Department of Physics, Chemistry and Biology

Master Thesis

Trapped in the forest:

The longhorn beetle *Tragosoma depsarium* L. in south-east Sweden

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Sammanfattning/Abstract:

The rare and elusive wood-living beetle *Tragosoma depsarium*, once widespread all over Sweden, is associated with large, sun-exposed pine logs required for breeding. Due to modern forestry and fire suppression, this type of substrate has become so rare in the landscape that the beetles' existence in Sweden is threatened. Recently, the female sex pheromone of this species was synthesised, providing a new method to monitor beetle populations using pheromone traps. Such a method was used in the current study to relate the presence-absence of *T. depsarium* with different landscape variables at different scales; 100, 500, 1000 and 2000 meters, respectively. The occurrence of *T. depsarium* in Östergötland County was associated with the amount of protected areas and clear-cuts at 500 and 1000 meters, respectively. Additionally, the amount of pine forest within 2000 m from the trap showed a weak, positive effect on the number of beetles. In the whole south-east boreo-nemoral zone of Sweden, a positive correlation between beetle occurrence and protected areas were found at 2000 m together with a negative correlation for volume pine wood within 100 m. Also, emergence holes on pine logs around each trap were strongly associated with beetle occurrences. To conclude, using pheromone traps were an easy way of detecting beetles. Although the number of caught *T. depsarium* varied greatly over time, the sampling period matched the flight period well. For long-term survival of this beetle, the forests must contain breeding substrates and be opened up through prescribed burning, selective cutting and active forestry.

Nyckelord/Keyword:

Tragosoma depsarium, scale, pine, pheromone, landscape variables

Content

1 Abstract

The rare and elusive wood-living beetle *Tragosoma depsarium*, once widespread all over Sweden, is associated with large, sun-exposed pine logs required for breeding. Due to modern forestry and fire suppression, this type of substrate has become so rare in the landscape that the beetles' existence in Sweden is threatened. Recently, the female sex pheromone of this species was synthesised, providing a new method to monitor beetle populations using pheromone traps. Such a method was used in the current study to relate the presence-absence of *T. depsarium* with different landscape variables at different scales; 100, 500, 1000 and 2000 meters, respectively. The occurrence of *T. depsarium* in Östergötland County was associated with the amount of protected areas and clear-cuts at 500 and 1000 meters, respectively. Additionally, the amount of pine forest within 2000 m from the trap showed a weak, positive effect on the number of beetles. In the whole south-east boreo-nemoral zone of Sweden, a positive correlation between beetle occurrence and protected areas were found at 2000 m together with a negative correlation for volume pine wood within 100 m. Also, emergence holes on pine logs around each trap were strongly associated with beetle occurrences. To conclude, using pheromone traps were an easy way of detecting beetles. Although the number of caught *T. depsarium* varied greatly over time, the sampling period matched the flight period well. For long-term survival of this beetle, the forests must contain breeding substrates and be opened up through prescribed burning, selective cutting and active forestry.

2 Introduction

Today about one third of the land on earth is covered by forest, but it is rapidly decreasing at a rate of more than 5 million hectares annually (FAO 2013). In total, we have lost about half of the earth's original forest cover (Bryant et al. 1997). The loss causes problems for many, but not all, organisms when the natural forests they live in become degraded fragments or unsuitable tree plantations. In boreal coniferous forests, some species of for example saproxylic beetles are adapted to natural large-scale disturbances but could also be found in man-made disturbed areas such as clear-cuts (Ahnlund & Lindhe 1992, Davidsson 2014, Evans 1966, Laestander 2014, Muona & Rutanen 1994, Wikars 1992). The beetles take advantage of the more open and warmer habitats that these disturbed areas offer, provided that suitable substrates in the form of dead or dying wood exists (Gibb et al. 2006a). Large-scale natural disturbances in northern Europe are primarily storms, insect outbreaks and fires (Lindbladh et al. 2013), where fire is considered to be the most important (Esseen et al. 1997, Toivanen et al. 2014). Forest fires were frequent until about 1770 in southern Sweden (Niklasson & Drakenberg 2001), whereas in northern Sweden the frequency of fires did not drop significantly for another 100 years, around 1860 (Niklasson & Granström 2000, Zackrisson 1977). After a forest fire, new substrates are created and existing pine logs are blackened with soot which, together with more open and sunlit forest floor, favours many beetles of which *T. depsarium* is one (Gärdenfors et al. 2002, Wikars 2003). Today fires are not only less common in Swedish forests (Lindbladh et al. 2003, Niklasson & Granström 2000), but also in other Scandinavian coniferous forests (Toivanen et al. 2014). This is a result of restricted burning of grazing land as well as a long period with relatively organised forestry starting when the value of timber was recognised (Niklasson & Drakenberg 2001, Zackrisson 1977). Thus, human-induced habitat loss and fragmentation has together with modern fire suppression caused difficult challenges for many species while creating a few new opportunities for a smaller number of species.

The efficiency and mechanisation within the Fennoscandian forestry is now one of the highest in the world (Esseen et al. 1997), and it began in Sweden when the modern large-scale silviculture practice, with clear-felling forest operations and subsequent tree plantation and management, became the main form of forestry in the 1950's (Albrektson et al. 2012). The management of the forest, particularly fire suppression, increases the number of fire-sensitive and shadow tolerant species such as Norway spruce (*Picea abies*) at the cost of fire-resistant and pioneer species such as Scots pine (*Pinus sylvestris*) (Linder et al. 1997, Linder & Östlund 1998, Niklasson & Drakenberg 2001, Zackrisson 1977). This is not unique to Sweden as the same pattern also emerges in the fire-adapted giant sequoia forests of North America (Swetnam 1993).

Another more direct effect of forest management is the huge loss of coarse woody debris (CWD) seen in all stages of managed forests compared to old-growth forests (Siitonen et al. 2000), which negatively affects saproxylic beetles and other organisms dependent on the CWD (Siitonen 2001). The loss of suitable substrates is ongoing, and this have led to the state where most species associated with dead wood are restricted to live in remnants of natural or old-growth forest (Gärdenfors 2010). To facilitate the survival of some species affected by the loss of CWD, high (several meters) stumps of trees are often saved on clear-cuts since 1990's for conservation purposes with good results (Ahnlund & Lindhe 1992, Djupström et al. 2012, Fries et al. 1997, Hjältén et al. 2010, Weslien et al. 2014). This is especially done in certified forestry such as FSC (http://se.fsc.org/), with positive effects on certain red-listed saproxylic beetles such as *Peltis grossa* (Djupström et al. 2012). Another way is retention forestry, where whole clusters of trees are saved to alleviate the negative impacts of clear-cuts (Fedrowitz et al. 2014, Gustafsson et al. 2010). The density and amount of substrates needed in today's forests for conservation purpose is affected by a species' dispersal abilities, where poor dispersers need a continuous supply of substrate at the local, e.g. forest stand, level while good dispersers might be satisfied with a supply at a larger scale.

Scale is also an important factor to take into consideration when assessing to what extent fragmentation and habitat loss affect animal populations. Fragmentation splits suitable habitats where a species can live into several smaller areas of equal size separated by unsuitable habitat (Fahrig 2003). However, fragmentation is more commonly accompanied by habitat loss where the suitable habitat disappears, resulting in divided areas with a smaller total size. Different species of for example oak-living saproxylic beetles, utilise resources within widely different spatial scales, from 52 meters up to 5284 meters (0.85-8772 ha) (Bergman et al. 2012). Therefore, they are unequally sensitive to fragmentation. The beetles with the shortest dispersal will likely not be affected by fragmentation at the landscape scale in the short term if the woodland where they live becomes isolated from other similar areas (Gibb et al. 2006b), as they do not move outside the area, but it could have an effect in the long-term (Franc et al. 2007). The potential intermediate or long-dispersers on the other hand are affected by what is going on outside the local area where they currently live (Gibb et al. 2006b). In these cases, a larger scale is needed to explain occurrences and distribution of populations. Noteworthy is also that drawing conclusions from investigated factors based on merely a single scale may in some cases lead to a misleading understanding (Cushman & McGarigal 2004). Additionally, the relevant scale is also in many cases dependent on the size of the study animal, demonstrated with examples of two unrelated species; the pitcher plant midge (*Metriocnemus knabi*) with a poor flight ability who uses resources mainly within a 20-100 meter radius (0.13-3.14 ha) (Millette & Keyghobadi 2015) and the grizzly bear who could search for new good habitats within a 160,000 ha area (Nams et al. 2006). This shows the importance of knowing the study species in order to apply the appropriate scale(s) and to correctly assess the effects of fragmentation and habitat loss.

Currently 855 (19 %) out of more than 4,400 beetle species are red-listed in Sweden (ArtDatabanken 2015) whereof a clear majority are associated with different stages of senescence or decay in trees, from the old to the dead (Gärdenfors 2010). Some threatened beetles are larger and more appealing than others. If such a beetle also coexists with several other red-listed species, it has not only the potential to become a flagship species to raise public interest in this group of animals, but also to be an umbrella species in conservation efforts (Barua 2011). One of these interesting and important species is the longhorn beetle *Tragosoma depsarium* (Linnaeus 1767). This red-listed, large beetle is 16-32 mm long (Figure 2, Gärdenfors et al. 2002) and develops inside sun-exposed, bark free logs of Scots pine (Palm 1951, Wikars 2003). It was once widespread across most of Sweden, but has relatively recently declined dramatically and is now thought to be locally extinct in some provinces in Sweden (Gärdenfors et al. 2002). A continued lack of suitable breeding substrates predicts a further decrease in the Swedish population (Wikars 2004). One reason for such a decrease is that many locations only harbour very small subpopulations, each with a tiny chance of long-term survival (Gärdenfors et al. 2002). If the public, and especially land owners, starts to recognise the value of threatened beetles and other insects through increased awareness from e.g. flagship or umbrella species programs, there is a higher chance to successfully stop or even reverse the human-induced declines in many of the threatened populations.

The aim of this study was to first map the current distribution of this beetle on the mainland in south-eastern Sweden. Then, in a second step, the data on the presence-absence of the beetle is related to different landscape attributes on both a large landscape scale and a small, site-specific scale. The purpose is to find certain landscape elements or features that can explain the presence of the beetle.

3 Material & methods

3.1 Study species

The worldwide distribution of *Tragosoma depsarium* ranges from the mountainous areas in the middle and south of Europe to eastern Russia (Ehnström & Wikars, 2010). It is a red-listed long-horned beetle (Coleoptera: Cerambycidae) currently classified as Near Threatened (NT) in Sweden (ArtDatabanken 2015) after being classified as vulnerable (VU) in previous years (Gärdenfors 2010). It is not known from Denmark (Gärdenfors et al. 2002), but it is classified as VU in Norway and Finland

(National Red Lists - IUCN 2015). *T. depsarium* is locally distributed in Sweden from the county of Kalmar in the south up to Norrbotten County in the north (Gärdenfors 2010), with the exception of the Scandinavian mountain range area (Ehnström & Wikars 2010, Gärdenfors et al. 2002).

The eggs are almost exclusively laid deep inside small cracks in sun-exposed logs of Scots pine (*Pinus sylvestris*) or, rarely, Norwegian spruce (*Picea abies*) (Ehnström & Wikars 2010, Palm 1951, Wikars 2003, Wikars 2004). The best substrate for the larvae's development is sun-exposed, 10-15 years old, bark-free, large-diameter pine logs with a hard silver-coloured sapwood surface located in a dry or semi-dry environment (Palm 1951, Wikars 2003, Wikars 2004). It has been estimated to take about four years for the beetle to develop from an egg into an adult, since at least four different sizes of the larvae can be found within the same pine log at the same time (Palm 1951). Palm also points out that the larvae presumably do not have a predetermined time of development before metamorphosis, but rather adjust the larval stage to environmental conditions and food supply.

A log that becomes too shaded or gets infected by brown-rotting fungi, which happens quickly in younger pine logs, is rapidly abandoned and any larvae still inside are often found dead (Wikars 2003). Adult larvae pupate in late June and hatches during July in the southern parts of Sweden (Ehnström & Wikars, 2010). When the adult beetle eventually leave the log, it creates a characteristic, oval, exit hole up to 12 mm wide with rough edges that cannot be mistaken for any other species on the Scandinavian mainland (Gärdenfors et al. 2002, Figure 1).

Figure 1. A fresh exit hole from an adult T. depsarium *in a silver-coloured pine log, created between July 16th and July 18th 2014. Note the typical size (12 mm) and rough edges.* Photo: Alexander Nilsson

Figure 2. A male T. depsarium *about 23 mm long (without the antennae) found in the pheromone trap next to the emergence hole in Figure 1 on July 18th 2014.* Photo: Alexander Nilsson

3.2 Study area

The primary study area was the county of Östergötland, located in south east Sweden (Figure 3). Additionally, study areas from the county of Kalmar were included in this study together with a few scattered data from the counties of Södermanland and Stockholm, north of Östergötland (Figure 3). The sampling sites were located in dry-mesic Scots pine (*Pinus sylvestris*) dominated forests, forest edges or slow-growing pine forests on hilltops.

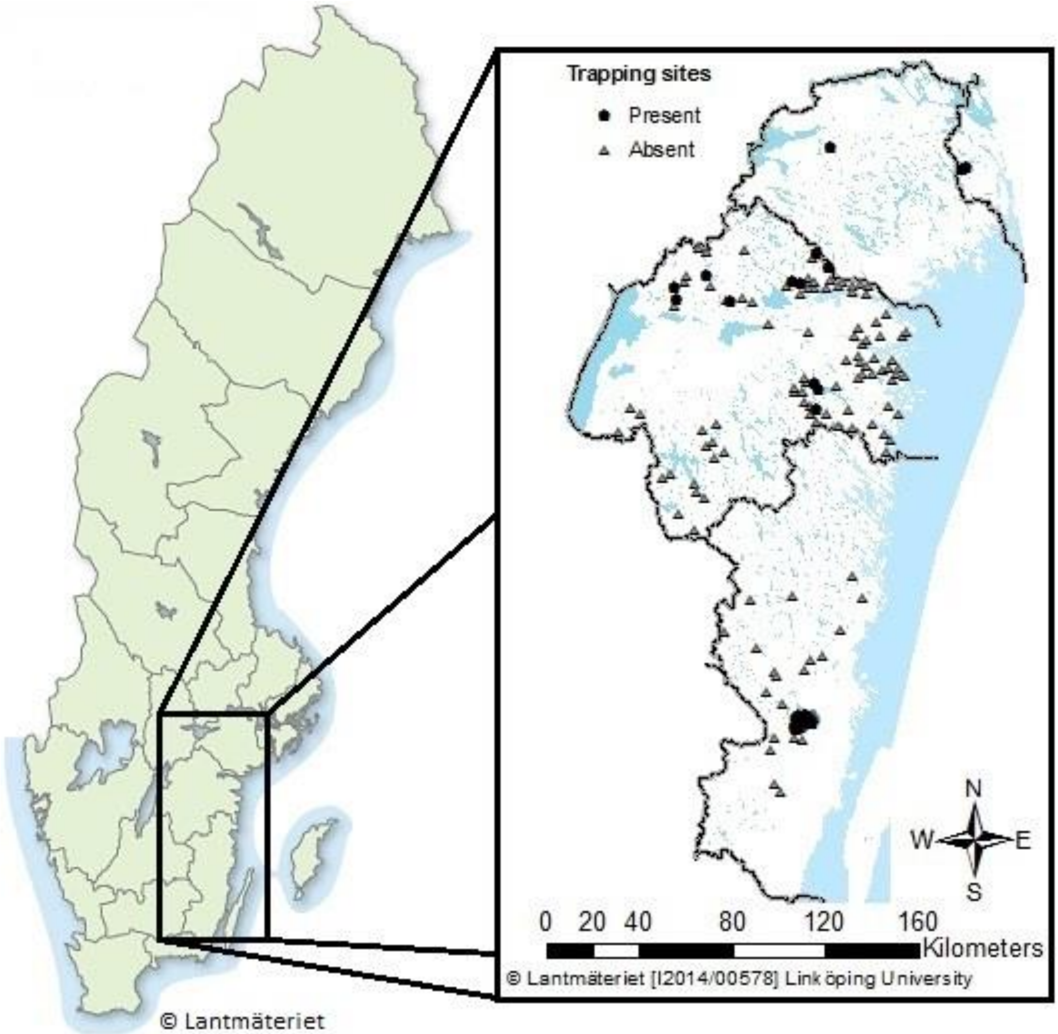

Figure 3. Overview of the study sites in south-east Sweden (left) and the trapping sites in each County marked as present/absent. From south to north; Kalmar, Östergötland, Södermanland and Stockholm (top right corner). The left map is designed by Sveriges domstolar (domstol.se).

3.3 Beetle sampling

In order to map the distribution of this elusive, night-active beetle the most common way has been to either search for the characteristic exit holes in the breeding logs made by emerging adults (Figure 1) or to search for larvae inside dissected logs (Palm 1951, Wikars 2003, Wikars 2004). Now, when the female sex pheromone of this species has been found (Ray et al. 2012), the efficiency of monitoring flying adult males is thought to be greatly improved. Although the number of females remains unknown with this method, it can be used to detect populations of *T. depsarium* or at least where a female has laid her eggs. The beetles in this study were sampled by using a non-harmful, pheromone (odour) based trapping method that allowed the beetles to be released alive once being counted. The non-lethal method was selected to minimise the impact on breeding and mortality in potentially fragile populations.

The pheromone for this study was synthesised by Jocelyn Millar (department of Entomology, University of California, Riverside) and distributed through Mattias Larsson (Swedish University of Agricultural Sciences). The formula of the pheromone isomer used here was R*,S*-2,3-hexanediol. It had been dissolved in isopropanol with a resulting concentration of 100 mg/ml, which enabled diffusion through plastic bags. The pheromone was stored in vials, at +4 °C when possible, to keep it fresh for longer. In the field it was always kept inside a cooling bag with ice clamps, except for when baiting traps (less than 2 minutes/trap) and a few occasions shorter than 20 minutes (ambient temperature around 20 °C).

3.3.1 Östergötland County

Traps were baited with pheromone between July 7th and July 25th 2014 on the trapping site by filling a transparent plastic zip-lock bag (LD-polyethene, 55x65 mm, 0.050 mm) with 0.5 ml of pheromone solution (equal to 50 mg of pheromone), closing it and hanging it up in a string inside the trap (Figure 4). These baited traps are hereafter called "activated" traps. The activated traps were generally re-visited after two or three days, depending on the weather conditions, from July 8th to July 31st. A re-visit was made after two days during sunny and warm conditions (above 20 °C), but after three days during colder and/or rainy periods. The different days intended to maximise the chance of capture, while minimising the risk of killing beetles due to e.g. overheating. The beetles were also expected to be less active during cold and/or rainy nights, compared to warm and clear, and thus the chance of capture between visits should also be more equal than having the same number of days between visits regardless of the weather.

When a trap contained *T. depsarium* during a visit, it was noted in the field protocol and the trap was taken down. A trap found empty was left in the same place until the next time two or three days later. If no catch had been recorded in the third check, it was taken down anyway assuming there were no beetles in the area. Transports of the pheromone bag were always done inside a glass jar to avoid delusive scent trails.

Figure 4. The pheromone trap used in the study. The configuration of the pheromone zip-lock bag inside the trap is shown in the upper left corner. Photo: Alexander Nilsson

3.3.2 Kalmar County

In Kalmar County, the method was slightly different from that in Östergötland County. Instead of removing a trap after a catch, they were set out for a certain period of 7-31 days (but still re-visited regularly). To maintain the effectiveness, the pheromone was renewed after two weeks according to the manufacturers' instructions. All *T. depsarium* caught in the traps were individually marked with a pen. Each beetle was then noted in the protocol with a date and place where it was caught, and finally released within a 50 meter radius from the trap. Re-capture events can be distinguished from new catches in the data, and thus the total number of unique individuals can be extracted. To make the capture effort more equal between Östergötland (maximum 6-9 days) and Kalmar (maximum 31 days) with regard to trapping time, only the catches during the "main period" (17^{th}-23^{rd} July in Östergötland County) were counted from Kalmar County. Sometimes there were catches in Kalmar County in the first week, but not later on in the "main period". To include the early beetles not present during the "main period", a secondary selection period (only applied when there was not a single catch in the "main period") was added between the 1st and the 7th of July. The reason for this secondary selection was to reduce false zeroes in the data, and thus increase the statistical accuracy.

3.4 Sampling strategy

3.4.1 Map selection

In the county of Östergötland, we used a strategic sampling strategy to increase probability of catching beetles. The selection process was divided into two steps. The first step was to choose areas with the right basic habitat conditions for the beetle, i.e. sparse pine forest that contain sunlit dead pine logs. A digital map over woodland key biotopes and their associated attribute table was used to separate rocky outcrops from other areas. Due to the sites' inaccessibility for forestry and dry conditions when located at hills, they often contain many old pines in relatively open stands (Gustafsson 1999, personal observation). The category "rocky outcrops" contained some information about what the area looked like, such as "rich in dead wood", and this information was used to distinguish the potentially more valuable areas from all other "rocky outcrop" areas that did not have much dead wood or any at all. This resulted in about 200 sites, of which 100 were used.

3.4.2 Field selection

The second step was to judge, in the field, whether or not the rocky outcrop areas were at least somewhat suitable for *T. depsarium*. One reason for the second selection in the field was because the descriptions of the areas were sometimes 20 years old and not very reliable anymore. Another reason was to find out if it was possible to reach the location within a reasonable time from the nearest place where the car could be parked, i.e. if the road was okay or blocked too far from the trap location. About 100 sites were discarded.

3.4.3 Trapping

All the traps could not be baited with pheromone at the same time due to logistic reasons. Instead they were baited if there was any time left after the necessary re-visits of activated traps the same day, or when other traps had been taken down at the previous route. Re-visits of traps occurred during a period from July 8th to July 31st 2014 in Östergötland County, and from June 30th to July 31st 2014 in Kalmar County. This corresponds to the main flight period of the beetle (Ehnström & Wikars 2010, Gärdenfors et al. 2002, Palm 1951).

The placement of the traps in each area was such that the sunlight did not reach the trap directly at all or merely early mornings and evenings, to prevent the beetles from being overheated and killed by strong sunlight during the day. To increase the chance of beetle survival, a piece of bark was added inside the otherwise empty plastic container attached below the trapping device. Even though there were some small drilled holes at the bottom, a combination of debris falling down into the trap, covering the draining holes, and heavy rainfall could possibly fill the trap with water. The piece of bark was a measure to prevent drowning of the beetles, as they could climb up on and float in case of water accumulation in the trap. The bark also provided a shelter to hide beneath during the days for caught specimens of this night-living beetle (Palm 1951) when there was no water in the trap.

3.4.4 Östergötland data set

The data set from Östergötland County consisted of 100 traps scattered over the landscape. The sampling sites were situated at least 2.5 km apart. This specific distance was primarily set to avoid overlapping of landscape variables between different sites, but also since it was thought to be enough to prevent most of the inference between activated traps. This estimation was partly based on the dispersal ability of *Rosalia alpina*, another large long-horn beetle ecologically and morphologically similar to *T. depsarium* (Drag et al. 2011). Due to a lack of suitable areas at the guideline distance, some traps were located between 1.9 and 2.5 km away from each other. A GPS (Garmin GPSmap 62st) was used to take the coordinates for each of the 100 areas.

Within 30 meters of each trap in Östergötland County (but not elsewhere), two variables were measured; 1) The number of pine logs (fallen trees only) exceeding 25 cm at 1.3 m from the root end 2) the number of pine logs with presumed exit holes from *T. depsarium* while the third was subjectively estimated; 3) the average crown cover. These variables are later called “Pine logs above 25 cm in diameter”, “pine logs with exit holes” and “Crown cover”, respectively, or simply grouped together as “onsite” variables.

3.4.5 Kalmar data set

The data set from Kalmar County was based on a total of 152 traps (with 43 catches), mainly set out in clusters of 3 with a minimum distance between clusters of about 500 meters. To compensate for the triple amount of pheromone and traps in the clusters, an average of caught individuals and their average date of catch was used (both rounded up to whole numbers). The data set from Kalmar with these modifications are hereafter referred to as "reduced data set" from Kalmar and consists of 50 sites with 23 catches. The reduced data set has been treated as fully comparable with the Östergötland data set.

3.4.6 Stockholm and Södermanland data set

The data from the county of Stockholm are based on four pheromone traps active during one night (7th-8th of July 2014). These four traps were divided into two sites with two traps at each and with about 30 m between the traps within a site. After one night, the caught *T. depsarium* were counted and released before all traps were removed. At the second site two traps were activated again about one week later, between July 16th and 17th. The catch at site one was 1 beetle, while at the second site it was 9 + 6 for the different days resulting in a total of 16 catches. As this data was clustered like in Kalmar County, the same method was applied to make it comparable with other sites (average of catches and catch dates for traps next to each other). After reduction, the first and second site had one and eight catches, respectively. In Södermanland County, a pheromone bag was laid on a pine log and males of *T. depsarium* were observed on approach, i.e. not catches based on traps.

3.5 Data analyses

3.5.1 Landscape variables

The landscape variables; nature reserves, woodland key biotopes, voluntary woodland key biotopes set aside by large forest companies, biotope protection, nature conservation agreements and nature conservation values, were based on data from skogsdataportalen (Swedish Forest Agency 2014) while the volume of pine was based on data from kNN-Sverige (Pahlén et al. 2004, Reese et al. 2003). The software program used to process the landscape variables and extract County-wide data was ArcMap 9.3 (ESRI 2009), a GIS (Geographic Information System) program using digital maps. The landscape variables from skogsdataportalen were grouped together as “protected areas”, since the area of any single variable was assumed to be too small to explain occurrences of the beetle. The clear-cut areas were based on actual cut area between 1999-2009 calculated from aerial photos, not just reported area to be cut, since these two often not conform. The age of the clear-cuts were selected to be 5-15 years old, which was based on the females’ preferences for log age when laying eggs (Gärdenfors et al. 2002, Wikars 2003). Older logs on clear-cuts with planted forest are likely to be too shadowed by the young growing trees. Volume pine was the only variable derived from kNN-data, which uses an algorithm to calculate forest properties based on satellite data and inventory plots from the national forest inventory. All areas were measured in hectares, and volume pine (*P. sylvestris*) was measured in m^3 forest/ha.

Starting from the traps’ GPS coordinates (or the center point for each cluster of merged traps), the amount of all landscape variables above were extracted by using a buffer zone of 100 m, 500 m, 1000 m, and 2000 m, respectively. These buffer zones were chosen to cover the different ranges of dispersal which could be relevant, compared with other large beetles, from a common observed distance of 50 m (maximum about 250 m) for *Osmoderma eremita* (Ranius 2006, Svensson et al. 2011), 0-1600 m for *Rosalia alpina* (Drag et al. 2011) and 50-2000 m for *Lucanus cervus* (Rink & Sinsch 2007).

Except for “nature reserves” and “voluntary woodland key biotopes set aside by large forest companies”, the variables contained information that allowed them to be sorted into categories of different habitat types. In an attempt to increase the relative importance of those variables and to reduce noise in the analyses, only categories that potentially could include the beetles’ habitat were used (i.e. deciduous forest, swamps and more, were not considered as a habitats and thus removed).

3.5.2 Statistical analysis in R

Negative binomial generalised linear models (GLZ; log-link; statistical software R [R Core Team 2014]) were used in order to relate the number of caught *T. depsarium* at each trapping site with different landscape variables at different scales. One GLZ was used for each of the three landscape variables (protected areas, clear-cut areas and volume pine), with “number of caught individuals” as the response variable and corresponding data from the four scales as the explanatory variables. The three additional variables (only available from the main study in the county of Östergötland) collected in the proximity of each trap, were related to the occurrence of *T. depsarium* in another GLZ using them as explanatory variables and the same response variable (individuals) as the landscape variables above.

4 Results

In total, 57 specimens of *T. depsarium* from the counties of Kalmar, Östergötland, Södermanland and Stockholm were included in the analyses. Of the 153 sites, 24 % harboured the beetle (Table 1).

Table 1. Contributions by county to a) number of sites visited b) number of T. depsarium *individuals found in the traps and c) percentage of sites with occurrences.*

County of:	Number of sites	Individuals found	Site occurrence %
Kalmar	50	23	44
Stockholm	2	9	100
Södermanland	1	3	100
Östergötland	100	22	11
Total:	153	57	24

There was a similar amount of new catches in Kalmar County compared to Östergötland County during the same time period (Figure 5). The dates for the “first-time” catch, extracted from the full data set from Kalmar (unpublished data), showed one peak in the beginning of July and another one about two weeks later. This resembles the catches in Östergötland (Figure 5). One beetle in Östergötland emerged between visits on the 16th and 18th of July 2014 (personal observation) (Figure 1).

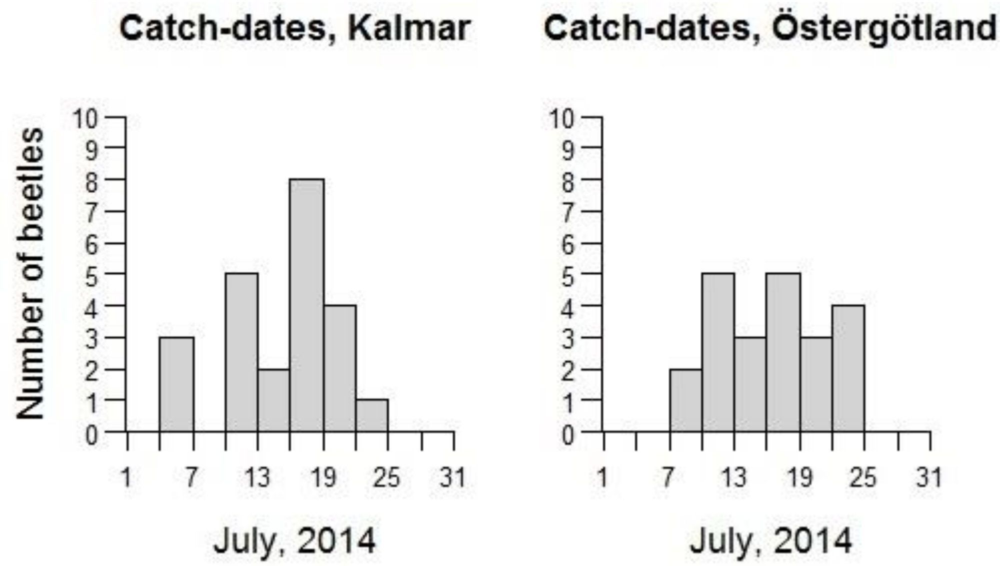

Figure 5. Catch dates of T. depsarium *during July 2014 (x-axes). To the left; number of beetles from 50 sites based on the reduced data set in Kalmar, comparable with the Östergötland data set. To the right; number of beetles from 100 sites in Östergötland County between July 8th and 31st.*

Table 2. Relationship between the landscape variables at different scales around trap sites (explanatory variables) and the number of beetles found at each site (N=153) using three negative binomial Generalized Linear Models. The three models analysed protected areas, cut areas and volume pine at 100, 500, 1000 and 2000 meters from each trap. In protected areas, unsuitable habitats were excluded as far as possible. Clear-cut areas were 5-15 years old (cut in 1999-2009). Volume pine refers to volume wood of alive Scots pine trees.

Explanatory variables, all areas	**Estimate**	**SE**	**z-value**	**p-value**
Intercept (protected area)	-1.066	0.227	-4.689	**<0.001**
Protected areas (ha) 100 m	-0.534	0.433	-1.232	0.218
Protected areas (ha) 500 m	0.023	0.044	0.535	0.593
Protected areas (ha) 1000 m	-0.010	0.014	-0.721	0.471
Protected areas (ha) 2000 m	0.004	0.002	1.995	**0.046**
Intercept (clear-cut)	-0.577	0.314	-1.841	0.066
Clear-cut areas (ha) 100 m	0.668	0.627	1.065	0.287
Clear-cut areas (ha) 500 m	-0.152	0.091	-1.668	0.095
Clear-cut areas (ha) 1000 m	0.041	0.036	1.147	0.252
Clear-cut areas (ha) 2000 m	-0.015	0.010	-1.437	0.151
Intercept (volume pine)	-2.501	0.692	-3.612	**<0.001**
Volume pine (m^3/ha) 100 m	-0.005	0.002	-2.486	**0.013**
Volume pine (m^3/ha) 500 m	8.04E-05	<0.001	0.333	0.739
Volume pine (m^3/ha) 1000 m	3.80E-05	<0.001	0.365	0.715
Volume pine (m^3/ha) 2000 m	2.28E-05	<0.001	1.158	0.247

The area of protected land had a significant, positive effect on the occurrence of *T. depsarium* within a 2000 m radius from the trapping site when including all counties (Table 2). Volume pine, as well as cut areas, did not show a positively significant response to the occurrence of the beetle at any scale. Instead, the volume of pine wood had a significantly negative effect on the beetles at a distance less than 100 m from each site (Table 2).

The GLZ with "site-specific data in Östergötland" (Table 3) showed that pine logs above 25 cm in diameter did not explain presence-absence of the beetle at all. The same is also valid for crown cover less than 25 % and crown cover between 25-50 %. However, there is a strong, highly significant, correlation between presence-absence of *T. depsarium* and presumed exit holes regardless of their age (Table 3).

Table 3. A negative binomial GLZ of the site-specific data in Östergötland County (N=100). Pine logs refers to all logs of Scots pine that were not completely decayed, and crown cover was subjectively estimated as an average of the tree canopy cover. Crown cover above 50 % was included in the intercept and thus not shown separately in the table. All parameters were measured within approximately 30 m from each trap.

Explanatory variables	**Estimate**	**SE**	**z value**	**p-value**
Intercept	-1.959	0.932	-2.103	**0.035**
Pine logs, above ø 25 cm	0.085	0.165	0.514	0.607
Pine logs, with exit holes	1.069	0.315	3.394	**<0.001**
Crown cover < 25 % (compared to crown cover above 50 %)	-1.983	1.839	-1.079	0.281
Crown cover 25-50 % (compared to crown cover above 50 %)	-0.786	0.940	-0.836	0.403

Table 4. Three negative binomial Generalized Linear Models with the landscape variables in Östergötland County only (N=100). The response variable was "individuals", and the explanatory variables were protected areas, cut areas and volume pine at 100, 500, 1000 and 2000 meters from each trap, respectively. In protected areas, unsuitable habitats were excluded as far as possible. Clear-cut areas were 5-15 years old (cut in 1999-2009). Volume pine refers to volume wood of alive Scots pine trees.

Explanatory variables, Östergötland	Estimate	SE	z-value	p-value
Intercept (protected area)	-1.909	0.452	-4.221	**<0,001**
Protected areas (ha) 100 m	-0.808	0.798	-1.013	0.311
Protected areas (ha) 500 m	0.182	0.088	2.074	**0.038**
Protected areas (ha) 1000 m	-0.066	0.035	-1.890	0.059
Protected areas (ha) 2000 m	0.008	0.007	1.206	0.228
Intercept (clear-cut)	-2.179	0.742	-2.936	**0.003**
Clear-cut areas (ha) 100 m	0.129	1.863	0.069	0.945
Clear-cut areas (ha) 500 m	-0.375	0.202	-1.857	0.063
Clear-cut areas (ha) 1000 m	0.169	0.069	2.457	**0.014**
Clear-cut areas (ha) 2000 m	-0.010	0.020	-0.520	0.603
Intercept (volume pine)	-4.231	1.773	-2.387	**0.017**
Volume pine (m^3/ha) 100 m	-0.010	0.005	-1.837	0.066
Volume pine (m^3/ha) 500 m	2.66E-04	<0,001	0.562	0.574
Volume pine (m^3/ha) 1000 m	-9.00E-05	<0,001	-0.432	0.666
Volume pine (m^3/ha) 2000 m	7.76E-05	4.03E-05	1.927	0.054

In Östergötland County, protected areas were positively correlated with the abundance of *T. depsarium* at a 500 meter scale (Table 4) but not at 2000 meters as was the case when all counties were included (Table 2). The area of clear-cuts within 1000 meters from the trapping site could explain the presence of the beetle in Östergötland County when it was analysed separately (Table 4). For volume pine, a tendency for a negative correlation can be seen at 100 meters, similar to the data set with all areas. However, at 2000 m, there is a strong tendency for a positive relationship between the amount of pine wood and beetle occurrence (Table 4).

5 Discussion

5.1 Landscape variables and scale

Generally protected forest areas, including e.g. voluntary set asides, significantly explained the occurrence of *T. depsarium* at a landscape scale of 2000 m (1257 ha) (Table 2). Gibb et al. (2006c) showed that a 1-10 km scale likely is important for many saproxylic beetles with regard to availability of suitable habitats. This 2000 m scale is also similar to the 1600 m scale sometimes used by *Rosalia alpina*, another large longhorn saproxylic beetle living in logs (Drag et al. 2011). However, this might not give a representative view of the beetles' general occurrence in protected areas due to spatial autocorrelation between several sites. The aggregated distribution of trapping locations from Kalmar County might have created a bias in the analysis of the explanatory landscape variables (Figure 3), despite efforts made to reduce bias in the analysis. Additionally, all catches in Kalmar County were located in a large nature reserve and thus more or less covered by the same nature reserve at all scales. The same issue with bias also exists in Östergötland as the trapping sites were selected using protected areas and nature reserves, though not as prominent as in Kalmar County due to the small size (commonly 0.5-2 ha) of visited woodland key biotopes and generally quite small nature reserves.

A sub-analysis, using the Östergötland data only, did not reveal a response to protected forest at the same scale. Here the beetle had no preference for sites with large amounts of protected areas within 2000 meters, but instead for 500 meters (79 ha) (Table 4). Other studies have mainly found individuals of *T. depsarium* outside protected areas (Gärdenfors et al. 2002, Wikars 2003), although important to note that protected forests below the Scandinavian mountain range only cover 2 % of the total forest (Höjer 2014). On the other hand Gustafsson (1999), studying species richness, found more red-listed species in the woodland key biotopes than in the production forest. Protected areas are indeed valuable for a variety of organisms, from saproxylic beetles (D'Amen et al. 2013) to birds and hundreds of invertebrate species (Thomas et al. 2012), lichens (Thor 1998) and mosses (Plášek 2014). The aggregated sampling sites in Kalmar County likely inflated the importance of protected areas but, since the data from Östergötland still shows an effect at 500 m, this can not only reflect the smaller sizes of protected areas as there is no effect at 100 m (Table 4). Thus, it indicates that protected forests are beneficial to *T. depsarium*.

Another explanation for the specimens found within the small protected areas might be a migration from populations in nearby clear-cuts or from logs at the border of protected areas that experience an increased sun-exposure when clear-cutting occur next to it (Wikars 2003). Other findings by Wikars (2003) concludes that occurrences of *T. depsarium* nowadays is mainly restricted to the open clear-cuts, not to the often increasingly more dense protected areas invaded by spruce (Linder et al. 1997), but he found no correlation between beetles and clear-cuts. This could explain why clear-cuts have a significant effect on the beetles' occurrence at an intermediate scale of 1000 meters (314 ha) in Östergötland (Table 4).

The negative correlation between the amount of pine wood (volume pine) within 100 m (3 ha) (Table 2) and beetle presence can be an effect of too high tree densities. Although this beetle is a pine specialist, and pine forests provide breeding substrates, these forests are often too young and dense to contain suitable pine logs in comparison with older forests (Siitonen et al. 2000). A weak tendency for a preference of pine trees, potentially reflecting the need of enough pine trees in the landscape, can be seen at the 2000 meter scale although the effect is very small (Table 4).

5.2 Concordance with related studies

All landscape variables listed above (protected areas, clear-cuts and volume pine) were relevant only at particular scales. This further demonstrates the importance and benefit of utilising multiple, instead of single, spatial scales, which has also been concluded by several other authors that performed a multi-scale approach (Bergman et al. 2012, Ibarra et al. 2014, Sergio et al. 2003). The outcome of my study is in line with several others showing that a species react on different scales dependent on the landscape variable in focus. Examples do not only include the different anuran species studied by Price et al. (2005) and the birds studied by Lee et al. (2002), that reacted to the investigated landscape variables at species specific scales, but also studies about beetles. The beetle studies showed an importance of variables on the small scale such as distance to the next colonised tree and bark depth (age of tree substrate) (Buse et al. 2007). On the large landscape scale, the amount of oak trees (substrate availability) together with oak woodland key habitat (corresponding to the pine woodland key habitats in this study) within 1 km were significant predictors of beetle occurrence (Franc et al. 2007). A third study, by Musa et al. (2013), used pheromone traps and showed that the density of oaks explained the occurrence of *Elater ferrugineus*, a saproxylic beetle species living in tree hollows of primarily oak. The scale at which a species react is often species specific, and this study agrees with previous studies from beetles to birds that a more complete understanding of a species' response is possible to acquire when using multiple scales rather than a single scale approach.

5.3 "Onsite" variables at trapping sites

The "onsite" variable crown cover did not significantly affect the abundance of beetles based on my collected data, which indicates that the amount of sunlight that reaches the spot around the trap is not of major importance when selecting a tree to hang up the trap (Table 3). However, in a study with hollow oaks, a reduced canopy cover was related to increased frequency of several saproxylic species living in the trees (Ranius & Jansson 2000). A difference between Ranius & Jansson's study and the current study is that the traps for *T. depsarium,* and thus crown cover, were not necessarily located in the same spot as a suitable breeding substrate, which was the case for the oak-living beetles.

Another onsite variable that did not explain presence-absence was pine logs above 25 cm in diameter (Table 3). The idea with this variable was to get some kind of substrate availability at each site since logs above 25 cm has proven to be the most suitable size for the larvae of *T. depsarium* (Wikars 2003). In my study, the logs had unspecified properties (old or fresh, soft or firm sapwood or just heartwood, sunlit or shadowed) and did not significantly explain the beetles' occurrence. The inadequate quality of some logs for *T. depsarium* partly explains why pine logs in general were not correlated with occurrence (Wikars 2003). Another explanation for this offered by Wikars (2003) is that of dispersal limitations, if the suitable logs are located too far away or are too scattered they will not be found and utilised. If this variable would be tested again for *T. depsarium,* it might be better to only record pine logs that are sunlit or in semi-shade with an outer layer of sapwood, partly or completely free from bark, to better match the breeding criteria of *T. depsarium* (Gärdenfors et al. 2002, Palm 1951, Wikars 2003). This modification would give a number on the unused, but suitable, logs and help to explain the dispersal limits of the beetle (Wikars 2003). It would also be advantageous to lower the search diameter to 15 cm instead of 25 cm, since a fresh exit hole of this beetle was found in a log (Figure 1) not more than 15-20 cm in diameter (personal observation) which also has been recorded by Wikars (2003). To validate the older technique of studying emergence holes for surveillance of *T. depsarium* (Ahnlund & Lindhe 1992, Palm 1951, Wikars 2003), I also tested if presumed emergence holes from *T. depsarium* were a good predictor of beetle presence. Indeed, there is a strong correlation between beetles and old/new emergence holes (Table 3). Smith et al. (2004) similarly tested if previously found emergence holes could predict new ones among the Asian longhorn beetle *Anoplophora glabripennis*, with the same result.

5.4 Influences on variation in beetle capture

In Kalmar County where most traps were up during all of July 2014, the capture success of "first time caught" *T. depsarium* was seen to vary greatly in time in the full data set, creating two distinct peaks (Larsson, unpublished data from Kalmar). Also, based on this data, it can be confirmed that the sampling period in Östergötland County occurred within the middle of the beetles' flight period. Longevity experiments on *Rosalia alpina*, a saproxylic species with a similar ecology as *T. depsarium* also within the same family (Cerambycidae), showed that females survived for at least 15 days and males up to 24 days (Drag et al. 2011). Thus it is likely not a huge issue that the trapping period began seven days later in Östergötland County compared to Kalmar County, since early males flying in the beginning of July would likely still be alive at least until the middle of July. Nevertheless, traps at some sites were not activated until the last week in July and could therefore have missed early males.

There are several factors that could have influenced this variation in captured individuals. First of all, the pheromone might not have lasted the two weeks in the field that was set by the manufacturer as the pheromone bag was almost dried out completely after the one week trials in Östergötland County during the unusually warm and dry weather conditions that predominated this period.

Another explanation for the peaks is a synchronised hatching following a critical temperature threshold, observed by both Bentz et al. (1991) and Powell & Logan (2005) during development in the mountain pine beetle *Dendroctonus ponderosae*. These findings are also in line with the seasonality and effect of temperature among insects in general (Régnière et al. 2012).

A third explanation could be a temperature dependence for flying. The peaks of catches coincides with warmer periods (20-26 °C in evening/night) following slightly colder days (14-20 °C in evening/night) during which catches were low, indicating that temperature is important for movements. This finding is consistent with that of Machin et al. (1962), who found a positive effect of temperature on a tested beetle's wing muscle performance, and thus flight capacity. This relationship between temperature and movements has also been observed in other studies. Palm (1951) observed specimens of *T. depsarium* during a relatively cold summer evening, and a beetle could sit for hours without moving. This led him to the conclusion that they are sedentary and unwilling to move, at least in cold weather. A mark-recapture study of the eucalyptus longhorn borer, *Phoracantha semipunctata*, also showed an unwillingness of long dispersal movements among the beetles in cold weather (Hanks et al. 1998).

5.5 Sex ratio and its implications

The sex ratio of *T. depsarium* has not been found in the literature by the author, but another saproxylic beetle of the same family, *Rosalia alpina*, have no bias (1:1) (Drag et al. 2011). Yet another saproxylic beetle, *Leptura maculata*, had a male biased sex ratio (2:1) in a field experiment, but it could not be ruled out that the sex ratio found was due to behavioural differences between sexes and not a true bias (Tikkamäki & Komonen 2011). If there would be a male biased sex-ratio for *T. depsarium*, populations at a few sites with only one catch after a whole week might be at a serious risk of extinction, provided no more beetles existed at that site not caught in the trap. The effectiveness of the traps, i.e. actually catching male beetles present in the surroundings, is not known for *T. depsarium*. However, the accuracy of pheromone traps has been estimated to reach 100 % for both *Elater ferrugineus* and *Osmoderma eremita* within 6-9 days and about a month, respectively, when used during the optimal time of year (Andersson et al. 2014). In the same study, the pheromone traps outperformed the older survey methods of saproxylic beetles with window/pitfall traps in a comparison, with a beetle detection on 19 and 5 sites, respectively, out of 47 in total.

Another problem by only catching males is the risk of false occurrences at trapping sites, as male beetles often tend to fly longer distances and move more actively than females (Hanks 1999, Tikkamäki & Komonen 2011). The use of long-range pheromones in cerambycids often coincide with no feeding in adults and a sedentary behaviour in the pheromone producing sex (Hanks 1999), which in the case of *T. depsarium* is the females. A male, attracted by the pheromone in a trap set out in a previously unoccupied area, might thus fly from a neighbouring population all the way to the trap where it is caught. A female, contrary to the males, would more likely stay in the old area although the "new" area is equally suitable. This is what Wikars (2003) concluded after studying the spatial distribution of *T. depsarium* and found that occupancy patterns were clumped together in 1-10 ha large areas within his investigated 1x1 km (100 ha) squares. He also found a lot of suitable substrates completely unused between the colonised areas, just like in this study where pine logs did not explain beetle presence (Table 3), suggesting dispersal limitations even though the beetle in some cases is not physically constrained. Other studies have shown that connectivity (how well areas are connected) has proven to be important for both colonisation and dispersal success (Walters 2007). In turn, the connectivity in a landscape is dependent on the number and sizes of habitat patches, together with the dispersal ability by the species of interest (Laita et al. 2010).

5.6 Positive effects of disturbances

Threatened species has been shown to often be specialists with narrow habitat requirements and more prone to suffer from fragmentation (Clavel et al. 2010, Devictor et al. 2008, Ibarra et al. 2014). In a study by Gibb et al. (2006b), two out of the three tested red-listed beetle species showed a preference for habitats threatened by forestry. The same pattern, with specialisation among threatened beetles, has also been documented by Oleksa et al. (2013). There is a large variety of specialised beetles (Coleoptera), not just *T. depsarium*, that are highly favoured by, or even require, large-scale disturbances in the forest for their breeding (Ahnlund & Lindhe 1992). The reason for this requirement is not the disturbance itself, but rather the resulting open, sun-lit conditions with a warm microclimate that is suitable for many of these threatened beetles.

One effective way to increase the diversity of habitats for saproxylic beetles in managed forests is prescribed burning (Heikkala et al. 2014). The study demonstrated that a retention level of 10-20 % after logging is optimal for prescribed fires, giving a long-term benefit for many saproxylic beetles favoured by fires (Ahnlund & Lindhe 1992, Muona & Rutanen 1994), while minimising the economic loss from uncut trees. In the cases where an uneven mortality pattern arises after a fire, benefits for an even larger diversity of saproxylic insects are created over an extended period of time due to a continuous supply of dead wood from weakened trees not killed immediately after the fire (Heikkala et al. 2014). Benefits to fire-dependent organisms when applying fire at cut areas has been predicted before, e.g. by Fries et al. (1997).

5.7 Implications for conservation

The results of this study shows that Kalmar County has one large population of *T. depsarium* whereas Östergötland County has several smaller. Therefore, it is recommended to first enhance the populations in Östergötland by creating breeding substrates. This could done by felling a few larger pines in sun-exposed areas at occupied sites, e.g. in connection with clear-felling operations. This should enhance the presumed small populations of *T. depsarium* in Östergötland County. Prescribed fires and selective cutting are two management options that counteract the increased densification of (sometimes protected) pine forests. All these actions can reverse the negative impacts on *T. depsarium* and other saproxylic beetles. Some of these saproxylic beetles are favoured by or even require the dead or dying burnt wood as breeding substrates (Ahnlund & Lindhe 1992, Davidsson 2014, Evans 1966, Laestander 2014, Muona & Rutanen 1994, Wikars 1992). In production forests with pine, even an active forestry might contribute with a positive effect when temporary open gaps are created in the otherwise dense forest landscape.

5.8 Conclusions

In this study, protected areas and clear-cuts significantly correlated with the presence of *T. depsarium*. This is in contrary to a study by Wikars (2003), although he found clear-cuts with coarse pine debris to be important short-term habitats in todays managed forests. Further, the distribution of *T. depsarium* is concentrated to a few areas in the landscape shown both in this study and proposed earlier by Wikars (2003). Unfortunately, many of the beetle populations found will likely face a high risk of extinction in the near future (Gärdenfors et al. 2002). The loss of large and old logs, so called "buffering logs" used by multiple generations of beetles (Wikars 2003), negatively affect the long term persistence of *T. depsarium* populations at specific sites. The fire suppression on the other hand, with a subsequent invasion of shadow tolerant species such as Norway spruce (Linder et al. 1997, Linder 1998, Niklasson & Drakenberg 2001, Zackrisson 1977), have a more widespread negative impact on this species as it affects the whole forest where they live and making most or all logs unsuitable regardless of their thickness. This negative trend can be stopped and reversed if at least 10-20 % of pine forests next to areas with *T. depsarium* are saved and then burnt at the final logging (Heikkala et al. 2014). A successful burning in retention forests on clear-cuts generates a continuous supply of both dead and dying trees (Heikkala et al. 2014). This, together with selective cutting and a responsible active forestry, will help to keep the forests warm and open and aid the work for a safe future for *T. depsarium* and many other currently threatened saproxylic insects.

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