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Oaks retained in production spruce forests help maintain saproxylic beetle diversity in southern Scandinavian landscapes

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ABSTRACT

In Northern Europe, human activities have caused a substantial decrease in the number of old deciduous trees over the last two centuries, leading to a decline in species populations associated with this habitat. One way to mitigate this trend is to increase the abundance of mature and old deciduous trees in commercial forests, such as by tree retention at final harvest. We analysed the biodiversity value of retained mature oaks in the production forests of Norway spruce in southern Sweden, using oaks in pastures as reference. The forest oaks were grown in two different levels of shade. We analysed two categories of saproxylic (i.e. dead wood-dependent) beetles: those utilizing oaks (Group I) and those utilizing oak but not spruce (Group II, which was, therefore, a subcategory of Group I). We found that forest oaks sustained high beetle diversity, in particular, Group I beetles, which were significantly more abundant in forest oaks in heavily thinned patches, as compared with pasture oaks and oaks in moderately thinned patches. For both beetle groups, the composition differed between the forest oaks and pasture oaks, indicating that the forest oaks can be a complementary habitat to that of pasture oaks. There was a positive relationship between oak dead branch diameter and beetle biodiversity, but only for older oaks (~200 years old). We conclude that retaining oaks in production spruce forests can increase the diversity of oak-associated beetles at the landscape scale. Since many oak associated species depend on relatively high levels of insolation, management of retained oaks in production forests should include periodic removal of encroaching trees.

1. Introduction

In Northern Europe, land use practices have led to a substantial decrease of old deciduous trees since the second half of the 1800s (Östlund and Linderson, 1995; Eliasson and Nilsson, 2002). This trend has resulted in habitat loss and population decline for many insects, birds, and lichens associated with old trees. Species that are dispersal limited have been shown to be particularly vulnerable (Siitonen and Ranius, 2015), despite the recent finding of a rather common long-distance dispersal among deadwood-dependent organisms (Komonen and Müller, 2018). Ecologically important habitats in reserves often represent small islands in a landscape that is heavily dominated by production coniferous forests (Lindenmayer and Franklin, 2002; Bengtsson et al., 2003), and may not fully mitigate the loss of habitats. Conservation measures should, therefore, also include areas within commercial forests to increase the habitat amount and connectivity for species that are dependent on old deciduous trees.

Green tree retention, i.e. leaving trees in production forests at final felling, has become a standard management practice in many boreal and temperate regions (Gustafsson et al., 2012). Green tree retention aims to maintain important structural features, such as large and old trees, and to prevent population isolation by connecting habitat patches (Burkey, 1989, Franklin et al., 1997, Kouki et al., 2001). The positive effects of green tree retention on biodiversity have been shown for epiphytic bryophytes and lichens (Hazell and Gustafsson, 1999), vascular plants (Halpern et al., 2005, Nelson and Halpern, 2005), mammals (Moses and Boutin, 2001, Sullivan et al., 2005), and birds (Merrill et al., 1998, Rodewald and Yahner, 2000, Schieck et al., 2000). Green tree retention has also been shown to benefit insect species, in particular saproxylic beetles, which are beetles that are associated with dead wood (Hyvärinen et al., 2006, Rosenvald and Lõhmus, 2008, Sahlin and Ranius, 2009). This group constitutes a considerable part of the species diversity in temperate and boreal forests (Grove, 2002).

In Northern Europe, oaks (*Quercus robur* and *Q. petraea*) host a high

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amount of insect species (Siitonen and Ranius, 2015). In traditionally managed agricultural landscapes, oaks sustain a large number of saproxylic beetles (Ranius and Jansson, 2000), and are, therefore, if present, often retained in production forests. There are, however, concerns that these commonly dense plantations may be too dark for saproxylic beetles. Since oak is a light demanding species, the same could be expected of the beetle fauna of these trees. This could make oaks in spruce production forests less attractive for beetles associated to oak. The number of beetle species on oaks has been shown to be positively correlated with light levels (Koch Widerberg et al., 2012), sun exposure (Sverdrup-Thygeson and Ims, 2002; Bouget et al., 2014) and temperature (Müller et al., 2015). These patterns suggest that increasing light levels may improve oak capacity to host beetle diversity.

The main aim of the current study was to explore the contribution to biodiversity of retained oaks in Norway spruce (*Picea abies*) plantations in relation to oaks growing in pastures, the latter which is known to host a species rich and specialized beetle fauna (Ranius and Jansson, 2000). We studied trees in mid-age plantations, in contrast to earlier studies on biodiversity associated with green tree retention, which have been done on retained trees relatively soon (≤20 years) after clear-cutting (Gustafsson et al., 2010). We tested two hypotheses:

(I) Pasture and forest oaks host different communities of saproxylic beetles and exhibit different diversity levels of beetle fauna, and
(II) Oak properties, such as tree size, age and the amount of dead wood in the crown, affect the diversity of species associated with oaks.

Along with the testing of these hypotheses, the study provides advice for forest owners and policymakers regarding the justification of tree retention and the management of retained trees in production forests.

2. Materials and methods

2.1. Study area and the sites

We studied oaks in eight locations (Fig. 1A, Table 1) in the hemiboreal vegetation zone of Sweden (Ahti et al., 1968). The mean temperature in the study region ranges between −4 °C and 0 °C in January and between 15 °C and 16 °C in July. There is a large variability in the precipitation between the western part (up to 1200 mm/year) and the eastern part (approximately 500 mm/year) of the study area.

Forests cover 63% of the land area in southern Sweden (Götaland). Commercial forestry dominates in the region, with just approximately 2% of productive forest land (forest area with the annual growth > 1 m^3 ha^{-1}) being formally protected (Table 1.5 in Nilsson and Cory, 2016). Norway spruce is the most common tree species, comprising 47% of the total volume (SFA, 2017). Norway spruce dominated forests are generally managed using rotationally clear cut even-aged stands which are pre-commercially and commercially thinned two to three times during a rotation period, which can vary between 45 and 70 years. All locations in this study, except for the Tönnersjö, were situated in a region with a high number of beetle species associated with old oaks (Niklasson and Nilsson, 2005). In the 1800s, oaks were common in the study region (Lindbladh and Foster, 2010). However, today oak represents only around 3% of the total timber volume in Southern Sweden.

The studied forest stands have been pastures until the middle of the 20th century. Each stand contained a number of retained mature oaks shaded to a varying degree by the surrounding spruce trees. The latter represented at least 90% of the total stand basal area. The age of the spruce stands ranged from about 40 to 70 years, and was on average about 50 years (Table 1). On six of the eight stands, the spruces were planted, and on two sites they were naturally regenerated following the abandonment of the pastures (sites Strömsrum and Tönnersjö, Fig. 1A). All stands had been subjected to pre-commercial and all but two – to commercial thinning.

We sampled six mature oaks from each location, with four oaks located in the spruce stand and two oaks in nearby pastures. Within each location, we selected oaks to be as similar as possible (except for light levels, see below) in respect to DBH (diameter at breast height), height, tree vitality, and the amount of dead wood in the tree crown. To reduce the correlation in species composition among oaks growing close to each other, we selected only trees with crowns that were isolated by at least three rows of spruce, which corresponded to about 30 m. Most of the forest oaks, however, were located at least 50 m from each other. The pasture oaks were in open conditions, with no or only little shade from neighbouring trees. The distance between the spruce stands and the pasture oaks did not exceed 500–700 m and, in some cases, the pasture and forest oaks were part of the same pasture prior to the spruce establishment.

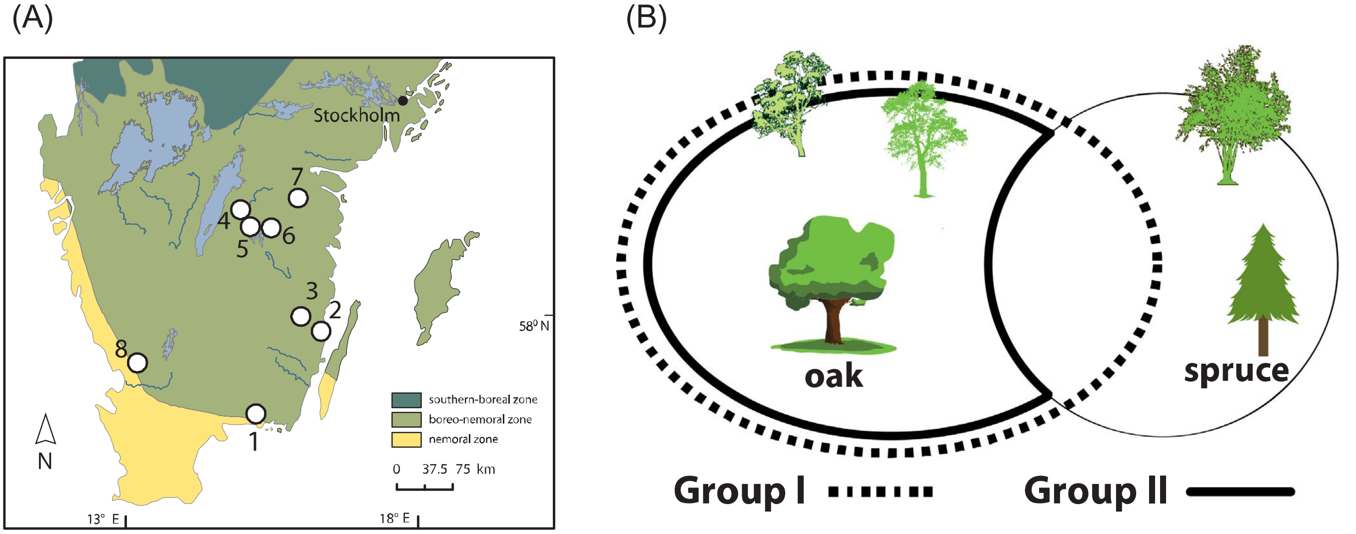

Fig. 1. Location of the eight study sites (A) and definition of beetle groups (B). Numerical location IDs correspond to those in Table 1. Group I represents all species associated with oak, and Group II represents all species associated to oak, except those also associated with spruce. By symbolically showing other trees on Figure B we indicate that both oak- and spruce-associated beetles may have used other tree species, which are present in Southern Sweden (but was largely absent in the studied landscapes).

Table 1
Stand and tree data from the studied locations, *n* is the total number of oaks in the forest stand, *Age* is the mean age of the sampled oaks in each location (forest oaks/pasture oaks) determined through dendrochronological dating. The spruce data were obtained from the estates' forestry plans.

Location	Stand data			Oak data		Spruce data		
	Coordinates	Size (ha)	*n*	Age	SD of age	Age	Basal area, ($m^2\,ha^{-1}$)	Year of thinning
(1) Johannishus	56.24 N 15.52 E	1.6	11	149/95	40/2	43–45	184	1997
(2) Strömsrum	56.93 N 16.46 E	4.3	18	194/234	19/12	Varying	113	None
(3) Hornsö	57.02 N 16.23 E	0.8	20	110/120	5/21	70	141	1999
(4) Boxholm	58.19 N 15.13 E	1.4	11	150/127	12/33	53	102	1997
(5) Sandvik	58.12 N 15.17 E	1.6	18	123/83	13/40	48	124	2002
(6) Malexander	58.07 N 15.36 E	0.7	12	141/100	31/21	50	133	1999
(7) Adelsnäs	58.14 N 15.95 E	0.4	8	146/76	13/47	47	173	2000
(8) Tönnersjö	56.70 N 13.14 E	0.4	8	168/165	56/20	Varying	111	None

2.2. Sampling of saproxylic beetles

We collected beetles from the 48 oaks in the eight locations (six oaks per location) from mid-May to early September in 2008, using window traps. The traps consisted of a plexiglass window (40×60 cm^2) attached to a funnel with a bottle of propylene glycol (approx. 60%) and a few drops of detergent. The traps were mounted close to the trunk on the southern side of the tree, at a height of approximately 5 m (i.e. at the same height as the majority of dead branches). To reduce disturbing solar reflections, the window was fixed with wires so that the edge of the glass pointed south. The traps were emptied once a month and the beetles were stored in 60% ethanol solution. All saproxylic beetles (*Coleoptera*) were identified to the species level by taxonomist Rickard Andersson, Höör, Sweden.

We assessed the beetles' association to oak and spruce on the basis of their ability to use the wood of these tree species for at least some part of their life-cycle (Palm, 1959; Dahlberg and Stokland, 2004). We classified the beetles into two groups: (a) all beetles using oaks during at least part of their life-cycle (Group I, Fig. 1B), and (b) all beetles using oaks during at least part of their life-cycle except those using spruce (Group II). Group II was, therefore, a subset of Group I. The proposed division reflects a management-oriented perspective which considers the presence (abundance and diversity) of each group as a proxy for the overall efficiency of conservation management. Group I species had a documented association with oak while with Group II species had narrower niche requirements, i.e. utilizing oak but not spruce. Our insect traps, even if attached to oak trees, might also have caught beetles attracted to spruce trees, i.e. the trees dominating in the stands. The group definitions that were used filtered out this group of beetles, which was of minor interest and, therefore, fell outside the scope of our study. Both beetle groups included species which could use other trees. Thus, our classification into Group I and II beetles reflected their relationship to oak and spruce only.

2.3. Sampling of environmental variables

We classified the oaks in each location into three categories: pasture oaks (factor level *Pasture*), forest oaks growing under increased light in patches where the spruces had been heavily pre-commercially or commercially thinned (factor level *Light*) and forest oaks growing under reduced light in moderately thinned patches (factor level *Dark*). Around the *Dark* oaks, all spruces within the crown radius of the focal oaks had been removed. Around the *Light* oaks, spruces within 1.5 times the radius of the focal oak crown had been removed. To objectively assess the light levels around oak trees and to ensure that oak selection in the field actually resulted in two tree groups with contrasting light environments, we used an angular Shade Index (SIa), calculated for each forest oak (Widerberg, 2013). The index was calculated from the density, height, and position of the surrounding spruce trees in relation to the insolation angle. Two oak groups (*Light* and *Dark* oaks) were well-discriminated by SIa values (Supplementary Information Fig. 1).

Oak DBH (variable *DBH*), oak age (var. *Oak age*), the maximum dead branch diameter (var. *DBD*), and the percentage of dead crown (var. *Dead crown*) were measured for each oak. *Dead crown* was visually estimated as the percentage volume of dead branches in relation to the total branch volume. *Oak age* was determined by dendrochronological dating using standard methods (Stokes and Smiley, 1968). We collected up to three increment cores per tree, depending on the degree of wood rot.

2.4. Statistical analyses

To analyse the difference in the beetle composition and associated diversity levels among the three types of habitats (hypothesis I), we used three approaches. First, we compared the species composition of Group I and Group II among the three oak categories in a multiple response permutation procedure (MRPP), using function *mrpp* in the R package *vegan* (Oksanen et al., 2016). MRPP is a non-parametric test of differences between two or more groups, based on a comparison of the observed within-group homogeneity in species composition to the one expected by chance (Mielke and Berry, 2001). Pair-wise comparisons of beetle species composition between the three oak categories were based on the Sørensen index (Sørensen, 1948). Second, we used ANOVA on abundances (i.e. numbers of individuals captured) of both groups as the dependent variable to evaluate differences among the three oak categories. Third, we ran ANOVA on species numbers, Shannon and Gini-Simpson indices as the dependent variables to provide an assessment of diversity patterns. The Shannon index (H′, Shannon, 1948) positively correlates with the number of species and their evenness within a sample:

$$H' = -\sum_{i=1}^{R} p_i \ln(p_i)$$

where p_i is the proportion of ith species in the total number of individuals in the sample.

The Gini-Simpson index is the inverse version of the original Simpson diversity index (Jost, 2007). It increases with higher diversity which is, similar to the Shannon index, proportion-based but gives more weight to more abundant species:

$$SG = 1 - \sum_{i=1}^{R} p_i^2$$

Prior to the analyses, we transferred values of both indices into effective species numbers, so-called Hill numbers, to address the highly non-linear relationship between their values, on one side, and the species numbers and abundances, on the other (Hill, 1973; Jost, 2007). The function *Diversity* of the R package *vegan* (Oksanen et al., 2013) was used for this purpose.

To analyse abundance and the number of species for Group I and Group II beetles in relation to the oak tree category, we fitted generalized linear mixed models in the package *glmmADMB* (Fournier et al., 2012), using a negative binominal distribution. The choice of this distribution was justified by the fact that the model deviance considerably (×3–4 times) exceeded model's degrees of freedom, indicating over-dispersion, which precluded the use of the Poisson distribution (NOE et al., 2010). For analyses of diversity indices, we used generalized linear mixed-effects models realized in the function *glmer* from R package *lmer4* (Pinheiro et al., 2014; Bates et al., 2015), assuming the Poisson distribution of the response variable. The choice of the model implementation in both cases allowed us to test nested random effects, while permitting for the correlation of within group errors. Independent factors in both groups of analyses were *DBH*, *Oak age, Dead branch diameter*, *Dead crown* and *Oak Category* (factor levels *Pasture*, *Light*, or *Dark*). Site location was a random effect in the models. Continuous independent variables (factors) were normalized (i.e. transformed to zero mean and the variance of one) prior to analyses and the maximum log-likelihood (ML) was used to fit the model parameters. Finally, we relied on the AIC score (Akaike, 1974) to select the most parsimonious model from the initial pool of candidate models, including all 2-level interactive and non-interactive effects in R package *AICcmodavg* (Mazerolle, 2006).

We analysed the relationships between diversity metrics and habitat properties (hypothesis II) within the framework of the same mixed effect models employed to test hypothesis I, benefiting from the fact that both oak type and oak tree properties were simultaneously included as factors in the set of models used to identify the model with the lowest AIC score.

To evaluate the differences in the amount of crown deadwood among oaks in different habitats, we used pair-wise comparisons based on the least square means. We used the same model structure and set of independent variables as in the analyses of species abundance and diversity indices and applied similar AIC-based protocol to identify the most parsimonious model.

3. Results

We sampled a total of 1173 individuals, belonging to 168 species of saproxylic beetles (Supplementary Information Table 1). In total, 97 species (891 individuals) were associated with oak (Group I beetles) and 59 (510) were associated with oak but not with spruce (Group II beetles) (Table 2). Four species (five individuals) were red-listed and belonged to the NT category (Near Threatened), according to the Swedish red-list (Swedish Species Information Centre, 2015). Of these, two species were found on *Pasture* oaks, two species on *Light* oaks, and no species on *Dark* oaks (Supplementary Information Table 1). MRPP analyses revealed that, for both groups of beetles, there was a tendency of the *Pasture* oaks to exhibit different species composition as compared to the other two groups (Table 3). For Group II species, the statistical significance of the differences was generally higher than for Group I species (Table 3).

Table 3
MRPP pair-wise comparison of species composition between oak categories. Results are shown for Group I (all beetles associated to oak) and Group II (all beetles associated to oak, but not to spruce), and three oak categories (Light, Dark, and Pasture). *delta* refers to the overall weighted mean of group mean distance. For each analysis the theoretically expected value of delta is given after slash sign. The method used here operates with Sørensen distances. The overall weighted mean is based on within-group pair-wise distances, with the group mean weighted by number of observations per group. Number of permutation was 1000.

Oak categories	Group I		Group II	
	delta	*p*	delta	*p*
Dark (1) vs. Light (2)	9.80 (1) vs. 12.2 (2)/10.95	0.687	7.98 (1) vs. 9.25 (2)/8.51	0.893
Light (2) vs. Pasture (3)	12.2 (2) vs. 10.3 (3)/11.46	0.039	9.25 (2) vs. 7.77 (3)/8.73	0.011
Dark (1) vs. Pasture (3)	9.80 (1) vs. 10.3 (3)/10.14	0.095	7.98 (1) vs. 7.77 (3)/8.06	0.028

The abundance of Group I beetles was significantly higher on *Light* oaks, as compared to the other two habitat types, whereas Group II abundance revealed a tendency to increase with the increasing *Dead branch diameter* (Table 4).

Relationships between beetle diversity indices and oak metrics were similar for both species groups (Table 4, Fig. 2). In the vast majority of analyses, the most parsimonious model included the interaction between *Dead branch diameter* (DBD) and *Oak age*. In particular, a positive correlation between *Dead branch diameter* and diversity metrics was absent in younger oaks, but was strong in trees around 200 years old (Fig. 2), the latter representing the upper 10% of the total tree age distribution in our dataset. Although these variables were strongly correlated (r = 0.58), the model including both variables and their interactions was, nevertheless, superior over models with alternative formulations (Supplementary Information Table 2). In many analyses, the most parsimonious model included *Dead branch diameter* as an independent variable (not in interaction) with a positive effect at significance levels of 0.06–0.10 (Table 4).

Dead wood was abundant on the forest oaks (Table 5) and *Dead Crown* was significantly related to the oak category (Table 4, Fig. 3). We observed a significantly higher percentage of dead crown on both *Light* oaks ($p = 0.004$) and *Dark* oaks ($p < 0.001$), as compared to *Pasture* oaks (Fig. 3). There was, however, no significant difference between *Light* and *Dark* oaks ($p = 0.122$). We noted that oak age was not included in the most parsimonious model.

Table 2
Total number of sampled beetle species/average Shannon's diversity index/average Gini-Simpson index for each location, oak category (*Dark*, *Light*, and *Pasture*), and beetle group. Group I refers to all beetles associated to oak, and Group II refers to all beetles associated to oak, but not to spruce.

Location	*Dark*		*Light*		*Pasture*	
	Group I	Group II	Group I	Group II	Group I	Group II
Johannishus	20/2.37/0.283	12/1.62/0.456	30/3.12/0.187	16/2.45/0.123	23/2.63/0.221	19/2.43/0.239
Strömsrum	19/2.94/0.112	13/2.39/0.164	16/2.43/0.221	11/1.85/0.333	25/3.44/0.054	20/3.12/0.050
Hornsö	15/2.64/0.130	8/1.83/0.192	34/3.08/0.129	10/2.03/0.205	17/2.39/0.279	11/2.12/0.138
Boxholm	12/2.33/0.120	5/1.13/0.367	16/2.54/0.165	7/1.24/0.389	13/2.39/0.104	6/1.46/0.050
Sandvik	15/2.61/0.138	10/2.03/0.195	19/2.94/0.086	9/1.99/0.183	14/2.39/0.193	8/1.95/0.000
Malexander	11/2.21/0.190	6/1.28/0.381	21/3.15/0.093	8/1.82/0.246	10/2.24/0.081	4/0.75/0.583
Adelsnäs	19/2.64/0.194	9/1.55/0.412	19/2.83/0.147	8/1.38/0.448	19/2.79/0.101	9/1.67/0.110
Tönnersjö	7/2.50/0.071	5/1.91/0.133	19/2.96/0.084	7/1.47/0.339	6/1.16/0.133	2/0.46/0.417
Mean ± SD:						
Species numbers	14.8 ± 4.56	8.5 ± 3.07	20.5 ± 4.62	9.5 ± 2.98	15.86 ± 6.42	9.88 ± 6.58
Shannon index	2.51 ± 0.23	1.71 ± 0.41	2.88 ± 0.27	1.78 ± 0.40	2.43 ± 0.64	1.74 ± 0.87
Simpson-Gini index	0.155 ± 0.066	0.287 ± 0.128	0.139 ± 0.050	0.283 ± 0.111	0.146 ± 0.077	0.198 ± 0.204

Table 4
Influence of tree-level variables on beetle diversity and the amount of dead crown, as revealed by mixed-effect model analyses. Results are shown for Group I (all beetles associated to oak) and Group II (all beetles associated to oak, but not to spruce). *DBD* is the maximum dead branch diameter; *DBH* is the oak diameter at breast height. R^2 refers to the marginal R^2 in the sense of Nakagawa and Schielzeth (2013).

Analysis	Parameter	SE	z/t-value	p-value
Abundance, Group I				
R^2 = 0.155				
Intercept	1.739	0.193	9.02	< 0.001
Light Forest Oaks	0.618	0.195	3.16	0.002
Dark Forest Oaks	0.111	0.210	0.53	0.596
Species number, Group I				
R^2 = 0.279				
Intercept	1.923	0.116	16.55	< 0.001
DBD	0.166	0.078	2.13	0.033
Age	−0.020	0.072	−0.27	0.786
Light Forest Oaks	0.280	0.130	2.16	0.031
Dark Forest Oaks	−0.064	0.149	−0.43	0.669
DBD × Oak age	0.199	0.057	3.52	< 0.001
Shannon index, Group I				
R^2 = 0.209				
Intercept	11.0	0.936	11.81	< 0.001
DBD	1.93	1.04	1.86	0.071
Oak age	0.420	1.00	0.42	0.678
DBD × Oak age	2.23	0.821	2.72	0.010
Gini-Simpson index, Group I				
R^2 = 0.084				
Intercept	6.45	1.02	6.31	< 0.001
Oak age	0.918	0.804	1.14	0.260
Abundance, Group II				
R^2 = 0.072				
Intercept	2.292	0.174	13.17	< 0.001
DBD	0.179	0.103	1.74	0.082
Species number, Group II				
R^2 = 0.206				
Intercept	1.352	0.130	10.41	< 0.001
DBD	0.186	0.099	1.88	0.060
DBD * Oak age	0.211	0.066	3.21	0.001
Species number, Group II				
R^2 = 0.205				
Intercept	1.35	0.130	10.44	< 0.001
DBD	0.185	$9.81 * 10^{-2}$	1.89	0.058
Oak age	0.039	$9.77 * 10^{-2}$	0.40	0.689
DBD × Oak age	0.211	$6.50 * 10^{-2}$	3.24	0.001
Shannon index, Group II				
R^2 = 0.429				
Intercept	5.03	0.902	5.58	< 0.001
DBD	1.19	0.711	1.67	0.103
Oak age	1.02	0.768	1.33	0.1925
DBD × Oak age	2.85	0.562	5.08	< 0.001
Gini-Simpson index, Group II				
R^2 = 0.034				
Intercept	5.03	0.902	5.58	< 0.001
DBD	1.19	0.711	1.67	0.103
Oak age	1.02	0.768	1.33	0.193
DBD × Oak age	2.85	0.562	5.08	< 0.001
Dead Crown				
R^2 = 0.229				
Intercept	1.03	0.338	3.05	0.005
Oak category	−0.516	0.145	−3.56	0.006
DBH	0.223	0.134	1.67	0.130

4. Discussion

4.1. Patterns of beetle species diversity and composition

Green tree retention following clear-cutting has only been applied in commercial forests of Scandinavia for about two decades (Gustafsson et al., 2010). Therefore, our knowledge of the long-term effects of retained trees on forest biodiversity is limited. Our study on oaks in mid-aged production stands may be seen as a "glimpse into the future", when retained trees will be a more common feature of mid-aged or older production forests.

We show that retained oaks in spruce production forests harbour a saproxylic beetle fauna as rich as that on pasture oaks, as indicated by the lack of significant effects of oak group identity on beetle diversity metrics in all analyses, except the one with species numbers for Group I beetles (Table 4). The rich fauna on the *Light oaks* is a surprising result, considering the high biodiversity value that has been associated predominantly with sun-exposed pasture oaks (Nilsson et al., 2006). It is possible that the high number of Group I beetles and their abundance (of which 39% also utilize spruce wood) in a forest habitat was driven by the spruce trees that attracted an additional number of beetle individuals that were absent on the oaks in the open pastures. The difference displayed by Group I could also be due to the specific microclimate on and around *Light* oaks in spruce forests, which might be favourable to beetles associated with both oak and spruce. A study comparing species richness and composition between old oaks in natural mixed forests and in parks, the latter being in similar conditions as the pasture oaks in our study, has shown a higher species richness and a different species composition on forest oaks (Sverdrup-Thygeson et al., 2010). The authors explained their result by the more diverse forest environment, due to a larger variation in both tree species composition and microclimate, as compared to the more homogeneous park environment.

Forest oaks in our study had a larger volume of crown dead wood as compared to pasture oaks (Tables 4 and 5). The diversity of Group II beetles was positively and consistently correlated with the amount of maximum dead branch diameter, which appears as the main determinant of high species diversity in the forest oaks. Local abundance of dead oak wood has been found to be an important determinant of local species diversity in saproxylic oak beetles (Pilskog et al., 2016). The high level of dead wood on the forest oaks might be a result of the tree's response to the onset of darker conditions following the spruce forest development. The high volumes of dead wood and associated beetle diversity might, however, be a short-lived pattern, which will progressively disappear as a result of continuing darkening of the forest conditions.

Regarding species composition, both beetle groups revealed differences between *Pasture* and *Light* forest oaks (Table 3). This pattern implies that at least one group of forest oaks hosted compositionally different beetle fauna as compared to *Pasture* oaks. The finding highlights the role of forest oaks as a complementary habitat and thus assisting in maintaining beetle populations. For oak beetle species not using spruce (Group II), the obtained pattern suggests that a change from oaks in pastures to a forest setting does not imply a negative impact on species diversity. We did not observe differences in the number of species nor in the Shannon index for this species group among habitats. However, the high species richness in forest oaks may decrease as they may eventually experience progressively darker conditions.

The beetle biodiversity was affected by an interaction between maximum dead branch diameter and oak age, with a positive relationship between branch diameter and beetle diversity observed only in older oaks (Fig. 2). The result suggested that it is only in old trees (around 200 years old) that dead and large branches constitute an important beetle habitat. We speculate that the effect is due to an increase in the probability of hollow formation with age. Statistically, the result was a likely product of the increased variability of deadwood amounts with an increase in oak age (SI Fig. 2). The pattern is consistent with earlier studies suggesting that certain structures of importance for the saproxylic fauna (such as tree hollows, Ranius et al., 2009) develop while trees age. A positive effect of dead branch diameter is consistent with earlier observations of a higher species richness in dead wood with a larger diameter (Grove, 2002).

A feature of the studied landscapes which might have affected the

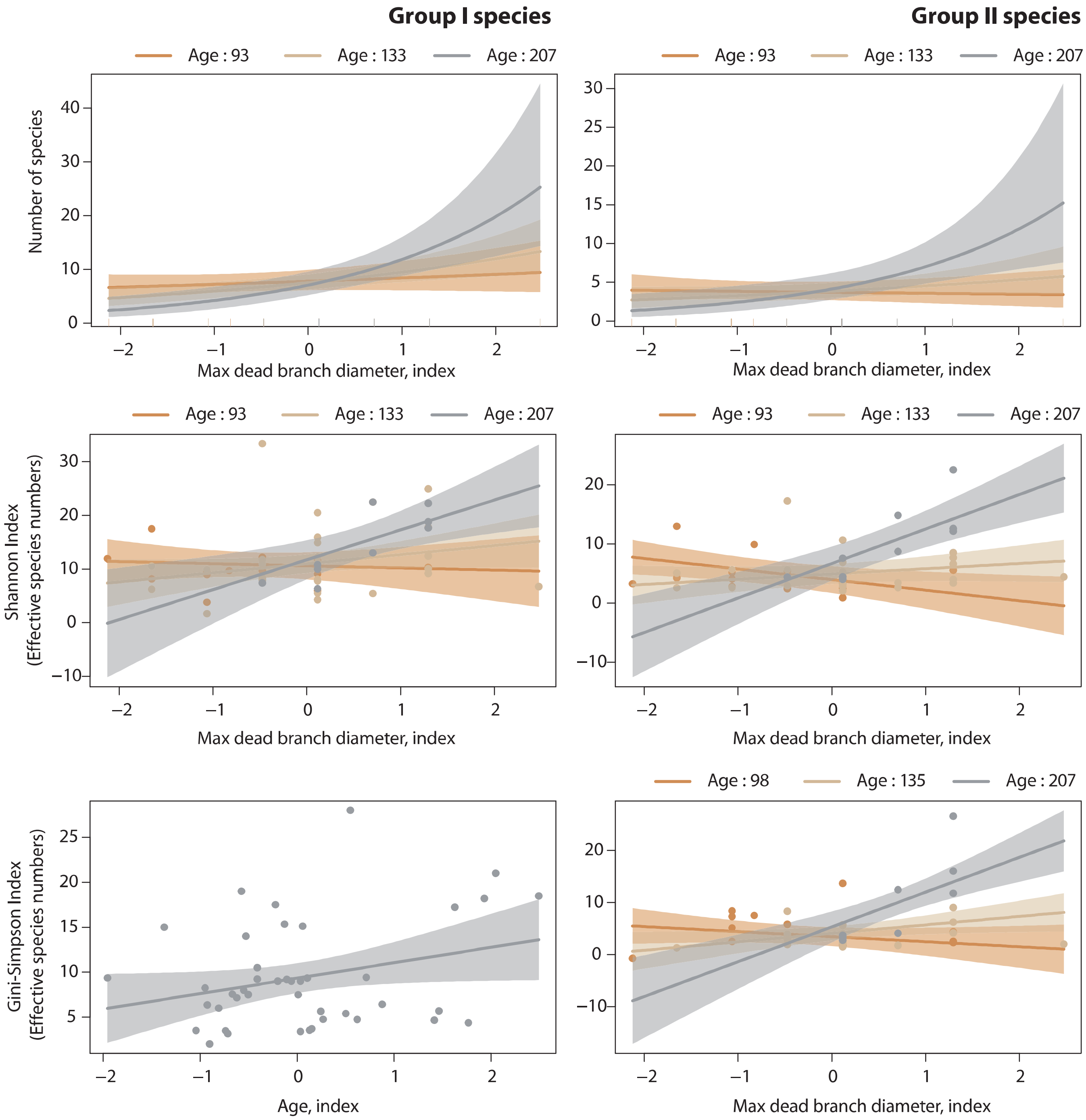

Fig. 2. Relationship between species diversity and habitat properties for Group I and II beetles. To demonstrate interactions between tree age and branch diameter, the age of trees was fixed at 10th, 50th, and 90th quantiles of the respective distributions and the resulting relationships between branch diameter and the response variable are shown by different colours. Confidence limits (0.95) are shown as shaded areas. The variables shown are those with a statistical significant effect on respective predictand, as revealed by mixed effect models (Table 4).

beetle diversity was the abundance of the oaks, both within each habitat type (forest and pasture) and within landscapes as a whole (Franc et al., 2007). We realize that even ensuring a certain minimum distance between studied trees we might not completely remove the effects of spatial autocorrelation among trees, driven by oak abundance. Although we did not evaluate the relative role of landscape-level oak density in this study, a consistent and positive effect of the maximum dead branch diameter, a tree-level factor, gives us confidence that there is potential to optimize conservation treatments operating at the scale of single stands and trees.

4.2. Management and conservation implications

Oaks retained in commercial spruce forests provide an important habitat for saproxylic beetles. The potential conservation value of tree retention is likely higher for oak than for other tree species (Müller and Gossner, 2007, Sverdrup-Thygeson et al., 2010). Retaining such trees can increase the diversity of oak associated beetles at the landscape scale and should be integrated into management plans for commercial forests. Biodiversity-oriented management can also include oaks naturally regenerated after final harvest as future retention trees.

The higher abundance of Group I beetles on *Light* (i.e. heavily

Table 5
Means of the estimated percentage of dead crown volume, calculated per oak category in each studied location.

Location	Dead crown (%)		
	Dark	Light	Pasture
Johannishus	60	50	5
Strömsrum	25	13	10
Hornsö	13	8	5
Boxholm	20	18	11
Sandvik	30	25	2
Malexander	20	50	2
Adelsnäs	20	15	3
Tönnersjö	8	4	9
Mean	25	23	6

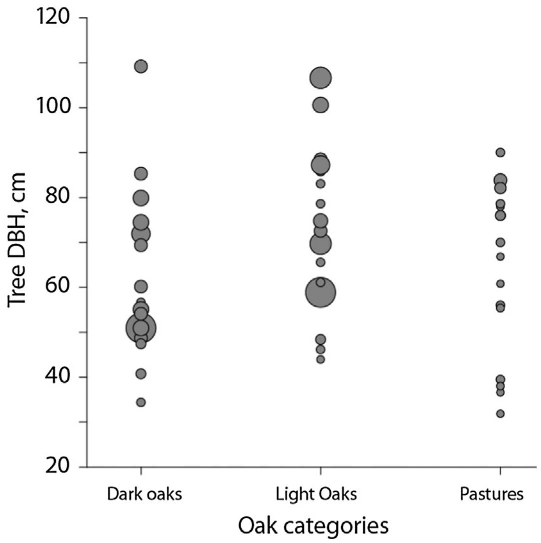

Fig. 3. Relationship between dead wood abundance in oak crown, oak category and tree DBH. The size of the circle represents the amount of dead wood for each tree sampled. Statistical details of analyses are given in Table 4.

thinned) oaks suggests that neighbouring production trees should be kept at some distance to maximize the value of forest oaks as beetle habitat for these species. Increasing the amount of light around forest oaks may also help oaks reach a higher age (Drobyshev et al., 2008), further enhancing their value for biodiversity. We argue that it is better to let the conservation values of oaks develop with the ageing of trees that survive for a long time, rather than by maximizing the amount of dead wood at a single point of time. Due to the positive correlation between maximum branch diameter of oak deadwood in the crown and beetle abundance and diversity proxies, we propose the use of in-crown deadwood inventory for fast indirect assessments of the conservation value of forest stands. Finally, our study highlights the need for more research on the saproxylic beetle fauna and other species groups potentially benefiting from retained trees in commercial plantations to better quantify the value of retained tree properties in hosting beetle diversity.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2018.02.048.

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