Beetles in hollow oaks: the effects of traits on community structure

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Acknowledgements

Ås, December 2020
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Abstract

Habitat fragmentation and habitat loss have long been acknowledged as two of the most important drivers of biodiversity loss all over the world. A way to preserve biodiversity is to protect the remaining hotspots. Hotspots can be large-scale areas representing the rich biodiversity of a biographic region. Yet there are also local hotspots which house high richness of threatened species that depend on the unique qualities of smaller habitat patches. Hollow oaks represent one important local hotspot habitat because they contain important dead wood that houses many threatened saproxylic species.

In Norway, the number of hollow oaks is in decline, and most of the remaining trees are scattered in small isolated patches across the southern part of the country. Within Norway, there are also regional differences in the species richness patterns of saproxylic beetles inhabiting hollow oaks. The western hollow oak region represents a different region than the east with tall mountains and fjords leading to a different landscape structure and a different climate pattern than the eastern hollow oak region. Species richness of hollow oak specialist species has been shown to be lower in the western region, but the understanding of the causes behind this east-west decline gradient remain limited.

How these oak-associated beetle communities respond to both isolation effects and geographical differences likely depends on their morphological traits, which influence their ecology. Species with good dispersal abilities have a greater chance to reach isolated habitats that are more scattered in the landscape. Further, the extinction risk of beetles has been shown to depend on body size. Smaller species are more resilient to isolation effects, because of their broader habitat breadth, higher reproduction rate and higher abundance. The focus in this study was therefore to investigate the effects of traits on community structure of oak associated beetles, including red-listed beetles. I have therefore chosen relative wing length as a proxy for dispersal ability and body size as a proxy for extinction risk of oak associated beetle communities. Traits were summarized as community weighed means, as I wanted to see a generalized pattern of how trait diversity of all oak- associated beetles respond to isolation effects and regional effects. I used a dataset in which beetles were sampled from eleven solitary hollow oaks and four groups of

clustered hollow oaks to investigate isolation effects. These sites were distributed across two geographical zones to represent the eastern and western distribution of hollow oak habitats in Norway. This dataset included 116 saproxylic oak-associated beetle species (1706 individuals), of which 8 species (938 individuals) were red-listed. Mean relative wing length and mean body size did not differ significantly by habitat isolation status or between western and eastern regions. However, in the western region, species richness was 35% lower ($p = 0.01$) and red-listed species richness was 92% lower ($p = <0.0001$) relative to the eastern region. Richness did not differ significantly by isolation status.

A relatively small sample size likely made detecting any differences among highly variable beetle communities difficult. My results showed an east/west difference of species richness of all and red-listed beetle species associated with hollow oaks. I encourage researchers to also investigate species composition, as that was not included in this study design. The importance of region vs. isolation effects for richness patterns implies that region has a great impact on the variation in community structure of saproxylic beetles. On a small scale, conservation planning must focus on habitats with high density of large hollow oaks and promote occurrence of dead wood. Planning on large scale must focus on preventing further increasing the distance between habitat patches, as it is important to protect the large variation of all saproxylic oak-associated communities.

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Introduction

Biodiversity loss has long been acknowledged as a global problem, and habitat loss and fragmentation is currently two of its most important drivers (Butchart et al., 2010; Díaz et al., 2019). Land use change is expected to be the largest threat to biodiversity in forest ecosystems across the world (Hannah et al., 1995; Sala et al., 2000), thus it affects numerous terrestrial species across a range of groups that depend on these habitats (Grove, 2002; Newbold et al., 2014). Old trees represent unique and species rich microhabitats in these diverse and large forest ecosystems (Grove, 2002; Jaworski et al., 2019), but are in decline throughout Europe from humans intense use of forest resources to forest industry, agriculture or urban development (Gauthier et al., 2015; Komonen et al., 2008; Mery et al., 2010; Nieto et al., 2010; Ranius & Jansson, 2000).

Hollow oaks are important hotspot habitats

Threatened biodiversity that are concentrated in small sites or larger regions are globally known as hotspots (Gaston & David, 1994; Mittermeier et al., 2011; Myers et al., 2000; Skarpaas et al., 2017). A vital strategy to prevent further biodiversity loss is therefore to preserve biodiversity hotspots (Brooks et al., 2002; Mace et al., 2018; Mittermeier et al., 2011; Sverdrup-Thygeson et al., 2010a). Hollow oaks (*Quercus sp.*) represent important local hotspot habitat for many threatened species from their important component of dead wood (Buse et al., 2010; Davies et al., 2008; Sverdrup-Thygeson, 2009). They provide both stable and highly diverse habitats because they are long-lived and slow growing trees that develop deep crevices in their bark, internal cavities, and great amounts of dead wood. (Stokland et al., 2012). One of the most important residents of hollow oaks are the saproxylic beetles, as many of these beetles can only be found in hollow oaks (Grove, 2002; Komonen et al., 2008; Sverdrup-Thygeson et al., 2011).

Saproxylic beetle species

Saproxylic beetles is a highly diverse species group that depend on dead or decaying wood at some point in their life cycle (Grove, 2002; Stokland et al., 2012). Thus they play an important role in the decomposition cycle in forests (Grove, 2002). They also include fungivores that feed

on fungi that depends on dead wood, or predators that depend on the presence of other saproxylics (Stokland et al., 2012). There are differences in the species richness patterns of saproxylic beetles inhabiting hollow oaks depending on both size of tree and the abundance of dead wood (e.g. Ranius & Jansson, 2000; Siitonen, 2001). Large hollow oaks with abundance of dead wood is found especially important to red-listed saproxylic species in Norway (Pilskog et al., 2016; Sverdrup-Thygeson et al., 2010b).

The effects of isolation

Habitat fragmentation is the process of different isolation effects namely caused by humans dividing habitat patches into smaller fragments (Lindenmayer & Fischer, 2013). The effects of isolation on species are often referred to the biography theory (MacArthur & Wilson, 2001), which considers species richness to depend on island size and the degree of isolation effect. In the context of hollow oak habitats, extinction risk of hollow oak beetle species is induced by the process of decreasing stands of hollow oaks and by increasing the distance between the remaining habitat patches leading to decrease resource availability and immigration between the remaining patches.

Isolation effects may affect saproxylic species in different ways at different scales, depending on their habitat specialisation function which affects the niche breadth–range size relationship (Chase & Leibold, 2003; Slatyer et al., 2013) A study in Norway (Sverdrup-Thygeson et al., 2017) found that high density of hollow oaks on a habitat range of 0.5 km are more important to specialists than generalists of saproxylic beetle communities. Also a large circumference is found to be more important to specialists than generalists (Pilskog et al., 2016; Ranius & Jansson, 2000; Sverdrup-Thygeson et al., 2010b) Density (Bergman et al., 2012).

The impacts of geography

Geographical scales often combine climatically conditions and land use changes when trying to understand the distribution of species (Gough et al., 2015; Müller et al., 2015; Parmesan, 2006). Saproxylic specialists are highly affected by both climate and land use changes (Gough et al., 2015), Based on a study in Norway (Pilskog et al., 2020), the composition of saproxylic beetle communities change along a coastal-inland gradient.

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The study also found specialists highly influenced from precipitation, as species richness of saproxylic specialist had a negative relationship to precipitation. This relation has also been revealed on a larger scale, were saproxylic specialists were affected negatively by precipitation across the oak range of both Norway and Sweden (Gough et al., 2015). Mean summer precipitation is higher in the western region compared to the eastern region of the southern part of Norway (Moen et al., 1998) of which hollow oaks are in both areas. Climatic conditions on a regional scale is therefore important to the saproxylic beetle community structure. Beetles living in hollow oaks in the west could be limited to disperse as increasing precipitation likely reduces their opportunities to fly (Gough et al., 2015).

Forestry logging history are an important driver to why hollow oak habitats are reduced into small isolated patches across the southern part of Norway (Pilskog et al., 2018). Based on studies in Norway, a coastal-inland gradient can explains an overall higher species richness in the inland by the effects of logging history and climatic differences (Pilskog et al., 2018; Pilskog et al., 2020).

Both distance and structure within a landscape determines the availability for species to disperse between local habitats (Feldhaar & Schauer, 2018; Wiens, 1995). The impact of landscape structure and landscape connectivity are therefore important factors to consider when studying dispersal limitations of saproxylic beetle communities.

The effects of traits
Traits express different strategies or ecological functions which species have adapted in order to best cope with abiotic and biotic factors in their environment (McKinney, 1997; Reiss et al., 2009). As traits respond to abiotic factors, they can be used to predict probability of extinction from habitat loss and habitat fragmentation (Chichorro et al., 2019; Davies et al., 2004; Henle et al., 2004; Kouki et al., 2001; McKinney, 1997). Dispersal traits can relate to both habitat specialisation and body size of which saproxylic species adapted to long-lived habitats often are found to have a larger body size and limited dispersal abilities, whereas species adapted to short-lived habitats are found to have a smaller body size and better dispersal abilities (Chichorro et al., 2019; McKinney, 1997; Ranius, 2006; Southwood, 1962) One can therefore divide beetles into groups from their similar traits to investigate how communities respond to different habitat environments or isolation effects.

Relative wing length is an example of a trait sometimes used to assess dispersal ability (Bouget et al., 2015; Gibb et al., 2006; Hagge et al., in review). Relative wing length is the ratio of wing length to body length, and a higher relative wing length is thought to increase a species' dispersal ability (Rundle et al., 2007). Based on a comparison of red-listed saproxylic beetles in Germany, species with higher relative wing length showed a lower risk of extinction than those with a shorter relative wing length (Hagge et al., in review).

Body size is one of the most studied traits of saproxylic beetles, because it correlates with life cycle, habitat specialisation and abundance (Chichorro et al., 2019; McKinney, 1997; Seibold et al., 2015). Species with larger body size (length) are correlated with a higher extinction risk by having a longer life cycle, lower reproduction rate and lower abundance (Fisher et al., 2001; Fisher & Owens, 2004; Gillespie et al., 2017; Seibold et al., 2015). Based on a study in Germany, saproxylic species with a larger body size had increasing risk of extinction by requiring more dead wood resources to fulfil their larvae development (Seibold et al., 2015). Smaller species correlates to a lower extinction risk by their higher reproduction rate, higher abundances and better ability to disperse than larger species (Fisher & Owens, 2004; Gillespie et al., 2017). A larger body size also shows a negative effect on dispersal phenology(Gillespie et al., 2017). Because smaller species are better dispersers and faster colonizers than larger species, smaller species are also likely more resilient to habitat isolation effects. However, the effects of body size has been found to vary and therefore it is challenging to unify a generalized effect of traits across taxa (Chichorro et al., 2019; Davies et al., 2000; Ewers & Didham, 2006).

Present status of saproxylic species in Norway

Hollow oaks exist along the coastline and fjords of the southern part of Norway (Sverdrup-Thygeson et al., 2018). Counties east from the Oslo fjord, such as Vestfold, Telemark and partly Agder are known as core hollow oak areas with high richness of red-listed saproxylic beetles (Pilskog et al., 2014). Currently hollow oaks are in decline in Norway and the government have designated these hotspot habitats as a 'selected habitat type' under the Regulation on Selected habitats 2011 (Lovdata, 2011) to resolve the decline and increase oak recruitment (Directorate for Nature Management, 2012).

Slightly more than 100 red-listed beetle species are listed from oak in Norway, and about 60 red-listed beetles are associated with hollow trees (Sverdrup-Thygeson et al., 2011). The effects of isolation and increasing the distance between hollow oak habitats have led to a negative effect on the abundance of many saproxylic species leading to the result of why many saproxylic beetles are red-listed (Sverdrup-Thygeson et al., 2011; Ødegaard et al., 2015).

Within Norway, there are regional differences in the species richness patterns of saproxylic beetles inhabiting hollow oaks. Westwards from Agder, saproxylic beetle specialists associated with hollow oaks are showing a decreasing pattern (Pilskog et al., 2020; Sverdrup-Thygeson et al., 2018), but the understanding of the causes behind this east-west decline gradient remain limited.

The landscape in the western hollow oak region differs from the eastern hollow oak region of the southern part of Norway. In the west the landscape is dominating with tall mountains and fjords leading to a different landscape structure and a higher oceanic influence than the eastern hollow oak region (Moen et al., 1998). The regional factors in the west are likely to affect species richness more negative compared to the eastern region from a different landscape structure, higher mean summer-temperature and precipitation compared to the eastern region.

The focus in this study is to investigate the effects of traits on community structure of oak-associated beetles, including red-listed beetles. I have therefore chosen relative wing length as a proxy for dispersal ability and body size as a proxy for extinction risk of oak-associated beetle communities. Because species with good dispersal abilities have a greater chance to reach isolated habitats (Davies et al., 2004; Southwood, 1962), it is likely that only the good dispersers also would have the chance to reach habitats in the west from a landscape structure and climate that is less favourable to all oak-associated saproxylic species, compared to the east. Smaller species are more resilient to isolation effects, because of their broader habitat breadth, higher reproduction rate and higher abundance (Nilsson & Baranowski, 1997; Percel et al., 2019; Slatyer et al., 2013) and therefore these species are more likely to be found in isolated habitats and in the western region because they are more resilient against the less favourable conditions in the western hollow oak region compared to the eastern region.

Beetles were sampled from eleven solitary hollow oaks and four groups of clustered hollow oaks to investigate isolation effects. I have divided the hollow oak region into two geographical zones in order to investigate the geographical effects between the eastern and western hollow oak region of Norway. I have used community-weighed means sampled by each tree to test how diversity of traits in beetle communities of all oak-associated beetle species respond to habitat isolation and regional effects. Species richness of all oak-associated beetles and red-listed beetles were investigated from the effects of isolation. Species richness was also investigated from the implications of a regional difference in species richness between east and west leading to a lower species richness in the western region. I therefore expect:

i.   Mean relative wing length will be higher in beetle communities that are isolated (i.e. from solitary trees vs. clustered). Mean relative wing length will also be higher in beetle communities from oaks in the western region, compared to the eastern region.

ii.   Mean body size will be lower in beetle communities that are isolated (i.e. from solitary trees vs. clustered). Mean body size will also be lower in beetle communities from oaks in the western region, compared to the eastern region.

iii.   The species richness or richness of red-listed oak-associated beetles will be lower in communities that are isolated (i.e. from solitary trees vs. clustered) or in the western region, compared to the eastern region.

Materials and methods

Study sites

Hollow oaks of high conservation value (categorized as A or B – se appendix 2 for details) were selected from the entire distribution of hollow oaks in the southern part of Norway (figure 1). All of these trees were previously inventories as part of the national monitoring program of hollow oaks (Sverdrup-Thygeson et al., 2018) in Norway.

Geographical zones were divided between hollow oaks in southeast counties (East-Agder and Telemark) and hollow oaks placed in southwest counties (West-Agder, Sogn & Fjordane, Hordaland). The sample of trees was divided into two areas to both balance the study design and represent the difference in species richness of the eastern and western hollow oak regions (see

figure 1). In total I chose eleven solitary hollow oaks and five groups of hollow oak trees consisting of five trees each, resulting in a sample of thirty-one trees in total.

Solitary hollow oaks were categorized as isolated habitats. This means that each solitary hollow oak was registered as the only tree within a square of 500x500 meters. The solitary hollow oaks could stand anywhere within this square, which means I cannot exclude the possibility that other trees would be close by. Hollow oaks that were standing in groups of minimum five trees were categorized as not isolated habitats. Each group of minimum five hollow oaks were standing clustered in the same square. They were selected from having high density of hollow oaks spread out in the area. I have chosen hollow oak trees mainly from forested areas but have also included five trees from an alley in Eidanger and two solitary trees from agricultural landscapes in Kvåle and Soldalen.
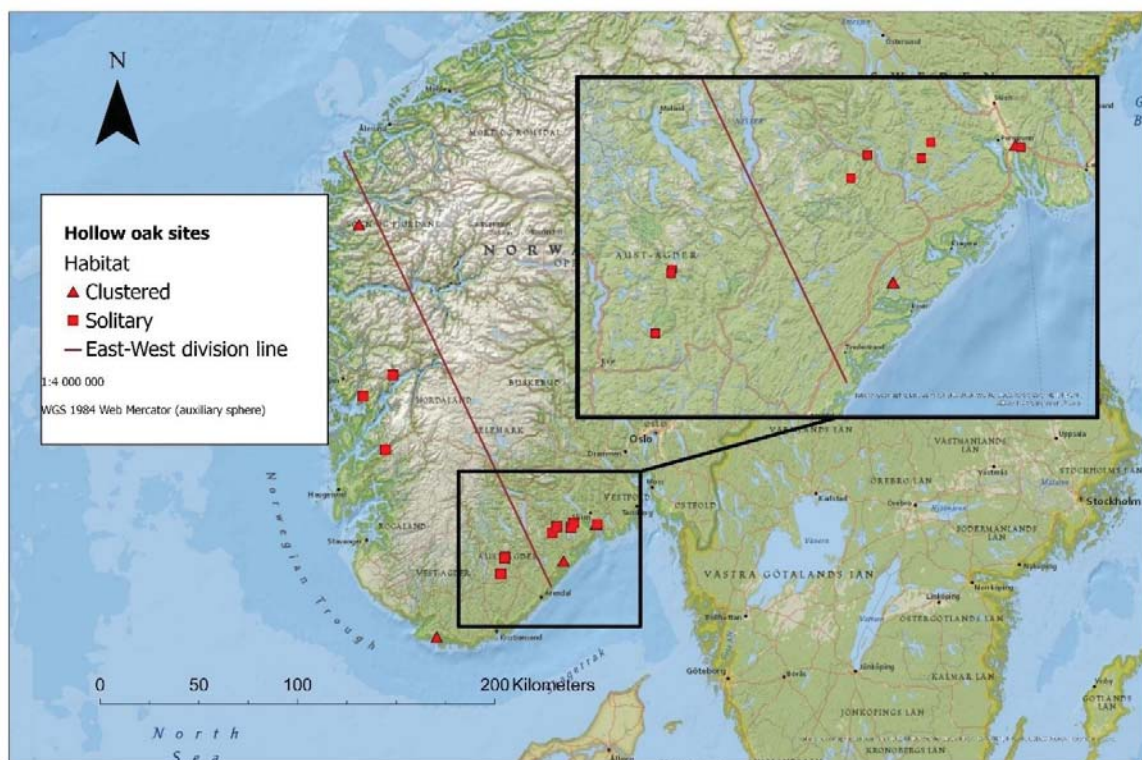
Figure 1: An overview of the study area of all 15 hollow oak sites (31 hollow oaks) distributed in the southern part of Norway. Solitary hollow oaks were classified as isolated habitats. Clustered hollow oaks were classified as not isolated habitats. Red boarder line indicates the division of the eastern and western geographical zones. The division were made to balance the sample of trees in the study design and represent the difference in species richness of the eastern and western hollow oak regions.

Beetle sampling

I collected all data from fieldwork that was already conducted by other field registrants. Beetles were sampled with window traps in the summers of 2016 and 2017. Two traps were placed in each tree, one trap in front of the hollow and one trap in the canopy, from May-August. Propylene glycol was used as preserving agent in the traps. Traps consisted of two clear glass panes 20x40 cm. The beetle sampling method follows the same method after an earlier study on saproxylic beetles associated with hollow oaks in Norway (see Sverdrup-Thygeson et al., 2010b for more details).

Beetle species

All beetles were identified to species level by an expert taxonomist. Saproxylic beetles in the study design were considered as oak-associated beetles based on the 'saproxylic database' by Stokland et al. (2006). I included saproxylic species from four groups based on their association with hollow oaks: ´Hollow oak specialists', 'hollow oak generalists', 'hollow oak and broadleaved boreal trees' or 'hollow oak and broadleaved temperate trees' (Stokland et al., 2006). As all the groups above were included into one group classified as oak-associated beetles, my analysis does not separate oak-specialists from oak-generalists. I excluded all other beetle species that were not saproxylic species associated to hollow oaks.

Red-listed species were classified from the four red-listed categories given by the Norwegian red-list database (Artsdatabanken, 2015): Near Threatened (NT), Vulnerable (V), Endangered (EN) and Critically Endangered (CR). All oak-associated species were included in the group classified as Red-listed species.

Analysis

I used R-studio in R (R Core Team 2013) for all statistical analysis. For the mixed effect modelling the packages "lme4" (Douglas Bates, 2015) and "lmerTest" (Kuznetsova A, 2017). Package "glmmADMB" (Fournier DA, 2012) was used for the negative binomial GLMM models in the analysis.

Obtaining trait variables

Hagge et al. (in review), recently analysed different dispersal traits (relative wing length, wing load and wing aspect) of which all three were found related to extinction risk. The effects of the dispersal traits were strongly correlated, and relative wing length gave the clearest results. I chose therefore to use this trait as the measurement of dispersal ability in this analysis. I obtained body length and wing length from Hagge et al. (in review) Relative wing length was calculated by standardizing it around 0, from using the residuals of a simple linear regression model of wing length ~ body length.

Body size is closely correlated to extinction risk (Hagge et al., in review) which has also been shown in previous studies (e.g.,Kotze & O'hara, 2003; Seibold et al., 2015). I classified body size from obtaining body length from Hagge et al. (in review).

Response variables

I used community weighed means (CWM) to summarize the overall trait values of each beetle community sampled from each tree. I chose to use CWM as a method because this approach combines species traits with weighed abundances of all oak-associated beetle communities (Ricotta & Moretti, 2011) to investigate the effects of isolation or regional differences from the different sample sites in this study design. Community weighed means for each community were calculated by recording trait values of each species sampled in a given tree and calculating a weighted average of these means, weighted based on the number of individuals captured of each species. Linear mixed effect models (LMER) were chosen for the community weighed means trait models (Bates et al., 2007).

The response variable community weighed mean of relative wing length was called `mean relative wing length´. 'Mean relative wing length' was inspected before modelling, were I saw indications of a heavy tail in both ends of its histogram and QQ-plot. Because transformation did not give better results, I determined that the original data were most appropriate for modelling.

The response variable community weighed mean of body size was called `mean body size´. 'Mean body size' had a right tailed skewness in its histogram and QQ-plot. Log transforming the data improved the fit to a normal distribution and therefore a log transformed response variable was used of this response trait.

Because I expected that the red-listed beetles are especially affected by habitat isolation or region, response variables of relative wing length and body size was made separately for this group as well. The response variables 'mean relative wing length of red-listed beetles' and 'mean body size of red-listed beetles' were affected by a small sample size, with many zeros detected in histograms and QQ-plots because no red-listed species were captured in many of the sites.

Species richness was estimated by recording the total number of species recorded of each tree. I tested if the distribution of species richness would fit a Poisson distribution and found count values to be affected from overdispersion. Instead I used a negative binomial distribution model (negative GLMM) (Bates et al., 2007; Zeileis et al., 2008).

Red-listed species were estimated by counting the total number of red-listed saproxylic beetles within each site from the four vulnerability categories: Near Threatened (NT), Vulnerable (V), Endangered (EN) and Critically Endangered (CR). To account for excessive zeros in its histogram and QQ-plot, I decided to use a negative binomial distribution model (negative GLMM) (Bates et al., 2007; Zeileis et al., 2008).

Selecting the random effect

Mixed effect models introduces a random effect that can account for the many variations that is hard to detect and explain from all the uncountable variations in nature (Pinheiro & Bates, 2006).

My study design is nested in four spatial scales. The largest scale is region, followed by site, tree and finally traps as the smallest scale. It was appropriate to include mixed effects models as it presented the random effect that could account for the complexity of variation given from the multiple scales in the study hierarchy. The hierarchy level of site was determined as the random effect to best account for the highest level of variation, as there were clustered trees or solitary trees at a given site.

Site represents the locations of where I sampled beetles from the different hollow oak trees (in total 15 sites – see appendix 2). Each solitary tree was its own site and each cluster of five trees was its own site. Site as the random effect could therefore account for the unbalanced variation of beetles observed between solitary and clustered trees. I could have used site and tree as two random effects in the model, but this led to complications as the solitary tree sites are synonymous to observations of some trees in the tree level, and the mixed effect model cannot

estimate the same thing. However, some models failed estimating a random effect of site or tree (see figure 2). For these models I instead chose to use a standard linear model.

Selecting the explanatory variables

 Zuur et al. (2009) recommends starting with the most complex model, so I included both covariates in the different models. In this study I decided to keep the two nominal variables, 'region' and 'isolation status' as the fixed effects in the different models. I therefore started out having the optimal models for the analysis. I used VIF estimations from the package "CAR" (John Fox, 2019) to check for collinearity and no collinearity was detected between the co varieties 'region' and 'isolation status'.

I fitted the fixed effects 'region' and 'isolation status' to all response variables. There was not enough variation to fit a random effect to the response value of 'mean relative wing length' of allsaproxylic specialists mainly living in hollow oaks, so instead I used a standard fixed effects linear model (see figure 2 for more details). The same problem was found for the response variable of 'mean body size' of red-listed saproxylic specialists mainly living in hollow oaks and therefore I used the same linear model for this response variable.
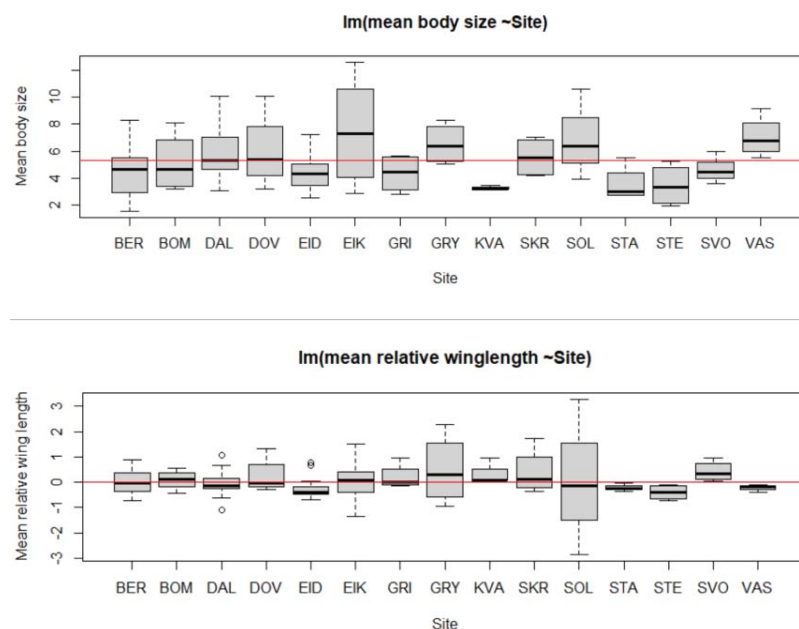
Figure 2: Boxplot of lm(mean body size~site) and of lm(mean relative wing length)~site. Because mixed effect models use random effects to estimate variation, the variation among groups must differ sufficiently from 0. The very little variation in mean relative wing among the sites made it likely not suited for mixed modelling.

Validating the optimal models

Residual plots and QQ plots were inspected for each model. Model assumptions were good for all models except for the models only including red-listed beetles. This comes from many traps not observing any red-listed beetles in addition to an unbalanced sample of red-listed beetles between east and west. These complications are likely the cause to why the model assumption of a normal distribution was violated. Thus, parameter estimates are biased and would not make good predictions.

I evaluated the model fit of the LM models using R^2 model values. These were estimated using the package 'MASS' (Venables, 2002).

R^2 For the mixed models (LMER) were estimated using package "MuMIn" in R (Barton, 2020), which provides an overall r^2 value as well as r^2 value only the fixed effects.

Outliers

I found potential influential observations when investigating the response variable 'mean relative wing length' from all oak-associated saproxylic beetle communities in the analysis. The outliers were from traps recorded with few beetle individuals which either happened to have a small or large relative wing length. I did the analysis with and without the outliers and found no notable difference, thus I kept the outliers in. One species, *Euglenes oculatus* (NT), had extreme observations and was therefore also a potential influence in the statistical modelling. I therefore also ran all models with and without this species, but it was not found to affect the results notably. As it is in the nature of this species to sometimes occur in extreme abundance it would therefore be wrong to exclude it (Sverdrup-Thygeson et al., 2018).

Results

Beetle samples

The dataset contained 4183 beetle individuals belonging to 346 species. Of these, 1706 individuals were selected for the analyses as saproxylic, oak-associated beetles belonging to 116 species (see Materials and methods for more details).

The data sample of oak-associated beetles contained eight species that were red-listed (938 individuals – se appendix 1 for more details of species and categorization used in the study). The highest values of species richness where detected in the eastern region with 50 species observed in a habitat with clustered trees. Observation of 2 species was the lowest species richness value detected in a western habitat in a solitary tree. One habitat with clustered trees had extreme observations of the red-listed species *Euglenes oculatus* (NT). This species was therefore most abundant in the traps and represents 44.6 % (761 individuals) of all oak-associated beetles sampled (see figure 3 for more details of beetle observations).
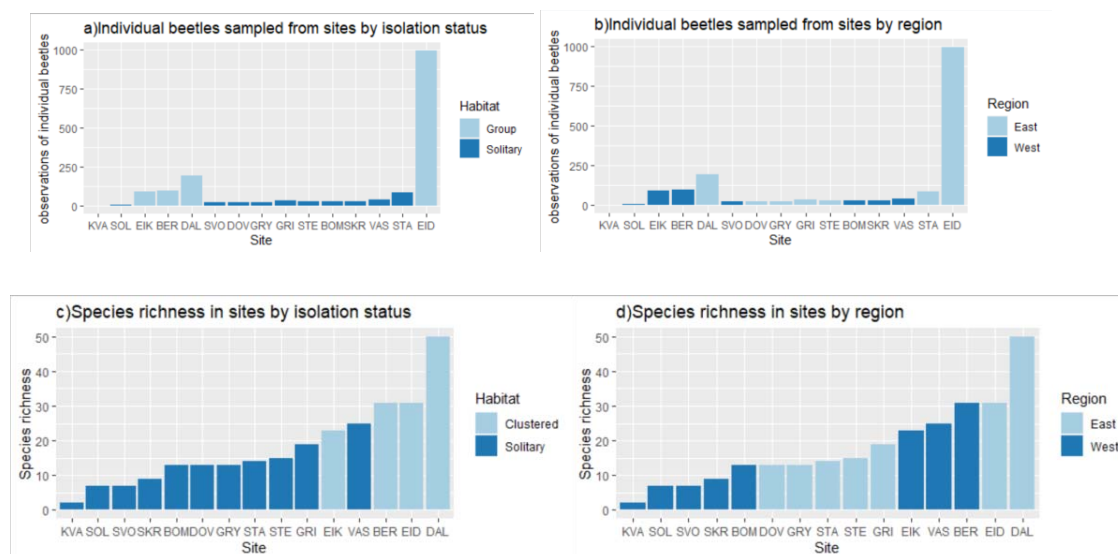
Figure 3: figure **a** and **b** show sum of oak-associated individuals sampled in the 15 sampling sites by isolation status or region. Figure **c** and **d** shows sum of species richness of oak-associated beetles sampled by isolation status or region. Figures showing species richness are sorted in ascending order (**c** & **d)**. The highest species richness value was 50 species observed in a habitat with clustered trees in site 'Dal' located in the eastern region. Observation of 2 species was the lowest species richness value detected in a western habitat in a solitary tree in site ´Kva´. 761 of 1706 individual beetles captured at one site, 'EID', were of one species, *Euglenes oculatus*. This species alone made up 44.6 % of the total proportion of oak-associated beetle individuals selected from the dataset.

The effects of dispersal abilities

 I did not find any significant differences in mean relative wing length of all saproxylic beetle communities from the effects of isolation status or region (table 1).

Table 1: Standard linear regression model with the response variable of 'mean relative wing length' of all oak-associated beetles

Parameters	Estimate	SE	t value	P-value	
Model: mean relative wing length ~ region + isolation status					
intercept - region east/clustered trees	-0.16	0.1	-1.61	0.11	
region west	0.15	0.13	1.17	0.24	NS
solitary trees	0.21	0.13	1.58	0.12	NS

Significance codes: <0.001***, 0.01**, 0.05*, not significant 'NS'. AICc: 255. Residual standard error: 0.69 on 116 degrees of freedom. Multiple R-squared: 0.03. Adjusted R-squared: 0.02.

Mean relative wing length was also not significant different of red-listed beetle communities from the effects of region or isolation status (table 2).

Table 2: Linear mixed effect model with the response variable 'mean relative wing length' of only red-listed oak-associated beetles

Parameters	Estimate	SE	df	t value	P-value	
Model: red-list mean relative wing length ~ region + isolation status + (1 | Site)						
intercept – region east/clustered trees	-0.16	0.08	9.22	-1.94	0.08	
region west	0.14	0.08	12.24	1.66	0.12	NS
solitary trees	0.09	0.09	10.08	1.02	0.33	NS
random effect	**Variance**	**SD**				
(1 | Site)	0.02	0.14				
residual	0.33	0.18				

Significance codes: <0.001***, 0.01**, 0.05*, not significant 'NS'. AICc: 34.8. Number of obs: 47, groups: Site = 9. The variation explained by fixed effects: R^2 marginal: 0.13, and the variation explained by both fixed and random effects, R^2 conditional: 0.61.

The effects of body size

I did not find significant results for the response variable 'mean body size' of all oak-associated beetle communities affected by isolation status or region (table 3).

Table 3 Linear mixed effect model with the response variable 'mean body size' of all oak-associated beetle species.

Parameters	Estimate	SE	df	t-value	P-value	
Model: log(mean body length) ~ region + isolation status + (1 | Site)						
intercept - region east/clustered trees	1.55	0.13	6.88	12.36	<0.000	***
region west	0.13	0.13	10.68	0.96	0.36	
solitary trees	-0.06	0.14	8.38	-0.47	0.65	
Random effect	**Variance**	**SD**				
(1 | Site)	0.04	0.2				
residual	0.15	0.38				

Significance codes: <0.001***, 0.01**, 0.05*, not significant 'NS'. AICc: 139. Number of obs: 119, groups: Site = 15. The variation explained by fixed effects: R^2 marginal: 0.03, and the variation explained by both fixed and random effects, R^2 conditional: 0.23.

I did not find a clear difference in body size of red-listed beetles affected by region. Difference in body size between isolated and not isolated habitats was also not significant (table 4).

Table 4 Linear mixed effect model with the response variable 'mean body size' of only red-listed oak-associated beetles

Parameters	Estimates	SE	t value	P-value	
Model: red-list mean body size ~ region + isolation status					
intercept - region east/clustered trees	2.62	0.26	9.98	0	***
region west	-0.41	0.72	-0.56	0.58	NS
solitary trees	-0.45	0.49	-0.93	0.36	NS

Significance codes: <0.001***, 0.01**, 0.05*, not significant 'NS'. AICc:176. Residual standard error: 1.48 on 44 degrees of freedom. Multiple R-squared: 0.03. Adjusted R-squared: -0.01

The effects of habitat isolation or region on species richness

There was a significant difference in species richness of saproxylic beetles between the eastern and western regions; mean species richness in hollow oak trees in the west was 35 % lower than in the east (Region west; p-value = 0.01 - Table 5) Mean estimated species richness in the eastern region was 5.0, but only 3.3 in the western region. Difference in species richness between isolated and not isolated habitats was not significant.

Table 5: Negative binomial GLMM model with species richness of all oak-associated beetles as the response variable.

Parameters	Estimates	SE	z value	P-value	
Model: species richness ~ region + isolation status + (1 | Site)					
intercept - region east/clustered trees	1.63	0.15	11.05	<0.0001	***
region west	-0.43	0.17	-2.61	0.01	*
solitary trees	-0.04	0.17	-0.21	0.83	
random effect	**Variance**	**SD**			
intercept: (1 | Site)	0.05	0.21			
estimates of mean species richness	**East**	**West**			
region	5	3.3			
isolation status	**clustered**	**solitary**			
mean estimates	4.2	4			

Significance codes: <0.001***, 0.01**, 0.05*, not significant 'NS'. Negative binomial dispersion parameter: 11 (SE: 5.89). Log-likelihood: -281. AIC: 571. Number of obs: 124, groups: Site = 15

The effects of habitat isolation or region on richness of red-listed species

Richness of red-listed saproxylic beetles was significantly 92 % lower in hollow oaks in western Norway (Region west; p-value = <0.0001 - Table 6). Mean estimated richness of red-listed species was 0.99 in the east, but only 0.08 in the west; most sites did not have any red-listed species. However, difference in red-list richness of saproxylic beetles between 'solitary' and 'clustered' hollow oaks was not statistically significant.

Table 6: Negative binomial model with richness of only red-listed species as the response variable

Parameters	Estimates	SE	z value	P-value	c
Model: richness red-listed ~ region + isolation status + (1 | Site)					
Intercept: region east/clustered trees	0.09	0.41	0.22	0.82	
region west	-2.55	0.59	-4.33	<0.0001	***
solitary trees	-0.36	0.49	-0.74	0.46	
Random effect	**Variance**	**SD**			
Intercept: (1 | Site)	0.29	0.54			
estimates of mean richness of red-listed beetles	**East**	**West**			
region	0.99	0.08			
isolation status	**clustered**	**solitary**			
mean estimates	0.59	0.38			

Significance codes: <0.001***, 0.01**, 0.05*, not significant 'NS'. Negative binomial dispersion parameter: 403 (SE: 4.21)Log-likelihood: -94.8. AIC:200. Number of obs: 124, groups: Site = 15

Discussion

In contrast to my expectations, there were no clear indications to that all or red-listed oak-associated communities had a higher dispersal ability in isolated hollow oak habitats or in the western region.

Mean body size did not clearly differ between all or red-listed saproxylic beetle communities in isolated hollow oak habitats or between the different regions.

In contrast to my expectations, no significant difference in species richness of all beetle communities, including the red-listed beetles were clearly affected from the different state of isolation between solitary trees and clustered trees.

In line with my third expectations species richness decreased with 35 % between the two regions (table 5) and red-listed species was also clearly lower in the western region by 92 % relative to the eastern hollow oak region (table 6).

The effects of dispersal ability on community structure

As no results were significant, we cannot conclude that any saproxylic communities in solitary trees have communities with a higher relative wing length.

I could also not confirm a significant difference of a lower dispersal ability in the western region, compared to the eastern region. Hagge et al. (in review), reports that relative wing length has a strong effect on the extinction risk of red-listed saproxylic beetles, of which a higher relative wing length (higher = increased dispersal capacity), leads to increased extinction risk. Had my results shown significance, it could have implied an indirect relation to why there is a clear lower species richness in the west in all and red-listed oak-associated communities.

It is difficult to say if the pattern had been more clear if I had separated specialists and generalists as encouraged in previous research on traits and dispersal abilities (Chichorro et al., 2019; Percel et al., 2019). My design has a more simplified approach, as I used community weighed means to measure dispersal capacity patterns (mean relative wing length in this context) of all oak-associated beetles depending on habitat isolation or regional differences. By included both generalists and specialists in the same group, the results do not differentiate how oak-

specialists and oak-generalists would likely respond differently to isolation effects (Chichorro et al., 2019; Percel et al., 2019). At the same time it is important to also understand the respond of the whole oak-associated community at a given habitat patch, as it gives the ability to interpret how all saproxylic beetle species may be struggling to disperse from the effects of isolation or regional differences. At the same time one of the greatest challenges in understanding how traits of species make them vulnerable, is that there are often are more than one trait connected to extinction risk (Chichorro et al., 2019). Thus detecting the general trend of the dispersal ability of all saproxylic beetle communities is highly complex.

The effects of body size on community structure

There were no significant patterns of mean body size in communities of all or red-listed oak-associated beetles affected by isolation or regional differences.

Previous research supports that beetles with a smaller body size have a greater resilience to habitat isolation as these species correlates with a higher abundance and better colonizing ability (Fisher & Owens, 2004; Gillespie et al., 2017) Species with larger body size are also highly dependent on tree size (Seibold et al., 2015). Density of trees within a habitat is also positively correlated with species richness of specialists (Bergman et al., 2012), which implies a positive relationship between body size, tree size and density of trees. This implies that oak-associated beetle communities would have a pattern of a smaller mean body size in isolated habitats, as lower density of trees affects negatively species richness thus likely correspond also negatively with body size. However, since my results are not significant, I cannot conclude that habitat isolation would lead to a smaller mean body size of oak-associated beetles.

I could not confirm a significant difference in mean body size between the western region and eastern region of all or only the red-listed oak-associated beetles. There is little research of how the distribution of hollow oaks in Norway could be related to community weighed mean body size of saproxylic specialist communities from a regional scale. However, Gillespie et al. (2017) studied the relationship between dispersal phenology and body size of all saproxylic forest beetles in Norway. Body size had a negative relationship with abundance which indicated a shortened flight period and flight activity during the summer. In contrast, a smaller body size had a positive correlation to abundance and indicated increased flight period and flight activity during the summer. Because Gillespie et al. (2017) looked at all forest trees that are important for

saproxylic beetles instead of only hollow oak trees, it does not distinguish how dispersal phenology of oak-associated beetles respond to body size. Mean summer precipitation is higher in the western hollow oak region compared to the eastern region. Therefore, the findings do provide a generalizing result of all saproxylic forest communities and to some degree support that if dispersal phenology to all forest beetles are correlated to a large body size, than it suggests that most of my oak-associated beetles also are. Thus, longer periods of rain in the western region likely limits the larger sized beetle species window to disperse more than the smaller body sized beetles. In the complex picture of traits connecting to other traits, it could further indicate that the larger beetles would include mainly the specialists, which are shown to be negatively affected by precipitation (Gough et al., 2015; Pilskog et al., 2020).

The effects of isolation on species richness

My results could not indicate any significant trend of a different species richness of all or only red-listed oak-associated beetles from the effects of habitat isolation.

There are many structural variables that can influence the effects of habitat isolation on species richness, of which habitat size, habitat quality and degree of isolation are confirmed as influential factors to saproxylic species in several studies (Pilskog et al., 2016; Ranius & Jansson, 2000; Ranius, 2002; Sverdrup-Thygeson et al., 2010b). Scale is highlighted as another important factor when understanding the effects of isolation on species richness in a given landscape context (Della Rocca & Milanesi, 2020; Ewers & Didham, 2006; Percel et al., 2019; Sverdrup-Thygeson et al., 2014). An example can be given by Pilskog et al. (2016) that surprisingly did not find species richness effected by isolation at a small scale although species abundance was affected in some species groups.

There is an east/west pattern in species richness for all and red-listed oak-associated beetle communities

My results confirm a strong difference in species richness on a regional scale. This could indicate that the western hollow oak region represents a different landscape structure and a different climate pattern than the eastern hollow oak region that would affect species richness of the saproxylic beetle communities included in this study.

However, the study design restricts my results to only hypothesise the possible effects. It is challenging to test how species richness respond to regional drivers as regional differences are complex structures to identify. For example, a German study (Müller et al., 2015) found a generalized pattern between species richness of saproxylic species and the effects of temperature, of which increasing temperature overpowered the negative effects by lower amounts of dead wood. Another study from Switzerland (Della Rocca & Milanesi, 2020) challenges this generalizing trend, as saproxylic specialists would only benefit from increasing temperature, if they were not limited by the effects of habitat isolation caused by human land use change. A Norwegian study Pilskog et al. (2016) further highlights the complexity of species richness depending also on the local context, by the importance of considering the proportion of oak trees within an area, variation of stand age and the effects of temperature that varies along a costal-inland gradient.

Limitations in the study design

A limitation of my study design is that the sample size to not cover enough habitat patches too show any clear trends. To imply dispersal patterns, saproxylic insects needs to be captured in every habitat patch in an entire landscape, a problem that is stated as one of the greatest challenges with studying saproxylic species (Ranius, 2006). Hollow oak habitats are hyper diverse and highly variable communities; therefore, a large sample size is important in order to observe any patterns.

Increasing study areas and sample size would possibly lead to the trend becoming more robust. Unfortunately, it is likely difficult to increase observations, as red-listed specialists and saproxylic specialists generally are rarer than generalists, and therefore more difficult to observe in large enough numbers (Skarpaas et al., 2011). Red-listed beetles that were observed in traps, were strongly unevenly sampled between east and west. The dataset included red-listed beetles from 5 traps in the west and 42 traps in the east. Even though a limited number of study areas, I had balanced the number of traps and number of study areas between regions. Thus, the western region only obtaining 1/8 of the total proportion of red-listed beetles sampled in this study says a great deal.

An important question we did not ask in this study design is if species composition changes along the same east-west division. Pilskog et al. (2020), found similar species richness between the counties Agder and Larvik, but species composition differed between the two counties. Future research should therefore include species composition as well as species richness, as it is likely that unique species in the east may not be found in the west and vice versa.

Because the habitat scale was only investigated within a square of 500x500 meters, it is possible that the solitary trees were connected to other hollow oaks outside the square, thus confounding the isolation effects. Because sample size was limited, I included both specialists and generalists which means that my study design is a more generalized approach to understand the respond of community weighed means of all oak-associated species. However, incorporating specialists and generalists in different groups is also important to provide more detailed results to how vulnerable the different groups are to different environmental changes as found by Percel et al. (2019).

Conclusion

I could not confirm the expectations of finding a lower mean relative wing length in isolated habitats or in the western region, and therefore cannot conclude that only the good dispersers could reach these areas. Mean body size of oak-associated beetle communities including red-listed beetles did not differ from the effects of habitat isolation or between the western and eastern region. I encourage researches to increase sample size and study areas to potentially detect stronger generalized patterns of how traits of relative wing length and body size in oak-associated beetle communities affect community structure from habitat isolation or regional differences.

The study confirms a strong pattern of species richness of all oak-associated communities, including red-listed to be lower in the western hollow oak region, compared to the eastern region in the southern part Norway. Both regions should prioritize conservation strategies at a local scale by conserving or increasing high density of large hollow oaks and promote occurrence of dead wood by leaving snags and stumps of fallen tree as important resource components for the

species with limiting dispersal abilities (Grove, 2002; Huxel & Hastings, 1999). On a large scale, there is still not a consensus in conservation planning (Sverdrup-Thygeson et al., 2014), however management should strive to prevent further patterns of increasing the distance between habitat patches, as at one point the distance between habitats will become to great even for the good dispersers to immigrate. It is therefore important to consider the status of hollow oak stands and the occurrence of dead wood in the landscape from the large variation in responses of hollow oak beetle communities.

References

Artsdatabanken. (2015). *The Norwegian Red List Database*. Available at: https://www.artsdatabanken.no/Rodliste2015/sok?Kategori=re,cr,en,vu,nt,dd&Vurderings%C3%85r=2015&VurderingsContext=n&TaxonRank=species.

Barton, K. (2020). MuMIn: Multi-Model Inference. (R package version 1.43.17).

Bates, D., Sarkar, D., Bates, M. D. & Matrix, L. (2007). The lme4 package. *R package version*, 2 (1): 74.

Bergman, K.-O., Jansson, N., Claesson, K., Palmer, M. W. & Milberg, P. (2012). How much and at what scale? Multiscale analyses as decision support for conservation of saproxylic oak beetles. *Forest Ecology and Management*, 265: 133-141.

Bouget, C., Brin, A., Tellez, D. & Archaux, F. (2015). Intraspecific variations in dispersal ability of saproxylic beetles in fragmented forest patches. *Oecologia*, 177 (3): 911-920. doi: 10.1007/s00442-014-3162-9.

Brooks, T. M., Mittermeier, R. A., Mittermeier, C. G., Da Fonseca, G. A., Rylands, A. B., Konstant, W. R., Flick, P., Pilgrim, J., Oldfield, S. & Magin, G. (2002). Habitat loss and extinction in the hotspots of biodiversity. *Conservation biology*, 16 (4): 909-923.

Buse, J., Levanony, T., Timm, A., Dayan, T. & Assmann, T. (2010). Saproxylic beetle assemblages in the Mediterranean region: Impact of forest management on richness and structure. *Forest ecology and Management*, 259 (8): 1376-1384.

Butchart, S. H., Walpole, M., Collen, B., Van Strien, A., Scharlemann, J. P., Almond, R. E., Baillie, J. E., Bomhard, B., Brown, C. & Bruno, J. (2010). Global biodiversity: indicators of recent declines. *Science*, 328 (5982): 1164-1168.

Chase, J. M. & Leibold, M. A. (2003). *Ecological niches: linking classical and contemporary approaches*: University of Chicago Press.

Chichorro, F., Juslén, A. & Cardoso, P. (2019). A review of the relation between species traits and extinction risk. *Biological Conservation*, 237: 220-229.

Davies, K. F., Margules, C. R. & Lawrence, J. F. (2000). Which traits of species predict population declines in experimental forest fragments? *Ecology*, 81 (5): 1450-1461.

Davies, K. F., Margules, C. R. & Lawrence, J. F. (2004). A synergistic effect puts rare, specialized species at greater risk of extinction. *Ecology*, 85 (1): 265-271. doi: 10.1890/03-0110.

Davies, Z. G., Tyler, C., Stewart, G. B. & Pullin, A. S. (2008). Are current management recommendations for saproxylic invertebrates effective? A systematic review. *Biodiversity and conservation*, 17 (1): 209-234.

Della Rocca, F. & Milanesi, P. (2020). Combining climate, land use change and dispersal to predict the distribution of endangered species with limited vagility. *Journal of Biogeography*, 47 (7): 1427-1438. doi: 10.1111/jbi.13804.

Díaz, S. M., Settele, J., Brondízio, E., Ngo, H., Guèze, M., Agard, J., Arneth, A., Balvanera, P., Brauman, K. & Butchart, S. (2019). The global assessment report on biodiversity and ecosystem services: Summary for policy makers.

Directorate for Nature Management. (2012). *Handlingsplan for utvalgt naturtype hule eiker*.

Douglas Bates, M. M., Ben Bolker, Steve Walker. (2015). Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software*, 67 (1): 48. doi: 10.18637/jss.v067.i01.

Ewers, R. M. & Didham, R. K. (2006). Confounding factors in the detection of species responses to habitat fragmentation. *Biological reviews*, 81 (1): 117-142.

Feldhaar, H. & Schauer, B. (2018). *Dispersal of Saproxylic Insects*. Cham: Cham: Springer International Publishing. pp. 515-546.

Fisher, D. O., Owens, I. P. & Johnson, C. N. (2001). The ecological basis of life history variation in marsupials. *Ecology*, 82 (12): 3531-3540.

Fisher, D. O. & Owens, I. P. (2004). The comparative method in conservation biology. *Trends in ecology & evolution*, 19 (7): 391-398.

Fournier DA, S. H., Ancheta J, Ianelli J, Magnusson A, Maunder M, Nielsen A, Sibert J. (2012). AD Model Builder: using automatic differentiation for statistical inference of highly parameterized complex nonlinear models. *Optim. Methods Softw*, 27: 233-249.

Gaston, K. J. & David, R. (1994). Hotspots across Europe. *Biodiversity letters*: 108-116.

Gauthier, S., Bernier, P., Kuuluvainen, T., Shvidenko, A. & Schepaschenko, D. (2015). Boreal forest health and global change. *Science*, 349 (6250): 819-822.

Gibb, H., Hjältén, J., Ball, J. P., Pettersson, R., Landin, J., Alvini, O. & Danell, K. (2006). Wing loading and habitat selection in forest beetles: Are red-listed species poorer dispersers or more habitat-specific than common congenerics? *Biological Conservation*, 132 (2): 250-260.

Gillespie, M. A., Birkemoe, T. & Sverdrup-Thygeson, A. (2017). Interactions between body size, abundance, seasonality, and phenology in forest beetles. *Ecology and evolution*, 7 (4): 1091-1100.

Gough, L. A., Sverdrup-Thygeson, A., Milberg, P., Pilskog, H. E., Jansson, N., Jonsell, M. & Birkemoe, T. (2015). Specialists in ancient trees are more affected by climate than generalists. *Ecology and Evolution*, 5 (23): 5632-5641. doi: 10.1002/ece3.1799.

Grove, S. J. (2002). Saproxylic Insect Ecology and the Sustainable Management of Forests. *Annual Review of Ecology and Systematics*, 33 (1): 1-23. doi: 10.1146/annurev.ecolsys.33.010802.150507.

Hagge, J., Müller, J., Birkemoe, T., Buse, J., Christensen, R. H. B., Gossner, M. M., Gruppe, A., Jarzabek-Müller, A., Seibold, S., Siitonen, J., et al. (in review). *A new trait database allows modelling of the relationships between morphological features and the extinction risk of saproxylic beetles*.

Hannah, L., Carr, J. L. & Lankerani, A. (1995). Human disturbance and natural habitat: a biome level analysis of a global data set. *Biodiversity & Conservation*, 4 (2): 128-155.

Henle, K., Davies, K. F., Kleyer, M., Margules, C. & Settele, J. (2004). Predictors of species sensitivity to fragmentation. *Biodiversity & Conservation*, 13 (1): 207-251.

Huxel, G. R. & Hastings, A. (1999). Habitat loss, fragmentation, and restoration. *Restoration ecology*, 7 (3): 309-315.

Jaworski, T., Plewa, R., Tarwacki, G., Sucko, K., Hilszczanski, J. & Horak, J. (2019). Ecologically similar saproxylic beetles depend on diversified deadwood resources: From habitat requirements to

management implications. *Forest Ecology and Management*, 449. doi: 10.1016/j.foreco.2019.117462.

John Fox, S. W. (2019). An {R} Companion to Applied Regression. (Third Edition).

Komonen, A., Jonsell, M. & Ranius, T. (2008). Red-listing saproxylic beetles in Fennoscandia: current status and future perspectives. *Endangered Species Research*, 6 (2): 149-154.

Kotze, D. J. & O'hara, R. B. (2003). Species decline—but why? Explanations of carabid beetle (Coleoptera, Carabidae) declines in Europe. *Oecologia*, 135 (1): 138-148.

Kouki, J., Löfman, S., Martikainen, P., Rouvinen, S. & Uotila, A. (2001). Forest fragmentation in Fennoscandia: linking habitat requirements of wood-associated threatened species to landscape and habitat changes. *Scandinavian Journal of Forest Research*, 16 (S3): 27-37.

Kuznetsova A, B. P., Christensen RHB. (2017). lmerTest Package: Tests in Linear Mixed Effects Models. *Journal of Statistical Software*, 82 (13): 26. doi: doi: 10.18637/jss.v082.i13.

Lindenmayer, D. B. & Fischer, J. (2013). *Habitat fragmentation and landscape change: an ecological and conservation synthesis*: Island Press.

Lovdata. (2011). *Forskrift om utvalgte naturtyper etter naturmangfoldloven*. Available at: http://lovdata.no/dokument/SF/forskrift/2011-05-13-512.

MacArthur, R. H. & Wilson, E. O. (2001). *The theory of island biogeography*, vol. 1: Princeton university press.

Mace, G. M., Barrett, M., Burgess, N. D., Cornell, S. E., Freeman, R., Grooten, M. & Purvis, A. (2018). Aiming higher to bend the curve of biodiversity loss. *Nature Sustainability*, 1 (9): 448-451.

McKinney, M. L. (1997). Extinction vulnerability and selectivity: combining ecological and paleontological views. *Annual review of ecology and systematics*, 28 (1): 495-516.

Mery, G., Katila, P., Galloway, G., Alfaro, R. I., Kanninen, M., Lobovikov, M. & Varjo, J. (2010). *Forests and society-responding to global drivers of change*: IUFRO Vienna.

Mittermeier, R. A., Turner, W. R., Larsen, F. W., Brooks, T. M. & Gascon, C. (2011). Global biodiversity conservation: the critical role of hotspots. In *Biodiversity hotspots*, pp. 3-22: Springer.

Moen, A., Norges geografiske, o. & Statens, k. (1998). *Vegetasjon*. Atlas : vegetasjon. Hønefoss: Norges geografiske oppmåling.

Myers, N., Mittermeier, R. A., Mittermeier, C. G., Da Fonseca, G. A. & Kent, J. (2000). Biodiversity hotspots for conservation priorities. *Nature*, 403 (6772): 853-858.

Müller, J., Brustel, H., Brin, A., Bussler, H., Bouget, C., Obermaier, E., Heidinger, I. M., Lachat, T., Förster, B. & Horak, J. (2015). Increasing temperature may compensate for lower amounts of dead wood in driving richness of saproxylic beetles. *Ecography*, 38 (5): 499-509.

Newbold, T., Hudson, L. N., Phillips, H. R., Hill, S. L., Contu, S., Lysenko, I., Blandon, A., Butchart, S. H., Booth, H. L. & Day, J. (2014). A global model of the response of tropical and sub-tropical forest biodiversity to anthropogenic pressures. *Proceedings of the Royal Society B: Biological Sciences*, 281 (1792): 20141371.

Nieto, A., Alexander, K., International Union for Conservation of, N. & European, U. (2010). *European red list of saproxylic beetles*. Luxembourg: Publications Office of the European Union.

Nilsson, S. G. & Baranowski, R. (1997). Habitat predictability and the occurrence of wood beetles in old-growth beech forests. *Ecography*, 20 (5): 491-498.

Parmesan, C. (2006). Ecological and evolutionary responses to recent climate change. *Annu. Rev. Ecol. Evol. Syst.*, 37: 637-669.

Percel, G., Laroche, F. & Bouget, C. (2019). The scale of saproxylic beetles response to landscape structure depends on their habitat stability. *Landscape Ecology*, 34 (8): 1905-1918. doi: 10.1007/s10980-019-00857-0.

Pilskog, H. E., Sverdrup-Thygeson, A. & Birkemoe, T. (2014). Biller i hule eiker i Vestfold, Telemark og Agder.

Pilskog, H. E., Birkemoe, T., Framstad, E. & Sverdrup-Thygeson, A. (2016). Effect of Habitat Size, Quality, and Isolation on Functional Groups of Beetles in Hollow Oaks. *Journal of Insect Science*, 16 (1). doi: 10.1093/jisesa/iev145.

Pilskog, H. E., Sverdrup-Thygeson, A., Evju, M., Framstad, E. & Birkemoe, T. (2018). Long-lasting effects of logging on beetles in hollow oaks. *Ecology and evolution*, 8 (20): 10126-10137.

Pilskog, H. E., Birkemoe, T., Evju, M. & Sverdrup-Thygeson, A. (2020). Species composition of beetles grouped by host association in hollow oaks reveals management-relevant patterns. *Journal of Insect Conservation*, 24 (1): 65-86.

Pinheiro, J. & Bates, D. (2006). *Mixed-effects models in S and S-PLUS*: Springer Science & Business Media.

R Core Team (2013). R: A language and environment for statistical computing. *R Foundation for Statistical Computing*.

Ranius, T. & Jansson, N. (2000). The influence of forest regrowth, original canopy cover and tree size on saproxylic beetles associated with old oaks. *Biological Conservation*, 95 (1): 85-94.

Ranius, T. (2002). Influence of stand size and quality of tree hollows on saproxylic beetles in Sweden. *Biological Conservation*, 103 (1): 85-91.

Ranius, T. (2006). Measuring the dispersal of saproxylic insects: a key characteristic for their conservation. *Population Ecology*, 48 (3): 177-188. doi: 10.1007/s10144-006-0262-3.

Reiss, J., Bridle, J. R., Montoya, J. M. & Woodward, G. (2009). Emerging horizons in biodiversity and ecosystem functioning research. *Trends in ecology & evolution*, 24 (9): 505-514.

Ricotta, C. & Moretti, M. (2011). CWM and Rao's quadratic diversity: a unified framework for functional ecology. *Oecologia*, 167 (1): 181-188.

Rundle, S. D., Bilton, D. T. & Foggo, A. (2007). By wind, wings or water: body size, dispersal and range size in aquatic invertebrates. *Body size: the structure and function of aquatic ecosystems. Cambridge University Press, Cambridge*: 186-209.

Sala, O. E., Chapin, F. S., Armesto, J. J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L. F., Jackson, R. B. & Kinzig, A. (2000). Global biodiversity scenarios for the year 2100. *science*, 287 (5459): 1770-1774.

Seibold, S., Brandl, R., Buse, J., Hothorn, T., Schmidl, J., Thorn, S. & Müller, J. (2015). Association of extinction risk of saproxylic beetles with ecological degradation of forests in Europe. *Conservation Biology*, 29 (2): 382-390. doi: 10.1111/cobi.12427.

Siitonen, J. (2001). Forest management, coarse woody debris and saproxylic organisms: Fennoscandian boreal forests as an example. *Ecological bulletins*: 11-41.

Skarpaas, O., Diserud, O. H., SVERDRUP-THYGESON, A. & ØDEGAARD, F. (2011). Predicting hotspots for red-listed species: Multivariate regression models for oak-associated beetles. *Insect Conservation and Diversity*, 4 (1): 53-59.

Skarpaas, O., Blumentrath, S., Evju, M. & Sverdrup-Thygeson, A. (2017). Prediction of biodiversity hotspots in the Anthropocene: The case of veteran oaks. *Ecology and evolution*, 7 (19): 7987-7997.

Slatyer, R. A., Hirst, M. & Sexton, J. P. (2013). Niche breadth predicts geographical range size: a general ecological pattern. *Ecology letters*, 16 (8): 1104-1114.

Southwood, T. (1962). Migration of terrestrial arthropods in relation to habitat. *Biological reviews*, 37 (2): 171-211.

Stokland, J., Dahlberg, A., Meyke, E., Schigel, D. & Siitonen, J. (2006). *The Nordic saproxylic database - a comprehensive overview of the biological diversity in dead wood*. 1st European Congress of Conservation Biology - "Diversity for Europe". . Hungary: Society of Conservation Biology (USA) & Blackwell Publishing (UK).

Stokland, J. N., Jonsson, B. G. & Siitonen, J. (2012). *Biodiversity in Dead Wood*. Ecology, Biodiversity, and Conservation. Cambridge: Cambridge University Press.

Sverdrup-Thygeson, A. (2009). *Oaks in Norway: hotspots for red-listed beetles (Coleoptera)*. Saproxlic beetles: their role and diversity in European woodland and tree habitats. Proceedings of the 5th Symposium and Workshop on the Conservation of Saproxylic Beetles, Lüneberg, Germany, 14-16 June 2008: Pensoft Publishers.

Sverdrup-Thygeson, A., Bratli, H., Brandrud, T. E. & Ødegaard, F. (2010a). Eikeskog og gamle eiketrær: Viktige hotspot-habitater for rødlistearter i Norge. *Naturen*, 134 (2): 74-89.

Sverdrup-Thygeson, A., Skarpaas, O. & Ødegaard, F. (2010b). Hollow oaks and beetle conservation: the significance of the surroundings. *Biodiversity and Conservation*, 19 (3): 837-852. doi: 10.1007/s10531-009-9739-7.

Sverdrup-Thygeson, A., Bratli, H., Brandrud, T. E., Endrestøl, A., Evju, M., Hanssen, O., Skarpaas, O., Stabbetorp, O. E. & Ødegaard, F. (2011). Hule eiker-et hotspot-habitat. Sluttrapport under ARKO-prosjektets periode II. *NINA rapport*.

Sverdrup-Thygeson, A., Gustafsson, L. & Kouki, J. (2014). Spatial and temporal scales relevant for conservation of dead-wood associated species: current status and perspectives. *Biodiversity and conservation*, 23 (3): 513-535.

Sverdrup-Thygeson, A., Skarpaas, O., Blumentrath, S., Birkemoe, T. & Evju, M. (2017). Habitat connectivity affects specialist species richness more than generalists in veteran trees. *Forest Ecology and Management*, 403: 96-102.

Sverdrup-Thygeson, A., Evju, M., Skarpaas, O., Jacobsen, R. M. & Birkemoe, T. (2018). Nasjonal overvåking av hule eiker: Resultat første omløp og forslag til videreføring. *MINA fagrapport*, 50: 33.

Venables, W. N., Ripley, B. D.,. (2002). *Modern Applied Statistics with S.* . Fourth ed.: Springer.

Wiens, J. A. (1995). Landscape mosaics and ecological theory. In *Mosaic landscapes and ecological processes*, pp. 1-26: Springer.

Zeileis, A., Kleiber, C. & Jackman, S. (2008). Regression models for count data in R. *Journal of statistical software*, 27 (8): 1-25.

Zuur, A., Ieno, E. N., Walker, N., Saveliev, A. A. & Smith, G. M. (2009). *Mixed effects models and extensions in ecology with R*: Springer Science & Business Media.

Ødegaard, F., Olberg, S. & Hanssen, O. (2015). *Biller (Coleoptera)*. Norsk rødliste for arter 2015: Artsdatabanken. Available at: http://www.artsdatabanken.no/Rodliste/Artsgruppene/Biller.

Appendix S1 Species list of saproxylic specialists and categorization

Table S1: List of study species with information on number of individuals observed by isolation status by region, red-list status and oak association. Oak association is obtained from the Nordic saproxylic database by Stokland et al. (2006) and red-list status is obtained from the Norwegian red-list database (Artsdatabanken, 2015).

Species names	Solitary / East	Solitary/ West	Clustered/ East	Culstered/ West	Red-list status	Oak association
Agathidium confusum	0	1	0	1	LC	Oak Generalist
Agathidium nigripenne	0	0	0	1	LC	Oak Generalist
Alosterna tabacicolor	6	3	7	0	LC	OakSpecialist
Ampedus balteatus	3	5	9	9	LC	OakGeneralist
Ampedus hjorti	5	0	98	0	VU	OakSpecialist
Ampedus nigerrimus	1	0	0	2	NA	OakSpecialist
Ampedus nigrinus	3	0	0	4	LC	OakSpecialist
Ampedus pomorum	0	0	1	8	LC	OakGeneralist
Anaspis frontalis	0	1	0	0	LC	OakGeneralist
Anaspis rufilabris	31	21	67	22	LC	OakGeneralist
Anaspis thoracica	2	0	13	1	LC	OakGeneralist
Anisotoma humeralis	5	2	1	6	LC	OakGeneralist
Anisotoma orbicularis	0	0	0	4	LC	OakGeneralist
Anoplodera sexguttata	0	0	5	0	LC	OakSpecialist
Aplocnemus nigricornis	1	0	3	0	LC	OakGeneralist
Atrecus affinis	0	0	2	0	LC	OakGeneralist
Bibloporus bicolor	13	4	2	1	LC	OakGeneralist
Calambus bipustulatus	0	0	3	0	EN	OakBroadLBoreal
Cerylon fagi	0	0	2	0	LC	OakBroadLBoreal
Cerylon ferrugineum	5	1	1	9	LC	OakGeneralist
Cis boleti	0	0	0	4	LC	OakBroadLBoreal
Cis micans	0	1	0	3	LC	OakGeneralist
Clytus arietis	0	1	0	0	LC	OakSpecialist
Conopalpus testaceus	3	3	0	0	LC	OakSpecialist
Corticaria longicollis	1	0	0	0	LC	OakGeneralist
Crepidophorus mutilatus	0	0	2	0	EN	OakBroadLBoreal
Cryptarcha strigata	1	0	4	0	NT	OakBroadLBoreal
Cryptarcha undata	1	0	1	0	NT	OakBroadLBoreal
Ctesias serra	0	3	11	0	LC	OakBroadLBoreal
Cychramus variegatus	0	1	1	0	LC	OakGeneralist
Dacne bipustulata	0	0	6	2	LC	OakBroadLBoreal
Dadobia immersa	0	0	1	0	LC	OakGeneralist
Dasytes niger	4	0	0	2	LC	OakGeneralist
Dasytes plumbeus	8	4	16	0	LC	OakBroadLBoreal
Dendrophilus punctatus	0	0	1	0	LC	OakGeneralist

Species					Status	Category
Denticollis linearis	0	0	0	9	LC	OakGeneralist
Dorcatoma chrysomelina	0	1	17	0	LC	OakSpecialist
Dorcatoma dresdensis	0	1	44	0	LC	OakGeneralist
Dromius agilis	3	1	2	0	LC	OakGeneralist
Dropephylla ioptera	0	2	0	0	LC	OakGeneralist
Dropephylla linearis	1	0	0	0	LC	OakGeneralist
Dryocoetes villosus	0	0	10	0	LC	OakSpecialist
Endomychus coccineus	0	1	0	0	LC	OakBroadLBoreal
Enicmus testaceus	2	0	0	3	LC	OakGeneralist
Ennearthron cornutum	3	0	0	0	LC	OakGeneralist
Ernoporus tiliae	0	0	0	1	LC	OakBroadLTemp
Euglenes oculatus	49	0	712	0	NT	OakSpecialist
Euplectus punctatus	1	0	0	0	LC	OakGeneralist
Gabrius splendidulus	0	2	1	2	LC	OakGeneralist
Gastrallus immarginatus	2	0	2	0	EN	OakSpecialist
Glischrochilus quadriguttatus	1	0	1	0	LC	OakBroadLBoreal
Gnorimus nobilis	1	0	0	0	NT	OakBroadLTemp
Grammoptera ruficornis	0	0	0	1	LC	OakBroadLBoreal
Grynobius planus	0	6	0	17	LC	OakBroadLBoreal
Grynocharis oblonga	0	0	4	0	VU	OakGeneralist
Hallomenus axillaris	0	0	6	0	NT	OakGeneralist
Hapalaraea pygmaea	1	0	0	0	LC	OakBroadLTemp
Hylobius abietis	2	0	0	0	LC	OakGeneralist
Ischnoglossa prolixa	0	0	0	2	LC	OakGeneralist
Laemophloeus monilis	0	0	1	0	CR	OakBroadLTemp
Leiopus nebulosus	0	1	2	1	LC	OakSpecialist
Leptura quadrifasciata	0	1	0	0	LC	OakGeneralist
Leptusa pulchella	0	0	0	4	LC	OakGeneralist
Leptusa ruficollis	2	1	0	5	LC	OakBroadLBoreal
Malachius bipustulatus	0	0	1	0	LC	OakGeneralist
Malthodes spathifer	1	0	1	1	LC	OakBroadLBoreal
Megatoma undata	1	0	0	0	LC	OakGeneralist
Melasis buprestoides	0	0	1	0	NT	OakBroadLBoreal
Mycetophagus piceus	0	0	2	0	NT	OakSpecialist
Orchesia micans	0	1	0	0	LC	OakGeneralist
Orchesia minor	0	0	0	1	LC	OakGeneralist
Orchesia undulata	1	0	2	0	LC	OakBroadLBoreal
Orthocis alni	3	0	2	0	LC	OakGeneralist
Oxymirus cursor	0	0	1	0	LC	OakGeneralist
Phloeocharis subtilissima	0	0	0	1	LC	OakGeneralist
Phloeonomus pusillus	1	0	0	0	LC	OakGeneralist
Phloeophagus lignarius	0	0	1	0	VU	OakBroadLBoreal
Phloeopora testacea	0	0	5	2	LC	OakGeneralist
Phloiotrya rufipes	2	0	2	0	NT	OakBroadLBoreal
Phyllodrepa melanocephala	1	1	0	0	LC	OakBroadLBoreal

Species						
Phymatodes testaceus	0	0	5	0	LC	OakSpecialist
Platycerus caraboides	0	1	0	0	LC	OakBroadLBoreal
Pogonocherus hispidus	1	0	0	0	LC	OakBroadLBoreal
Prionocyphon serricornis	0	13	20	3	NT	OakBroadLTemp
Pseudocistela ceramboides	6	12	43	0	LC	OakGeneralist
Pteryx suturalis	1	0	0	0	LC	OakGeneralist
Quedius brevicornis	0	1	0	0	NT	OakGeneralist
Quedius maurus	0	2	0	1	LC	OakGeneralist
Quedius plagiatus	0	0	0	1	LC	OakGeneralist
Quedius scitus	0	0	1	0	LC	OakSpecialist
Quedius xanthopus	2	3	1	4	LC	OakGeneralist
Rhagium mordax	1	2	2	5	LC	OakGeneralist
Rhizophagus bipustulatus	0	0	2	0	LC	OakSpecialist
Rhizophagus cribratus	0	2	0	0	LC	OakSpecialist
Rhyncolus ater	0	14	4	0	LC	OakGeneralist
Rhyncolus sculpturatus	1	0	0	0	LC	OakGeneralist
Salpingus planirostris	1	6	5	14	LC	OakBroadLBoreal
Salpingus ruficollis	1	1	1	5	LC	OakGeneralist
Scaphisoma agaricinum	0	1	0	1	LC	OakGeneralist
Schizotus pectinicornis	0	0	1	1	LC	OakGeneralist
Scolytus intricatus	0	0	1	0	LC	OakSpecialist
Sepedophilus testaceus	3	0	0	0	LC	OakGeneralist
Soronia grisea	0	0	7	0	LC	OakBroadLBoreal
Stenichnus bicolor	1	0	0	0	LC	OakGeneralist
Stenichnus godarti	1	0	0	0	LC	OakSpecialist
Stenocorus meridianus	0	0	1	0	VU	OakBroadLBoreal
Stenostola dubia	0	0	0	1	LC	OakBroadLBoreal
Thamiaraea cinnamomea	0	0	1	0	LC	OakBroadLBoreal
Thymalus limbatus	0	0	1	0	LC	OakGeneralist
Tillus elongatus	1	0	1	0	LC	OakGeneralist
Trachodes hispidus	0	0	0	1	LC	OakBroadLBoreal
Trichius fasciatus	0	5	0	24	LC	OakBroadLBoreal
Triplax russica	1	0	2	0	LC	OakBroadLBoreal
Xestobium rufovillosum	1	0	6	0	LC	OakSpecialist
Xyleborinus saxesenii	1	0	0	0	LC	OakBroadLBoreal
Xylophilus corticalis	0	1	4	0	LC	OakGeneralist

Appendix S2 Table of study site locations and tree variables

Table S2: Site, TreeID, location, Isolation status, coordinates, old county names, geographical zones by region, circumference of all hallow oaks and tree value of the 31 hollow oaks used in the study. Tre value criteria of A, B, or C are based on tree size, hollowness, abundance of wood mould, crevices and high density of clustered hollow oaks in the habitat. A- tree would be a large tree with hollow, high wood mould abundance and deep crevices surrounded by high density of oaks. B- tree could be large trees but with less would mould. C-tree are generally smaller trees and could have early developed hollows and low abundance of would mould. Tree values are obtained from the National monitoring of hollow oaks (Sverdrup-Thygeson et al., 2018). TreeIDs that had no information on circumference and tree value are marked with an asterisk (*).

Site	TreeID	Location	Status	X UTM32	Y UTM33	Old county names	Region	Circumference	Tre-value
DAL	DAL1	Dale , Risør	Clustered	508478	6516675	Aust-Agder	East	160	B
DAL	DAL2*	Dale , Risør	Clustered	508377	6516601	Aust-Agder	East	Unknown	Unknown
DAL	DAL3	Dale , Risør	Clustered	508514	6516672	Aust-Agder	East	226	B
DAL	DAL4	Dale , Risør	Clustered	508524	6516658	Aust-Agder	East	201	B
DAL	DAL5*	Dale , Risør	Clustered	508518	6516648	Aust-Agder	East	Unknown	Unknown
EID	EID1	Eidanger prestegård, Porsgrunn	Clustered	540241	6552732	Telemark	East	530	A
EID	EID2	Eidanger prestegård, Porsgrunn	Clustered	540245	6552752	Telemark	East	580	A
EID	EID3	Eidanger prestegård, Porsgrunn	Clustered	540247	6552774	Telemark	East	640	A
EID	EID4	Eidanger prestegård, Porsgrunn	Clustered	540259	6552862	Telemark	East	830	A

EID	EID5*	Eidanger prestegård, Porsgrunn	Clustered	540263	6552898	Telemark	East	Unknown	Unknown
DOV	DOV1	Døvika, Porsgrunn	Solitary	541669	6552104	Telemark	East	380	A
STA	STA1	Stålfjellsaksla, Skien	Solitary	518226	6553267	Telemark	East	270	A
STE	STE1	Steinknapp, Drangedal	Solitary	501661	6549871	Telemark	East	158	B
GRY	GRY1	Gryntjennåsen	Solitary	515778	6549030	Telemark	East	280	B
GRI	GRI1	Grimsdalen, Drangedal	Solitary	497390	6543841	Telemark	East	290	B
EIK	EIK1	Eikedalen, Florø	Clustered	321072	6842157	Sogn og Fjordane	West	452	A
EIK	EIK2	Eikedalen, Florø	Clustered	320986	6842221	Sogn og Fjordane	West	250	A
EIK	EIK3	Eikedalen, Florø	Clustered	321052	6841939	Sogn og Fjordane	West	230	A
EIK	EIK4	Eikedalen, Florø	Clustered	321035	6841880	Sogn og Fjordane	West	197	A
EIK	EIK5*	Eikedalen, Florø	Clustered	320999	6842002	Sogn og Fjordane	West	Unknown	Unknown
SOL	SOL1	Soldalen, Øystese	Solitary	346201	6700254	Hardanger	West	245	B
BER	BER1	Berghydne, Farsund	Clustered	379779	6442013	Vest-Agder	West	200	B
BER	BER2	Berghydne, Farsund	Clustered	379823	6441939	Vest-Agder	West	163	C
BER	BER3	Berghydne, Farsund	Clustered	379699	6441851	Vest-Agder	West	227	B
BER	BER4	Berghydne, Farsund	Clustered	379655	6441851	Vest-Agder	West	184	B
BER	BER5	Berghydne, Farsund	Clustered	379763	6441719	Vest-Agder	West	204	B
KVA	KVA1	Kvåle, Fusa	Solitary	316588	6681199	Hordaland	West	350	A
SVO	SVO1*	Svovika, Kvinnherad	Solitary	335683	6628790	Hardanger	West	Unknown	Unknown
SKR	SKR1	Skrivestøyldalen, Åmli	Solitary	450107	6519197	Aust-Agder	West	260	A
VAS	VAS1	Vassvatn, Risdal	Solitary	445788	6503510	Aust-Agder	West	252	B
BOM	BOM1	Bomsberget, Åmli	Solitary	450345	6520357	Aust-Agder	West	162	C