silk, P. & Flaherty, L. (2010) Phenology and spatial distribution of native and exotic *Tetropium* longhorned beetles (Coleoptera: Cerambycidae). *Environmental Entomology*, **39**, 1794–1800.

Ruuskanen, T.M., Hakola, H., Kajos, M.K., Hellen, H., Tarvainen, V. & Rinne, J. (2007) Volatile organic compound emissions from Siberian larch. *Atmospheric Environment*, **41**, 5807–5812.

Sama, G. & Löbl, I. (2010) Spondylinae. *Catalogue of Palearctic Coleoptera*, Vol. **6** (ed. by I. Löbl and A. Smetana), pp. 137–139. Apollo Books, Stenstrup 924 pp.

Schimitschek, E. (1929) *Tetropium gabrieli* Weise and *Tetropium fuscum* F. Ein Beitrag zu ihrer Lebensgeschichte and Lebensgemeinschaft. *Zeitschrift für Angewandte Entomologie*, **15**, 229–334.

Silk, P.J., Sweeney, J., Wu, J., Price, J., Gutowski, J.M. & Kettela, E.G. (2007) Evidence for a male-produced pheromone in *Tetropium fuscum* (F.) and *Tetropium cinnamopterum* (Kirby) (Coleoptera: Cerambycidae). *Naturwissenschaften*, **94**, 697–701.

Sweeney, J., Groot, P., Macdonald, L., Smith, S., Cocquempot, C., Kenis, M. & Gutowski, J.M. (2004) Host volatile attractants and traps for detection of *Tetropium fuscum* (F.), *Tetropium castaneum* L., and other longhorned beetles (Coleoptera: Cerambycidae). *Environmental Entomology*, **33**, 844–854.

Sweeney, J., Gutowski, J.M., Price, J. & De Groot, P. (2006) Effect of semiochemical release rate, killing agent, and trap design on detection of *Tetropium fuscum* (F.) and other longhorn beetles (Coleoptera: Cerambycidae). *Environmental Entomology*, **35**, 645–654.

Sweeney, J., Silk, P.J., Gutowski, J.M., Wu, J., Lemay, M.A., Mayo, P.D. & Magee, D.I. (2010) Effect of chirality, release rate, and host volatiles on response of *Tetropium fuscum* (F.), *Tetropium cinnamopterum* Kirby, and *Tetropium castaneum* (L.) to the aggregation pheromone, Fuscumol. *Journal of Chemical Ecology*, **36**, 1309–1321.

Von Rudloff, E. (1987) The volatile twig and leaf oil terpene composition of three western North American larches, *Larix laricina*, *Larix occidentalis*, and *Larix lyalli*. *Journal of Natural Products*, **50**, 317–321.

Yanega, D. (1996) Field Guide to Northeastern Longhorned Beetles (Coleoptera: Cerambycidae). Illinois Natural History Survey Manual 5. 184 pp.

Žunič-Kosi, A., Stritih-Peljhan, N., Zou, Y., McElfresh, J.S. & Millar, J.G. (2019) A male-produced aggregation-sex pheromone of the beetle *Arhopalus rusticus* (Coleoptera: Cerambycidae, Spondylidinae) may be useful in managing this invasive species. *Scientific Reports*, **9**, 19570.

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RESEARCH ARTICLE

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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. aminitus* 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).

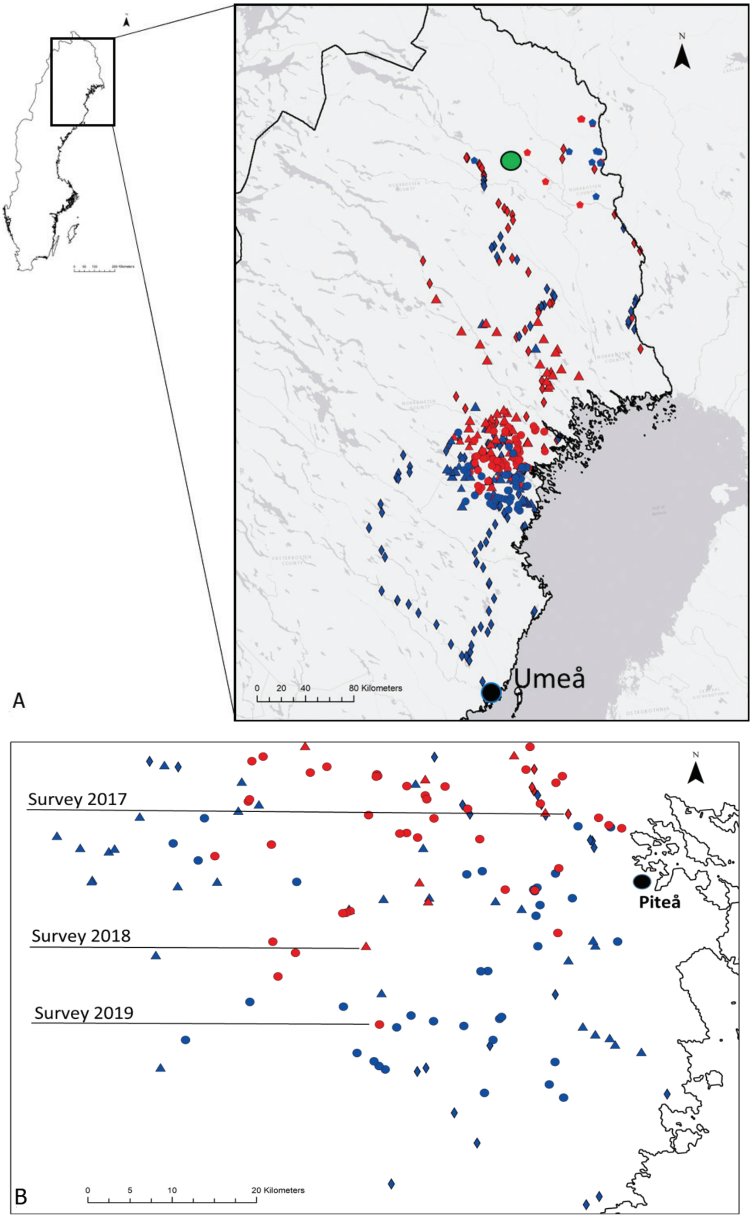

Figure 1. A locations checked for presence of *Ips amitinus* in northern Sweden in 2016 – 2019. Red symbols = presence and blue symbols = absence. Green symbol = first record in 2012. 2016 = pentagon, 2017 = diamond, 2018 = triangle and 2019 = circle. Umeå (63°49.877'N, 20°15.651'E) **B** *Ips amitinus* 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 colonisation	Intercept	**312.88**	**1**	**-6.20**	**0.35**	**<0.0001**	0.96	0.10
	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.

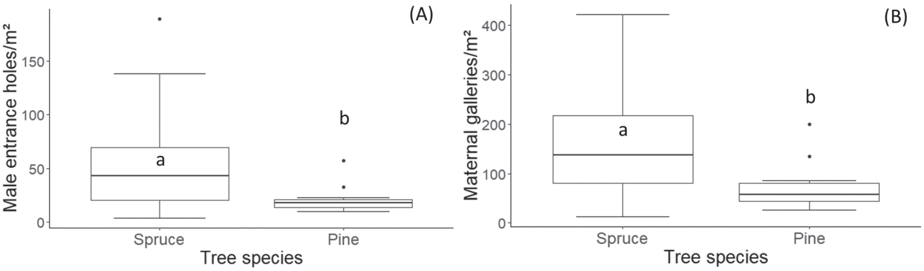

Figure 3. Male attack and female gallery density in host material naturally colonised by *Ips amitinus*. (**A**) Male entrance holes per m^2 bark and (**B**) maternal galleries per m^2 bark.

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.

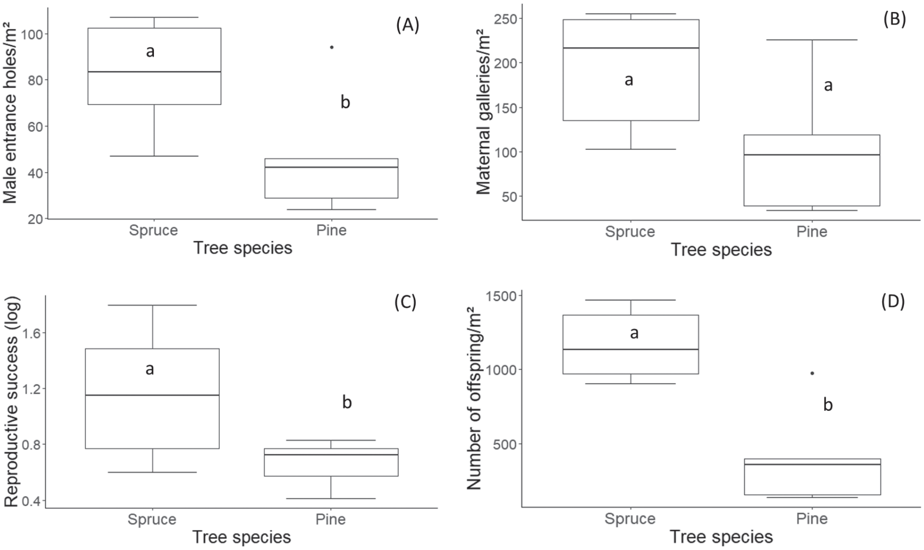

Figure 4. The results from the no-choice rearing experiment with *Ips amitinus*. Male entrance holes per m^2 bark (**A**), maternal galleries per m^2 bark (**B**), reproductive success (log transformed), (**C**) and number of offspring produced per m^2 bark (**D**). Means with different lowercase letters 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*

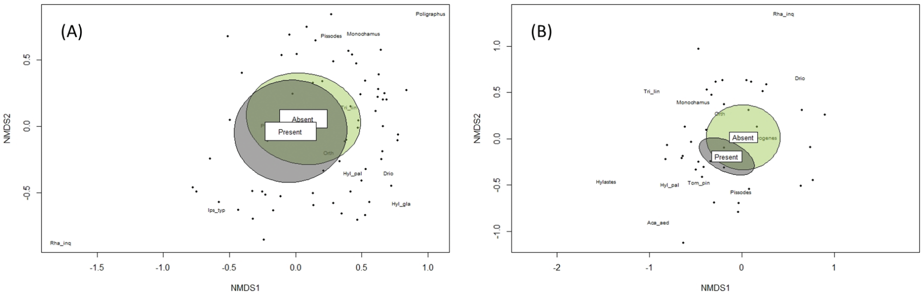

Figure 5. NMDS visualisation of the relationship between the other species found in spruce (**A**) and pine (**B**) in relation to the presence/absence of *I. amitinus*. Stress: 0.1868 (spruce) and 0.1173 (pine).

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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References

Annila E, Nuorteva M (1976) Dates of attack and emergence of *Ips amitinus* Eichh. (Col., Scolytidae) in Finland. Annales Entomologici Fennici 42: 28–30.

Aukema JE, Leung B, Kovacs K, Chivers C, Britton KO, Englin J, Frankel SJ, Haight RG, Holmes TP, Liebhold AM, McCullough DG, Von Holle B (2011) Economic Impacts of Non-Native Forest Insects in the Continental United States. PLoS ONE 6(9): e24587. https://doi.org/10.1371/journal.pone.0024587

Bates D, Maechler M, Bolker M, Walker S (2015) Fitting linear mixed-effects models using lme4. Journal of Statistical Software 67(1): 1–48. https://doi.org/10.18637/jss.v067.i01

Brockerhoff EG, Liebhold AM (2017) Ecology of forest insect invasions. Biological Invasions 19(11): 3141–3159. https://doi.org/10.1007/s10530-017-1514-1

Brockerhoff EG, Bain J, Kimberley M, Knižek M (2006) Interception frequency of exotic bark and ambrosia beetles (Coleoptera: Scolytinae) and relationship with establishment in New Zealand and worldwide. Canadian Journal of Forest Research 36(2): 289–298. https://doi.org/10.1139/x05-250

Dexter E, Rollwagen-Bollens G, Bollens SM (2018) The trouble with stress: A flexible method for the evaluation of nonmetric multidimensional scaling. Limnology and Oceanography: Methods 16(7): 434–443. https://doi.org/10.1002/lom3.10257

Dodds KJ, Aoki CF, Arango-Velez A, Cancelliere J, D'Amato AW, DiGirolomo MF, Rabaglia RJ (2018) Expansion of Southern Pine Beetle into Northeastern Forests: Management and Impact of a Primary Bark Beetle in a New Region. Journal of Forestry 116(2): 178–191. https://doi.org/10.1093/jofore/fvx009

Ehnström B, Axelsson R (2002) Insektsgnag i bark och ved. ArtDatabanken, SLU, Uppsala, 512 pp.

EPPO (2022) *Ips amitinus*. EPPO datasheets on pests recommended for regulation. https://gd.eppo.int/taxon/IPSXAM/hosts [accessed on 4 March 2022]

Essl F, Dullinger S, Genovesi P, Hulme P, Jeschke JM, Katsanevakis S, Kühn I, Lenzner B, Pauchard A, Pyšek P, Rabitsch W, Richardson DM, Seebens H, Kleunen M, Putten WV, Vilà M, Bacher S (2019) A Conceptual Framework for Range-Expanding Species that Track Human-Induced Environmental Change. BioScience 69: 908–919. https://doi.org/10.1093/biosci/biz101

Foit J (2012) Felling date affects the occurrence of *Pityogenes chalcographus* on Scots pine logging residues. Agricultural and Forest Entomology 14(4): 383–388. https://doi.org/10.1111/j.1461-9563.2012.00579.x

Foit J (2015) Bark- and wood-boring beetles on Scots pine logging residues from final felling: Effects of felling date, deposition location and diameter of logging residues. Annals of Forest Research 58(1): 67–79. https://doi.org/10.15287/afr.2015.302

Grodzki W (1997) Changes in the occurrence of bark beetles on Norway spruce in a forest decline area in the Sudety Mountains in Poland. In: Grégoire JC, Liebhold AM, Stephen FM, Day KR, Salom SM (Eds) Proceedings: Integrating cultural tactics into the management of bark beetle and reforestation pests, USDA, Forest Service General Technical Report, NE-236, 105–111. https://doi.org/10.1515/frp-2016-0033

Grodzki W (2009) Entomofauna of dying young spruces *Picea abies* (L.) Karst. in the area after forest decline in the Izerskie Mountains. Folia Forestalia Polonica 51: 161–170.

Holuša J, Lukášová K, Grodzki W, Kula E, Matoušek P (2012) Is *Ips amitinus* (Coleoptera: Curculionidae) abundant in wide range of altitudes? Acta Zoologica Bulgarica 64: 219–228.

Jakuš R (1998) Patch level variation on bark beetle attack (Col., Scolytidae), on snapped and uprooted trees in Norway spruce primeval natural forest in endemic condition: Effects of host and insolation. Journal of Applied Entomology 122(1–5): 409–421. https://doi.org/10.1111/j.1439-0418.1998.tb01521.x

Jonsell M, Hansson J, Wedmo L (2007) Diversity of saproxylic beetle species in logging residues in Sweden - comparisons between tree species and diameters. Biological Conservation 138(1–2): 89–99. https://doi.org/10.1016/j.biocon.2007.04.003

Jurc M, Bojović S (2004) Bark beetle outbreaks during the last decade with special regard to the eight-toothed bark beetle (*Ips amitinus* Eichh.) outbreak in the Alpine region of Slovenia. In: Csóka G, Hirka A, Koltay A (Eds) 2006: Biotic damage in forests. Proceedings of the IUFRO (WP7.03.10) Symposium held in Mátrafüred, Hungary, September 12–16, 2004.

Kerchev IA, Krivets SA (2021) An attack of Ips amitinus (Coleoptera: Curculionidae: Scolytinae) on arboretum in West Siberia: new host of invasive bark beetle among exotic conifers. Journal of Asia-Pacific Entomology 24(2): 148–152. https://doi.org/10.1016/j.aspen.2021.03.003

Koponen M (1975) Distribution of *Ips amitinus* Eichh. (Coleoptera, Scolytidae) in Finland in 1950–1973. Ann. Ent. Fenn. 41: 65–69.Koponen M (1980) Distribution of *Ips amitinus* (Eichhoff) (Coleoptera, Scolytidae) in Finland in 1974–1979. Notulae Entomologicae 60: 223–225.

Lekander B, Bejer-Petersen B, Kangas E, Bakke A (1977) The distribution of bark beetles in the Nordic countries. Acta Entomologica Fennica 32: 1–37.

Lenoir J, Svenning J-C (2015) Climate-related range shifts – a global multidimensional synthesis and new research directions. Ecography 38(1): 15–28. https://doi.org/10.1111/ecog.00967

Lindelöw Å (2013) Väntad barkborre funnen i Sverige - fynd av *Ips amitinus* (Coleoptera, Scolytinae). Entomologisk Tidskrift 134: 203–206. [*Ips amitinus* (Coleoptera, Scolytinae) expected and found in Sweden]

Mandelshtam MJ (1999) Current status of *Ips amitinus* Eichh. (Coleoptera, Scolytidae) in North-West Russia. Entomologica Fennica 10(1): 29–34. https://doi.org/10.33338/ef.83996

Martikainen P, Siitonen J, Kaila L, Punttila P (1996) Intensity of forest management and bark beetles in non-epidemic conditions: A comparison between Finnish and Russian Karelia. Journal of Applied Entomology 120(1–5): 257–264. https://doi.org/10.1111/j.1439-0418.1996.tb01603.x

Mazur A, Kuźmiński R (2013) Phenology of development and population characteristics of the small spruce bark beetle *Ips amitinus* (Eichh.) in the Karkonoski National Park. Folia Forestalia Polonica 55(2): 89–96. https://doi.org/10.2478/ffp-2013-0009

Økland B, Skarpaas O (2008) Draft pest risk assessment report on the small spruce bark beetle, *Ips amitinus*. Commissioned report from Norwegian Forest and Landscape Institute, 10–2008, 1–24.

Økland B, Flø D, Schroeder M, Zach P, Cocos D, Martkainen P, Siitonen J, Mandelshtam MY, Musolin DL, Neuvonen S, Vakula J, Nikolov C, Lindelöw Å, Voolma K (2019) Range Expansion of the Small Bark Beetle *Ips amitinus*: A Newcomer in Northern Europe. Agricultural and Forest Entomology 21: 286–298. https://doi.org/10.1111/afe.12331

Oksanen J, Simpson GL, Blanchet FG, Kindt R, Legendre P, Minchin PR, O'Hara RB, Solymos P, Stevens MHH, Szoecs E, Wagner H, Barbour M, Bedward M, Bolker B, Borcard D, Carvalho G, Chirico M, De Caceres M, Durand S, Evangelista HBA, Fitz-John R, Friendly M, Furneaux B, Hannigan G, Hill MO, Lahti L, McGlinn D, Ouellette M-H, Cunha ER, Smith T, Stier A, Braak CJFT, Weedon J (2013) Package 'vegan'. Community ecology package, R package version 2.3-2. The R Foundation for Statistical Computing, Vienna.

Olver FWJ, Lozier DM, Boisvert RF, Clark CW [Eds] (2010) Quadrature: Gauss–Hermite Formula, NIST Handbook of Mathematical Functions, Cambridge University Press.

Pyšek P, Jarošík V, Hulme PE, Pergl J, Hejda M, Schaffner U, Vilà M (2012) A global assessment of invasive plant impacts on resident species, communities and ecosystems: The interaction of impact measures, invading species traits and environment. Global Change Biology 18(5): 1725–1737. https://doi.org/10.1111/j.1365-2486.2011.02636.x

R Core Team (2019) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. https://www.R-project.org/

Roques A, Rabitsch W, Rasplus JY, Lopez-Vamonde C, Nentwig W, Kenis M (2009) Alien terrestrial invertebrates of Europe. In: DAISIE (Ed.) Handbook of Alien Species in Europe. Springer, Berlin, 63–79. https://doi.org/10.1007/978-1-4020-8280-1_5

Seebens H, Blackburn T, Dyer E, Genovesi P, Hulme PE, Jeschke JM, Pagad S, Pyšek P, Winter M, Arianoutsou M, Bacher S, Blasius B, Brundu G, Capinha C, Celesti-Grapow L, Dawson W, Dullinger S, Fuentes N, Jäger H, Kartesz J, Kenis M, Kreft H, Kühn I, Lenzner B, Liebhold A, Mosena A, Moser D, Nishino M, Pearman D, Pergl J, Rabitsch W, Rojas-Sandoval J, Roques A, Rorke S, Rossinelli S, Roy HE, Scalera R, Schindler S, Štajerová K, Tokarska-Guzik B, van Kleunen M, Walker K, Weigelt P, Yamanaka T, Essl F (2017) No saturation in the accumulation of alien species worldwide. Nature Communications 8(1): 14435. https://doi.org/10.1038/ncomms14435

Stauffer C, Zuber M (1998) *Ips amitinus* var. *montana* (Coleoptera, Scolytidae) is synonymous to *Ips amitinus*: A morphological, behavioural and genetic re-examination. Biochemical Systematics and Ecology 26(2): 171–183. https://doi.org/10.1016/S0305-1978(98)80004-5

Wang Y, Naumann U, Wright S, Warton DI (2012) mvabund: An R package for model-based analysis of multivariate data. Methods in Ecology and Evolution 3(3): 471–474. https://doi.org/10.1111/j.2041-210X.2012.00190.x

Wermelinger B, Schneider Mathis D, Knížek M, Forster B (2020) Tracking the spread of the northern bark beetle (*Ips duplicatus* [Sahlb.]) in Europe and first records from Switzerland and Liechtenstein. Alpine Entomology 4: 179–184. https://doi.org/10.3897/alpento.4.53808

Witrylak M (2008) Studies of the biology, ecology, phenology, and economic importance of *Ips amitinus* (Eichh.) (Col., Scolytidae) in experimental forests of Krynica (Beskid Sadecki, southern Poland). Acta Scientinarum Polonorum 7: 75–92.

Zolk K (1932) Kodumaa ürasklased (Ipidae) ühes lühikese ülevaatega nende bionoomiast ja levimisest Eestis (Die Borkenkäfer (Ipidae) Estlands mit kurzer Berücksichtigung ihrer Bionomie und Verbreitung). Eesti Metsanduse Aastaraamat (Estländischesforstwirtschaftliches Jahrbuch), VI. Tartu: 127–176.

Supplementary material 1.

Ips amitinus description

Ips amitinus adults were collected for identification when possible. *Ips amitinus* differ from other *Ips* species present in Sweden by the shape of the body and a shiny declivity at the back of the elytra (Knižek 2001; Nierhaus-Wunderwald and Forster 2004; Åke Lindelöw, pers. communication).

The gallery system is very 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 fiber, then turn after about one centimeter and continue along the wood fiber 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).

References

Knižek M (2001) Progradation of small spruce bark beetle species. Journal of Forest Science 47: 113-114.

Nierhaus-Wunderwald D, Forster B (2004) Zur Biologie der Buchdruckerarten. Merkblatt fur die Praxis 18: 1-8.

Table S1. Percentages of localities and wood objects colonized by bark- and wood-boring beetle taxa north and south of the *Ips amitinus* 2019 southern distribution limit. The number of colonized localities and objects is given within parenthesis. Species were ordered based on the percentage (and number) of colonized 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 colonized objects is calculated based on the number of objects from their host tree species

		Colonized localities		**Colonized objects**		
		North	**South**	**North**	**South**	
Species	**Beetle group**	% (number)	% (number)	% (number)	% (number)	**Host tree**
Pityogenes chalcographus	B	82.1 (261)	73.4 (47)	87.4 (4348)	91.4 (1008)	S
***Pityogenes* spp.**	B	75.4 (240)	61 (39)	57.5 (2114)	55.9 (405)	P
Ips amitinus	B	57.9 (184)	0	8.6 (741)	0	S/P
***Orthotomicus* spp.**	B	54.7 (174)	28.1 (18)	7.5 (647)	5.1 (94)	S/P
Tomicus piniperda	B	45.6 (145)	42.2 (27)	18.1 (665)	19.6 (142)	P
***Pissodes* spp.**	W	29.6 (94)	15.6 (10)	1.8 (153)	1.0 (18)	S/P
***Dryocoetes* spp.**	B	28.9 (92)	35.9 (23)	3.9 (194)	7.2 (80)	S
***Monochamus* spp.**	L	23.6 (75)	12.5 (8)	3.9 (341)	1.3 (24)	S/P
Ips typographus	B	19.5 (62)	25.0 (16)	1.4 (118)	2.3 (42)	S
Hylurgops glabratus	B	9.7 (31)	4.7 (3)	0.8 (42)	0.4 (4)	S
Hylurgops palliatus	B	9.4 (30)	7.8 (5)	0.6 (53)	0.4 (7)	S/P
***Polygraphus* spp.**	B	2.5 (8)	1.6 (1)	0.2 (11)	0.1 (1)	S
Trypodendron lineatum	B	2.2 (7)	1.6 (1)	0.2 (13)	0.1 (1)	S/P
Rhagium inquisitor	L	1.9 (6)	6.3 (4)	0.1 (9)	1.4 (25)	S/P
***Hylastes* spp.**	B	1.6 (5)	3.1 (2)	0.1 (7)	0.2 (4)	S/P
Acanthocinus aedilis	L	0.9 (3)	0.0	0.1 (3)	0	P

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Non-native bark- and woo-boring beetle species can have devastating consequences on the local forest ecosystems. Thus, the use of an appropriate method for delimiting the distribution areas for such species is fundamental. This thesis examines factors that influence the probability of colonization and how the distance to the range limit influences the probability of patch colonization.

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