Effects of climate, historical logging and spatial scales on beetles in hollow oaks

Betydningen av klima, historisk hogst og omgivelser for biller i hule eiker

Philosophiae Doctor (PhD) Thesis

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"Lengthy forest logging and the related use of timber and sawmills have caused grave damage to his Majesty the King and driven the country into ruin"

—Report to the Danish-Norwegian King regarding the state of the Norwegian oak forests in 1631[1]

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[1] Translated to English from Tvethe, M. B. 1852. Bidrag til Kundskab om Skovenes Tilstand i det 17de Aarhundrede. Norske Samlinger. Feilberg & Landmark, pp. 112-119

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Four years have passed quickly, and this PhD have given me opportunity to investigate and learn about the fascinating world of deadwood-dependent insects living in the oldest beings you are likely to encounter—centuries old oaks. But this PhD have also given me the chance to get involved in teaching of zoology, entomology and nature management courses, of which I am very grateful.

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I dedicate this thesis to my mother, Aase Randi Eik, who always believed in me and that I will miss very much.

Hanne Eik Pilskog
Ås, 30. September 2016

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List of papers

This thesis consists of the following papers, referred to by the Roman numerals (I−IV) in the text:

Paper I

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, 5632-41.

Paper II

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, 1-8.

Paper III

Pilskog, H. E., Sverdrup-Thygeson, A., Evju, M., Framstad, E. and Birkemoe, T. Long-lasting effects of logging on beetles in hollow oaks. *Submitted.*

Paper IV

Pilskog, H. E., Birkemoe, T., Evju, M. and Sverdrup-Thygeson, A. Investigating species composition of beetles in hollow oaks reveals management-relevant patterns. *Manuscript.*

Summary

Veteran trees are keystone structures and important biodiversity habitats, but they are declining on a global scale. In Europe, old oaks (*Quercus* spp.) are one of the most important habitat trees for biodiversity, yet the knowledge about most of these associated species is limited. One important group is the deadwood-dependent beetles associated with old oaks. The aim of this thesis is to increase the knowledge of how beetles in old oaks with different oak-dependency respond to the surroundings on different spatial scales, and if other drivers such as climate and past habitat loss also affect these communities. We collected beetles with insect traps on hollow oaks in four studies: along a climatic gradient, in solitary and aggregated oaks, and along a coast-inland gradient for the two last studies. The climatic gradient went from west to east across Norway and Sweden, and the remaining studies were conducted in southern Norway. We grouped the beetles according to oak-dependency to test if the more specialised species with narrower host-tree range responded differently in comparison to species less dependent on oaks, and focused on the species richness, abundances and species composition.

Along the climatic gradient we found that only a small group of specialists with northern distribution responded positively to the 4ºC increase in summer temperature, but increased summer precipitation had a negative impact on the remaining specialists. The generalists did not respond. Similarly, no groups responded to an increase of 2.6ºC and 180 mm summer rain along the coast-inland gradient. In light of climate change, we can therefore expect most species to be quite robust to smaller changes in summer temperature and precipitation. However, larger changes is likely to benefit a smaller group of specialists only, whereas the remaining specialists can be expected to decline in response to increased precipitation.

We found that species richness did not differ between solitary and aggregated oaks, indicating that solitary oaks can be just as species rich and valuable for conservation as oaks in groups. Still, lower abundance for two groups in solitary oaks indicated that some groups are vulnerable to small-scale isolation, possibly due to their high degree of specialization. In the same study, the species richness only responded to habitat quality (measured as tree shape) and the abundances were influenced by both patch size (measured as circumference) and habitat quality. When the different studies were compared, however, patch size was also found to be important for the species richness, showing that patch size and habitat quality are influencing both species richness and abundances in our study regions.

Tree characteristics and the close surroundings influenced the population sizes of the oak-specialization groups, whereas the species richness increased with deciduous forest cover on the landscape scale. There was a high proportion of species unique to each of the two sampling regions along the coast-inland gradient, and sampling region affected the species composition of all groups. Conservation strategies should therefore aim to conserve hollow oaks across regional scales to maintain the overall biodiversity.

Distance to coast along the coast-inland gradient was used as a proxy for historical logging intensity and duration. We found higher species richness and total abundance inland, indicating that historical logging could be influencing a considerable part of the oak-community, although the most specialised species did not respond. Our results indicate that there could be an extinction debt inland if the habitat in the surroundings today are similar along the coast-inland gradient. Semi-specialists appear to be extra vulnerable to fragmentation compared to the other groups; with the abundance being positively affected by hollow oaks in the close surroundings, species richness responding positively to deciduous forest cover and being negatively affected by historical logging. Overall, our results indicate that there could be a considerable time-lag in the response of the species to habitat loss, calling for more active management to avoid the potential delayed extinctions. This also implies that actions taken today can have implications far into the future.

Sammendrag

Gamle trær er nøkkelstrukturer og et viktig habitat for et rikt og unikt artsmangfold, men dette habitatet minker globalt. I Europa er gamle eiker (*Quercus* spp.) et av de viktigste trærne for slik artsdiversitet. Likevel er kunnskapen om de fleste tilhørende arter begrenset. En viktig gruppe tilknyttet hule eiker er vedlevende biller. Formålet med denne avhandlingen er å øke kunnskapen om hvordan biller med ulik grad av tilknytning til eik påvirkes av nære og fjerne omgivelser, samt av andre faktorer som klima og historisk habitattap.

Vi samlet biller ved hjelp av insektfeller på hule eiker i fire studier: Langs en klimatisk gradient, i solitære og grupperte eiker, og langs en kyst-innlandsgradient i de to siste studiene. Den klimatiske gradienten strakk seg fra øst i Sverige til vest i Norge. De øvrige tre studiene ble utført i Sør-Norge. Vi grupperte billene basert på eiketilknytning, for å teste om spesialiserte arter som er tilknyttet få vertstrær responderer ulikt arter med bredere vertstilknytning. Vi undersøkte både antall arter, antall individer og artssammensetning.

Langs klimagradienten responderte en liten gruppe spesialister med nordlig utbredelse positivt på en 4°C økning i sommertemperatur, samtidig som økt sommernedbør hadde negativ påvirkning på de resterende spesialistene. Generalistene responderte ikke på klimavariablene. Vi fant lignende resultat langs kyst-innlandsgradienten, hvor ingen spesialiseringsgrupper responderte på en 2.6°C og 180 mm økning i sommertemperatur og nedbør. I lys av globale klimaendringer kan vi forvente at de fleste artene er ganske robuste i forhold til små endringer i sommertemperatur og nedbør. Større endringer derimot vil trolig kunne gi positive effekter for en liten gruppe spesialister, mens resten av spesialistene kan forventes å bli negativt påvirket av økt nedbør.

Vi fant ikke forskjeller i artsrikdom mellom solitære eiker og eiker i grupper. Dette viser at solitære eiker kan være like artsrike og verdifulle for bevaring som eiker i grupper. Vi fant likevel færre individer i to av spesialiseringsgruppene i de solitære eikene. Dette kan indikere at noen spesialiseringsgrupper likevel er sårbare for isolasjon på en liten skala, muligens på grunn av høy grad av spesialisering. I samme studie fant vi at artsrikdommen kun responderte på habitatkvalitet (representert ved treets fasong), mens antall individer responderte både på habitatstørrelse (målt som eikas omkrets) og kvalitet. I de øvrige studiene var også habitatstørrelse en viktig forklaringsvariabel for artsrikdom. Dette betyr at habitatstørrelse og kvalitet påvirker både artsrikdom og individantall i våre regioner.

Antall individer med ulik spesialisering ble påvirket av trevariabler og de nære omgivelsene, mens artsrikdom i gruppene økte med areal av løvskog på en større landskapsskala. Mange arter ble kun funnet i én av de to undersøkte regionene, og artssammensetning varierte mellom regionene for alle spesialiseringsgrupper. Bevaringsstrategier burde derfor ha som mål å bevare hule eiker på tvers av regioner for å sikre det totale artsmangfoldet.

Avstand til kyst langs kyst-innlandsgradienten ble brukt som et mål på varighet og intensitet av historisk hogst. Vi fant høyere artsrikdom og flere individer i innlandet, noe som tyder på at historisk hogst kan ha påvirket en betydelig del av eikesamfunnet, selv om de mest spesialiserte artene ikke hadde noen respons. Resultatene våre antyder at det kan være en utdøingsgjeld i innlandet, gitt at dagens habitatmengder i omgivelsene langs kyst-innlandsgradienten er like. Videre tyder resultatene på at de middels spesialiserte artene kan være ekstra sårbare for fragmentering sammenlignet med de andre spesialiseringsgruppene: Antall individer økte med mengden hule eiker i nære omgivelser, artsrikdommen økte med areal av løvskog og historisk hogst påvirket artsrikdommen negativt. Resultatene stemmer overens med en betydelig forsinket respons hos artene når habitat forsvinner. Dette betyr at en mer aktiv forvaltning kan være nødvendig for å unngå framtidig tap av arter som følge av en utdøingsgjeld. Dagens forvaltning av hule eiker kan få konsekvenser langt inn i framtiden.

Synopsis

Introduction

Species are currently going extinct a thousand times faster than expected from the natural background rates (Millennium Ecosystem Assessment 2005). The rapid loss of species could suggest that we are entering a new mass extinction, only known to have occurred five times previously in the history of Earth (Barnosky et al. 2011). Globally, land use change is the strongest driver, causing habitat loss and fragmentation of the remaining landscapes (Andrén 1994, Millennium Ecosystem Assessment 2005), although other major drivers of biodiversity change include climate change, nitrogen deposition and invasive species (Sala et al. 2000). A range of important ecosystem services are provided by species and are essential for human well-being (Millennium Ecosystem Assessment 2005), and maintaining biodiversity is essential for the resilience of these ecosystem functions (Oliver et al. 2015).

The species' responses to the environment is likely to be scale-dependent and species-specific (Wiens 1989, Jackson and Fahrig 2015), but the spatial scales of response are unknown for many species, and conducting multiple single-species studies can be demanding and difficult (Jackson and Fahrig 2015). Furthermore, several recent studies have shown that past habitat loss can have substantial impact on current communities (Helm et al. 2006, Kuussaari et al. 2009, Sverdrup-Thygeson et al. 2014a). When populations are not in equilibrium with their environment due to past habitat loss or disturbances, species can be expected to become extinct locally even if no more habitat is lost, a phenomenon known as extinction debt (Kuussaari et al. 2009). Multi-scale studies and knowledge of the relevant habitat history can therefore be essential in understanding current species responses in fragmented landscapes (Kuussaari et al. 2009).

Vulnerability to extinction by habitat loss and fragmentation varies with species traits (Henle et al. 2004), and several studies have found that species with specialised food or habitat requirements are more vulnerable than generalist species (Henle et al. 2004, Benedick et al. 2006, Nordén et al. 2013, Slatyer et al. 2013). Therefore, grouping ecological similar species with shared species traits (Henle et al. 2004, Franzén et al. 2012) can be beneficial for conservational purposes where the goal often is to conserve multiple species within the same landscape.

Veteran trees are important habitats for a range of species (Hultengren et al. 1997, Butler et al. 2002, Dudley and Vallauri 2004), but they are declining on a global scale (Gibbons et al. 2008, Lindenmayer et al. 2012, Lindenmayer et al. 2014). Veteran trees are often keystone structures in landscapes with a disproportionate large effect on ecosystems relative to the small area they occupy (Manning et al. 2006, Gibbons et al. 2008, Lindenmayer et al. 2012). In Northern Europe, oaks (*Quercus* spp.) are one of the most important trees for biodiversity (Hultengren et al. 1997, Siitonen and Ranius 2015). As oaks grow old, a range of microhabitats develop that are not present on younger trees, such as coarse bark, dead branches and cavities in the trunk. Cavity bearing oaks are normally more than 200 years old (Ranius et al. 2009) and a hollow develops over time by the help of wood-decaying fungi and insects. Inside the cavity wood mould accumulates that consists of decaying wood and fungi that mix with remnants from bird nests, bird droppings, dead insects and other detritus (Sverdrup-Thygeson 2009). Many invertebrates live in this wood mould (Hultengren et al. 1997, Siitonen and Ranius 2015), but the cavities also provide shelter and nesting sites for birds and bats (Bütler et al. 2013).

Hollow oaks are hot-spots for rare and red-listed species (Hultengren et al. 1997, Sverdrup-Thygeson 2009, Direktoratet for naturforvaltning 2012), and one of the large and important groups associated with hollow oaks are the deadwood-dependent (saproxylic) beetles (Sverdrup-Thygeson 2009, Siitonen and Ranius 2015). Several factors on different spatial scales have been found to have an affect on the species richness of beetles in these communities: On the tree scale, size of the oaks (Ranius and Jansson 2000, Buse et al. 2008, Sverdrup-Thygeson et al. 2010, Buse et al. 2016), on a local scale the openness around the oaks (Ranius and Jansson 2000, Widerberg et al. 2012, Gough et al. 2014), and on several scales the amount of dead-wood and connectivity (Franc et al. 2007, Sverdrup-Thygeson et al. 2010, Bergman et al. 2012). Microclimate with high sun-exposure and higher temperatures has also been found to have positive effects on the species richness (Vodka et al. 2009, Müller et al. 2015). Still, there is limited knowledge of how the response of the overall oak community compares to the response of the more specialised or vulnerable species groups at multiple spatial scales (but see Franc et al. 2007). As species dependent on long-lasting and stable habitats can be expected to have low dispersal rates (Nilsson and Baranowski 1997, Hedin et al. 2008), it is possible that species highly dependent on old oaks are more vulnerable to fragmentation and habitat loss than species with broader habitat preferences (Slatyer et al. 2013).

Objectives

To conserve the high species richness dependent on hollow oaks, we must have knowledge of how the environment affects the communities and whether some groups are more vulnerable to habitat loss and fragmentation than others. The aim of this thesis was therefore to increase the knowledge of how saproxylic beetles in old oaks with different oak-dependency respond to the surroundings on different spatial scales, and if other drivers such as climate and past habitat loss also affect these communities. We focused on the species richness, abundance and species composition of beetles in hollow oaks and categorised the species according to oak-association, to test if species with narrower habitat preferences responded differently to their environments than species with a broader host-tree range. We also included trophic level and red-listed status in one of the papers (Paper II). A proxy representing historical logging-pressure was included in two of the papers to investigate whether the species are responding to past habitat densities.

We specifically asked the following questions:

1) How is summer temperature and precipitation affecting species richness, abundance and species composition in hollow oaks? (**Paper I, III-IV**)
2) How is species richness and abundance of beetles in hollow oaks affected by patch size, habitat quality and small-scale isolation? Are different oak-association groups, trophic levels and red-listed species differently affected? **(Paper II)**
3) Is historical logging of oak affecting the species richness, abundance and species composition of beetles in hollow oaks today? (**Paper III, IV**)
4) How are abundance, species richness and species composition in hollow oaks responding to the surroundings on different spatial scales? (**Paper III, IV**)

In all papers, we addressed these questions both for the overall species richness, abundance or species composition, as well as for the different oak-association groups.

Methods

Study system and insect sampling

Oak is a temperate deciduous tree with a wide European distribution, reaching its northern distributional limits in northwestern Norway, with two species naturally occurring in Norway and Sweden, the pedunculate oak (*Quercus robur*) and the sessile oak (*Q. petraea*). The pedunculate oak is most common, and the sessile oak is more restricted to warm coastal areas (Hultengren et al. 1997, Direktoratet for naturforvaltning 2012). Still, old oaks generally have a fragmented distribution where they occur in forests, agricultural and urban landscapes. In our study, we sampled beetles in old oaks (*Q. robur* and *Q. petraea*) with a visual hollow for all the papers. The oaks were situated in southern Norway (Paper I-IV) and southern Sweden (Paper I).

To sample beetles in hollow oaks we used flight interception traps with one trap placed in front of the cavity opening (Paper I-IV) and one in the canopy (Paper II-IV) (Sverdrup-Thygeson 2009, Sverdrup-Thygeson et al. 2010) (Figure 1). The traps collected insects throughout the summer and were emptied once a month. The sampled beetles were then identified and categorized according to oak-association (Paper I-IV), trophic level (Paper II) and red-listed status (Paper II, IV). We defined *oak specialists* as species preferring oak or occurring only on oak, *oak semi-specialist* as species occurring only on broadleaved trees in addition to oak, and *oak generalists* as species occurring on coniferous trees in addition to oak. In Paper I only two categories were used, and semi-specialist were merged with oak generalists. This classification was based on Dahlberg and Stokland (2004). Species that were not associated with oak were excluded for further analyses.

Figure 1 Two flight-interception traps were placed on each hollow oak, one in front of the cavity opening and one in the canopy.

Description of each study

Paper I

In this study, we wanted to investigate how beetles in hollow oak respond to current summer climate as this can give valuable information on how the species are likely to respond to expected climate change. We therefore used an extensive dataset of beetles from 308 hollow oaks from 105 sites situated along a climatic gradient from southern Sweden to southwestern Norway (Figure 2). Sites along this gradient spanned 700 km and had a difference in summer temperature of 4^{o}C

(12.5−16.9ºC) and difference in summer precipitation of 620 mm (178−798 mm), or 303 mm without the two westernmost sites (Figure 2). All oaks were sampled for one year only in the period 1999−2013. In the statistics, we included 152 oak-associated species from families represented in both the Swedish and Norwegian datasets, and therefore comparable along the gradient. As the geographic range of a species can indicate the climate regime it is adapted to, we grouped the species according to geographic distribution into: *Southern species* defined as occurring primarily in southern Europe (south of ~47 degrees N), *Northern species* as occurring primarily in the north of Europe (north of ~50 degrees N), and *Widespread species* were the remaining species that did not fall into either group.

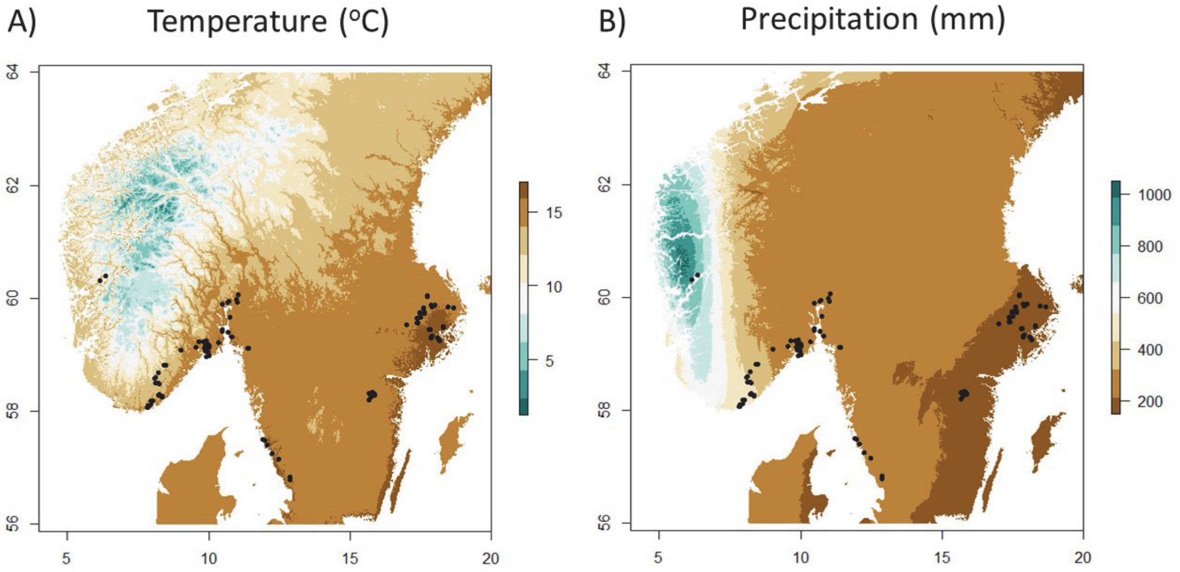

Figure 2 The climate gradient and location of the study sites (n = 105) used in **Paper I**. A) Mean temperature during warmest quarter of the year, and B) mean precipitation during the warmest quarter of the year. Climate data was downloaded from BIOCLIM (Hijmans et al. 2005). Axes are longitude and latitude. Adapted from **Paper I**.

In addition to summer temperature and precipitation, we included circumference of the oaks and openness around the oaks as predictor variables in generalised linear mixed-effects models (GLMMs). We used species richness in each group as the response variable and country (Norway/Sweden) and site as random effects.

Paper II

In this study, we investigated the effect of habitat size, quality and isolation on beetles in hollow oaks in relation to oak-association, trophic guild and red-listed status. We included one-year data from 40 hollow oaks from forests (n = 20) and agricultural landscapes (n = 20) collected in the period 2004–2013 in Norway (Figure 3). Half of the oaks were locally isolated with no or few other oaks nearby (*high isolation*), whereas the other half were situated in areas with close distance (<200 m) to at least four other hollow oaks (*low isolation*). We used the amount of dead branches in the tree crown and circumference as proxies for *patch size*. The tree form and openness around the oak were used as proxies for *habitat quality*, and the beetles were expected to prefer trees with low wide tree crowns and open surroundings (Widerberg et al. 2012). The species were categorized according to red-list status (Kålås et al. 2010) and trophic guild, mainly based on Koehler (2000) and the BugsCEP database (Buckland and Buckland 2006). The following trophic groups were used: *xylophage* for species eating wood, *xylomycetophage* for species dependent on wood and fungi, *fungivore* for species only eating fungi, *predator* for predatory species, and *mixed feeding group* for other species (mainly omnivores). The optimal models best explaining the species richness of the different groups were found by backward elimination of GLMMs with geographical position (Universal Transverse Mercator (UTM) coordinates) used as a random effect. For analyses of the abundances, we used backward elimination of linear mixed models (LMMs) on log-transformed abundances. For the LMMs the random effects had to be categorical, and a commonly used categorical variable ('entomological region') was used that reflects the sampling region for insects in Norway.

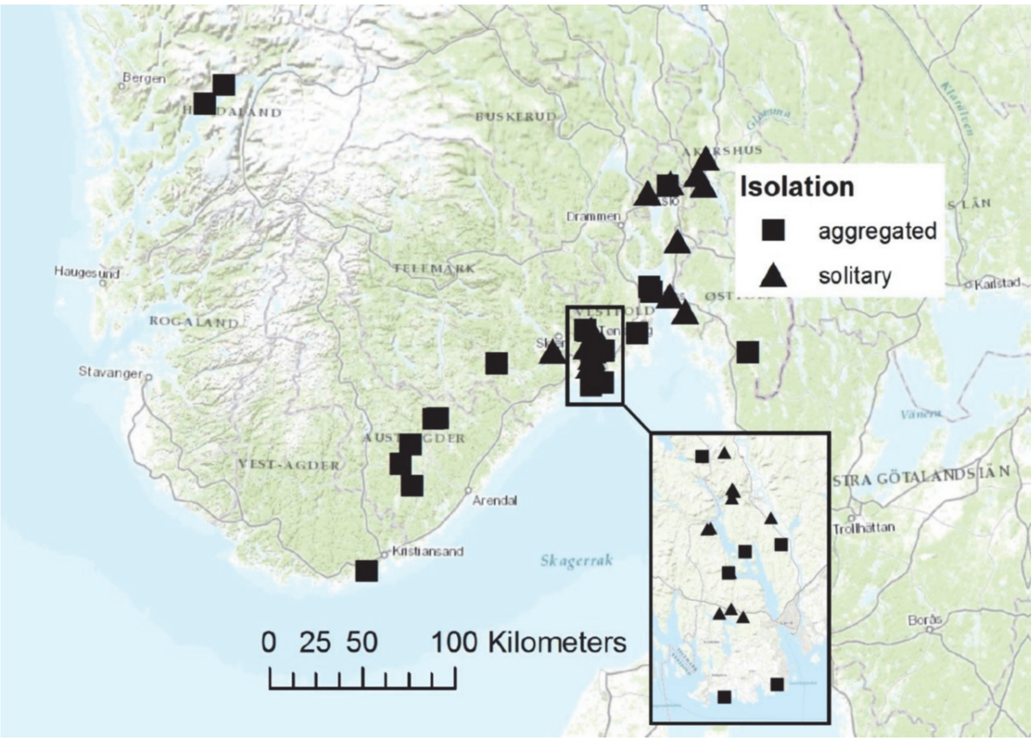

Figure 3 Location of the hollow oaks (*n* = 40) in southern Norway included in **Paper II**. The symbols show isolation category: solitary (*high isolation*) and aggregated (*low isolation*). Adapted from **Paper II**.

Paper III - IV

In these two studies, we sampled beetles along a coast-inland gradient in two regions, Agder and Larvik, in Southern Norway (Figure 4) to study the change in species richness and abundance (Paper III), and species composition (Paper IV) along this gradient. We selected oaks along a coast-inland gradient spanning 40 km inland to use the gradient as a proxy for historical logging pressure, although the gradient also represented changes in climate with warmer and dryer climate along the coast. Norway used to have large oak forests along the southern coastline, but the introduction of the gate saw in the 1520s set the scene for large-scale logging (Central Bureau of Statistics of Norway 1977, Moore 2010). Timber transport was difficult and the easily-accessible oaks along the coast were therefore logged first and logging happened later inland (Vevstad 1998), creating a gradient in the onset of large-scale logging. Due to coastal settlements and cities, the land-use pressure has in general also been more continuous along the coast. We therefore used distance to coast (km) as a proxy for historical logging pressure and intensity, with sites along the coast assumed to have been logged earlier and in general exposed to higher land-use pressure than inland oaks (Figure 5). We included 32 oaks along this gradient with 16 oaks in each region. Approximately half of the oaks were situated in semi-natural landscapes (*n* = 15) and the other half in forests (*n* = 17) (Figure 4). We sampled beetles through two summers in 2013 and 2014. We included variation on the tree, local and landscape scale by registering tree variables and the close surroundings (42 × 42 m) in the field and extracting information of the surroundings on a 2-km landscape scale by using available databases (Norwegian Environment Agency 2015, NIBIO 2016) (Figure 5). We used correlation tests to identify how the variables changed along the gradient (Pearson's r) and backward elimination of generalised linear models (GLMs) to find the optimal models for species richness and abundance (Paper III). To determine the relative importance of the environmental variables on different spatial scales in structuring the species composition, we used variation partitioning techniques and partial constrained correspondence analyses (CCAs) (Økland 2003) (Paper IV). To separate the effects of sampling region and distance to coast, a categorical coast-inland variable was included.

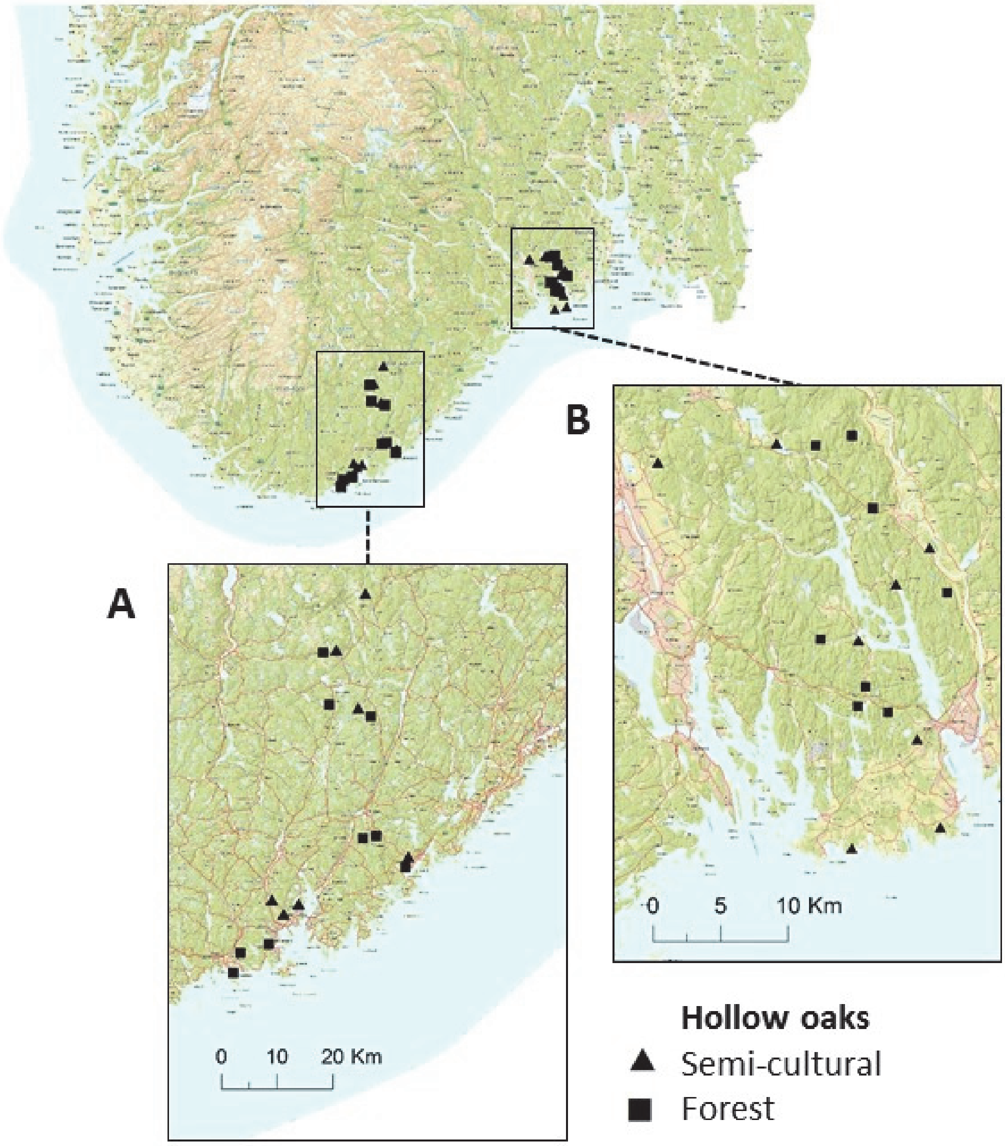

Figure 4 Locations of the sampled hollow oaks (*n* = 32) included in **Paper III-IV**. The oaks were sampled along a coast-inland gradient in southern Norway, representing historical logging intensity and changes in climate. The hollow oaks were situated in forests and semi-natural landscapes (squares and triangles) in the Agder (A) and Larvik (B) regions. Adapted from **Paper III**.

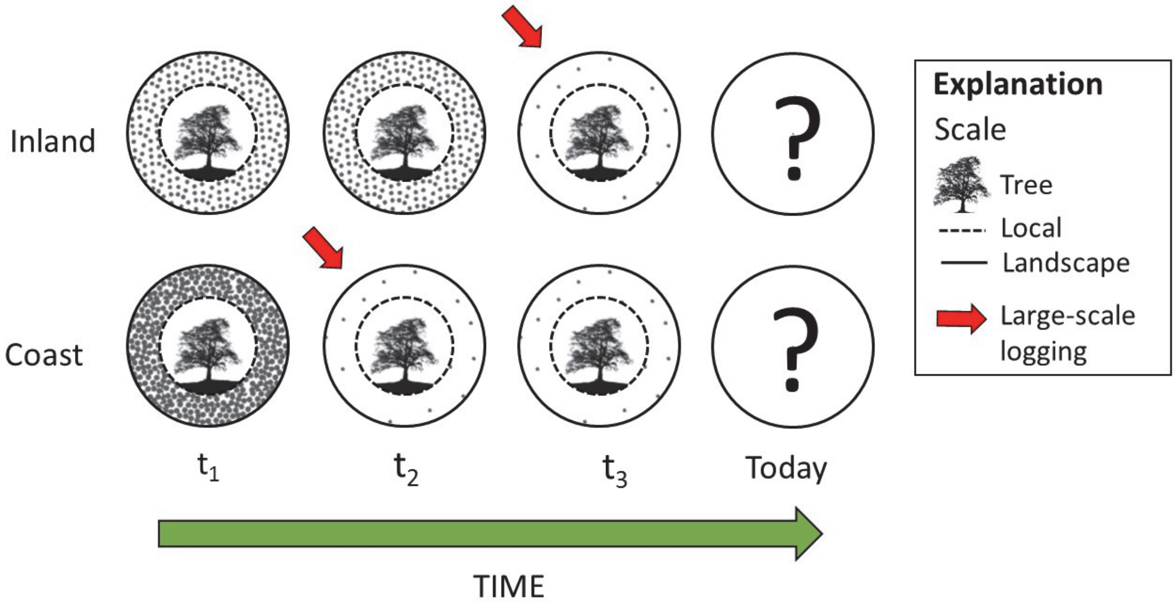

Figure 5 Study design and logging history of oak in southern Norway. Hollow oaks (*n* = 32) were selected along a coast-inland gradient used as a proxy for historical logging intensity and duration. We included variables on the tree, local and landscape scale. The number of grey dots reflects oak density. Before large-scale logging (t_1) there were large oak forests along the coast and a high density of mature and old oaks, but naturally lower abundance inland due to colder climate. After the introduction of the river saws the coastal areas were logged (t_2), whereas the inland areas were logged later due to their inaccessibility and log-floating challenges (t_3). Today the distribution of mature and old oaks are fragmented and scattered in the landscape along both the coast and inland, but the exact densities and their impact on associated species are not known. In our study, the hollow oaks' distance to the coast was therefore used as a proxy for historical logging intensity with variables on the tree scale, local scale and landscape scale to identify current habitat differences. The start of large-scale logging of oak is indicated by a red arrow along the coast and inland.

Main results

Paper I

We found that the species richness of all three specialist groups responded to climate, but none of the generalists were affected (Figure 6). The Northern Specialists (*n* = 6) were positively affected by increased summer temperatures, whereas the Southern (*n* = 24) and Widespread Specialists (*n* = 7) were negatively affected by increased summer precipitation. Tree circumference had a positive effect on most of the groups, but the Southern Specialists and Widespread Generalists (*n* = 12) did not have a significant response. The openness around the oaks did not affect any of the groups (Figure 6).

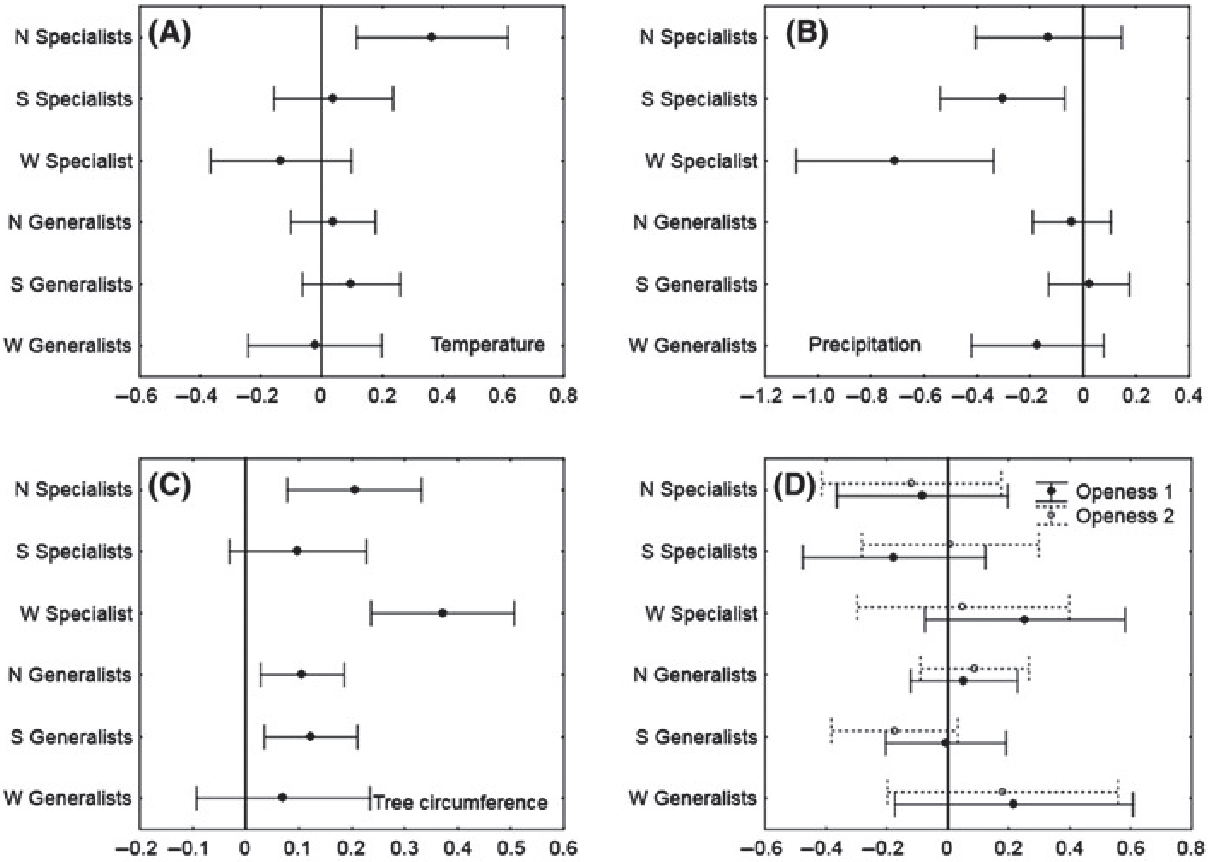

Figure 6 Partial regression coefficients (with 95% CI) from six regression models, one for each species group (Generalist and Specialists divided into Northern (N), Southern (S), and Widespread (W) species). In the models, the richness was predicted by summer temperature (A), summer precipitation (B),

Figure 6 continued: hollow oak circumference (C), the openness of the immediate surroundings of a tree (D); 1 = partly closed canopy, 2 = closed canopy, 0 = open canopy, used as the baseline in model estimates. Adapted from **Paper I**.

Paper II

When solitary and aggregated oaks with varying patch size and habitat quality were compared, the species richness only responded to habitat quality, represented by low and intermediate tree form. Species richness of red-listed species, oak specialists, xylomycetophages and the mixed feeding group, however, did not have a significant response to any of the variables (Table 1). Only the abundances responded to patch size and isolation. Patch size, represented by circumference and dead branches in the tree crown, had a positive effect on eight of the ten groups, and only the predators and mixed feeding group did not respond. The response to openness (characterised by presence of surrounding shrubs or trees) was mixed: predators and the mixed feeding group preferred shrubs, and xylomycetophages preferred open surroundings. Species richness did not differ between solitary oaks and aggregated oaks for any groups, but high isolation had a negative effect on the abundances of xylomycetophages and semi-specialists (Table 1).

Table 1 Effect of patch size, habitat quality and isolation on species richness and abundance of beetles in hollow oaks in relation to red-listed status, trophic guild and oak-association. Adapted from **Paper II**.

	Patch size		**Habitat quality**		**Isolation**
	Circum.	Dead branches high/inter. vs. low	Tree form low/inter. vs. high	Openness tree/shrub vs. open	high vs. low
SPECIES RICHNESS					
Red-listed species		(+)[a]			
All oak species			+		
Trophic level					
Xylophage	(+)[a]		+		
Xylomycetophage		(+)[a]			(−)[a]
Fungivore			+		
Predator			+		
Mixed feeding					
Oak association					
Specialist					
Oak semi-specialist			+		
Generalist			+		
ABUNDANCE					
Red-listed individuals	+				
All oak individuals	(+)[b]	+			(−)[b]
Trophic level					
Xylophage	+	+	+		
Xylomycetophage	+	+	+	−	−
Fungivore		+	(+)[a]		
Predator				+	
Mixed feeding				+	
Oak association					
Specialist	+				
Oak semi-specialist		+			−
Generalist		+		(+)[a]	(−)[b]

Table 1 continued: Only the strongest trend is shown for variables with several levels. Significant effects ($p<0.05$) are indicated with a + or − only, whereas the non-significant variables ($p>0.05$) kept in the optimal models are given with the corresponding p-values. For full details, see supplemental material of Paper II. *Explanation*: Circum, circumference, Inter., intermediate, a, $0.1>p>0.05$, b, $0.15>p>0.1$

Paper III

Along the coast-inland gradient, we found that the coastal areas were warmer, had less summer rain, higher forest volume per hectare and less area of old forest than the inland sites, although only temperature remained significant when the Agder and Larvik region was evaluated separately (Paper IV). The species richness of all groups except the specialists increased inland, indicating a response to historical logging. In addition, circumference on the tree scale and cover of deciduous forest on the landscape scale had a positive effect on the species richness of all beetles, the specialists (responded to circumference) and semi-specialists (deciduous tree cover) (Table 2). The total beetle abundance also increased inland, although only the tree scale and local scale were important for the different specialisation groups (Table 2). All groups except the oak semi-specialists were positively affected by tree circumference and negatively affected by low and middle tree forms. The semi-specialists only responded to the number of hollow oaks on the local scale, while the local forest density had a negative impact on the abundance of the oak specialists and all beetles.

Table 2 Summary of the optimal models for species richness and abundance of oak-associated beetles in hollow oaks in southern Norway. Only variables kept in the models are shown and their positive or negative response is indicated. Non-significant variables ($p > 0.05$) are shown in brackets. *Abbreviations*: Circum = circumference; Tree form = low and middle vs. high (base line level); Decid = deciduous forest; Dist = distance to coast (km), used as a proxy for the historical logging intensity and duration. Adapted from **Paper III**.

	Tree		**Local**		**Landscape**	**Coast-inland gradient**
	Circum.	Tree form low/middle	Forest density	Hollow oaks	Decid.	Dist.
Species richness						
All beetles	+				+	+
Oak generalists					(+)	+
Oak semi-specialists					+	+
Oak specialists	+					
Abundance						
All beetles	+	−	−			+
Oak generalist	+	−				
Oak semi-specialists		(−/+)		+		
Oak specialists	+	−	−			

Paper IV

The tree scale appeared as the most important scale for species composition of all beetles, generalists and specialists, explaining 47-67% of the explained variation. Depth of bark crevices was important for all these groups, whereas bryophyte cover on the stem affected the species composition of all beetles and the generalists; wood mould only influenced the specialists. The semi-specialists however, did not respond on this scale. The species composition of all beetles and the generalists had similar response to the environmental variables (Figure 7 A-B), probably due to the numerical dominance of the generalists in the all beetles dataset. These two group responded to the local scale with effect of surroundings (forest or semi-natural landscape) and tree density for generalists. Half of the species (*n* = 101) were only found in one of the two sampling regions and sampling region therefore affected the species composition of all groups, but the effect was largest for the semi-specialists where it accounted for more than half of the total variation explained (Figure 7). The semi-specialists differed from the other groups by only responding to the coast-inland gradient and sampling region. Inspections of CCA plots showed that several of the semi-specialist species in our study were restricted to coastal and inland sites in each region (see Paper IV). The proportion of red-listed species (*n* = 27) increased with the specialisation level of the beetles, with most red-listed species being either semi-specialists or specialists. Landscape variables were not important in explaining the species composition for any of the groups.

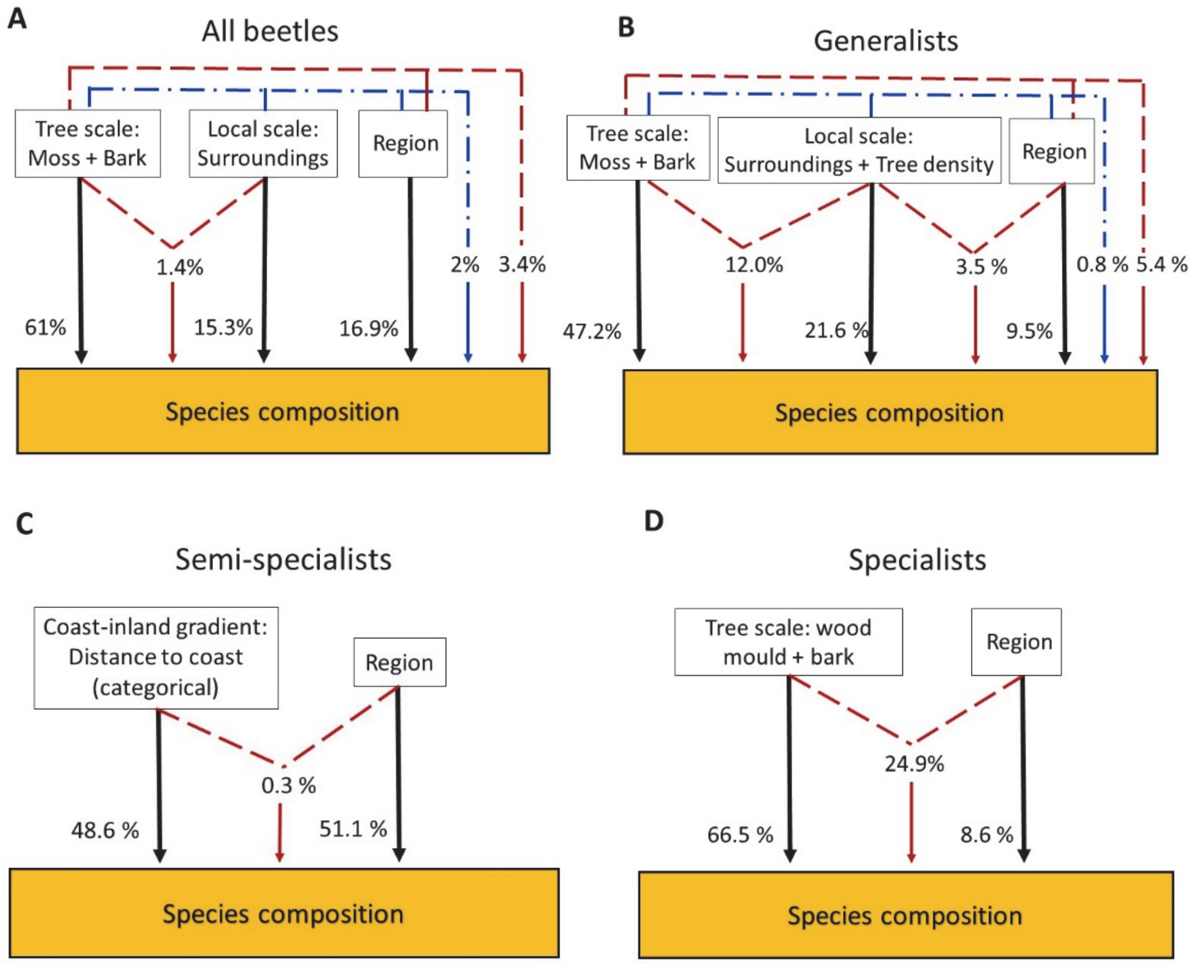

Figure 7 Relationship between species composition and relative amount of variation explained by different sets of environmental variables in partial constrained ordination (CCA). Only variables with a significant independent contribution ($p<0.05$) were included and percentage of variation explained is shown for A) all beetles, B) generalists, C) semi-specialists and D) specialists. *Explanation*: Variation explained by one set of variables is shown with solid black lines and shared explained variation is shown with dashed lines. Red lines represent variation shared between two sets of variables and blue lines represent variation shared between three sets of variables. Moss = cover of bryophytes on the stem (see Table 1). Adapted from **Paper IV.**

Discussion

We found that the oak-dependency of the species affected their responses to climate, historical logging, habitat quality and amount on different spatial scales (Paper I-IV). A general trend was that variables on the tree scale were important for the communities in hollow oaks, regardless of whether the species richness, abundance or species composition was studied, although there was variation in which groups responded and to which characteristics of the tree they responded to (Paper I-IV). Climate only affected the specialist species, with positive effect of higher summer temperature on a small group, and negative effects of precipitation for the remaining specialists (Paper I), but no response to climate was found along the coast-inland gradient (Paper III-IV). The species richness responded on a larger spatial scale than the population sizes, which were more controlled by local conditions of the tree and close surroundings (Paper III). The species richness increased inland for all groups except the specialists, and hence our results indicate that historical habitat loss likely affects most of the oak-associated species in our study areas (Paper III). When we studied species composition (Paper IV), new patterns were revealed compared to the species richness and abundance studies (Paper I-III): we found regional differences in the species composition for all groups and new variables on the tree scale to influence the species composition, with effect of bark type, bryophyte cover and wood mould. Furthermore, the response in species composition of all beetles was dominated by the generalists and this overshadowed important responses of the semi-specialists and specialists. Hence, we show that including species identities can reveal new patterns important to management, not easily revealed by studying species richness and abundance alone.

Only specialists are affected by climate

Climate change is an important threat to biodiversity, and likely to become one of the strongest drivers of biodiversity change by the year 2100 (Sala et al. 2000). In Paper I we sampled beetles along a climatic gradient from southern Sweden to western Norway representing a 4°C increase in summer temperature, comparable to the predicted global rise in temperature by the end of the century (Thuiller 2007, IPCC 2013). We had expected positive effects of higher temperature to benefit all beetles, as temperature has been found to increase the saproxylic species richness in other studies (Gossner et al. 2013a, Müller et al. 2015, Seibold et al. 2016), but only a small group of specialists with northern distribution responded positively to the increased temperatures along the climatic gradient (Paper I). Summer precipitation on the other hand had a negative impact on the remaining groups of southern and widespread specialists, although the generalists did not respond to any of the climate variables. Similarly, none of the species group responded to a change of 2.6°C and 180 mm summer rain along the coast-inland gradient in southern Norway (Paper III-IV). Gossner et al. (2013a) found that the effect of summer temperature and precipitation on beetles attracted to fresh deadwood of beech and spruce varied with trophic guild, and that the response to precipitation was mixed. Increased precipitation is likely to reduce the flight time and dispersal distances of the species, as insects are likely to avoid flying when it is raining (Klueken et al. 2009). As hollow oak ecosystems are very complex and changes in moisture is also likely to affect other oak-associated species of fungi, lichens and bryophytes, this could cause indirect effects on the beetles. For example, many beetles are dependent on fungi or fungi-infested wood (Paper II) and bryophyte cover on the stem can be a determining factor for the species composition (Paper IV).

Our findings show that the species richness in hollow oaks to a lesser degree can be explained by climate, with only specialists responding to a considerable change in temperature and precipitation (Paper I, III). As species in hollow oaks are likely to experience a more stable microclimate than the ambient surroundings or small pieces of deadwood (Siitonen and Ranius 2015, Pilskog et al. unpublished material), it could potentially buffer against some of the climatic changes. However, the more specific habitat requirement of the specialists could make them more vulnerable to environmental change. Different species composition of semi-specialists between coastal and inland sites could indicate that some species are restricted to the warmer coastal sites in our study regions in Norway (Paper IV). In light of climate change, our results indicate that the temperature increase predicted to occur by 2100 could benefit a small group of specialists with northern distribution, although most specialists are likely to decline due to increased precipitation. The most specialised species are already severely affected by the decline of large hollow trees both in Scandinavia and globally (Naturvårdsverket 2004, Gibbons et al. 2008, Lindenmayer et al. 2014, Sverdrup-Thygeson et al. 2014b). Hence, halting the decline of large oaks is important to conserve the most vulnerable species and to avoid synergic effects of climate change and habitat loss.

Tree and local scale

Patch size and habitat quality

In paper II, circumference and dead branches in the tree crown were used as proxies for patch size, and tree form and openness were used as proxies for habitat quality of wood living beetles. In this paper, we found that only habitat quality (tree form) affected the species richness regardless of functional group, although some groups did not respond to any variables. The abundances responded to both patch size and habitat quality. However, when the same variables were included in Paper III, this pattern changed slightly: habitat quality represented by tree form was now only influencing the abundances, and patch size had effect on both the abundances and species richness of all beetles and the specialists. This means that both patch size and habitat quality are likely to be important predictors of species richness and abundance of wood living beetles.

Tree size has been found to increase species richness of beetles in old oaks in several studies (Ranius and Jansson 2000, Sverdrup-Thygeson et al. 2010, Gough et al. 2014, Buse et al. 2016). Patch size was one of the most important variables to the specialists influencing species richness and abundance (Paper I-III). Large trees make room for more individuals and species, but the number of microhabitats also tend to increase with size (Sverdrup-Thygeson et al. 2010, Siitonen and Ranius 2015). This was also evident in our study where large oaks tended to have more wood mould and deeper bark crevices (Paper IV). The species richness and abundance always had a positive response to size of the tree (Paper I-III), but the response to tree form and openness (used as proxies for habitat quality), diverged between the studies (Paper II-III). The tree form indicates whether the tree has grown in open or closed conditions, and therefore both tree form and openness can be related to past or current sun-exposure that is likely to affect the microclimate in the oaks. Microclimate is important to saproxylic beetles, and several studies have found higher temperatures or open conditions to be positive for saproxylic species richness in deadwood and hollow oaks (Ranius and Jansson 2000, Widerberg et al. 2012, Müller et al. 2015, Seibold et al. 2016). As many saproxylic beetles in hollow oaks are flower-visiting as adults, it is possible that the preference for open surroundings found by many authors also could be linked to higher flower densities where sun-exposure is high (Bouget 2005). Sverdrup-Thygeson et al. (2010) found hollow oaks in parks and forests to have a different species composition of beetles and, similarly, Seibold et al. (2016) found the species composition to change between deadwood in sunny and shady forest plots. In our study, we found species composition of generalists to differ between oaks in semi-natural habitats and forests (Paper IV). It is possible that the positive effects of high tree form in Paper III therefore reflects the species' preference for forest surroundings rather than preference for shade. This was also supported by the negative response in the abundance of all beetles and specialists to forest density in the same study (Paper III), although we acknowledge that some species also can prefer shade (Seibold et al. 2016). We probably favoured forest species by including hollow oaks in forests and in the transition zone between agricultural landscapes and forests (semi-natural landscapes), but not including wide-branched agricultural trees that typically have low tree form and can be expected to have different species assemblies compared to forest oaks (Sverdrup-Thygeson et al. 2010).

When species composition was investigated, we found cover of bryophytes and depth of bark crevices to be important determinants of species composition (Paper IV). To our knowledge, these variables have not previously been found to be important in structuring the beetle communities in hollow oaks. Deep bark crevices is a characteristic associated with large and old oaks (Ranius et al. 2008b) and the oaks in our studies with coarse bark were characterised by large circumference, low or intermediate tree form and more wood mould (Paper IV). Hence, the response to bark type could possibly represent an overall response to changes in microhabitat diversity, although the bark itself is also likely to represent habitat for some species.

In conclusion, we found tree characteristics in general to be important to species richness, abundance and species composition, and both patch size and habitat quality affects the species richness and abundances of beetles in hollow oaks.

Small-scale isolation

Although small-scale isolation did not affect most species groups when solitary and grouped oaks were compared, the abundance of two groups, the semi-specialists and the species feeding on both wood and fungi (xylomycetophages), were negatively affected (Paper II). Similarly, the semi-specialists were the only group that responded to number of hollow oaks in their close surroundings (local scale) along the coast-inland gradient (Paper III). Both groups are quite specialised in their habitat requirements: the xylomycetophages are dependent on wood and fungi and the semi-specialists are restricted to deciduous host trees. This high degree of specialisation could make them especially vulnerable to habitat loss and fragmentation (Nordén et al. 2013, Slatyer et al. 2013). The lack of response in the specialists and red-listed species could indicate that they respond on larger spatial scales (Franc et al. 2007, Ranius et al. 2011) or that the difference between the low and high isolation sites were too small (Götmark et al. 2011). In a similar study, Buse et al. (2016) found negative response in the abundance of predators to small-scale isolation (low connectivity within 50 m), but the wood feeding species had an opposite response, possibly due to more open surroundings and higher sun-exposure for isolated oaks (Buse et al. 2016). Although most groups did not respond to the small-scale isolation in our study, others have found connectivity at various scales to be important for beetles in hollow oaks (Ranius 2002, Ranius et al. 2011, Bergman et al. 2012) and some rare species require high connectivity (Ranius 2002). The most vulnerable species could therefore have disappeared already from many of our sites.

Semi-specialists and specialists respond differently to the environment

Overall, the semi-specialists seem to be vulnerable to isolation and fragmentation on the local and landscape scale as they were the only oak-association group that responded to connectivity of oaks in their close surroundings (Paper II-III), but also responded positively to deciduous forest on the landscape scale (Paper III). This is in contrast to the specialists that did not respond to connectivity of hollow oaks or any landscape variables (Paper II-IV). For the specialists the tree scale was the most important scale of response, influencing species richness (Paper III), abundance (Paper II-III) and species composition (Paper IV). The semi-specialists on the other hand only responded to amount of dead branches on the tree scale (Paper II). This demonstrates that although the two groups are restricted in their host-preferences, their responses to the environment are very different. While the specialists seem to be highly dependent on tree characteristics, the semi-specialists are mostly affected by environmental variables on larger spatial scales that indicate vulnerability to fragmentation. The semi-specialists' response fits well with Seibold et al. (2015) that found higher extinction risk for saproxylic beetles depending on broad-leaved trees. The low number of species in the specialist group could make it more difficult to reveal their response to connectivity, as our connectivity measures on larger scales were quite coarse (Paper III-IV). Still, the specialists seem to depend on large veteran oaks of high quality, and in light of the fragmented distribution of this habitat in our regions (Direktoratet for naturforvaltning 2012) and the high proportion of red-listed species in this group (Paper IV), it is likely that this group is also vulnerable to fragmentation and isolation.

Landscape and regional effects

In Paper III-IV, we included variables on a 2 km landscape scale and found that deciduous forest cover was positive for the species richness of all beetles and the semi-specialists, but a non-significant response also remained in the optimal model of the generalists (Paper III). This indicates that abundances and species richness are affected by different spatial processes: population sizes appear to be mainly controlled by the local resources of the tree and close surroundings, but larger areas of suitable habitat are needed to maintain populations through time. This is in line with metapopulation theory, that a network of habitat patches and populations is necessary for species to persist through time (Hanski 1998). As the semi-specialists cannot use coniferous trees, they are likely to experience higher isolation than species that can use the deadwood of pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*), which together dominate the forests in our sampling regions (Tomter and Eriksen 2001, Tomter et al. 2001, Eriksen et al. 2006). A 2 km landscape scale has been found to be important to species richness in other studies (Bergman et al. 2012, Jacobsen et al. 2015), although the characteristic scale of response for individual species in hollow oaks can vary greatly (Bergman et al. 2012).

In Paper III-IV, we sampled in two regions and there could be regional differences in climate, surrounding landscapes or habitat history influencing the beetles in hollow oaks. Although sampling region did not affect species richness (Paper III), it influenced the species composition of all groups with a considerable proportion of the species being unique to only one of the regions (Paper IV). This show that important patterns emerge when the identities of the species are included, as these patterns were not revealed by studying species richness and abundance alone. Some of the differences could be due to changes in forest variables and climate along the gradient in the two regions, but local forest history is probably also important. For instance are oaks in Larvik in general larger than in Agder (but not different in our study) (Tomter and Eriksen 2001, Tomter et al. 2001, Eriksen et al. 2006), probably a result of different oak management in the past.

Historical logging is influencing the species richness in hollow oaks

That logging affects saproxylic species negatively is well documented (Siitonen 2001, Müller et al. 2007, Paillet et al. 2010, Gossner et al. 2013b), but several studies indicate that species dependent on old trees or old-growth forest also could be responding to past habitat loss (Ranius et al. 2008a, Buse 2012). In our study, we used a coast-inland gradient as a proxy for historical logging intensity and duration, and in absence of historical logging it would be reasonable to expect higher species richness along the coast, due to a more favourable coastal climate. However, the species richness of almost all groups and the overall abundance increased inland (Paper III). This was in line with our expectations, as the onset of historical large-scale logging started earlier and was more intensive along the coast than inland. Although some of the environmental variables changed systematically along the coast-inland gradient, our results do not indicate these variables to be the cause of the species response (Paper III). We also found the species composition of semi-specialists to change along the gradient with several red-listed species only found in inland sites (Paper IV). This supports the notion that species have gone locally extinct in the coastal areas, and could indicate an extinction debt inland if habitat amount along the gradient is similar today. It is possible that populations in hollow oaks are especially prone to exhibit time-lagged responses as populations of beetles can live many generations within the same oak without needing to disperse (Nilsson and Baranowski 1997, Ranius and Hedin 2001), which could slow down their response to environmental change. The lack of response in the most specialised species to the gradient could possibly indicate that the historical habitat loss lead to rapid local extinctions for this group and that they are in equilibrium with their environment today.

Concluding remarks and management implications

In this thesis, I show that beetles in hollow oaks are affected by variables on different spatial scales, but that the response in species richness, abundance and species composition vary with oak-association and trophic level. Our findings show that veteran oaks in different regions in southern Norway cannot be expected to host the same species assemblages. This means that to conserve the overall diversity of oak-associated beetle species, hollow oaks must be conserved across regional scales, with variation in tree characteristics and surroundings. Still, care should be taken in future studies to identify specialisation levels, as the response of the most vulnerable groups can be overshadowed by more common and abundant species. Both semi-specialists and specialists are likely to host a considerable number of rare species, but they respond differently to their environment. Hence, to benefit both groups, conservation should aim to conserve the large hollow oaks of high quality that is important to the oak specialists, as well as habitat in the close surroundings and at larger scales, found to benefit the semi-specialists. Our results further indicate that historical logging could have considerable impact on current communities in hollow oaks, as we found higher species richness inland for all groups except the specialists (Paper III). If habitat amount in the surroundings are similar inland and along the coast today, this difference could indicate a considerable time-lagged response to past habitat loss. Comprehensive mapping of hollow oaks and other relevant habitat could therefore help to resolve the status of inland populations. Still, the indication of a possible extinction debt could call for a more active management to improve the current habitats and to avoid potential extinctions. This could for instance include veteranisation of oaks (Bengtsson et al. 2012) or artificial hollows (Jansson et al. 2009), although halting the decline of old oaks and secure recruitment should be a main priority. Improving the habitat could also be important to avoid synergic negative effects of habitat loss and increased precipitation for the specialists in light of climate change. In general, we recommend taking habitat history into consideration when investigating long-lasting habitats such as veteran oaks, and our results indicate that actions taken today can affect the oak-associated communities far into the future.

To build on our results and gain further insight into the responses of beetles in hollow oaks, future studies could focus on:

1) Comparing the responses of beetles in hollow oaks to current and historical habitat densities in other countries and regions. This could reveal if

extinction debts are common in hollow oaks in general, and could give valuable directions for how active the managment should be to avoid species loss.

2) The dispersal biology of varying hollow oak-dependent species, for instance by using population genetics. Many species dependent on hollow oaks are assumed to have low dispersal rates and hollow oaks often occur fragmented in the landscape. Hence, identifying how genetically isolated the populations in different oaks are could give valuable information on dispersal patterns between close and distant populatons in hollow oaks, and hence at what scales connectivity is important to different species.

References

Andrén, H. 1994. Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: A Review. – Oikos 71: 355-366.

Barnosky, A. D., Matzke, N., Tomiya, S., Wogan, G. O. U., Swartz, B., Quental, T. B., Marshall, C., McGuire, J. L., Lindsey, E. L., Maguire, K. C., Mersey, B. and Ferrer, E. A. 2011. Has the Earth's sixth mass extinction already arrived? – Nature 471: 51-57.

Benedick, S., Hill, J. K., Mustaffa, N., Chey, V. K., Maryati, M., Searle, J. B., Schilthuizen, M. and Hamer, K. C. 2006. Impacts of rain forest fragmentation on butterflies in northern Borneo: species richness, turnover and the value of small fragments. – J. Appl. Ecol. 43: 967-977.

Bengtsson, V., Hedin, J. and Niklasson, M. 2012. Veteranisation of oak – managing trees to speed up habitat production. – In: Rotherham, I.Handley, C.Samojolik, T. and Agnoletti, M. (eds), Trees Beyond the Wood. Sheffield Hallam University, pp. 1-11.

Bergman, K.-O., Jansson, N., Claesson, K., Palmer, M. W. and Milberg, P. 2012. How much and at what scale? Multiscale analyses as decision support for conservation of saproxylic oak beetles. – For. Ecol. Manage. 265: 133-141.

Bouget, C. 2005. Short-term effect of windstorm disturbance on saproxylic beetles in broadleaved temperate forests: Part II. Effects of gap size and gap isolation. – For. Ecol. Manage. 216: 15-27.

Buckland, P. I. and Buckland, P. C. 2006. BugsCEP Coleopteran Ecology Package. IGBP PAGES/World Data Center for Paleoclimatology Data Contribution Series # 2006-116. NOAA/NCDC Paleoclimatology Program, Boulder CO, USA.(Accessed 11 January, 2013) http://www.bugscep.com

Buse, J. 2012. “Ghosts of the past”: flightless saproxylic weevils (Coleoptera: Curculionidae) are relict species in ancient woodlands. – J. Insect Conserv. 16: 93-102.

Buse, J., Entling, M. H., Ranius, T. and Assmann, T. 2016. Response of saproxylic beetles to small-scale habitat connectivity depends on trophic levels. – Landscape Ecol. 31: 939-949.

Buse, J., Levanony, T., Timm, A., Dayan, T. and Assmann, T. 2008. Saproxylic beetle assemblages of three managed oak woodlands in the Eastern Mediterranean. – Zool. Middle East 45: 55-66.

Butler, J., Alexander, K. and Green, T. 2002. Decaying wood: an overview of its status and ecology in the United Kingdom and Continental Europe. – USDA For. Serv. Gen. Tech. Rep. PSW-GTR-181 11-19.

Bütler, R., Lachat, T., Larrieu, L. and Paillet, Y. 2013. Habitat trees: key elements for forest biodiversity. – In: Kraus, D. and Krumm, F. (eds), Integrative approaches as an opportunity for the conservation of forest biodiversity. European Forest Institute, pp. 84-91.

Central Bureau of Statistics of Norway 1977. Timber Floating 1871-1975. Statistiske analyser. p 79.

Dahlberg, A. and Stokland, J. 2004. Substrate requirements of wood-inhabiting species - a synthesis and analysis of 3600 species. – Skogsstyrelsen, Report 7-04. p 75.

Direktoratet for naturforvaltning 2012. Handlingsplan for utvalgt naturtype hule eiker. – Direktoratet for naturforvaltning.

Dudley, N. and Vallauri, D. 2004. Deadwood – Living forests: The importance of veteran trees and deadwood to biodiversity. WWF Report. pp. 1-19

Eriksen, R., Tomter, S. M. and Ludahl, A. 2006. Statistikk over skogforhold og -ressurser i Vestfold. Landsskogtakseringen 2000-2004. – NIJOS-ressursoversikt 03/06, p 57.

Franc, N., Götmark, F., Økland, B., Nordén, B. and Paltto, H. 2007. Factors and scales potentially important for saproxylic beetles in temperate mixed oak forest. – Biol. Conserv. 135: 86-98.

Franzén, M., Schweiger, O. and Betzholtz, P.-E. 2012. Species-area relationships are controlled by species traits. – PLoS ONE 7: e37359.

Gibbons, P., Lindenmayer, D. B., Fischer, J., Manning, A. D., Weinberg, A., Seddon, J., Ryan, P. and Barrett, G. 2008. The future of scattered trees in agricultural landscapes. – Conserv. Biol. 22: 1309-1319.

Gossner, M. M., Floren, A., Weisser, W. W. and Linsenmair, K. E. 2013a. Effect of dead wood enrichment in the canopy and on the forest floor on beetle guild composition. – For. Ecol. Manage. 302: 404-413.

Gossner, M. M., Lachat, T., Brunet, J., Isacsson, G., Bouget, C., Brustel, H., Brandl, R., Weisser, W. W. and Müller, J. 2013b. Current near-to-nature forest management effects on functional trait composition of saproxylic beetles in beech forests. – Conserv. Biol. 1–10.

Gough, L. A., Birkemoe, T. and Sverdrup-Thygeson, A. 2014. Reactive forest management can also be proactive for wood-living beetles in hollow oak trees. – Biol. Conserv. 180: 75-83.

Götmark, F., Asegard, E. and Franc, N. 2011. How we improved a landscape study of species richness of beetles in woodland key habitats, and how model output can be improved. – For. Ecol. Manage. 262: 2297-2305.

Hanski, I. 1998. Metapopulation dynamics. – Nature 396: 41-49.

Hedin, J., Ranius, T., Nilsson, S. and Smith, H. 2008. Restricted dispersal in a flying beetle assessed by telemetry. – Biodivers. Conserv. 17: 675-684.

Helm, A., Hanski, I. and Pärtel, M. 2006. Slow response of plant species richness to habitat loss and fragmentation. – Ecol. Lett. 9: 72-77.

Henle, K., Davies, K. F., Kleyer, M., Margules, C. and Settele, J. 2004. Predictors of species sensitivity to fragmentation. – Biodivers. Conserv. 13: 207-251.

Hijmans, R. J., Cameron, S. E., Parra, J. L., Jones, P. G. and Jarvis, A. 2005. Very high resolution interpolated climate surfaces for global land areas. http://www.worldclim.org/bioclim (accessed June 2014). – International Journal of Climatology 25: 1965-1978.

Hultengren, S., Pleijel, H. and Holmer, M. 1997. Ekjätter – historia, naturvård och vård. p 32.

IPCC 2013. Summary for policymakers. – In: Stocker, T. F.Qin, D.Plattner, G.-K.Tignor, M.Allen, S. K.Boschung, J.A., N.Xia, Y.Bex, V. and Midgley, P. M. (eds), Climate Change 2013: The physical science basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press,.

Jackson, H. B. and Fahrig, L. 2015. Are ecologists conducting research at the optimal scale? – Global Ecol. Biogeogr. 24: 52-63.

Jacobsen, R. M., Sverdrup-Thygeson, A. and Birkemoe, T. 2015. Scale-specific responses of saproxylic beetles: combining dead wood surveys with data from satellite imagery. – J. Insect Conserv. 19: 1053-1062.

Jansson, N., Ranius, T., Larsson, A. and Milberg, P. 2009. Boxes mimicking tree hollows can help conservation of saproxylic beetles. – Biodivers. Conserv. 18: 3891-3908.

Klueken, A. M., Hau, B., Ulber, B. and Poehling, H. M. 2009. Forecasting migration of cereal aphids (Hemiptera: Aphididae) in autumn and spring. – J. Appl. Entomol. 133: 328-344.

Koehler, F. 2000. Saproxylic beetles in nature forests of the northern Rhineland: comparative studies on the saproxylic beetles of Germany and contributions to German nature forest research. Schrr. LO¨ BF/LAFAO NRW (Recklinghausen) 18: 1–351.

Kuussaari, M., Bommarco, R., Heikkinen, R. K., Helm, A., Krauss, J., Lindborg, R., Öckinger, E., Pärtel, M., Pino, J., Rodà, F., Stefanescu, C., Teder, T., Zobel, M. and Steffan-Dewenter, I. 2009. Extinction debt: a challenge for biodiversity conservation. – Trends Ecol. Evol. 24: 564-571.

Kålås, J. A., Viken, Å., Henriksen, S. and Skjelseth, S. 2010. Norsk rødliste for arter 2010. – Artsdatabanken.

Lindenmayer, D. B., Laurance, W. F. and Franklin, J. F. 2012. Global decline in large old trees. – Science 338: 1305-1306.

Lindenmayer, D. B., Laurance, W. F., Franklin, J. F., Likens, G. E., Banks, S. C., Blanchard, W., Gibbons, P., Ikin, K., Blair, D., McBurney, L., Manning, A. D. and Stein, J. A. R. 2014. New policies for old trees: averting a global crisis in a keystone ecological structure. – Conservation Letters 7: 61-69.

Manning, A. D., Fischer, J. and Lindenmayer, D. B. 2006. Scattered trees are keystone structures – Implications for conservation. – Biol. Conserv. 132: 311-321.

Millennium Ecosystem Assessment 2005. Ecosystems and Human Well-being: Synthesis. – Island Press.

Moore, J. W. 2010. 'Amsterdam is standing on Norway' Part II: The global North Atlantic in the ecological revolution of the long seventeenth century. – Journal of Agrarian Change 10: 188-227.

Müller, J., Brustel, H., Brin, A., Bussler, H., Bouget, C., Obermaier, E., Heidinger, I. M. M., Lachat, T., Förster, B., Horak, J., Procházka, J., Köhler, F., Larrieu, L., Bense, U., Isacsson, G., Zapponi, L. and Gossner, M. M. 2015. Increasing temperature may compensate for lower amounts of dead wood in driving richness of saproxylic beetles. – Ecography 38: 499-509.

Müller, J., Hothorn, T. and Pretzsch, H. 2007. Long-term effects of logging intensity on structures, birds, saproxylic beetles and wood-inhabiting fungi in stands of European beech *Fagus sylvatica* L. – For. Ecol. Manage. 242: 297-305.

Naturvårdsverket 2004. Naturvårdsverket 2004. Åtgärdsprogram för särskilt skyddsvärda träd i kulturlandskapet. Rapport 5411:1–81. –, p.

NIBIO 2016. Nedlasting av kartdata - SAT-SKOG. – The Norwegian Institute of Bioeconomy Research (NIBIO) (Accessed 18 January, 2016) http://www.skogoglandskap.no/artikler/2009/nedlasting_satskog/newsitem

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

Nordén, J., Penttilä, R., Siitonen, J., Tomppo, E. and Ovaskainen, O. 2013. Specialist species of wood-inhabiting fungi struggle while generalists thrive in fragmented boreal forests. – J. Ecol. 101: 701-712.

Norwegian Environment Agency 2015. Norwegian database for habitats (Naturbase) –Norwegian Environment Agency (Accessed 30 September, 2015) http://karteksport.miljodirektoratet.no/#page=tab1

Oliver, T. H., Heard, M. S., Isaac, N. J. B., Roy, D. B., Procter, D., Eigenbrod, F., Freckleton, R., Hector, A., Orme, C. D. L., Petchey, O. L., Proença, V., Raffaelli, D., Suttle, K. B., Mace, G. M., Martín-López, B., Woodcock, B. A. and Bullock, J. M. 2015. Biodiversity and resilience of ecosystem functions. – Trends Ecol. Evol. 30: 673-684.

Paillet, Y., Bergès, L., Hjältén, J., Ódor, P., Avon, C., Bernhardt-Römermann, M., Bijlsma, R.-J., De Bruyn, L. U. C., Fuhr, M., Grandin, U. L. F., Kanka, R., Lundin, L., Luque, S., Magura, T., Matesanz, S., MÉSzÁRos, I., SebastiÀ, M. T., Schmidt, W., StandovÁR, T., TÓThmÉRÉSz, B., Uotila, A., Valladares, F., Vellak, K. A. I. and Virtanen, R. 2010. Biodiversity differences between managed and unmanaged forests: meta-analysis of species richness in Europe. – Conserv. Biol. 24: 101-112.

Ranius, T. 2002. Influence of stand size and quality of tree hollows on saproxylic beetles in Sweden. – Biol. Conserv. 103: 85-91.

Ranius, T., Eliasson, P. and Johansson, P. 2008a. Large-scale occurrence patterns of red-listed lichens and fungi on old oaks are influenced both by current and historical habitat density. – Biodivers. Conserv. 17: 2371-2381.

Ranius, T. and Hedin, J. 2001. The dispersal rate of a beetle, *Osmoderma eremita*, living in tree hollows. – Oecologia 126: 363-370.

Ranius, T. and Jansson, N. 2000. The influence of forest regrowth, original canopy cover and tree size on saproxylic beetles associated with old oaks. – Biol. Conserv. 95: 85-94.

Ranius, T., Johansson, P., Berg, N. and Niklasson, M. 2008b. The influence of tree age and microhabitat quality on the occurrence of crustose lichens associated with old oaks. – J. Veg. Sci. 19: 653-662.

Ranius, T., Johansson, V. and Fahrig, L. 2011. Predicting spatial occurrence of beetles and pseudoscorpions in hollow oaks in southeastern Sweden. – Biodivers. Conserv. 20: 2027-2040.

Ranius, T., Niklasson, M. and Berg, N. 2009. Development of tree hollows in pedunculate oak (*Quercus robur*). – For. Ecol. Manage. 257: 303-310.

Sala, O. E., Chapin III , F. S., Armesto, J. J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L. F., Jackson, R. B., Kinzig, A., Leemans, R., Lodge, D. M., Mooney, H. A., Oesterheld, M. n., Poff, N. L., Sykes, M. T., Walker, B. H., Walker, M. and Wall, D. H. 2000. Global Biodiversity Scenarios for the Year 2100. – Science 287: 1770-1774.

Seibold, S., Brandl, R., Buse, J., Hothorn, T., Schmidl, J., Thorn, S. and Müller, J. 2015. Association of extinction risk of saproxylic beetles with ecological degradation of forests in Europe. – Conserv. Biol. 29: 382-390.

Seibold, S., Bässler, C., Brandl, R., Büche, B., Szallies, A., Thorn, S., Ulyshen, M. D. and Müller, J. 2016. Microclimate and habitat heterogeneity as the major drivers of beetle diversity in dead wood. – J. Appl. Ecol. 53: 934-943.

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

Siitonen, J. and Ranius, T. 2015. The importance of veteran trees for saproxylic insects. – In: Kirby, K. J. and Watkins, C. (eds), Europe's changing woods and forests: from wildwood to managed landscapes. CABI, pp. 140-153.

Slatyer, R. A., Hirst, M. and Sexton, J. P. 2013. Niche breadth predicts geographical range size: a general ecological pattern. – Ecol. Lett. 16: 1104-1114.

Sverdrup-Thygeson, A. 2009. Oaks in Norway: Hotspots for red-listed beetles (Coleoptera). – In: Buse, J.Alexander, K. N. A.Ranius, T. and Assmann, T. (eds), Saproxylic beetles: their role and diversity in European woodland and tree habitats - Proceedings of the 5th symposium and workshop. Pensoft Publishers, pp. 13-26.

Sverdrup-Thygeson, A., Gustafsson, L. and Kouki, J. 2014a. Spatial and temporal scales relevant for conservation of dead-wood associated species: current status and perspectives. – Biodivers. Conserv. 23: 513-535.

Sverdrup-Thygeson, A., Rasmussen, A., Hanssen, O. and Evju, M. 2014b. Gjenbesøk av hule eiker kartlagt for 30 år siden. INA fagrapport. – Norwegian University of Life Sciences (NMBU), p 30.

Sverdrup-Thygeson, A., Skarpaas, O. and Ødegaard, F. 2010. Hollow oaks and beetle conservation: the significance of the surroundings. – Biodivers. Conserv. 19: 837-852.

Thuiller, W. 2007. Biodiversity: Climate change and the ecologist. – Nature 448: 550-552.

Tomter, S. and Eriksen, R. 2001. Statistikk over skogforhold og -ressurser i Vest-Agder - Landsskogtakseringen 1995-99. – NIJOS ressursoversikt 02/01, p 60.

Tomter, S. M., Eriksen, R. and Aalde, H. 2001. Statistikk over skogforhold og – ressurser i Aust-Agder: Landsskogtakseringen 1995 – 99. – NIJOS-ressursoversikt 03/01, p 61.

Vevstad, A. 1998. Agderskog, Agder skogeierlag 1948-1998 og om skog og skogbruk på Agder gjennom tidene. – Agder Skogeigarlag.

Vodka, S., Konvicka, M. and Cizek, L. 2009. Habitat preferences of oak-feeding xylophagous beetles in a temperate woodland: implications for forest history and management. – J. Insect Conserv. 13: 553-562.

Widerberg, M. K., Ranius, T., Drobyshev, I., Nilsson, U. and Lindbladh, M. 2012. Increased openness around retained oaks increases species richness of saproxylic beetles. – Biodivers. Conserv. 21: 3035-3059.

Wiens, J. A. 1989. Spatial scaling in ecology. – Funct. Ecol. 3: 385-397.

Økland, R. H. 2003. Partitioning the variation in a plot-by-species data matrix that is related to *n* sets of explanatory variables. – J. Veg. Sci. 14: 693-700.

Paper I

Ecology and Evolution

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Specialists in ancient trees are more affected by climate than generalists

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Abstract

Ancient trees are considered one of the most important habitats for biodiversity in Europe and North America. They support exceptional numbers of specialized species, including a range of rare and endangered wood-living insects. In this study, we use a dataset of 105 sites spanning a climatic gradient along the oak range of Norway and Sweden to investigate the importance of temperature and precipitation on beetle species richness in ancient, hollow oak trees. We expected that increased summer temperature would positively influence all wood-living beetle species whereas precipitation would be less important with a negligible or negative impact. Surprisingly, only oak-specialist beetles with a northern distribution increased in species richness with temperature. Few specialist beetles and no generalist beetles responded to the rise of 4°C in summer as covered by our climatic gradient. The negative effect of precipitation affected more specialist species than did temperature, whereas the generalists remained unaffected. In summary, we suggest that increased summer temperature is likely to benefit a few specialist beetles within this dead wood community, but a larger number of specialists are likely to decline due to increased precipitation. In addition, generalist species will remain unaffected. To minimize adverse impacts of climate change on this important community, long-term management plans for ancient trees are important.

Introduction

Ancient trees are keystone structures in natural, agricultural, and urban ecosystems around the globe (Vera 2000; Brawn 2006; Gibbons et al. 2008; Andersson et al. 2011; Lindenmayer et al. 2012; Buse et al. 2013; Bouget et al. 2014). In the northern temperate zone, ancient hollow oak trees (*Quercus* spp.) are considered one of the most important habitats for biodiversity, both in Europe (Vera 2000; Andersson et al. 2011; Bouget et al. 2014) and in North America (Brawn 2006). They support exceptional numbers of specialized biodiversity, including a range of rare and endangered species of wood-living insects (Ranius and Jansson 2000; Buse et al. 2010; Sverdrup-Thygeson et al. 2010). These specialist species have important ecological roles, particularly as decomposers (Ulyshen 2014) and as they tend to be rare in a community, the roles are often irreplaceable (Mouillot et al. 2013). They contribute to maintaining functional diversity, the importance of which for ecosystem services is increasingly acknowledged (Diaz and Cabido 2001; Díaz et al. 2007; Arnan et al. 2013). Specialists are known to be more negatively affected by habitat loss than are generalists (Slatyer et al. 2013), but their responses to climate change are little understood.

Climate change is an ever-increasing threat to biodiversity (Bellard et al. 2012). Temperature has increased by 0.74°C and precipitation by 6–8% in the northern hemisphere during the last century alone (IPCC, 2007). Conservative projections of climate change estimate a further 2°C rise in temperature by 2100. But as recent greenhouse gas emission rates are the highest ever observed (World Meteorological Organization, 2014), we are more likely to experience a global temperature increase closer to the 4°C predicted under both constant and high emissions scenarios (IPCC, 2013). In tandem with these vast temperature changes, precipitation in the northern hemisphere is likely to increase over the coming decades (Kjellström et al. 2011).

In response to the recent temperature changes, bark beetles have expanded to higher elevations and latitudes beyond their historic limits (Logan et al. 2003; Parmesan 2006). Butterflies, representing the best-known insect group, appear several weeks earlier than three decades ago on various continents (Roy and Sparks 2000; Forister and Shapiro 2003; Diamond et al. 2011). Multibrooded species have longer flight periods (Roy and Sparks 2000), and some bark beetles, butterflies, and moths have shifted from one to several generations in warmer summers (Jönsson et al. 2009; Altermatt 2010). Compared to temperature, few studies have focused on the possible effects of increased precipitation on insect communities. Existing studies have found that high precipitation may limit insect flight ability (Bale et al. 2002; Klueken et al. 2009; Jaramillo et al. 2011; Sturtevant et al. 2013), but it is not possible to anticipate effects at a wider community level.

Despite their importance for ecosystem functioning and high proportion of threatened species, the effect of climate on the dead wood beetle community is little studied. There is some indication that climate will affect species richness. Temperature has been found to be a predictor of dead wood-living beetle species richness along geographical and altitudinal gradients in Europe (Gossner et al. 2013; Müller et al. 2014). Precipitation has been found to have either no effect on species richness (Müller et al. 2014) or a mixed response, depending on functional group (Gossner et al. 2013). However, it is not known how these effects vary between host tree species, and whether specialists and generalists respond in the same way. Species may respond quite differently in oak as opposed to other host trees such as beech, and in ancient, natural forest to managed productive woodland. Specialists and generalists are known to respond differently to habitat change and so may respond differently to climate change. Specialists might experience larger challenges from temperature change alone or in combination with habitat degeneration than generalists (Stefanescu et al. 2011; Filz et al. 2013; Ball-Damerow et al. 2014). Specialists might be more sensitive than generalists to precipitation (Leckey et al. 2014).

Geographical range is also important. The current geographical range of a species indicates the climate regime to which it is adapted. Also, the size of a species geographical range often correlates with niche-breadth; the larger the range, the wider the niche-breadth (Slatyer et al. 2013). Taking geographical range into account when analyzing species responses to climate may reveal important patterns that are otherwise overlooked. Thus, to predict future changes in species diversity and subsequently ecosystem services, specialist and generalist species ought to be treated separately and geographical range taken into account. With the prospect of rapid and sustained change in both temperature and precipitation, it is important to understand how specialist and generalist wood-living insects may respond to inform conservation and begin to understand the implications for the services they provide.

In this study, we use a huge dataset of 105 sites – spanning a climatic gradient that mimics the temperature increase of 4°C and precipitation changes likely to occur to 2100 along the oak range of Norway and Sweden – to investigate the likely consequences of future climate change for the species richness of wood-living beetles in ancient, hollow oak trees. We examine specialists and generalists, and those with differing geographical ranges separately. We expect that (1) increased summer temperature will positively influence all wood-living beetle species and in particular, those with a southern distribution and (2) precipitation may be less important than temperature, with a negligible or negative impact.

Materials and Methods

Data collection

The study contains data from 308 hollow oak trees at 105 sites, spread along a 700-km climatic gradient mainly going from west to east across southern Norway and Sweden (Fig. 1). The gradient covers a range of 4°C (12.5–16.9°C) difference in temperature during the warmest quarter of the year. As for precipitation, there is a 620-mm difference between the highest (798 mm) and lowest (178 mm) values in our study sites (Fig. 1). Excluding the two westernmost sites, the range spans 303 mm.

The sites fall within the hemiboreal zone (Ahti et al. 1968) which, although dominated by boreal tree species, is also characterized by a considerable element of southern deciduous tree species, for example oak *Quercus robur* and *Quercus petraea*, lime *Tilia cordata*, maple *Acer platanoides*, ash *Fraxinus excelsior*, elm *Ulmus glabra*, and hazel *Corylus avellana*, on richer soils and on sites with a warmer microclimate.

We surveyed all sites during 1 year in the period 1999–2009. We sampled one to four hollow oaks (defined as having a minimum of 60-cm circumference at breast height with a visible cavity in the trunk) at each site (Table S1). Oaks were randomly chosen within a site. Where more than one tree was sampled at a site, trees were between 6 m and 250 m apart. Sites were at least 1500 m apart. Tree age was not known precisely, but the age of a subset of the Swedish oaks was estimated to be 150–500 years old. Each tree was sampled for beetles using one flight interception (window) trap with a trans-

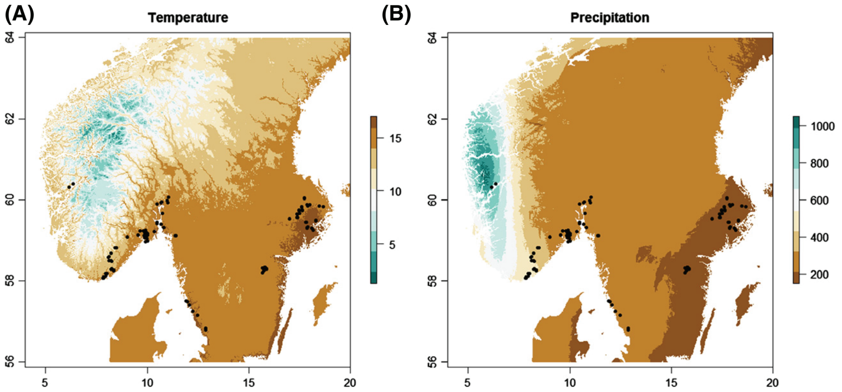

Figure 1. Study sites location with (A) mean temperature during warmest quarter of the year and (B) mean precipitation during warmest quarter of the year in millimeter. Climate data were downloaded from BIOCLIM (variables BIO10 and BIO18) (Hijmans et al. 2005). Axes are longitude and latitude.

parent plastic window above a container of preservative solution and detergent to break surface tension. Trap windows were either 20 × 40 cm or 30 × 50 cm and placed as close to the cavity opening as possible (within 1 m). Height above the ground varied from 1.5 m to 7 m (average 2–3 m) dependent on the height of the cavity opening. They were active during the summer beetle flight season from May to September, and emptied once per month. The sites were originally surveyed for slightly different purposes, but all for wood-living beetles and the sampling methods were consistent across sites and years. The tree selection and sampling process for all sites is described in detail in Jansson et al. (2009), Sverdrup-Thygeson et al. (2010), Pilskog et al. (2014), Jonsell and Eriksson (2002) and Jonsell (2008).

The original surveys had slightly different taxonomic ambition (i.e. ignoring some groups). However, for all sites, beetle species known to be associated with oak were identified, and based on this criterion, we made a common species list of 152 species that was comparable across sites (Table S2). We classified the species into specialists and generalists according to their association with oak trees based on an open database on host tree association from Fennoscandia (The Saproxylic Database, 2014). Specialists were defined as species occurring primarily on dead wood from oak and occasionally on other broadleaved temperate species and generalists as species occurring on dead wood from a range of trees (deciduous and coniferous), including oak (see Table S2 and The Saproxylic Database for classification details). Species not associated with oak at all were excluded from the analysis. In addition, the species were categorized according to their geographical distribution; Southern species, occurring primarily in the south of Europe (south of ~47 degrees N); Northern species, occurring primarily in the north of Europe (north of ~50 degrees N); and Widespread species which do not fall into either group and are widespread. The Widespread group also includes a few species with a central European distribution. The distribution was based on the European Nature Information System (eunis.eea.europa.eu), Global Biodiversity Information Facility (www.gbif.org), Fauna Europaea (www.faunaeur.org), Encyclopedia of Life (www.eol.org), and various other resources depending on species. This resulted in six species groups: (1) Northern Specialists, (2) Southern Specialists, (3) Widespread Specialists, (4) Northern Generalists, (5) Southern Generalists, and (6) Widespread Generalists (Table S2). We summed the species counts per group and tree.

We chose to use an open database (Dahlberg and Stokland 2004; The Saproxylic Database, 2014) on host tree association to classify the species' host tree dependence. However, we found that the classification did not fully correspond with our own experience of beetle specialization. To test the results' sensitivity to the classification, we revised the original classification based on our field sampling experiences of oak and other host trees (Table S2) and compared the importance of our explanatory variables to the response variables based on univariate statistics with the two classifications. The new classification gave similar but stronger results for the specialist species and similar but weaker results for the generalists. Few species were categorized as Widespread in the new classification, so the comparison was inconclusive for these species.

Two climate variables and two environmental variables were included in all analyses. Climate data were derived from BIOCLIM (Hijmans et al. 2005). We chose the variables BIO10 Mean Temperature during the Warmest Quarter of the Year and BIO18 Mean Precipitation during the Warmest Quarter of the Year as the most relevant climate measures for beetle development and swarming (Fig. 1). We extracted the data for each tree using the extract function in the "raster" package in R (Hijmans 2014) and we used the "RColorBrewer" package (Neuwirth 2014) to visualize the changes in temperature and precipitation across the gradient (Fig. 1). To account for additional variation in species richness, we also included Circumference of the sampled hollow oak (cm at breast height, measured with a tape) and Openness immediately around the oak (0 = open, 1 = partly closed canopy, 2 = closed canopy). These are ecologically meaningful variables known to affect wood-living beetle species richness (Ranius and Jansson 2000; Sverdrup-Thygeson et al. 2010; Gough et al. 2014). Openness reflects the amount of surrounding vegetative growth and the amount of sunlight that reaches the trunk (and hence cavity) and crown of the oak. The openness around the oak tree has been found to be the most important factor for wood-living beetle species richness in previous work (Gough et al. 2014), and it provides an insight into the microclimate of the tree within the broader climate gradient.

Statistical analysis

All analyses were carried out in R version 3.1.0 (R Core Team, 2014). We used species richness per tree within each category of species as a response variable. To evaluate whether temperature and precipitation influence species richness, we applied generalized linear mixed-effects models (GLMMs) using function glmer from package "lme4" (Bates et al. 2014) with a Poisson error distribution, log-link function, and Nelder–Mead optimizer from package "nloptr" (Nelder and Mead 1965; Johnson 2014). Continuous variables (Circumference, Temperature, and Precipitation) were checked for collinearity through calculation of correlation coefficients and inspection of variance inflation factors (VIF), then centered and scaled. We used Site as a random effect to account for large variances between species richness of different sites, and to allow generalization of the results beyond the sampled trees. Country (Norway/Sweden) was used as a random effect to account for large variances between the species richness of the different countries. To validate model fit, we checked overdispersion of the residuals for each species group (it was between 0.9 and 1 for all groups) and visually assessed the distribution of the residuals using QQ plots and plots of residual against fitted values. An additional analysis using backwards stepwise selection by use of the drop1 function, based on Akaike's Information Criterion (AIC), was carried out to select the most parsimonious model for each species group (Table S3).

Results

The dataset we used consisted of 3036 occurrences of 152 beetle species. For generalists, there were an even number of Northern and Southern species (51 Northern, 52 Southern). It was highly uneven for specialists, with four times as many Southern Specialists (24 species) as Northern Specialists (six species) in total, although the mean, minimum, and maximum number of Northern Specialists and Southern Specialists per tree was identical. There were few Widespread species, with a mode of zero counts per tree and a mean of less than one species per tree (Table 1).

Climate

The species richness of all three specialist groups (Northern, Southern, and Widespread) was significantly affected by either Temperature (positive) or Precipitation (negative). In contrast, no generalist group was affected by a climate variable (Fig. 2).

The effect of Temperature was significant for only one group, the Northern Specialists, for which species richness increased with Temperature (Fig. 2A). Precipitation overall had a stronger impact than Temperature, as it negatively affected Southern as well as Widespread Specialists (Fig. 2B). No group was significantly affected by both Temperature and Precipitation. This pattern, and Precipitation having an effect of larger magnitude than Temperature, was confirmed and even strengthened, in the most parsimonious models; the Northern Specialists were the only model that contained temperature (significant positive effect), while three models – Southern and Widespread Specialists and Widespread Generalists – contained Precipitation (negative effect) (Table S3). Precipitation was, however, not significant ($p = 0.86$) in the model with Widespread Generalists.

As the results for specialists were found to be strengthened under an alternative classification (see Methods), we consider the results presented here to be a conservative estimate of the effect of temperature and precipitation on Specialists.

Environmental variables

Every group except Widespread Generalists was significantly affected by the size of the tree, with species richness increasing as Circumferences increases (Fig. 2C,

Table 1. Number of species per group.

Species group	Total number of species	Mean richness per tree (min, max)
Northern specialists	6	1.1 (0, 5)
Southern specialists	24	1.1 (0, 5)
Widespread specialists	7	0.7 (0, 4)
Northern generalists	51	3.9 (0, 14)
Southern generalists	52	2.5 (0, 13)
Widespread generalists	12	0.6 (0, 3)

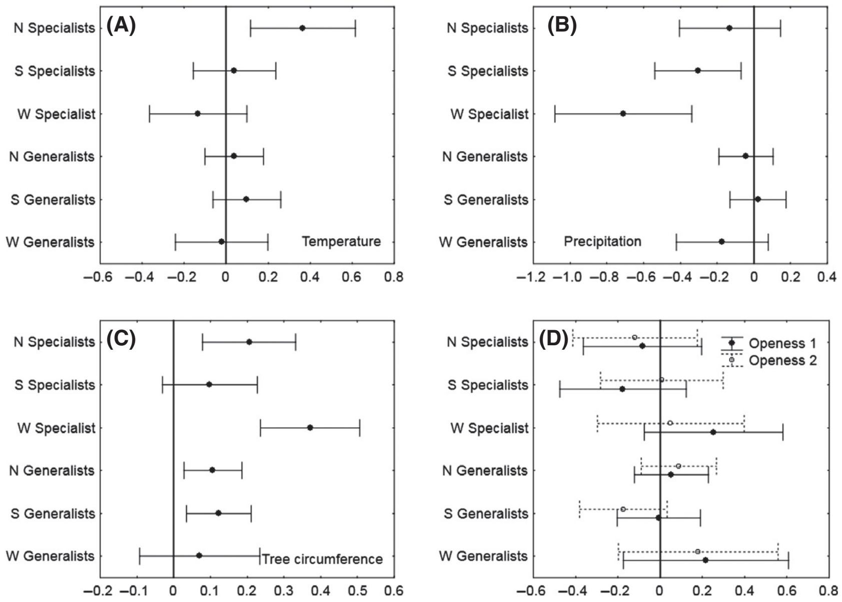

Figure 2. Partial regression coefficients (with 95% CI) from six regression models, one for each species group (Generalist and Specialists divided into Northern (N), Southern (S), and Widespread (W) species). In the models, the richness was predicted by summer temperature (A), summer precipitation (B), hollow oak circumference (C), the openness of the immediate surroundings of a tree (D); 1 = partly closed canopy, 2 = closed canopy. 0 = open canopy, used as the baseline in model estimates.

Table S3). Openness is known to be very important for hollow oak beetle species and was a significant variable when tested alone (results not shown), but did not significantly affect any group in the full models (Fig. 2D). Openness was removed from all models early in the selection process during stepwise selection and was not included in any of the most parsimonious models (Table S3).

Discussion

Our study of beetle species richness in ancient trees along a climate gradient provides a starting point to understand and predict wood-living beetles' responses to climate change. Our results indicate that increased summer temperature and summer rain could substantially affect wood-living beetle species richness and that the effect is likely to be more profound for oak specialists than generalists.

Effect of increased mean summer temperature

Our specialist beetle species are primarily found on *Q. robur* and *Q. petraea*, which need warm, sunny conditions to successfully grow to a great age (Vera 2000). The beetles are therefore likely to be adapted to stable and warm conditions, and we expected their species richness to increase with temperature independent of their present geographical distribution. Such patterns have been demonstrated for wood-living beetles in other European studies. In a study of beech forest, Müller et al. (2014) found an increase in species richness of wood-living beetles along temperature gradients in Europe. A recent report also concluded that species richness of wood-living beetles has increased during the last 20 years, probably as a result of global warming (Köhler 2014). Contrary to our expectation, our study did not confirm this pattern for the majority of the species; only specialist species with a Northern distribution responded positively to temperature in our gradient.

It is difficult to untangle the underlying processes determining the richness of hollow oak species along temperature gradients. Some explanation might be related to the fact that specialists, with their narrower habitat demands compared to generalists, may be particularly sensitive to additional constrains such as biotic interactions which may interfere with climate predictions (Preston et al. 2008). Hollow tree specialists were also found to be less affected by global warming than the total species richness reported by Köhler (2014). This could be due to a potential buffering effect of living within a tree cavity, where, depending on the size of the cavity and amount of wood-mold within it, temperatures tend to be more stable than outside or in small pieces of dead wood (Ranius and Nilsson 1997). The responses of the specialist hollow oak beetles could therefore be modified by the immediate microclimate of the hollow. In order to understand the contrasting responses, more detailed studies are clearly needed.

The temperature range of our study, a difference of 4°C, corresponds to the predicted temperature rise in the study region of 4.6 degrees by 2100 (Hanssen-Bauer et al. 2009). Thus, our findings along the geographical gradient may potentially describe the changes to be expected toward the end of this century – acting as a warning of possible changes in abundance patterns in the important community of beetles in ancient trees in Northern Europe.

Effect of increased mean summer precipitation

We expected that precipitation would have a negligible or possibly negative effect on species richness. This was confirmed, with no effect for four and negative effect for two (both specialists) of the six species groups in the hollow oaks.

It is likely that precipitation reduces flight time and dispersal distance, as insects may fly less during wet periods (Klueken et al. 2009; Jaramillo et al. 2011). This could shorten or interrupt the overall flight period and disrupt dispersal and colonization of new trees. The Southern and Widespread specialists responded most strongly to precipitation. Possibly, they are less likely to fly in rain than the other beetles, as they generally live in drier and warmer climates. However, the importance of indirect effects should not be overlooked. Changes in wood-rot fungi might be of particular importance, as many beetle species in dead wood interact with the fungal community (Crowson 1981; Müller et al. 2002), and fungi generally are sensitive to changes in moisture. Gossner et al. (2013) found an increase in the proportion of fungivorous beetle species in dead wood with increasing precipitation in Germany, whereas fresh wood feeders decreased. Thus, it is possible that our observed decrease in species richness among two specialist groups could be at least partly explained by changes in fungi-interacting beetles along the gradient. However, two genera of known fungi-interacting beetles in our study, *Cryptophagus* and *Mycetophagus,* were classified as generalists in groups that overall did not respond to precipitation, in contrast to Gossner et al.'s result. It is likely that the ecology and relationships between hollow oak species are highly complex and there are interactions taking place that are not yet understood. This highlights an advantage of studying wood-living beetles at the overall community level. Indications that two specialist groups may be negatively affected by precipitation can guide future work to elicit the mechanisms behind the response, while still informing wider wood-living beetle ecology and conservation, before individual species' responses can be studied in detail. In contrast to Gossner et al. (2013) and in line with most species in the present study, Müller et al. (2014) found no effect of precipitation on wood-living beetle richness across European beech forests.

In the study area, precipitation is expected to increase by 5–30% by 2100 and most additional precipitation is predicted to occur in the already wet areas (Hanssen-Bauer et al. 2009). As the proportional changes will be smaller in the dry as to compared to the wettest areas, the precipitation gradient is likely to be extended within the same geographical region and the specialist species richness may consequently decline even more toward the wetter end of the gradient.

Extreme climate events are likely to happen more frequently as the climate changes, with a potential for both increased drought and extreme precipitation events (IPCC, 2007). Whilst we did not examine the effect of extreme events, the results may provide some indication of their consequences. Drought with a lack of summer precipitation would not be likely to directly influence species richness of hollow oak beetle species, although it could be perceived as beneficial for the two specialist groups that were negatively affected by higher precipitation. It would likely affect the cavity microclimate and fungal community as discussed above. A greater impact could occur through the effects of a sustained drought on the host trees. Ancient trees are already in decline (Paillet et al. 2010; Lindenmayer et al. 2012), and drought can be a major stress contributing to oak tree aging and death (Vera 2000; Allen et al. 2010). Extreme precipitation events in the summer with intense periods of summer rain could affect beetle flight and enhance the negative effect observed in two groups. However, the contrasting response between groups and to climate and precipitation indicates that responses to extreme climate events are likely to be difficult to predict.

Trap catches are always a combination of population density and insect activity. Generally, insects are more flight active in warmer and dry weather as compared to cold and wet weather. Thus, one might argue that the coldest and wettest sites are being undersampled compared with warmer sites; it would take more trapping effort to catch beetles flying infrequently. However, if the results had been an artifact of sampling, we would expect a similar decline of species richness with high precipitation and low temperature in all species groups, but this was not observed. Müller et al. (2014) also found a consistent effect of temperature and precipitation on species richness comparing trapping data to data based on hatching from log units along a climatic gradient. Thus, it is unlikely that our findings are a result of a sampling bias.

Environmental variables

Circumference and openness were included in the analyses as they are known to influence hollow oak beetle richness (Ranius and Jansson 2000). Circumference was confirmed as important with a significant positive effect for all species groups, likely related to the greater range and availability of habitat in the largest trees, and was retained in the most parsimonious model for all species groups except one (Widespread Generalists). However, the positive effect of circumference does not negate the effect of precipitation. The magnitude of the negative effect of precipitation was greater than the positive effect of circumference (Fig 2B,C). This means that even oak specialists in the “best trees” and “best quality habitat” are likely to be adversely affected by increased summer rain.

Openness, although significant alone and known to be important for beetle species composition (Lindhe et al. 2005; Vodka et al. 2009; Gough et al. 2014), did not affect species richness in the full models. Openness is a measure of how open or shaded the hollow oak tree is, and is a proxy for microclimate of the oak hollow. Thus, it is possible that the changes in species richness due to openness around the oak are eclipsed by a more profound gradient in climate. The result for openness in these models emphasizes the complex nature of climate change effects, and the synergy between climate and habitat change.

We did not include any measure of dead wood quantity or forest history in our analysis as this was only available for subsets of the entire dataset and measures used at different sites were not comparable. As the extent and abundance of ancient oaks in Sweden in recent times have been higher than in Norway (Eliasson and Nilsson 2002; Direktoratet for naturforvaltning, 2012), country was used as a random variable in all models as a proxy for forest history to account for any effect this may have had. This difference between Norway and Sweden in ancient oak abundance is driven by human activity and oak protection measures rather than climate (Direktoratet for Naturforvaltning, 2012), and so we find it unlikely that dead wood amount and forest history correlate strongly with the temperature and precipitation gradients in this particular study. However, we acknowledge that some variation within the dataset is likely to be explained by these variables and it would be beneficial to include them in future work.

Potential impacts of future climate change

Our results indicate that with predicted climate change, only the specialists in hollow oaks with a Northern distribution are likely to benefit overall, as they were positively affected by temperature and did not respond to precipitation. Most specialists are likely to decline as they are negatively affected by precipitation and not affected by temperature, whereas generalists are likely to remain unchanged. Still, species expanding at the margins of their range may evolve greater dispersal abilities than those in the core (Hill et al. 2011; Lindstrom et al. 2013). Such an expansion cannot be ruled out and may potentially counteract the negative effect of precipitation on the Southern Specialist and increase species richness of Southern Generalists.

In general, hollow oak specialist beetles will be far more affected than generalists by climate change, and we may face an overall decrease in species richness in this community in Northern Europe. Although the specialists make up a relatively small species group compared to the generalists, they might be proportionally more important. They are often locally rare species, and as such often have functional traits with low redundancy, meaning that other species cannot easily replace their role if lost from the ecosystem (Mouillot et al. 2013).

The results discussed above assume that hollow oak habitats remain stable, which is questionable. Large, hollow oaks are considered to be in decline in Norway and Sweden due to direct removal, mechanical damage, and competition from dense surrounding growth (Naturvårdsverket, 2004, Sverdrup-Thygeson et al. 2014). Action Plans are now in place in both countries aimed at halting the decline (Direktoratet for Naturforvaltning 2012, Naturvårdsverket, 2012). It is of course an open issue whether these attempts will impact the future abundance of large, hollow oaks and hence whether the possible adverse impacts of climate will be exacerbated. In any case, it will take several decades for the results of the Action Plans to become apparent due to the long lifespan of oak trees, and immediate (next 20+ years) climate change is not likely to be mitigated by a habitat increase.

Oak ecosystems in general are suffering a drastic decline worldwide (Vera 2000; Bjorkman and Vellend 2010; Paillet et al. 2010; Horak et al. 2014), and large, hollow trees are often disproportionately affected (Lindenmayer et al. 2014). Given the overall inability of hollow oak species to respond positively to temperature and their possible negative response to precipitation, a decline in the number of rare and threatened species is likely.

To conclude, the responses of wood-living beetles to climate change are likely to be complex and to vary with geographical distribution and specialization. For hollow oak species, increased summer temperature is likely to benefit a few oak specialists with a northern distribution, but the majority of specialists is likely to decline due to increased precipitation. Oak generalist beetles are expected to remain unaffected. To minimize adverse impacts and allow for positive responses to climate change, it is important to halt the decline in ancient trees and consider restoration efforts that can maximize the quantity and quality of available habitat.

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Conflict of Interest

None declared.

References

Ahti, T., L. Hämet-Ahti, and J. Jalas. 1968. Vegetation zones and their sections in north-western Europe. Ann. Zool. Fenn. 5:169–211.

Allen, C. D., A. K. Macalady, H. Chenchouni, D. Bachelet, N. McDowell, M. Vennetier, et al. 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. For. Ecol. Manage. 259:660–684.

Altermatt, F. 2010. Climatic warming increases voltinism in European butterflies and moths. Proc. R. Soc. B Biol. Sci. 277:1281–1287.

Andersson, M., P. Milberg, and K.-O. Bergman. 2011. Low pre-death growth rates of oak (*Quercus robur* L.)—Is oak death a long-term process induced by dry years? Ann. For. Sci. 68:159–168.

Arnan, X., X. Cerda, A. Rodrigo, and J. Retana. 2013. Response of ant functional composition to fire. Ecography 36:1182–1192.

Bale, J. S., G. J. Masters, I. D. Hodkinson, C. Awmack, T. M. Bezemer, V. K. Brown et al. 2002. Herbivory in global climate change research: direct effects of rising temperature on insect herbivores. Glob. Change Biol. 8:1–16.

Ball-Damerow, J. E., L. K. M'gonigle, and V. H. Resh. 2014. Changes in occurrence, richness, and biological traits of dragonflies and damselflies (Odonata) in California and Nevada over the past century. Biodivers. Conserv. 23:2107–2126.

Bates, D., M. Maechler, B. Bolker, and S. Walker. 2014. lme4: linear mixed-effects models using Eigen and S4. R package version 1.1–6. Available at http://CRAN.R-project.org/package=lme4.

Bellard, C., C. Bertelsmeier, P. Leadley, W. Thuiller, and F. Courchamp. 2012. Impacts of climate change on the future of biodiversity. Ecol. Lett. 15:365–377.

Bjorkman, A. D., and M. Vellend. 2010. Defining historical baselines for conservation: ecological changes since European settlement on Vancouver Island, Canada. Conserv. Biol. 24:1559–1568.

Bouget, C., L. Larrieu, and A. Brin. 2014. Key features for saproxylic beetle diversity derived from rapid habitat assessment in temperate forests. Ecol. Ind. 36:656–664.

Brawn, J. D. 2006. Effects of restoring oak savannas on bird communities and populations. Conserv. Biol. 20:460–469.

Buse, J., T. Levanony, A. Timm, T. Dayan, and T. Assmann. 2010. Saproxylic beetle assemblages in the Mediterranean region: impact of forest management on richness and structure. For. Ecol. Manage. 259:1376–1384.

Buse, J., T. Assmann, A.-L.-L. Friedman, O. Rittner, T. R. Pavlicek, S. Leather, et al. 2013. Wood-inhabiting beetles (Coleoptera) associated with oaks in a global biodiversity hotspot: a case study and checklist for Israel. Insect Conserv. Divers. 6:687–703.

Crowson, R. A. 1981. Biology of the coleoptera. Academic Press, London.

Dahlberg, A., and J. Stokland. 2004. Substrate requirements of wood-inhabiting species - a synthesis and analysis of 3600 species. Skogsstyrelsen, Report 7-04.

Diamond, S. E., A. M. Frame, R. A. Martin, and L. B. Buckley. 2011. Species' traits predict phenological responses to climate change in butterflies. Ecology 92:1005–1012.

Diaz, S., and M. Cabido. 2001. Vive la difference: plant functional diversity matters to ecosystem processes. Trends Ecol. Evol. 16:646–655.

Díaz, S., S. Lavorel, F. De Bello, F. Quétier, K. Grigulis, and T. M. Robson. 2007. Incorporating plant functional diversity effects in ecosystem service assessments. PNAS 104:20684–20689.

Direktoratet for Naturforvaltning 2012. Handlingsplan for utvalgt naturtype hule eiker. DN-rapport 1-2012.

Eliasson, P., and S. G. Nilsson. 2002. 'You should hate young oaks and young noblemen' - The environmental history of oaks in eighteenth- and nineteenth-century Sweden. Environ. Hist. 7:659–677.

Filz, K. J., M. Wiemers, A. Herrig, M. Weitzel, and T. Schmitt. 2013. A question of adaptability: climate and habitat change lower trait diversity in butterfly communities in south-western Germany. Eur. J. Entomol. 110:633–642.

Forister, M. L., and A. M. Shapiro. 2003. Climatic trends and advancing spring flight of butterflies in lowland California. Glob. Change Biol. 9:1130–1135.

Gibbons, P., D. B. Lindenmayer, J. Fischer, et al. 2008. The future of scattered trees in agricultural landscapes. Conserv. Biol. 22:1309–1319.

Gossner, M. M., A. Floren, W. W. Weisser, and K. E. Linsenmair. 2013. Effect of dead wood enrichment in the canopy and on the forest floor on beetle guild composition. For. Ecol. Manage. 302:404–413.

Gough, L. A., T. Birkemoe, and A. Sverdrup-Thygeson. 2014. Reactive forest management can also be proactive for wood-living beetles in hollow oak trees. Biol. Conserv. 180:75–83.

Hanssen-Bauer, I., H. Drange, and E. J. Førland. 2009. Klima i Norge 2100, Bakgrunnsmateriale til NOU Klimatilplassing. Norsk klimasenter, Oslo.

Hijmans, R. J. 2014. Geographic data analysis and modeling. R package version 2.3-12. Available at http://CRAN-R-project.org/package-raster.

Hijmans, R. J., S. E. Cameron, J. L. Parra, P. G. Jones, and A. Jarvis. 2005. Very high resolution interpolated climate surfaces for global land areas. www.worldclim.org/bioclim (accessed June 2014). Int. J. Climatol. 25:1965–1978.

Hill, J. K., H. M. Griffiths, and C. D. Thomas. 2011. Climate change and evolutionary adaptations at species' range margins. Annu. Rev. Entomol. 56:143–159.

Horak, J., S. Vodka, J. Kout, J. P. Halda, P. Bogusch, and P. Pech. 2014. Biodiversity of most dead wood-dependent organisms in thermophilic temperate oak woodlands thrives on diversity of open landscape structures. For. Ecol. Manage. 315:80–85.

IPCC 2007. Climate change 2007: synthesis report. Pp. 23–73 *in* Core Writing Team, R. K. Pachauri, A. Reisinger, eds. Contribution of working groups I, II and III to the fourth assessment report of the intergovernmental panel on climate change. IPCC, Geneva.

IPCC 2013. Climate change 2013: the physical science basis. IPCC Working Group 1 Contribution to AR5. IPCC, Geneva.

Jansson, N., K.-O. Bergman, M. Jonsell, and P. Milberg. 2009. An indicator system for identification of sites of high conservation value for saproxylic oak (*Quercus* spp.) beetles in southern Sweden. J. Insect Conserv. 13:399–412.

Jaramillo, J. L., C. M. Ospina, Z. N. Gil, E. C. Montoya, and P. Benavides. 2011. Advances in the biology of *Corthylus zulmae* (Coleoptera: Curculionidae) in plantations of *Alnus acuminata* (Betulaceae). Revista Colombiana de Entomología 37:48–55.

Johnson, S. G. 2014. The Nlopt nonlinear-optimization package. Available at http://ab-initio.mit.edu/nlopt.

Jonsell, M. 2008. Vedlevande skalbaggar i Drottningholms slottspark [Saproxylic beetles in the park at Drottningholm, Stockholm]. Entomologisk Tidskrift 129:103–120.

Jonsell, M., and P. Eriksson. 2002. Harparbollund revisited - återinventering av en välkänd vedinsektslokal [Harparbollund revisited - reinventory of a well known locality for saproxylic beetles]. Entomologisk Tidskrift 123:205–218.

Jönsson, A. M., G. Appelberg, S. Harding, and L. Bärring. 2009. Spatio-temporal impact of climate change on the activity and voltinism of the spruce bark beetle, Ips typographus. Glob. Change Biol. 15:486–499.

Kjellström, E., G. Nikulin, U. L. F. Hansson, G. Strandberg, and A. Ullerstig. 2011. 21st century changes in the European climate: uncertainties derived from an ensemble of regional climate model simulations. Tellus A 63:24–40.

Klueken, A. M., B. Hau, B. Ulber, and H. M. Poehling. 2009. Forecasting migration of cereal aphids (Hemiptera: Aphididae) in autumn and spring. J. Appl. Entomol. 133:328–344.

Köhler, F. 2014. Die klimabedingte Veränderung der Totholzkäferfauna (Coleoptera) des nördlichen Rheinlandes – Analysen zur Gesamtfauna und am Beispiel von Wiederholungsuntersuchungen in ausgewählten Naturwaldzellen. Pp. 1–198. Wald und Holz NRW. Münster.

Leckey, E. H., D. M. Smith, C. R. Nufio, and K. F. Fornash. 2014. Oak-insect herbivore interactions along a temperature and precipitation gradient. Acta Oecol. 61:1–8.

Lindenmayer, D., W. F. Laurance, and J. Franklin. 2012. Global decline in large old trees. Science 338:1305–1306.

Lindenmayer, D. B., W. F. Laurance, J. F. Franklin, et al. 2014. New policies for old trees: averting a global crisis in a keystone ecological structure. Conserv. Lett. 7:61–69.

Lindhe, A., A. Lindelöw, and N. Åsenblad. 2005. Saproxylic beetles in standing dead wood density in relation to substrate sun-exposure and diameter. Biodivers. Conserv. 14:3033–3053.

Lindstrom, T., G. P. Brown, S. A. Sisson, B. L. Phillips, and R. Shine. 2013. Rapid shifts in dispersal behavior on an expanding range edge. Proc. Natl Acad. Sci. USA 110:13452–13456.

Logan, J. A., J. Regniere, and J. A. Powell. 2003. Assessing the impacts of global warming on forest pest dynamics. Front. Ecol. Environ. 1:130–137.

Mouillot, D., D. R. Bellwood, C. Baraloto, J. Chave, R. Galzin, M. Harmelin-Vivien, et al. 2013. Rare species support vulnerable functions in high-diversity ecosystems. PLoS Biol. 11:e1001569.

Müller, M. M., M. Varama, J. Heinonen, and A. M. Hallaksela. 2002. Influence of insects on the diversity of fungi in decaying spruce wood in managed and natural forests. For. Ecol. Manage. 166:165–181.

Müller, J., H. Brustel, A. Brin, H. Bussler, C. Bouget, E. Obermaier et al. 2014. Increasing temperature may compensate for lower amounts of dead wood in driving richness of saproxylic beetles. Ecography 37:1–11.

Naturvårdsverket 2004. Åtgärdsprogram för särskilt skyddsvärda träd i kulturlandskapet. Rapport 5411:1–81.

Naturvårdsverket 2012. Åtgärdsprogram för särskilt skyddsvärda träd. Mål och åtgärder 2012–2016. Rapport 6496:1–53.

Nelder, J. A., and R. Mead. 1965. A simplex method for function minimization. Comp. J. 7:308–313.

Neuwirth, E. 2014. RColorBrewer: ColorBrewer Palettes. R package version 1.1–2. Available at http://CRAN.R-project.org/package=RColorBrewer.

Paillet, Y., L. Bergès, J. Hjältén, P. Ódor, C. Avon, M. Bernhardt-Römermann, et al. 2010. Biodiversity differences between managed and unmanaged forests: meta-analysis of species richness in Europe. Conserv. Biol. 24:101–112.

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

Pilskog, H. E., A. Sverdrup-Thygeson, and T. Birkemoe. 2014. Biller i hule eiker i Vestfold, Telemark og Agder. INA Fagrapport 27:1–35.

Preston, K., J. T. Rotenberry, R. A. Redak, and M. F. Allen. 2008. Habitat shifts of endangered species under altered climate conditions: importance of biotic interactions. Glob. Change Biol. 14:2501–2515.

R Core Team 2014. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Ranius, T., and N. Jansson. 2000. The influence of forest regrowth, original canopy cover and tree size on saproxylic beetles associated with old oaks. Biol. Conserv. 95:85–94.

Ranius, T., and S. G. Nilsson. 1997. Habitat of *Osmoderma eremita* Scop. (Coleoptera: Scarabidae), a beetle living in hollow trees. J. Insect Conserv. 1:193–204.

Roy, D. B., and T. H. Sparks. 2000. Phenology of British butterflies and climate change. Glob. Change Biol. 6:407–416.

Slatyer, R. A., M. Hirst, and J. P. Sexton. 2013. Niche breadth predicts geographical range size: a general ecological pattern. Ecol. Lett. 16:1104–1114.

Stefanescu, C., J. Carnicer, and J. Penuelas. 2011. Determinants of species richness in generalist and specialist Mediterranean butterflies: the negative synergistic forces of climate and habitat change. Ecography 34:353–363.

Sturtevant, B. R., G. L. Achtemeier, J. J. Charney, D. P. Anderson, B. J. Cooke, and P. A. Townsend. 2013. Long-distance dispersal of spruce budworm (Choristoneura fumiferana Clemens) in Minnesota (USA) and Ontario (Canada) via the atmospheric pathway. Agric. For. Meteorol. 168:186–200.

Sverdrup-Thygeson, A., O. Skarpaas, and F. Ødegaard. 2010. Hollow oaks and beetle conservation: the significance of the surroundings. Biodivers. Conserv. 19:837–852.

Sverdrup-Thygeson, A., A. Rasmussen, O. Hanssen, and M. Evju. 2014. Gjenbesøk av hule eiker kartlagt for 30 år siden. INA Fagrapport 23:1–30.

The Saproxylic Database 2014. Available at http://radon.uio.no/WDD/Login.aspx?ReturnUrl=%2fwdd%2fDefault.aspx.

Ulyshen, M. D. 2014. Wood decomposition as influenced by invertebrates. Biol. Rev. Camb. Philos. Soc. 1–17. doi:10.1111/brv.12158.

Vera, F. W. M. 2000. Grazing ecology and forest history. CABI Publishing, Wallingford, U.K.

Vodka, S., M. Konvicka, and L. Cizek. 2009. Habitat preferences of oak-feeding xylophagous beetles in a temperate woodland: implications for forest history and management. J. Insect Conserv. 13:553–562.

World Meteorological Organization. 2014. Greenhouse Gas Bulletin - The state of greenhouse gases in the atmosphere based on global observations through 2013. World Meteorological Organization, Geneva.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Location of all 308 oaks from 105 sites sampled for beetles in the present study.

Table S2. Categorization of dead wood inhabiting beetles species according to oak association and primary geographical distribution.

Table S3. Results of backwards stepwise selection of six models all including four predictor variables: Temperature, Precipitation, Oak Circumference and Openness around trees.

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Supplementary material

Table S1. Location of all 308 oaks from 105 sites sampled for beetles in the present study.

Country	Site	OakID	UTM33_X	UTM33_Y	Responsible Author
Norway	Vollebekk/Korsegården	AA1	260867	6621558	Anne Sverdrup-Thygeson
Norway	Årosveten	AR1	77806	6458628	Anne Sverdrup-Thygeson
Norway	Årosveten	AR2	77683	6458842	Anne Sverdrup-Thygeson
Norway	Årosveten	AR3	77638	6458847	Anne Sverdrup-Thygeson
Norway	Årosveten	AR4	77608	6458967	Anne Sverdrup-Thygeson
Norway	Årosveten	AR5	77684	6459096	Anne Sverdrup-Thygeson
Norway	Askedalsåsane	AS1	207211	6558501	Anne Sverdrup-Thygeson
Norway	Bøhler, Gjelleråsen	BG1	274885	6656350	Anne Sverdrup-Thygeson
Norway	Berge landskapsvernområde	BL1	12946	6718980	Anne Sverdrup-Thygeson
Norway	Berge landskapsvernområde	BL2	12936	6719005	Anne Sverdrup-Thygeson
Norway	Berge landskapsvernområde	BL3	12901	6718952	Anne Sverdrup-Thygeson
Norway	Berge landskapsvernområde	BL4	12858	6718864	Anne Sverdrup-Thygeson
Norway	Berge landskapsvernområde	BL5	12819	6718853	Anne Sverdrup-Thygeson
Norway	Bog (ved Carlberg)	BO1	253816	6592437	Anne Sverdrup-Thygeson
Norway	Brenndalsskarven	BR1	206851	6578045	Anne Sverdrup-Thygeson
Norway	Brenndalsskarven	BR2	206846	6578019	Anne Sverdrup-Thygeson
Norway	Brenndalsskarven	BR3	206876	6578016	Anne Sverdrup-Thygeson
Norway	Brenndalsskarven	BR4	206958	6578016	Anne Sverdrup-Thygeson
Norway	Brenndalsskarven	BR5	206828	6578102	Anne Sverdrup-Thygeson
Norway	Budalsåsen	BU1	215785	6566196	Anne Sverdrup-Thygeson
Norway	Budalsåsen	BU2	215804	6566182	Anne Sverdrup-Thygeson
Norway	Budalsåsen	BU3	215755	6566302	Anne Sverdrup-Thygeson
Norway	Budalsåsen	BU4	215638	6566262	Anne Sverdrup-Thygeson
Norway	Budalsåsen	BU5	215643	6566317	Anne Sverdrup-Thygeson
Norway	Fjellstad (Asbjørnseneika)	FJ1	280218	6664849	Anne Sverdrup-Thygeson
Norway	Gangseid	GA1	123223	6537857	Anne Sverdrup-Thygeson
Norway	Gangseid	GA2	123196	6537853	Anne Sverdrup-Thygeson
Norway	Gangseid	GA3	123190	6537816	Anne Sverdrup-Thygeson
Norway	Gangseid	GA4	123214	6537943	Anne Sverdrup-Thygeson
Norway	Gangseid	GA5	123221	6537942	Anne Sverdrup-Thygeson
Norway	Gjønnesvannet	GJ1	214657	6569733	Anne Sverdrup-Thygeson
Norway	Karljohansvern	KJ1	244248	6595798	Anne Sverdrup-Thygeson
Norway	Karljohansvern	KJ2	244272	6595842	Anne Sverdrup-Thygeson
Norway	Karljohansvern	KJ3	244243	6595743	Anne Sverdrup-Thygeson
Norway	Karljohansvern	KJ4	244270	6595730	Anne Sverdrup-Thygeson
Norway	Karljohansvern	KJ5	244185	6595730	Anne Sverdrup-Thygeson
Norway	Knardal	KN1	293303	6558409	Anne Sverdrup-Thygeson
Norway	Knardal	KN2	293281	6558471	Anne Sverdrup-Thygeson
Norway	Knardal	KN3	293309	6558516	Anne Sverdrup-Thygeson
Norway	Knardal	KN4	293343	6558500	Anne Sverdrup-Thygeson
Norway	Knardal	KN6	293678	6558433	Anne Sverdrup-Thygeson
Norway	Eikvang (Kjoseeika)	KO1	208960	6563444	Anne Sverdrup-Thygeson
Norway	Kvelderønningen	KR1	210364	6573419	Anne Sverdrup-Thygeson
Norway	Kvelderønningen	KR2	210167	6573730	Anne Sverdrup-Thygeson
Norway	Kurland	KU1	277665	6650544	Anne Sverdrup-Thygeson
Norway	Store Limtjønn	LI1	210047	6572601	Anne Sverdrup-Thygeson

Norway	Melsomvik	ME1	234339	6574060	Anne Sverdrup-Thygeson
Norway	Melsomvik	ME2	234286	6574111	Anne Sverdrup-Thygeson
Norway	Melsomvik	ME3	234266	6573868	Anne Sverdrup-Thygeson
Norway	Melsomvik	ME4	234473	6573642	Anne Sverdrup-Thygeson
Norway	Melsomvik	ME5	234466	6573616	Anne Sverdrup-Thygeson
Norway	Montebello	MO1	257996	6651634	Anne Sverdrup-Thygeson
Norway	Montebello	MO2	257972	6651646	Anne Sverdrup-Thygeson
Norway	Montebello	MO3	257953	6651587	Anne Sverdrup-Thygeson
Norway	Montebello	MO4	257953	6651625	Anne Sverdrup-Thygeson
Norway	Montebello	MO5	257962	6651606	Anne Sverdrup-Thygeson
Norway	Østøya	OO1	243320	6598057	Anne Sverdrup-Thygeson
Norway	Østøya	OO2	243310	6598038	Anne Sverdrup-Thygeson
Norway	Østøya	OO3	243223	6598287	Anne Sverdrup-Thygeson
Norway	Østøya	OO4	243283	6598373	Anne Sverdrup-Thygeson
Norway	Østøya	OO5	243212	6598402	Anne Sverdrup-Thygeson
Norway	Pauler	PA1	210086	6557777	Anne Sverdrup-Thygeson
Norway	Ris (Risbakken 22)	RB1	259883	6653023	Anne Sverdrup-Thygeson
Norway	Søndre Odbergsetra (Rimstad)	RI1	209614	6578345	Anne Sverdrup-Thygeson
Norway	Sandvikskollane	SA1	207040	6569131	Anne Sverdrup-Thygeson
Norway	Sandvikskollane	SA2	206601	6569019	Anne Sverdrup-Thygeson
Norway	Simonstona	SI1	121002	6537596	Anne Sverdrup-Thygeson
Norway	Simonstona	SI2	121018	6537765	Anne Sverdrup-Thygeson
Norway	Simonstona	SI3	121079	6537808	Anne Sverdrup-Thygeson
Norway	Simonstona	SI4	121112	6537824	Anne Sverdrup-Thygeson
Norway	Simonstona	SI5	121080	6537755	Anne Sverdrup-Thygeson
Norway	Skeianes	SK1	24179	6727712	Anne Sverdrup-Thygeson
Norway	Skeianes	SK2	24185	6727746	Anne Sverdrup-Thygeson
Norway	Skeianes	SK3	24202	6727756	Anne Sverdrup-Thygeson
Norway	Skeianes	SK4	24211	6727785	Anne Sverdrup-Thygeson
Norway	Skeianes	SK5	24286	6727809	Anne Sverdrup-Thygeson
Norway	Steinknapp Øst	SO1	157912	6564176	Anne Sverdrup-Thygeson
Norway	Steinknapp Øst	SO2	157780	6564330	Anne Sverdrup-Thygeson
Norway	Steinknapp Øst	SO4	157747	6564385	Anne Sverdrup-Thygeson
Norway	Steinknapp Øst	SO5	157739	6564401	Anne Sverdrup-Thygeson
Norway	Steinknapp Øst	SO6	157770	6564326	Anne Sverdrup-Thygeson
Norway	Steinknapp Vest	SV1	157012	6563991	Anne Sverdrup-Thygeson
Norway	Steinknapp Vest	SV2	157003	6564000	Anne Sverdrup-Thygeson
Norway	Steinknapp Vest	SV3	157005	6564009	Anne Sverdrup-Thygeson
Norway	Steinknapp Vest	SV4	156965	6564090	Anne Sverdrup-Thygeson
Norway	Tanum	TA1	247154	6648790	Anne Sverdrup-Thygeson
Norway	Tomb	TO1	261734	6583346	Anne Sverdrup-Thygeson
Norway	Vassbotn	VA1	208708	6558882	Anne Sverdrup-Thygeson
Norway	Vemannsås	VE1	211336	6565841	Anne Sverdrup-Thygeson
Norway	Vemannsås	VE2	211233	6565815	Anne Sverdrup-Thygeson
Norway	Vemannsås	VE3	211277	6566151	Anne Sverdrup-Thygeson
Norway	Vemannsås	VE4	211098	6565824	Anne Sverdrup-Thygeson
Norway	Vemannsås	VE5	211174	6565846	Anne Sverdrup-Thygeson
Norway	Veholt	VH1	188322	6568387	Anne Sverdrup-Thygeson
Norway	Bjørnehula i Kjosdalen	BjVA1	84431	6463516	Hanne Eik Pilskog
Norway	Brekkeseter	BrVE3	210489	6557857	Hanne Eik Pilskog
Norway	Engene, Kjose	EnVE10	205985	6563697	Hanne Eik Pilskog
Norway	Fuglevik	FuVE1	213582	6549028	Hanne Eik Pilskog

Norway	Gangdalen mot Otra	GaVA1	85713	6471429	Hanne Eik Pilskog
Norway	Gillsveien v/Gillsvann	GiVA1	90446	6470269	Hanne Eik Pilskog
Norway	Håstøl	HaaAA5	106295	6502760	Hanne Eik Pilskog
Norway	Håverstad	HaavAA9	99125	6505579	Hanne Eik Pilskog
Norway	Håvaldsrød	HaaVE2	212459	6555682	Hanne Eik Pilskog
Norway	Hushovd	HuAA3	107380	6524889	Hanne Eik Pilskog
Norway	Hovland Ø	Hul3	98818	6514990	Hanne Eik Pilskog
Norway	Kverndalen	KdAA13	110814	6476980	Hanne Eik Pilskog
Norway	Kiste ved Lakssjø	KiTE1	204060	6578440	Hanne Eik Pilskog
Norway	Lysebo	LyVE3	211936	6567273	Hanne Eik Pilskog
Norway	Ødegården	OdVE2	206920	6548066	Hanne Eik Pilskog
Norway	Øgården	OgVE8	209015	6559909	Hanne Eik Pilskog
Norway	Retterholt	ReAA3	104232	6504430	Hanne Eik Pilskog
Norway	Røsaker S	ROSK2	195184	6577850	Hanne Eik Pilskog
Norway	Sekkebekk	SeAA5	110133	6475185	Hanne Eik Pilskog
Norway	Skåre	SkAA3	101228	6515241	Hanne Eik Pilskog
Norway	Skjærsjø	SkVE11	210731	6573043	Hanne Eik Pilskog
Norway	Søndre Odbergsetra	SOVE3	209688	6578532	Hanne Eik Pilskog
Norway	Stueåsen	StVE1	208784	6563384	Hanne Eik Pilskog
Norway	Eg Sykehus	SyVA1	87590	6468677	Hanne Eik Pilskog
Norway	Tjomsevann	TjVA1	79244	6462450	Hanne Eik Pilskog
Norway	Tveitetjønnane SØ	TvAA1	103056	6481036	Hanne Eik Pilskog
Norway	Tveitemyrane	TveAA2	105452	6481213	Hanne Eik Pilskog
Norway	Vassbotnvannet	VaVE3	208308	6558526	Hanne Eik Pilskog
Sweden	Sundsbro	SvLiSun1	545137	6466251	Nicklas Jansson
Sweden	Sundsbro	SvLiSun2	545129	6466231	Nicklas Jansson
Sweden	Sundsbro	SvLiSun3	545184	6466233	Nicklas Jansson
Sweden	Sundsbro	SvLiSun5	545114	6466338	Nicklas Jansson
Sweden	Sturefors-S	SvLiStS1	544876	6466295	Nicklas Jansson
Sweden	Sturefors-S	SvLiStS3	544692	6466346	Nicklas Jansson
Sweden	Sturefors-N	SvLiStN1	544764	6466347	Nicklas Jansson
Sweden	Sturefors-N	SvLiStN2	544842	6466528	Nicklas Jansson
Sweden	Sturefors-N	SvLiStN4	544801	6466539	Nicklas Jansson
Sweden	Sturefors-N	SvLiStN5	544832	6466508	Nicklas Jansson
Sweden	Hjorthägnet-N	SvLiHjN1	543306	6459665	Nicklas Jansson
Sweden	Hjorthägnet-N	SvLiHjN2	543333	6459708	Nicklas Jansson
Sweden	Hjorthägnet-N	SvLiHjN3	543375	6459679	Nicklas Jansson
Sweden	Hjorthägnet-N	SvLiHjN4	543395	6459668	Nicklas Jansson
Sweden	Hjorthägnet-N	SvLiHjN5	543415	6459679	Nicklas Jansson
Sweden	Hjorthägnet-S	SvLiHjS1	543300	6459559	Nicklas Jansson
Sweden	Hjorthägnet-S	SvLiHjS2	543336	6459548	Nicklas Jansson
Sweden	Hjorthägnet-S	SvLiHjS3	543366	6459528	Nicklas Jansson
Sweden	Hjorthägnet-S	SvLiHjS4	543364	6459532	Nicklas Jansson
Sweden	Hjorthägnet-S	SvLiHjS5	543293	6459581	Nicklas Jansson
Sweden	Bjärka äng	SvLiBjä1	544379	6459714	Nicklas Jansson
Sweden	Bjärka äng	SvLiBjä2	544417	6459740	Nicklas Jansson
Sweden	Bjärka äng	SvLiBjä3	544431	6459635	Nicklas Jansson
Sweden	Bjärka äng	SvLiBjä4	544322	6459598	Nicklas Jansson
Sweden	Bjärka äng	SvLiBjä5	544253	6459662	Nicklas Jansson
Sweden	Fornhagen	SvLiFor1	543865	6459257	Nicklas Jansson
Sweden	Fornhagen	SvLiFor2	543938	6459288	Nicklas Jansson
Sweden	Fornhagen	SvLiFor3	543871	6459285	Nicklas Jansson
Sweden	Fornhagen	SvLiFor4	543875	6459293	Nicklas Jansson

Sweden	Fornhagen	SvLiFor5	543885	6459374	Nicklas Jansson
Sweden	Orräng 1	SvLiOrA1	550310	6461762	Nicklas Jansson
Sweden	Orräng 1	SvLiOrA2	550316	6461797	Nicklas Jansson
Sweden	Orräng 1	SvLiOrA3	550448	6461810	Nicklas Jansson
Sweden	Orräng 1	SvLiOrA4	550377	6461712	Nicklas Jansson
Sweden	Orräng 1	SvLiOrA5	550416	6461742	Nicklas Jansson
Sweden	Orräng 2	SvLiOrB1	550166	6461569	Nicklas Jansson
Sweden	Orräng 2	SvLiOrB2	550147	6461531	Nicklas Jansson
Sweden	Orräng 2	SvLiOrB3	550162	6461524	Nicklas Jansson
Sweden	Orräng 2	SvLiOrB4	550152	6461502	Nicklas Jansson
Sweden	Orräng 2	SvLiOrB5	550156	6461513	Nicklas Jansson
Sweden	Orräng 3	SvLiOrC2	550026	6461563	Nicklas Jansson
Sweden	Orräng 3	SvLiOrC3	549940	6461595	Nicklas Jansson
Sweden	Orräng 3	SvLiOrC4	549950	6461636	Nicklas Jansson
Sweden	Orräng 3	SvLiOrC5	549954	6461627	Nicklas Jansson
Sweden	Skaggebo	SvLiSka1	543201	6457103	Nicklas Jansson
Sweden	Skaggebo	SvLiSka2	543198	6457131	Nicklas Jansson
Sweden	Skaggebo	SvLiSka3	543225	6457077	Nicklas Jansson
Sweden	Skaggebo	SvLiSka4	543241	6457062	Nicklas Jansson
Sweden	Skaggebo	SvLiSka5	543223	6457021	Nicklas Jansson
Sweden	Labbenäs	SvLiLab1	539407	6463751	Nicklas Jansson
Sweden	Labbenäs	SvLiLab2	539415	6463759	Nicklas Jansson
Sweden	Labbenäs	SvLiLab3	539480	6463691	Nicklas Jansson
Sweden	Labbenäs	SvLiLabextra	539457	6463730	Nicklas Jansson
Sweden	Labbenäs	SvLiLab4	539557	6463684	Nicklas Jansson
Sweden	Labbenäs	SvLiLab5	539573	6463681	Nicklas Jansson
Sweden	Labbenäs	SvLiLab6	539577	6463670	Nicklas Jansson
Sweden	Brokind skolh.	SvLiBro1	539027	6452097	Nicklas Jansson
Sweden	Brokind skolh.	SvLiBro2	539053	6451994	Nicklas Jansson
Sweden	Brokind skolh.	SvLiBro3	539036	6451932	Nicklas Jansson
Sweden	Brokind skolh.	SvLiBro4	539115	6451822	Nicklas Jansson
Sweden	Brokind skolh.	SvLiBro5	538998	6451766	Nicklas Jansson
Sweden	Sätra Humpen	SvLiSät1	544161	6461319	Nicklas Jansson
Sweden	Sätra Humpen	SvLiSät2	544173	6461332	Nicklas Jansson
Sweden	Sätra Humpen	SvLiSät3	544124	6461331	Nicklas Jansson
Sweden	Sätra Humpen	SvLiSät4	544098	6461376	Nicklas Jansson
Sweden	Sätra Humpen	SvLiSät5	543981	6460500	Nicklas Jansson
Sweden	Långvassudde Ö	SvLiLåÖ1	546269	6466248	Nicklas Jansson
Sweden	Långvassudde Ö	SvLiLåÖ2	546273	6466253	Nicklas Jansson
Sweden	Långvassudde Ö	SvLiLåÖ3	546267	6466287	Nicklas Jansson
Sweden	Långvassudde Ö	SvLiLåÖ4	546226	6466089	Nicklas Jansson
Sweden	Långvassudde Ö	SvLiLåÖ5	546246	6466058	Nicklas Jansson
Sweden	Långvassudde V	SvLiLåV1	546083	6466427	Nicklas Jansson
Sweden	Långvassudde V	SvLiLåV3	546073	6466481	Nicklas Jansson
Sweden	Långvassudde V	SvLiLåV5	546034	6466392	Nicklas Jansson
Sweden	Biskopstorp	SvHaBis1	369494	6296135	Nicklas Jansson
Sweden	Biskopstorp	SvHaBis2	369494	6296135	Nicklas Jansson
Sweden	Biskopstorp	SvHaBis3	369494	6296135	Nicklas Jansson
Sweden	Biskopstorp	SvHaBis4	369494	6296135	Nicklas Jansson
Sweden	Biskopstorp	SvHaBis5	369494	6296135	Nicklas Jansson
Sweden	Gässlösa	SvHaGäs4	348275	6336763	Nicklas Jansson
Sweden	Gässlösa	SvHaGäs5	348275	6336763	Nicklas Jansson
Sweden	Gässlösa	SvHaGäs6	348275	6336763	Nicklas Jansson

Sweden	Hördalen	SvHaHör1	318724	6376467	Nicklas Jansson
Sweden	Hördalen	SvHaHör2	318724	6376467	Nicklas Jansson
Sweden	Hördalen	SvHaHör3	318724	6376467	Nicklas Jansson
Sweden	Hördalen	SvHaHör6	318724	6376467	Nicklas Jansson
Sweden	Stövlaberget	SvHaStö1	370454	6301154	Nicklas Jansson
Sweden	Stövlaberget	SvHaStö2	370454	6301154	Nicklas Jansson
Sweden	Stövlaberget	SvHaStö3	370454	6301154	Nicklas Jansson
Sweden	Stövlaberget	SvHaStö5	370454	6301154	Nicklas Jansson
Sweden	Särö	SvHaSär1	315806	6377854	Nicklas Jansson
Sweden	Särö	SvHaSär2	315806	6377854	Nicklas Jansson
Sweden	Särö	SvHaSär3	315806	6377854	Nicklas Jansson
Sweden	Särö	SvHaSär5	315806	6377854	Nicklas Jansson
Sweden	Särö	SvHaSär6	315806	6377854	Nicklas Jansson
Sweden	Tjolöholm	SvHaTjo1	324942	6365970	Nicklas Jansson
Sweden	Tjolöholm	SvHaTjo2	324942	6365970	Nicklas Jansson
Sweden	Tjolöholm	SvHaTjo3	324942	6365970	Nicklas Jansson
Sweden	Tjolöholm	SvHaTjo4	324942	6365970	Nicklas Jansson
Sweden	Åkraberga	SvHaÅkr1	332990	6349744	Nicklas Jansson
Sweden	Åkraberga	SvHaÅkr2	332990	6349744	Nicklas Jansson
Sweden	Åkraberga	SvHaÅkr5	332990	6349744	Nicklas Jansson
Sweden	Åkraberga	SvHaÅkr6	332990	6349744	Nicklas Jansson
Sweden	Åkersberga	Akersberga1	686091	6599064	Mats Jonsell
Sweden	Åkersberga	Akersberga2	686031	6599097	Mats Jonsell
Sweden	Åkersberga	Akersberga3	686001	6599409	Mats Jonsell
Sweden	Åkersberga	Akersberga4	685946	6599366	Mats Jonsell
Sweden	Biskops-Arnö	Arno1	640808	6616772	Mats Jonsell
Sweden	Biskops-Arnö	Arno2	640758	6616826	Mats Jonsell
Sweden	Biskops-Arnö	Arno3	640733	6616854	Mats Jonsell
Sweden	Biskops-Arnö	Arno4	640989	6616542	Mats Jonsell
Sweden	Biskops-Arnö	Biskops_Arno1	640808	6616772	Mats Jonsell
Sweden	Biskops-Arnö	Biskops_Arno2	640758	6616826	Mats Jonsell
Sweden	Biskops-Arnö	Biskops_Arno3	640989	6616542	Mats Jonsell
Sweden	Biskops-Arnö	Biskops_Arno4	641011	6616511	Mats Jonsell
Sweden	Drottningholm	Drottningholm5	663583	6578978	Mats Jonsell
Sweden	Drottningholm	Drottningholm6	663472	6579182	Mats Jonsell
Sweden	Drottningholm	Drottningholm7	663410	6579189	Mats Jonsell
Sweden	Drottningholm	Drottningholm8	663813	6579120	Mats Jonsell
Sweden	Edeby ekhagar	Edeby_ekhagar1	662777	6577252	Mats Jonsell
Sweden	Edeby ekhagar	Edeby_ekhagar2	662848	6577280	Mats Jonsell
Sweden	Edeby ekhagar	Edeby_ekhagar3	662926	6577247	Mats Jonsell
Sweden	Edeby ekhagar	Edeby_ekhagar4	662842	6577130	Mats Jonsell
Sweden	Ekudden	Ekudden1	679620	6572827	Mats Jonsell
Sweden	Ekudden	Ekudden2	679588	6572647	Mats Jonsell
Sweden	Ekudden	Ekudden3	679638	6572701	Mats Jonsell
Sweden	Ekudden	Ekudden4	679618	6572717	Mats Jonsell
Sweden	Fånö	F1	634890	6605446	Mats Jonsell
Sweden	Fånö	F2	634759	6605506	Mats Jonsell
Sweden	Fånö	F3	634805	6605639	Mats Jonsell
Sweden	Fånö	F4	634494	6606038	Mats Jonsell
Sweden	Hågadalen	Hagadalen1	645956	6633895	Mats Jonsell
Sweden	Hågadalen	Hagadalen2	645617	6634002	Mats Jonsell
Sweden	Hågadalen	Hagadalen3	645820	6633534	Mats Jonsell
Sweden	Hågadalen	Hagadalen4	645260	6635470	Mats Jonsell

Sweden	Harparbollund	Harparbol1	667947	6641276	Mats Jonsell
Sweden	Harparbollund	Harparbol2	668018	6641231	Mats Jonsell
Sweden	Harparbollund	Harparbol3	668065	6641285	Mats Jonsell
Sweden	Harparbollund	Harparbol4	668085	6641314	Mats Jonsell
Sweden	Hjulsta	Hjul1	613446	6601220	Mats Jonsell
Sweden	Hjulsta	Hjul2	613864	6601473	Mats Jonsell
Sweden	Hjulsta	Hjul3	613862	6601194	Mats Jonsell
Sweden	Hjulsta	Hjul4	613917	6601294	Mats Jonsell
Sweden	Kalhäll. Lädersättra	KL1	659580	6593086	Mats Jonsell
Sweden	Kalhäll. Lädersättra	KL2	659602	6593137	Mats Jonsell
Sweden	Kalhäll. Lädersättra	KL3	659709	6593097	Mats Jonsell
Sweden	Kalhäll. Lädersättra	KL4	659755	6593054	Mats Jonsell
Sweden	Kristineholm	Kristineholm1	694231	6639502	Mats Jonsell
Sweden	Kristineholm	Kristineholm2	694266	6639535	Mats Jonsell
Sweden	Kristineholm	Kristineholm3	694617	6639777	Mats Jonsell
Sweden	Kristineholm	Kristineholm4	694533	6639626	Mats Jonsell
Sweden	Krusenberg	Krus1	648520	6624922	Mats Jonsell
Sweden	Krusenberg	Krus2	648710	6625075	Mats Jonsell
Sweden	Krusenberg	Krus3	648564	6625040	Mats Jonsell
Sweden	Krusenberg	Krus4	648498	6625281	Mats Jonsell
Sweden	Krusenberg	Krus5	648600	6625607	Mats Jonsell
Sweden	Näsudden	Nasudden1	660635	6641834	Mats Jonsell
Sweden	Näsudden	Nasudden2	660588	6641757	Mats Jonsell
Sweden	Näsudden	Nasudden3	660633	6641591	Mats Jonsell
Sweden	Näsudden	Nasudden4	660538	6641610	Mats Jonsell
Sweden	Norrmalma	Norrmalma1	704715	6638551	Mats Jonsell
Sweden	Norrmalma	Norrmalma2	704743	6638640	Mats Jonsell
Sweden	Norrmalma	Norrmalma3	704681	6638520	Mats Jonsell
Sweden	Norrmalma	Norrmalma4	704615	6638680	Mats Jonsell
Sweden	Olivedal	Olivedal1	662444	6637377	Mats Jonsell
Sweden	Olivedal	Olivedal2	662382	6637377	Mats Jonsell
Sweden	Olivedal	Olivedal3	662293	6637402	Mats Jonsell
Sweden	Olivedal	Olivedal4	662328	6637459	Mats Jonsell
Sweden	Parnassen	Parnassen1	634496	6615423	Mats Jonsell
Sweden	Parnassen	Parnassen3	634091	6615256	Mats Jonsell
Sweden	Parnassen	Parnassen4	633974	6615305	Mats Jonsell
Sweden	Salsta	Salsta1	652388	6659194	Mats Jonsell
Sweden	Salsta	Salsta2	652442	6658968	Mats Jonsell
Sweden	Salsta	Salsta3	653131	6657896	Mats Jonsell
Sweden	Salsta	Salsta4	653031	6657949	Mats Jonsell
Sweden	Sickla udde	Sickla_udde1	677076	6578012	Mats Jonsell
Sweden	Sickla udde	Sickla_udde2	676987	6578118	Mats Jonsell
Sweden	Sickla udde	Sickla_udde3	676985	6578171	Mats Jonsell
Sweden	Sickla udde	Sickla_udde4	677164	6578010	Mats Jonsell
Sweden	Tyska botten	Tyska_botten1	664260	6581324	Mats Jonsell
Sweden	Tyska botten	Tyska_botten2	664202	6581377	Mats Jonsell
Sweden	Tyska botten	Tyska_botten3	664099	6581406	Mats Jonsell
Sweden	Tyska botten	Tyska_botten4	664053	6581401	Mats Jonsell
Sweden	Vik	Vik1	639222	6624858	Mats Jonsell
Sweden	Vik	Vik2	639257	6625060	Mats Jonsell
Sweden	Vik	Vik3	639077	6625219	Mats Jonsell
Sweden	Vik	Vik4	638915	6625049	Mats Jonsell

Table S2. Categorization of dead wood inhabiting beetles species according to oak association and primary geographical distribution. Oak association follows The Saproxylic Database (http://radon.uio.no/WDD/Login.aspx?ReturnUrl=%2fwdd%2fDefault.aspx) with specialists defined as species marked with p for oak or with only one tree association (x for oak). Generalists include all other species associated with oak (x for oak). The authors Mats Jonsell (MJ) and Niclas Jansson (NJ) also noted divergence between The Saproxylic database and their field experience. The species are according to Löbl, I. & A. Smetana 2003-2012. Catalogue of Palaearctic Coleoptera Vol I-VIII. – Apollo Books, Stenstrup, Denmark.

Family	**Name**	**Oak association used**	**Oak association divergence MJ and NJ**	**Primary geographical distribution**
Histeridae				
	Plegaderus caesus (Herbst, 1792)	Generalist	-	Southern
	Gnathoncus nannetensis (Marseul, 1862)	Generalist	-	Northern
	Dendrophilus punctatus (Herbst, 1792)	Generalist	-	Northern
	Paromalus flavicornis (Herbst, 1792)	Generalist	-	Southern
Leiodidae				
	Nemadus colonoides (Kraatz, 1851)	Specialist	Generalist	Northern
Staphylinidae				
	Stenichnus godarti (Latreille, 1806)	Specialist	Generalist	Southern
	Stenichnus bicolor (Denny, 1825)	Generalist	-	Northern
	Scydmaenus hellwigii (Herbst, 1792)	Specialist	Generalist	Southern
	Velleius dilatatus (Fabricius, 1787)	Generalist	-	Southern
	Quedius microps (Gravenhorst, 1847)	Generalist	-	Southern
	Quedius mesomelinus (Marsham, 1802)	Generalist	-	Other
	Quedius maurus (Sahlberg, 1830)	Generalist	-	Northern
	Quedius cruentus (Olivier, 1795)	Generalist	-	Southern
	Quedius invreae Gridelli, 1924	Specialist	Generalist	Southern
	Quedius brevicornis Thomson, 1860	Generalist	-	Southern
	Quedius scitus (Gravenhorst, 1806)	Specialist	Generalist	Southern
	Quedius xanthopus Erichson, 1839	Generalist	-	Northern
	Quedius plagiatus (Mannerheim, 1843)	Generalist	-	Northern
	Euplectus brunneus (Grimmer, 1841)	Generalist	-	Southern
	Euplectus nanus (Reichenbach, 1816)	Generalist	-	Northern
	Euplectus piceus Motschulsky, 1835	Generalist	-	Southern
	Euplectus punctatus Mulsant, 1861	Generalist	-	Northern
	Euplectus karstenii (Reichenbach, 1816)	Generalist	-	Northern
	Euplectus mutator Fauvel, 1895	Generalist	-	Northern
	Batrisodes adnexus (Hampe, 1863)	Specialist	Generalist	Southern
	Batrisodes delaporti (Aubé, 1833)	Specialist	Generalist	Southern
	Batrisodes venustus (Reichenbach, 1816)	Generalist	-	Southern
	Bibloporus bicolor (Denny, 1825)	Generalist	-	Northern
	Bibloporus minutus Raffray, 1914	Generalist	-	Northern
	Hapalaraea pygmaea (Paykull, 1800)	Generalist	Not in Oak	Northern
Trogidae				
	Trox scaber (Linnaeus, 1767)	Generalist	-	Southern
Scarabaeidae				
	Osmoderma eremita (Scopoli, 1763)	Specialist	Generalist	Southern
	Gnorimus nobilis (Linnaeus, 1758)	Generalist	-	Southern
	Protaetia marmorata (Fabricius, 1792)	Specialist	Generalist	Southern

	Protaetia metallica (Herbst, 1786)	Generalist	-	Southern
Lucanidae				
	Sinodendron cylindricum (Linnaeus, 1758)	Generalist	-	Southern
	Platycerus caraboides (Linnaeus, 1758)	Generalist	-	Southern
Scirtidae				
	Prionocyphon serricornis (Müller, 1821)	Generalist	-	Southern
Buprestidae				
	Agrilus angustulus (Illiger, 1803)	Generalist	Specialist	Southern
	Agrilus sulcicollis Lacordaire, 1835	Specialist	-	Southern
Elateridae				
	Stenagostus rhombeus (Olivier, 1790)	Generalist	-	Southern
	Denticollis linearis (Linnaeus, 1758)	Generalist	-	Northern
	Crepidophorus mutilatus (Rosenhauer, 1847)	Generalist	-	Northern
	Hypoganus inunctus (Lacordaire, 1835)	Generalist	-	Southern
	Calambus bipustulatus (Linnaeus, 1767)	Generalist	-	Southern
	Procraerus tibialis (Lacordaire, 1835)	Generalist	Specialist	Southern
	Ampedus cardinalis (Schiödte, 1865)	Specialist	-	Other
	Ampedus hjorti (Rye, 1905)	Specialist	-	Other
	Ampedus nigroflavus (Goeze, 1777)	Generalist	-	Southern
	Ampedus praeustus (Fabricius, 1792)	Generalist	-	Other
	Ampedus pomorum (Herbst, 1784)	Generalist	-	Northern
	Ampedus balteatus (Linnaeus, 1758)	Generalist	-	Northern
	Ampedus nigrinus (Herbst, 1784)	Specialist	-	Northern
	Elater ferrugineus Linnaeus, 1758	Specialist	Generalist	Other
	Melanotus villosus (Geoffroy, 1785)	Generalist	-	Southern
Eucnemidae				
	Melasis buprestoides (Linnaeus, 1760)	Generalist	-	Southern
	Xylophilus corticalis (Paykull, 1800)	Generalist	-	Other
Dermestidae				
	Attagenus pellio (Linnaeus, 1758)	Generalist	-	Other
	Megatoma undata (Linnaeus, 1758)	Generalist	-	Northern
	Ctesias serra (Fabricius, 1792)	Generalist	-	Northern
	Anthrenus scrophulariae (Linnaeus, 1758)	Generalist	-	Southern
	Anthrenus museorum (Linnaeus, 1760)	Generalist	-	Southern
Ptinidae				
	Ptinomorphus imperialis (Linnaeus, 1767)	Generalist	-	Southern
	Ptinus rufipes Olivier, 1790	Specialist	-	Southern
	Ptinus fur (Linnaeus, 1758)	Generalist	-	Other
	Ptinus subpillosus Sturm, 1837	Specialist	Generalist	Southern
	Grynobius planus (Fabricius, 1787)	Generalist	-	Northern
	Xestobium rufovillosum (Degeer, 1774)	Specialist	-	Other
	Oligomerus brunneus (Olivier, 1790)	Specialist	-	Southern
	Hadrobregmus pertinax (Linnaeus, 1758)	Generalist	-	Northern
	Gastrallus immarginatus (Müller, 1821)	Generalist	Specialist	Southern
	Cacotemnus rufipes (Fabricius, 1792)	Generalist	-	Northern
	Hemicoelus canaliculatus (Thomson, 1863)	Generalist	-	Northern
	Ptilinus pectinicornis (Linnaeus, 1758)	Generalist	-	Southern
	Xyletinus pectinatus (Fabricius, 1792)	Specialist	Generalist	Northern
	Dorcatoma flavicornis (Fabricius, 1792)	Generalist	Specialist	Northern
	Dorcatoma chrysomelina Sturm, 1837	Specialist	-	Northern
	Dorcatoma dresdensis Herbst, 1792	Generalist	-	Northern
Lymexylidae				
	Elateroides dermestoides (Linnaeus, 1760)	Generalist	-	Northern
	Lymexylon navale (Linnaeus, 1758)	Specialist	Generalist	Southern

Malachiidae				
	Hypebaeus flavipes (Fabricius, 1787)	Generalist	-	Southern
	Malachius bipustulatus (Linnaeus, 1758)	Generalist	-	Other
Trogossitidae				
	Grynocharis oblonga (Linnaeus, 1758)	Generalist	-	Northern
Cleridae				
	Tillus elongatus (Linnaeus, 1758)	Generalist	-	Southern
Dasytidae				
	Trichoceble memnonia (Kiesenwetter, 1861)	Generalist	-	Southern
Cryptophagidae				
	Cryptophagus confusus Bruce, 1934	Generalist	-	Northern
	Cryptophagus labilis Erichson, 1846	Generalist	-	Northern
	Cryptophagus populi Paykull, 1800	Generalist	-	Northern
	Cryptophagus quercinus Kraatz, 1852	Generalist	-	Northern
	Cryptophagus badius Sturm, 1845	Generalist	-	Northern
	Cryptophagus dentatus (Herbst, 1793)	Generalist	-	Southern
	Cryptophagus denticulatus Heer, 1841	Generalist	-	Northern
	Cryptophagus scanicus (Linnaeus, 1758)	Generalist	-	Northern
	Cryptophagus scutellatus Newman, 1834	Generalist	-	Other
	Cryptophagus setulosus Sturm, 1845	Generalist	-	Northern
	Atomaria morio Kolenati, 1846	Generalist	-	Southern
	Atomaria umbrina (Gyllenhal, 1827)	Generalist	-	Northern
Erotylidae				
	Dacne bipustulata (Thunberg, 1781)	Generalist	-	Northern
	Triplax russica (Linnaeus, 1758)	Generalist	-	Northern
	Cerylon histeroides (Fabricius, 1792)	Generalist	-	Northern
	Cerylon ferrugineum Stephens, 1830	Generalist	-	Northern
Endomychidae				
	Mycetaea subterranea (Fabricius, 1801)	Generalist	-	Southern
Zopheridae				
	Colydium filiforme Fabricius, 1792	Specialist	-	Southern
	Synchita humeralis (Fabricius, 1792)	Generalist	-	Other
Mycetophagidae				
	Triphyllus bicolor (Fabricius, 1777)	Generalist	-	Southern
	Litargus connexus (Geoffroy, 1785)	Generalist	-	Other
	Mycetophagus piceus (Fabricius, 1777)	Specialist	Generalist	Northern
Tenebrionidae				
	Mycetophagus multipunctatus Fabricius, 1792	Generalist	-	Northern
Salpingidae				
	Salpingus planirostris (Fabricius, 1787)	Generalist	-	Southern
	Salpingus ruficollis (Linnaeus, 1760)	Generalist	-	Northern
Aderidae				
	Aderus populneus (Creutzer, 1796)	Generalist	-	Southern
	Euglenes oculatus (Paykull, 1798)	Specialist	-	Northern
	Euglenes pygmaeus (Degeer, 1774)	Specialist	-	Other
Tenebrionidae				
	Uloma culinaris (Linnaeus, 1758)	Generalist	-	Southern
	Tenebrio opacus Duftschmid, 1812	Specialist	-	Southern
	Tenebrio molitor Linnaeus, 1758	Generalist	-	Southern
	Eledona agricola (Herbst, 1783)	Specialist	-	Other
	Palorus depressus (Fabricius, 1790)	Specialist	Generalist	Southern
	Allecula morio (Fabricius, 1787)	Generalist	-	Northern
	Prionychus ater (Fabricius, 1775)	Generalist	-	Southern

	Pseudocistela ceramboides (Linnaeus, 1758)	Generalist	-	Southern
	Mycetochara humeralis (Fabricius, 1787)	Generalist	-	Southern
	Mycetochara flavipes (Fabricius, 1792)	Generalist	-	Northern
	Mycetochara maura (Fabricius, 1792)	Generalist	-	Southern
	Corticeus fasciatus (Fabricius, 1790)	Specialist	-	Southern
	Diaperis boleti (Linnaeus, 1758)	Generalist	-	Southern
	Pentaphyllus testaceus (Hellwig, 1792)	Specialist	-	Southern
Scraptiidae				
	Scraptia fuscula Müller, 1821	Specialist	-	Southern
Tetratomidae				
	Hallomenus binotatus (Quensel, 1790)	Generalist	-	Other
Melandryidae				
	Orchesia fasciata (Illiger, 1798)	Generalist	-	Northern
	Orchesia micans (Panzer, 1793)	Generalist	-	Northern
	Orchesia minor Walker, 1837	Generalist	-	Northern
	Orchesia undulata Kraatz, 1853	Generalist	-	Southern
	Phloiotrya rufipes (Gyllenhal, 1810)	Generalist	-	Southern
	Conopalpus testaceus (Olivier, 1790)	Generalist	Specialist	Southern
Cerambycidae				
	Rhagium mordax (Degeer, 1775)	Generalist	-	Northern
	Rhagium inquisitor (Linnaeus, 1758)	Generalist	Not in Oak	Other
	Stenocorus meridianus (Linnaeus, 1758)	Generalist	-	Southern
	Grammoptera ruficornis (Fabricius, 1781)	Generalist	-	Southern
	Alosterna tabacicolor (Degeer, 1775)	Specialist	Generalist	Other
	Anoplodera sexguttata (Fabricius, 1775)	Specialist	-	Southern
	Leptura quadrifasciata Linnaeus, 1758	Generalist	-	Northern
	Stictoleptura maculicornis (Degeer, 1775)	Generalist	-	Southern
	Rutpela maculata (Poda, 1761)	Specialist	-	Southern
	Oxymirus cursor (Linnaeus, 1758)	Generalist	-	Northern
	Phymatodes testaceus (Linnaeus, 1758)	Generalist	-	Southern
	Clytus arietis (Linnaeus, 1758)	Specialist	Generalist	Southern
	Plagionotus detritus (Linnaeus, 1758)	Specialist	-	Southern
	Leiopus nebulosus (Linnaeus, 1758)	Specialist	Generalist	Southern
	Stenostola dubia (Laicharting, 1784)	Generalist	-	Southern
Curculionidae				
	Rhyncolus ater (Linnaeus, 1758)	Generalist	-	Northern
	Rhyncolus sculpturatus Waltl, 1839	Generalist	-	Other

Table S3. Results of backwards stepwise selection of six models all including four predictor variables: Temperature, Precipitation, Oak Circumference and Openness around trees. The analysis is performed in R using function glmer from package lme4 with a Poisson error distribution, log-link function and Nelder-Mead optimizer from package nloptr. The backward selection is based on Akaike's Information Criterion and the drop1 function.

Variable	Estimate	Std. Error	Z value	*p*-value
Response: Northern Specialists				
AIC Final Model: 769.5 (Initial: 774.1)				
Intercept	-0.186	0.201	-0.92	0.356
Circumference	0.213	0.061	3.48	<0.001
Temperature	0.425	0.114	3.74	<0.001
Response: Southern Specialists				
AIC Final Model: 801.4 (Initial: 804.8)				
Intercept	-0.024	0.073	-0.32	0.748
Circumference	0.107	0.062	1.74	0.082
Precipitation	-0.316	0.092	-3.44	<0.001
Response: Ubiquitous Specialists				
AIC Final Model: 634.8 (Initial: 637.7)				
Intercept	-0.537	0.085	-6.34	<0.001
Circumference	0.348	0.065	5.38	<0.001
Precipitation	-0.618	0.144	-4.30	<0.001
Response: Northern Generalists				
AIC Final Model: 1347.7 (Initial: 1352.9)				
Intercept				
Circumference	1.272	0.068	18.61	<0.001
	0.101	0.038	2.64	0.008
Response: Southern Generalists				
AIC Final Model: 1143.5 (Initial: 1146.5)				
Intercept	0.738	0.222	3.33	<0.001
Circumference	0.154	0.043	3.60	<0.001
Response: Ubiquitous Generalists				
AIC Final Model: 584.1 (Initial: 590.2)				
Intercept	-0.592	0.077	-7.68	<0.001
Precipitation	-0.167	0.097	-1.72	0.086

Paper II

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Research article

Effect of Habitat Size, Quality, and Isolation on Functional Groups of Beetles in Hollow Oaks

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Abstract

One of the largest threats to biodiversity is land use change and habitat loss. Hollow oaks (*Quercus* spp. L.) are well-defined patches that are hotspots for biodiversity and red-listed species, but they are often rare and fragmented in the landscape. We investigated the effect of patch size, habitat quality, and isolation on functional groups and red-listed saproxylic beetles in hollow oaks ($n = 40$) in Norway. The groups were defined by host tree association, trophic grouping, and red-listed status. Habitat quality, represented by tree form was most important in explaining species richness for most groups. Patch size, represented by circumference and amount of dead branches, was most important in explaining abundance. Isolation, that is single oaks compared with oaks in groups, had a negative effect on the abundance of beetles feeding both on wood and fungi (xylomycethopagous), as well as on species associated with broadleaved trees (oak semi-specialists), but did not affect species richness. This indicates that at this scale and in this landscape, isolated oaks are as species rich and valuable for conservation as other oaks, although some functional groups may be more vulnerable to isolation than others. The red-listed species only responded to patch size, indicating that oaks with large circumference and many dead branches are especially important for red-listed species and for conservation.

Key words: saproxylic, ancient tree, trophic group, fragmentation, Coleoptera

Currently, species are going extinct a thousand times faster than expected by fossil records (Millennium Ecosystem Assessment 2005) and we may already be entering the sixth mass extinction in the history of Earth (Barnosky et al. 2011). The largest threat to biodiversity and ecosystems is land use change and the subsequent loss of habitat (Sala et al. 2000, Millennium Ecosystem Assessment 2005). Loss of habitat also leads to fragmentation of the remaining patches with varying degrees of isolation (Andrén 1994). The effect of landscape fragmentation on species has been studied by several approaches, of which metapopulation theory and island biogeography (Hanski 1999, Ricketts 2001) are among the most important. Island biogeography, focusing on the effect of island size and isolation on populations and species, has been extended to include habitat patches on land, surrounded by nonhabitat referred to as the matrix (Hanski 1998, Dover and Settele 2009, Fischer et al. 2009, Franzén et al. 2012). Other important factors that can affect species richness of fragmented habitats is the degree of isolation and the size of the habitat patch (Andrén 1994, Benedick et al. 2006), as well as habitat patch quality (Thomas et al. 2001). To successfully conserve species richness, we need a better understanding of the responses to fragmentation. This is particularly true for species-rich groups such as insects, which include 1 million described species (IUCN Red List 2014) and contribute to important ecosystem services (Losey and Vaughan 2006). Understanding the patterns and responses of species in fragmented landscapes are essential for their conservation and should be a prioritized research task.

Several studies have tried to identify the traits that make species vulnerable to fragmented landscapes (Henle et al. 2004). Studies of insects reveal that degree of specialization in habitat and food requirements, dispersal ability, body size, population size, and reproductive capacity are traits that can influence species vulnerability (Henle et al. 2004, Benedick et al. 2006, Cagnolo et al. 2009). Species that are highly specialized with narrow niches are most vulnerable, whereas species that are more general in their habitat and food requirements, breed in ephemeral habitats or have rapid growth and dispersal are more likely to be successful (McKinney and Lockwood 1999, Franzén et al. 2012). Species are categorized according to their extinction risk in international and national red lists (IUCN Red List 2014), but the number of species at risk are likely to be higher (McKinney and Lockwood 1999) and a large number of species are not evaluated due to information deficiency (Nieto et al. 2014). The vulnerability of specialization and the

Holt's hypothesis, which proposed that specialized species on top of the food chain should have a stronger response to fragmentation and habitat loss than generalists (Holt et al. 1999), have been confirmed in several studies (Komonen et al. 2000, Valladares et al. 2006, Cagnolo et al. 2009).

Saproxylic species are species dependent on dead wood habitats or its inhabitants (Speight 1989), and they represent important decomposers with high species richness which is severely affected by land use changes. Modern forestry with clear-cutting and monocultures of planted trees has reduced the volumes of available dead wood and made old-growth forests rare or lacking in much of Europe (Grove 2002, Hanski 2008). Some species are highly specialized to certain host trees, whereas others can use a range of dead wood habitats independent of tree species (Grove 2002, Stokland et al. 2012). Oak (*Quercus* spp. L.) is a temperate broadleaved tree that can become close to 1,000 years old (Drobyshev and Niklasson 2010). As the tree grows old, the architectural diversity increases and a range of new microhabitats appear, such as dead branches, coarse bark, wood mould, and different types of rot (Alexander 2008). Oaks with hollows are normally older than 200 years (Ranius et al. 2009) and represent biodiversity hotspots (Kennedy and Southwood 1984, Sverdrup-Thygeson 2009, Bouget et al. 2014). The recruitment of such oaks is low. Most old-growth deciduous forests disappeared from Europe centuries ago, but the mature and ancient trees that still remain are threatened in large parts of Europe due to direct removal, intensification in forestry and agricultural landscapes, regrowth creating shade, lack of recruitment and pollution (Ranius et al. 2005, Gibbons et al. 2008, The Directorate for Nature Management 2012, Lindenmayer et al. 2012).

Hollow oaks are well defined 'patches' with a large number of rare and red-listed species (Ranius 2002b, Sverdrup-Thygeson 2009, The Directorate for Nature Management 2012). Although areas of high density of ancient hollow oaks in Europe do exist, most hollow oaks are scattered and isolated, either in agricultural landscapes or in woodlands (Gibbons et al. 2008, Ranius et al. 2009). For dispersing insects, the distance between suitable trees is likely to represent a challenge, and some beetles associated with hollow trees are known to be poor dispersers (Ranius 2006). The current spatial distribution and connectivity of hollow oaks are therefore of major importance for the oak-dependent species living in hollow trees.

To categorize the species into functional groups can help to identify if some groups are more vulnerable to fragmentation than others, which can in worst case lead to loss of important ecosystem functions. Therefore, to make sound management decisions it would be an advantage to know the most important aspects for maintaining species richness, rare species and ecosystem functions related to hollow oaks. Further, these aspects should be easily detectable in the field. Often, time or money does not allow expensive and time-consuming insect surveys. Recognizing important structures of the oak, or the surroundings, could provide valuable indication of which trees that are associated with high species richness or high number of rare species (Skarpaas et al. 2011). In our study, we have identified important structural variables related to patch size, habitat quality, and isolation, to test if these aspects affect the species richness and abundances in functional groups and red-listed species. We compared responses of different groups of beetles in highly isolated oaks to clustered hollow oaks (low isolation) while including variation in patch size and quality.

The aim of our study was to evaluate the effect of patch size, habitat quality, and isolation on species richness and abundance of functional groups and red-listed oak species in hollow oaks.

We expected a general positive effect of patch size and habitat quality on abundance and species richness, with open surroundings and low tree crown as proxies of high quality. We expected isolation to have strongest effect on the most specialized and vulnerable groups, such as the oak specialists and the red-listed species.

Materials and Methods

Study Design

The hollow oaks in the study (Fig. 1) were selected from the main oak-distribution area in southern Norway. We defined a hollow oak as an oak with a minimum circumference of 60 cm at breast height, with a visible hollow of at least 5 cm in diameter. The study is related to an ongoing study of hollow oaks under the National Program for Surveying and Monitoring Biodiversity—Threatened Species in Norway (Sverdrup-Thygeson et al. 2011).

Previous studies have indicated that the species composition differs between oaks in forests and parks (Sverdrup-Thygeson et al. 2010). To be able to generalize from our results, half of our hollow oaks were selected from the forest and half from the agricultural landscape. In total, 40 hollow oaks were included. In each of the two landscapes, half of the oaks ($n = 20$) were situated in areas where we found no or very few other hollow oaks nearby ('high isolation'), whereas the other half were situated in areas where we found several hollow oaks ('low isolation') with close distance (<200 m) to at least four other hollow oaks (Table 1). The 'high isolation' trees had a more northerly distribution than the 'low isolation' trees (Fig. 1). This could mean that the isolation is even more severe as cold weather might reduce the number of days suitable for flying.

Insect Trapping, Habitat Quality, and Patch Sizes

Beetles were collected from each oak by window traps (flight interception traps) from mid-May until mid-August for 1 year only, during the period 2004–2013. Mean and median number of oak species was similar for all sampled years, and although all the highly isolated hollow oaks were sampled in 2009, there were no differences in the number of oak-associated or red-listed beetle species in 2009 compared with other years (see Birkemoe and Sverdrup-Thygeson 2012). We used two traps per tree, one placed in front of the opening of the hollow and the other one in the canopy (see Sverdrup-Thygeson et al. 2010 for details).

We used circumference and amount of dead branches as proxies of 'patch size' for the saproxylic beetles (Table 1). Circumference was measured at breast height 1.3 m above ground, and amount of dead branches present on the tree was categorized into three groups: low, <50% of branches dead, intermediate, 50–80% of branches dead, and high, >80%. We further used tree form and openness around the trees as proxies of 'habitat quality'. We categorized our oaks' tree shape based on the positon of the tree crown into low, middle, or high tree form (Table 1). Low tree forms are typically wide-branched and a result of growing in open areas with high sun exposure (Read 2000), believed to create positive thermal conditions for insects. Additionally, low-branched hollow oaks tend to contain a high number of microhabitats, both of which will contribute to increased habitat quality. The openness status was categorized according to presence of woody vegetation around the oak: open, surrounded by shrubs, or surrounded by trees (Table 1). This variable has been found to affect habitat quality in earlier studies (Ranius and Jansson 2000, Widerberg et al. 2012) due to negative effects of shade on both the oak and the beetle diversity within. Landscape type (forest or agricultural) may affect species composition (Sverdrup-Thygeson et al. 2010, Skarpaas et al. 2011) and was included as a covariate in the analysis.

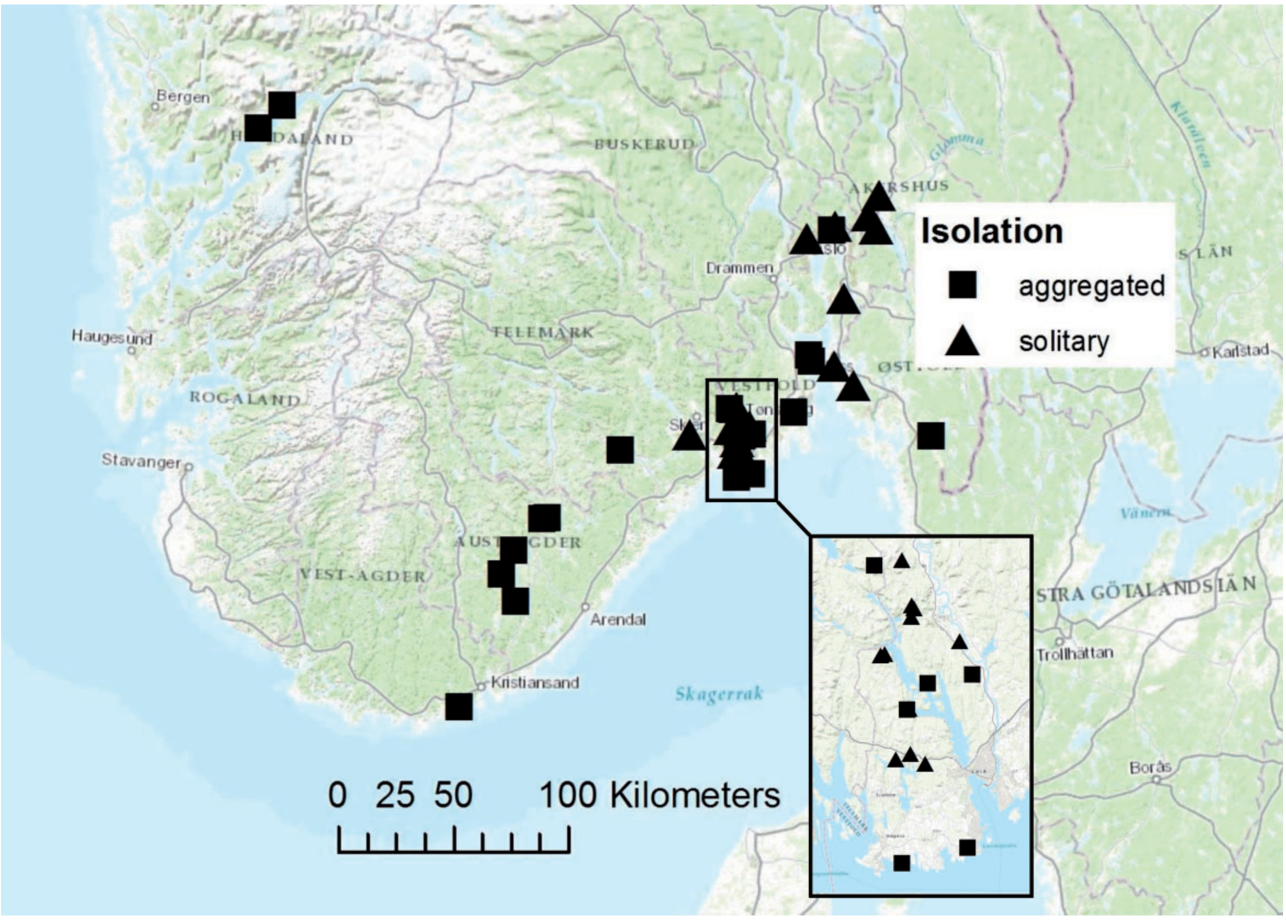

Fig. 1. Map of southern Norway with the locations of the hollow oaks ($n = 40$). The symbols show isolation category: solitary (high isolation) and aggregated (low isolation).

Table 1. Variables used in the statistical analyses of oak-associated beetles in hollow oaks ($n = 40$)

	Variable	Cont. or Cat.	Units or levels	Explanation
Isolation	Isolation	Cat.	High	Hollow oaks situated in areas with no or few other hollow oaks nearby (within 200 m) ($n = 20$)
			Low	Hollow oaks situated in areas with several hollow oaks and close distance (<200 m) to at least four other hollow oaks ($n = 20$).
Patch size	Circumference	Cont.	Cm	Circumference measured in breast height (1.3 m above ground) (min: 60 cm, max: 953 cm, median: 310 cm)
	Dead branches	Cat.	low, intermediate, high	Amount of dead branches present on the tree was categorized into: low, <50% of branches dead ($n = 12$), intermediate, 50-80% of branches dead ($n = 26$), and high, >80% ($n = 2$)
Habitat quality	Tree form	Cat.	low, middle, high	The shape of the oaks were categorized based on the positon of the tree crown into low ($n = 14$), middle ($n = 20$), or high ($n = 6$) position. The shape of the tree is a combination of past and current growing conditions reflecting whether it has grown in open or closed conditions
	Openness	Cat.	open, shrub, trees	The hollow oaks were categorized according to presence of woody vegetation within 5 m around the oak creating shade: open ($n = 18$), surrounded by shrubs ($n = 7$) or surrounded by trees ($n = 15$)
Covariate	Landscape	Cat.	cultural	Hollow oaks within agricultural landscapes ($n = 20$)
			forest	Hollow oaks in forests ($n = 20$)
Random factor	Geographical position	Cont.	UTM32V coordinates	X and Y coordinates from GPS coordinates (WGS84), rounded to nearest 100 m to adjust for uneven spatial distribution. Used in the GLMMs
	Entomological region	Cat.	regions	Sampling regions commonly used for insects in Norway (University of Oslo 2009) ($n = 8$). Used in the LMMs

Cont., continuous, Cat., categorical.

Functional Groups

All beetles were determined to species and categorized to functional groups based on their oak association and trophic guild. Only saproxylic species were included. The classification of oak association was based on Dahlberg and Stokland (2004) and The Saproxylic Database (2014) (Supp 1 [online only]). For oak association the following groups were used: oak specialists, oak semi-specialist, oak generalists, and not oak species. 'Oak specialists' were defined as preferring oak, only occurring on oak or only occurring on temperate broadleaved trees in addition to oak. 'Oak semi-specialists' were defined as occurring on boreal broadleaved trees in addition to oak, 'oak generalists' were defined as occurring on coniferous trees in addition to oak, and 'not oak' species were defined as saproxylic species not associated with oak or having unknown host association. The 'not oak species' group was not included in the statistical analyses.

Trophic guild information is mainly based on Koehler (2000), supplemented by the BugsCEP database (Buckland and Buckland 2006) and various other resources (including Ehnström and Axelsson 2002, Heliövaara et al. 2004, Lindhe et al. 2010, Norwegian Biodiversity Information Centre 2015, The Swedish Species Information Centre 2015). The following groups were used: '*xylophage*' for species eating wood, '*xylomycetophage*' for species dependent on wood and fungi, '*fungivore*' for species eating fungi, '*predator*' for predatory species, and 'mixed feeding group' for other species, mainly omnivores or species belonging to several of the trophic levels. Species were regarded as xylomycetophagous if they were both listed as xylophage and xylomycetophagous by different authors. When information on larva and imago were different (for example predatory larva and pollenophagous imago), information on the larva was used as the larva for most species is the dominant life stage in dead wood. Similarly, species were categorized as 'mixed feeding group' if different authors listed them in different categories (see Supp 1 [online only] for further details on categorization). In addition, red-listed oak species were included as a single group as they are of particular concern for conservation and likely to respond to fragmentation.

Statistics

We used generalized linear mixed effect models (GLMM) with a poisson error distribution and log-link function, using the glmer function in the lme4 package in R to test which predictors that best explained the species richness in the functional groups (trophic levels and host tree association) and red-listed species. Predictor variables were isolation (low and high), landscape (forest or agricultural), dead branches, openness, circumference, and tree form. The variables were checked for collinearity prior to analyses. We used geographical position (in the form of Universal Transverse Mercator (UTM) coordinates) as a random factor to adjust for spatial structure in the data and between site differences. The drop1 function was used to do backward elimination and the optimal models were found by favoring the GLMM model with lowest possible AIC (Akaike Information Criterion) (Zuur et al. 2009). The optimal models were then tested for significance against a null-model in a likelihood ratio test. When AIC values were almost identical for two models, we chose the simplest model. Nonsignificant predictors were included in some of the models to achieve the best model fit (lowest AIC).

One tree had considerably higher species richness than the other oaks and was therefore an outlier in the dataset. To decide whether the outlier should be omitted, the GLMMs were run with and without the outlier to see how much this tree contributed to the optimal models. The outlier had considerable effect on which predictors that were kept in the optimal models, and the outlier was hence excluded in the GLMMs. After exclusion of the outlier, the dead branch variable was used with only two levels (low $<50\%$ and intermediate $\geq 50\%$) as there were not enough trees with $>80\%$ dead branches to keep it as a separate category. The dispersion parameter in the GLMMs ranged from 0.67 to 1.08 and indicated some under-dispersion in some of the models.

For analyses of abundance in each functional group, we used backward elimination in linear mixed models (LMMs) on log-transformed abundances (to achieve homogeneity). There were no outliers after log transformation. In LMMs the random effect has to be categorical, therefore geographic position was grouped into a commonly used categorical variable ('entomological region') reflecting sampling region for insects in Norway (University of Oslo 2009). The optimal models were found with the same procedure as for the species. The optimal models were fitted by restricted maximum likelihood, and *P*-values for the variables were calculated based on a z-distribution as recommended by Zuur et al. (2013). Confidence intervals were checked to ensure that the 95% confidence interval of significant values did not overlap with zero (Zuur et al. 2013).

Results

We sampled a total of 350 saproxylic beetle species, of which 221 species and 4,548 individuals were associated with oak. Of the oak-associated species, 40 were on the Norwegian Red-List (Supp. Table 1 [online only]). The different functional groups were heterogeneous in terms of oak association (Fig. 2). Overall the predators had the highest species richness, and both predators and fungivore species had a decreasing trend from the oak generalists to the specialists in species richness and abundance. The xylophagous species dominated

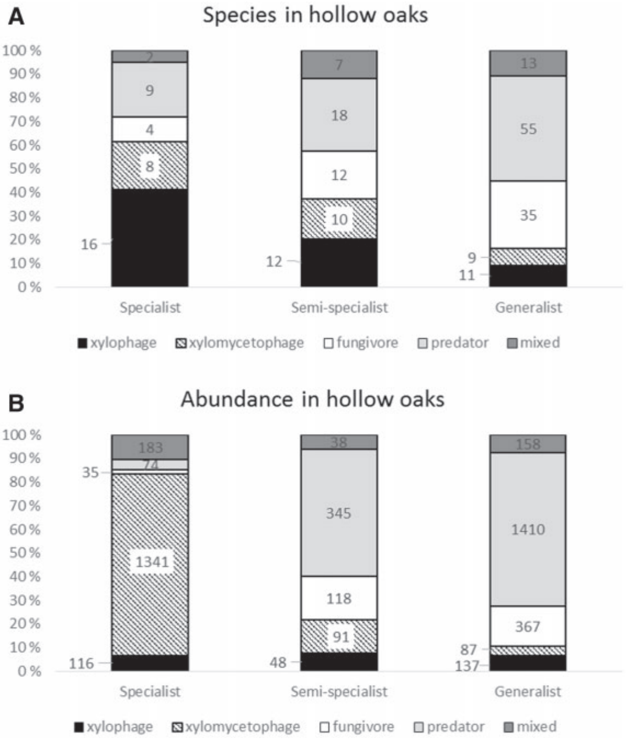

Fig. 2. Percentage of saproxylic beetles in hollow oaks split into specialization and trophic levels. (A) Species richness. (B) Number of individuals. The number of species or individuals in each category is shown.

among the oak specialist species (41% of the species), whereas predators and fungivores dominated in the oak generalist group with 45% and 28% of the species, respectively (Fig. 2A). This pattern was slightly different for abundance, as the specialists were dominated by xylomycetophages (77% of all species) (Fig. 2B). This was mainly due to two species, *Euglenes oculatus* Paykull, 1798 and *Dorcatoma chrysomelina* Sturm, 1837, represented by 784 and 541 individuals. The predators dominated the abundance of oak generalists (65% of the individuals), but only one species was very abundant, *Haploglossa villosula* Stephens, 1832, with 996 individuals.

Effect of Patch Size, Habitat Quality, and Isolation on Functional Groups

Patch size (circumference and amount of dead branches) and isolation did not affect species richness in any of the 10 groups, although it remained in some optimal models (Table 2). Habitat quality (low and intermediate tree crown) on the other hand affected species richness positively in all groups except xylomycetophages, red-listed species, oak specialists, and the mixed feeding group that did not show any response (Table 2, see full details in Supp Table 2 [online only]).

Contrary to species richness, the abundance responded to patch size. An increasing patch size increased abundance of 8 of the 10 groups, and only the predators and the mixed feeding group were not affected (Table 2, Supp Table 3 [online only]). The xylomycetophages and oak semi-specialists also responded negatively to isolation. Isolation remained in the optimal model for all oak individuals and oak generalists, but its negative effect was not significant (Table 2). Habitat quality had a mixed effect on the abundances: the xylomycetophages decreased with shrubs and trees whereas the predators and the mixed feeding group increased with shrubs (Supp Table 3 [online only]). The xylomycetophages also increased in abundance with openness. The habitat quality determined by tree form was positive (low and intermediate tree crown) for the abundance of xylomycetophages and xylophages.

Discussion

Our study revealed that beetle species richness in hollow oaks was primarily affected by habitat quality whereas beetle abundance was affected by patch size and isolation. This general pattern emerged despite the varying importance of patch size, habitat quality, and isolation on the different groups.

Habitat Patch Size

Large patch size, represented by circumference and a high proportion of dead branches, was important for the abundance of most functional groups except the predators and the mixed feeding group. Species

Table 2. Effect of patch size, habitat quality, and isolation on species richness and abundance of red-listed species and functional groups of oak-associated beetles in hollow oaks

	Patch size		Habitat quality		Isolation
	Circum.	Dead branches high/inter. versus low	Tree form low/inter. versus high	Openness tree/shrub versus open	high versus low
Species richness					
Red-listed species		(+)^a			
All oak species			+		
Trophic level					
Xylophage	(+)^a		+		
Xylomycetophage		(+)^a			(−)^a
Fungivore			+		
Predator			+		
Mixed feeding					
Oak association					
Specialist					
Oak semi-specialist			+		
Generalist			+		
Abundance					
Red-listed individuals	+				
All oak individuals	(+)^b	+			(−)^b
Trophic level					
Xylophage	+	+	+		
Xylomycetophage	+	+	+	−	−
Fungivore		+	(+)^a		
Predator				+	
Mixed feeding				+	
Oak association					
Specialist	+				
Oak semi-specialist		+			−
Generalist		+		(+)^a	(-)^b

Optimal models of GLMMs were used for species richness and LMMs for log-transformed abundance data. The optimal models were found by backward elimination using the drop1 function in R and AIC as selection criterion. For species, UTM coordinates were used as random effect and entomological region was used as random effect in the LMMs for log-transformed abundance. Only the strongest trend is shown for variables with several levels. Significant effects ($P < 0.05$) are indicated with a + or − only, whereas the nonsignificant variables ($P > 0.05$) kept in the optimal models are shown in brackets. For full details, see Supplementary Tables 2 and 3. *Explanation*: Circum, circumference; Inter., intermediate; $^a0.1 > P > 0.05$; $^b0.15 > P > 0.1$.

richness was not affected by patch size, although the xylophage, xylomycetophage and red-listed species had a positive response that was close to significant. In-line with species-area relationships larger patches have room for more species and individuals, and it is likely that decreasing population size occur before extinction in local patches.

Several studies have shown that tree size (measured as circumference) is important for the species richness of beetles (Ranius and Jansson 2000, Sverdrup-Thygeson et al. 2010, Gough et al. 2014). This could be related to larger oaks normally have larger hollows with more wood mould as well as more dead wood overall. Furthermore, the structural heterogeneity in the form of microhabitats also tend to increase with size (Ranius and Jansson 2000, Sverdrup-Thygeson et al. 2010). Large size also provides more stable microclimates, and Ranius and Jansson (2000) suggested that large tree size make it easier for more fungus to establish, thus providing more habitat for fungi-associated beetles. In this study, we show that the proportion of dead wood in the canopy also plays a part, as more of the tree is available for saproxylic insects.

Habitat Quality

Habitat quality was the most important and only significant predictor of species richness for the functional groups. Six of the ten groups, including the all oak group, had a positive response in species richness to low or intermediate tree form. The effect of openness at the other hand was mixed and only abundances were affected. Thus, our results fit party with our expectations; higher species richness in hollow oaks with low tree form and open surroundings. Open surroundings have been found to be important in previous studies (Ranius and Jansson 2000, Widerberg et al. 2012, Gough et al. 2014), and low tree form normally indicates higher structural diversity and also that the tree has been growing in open sunny conditions over time. Our results indicate that abundances of some functional groups (predators and the mixed feeding group) can have a positive response to woody vegetation in the surroundings. Gough et al. (2014) found that oak generalists preferred hollow oaks surrounded by shrubs and trees, and suggested that this could be explained by the amount of forest around these oaks, as tree host diversity would be higher for oak generalists. Sverdrup-Thygeson et al. (2010) also found more dead wood around hollow oaks in forests than in parks, which could increase the habitat patch for certain species. Our study fits well with these results as most of the predators and the mixed feeding species were oak generalists. Still, regrowth of woody vegetation around oaks that are adapted to open conditions creates competition for space and light that can reduce the life span of the oak (Read 2000). It is therefore often advocated to carefully open up around oaks to increase the diversity of insects and to secure the longevity of the oak (Read 2000, Widerberg et al. 2012).

Isolation and Spatial Scales

Isolation only had a negative effect on 2 of 10 groups in the optimal models; on the abundance of xylomycetophages and oak semi-specialists. However, xylomycetophage species richness also showed a negative trend that was close to significant (Table 2). Xylomycetophages are dependent upon the combination of wood and fungi and two-thirds of these species were oak specialists or semi-specialists. This overall high degree of specialization could make them particularly vulnerable to isolation. Overall, we had expected isolation to have an effect on the species richness and abundances of oak specialists and the vulnerable red-listed species. Although these groups had no response to isolation, isolation was always negative whenever it was included in the optimal models, indicating that connectivity is important for several of the functional groups. In our study, we only investigated the immediate surroundings around each oak (within 200 m). Bergman et al. (2012) found that the spatial scales that were most important for different oak beetle species ranged from 52 m to >5 km. Thus, the real scale of response may not have been reached for many species in this study.

Contrary to our expectations, the species richness of oak specialists could not be explained by patch size, habitat quality, or isolation. This could indicate that other factors, not included in our study, may be of importance. As we only investigated the local scale, it is possible that the highly isolated oaks were less isolated at larger scales and available for species with good dispersal abilities. Unfortunately we could not include connectivity on a larger spatial scale in our study as no complete mapping of hollow oaks exists in our study areas. Andrén (1994) demonstrated that fragmentation of a landscape would primarily affect the species in terms of habitat loss, and the additional negative effects of isolation and patch size would mainly occur when the original landscape was truly fragmented and only smaller proportions remained. It is possible that the fragmentation thresholds for some of the functional groups were not reached in our study, especially since several of the groups probably can use other resources than hollow oaks, such as other hollow trees or dead wood in the surroundings. Bergman et al. (2012) also demonstrated that several of the studied species responded to two spatial scales; a very local scale (such as within a 100 m radius) and a scale of several kilometers. Studies on saproxylic beetles have shown that many beetle species associated with hollow trees are considered to be poor dispersers (Hedin et al. 2008). This may be an adaptation to the stability of their habitat, hosting generation upon generation of beetles with limited needs for long-distance dispersal (Ranius 2006, Hedin et al. 2008). Knowledge of which spatial scales that is most important for saproxylic species is limited and difficult to study (Ranius 2006, Sverdrup-Thygeson et al. 2014). Still, the decrease in abundance of the functional groups with isolation in our study indicates that some groups are vulnerable to fragmentation at the very local scale. High connectivity would therefore be advisable to secure survival in the long term.

Red-Listed Species

We found that red-listed species richness and abundance responded to patch size, although the effect on species richness was only close to significant (Table 2). This indicates that large oaks with many dead branches are especially important for the conservation of threatened species. An earlier study of red-listed beetles in hollow oaks in Norway found that species richness was positively related to circumference (patch size), proportion of oaks (low isolation), cavity decay stage, and coarse woody debris (i.e., dead wood) in the surroundings (Sverdrup-Thygeson et al. 2010). They also suggested that coarse woody debris in the surroundings could compensate for small circumference and limited sun exposure. Similarly, Gough et al. (2014) found circumference to be important, and they found a negative effect of regrowth on red-listed species.

We expected red-listed species to be especially vulnerable to isolation, as these species typically are rare or have declining populations. However, no such pattern was found. Nilsson and Baranowski (1997) found an effect of isolation and habitat size on saproxylic red-listed beetles in old-growth beech (*Fagus sylvatica* L.) forests in Sweden. Ranius (2002a) found that the percentage of trees with presence of certain rare species increased with stand size of hollow oaks. Two of the red-listed species, the rare click beetle *Elater ferrugineus* Linnaeus, 1758 (Elateridae) and the pseudoscorpion *Larca lata* H. J. Hansen, 1884, were not present at all in groups of only 1–3 hollow oaks standing <250 m apart. This is comparable to our high isolation sites where there were no or few other hollow oaks within 200 m of the oak. *E. ferrugineus* needed almost a hundred hollow oaks to be present in a considerable amount of the oaks (Ranius 2002a, 2006), clearly demonstrating that the number of hollow oaks in the immediate surroundings can be important for rare species. The lack of response to isolation in our study could indicate that the most vulnerable species may already have disappeared from our Norwegian sites, and that the difference between high and low isolation was too small. Large hollow oaks with many dead branches (i.e., large patch size) were more important for red-listed species richness and abundance in our study than the type of surroundings or neighbouring hollow oaks. These oaks are therefore especially important to protect to conserve rare species, regardless of whether they stand isolated or not.

Overall habitat quality was most important in explaining species richness for most functional groups, and patch size was most important in explaining abundance. The lack of response in the species richness to high isolation indicates that solitary oaks are as species rich as clustered oaks, but the negative response in the abundance indicates vulnerability to fragmentation in some groups. Hence, it would be advisable to maintain oaks in groups, as lower abundances over time could make species vulnerable to extinctions. The red-listed species only responded to patch size, indicating that hollow oaks with large circumference and high amounts of dead branches are especially important to conserve.

Supplementary Data

Supplementary data are available at *Journal of Insect Science* online.

Acknowledgments

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References Cited

Alexander, K. N. A. 2008. Tree biology and saproxylic Coleoptera: issues of definitions and conservation language. Rev Écol-Terre Vie 10: 9–13.

Andrén, H. 1994. Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. Oikos 71: 355–366.

Barnosky, A. D., N. Matzke, S. Tomiya, G. O. U. Wogan, B. Swartz, T. B. Quental, C. Marshall, J. L. McGuire, E. L. Lindsey, K. C. Maguire, B. Mersey, and E. A. Ferrer. 2011. Has the Earth's sixth mass extinction already arrived? Nature 471: 51–57.

Benedick, S., J. K. Hill, N. Mustaffa, V. K. Chey, M. Maryati, J. B. Searle, M. Schilthuizen, and K. C. Hamer. 2006. Impacts of rain forest fragmentation on butterflies in northern Borneo: species richness, turnover and the value of small fragments. J. Appl. Ecol. 43: 967–977.

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

Birkemoe, T., and A. Sverdrup-Thygeson. 2012. Importance of long-term surveys for beetle diversity in veteran oaks, pp. 291–296. *In* I. Rotherham, C. Handley, T. Samojolik, M. Agnoletti (eds.), Trees beyond the wood. Sheffield Hallam University, Sheffield, UK.

Bouget, C., L. Larrieu, and A. Brin. 2014. Key features for saproxylic beetle diversity derived from rapid habitat assessment in temperate forests. Ecol. Ind. 36: 656–664.

Buckland, P. I., and P. C. Buckland. 2006. BugsCEP Coleopteran Ecology Package. IGBP PAGES/World Data Center for Paleoclimatology Data Contribution Series # 2006-116. NOAA/NCDC Paleoclimatology Program, Boulder CO, USA (http://www.bugscep.com).

Cagnolo, L., G. Valladares, A. Salvo, M. Cabido, and M. Zak. 2009. Habitat fragmentation and species loss across three interacting trophic levels: effects of life-history and food-web traits. Conserv. Biol. 23: 1167–1175.

Dahlberg, A., J. Stokland. 2004. Substrate requirements of wood-inhabiting species - a synthesis and analysis of 3600 species. Skogsstyrelsen. Report 7-04, pp. 75.

Dover, J. and J. Settele. 2009. The influences of landscape structure on butterfly distribution and movement: a review. J. Insect. Conserv. 13: 3–27.

Drobyshev, I., and M. Niklasson 2010. How old are the largest southern Swedish oaks? A dendrochronological analysis. Ecol. Bull. 53: 155–163.

Ehnström B., and R. Axelsson. 2002. Insekters gnag i bark och ved. ArtDatabanken, SLU, Uppsala, Sweden. [in Swedish]

Fischer, J., D. B. Lindenmayer, and R. J. Hobbs. 2009. pp. 431–437. *In* S. A. Levin (ed.), The Princeton guide to ecology. Princeton University press, New Jersey.

Franzén, M., O. Schweiger, and P-E. Betzholtz. 2012. Species-area relationships are controlled by species traits. PLoS One 7: e37359.

Gibbons, P., D. B. Lindenmayer, J. Fischer, A. D. Manning, A. Weinberg, J. Seddon, P. Ryan, and G. Barrett. 2008. The future of scattered trees in agricultural landscapes. Conserv. Biol. 22: 1309–1319.

Gough, L. A., T. Birkemoe, and A. Sverdrup-Thygeson. 2014. Reactive forest management can also be proactive for wood-living beetles in hollow oak trees. Biol. Conserv. 180: 75–83.

Grove, S. J. 2002. Saproxylic insect ecology and the sustainable management of forests. Annu. Rev. Ecol. Syst. 33: 1–23.

Hanski, I. 1998. Metapopulation dynamics. Nature 396: 41–49.

Hanski, I. 1999. Metapopulation ecology. Oxford University Press, Oxford.

Hanski, I. 2008. Insect conservation in boreal forests. J. Insect Conserv. 12: 451–454.

Hedin, J., T. Ranius, S. Nilsson, and H. Smith. 2008. Restricted dispersal in a flying beetle assessed by telemetry. Biodivers. Conserv. 17: 675–684.

Heliövaara, K., I. Mannerkoski, and J. Siitonen. 2004. Suomen Sarvijaarat: Longhorn Beetles of Finland (Coleoptera, Cerambycidae). Tremex, Helsinki, Finland.

Henle, K., K. F. Davies, M. Kleyer, C. Margules, and J. Settele. 2004. Predictors of species sensitivity to fragmentation. Biodivers. Conserv. 13: 207–251.

Holt, R. D., J. H. Lawton, G. A. Polis, and N. D. Martinez. 1999. Trophic rank and the species-area relationship. Ecology 80: 1495–1504.

Kennedy, C. E. J., and T. R. E. Southwood. 1984. The number of species of insects associated with British trees: a re-analysis. J. Anim. Ecol. 53: 455–478.

Koehler, F. 2000. Saproxylic beetles in nature forests of the northern Rhineland: comparative studies on the saproxylic beetles of Germany and contributions to German nature forest research. Schrr. LÖBF/LAFAO NRW (Recklinghausen) 18: 1–351.

Komonen, A., R. Penttilä, M. Lindgren, and I. Hanski. 2000. Forest fragmentation truncates a food chain based on an old-growth forest bracket fungus. Oikos 90: 119–126.

Lindenmayer, D. B., W. F. Laurance, and J. F. Franklin. 2012. Global decline in large old trees. Science 338: 1305–1306.

Lindhe, A., T. Jeppsson, and B. Ehnström. 2010. Longhorn beetles in Sweden – distribution and abundance during two hundred years. Entomologisk Tidskrift 131: 241–510.

IUCN Red List. 2014. Table 1: numbers of threatened species by major groups of organisms (1996–2014) (http://cmsdocs.s3.amazonaws.com/summary stats/2014_3_Summary_Stats_Page_Documents/2014_3_RL_Stats_Table_1.pdf) (accessed 20 April 2015).

Losey, J. E., and M. Vaughan. 2006. The economic value of ecological services provided by insects. BioScience 56: 311–323.

McKinney, M. L., and J. L. Lockwood. 1999. Biotic homogenization: a few winners replacing many losers in the next mass extinction. Trends Ecol. Evol. 14: 450–453.

Millenium Ecosysem Assessment. 2005. Ecosystems and human well-being: synthesis. Island Press, Washington, DC.

Nieto, A., S. P. M. Roberts, J. Kemp, P. Rasmont, M. Kuhlmann, M. García Criado, J. C. Biesmeijer, P. Bogusch, H. H. Dathe, P. De la Rúa, et al. 2014. European Red List of bees. Publication Office of the European Union, Luxembourg.

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

Norwegian Biodiversity Information Centre. 2015. Norsk rødliste for arter 2010. Norwegian Biodiversity Information Centre. [in Norwegian] (http://www.artsportalen.artsdatabanken.no/) (accessed 20 February 2015).

Ranius, T. 2002a. Influence of stand size and quality of tree hollows on saproxylic beetles in Sweden. Biol. Conserv. 103: 85–91.

Ranius, T. 2002b. *Osmoderma eremita* as an indicator of species richness of beetles in tree hollows. Biodivers. Conserv. 11: 931–941.

Ranius, T. 2006. Measuring the dispersal of saproxylic insects: a key characteristic for their conservation. Popul. Ecol. 48:177–188.

Ranius, T., L. O. Aguado, K. Antonsson, P. Audisio, A. Ballerio, G. M. Carpaneto, K. Chobot, B. Gjurasin, O. Hanssen, and H. Huijbregts. 2005. *Osmoderma eremita* (Coleoptera, Scarabaeidae, Cetoniinae) in Europe. Anim. Biodiver. Conserv. 28: 1–44.

Ranius, T., and N. Jansson. 2000. The influence of forest regrowth, original canopy cover and tree size on saproxylic beetles associated with old oaks. Biol. Conserv. 95: 85–94.

Ranius, T., M. Niklasson, and N. Berg. 2009. Development of tree hollows in pedunculate oak (*Quercus robur*). Forest. Ecol. Manag. 257: 303–310.

Read, H. 2000. Veteran Trees: A guide to good management. English Nature, Peterborough.

Ricketts, T. H. 2001. The matrix matters: effective isolation in fragmented landscapes. Am. Nat. 158: 87–99.

Sala, O. E., F. S. Chapin III, J. J. Armesto, E. Berlow, J. Bloomfield, R. Dirzo, E. Huber-Sanwald, L. F. Huenneke, R. B. Jackson, A. Kinzig, R. Leemans, D. M. Lodge, H. A. Mooney, M. Oesterheld, N. L. Poff, M. T. Sykes, B. H. Walker, M. Walker, and D. H. Wall. 2000. Global biodiversity scenarios for the year 2100. Science 287: 1770–1774.

Skarpaas, O., O. H. Diserud, A. Sverdrup-Thygeson, and F. Ødegaard. 2011. Predicting hotspots for red-listed species: multivariate regression models for oak-associated beetles. Insect Conserv. Diver. 4: 53–59.

Speight, M. 1989. Saproxylic invertebrates and their conservation. Nature and environment series, vol. 42. Council of Europe, Strasbourg.

Stokland, J. N., J., Siitonen, and B. G. Jonsson. 2012. Biodiversity in dead wood. Ecology, biodiversity and conservation. Cambridge University Press, Cambridge.

Sverdrup-Thygeson, A. 2009. Oaks in Norway: Hotspots for red-listed beetles (Coleoptera), pp. 13–26. *In* J. Buse, K.N.A. Alexander, T. Ranius, T. Assmann (eds.), Saproxylic beetles: their role and diversity in European woodland and tree habitats - Proceedings of the 5th symposium and workshop. Pensoft Publishers, Sofia-Moscow.

Sverdrup-Thygeson, A., H. Bratli, T. E. Brandrud, A. Endrestøl, M. Evju, O. Hanssen, O. Skarpaas, O. Stabbetorp, and F. Ødegaard. 2011. Hule eiker - et hotspot-habitat: Sluttrapport under ARKO-prosjektets periode II. NINA rapport 710. Norsk institutt for naturforskning, Oslo. [in Norwegian].

Sverdrup-Thygeson, A., L. Gustafsson, and J. Kouki. 2014. Spatial and temporal scales relevant for conservation of dead-wood associated species: current status and perspectives. Biodivers. Conserv. 23: 513–535.

Sverdrup-Thygeson, A., O. Skarpaas, and F. Ødegaard. 2010. Hollow oaks and beetle conservation: the significance of the surroundings. Biodivers. Conserv. 19: 837–852.

The Directorate for Nature Management. 2012. Handlingsplan for utvalgt naturtype hule eiker, vol. 1, pp. 80. [in Norwegian]

The Saproxylic Database, 2014. (http://radon.uio.no/WDD/Login.aspx?ReturnUrl=%2fwdd%2fDefault.aspx)

The Swedish Species Information Centre. 2015. Artfakta - Sök rödlistade arter i Sverige 2010. ArtDatabanken - Swedish Species Information Centre. [in Swedish] (http://www.artfakta.se/GetSpecies.aspx?SearchType=Advanced) (accessed 20 February 2015).

Thomas, J. A., N. A. D. Bourn, R. T. Clarke, K. E. Stewart, D. J. Simcox, G. S. Pearman, R. Curtis, and B. Goodger. 2001. The quality and isolation of habitat patches both determine where butterflies persist in fragmented landscapes. Proc. R. Soc. Lond. Ser. B Biol. Sci. 268: 1791–1796.

Valladares, G., A. Salvo, and L. Cagnolo. 2006. Habitat fragmentation effects on trophic processes of insect-plant food webs. Efectos de la Fragmentación del Hábitat Sobre Procesos Tróficos de Redes Alimenticias Insecto-Planta. Conserv. Biol. 20: 212–217.

University of Oslo. 2009. Strand-systemet - en inndeling av Norge til bruk ved insektkartlegging. University of Oslo. [in Norwegian] (http://www.nhm.uio.no/fakta/zoologi/insekter/norcol/regioner_lang.html) (accessed 16 January 2015).

Widerberg, M. K., T. Ranius, I. Drobyshev, U. Nilsson, and M. Lindbladh. 2012. Increased openness around retained oaks increases species richness of saproxylic beetles. Biodivers. Conserv. 21: 3035–3059.

Zuur, A. F., J. Hilbe, and E. N. Ieno. 2013. A beginner's guide to GLM and GLMM with R: A frequentist and bayesian perspective for ecologists. Highland Statistics Ltd., Newburgh, UK.

Zuur, A. F., E. N. Ieno, N. J. Walker, A. A. Saveliev, and G. M. Smith. 2009. Mixed effects models and extensions in ecology with R. Statistics for Biology and Health, Springer, New York.

Supplementary material

Supplementary material 1-3 consists of the categorization of each species into functional groups and full statistical details of the different analyses. Oak-association, trophic level and red list category is shown in Supp. 1, including some comments to the categorization. Table S2-3 shows the full details of the optimal models for species richness and abundances of the functional groups.

Supplementary material 1

Some comments on classification of functional groups

For oak association *Alnus* trees were considered to be temperate broadleaved trees.
For some species where it was hard to find information on feeding habit, information on genera or family was used instead, assuming closely related species to have similar preferences. All *Atheta* species (Staphylinidae) were regarded as predators where information on diet was missing. Species eating slime moulds were regarded as fungivorous, although slime moulds technically no longer belong to the fungi kingdom, this is mainly concerning a few beetles in the Leiodidae family. Similarly was Ptiliidae regarded as fungivorous.

Table S1 Saproxylic beetle species and functional groups

Family	Species	Oak association	Trophic level	Ind.	Red list
Aderidae	*Aderus populneus*	semi-specialist	xylomycetophage	4	NT
	Euglenes oculatus	specialist	xylomycetophage	784	NT
Anthribidae	*Choragus horni*	not oak	not oak	1	NT
Buprestidae	*Agrilus sulcicollis*	specialist	xylophage	1	
Cantharidae	*Malthinus flaveolus*	generalist	predator	5	
	Malthinus frontalis	not oak	not oak	24	
	Malthinus seriepunctatus	not oak	not oak	1	VU
	Malthodes brevicollis	not oak	not oak	6	
	Malthodes crassicornis	not oak	not oak	6	
	Malthodes fuscus	not oak	not oak	7	
	Malthodes guttifer	not oak	not oak	16	
	Malthodes marginatus	not oak	not oak	10	
	Malthodes pumilus	not oak	not oak	1	
	Malthodes spathifer	semi-specialist	predator	8	
Carabidae	*Dromius agilis*	generalist	predator	7	
	Dromius fenestratus	generalist	predator	2	
	Dromius quadrimaculatus	specialist	predator	5	
Cerambycidae	*Alosterna tabacicolor*	specialist	xylophage	10	
	Anoplodera sexguttata	specialist	xylomycetophage	3	
	Clytus arietis	specialist	xylophage	2	
	Leiopus nebulosus	specialist	xylophage	3	
	Leptura quadrifasciata	generalist	xylophage	1	
	Molorchus minor	not oak	not oak	1	
	Phymatodes testaceus	specialist	xylophage	6	
	Rhagium inquisitor	generalist	xylophage	1	

Family	Species	Oak association	Trophic level	Ind.	Red list
	Rhagium mordax	generalist	xylophage	5	
	Rutpela maculata	specialist	xylophage	1	
	Saperda scalaris	semi-specialist	xylophage	1	
	Stenocorus meridianus	semi-specialist	xylophage	1	VU
	Stenurella melanura	generalist	xylophage	5	
	Stictoleptura maculicornis	generalist	xylophage	5	
Cerylonidae	*Cerylon fagi*	semi-specialist	predator	1	
	Cerylon ferrugineum	generalist	mixed	22	
	Cerylon histeroides	generalist	predator	13	
Ciidae	*Cis bidentatus*	generalist	fungivore	2	
	Cis boleti	semi-specialist	fungivore	8	
	Cis comptus	generalist	fungivore	1	
	Cis dentatus	not oak	not oak	1	
	Cis fagi	specialist	fungivore	5	NT
	Cis festivus	semi-specialist	fungivore	1	
	Cis vestitus	semi-specialist	fungivore	14	
	Cis villosulus	not oak	not oak	2	
	Dolichocis laricinus	not oak	not oak	1	NT
	Ennearthron cornutum	generalist	fungivore	10	
	Octotemnus glabriculus	semi-specialist	fungivore	2	
	Orthocis alni	generalist	fungivore	8	
	Orthocis linearis	not oak	not oak	1	NT
	Ropalodontus perforatus	not oak	not oak	1	
	Sulcacis nitidus	generalist	fungivore	1	
Coccinellidae	*Chilocorus bipustulatus*	not oak	not oak	1	
	Myzia oblongoguttata	not oak	not oak	1	
Corticariidae	*Corticaria orbicollis*	not oak	not oak	1	
Corylophidae	*Orthoperus corticalis*	not oak	not oak	6	
	Orthoperus rogeri	not oak	not oak	1	VU
Cryptophagidae	*Atomaria affinis*	not oak	not oak	1	
	Atomaria fuscata	not oak	not oak	7	
	Atomaria morio	generalist	fungivore	3	
	Atomaria nigrirostris	not oak	not oak	6	
	Cryptophagus badius	generalist	fungivore	3	
	Cryptophagus dentatus	semi-specialist	fungivore	35	
	Cryptophagus dorsalis	not oak	not oak	2	
	Cryptophagus fuscicornis	not oak	not oak	1	EN
	Cryptophagus lapponicus	not oak	not oak	1	
	Cryptophagus micaceus	not oak	not oak	47	
	Cryptophagus populi	semi-specialist	fungivore	11	
	Cryptophagus scanicus	generalist	fungivore	61	
	Cryptophagus subdepressus	not oak	not oak	1	NT
	Micrambe abietis	not oak	not oak	14	
Curculionidae	*Anisandrus dispar*	specialist	fungivore	25	

Family	Species	Oak association	Trophic level	Ind.	Red list
	Cryphalus asperatus	not oak	not oak	2	
	Crypturgus cinereus	not oak	not oak	5	
	Crypturgus pusillus	not oak	not oak	1	
	Crypturgus subcribrosus	not oak	not oak	3	
	Dryocoetes alni	not oak	not oak	3	
	Dryocoetes autographus	not oak	not oak	2	
	Dryocoetes villosus	specialist	xylophage	13	
	Hylastes brunneus	not oak	not oak	1	
	Hylastes cunicularius	not oak	not oak	14	
	Hylesinus fraxini	semi-specialist	xylophage	11	
	Hylobius abietis	generalist	xylophage	5	
	Hylobius pinastri	not oak	not oak	1	
	Ips acuminatus	not oak	not oak	1	
	Ips typographus	not oak	not oak	13	
	Magdalis cerasi	generalist	xylophage	1	NT
	Magdalis linearis	not oak	not oak	1	
	Phloeophagus turbatus	not oak	not oak	1	VU
	Pissodes pini	not oak	not oak	1	
	Pityogenes bidentatus	not oak	not oak	1	
	Pityogenes chalcographus	not oak	not oak	29	
	Pityogenes quadridens	not oak	not oak	1	
	Pityogenes trepanatus	not oak	not oak	5	
	Pityophthorus micrographus	not oak	not oak	13	
	Polygraphus poligraphus	not oak	not oak	5	
	Rhyncolus ater	generalist	xylophage	32	
	Scolytus intricatus	specialist	xylophage	6	
	Scolytus laevis	specialist	xylophage	1	
	Scolytus rugulosus	not oak	not oak	6	
	Strophosoma capitatum	generalist	mixed	28	
	Taphrorychus bicolor	specialist	xylophage	1	NT
	Trachodes hispidus	semi-specialist	xylophage	2	
	Trypodendron domesticum	semi-specialist	xylomycetophage	1	
	Trypodendron lineatum	not oak	not oak	3	
	Trypophloeus granulatus	not oak	not oak	2	
	Xyleborinus saxesenii	semi-specialist	xylomycetophage	52	
	Xyleborus cryptographus	not oak	not oak	1	
	Xylechinus pilosus	not oak	not oak	2	
Dasytidae	*Aplocnemus nigricornis*	generalist	predator	1	
	Dasytes caeruleus	generalist	predator	10	
	Dasytes niger	generalist	predator	4	
	Dasytes plumbeus	semi-specialist	predator	45	
Dermestidae	*Anthrenus museorum*	not oak	not oak	34	
	Attagenus pellio	semi-specialist	predator	5	
	Ctesias serra	semi-specialist	predator	24	

Family	Species	Oak association	Trophic level	Ind.	Red list
	Dermestes lardarius	not oak	not oak	1	
Elateridae	*Ampedus balteatus*	generalist	xylophage	65	
	Ampedus cinnabarinus	semi-specialist	mixed	1	NT
	Ampedus hjorti	specialist	xylophage	22	VU
	Ampedus nigrinus	generalist	xylophage	16	
	Ampedus nigroflavus	semi-specialist	mixed	1	NT
	Ampedus pomorum	generalist	xylophage	1	
	Athous subfuscus	not oak	not oak	63	
	Calambus bipustulatus	semi-specialist	mixed	2	EN
	Cardiophorus ruficollis	generalist	xylomycetophage	1	
	Denticollis linearis	generalist	mixed	5	
	Melanotus castanipes	not oak	not oak	55	
	Melanotus villosus	generalist	mixed	7	
	Sericus brunneus	not oak	not oak	3	
Endomychidae	*Endomychus coccineus*	semi-specialist	fungivore	1	
Erotylidae	*Dacne bipustulata*	semi-specialist	fungivore	21	
	Triplax aenea	not oak	not oak	2	
	Triplax russica	semi-specialist	fungivore	2	
Eucnemidae	*Eucnemis capucina*	not oak	not oak	1	EN
	Melasis buprestoides	semi-specialist	xylomycetophage	1	NT
	Microrhagus lepidus	not oak	not oak	2	NT
	Microrhagus pygmaeus	generalist	xylomycetophage	2	
	Xylophilus corticalis	generalist	xylomycetophage	12	
Histeridae	*Dendrophilus punctatus*	generalist	predator	3	
	Dendrophilus pygmaeus	not oak	not oak	1	
	Gnathoncus buyssoni	not oak	not oak	9	
	Gnathoncus nannetensis	generalist	predator	1	
	Plegaderus caesus	semi-specialist	predator	6	
Laemophloeidae	*Cryptolestes corticinus*	not oak	not oak	5	EN
Latridiidae	*Cartodere nodifer*	generalist	fungivore	3	
	Corticaria longicollis	generalist	fungivore	31	
	Corticarina minuta	not oak	not oak	3	
	Corticarina parvula	not oak	not oak	1	
	Corticarina similata	not oak	not oak	51	
	Cortinicara gibbosa	not oak	not oak	21	
	Dienerella vincenti	generalist	fungivore	7	
	Enicmus fungicola	generalist	fungivore	2	
	Enicmus rugosus	generalist	fungivore	106	
	Enicmus testaceus	generalist	fungivore	34	
	Enicmus transversus	not oak	not oak	7	
	Latridius hirtus	generalist	fungivore	7	
	Latridius minutus	generalist	fungivore	1	
	Latridius porcatus	not oak	not oak	1	
	Stephostethus rugicollis	not oak	not oak	1	

Family	Species	Oak association	Trophic level	Ind.	Red list
Leiodidae	*Agathidium badium*	generalist	fungivore	1	
	Agathidium confusum	generalist	fungivore	8	
	Agathidium pisanum	generalist	fungivore	1	
	Agathidium seminulum	generalist	fungivore	16	
	Agathidium varians	generalist	fungivore	2	
	Amphicyllis globus	not oak	not oak	1	
	Anisotoma castanea	not oak	not oak	6	
	Anisotoma glabra	not oak	not oak	1	
	Anisotoma humeralis	generalist	fungivore	9	
	Anisotoma orbicularis	generalist	fungivore	3	
	Nemadus colonoides	specialist	predator	6	NT
Lucanidae	*Platycerus caraboides*	semi-specialist	xylophage	1	
	Sinodendron cylindricum	semi-specialist	xylophage	5	
Lymexylidae	*Elateroides dermestoides*	generalist	xylomycetophage	18	
	Lymexylon navale	specialist	xylomycetophage	5	CR
Malachiidae	*Anthocomus fasciatus*	not oak	not oak	1	
Melandryidae	*Conopalpus testaceus*	semi-specialist	xylomycetophage	6	
	Orchesia luteipalpis	not oak	not oak	1	VU
	Orchesia undulata	semi-specialist	xylomycetophage	11	
	Osphya bipunctata	not oak	not oak	2	EN
	Phloiotrya rufipes	semi-specialist	xylomycetophage	2	NT
	Serropalpus barbatus	not oak	not oak	1	
Monotomidae	*Rhizophagus bipustulatus*	specialist	predator	30	
	Rhizophagus cribratus	specialist	predator	2	
	Rhizophagus dispar	generalist	predator	4	
	Rhizophagus fenestralis	generalist	predator	1	
	Rhizophagus parallelocollis	not oak	not oak	1	
Mordellidae	*Curtimorda maculosa*	generalist	xylomycetophage	1	
	Mordella aculeata	not oak	not oak	1	
	Mordellochroa abdominalis	not oak	not oak	2	
Mycetophagidae	*Litargus connexus*	generalist	fungivore	1	
	Mycetophagus piceus	specialist	fungivore	3	VU
	Mycetophagus populi	not oak	not oak	2	VU
Nitidulidae	*Cryptarcha strigata*	semi-specialist	predator	45	NT
	Cryptarcha undata	semi-specialist	predator	14	NT
	Cybocephalus politus	not oak	not oak	1	
	Cychramus luteus	not oak	not oak	18	
	Cychramus variegatus	generalist	fungivore	8	
	Epuraea aestiva	not oak	not oak	8	
	Epuraea biguttata	generalist	mixed	1	
	Epuraea guttata	specialist	predator	1	NT
	Epuraea longula	not oak	not oak	1	
	Epuraea marseuli	generalist	predator	1	
	Epuraea melanocephala	not oak	not oak	6	

Family	**Species**	**Oak association**	**Trophic level**	**Ind.**	**Red list**
	Epuraea terminalis	generalist	predator	1	
	Epuraea unicolor	generalist	predator	5	
	Glischrochilus hortensis	semi-specialist	mixed	25	
	Glischrochilus quadriguttatus	semi-specialist	mixed	2	NT
	Pityophagus ferrugineus	not oak	not oak	2	
	Pocadius ferrugineus	semi-specialist	fungivore	2	
	Soronia grisea	semi-specialist	mixed	4	
Oedemeridae	*Ischnomera caerulea*	specialist	xylophage	1	VU
Ptiliidae	*Acrotrichis rugulosa*	semi-specialist	fungivore	2	
	Ptenidium turgidum	semi-specialist	fungivore	19	
	Pteryx suturalis	generalist	fungivore	1	
	Ptiliolum caledonicum	generalist	fungivore	1	
Ptinidae	*Cacotemnus rufipes*	semi-specialist	xylophage	2	
	Dorcatoma chrysomelina	specialist	xylomycetophage	541	
	Dorcatoma dresdensis	generalist	fungivore	1	
	Dryophilus pusillus	not oak	not oak	1	
	Gastrallus immarginatus	specialist	xylophage	6	EN
	Grynobius planus	semi-specialist	xylophage	10	
	Hadrobregmus pertinax	generalist	xylomycetophage	9	
	Hemicoelus canaliculatus	semi-specialist	xylophage	7	
	Ptilinus pectinicornis	semi-specialist	xylophage	1	
	Ptinomorphus imperialis	semi-specialist	xylophage	4	
	Ptinus fur	generalist	mixed	4	
	Ptinus rufipes	specialist	xylomycetophage	1	
	Ptinus subpillosus	specialist	mixed	182	
	Xestobium rufovillosum	specialist	xylophage	34	
	Xyletinus pectinatus	specialist	xylophage	3	EN
Salpingidae	*Lissodema cursor*	semi-specialist	predator	1	NT
	Salpingus planirostris	semi-specialist	predator	24	
	Salpingus ruficollis	generalist	predator	11	
	Sphaeriestes castaneus	not oak	not oak	1	
Scarabaeidae	*Cetonia aurata*	not oak	not oak	1	
	Gnorimus nobilis	specialist	xylophage	6	
	Protaetia marmorata	specialist	xylomycetophage	1	VU
	Trichius fasciatus	semi-specialist	xylophage	3	
Scraptiidae	*Anaspis frontalis*	generalist	mixed	5	
	Anaspis marginicollis	not oak	not oak	57	
	Anaspis rufilabris	generalist	mixed	44	
	Anaspis thoracica	generalist	mixed	18	
	Scraptia testacea	specialist	mixed	1	
Silvanidae	*Silvanoprus fagi*	not oak	not oak	2	
Sphindidae	*Aspidiphorus orbiculatus*	generalist	fungivore	2	
Staphylinidae	*Acidota crenata*	not oak	not oak	13	
	Acrulia inflata	generalist	predator	3	

Family	Species	Oak association	Trophic level	Ind.	Red list
	Agaricochara latissima	not oak	not oak	18	
	Anomognathus cuspidatus	generalist	mixed	3	
	Atheta britanniae	not oak	not oak	1	
	Atheta castanoptera	not oak	not oak	2	
	Atheta harwoodi	not oak	not oak	1	
	Atheta hypnorum	not oak	not oak	1	
	Atheta laticollis	not oak	not oak	1	
	Atheta pilicornis	not oak	not oak	5	
	Atheta ravilla	not oak	not oak	2	
	Atheta sodalis	not oak	not oak	1	
	Atheta subtilis	not oak	not oak	1	
	Atheta vaga	generalist	mixed	17	
	Atrecus affinis	generalist	predator	1	
	Batrisodes venustus	generalist	predator	1	
	Bibloporus bicolor	generalist	predator	63	
	Bibloporus minutus	generalist	predator	5	
	Bisnius subuliformis	generalist	predator	2	VU
	Bolitochara mulsanti	generalist	predator	1	
	Bryaxis puncticollis	not oak	not oak	4	
	Dadobia immersa	generalist	predator	1	
	Dalotia coriaria	not oak	not oak	1	
	Dexiogyia forticornis	not oak	not oak	27	
	Dropephylla ioptera	generalist	predator	1	
	Euconnus claviger	generalist	predator	4	
	Euconnus maklinii	generalist	predator	2	
	Euplectus bescidicus	not oak	not oak	1	
	Euplectus brunneus	semi-specialist	predator	2	
	Euplectus decipiens	not oak	not oak	4	
	Euplectus karstenii	generalist	predator	54	
	Euplectus mutator	generalist	predator	5	
	Euplectus nanus	generalist	predator	7	
	Euplectus piceus	generalist	predator	3	
	Euplectus punctatus	generalist	predator	27	
	Euthiconus conicicollis	semi-specialist	predator	3	EN
	Gabrius splendidulus	generalist	predator	11	
	Gyrophaena boleti	not oak	not oak	2	
	Hapalaraea pygmaea	specialist	predator	7	
	Haploglossa gentilis	specialist	predator	20	NT
	Haploglossa marginalis	generalist	predator	9	NT
	Haploglossa villosula	generalist	predator	996	
	Holobus apicatus	generalist	predator	2	
	Holobus flavicornis	not oak	not oak	10	
	Ischnoglossa prolixa	generalist	predator	5	
	Leptusa fumida	generalist	predator	6	

Family	**Species**	**Oak association**	**Trophic level**	**Ind.**	**Red list**
	Leptusa pulchella	generalist	predator	4	
	Leptusa ruficollis	semi-specialist	predator	51	
	Lordithon exoletus	not oak	not oak	1	
	Lordithon trimaculatus	not oak	not oak	1	
	Megarthrus depressus	not oak	not oak	2	
	Microscydmus minimus	not oak	not oak	2	
	Microscydmus nanus	generalist	predator	4	NT
	Mniusa incrassata	not oak	not oak	2	
	Mycetoporus lepidus	not oak	not oak	7	
	Omalium rugatum	not oak	not oak	1	
	Oxypoda arborea	semi-specialist	predator	94	
	Pella cognata	generalist	predator	1	
	Philonthus decorus	not oak	not oak	1	
	Phloeonomus punctipennis	generalist	mixed	1	
	Phloeopora corticalis	generalist	predator	13	
	Phloeopora testacea	generalist	predator	14	
	Phloeostiba lapponica	generalist	predator	1	
	Phloeostiba plana	generalist	mixed	3	
	Phyllodrepa ioptera	generalist	predator	16	
	Phyllodrepa linearis	not oak	not oak	2	
	Phyllodrepa melanocephala	semi-specialist	predator	6	
	Placusa tachyporoides	generalist	predator	7	
	Plectophloeus nitidus	generalist	predator	2	EN
	Quedius brevicornis	generalist	predator	4	NT
	Quedius brevis	not oak	not oak	4	
	Quedius cruentus	semi-specialist	predator	5	
	Quedius fuliginosus	not oak	not oak	1	
	Quedius maurus	generalist	predator	7	
	Quedius mesomelinus	semi-specialist	predator	5	
	Quedius microps	specialist	predator	2	VU
	Quedius plagiatus	generalist	predator	1	
	Quedius xanthopus	generalist	predator	49	
	Scaphisoma agaricinum	generalist	fungivore	18	
	Scaphisoma boreale	not oak	not oak	1	
	Scydmaenus hellwigii	specialist	predator	1	NT
	Scydmoraphes minutus	generalist	predator	1	NT
	Sepedophilus littoreus	generalist	fungivore	1	
	Sepedophilus testaceus	generalist	fungivore	5	
	Stenichnus bicolor	generalist	predator	4	
	Thamiaraea cinnamomea	semi-specialist	predator	6	
	Tyrus mucronatus	generalist	predator	1	
	Xantholinus tricolor	not oak	not oak	1	
Tenebrionidae	*Bolitophagus reticulatus*	not oak	not oak	1	
	Diaperis boleti	generalist	fungivore	3	

Family	Species	Oak association	Trophic level	Ind.	Red list
	Eledona agricola	specialist	fungivore	2	VU
	Mycetochara axillaris	not oak	not oak	4	EN
	Mycetochara flavipes	semi-specialist	xylomycetophage	1	
	Mycetochara maura	semi-specialist	xylomycetophage	11	NT
	Palorus depressus	specialist	xylomycetophage	1	
	Prionychus ater	semi-specialist	xylomycetophage	2	NT
	Prionychus melanarius	specialist	xylomycetophage	5	VU
	Pseudocistela ceramboides	generalist	xylomycetophage	32	
Tetratomidae	*Hallomenus axillaris*	generalist	fungivore	1	NT
	Hallomenus binotatus	generalist	fungivore	5	
Trogidae	*Trox scaber*	generalist	predator	2	
Trogossitidae	*Grynocharis oblonga*	generalist	xylomycetophage	5	VU
	Nemozoma elongatum	not oak	not oak	1	
	Thymalus limbatus	generalist	xylomycetophage	7	
Zopheridae	*Bitoma crenata*	generalist	predator	1	
	Colydium elongatum	not oak	not oak	1	EN
	Synchita humeralis	semi-specialist	mixed	3	

Beetles were caught with windows traps on hollow oaks (N=40) in Southern Norway and oak association and trophic level are shown. For explanation of the categories of functional groups see the method section. Total individuals (Ind) and Norwegian red list status (Kålås et al. 2010) are shown: NT, Near Threatened, VU, Vulnerable, EN, endangered, CR, Critically Endangered

Supplementary material 2

Table S2 Optimal models of Generalized linear mixed models (GLMMs) for species richness

Model	Est.[a]	SE[b]	z value	*p*-value
Response: r**ed-listed**				
AIC final: 151.92 (start: 161.27) p=0.058				
Intercept	0.295	0.278	1.058	0.290
Dead branches intermediate	0.555	0.300	1.850	0.064
Response: **all oak**				
AIC final: 264.52 (start: 267.70)***				
Intercept	2.594	0.143	18.087	**0.000**
Landscape forest	0.308	0.085	3.622	**0.000**
Tree crown low	0.503	0.154	3.264	**0.001**
Tree crown middle	0.441	0.150	2.946	**0.003**
Response: **xylophage**				
AIC final: 162.19 (start: 168.52)***				
Intercept	-0.492	-0.492	-0.994	0.320
Landscape forest	0.852	0.226	3.769	**0.000**
Circumference	0.001	0.001	1.811	0.070
Tree crown low	0.885	0.406	2.177	**0.029**
Tree crown middle	1.032	0.396	2.607	**0.009**
Response: **xylomycetophage**				

AIC final: 143.62 (start: 152.66) p=0.089				
Intercept	0.869	0.194	4.475	**0.000**
Isolation high	-0.409	0.213	-1.918	0.055
Dead branches intermediate	0.417	0.240	1.735	0.083
Response: fungivore				
AIC final: 186.18 (start: 195.29) p=0.080				
Intercept	1.224	0.243	5.046	**0.000**
Tree crown low	0.556	0.266	2.089	**0.037**
Tree crown middle	0.499	0.260	1.917	0.055
Response: **predator**				
AIC final: 214.49 (start: 219.11)**				
Intercept	1.611	0.204	7.884	**0.000**
Landscape forest	0.414	0.119	3.487	**0.000**
Tree crown low	0.467	0.217	2.151	**0.032**
Tree crown middle	0.414	0.211	1.960	**0.050**
Response: **oak semi-specialist**				
AIC final: 181.68 (start: 188.51)**				
Intercept	0.925	0.275	3.368	**0.001**
Landscape forest	0.244	0.137	1.780	0.075
Tree crown low	0.779	0.288	2.701	**0.007**
Tree crown middle	0.717	0.283	2.532	**0.011**
Response: **generalist**				
AIC final: 239.00 (start: 245.74)***				
Intercept	2.025	0.174	11.644	**0.000**
Landscape forest	0.356	0.100	3.558	**0.000**
Tree crown low	0.537	0.185	2.907	**0.004**
Tree crown middle	0.477	0.180	2.652	**0.008**

UTM coordinates were used as random effects and optimal models were found by backward elimination, using the drop1 function in R and AIC as selection criterion. The optimal models were tested against nullmodels in likelihood ratio tests and stars indicate significant p-values, otherwise significant p-values are shown in bold (p<0.05). Only optimal models significantly better than a nullmodel or p-value <0.1 are shown. For the oak specialists and the mixed feeding group no predictors were kept in the model and results are not shown.

[a]Est, Estimate, [b]SE, Standard error, *, p≤ 0.05, **, p≤ 0.01 and ***, p≤ 0.001

Supplementary material 3

Table S3 Optimal models of linear mixed models fitted by REML for log-transformed abundance of oak associated beetles placed in functional groups

Model	Est.[a]	SE[b]	t value	p-verdi
Response: **red-listed**				
AIC final 73.93 (start: 84.35)*				
Intercept	0.113	0.221	0.510	0.610
circumference	0.001	0.000	2.980	**0.003**
Response: **all oak**				
AIC final 14.00 (start: 20.60)*				
Intercept	1.723	0.094	18.235	**0.000**

Model	Est.^{a}	SE^b	t value	p-verdi
Isolation high	-0.157	0.097	-1.608	0.108
circumference	0.000	0.000	1.467	0.142
Dead branches intermediate	0.245	0.102	2.402	**0.016**
Dead branches high	0.533	0.213	2.506	**0.012**
Response: **xylophage**				
AIC final 28.36 (start: 30.82)***				
Intercept	-0.158	0.204	-0.771	0.441
Landscape forest	0.469	0.118	3.959	**0.000**
circumference	0.001	0.000	3.062	**0.002**
Dead branches intermediate	-0.053	0.117	-0.456	0.648
Dead branches high	0.698	0.248	2.809	**0.005**
Tree crown low	0.325	0.152	2.132	**0.033**
Tree crown middle	0.404	0.150	2.689	**0.007**
Response: **xylomycetophage**				
AIC final 63.43 (start: 65.24) ***				
Intercept	0.119	0.308	0.386	0.700
Isolation high	-0.682	0.214	-3.194	**0.001**
circumference	0.002	0.000	4.246	**0.000**
Dead branches intermediate	0.171	0.185	0.923	0.356
Dead branches high	1.033	0.387	2.669	**0.008**
Tree crown low	0.579	0.238	2.434	**0.015**
Tree crown middle	0.675	0.258	2.620	**0.009**
Openness shrub	-0.632	0.214	-2.961	**0.003**
Openness tree	-0.756	0.242	-3.118	**0.002**
Response: **fungivore**				
AIC final 28.87 (start: 34.80)**				
Intercept	0.557	0.153	3.635	**0.000**
Landscape forest	0.276	0.102	2.715	**0.007**
Dead branches intermediate	0.152	0.108	1.410	0.158
Dead branches high	0.599	0.250	2.399	**0.016**
Tree crown low	0.297	0.152	1.948	0.051
Tree crown middle	0.145	0.150	0.965	0.335
Response: **predator**				
AIC final 21.78 (start: 28.08)*				
Intercept	1.366	0.099	13.776	**0.000**
Landscape forest	0.195	0.102	1.912	0.056
Openness shrub	0.249	0.120	2.069	**0.039**
Openness tree	0.095	0.106	0.894	0.372
Response: **mixed feeding group**				
AIC final 23.53 (start: 34.64)*				
Intercept	0.775	0.070	11.034	**0.000**
Openness shrub	0.335	0.133	2.523	**0.012**
Openness tree	0.189	0.104	1.812	0.070
Response: **specialist**				
AIC final 68.85 (start: 77.78)**				
Intercept	0.609	0.220	2.769	**0.006**
circumference	0.001	0.000	3.032	**0.002**

Model	**Est.**[a]	**SE**[b]	**t value**	**p-verdi**
Response: **oak semi-specialist**				
AIC final 23.18 (start: 28.66)**				
Intercept	1.001	0.098	10.206	**0.000**
Isolation high	-0.309	0.104	-2.979	**0.003**
Landscape forest	0.168	0.094	1.776	0.076
Dead branches intermediate	0.203	0.111	1.825	0.068
Dead branches high	0.745	0.243	3.062	**0.002**
Response: **generalist**				
AIC final 26.68 (start: 30.15) p=0.055				
Intercept	1.553	0.137	11.293	**0.000**
Isolation high	-0.179	0.111	-1.609	0.108
Landscape forest	0.200	0.107	1.856	0.063
Dead branches intermediate	0.087	0.116	0.750	0.453
Dead branches high	0.527	0.243	2.169	**0.030**
Openness shrub	0.218	0.127	1.726	0.084
Openness tree	-0.090	0.132	-0.681	0.496

Entomological region (categorical) was used as random effect. Optimal models were found by backward elimination using drop1 function in R and AIC as selection criterion. Only optimal models significantly better than a nullmodel or p-value <0.1 are shown. The optimal models were tested against nullmodels in likelihood ratio tests and significant p-values are indicated with stars, otherwise significant p-values are shown in bold ($p<0.05$).

[a]Est, Estimate, [b]SE, Standard error, *, $p\leq 0.05$, **, $p\leq 0.01$ and ***, $p\leq 0.001$

References cited

Kålås, J. A., Å. Viken, S. Henriksen, and S. Skjelseth. 2010. The 2010 Norwegian Red List for Species. Norwegian Biodiversity Information Centre, Norway.,

Paper III

Long-lasting effects of logging on beetles in hollow oaks

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Key words: *Quercus*, veteran tree, extinction debt, spatial scales, Coleoptera, saproxylic, historical logging, temporal scale

Abstract

Habitat loss is currently one of the largest threats to biodiversity worldwide, but an increasing number of studies show that accounting for past habitat loss is essential to understanding current distributional patterns. Hollow oaks (*Quercus* spp.) are important habitats for species that depend on deadwood. We used a gradient spanning 40 km from the coast to inland areas reflecting historical logging intensity through 500 years in Southern Norway, to investigate if the historical variation in oak density is influencing the structure of beetle communities in hollow oaks today. We trapped beetles in 32 hollow oaks along this gradient in forested and semi-natural landscapes over two summers. We expected species richness and abundance to be higher inland because of the later large-scale logging of oak there. We also expected oak specialists to respond more markedly, and that the effect of historical logging would be modified by scale-specific environmental variables. Higher species richness and total abundance inland indicate that historical logging has affected the beetle communities, but the oak specialists did not respond. Scale-specific environmental variables at tree, local and landscape scales also affected the beetles' response. Whereas population sizes of the oak specialization groups were controlled by local conditions of the tree and the close surroundings, species richness responded to deciduous forest at a landscape scale, indicating that larger areas are necessary to maintain species richness through time. If coastal and inland hollow oaks are equally isolated today, we should expect an extinction debt inland due to its more recent history of logging. We show that spatial scale and habitat history are both important in understanding the responses of communities in long-lasting habitats. Our findings suggest that current management of old oaks is likely to affect the species in hollow oaks not only today, but also far into the future.

Introduction

Habitat loss is currently one of the greatest threats to biodiversity and ecosystems worldwide (Sala et al. 2000, Millennium Ecosystem Assessment 2005), with species going extinct at a rate that suggests we are entering a sixth mass extinction (Barnosky et al. 2011). Not all species are equally likely to go extinct, however. Several studies have identified traits that make some species more vulnerable than others, including specialized food or habitat requirements, limited dispersal ability, naturally low population size, or limited reproductive capacity (Henle et al. 2004, Benedick et al. 2006, Cagnolo et al. 2009). These vulnerable species are also often rare, but may still perform vital functions in ecosystems that may not easily be performed by common species, making their conservation crucial for ecosystem functioning (Mouillot et al. 2013).

Species richness and composition are affected by processes at several spatial scales (Wiens 1989, Cornell and Harrison 2014, Jackson and Fahrig 2015). For example, at a regional scale, climate may control a species' distribution, but at a local scale, biological processes such as competition can override the climatic effects (Wiens 1989), making climate a poor predictor of a species' local occurrence. These spatial responses are probably species-dependent (Wiens 1989, Sverdrup-Thygeson et al. 2014a), but spatial studies of communities face two major challenges: First, the relevant species-specific scales are rarely known, and second, a community will normally contain species with a range of spatial responses (Holland et al. 2004, Jackson and Fahrig 2015). One way forward is to categorize species by their specific traits, as ecologically similar species are likely to have similar spatial responses (Dupré and Ehrlén 2002, Henle et al. 2004, Sverdrup-Thygeson et al. 2014b). Finding shared scales of response for species aggregates is also useful for conservation purposes as it might enable correct management recommendations (Bergman et al. 2012). To reveal important scale-dependent ecological patterns within a community, multi-scale studies are needed (Wiens 1989, Lindenmayer et al. 2000, Jackson and Fahrig 2015).

All species communities change through time and are affected by past immigrations, extinctions and fluctuation in environmental factors (Magurran and McGill 2011), but several recent studies show that also local and regional habitat loss history can have substantial impact on current communities (Helm et al. 2006, Kuussaari et al. 2009, Sverdrup-Thygeson et al. 2014a). Temporal scale is therefore important to consider in community studies because, where populations are not in equilibrium with their environment due to past changes, species can still be expected to go extinct locally even if habitat loss is halted, a phenomenon called extinction debt (Kuusaaari et al. 2009). For example, the number of specialist plant species occurring in the calcareous grasslands of Estonia cannot be explained by current habitat area or connectivity, but by that present 70 years previously, before the subsequent massive loss of habitat (Helm et al. 2006). An estimated 40% of species in the remaining grassland could yet go extinct, a legacy of this past loss. Recording species number without considering past events therefore risks overestimating long-term species richness and underestimating the threat of extinction (Helm et al. 2006). Despite their limited number, current studies of plants, lichens, insects, fish and birds indicate that extinction debt is more common than previously recognised (Kuussaari et al. 2009). More such studies are clearly needed, focusing on the combined effects of historical and geographic factors, ideally across several spatial scales.

In this study, we investigate how habitat history and current habitat distribution at different spatial scales affect the richness and abundance of species groups exhibiting varying degrees of habitat specialization. We studied beetles dependent on deadwood (saproxylic beetles) living in hollow oaks (*Quercus* spp.), and ask if the history of forest exploitation influences present patterns of species richness and abundance, beyond what can be explained by the properties of individual oak trees, their close surroundings, and the wider landscape.

Veteran trees, with or without hollows, are highly specialized habitats that have been recognized as biodiversity hotspots, rich in rare and red-listed species (Sverdrup-Thygeson 2009, Bütler et al. 2013). They provide ecological continuity through time and are keystone structures in many landscapes (Manning et al. 2006), but are often locally rare, occur in fragmented landscapes, and are declining globally (Gibbons et al. 2008, Lindenmayer et al. 2012, Lindenmayer et al. 2014, Siitonen and Ranius 2015). Ancient oaks are one of the most important environments for saproxylic species in Northern Europe (Hultengren et al. 1997, Siitonen and Ranius 2015) and form long-lasting habitat for these species (Ranius et al. 2009, Nordén et al. 2014). As the oaks age, a range of microhabitats develop that are not present in younger trees, such as coarse bark, dead branches and cavities with wood mould (Bütler et al. 2013, Siitonen and Ranius 2015). This process takes centuries, as most oaks start to develop cavities around 200 years of age (Ranius et al. 2009). Species that depend on long-lasting and stable habitats are often assumed to have low dispersal rates (Nilsson and Baranowski 1997, Hedin et al. 2008) and respond more slowly to fragmentation than those species adapted to exploiting short-lived, fluctuating resources (Nilsson and Baranowski 1997).

The hollow oaks in our study system have a fragmented distribution due to historical large-scale logging of oak, and it is possible that the associated beetles are responding both to historical and current habitat density. To investigate if the historical variation in oak density is important for beetles in hollow oaks, we used a gradient spanning 40 km from the coast to the inland reflecting historical logging intensity through 500 years. As large-scale logging started earlier and was more intensive along the coast than in inland areas, the remaining hollow oaks along the coast are expected to have been isolated for longer than those inland. To assess the importance of current habitat and surroundings we also included environmental variables at three spatial scales: the individual tree; its immediate surroundings; and the landscape.

We predict that (1) the richness and abundance of saproxylic oak-beetle species will be lower close to the coast than at inland sites, reflecting the inferred difference in logging intensity and duration with distance from the coast; (2) the effect described in (1) is stronger for species most dependent on oaks (oak specialists) than for those with broader habitat preferences (oak semi-specialists and oak generalists); and (3) the effect of historical land use will be modified by scale-specific environmental variables.

Methods

Study area and design

The logging of oak in Norway

Historically, Norway had large oak forests in Southern Norway growing right down to the coast (Vogt 1886, Vevstad 1998). The shortage of oak timber in Europe combined with the introduction of river sawmills in the 1520s set the scene for large-scale logging and export of oak (Central Bureau of Statistics of Norway 1977, Moore 2010). Transporting the timber was the most demanding part of the trade. River transport (log floating) was difficult, could take several years, and led to substantial timber loss (Vevstad 1998). Therefore, the easily accessible coastal areas were logged first (Vevstad 1998). Oak was heavily harvested there from the 1520s and throughout the 1600s, but by the end of the 17th century little oak suitable for logging was left (Central Bureau of Statistics of Norway 1977, Vevstad 1998, Moore 2010). Already in the 1630s many places along the coast lacked suitable oak timber (Tvethe 1852), and it is safe to assume that logging of oak in general occurred inland from the mid-seventeenth century and onwards as the logging had depleted the costal oak forests in southern Norway. As the availability of oak diminished, logging for pine and spruce escalated and these species replaced oak as the most important timber trees (Vevstad 1998). Oak never regained its dominance, even though the timber was highly valued as shipbuilding material until the late 19th century. For more information about the history of oak logging see Supplementary material Appendix 1.

Study areas

To study a geographical gradient representing historical logging intensity and duration, we selected hollow oaks *Quercus robur* and *Q. petraea* along a coast-inland gradient in two regions, Agder and Larvik, in southern Norway. Agder is situated in the south, with hollow oaks from the coast to 40 km inland, while Larvik is located in the southeast with hollow oaks from the coast to 25 km inland (Figure 1).

The two sampling regions are both within the main area of oak distribution in Norway and span the nemoral, boreonemoral and southern boreal vegetation zones (Moen 1999). In Agder (Vest- and Aust-Agder counties) the forests are dominated by pine *Pinus sylvestris* (45-53% of the forest), spruce *Picea abies* (20-24%) and deciduous trees (16-29%) (Tomter and Eriksen 2001, Tomter et al. 2001). Around 8% of the productive forest volume in the Agder region is oak. Larvik is part of Vestfold county, where forests are dominated by spruce (45%), deciduous trees (35%) and pine (15%) (Eriksen et al. 2006). Only 2.7% of the productive forest volume is oak but there is a higher percentage of large trees (9.5% with trunk diameters > 45 cm) compared with 1−4% in Agder (Tomter and Eriksen 2001, Tomter et al. 2001, Eriksen et al. 2006).

We sampled 16 hollow oaks in each region with a minimum distance of 1.5 km between each to ensure independent sampling. We selected individuals with a visible hollow above ground and the presence of wood mould. As the species composition of beetles in hollow oaks varies between forest trees and those in agricultural or urban landscapes (Sverdrup-Thygeson et al. 2010, Skarpaas et al. 2011), we avoided the most culturally influenced trees, such as heavily pollarded trees in parks or cities and wide-branched solitary trees in open landscapes. Our study included trees in forest (n = 17) and semi-natural habitats (n = 15). The latter represents oaks in forest edges along fields or close to settlements. The semi-natural and forest oaks were evenly distributed along the gradient and between the regions (Figure 1, Table 1). We did not differentiate between *Q. robur* and *Q. petraea* as this is unlikely to affect the beetles.

The coast-inland gradient

Distance to coast was measured on a regional scale along the coast-inland gradient and was used as a proxy for how accessible and attractive the oaks were for historical logging. Oaks close to the coast were assumed to be isolated earlier and exposed to generally higher land-use pressures. The shortest distance from the oaks to the coast was measured as a straight line (Euclidean distance) using ArcMap 10.2.2 (Table 1). In the Larvik region, a straight line to the known destination for logged timber (Larvik city) was used for four trees because the shortest distance to the coast represented an impossible transport route for timber because of the terrain.

Because climate is likely to vary along the coast-inland gradient, climate variables were included to separate the effects of climate and historical logging. We characterized each site by its mean summer temperature (°C) and total precipitation (mm) in the four warmest months (June to September). We used interpolated data from a 1 × 1 km grid made available by the Norwegian

Meteorological Institute (see http://met.no/) for the period 1961−1990, assuming this to be representative of the climatic conditions prevailing in the study area (Table 1).

Spatial scales

We characterized habitat quality at three spatial scales. The smallest spatial scale used was the *tree scale*. For each oak, we recorded the circumference at breast height (cm) and categorized the growth form of the tree (Table 1). The close surroundings were used to characterize the *local scale*. At each site we counted the total number of oaks, number of hollow oaks, and the downed and standing deadwood of all tree species in different size classes in an area of 42 × 42 m around the oak (see Table 1). As a measure of the openness around the sampled oaks we estimated forest density using stand basal area (m^2 ha^{-1}), measured through a relascope with a 1-cm wide opening.

To characterize the surroundings of each sampled oak on a *landscape scale*, we included forest variables and a measure of favorable habitat in a 2 km radius, as this scale has proved to be important for species richness of saproxylic beetles (Bergman et al. 2012, Jacobsen et al. 2015). For the forest variables we obtained information on forest cover and structure from satellite images of the landscape provided by the Norwegian Institute of Bioeconomy Research (NIBIO 2016). ArcMap 10.2.2 was used to extract information on the 2 km scale around the oak using the clip function, and we used information on forest cover, volume per hectare, area of deciduous trees and cover of old forest (average tree age >80 years old) (Table 1).

To include a measure of relevant habitat on the landscape scale, we used information from the Norwegian database for habitats (Naturbase) (Norwegian Environment Agency 2015) on occurrences of hollow and large oaks (recorded as points registrations or polygons), hollow deciduous trees (point records) and standing and downed deadwood (recorded in polygons). In Larvik, we also included supplementary records of woodland key habitats relevant for saproxylic species (Fritzøe Skoger 2016), as this can be important habitat for oak-associated beetles (Franc et al. 2007, Götmark et al. 2011). For polygons where information on size was not available in the database, area was measured in ArcMap 10.2.2, using a buffer function for the key woodland habitats in Larvik to check for overlap with point records, and calculating the size of the deadwood polygons with the measuring tool. We wanted to convert all the records to a common scale to create a single variable reflecting favorable habitat. All point registrations of hollow and large trees within 2 km of the hollow oak were therefore counted, which we supplemented with information from the database on the hollow-oak polygons to estimate the number of hollow oaks in each polygon. We then converted the number of trees to a common scale of 30 trees ha^{-1}, and merged these into one variable with the deadwood polygons (defined as minimum 20−40 trees ha^{-1}) (Baumann et al. 2001). As the woodland key habitats in Larvik are large and contain other nature types than just old oaks and deadwood, a conversion factor of 0.1 was used before adding this information to the same habitat variable (Table 1, see Supplementary material Appendix 3 for more details on this variable). Because not all areas were completely mapped, we acknowledge that our ‘favorable habitat’ variable could be underestimated in some areas.

Insect sampling

Each oak was sampled for insects by a standard method used in previous studies (Sverdrup-Thygeson 2009, Sverdrup-Thygeson et al. 2010): two flight interception traps (window size 20 × 40 cm) for each oak, one in front of the cavity opening and one in the canopy. The insect traps were active from mid-May to mid-August in 2013 and 2014, and emptied once a month. We used a solution of propylene glycol, water and liquid dish detergent in the collecting containers. The insects were transferred to a 7:3 mix of propylene glycol and ethanol and stored at −20ºC until identification.

All beetles were identified to species and categorized according to their association with oaks (Supplementary material Appendix 2). Only saproxylic species associated with oak were included in our analyses. We used the following categories: ‘oak specialists’ for species preferring oak or occurring only on oak; ‘oak semi-specialists’ for species occurring only on oak and broadleaved trees; and ‘oak generalists’ for species occurring on both oak and coniferous trees (Supplementary material Appendix 2).

Statistics

All statistical analyses were carried out in R. v. 3.1.0. To investigate if the recorded environmental variables varied systematically along the coast-inland gradient, we calculated the correlation coefficients (Pearson’s r) between the assorted site variables and distance to coast. We wanted to reduce the number of predictor variables prior to model selection, and therefore tested for collinearity and eliminated variables until variance inflation factors (VIFs) were below three, as recommended by Zuur et al. (2009). Temperature and all the 2-km forest variables other than the area of deciduous forest were excluded because of collinearity. Temperature was highly correlated with precipitation and distance to coast, and the forest variables co-varied with distance to coast and with each other (collinear variables shown in italics in Table 1).

We tested if our two study regions, Agder and Larvik, should be included as random variables in the models by comparing generalized least square (GLS) and linear mixed-effect (LME) models. We included all the variables in the GLS and LME models, and compared their Akaike information criterion (AIC) scores. The

GLS models generally had lower AIC-values, and we proceeded without random effects, using generalized linear models (GLMs) with a Poisson distribution and log-link function instead. For backward elimination, we used the drop1 function to find the optimal GLM models based on their AIC scores. The abundance data and species richness of all species and oak generalists were over-dispersed so we applied a negative binomial GLM using the glm.nb function from the MASS library in R, and stepAIC, to find the optimal models. When two models had almost identical AIC values (< 1), we chose the simplest model. The optimal models were then tested against null models in analyses of deviance (for Poisson GLMs) or log-likelihood tests (for negative binomial GLMs). An outlier was present in the negative binomial GLMs that caused substantial over-dispersion (dispersion parameter > 1.3) in both overall abundance and the oak generalist measures. The outlier resulted from high numbers of the ant-associated oak generalist *Haploglossa villosula* (Päivinen et al. 2002). It constituted 82% of the individuals in one tree, probably the result of the presence of a nest of the ant *Lasius fuliginosus*. As *H. villosula* was present in most of the oaks ($n = 27$) and could have a large influence on the analyses, we excluded it from the abundance data to remove the over-dispersion and to improve the diagnostic plots that were inspected for all models.

To investigate if the explanatory variables that co-varied with the coast-inland gradient were better predictors of the observed patterns of species richness and abundance than the gradient itself, we replaced distance-to-coast in the relevant optimal models with the excluded variables to see if this improved the fit.

Results

Environmental correlates with the coast-inland gradient

Only climate and landscape-scale variables were correlated with distance from the coast (Table 3). The coastal, historically first-logged areas, were warmer and dryer, had less area of old forest, and a greater forest volume per hectare than the inland sites (Table 3). There was also a non-significant trend of more forest cover and hollow oaks inland (Table 3).

Determinants of species richness and abundance

The total species richness increased with distance from the coast and was positively affected by tree circumference and the cover of deciduous forest in the landscape (Tables 4, 6). Species richness of oak generalists and oak semi-specialist beetles followed a similar pattern, being positively related to distance from the coast and with the cover of deciduous forest in the landscape. In contrast, oak specialists only responded to tree circumference (Table 4).

Overall abundance also increased with distance from the coast, but the various species groups did not (Table 5, 6). Tree characteristics and local variables were most important in determining abundance, with all groups except the oak semi-specialists being positively affected by tree circumference and negatively affected by low and middle tree forms. The oak semi-specialists only responded to the nearby abundance of hollow oaks (Tables 5, 6). The total oak-associated beetle abundance and the abundance of the oak specialists were also negatively influenced by local forest density, as indexed by stand basal area.

Models fitted with the excluded collinear predictor variables were weaker, with no significant effects of the predictors (forest cover, forest volume, old forest and temperature). Overall, distance-to-coast had the higher explanatory power for the observed patterns of species richness and abundance.

Discussion

In this study we hypothesized that beetle species richness and abundances should be highest inland as a result of later, lower intensity, historical logging compared with that in coastal areas. Our finding that total species richness and overall abundance increased significantly with distance from the coast supports this hypothesis, although the most specialized species, for which we expected the more pronounced relationship, did not respond as predicted. Present environmental conditions at tree and local scales apparently modify the abundances of the beetles, whereas these only affect beetle species richness at the tree and landscape scales.

Are the effects of historical logging real?

As logging history in southern Norway is not georeferenced in any way, we used distance to the coast as a proxy for past logging, with areas close to the coast assumed to have been logged longest and most intensively. Nevertheless, several variables—climate, area of old forest and volume—also change systematically along this gradient (see Table 3). Their influences cannot clearly be separated from those of historical logging. But if the observed species' responses were due solely to the changes in climate, we would expect a negative response to this gradient because of reduced summer temperatures and increased precipitation inland (Table 3). Saproxylic insects generally prefer high temperatures (Müller et al. 2015) and are likely to be negatively affected by precipitation (Gough et al. 2015). The forest structure changed along the gradient, with more extensive old forest and lower total forest volume inland than along the coast, but we found no relationship with beetle species richness or abundances when we replaced distance-to-coast with these variables in our models. As a hollow oak's distance to the coast, in itself, should not promote species richness, we therefore believe the most likely explanation of the observed pattern is a response to the historical logging intensity and duration.

The negative effects of logging on saproxylic species is well documented (Siitonen 2001, Müller et al. 2007, Paillet et al. 2010, Gossner et al. 2013) and we expected the beetles in our study to be affected by the historical logging of oak. Nordén et al. (2013) found that the specialist wood-inhabiting fungi were negatively affected by forest fragmentation, whereas generalist species thrived. The specialized fungi were host-specific and typically depend on forest characteristics, such as large diameter deadwood and late stages of decay, that are rare in managed forests (Nordén et al. 2013). Even in near-to-nature management forests, selective logging can affect the assembly of functional traits of saproxylic beetles, as such logging reduces the volume of deadwood, tree diameters, the number of veteran trees, and those in late stages of decay (Gossner et al. 2013). Intensive forest management in Finland has already led to the extinction of over a hundred forest-dwelling species, but an extinction debt is probably still be present in the northeast (Hanski and Ovaskainen 2002). Large-scale historical logging of oak in Norway is therefore likely also to have had severe negative effects on oak-associated beetles. For example, the rare ship timber beetle *Lymexylon navale*, present in only one of our hollow oaks, was once a pest species in shipyards where oak timber was used, but today it is critically endangered in Norway (Norwegian Biodiversity Information Centre 2015). Other beetles that are rare today, but were probably more common in oak forests historically include the hermit beetle *Osmoderma eremita* and its predator, *Elater ferrugineus*, each now present only in single locations in Norway (Norwegian Biodiversity Information Centre 2015) and not observed in our study.

Why do oak specialists not respond to historical logging?

The oak specialists in our study did not respond as expected along the coast-inland gradient representing historical logging. As the specialists must have experienced the most severe habitat loss following large-scale logging, it is possible that local extinctions happened rapidly and that the current populations are already in equilibrium with their environment. Another possibility could be due to climate, as several of the specialist species in our study appear to be restricted to the warmest parts of Norway within the main region of oak distribution (Norwegian Biodiversity Information Centre 2016). In a study of beetles in hollow oaks over a 700-km climatic gradient across Norway and Sweden, Gough et al. (2015) found that oak specialists responded negatively to summer precipitation and positively to increased summer temperatures. Because oak is at its northern distributional limits in Norway, many oak specialists are probably also close to their northern limits. Our inland sites could therefore be climatically less favorable. But micro-climate is also important for saproxylic beetles (Müller et al. 2015) and hollow oaks situated on southern slopes or the top of hills could experience higher temperatures than the average climate on a landscape scale that we used in our study.

From tree to landscape scale

We found that the environment at several spatial scales affected the oak-associated beetle community. The tree scale was important for species richness and abundance, whereas the local scale was important only for abundances and the landscape scale important only for species richness (Table 6). This indicate that different processes are important in determining abundance and species richness. Population sizes appear to be controlled by local resources, such as patch size and quality. For a species to maintain populations through time, however, larger areas of suitable habitat are needed and, in disturbed habitats, species could have died out because of increased isolation. If so, the greater species richness in deciduous forest at a landscape level makes sense, because deciduous forest provides more habitat in the form of host trees and deciduous deadwood.

Spatial patterns likely reflect differences in species' dispersal biology (Ranius 2006, Bergman et al. 2012). Many species living in hollow trees today could be dispersal-limited, given that such species, which live in stable and long-lived habitats, less frequently need to disperse to new habitats (Nilsson and Baranowski 1997, Ranius and Hedin 2001, Ranius 2006). Detailed studies of saproxylic beetles in hollow oaks indicate that their spatial responses to the surrounding environment varies at a range of scales (52 m to ≥ 5000 m: Bergman et al. 2012; 135−2800 m: Ranius et al. 2011) depending on species. In particular, the beetle species richness was best explained by oak density on a 2.3 km scale (Bergman et al. 2012). This is a similar scale of response to the 2-km landscape scale that we used, to which overall beetle-species richness and that of oak semi-specialists responded to. Because semi-specialists only use deciduous host trees, the positive effects of deciduous forest in the landscape could be partly offsetting the negative effects of historical logging in areas with a high proportion of deciduous trees.

At the tree level, the positive relationship between circumference and both species richness and abundances accords with previous studies (Ranius and Jansson 2000, Sverdrup-Thygeson et al. 2010, Buse et al. 2016, Pilskog et al. 2016). At this scale, circumference can be viewed as a proxy for patch size (Pilskog et al. 2016), often being associated with more wood mould and greater architectural diversity, and therefore an increasing number of available niches (Siitonen and Ranius 2015). At the local scale, the observed negative relationship between forest density and beetle abundance fits well with previous studies showing that openness or limited regrowth around hollow oaks positively influences abundance (Ranius and Jansson 2000, Widerberg et al. 2012, Gough et al. 2014). Lower forest density means less shade, increased insolation and higher temperatures, likely to favor saproxylic beetles (Widerberg et al. 2012, Müller et al. 2015).

Unlike circumference, low tree form negatively affected beetle abundance, contrary to earlier findings (Pilskog et al. 2016). This could reflect differences in study design, as we focused on hollow oaks in forests and in the transition zone between agricultural landscapes and forests (semi-natural landscapes), but excluded wide-branched solitary trees in agricultural landscapes that typically have a low tree form. Hence, we possibly favored forest species. As tall trees are the typical growth form in forests, growth form could represent some other forest characteristic not measured in our study. For example, Gough et al. (2014) found higher species richness of oak generalists in hollow oaks surrounded by trees than in open surroundings, and suggested that the oak generalists may be responding to greater tree-host diversity in the surroundings, rather than to increased shade cast by the trees. Sverdrup-Thygeson et al. (2010) found different species assemblages in hollow oaks in forests and parks, partly explained by more deadwood in the surroundings in the forest. We suggest a similar explanation for our findings, that the beetles are responding to current or previous forest conditions, rather than to tree form itself.

Do the beetle communities in hollow oaks have an extinction debt?

Pollen from the last 4000 years show that oak abundance in Denmark and southern Sweden is currently at a historical minimum (Lindbladh and Foster 2010). It also supports historical records of a rapid decline in 18th and 19th century Sweden (Ranius et al. 2008, Lindbladh and Foster 2010). Although large-scale logging happened earlier in Norway (16th −17th century) than Sweden, and no similar oak-study exists from our regions, the decline following large-scale logging was extremely rapid for a long-lived species such as oak, where a millennium only represents a few generations (Drobyshev and Niklasson 2010, Lindbladh and Foster 2010). Species dependent on long-lived and stable resources such as veteran trees, are often assumed to be poor dispersers (Nilsson and Baranowski 1997, Hedin et al. 2008) and can be expected to respond more slowly to environmental changes than species in more ephemeral habitats (Ranius et al. 2008). At a meta-population level, local extinctions must be balanced by immigration and establishment of new local populations. But if isolation is too severe, colonization will no longer balance extinctions and the meta-population may go extinct (Hylander and Ehrlén 2013). Although our knowledge of historical habitat density for species in hollow oaks in most of Europe is limited, there is growing evidence that veteran trees and old-growth forest are harboring extinction debts (Berglund and Jonsson 2005, Sverdrup-Thygeson et al. 2014a). For example, occurrence of red-listed lichen and fungus species on old oaks in Sweden was best explained by including the early 19th century oak density prior to large-scale logging, indicating a probable extinction debt (Ranius et al. 2008). Buse (2012) found that saproxylic flightless weevils were absent from forests younger than 200 years and that their occurrence was explained by historical habitat density, but not current woodland size. Moreover, Nilsson and Baranowski (1997) found lower species richness of beetles in hollow trees in stands that had been managed 50−100 year ago, than in nearly primeval stands, suggesting slow recolonization.

As hollow oaks can last for centuries, it is possible that those in our study were colonized by beetles in the past when there was greater connectivity between oaks. Beetle populations living in hollow oaks can remain for decades, potentially even centuries (Hedin et al. 2008). It is quite possible that the beetle populations in our regions are not in equilibrium with their current surroundings (Ranius 2002), given that historical logging occurred later inland than along the coast. The observed increase in species richness inland could suggest an extinction debt if isolation inland and along the coast are similar today. Although some changes in forest structure were identified along the coast-inland gradient (Table 3), our results do not suggest these to be the cause of the greater species richness and abundance inland. Rather, it is likely that the species are responding to the later historical logging and subsequent isolation of the oaks inland.

The question of current isolation is therefore relevant to determining if the populations today are in equilibrium with their current surroundings or not. Unfortunately, no comprehensive mapping of hollow oaks exists in our regions. Our constructed habitat variable was based on current records of relevant habitat at the landscape scale, but it did not change along the gradient. But because our measures of habitat were quite coarse, there could still be important differences in habitat along the coast-inland gradient that were not revealed in our study. For example, the volume of deadwood or the quality of veteran trees as habitat may be more relevant than the area they cover, but unfortunately we did not have relevant data on this to include in our study. Detailed mapping at the landscape scale could help to reveal if the current populations are in equilibrium with their surroundings, or if we should expect an extinction debt inland because of more recent logging of oak there.

Implications for management

The number of hollow oaks in Norway is declining (Sverdrup-Thygeson et al. 2014c), a similar trend to that globally where large old trees are disappearing at a faster rate than new ones are being recruited (Gibbons et al. 2008, Lindenmayer et al. 2014). Our results demonstrate the importance of including both spatial scales and habitat history when aiming to understand community dynamics in long-lasting habitats. Our study further suggests that habitat history, spanning several centuries, may be important in understanding current patterns of species richness of beetles in veteran oaks. As such, more account should be taken of history when studying these long-lasting and stable ecological systems. The echoes of the past also carry another important message: actions taken today when managing hollow oaks can affect species far into the future. The good news is that the slow response of these species gives us time to improve their habitats and hopefully save those carrying an extinction debt, as many populations probably are. In Norway, we can expect highest species richness inland because of our logging history, but in other systems with different forest histories the pattern could be different. Local and national history therefore can help predict where the most valuable oaks could be.

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References

Barnosky, A. D. et al. 2011. Has the Earth's sixth mass extinction already arrived? – Nature 471: 51-57.

Baumann, C. et al. 2001. Miljøregistrering i skog - biologisk mangfold. Håndbok i registrering av livsmiljøer i skog. Hefte 3. Instruks for registrering 2001. – Skogforsk, NIJOS and Landbruksdepartementet.

Benedick et al. 2006. Impacts of rain forest fragmentation on butterflies in northern Borneo: species richness, turnover and the value of small fragments. – J. Appl. Ecol. 43: 967-977.

Berglund, H. and Jonsson, B. G. 2005. Verifying an extinction debt among lichens and fungi in northern Swedish boreal forests. – Conserv. Biol. 19: 338-348.

Bergman, K.-O. et al. 2012. How much and at what scale? Multiscale analyses as decision support for conservation of saproxylic oak beetles. – For. Ecol. Manage. 265: 133-141.

Buse, J. 2012. “Ghosts of the past”: flightless saproxylic weevils (Coleoptera: Curculionidae) are relict species in ancient woodlands. – J. Insect Conserv. 16: 93-102.

Buse, J. et al. 2016. Response of saproxylic beetles to small-scale habitat connectivity depends on trophic levels. - Landscape Ecol. 31: 939-949.

Bütler, R. et al. 2013. Habitat trees: key elements for forest biodiversity. - In: Kraus, D. and Krumm, F. (eds), Integrative approaches as an opportunity for the conservation of forest biodiversity. European Forest Institute, pp. 84-91.

Cagnolo, L. et al. 2009. Habitat fragmentation and species loss across three interacting trophic levels: effects of life-history and food-web traits. – Conserv. Biol. 23: 1167-1175.

Central Bureau of Statistics of Norway 1977. Timber Floating 1871-1975. Statistiske analyser. p 79.

Cornell, H. V. and Harrison, S. P. 2014. What are species pools and when are they important? – Annu. Rev. Ecol. Evol. Syst. 45: 45-67.

Drobyshev, I. and Niklasson, M. 2010. How old are the largest southern Swedish oaks? A dendrochronological analysis. – Ecol. Bull. 53: 155-163.

Dupré, C. and Ehrlén, J. 2002. Habitat configuration, species traits and plant distributions. - J. Ecol. 90: 796-805.

Eriksen, R. et al. 2006. Statistikk over skogforhold og -ressurser i Vestfold. Landsskogtakseringen 2000-2004. – NIJOS-ressursoversikt 03/06, p 57.

Franc, N. et al. 2007. Factors and scales potentially important for saproxylic beetles in temperate mixed oak forest. – Biol. Conserv. 135: 86-98.

Fritzøe Skoger 2016. Miljøsertifisering. - Fritzøe Skoger. (Accessed 29 March, 2016) http://www.fritzoe-skoger.no/SKOGBRUK/Miljosertifisering.aspx

Gibbons, P. et al. 2008. The future of scattered trees in agricultural landscapes. - Conserv. Biol. 22: 1309-1319.

Gossner, M. M. et al. 2013. Current near-to-nature forest management effects on functional trait composition of saproxylic beetles in beech forests. - Conserv. Biol. 27: 605-14.

Götmark, F. et al. 2011. How we improved a landscape study of species richness of beetles in woodland key habitats, and how model output can be improved. - For. Ecol. Manage. 262: 2297-2305.

Gough, L. A. et al. 2014. Reactive forest management can also be proactive for wood-living beetles in hollow oak trees. - Biol. Conserv. 180: 75-83.

Gough, L. A. et al. 2015. Specialists in ancient trees are more affected by climate than generalists. – Ecol. Evol. 5: 5632-5641.

Hanski, I. and Ovaskainen, O. 2002. Extinction debt at extinction threshold. - Conserv. Biol. 16: 666-673.

Hedin, J. et al. 2008. Restricted dispersal in a flying beetle assessed by telemetry. - Biodivers. Conserv. 17: 675-684.

Helm, A. et al. 2006. Slow response of plant species richness to habitat loss and fragmentation. - Ecol. Lett. 9: 72-77.

Henle, K. et al. 2004. Predictors of species sensitivity to fragmentation. – Biodivers. Conserv. 13: 207-251.

Holland, J. D. et al. 2004. Determining the spatial scale of species' response to habitat. - BioScience 54: 227-233.

Hultengren, S. et al. 1997. Ekjätter – historia, naturvård och vård. Naturcentrum AB, p 32.

Hylander, K. and Ehrlén, J. 2013. The mechanisms causing extinction debts. - Trends Ecol. Evol. 28: 341-346.

Jackson, H. B. and Fahrig, L. 2015. Are ecologists conducting research at the optimal scale? - Global Ecol. Biogeogr. 24: 52-63.

Jacobsen, R. M. et al. 2015. Scale-specific responses of saproxylic beetles: combining dead wood surveys with data from satellite imagery. - J. Insect Conserv. 19: 1053-1062.

Kuussaari, M. et al. 2009. Extinction debt: a challenge for biodiversity conservation. - Trends Ecol. Evol. 24: 564-571.

Lindbladh, M. and Foster, D. R. 2010. Dynamics of long-lived foundation species: the history of *Quercus* in southern Scandinavia. - J. Ecol. 98: 1330-1345.

Lindenmayer, D. B. et al. 2000. Factors at multiple scales affecting distribution patterns and their implications for animal conservation – Leadbeater's Possum as a case study. - Biodivers. Conserv. 9: 15-35.

Lindenmayer, D. B. et al. 2012. Global decline in large old trees. - Science 338: 1305-1306.

Lindenmayer, D. B. et al. 2014. New policies for old trees: averting a global crisis in a keystone ecological structure. – Conserv. Lett. 7: 61-69.

Magurran, A. E. and McGill, B. J. 2011. Biological diversity. Frontiers in measurement and assessment. – Oxford University Press.

Manning, A. D. et al. 2006. Scattered trees are keystone structures – Implications for conservation. - Biol. Conserv. 132: 311-321.

Millennium Ecosystem Assessment 2005. Ecosystems and Human Well-being: Synthesis. – Island Press.

Moen, A. 1999. National Atlas of Norway: Vegetation. – Norwegian Mapping Authority.

Moore, J. W. 2010. ‘Amsterdam is Standing on Norway’ Part II: The Global North Atlantic in the Ecological Revolution of the Long Seventeenth Century. – J. Agrar. Change 10: 188-227.

Mouillot, D. et al. 2013. Rare species support vulnerable functions in high-diversity ecosystems. - PLoS Biol. 11: e1001569.

Müller, J. et al. 2007. Long-term effects of logging intensity on structures, birds, saproxylic beetles and wood-inhabiting fungi in stands of European beech *Fagus sylvatica* L. - For. Ecol. Manage. 242: 297-305.

Müller, J. et al. 2015. Increasing temperature may compensate for lower amounts of dead wood in driving richness of saproxylic beetles. - Ecography 38: 499-509.

NIBIO 2016. Nedlasting av kartdata - SAT-SKOG. - The Norwegian Institute of Bioeconomy Research (NIBIO) (Accessed 18 January, 2016) http://www.skogoglandskap.no/artikler/2009/nedlasting_satskog/newsitem

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

Nordén, B. et al. 2014. Effects of ecological continuity on species richness and composition in forests and woodlands: A review. - Ecoscience 21: 34-45.

Nordén, J. et al. 2013. Specialist species of wood-inhabiting fungi struggle while generalists thrive in fragmented boreal forests. - J. Ecol. 101: 701-712.

Norwegian Biodiversity Information Centre 2015. Norsk rødliste for arter [Norwegian red list for species]. – Norwegian Biodiversity Information Centre (Accessed 31 August 2016) http://data.artsdatabanken.no/Rodliste2015/Sok

Norwegian Biodiversity Information Centre 2016. Species Map Service 1.6. – The Norwegian Biodiversity Information Centre (Accessed 30 August, 2016) https://artskart.artsdatabanken.no/Default.aspx

Norwegian Environment Agency 2015. Norwegian database for habitats (Naturbase) -Norwegian Environment Agency (Accessed 30 September, 2015) http://karteksport.miljodirektoratet.no/#page=tab1

Paillet, Y. et al. 2010. Biodiversity differences between managed and unmanaged forests: meta-analysis of species richness in Europe. - Conserv. Biol. 24: 101-112.

Päivinen, J. et al. 2002. Ant-associated beetles of Fennoscandia and Denmark. - Entomol. Fenn. 13: 20-40.

Pilskog, H. E. et al. 2016. Effect of habitat size, quality, and isolation on functional groups of beetles in hollow oaks. – J. Insect Sci. 16: 1-8.

Ranius, T. 2002. Influence of stand size and quality of tree hollows on saproxylic beetles in Sweden. - Biol. Conserv. 103: 85-91.

Ranius, T. 2006. Measuring the dispersal of saproxylic insects: a key characteristic for their conservation. - Popul. Ecol. 48: 177-188.

Ranius, T. and Hedin, J. 2001. The dispersal rate of a beetle, *Osmoderma eremita*, living in tree hollows. - Oecologia 126: 363-370.

Ranius, T. and Jansson, N. 2000. The influence of forest regrowth, original canopy cover and tree size on saproxylic beetles associated with old oaks. - Biol. Conserv. 95: 85-94.

Ranius, T. et al. 2008. Large-scale occurrence patterns of red-listed lichens and fungi on old oaks are influenced both by current and historical habitat density. - Biodivers. Conserv. 17: 2371-2381.

Ranius, T. et al. 2009. Development of tree hollows in pedunculate oak (*Quercus robur*). - For. Ecol. Manage. 257: 303-310.

Ranius, T. et al. 2011. Predicting spatial occurrence of beetles and pseudoscorpions in hollow oaks in southeastern Sweden. - Biodivers. Conserv. 20: 2027-2040.

Sala, O. E. et al. 2000. Global Biodiversity Scenarios for the Year 2100. - Science 287: 1770-1774.

Siitonen, J. 2001. Forest management, coarse woody debris and saproxylic organisms: Fennoscandian boreal forests as an example. – Ecol. Bull. 11-41.

Siitonen, J. and Ranius, T. 2015. The importance of veteran trees for saproxylic insects. - In: Kirby, K. J. and Watkins, C. (eds), Europe's changing woods and forests: from wildwood to managed landscapes. CABI.

Skarpaas, O. et al. 2011. Predicting hotspots for red-listed species: multivariate regression models for oak-associated beetles. - Insect Conserv. Divers. 4: 53-59.

Sverdrup-Thygeson, A. 2009. Oaks in Norway: Hotspots for red-listed beetles (Coleoptera). - In: Buse, J. et al. (eds), Saproxylic beetles: their role and diversity in European woodland and tree habitats - Proceedings of the 5th symposium and workshop. Pensoft Publishers, pp. 13-26.

Sverdrup-Thygeson, A. et al. 2010. Hollow oaks and beetle conservation: the significance of the surroundings. - Biodivers. Conserv. 19: 837-852.

Sverdrup-Thygeson, A. et al. 2014a. Spatial and temporal scales relevant for conservation of dead-wood associated species: current status and perspectives. - Biodivers. Conserv. 23: 513-535.

Sverdrup-Thygeson, A. et al. 2014b. Do conservation measures in forest work? A comparison of three area-based conservation tools for wood-living species in boreal forests. - For. Ecol. Manage. 330: 8-16.

Sverdrup-Thygeson, A. et al. 2014c. Gjenbesøk av hule eiker kartlagt for 30 år siden. INA fagrapport. Norges miljø- og biovitenskapelige universitet (NMBU), p 30.

Tomter, S. and Eriksen, R. 2001. Statistikk over skogforhold og -ressurser i Vest-Agder - Landsskogtakseringen 1995-1999. – NIJOS ressursoversikt 02/01, p 60.

Tomter, S. M. et al. 2001. Statistikk over skogforhold og –ressurser i Aust-Agder: Landsskogtakseringen 1995 – 99. – NIJOS-ressursoversikt 03/01, p 61.

Tvethe, M. B. 1852. Bidrag til Kundskab om Skovenes Tilstand i det 17de Aarhundrede. Norske Samlinger. Feilberg & Landmark, pp. 112-119 and pp. 592-608.

Vevstad, A. 1998. Agderskog, Agder skogeierlag 1948-1998 og om skog og skogbruk på Agder gjennom tidene. – Agder Skogeigarlag.

Vogt, L. J. 1886. Om Norges Udførsel af Trælast i ældre Tider. Historisk Tidsskrift. Den Norske Historiske Forening, pp. 81-120 and 273-384.

Widerberg, M. K. et al. 2012. Increased openness around retained oaks increases species richness of saproxylic beetles. - Biodivers. Conserv. 21: 3035-3059.

Wiens, J. A. 1989. Spatial scaling in ecology. - Funct. Ecol. 3: 385-397.

Zuur, A. F. et al. 2009. Mixed effects models and extensions in ecology with R. – Springer.

Figure 1

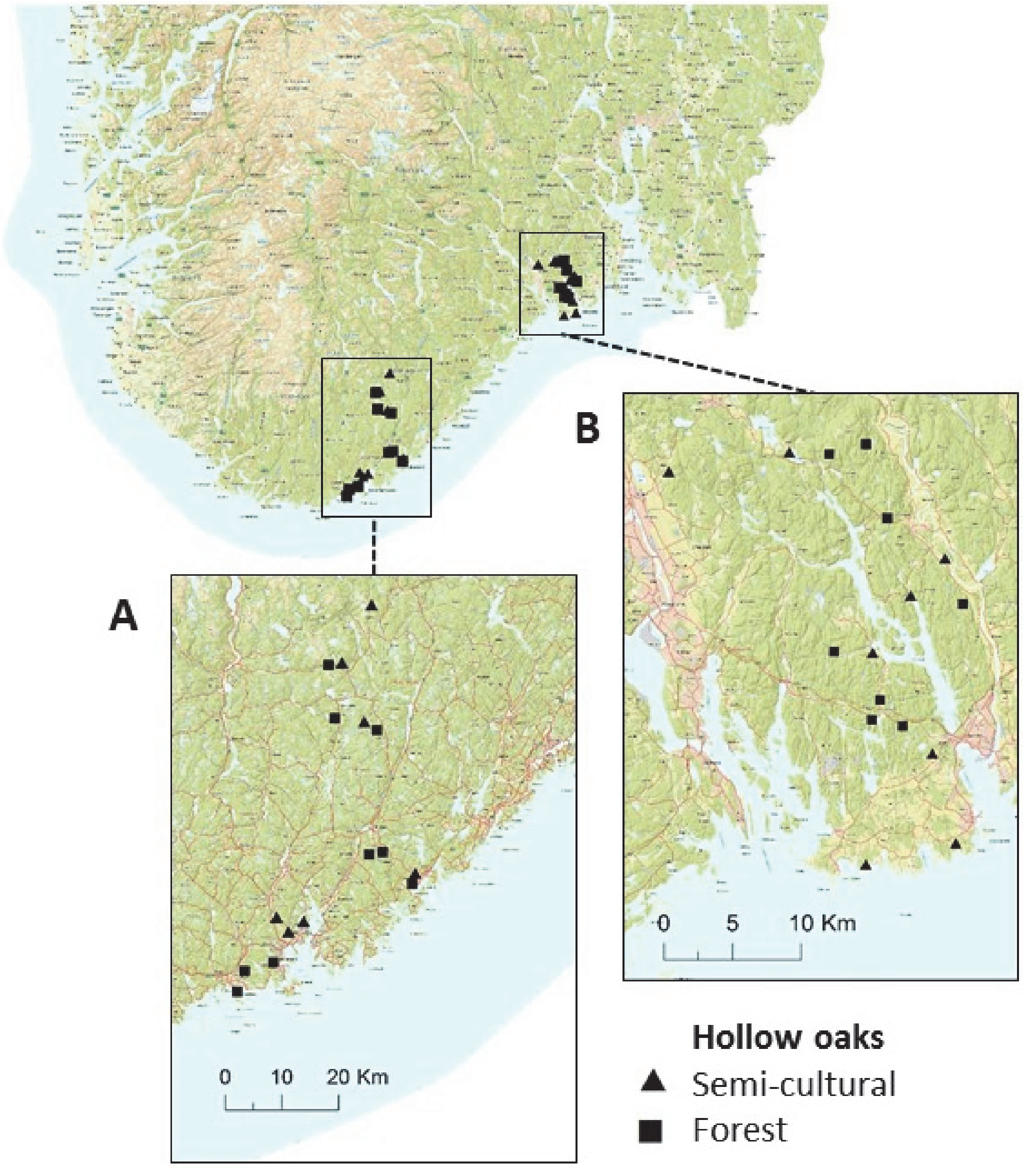

Figure 1. Locations of the sampled hollow oaks ($n = 32$) along the coast-inland gradient in Southern Norway. The hollow oaks were situated in forests and semi-natural landscapes (squares and triangles) in the Agder (A) and Larvik (B) regions.

Tables

Table 1. Predictor variables included in the statistical analyses (variables in italics were not included in the model selection due to collinearity with other variables).

Scale	**Name**	**Units or categories**	**Explanation**
Tree	Circumference	cm	Circumference measured at breast height (1.3 m above ground) (min. 80, mean 228, max. 500)
	Tree form	low, middle, high	The shape of the tree was categorized based on the position of the tree crown into low (n = 8 trees), middle (n = 16) or high (n = 8) position. The growth form is a combination of current and past growing conditions
Local	Forest density	basal area (m^2/ha)	Forest density was measured as the basal area of trees around the hollow oak using a relascope with 1 cm opening (min. 5, mean 16.6, max. 36)
	Landscape	forest, semi-natural	Oaks were situated either in forests (n = 17) or in semi-natural habitats (n = 15). Both types were evenly distributed in the regions and along the coast-inland gradient (forest sites: Agder: n = 7, Larvik: n = 8; semi-natural: Agder: n = 9, Larvik: n = 8)

	Oaks	oak trees	Number of oak trees ≥ 20 cm in diameter at breast height within 42 × 42 m square around the oak (min. 0, mean 12.2, max. 32)
	Hollow oaks	hollow oaks	Number of hollow oaks ≥ 20 cm in diameter at breast height, within 42 × 42 m (0.18 ha) square around the oak (min. 0, mean 1.9, max. 6)
	Deadwood	m^3/ha	Minimum volume of deadwood within a 42 × 42 m square around the oak. Standing and lying deadwood ≥ 1m in length was counted in size classes: small (diameter: 10–20 cm), medium (21–40 cm) and large (>40 cm) and minimum deadwood volume was estimated based on the smallest diameter in each size class. (min. 0.039, mean 0.466, max. 1.172)
Landscape	Favorable habitat	ha	Area of favorable habitat measured in hectare within 2 km radius of the hollow oaks. See the main text for more details (min. 0.17, mean 3.00, max. 11.17)
	Deciduous forest	ha	Area covered by deciduous dominated forest within 2 km of the hollow oaks. Deciduous dominated was defined as > 50% of the volume

			being deciduous trees (min. 19.53, mean 175.23, max. 412.87)
	Forest cover	*ha*	Area covered by forest within 2 km of the hollow oaks (min. 173.24, mean 780.45, max. 1119.59)
	Old forest	*ha*	Area of old forest (average age >80 years) within 2 km of the hollow oaks (min. 3.15, mean 131.28, max. 412.72)
	Forest volume	m^3/ *ha*	Average forest volume (measured without bark) per hectare within 2 km of the hollow oaks (min. 61.74, mean 99.26, max. 126.30)
Coast-inland gradient	Distance to coast	km	Shortest distance to the coast measured as a straight line, used as a proxy for historical logging intensity and duration. For some sites a straight line to the likely destination was used as the shortest line did not reflect the probable transport route of timber due to difficult terrain (min. 0.04, mean 12.89, max. 40.47)
	Precipitation	mm	Sum of average precipitation in the four warmest months (June−September) for the period 1961−1990 (min. 338, mean 411, max. 518)

Temperature	^{o}C	Average summer temperature in the four warmest months for the period 1961−1990 (min. 11.7, mean 13.2, max. 14.3)

Table 2. Summary statistics for all response variables measured in this study. Only oak-associated beetle species were included. Abbreviations: min = minimum, max = maximum, med = median, tot = total.

Response variable	**Species richness**					**Abundance**					
	min	**max**	**mean**	**med**	**tot**	**min**	**max**	**mean**	**med**	**tot**	**Explanation**
All oak species	18	55	32.7	30.5	205	36	451	127.4	109	4077	All oak-associated species
Oak specialists	1	9	4.4	4	25	1	73	17.4	10.5	557	Preferring oak or occurring only on oak
Oak semi-specialists	3	15	7.8	7	55	4	70	17.8	15	571	Occurring only on broadleaved trees in addition to oak
Oak generalists	11	36	20.5	19.5	125	22	432	92.2	74.5	2949	Occurring on coniferous trees in addition to oak

Table 3. Pearson's correlation coefficients between selected continuous variables at different scales and the shortest distance to the coast (km) (df = 30 for all tests). The local scale was the surrounding landscape in a 42 × 42 m area centered on the hollow oak, whereas variables at the landscape scale were measured within a 2-km radius of that tree (see Table 1 for further details).

Variables	**corr.**	**p-value**
Tree variables		
Circumference	−0.012	0.948
Local scale		
Forest density	0.282	0.119
Deadwood	0.075	0.684
Number of oaks	0.135	0.462
Hollow oaks	0.337	0.059
Landscape scale		
Forest cover	0.347	0.052
Old forest	0.701	<0.001
Forest volume	−0.600	<0.001
Deciduous forest	−0.227	0.211
Favorable habitat	−0.019	0.916
Climate		
Precipitation	0.482	0.005
Temperature	−0.773	<0.001

Table 4. Determinants of saproxylic beetle species richness derived from the optimum generalized linear Poisson models and negative binomial models (for the all beetles and oak generalist dataset due to overdispersion). We used backwards elimination with AIC as the selection criterion and the optimal models were tested against null models in analyses of deviance (for poisson GLMs) or log-likelihood tests (for negative binomial GLMs). The dispersion parameter (Disp.) of the model is shown and the p-value from the tests against null models. Bold p-values indicate significant predictor variables.

Response variable	**p-value**	**Disp.**	**Predictor variable**	**Est.**	**SE**	**z-value**	**p-value**
All beetles	**0.011**	1.204	Intercept	3.014	0.143	21.050	**<0.001**
			Circumference	0.001	0.000	1.964	**0.050**
			Distance	0.008	0.003	2.465	**0.014**
			Deciduous area	0.001	0.000	2.405	**0.016**
Oak generalists	0.057	1.149	Intercept	2.741	0.132	20.831	**<0.001**
			Distance	0.010	0.004	2.278	**0.023**
			Deciduous area	0.001	0.001	1.569	0.117
Oak semi-specialists	**0.012**	0.759	Intercept	1.650	0.160	10.301	**<0.001**
			Distance	0.013	0.005	2.435	**0.015**
			Deciduous area	0.001	0.001	2.270	**0.023**
Oak specialists	0.054	1.111	Intercept	1.074	0.227	4.737	**<0.001**
			Circumference	0.002	0.001	1.972	**0.049**

Table 5. Determinants of saproxylic beetle abundance present in the optimum negative binomial generalized linear models. We used backwards elimination with AIC as the selection criterion and the optimal models were tested against null models in log-likelihood tests. The dispersion parameter (Disp.) of the model is shown and the p-value from the tests against null models. Bold p-values indicate significant predictor variables.

Response variable	**p-value**	**Disp.**	**Predictor variable**	**Est.**	**SE**	**z-value**	**p-value**
All beetles	< **0.001**	1.212	Intercept	4.441	0.213	20.803	<**0.001**
			Circumference	0.002	0.001	3.367	**0.001**
			Distance	0.013	0.005	2.678	**0.007**
			Forest density	−0.015	0.008	−2.007	**0.045**
			Tree form low	−0.850	0.165	−5.141	<**0.001**
			Tree form middle	−0.587	0.141	−4.175	<**0.001**
Oak generalists	**0.001**	0.979	Intercept	3.851	0.227	16.962	<**0.001**
			Circumference	0.002	0.001	2.217	**0.027**
			Tree form low	−0.826	0.224	−3.691	<**0.001**
			Tree form middle	−0.639	0.192	−3.329	**0.001**
Oak semi-specialists	**0.010**	1.025	Intercept	2.517	0.200	12.575	<**0.001**
			Tree form low	−0.344	0.262	−1.314	0.189
			Tree form middle	0.348	0.216	1.609	0.108
			Hollow oaks	0.119	0.050	2.398	**0.017**

Oak specialists	**< 0.001**	1.041	Intercept	3.39	0.493	6.87	**<0.001**
			Circumference	0.004	0.001	2.526	**0.012**
			Tree form low	−1.607	0.384	−4.189	**<0.001**
			Tree form middle	−1.226	0.325	−3.770	**<0.001**
			Forest density	−0.034	0.017	−1.990	**0.047**

Table 6. Summary of the optimal models for species richness and abundance of oak-associated beetles in hollow oaks in southern Norway. Only variables kept in the models are shown and their positive or negative response is indicated. Non-significant variables (p > 0.05) are shown in brackets. Abbreviations: Circum = circumference; Tree form = low and middle vs. high (base line level); Decid = deciduous forest; Dist = distance to coast (km), used as a proxy for the historical logging intensity and duration (see Table 1 for details).

	Tree		**Local**		**Land-scape**	**Coast-inland gradient**
	Circum.	Tree form low/middle	Forest density	Hollow oaks	Decid.	Dist.
Species richness						
All beetles	+				+	+
Oak generalists					(+)	+
Oak semi-specialists					+	+
Oak specialists	+					
Abundance						
All beetles	+	−	−			+
Oak generalist	+	−				
Oak semi-specialists		(−/+)		+		
Oak specialists	+	−	−			

Supplementary material

Pilskog, H. E., Sverdrup-Thygeson, A., Evju, M., Framstad, E. and Birkemoe, T. 2016. Long-lasting effects of logging on beetles in hollow oaks. – Ecography 000: 000–000

Appendix 1

The logging of oak in southern Norway

Historically, oak has been important to humans for centuries for building houses, ships, furniture, tanning, firewood and animal food. In Norway, timber export and log-floating has been known from around a thousand years ago (Vogt 1886, Central Bureau of Statistics of Norway 1977). Although there are records of timber trade with the Netherlands, England, Scotland and Denmark from the 13th century and onwards (Vogt 1886, Vevstad 1998, Daly 2007), the largest exploitation of oaks in Norway happened after the waterwheel-driven gate saw was introduced and became common in rivers in the 1520s. At this time, there were large oak forests growing along the coastline of southern Norway (Vogt 1886, Vevstad 1998), and Scots and Dutch merchants came by ship and bought oak timber directly from farmers on the coast (Vevstad 1998, Moore 2010). Oak was especially important for building ships, but many places in Western Europe oaks were scarce or situated inland (Vevstad 1998, Moore 2010).

From around 1580 the timber trade could be characterized as large scale, with oak as the most sought-after timber and Holland one of its main destinations (Moore 2010), although the best oaks in general were reserved for the Danish-Norwegian king (Vevstad 1998). By the 1630s, many places along the coast lacked suitable oak timber (Tvethe 1852), and by the mid-17th century it was difficult to supply the Dutch with large oaks, causing them to switch their purchasing to the Baltic and Russia (Moore 2010). One can assume that, in general, logging of oak occurred inland from the mid-17th century onwards as the coastal oak forests in southern Norway became depleted, ending of the oak-logging boom there (Moore 2010). As oak became scarce, logging for pine and spruce intensified, progressively replacing oak as the most important timber tree (Vevstad 1998). The large coastal oak forests were gone and oak never regained its dominant role in the logging industry. Still oak timber was highly valued until the late-19th century, before other shipbuilding materials became available. Because long-distance timber transport depended on water, the most attractive inland forests were those near large rivers on which logs could be floated. Throughout the 18th and 19th centuries the network of such rivers expanded and many rivers were modified to facilitate the timber transport. Log-floating remained the main mode of timber transport until the 1950s (Central Bureau of Statistics of Norway 1977). The coastal forests in the Larvik and Agder regions of our study have also been under more continuous land-use pressure than the inland forests as a result of the coastal development of cities and larger settlements. Logging to meet the demand for firewood and charcoal production for the metallurgical industries, along with grazing and collecting bark for tanning, all created constant pressure on forest resources.

Unfortunately, there are no good estimates of the extent of the original 16th century oak forests or how much oak was logged, as there are no complete log-floating statistics prior to the 1870s (Central Bureau of Statistics of Norway 1977). Nevertheless, fragmentary records from customs accounts, the number of saws and forest registrations clearly show oak being heavily exploited from 1520 through to the 1600s (Tvethe 1852, Central Bureau of Statistics of Norway 1977), with little oak suitable for logging left by the end of the 17th century (Fryjordet 1968, Moore 2010). It has been suggested that the export of oak in the period 1520−1630 increased 50-fold (Central Bureau of Statistics of Norway 1977). According to Moore (2010 and references therein), the Dutch imported 300 000 − 375 000 m^3 timber annually (including pine) from Norway in the 17th century, with an estimated 25 000 m^3 of high quality oak being needed yearly in the 18th century to maintain the Danish-Norwegian fleet (Vevstad 1995), despite there being a shortage of oak both in Norway and most of Western Europe at the time. The limited sawmill records seldom differentiate between oak and other trees after the 17th century and only list the total quantum sawed in specific rivers, hence making it difficult to draw general trends about the oak quantum logged in this period. Throughout the 18th and 19th centuries Norway continued to be an international timber-producer nation with pine and spruce as the main products (Central Bureau of Statistics of Norway 1977, Hutchison 2012), although from the early 1900s onwards the value of oak was low.

References

Central Bureau of Statistics of Norway 1977. Timber Floating 1871-1975. Statistiske analyser. p 79.

Daly, A. 2007. Timber, Trade and Tree-rings. A dendrochronological analysis of structural oak timber in Northern Europe, c. AD 1000 to c. AD 1650. PhD thesis. University of Southern Denmark, p 270.

Fryjordet, T. 1968. Generalforstamtet 1739-1746. – Norsk skogbruksmuseum.

Hutchison, R. 2012. The Norwegian and Baltic timber trade to Britain 1780–1835 and its interconnections. – Scand. J. Hist. 37: 578-599.

Moore, J. W. 2010. ‘Amsterdam is Standing on Norway’ Part II: The Global North Atlantic in the Ecological Revolution of the Long Seventeenth Century. – J. Agrar. Change 10: 188-227.

Tvethe, M. B. 1852. Bidrag til Kundskab om Skovenes Tilstand i det 17de Aarhundrede. Norske Samlinger. Feilberg & Landmark, pp. 112-119 and pp. 592-608.

Vevstad, A. 1995. Skogen i Aust-Agder frå Skagerrak til fjellet. – Aust Agder Skogselskap.

Vevstad, A. 1998. Agderskog, Agder skogeierlag 1948-1998 og om skog og skogbruk på Agder gjennom tidene. – Agder Skogeigarlag.

Vogt, L. J. 1886. Om Norges Udførsel af Trælast i ældre Tider. Historisk Tidsskrift. Den Norske Historiske Forening, pp. 81-120 and 273-384.

Appendix 2

Table A1. The saproxylic beetle species and categorizations used in this study, along with the number of individuals collected. The categorization of these species and their oak associations was based on Dahlberg and Stokland (2004). We defined 'oak specialists' as species preferring oak or occurring only on oak; 'oak semi-specialists' as species occurring only on both oak and other broadleaved trees; 'oak generalists' as species occurring on both oak and coniferous trees; and 'not oak' for species not occurring on oak. The last group was not included in the analyses.

Family	Species	Oak association	Individuals
Aderidae	*Euglenes pygmaeus*	specialist	3
Anthribidae	*Anthribus nebulosus*	generalist	1
Buprestidae	*Anthaxia quadripunctata*	not oak	1
Cantharidae	*Malthinus flaveolus*	generalist	1
	Malthinus frontalis	not oak	10
	Malthodes brevicollis	not oak	4
	Malthodes crassicornis	not oak	3
	Malthodes fibulatus	not oak	2
	Malthodes fuscus	not oak	3
	Malthodes guttifer	not oak	17
	Malthodes marginatus	not oak	6
	Malthodes mysticus	not oak	1
	Malthodes spathifer	semi-specialist	1
Carabidae	*Dromius agilis*	generalist	12
	Dromius fenestratus	generalist	2
	Dromius quadrimaculatus	specialist	3
	Platynus assimilis	not oak	7
Cerambycidae	*Alosterna tabacicolor*	specialist	10
	Anastrangalia sanguinolenta	not oak	1
	Leiopus nebulosus	specialist	4
	Molorchus minor	not oak	1
	Oxymirus cursor	generalist	1

	Phymatodes testaceus	specialist	13
	Rhagium inquisitor	generalist	1
	Rhagium mordax	generalist	7
	Stenurella melanura	generalist	2
	Stictoleptura maculicornis	generalist	2
	Tetropium fuscum	not oak	1
	Tetrops praeusta	not oak	1
Cerylonidae	*Cerylon fagi*	semi-specialist	1
	Cerylon ferrugineum	generalist	23
	Cerylon histeroides	generalist	12
Ciidae	*Cis bidentatus*	generalist	2
	Cis boleti	semi-specialist	12
	Cis castaneus	semi-specialist	2
	Cis comptus	generalist	1
	Cis festivus	semi-specialist	16
	Cis jacquemarti	generalist	1
	Cis nitidus	generalist	1
	Cis punctulatus	not oak	1
	Cis submicans	generalist	11
	Cis vestitus	semi-specialist	1
	Cis villosulus	not oak	3
	Ennearthron cornutum	generalist	12
	Octotemnus glabriculus	semi-specialist	2
	Orthocis alni	generalist	21
	Sulcacis nitidus	generalist	2
Cleridae	*Thanasimus formicarius*	generalist	2
	Tillus elongatus	generalist	1
Coccinellidae	*Anatis ocellata*	not oak	1
	Aphidecta obliterata	generalist	2
	Myrrha octodecimguttata	not oak	1
	Scymnus suturalis	not oak	1
Corylophidae	*Orthoperus rogeri*	not oak	3
	Sericoderus lateralis	not oak	1
Cryptophagidae	*Atomaria diluta*	not oak	3
	Atomaria morio	generalist	1
	Atomaria ornata	not oak	1
	Cryptophagus dentatus	semi-specialist	32

	Cryptophagus dorsalis	not oak	18
	Cryptophagus lapponicus	not oak	1
	Cryptophagus micaceus	not oak	62
	Cryptophagus parallelus	not oak	1
	Cryptophagus scanicus	generalist	13
	Cryptophagus setulosus	semi-specialist	1
	Micrambe abietis	not oak	5
	Pteryngium crenatum	not oak	1
Curculionidae	*Cryphalus asperatus*	not oak	3
	Crypturgus hispidulus	not oak	6
	Dryocoetes alni	not oak	13
	Dryocoetes autographus	not oak	6
	Dryocoetes villosus	specialist	16
	Hylastes brunneus	not oak	1
	Hylastes cunicularius	not oak	5
	Hylastes opacus	not oak	1
	Hylesinus crenatus	semi-specialist	2
	Hylobius abietis	generalist	5
	Kyklioacalles roboris	not oak	8
	Magdalis armigera	not oak	1
	Phloeophagus lignarius	semi-specialist	1
	Phloeotribus spinulosus	not oak	4
	Pissodes pini	not oak	1
	Pityogenes bidentatus	not oak	2
	Pityogenes chalcographus	not oak	15
	Pityophthorus lichtensteinii	not oak	19
	Pityophthorus micrographus	not oak	1
	Polydrusus cervinus	not oak	2
	Polydrusus tereticollis	not oak	2
	Polygraphus poligraphus	not oak	1
	Rhyncolus ater	generalist	76
	Rhyncolus elongatus	not oak	3
	Rhyncolus sculpturatus	generalist	1
	Scolytus intricatus	specialist	12
	Strophosoma capitatum	generalist	36
	Trypodendron domesticum	semi-specialist	3
	Trypodendron lineatum	not oak	3

	Trypodendron signatum	semi-specialist	14
	Xyleborinus saxeseni	semi-specialist	5
	Xyleborus dispar	specialist	3
Dasytidae	*Aplocnemus nigricornis*	generalist	1
	Dasytes caeruleus	generalist	5
	Dasytes niger	generalist	11
	Dasytes plumbeus	semi-specialist	18
Dermestidae	*Anthrenus museorum*	not oak	11
	Attagenus pellio	semi-specialist	3
	Ctesias serra	semi-specialist	3
	Megatoma undata	generalist	5
Elateridae	*Ampedus balteatus*	generalist	274
	Ampedus hjorti	specialist	31
	Ampedus nigrinus	generalist	38
	Ampedus nigroflavus	semi-specialist	1
	Ampedus pomorum	generalist	3
	Athous subfuscus	not oak	167
	Cardiophorus ruficollis	generalist	1
	Crepidophorus mutilatus	semi-specialist	1
	Denticollis linearis	generalist	10
	Hypoganus inunctus	semi-specialist	1
	Melanotus castanipes	not oak	109
	Sericus brunneus	not oak	1
Endomychidae	*Endomychus coccineus*	semi-specialist	3
	Leiestes seminiger	not oak	2
	Mycetina cruciata	generalist	2
Erotylidae	*Dacne bipustulata*	semi-specialist	8
	Triplax aenea	not oak	2
	Triplax russica	semi-specialist	21
Eucnemidae	*Eucnemis capucina*	not oak	4
	Hylis procerulus	not oak	1
	Microrhagus lepidus	not oak	3
	Microrhagus pygmaeus	generalist	2
	Xylophilus corticalis	generalist	35
Histeridae	*Gnathoncus buyssoni*	not oak	31
	Plegaderus caesus	semi-specialist	4
	Plegaderus vulneratus	not oak	1

Latridiidae	*Cartodere constricta*	generalist	1
	Cartodere nodifer	generalist	1
	Corticaria longicollis	generalist	5
	Corticarina fuscula	not oak	1
	Corticarina obfuscata	not oak	1
	Corticarina similata	not oak	2
	Cortinicara gibbosa	not oak	13
	Dienerella vincenti	generalist	3
	Enicmus fungicola	generalist	3
	Enicmus rugosus	generalist	70
	Enicmus testaceus	generalist	29
	Enicmus transversus	not oak	1
	Latridius consimilis	generalist	2
	Latridius gemellatus	generalist	1
	Latridius hirtus	generalist	14
	Latridius minutus	generalist	2
	Stephostethus alternans	not oak	1
	Stephostethus rugicollis	not oak	3
Leiodidae	*Agathidium badium*	generalist	3
	Agathidium confusum	generalist	4
	Agathidium mandibulare	generalist	1
	Agathidium rotundatum	generalist	1
	Agathidium seminulum	generalist	24
	Agathidium varians	generalist	5
	Anisotoma castanea	not oak	2
	Anisotoma humeralis	generalist	66
	Anisotoma orbicularis	generalist	1
	Nemadus colonoides	specialist	6
Lucanidae	*Platycerus caraboides*	semi-specialist	1
	Sinodendron cylindricum	semi-specialist	4
Lycidae	*Dictyoptera aurora*	not oak	6
	Pyropterus nigroruber	generalist	2
Lymexylidae	*Elateroides dermestoides*	generalist	4
	Lymexylon navale	specialist	1
Melandryidae	*Abdera flexuosa*	not oak	1
	Conopalpus testaceus	semi-specialist	6
	Hypulus quercinus	specialist	1

	Orchesia micans	generalist	5
	Orchesia undulata	semi-specialist	18
	Phloiotrya rufipes	semi-specialist	3
	Serropalpus barbatus	not oak	3
	Xylita laevigata	not oak	2
Monotomidae	*Rhizophagus bipustulatus*	specialist	30
	Rhizophagus cribratus	specialist	19
	Rhizophagus dispar	generalist	14
	Rhizophagus fenestralis	generalist	3
	Rhizophagus ferrugineus	not oak	1
	Rhizophagus nitidulus	generalist	1
	Rhizophagus parallelocollis	not oak	2
Mordellidae	*Mordella holomelaena*	not oak	2
	Tomoxia bucephala	generalist	1
Mycetophagidae	*Litargus connexus*	generalist	3
	Mycetophagus atomarius	semi-specialist	1
	Mycetophagus piceus	specialist	8
	Mycetophagus populi	not oak	2
	Triphyllus bicolor	semi-specialist	9
Nitidulidae	*Cryptarcha strigata*	semi-specialist	25
	Cryptarcha undata	semi-specialist	15
	Cychramus luteus	not oak	10
	Cychramus variegatus	generalist	1
	Epuraea abietina	generalist	1
	Epuraea aestiva	not oak	6
	Epuraea guttata	specialist	1
	Epuraea marseuli	generalist	2
	Epuraea neglecta	semi-specialist	2
	Epuraea rufomarginata	generalist	3
	Epuraea silacea	not oak	1
	Epuraea unicolor	generalist	1
	Glischrochilus hortensis	semi-specialist	72
	Glischrochilus quadriguttatus	semi-specialist	6
	Ipidia binotata	generalist	2
	Pityophagus ferrugineus	not oak	2
	Soronia grisea	semi-specialist	33

Ptiliidae	*Pteryx suturalis*	generalist	1
Ptinidae	*Cacotemnus rufipes*	semi-specialist	2
	Dorcatoma chrysomelina	specialist	111
	Dorcatoma dresdensis	generalist	2
	Dryophilus pusillus	not oak	3
	Ernobius mollis	not oak	1
	Grynobius planus	semi-specialist	24
	Hemicoelus canaliculatus	semi-specialist	6
	Ptilinus pectinicornis	semi-specialist	3
	Ptinomorphus imperialis	semi-specialist	5
	Ptinus fur	generalist	6
	Ptinus rufipes	specialist	1
	Ptinus subpillosus	specialist	172
	Xestobium rufovillosum	specialist	70
Salpingidae	*Salpingus planirostris*	semi-specialist	7
	Salpingus ruficollis	generalist	10
	Sphaeriestes castaneus	not oak	1
Scarabaeidae	*Cetonia aurata*	not oak	1
	Trichius fasciatus	semi-specialist	1
Scirtidae	*Prionocyphon serricornis*	semi-specialist	1
Scraptiidae	*Anaspis frontalis*	generalist	6
	Anaspis marginicollis	not oak	51
	Anaspis rufilabris	generalist	64
	Anaspis thoracica	generalist	4
Silphidae	*Phosphuga atrata*	generalist	1
Silvanidae	*Silvanoprus fagi*	not oak	2
Sphindidae	*Aspidiphorus orbiculatus*	generalist	3
Staphylinidae	*Acidota crenata*	not oak	18
	Atheta amicula	not oak	1
	Atheta corvina	not oak	2
	Atheta crassicornis	not oak	6
	Atheta euryptera	not oak	1
	Atheta hypnorum	not oak	2
	Atheta laticollis	not oak	1
	Atheta picipes	generalist	1
	Atheta sodalis	not oak	11
	Atheta vaga	generalist	31

Atrecus affinis	generalist	2
Batrisodes venustus	generalist	5
Bibloporus bicolor	generalist	90
Bisnius fimetarius	not oak	2
Bryaxis puncticollis	not oak	1
Coprophilus striatulus	not oak	2
Dadobia immersa	generalist	7
Dexiogyia forticornis	not oak	8
Dinaraea aequata	generalist	1
Dropephylla ioptera	generalist	3
Euconnus claviger	generalist	3
Euplectus bescidicus	not oak	9
Euplectus karstenii	generalist	33
Euplectus mutator	generalist	7
Euplectus nanus	generalist	8
Euplectus piceus	generalist	16
Euplectus punctatus	generalist	13
Euryusa castanoptera	not oak	2
Gabrius splendidulus	generalist	21
Gyrophaena boleti	not oak	1
Gyrophaena joyioides	not oak	1
Hapalaraea pygmaea	semi-specialist	7
Haploglossa gentilis	specialist	35
Haploglossa villosula	generalist	1484
Holobus apicatus	generalist	2
Holobus flavicornis	not oak	3
Ischnoglossa prolixa	generalist	8
Leptusa fumida	generalist	12
Leptusa pulchella	generalist	8
Leptusa ruficollis	semi-specialist	56
Lordithon lunulatus	generalist	2
Mniusa incrassata	not oak	4
Mycetoporus lepidus	not oak	33
Neuraphes elongatulus	not oak	1
Neuraphes plicicollis	not oak	2
Omalium rugatum	not oak	1
Oxypoda arborea	semi-specialist	68

	Pella cognata	generalist	8
	Pella funesta	generalist	1
	Pella laticollis	generalist	4
	Pella lugens	generalist	13
	Philonthus succicola	not oak	5
	Phloeocharis subtilissima	generalist	2
	Phloeopora corticalis	generalist	3
	Phloeopora testacea	generalist	5
	Phloeostiba plana	generalist	1
	Phyllodrepa melanocephala	semi-specialist	1
	Plectophloeus nitidus	generalist	2
	Quedius brevicornis	generalist	6
	Quedius brevis	not oak	1
	Quedius cruentus	semi-specialist	1
	Quedius fuliginosus	not oak	1
	Quedius maurus	generalist	6
	Quedius mesomelinus	semi-specialist	12
	Quedius scitus	specialist	2
	Quedius xanthopus	generalist	52
	Scaphisoma agaricinum	generalist	15
	Scaphisoma boreale	not oak	4
	Scydmoraphes minutus	generalist	3
	Sepedophilus littoreus	generalist	2
	Sepedophilus testaceus	generalist	9
	Stenichnus bicolor	generalist	5
	Stenichnus godarti	specialist	2
	Syntomium aeneum	not oak	1
	Thamiaraea cinnamomea	semi-specialist	3
	Thamiaraea hospita	specialist	1
	Xantholinus tricolor	not oak	1
Tenebrionidae	*Mycetochara axillaris*	not oak	5
	Mycetochara flavipes	semi-specialist	4
	Mycetochara maura	semi-specialist	16
	Palorus depressus	specialist	2
	Prionychus ater	semi-specialist	3
	Pseudocistela ceramboides	generalist	22
	Uloma rufa	not oak	1

Tetratomidae	*Hallomenus binotatus*	generalist	5
	Tetratoma ancora	generalist	1
Trogossitidae	*Grynocharis oblonga*	generalist	1
	Thymalus limbatus	generalist	11
		Total	**4919**

References

Dahlberg, A., Stokland. J. 2004. Substrate requirements of wood-inhabiting species - a synthesis and analysis of 3600 species. Skogsstyrelsen. Report 7- 04, pp. 75.

Appendix 3

We used records from the Norwegian database for habitats (Naturbase) (Norwegian Environment Agency 2015) and non-digitalized maps from Larvik to construct the habitat variable. This variable was measured at the landscape scale. From the Norwegian database for habitats we used ‘selected habitat type’ for hollow and large oaks (point registrations and polygons), and standing and lying deadwood (polygons). Point registrations of hollow deciduous trees were obtained from Complementary Hotspot Inventories. In addition, non-digitized woodland key habitats from Larvik were acquired by entering the center point of the polygons in ArcMap 10.2.2 and using the buffer function to make the polygons with their corresponding sizes. All polygon types and points registrations were checked for overlap in ArcMap, and only the largest overlapping values were included.

In contrast to the other polygons, the deadwood polygons from the Norwegian database for habitats had a defined number of trees per hectare (20-40 trees ha^{-1}) (Baumann et al. 2001). We therefore converted the other records to this scale. Point registrations of trees were counted and the total was converted to a hectare measure using the definition of 30 trees ha^{-1}. The large oak polygons generally included more habitat than old oaks, and we therefore used information from the database on number of oaks in each polygon and converted this number to create new polygons whose size was equivalent to 30 trees ha^{-1}. For polygons with insufficient information, we used a conversion factor of 0.22, which corresponded to the average conversion factor used for the other hollow oak polygons. A conversion factor of 0.1 was used for the woodland key habitats in Larvik, as this conversion factor made the polygons more comparable to the other registrations, and more likely to reflect the definition of 30 trees ha^{-1}. Lastly, all these converted records were added to the deadwood polygons to make one habitat variable reflecting area of favorable habitat at the 2-km scale around each studied hollow oak.

References

Baumann, C. et al. 2001. Miljøregistrering i skog - biologisk mangfold. Håndbok i registrering av livsmiljøer i skog. Hefte 3. Instruks for registrering 2001. – Skogforsk, NIJOS and Landbruksdepartementet.

Norwegian Environment Agency 2015. Norwegian database for habitats (Naturbase) -Norwegian Environment Agency (Accessed 30 September, 2015) http://karteksport.miljodirektoratet.no/#page=tab1

Paper IV

Investigating species composition of beetles in hollow oaks reveals management-relevant patterns

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Abstract

Veteran trees are keystone structures currently in decline worldwide. In Europe, veteran oaks (*Quercus* spp.) are important habitat trees for wood-living beetles. Still, we have limited knowledge of the drivers determining the *composition* of these communities and the relevant spatial and temporal scales for these drivers.

We collected beetles from 32 hollow oaks in two regions in Southern Norway along a coast-inland gradient paralleling historical onset of oak harvesting. We focused on species with different host-association to oak and identified the relative importance of processes working on different spatial scales, ranging from tree-scale to region-scale, as well as effects of the coast-inland gradient. Our results were also compared to a previous study of species richness using the same data. We found differences in species composition between the regions for all oak association groups. The tree scale was the most important scale for overall species composition, for oak generalists and specialists, with bryophyte cover on the stem, depth of bark crevices and amount of wood mould to be the important variables. The beetle species restricted to broadleaved trees (semi-specialists) responded to the coast-inland gradient and red-listed species only found inland could indicate long-lasting responses to historical logging. In summary, our results highlight the importance of protecting veteran oaks across large regional scales, in different surroundings and with a range of tree characteristics, if the aim is to conserve the entire suite of oak-associated species.

Our study revealed new patterns compared to a previous study of species richness in the same study system, illustrating the relevance of a community focus with different specialization groups. Firstly, we revealed new relationships between oak-associated beetles and relevant drivers on the tree and regional scale, but found no effect of the landscape scale. Secondly, while the proportion of red-listed species increased with specialization level, important responses of the specialists and semi-specialists were concealed when analyzing the complete community. This means that making management recommendations based on the overall community responses can lead to recommendations that are not beneficial for the most vulnerable species.

Key-words: *Quercus*, veteran tree, spatial scales, Coleoptera, saproxylic, historical logging, specialists, generalists

Introduction

As a consequence of a rapidly expanding human population and our increasing consumption of resources, Earth's biodiversity is declining at an alarming rate (Barnosky et al. 2011). The decline of biodiversity and the accompanying loss of ecosystem services is a major threat to the biosphere and to human wellbeing (Millennium Ecosystem Assessment 2005). Alongside biodiversity loss, biotas are also becoming increasingly homogenized across space (McKinney and Lockwood 1999). Endemic or native species are often replaced by a few common or invasive species thriving in human-modified habitats (McKinney and Lockwood 1999, Socolar et al. 2016), and such community homogenization on large scales might reduce the stability of regional ecosystems (Wang and Loreau 2016). This calls for an improved understanding of the organization of biodiversity in a spatial context, and the factors that govern it (Socolar et al. 2016, Wang and Loreau 2016).

A range of different methods and diversity indices exists to measure biodiversity (Magurran and McGill 2011). Species richness and diversity indices are widely used measures in ecological studies, as they often are simple to use and in-line with conservational goals of monitoring and maintaining biodiversity. Still, we miss important information by not considering the identities of the species that make up the communities, as responses of species of interest can be masked by the responses of dominating and common species (Magurran and McGill 2011, Mouillot et al. 2013). To manage and protect native and vulnerable species we must therefore know where they occur and how they vary across spatial scales (Ferrier 2002).

The interaction of species with the environment is likely to be both species specific and scale dependent (Wiens 1989, Sverdrup-Thygeson et al. 2014). As the capacity for management-related single-species analyses is limited, a solution is to group ecological similar species that can be expected to have similar responses to environmental change (Henle et al. 2004, Franzén et al. 2012). Such grouping can for instance be based on niche breadth (Slatyer et al. 2013): Specialist species and generalist species often respond differently to environmental constraints (Henle et al. 2004), and specialists can be especially vulnerable to habitat loss and fragmentation (Franzén et al. 2012, Nordén et al. 2013, Slatyer et al. 2013).

Veteran trees are keystone structures in many landscapes and home to a range of species (Dudley and Vallauri 2004, Siitonen and Ranius 2015), but they are experiencing fragmentation and decline on a global scale (Gibbons et al. 2008, Lindenmayer et al. 2014). In Europe, old oaks (*Quercus* spp.) are known as hotspots for biodiversity and rare species alike (Sverdrup-Thygeson 2009, Siitonen and Ranius 2015), and one of the large and important groups associated with them are the wood-living (saproxylic) beetles (Buse et al. 2008, Jansson et al. 2009a, Sverdrup-Thygeson 2009, Gough et al. 2014, Siitonen and Ranius 2015).

Several studies have addressed the species richness of these systems and found factors on different spatial scales to influence the species number of saproxylic beetles in old oaks: On the tree scale, size and shape of the oak are known to be important factors (Ranius and Jansson 2000, Buse et al. 2008, Sverdrup-Thygeson et al. 2010, Buse et al. 2016, Pilskog et al. 2016). On a local scale, increasing openness around oaks has been found to increase species numbers of associated beetles (Ranius and Jansson 2000, Widerberg et al. 2012, Gough et al. 2014). Finally, the amount of deadwood and habitat connectivity has been shown to be important for oak-associated beetle richness on a range of scales (Franc et al. 2007, Sverdrup-Thygeson et al. 2010, Bergman et al. 2012).

Still, we do not know whether the same drivers also determine the *species composition* of these communities. Nor do we know the relevant spatial scales for the factors shaping the community composition. As analyses of species richness alone might mask important changes in species identity, especially of the rarer species of high conservation interest, a community approach might shed new light on the processes governing this system. Also, because we might expect different responses to main drivers depending on the species' niche breadth, a grouping into sub-communities with different degrees of habitat specialization seems highly relevant for management.

In this study, we use a study system consisting of hollow oaks along a coast-inland gradient (representing historical logging intensity as well as changes in climate), replicated across two regions in Southern Norway. We investigate the species composition of both specialized beetles and beetles with wider habitat niches, aiming to identify the relative importance of habitat amount and quality - on different spatial scales - in structuring these sub-communities. We also compare the findings to studies of species richness, including a previous study from the same study system (Pilskog et al. submitted), to reveal possible benefits of a community approach. Our main aim is to increase the understanding of the veteran oak system, possibly revealing new patterns of relevance for the conservation of old oaks and the associated biodiversity in them.

Methods

Study design

We sampled a total of 32 hollow oaks (*Quercus robur* and *Q. petraea*) in Southern Norway. To incorporate possible regional variation in species composition, we sampled across two different regions: the Agder region (16 oaks) and the Larvik region (16 oaks) (Appendix 1). In each region, we selected oaks along a gradient from the coast to inland areas. This sampling design represents a gradient in climate, from dry and warm along the coast to wetter and colder in inland sites, as well as a gradient in historical exploitation of oak timber (see Pilskog et al. submitted). The Agder region is situated in southern Norway with hollow oaks from the coast to 40.5 km inland, and the Larvik region is situated in southeastern Norway with hollow oaks situated from the coast to 24.6 km inland. The sites span the nemoral, boreonemoral and southern boreal vegetation zones (Moen 1999). In the Agder region (Vest- and Aust-Agder counties) oak makes up 8% of the productive forest volume, whereas in Vestfold county that Larvik is a part of, the proportion is lower, only 2.7%. However, a considerably larger proportion of the oaks in Vestfold has a large diameter (9.5% >45 cm) compared to Agder (1−4%) (Tomter and Eriksen 2001, Tomter et al. 2001, Eriksen et al. 2006).

We used the Norwegian database for habitats (Naturbase) (Norwegian Environment Agency 2015) to identify relevant study sites. We selected oak trees with cavities containing wood mould (preferably with its opening above ground), and only oaks situated in forests (17 oaks) or semi-natural habitats (forest edges, along fields or close to settlement; 15 oaks), with a minimum distance of 1.5 km between the selected oaks. We avoided heavily pollarded trees in parks or cities and wide-branched solitary trees in open agricultural landscapes, as oaks in urban or agricultural landscapes have different species assemblages than forest oaks (Sverdrup-Thygeson et al. 2010, Skarpaas et al. 2011).

Insect sampling

To sample beetles, we used two flight interception traps per oak (window size 20 cm × 40 cm), one in front of the cavity opening and one in the canopy (Sverdrup-Thygeson 2009, Sverdrup-Thygeson et al. 2010). The traps collected insects from mid-May to mid-August in 2013 and 2014. We emptied the traps once a month and used a solution of propylene glycol, water and liquid dish detergent in the collecting containers.

We identified all beetles to species and categorized them according to oak association, based mainly on information from Dahlberg and Stokland (2004). Only saproxylic species associated with oak were included in further analyses (Appendix 2). Species associated with oak were grouped into: 'specialists' for species preferring oak or occurring only on oak, 'semi-specialist' for species occurring only on broadleaved trees in addition to oak, and 'generalists' for species occurring on coniferous trees in addition to oak (Appendix 2).

Environmental variables

A total of 20 variables were used in order to characterize the sample sites. The variables were collected at different spatial scales: The tree scale (5 variables), the local surrounding (5 variables) and the landscape scale (5 variables), in addition to variables describing the coast-inland gradient (4 variables) and sampling region (1 variable) (Table 1).

On the tree scale we recorded the circumference at breast height (1.3 m above the ground), visually estimated the amount of wood mould, categorized the bark type based on the depth of the deepest bark crevices, estimated the cover of bryophytes on the lowest 2 m of the trunk and categorized the tree form according to the position of the tree crown (Table 1). The growth form of the tree is a combination of current and past growing conditions; trees growing in open surroundings typically develop low wide-branched tree crowns with high levels of sun exposure whereas closed surroundings typically result in high tree crown (see Pilskog et al. submitted).

The local scale was defined as the area of 42 × 42 m around the focal oak and was measured in the field by going 30 meters in each cardinal direction from the oak to create a square. Within this square we counted the total number of oaks and hollow oaks ≥20 cm in diameter at breast height. Downed and standing deadwood with length of ≥1 m was counted in size classes: small (diameter: 10−20 cm), medium (21−40 cm) and large (>40 cm) and minimum deadwood volume was estimated based on the smallest diameter in each size class. We estimated forest density (basal tree area) by use of a relascope as a measure of openness around the sampled oak. The surroundings were classified as either forest or semi-natural landscape.

We defined the landscape scale to a 2 km-radius around the focal oaks, as this scale has been found to be important for species richness of saproxylic beetles in previous studies (Bergman et al. 2012, Jacobsen et al. 2015). We included relevant habitat and forest variables extracted from online databases. The amount of favorable habitat measured as area on the landscape scale included registrations of hollow and large oaks (recorded as points registrations or polygons), hollow deciduous trees (point records) and standing and downed deadwood (recorded in polygons) in the Norwegian database for habitats (Naturbase) (Norwegian Environment Agency 2015). Supplementary records of woodland key habitats relevant for saproxylic species were available from Larvik (Fritzøe Skoger 2016). We counted all the point registrations within 2 km of the sampled oaks, estimated the number of hollow and large oaks in the oak polygons, and converted the number of trees to a common scale of 30 trees per hectare, which was subsequently merged with the deadwood polygons (defined as minimum 20−40 trees per ha) (Baumann et al. 2001) to make the favorable habitat variable. To add the woodland key habitats in Larvik to the same variable, we used a conversion factor of 0.1 as these polygons were large and contained several nature types in addition to old oaks and deadwood (Table 1). See Pilskog et al. (submitted) for details. ArcMap 10.2.2 was used to process the data.

Data on forest structure were downloaded from The Norwegian Institute of Bioeconomy Research (NIBIO 2016). These forest variables are derived from satellite images, and ArcMap 10.2.2 was used to extract information on the 2 km scale around each oak using the 'clip function'. We included area covered by forest, forest volume per hectare, area of deciduous trees and cover of old forest (average tree age >80 years old) (Table 1).

To characterize the historical logging along the coast-inland gradient, we used distance to coast as a proxy to reflect how accessible and attractive the oaks were for historical logging. Historically, there were large oak forests along the Norwegian southern coast (Vogt 1886, Vevstad 1998) and large-scale logging of oak was enabled after the introduction of the river saws in the 1520s (Central Bureau of Statistics of Norway 1977; Moore 2010). As the timber transport along the rivers was difficult, the easily accessible coastal areas were logged first, and less accessible areas inland were logged later (Vevstad 1998), creating a gradient in logging intensity and duration (see Pilskog et al. submitted for details). We therefore measured the distance from the focal oaks to the coast to use as a proxy of the historical logging. The distance was measured as the shortest distance in km using ArcMap 10.2.2. In the Larvik region, a straight line to the known destination (Larvik city) was used for four oaks where the shortest distance represented an impossible transport route for timber due to the terrain. The coast-inland gradient spanned a longer distance in Agder (40.5 km) than in Larvik (24.6 km). To be able to separate effects of sampling region from effects of distance to the coast, we classified all oak sites in each region as being either close to the coast (the eight oaks in each region with shortest distance to the coast) or far from the coast (the eight oaks in each region with longest distance to the coast).

Each site was characterized by mean summer temperature (°C) and total summer precipitation (mm) in the four warmest months (June to September). We used interpolated data from a 1 × 1 km-grid from the period 1961−1990, (Table 1). The data were downloaded from the Norwegian Meteorological Institute (see http://met.no/).

Table 1 Environmental variables included in the study. For continuous variables mean, min and max values are given. For categorical variables, categories are defined and the number of trees within each category given in brackets.

Spatial scale	**Variable**	**Cat./Cont.**	**Description**
Tree	Bark	Cat.	Smooth: deepest bark crevice <15 mm, (n = 9), intermediate: 15−30 mm (n = 10), coarse: >30 mm, (n = 13)
	Circumference	Cont.	228 (80−500) cm
	Bryophytes	Cat.	Low: <25 % of trunk covered (n = 12), intermediate: 25−50 % (n = 14), high: >50 % (n = 6)
	Wood mould	Cat.	Little: ≤10 L (n = 15), intermediate: 10−99 L (n = 11), much: ≥100 L (n = 6)
	Tree form	Cat.	Low (n = 8), middle (n = 16), high (n = 8)
Local	Forest density	Cont.	16.6 (5−36) m^2/ha
	Surroundings	Cat.	Forest (n = 17), semi-natural (n = 15)
	Oaks	Cont.	12.2 (0−32)

	Hollow oaks	Cont.	1.9 (0−6)
	Deadwood	Cont.	0.47 (0.04−1.17) m^3/ha
Landscape	Favorable habitat	Cont.	3.0 (0.2−11.2) ha
	Deciduous forest	Cont.	175.2 (19.5−412.9) ha
	Forest cover	Cont.	780.5 (173.2−1119.6) ha
	Old forest	Cont.	131.3 (3.2−412.7) ha
	Forest volume	Cont.	99.3 (61.7−126.3) m^3/ ha
Coast-inland gradient	Distance to coast - continuous	Cont.	12.9 (0.04−40.5) km
	Distance to coast - categorical	Cat.	Coast; Agder: <8.33 km from the coast, Larvik: <11.2 km (*n* = 16), inland; Agder: >8.33 km, Larvik: >11.2 km (*n* = 16)
	Precipitation	Cont.	411 (338−518) mm
	Temperature	Cont.	13.2 (11.7−14.3) °C
Region	Region	Cat.	Agder (*n* = 16), Larvik (*n* = 16)

Statistics

For each oak we pooled the data from both traps and both years. All analyses were performed in in R. v. 3.1.0. using the vegan package v. 2.3-3 for the multivariate analyses.

We wanted to explore the interdependence of environmental variables. For this purpose, we used one-way ANOVAs, Pearson's Chi-squared test of independence and correlation coefficients (Pearson's r) to test the relationship among the tree scale variables, and to investigate whether the environmental variables changed in a consistent pattern along the coast-inland gradient, for both regions combined and for each region separately.

To investigate the relative importance of environmental variables at different spatial scales for structuring species assemblages of the different oak-association groups, we used variation partitioning techniques (Økland 2003). We used partial constrained correspondence analyses (CCA) that assume a unimodal relationship between species and the underlying gradients. For each oak group we performed forward selection using permutation tests ('permutest' function) with 999 permutations within each set of variables (tree, local and landscape), to select the variables that explained most variation in the species composition at each spatial scale. Only variables that had a significant independent contribution ($\alpha = 0.05$ level) were included (Økland 2003). We constructed site and species plots of the CCAs to interpret the variation in species composition related to the main explanatory variables, and used partial CCAs to distribute the total explained variation on the unique, non-overlapping partial intersections among the spatial scales, identifying the relative contribution of each scale for explaining species composition (Økland 2003).

Results

We collected 4077 oak-associated beetle individuals that belonged to 205 species. Half of these were unique to either of the two regions, whereas the rest made up a shared species pool. The Larvik region had more unique species than Agder, with a considerably higher proportion of specialists (11 species) compared to

Agder (3 species) (Table 2). In total, 27 of the oak-associated species were red-listed, and the proportion of red-listed species increased with specialization level (Table 3).

Covariation of explanatory variables

The large trees had deeper bark crevices, more wood mould and were more common in semi-natural landscapes than in forests (Appendix 3, Figure A1). Oaks in Larvik had a higher cover of bryophytes and deeper bark crevices than oaks in Agder (Appendix 3, Figure A2 d-e). There was a tendency for trees with deep bark crevices to have more wood mould (Chi-squared test, $p = 0.070$) and being more common in semi-natural landscapes than in forests (Chi-squared test, $p = 0.082$) (Appendix 3, Figure A2).

The distance from coast (continuous) correlated with climate and variables on the landscape scale (Table 4). The coastal areas were warmer, had less summer rain, higher forest volume per hectare and less area of old forest than the inland sites. Analyzed separately, only the correlation between temperature and distance to coast remained significant in both regions, but new region-specific patterns were revealed: In Agder the amount of deciduous forest decreased inland, whereas the number of hollow oaks on the local scale increased. In Larvik both the forest cover in general and the amount of deciduous forest increased inland (Table 4). Neither tree size (Table 4) or other tree characteristics (ANOVA, $p>0.05$) varied along the gradient.

Table 2 Number of unique and shared oak-associated saproxylic beetle species in the two sampling regions in Southern Norway. The species are grouped according to level of specialization on oak.

Species	**Region**	**Specialist**	**Semi-specialist**	**Generalist**	**All species**
Unique	Agder	3	12	30	45
	Larvik	11	16	29	56
Shared		11	27	66	104
Total		**25**	**55**	**125**	**205**

Table 3 Number of red-listed beetle species grouped according to level of specialization on oak. Proportions of red-listed species within each group are shown in brackets. Red-listed status are from the Norwegian red list (Kålås et al. 2010), see Appendix 2 for species names.

	Specialist	**Semi-specialist**	**Generalist**	**All species**
Red-listed	9 (0.36)	12 (0.22)	6 (0.05)	27 (0.13)
Not red-listed	16 (0.64)	43 (0.78)	119 (0.95)	178 (0.87)
Total	**25**	**55**	**125**	**205**

Table 4 Pearson's correlation coefficients between the coast-inland gradient (km from the coast) and the other continuous variables. The coefficients are shown for the whole dataset combined and for the regions separately. The local scale included a 42 × 42 m square, and the landscape scale a 2 km radius, around the hollow oaks (see Table 1 for details). Df = 30 for the whole dataset and df = 14 for the separate regions. Stars indicate significant p-values: **.** p < 0.10, *p<0.05, **p<0.0.1,***p<0.001.

Variables	Both regions	Agder	Larvik
Tree variables			
Circumference	−0.012	−0.029	0.059
Local scale			
Forest density	0.282	0.419	0.030
Deadwood	0.075	0.235	−0.121
Number of oaks	0.135	0.294	−0.189
Hollow oaks	0.337 **.**	0.584 *	0.046
Landscape scale			
Forest cover	0.347 **.**	0.316	0.621 *
Old forest	0.701 ***	0.777 ***	0.075
Forest volume	−0.600 ***	−0.719 **	−0.254
Deciduous forest	−0.227	−0.650 **	0.578 *
Habitat variable	−0.019	0.117	−0.087
Coast-inland gradient			
Precipitation	0.482 **	0.548 *	0.399
Temperature	−0.773 ***	−0.926 ***	−0.543 *

Variation partitioning

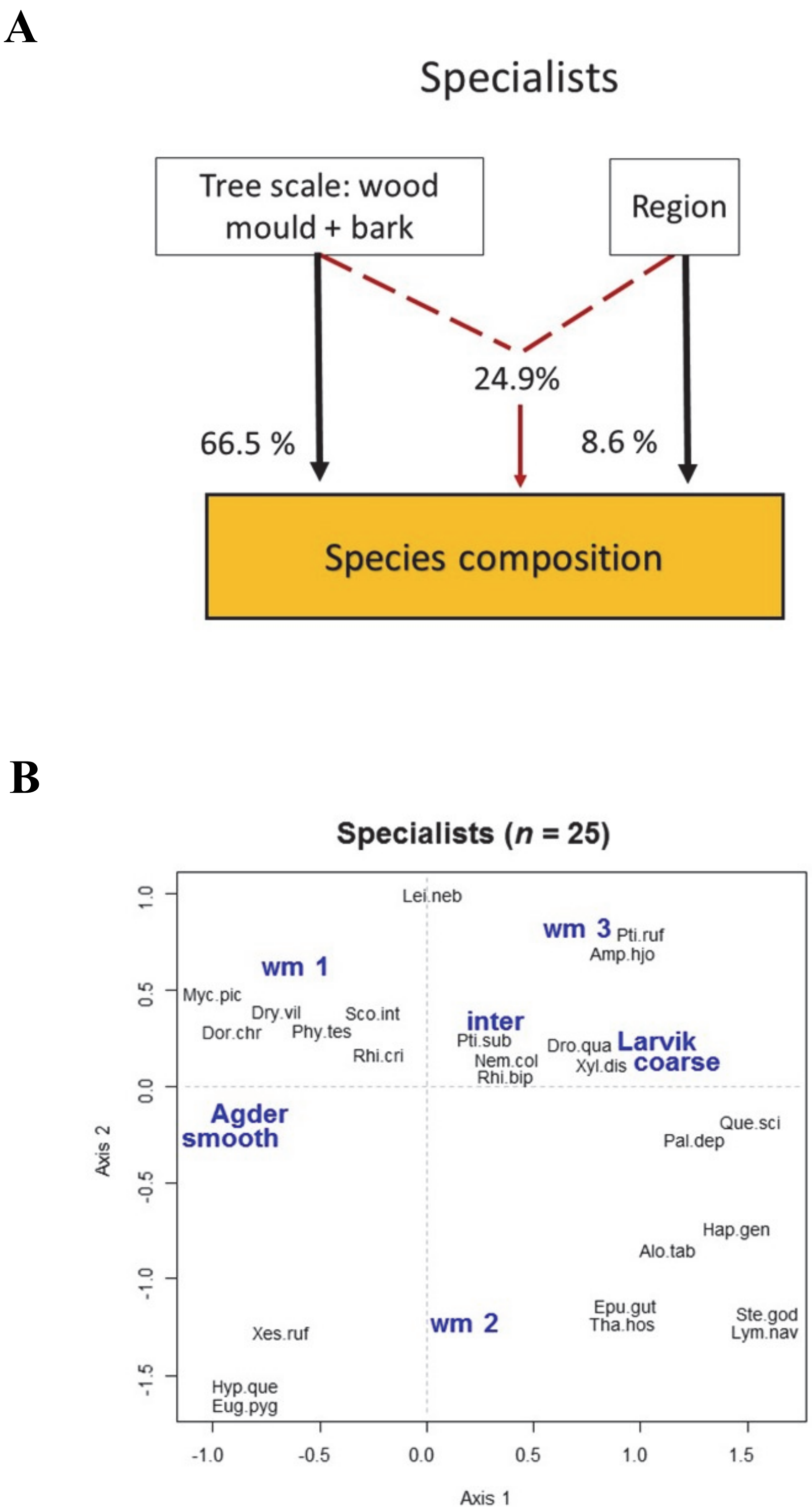
The best combination of variables explained 25−30% of the variation (total inertia) in the partial CCA for generalists and specialist species, but only 12% for the semi-specialists (Appendix 4).

The species composition of specialist beetles was best explained by a combination of tree scale variables, in particular bark structure and amount of wood mould, and region, with almost 25% of the explained variation shared between the two scales (Figure 1A). The CCA plot revealed a gradient along axis 1 of increasingly deeper bark crevices and more wood mould, which coincided with region, with Agder on the left hand and Larvik on the right hand of the axis (Figure 1B).

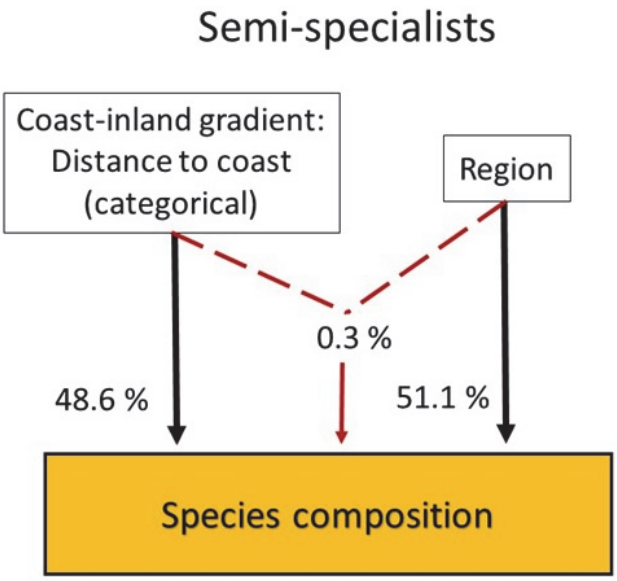
For semi-specialists, species composition was equally explained by distance to coast (coast vs. inland sites) and region (Figure 1C). Several of the species were confined to clusters representing species unique to each region and found only in coastal or inland oaks (Figure 1D): Cluster A consisted of species present only in inland Larvik oaks, whereas the species in Cluster B were primarily found in Larvik, but both in inland and costal oaks. Species only found in coastal Agder aggregated in Cluster C, and Cluster D consisted of species only found in inland Agder oaks.

For the generalists, the tree scale accounted for nearly half of the variation explained in the species composition, with bryophyte cover and bark structure being the important variables (Figure 1E). The local scale, with tree density and type of surroundings (semi-natural or forest) accounted for 22% of the variation and region for about 10 %. The first axis of the CCA corresponded to a gradient in bark structure from smooth in Agder to coarse in Larvik, and partly to a gradient from forested sites to semi-natural sites (Figure 1F).

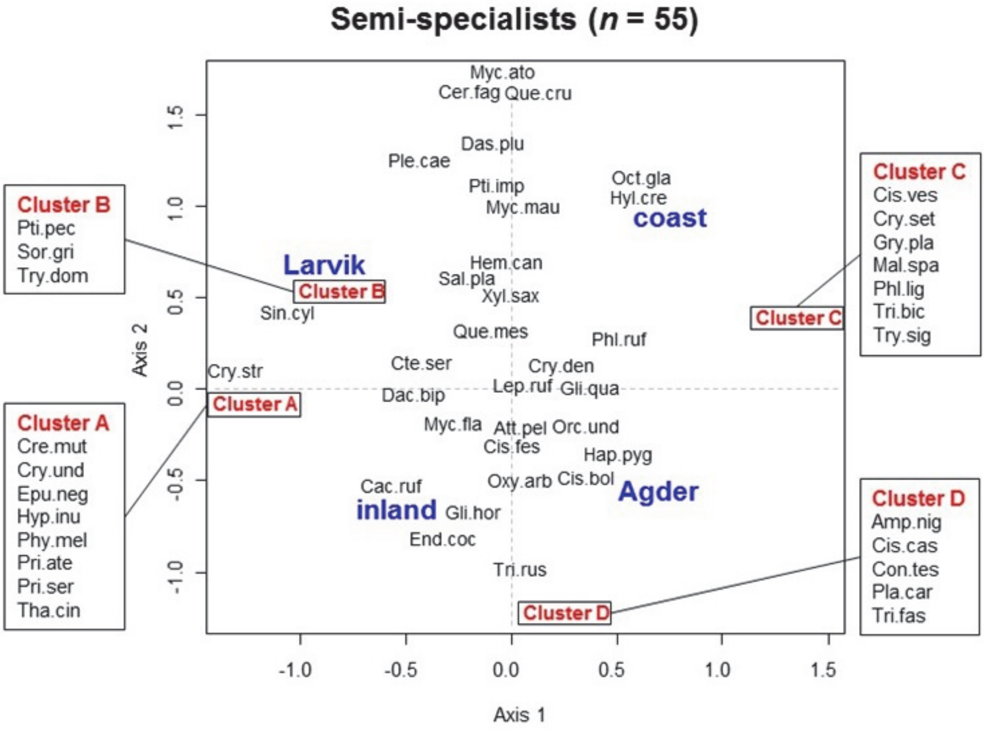
The species composition of all beetles was explained by the same spatial scales as the generalists (Figure 1G). The tree scale explained more than half of the explained variation, with most of the remaining variation being explained by region and the surroundings. In the CCA plot the semi-natural sites grouped together, indicating that they were more similar in species composition than the forest sites, particularly in Agder (Figure 1H).



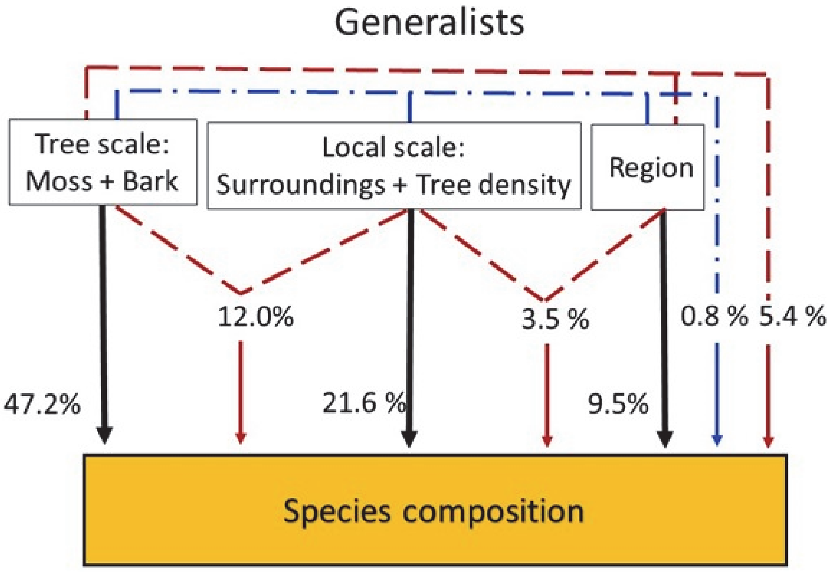
C


Semi-specialists
Coast-inland gradient: Distance to coast (categorical)
Region
0.3 %
48.6 %
51.1 %
Species composition

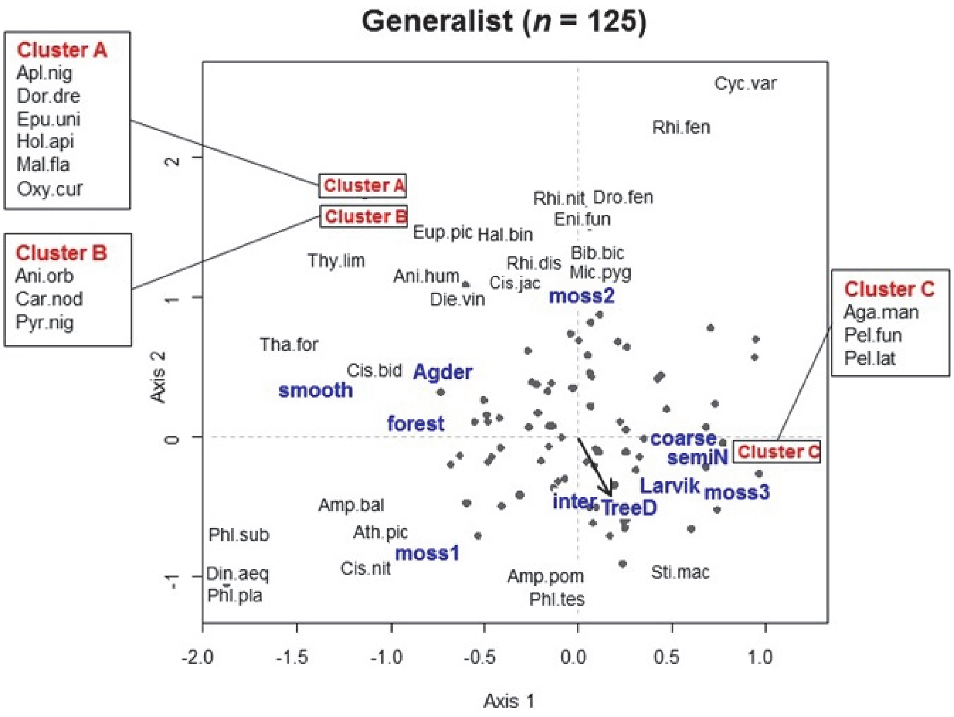
D


Semi-specialists (*n* = 55)
Cluster B
Pti.pec
Sor.gri
Try.dom
Cluster A
Cre.mut
Cry.und
Epu.neg
Hyp.inu
Phy.mel
Pri.ate
Pri.ser
Tha.cin
Cluster C
Cis.ves
Cry.set
Gry.pla
Mal.spa
Phl.lig
Tri.bic
Try.sig
Cluster D
Amp.nig
Cis.cas
Con.tes
Pla.car
Tri.fas
Myc.ato
Cer.fag
Que.cru
Das.plu
Ple.cae
Pti.imp
Myc.mau
Oct.gla
Hyl.cre
coast
Larvik
Cluster B
Hem.can
Sal.pla
Xyl.sax
Sin.cyl
Cluster C
Que.mes
Phl.ruf
Cte.ser
Cry.den
Cry.str
Lep.ruf
Gli.qua
Dac.bip
Cluster A
Myc.fla
Att.pel
Orc.und
Cis.fes
Hap.pyg
Cac.ruf
Oxy.arb
Cis.bol
Agder
inland
Gli.hor
End.coc
Tri.rus
Cluster D
Axis 2
1.5
1.0
0.5
0.0
-0.5
-1.0
-1.0
-0.5
0.0
0.5
1.0
1.5
Axis 1

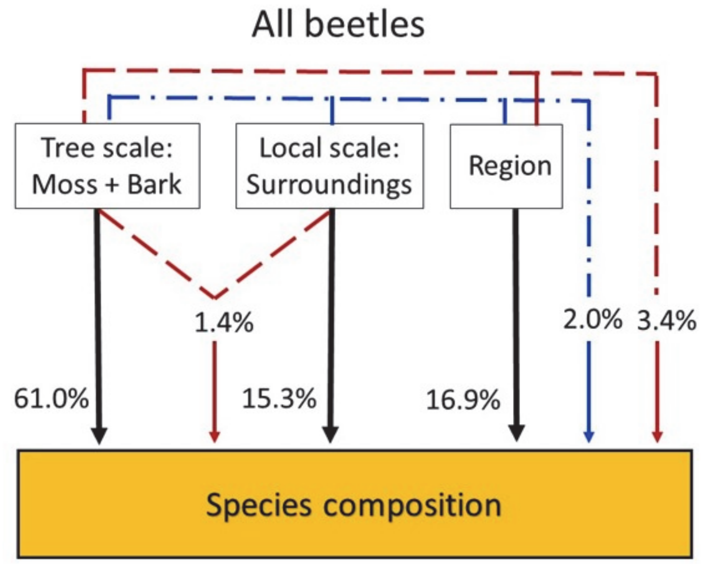
E


Generalists
Tree scale: Moss + Bark
Local scale: Surroundings + Tree density
Region
12.0%
3.5 %
0.8 %
5.4 %
47.2%
21.6 %
9.5%
Species composition

F


Generalist (n = 125)
Cluster A
Apl.nig
Dor.dre
Epu.uni
Hol.api
Mal.fla
Oxy.cur
Cluster B
Ani.orb
Car.nod
Pyr.nig
Cluster C
Aga.man
Pel.fun
Pel.lat
Cyc.var
Rhi.fen
Rhi.nit
Dro.fen
Eni.fun
Eup.pic
Hal.bin
Thy.lim
Bib.bic
Mic.pyg
Rhi.dis
Ani.hum
Cis.jac
Die.vin
moss2
Tha.for
Cis.bid
Agder
smooth
forest
coarse
semiN
Larvik
moss3
inter
TreeD
Amp.bal
Phl.sub
Ath.pic
moss1
Cis.nit
Din.aeq
Phl.pla
Amp.pom
Phl.tes
Sti.mac
Axis 2
Axis 1
2
1
0
-1
-2.0
-1.5
-1.0
-0.5
0.0
0.5
1.0

G



H

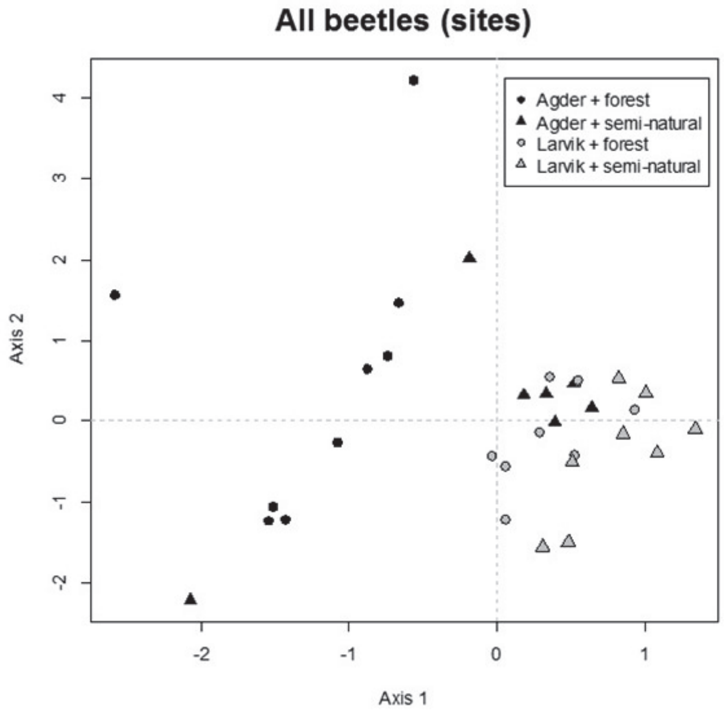


Figure 1 Amount of variation explained by different sets of environmental variables in partial constrained ordination (CCA) (left panel) and ordination plots (right panel) for specialist beetles, semi-specialists, generalists and all beetles.

Only variables with a significant independent contribution ($p<0.05$) were included. In the variation partitioning plots, variation explained by one set of variables is shown with solid black lines. Red dashed lines represent variation shared between two sets of variables and blue dashed lines represent variation shared between three sets of variables. In the ordination plots, categorical variables are shown by their centroid and continuous variables by arrows pointing in the direction of effect. Abbreviation of variable names: wm = wood mould (1 = little, 2 = intermediate, 3 = much), moss = cover of bryophytes (1 = little, 2 = medium, 3 = much), smooth = smooth bark, inter = intermediate bark, coarse = coarse bark, TreeD = tree density, forest = forest surroundings, semiN = semi-natural surroundings. Clusters in the species ordination plots represent species with identical coordinates in the CCA. The plots have been slightly modified to make them readable. See Table 1 for details on the variables and Appendix 2 for full species names.

Discussion

The main aim of the present study was to understand the drivers influencing community composition of beetles with different specialization in veteran trees. We found that regional variation structured all beetle communities independent on niche breadth. Tree quality proved important for the most and least specialized species, whereas the medium specialized species were the only group responding to a coast-inland gradient. The immediate surroundings of the veteran trees affected the generalist community, whereas no characteristics at the landscape scale (2 km radius) proved important for either beetle group.

Region matters for all beetles

This study clearly demonstrates that the beetle communities in veteran oaks vary between close geographical regions, a pattern not detected when analyzing species richness only (Pilskog et al. submitted). The variation between regions was present in all groups of oak specialization, indicating an overall regional effect on the beetles communities in hollow oaks. Most likely this is a result of complex region-specific conditions. For instance, we know that oak makes up 8% of the productive forest volume in Agder, whereas in the Larvik area this proportion is only 2.7%. At the same time, the oaks in Larvik are generally larger than in Agder (Tomter and Eriksen 2001, Tomter et al. 2001, Eriksen et al. 2006) (although there were no differences between our study oaks). Factors related to historical use of forests or randomness in colonization patterns may also contribute to the differences, as might the slightly higher summer temperatures in Larvik (http://met.no/). Whereas the pattern found by Franc et al. (2007) in an east-west gradient in Sweden revealed a change in species composition paralleled by a change in species richness, our patterns are different, with unique species in both areas (Table 2) despite similar species richness. This calls for a conservation strategy including regional variation to maintain overall biodiversity. Clearly, further studies covering multiple scales are needed in order to detect important shifts in species composition.

Tree characteristics matters for specialists and generalists

The tree itself was the most important scale explaining species composition for specialist and generalist beetles. Earlier studies have found amount of wood mould to increase species richness of red-listed beetles (Skarpaas et al. 2011), affect population sizes (Ranius et al. 2009) and attract colonizing species (Jansson et al. 2009b), and similarly in our study wood mould came out as an important structuring factor for the specialists. Several highly specialized beetles are known to depend on wood mould in veteran trees (Ranius 2007, Siitonen and Ranius 2015), like the click beetle *Ampedus hjorti*, listed as vulnerable in IUCNs European assessment and in Norway (Norwegian Biodiversity Information Centre 2015, IUCN Red List of Threatened Species 2016), and only present in our study in oaks with high amounts of wood mould (Figure 1B).

The two other important tree characteristics, depth of bark crevices and cover of bryophytes, has to our knowledge not previously proved important for beetles in veteran trees. Bark crevices is known to have a positive effect on the diversity of epiphytic lichens (Ranius et al. 2008, Nordén et al. 2012, Lättman et al. 2014) and is a characteristic associated with large and old oaks (Ranius et al. 2008). In our study, two specialist species, *Ptinus subpilosus* and *Alosterna tabacicolor*, have larvae developing in coarse bark (Ehnström and Axelsson 2002). Also, the oak specialist predator *Dromius quadrimaculatus* patrolling trunk and branches (Lindroth 1986), may profit from larvae living in the bark and an increased number of hiding places in deep crevices. Thus, the species composition of specialists might be determined partly by bark characteristics. However, the fact that deep bark crevices is a characteristic associated with large oak trees and correlates with both trunk diameter, wood mould amount and tree form in our study also indicates that this variable may represent other tree characteristics than the bark itself. Many studies of species richness in hollow oaks have found effect of tree diameter (Ranius and Jansson 2000, Sverdrup-Thygeson et al. 2010, Buse et al. 2016, Pilskog et al. submitted). With increasing age, a veteran oak provides an overall larger resource with more diverse microhabitats (Siitonen and Ranius 2015). Thus, variation in depth of bark crevices could indicate an overall increase in available niches correlated with tree size and age. This would indeed affect species composition of specialists and generalist in accordance with the patterns found in our study.

Cover of bryophytes on the tree trunk affected the overall species composition and the generalists, but the pattern for all beetles was probably determined by the numerical dominant generalists (Table 2). Djupström et al. (2010) found a positive correlation between species richness of bryophytes and species richness of saproxylic beetles in boreal forests in Sweden, while the opposite pattern was found by Jonsson and Jonsell (1999). Bryophytes generally depend on high moisture conditions, as found also for epiphytic bryophytes on oaks by Ranius et al. (2008). Warm microclimate is known to be important for many saproxylic beetles (Jonsell et al. 1998, Vodka et al. 2009, Müller et al. 2015, Milberg et al. 2016), but there are also beetle species that prefer shade (Ranius and Jansson 2000, Vodka et al. 2009). Thus, more bryophytes on the tree trunk might indicate favorable microclimatic conditions especially for beetle species in the generalist community. In addition, Pilskog et al. (2016) found a dominance of predators among the generalist beetles in hollow oaks. Increasing bryophyte cover might also represent more variation in hiding and hunting opportunities for this species group.

Semi-specialists change from coast to inland

In our study, the coast-inland gradient represents changes in historical logging of oak as well as climate. Pilskog et al. (submitted) found more semi-specialists and a higher overall species richness inland, in spite of a less attractive climate, which suggests the presence of an extinction debt in the inland veteran trees. In our study, the coast-inland gradient was also found to be a driver of species assemblages, but this effect was only seen among the medium specialized beetles.

As oaks grow to be several centuries old (Drobyshev and Niklasson 2010) they can be regarded as legacies from the past where many generations of beetles can live within the same oak before needing to disperse (Ranius 2006, Hedin et al. 2008). Being adapted to stable ecosystems, the species are in general assumed to be poor dispersers (Nilsson and Baranowski 1997, Hedin et al. 2008) and can be expected to have a slow response to environmental change. Many beetles living in hollow oaks do also have long life cycles (Ranius et al. 2005, Bütler et al. 2013) making these species extra vulnerable to fragmentation and habitat loss (Nordén et al. 2014).

By looking at the ordination plots of our semi-specialists, we identified several species only found inland or along the coast (Figure 1D, Cluster A, C-D). The eight species in cluster A is especially interesting, as these are all caught inland in Larvik with as many as five nationally red-listed species dependent on old or hollow deciduous trees (Kålås et al. 2010, Norwegian Biodiversity Information Centre 2015). This include the endangered click beetles *Crepidophorus mutilatus* and *Hypoganus inunctus*. Similarly, cluster D consisted of species only found inland in Agder (Figure 1D), including the near threatened click beetle *Ampedus nigroflavus*. This pattern, as well as overall higher species richness inland, support the notion that species have gone locally extinct in the coastal areas. This could be a reasonable result of the more enduring and advanced fragmentation resulting from historical logging of large oaks. In other words, while the extinction debt seems to have been paid off already in the coastal areas, the situation inland is unclear (Pilskog et al. submitted). We do not know if the present amount and distribution of veteran oaks inland is sufficient to sustain today's communities of red-listed beetles into the future.

Climate did not affect the species composition, although the temperature changed by 2.6 °C along the coast-inland gradient. This is in line with the patterns of species richness (Pilskog et al. submitted). The fact that species richness has been found to increase with temperature in earlier studies of insects in deadwood (Vodka et al. 2009, Gough et al. 2015, Müller et al. 2015) indicate that other factors, such as logging history, are indeed working against the effect of temperature in the present study. The few semi-specialists restricted to coastal sites were partly singletons (cluster C in Figure 1D, Agder only), but some of them could possibly be explained by coastal preferences or a need for warmer and drier climate than we find in inland sites. For example the two red-listed species *Phloeophagus lignarius* and *Triphyllus bicolor* in cluster C are only known from a few coastal locations in Southern Norway and dependent on veteran trees (Norwegian Biodiversity Information Centre 2015, 2016).

Only generalists are affected by close surroundings

Whereas the more specialized beetles only responded to region, tree characteristics and the coast-inland gradient, the generalist community was also structured by the immediate surroundings of the trees. As these species might inhabit a wide range of deadwood habitat, this is not surprising; the immediate surroundings might reflect variation in resources and determine the presence of broad-niched species also benefitting from oak wood. The categorization of sites into semi-natural habitats and forest are likely to represent such differences. Different species assemblages have previously been found for red-listed species in veteran oaks in parks and forests, partly as a result of a higher amount of coarse woody debris in the forest surroundings (Sverdrup-Thygeson et al. 2010). While the park vs. forest categories represent a much larger contrast than our trees, a similar mechanism could be at work and structure our generalist community.

The generalists also responded to forest density. This driver has previously been identified by Gough et al (2014), who found the variation in openness around the oaks to influence the species richness and composition of generalists. Pilskog et al. (2016) also found that beetles at different trophic levels diverged in their response to openness which further indicate species-specific responses to shading. The importance of openness is also paralleled by studies of species richness; shaded oak trees generally have lower species richness than more sun-exposed oaks (Ranius and Jansson 2000, Widerberg et al. 2012).

Implications for conservation of hollow oaks

When analyzing species richness data without considering the identity of the species, we might miss important patterns of high relevance for conservation. The large regional differences between beetle communities in the present study exemplifies this: Although only separated by approximately 120 km, a considerable number of unique and red-listed species was detected in each region in this study. Still, no effect of region was identified in a previous study comparing only species richness, in the exact same study system (Pilskog et al. submitted). Regional variation should therefore be included in conservation plans in order to maintain the oak-associated biodiversity, although we need further studies in order to identify the relevant scales of species turnover and gain a better understanding of the regional patterns of rare species in these communities. When it comes to the characteristics of the oak itself, our results emphasize the well-known importance of high amounts of wood mould for the specialized beetles of high conservation interest, but also add deeply creviced bark to the list of important oak tree qualities. To our knowledge, this has not previously been noted as an important factor for beetle communities, although it is well known to influence communities of epiphytic red-listed lichens on oak (Paltto et al. 2010).

Extinction debt is a challenge for conservation (Kuussaari et al. 2009); as past changes in landscapes may still affect present biodiversity. Our patterns of species composition indicate a possible extinction debt in the inland veteran trees, also identified by patterns in species richness (Pilskog et al. submitted). If our aim is to ensure the viability of the unique and vulnerable species found at these and similar locations that possibly are experiencing extinction debts, a more active management approach might be needed. This could for instance include restoration efforts like ‘veteranisation’ of younger oaks (Bengtsson et al. 2012) or artificial boxes with wood mould on trees to mimicking hollows (Jansson et al. 2009b).

In general, we found that when analyzing drivers of the total community composition, the generalists masked the changes in the more specialized species groups. As the proportion of red-listed beetle species increased with specialization, we need to pay more attention to the drivers of the specialist and semi-specialist communities, otherwise we risk designing conservation approaches that may not benefit the most vulnerable species. Loosing such species is not only of ethical concern, but may also remove important functions from the ecosystem (Mouillot et al. 2013, Leitão et al. 2016).

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References

Barnosky, A. D., Matzke, N., Tomiya, S., Wogan, G. O. U., Swartz, B., Quental, T. B., Marshall, C., McGuire, J. L., Lindsey, E. L., Maguire, K. C., Mersey, B. and Ferrer, E. A. 2011. Has the Earth's sixth mass extinction already arrived? - Nature 471: 51-57.

Baumann, C., Gjerde, I., Blom, H. H., Sætersdal, M., Nilsen, J. E., Løken, B. and Ekanger, I. 2001. Miljøregistrering i skog - biologisk mangfold. Håndbok i registrering av livsmiljøer i skog. Hefte 3. Instruks for registrering 2001. – Skogforsk, NIJOS and Landbruksdepartementet.

Bengtsson, V., Hedin, J. and Niklasson, M. 2012. Veteranisation of oak – managing trees to speed up habitat production. - In: Rotherham, I. Handley, C.S amojolik, T. and Agnoletti, M. (eds), Trees Beyond the Wood. Sheffield Hallam University, pp. 1-11.

Bergman, K.-O., Jansson, N., Claesson, K., Palmer, M. W. and Milberg, P. 2012. How much and at what scale? Multiscale analyses as decision support for conservation of saproxylic oak beetles. - For. Ecol. Manage. 265: 133-141.

Buse, J., Entling, M. H., Ranius, T. and Assmann, T. 2016. Response of saproxylic beetles to small-scale habitat connectivity depends on trophic levels. - Landscape Ecol. 31: 939-949.

Buse, J., Levanony, T., Timm, A., Dayan, T. and Assmann, T. 2008. Saproxylic beetle assemblages of three managed oak woodlands in the Eastern Mediterranean. - Zool. Middle East 45: 55-66.

Bütler, R., Lachat, T., Larrieu, L. and Paillet, Y. 2013. Habitat trees: key elements for forest biodiversity. - In: Kraus, D. and Krumm, F. (eds), Integrative approaches as an opportunity for the conservation of forest biodiversity. European Forest Institute, pp. 84-91.

Central Bureau of Statistics of Norway 1977. Timber Floating 1871-1975. Statistiske analyser. p 79.

Dahlberg, A. and Stokland, J. 2004. Substrate requirements of wood-inhabiting species - a synthesis and analysis of 3600 species. Skogsstyrelsen, Report 7-04, p 75.

Djupström, L. B., Perhans, K., Weslien, J., Schroeder, L. M., Gustafsson, L. and Wikberg, S. 2010. Co-variation of lichens, bryophytes, saproxylic beetles and dead wood in Swedish boreal forests. - Syst. Biodivers. 8: 247-256.

Drobyshev, I. and Niklasson, M. 2010. How old are the largest southern Swedish oaks? A dendrochronological analysis. - Ecological Bulletins 53: 155-163.

Dudley, N. and Vallauri, D. 2004. Deadwood – Living forests: The importance of veteran trees and deadwood to biodiversity. WWF Report. pp. 1-19.

Ehnström, B. and Axelsson, R. 2002. Insekters gnag i bark och ved. – ArtDatabanken, SLU.

Eriksen, R., Tomter, S. M. and Ludahl, A. 2006. Statistikk over skogforhold og -ressurser i Vestfold. Landsskogtakseringen 2000-2004. p 57.

Ferrier, S. 2002. Mapping spatial pattern in biodiversity for regional conservation planning: Where to from here? - Syst. Biol. 51: 331-363.

Franc, N., Götmark, F., Økland, B., Nordén, B. and Paltto, H. 2007. Factors and scales potentially important for saproxylic beetles in temperate mixed oak forest. - Biol. Conserv. 135: 86-98.

Franzén, M., Schweiger, O. and Betzholtz, P.-E. 2012. Species-area relationships are controlled by species traits. - PLoS ONE 7: e37359.

Fritzøe Skoger 2016. Miljøsertifisering. - Fritzøe Skoger (Accessed 29 March, 2016) http://www.fritzoe-skoger.no/SKOGBRUK/Miljosertifisering.aspx

Gibbons, P., Lindenmayer, D. B., Fischer, J., Manning, A. D., Weinberg, A., Seddon, J., Ryan, P. and Barrett, G. 2008. The future of scattered trees in agricultural landscapes. - Conserv. Biol. 22: 1309-1319.

Gough, L. A., Birkemoe, T. and Sverdrup-Thygeson, A. 2014. Reactive forest management can also be proactive for wood-living beetles in hollow oak trees. - Biol. Conserv. 180: 75-83.

Gough, L. A., Sverdrup-Thygeson, A., Milberg, P., Pilskog, H. E., Jansson, N., Jonsell, M. and Birkemoe, T. 2015. Specialists in ancient trees are more affected by climate than generalists. - Ecology and Evolution 5: 5632-5641.

Hedin, J., Ranius, T., Nilsson, S. and Smith, H. 2008. Restricted dispersal in a flying beetle assessed by telemetry. - Biodivers. Conserv. 17: 675-684.

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

IUCN Red List of Threatened Species 2016. Ampedus hjorti (Accessed 24 September, 2016) http://www.iucnredlist.org/details/157692/0

Jacobsen, R. M., Sverdrup-Thygeson, A. and Birkemoe, T. 2015. Scale-specific responses of saproxylic beetles: combining dead wood surveys with data from satellite imagery. - J. Insect Conserv. 19: 1053-1062.

Jansson, N., Bergman, K.-O., Jonsell, M. and Milberg, P. 2009a. An indicator system for identification of sites of high conservation value for saproxylic oak *(Quercus* spp.) beetles in southern Sweden. - J. Insect Conserv. 13: 399-412.

Jansson, N., Ranius, T., Larsson, A. and Milberg, P. 2009b. Boxes mimicking tree hollows can help conservation of saproxylic beetles. - Biodivers. Conserv. 18: 3891-3908.

Jonsell, M., Weslien, J. and Ehnstrom, B. 1998. Substrate requirements of red-listed saproxylic invertebrates in Sweden. - Biodivers. Conserv. 7: 749-764.

Jonsson, B. G. and Jonsell, M. 1999. Exploring potential biodiversity indicators in boreal forests. - Biodiversity & Conservation 8: 1417-1433.

Kuussaari, M., Bommarco, R., Heikkinen, R. K., Helm, A., Krauss, J., Lindborg, R., Öckinger, E., Pärtel, M., Pino, J., Rodà, F., Stefanescu, C., Teder, T., Zobel, M. and Steffan-Dewenter, I. 2009. Extinction debt: a challenge for biodiversity conservation. - Trends Ecol. Evol. 24: 564-571.

Kålås, J. A., Viken, Å., Henriksen, S. and Skjelseth S. (eds.). 2010. The 2010 Norwegian Red List for Species. – Norwegian Biodiversity Information Centre, Norway.

Leitão, R. P., Zuanon, J., Villéger, S., Williams, S. E., Baraloto, C., Fortunel, C., Mendonça, F. P. and Mouillot, D. 2016. Rare species contribute disproportionately to the functional structure of species assemblages. - Proc. R. Soc. B 283: 20160084.

Lindenmayer, D. B., Laurance, W. F., Franklin, J. F., Likens, G. E., Banks, S. C., Blanchard, W., Gibbons, P., Ikin, K., Blair, D., McBurney, L., Manning, A. D. and Stein, J. A. R. 2014. New policies for old trees: averting a global crisis in a keystone ecological structure. - Conservation Letters 7: 61-69.

Lindroth, C. H. 1986. The Carabidae (Coleoptera) of Fennoscandia and Denmark. – E. J. Brill/Scandinavian Science Press Ltd.

Lättman, H., Bergman, K.-O., Rapp, M., Tälle, M., Westerberg, L. and Milberg, P. 2014. Decline in lichen biodiversity on oak trunks due to urbanization. - Nord. J. Bot. 32: 518-528.

Magurran, A. E. and McGill, B. J. 2011. Biological diversity. Frontiers in measurement and assessment. – Oxford University Press.

McKinney, M. L. and Lockwood, J. L. 1999. Biotic homogenization: a few winners replacing many losers in the next mass extinction. - Trends Ecol. Evol. 14: 450-453.

Milberg, P., Bergman, K. O., Sancak, K. and Jansson, N. 2016. Assemblages of saproxylic beetles on large downed trunks of oak. - Ecology and evolution 6: 1614–1625.

Millennium Ecosystem Assessment 2005. Ecosystems and Human Well-being: Synthesis. – Island Press.

Moen, A. 1999. National Atlas of Norway: Vegetation. – Norwegian Mapping Authority.

Moore, J. W. 2010. ‘Amsterdam is standing on Norway’ Part II: The global North Atlantic in the ecological revolution of the long seventeenth century. - Journal of Agrarian Change 10: 188-227.

Mouillot, D., Bellwood, D. R., Baraloto, C., Chave, J., Galzin, R., Harmelin-Vivien, M., Kulbicki, M., Lavergne, S., Lavorel, S., Mouquet, N., Paine, C. E. T., Renaud, J. and Thuiller, W. 2013. Rare species support vulnerable functions in high-diversity ecosystems. - PLoS Biol. 11: e1001569.

Müller, J., Brustel, H., Brin, A., Bussler, H., Bouget, C., Obermaier, E., Heidinger, I. M. M., Lachat, T., Förster, B., Horak, J., Procházka, J., Köhler, F., Larrieu, L., Bense, U., Isacsson, G., Zapponi, L. and Gossner, M. M. 2015. Increasing temperature may compensate for lower amounts of dead wood in driving richness of saproxylic beetles. - Ecography 38: 499-509.

NIBIO 2016. Nedlasting av kartdata - SAT-SKOG. - The Norwegian Institute of Bioeconomy Research (NIBIO) (Accessed http://www.skogoglandskap.no/artikler/2009/nedlasting_satskog/newsitem

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

Nordén, B., Dahlberg, A., Brandrud, T. E., Fritz, Ö., Ejrnaes, R. and Ovaskainen, O. 2014. Effects of ecological continuity on species richness and composition in forests and woodlands: A review. - Ecoscience 21: 34-45.

Nordén, B., Paltto, H., Claesson, C. and Götmark, F. 2012. Partial cutting can enhance epiphyte conservation in temperate oak-rich forests. - For. Ecol. Manage. 270: 35-44.

Nordén, J., Penttilä, R., Siitonen, J., Tomppo, E. and Ovaskainen, O. 2013. Specialist species of wood-inhabiting fungi struggle while generalists thrive in fragmented boreal forests. - J. Ecol. 101: 701-712.

Norwegian Biodiversity Information Centre 2015. Norsk rødliste for arter [Norwegian red list for species]. - Norwegian Biodiversity Information Centre (Accessed 31 August 2016) http://data.artsdatabanken.no/Rodliste2015/Sok

Norwegian Biodiversity Information Centre 2016. Species Map Service 1.6. - The Norwegian Biodiversity Information Centre (Accessed 30 August, 2016) https://artskart.artsdatabanken.no/Default.aspx

Norwegian Environment Agency 2015. Norwegian database for habitats (Naturbase) -Norwegian Environment Agency (Accessed 30 September, 2015) http://karteksport.miljodirektoratet.no/#page=tab1

Paltto, H., Thomasson, I. and Nordén, B. 2010. Multispecies and multiscale conservation planning: setting quantitative targets for red-listed lichens on ancient oaks. - Conserv. Biol. 24: 758-768.

Pilskog, H. E., Birkemoe, T., Framstad, E. and Sverdrup-Thygeson, A. 2016. Effect of habitat size, quality, and isolation on functional groups of beetles in hollow oaks. - Journal of Insect Science 16: 1-8.

Pilskog, H. E., Sverdrup-Thygeson, A., Evju, M., Framstad, E. and Birkemoe, T. submitted. Long-lasting effects of logging on beetles in hollow oaks.

Ranius, T. 2006. Measuring the dispersal of saproxylic insects: a key characteristic for their conservation. - Popul. Ecol. 48: 177-188.

Ranius, T. 2007. Extinction risks in metapopulations of a beetle inhabiting hollow trees predicted from time series. - Ecography 30: 716-726.

Ranius, T., Aguado, L. O., Antonsson, K., Audisio, P., Ballerio, A., Carpaneto, G. M., Chobot, K., Gjurasin, B., Hanssen, O. and Huijbregts, H. 2005. *Osmoderma eremita* (Coleoptera, Scarabaeidae, Cetoniinae) in Europe. - Anim. Biodivers. Conserv. 28: 1-44.

Ranius, T. and Jansson, N. 2000. The influence of forest regrowth, original canopy cover and tree size on saproxylic beetles associated with old oaks. - Biol. Conserv. 95: 85-94.

Ranius, T., Johansson, P., Berg, N. and Niklasson, M. 2008. The influence of tree age and microhabitat quality on the occurrence of crustose lichens associated with old oaks. - J. Veg. Sci. 19: 653-662.

Ranius, T., Svensson, G. P., Berg, N., Niklasson, M. and Larsson, M. C. 2009. The successional change of hollow oaks affects their suitability for an inhabiting beetle, *Osmoderma eremita*. - Ann. Zool. Fenn. 46: 205-216.

Siitonen, J. and Ranius, T. 2015. The importance of veteran trees for saproxylic insects. - In: Kirby, K. J. and Watkins, C. (eds), Europe's changing woods and forests: from wildwood to managed landscapes. CABI.

Skarpaas, O., Diserud, O. H., Sverdrup-Thygeson, A. and Ødegaard, F. 2011. Predicting hotspots for red-listed species: multivariate regression models for oak-associated beetles. - Insect Conserv. Diver. 4: 53-59.

Slatyer, R. A., Hirst, M. and Sexton, J. P. 2013. Niche breadth predicts geographical range size: a general ecological pattern. - Ecol. Lett. 16: 1104-1114.

Socolar, J. B., Gilroy, J. J., Kunin, W. E. and Edwards, D. P. 2016. How should beta-diversity inform biodiversity conservation? - Trends Ecol. Evol. 31: 67-80.

Sverdrup-Thygeson, A. 2009. Oaks in Norway: Hotspots for red-listed beetles (Coleoptera). - In: Buse, J.Alexander, K. N. A.Ranius, T. and Assmann, T. (eds), Saproxylic beetles: their role and diversity in European woodland and tree habitats - Proceedings of the 5th symposium and workshop. Pensoft Publishers, pp. 13-26.

Sverdrup-Thygeson, A., Gustafsson, L. and Kouki, J. 2014. Spatial and temporal scales relevant for conservation of dead-wood associated species: current status and perspectives. - Biodivers. Conserv. 23: 513-535.

Sverdrup-Thygeson, A., Skarpaas, O. and Ødegaard, F. 2010. Hollow oaks and beetle conservation: the significance of the surroundings. - Biodivers. Conserv. 19: 837-852.

Tomter, S. and Eriksen, R. 2001. Statistikk over skogforhold og -ressurser i Vest-Agder - Landsskogtakseringen 1995-99. p 60.

Tomter, S. M., Eriksen, R. and Aalde, H. 2001. Statistikk over skogforhold og –ressurser i Aust-Agder: Landsskogtakseringen 1995 – 99. p 61.

Vevstad, A. 1998. Agderskog, Agder skogeierlag 1948-1998 og om skog og skogbruk på Agder gjennom tidene. – Agder Skogeigarlag.

Vodka, S., Konvicka, M. and Cizek, L. 2009. Habitat preferences of oak-feeding xylophagous beetles in a temperate woodland: implications for forest history and management. - J. Insect Conserv. 13: 553-562.

Vogt, L. J. 1886. Om Norges Udførsel af Trælast i ældre Tider. Historisk Tidsskrift. Den Norske Historiske Forening, pp. 81-120 and 273-384.

Wang, S. and Loreau, M. 2016. Biodiversity and ecosystem stability across scales in metacommunities. - Ecol. Lett. 19: 510-518.

Widerberg, M. K., Ranius, T., Drobyshev, I., Nilsson, U. and Lindbladh, M. 2012. Increased openness around retained oaks increases species richness of saproxylic beetles. - Biodivers. Conserv. 21: 3035-3059.

Wiens, J. A. 1989. Spatial scaling in ecology. - Funct. Ecol. 3: 385-397.

Økland, R. H. 2003. Partitioning the variation in a plot-by-species data matrix that is related to *n* sets of explanatory variables. - J. Veg. Sci. 14: 693-700.

Appendix 1

Table A1 The hollow oak sites used for insect collection in this study. The hollow oaks were situated along a coast-inland gradient in Southern Norway in two regions, Agder and Larvik, with a minimum of 1.5 km between the sites. Only one hollow oak in each site was used and the UTM-coordinates of the oaks are shown.

Site	Municipality	County	Region	UTM 32V E	UTM 32V N
Bjørnehula i Kjosdalen	Kristiansand	Vest-Agder	Agder	437464	6442220
Gangdalen mot Otra	Kristiansand	Vest-Agder	Agder	438035	6450199
Gillsveien v/Gillsvann	Kristiansand	Vest-Agder	Agder	442843	6449467
Eg Sykehus	Kristiansand	Vest-Agder	Agder	440146	6447630
Årosveten	Søgne	Vest-Agder	Agder	431126	6436976
Tjomsevann	Søgne	Vest-Agder	Agder	432403	6440700
Kverndalen	Lillesand	Aust-Agder	Agder	462495	6457948
Sekkebekk	Lillesand	Aust-Agder	Agder	461977	6456103
Håstøl	Birkenes	Aust-Agder	Agder	455708	6483175
Håverstad	Birkenes	Aust-Agder	Agder	448328	6485339
Hovland Ø	Birkenes	Aust-Agder	Agder	447184	6494667
Retterholt	Birkenes	Aust-Agder	Agder	453508	6484652
Tveitetjønnane SØ	Birkenes	Aust-Agder	Agder	454421	6461290
Tveitemyrane	Birkenes	Aust-Agder	Agder	456788	6461680
Skåre	Birkenes	Aust-Agder	Agder	449557	6495131
Hushovd	Froland	Aust-Agder	Agder	454812	6505271
Brenndalsskarven	Siljan	Telemark	Larvik	549045	6567077
Røsaker S	Skien	Telemark	Larvik	537389	6565804
Brekkeseter	Larvik	Vestfold	Larvik	554410	6547287
Budalsåsen	Larvik	Vestfold	Larvik	558779	6556166
Engene, Kjose	Larvik	Vestfold	Larvik	549405	6552693

Fuglevik	Larvik	Vestfold	Larvik	558279	6538779
Gjønnesvannet	Larvik	Vestfold	Larvik	557491	6559477
Håvaldsrød	Larvik	Vestfold	Larvik	556565	6545299
Kiste ved Lakssjø	Siljan	Vestfold	Larvik	546166	6567188
Lysebo	Larvik	Vestfold	Larvik	555005	6556785
Ødegården	Larvik	Vestfold	Larvik	551736	6537225
Øgården	Larvik	Vestfold	Larvik	552759	6549196
Skjærsjø	Larvik	Vestfold	Larvik	553288	6562418
Søndre Odbergsetra	Larvik	Vestfold	Larvik	551757	6567786
Stueåsen	Larvik	Vestfold	Larvik	552218	6552633
Vassbotnvannet	Larvik	Vestfold	Larvik	552180	6547757

Appendix 2

Species list and categorization.

Table A2 The oak-associated beetles collected from hollow oaks (*n* = 32) in Southern Norway and oak association. We defined 'oak specialists' as species preferring oak or occurring only on oak, 'oak semi-specialist' as species occurring only on broadleaved trees in addition to oak and 'oak generalists' as species occurring on coniferous trees in addition to oak. *Explanation*: Abbr. = abbreviations used in Figure 1, Ass. = Oak association; S, specialist, SS, semi-specialist, G, generalist, RL = red-list category according to the Norwegian red list for species (Kålås et al. 2010); NT, near threatened, VU, vulnerable, EN, endangered, CR, critically endangered, Ind. = number of individuals, R = region where the species was collected in our study: A = Agder, L = Larvik.

Family	**Species**	**Abbr.**	**Ass.**	**RL**	**Ind.**	**R**
Aderidae	*Euglenes pygmaeus*	Eug.pyg	S	NT	3	A
Anthribidae	*Anthribus nebulosus*		G		1	L
Cantharidae	*Malthinus flaveolus*	Mal.fla	G		1	A
	Malthodes spathifer	Mal.spa	SS		1	A
Carabidae	*Dromius agilis*		G		12	A, L
	Dromius fenestratus	Dro.fen	G		2	A
	Dromius quadrimaculatus	Dro.qua	S		3	L
Cerambycidae	*Alosterna tabacicolor*	Alo.tab	S		10	A, L
	Leiopus nebulosus	Lei.neb	S		4	A, L
	Oxymirus cursor	Oxy.cur	G		1	A
	Phymatodes testaceus	Phy.tes	S		13	A, L
	Rhagium inquisitor		G		1	A
	Rhagium mordax		G		7	A, L
	Stenurella melanura		G		2	L
	Stictoleptura maculicornis	Sti.mac	G		2	L
Cerylonidae	*Cerylon fagi*	Cer.fag	SS		1	L
	Cerylon ferrugineum		G		23	A, L
	Cerylon histeroides		G		12	A, L
Ciidae	*Cis bidentatus*	Cis.bid	G		2	A
	Cis boleti	Cis.bol	SS		12	A, L
	Cis castaneus	Cis.cas	SS		2	A

	Cis comptus		G		1	L
	Cis festivus	Cis.fes	SS		16	A, L
	Cis jacquemarti	Cis.jac	G		1	A
	Cis nitidus	Cis.nit	G		1	A
	Cis submicans		G	NT	11	A, L
	Cis vestitus	Cis.ves	SS		1	A
	Ennearthron cornutum		G		12	A, L
	Octotemnus glabriculus	Oct.gla	SS		2	A, L
	Orthocis alni		G		21	A, L
	Sulcacis nitidus		G		2	L
Cleridae	*Thanasimus formicarius*	Tha.for	G		2	A
	Tillus elongatus		G		1	L
Coccinellidae	*Aphidecta obliterata*		G		2	L
Cryptophagidae	*Atomaria morio*		G		1	A
	Cryptophagus dentatus	Cry.den	SS		32	A, L
	Cryptophagus scanicus		G		13	A, L
	Cryptophagus setulosus	Cry.set	SS		1	A
Curculionidae	*Dryocoetes villosus*	Dry.vil	S		16	A, L
	Hylesinus crenatus	Hyl.cre	SS		2	A, L
	Hylobius abietis		G		5	A, L
	Phloeophagus lignarius	Phl.lig	SS	VU	1	A
	Rhyncolus ater		G		76	A, L
	Rhyncolus sculpturatus		G		1	L
	Scolytus intricatus	Sco.int	S		12	A, L
	Strophosoma capitatum		G		36	A, L
	Trypodendron domesticum	Try.dom	SS		3	L
	Trypodendron signatum	Try.sig	SS		14	A
	Xyleborinus saxeseni	Xyl.sax	SS		5	A, L
	Xyleborus dispar	Xyl.dis	S		3	L
Dasytidae	*Aplocnemus nigricornis*	Apl.nig	G		1	A
	Dasytes caeruleus		G		5	A, L
	Dasytes niger		G		11	A, L
	Dasytes plumbeus	Das.plu	SS		18	A, L
Dermestidae	*Attagenus pellio*	Att.pel	SS		3	A, L
	Ctesias serra	Cte.ser	SS		3	A, L
	Megatoma undata		G		5	A, L
Elateridae	*Ampedus balteatus*	Amp.bal	G		274	A, L
	Ampedus hjorti	Amp.hjo	S	VU	31	L

	Ampedus nigrinus		G		38	A, L
	Ampedus nigroflavus	Amp.nig	SS	NT	1	A
	Ampedus pomorum	Amp.pom	G		3	A, L
	Cardiophorus ruficollis		G		1	L
	Crepidophorus mutilatus	Cre.mut	SS	EN	1	L
	Denticollis linearis		G		10	A, L
	Hypoganus inunctus	Hyp.inu	SS	EN	1	L
Endomychidae	*Endomychus coccineus*	End.coc	SS		3	A, L
	Mycetina cruciata		G		2	L
Erotylidae	*Dacne bipustulata*	Dac.bip	SS		8	A, L
	Triplax russica	Tri.rus	SS		21	A, L
Eucnemidae	*Microrhagus pygmaeus*	Mic.pyg	G		2	A, L
	Xylophilus corticalis		G		35	A, L
Histeridae	*Plegaderus caesus*	Ple.cae	SS		4	L
Latridiidae	*Cartodere constricta*		G		1	A
	Cartodere nodifer	Car.nod	G		1	A
	Corticaria longicollis		G		5	A, L
	Dienerella vincenti	Die.vin	G		3	A
	Enicmus fungicola	Eni.fun	G		3	A
	Enicmus rugosus		G		70	A, L
	Enicmus testaceus		G		29	A, L
	Latridius consimilis		G		2	L
	Latridius gemellatus		G		1	A
	Latridius hirtus		G		14	A, L
	Latridius minutus		G		2	A, L
Leiodidae	*Agathidium badium*		G		3	L
	Agathidium confusum		G		4	A, L
	Agathidium mandibulare	Aga.man	G	VU	1	L
	Agathidium rotundatum		G		1	L
	Agathidium seminulum		G		24	A, L
	Agathidium varians		G		5	A, L
	Anisotoma humeralis	Ani.hum	G		66	A, L
	Anisotoma orbicularis	Ani.orb	G		1	A
	Nemadus colonoides	Nem.col	S	NT	6	A, L
Lucanidae	*Platycerus caraboides*	Pla.car	SS		1	A
	Sinodendron cylindricum	Sin.cyl	SS		4	L

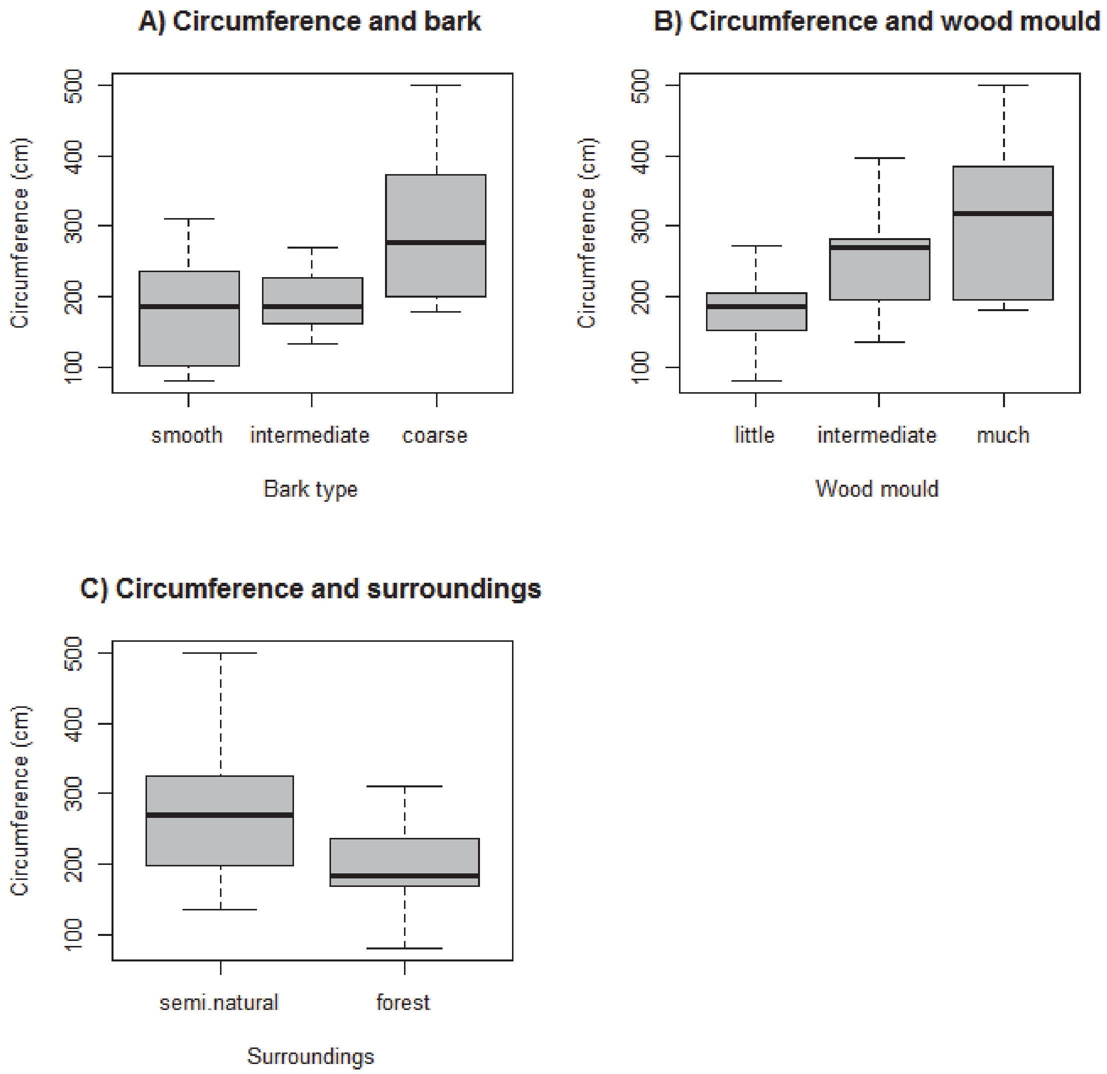
Lycidae	*Pyropterus nigroruber*	Pyr.nig	G		2	A
Lymexylidae	*Elateroides dermestoides*		G		4	A, L
	Lymexylon navale	Lym.nav	S	CR	1	L
Melandryidae	*Conopalpus testaceus*	Con.tes	SS		6	A
	Hypulus quercinus	Hyp.que	S	EN	1	A
	Orchesia micans		G		5	A
	Orchesia undulata	Orc.und	SS		18	A, L
	Phloiotrya rufipes	Phl.ruf	SS	NT	3	A, L
Monotomidae	*Rhizophagus bipustulatus*	Rhi.bip	S		30	A, L
	Rhizophagus cribratus	Rhi.cri	S		19	A, L
	Rhizophagus dispar	Rhi.dis	G		14	A, L
	Rhizophagus fenestralis	Rhi.fen	G		3	A
	Rhizophagus nitidulus	Rhi.nit	G		1	A
Mordellidae	*Tomoxia bucephala*		G		1	L
Mycetophagidae	*Litargus connexus*		G		3	A, L
	Mycetophagus atomarius	Myc.ato	SS		1	L
	Mycetophagus piceus	Myc.pic	S	VU	8	A
	Triphyllus bicolor	Tri.bic	SS	EN	9	A
Nitidulidae	*Cryptarcha strigata*	Cry.str	SS	NT	25	L
	Cryptarcha undata	Cry.und	SS	NT	15	L
	Cychramus variegatus	Cyc.var	G		1	A
	Epuraea abietina		G		1	A
	Epuraea guttata	Epu.gut	S	NT	1	L
	Epuraea marseuli		G		2	A, L
	Epuraea neglecta	Epu.neg	SS		2	L
	Epuraea rufomarginata		G		3	A, L
	Epuraea unicolor	Epu.uni	G		1	A
	Glischrochilus hortensis	Gli.hor	SS		72	A, L
	Glischrochilus quadriguttatus	Gli.qua	SS	NT	6	A, L
	Ipidia binotata		G		2	L
	Soronia grisea	Sor.gri	SS		33	A, L
Ptiliidae	*Pteryx suturalis*		G		1	L
Ptinidae	*Cacotemnus rufipes*	Cac.ruf	SS		2	A, L
	Dorcatoma chrysomelina	Dor.chr	S		111	A, L

	Dorcatoma dresdensis	Dor.dre	G		2	A
	Grynobius planus	Gry.pla	SS		24	A
	Hemicoelus canaliculatus	Hem.can	SS		6	A, L
	Ptilinus pectinicornis	Pti.pec	SS		3	L
	Ptinomorphus imperialis	Pti.imp	SS		5	A, L
	Ptinus fur		G		6	A, L
	Ptinus rufipes	Pti.ruf	S		1	L
	Ptinus subpillosus	Pti.sub	S		172	A, L
	Xestobium rufovillosum	Xes.ruf	S		70	A, L
Salpingidae	*Salpingus planirostris*	Sal.pla	SS		7	A, L
	Salpingus ruficollis		G		10	A, L
Scarabaeidae	*Trichius fasciatus*	Tri.fas	SS		1	A
Scirtidae	*Prionocyphon serricornis*	Pri.ser	SS	NT	1	L
Scraptiidae	*Anaspis frontalis*		G		6	L
	Anaspis rufilabris		G		64	A, L
	Anaspis thoracica		G		4	L
Silphidae	*Phosphuga atrata*		G		1	L
Sphindidae	*Aspidiphorus orbiculatus*		G		3	A, L
Staphylinidae	*Atheta picipes*	Ath.pic	G		1	A
	Atheta vaga		G		31	A, L
	Atrecus affinis		G		2	L
	Batrisodes venustus		G		5	A, L
	Bibloporus bicolor	Bib.bic	G		90	A, L
	Dadobia immersa		G		7	A, L
	Dinaraea aequata	Din.aeq	G		1	A
	Dropephylla ioptera		G		3	A, L
	Euconnus claviger		G		3	L
	Euplectus karstenii		G		33	A, L
	Euplectus mutator		G		7	L
	Euplectus nanus		G		8	A, L
	Euplectus piceus	Eup.pic	G		16	A, L
	Euplectus punctatus		G		13	A, L
	Gabrius splendidulus		G		21	A, L
	Hapalaraea pygmaea	Hap.pyg	SS		7	A, L
	Haploglossa gentilis	Hap.gen	S	NT	35	L

	Haploglossa villosula		G		1484	A, L
	Holobus apicatus	Hol.api	G		2	A
	Ischnoglossa prolixa		G		8	A, L
	Leptusa fumida		G		12	A, L
	Leptusa pulchella		G		8	A, L
	Leptusa ruficollis	Lep.ruf	SS		56	A, L
	Lordithon lunulatus		G		2	A, L
	Oxypoda arborea	Oxy.arb	SS		68	A, L
	Pella cognata		G		8	A, L
	Pella funesta	Pel.fun	G		1	L
	Pella laticollis	Pel.lat	G		4	L
	Pella lugens		G		13	A, L
	Phloeocharis subtilissima	Phl.sub	G		2	A
	Phloeopora corticalis		G		3	A, L
	Phloeopora testacea	Phl.tes	G		5	A, L
	Phloeostiba plana	Phl.pla	G		1	A
	Phyllodrepa melanocephala	Phy.mel	SS		1	L
	Plectophloeus nitidus		G	EN	2	L
	Quedius brevicornis		G	NT	6	A, L
	Quedius cruentus	Que.cru	SS		1	L
	Quedius maurus		G		6	A, L
	Quedius mesomelinus	Que.mes	SS		12	A, L
	Quedius scitus	Que.sci	S		2	L
	Quedius xanthopus		G		52	A, L
	Scaphisoma agaricinum		G		15	A, L
	Scydmoraphes minutus		G	NT	3	L
	Sepedophilus littoreus		G		2	A, L
	Sepedophilus testaceus		G		9	A, L
	Stenichnus bicolor		G		5	A, L
	Stenichnus godarti	Ste.god	S		2	L
	Thamiaraea cinnamomea	Tha.cin	SS		3	L
	Thamiaraea hospita	Tha.hos	S	NT	1	L
Tenebrionidae	*Mycetochara flavipes*	Myc.fla	SS		4	A, L
	Mycetochara maura	Myc.mau	SS	NT	16	A, L
	Palorus depressus	Pal.dep	S		2	L
	Prionychus ater	Pri.ate	SS	NT	3	L

	Pseudocistela ceramboides		G		22	A, L
Tetratomidae	*Hallomenus binotatus*	Hal.bin	G		5	A, L
	Tetratoma ancora		G		1	L
Trogossitidae	*Grynocharis oblonga*		G	VU	1	L
	Thymalus limbatus	Thy.lim	G		11	A
Grand Total					**4077**	

Appendix 3



A) Circumference and bark

B) Circumference and wood mould

C) Circumference and surroundings

Figure A1 Significant relationship ($p<0.05$) between circumference and the tree variables and surroundings in analysis of variance (ANOVA). The boxes show the 25th and 75th percentiles, the median is indicated by the horizontal line and dotted lines show the minimum and maximum values. Test results: A) circumference and bark; df = 2, F = 6.048, p = 0.006, B) circumference and wood mould; df = 2, F = 7.190, p = 0.003 and C) circumference and surroundings; df = 1, F = 7.1977, p = 0.012.

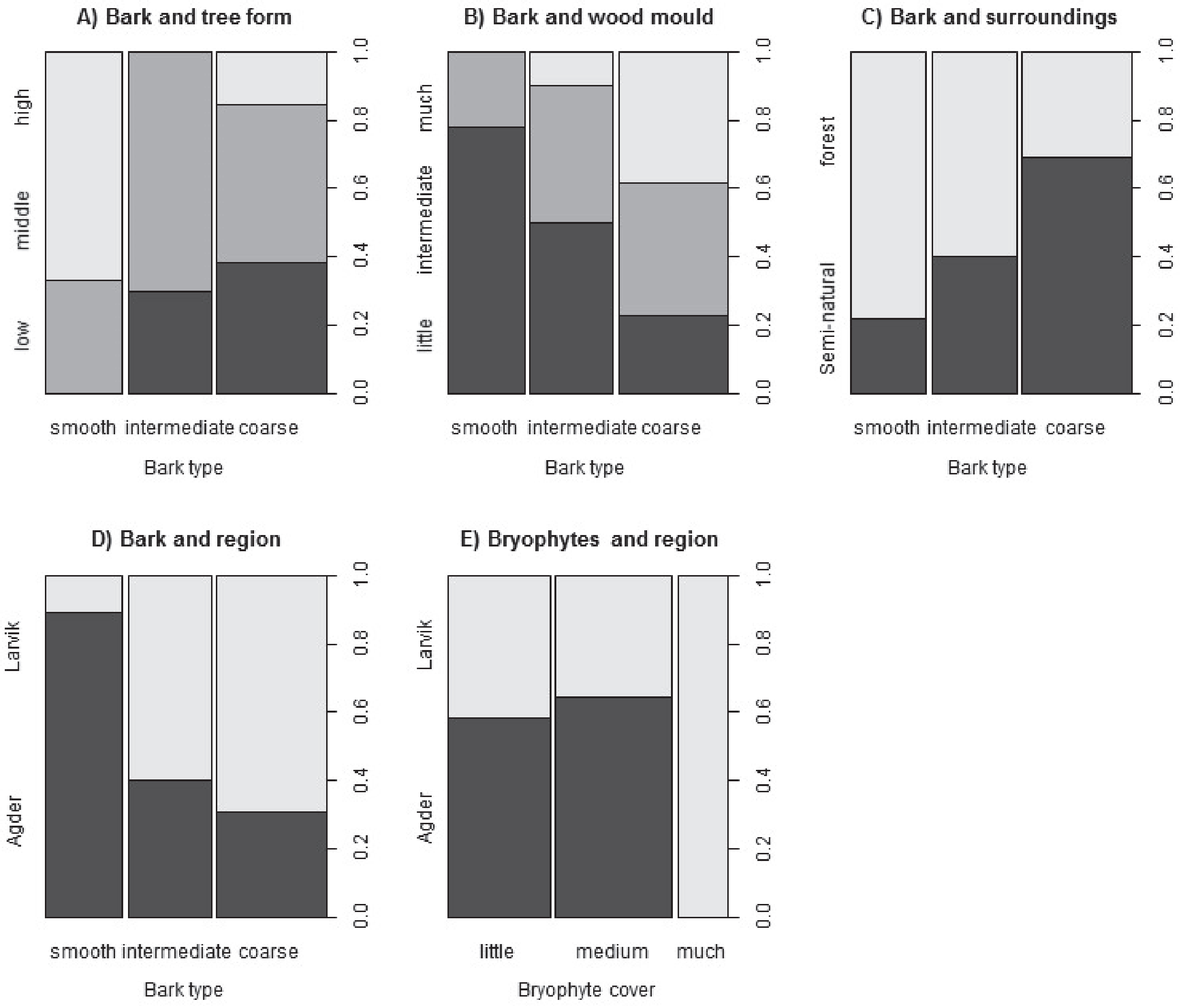


Figure A2 Categorical variables with significant (p<0.05) or close to significant relationship (0.1>p≥0.05) in Pearson's Chi-squared test for independence. The plots show the relative distribution of oaks (*n* = 32) within each combination of categories. The colors correspond to the categories on the y-axis with the category on the bottom shown in dark grey, the category in the middle in lighter grey and the category on the top in lightest grey. The width of the bars indicate sample size (i.e. number of oaks). Test results: A) bark and tree form; df = 4, p-value = 0.008, B) bark and wood mould; df = 4, p-value = 0.070, C) Bark and surroundings; df = 2, p-value = 0.082, D) bark and region; df = 2, p-value = 0.021, E) Bryophytes and region, df = 2, p-value = 0.024.

Appendix 4

Table A3 Variation in species composition of oak-associated beetles in hollow oaks explained by variables on different spatial scales, found by partial constrained correspondence analysis (pCCA) and variation partitioning. On each spatial scale variables were selected by forward selection and only variables with a significant independent contribution ($p<0.05$) were included in the final model. *Explanation*: ∪ = union: variation explained by the variables and the variation shared between them, ∩ = intersection: only variation that is shared between the variables, | = given, TI = total inertia, VE = variation explained (constrained inertia), FVE = fraction of variation explained by the full model and the contribution of each set of variables to the constrained inertia. Significance level of the full model is indicated by stars: *p<0.05, **, p<0.0.1. See the main text and Table 1 for explanation of the variables.

	Scale	**Variables**	**TI**	**VE**	**FVE**
All beetles					
Full model**		Bryophytes + Bark + Surroundings + Region	4.550	1.144	0.251
Individual fraction	Tree	(Bark ∪ Bryophytes) | (Local ∪ Region)		0.698	0.610
	Local	Surroundings | (Tree ∪ Region)		0.175	0.153
	Region	Region | (Tree ∪ Local)		0.193	0.169
Shared fraction		(Tree ∩ Local) | Region		0.015	0.014
		(Tree ∩ Region) | Local		0.039	0.034
		Tree ∩ Local ∩ Region		0.023	0.020
Generalists					
Full model**		Bryophytes + Bark + Forest density + Surroundings + Region	3.092	0.928	0.300
Individual fraction	Tree	(Bark ∪ Bryophytes) | (Local ∪ Region)		0.438	0.472
	Local	(Surroundings ∪ Tree density) | (Tree ∪ Region)		0.201	0.216
	Region	Region | (Tree ∪ Local)		0.088	0.095
Shared fraction		(Tree ∩ Local) | Region		0.112	0.120
		(Tree ∩ Region) | Local		0.050	0.054

		(Local ∩ Region) | Tree		0.032	0.035
		Tree ∩ Local ∩ Region		0.008	0.008
Semi-specialists					
Full model**		Distance to coast (categorical) + Region	6.379	0.781	0.122
Individual fraction	Coast-inland	Distance to coast (categorical) | Region		0.379	0.486
	Region	Region | Coast-inland		0.399	0.511
Shared fraction		Coast-inland gradient ∩ Region		0.002	0.003
Specialists					
Full model*		Bark + Wood mould + Region	4.568	1.371	0.300
Individual fraction	Tree	(Bark ∪ Wood mould) | Region		0.912	0.665
	Region	Region | Tree		0.117	0.086
Shared fraction		Tree ∩ Region		0.342	0.249