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# The significance of tree, site and landscape variables on eight saproxylic beetles in hollow oaks.

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This thesis concludes my master's degree in Management of Natural Resources at the Norwegian University of Life Sciences (NMBU).

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Senia Hagen

# Abstract

Fragmentation of habitats is a great threat to biodiversity. An especially vulnerable species group is saproxylic beetles. Many of these are associated with hollow oaks, which provide a unique and stable habitat. The number of hollow oak trees in Norway has declined, resulting in hollow oaks being scattered in the landscape with varying degrees of isolation. How species associated with hollow oaks respond to fragmentation depends on their life history characteristics, two of which are a subject of this thesis, namely trophic level and specialization. I investigated what variables and scales had the greatest effect on four oak specialist beetles on different trophic levels. The same variables and scales were also used to understand why two pairs of closely related saproxylic beetles, one common and one rare had different occurrence frequencies on hollow oaks. Tree, site and landscape variables representing habitat size, isolation and climate were obtained though field registrations and from map sources. These variables were analyzed in GIS and used in stepwise multiple regression to create optimal models for each species. The results for the four oak specialists showed that the species dependent on wood (xylophage) and the species dependent on wood and fungi (xylomycetopage) responded to small-scale tree variables representing habitat size. The predator species and the species with mixed feeding preferences responded to large-scale landscape variables representing climate and isolation, respectively. The variables and scales did, to some degree contribute to the understanding of why two species within the same family occurred at different frequencies. For instance, both of the rare species responded to dead wood. Their dependence on this substrate could have made them vulnerable to habitat change and fragmentations, and in turn rare.

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# 1. Introduction

Habitat loss has been identified as one of the main threats to biodiversity on a global scale (Primack, 2012). The driving force behind this is primarily anthropogenic activities, which cause land use changes and with it the degradation and destruction of habitats. After habitat loss, the remaining habitat is left fragmented, only consisting of smaller patches with varying degrees of isolation (Collinge, 2009). The process of fragmentation can make the distance between habitat patches too great for species to be able to utilize them. Limited dispersal possibilities can create small populations, which are vulnerable to deterministic and stochastic variations. The Norwegian Red List for Species (Kålås et al., 2010) include species that have decreasing populations or have a risk of becoming extinct in Norway. Species dependent upon dead wood habitats (saproxylic species) make up 17% of the red-listed species (Kålås et al., 2010). Many of these are involved in dead wood decomposition and play an important role in recycling nutrients back to the forest ecosystems (Sverdrup-Thygeson and Ims, 2002).

Oak trees (*Quercus* spp.) are considered the most important host trees for lichens, bryophytes, fungi and insects in Scandinavia (Miljødirektoratet, 2012). The longevity of oak trees creates a stable and temporally continuous habitat for these groups of species (Antonsson and Jansson, 2001, Hultengren et al., 1997). When an oak tree exceeds 200 years, a cavity is often created as a result of branches breaking off (Ranius et al., 2009), which allows colonization of particular "cavity creating" fungi (*Laetiporus sulphureus* and *Fistulina hepatica*) (Miljødirektoratet, 2012). Over time the cavity is filled with wood mould; a mix of decaying wood, fungal hyphae and other organic substances (Franc et al., 2007). In addition, coarse bark and dead wood in the canopy add several microhabitats to the oak tree (Hultengren et al., 1997). Hollow oaks are considered as hotspots for biodiversity and host many saproxylic species (Sverdrup-Thygeson et al., 2011). The saproxylic organisms are dominated by beetles (Coleoptera), which can be dependent or more loosely associated with oak.

The number of hollow oak trees in Europe has severely declined (Sverdrup-Thygeson et al., 2011). This is primarily due to removal, either for logging purposes or because of land use change. The distribution of the two naturally occurring oak species in Norway (*Quercus robur* and *Quercus petraea*) is mainly confined to a belt along the southern and western coastline of Norway (Miljødirektoratet, 2012) (**Appendix I**).

As the distance between hollow oaks increases, the dispersal opportunities for many saproxylic beetles decreases. The same applies to various fungi, which many saproxylic beetles are feeding on. Species dependent on hollow oak trees are generally regarded to have low dispersal ability compared to other saproxylic insects (Bergman et al., 2012), which fits well with adaptations to their stable and long-lived habitats where only occasional dispersal is needed. The biogeography theory suggests that the size of an island and the degree of isolation affects the immigration and extinction rate of species (Cox and Moore, 2010). Following this theory, the smaller and more isolated the island is (here: stands of hollow oak trees), the less stability and higher risk of extinction (Collinge, 2009). Subsequently, Ranius (2002) describes the remaining hollow oak stands in Sweden as "(…) small and isolated habitat islands in a 'sea' of managed forests and agricultural fields".

## 1.1 Ecological traits

How species respond to fragmentation will depend on their life history characteristics, for example body size, population size, specialization, dispersal ability and trophic position (Henle et al., 2004). Species traits can work together; to either enhance the species survival chance, or reducing it. Identification of these traits provides valuable knowledge, which may, in some cases, be applied to whole groups of species - resulting in cost- and time-efficient management.

Trophic levels describe a species position in the food web. Hollow oaks provide habitat for species on many trophic levels, from detrivores to predators. A study done on landscape simplification and the responses of various carabid trophic groups revealed that carnivores (higher trophic level) are more sensitive to increased homogeneity of landscapes than for instance omnivores (lower trophic level) (Purtauf et al., 2005). These results are consistent with the "trophic-rank hypothesis", which suggests that species at higher levels may be more susceptible to extinction because they, among other, are affected by the fluctuations in their prey's population size (Holt et al., 1999). However, research on the significance of trophic levels in relation to fragmentation vulnerability has yielded contrasting results. A study found, for instance, that detrivores were more sensitive to fragmentation than predators (Didham et al., 1998) and another found that there was no indication of a connection between trophic level and extinction risk (Mikkelson, 1993).

Specialization is another species trait often included in studies of species responses to habitat change or fragmentation. Generally, specialized species are regarded as more prone to extinction because they often have a narrow range of tolerance when it comes to their diet or the environment they live in (Cox and Moore, 2010). Hollow oaks house many specialist species due to the high diversity of microhabitats and the stability the trees offer. In such environments specialization may be beneficial. However, this advantage is lost when the hollow oaks become few and far between and the environmental conditions around the trees become unstable and unsuited. Specialists are then likely to be negatively affected. For example, the rare click beetle *Elater ferrugineus* (Elateridae) is a highly specialized predator in hollow trees, primarily oak. It specializes mainly on the larvae of the hermit beetle*, Osmoderma eremita* (Scarabaeidae), resulting in the species becoming as rare and threatened as *O. eremita* itself, with only one known location in Norway (Miljødirektoratet, 2010). Likewise, a study of bumblebees (*Bombus* spp.) revealed a strong relationship between abundance and diet breadth, where the specialized species were the least abundant (Goulson and Darvill, 2004). This recurring pattern is why specialization in many cases is linked to rarity. Species are often considered rare when they are not abundant in those communities they are a part of (Cunningham and Lindenmayer, 2005). Nevertheless, it is common to be rare. Several studies have suggested that a community consist mostly of rare species, with a few common ones that dominate (Cunningham and Lindenmayer, 2005, MacArthur, 1967, Preston, 1962). Unfortunately, there is often a lack of knowledge about habitat requirements, dispersal ability and population dynamics of the rare species (Byers and Meagher, 1997). To this date there has not been performed any studies on what habitat features and scales common and rare species within the same saproxylic beetle family respond to. When dealing with the question of rarity, much focus has been on plants (Byers and Meagher, 1997, Novotný and Basset, 2000, Pate and Hopper, 1994).

## 1.2 Environmental variables and scales

Species respond to changes in environmental variables on different spatial scales. Finding the right scale of response for each species provides important information when managing them, especially the rare and threatened species (Bergman et al., 2012).

At a small scale, habitat size in terms of different tree characteristics have proven to be important when predicting richness of saproxylic beetles. High species richness has, for instance been shown to be associated with large circumference (Ranius and Jansson, 2000, Ranius et al., 2011, Sverdrup-Thygeson et al., 2010).

The same applies to large volumes of wood mould, which contributes to making hollow trees functionally diverse and provide substrate for many saproxylic beetle larvae (Micó et al., 2015). For instance, at least three studies have found that *O. eremita* occurs more frequently in hollows that contain large volumes of wood mould (Ranius, 2000, Ranius and Nilsson, 1997, Ranius et al., 2009).

The density of hollow oaks or other deciduous trees and dead wood as habitat patches can be decisive for species occurrence on small or large scales, depending on the species of interest (Bergman et al., 2012). This will decide the frequency at which the saproxylic beetles species occur and to what degree they are affected by fragmentation of their habitat. Bergman et al. (2012) found that for a rich specialist beetle fauna to persist, at least 250 old/hollow oaks spread out in an area of 1600 ha are needed. Other studies also corroborate the positive effect of larger hollow oak stands (Franc et al., 2007, Ranius, 2002). Many saproxylic beetle species associated with hollow oaks also utilize other deciduous trees and require the presence of these to survive.

Further on, dead wood is created through natural disturbances and form a habitat patch for various saproxylic species (Johansson et al., 2007) and is important on many spatial scales, including the dead wood on hollow oaks. Dead wood undergoes a succession; the newly dead material attracts certain species and as the succession continues new species will colonize the wood and replace each other (Hultengren et al., 1997). This variable is surveyed at a larger scale than tree characteristics, often as a site, stand or landscape variable. Several studies have found it to be a significant factor for biodiversity of beetles on different spatial scales, for instance Økland et al. (1996) and Sverdrup-Thygeson et al. (2014b).

Finally, climatic variation must be considered on different scales. On a small scale, the hollow oaks' surroundings will affect the microclimate on the tree. High degree of forest openness with little regrowth leads to high sun-exposure, which is beneficial for various saproxylic species living on hollow oaks (Bouget et al., 2013, Ranius, 2002, Ranius and Jansson, 2000, Vodka et al., 2009). However, a dense tree cover will create better moisture conditions on the hollow oak, something fungi, and fungi associated species may favor (Ranius and Jansson, 2000). On a larger scale, the regional climatic conditions become influential. Seeing as hollow oaks are located in the coastal and inland areas of southern and western Norway, there are noticeable climatic variations in regard to temperature and precipitation.

## 1.3 Management challenges

In order to counteract the decline of hollow oak trees, and subsequently the decline in saproxylic beetle biodiversity, an adequate management strategy must be in place. Hollow oaks have a specific legal status in Norway, as a selected habitat type according to the Nature Diversity Act (2009). This insures that special consideration needs to be taken when implementing measures that can affect hollow oaks. Hollow oak trees that are encompassed by the regulation are oaks with a girth >200 cm (130 cm above ground) or oaks with a visible cavity (larger than an opening of at least 5 cm) and a girth >95 cm at breast height (Miljødirektoratet, 2012). Hollow oak trees in productive forests are excluded from the regulation (Miljødirektoratet, 2012), but included in this study as they are as important for biodiversity as trees in agricultural landscapes (Sverdrup-Thygeson et al., 2010).

Several factors make management of saproxylic beetles associated with hollow oaks difficult. First, hollow oak trees are often only found as scattered remnants in forests, agricultural- and urban landscapes. Hollow oaks located in populated areas are especially prone to removal due to land use change or for public safety if old branches are regarded as hazards. Secondly, specific data on species dispersal and colonization abilities are scarce. It is of interest to know how far apart hollow oaks trees can be located and still be able to obtain a continuous exchange of species. Thirdly, it is challenging to find the right spatial scale on which to apply management actions. Management action applied on the wrong scale may not have any effect or even contribute to undesirable outcomes (Macdonald and Service, 2009).

## 1.4 Research goals

This master thesis aims to address these challenges, by studying single-species responses of eight selected beetle species associated with hollow oak, in relation to environmental variables at three spatial scales. Four species are oak specialists at different trophic levels; one dependent on wood and fungi (xylomycetopage), one eating wood (xylophage), one predator and a species with mixed feeding preferences. The four remaining species make up two pairs of closely related species with different occurrence frequency. Comparison can contribute to the understanding of what habitat factors and scales affect the commonness and rarity of these saproxylic beetles species.

More specifically, the research questions for this study are:

1) What variables and scales are important for the four oak specialists representing different trophic levels?
2) Can the selected variables and scales explain why two closely related species, one common and one rare, occur at different frequencies?

The environmental variables representing habitat size, isolation and climate are all relevant for all these oak associated beetles. Still, for some species we have some predictions:

- Variables affecting moisture levels, for instance diameter and forest regrowth are predicted to be of importance for xylomycetophagous species due to its association with fungi. Dead wood is also expected to be a decisive factor.
- The xylophage species is expected to respond positively to dead wood, but also to variables linked to increased sun-exposure.
- Seeing as the species with the mixed feeding preference is a trophic generalist, a weaker response to the environmental variables is predicted.
- It is expected that the common species (within the species pairs) have a weaker response to the different variables and scales than the rare ones.

# 2. Methods

This master thesis is done in collaboration with an on-going PhD research project conducted by Hanne Eik Pilskog at the Department of Ecology and Natural Resource Management (INA) at the Norwegian University of Life Sciences (NMBU). The project started in 2012 and addresses biodiversity of beetles in hollow oaks in relation to different temporal and spatial aspects (Pilskog et al., 2014). For this purpose, 32 hollow oak trees were selected, and several tree- and site variables were mapped. These measurements, together with species data are made available for this master thesis.

## 2.1 Study sites

The study sites consist of 32 locations divided into two regions (**Appendix II**). There were 16 sites in the municipalities of Larvik, Siljan and Skien and 16 in the Agder-counties in southern Norway (**Figure 1**). There was one hollow oak per location and at least 1.5 km between them. Half of the oak trees in each region were situated in anthropogenic landscapes equivalent to pastures, road verges and residential areas, while the other half in forests. Furthermore, the hollow oaks were situated along a coast-inland gradient in both regions, where approximately half the trees are less than 10 km from the coast and the other half were situated further inland (**Appendix III**). The oaks were chosen on the basis of being visibly hollow above ground with presence of wood mould (Pilskog et al., 2014).

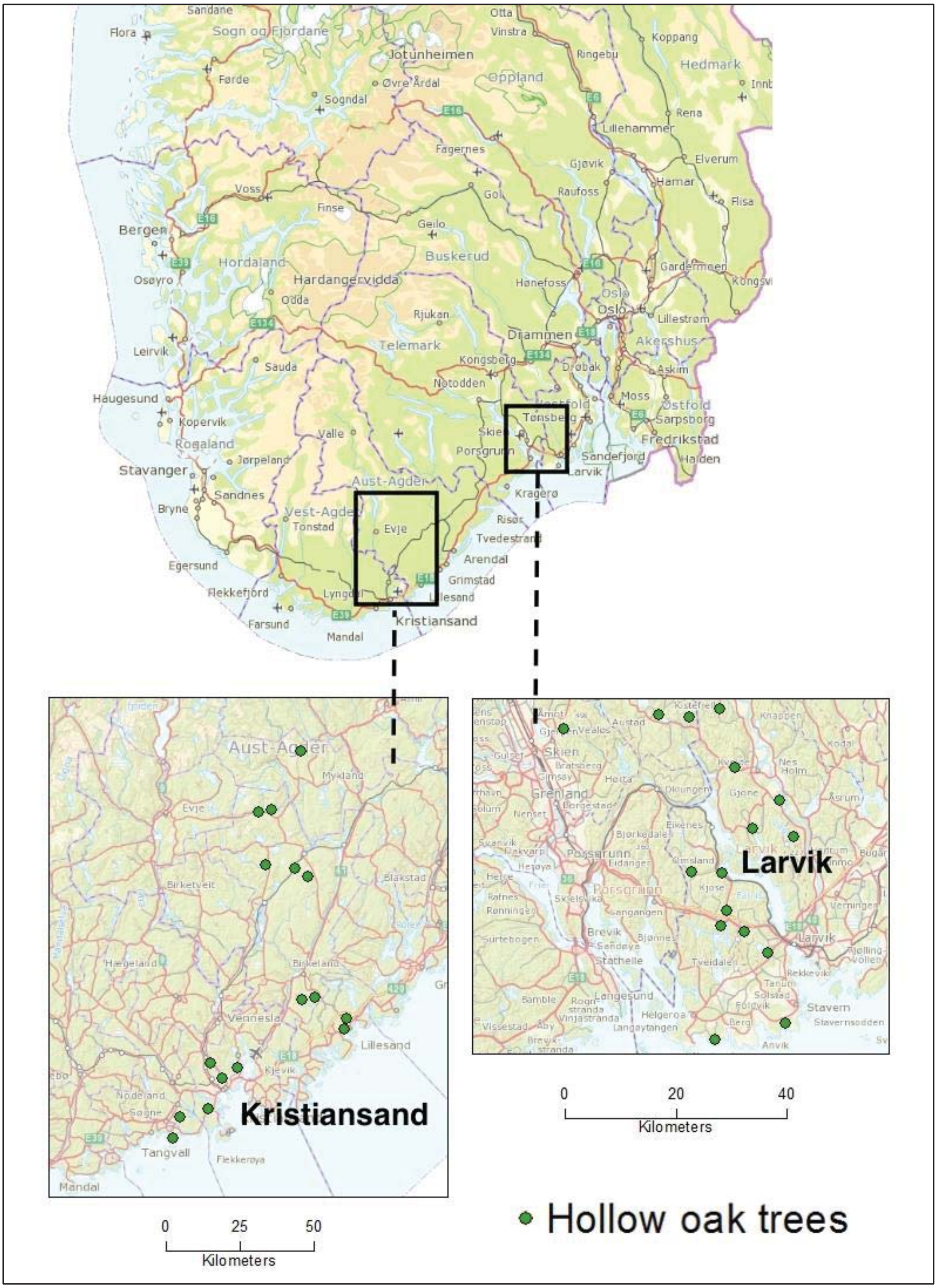

**Figure 1.** The 32 study sites divided between two regions, with one hollow oak per location

## 2.2 Data collection

Insects were sampled by Hanne Eik Pilskog in 2013 and by Senia Hagen and Hanne Eik Pilskog in 2014. Window traps with a propylene glycol solution for conservation were used to collect beetles. In 2013, the traps were placed out May 16th and emptied in June and July, and removed again August 23rd. In 2014, the traps were set up May 5th and emptied in June and July, and removed August 11th.  Each tree contained two traps, one in front of the hollow and one hanging from a dead wood branch (**Figure 2**). The beetles (Coleoptera) were identified to species level by Sindre Ligaard (taxonomist).

**Figure 2.** A hollow oak with two window traps

## 2.3 Study species

A total of eight beetle species were chosen to be a part of this thesis. The four oak specialist species were selected on the basis of their abundance and different preferences for microhabitats (Koehler, 2000), (**Table 1-2, Figure 3**). Oak specialist are in this thesis defined as species that prefer oak or only occur on oak, while the oak generalists occur on coniferous trees in addition to oak (Pilskog et al. in prep.).

The four oak specialists belong to different trophic groups: one xylomycetophage feeding on both fungi and wood, one xylophage species feeding on wood, one predator and one species with mixed food preferences, see Pilskog et al. (in prep.) for details on the categories. The pairs represent both oak generalists and specialists from the same genus, with one common and one rare species in each pair. *Ampedus balteatus* and *Ampedus nigrinus* make up the first pair and *Haploglossa villosula* and *Haploglossa gentilis,* the second. An overview of the distribution of all eight species in Norway is available in appendix (**Appendix IV**).

**Table 1.** Study species with information on family and number of individuals sampled. Occurrence = the percentage of hollow oaks where the species is present, all 32 hollow oaks = 100 %. The species status on the Norwegian Red List is displayed, NT = Near Threatened (Kålås et al., 2010)

| Species | Family | Individuals sampled | Occurrence (%) |
|---|---|---|---|
| *Dorcatoma chrysomelina* | Anobiidae | 111 | 31 |
| *Xestobium rufovillosum* | Anobiidae | 70 | 34 |
| *Rhizophagus bipustulatus* | Monotomidae | 30 | 59 |
| *Ptinus subpillosus* | Ptinidae | 172 | 88 |
| | | | |
| *Ampedus balteatus* | Elateridae | 274 | 66 |
| *Ampedus nigrinus* (NT) | Elateridae | 38 | 38 |
| | | | |
| *Haploglossa villosula* | Staphylinidae | 1484 | 100 |
| *Haploglossa gentilis* | Staphylinidae | 35 | 22 |

**Figure 3.** The eight study species. From the upper left: *Dorcatoma chrysomelina*, *Xestobium rufovillosum, Rhizophagus bipustulatus, Ptinus subpillosus*, *Ampedus balteatus*, *Ampedus nigrinus*, *Haploglossa villosula* and *Haploglossa gentilis.* Copyright Borowiec (2015). Permission for usage given. The pictures are scaled to represent the species sizes in relation to each other.

**Table 2.** The study species with information on distribution, trophic group, oak association, host tree preference, other host trees the species can occupy (includes coniferous and deciduous trees. Few = 0-5 other host trees, several = 6-10, many = 11-15), dead wood association and dispersal ability. Data marked with an asterisk (*) is obtained from The Saproxylic Database (2014) and Dahlberg and Stokland (2004)

| Species | Distribution | Trophic group | Oak association | Host tree preference | Other host trees the species can occupy | Dead wood association | Dispersal ability |
|---|---|---|---|---|---|---|---|
| *Dorcatoma chrysomelina* | Along the coast and inland of southeast Norway. | Xylomycetophage | Specialist | *Quercus* | Few | Rotten wood in any part of the trunks (Ranius and Jansson, 2000), from initial and advanced decayed trees*. | Unknown |
| *Xestobium rufovillosum* | Along the coast and inland of southeast Norway. | Xylophage | Specialist | *Quercus, Salix* | Several | From recently decayed trees to advanced decayed trees*. Dead, dry wood in trunks (Ranius and Jansson, 2000). | Low ability. Very rarely seen to fly (Hickin, 1968) and not expected to walk far (Buck, 1958). |
| *Rhizophagus bipustulatus* | Mainly along the coast and inland of southeast Norway. | Predator | Specialist | *Quercus*, *Betula* | Several | From healthy trees to very decayed trees*. Under the bark (Palm, 1951). | High ability (Irmler et al., 2010). |
| *Ptinus subpillosus* | Mainly along the coast and inland of southeast Norway, but also in the west and as far north as Hedmark county. | Mixed feeding | Specialist | *Quercus* | Many | From healthy trees to advanced decayed trees*. Under bark, moss and in leaves (Koch et al., 1989). | Low ability. Wingless females (Crowson, 1984). |
| *Ampedus balteatus* | Mainly along the coast and inland of southeast Norway, but also in the west and as far north as Hedmark county. | Xylophage | Generalist | Deciduous, coniferous | Few | From recently decayed trees to advanced decayed trees*. Rotten wood in any part of the trunks (Ranius and Jansson, 2000). | Unknown |
| *Ampedus nigrinus* | Mainly along the coast and inland of southeast Norway, but also in the west and as far north as Hedmark county. | Xylophage | Generalist | No preference | Several | From recently decayed trees to advanced decayed trees*. Red-rotted wood, under mould-rich bark (Koch et al., 1989). | Unknown |
| *Haploglossa villosula* | Mainly along the coast and inland of southeast Norway, but also in the west and as far north as Hedmark county. | Predator | Generalist | No preference | Few | Advanced decayed trees* with ants and in bird nests (Rothschild and Clay, 1957). | Unknown |
| *Haploglossa gentilis* | Limited to a few places in eastern Norway. | Predator | Specialist | *Quercus* | Few | Advanced decayed trees*. With ants and in bird nests (Donisthorpe, 1927). | Unknown |

## 2.4 Explanatory variables

A series of explanatory variables have been collected in order to explain variation in the eight chosen species of beetles (**Table 3-4**). These variables were gathered from a variety of sources and can be divided into three spatial levels; tree, site and landscape. The tree variables consist of Diameter and Wood Mould. Diameter was measured, while Wood Mould was visually estimated. Site variables were surveyed by walking 30 m in each cardinal direction, creating a 43x43 m cell (1849m$^2$) around each hollow oak. Site variables include relascope sum (measuring the basal area of the stand around each hollow oak, as a proxy for forest regrowth), dead wood amount and number of hollow oaks. The hollow oaks included in the latter variable were trees that had a diameter larger than 20 cm (at breast height) and were visibly hollow. Dead wood larger than 1 m in length was registered according to whether it was standing (snags) or lying (logs) and size: small (diameter: 10-20 cm), medium (21-40 cm) and large (>41 cm). To simplify this for the purpose of this thesis, logs and snags were combined. Then, the minimum dead wood volume for each size category was calculated based on the smallest diameter in each category (10, 21 and 41 cm) and the minimum length of counted logs, i.e. 1 m, using the formula $\pi$ r2h, where r was is the radius and h the length. The purpose for this categorization was to give the largest logs and snags more weight than the small ones. These values were then multiplied with the number of dead wood entities that were registered around every hollow oak and finally added together to represent the minimum local dead wood volume.

The landscape variables were derived from various online map sources and include the distance to the nearest coast, as well as amount of deciduous trees, hollow oaks and dead wood, all for both 1 and 2 km scale. The dataset SAT-SKOG was downloaded as a shapefile for each county from The Norwegian Forest and Landscape Institute (Skog og Landskap, 2009). SAT-SKOG provides information on forest type, age and volume calculated from satellite imaging and field data from the Norwegian Forest Inventory (Skog og Landskap, 2009).

On landscape level, dead wood data was derived from the Complementary Hotspot Inventory (CHI), which is an approach developed by The Norwegian Forest and Landscape Institute and used to identify important areas for biodiversity (Gjerde et al., 2007). Standing and lying dead wood were combined into one variable. It must be noted that CHI coverage is absent in some areas in Larvik (Vestfold) and Siljan (Telemark), as these grounds are owned by Fritzøe Skoger.

Fritzøe have conducted their own mapping of woodland key habitats, for which no measurements of dead wood content are accessible and therefore it was not possible to include this in the thesis. To compensate for the loss of data, the mean of the areas with information on dead wood was used to represent the areas where data was missing.

The lack of complete coverage in the study areas was the reason CHI data on hollow deciduous trees was not used in this thesis. Also, the proportion of hollow oaks in the CHI dataset is not known and might have given an incorrect impression of the amount of hollow oaks in the landscape. Instead, the selected habitat type dataset was used, which contain locations of hollow oaks that meet the requirements for being a selected habitat type. Data on selected habitat types was also obtained through WMS (Miljødirektoratet, 2014), see next subchapter for details on data processing. Finally, Distance to Coast was measured in ArcMap 10.2.2.

**Table 3.** The explanatory variables used in this study

| Name | Description | Source |
|---|---|---|
| *Tree variables* | | |
| Diameter | Trunk diameter measured at breast height (DBH), 1.3 m above ground | Hanne Eik Pilskog |
| Wood Mould | An estimate of the amount of wood mould found in each hollow oak tree.<br>Categories: small (<10 liters),<br>moderate (10 - <100 liters) and<br>large (>100 liters) amount | Hanne Eik Pilskog |
| *Site variables* | *Measured within 43x43 m (0.18 ha)* | |
| Forest Regrowth North | Relascope sum of forest regrowth, measured as basal area of trees, facing north | Hanne Eik Pilskog |
| Forest Regrowth South | Relascope sum of forest regrowth, measured as basal area of trees, facing south | Hanne Eik Pilskog |
| Dead Wood Local | Volume of dead wood ($m^3$/ha) | Hanne Eik Pilskog |
| Hollow Oaks Local | Number of hollow oaks | Hanne Eik Pilskog |
| *Landscape variables* | | |
| Distance to Coast | Distance to nearest coast measured in km | Measured in ArcMap |
| Deciduous Trees_1km | Average $m^3$/ha deciduous trees within a buffer zone of 1 km | SAT-SKOG |
| Hollow Oaks_1km | Selected habitat type: hollow oaks as area (ha) within a buffer zone of 1 km | Selected habitat type |
| Dead Wood_1km | Standing and lying dead wood as area (ha) within a buffer zone of 1 km | CHI |
| Deciduous Trees_2km | Average $m^3$/ha deciduous trees within a buffer zone of 2 km | SAT-SKOG |
| Hollow Oaks_2km | Selected habitat type: hollow oaks as area (ha) within a buffer zone of 2 km | Selected habitat type |
| Dead Wood_2km | Standing and lying dead wood as area (ha) within a buffer zone of 2 km | CHI |

**Table 4.** Descriptive statistics of the explanatory variables used in this study. WoodMould is not a continuous variable and was therefore excluded from this overview

| Variable | Minimum | Median | Maximum | Mean |
|---|---|---|---|---|
| Diameter | 25 cm | 65.55 cm | 159 cm | 72.503 cm |
| Forest Regrowth North | 3 | 8 | 20 | 8.718 |
| Forest Regrowth South | 1 | 8 | 19 | 7.906 |
| Dead Wood Local | 0.21 $m^3$/ha | 2.244 $m^3$/ha | 6.333 $m^3$/ha | 2.52 $m^3$/ha |
| Hollow Oaks Local | 0 | 0 | 6 | 0.87 |
| Distance to Coast | 0.26 km | 8.95 km | 42.73 km | 13.507 km |
| Deciduous Trees_1km | 13.36 $m^3$/ha | 40.154 $m^3$/ha | 51.521 $m^3$/ha | 37.264 $m^3$/ha |
| Hollow Oaks_1km | 0 ha | 0.157 ha | 7.68 ha | 0.866 ha |
| Dead Wood_1km | 0.189 ha | 1.521 ha | 5.103 ha | 1.521 ha |
| Deciduous Trees_2km | 17.069 $m^3$/ha | 43.686 $m^3$/ha | 75.149 $m^3$/ha | 41.218 $m^3$/ha |
| Hollow Oaks_2km | 0 ha | 0.172 ha | 37.502 ha | 3.006 ha |
| Dead Wood_2km | 0.189 ha | 1.891 ha | 5.824 ha | 1.895 ha |

## 2.5 Data processing

### GIS

ArcMap was used to process landscape variables, in addition to creating maps and measuring distances. The coordinates of the 32 hollow oaks were imported to ArcMap as a basis for analysis. Buffer zones of 1 km and 2 km were created around the oaks, using the *buffer* function (**Figure 4**). This created some overlap between the buffer zones. Overlap is generally something to avoid as it could lead to spatial autocorrelation. Eigenbrod (2011) states that overlap is a form of pseudoreplication and should be avoided. Seeing as some hollow oak trees are located less than 2 km from each other, they do in fact share some explanatory variables. Even though this may not be ideal it must be mentioned that species on hollow oak trees do not respond less to some variables because they overlap with another tree. Removing duplicates would therefore not be beneficial. Moreover, Zuckerberg et al. (2012) found no direct link between overlap and spatial autocorrelation.

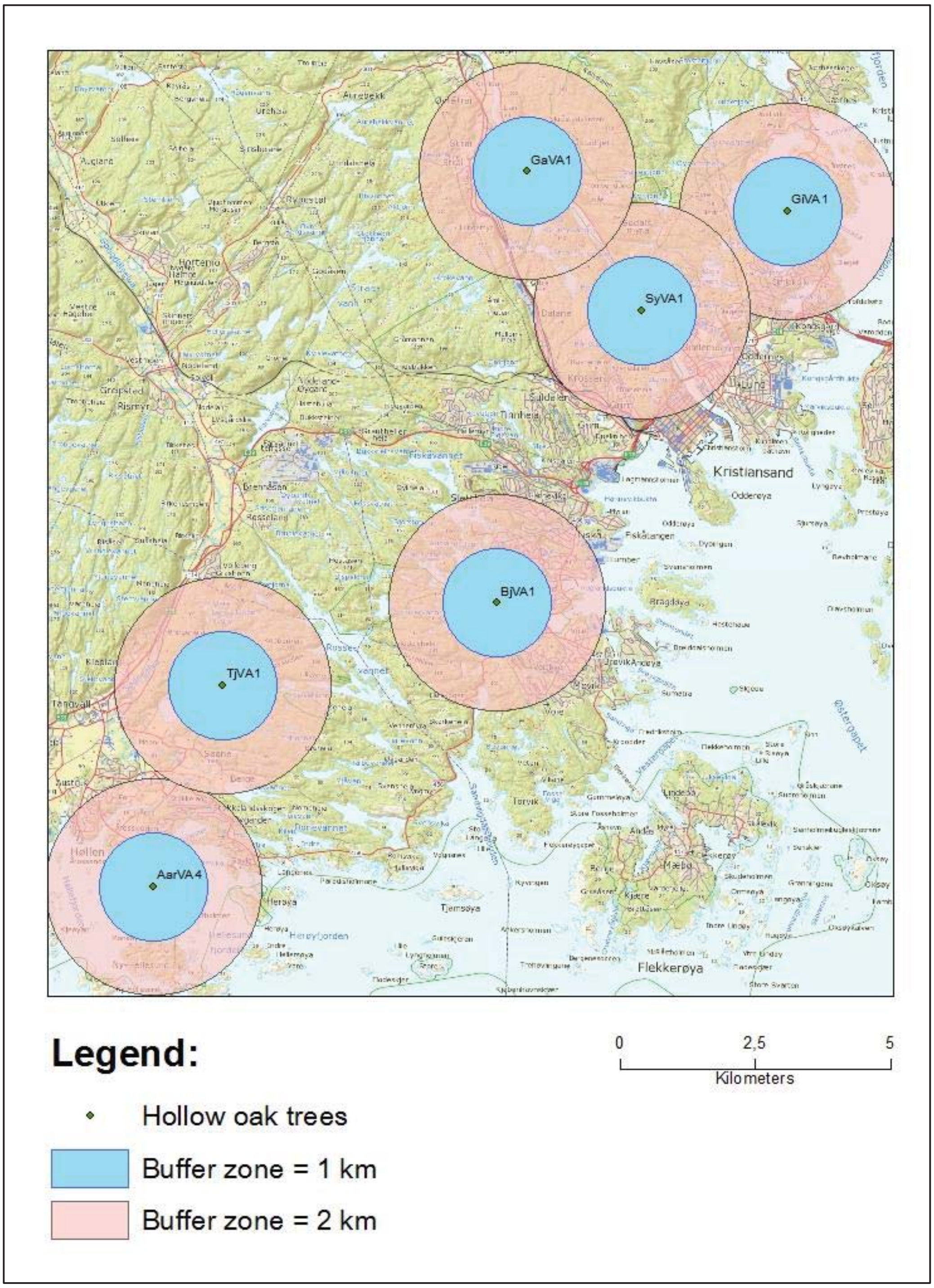

**Figure 4.** Hollow oak trees with buffer zones of 1 km and 2 km

The variable Deciduous Trees_1km and 2 km was based on volume of deciduous trees measured in $m^3$ per hectare from the SAT-SKOG dataset. This data was overlapped with the oaks buffer zones, using *intersect* and converted to display the average $m^3$ per hectare of deciduous trees within 1 km and 2 km radii for each hollow oak tree.

Categories of CHI data were made available in ArcMap through WMS services. Due to the limited nature of WMS data, it was not possible to perform any analysis. Instead, Dead Wood_1km and 2 km were collected by measuring the area of the dead wood polygons that were found within the buffer zones of 1 km and 2 km, respectively. Figure 5 shows how Dead Wood_1km and 2 km was displayed in ArcMap.

The selected habitat types dataset contained both and point features, therefore there was a need for uniformity. This was solved by assigning all point features a given radius of 10 m and converting them to hectare. WMS services are not available for analysis, so hollow oaks points and polygons were simply counted and measured within the two buffer zones and then added together (**Figure 5**).

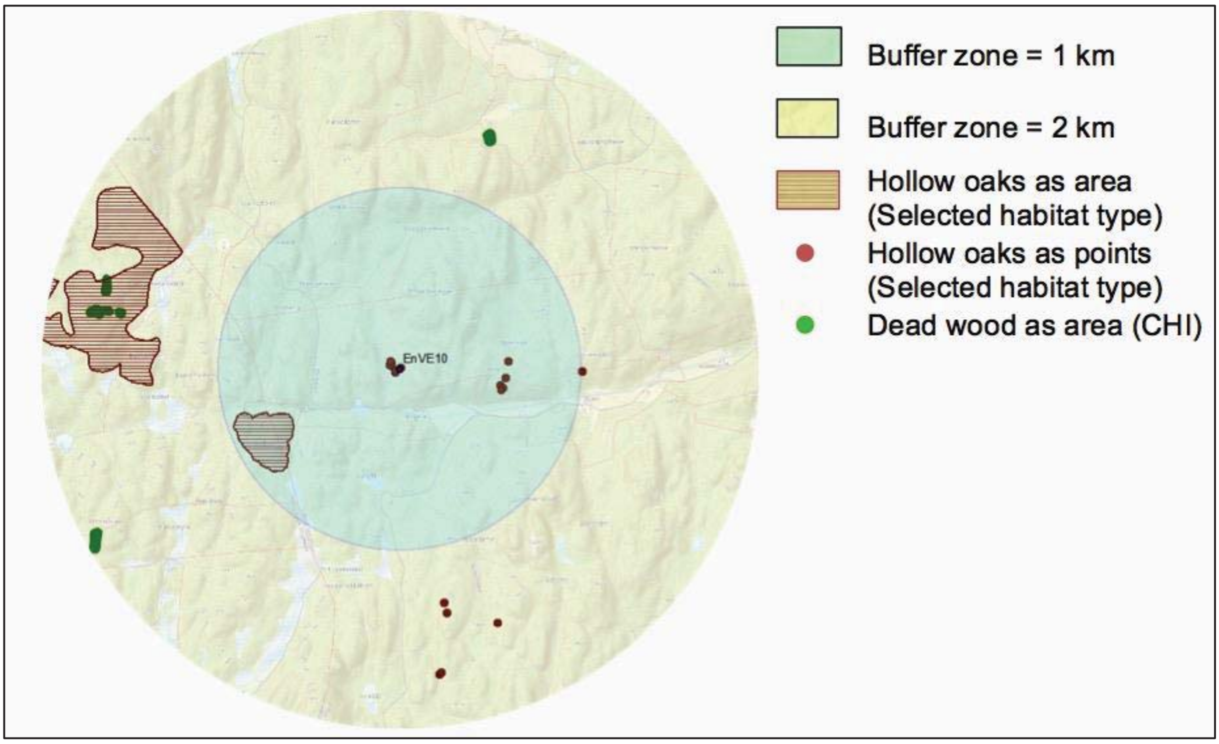

**Figure 5.** An overview of a hollow oak and the buffer zones of 1 km and 2 km overlapped with three variables; hollow oaks as area features, hollow oaks as point features and dead wood as area feature

### Statistics

The statistical software SAS JMP Pro 10.0 was used for all statistical operations.

As the response variables, the eight species of beetles were tested for normality using the *distribution* option, which generated histograms. These were visually inspected and revealed that none were normally distributed.

Five had a severely skewed distribution and were converted to presence-absence data (1, 0), two other variables were log-transformed (log x+1) to reach normality and the final response variable was left untransformed. The reason for this was that the species, *Haploglossa gentilis'* distribution is limited to seven hollow oaks in the region of Larvik, Siljan and Skien. The analyses ran smoother when the species data was not log transformed or converted to presence-absence.

Due to numerous explanatory variables multicollinearity was a possibility (Rogerson, 2010). In order to test for this, the *multivariate* option was used, creating a correlation table (**Appendix V**). It revealed an association (0.81) between Dead Wood _1km and Dead Wood_2km and between Hollow Oaks_1km and Hollow Oaks_2km (0.86). Therefore, separate analyses were carried out with 1 km and 2 km variables. Seeing as Wood Mould is an ordinal variable it could not be included in the multivariate analysis together with the continuous variables. Instead, ordinal logistic was performed, which showed a strong relationship between Wood Mould and Diameter ($p$ = 0.005). Nevertheless, this relationship did not interfere with the final results, as it was performed separate correlation tests in the two cases where Diameter and Wood Mould were found to be significant predictors.

Backward stepwise multiple regression was performed on the eight response variables. For each species two analyses were done, one with 1 km landscape variables and the other with 2 km. Tree- and site variables were for the most part included in both of these analyses. Because the occurrence of *Haploglossa gentilis* was limited to Larvik, only 16 hollow oaks were included in the analyses for this species.

In some cases there were too many explanatory variables relative to the amount of data in the response variables and JMP would generate a warning when running the stepwise regression. Then the explanatory variables with the least explanatory value were excluded. Some explanatory variables were not significant predictors, but were included because they added to a better model. Two optimal models were selected for each of the eight study species, one for 1 km and one for 2 km.

The corrected Akaike information criterion (AICc), which is used in JMP instead of the Akaike information criterion (AIC), ranks competing models and was used as a basis for model selection in the stepwise regression (Symonds and Moussalli, 2011).

The model with lowest AICc value was chosen. AICc gives a more accurate score than AIC when the sample sizes are small (Burnham and Anderson, 2004), which fits well with this dataset.

$R^2$ is a measure of goodness of fit, which tells how much variation in the response variables can be explained by the explanatory variables (Rogerson, 2010). $R^2$ was used to evaluate and compare the two optimal models created for each species through the logistic regression. $R^2$ adjusted value was obtained for the parametric response variables. To compare models with nominal response variables the *model comparison* option was used. This analysis generated Receiver Operating Characteristic (ROC) curves for the two comparing models, where the predictive abilities of the models could be compared (SAS Institute, 2013). On the basis of the ROC curves, the Area under the curve (AUC) values could be found and a hypothesis test was performed. The hypothesis test showed whether there was a significant difference between the two models or not. Using the AUC values, a comparison between the different models was possible, where the model with the value closes to 1 was regarded as the better of the two. There was not any point in comparing models for the three species with continuous occurrence data as one only had one model, and the other two species had identical models on both scales.

# 3. Results

Of the 13 explanatory variables used in the analyses, as many as 11 were included at least once in the optimal models (**Table 5**), excluding only Forest Regrowth North and Dead Wood_1km. A complete overview over the results is displayed in Table 6.

**Table 5.** The explanatory variables that were included in the chosen models generated by the backward stepwise regression analysis, divided between tree, site and landscape scale

| Tree variables | Site variables | Landscape variables |
|---|---|---|
| Diameter | Forest Regrowth South | Distance to Coast |
| Wood Mould | Dead Wood Local | Deciduous Trees_1km |
| | Hollow Oaks Local | Deciduous Trees_2km |
| | | Hollow Oaks_1km |
| | | Hollow Oaks_2km |
| | | Dead Wood_2km |

**Table 6.** Complete results from the backward stepwise regression. Separate analyses done for 1 km and 2 km landscape variables (scale). Variables with *p*-values < 0.05 are highlighted in bold. Binary (presence-absence) occurrence data is marked with an asterisk (*)

| Species | Scale | Output | Estimate | SE | $\chi^2$ | Prob>$\chi^2$ | t Ratio | Prob>\|t\| |
|---|---|---|---|---|---|---|---|---|
| *Dorcatoma chrysomelina** | 1 km | Intercept | -4.808 | 1.971 | 5.95 | 0.014 | | |
| | | **Diameter** | **0.068** | **0.028** | **5.62** | **0.017** | | |
| | | Hollow Oaks_1km | -3.447 | 2.431 | 2.01 | 0.156 | | |
| | 2 km | Intercept | -5.654 | 2.335 | 5.71 | 0.015 | | |
| | | **Diameter** | **0.063** | **0.028** | **5.02** | **0.025** | | |
| | | Hollow Oaks_2km | -0.985 | 0.515 | 3.66 | 0.055 | | |
| *Xestobium rufovillosum** | 1 km | Intercept | -0.589 | 0.418 | 1.98 | 0.159 | | |
| | | **Wood Mould** | **0.877** | **0.418** | **4.38** | **0.036** | | |
| | 2 km | Intercept | -0.589 | 0.418 | 1.98 | 0.159 | | |
| | | **Wood Mould** | **0.877** | **0.418** | **4.38** | **0.036** | | |
| *Rhizophagus bipustulatus** | 1 km | Intercept | 1.568 | 0.627 | 6.24 | 0.012 | | |
| | | **Distance to Coast** | **-0.086** | **0.035** | **5.77** | **0.016** | | |
| | 2 km | Intercept | 1.568 | 0.627 | 6.24 | 0.012 | | |
| | | **Distance to Coast** | **-0.086** | **0.035** | **5.77** | **0.016** | | |
| *Ptinus subpillosus* | 1 km | - | - | - | - | - | - | - |
| | 2 km | Intercept | 3.534 | 0.564 | | | 6.26 | <.0001 |
| | | **Deciduous Trees_2km** | **-0.026** | **0.012** | | | **-2.06** | **0.049** |
| *Ampedus balteatus** | 1 km | Intercept | 7.629 | 2.976 | 6.57 | 0.010 | | |
| | | Forest Regrowth South | -0.195 | 0.110 | 3.12 | 0.077 | | |
| | | **Deciduous Trees_1km** | **-0.138** | **0.060** | **5.16** | **0.023** | | |
| | 2 km | Intercept | -0.072 | 0.543 | 0.02 | 0.893 | | |
| | | Distance to Coast | 0.061 | 0.038 | 2.57 | 0.108 | | |
| *Ampedus nigrinus** | 1 km | Intercept | 3.377 | 1.589 | 4.52 | 0.033 | | |
| | | Hollow Oaks Local | -1.350 | 0.733 | 3.39 | 0.065 | | |
| | | Forest Regrowth South | -0.298 | 0.154 | 3.75 | 0.053 | | |
| | | Hollow Oaks_1km | -2.430 | 1.814 | 1.79 | 0.180 | | |
| | 2 km | Intercept | 0.103 | 1.381 | 0.01 | 0.940 | | |
| | | Forest Regrowth South | -0.271 | 0.144 | 3.56 | 0.059 | | |
| | | Hollow Oaks_2km | -1.118 | 0.863 | 1.89 | 0.168 | | |
| | | **Dead Wood_2km** | **1.223** | **0.605** | **4.08** | **0.043** | | |
| *Haploglossa villosula* | 1 km | Intercept | 4.234 | 0.163 | | | 25.87 | <.0001 |
| | | **Wood Mould** | **0.374** | **0.163** | | | **2.29** | **0.029** |
| | 2 km | Intercept | 4.234 | 0.163 | | | 25.87 | <.0001 |
| | | **Wood Mould** | **0.374** | **0.163** | | | **2.29** | **0.029** |
| *Haploglossa gentilis* | 1 km | Intercept | -1.433 | 1.753 | | | -0.82 | 0.427 |
| | | **Dead Wood Local** | **7.525** | **3.058** | | | **2.46** | **0.027** |
| | 2 km | Intercept | -1.433 | 1.753 | | | -0.82 | 0.427 |
| | | **Dead Wood Local** | **7.525** | **3.058** | | | **2.46** | **0.027** |

**Table 7.** The table displays each species' two optimal models (1 and 2 km spatial scale). The AICc, $R^2$ and AUC value for comparison is also displayed. Binary (presence-absence) occurrence data is marked with an asterisk (*). The model with the highest $R^2$ and AUC value is highlighted in bold

| Species | | 1 km Optimal Model | 2 km Optimal Model |
|---|---|---|---|
| *Dorcatoma chrysomelina** | | | |
| | AICc, initial/final | 57.474 / 28.743 | 56.978 / 30.996 |
| | $R^2$ | **0.386** | 0.315 |
| | AUC | **0.877** | 0.831 |
| *Xestobium rufovillosum** | | | |
| | AICc, initial/final | 67.959 / 39.008 | 66.671 / 39.008 |
| | $R^2$ | 0.123 | 0.123 |
| | AUC | 0.705 | 0.705 |
| *Rhizophagus bipustulatus** | | | |
| | AICc, initial/final | 69.297 / 38.272 | 69.962 / 38.272 |
| | $R^2$ | 0.175 | 0.175 |
| | AUC | 0.740 | 0.740 |
| *Ptinus subpillosus* | | | |
| | AICc, initial/final | - | 116.501 / 71.342 |
| | $R^2$, adjusted | - | 0.106 |
| | AUC | - | - |
| *Ampedus balteatus** | | | |
| | AICc, initial/final | 63.024 / 38.667 | 67.739 / 39.889 |
| | $R^2$ | **0.217** | 0.080 |
| | AUC | **0.792** | 0.662 |
| *Ampedus nigrinus** | | | |
| | AICc, initial/final | 49.917 / 36.538 | 49.894 / 33.015 |
| | $R^2$ | 0.361 | **0.480** |
| | AUC | 0.875 | **0.920** |
| *Haploglossa villosula* | | | |
| | AICc, initial/final | 113.464 / 83.297 | 119.585 / 83.297 |
| | $R^2$, adjusted | 0.127 | 0.127 |
| | AUC | - | - |
| *Haploglossa gentilis* | | | |
| | AICc, initial/final | 168.615 / 94.145 | 170.737 / 94.145 |
| | $R^2$, adjusted | 0.252 | 0.252 |
| | AUC | - | - |

## 3.1 Model selection

Based on the AUC hypothesis testing there was no significant differences between the 1 km and 2 km optimal models for any of the species (**Table 7**). Nevertheless, for the three dissimilar models, AUC and $R^2$ values gave an indication of the goodness of fit and which model of the two was the better. For *D. chrysomelina* and *A. balteatus* the 1 km model was the better one, while for *A. nigrinus* the 2 km model performed better.

## 3.2 Responses of oak specialists

### Tree variables

The xylomycetophagous oaks specialist *D. chrysomelina* increased with Diameter ($p = 0.035$) (**Figure 6**) and the xylophage specialist *X. rufovillosum* appeared more frequently when the amounts of Wood Mould were moderate and large ($p = 0.036$) (**Figure 7**).

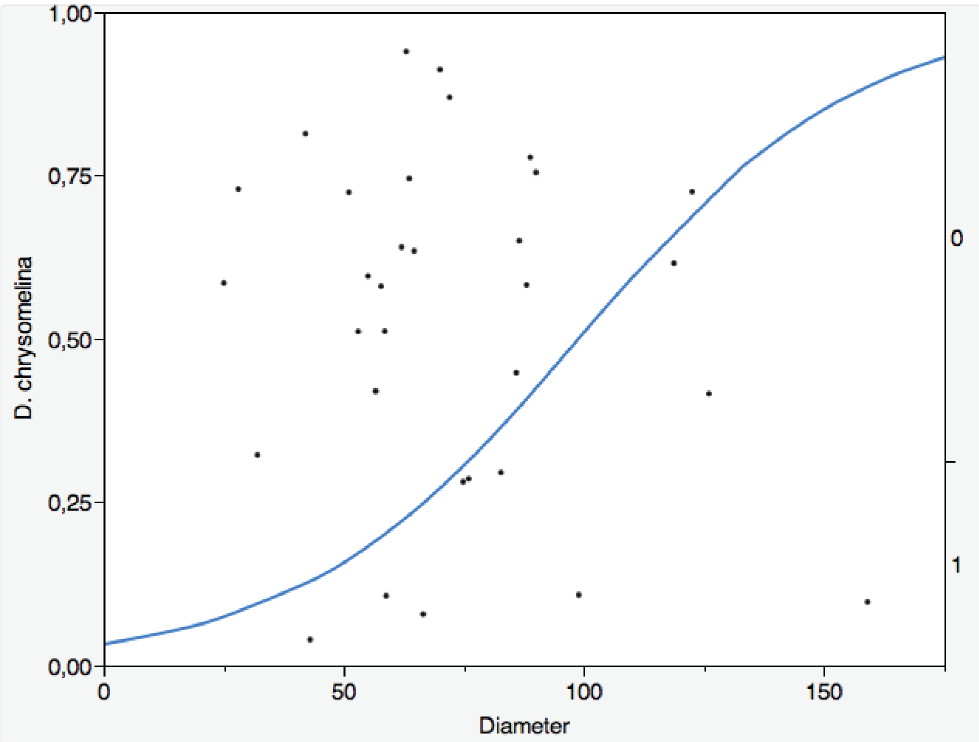

**Figure 6.** Logistic fit of *D. chrysomelina* (y) by Diameter (x). Right side represents the marginal proportion of 1 (presence) and 0 (absence), while the left side displays the probability of the species being present. As the success category is set to presence (bottom), the points under the curve drive it upward, displaying the increasing probability of success (here: that the species is present) with increasing Diameter

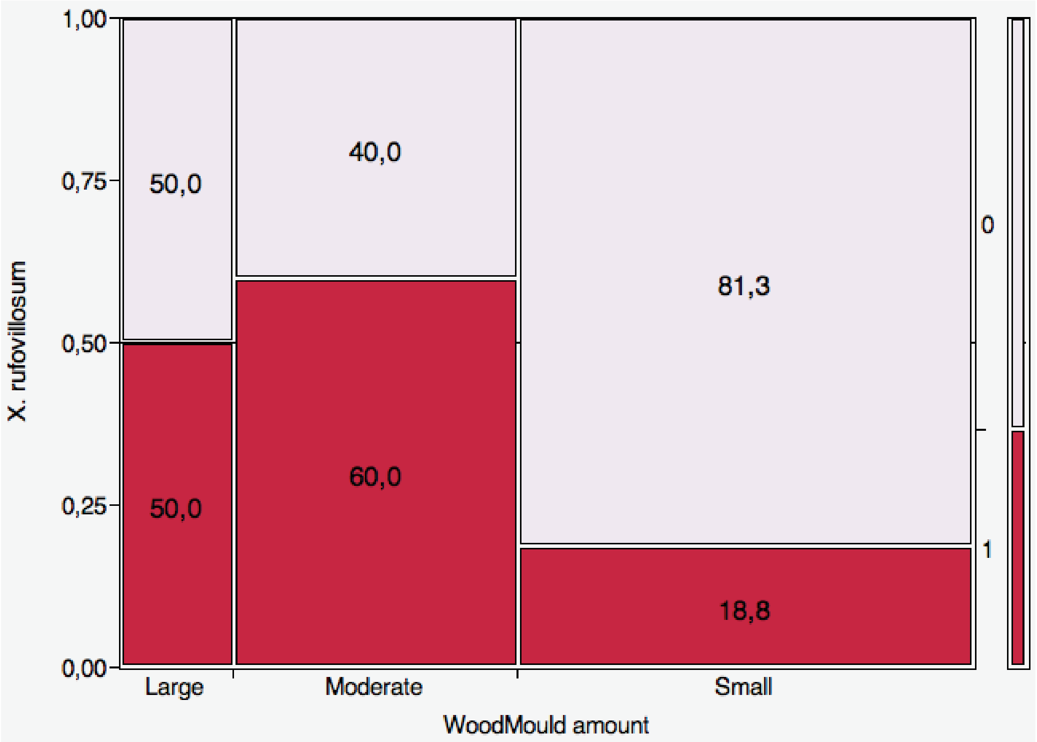

**Figure 7.** Contingency analysis of *X. rufovillosum* (y) by Wood Mould amount (x). Dark fill represents presence (1), light represents absence (0). Right side represents the marginal proportion of 1 (presence) and 0 (absence), while the left side displays the probability of the species being present. Information on percentages (presence/absence)

### Site variables

None of the four oak specialists species responded to a site variable.

### Landscape variables

*P. subpillosus,* belonging to the mixed feeding group responded negatively to Deciduous Trees_2km ($p$ = 0.049) (**Figure 8**). Distance to Coast had a negative effect on the predator *R. rufovillosum* signalizing that the species was more frequently found on hollow oak trees near the coast ($p$ = 0.016) (**Figure 9**).

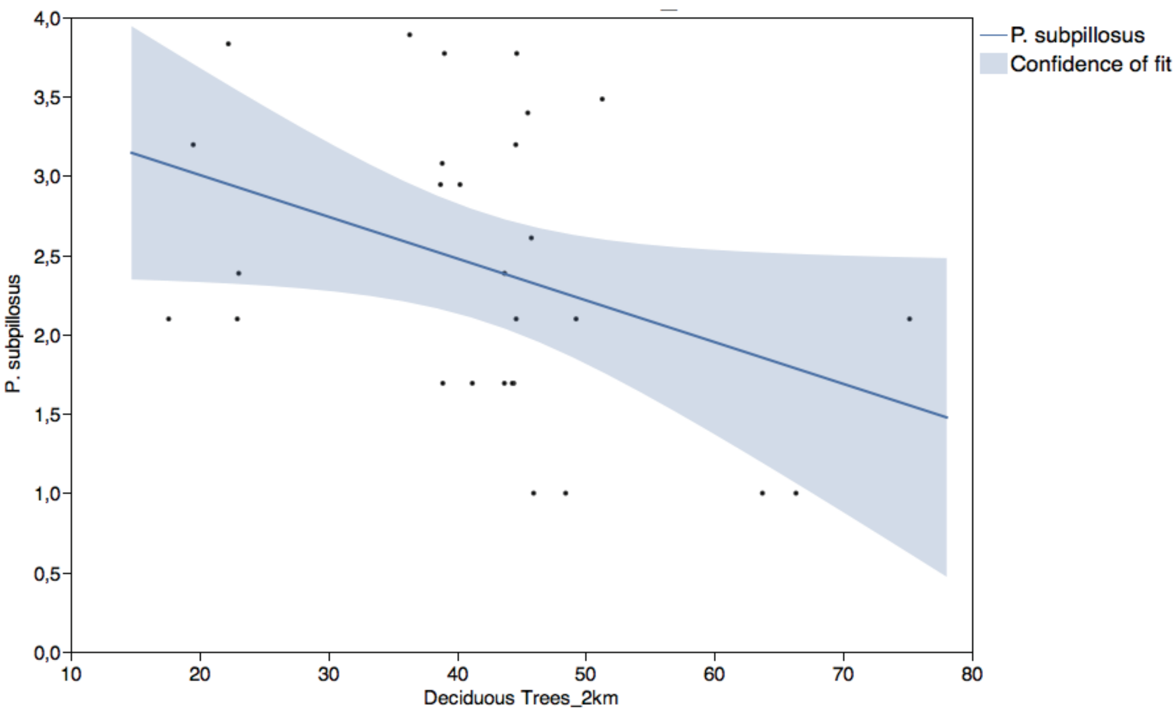

**Figure 8.** Bivariate fit of log transformed *P. subpillosus* (y = number of individuals) by Deciduous Trees_2km (x), showing the negative relationship between *P. subpillosus* and average m$^3$/ha deciduous trees with buffer zone of 2 km. The confidence of fit is also displayed

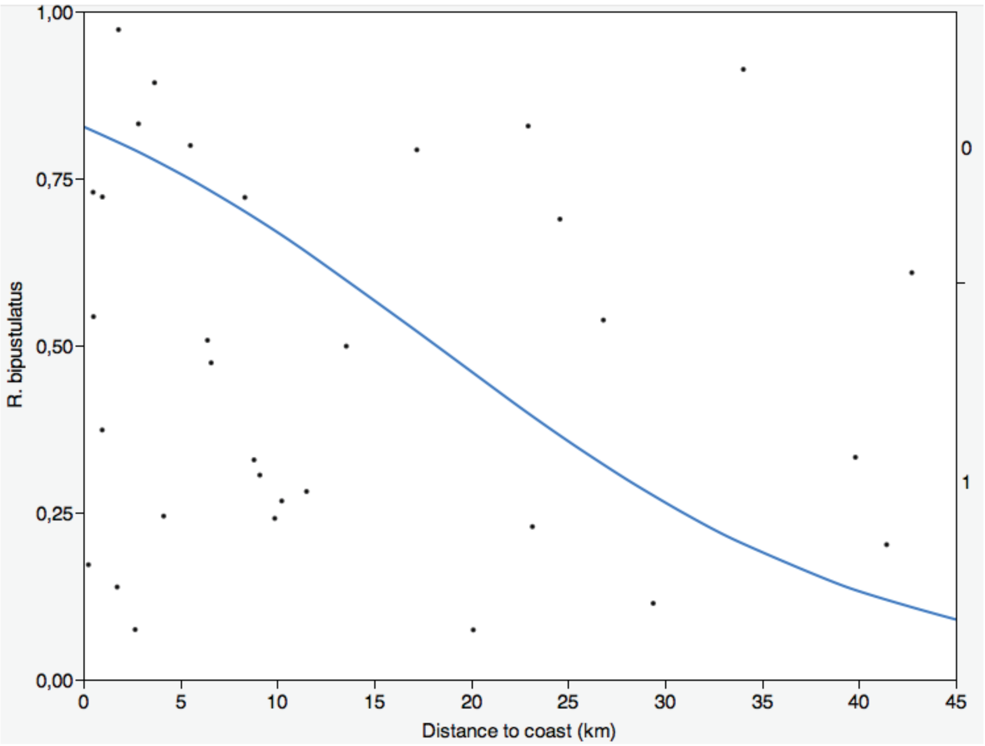

**Figure 9.** Logistic fit of *R. bipustulatus* (y) by Distance to Coast (x). Right side represents the marginal proportion of 1 (presence) and 0 (absence), while the left side displays the probability of the species being present. As the success category is set to presence (bottom), the points under the curve drive it downward, displaying the decreasing probability of success (here: that the species is present) with increasing distance to the coast

## 3.3 Responses within species pairs

### Tree variables

For one of the two species pairs, the count of the oak generalist *H. villosula* increased when the Wood Mould amounts were moderate and large ($p = 0.029$), whereas the similar species *H. gentilis* did not respond to any tree variables.

### Site variables

There was a positive relationship between the rare oak specialist *H. gentilis* and Dead Wood Local ($p = 0.275$) (**Figure 10**).

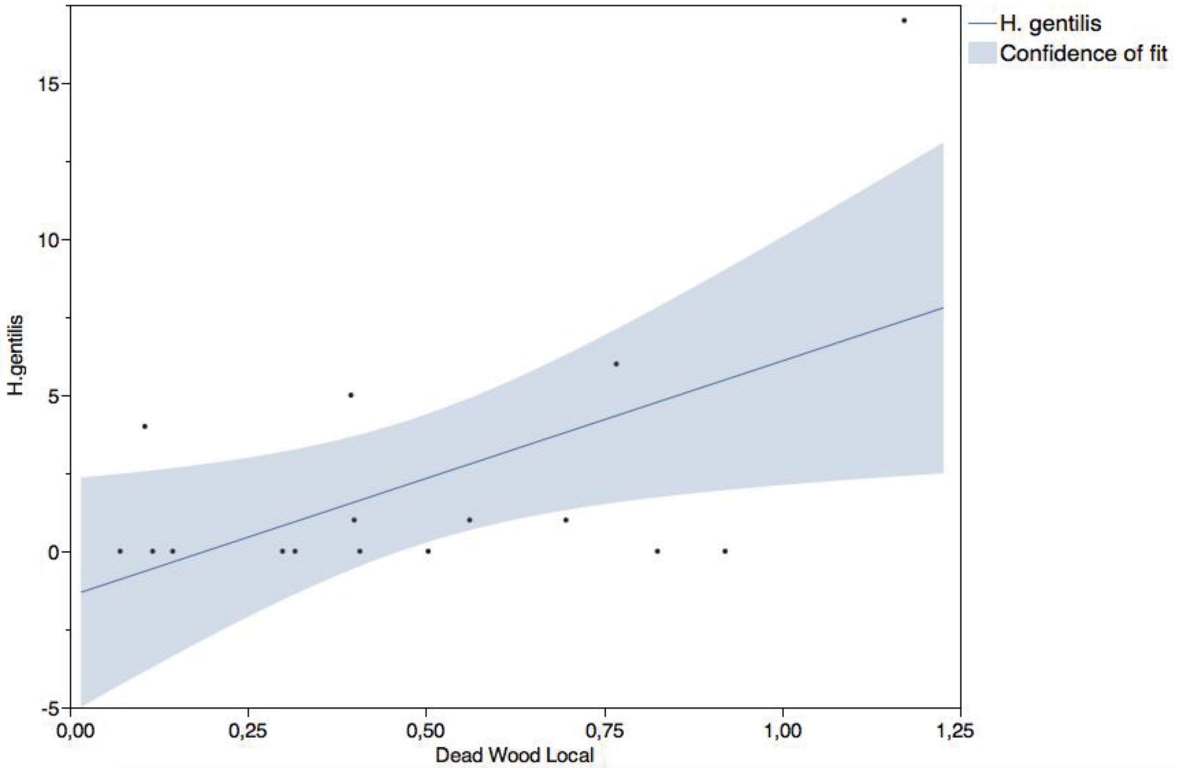

**Figure 10.** Bivariate fit of *H. gentilis* (y = number of individuals) by Dead Wood Local (x), showing the positive relationship between *H. gentilis* and the local dead wood volume. The confidence of fit is also displayed

### Landscape variables

One of the two species pairs, the oaks generalist *A. balteatus* decreased with increasing Deciduous Trees_1km ($p = 0.023$) (**Figure 11**), while the closely related *A. nigrinus* had a positive relationship with Dead Wood_2km ($p = 0.275$) (**Figure 12**). None of the *Haploglossa* species responded to landscape variables.

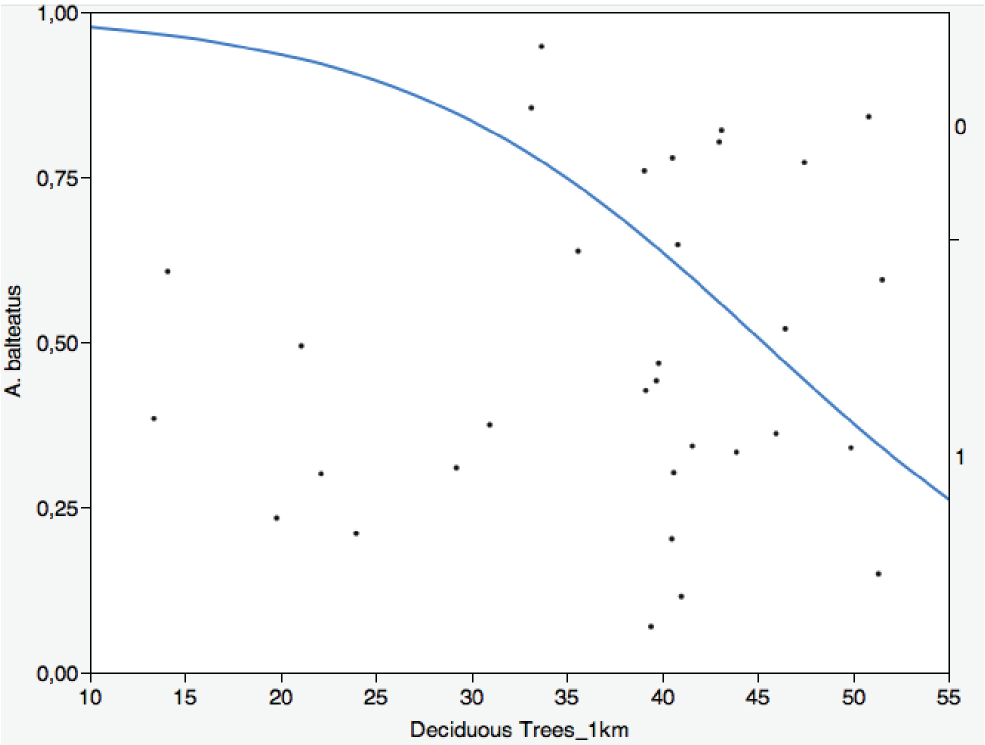

**Figure 11.** Logistic fit of *A. balteatus* (y) by Deciduous Trees_1km (x). Right side represents the marginal proportion of 1 (presence) and 0 (absence), while the left side displays the probability of the species being present. As the success category is set to presence (bottom), the points under the curve drive it downward, displaying the decreasing probability of success (here: that the species is present) with increasing average m$^3$/ha deciduous trees with buffer zone of 1 km.

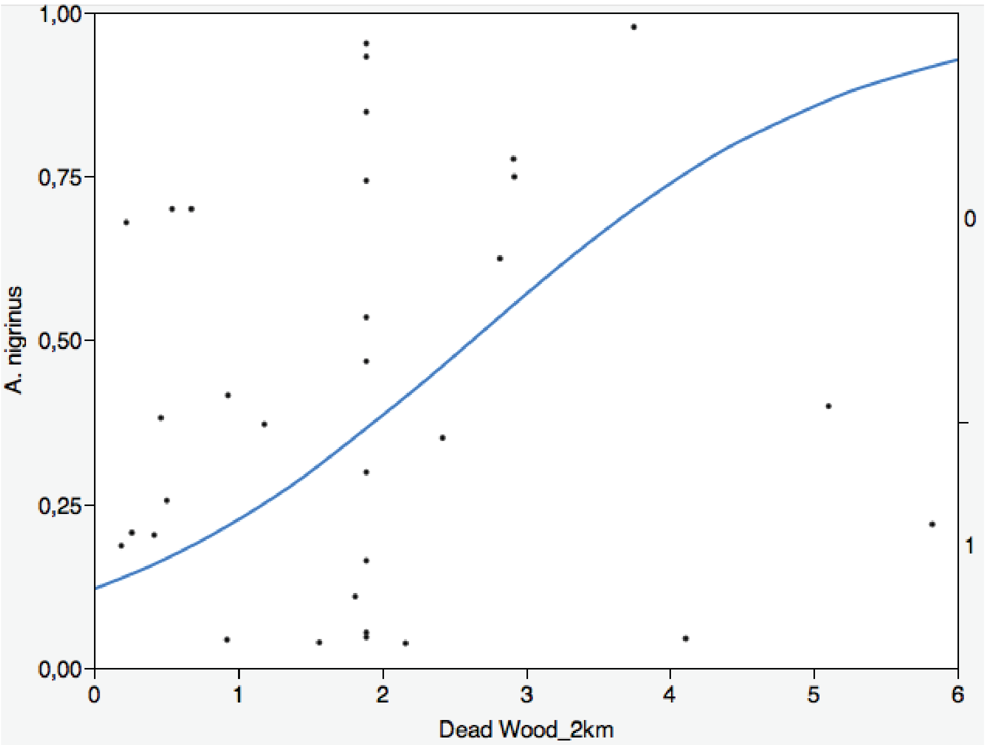

**Figure 12.** Logistic fit of *A. nigrinus* (y) by Dead Wood_2km (x). Right side represents the marginal proportion of 1 (presence) and 0 (absence), while the left side displays the probability of the species being present. As the success category is set to presence (bottom), the points under the curve drive it downward, displaying the increasing probability of success (here: that the species is present) with increasing dead wood area (ha) trees with buffer zone of 2 km

# 4. Discussion

The results show that different variables and scales were important for the four specialists belonging to different trophic levels. The first species pair, *A. balteatus* and *A. nigrinus* responded to landscape variables at 1 km and 2 km scales, respectively. *H. villosula* responded to a tree variable, while the less common *H. gentilis* responded to a site variable.

## 4.1 Effects of habitat size, isolation and climate

### Habitat size

The ecological principle of species-area relationships states that the larger the area, the more species can be found there (Collinge, 2009). This study found support for this as one study species responded positively to large diameter and two to larger amounts of wood mould. Large patches can also offer a more stable microhabitat (Ranius and Jansson, 2000), which can be linked to the metapopulation theory. The theory suggests that, in this case, large hollow oak trunks are able to sustain more stable and viable populations (Sverdrup-Thygeson et al., 2010). Stability is often a necessity for supporting an assemblage of specialist species, which many of the study species are.

### Isolation

It was expected that all species should respond positively to increased amounts of dead wood, hollow oaks and deciduous trees in their surroundings, suggesting a lower degree of isolation.
If addressing each tree and dead wood log or snag as individual habitat patches with a local population of species (Ranius, 2007), it becomes evident how important it is that these patches are connected with minimal matrix between them.

Dead wood turned out to be a significant variable on both site- and 2 km landscape scale and had a positive effect on two study species. The findings of Schiegg (2000) found a positive relationship between connectivity of dead wood and higher species abundance of saproxylic Diptera and Coleoptera. In our study, the study trees located in forests had a larger amount of dead wood surrounding them on both site- and landscape scales. This is probably one of the main factors explaining why five of the eight study species were most abundant in forests, which was obvious when inspecting the dataset. As Sverdrup-Thygeson et al. (2010) suggested, it seems as dead wood amounts in forests compensate for the smaller diameter and less sun-exposure hollow oaks in forests have, empathizing the importance of dead wood.

It was, however puzzling that none of the eight study species responded to the hollow oaks variables. In general, local connectivity should be important, as specialist species living in hollow oaks often are poor dispersers. One reason for the lack of response to Hollow Oaks Local can be that the site scale, on which hollow oaks were counted (1849 $m^2$) was simply too small, which is visible in the dataset through many zero values. Also, the hollow oaks that are in the vicinity might not necessarily be suitable as habitat, due to tree characteristics. Finally, species can have a scale of response to local amount of hollow oaks not included in this thesis. For Hollow Oaks_1km and 2 km the most prominent reason for the lack of response is the lack of complete mapping of the hollow oaks that are considered to be a selected habitat type in Norway. Nevertheless, this is the best data available. Because of this, some of the hollow oaks in this study did not have any "selected habitat type hollow oaks" within the radius of 1 km and 2 km. This did not correspond with what we saw during fieldwork, supporting the impression that the data from Miljødirektoratet (2014) is incomplete.

Several of the study species also use other deciduous trees as host trees. The variable was intended to catch a possible variation in species occurrence due to this and because oak trees are a part of the Deciduous Trees variable. It was not expected that two species would respond negatively to the volume of deciduous trees on 1 km and 2 km landscape scale. There are multiple possible reasons for the negative response in this study. If the proportion of oak in the Deciduous Trees variables was very low, the species might not benefit from the supplementary host trees the other deciduous trees offer. There is support for this theory in the fact that the Deciduous Trees and Hollow Oaks variables should, to some degree, correlate, which they do not do in this study. The Deciduous Trees variables might also be correlated with some negative biotic or abiotic variables outside the scope of this study, making the species respond to something else than the deciduous volume itself. For instance, the hollow oaks located in anthropogenic landscapes had larger amounts of Deciduous Trees in their surroundings, than those in forests. The decline in species occurrence may therefore be linked to the unstable and fragmented habitat patches this landscape offers. Both of the responding species were more abundant in forest hollow oaks, and evidently decline with increasing anthropogenic influence. Finally, the variable itself may not be foolproof. Seeing as SAT-SKOG is derived from satellite data, it provides information on a coarse-scale and may therefore not be suitable for small-scale studies, as this study ultimately is. This assumption is in correspondence with the findings of Blindheim et al. (in prep.).

**Climate**

None of the Forest Regrowth variables were significant, but Forest Regrowth South was included in three optimal models for a better result. The Forest Regrowth variables were used as an indicator of the degree of regrowth around the hollow oaks, which would affect the microclimate. It is possible that relascope measurements used were not the best method to estimate regrowth; an assessment of canopy cover may have been more accurate.

One species responded negatively to the large-scale climatic variable, Distance to Coast. It is generally warmer in the coastal areas of Norway than further inland; the inland areas also experience more precipitation (**Appendix III**). Increased precipitation has been shown to have an especially negative effect on specialist beetle species in hollow oaks (Gough et al. Submitted). Therefore, we should have seen more species respond to Distance to Coast. The inland trees were, on the other hand surrounded by more dead wood on both site- and landscape scale, which could have influenced the results.

## 4.2 Responses of oak specialists

The responses of the four oak specialists representing different trophic levels are summarize in Table 8.

**Table 8.** A simplified overview of the main results for the four oak specialist species. A positive relationship between the species and a variable is marked with +, while a negative is marked with **-**

| Species/Variables | Tree | | Landscape | |
|---|---|---|---|---|
| | Diameter | Wood Mould | Distance to Coast | Deciduous Trees_2km |
| *Dorcatoma chrysomelina*<br>(xylomycetophage) | + | | | |
| *Xestobium rufovillosum*<br>(xylophage) | | + | | |
| *Rhizophagus bipustulatus*<br>(predator) | | | - | |
| *Ptinus subpillosus*<br>(mixed feeding) | | | | - |

***Dorcatoma chrysomelina***

*D. chrysomelina*, the xylomycetophagous oak specialist responded positively to Diameter in the analyses at both spatial scales. It was generally predicted that habitat size would affect the species positively. Additionally, because *D. chrysomelina* is partially feeding on fungi, it was expected that variables enhancing fungal presence would be of importance, which was thought to be Diameter and Forest Regrowth.

Following the "habitat heterogeneity theory" there is a correlation between large areas and great habitat diversity (Boecklen, 1986, Williams, 1964). A large hollow oak will contain more variety in microhabitat in terms of different bark structures and depth, which cannot develop on smaller trunks. This diversity can facilitate fungal colonization by creating different "points of entry". Further on, Ranius and Jansson (2000) found that fungi associated beetles in Sweden actually favor trees with large circumference and dense tree cover. The cover may contribute to higher moisture levels and a large trunk can make fungi colonization easier (Ranius and Jansson, 2000). Seeing as diameter may increase with age, a large diameter might reflect a tree's old age, which in turn reflects the possibility of a longer colonization period for fungi, increasing the odds of success.

Why *D. chrysomelina* did not respond to Forest Regrowth could possibly be explained by the fact that a relascope sum may not be representative for the optimal growth conditions for the fungi this species is associated with. On a larger scale, *D. chrysomelina* should also have responded positively to Distance to Coast, seeing as inland areas have more precipitation and subsequently, the microclimate should be moister.

### *Rhizophagus bipustulatus*

There were no specific predictions tied to the predator *R. bipustulatus* due to the lack of knowledge about the species possible dietary specialization. The results showed a negative relationship with Distance to Coast. The species occurrence frequency decreased with increasing distance to the coast, which most likely is due to lower temperature and more precipitation in the inland sites (**Appendix III**). As stated, increased precipitation was not favored by specialist species associated with hollow oaks (Gough et al. Submitted).

### *Xestobium rufovillosum*

The xylophage species, *X. rufovillosum* was predicted to respond to dead wood and climatic variables, like Forest Regrowth and Distance to Coast. As stated earlier, many saproxylic beetles favor high sun-exposure. While *X. rufovillosum* did not directly respond to a climatic variable or dead wood, its positive response to Wood Mould may be linked to its preferred microhabitat, which consist of dead, dry wood in trunks (Ranius, 2002). Seeing as tree characteristic may affect wood mould quality, I ran a quick correlation test on Wood Mould and the size of the entrance of the cavity (field registration), which showed a significant relationship between the two; a large entrance had large and moderate amounts of Wood Mould.

It is suggested that a large entrance would allow for more sun-exposure, reducing the humidity (Ranius, 2002), which fits well with what we know about the microhabitat preferences of *X. rufovillosum*. The expectations tied to a positive response to dead wood, was to some degree met, seeing as Wood Mould may represent the dead wood in hollow oaks.

***Ptinus subpillosus***

*P. subpillosus* has mixed feeding preferences and is assumed to be a dietary generalist, therefore the species was predicted to have a weaker response to the environmental variables than the species with more narrow food preferences. *P. subpillosus* did not have a notably weaker response to the variables compared to the other three oaks specialists, and responded negatively to Deciduous Trees_2 km. As stated above, this response may be caused by a too small proportion of oak in the Deciduous Trees variable, an associated with some negative factor or the variable being too coarse-scaled. Adding to this, *P. subpillosus* prefers hollow oaks, but the species might also be associated with spruce (*Picea*) (Widerberg et al., 2012), which could have contributed to this result.

## 4.3 Responses within species pairs

The responses of the two species pairs are summarize in Table 9.

**Table 9.** A simplified overview of the main results for the two species pairs. A positive relationship between the species and a variable is marked with +, while a negative is marked with -

| Species/Variables | Tree | Site | Landscape | |
|---|---|---|---|---|
| | Wood Mould | Dead Wood Local | Deciduous Trees_1km | Dead Wood_2km |
| *Ampedus balteatus*<br>(common) | | | - | |
| *Ampedus nigrinus*<br>(rare) | | | | + |
| *Haploglossa villosula*<br>(common) | + | | | |
| *Haploglossa gentilis*<br>(rare) | | + | | |

***Ampedus balteatus* and *Ampedus nigrinus***

As with *P. subpillosus*, *A. balteatus* also had a negative relationship with Deciduous Trees. The species is also using coniferous trees as host trees and was most abundant on hollow oaks in forests. However, *A. balteatus* is an abundant oak generalist and therefore I also predict the species to be less specialized and hence, less particular in its habitat preferences.

As a wood boring species, it was not surprising that a positive relationship between *A. nigrinus* and dead wood arose. Dead wood on large scales have proven to be important in many studies, for example Franc et al. (2007), Gibb et al. (2006) and Økland et al. (1996). Species like *A. nigrinus* and *H. gentilis* which already are somewhat uncommon, may be vulnerable to habitat change and fragmentation due to their dependence on dead wood. Dead wood quantity in managed forests is generally lower than in unmanaged, old growth forests (Siitonen, 2001) and *A. nigrinus* is probably dependent on having a minimum amount of dead wood to persist. Therefore, if the surrounding forest around the hollow oaks where *A. nigrinus* is present become managed or more intensively managed, *A. nigrinus* may have a hard time adapting and become even more uncommon.

### ***Haploglossa villosula* and *Haploglossa gentilis***

It was expected that the common generalist *H. villosula* would have a weaker response to variables than the more rare *H. gentilis*. As with the other species, there was not a notably large difference between the responses.

*H. villosula's* response to Wood Mound can possibly be explained by the high occurrence frequency this species had on hollow oaks outside of forests, which had more wood mould than the forest trees. The openness such landscapes offer, often results in larger diameter (Sverdrup-Thygeson et al., 2010), which in the oaks in this study was correlated with larger amounts of Wood Mould. The general impression of this species ecology is that the species is not necessarily linked to wood mould and seem, as *A. balteatus* less particular in its habitat preferences. Both in this study, and in others (Sverdrup-Thygeson et al., 2014a), *H. villosula* was the species with the highest number of individuals caught. The species was most abundant in anthropogenic landscapes, but many individuals were also caught on forest oaks. An apparent tolerance for the challenges both these landscapes offer is perhaps the reason for the commonness of this species, compared to *H. gentilis*.

Besides being an oak specialist with a very limited distribution in Norway, *H. gentilis* is also listed as Near Threaten (NT) in the Norwegian Red List (Kålås et al., 2010). As a specialist species that considers oak as one of its few suitable host trees, it was in general expected that *H. gentilis* should have had a positive relationship with a tree variable. However, *H. gentilis* was only present with 35 individuals on seven of 32 trees. Of these seven trees only five had registered wood mould values, a value count far too low to preform an analysis. It was therefore expected that Wood Mould would not be a significant predictor for *H. gentilis* in this study.

As for Diameter, a visual examination of the data revealed that *H. gentilis* was only present on trees with a diameter larger than 57.7 cm. The species may also respond to tree characteristics that are not included in this thesis, like age or the composition of nutrients in the wood mould.

Instead, the species had a positive relationship with Dead Wood Local. While several studies have reported that local volume of dead wood is a good predictor of species richness or abundance (Götmark et al., 2011, Martikainen et al., 2000, Müller et al., 2008), others have dismissed this (Gibb et al., 2006, Økland et al., 1996, Siitonen, 1994). Nevertheless, it is probable to suggest that *H. gentilis* has low dispersal ability, and is therefore dependent on a local network of dead wood patches. It must though be mentioned that several of the hollow oaks in this study are located in productive forests. The dead wood surveyed at these sites might therefore not reflect the natural succession process and be rather homogeneous in terms of decay stage and tree type.

The prediction that the common species within the pairs should have a weaker response to the variables than the rare species did not come true. *A. balteatus* actually had a slightly stronger response to Deciduous Trees_1km than *A. nigrinus* had to Dead Wood_2km. There was no notable difference for *H. villosula* and *H. gentilis*. However, when studying the optimal models for the rare species, we can see that they have better models (higher $R^2$) than the models for the common species.

### 4.4 Management consequences

As many studies before, this current study also reached the conclusion that different variables and scales are important to sustain a viable saproxylic beetle community in hollow oaks. For this to happen, sufficient connectivity of hollow oaks on all scales is required, even though my results did not support this notion. The concept of substrate availability and connectivity also applies to dead wood. Both of the rare species responded to dead wood, stressing the fact that many rare and specialized species are dependent on this substrate on different scales. For hollow oaks located in managed forest, action must be taken to ensure a diverse selection of dead wood is left behind available for saproxylic species.

This study has only highlighted two life attributes, namely trophic level and specialization, but many more are at work, influencing a species response to habitat change and fragmentation. It is also suggested that some traits work together, creating a synergistic combination of extinction promoting traits in regard to sensitivity to fragmentation (Davies et al., 2004). It must therefore be stressed that management must be based on an overall assessment of the species traits, not just a single one (Davies et al., 2004). Further on, management is needed not only to keep the rare and extinction prone species alive, but also to prevent that common species become threatened (Lindenmayer et al., 2011). One should be careful disregarding a common species' vulnerability to extinction just because they are abundant. A rapid decline in population of common species might still occur if management is not aware of the possible threats to the species habitat or pro-active action is not taken (Lindenmayer et al., 2011).

The conservation of hollow oaks as habitat patches should therefore be of high priority. First, the status hollow oaks have as a selected habitat type must be better reinforced, so illegal removal of hollow oaks does not happen. Many traits that make a hollow oak tree valuable to saproxylic beetles are not something one can restore, for instance large diameter and wood mould. Preventive action must therefore be taken to avoid removing or degrading such trees. Secondly, attention must also be given to recruitment of new oak trees. Thirdly, considering hollow oaks are located in many different landscapes, it would be beneficial to have an approach to management that included concepts and principals of landscape ecology. Finally, more knowledge is needed. Therefore, studies with similar purpose as this one are necessary to identify the vulnerability factors of oak associated species.

## 4.5 Conclusions

This study of single-species responses aimed to untangle some of the complicated interactions of habitat quality and scale affecting the community of saproxylic beetles on hollow oaks. We saw that variables representing habitat size, isolation and climate affected the study species on different scales, emphasizing the significance of the surroundings.

The research question were:

1) What variables and scales are important for the four oak specialists representing different trophic levels?
   The results showed that the xylophage and xylomycetophage species responded to tree variables, while the predator and the species with mixed feeding preferences responded to landscape variables.

2) Can the selected variables and scales explain why two closely related species, one common and one rare, occur at different frequencies?
   To some degree, yes. The variables and scales the species responded to gave us a possibility to infer about the species habitat requirements and subsequently what makes them common and rare. However, for accurately comparing a rare and common species one must have more data on species traits and population dynamics than what was made available in this thesis.

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# Appendix

## **Appendix I:** Map of selected habitat type hollow oaks in Norway

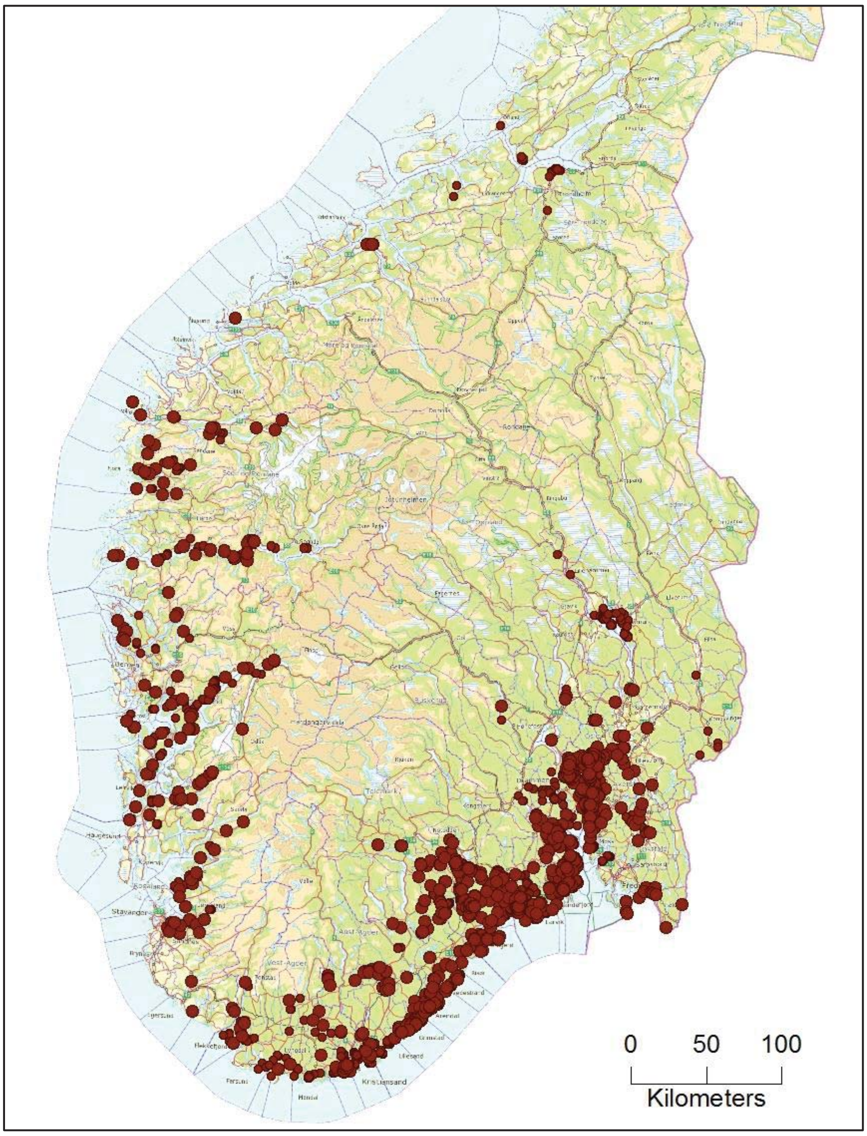

**Figure 1**. Map displays the selected habitat type; hollow oaks in Norway (Norwegian Biodiversity Information Centre, 2015)

## **Appendix II:** Table of study site locations

**Table 1.** The location and coordinates of the 32 hollow oak trees used in this study

| Tree ID | Location | Municipality | County | UTM32_X | UTM32_Y |
|---|---|---|---|---|---|
| HaaVE2 | Håvaldsrød | Larvik | Vestfold | 556565 | 6545299 |
| OgVE8 | Øgården | Larvik | Vestfold | 552759 | 6549196 |
| StVE1 | Stueåsen | Larvik | Vestfold | 552218 | 6552633 |
| EnVE10 | Engene, Kjose | Larvik | Vestfold | 549405 | 6552693 |
| OdVE2 | Ødegården | Larvik | Vestfold | 551736 | 6537225 |
| FuVE1 | Fuglevik | Larvik | Vestfold | 558279 | 6538779 |
| LyVE3 | Lysebo | Larvik | Vestfold | 555005 | 6556785 |
| BuVE5 | Budalsåsen | Larvik | Vestfold | 558779 | 6556166 |
| GjVE1 | Gjønnesvannet | Larvik | Vestfold | 557491 | 6559477 |
| SkVE11 | Skjærsjø | Larvik | Vestfold | 553288 | 6562418 |
| SOVE3 | Kiste at Lakssjø | Larvik | Vestfold | 551757 | 6567786 |
| BrVE3 | Brenndalsskarven | Larvik | Vestfold | 554410 | 6547287 |
| VaVE3 | Søndre Odbergsetra | Larvik | Vestfold | 552180 | 6547757 |
| KiTE1 | Brekkeseter | Siljan | Telemark | 546166 | 6567188 |
| BrTE9 | Vassbotnvannet | Siljan | Telemark | 549045 | 6567077 |
| RoSK2 | Røsaker S | Skien | Telemark | 537389 | 6565804 |
| SyVA1 | Eg Hospital | Kristiansand | Vest-Agder | 440146 | 6447630 |
| BjVA1 | Bjørnehula | Kristiansand | Vest-Agder | 437464 | 6442220 |
| GaVA1 | Håstøl | Kristiansand | Vest-Agder | 438035 | 6450199 |
| GiVA1 | Gangdalsveien | Kristiansand | Vest-Agder | 442843 | 6449467 |
| AarVA4 | Gillsveien at Gillsvann | Søgne | Vest-Agder | 431126 | 6436976 |
| TjVA1 | Tveitemyrane | Søgne | Vest-Agder | 432403 | 6440700 |
| HaaAA5 | Håverstad | Birkenes | Aust-Agder | 455708 | 6483175 |
| TveAA2 | Skåre | Birkenes | Aust-Agder | 456788 | 6461680 |
| HaaVAA9 | East of Hovland | Birkenes | Aust-Agder | 448328 | 6485339 |
| SkAA3 | Hushovd | Birkenes | Aust-Agder | 449557 | 6495131 |
| Hul3 | Årosveten | Birkenes | Aust-Agder | 447184 | 6494667 |
| HuAA3 | Tjomsevann | Froland | Aust-Agder | 454812 | 6505271 |
| KdAA13 | Kverndalen | Lillesand | Aust-Agder | 462495 | 6457948 |
| ReAA3 | Retterholt | Birkenes | Aust-Agder | 453508 | 6484652 |
| TvAA1 | Tveitetjønnane | Birkenes | Aust-Agder | 454421 | 6461290 |
| SeAA5 | Sekkebekk | Lillesand | Aust-Agder | 461977 | 6456103 |

## **Appendix III:** Climatic gradient from coast to inland

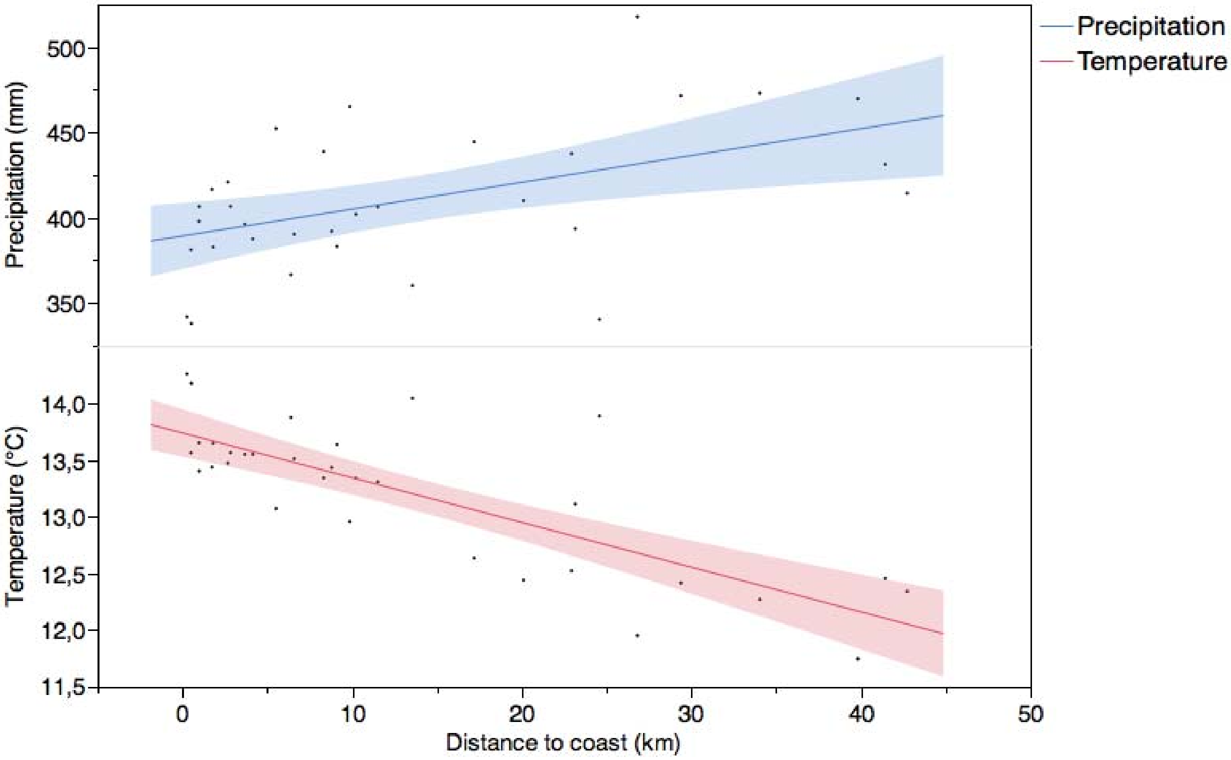

**Figure 2**. Bivariate fit of temperature and precipitation by distance to coast (both $p = <0.05$). The temperature data is based on the average temperature of the four hottest months. The precipitation data is the average precipitation for the months May, June, July and August, following the long-term average from the period 1961-1990. Data from the Norwegian Meteorological Institute (2015)

**Appendix IV**: The distribution of the eight study species in Norway. Data from the online database, *Species Map Service* (Norwegian Biodiversity Information Centre, 2015).

**Figure 2.** The distribution of *Dorcatoma chrysomelina*

**Figure 3**. The distribution of *Ptinus subpillosus*

**Figure 4.** The distribution of *Rhizophagus bipustulatus*

**Figure 5.** The distribution of *Xestobium rufovillosum*

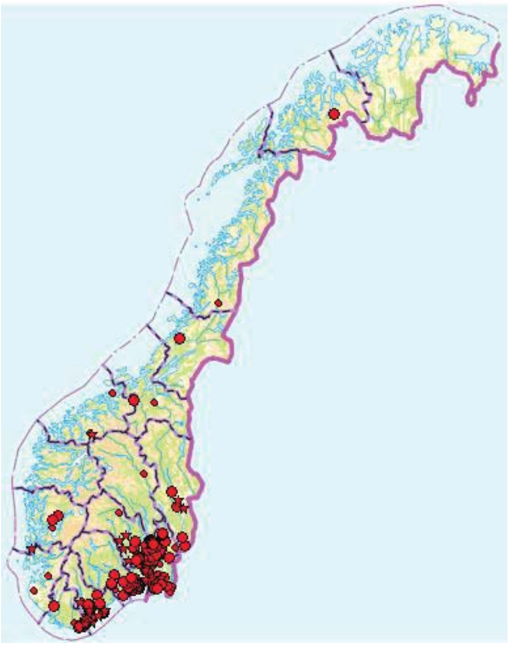

**Figure 6.** The distribution of *Ampedus balteatus*

**Figure 7.** The distribution of *Ampedus nigrinus*

**Figure 8.** The distribution of *Haploglossa villosula*

**Figure 9.** The distribution of *Haploglossa gentilis*

# **Appendix V:** Table of results from the multivariate analysis

**Table 2.** A multivariate analysis of the explanatory variables used in this study (Wood Mould was tested separately). Strong correlations (r = >0.75) are marked with an asterisk (*)

| | Diameter | Hollow Oaks Local | Dead wood Local | Forest Regrowth North | Forest Regrowth South | Distance to Coast | Deciduous Trees_1km | Hollow Oaks_1km | Dead Wood_1km | Deciduous Trees_2km | Hollow Oaks_2km | Dead Wood_2km |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Diameter | 1.000 | 0.071 | -0.040 | 0.039 | -0.083 | 0.007 | 0.205 | 0.174 | -0.293 | 0.036 | 0.069 | -0.330 |
| Hollow Oaks Local | 0.071 | 1.000 | -0.186 | -0.086 | -0.018 | -0.222 | 0.249 | -0.015 | -0.095 | 0.142 | 0.105 | -0.130 |
| Dead wood Local | -0.040 | -0.186 | 1.000 | 0.139 | 0.089 | 0.084 | -0.044 | -0.146 | 0.338 | -0.173 | -0.229 | 0.223 |
| Forest Regrowth North | 0.039 | -0.086 | 0.139 | 1.000 | 0.535 | 0.271 | -0.242 | -0.023 | 0.013 | -0.239 | -0.119 | -0.045 |
| Forest Regrowth South | -0.083 | -0.018 | 0.089 | 0.535 | 1.000 | 0.241 | -0.333 | -0.143 | -0.176 | -0.302 | -0.247 | -0.146 |
| Distance to Coast | 0.007 | -0.222 | 0.084 | 0.271 | 0.241 | 1.000 | -0.660 | 0.070 | 0.121 | -0.564 | -0.142 | 0.066 |
| Deciduous Trees_1km | 0.205 | 0.249 | -0.044 | -0.242 | -0.333 | -0.660 | 1.000 | 0.106 | -0.240 | 0.680 | 0.161 | -0.218 |
| Hollow Oaks_1km | 0.174 | -0.015 | -0.146 | -0.023 | -0.143 | 0.070 | 0.106 | 1.000 | -0.144 | 0.090 | 0.862* | 0.040 |
| Dead Wood_1km | -0.293 | -0.095 | 0.338 | 0.013 | -0.176 | 0.121 | -0.240 | -0.144 | 1.000 | -0.273 | -0.151 | 0.815* |
| Deciduous Trees_2km | 0.036 | 0.142 | -0.173 | -0.239 | -0.302 | -0.564 | 0.680 | 0.090 | -0.273 | 1.000 | 0.193 | -0.188 |
| Hollow Oaks_2km | 0.069 | 0.105 | -0.229 | -0.119 | -0.247 | -0.142 | 0.161 | 0.862* | -0.151 | 0.193 | 1.000 | 0.139 |
| Dead Wood_2km | -0.330 | -0.130 | 0.223 | -0.045 | -0.146 | 0.066 | -0.218 | 0.040 | 0.815* | -0.188 | 0.139 | 1.000 |