



# Reactive forest management can also be proactive for wood-living beetles in hollow oak trees



Leonie A. Gough\*, Tone Birkemoe, Anne Sverdrup-Thygeson

Norwegian University of Life Sciences, Department of Ecology and Natural Resource Management, P.O. Box 5003, NO-1432 Ås, Norway

## ARTICLE INFO

### Article history:

Received 14 May 2014

Received in revised form 18 September 2014

Accepted 23 September 2014

Available online 18 October 2014

### Keywords:

Ancient trees

Conservation strategy

Hollow oaks

Proactive conservation

Reactive conservation

Wood-living beetles

## ABSTRACT

The debate about whether proactive (focused on irreplaceable species) or reactive (focused on vulnerable species) conservation is more effective usually focuses on the global or multinational scale and knowledge of how these principles interact on-the-ground is lacking. Here we use the first long-term dataset on an entire oak-living beetle community in hollow oaks (*Quercus spp.*) to ask whether policy-driven conservation actions aimed at vulnerable species can also be proactive for unthreatened, but irreplaceable species. Hollow oaks are vital keystone structures that are rich in both vulnerable and irreplaceable wood-living beetles. We sampled in excess of 23,000 individuals from 307 species over four seasons, across the oak range in Norway. We assessed the importance of key environmental variables for vulnerable, irreplaceable and generalist species. We show that simple management actions taken to benefit vulnerable species in hollow trees could also contribute to preventing the decline of important, irreplaceable species. Clearing regrowth is predicted to increase vulnerable species richness by 75–100%, specialist richness by 65%, and to benefit two generalist species. Regrowth clearance is likely to be similarly beneficial in all oak-based habitats with hollow trees across Europe and North America. Increased oak circumference and local habitat quantity were also beneficial for species richness and influenced species composition. Based on this we provide advice for targeting conservation action. We suggest economic, carbon and recreational benefits of clearance that could increase the attractiveness of conservation for policy-makers. We show the importance of examining large-scale conservation planning principles at a local scale to elicit how they work on the ground where conservation actually happens.

© 2014 The Authors. Published by Elsevier Ltd. This is an open access article under the CC BY-NC-SA license (<http://creativecommons.org/licenses/by-nc-sa/3.0/>).

## 1. Introduction

Current species extinction rates are among the highest ever observed (Barnosky et al., 2011; Naeem et al., 2012). In the face of this daunting scale of loss, it is important to target conservation resources as effectively and efficiently as possible to achieve greatest biodiversity benefit (Wilson et al., 2007). One approach is to focus conservation action on hotspots of biodiversity, areas where many species co-occur (Brooks et al., 2006; Myers et al., 2000; Redford et al., 2003). Hotspots can be designed to be reactive, focusing on highly vulnerable (threatened) species to prevent their extinction, or proactive focusing on highly irreplaceable (rare, but unthreatened) species to prevent them becoming threatened in the future (Brooks et al., 2006).

There has been much debate about the merits of implementing proactive vs. reactive conservation, mainly in the field of conservation planning related to global or multinational priority-setting

(Brooks et al., 2006; Margules and Pressey, 2000; Wilson et al., 2007). In reality much current conservation action and spending on the ground is reactive regardless of this debate, as it is determined by policy at a variety of levels from international to local. Policy makers can be reluctant to act to protect biodiversity until there is a clear threat to it, because of the perceived costs of intervention and conflicting interests (Drechsler et al., 2011). Conservation often therefore focuses on actions targeted to slow threatened species' decline and prevent their extinction.

Oak (*Quercus spp.*) based systems are global hotspots of biodiversity (Buse et al., 2010; Sverdrup-Thygeson, 2009) and are considered as one of the most important habitats in a variety of ecosystems across the temperate zone from boreonemoral woodland (Andersson et al., 2011), lowland European wood-pasture and woodland (Bouget et al., 2014; Vera, 2000) and Mediterranean forests (Buse et al., 2013) to North American savannah (Brawn, 2006) and American and European agricultural lands (Gibbons et al., 2008). Ancient, hollow oak trees are an integral component of these systems. They are keystone structures, their great size and age conferring vital ecological roles that cannot be replicated

\* Corresponding author. Tel.: +44 79 80 45 78 27.

E-mail addresses: [leonie.gough@nmbu.no](mailto:leonie.gough@nmbu.no), [leonie.gough@oxon.org](mailto:leonie.gough@oxon.org) (L.A. Gough).

by younger, smaller trees (Lindenmayer et al., 2014). Hollow oaks are 'habitat trees' (Bouget et al., 2014) that contain varied microhabitats including cavities, wood mould, dead wood, and fissured bark which support a multitude of different species (Ranius et al., 2011; Stokland and Siitonen, 2012) including fungi, lichens, birds, small mammals and insects (Bergman et al., 2012; Siitonen, 2012). Oak ecosystems are suffering a drastic decline due to direct removal, a lack of traditional forest management in areas where it historically occurred, intensive forestry and climate events such as severe drought (Bjorkman and Vellend, 2010; Horak et al., 2014; Paillet et al., 2010; Vera, 2000) and large, hollow trees are often disproportionately affected (Lindenmayer et al., 2014). Hollow oak trees are incredibly rich in wood-living beetles, a group of animals with one of the highest proportions of threatened species in Europe (Davies et al., 2008; Grove, 2002; Nieto and Alexander, 2010; Speight, 1989). In Norway over 60 red-listed wood-living beetle species are found exclusively on hollow trees, primarily oak, and many hundreds more are associated with other microhabitats in veteran oaks (Kålås et al., 2010). The vulnerability of hollow oaks and their importance for red-listed species has been recognized by the Norwegian government and hollow oak trees are designated as a 'selected habitat type' ('utvalgt naturtype') under the Regulation on Selected Habitats 2011 (associated with the Nature Diversity Act 2009). A key aim of the Regulation is to ensure that hollow oaks are managed appropriately to halt their decline, increase oak recruitment and benefit red-listed species. There is a national Action Plan which sets out the need for action (Norwegian Environment Agency, 2012).

This protection of hollow oaks in Norway is a reactive approach (prioritizing high vulnerability) to conservation as defined by Brooks et al. (2006), as it focuses on red-listed species that are in need of urgent action to prevent a slide towards extinction. Most existing research into conservation of hollow oak trees and wood-living beetles has been reactive, attempting to determine how best to conserve red-listed species associated with the oaks. However, there are hundreds of beetle species associated with hollow oak trees that are not currently threatened but are highly irreplaceable due to rarity through endemism or limited distribution. A proactive conservation approach (prioritizing high irreplaceability) aiming to prevent further species from reaching the red list could also be taken.

Whether conservation is proactive or reactive, it usually occurs in the context of limited resources and requires targeted on-the-ground action. Conservation managers in Norway are currently in need of advice on how to target their resources most efficiently to fulfil the aims of the Action Plan. Hollow oak trees in Norway therefore provide an ideal system to investigate the potential of reactive conservation actions to benefit other species. In order to advise landowners and managers on how best to selectively target trees for management, we need to know how actions taken influence beetle species richness. Ecological knowledge is growing about wood-living beetle requirements. We know that increasing the amount of dead wood in the wider surroundings can benefit species richness (Sverdrup-Thygeson et al., 2010), and that a landscape-level approach to habitat restoration is required to increase oak recruitment, reduce fragmentation and facilitate insect dispersal (Franc et al., 2007). We also know that various tree factors influence beetle species richness, including amount of wood mould, age and size of the tree, and whether a tree is in a forest or open landscape (Ranius et al., 2009a,b; Sverdrup-Thygeson et al., 2010). However, it is often hard to draw inferences from these existing studies about how to specifically and immediately manage the existing trees and immediate area around them on-the-ground to improve the prospects of associated biota. Most studies have taken a reactive view, focused on red-listed species. It is not clear whether the conclusions drawn about red-listed species also apply to other species.

The studies providing the most practical management advice have focused on only one (Ranius, 2002; Ranius et al., 2009b) or a few species (Vodka et al., 2009), which due to their restricted geographical distribution (such as *Osmoderma eremita*, a focus of research in Sweden but known from only one location in Norway) or specialist ecology makes it hard to generalize recommendations for a whole community. Another shortcoming of existing studies is the short time frame (one or two seasons) used for sampling (Koch Widerberg et al., 2012; Ranius et al., 2010, 2009b; Sverdrup-Thygeson et al., 2010). Long-term wood-living insect sampling designs are non-existent for hollow oaks, although there are examples from birch (Martikainen and Kaila, 2004) and mixed forests (Grove and Forster, 2011; Hjalten et al., 2012; Parmain et al., 2013). Beetles are known to experience large population fluctuations between years and wood-living species are elusive, with limited detection probability. In addition, the very high number of rare species associated with oaks are likely to have stochastic occurrence or patchy distribution, meaning a high proportion of the community may be missed in one year's sampling (Engen et al., 2008; Jansson et al., 2009; Thompson, 2004). Rare beetles accumulate in samples slowly over years (Martikainen and Kaila, 2004), but just one extra sampling year (two years total instead of one) vastly increases the number and diversity of species caught (Parmain et al., 2013). For these reasons conclusions based on one year's sampling, particularly of rare species, may not be robust.

In this study we use the first, to our knowledge, long-term dataset on an entire oak-living beetle community in hollow oak trees to investigate whether reactive conservation actions aimed at vulnerable species in a hotspot habitat can also be proactive for currently unthreatened, but highly irreplaceable species. It is a large-scale study, with samples from across the whole oak range in Norway. We use the results to provide management recommendations for species conservation and explore the policy implications of the recommendations.

## 2. Materials and methods

### 2.1. Data collection

The data set used in this study is a part of an ongoing study of hollow oaks under the National Program for Surveying and Monitoring Biodiversity – Threatened Species in Norway (ARKO project (ARKO, 2011)). The study contains data from 50 hollow oak (*Quercus robur* and *Q. petraea*) trees in 10 sites, spread across the geographical range of oak in Norway (Fig. 1). All sites had at least five hollow oaks close to each other (6–250 m). A hollow oak was defined as a tree of at least 95 cm circumference with a visible cavity in the trunk, in line with the Regulation on Selected Habitats 2011, although one tree with a visible cavity included in the analysis was slightly smaller.

Five environmental variables were included in the analysis – Circumference, Regrowth, Cavity Stage, Number of Big and Hollow Oaks and Amount of Forest (Table 1). These were selected from an initial larger set of measured variables after assessing collinearity between variables through calculation of correlation coefficients and inspecting Variance Inflation Factors (VIFs). We prioritized variables that were ecologically meaningful and could either be directly influenced by management or easily measured by conservation managers at new sites.

Each tree was sampled for beetles in four years between 2004 and 2011. Two flight interception traps (20 cm × 40 cm windows, traps with ethylene glycol and detergent) were used per tree, one directly in front of the cavity opening and one in the canopy, and they were emptied once a month between May and August.

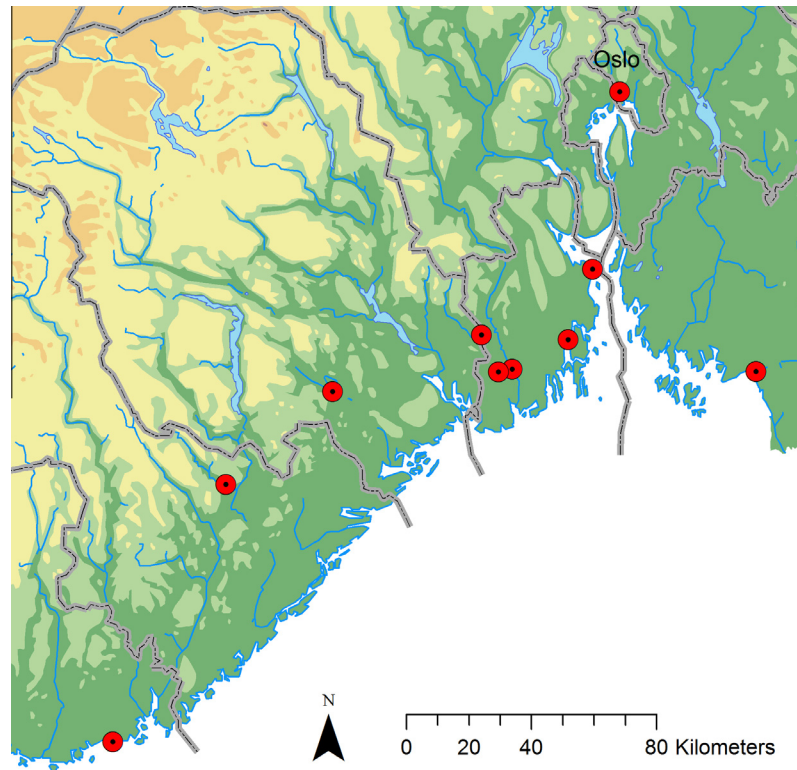


Fig. 1. Distribution of the study sites within southern Norway. Grey lines represent County boundaries.

**Table 1**  
Environmental variables used in the analyses.

Variable name	Description	Measurement method	Summary
Circumference	cm gbh girth at breast height, 1.3 m above the ground	Tape measure	Min: 80.0 Max: 660.0 Mean: 296.7 Median: 280.0
Regrowth <sup>a</sup>	None, scrub, trees vegetation which directly shades the trunk or crown of the oak	Visual estimate	None: 25 oaks Scrub: 6 oaks Trees: 19 oaks
Cavity stage	1,2,3,4,5	Visual estimate based on the method of <a href="#">Antonsson and Jansson (2001)</a> . Level 1 is least decayed	1: 0 oaks 2: 13 oaks 3: 11 oaks 4: 18 oaks 5: 8 oaks
Number of big and hollow oaks	The number of hollow oak trees in surrounding 1 km	Assessed by counting along two perpendicular 1000 m long transects with the focal oak at the central crossing point	Min: 6.0 Max: 21.0 Mean: 14.5 Median: 17.0
Amount of forest	The number of 10 × 10 m cells occupied by forest in the surrounding 1 km	Calculated using ( <a href="#">AR5 Land Resource Map</a> ). High values indicate high density and connectivity of forest	Min: 2641 Max: 30372 Mean: 18720 Median: 19765

<sup>a</sup> All but two of the hollow oaks surrounded by scrub or trees Regrowth occurred in forests.

The sampling process is described in detail in [Sverdrup-Thygeson et al. \(2010\)](#).

All beetle individuals were identified to species level and classified according to threat (approximate measure of vulnerability) and habitat specialization (approximate measure of irreplaceability) as (a) not red-listed oak-generalist; species that occur on oak, but also use other trees (b) not red-listed oak-specialist; defined as species that prefer oak and (c) red-listed; defined as oak-associated species listed as Near Threatened (NT) and threatened (VU, EN, CR) on the Norwegian Red List ([Kålås et al., 2010](#)) and d) others. The classification was based on relevant literature, mainly [Dahlberg and Stokland \(2004\)](#), and [The Saproxyllic](#)

[Database \(2014\)](#). Only oak-associated beetle species were included in the analysis. Species counts were summed per tree across years.

## 2.2. Statistical analysis

All analyses were carried out in R version 3.0.1 (R Core Team 2013).

To test which environmental variables were the most influential for species richness, generalized linear mixed-effects models (GLMMs) with a Poisson error distribution and log-link function were used. Site was used as a random effect to account for repeated sampling of the same sites, large variances between species

richness of different sites, and to allow generalization of the results beyond the sampled trees. Function `glmer` in package `lme4` was used (Bates et al., 2014). Backwards stepwise selection based on Akaike's Information Criterion was used to determine the optimal model by use of the `drop1` function. Where several models were equally or almost as good, the optimal model was chosen based on ecological and practical knowledge. Overdispersion of the residuals was checked in the global model for each species group. Overdispersion was above 1 for all species groups. To assess whether the chosen GLMM method was robust to this overdispersion, an alternative GLMM method with a negative binomial error distribution was tested using function `glmmadmb` from `glmmADMB` package (Skaug et al., 2013). An information-theoretic selection process was used (Burnham and Anderson, 2002) as the `drop1` function is not compatible with this function. 37 candidate models were tested for each species group. The results were very similar to those obtained using `glmer`, with only slight differences in estimates and no change in the overall conclusions. The poisson-distributed `glmer` was therefore assumed to be robust to the slight overdispersion in the data and was used for all analyses.

To assess whether the species composition of the different species groups was affected by the measured variables, multivariate analyses were carried out. To examine patterns of species composition and determine which variables affect composition, redundancy analysis (RDA) using package `vegan` (Oksanen et al., 2013) was used. The data was subjected to a Hellinger transformation to account for double zeros and asymmetry in the data, whilst preserving Euclidean distance between sites (Legendre and Gallagher, 2001). Unconstrained Principal Components Analysis was used to look for outliers (one outlier, site SI4, was removed from the generalist species analysis). Constrained RDA was then used to examine the effect of the measured variables. Backwards stepwise selection using step function with permutations set at 4999 was used to determine which environmental variables were the most important for explaining differences in species composition between sites. Finally, a type of species indicator analysis was carried out to identify species that are associated with sites with particular environmental characteristics. Function `multipatt` (method `r.g`, which corrects for differing numbers of species between site groups) in package `indicspecies` was used (De Cáceres and Legendre, 2009). This uses a correlation matrix to determine the strength of the association between a species and a particular group of sites, expressed as the point-biserial phi coefficient of association (De Cáceres, 2013; De Cáceres et al., 2010). It takes into account species abundances and absences both within and outside each group of sites, with the strength of a species association to a group increased by absences outside of that group. Abundance data was square-rooted to correct for extremely abundant species in the species indicator analysis.

### 3. Results

We sampled a total of 23 745 individuals from 307 oak-associated species, of which 68 (9079 individuals) were red-listed, 24 (4051 individuals) were non-red-listed specialists and 215 (10615 individuals) were non-red-listed generalist. In addition, 39 red-listed species (102 individuals) were caught that were not wood-living.

#### 3.1. Effect of long-term sampling

Over the four years we caught a greater number and variety of species than in the first year. The species accumulation curves for both specialist and red-listed species appear to have reached an asymptote, demonstrating that the long-term sampling has caught

the majority of those two communities (Fig. 2). The generalist species curve is beginning to plateau, but more effort is needed before reaching the same completeness as for the other two groups. The longer-term sampling was especially effective at increasing the number of red-listed species that were caught. 68 red-listed oak-associated species were caught over four seasons sampling, compared to just 46 in the first year. This is a very considerable increase of 48% (22 species) in the number of red-listed species caught. A wider variety of red-listed species were caught in general as demonstrated by the relatively high number of non-wood-living red-listed species sampled. 39 such species were sampled in the multi-year dataset, only 18 in the single year dataset, an increase of 117%.

#### 3.2. Species richness in vulnerable, irreplaceable and general species groups

The optimal model for red-listed (vulnerable) species was best described by Regrowth and Circumference (Table 2). At any size (Circumference) of tree, there was approximately double the number of red-listed species in oaks with no regrowth compared to maximum regrowth in the surroundings (Fig. 3) and the intermediate regrowth (scrub) was intermediate to those two extremes. The model predicted that trees with the highest red-listed species richness were therefore likely to be of large girth in a relatively open setting with no regrowth shading the trunk or crown.

The optimal model for oak generalists was also described by Regrowth and Circumference, in addition to Amount of Forest. However, the effect of the Circumference and Regrowth were inverted compared to the model explaining the red-listed beetles richness (Table 2); oaks surrounded by the highest level of regrowth are likely to support more species than oaks in the open, and smaller trees are likely to support more generalist species than larger trees at all regrowth levels. Generalists also respond similarly to scrub and trees regrowth levels, with a large increase in species number between none and scrub. The effect of Forest amount is positive, but small. To sum up, species richness of oak generalists was predicted to be likely to be highest in trees of relatively small girth, surrounded by scrub or trees, where amount of forest in the surrounding 1 km is high.

The oak specialists (irreplaceable) were the only group not to respond to Circumference, and the optimal model contained Regrowth, Number of Big Hollow Oaks, and Amount of Forest. As with the red-listed species, there was a much reduced species richness in oaks surrounded by other trees as compared to no regrowth, but there was no difference between trees surrounded by scrub and those with no regrowth. Species richness increased

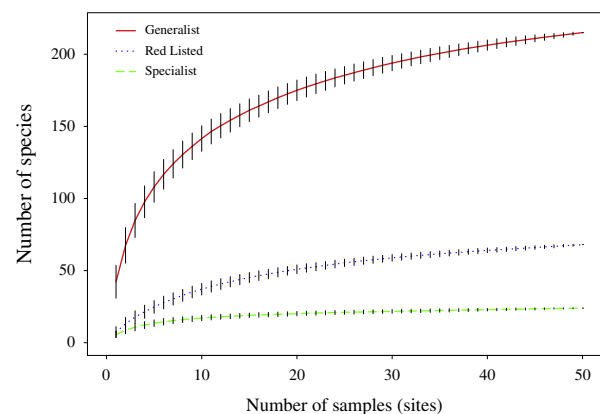
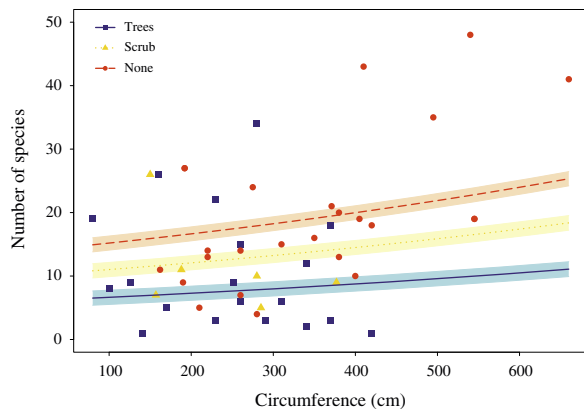


Fig. 2. Species accumulation curves. Confidence intervals are represented by vertical lines. Calculated using a random method, which subsamples the data without replacement. Permutations = 499.

**Table 2**Results of model selection (generalized linear mixed models, Poisson distribution, log link) showing the optimal model for explaining species richness.  $n = 50$  sites in all analyses.

Variable	Estimate	Std. error	z-Value	p-Value
<i>Response: red-listed species</i>				
AIC Final Model: 387.77 (Initial: 395.33)				
Intercept	2.6298	0.2363	11.13	<0.001
Circumference	0.0009	0.0004	2.21	0.027
Regrowth scrub	-0.3211	0.1501	-2.14	0.032
Regrowth trees	-0.8266	0.2281	-3.62	<0.001
<i>Response: generalist species</i>				
AIC Final Model: 636.23 (Initial: 638.2)				
Intercept	4.3600	0.0114	38.40	<0.001
Circumference	-0.0004	0.0002	-2.20	0.029
Regrowth scrub	0.2400	0.0049	4.90	<0.001
Regrowth trees	0.2199	0.0637	3.30	<0.001
Amount of forest	0.00001	0.000004	3.20	0.002
<i>Response: specialist species</i>				
AIC Final Model: 435.90 (Initial: 439.00)				
Intercept	2.3600	0.1310	18.00	<0.001
Number of big and hollow oaks	0.0513	0.0073	7.01	<0.001
Regrowth scrub	0.105	0.1070	0.98	0.326
Regrowth trees	-0.317	0.0867	-3.66	<0.001
Amount of forest	-0.00001	0.000004	-2.87	0.004

**Fig. 3.** The optimal model for red-listed species richness. Points represent observed values, lines represent model fit. Standard errors are represented by shading.

as the number of big, hollow oaks in the surrounding 1 km increased, and declined slightly as the amount of forest in the surrounding 1 km increased (Table 2). Species richness of oak specialists was therefore predicted to be highest in any hollow oak surrounded by no regrowth or scrub, with a high number of other hollow oak trees in the surrounding 1 km, in a relatively open landscape.

### 3.3. Species composition

For red-listed and specialist species, the optimal redundancy model for explaining species composition contained Regrowth and Number of Big and Hollow Oaks. For generalist species, the optimal model contained only Regrowth.

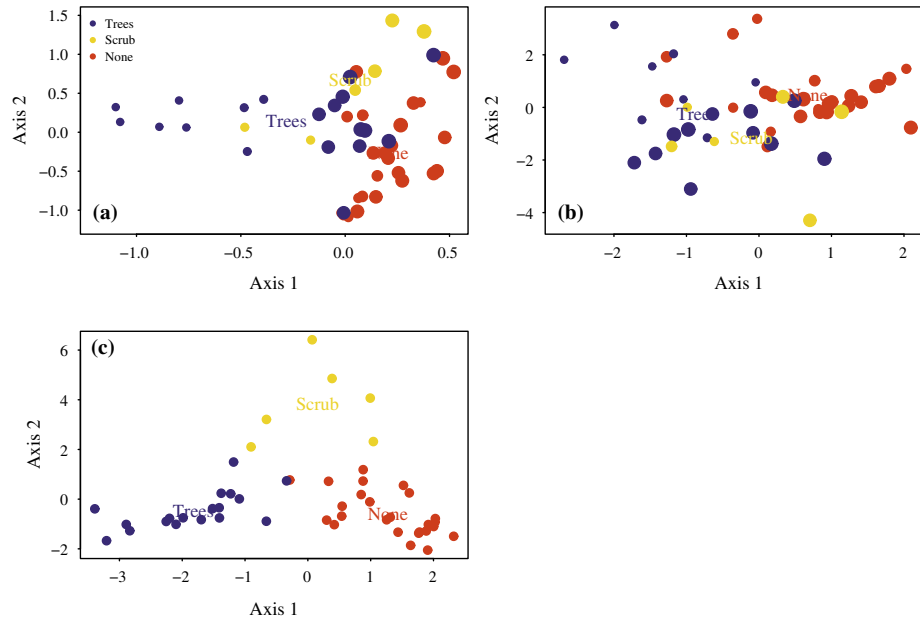
Sites in the different Regrowth groups had different species compositions, with sites in the different Regrowth groups occupying mostly distinct ordination space (Fig. 4). The patterns differed between groups. For red-listed species, 'trees' sites varied greatly along Axis 1, whilst 'scrub' and 'none' sites varied mostly along Axis 2. For generalists, 'trees' and 'none' varied along Axis 1, and 'scrub' sites varied mostly along Axis 2 (Fig. 3). Despite the visible patterns, the explanatory power of the optimal redundancy models was quite low, explaining a small proportion of the variation in species composition (Table 3).

The species association analysis showed that there are red-listed and generalist species that were strongly associated with a particular Regrowth group (Table 4). Generalists had the highest number of selected species, with 22 species selected as associated with one or more Regrowth groups. Only two red-listed species were selected, both associated with Regrowth level 'none'. No specialist species were selected. This reflects the pattern of the redundancy analysis (Fig. 4), where generalists showed almost no overlap between regrowth groups, and specialists showed a large amount of overlap.

## 4. Discussion

We have shown for the first time that vulnerable and irreplaceable species in hollow oaks can be affected by a single environmental factor – Regrowth, a description of the vegetation shading the oak. Oak Circumference and the Number of Big and Hollow Oaks in the local landscape were also influential.

We found that Regrowth has a significant impact on the species richness of all species groups. The strong effect of Regrowth for red-listed species and specialist species richness, with the highest richness in oaks with no regrowth shading the trunk or crown, is expected. Oaks prefer an open canopy, so many of the wood-living species they support are likely to be adapted to open, light and warm conditions (Horak et al., 2014; Vera, 2000). The red-listed and specialist results agree with other studies that have found that increased canopy openness increases wood-living beetle species richness, with openness to the south having the most beneficial effect (Widerberg et al., 2012). The result for generalist richness is a complete contrast, with species richness highest in oaks surrounded by regrowth. However, this can be explained by the Amount of Forest surrounding the oaks. Generalist species use a wide range of host tree species and it is likely that generalist richness is high in oaks with Regrowth as those oaks are in the main surrounded by large amounts of mixed forest, where host tree diversity is high. The effect of regrowth may also be due to the habitat preferences of the generalists. The generalists group contains species that are known to prefer another particular type of tree, but use oak if it is present. Alternative host tree species, such as beech or lime, are more shade-tolerant than oak (Vera, 2000) and the species more particularly associated with them are likely to be less warmth-loving than those particularly associated with oak.



**Fig. 4.** The optimal redundancy models for species composition of (a) red-listed species, (b) specialist species and (c) generalist species. Point size is proportional to the Number of Big and Hollow Oaks for red-listed and specialist species. Text represents the centroid of each Regrowth group.

**Table 3**  
Results of backwards stepwise model selection (redundancy analysis). One outlier site was removed from the generalist species analysis.  $n = 50$  sites for red-listed (68 species) and specialist species (24 species), 49 sites (215 species) for generalist species.

Model	Total inertia	Constrained inertia (proportion of total)	Eigenvalues of constrained axes		Model significance			
			Axis 1	Axis 2	DF	Var	F	P
Red-listed species ~ regrowth + BigHOak	0.77	0.07 (0.10)	0.052	0.017	3, 46	0.08	1.75	0.005
Generalist species ~ regrowth	0.47	0.06 (0.12)	0.047	0.007	7, 41	0.12	2.05	0.005
Specialist species ~ regrowth + BigHOak	0.47	0.08 (0.17)	0.067	0.007	3, 46	0.08	3.13	0.005

**Table 4**  
Results of species-habitat association analysis. Species that are strongly associated to one or more regrowth groups.  $n = 215$  generalist species, 24 specialist species, 68 red-listed species.

Regrowth level	Species	Coefficient value	P value
Red-listed species	None		
	<i>Prionychus ater</i>	0.533	0.001
	<i>Mycetochara maura</i>	0.395	0.030
Generalist species	None		
	<i>Ctesias serra</i>	0.426	0.023
	<i>Ptinomorphus imperialis</i>	0.420	0.027
	Scrub		
	<i>Quedius xanthopus</i>	0.523	0.007
	<i>Cerylon histeroideus</i>	0.518	0.012
	<i>Xylophilus corticalis</i>	0.475	0.019
	<i>Phyllocladus ioptera</i>	0.466	0.015
	<i>Enicmus rugosus</i>	0.433	0.035
	<i>Gabrieus splendidulus</i>	0.423	0.033
	<i>Atomaria morio</i>	0.401	0.026
	Trees		
	<i>Bibloporus bicolor</i>	0.553	0.003
	<i>Cis festivus</i>	0.492	0.005
	<i>Cis boleti</i>	0.483	0.010
<i>Leptusa fumida</i>	0.479	0.019	
<i>Anisotoma humeralis</i>	0.454	0.012	
<i>Grynobius planus</i>	0.439	0.008	
<i>Thymalus limbatus</i>	0.421	0.022	
None + scrub			
<i>Xyleborinus saxesenii</i>	0.521	0.006	
<i>Hemicoelus canaliculatus</i>	0.500	0.009	
<i>Thamniaea cinnamomea</i>	0.427	0.032	
Scrub + trees			
<i>Ampedus balteatus</i>	0.458	0.034	
<i>Oxyopoda arborea</i>	0.455	0.022	
<i>Leptusa ruficollis</i>	0.448	0.025	
Specialist species	None selected		

Regrowth significantly affected the species composition of all groups. This was also expected, as insolation (which will increase as regrowth decreases) has been found to be an important factor for wood-living beetle species composition (Vodka et al., 2009). Although overall species composition was different between the Regrowth groups, the species association analysis showed that only two red-listed species (*Prionychus ater* and *Mycetochara maura*) were associated with any particular Regrowth group and no specialist species were associated with any Regrowth group. This pattern has been observed in other taxa in oak woodlands. Of 31 species of birds in open and closed oak woodlands, overall composition between open and closed forests was different but few species were specifically associated to a specific openness of woodland (Brawn, 2006).

The positive result of Circumference for red-listed and specialist species is likely to be related to the age and stage of decay of the oak. Older and larger oak trees contain more diverse microhabitats such as more dead wood in the crown, and larger and more developed cavities which are capable of supporting a greater variety and diversity of wood-living species than younger, smaller oaks. Large circumference has been found to be important for other threatened species on hollow oaks, including red-listed lichens (Johansson et al., 2009). The somewhat counterintuitive result for generalists, with higher species richness in the smallest oaks, was unexpected. It is likely to be due to the position of the hollow oaks. Although there is no collinearity between the variables (Variance Inflation Factors for all variables of between 1 and 1.9), it is known that in the study landscape, hollow oaks growing in forests are smaller than hollow oaks growing in the open (mean circumference:

242 cm in forests, 385 cm in open landscapes) (Sverdrup-Thygeson et al., 2010), probably due to lower productivity, increased competition for resources and lower light levels resulting in a lower growth rate. It is likely that the negative result for generalists reflects this - the wider species pool of generalists in the forests results in higher species richness of generalists in the smaller oaks in forests. It should also be borne in mind that the smallest hollow oaks in this study are 80–95 cm gbh. This is still a significant size.

Specialist species were the only group whose richness responded to the Number of Big and Hollow Oaks. This at first glance seems that specialist species are more responsive to connectivity of habitat in the landscape than red-listed species. Red-listed species could be so restricted that they are no longer able to disperse in sufficient numbers to take advantage of surrounding habitat. A study of *O. eremita*, a red-listed beetle in Sweden, found that only approximately 15% of beetle individuals disperse from their host oak and the rest stay resident, probably due to the stability of hollow oak habitat over centuries reducing the need to find new habitat (Bergman et al., 2012; Ranius and Hedin, 2001). Alternatively, the measured scale of 500 m could be too small to detect an effect. Red-listed species have been found to respond to measures of connectivity at larger scales of approximately 1 km (Ranius et al., 2011). In addition, red-listed species composition was significantly affected by the Number of Big and Hollow Oaks, so it seems the amount of habitat does have an effect on red-listed communities but only on composition, not richness.

The completely different response of generalist species to the other groups at first appears a little strange. It is however known that it is difficult to predict total species richness of a wood-living beetle community from red-listed species richness (Sebek et al., 2012) and that is supported by our results. The generalist species, of which there are many more than either red-listed or specialist species, are not reliant on oak while the other groups are to a large extent, so they would not be expected to respond in the same way.

#### 4.1. Effectiveness of long-term sampling

This study is the first, to our knowledge, on an entire oak-associated wood-living beetle community in hollow oak trees to use a long-term dataset. We sampled in total 80 more oak-associated species over the four years than in the first year (307 species over four years, 227 in the first year). Over the four seasons we sampled 68 red-listed species, which is 57% of the oak-associated beetle species on the Norwegian red-list (Kålås et al., 2010), compared to 46 species (39% of the oak-associated beetles on the red-list), in the first season. Ranius and Jansson (2002) compared the effectiveness of pitfall and window traps for sampling cavity-dwelling beetles over one season and found that eight species were not caught by window traps. One of these species only occurs in one location in Norway and would not be likely to be sampled. Of the remaining seven species, three species were caught in this study – *Elatер ferrugineus*, *Plegaderus caesus* and *Trox scaber*. This demonstrates the greater effectiveness of multi-year sampling.

#### 4.2. Management recommendations

To benefit the most threatened (red-listed) species, the best reactive approach is to clear all regrowth that shades the trunk or crown of a hollow oak. Provided there is a colonization source nearby, this is predicted to increase the number of red-listed species by between 75% and 100% and specialist richness by 65%. It would specifically benefit the two red-listed and two generalist species selected as being associated with oaks with no surrounding regrowth. Clearing regrowth, particularly trees, from around hollow oak trees can therefore act as both a reactive and proactive approach, improving conditions both for the most vulnerable

red-listed species, the not-yet-threatened specialist species, and two generalist species. Generalist species richness was highest in trees with surrounding regrowth and 20 species were selected as associated to oaks surrounded by either scrub or trees. However, the regrowth variable refers to growth that directly shades the trunk or crown of the oak tree. Removing this type of regrowth from around hollow oak trees, whilst not altering the position of the oak in a forest landscape, should not negatively affect generalist species as the remainder of the forest (and therefore the variety of host trees and generalist species pool), will be unaffected by the management. This should also be true for red-listed and specialist species, which had overall differences in composition between regrowth groups but only two and zero species, respectively, associated with any group. The differences in composition were probably due to the differences in richness between the regrowth groups evident in the species richness results and clearing regrowth should not cause the loss of any species.

There may be only a small positive impact of clearance upon generalist species, but the specialists are perhaps more likely than the generalist species to become threatened in the near future due to the decline of hollow oak trees. Only 24 specialist species were sampled, compared to the 215 generalist species. Whilst this may seem like a small number of species compared to the generalist group, if no proactive action is taken to prevent them declining and they ended up on the red-list as a result, that would be a 20% increase of the oak-associated wood-living beetle red-list. It would therefore be highly beneficial to focus on preventing these additional species becoming threatened at the same time as acting to prevent the already-threatened species declining further. Focusing on specialists rather than generalists could also contribute to maintaining ecosystem function, such as nutrient release from dead wood. Many of the sampled specialist species are locally rare. Rare species tend to have least-redundant functional traits, i.e. traits that cannot be replaced by other species (Moullot et al., 2013). Rare species, such as the oak specialists, may therefore be more important for ecosystem functioning than their relatively low species richness may imply.

Clearance of immediate regrowth will benefit oak trees themselves, which are thermophilic and need relatively open, sunny conditions to survive to maturity (Vera, 2000). Clearing will reduce the risk of mechanical damage to the tree from regrowth as well as reduce competition for water, light and nutrients, factors that can trigger oak death (Andersson et al., 2011).

As well as knowing how to manage hollow trees, it is important to be able to target management actions to ensure that limited conservation resources are used as efficiently as possible. Focusing on trees that have the potential to support the greatest number of species may be a good way of targeting action, and the largest trees are clearly the most valuable for red-listed and specialist species. As oaks in forests are generally smaller than oaks in open landscapes and oak circumference can vary between landscapes, there is little sense in defining a circumference at which management is most beneficial. Also, sites that contain only relatively small hollow oaks should not be ignored. The smaller oaks are likely to be younger and will, in time, replace the current largest, oldest oaks. If the smaller oaks are neglected now then it may hamper recruitment as they may not reach the sizes or ages of the current oaks. However, if a manager needs to choose which hollow oaks on his plot of land he/she should focus on, focusing on the largest ones will be the most immediately beneficial for species richness. This will be both reactive and proactive, benefitting both red-listed and specialist species. The oaks in this study occur in groups of at least five. These are high quality habitat patches and have the potential to act as colonization sources for other hollow oak trees. This is likely to be especially true for specialists, as the positive result for big and hollow oaks implies that a higher local habitat density increases

species richness. Their maintenance could therefore be especially valuable for maintaining wood-living beetle species richness beyond the immediate patch. Maintaining small groups of trees, especially in forests, may be preferable to solitary trees if there is a choice between managing solitary or group trees (Ulyshen, 2011).

#### 4.3. Policy implications

The conclusions are not only applicable to Norway. There has been a pattern of increased tree density and a reduction in open woodland habitats across Europe and North America over the last few centuries, as a reduction in grazing, changes in land use and alteration of fire regimes has led to development of closed canopy woodland from formerly open oak woodland and oak wood pasture. This regrowth has benefitted more shade tolerant trees that thrive in closed canopy positions, and caused a decline in shade-intolerant oak trees, and hence oak associated species (Bjorkman and Vellend, 2010; Horak et al., 2014; Koch Widerberg et al., 2012; Vera, 2000). Clearance of regrowth – scrub or trees that shade the trunk or crown of ancient oak trees – is therefore likely to be similarly beneficial in all oak-based habitats for a wider group of animals than wood-living beetles. Clearance of regrowth around oaks could also lead to important secondary benefits which would appeal to policy makers and the public, vital for conservation to succeed (Dudley et al., 2005). The increased light and warmth resulting from the removal of vegetation around the oaks will benefit more taxa than wood-living beetles. Opening the canopy around oak trees would lead to increased light at ground level which would be likely to increase the ground flora (Horak et al., 2014), leading to a greater abundance and diversity of flowering herb species. This increase in available nectar and pollen will in turn benefit pollinating insects, an important group that is currently under threat (Vanbergen et al., 2013). Hole-nesting birds and birds that prey on wood-living insects would be likely to benefit from the increased food resource and altered microclimate within the oak trees. In North America, abundance of 12 oak-associated bird species has been found to be higher in restored oak savannas than in closed canopy forests, with six species also experiencing greater nesting success and productivity in savannas compared to closed canopy forests (Brawn, 2006). The cleared material could be used to increase the amount of dead wood debris in the local surroundings by for example creating log piles, which is known to be extremely beneficial for wood-living species (Ranuis and Fahrig, 2006). The cleared material could also be used as an input for biofuel production (as ‘forest residues’ or ‘energy wood’), providing an economic and climate change benefit (Berger et al., 2013; Hakkila, 2006) as well as biodiversity benefit. Multiple benefits such as these can reduce competition between conservation and other land-uses, increasing the attractiveness of conservation action for policy makers and landowners (Obersteiner et al., 2010). There could also be less-tangible benefits. The increased openness of oak woodlands, and oak stands in open landscapes could have benefits for nature-based tourism. Increased woodland openness leads to increased visibility, useful for recreational hiking. Ancient oak trees have been culturally fascinating for hundreds of years (Lindenmayer et al., 2014; The Norwegian Ministry of the Environment, 2011) and restoring visibility to veteran trees by clearing regrowth around them could contribute to a renewed notice and affection of them.

## 5. Conclusion

In conclusion, we have shown for the first time that vulnerable and irreplaceable wood-living beetles in a biodiversity hotspot for

threatened species can be influenced by a single, easily manipulated factor – regrowth. Regrowth clearance within oak-based hotspots in Europe and North America can therefore be both reactive and proactive, regardless of the broader logic underpinning the hotspot description. Conservation managers can ensure resources are invested effectively by selectively targeting the larger oak trees for management. We suggest that economic, carbon and recreational benefits of clearance could reduce conflicts between conservation and other land uses which will increase the attractiveness of conservation for policy makers. The study shows the importance of examining large-scale conservation planning principles at a local scale to elicit how those principles work when applied on the ground where conservation actually happens. This can best show which conservation actions will be most effective in the battle against extinction.

## Acknowledgements

This study was carried out under the project “Survey and monitoring of red-listed species” (ARKO project, funded by the Norwegian Environment Agency) and used some landscape data courtesy of the project “Management of biodiversity and ecosystem services in spatially structured landscapes” (funded by the Norwegian Research Council, grant 208434/F40). We are grateful to O. Hanssen and F. Ødegaard for species identification, to forest owners for access to their properties and to two anonymous referees for helpful comments about the manuscript.

## References

- Andersson, M., Milberg, P., Bergman, K.-O., 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.
- Antonsson, K., Jansson, N., 2001. Ancient trees and their fauna and flora in the agricultural landscape in the County of Östergötland. In: Tools for preserving biodiversity. NACONEX Textbook 2. Read, H., Forfang, A.S., Marciau, R., Paltto, H., Andersson, L., Tardy, B., (Eds.). Töreboda Tryckeri AB, Sweden.
- AR5 Land Resource Map, <[http://www.skogoglandskap.no/en/subjects/ar5\\_land\\_resource\\_map](http://www.skogoglandskap.no/en/subjects/ar5_land_resource_map)>. Norwegian Forest and Landscape Institute.
- ARKO, 2011. [www.nina.no/Overvaking/ARKO.aspx](http://www.nina.no/Overvaking/ARKO.aspx).
- Barnosky, A.D., Matzke, N., Tomiya, S., Wogan, G.O., Swartz, B., Quental, T.B., Marshall, C., McGuire, J.L., Lindsey, E.L., Maguire, K.C., Mersey, B., Ferrer, E.A., 2011. Has the Earth's sixth mass extinction already arrived? *Nature* 471, 51–57.
- Bates, D., Maechler, M., Bolker, B., Walker, S., 2014. lme4: Linear mixed-effects models using Eigen and S4. R package version 1.1-6. <<http://CRAN.R-project.org/package=lme4>>.
- Berger, A.L., Palik, B., D'Amato, A.W., Fraver, S., Bradford, J.B., Nislow, K., King, D., Brooks, R.T., 2013. Ecological impacts of energy-wood harvests: lessons from whole-tree harvesting and natural disturbance. *J. For.* 111, 139–153.
- Bergman, K.-O., Jansson, N., Claesson, K., Palmer, M.W., Milberg, P., 2012. How much and at what scale? Multiscale analyses as decision support for conservation of saproxylic oak beetles. *For. Ecol. Manage.* 265, 133–141.
- Bjorkman, A.D., Vellend, M., 2010. Defining historical baselines for conservation: ecological changes since European Settlement on Vancouver Island. *Can. Conserv. Biol.* 24, 1559–1568.
- Bouget, C., Larrieu, L., Brin, A., 2014. Key features for saproxylic beetle diversity derived from rapid habitat assessment in temperate forests. *Ecol. Indic.* 36, 656–664.
- Brawn, J.D., 2006. Effects of restoring oak savannas on bird communities and populations. *Conserv. Biol.* 20, 460–469.
- Brooks, T.M., Mittermeier, R.A., Da Fonseca, G.A.B., Gerlach, J., Hoffman, M., Lamoreux, J.F., Mittermeier, C.G., Pilgrim, J.D., Rodrigues, A.S.L., 2006. Global biodiversity conservation priorities. *Science* 313, 58–61.
- Burnham, K.P., Anderson, D.R., 2002. Model Selection and Multimodel Inference: a Practical Information-Theoretic Approach. Springer, New York.
- Buse, J., Levanony, T., Timm, A., Dayan, T., Assmann, T., 2010. Saproxylic beetle assemblages in the Mediterranean region: impact of forest management on richness and structure. *For. Ecol. Manage.* 259, 1376–1384.
- Buse, J., Assmann, T., Friedman, A.-L.-L., Rittner, O., Pavlicek, T.R., Leather, S., Ribera, I., 2013. Wood-inhabiting beetles (Coleoptera) associated with oaks in a global biodiversity hotspot: a case study and checklist for Israel. *Insect Conserv. Diver.* 6, 687–703.
- Dahlberg, A., Stokland, J., 2004. Substrate requirements of wood-inhabiting species – a synthesis and analysis of 3600 species. Skogsstyrelsen, Report 7–04, 75.



- Davies, Z.G., Tyler, C., Stewart, G.B., Pullin, A.S., 2008. Are current management recommendations for saproxylic invertebrates effective? A systematic review. *Biodivers. Conserv.* 17, 209–234.
- De Cáceres, M., 2013. How to use the *indicspecies* package (ver. 1.7.1).
- De Cáceres, M., Legendre, P., 2009. Associations between species and groups of sites: indices and statistical inference. *Ecology* 90, 3566–3574.
- De Cáceres, M., Legendre, P., Moretti, M., 2010. Improving indicator species analysis by combining groups of sites. *Oikos* 119, 1674–1684.
- Drechsler, M., Eppink, F.V., Watzold, F., 2011. Does proactive biodiversity conservation save costs? *Biodivers. Conserv.* 20, 1045–1055.
- Dudley, N., Baldock, D., Nasi, R., Stolton, S., 2005. Measuring biodiversity and sustainable management in forests and agricultural landscapes. *Philos. Trans. R. Soc. Lond. Ser. B: Biol. Sci.* 360, 457–470.
- Engen, S., Sæther, B.E., Sverdrup-Thygeson, A., Grøtan, V., Ødegaard, F., 2008. Assessment of species diversity from species abundance distributions at different localities. *Oikos* 117, 738–748.
- Franc, N., Gotmark, F., Økland, B., Norden, B., Palto, H., 2007. Factors and scales potentially important for saproxylic beetles in temperate mixed oak forest. *Biol. Conserv.* 135, 86–98.
- Gibbons, P., Lindenmayer, D.B., Fischer, J., Manning, A.D., Weinberg, A., Seddon, J., Ryan, P., Barrett, G., 2008. The future of scattered trees in agricultural landscapes. *Cons. Biol.* 22, 1309–1319.
- Grove, S.J., 2002. The influence of forest management history on the integrity of the saproxylic beetle fauna in an Australian lowland tropical rainforest. *Biol. Conserv.* 104, 149–171.
- Grove, S.J., Forster, L., 2011. A decade of change in the saproxylic beetle fauna of eucalypt logs in the Warra long-term log-decay experiment, Tasmania. 1. Description of the fauna and seasonality patterns. *Biodivers. Conserv.* 20, 2149–2165.
- Hakkila, P., 2006. Factors driving the development of forest energy in Finland. *Biomass Bioenergy* 30, 281–288.
- Hjalten, J., Stenbacka, F., Pettersson, R.B., Gibb, H., Johansson, T., Danell, K., Ball, J.P., Hilszczanski, J., 2012. Micro and macro-habitat associations in saproxylic beetles: implications for biodiversity management. *Plos One* 7.
- Horak, J., Vodka, S., Kout, J., Haldá, J.P., Bogusch, P., Pech, P., 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.
- Jansson, N., Bergman, K.O., Jonsell, M., Milberg, P., 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.
- Johansson, V., Bergman, K.-O., Lättman, H., Milberg, P., 2009. Tree and site quality preferences of six epiphytic lichens growing on oaks in southeastern Sweden. *Ann. Bot. Fenn.* 46, 496–506.
- Kålås, J.A., Viken, Å., Henriksen, S., Skjelseth, S. (Eds.), 2010. The 2010 Norwegian Red List for Species. Norwegian Biodiversity Information Centre, Norway.
- Koch Widerberg, M., Ranius, T., Drobyshev, I., Nilsson, U., Lindbladh, M., 2012. Increased openness around retained oaks increases species richness of saproxylic beetles. *Biodivers. Conserv.* 21, 3035–3059.
- Legendre, P., Gallagher, E., 2001. Ecologically meaningful transformations for ordination of species data. *Oecologia* 129, 271–280.
- 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., Stein, J.A.R., 2014. New policies for old trees: averting a global crisis in a keystone ecological structure. *Conserv. Lett.* 7, 61–69.
- Margules, C.R., Pressey, R.L., 2000. Systematic conservation planning. *Nature* 405, 243–253.
- Martikainen, P., Kaila, L., 2004. Sampling saproxylic beetles: lessons from a 10-year monitoring study. *Biol. Conserv.* 120, 171–181.
- 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., Renaud, J., Thuiller, W., 2013. Rare species support vulnerable functions in high-diversity ecosystems. *PLoS Biol.* 11, e1001569.
- Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B., Kent, J., 2000. Biodiversity hotspots for conservation priorities. *Nature*, 853–858.
- Naeem, S., Duffy, J.E., Zavaleta, E., 2012. The functions of biological diversity in an age of extinction. *Science* 336, 1401–1406.
- Nieto, A., Alexander, K.N.A., 2010. European Red List of Saproxylic Beetles. Publications Office of the European Union, Luxembourg.
- Norwegian Environment Agency, 2012. Handlingsplan for utvalgt naturtype hule eiker, p. 80.
- Obersteiner, M., Böttcher, H., Yamagata, Y., 2010. Terrestrial ecosystem management for climate change mitigation. *Curr. Opin. Environ. Sustainability* 2, 271–276.
- Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H., Wagner, H., 2013. *vegan: Community Ecology Package*. R package version 2.0-10. <<http://CRAN.R-project.org/package=vegan>>.
- Paillet, Y., Berges, L., Hjalten, J., Odor, P., Avon, C., Bernhardt-Romermann, M., Bijlsma, R.J., De Bruyn, L., Fuhr, M., Grandin, U., Kanka, R., Lundin, L., Luque, S., Magura, T., Matesanz, S., Meszaros, I., Sebastia, M.T., Schmidt, W., Standovar, T., Tothmeresz, Uotila, A., Valladares, F., Vellak, K., Virtanen, R., 2010. Biodiversity differences between managed and unmanaged forests: meta-analysis of species richness in Europe. *Cons. Biol.* 24, 101–112.
- Parmain, G., Dufrene, M., Brin, A., Bouget, C., 2013. Influence of sampling effort on saproxylic beetle diversity assessment: implications for insect monitoring studies in European temperate forests. *Agric. For. Entomol.* 15, 135–145.
- Ranius, T., 2002. *Osmoderma eremita* as an indicator of species richness of beetles in tree hollows. *Biodivers. Conserv.* 11, 931–941.
- Ranius, T., Fahrig, L., 2006. Targets for maintenance of dead wood for biodiversity conservation based on extinction thresholds. *Scand. J. Forest Res.* 21, 201–208.
- Ranius, T., Hedin, J., 2001. The dispersal rate of a beetle, *Osmoderma eremita*, living in tree hollows. *Oecologia* 126, 363–370.
- Ranius, T., Jansson, N., 2002. A comparison of three methods to survey saproxylic beetles in hollow oaks. *Biodivers. Conserv.* 11, 1759–1771.
- Ranius, T., Niklasson, M., Berg, N., 2009a. Development of tree hollows in pedunculate oak (*Quercus robur*). *For. Ecol. Manage.* 257, 303–310.
- Ranius, T., Svensson, G.P., Berg, N., Niklasson, M., Larsson, M.C., 2009b. The successional change of hollow oaks affects their suitability for an inhabiting beetle, *Osmoderma eremita*. *Ann. Zool. Fenn.* 46, 205–216.
- Ranius, T., Johansson, V., Fahrig, L., 2010. A comparison of patch connectivity measures using data on invertebrates in hollow oaks. *Ecography* 33, 971–978.
- Ranius, T., Johansson, V., Fahrig, L., 2011. Predicting spatial occurrence of beetles and pseudoscorpions in hollow oaks in southeastern Sweden. *Biodivers. Conserv.* 20, 2027–2040.
- Redford, K.H., Coppolillo, P., Sanderson, E.W., Da Fonseca, G.A.B., Dinerstein, E., Groves, C., Mace, G., Maginnis, S., Mittermeier, R.A., Noss, R.F., Olson, D., Robinson, J.G., Vedder, A., Wright, M., 2003. Mapping the conservation landscape. *Conserv. Biol.* 17, 116–131.
- Sebek, P., Barnouin, T., Brin, A., Brustel, H., Dufrene, M., Gosselin, F., Meriguet, B., Micas, L., Noblecourt, T., Rose, O., Velle, L., Bouget, C., 2012. A test for assessment of saproxylic beetle biodiversity using subsets of “monitoring species”. *Ecol. Indic.* 20, 304–315.
- Siitonen, J., 2012. Microhabitats. In: Stokland, J., Siitonen, J., Jonsson, B.G., (Eds.). *Biodiversity in dead wood*. Cambridge University Press, Cambridge, p. 509.
- Skaug, H., Fournier, D., Nielsen, A., Magnusson, A., Bolker, B., 2013. *Generalized Linear Mixed Models using AD Model Builder*. R package version 0.7.7.
- Speight, M.C.D., 1989. Saproxylic Invertebrates and their Conservation. Council of Europe Publication, Strasbourg.
- Stokland, J., Siitonen, J., 2012. Mortality Factors and Decay Succession. In: Stokland, J., Siitonen, J., Jonsson, B.G., (Eds.). *Biodiversity in dead wood*. Cambridge University Press, Cambridge, p. 509.
- Sverdrup-Thygeson, A., 2009. Oaks in Norway: Hotspots for red-listed beetles (Coleoptera). In *Saproxylic Beetles – their role and diversity in European woodland and tree habitats*. In: J. Alexander, K.N.A., Ranius, T., Assmann, T., (Eds.). *Proceedings of the 5th Symposium and Workshop on the Conservation of Saproxylic Beetles*. Buse, Pensoft Publishers, Sofia-Moscow, pp. 13–26.
- Sverdrup-Thygeson, A., Skarpaas, O., Odegaard, F., 2010. Hollow oaks and beetle conservation: the significance of the surroundings. *Biodivers. Conserv.* 19, 837–852.
- The Norwegian Ministry of the Environment, 2011. *Hollow oaks – Noah's oaks*. The Norwegian Ministry of the Environment, <[http://www.regjeringen.no/pages/17018907/Hollow\\_oaks\\_Selected\\_habitat\\_types.pdf#search=hollowoaks&regj\\_oss=1](http://www.regjeringen.no/pages/17018907/Hollow_oaks_Selected_habitat_types.pdf#search=hollowoaks&regj_oss=1)>.
- The Saproxylic Database, 2014. <<http://radon.uio.no/WDD/Login.aspx?ReturnUrl=%2fwd%2fDefault.aspx>>.
- Thompson, W.L. (Ed.), 2004. *Sampling rare or elusive species: concepts, designs and techniques for estimating population parameters*. Island Press, Washington, DC.
- Ulyshen, M.D., 2011. Arthropod vertical stratification in temperate deciduous forests: implications for conservation-oriented management. *For. Ecol. Manage.* 261, 1479–1489.
- Vanbergen, A.J., Baude, M., Biesmeijer, J.C., Britton, N.F., Brown, M.J.F., Brown, M., Bryden, J., Budge, G.E., Bull, J.C., Carvel, C., Challinor, A.J., Connolly, C.N., Evans, D.J., Feil, E.J., Garratt, M.P., Greco, M.K., Heard, M.S., Jansen, V.A.A., Keeling, M.J., Kunis, W.E., Marris, G.C., Memmott, J., Murray, J.T., Nicolson, S.W., Osborne, J.L., Paxton, R.J., Pirk, C.W.W., Polce, C., Potts, S.G., Priest, N.K., Raine, N.E., Roberts, S., Ryabov, E.V., Shafir, S., Shirley, M.D.F., Simpson, S.J., Stevenson, P.C., Stone, G.N., Termansen, M., Wright, G.A., Initiative, Insect Pollinators., 2013. Threats to an ecosystem service: pressures on pollinators. *Front. Ecol. Environ.* 11, 251–259.
- Vera, F.W.M., 2000. *Grazing Ecology and Forest History*. CAB International, Wallingford, UK.
- Vodka, S., Konvicka, M., 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., Lindbladh, M., 2012. Increased openness around retained oaks increases species richness of saproxylic beetles. *Biodivers. Conserv.* 21, 3035–3059.
- Wilson, K.A., Underwood, E.C., Morrison, S.A., Klausmeyer, K.R., Murdoch, W.W., Reynolds, B., Wardell-Johnson, G., Marquet, P.A., Rundel, P.W., McBride, M.F., Pressey, R.L., Bode, M., Hoekstra, J.M., Andelman, S., Looker, M., Rondinini, C., Kareiva, P., Shaw, M.R., Possingham, H.P., 2007. Conserving biodiversity efficiently: what to do, where, and when. *PLoS Biol.* 5, e223.