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Factors affecting population density and colonization success of two non-native beetle species with different breeding/life-history strategies

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Introduction: Bark and longhorn beetles have become of increasing concern as invasive pests as they are transported across the globe. The larch bark beetle *Ips cembrae* and the larch longhorn beetle *Tetropium gabrieli* are two species that have recently established in Scandinavia. We asked the following questions for both *I. cembrae* and *T. gabrieli*: (i) How does habitat availability affect the relative population density? (ii) How is the colonization probability related to the relative population density? (iii) What is the relationship between relative population densities of the beetles and enemy pressure?

Methods: The relative population density of the two beetle species were assessed with two pheromone-baited traps for each beetle species in 36 pure larch stands distributed in southern Sweden and Denmark. In addition, colonization success was recorded on five cut larch trees in 30 of the 36 larch stands.

Results: *Ips cembrae* was trapped in 19 stands and had colonized cut trees in two stands, whereas *Tetropium gabrieli* was trapped in 18 stands and had colonized cut trees in 12 stands. Both species showed a positive relationship between the relative population density and the probability of colonization of the cut trees. For *I. cembrae* a higher population size was required for colonization than for *T. gabrieli*. The relative population density of both species was positively related to the amount of habitat.

Discussion: The difference in the population size required for colonization between the two studied species might be explained by their different reproductive strategies. The results are discussed in terms of host location and mate finding, and predation pressure.

KEYWORDS

Allee effects, habitat fragmentation, larch bark beetles, larch longhorn beetles, life history traits, *Ips cembrae*, *Tetropium gabrieli*

1 Introduction

Establishments of non-native species in new areas are a major challenge for forest ecosystems around the globe (Vilà et al., 2010; Simberloff et al., 2013), and their number have increased in the last decades (Brockerhoff and Liebhold, 2017). Increasing global trade volumes are a major factor for the increase in the unintended introductions of non-native species (Everett, 2000; Haack, 2006; Meurisse et al., 2019). Although species might be unwittingly transported, only a small percentage of incursions result in establishment (Liebhold and Tobin, 2008). Often incursions fail due to lack of suitable habitat (Brockerhoff and Liebhold, 2017), or too low numbers of arriving individuals (Brockerhoff et al., 2014). The number of arriving individuals is thought to be one of the most important driving forces behind the success of non-native species establishment (Lockwood et al., 2005; Drake and Lodge, 2006; Simberloff, 2009; Chase et al., 2023). After initial establishment in a new region, the spread, and subsequent colonization of new localities in the region, can be expected to be influenced by both population pressure and species-specific traits. In this study, we compare the success of colonization of new localities of two bark- and wood-boring beetle species that have recently established in Denmark and southern Sweden, and that differ regarding their life history traits.

Establishment success and spread of non-native species commonly follows the principles of the Allee effect (Taylor and Hastings, 2005), which describes the relationship between population density and individual fitness (Lewis and Kareiva, 1993; Berec et al., 2007) in relation to population growth. The Allee threshold defines the population density below which population growth will be negative and population establishment will fail. To distinguish species-specific factors contributing to the Allee effect, the Allee effect is divided into component and demographic Allee effects (Stephens et al., 1999). Component Allee effects use life history traits, like mate finding, foraging efficiency and enemy pressure, to understand their impact on the realized population growth rate (Courchamp and Macdonald, 2001; Grünbaum and Veit, 2003; Gascoigne et al., 2009; Tobin et al., 2011; Fauvergue, 2013; Bürgi et al., 2015).

Species life history traits are key behavioral predictors when it comes to success of establishment and spread because they determine how the component Allee effects contribute to the Allee threshold (Ducatez and Shine, 2019; Davies and Robert Britton, 2021). Previous research has shown that dispersal ability, location of suitable habitat (South and Kenward, 2001) and the duration of the flight period (Kolar and Lodge, 2001), are important determinants in population expansions. In addition, the reproduction strategies and the number of produced offspring influence probability of colonization and also establishment and spread (Caswell et al., 2003; Rhainds, 2010; Sekar, 2012; Allen et al., 2017; Demidko et al., 2021). Other factors, such as reduced impact from natural enemies (Roy et al., 2011) and competition (Berec and Mrkvička, 2013), may also affect the probability of establishment and spread (Roy et al., 2011).

Besides differences in life history traits of species, habitat fragmentation is another important factor affecting the establishment and spread of non-native species by influencing dispersal, mortality, foraging efficiency and mate finding (Drake and Lodge, 2006; Dewhirst and Lutscher, 2009; Maciel and Lutscher, 2015; Musgrave et al., 2015; Walter et al., 2016). Different species may be affected at different spatial scales (Holland et al., 2004, 2005; Martin and Fahrig, 2012) or at different phases in the establishment and spread process (Johnson et al., 1992).

In this study, we investigate how relative population densities of the European larch bark beetle, *Ips cembrae* (Heer) (Curculionidae), and the larch longhorn beetle, *Tetropium gabrieli* (Weise) (Cerambycidae), influence their colonization success. Both species are non-native in the study area and breed in the non-native larch trees (genus *Larix*), which occur in highly fragmented forest patches. Bark beetles and longhorn beetles, have become of increasing concern as invasive species as they are easily transported in wooden products and wood packing material used in shipping of goods (Brockerhoff et al., 2006; Haack, 2006; Vilardo et al., 2022).

We ask the following questions for *I. cembrae* and *T. gabrieli*: (i) How does habitat availability (amount of larch in the surrounding landscape), affect the relative population density? (ii) How is the colonization probability related to the relative population density? (iii) What is the relationship between local population densities of beetles and enemy pressure? Our hypotheses are that: (1) the relative population density is influenced by the availability of larch stands in the surrounding landscape, hence we expect higher populations in areas with larger total areas of larch stands; (2) a minimum population size is required for colonization in new localities and this threshold value is influenced by species reproductive strategies; (3) there are no relationships between the relative population densities of the two beetles and their enemies because the enemies are generalist species.

2 Materials and methods

2.1 Study system

Both *I. cembrae* and *T. gabrieli* are native to the Alps in Central Europe where European larch (*Larix decidua*, Mill.) is the host tree. Although Siberian larch (*Larix sibirica*, Ledeb.) occurred naturally in Scandinavia shortly after the last glacial period (Kullman, 1998), it disappeared from the Scandinavian peninsula probably due to changes in the climatic conditions (Larsson-Stern, 2003). In Sweden, the first recorded plantation of European larch dates from 1763 (Schotte, 1917 in Larsson-Stern, 2003). Today, *Larix* x *eurolepis*, (A Henry), a hybrid between the European and the Japanese larch, (*L. kaempferi*, Lamb. Carr), is the most planted larch variety in Sweden (Johansson, 2012; Larsson-Stern, 2003). In southern Sweden (Götaland), larch constitutes 0.2% of the total growing stock including all tree species (Swedish University of Agricultural Sciences, 2022) while in Denmark larch constitutes 3.4% of total growing stock (Nord-Larsen et al., 2020). The increased use of larch in forest plantations is thought to have enabled *I. cembrae* and *T. gabrieli* to spread and establish in new areas in Europe (Ravn, 2012; Lindelöw et al., 2015; Lynikiene et al., 2021; Grégoire et al., 2024).

The current known distribution of *I. cembrae* outside its native area ranges from UK and the Netherlands in the west (Luitjes, 1974; Alexander, 2007), to Denmark and Sweden in the north (Ravn, 2012; Lindelöw et al., 2015; Grégoire et al., 2024). *Ips cembrae* generally colonizes weakened trees. In the native range outbreaks of *I. cembrae* have occurred after storm feelings and snow-breakages (Grégoire and Evans, 2004; Grodzki, 2008). The flight period in central Europe occurs between the end of April to the middle of September (Grucmanová et al., 2014; Holuša et al., 2014). It is not known if *I. cembrae* is attracted to host volatiles although it is known that *I. cembrae* is not attracted to α-pinene (Stoakley et al., 1978). The male initiates colonization of breeding substrate by boring into the bark. After successful colonization, an aggregation pheromone is released by the males that is strongly attractive to both males and females. The males create a mating chamber and is joined by three to five females, which create maternal galleries where they oviposit. After producing a first brood the parent beetles may emerge to establish a second brood (sister brood) in another tree. The species can have one to two generations per year, depending on environmental conditions.

The current distribution of *T. gabrieli* outside its native area ranges from the UK in the west to Denmark and southern Sweden, and recently Lithuania, towards the northeast (Crawshay, 1907; Ericson, 2010; Kahanpää, 2017; Lynikiene et al., 2021). Like *I. cembrae*, *T. gabrieli* is considered a secondary pest, but when larch trees are weakened due to drought it may cause considerable tree mortality (Evans et al., 2004). The flight period starts in May and extends to early August in southern Sweden (Schroeder et al., 2020). Mating may take place right after the emergence of the new generation, possibly even before dispersal, as well as later in the summer (Hanks, 1999). Thus, in contrast to *I. cembrae*, mated females can colonize (i.e., lay their eggs) host trees independent of males, and aggregation with conspecifics to overwhelm tree defence is not required. It is not known if *T. gabrieli* uses host tree volatiles to locate breeding substrate, but it is shown that the species was not attracted to α-pinene and ethanol (Schroeder et al., 2020). However, as it has been demonstrated that a closely related species, *T. fuscum,* responds to a blend of five monoterpenes that are released from stressed spruce trees (Sweeney et al., 2004), it is possible that also *T. gabrieli* is attracted to host volatiles. Males of *T. gabrieli* are thought to release a pheromone (fuscumol) as it was found to attract both males and females (Schroeder et al., 2020). Three other *Tetropium* species are attracted to fuscumol and the pheromone has been demonstrated to be released by the males of two of these species (Silk et al., 2007; Sweeney et al., 2010).

2.2 Study area and stand selection

The study was conducted in Denmark (in the regions Zealand, Funen, South Denmark, Mid and North Jutland), and Southern Sweden (in the regions Skåne, Småland, Blekinge, Kalmar and Halland), during 2020. Both *I. cembrae* and *T. gabrieli* had previously been detected in many of the regions included in the current study (Isacsson, unpublished data; Ravn and Harding, 1995; Ravn, 2012; Lindelöw et al., 2015; Schroeder et al., 2020). With the above mentioned regions, we refer to the administrative entities in Denmark and southern Sweden, except for the island of Funen, which, although administratively belongs to Southern Jutland, we defined as its own entity due to its isolated location. The number of study locations differed between regions spanning from one (Funen) to 14 (Skåne). The first records of *T. gabrieli* in Denmark dates from 1890, with a few subsequent sightings, but with a limited distribution (Hansen, 1996). The first report of *I. cembrae* in Denmark dates from 1995 (Ravn and Harding, 1995) and it is currently established over large parts of the country (Ravn, 2012). The first record of *T. gabrieli* in Sweden occurred in 2007 in the province of Blekinge (Ericson, 2010). *Ips cembrae* was first reported in Sweden in 2011 in the province of Skåne (Lindelöw et al., 2015).

Forty-two stands of hybrid larch were selected, ranging from 0.79 to 9.74 ha in size. All stands were monocultures except for five stands, which had undergrowth trees, consisting mainly of spruce. A subset of the stands had previously been included in a monitoring program for *I. cembrae* conducted by Swedish Forest Agency (Lindelöw et al., 2015) while others were selected from larch stand data provided by forest owners. The minimum distance between selected stands was 1.8 km. For each stand the diameter at 1.3 m height of 40 randomly selected trees (10 trees around each trap position, see below) were measured. Only one standing tree, successfully attacked by *T. gabrieli* in the previous year (2019), was found in two of our focal stands (both in Sweden, one in Blekinge and one in Kalmar region). In the remaining stands, there were no signs of any local hibernating populations of neither *I. cembrae* nor *T. gabrieli*. In the 42 stands, the relative population density of *I. cembrae* and *T. gabrieli* were estimated with pheromone-baited traps. In addition, in 34 stands colonization success was assessed by felling larch trees in early spring that subsequently were inspected for attacks.

To analyze the relationship between amount of larch in the adjacent landscape and the relative population density of *I. cembrae* and *T. gabrieli,* we used two buffer zones with a radius of 500 and 1,000 m respectively, from the center of each focal stand. We chose 1,000 m as the maximum buffer radius not to violate the independence of our observations (i.e., overlapping buffers). In addition to the focal stand, the quantity of larch (in hectares) in the created buffer zones was calculated. We used the quantity of larch as a proxy for presence of suitable breeding material like weakened standing trees, wind-felled trees and logging residues. The mean, standard deviations and range of stand and landscape variables are provided in Table 1. For all stands in Denmark, and a subset of ten stands in Sweden, the forest owners provided detailed maps with all the larch stands around the focal stands. For the remaining stands in Sweden maps were lacking and we estimated the amount of larch based on aerial images Google maps and maps from the Swedish Forest Agency website.[1] The estimates from aerial images were accurate as demonstrated by a check against the detailed maps provided by the ten forest owners in Sweden.

2.3 Relative population density

To estimate the relative population density of *I. cembrae* and *T. gabrieli*, for each of the selected stands, we used two pheromone-baited traps (ECONEX MULTIFUNNEL-12®, Econex SL, Murcia, Spain) for each species. The trapping was standardized by placing the traps inside larch stands, at least 10 m from the stand edge with a minimum distance of 50 m between them. The traps were hung from two 1.8 m wooden poles. A 1:1 mixture of propylene glycol and water was used in the trap jars. Cemsan dispensers (Flügel Gmbh, Germany; active substance 3-Methyl-3-buten-1-ol), were used for attracting *I. cembrae* and aPhinity BSLB dispensers (racemic E-fuscumol, Andermatt Biocontrol, Switzerland) for attracting *T. gabrieli.* The lures were not changed during the experiment since the attraction of the lures should last for the duration of an entire trapping season based on the pheromone data sheet provided by the manufacturer. All traps were baited between 13th and 19th of April 2020 and emptied four times between 12th of May and 27th of July 2020, at approximately 3 weeks intervals. This period includes the major part of the flight activity of *T. gabrieli* as shown in an earlier trapping study conducted in the study area (Schroeder et al., 2020). There is no study on seasonal flight activity of *I. cembrae* from Scandinavia but the considerably slower development rate, and higher temperature

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[1] https://kartor.skogsstyrelsen.se/kartor/?startapp=skador

TABLE 1 Means ± SD, and ranges of the stand variables, landscape variables and trap catches of *Ips cembrae* and *Tetropium gabrieli* for the stands included in the statistical analyses.

Explanatory variables	Unit	Mean ± SD	Range
Ips cembrae			
Mean diameter stand[1]	cm	26.6 ± 4.2	18–35
Mean diameter cut trees[2]	cm	23.5 ± 1.0	22–26
Focal stand area	ha	3.2 ± 1.7	0.2–6.7
Larch area 500 m buffer	ha	2.1 ± 3.3	0–13.2
Larch area 1,000 m buffer	ha	6.8 ± 7.3	0–25.4
Mean trap catches[3]	no	16.3 ± 38.9	0–203.5
Mean *Thanasimus*[3]	no	111.3 ± 103.4	4.5–493.5
Tetropium gabrieli			
Mean diameter stand[1]	cm	26.8 ± 3.8	22–35
Mean diameter cut trees[2]	cm	23.5 ± 1.1	22–26
Focal stand area	ha	3.4 ± 1.7	1–6.7
Larch area 500 m buffer	ha	2.0 ± 3.4	0–13.2
Larch area 1,000 m buffer	ha	6.5 ± 7.7	0–25.4
Mean trap catches[3]	no	2.6 ± 4.3	0–16

[1] Mean diameter of the trees in the focal stand used for trapping.
[2] Mean diameter of the cut trees used in the experiment.
[3] Stands without catches are included as well.

requirements, compared with *I. typographus* (Schebeck and Schopf, 2017) suggests that most of the flight has occurred during the trapping period (c.f. Fritscher and Schroeder, 2022). As the important predator of *I. cembrae*, *Thanasimus* spp., is attracted to bark beetle pheromone, the funnel traps also provided an estimate of their relative population density.

Ips cembrae adults were determined based on morphological characteristics using the identification key from Douglas et al. (2019), and sexed by inspecting the genitalia through dissection. *Tetropium gabrieli* adults were determined based on Pfeffer (1995), and Ehnström and Holmer (2007), and sexed by inspection of the tip of the abdomen (Yanega, 1996). As in many Cerambycidae, a portion of the sixth abdominal tergite is visible beyond the pygidium of males.

2.4 Species colonization success

Both *I. cembrae* and *T. gabrieli* are known to colonize felled trees (Lindelöw et al., 2015; Resnerová et al., 2020; Schroeder et al., 2020). Five larch trees were felled in early spring (2–8 March in Denmark and 16–22 March 2020, in Sweden) in each of the 34 selected stands. Stands with felled trees had a minimum size of 1.8 ha. The minimum distance between the felled trees within stands was 30 m and with a minimum distance of 50 m from the pheromone-baited traps. The trees to be felled were randomly selected (although the distance to the previous felled tree was kept to a minimum of 30 meters). At each trap emptying, the whole length of the trunk, and branches with a diameter exceeding 3 cm of the felled trees, were inspected for the presence of boring dust and entrance holes, indicating possible attacks of *I. cembrae*. If boring dust was found, the bark was removed and species present were determined. At the final inspection (15–25 September), on every half meter of the trunk, pieces of bark were peeled off with an axe, to check for possible larval galleries of *Tetropium* (not possible to determine to species level from galleries) and *I. cembrae* attacks, as well as other non-target bark- and wood-boring beetles.

From each tree with *I. cembrae* or *Tetropium* attacks, one 1.2 m log was cut for rearing of adult beetles and enemies. As few trees were colonized by *I. cembrae* no data from rearing of this species is presented. All collected logs were placed in insect nets and stored outside the laboratory in Uppsala during winter. On 30 and 31 March 2021, one 60 cm stem section was cut from each log and waxed at both ends to prevent desiccation. Each stem section was hung under a translucent roof outside, in a cotton sack, with a plastic collection funnel attached to a collection jar located at the bottom of the sack. The collection jars were emptied throughout the summer. The data collection was completed by the end of August when all the logs were debarked, and dead adults and larvae were recorded. The only *Tetropium* species emerging was *T. gabrieli*. Emerging parasitoids belonged to either *Braconidae* or *Ichneumonidae* family based on morphological characteristics (see Schroeder et al., 2020 for more details). Parasitism rates of *T. gabrieli* larvae was estimated for each stem section by dividing the number of emerging parasitoids by the sum of emerging *T. gabrieli* adults and parasitoids [we assume that each emerged parasitoid killed one larva, based on the life history of the species found to parasitize *T. gabrieli* previously (see Schroeder et al., 2020)].

2.5 Statistical analyses

All statistical analyses were performed using R ver. 4.3.3 (R Core Team, 2024). For the analyses, locations without any catches or lacking colonization by either species were excluded. These locations were assumed to be outside the distribution area of the species based on the results from this and previous studies (Ravn and Harding, 1995; Ravn, 2012; Lindelöw et al., 2015). Thus, for the analyses of trap catches, 36 locations remained for *I. cembrae* and 32 locations for *T. gabrieli*. For the analyses of tree colonization, 30 locations remained for *I. cembrae* and 26 for *T. gabrieli*.

2.5.1 How does habitat availability affect the relative population density?

To test the effect of focal stand characteristics, and the amount of larch in the surrounding landscape, on the relative population density (i.e., trap catches), generalized linear mixed models with negative binomial distribution were fitted. Two separate models were run for each species. For each model, location was the level of replication, with 36 replicates for *I. cembrae* models and 32 for *T. gabrieli*. Size of the focal stand and the quantity of larch within a 500 m buffer or a 1000 m buffer were explanatory variables for the response variable trap catches. The negative binomial distribution was used instead of Poisson distribution as overdispersion was detected when inspecting the residuals (dispersion_glmer; blmeco package; Korner-Nievergelt et al., 2015). In all the models, Region was included as a random factor to account for potential difference in the trap catches related to different forestry practices between regions (glmer.nb(); lme4 package, Bates et al., 2015). Because we encountered problems with model convergence we fitted the model with adaptive Gauss-Hermite quadrature instead of Laplace approximation and (nAGQ) was set to zero (Olver et al., 2010). Anova type II Wald chi-square test was used to test for significance (Anova() function; car package; Fox and Weisberg, 2019).

2.5.2 How does colonization probability relate to the relative population density?

To examine the effect of mean tree diameter of the cut trees on the mean number of trapped beetles, as well as the mean number of trapped females and males (in three separate models), generalized linear models with a negative binomial distribution were applied. Location was the level of replication, with 30 replicates for *I. cembrae* models and 26 for *T. gabrieli*. Again, the negative binomial distribution was used instead of Poisson distribution as overdispersion was detected when inspecting the residuals, (dispersiontest; AER package; Kleiber and Zeileis, 2008). Anova type II Wald chi-square test was used to test for significance (Anova() function; car package; Fox and Weisberg, 2019). Unpaired *t*-test was used to test whether there was a difference in the mean population size between the locations with colonized trees compared to the locations without colonization för *I. cembrae*. For the reared *Tetropium*, chi-square test was used to test whether there was a difference in the sex ratio of emerged beetles.

2.5.3 What is the relationship between the relative population density of beetles and enemy pressure?

To assess the relationship between the relative population density of *I. cembrae* and of its enemy *Thanasimus* spp. (from trap catches) we fitted a generalized linear model with quasipoisson distribution. Quasipoisson distribution was used instead of Poisson as overdispersion was detected when inspecting the residuals (dispersiontest; AER package; Kleiber and Zeileis, 2008). To assess the relationship between the numbers of *T. gabrieli* larvae in the stem sections and proportion parasitism we fitted a generalized linear model with quasibinomial distribution, where proportion of parasitized individuals was used as the response variable and the number of emerged beetles plus emerged parasitoids as the explanatory variables. A similar model was used to test the relationship between the relative population density of *T. gabrieli* (trap catches) and proportions parasitized in stem sections. Each log was seen as an individual replicate. For the second model on the relationship between the proportion parasitized and the local population from trap catches, the proportion parasitized beetles from the logs from the same location were pooled against the average trap catch from the respective location. Anova type II test was used to test for significance (Anova() function; car package; Fox and Weisberg, 2019).

3 Results

In total, 1185 *I. cembrae* were caught in 19 larch stands out of the total 36 used in the analyses for trapping (Figure 1A). Of these 800 beetles were sexed that resulted in 46% trapped males and 54% trapped females. The mean (±SE) number of trapped beetles per trap and location was 16.3 (±6.5). At two different locations *I. cembrae* individuals (two males and six females) were caught in the traps baited with *T. gabrieli* pheromone (hence cross attraction was negligible). These individuals were not included in the analyses.

In total 165 *T. gabrieli* were caught in 18 out of 32 larch stands (Figure 1B). The mean number of trapped beetles per trap and location was 2.6 (±0.8). No *T. gabrieli* was caught in the traps baited with *I. cembrae* pheromones. Both native *Tetropium* species, the brown spruce longhorn beetle *T. fuscum* (F.) and the European longhorn beetle *T. castaneum* (L.) were caught in the traps as well, however, none of the species colonized any of the cut trees. In total, 157 *T. fuscum* and 359 *T. castaneum* were caught.

3.1 How does habitat availability affect the relative population density?

For *I. cembrae*, no significant correlation was found between any of the explanatory variables and the size of the local population in the model including the 500 m buffer zone. However, a positive significant relationship was found between relative population density and the amount of larch within the 1,000 m buffer (Table 2). Region explained some of the variance in both the 500 and 1,000 m model (between 0.88 and 9.06%, see Table 2). In both models for *T. gabrieli*, the relative

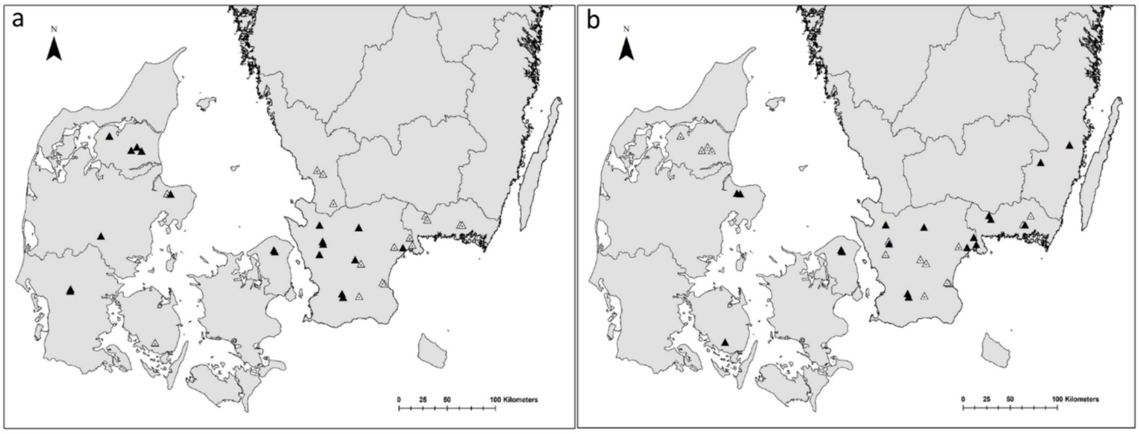

FIGURE 1
Locations of experimental stands with pheromone traps in Denmark and Sweden for **(A)** *Ips cembrae* (36 replicates) and **(B)** *Tetropium gabrieli* (32 replicates) which were considered to be within the species distribution areas and thus included in the analyzes. Black triangles represent locations with trapped beetles, empty triangles represent locations with no beetles trapped.

TABLE 2 Anova (type II test) and summary table for generalized linear mixed models testing the difference in number of beetles (*Ips cembrae* and *Tetropium gabrieli*) caught in traps against the size of the focal area and the total amount of larch within 500 and 1,000 m around the focal stand.

Model and variables included	X^2	DF	Est	SE	z	Pr(>|z|)
Ips cembrae 500 m						
Intercept			1.60	1.50	1.08	0.29
Focal stand area	0.44	1	−0.16	0.25	−0.67	0.51
Larch area 500 m buffer	0.29	1	0.08	0.14	0.53	0.60
Random factor	Variance	StD				
Region	9.06	3.01				
Ips cembrae 1,000 m						
Intercept			0.06	1.48	0.01	0.97
Focal stand area	0.00	1	−0.01	0.24	−0.06	0.96
Larch area 1,000 m buffer	7.77	1	0.17	0.06	2.77	**0.005**
Random factor	Variance	StD				
Region	8.19	2.86				
Tetropium gabrieli 500 m						
Intercept			−0.32	0.81	−0.40	0.69
Focal stand area	11.13	1	0.56	0.17	3.34	**<0.001**
Larch area 500 m buffer	1.67	1	−0.15	0.12	−1.30	0.20
Random factor	Variance	StD				
Region	0.88	0.93				
Tetropium gabrieli 1,000 m						
Intercept			−1.50	1.05	−1.44	0.15
Focal stand area	16.39	1	0.69	0.17	4.05	**<0.001**
Larch area 1,000 m buffer	1.12	1	0.05	0.04	1.06	0.29
Random factor	Variance	StD				
Region	3.27	1.81				

Region was used as a random factor. Two different models were run for each species. Significant values are indicated in bold.

population density showed a significant positive relationship with the size of the focal stand (Table 2), but not with the quantity of larch in the surrounding landscape.

3.2 How does colonization probability relate to the relative population density?

Ips cembrae colonized four felled larch trees, distributed among two of the 30 stands included in the analyses (Figure 2A). The two locations with colonized trees were those with the highest trap catches (Figure 2B) and, there was a significant difference in the mean (±SE) number of trapped beetles between the two locations with colonized trees and the 17 locations without colonized trees (287.5 ± 59.7 versus 35.4 ± 5.8, t-test, $p < 0.001$). No colonization occurred in stands with mean trap catches below 80 beetles. No standing trees were attacked by either of the species in the focal stands in the year of the experiment.

Tetropium gabrieli colonized 46 felled larch trees, distributed over 12 of the 26 stands included in the analyses (Figure 3A). The number of colonized trees varied from one to five per location. All five trees were colonized in 30% of the locations. Colonization occurred at mean catches as low as 0.5 beetles per stand, and took place in all stands with mean trap catches of two beetles or more (Figure 3B).

The number of felled trees colonized by *T. gabrieli* was significantly and positively related to the mean number of trapped individuals, and the mean number of trapped females and males (Table 3). We found a negative significant relationship between mean diameter of the cut trees and the number of colonized trees in the models including the mean number of trapped individuals and the mean number of trapped males.

A total of 676 *T. gabrieli* emerged from 42 stem sections out of the total 46 used in the rearing experiment. The mean (±SE) rate of emergence per stem section was 16.1 (±3.2) beetles. There was no significant difference between the number of emerged males and females ($p = 0.16$, chi-square test).

3.3 What is the relationship between the relative population density of beetles and enemy pressure?

A total of 7684 *Thanasimus* beetles (7649 *T. formicarius* and 35 *T. femoralis*), were caught in the *I. cembrae* traps at the 36 locations. There was no significant relationship between the mean numbers of trapped *I. cembrae* and *Thanasimus* (Figure 4). The ratio between trapped

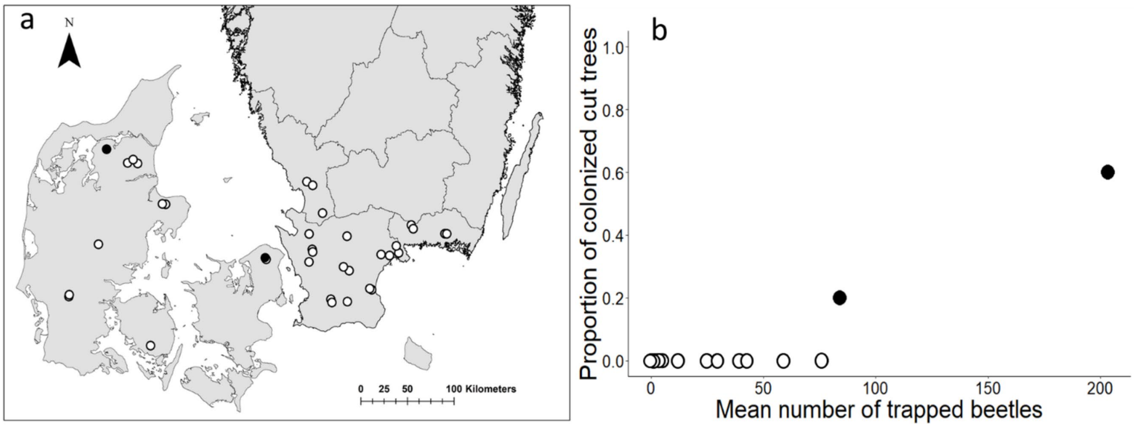

FIGURE 2
(A) Locations of experimental stands with cut trees in Denmark and Sweden, which were considered to be within the distribution area of *Ips cembrae*. Black circles represent locations with colonized cut trees; white circles represent locations without colonized cut trees. **(B)** Relationship between the mean number of trapped *I. cembrae* and the proportion of colonized cut trees per location (30 replicates).

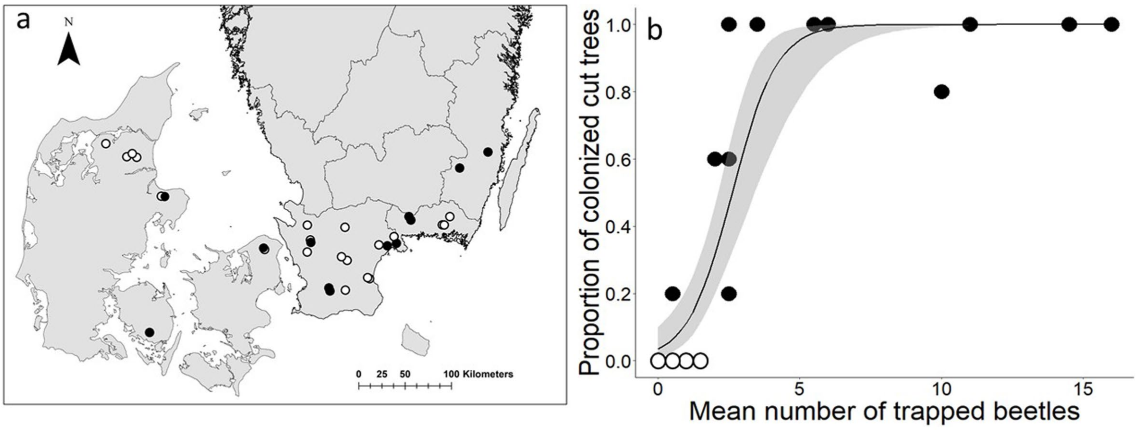

FIGURE 3
(A) Locations of experimental stands with cut trees in Denmark and Sweden which were considered to be within the distribution area of *Tetropium gabrieli*. Black circles represent locations with colonized cut trees; white circles represent locations without colonized cut trees. **(B)** Relationship between the mean number of trapped *T. gabrieli* and the proportion of colonized cut trees per location (26 replicates). Grey shaded areas represent the 95% confidence intervals.

Thanasimus/*I. cembrae* was 6.6 to 1. One location was removed from the model as it was considered an outlier; however it is included in the figure.

A total of 184 parasitoids emerged from the stem sections colonized by *T. gabrieli*. The average rate of parasitism was 30.1% (SE = 5.0%). There was no significant relationship between the proportion of parasitized *T. gabrieli* larvae and the density of larvae (Figure 5A) or the proportion of parasitized larvae and the mean number of trapped *T. gabrieli* (Figure 5B).

Three other bark- and wood-boring species emerged from the *T. gabrieli* colonized stem sections, *Serropalpus barbatus* (Schaller), (Coleoptera, Melandryidae), *Urocerus gigas* (L), (Hymenoptera, Siricidae) and *Cryphalus* sp. (Coleoptera, Scolytinae). A total of 121 *S. barbatus* adults emerged from 13 of the 47 stem sections, 28 *U. gigas* emerged from seven of the sections and two adults of *Cryphalus* sp. were found after debarking one stem section at the end of the rearing experiment.

4 Discussion

The aim of the study was to compare the colonization success of *I. cembrae* and *T. gabrieli*, two non-native beetle species with markedly different reproductive strategies. Our results provide important insights into the relationship between the relative population density and habitat availability, and how colonization probability is related to the relative population density. The relative population density of both *I. cembrae* and *T. gabrieli* was, as hypothesized, positively influenced by the amount of habitat but at different spatial scales. For both species colonization probability increased with relative population density. For *I. cembrae* a considerably higher population size was required for colonization than for *T. gabrieli*, which was according to our predictions, and may be explained by differences in reproductive strategy. As expected, there was no relationship between

TABLE 3 Anova (type II test) and summary table for generalized linear models testing the difference in the number of colonized trees by *Tetropium gabrieli* against the mean number of trapped individuals, mean number of trapped females and males and mean diameter of the cut trees.

Model and variables included	X^2	DF	Est	SE	z	Pr (>|z|)
Intercept			12.80	6.16	2.08	**0.04**
Mean diameter	5.11	1	−0.57	0.27	−2.14	**0.03**
Mean number of trapped individuals	20.52	1	0.22	0.04	5.01	**<0.001**
Intercept			10.47	6.09	1.72	0.09
Mean diameter	3.27	1	−0.47	0.26	−1.78	0.08
Mean number of trapped females	17.16	1	0.32	0.07	4.64	**<0.001**
Intercept			16.99	6.86	2.48	**0.02**
Mean diameter	7.97	1	−0.75	0.30	−2.50	**0.02**
Mean number of trapped males	20.54	1	0.62	0.12	5.03	**<0.001**

Significant values are indicated in bold.

population sizes of the beetles and their enemies, likely because both studied species are mainly affected by generalist predators.

4.1 How does habitat availability affect relative population density?

Our results show that relative population density of both species was positively related to habitat availability (see also Schroeder, 2013; Kautz et al., 2016; Gohli et al., 2024). However, the species differed in the spatial scale of their response to habitat quantity: *Tetropium gabrieli* showed a positive response to the size of the focal stand, in both the 500 m and 1,000 m buffer models. Whereas *I. cembrae* showed a positive response to the quantity of larch at the 1,000 m buffer. The result for *I. cembrae* might be explained by the presence of local populations in larch stands within the 1,000 m radius resulting from the previous year. The positive relationship of *T. gabrieli* with the size of the focal stand was not only due to the local hibernating populations in two of the stands. *Tetropium gabrieli* still showed a positive response to the size of the focal stand even after removing the only two localities with hibernating populations. Research has shown that responses to habitat availability at different spatial scales is often species specific due to different life history traits (Holland et al., 2004).

4.2 How does colonization probability relate to the relative population density?

Both species showed a positive relationship between the relative population density and the probability of colonization of the cut trees. At too low population sizes no colonization occurred. This indicates the presence of the component Allee effects for host finding (i.e., finding of suitable breeding material) and/or mate finding for both species. For the bark beetle *I. cembrae,* a much higher relative population density was required for colonization than for the longhorn beetle *T. gabrieli*. At the same time, the mean population size of *I. cembrae* in the colonized localities was significantly higher than in localities without colonization. The large difference in minimum relative population density (i.e., trap catch) required for colonization events strongly indicates that lower population density is required for *T. gabrieli* than for *I. cembrae*. Reproductive strategy could be an explanation for this difference. *Tetropium gabrieli* females can, after mating, oviposit in many substrates independent of males. Whereas, *for I. cembrae,* a male must first find the object and then successfully attract a female (i.e., the female cannot by herself colonize an object). In addition, each female colonizes potentially two objects. However, when comparing the trap catches of the two species, we need to be aware that it is hard to know if both species are equally attracted to the pheromone bait used. Regardless of the magnitude of the trap catch colonization of the felled logs is, however, a good indication of reproductive activity for both species.

4.3 What is the relationship between local population densities of beetles and enemy pressure?

Based on the trap catches, there was no relationship between the relative population density of *I. cembrae* and the predator *Thanasimus* spp. *Thanasimus formicarius*, the dominant species preys on over 20 species, and it is considered one of the most important predator for many bark beetle species, including *I. cembrae* (Schroeder, 2001; Kenis et al., 2004; Warzée and Grégoire, 2006). Being generalists, *Thanasimus* spp. densities most likely depend on the presence of other potential prey in the area. At low population densities of the prey generalist predators are thought to be important predators to maintain the population at low densities. In the present study, the average catch of *Thanasimus* was almost five times higher than that of *I. cembrae*. When present *Thanasimus* spp. adults feed on adult bark beetles and their larvae feed on bark beetle larvae under the bark. Thus, one *Thanasimus* beetle could kill more than one bark beetle and therefore, predation pressure at low density of *I. cembrae* could be high. In our study, this could mean that the predator may have prevented some colonization in localities with small populations of *I. cembrae* by being attracted to the felled trees by host volatiles and preying on *I. cembrae* males prior to boring into the bark. Following the start of pheromone production the predator may also prey on the *I. cembrae* females before they have managed to enter the mating chamber. Our findings indicate that the potential presence of a component Allee effect of predation pressure could influence successful colonization and establishment of *I. cembrae* negatively. Using trap catches enables us only to look at the presented relationship, other natural enemies, like parasitoids and woodpeckers, could be important predators as well. Unfortunately, we could not measure this because of the minimum colonization of our felled logs.

For *T. gabrieli* there was no significant relationship between neither the relative population density and the proportion of larvae parasitized, nor the number of larvae in the stem sections and the proportion of them that were parasitized. Hence, there does not seem to be a component Allee effect of enemy pressure on reproductive success after colonization. Although the rate of parasitism in our study was higher compared to Schroeder et al.

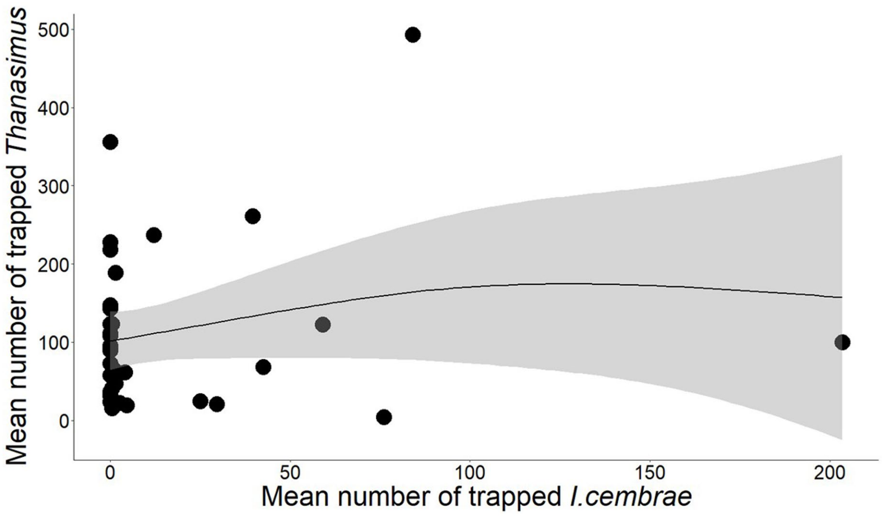

FIGURE 4
Relationship between the mean number of trapped *Thanasimus* spp. and the mean number of trapped *Ips cembrae*. Only locations with both *I. cembrae* and *Thanasimus* spp. were included in the graph. Each dot represents a different location. The location on the right hand side of the graph was considered an outlier, thus removed from the analysis. Grey shaded areas represent the 95% confidence intervals.

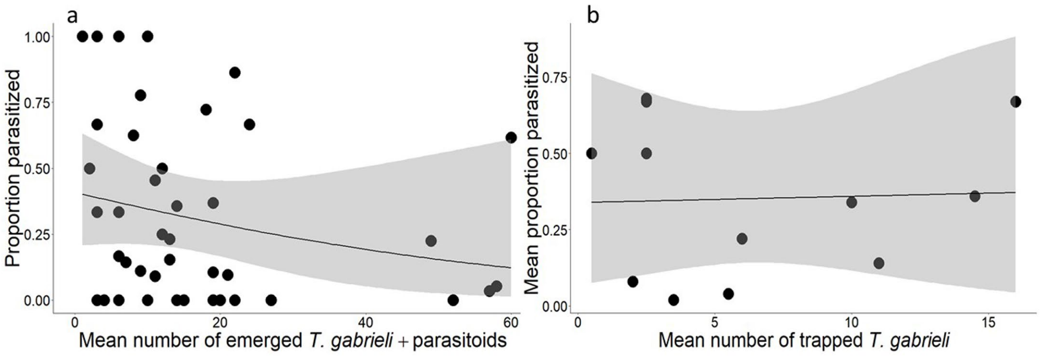

FIGURE 5
Relationship between **(A)** the number of emerging *T. gabrieli* plus emerging parasitoids and the proportion of parasitized *Tetropium gabrieli* larvae from the rearing experiment (each dot represent one stem section), and **(B)** mean number of trapped *T. gabrieli* per stand and the mean proportion of parasitized *T. gabrieli* larvae from the rearing experiment (each dot represent the mean values for stands with colonization).

(2020), it was still lower than the rate of parasitism reported from its native range (Kenis and Hilszczanski, 2004). In Schroeder et al. (2020) only three parasitoids species, classified as native, were found to parasitize the *T. gabrieli* larvae. All these species are also associated with the native *T. fuscum* and *T. castaneum*. The parasitoids of the present study were not determined to the species level but belonged to the same families as the ones in the study by Schroeder et al. (2020). The limited presence of other species under the bark suggests that *T. gabrieli* larvae faced no competition for food (phloem) from other species, as *S. barbatus* and *U. gigas* larvae feed in the wood instead.

To show a direct effect on population size (the demographic Allee effect) one often needs to investigate those factors that affect population size (component Allee effects) (Lewis and Kareiva, 1993; Berec et al., 2007). In this study, we investigated host location, mate finding and predation pressure as components of the demographic Allee effect. Our study species exhibit distinct ecological differences, and we find that enemy pressure, as well as the mechanisms for host and mate finding, are specific to each species. Based on the natural enemies included in our study, we suggest that component Allee effect involving enemy pressure is more important for *I. cembrae* than for *T. gabrieli* in the way it affects their success in population establishment and thus invasion of a new previously uncolonized area with fragmented habitat.

Species establishment and spread are processes that happen over time. Time series collected by the Swedish Forest Agency (Issacson unpublished data) show that trap catches of *I. cembrae* vary per year and it is general knowledge that based on weather conditions, insect populations can show large variation in densities between years. In that respect, our study is a snapshot in time. To circumvent replication over time, we designed the experiment at a large spatial scale including areas where the species were fully established (Denmark) and areas where evidence of establishment was more tentative (southern Sweden).

Based on the geographical scale and the extensive spatial replication, we believe that our results represent those ecological processes influencing population establishment we are aiming to measure.

5 Conclusion

In conclusion, as it has also been shown by other studies (Blackburn et al., 2009; Sekar, 2012; Ducatez and Shine, 2019), species ecology can be a strong indicator for establishment likelihood after introduction. For bark- and wood-boring species with mating strategies where many individuals are required, propagule pressure will be of higher importance than for species where females may disperse when they have already been mated. This species-specific knowledge needs to be integrated in risk assessments for species invasions and can help to prioritize monitoring efforts and subsequent actions to prevent species invasions. However, more studies are needed to fully understand such establishments and spread of non-native species.

Data availability statement

The datasets generated during and/or analyzed during the current study are available from the corresponding author on reasonable request.

Ethics statement

Ethical approval was not required for the study involving animals in accordance with the local legislation and institutional requirements because not required for our studied organisms (beetles).

Author contributions

DC: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Writing – original draft. MK: Conceptualization, Formal analysis, Methodology, Writing – review & editing. CB: Funding acquisition, Writing – review & editing. HR: Writing – review & editing. MS: Conceptualization, Funding acquisition, Methodology, Writing – review & editing.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Generative AI statement

The author(s) declare that no Generative AI was used in the creation of this manuscript.

Publisher's note

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