

## Near-natural forests harbor richer saproxylic beetle communities than those in intensively managed forests

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### ARTICLE INFO

#### Keywords:

Biodiversity  
Clear-cuts  
Coleoptera  
CWD  
Forest management  
Indicator species  
Landscape scale  
Near-natural forests  
Redundancy analysis (RDA)  
Saproxylic  
Window traps

### ABSTRACT

Globally, boreal forests cover 33 percent of Earth's forested area, constitute the largest terrestrial carbon source, and house an important biodiversity of forest-dependent species, many of which are saproxylic taxa reliant on a wide variety of dead wood. This dead wood is most prevalent in old-growth forest, yet intensive management means that little old growth is left, and the remaining forests rarely attain the necessary age and structure to resemble these original forests. There is increasing recognition, however, that forests that have not been subjected to modern, stand-replacing harvest methods (like clear-cutting), and in which management activities are no longer occurring, may be able to provide habitat similar to old-growth forest for many species (older mean age, higher deadwood volumes, and more age-class heterogeneity). These are called 'near-natural' forests.

We use linear mixed models and redundancy analysis (RDA) to compare beetle species richness and community composition using a large, mixed data set, containing more than one third of all beetle species known from Norway, from window trap records in three types of forest: intensively managed mature stands, recent clear-cuts, and 'near-natural forests'.

Even though location, study substrate and other sampling details vary substantially between sites, the signal from management still comes out as a significant factor explaining the patterns on beetle diversity. We find that species richness of saproxylic, natural-forest indicator, and red-listed beetle species is higher in both near-natural forests and recent clear-cuts than in managed mature forests. Community composition also differs significantly between the three forest types, and these differences are correlated with forest age and volume at the landscape (1 km radius) level.

These findings provide support for the idea that near-natural forests provide habitats that are distinct from those in managed forests and which are important for species of conservation concern. Clear-cuts briefly harbor some of these same species, probably due to the sun-exposed coarse woody debris (CWD) that is available immediately after felling, but this effect is transient. Conservation of existing near-natural forests, many of which are currently without legal protection, should therefore be prioritized.

### 1. Introduction

Boreal forest covers approximately 809 million hectares in Europe and Central Asia, mostly located in Fennoscandia and Russia (Fischer et al., 2018). Globally, boreal forest provide important ecosystem services, storing more carbon than any other terrestrial ecosystem (Bradshaw and Warkentin, 2015), including much carbon tied up in soil, litter and dead wood (Pan et al., 2011) and providing habitat for many forest-dependent species. A large proportion of these forest-dependent species are saproxylic species dependent on dead wood

(Stokland et al., 2012).

While European forests in general have been heavily influenced by deforestation and fragmentation (Fischer et al., 2018), boreal forests still cover vast areas. However, boreal forests have long been subject to timber extraction, in many areas with increasing intensity. Timber extraction will necessarily change the characteristics of the forest such as volume of living trees and dead wood, and leads to a shift in forest age structure and tree species composition (Martikainen et al., 2000; Penttilä et al., 2004). This results in plant and animal communities that differ from those of unmanaged, old-growth forests. Clear-cutting in

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<https://doi.org/10.1016/j.foreco.2020.118124>

Received 30 January 2020; Received in revised form 24 March 2020; Accepted 26 March 2020

Available online 06 April 2020

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particular drastically changes abiotic conditions and removes most structural elements from the stand.

In a meta-analysis of 49 papers testing the difference in biodiversity between managed and unmanaged forests, Paillet et al. (2010; but see Halme et al., 2010) found that forest management decreased species richness by 6.8% on average in comparison with unmanaged forests. However, the response to forest management differed between taxonomic groups. Beetles dependent on dead wood (saproxylic beetles), carabid beetles, fungi, lichens and (marginally) bryophytes had significantly higher species richness in unmanaged forests (Paillet et al., 2010). Clear-cut stands therefore host beetle species assemblages that differ significantly from those of closed-canopy forests, and mature forests regenerating from clear-cuts, especially when subject to thinning treatments, tend to deviate further from the species assemblages of old-growth forests than do mature forests subject to selective felling (Hjältén et al., 2012; Kraut et al., 2016; Joëlsson et al., 2018). Landscape-scale forest characteristics, in addition to management practices at the stand level, are also important for understanding beetle diversity (Gibb et al., 2006; Jacobsen et al., 2015; Pilskog et al., 2016), and these also depend on forest management practices.

When timber extraction ceases or is reduced in intensity, forests will over time develop old-growth characteristics such as heterogeneity in forest structure (e.g. multi-layered canopies and variation in tree dimensions), high volume and variety of dead wood, and higher average tree age. Therefore, the difference in species richness between actively managed forests and presently unmanaged forests generally increases with time since management was abandoned (Paillet et al., 2010). Forests with several old-growth characteristics, but which are not true old-growth or virgin forest, are often called ‘near-natural forests’ as natural dynamics begin to lessen the influence of past timber extraction. If allowed to progress without intervention, such near-natural forests might over time become as valuable for species conservation as old-growth forests (Ohlson et al., 1997; Stenbacka et al., 2010). In Norway several such forested areas, which have only been subject to some level of selective felling in the past but never stand-replacing harvesting, are now developing structural characteristics similar to those of old-growth forests (Storaunet et al., 2005). However, these near-natural forests are often poorly covered by forest protection measures (Sverdrup-Thygeson et al., 2014b), and risk clear-cutting, especially with current ambitions of a 50 percent increase in harvesting levels (Meld. St. 9, 2011–2012). To make informed management choices, it is necessary to know the extent to which these near-natural forests harbor higher species richness or different species assemblages than managed forests, and how this varies in different landscapes.

In the present paper, we compare the richness and composition of beetle assemblages in Norwegian boreal forests between near-natural forests that have never been clear-cut, recent clear-cuts, and forest stands that have regrown from past stand-replacing harvesting. We do this using the largest community dataset that has been employed to answer these questions – comprising 1267 species (35% of all Norwegian beetles) – and which covers a large spatial extent and includes landscape scale covariates. Our aim is to investigate whether the contrast between forest types is strong enough to explain patterns in beetle diversity for such a large group of species across southeastern Norway when landscape as well as stand-level covariates are included.

Specifically, we ask: a) whether there are significant differences in species richness and beetle assemblage composition among forest types, b) whether species richness is also correlated to differences in landscape-scale forest covariates, and c) whether these effects vary among saproxylic, red-listed, and natural-forest indicator species.

## 2. Methods

### 2.1. Sampling

Datasets from five different beetle-sampling projects (Sverdrup-Thygeson and Ims, 2002; Fossetøl and Sverdrup-Thygeson, 2009;

Birkemoe and Sverdrup-Thygeson, 2015; Sverdrup-Thygeson et al., 2017; Vindstad et al., 2020) were combined in the current study for a total of 407 sites in Norway, where beetles had been sampled with window traps (i.e. flight interception traps). One window trap was placed at each site, and each site was sampled in a single year (1997, 1998, 2001, 2004 or 2007). The sampling took place from May to August. Sites were located in nine different regions in southern Norway (Fig. 1), with the majority in Akershus (185).

Traps were all placed in boreal forest sites but were mounted on a variety of substrates: hollow, old oaks (52 sites), natural or artificially created aspen snags (193 sites), birch snags (15 sites), standing or downed dead spruces or spruce snags (117 sites), or freely without adjacent substrate (30 sites). Most sites were located in mixed coniferous and deciduous forest (285), but 104 sites were located in coniferous forest and 18 in deciduous-dominated forest. Trap substrates were roughly comparable between forest management categories.

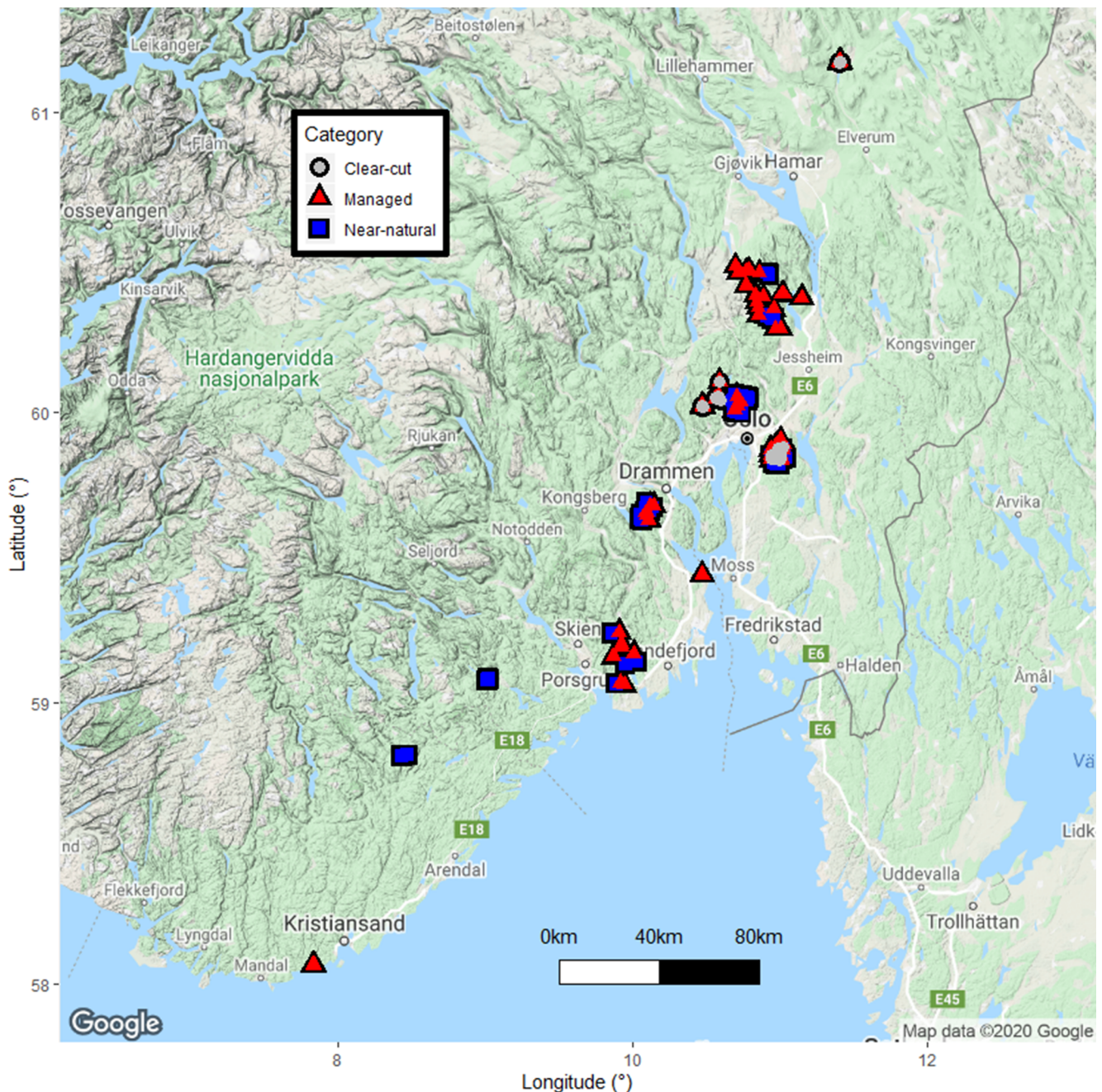
Most of the sites (317) were in forests managed as sustainable production forests within the regulations of the PEFC (the Programme for the Endorsement of Forest Certification schemes, Norway, pefc-norway.org). Of these, 105 sites were located at clear-cuts when beetles were sampled, and the other 195 sites were in closed canopy forests that have been heavily managed, most likely clear-cut, in the past. Additionally, there were 106 sites in near-natural forests. Near-natural forests, by our definition, are forests which have never been clear-cut, have high heterogeneity in forest structure (both horizontally and vertically), and have older trees and higher deadwood volumes when compared with managed forest (Storaunet et al., 2005). These sites were located in nature reserves or woodland key habitats or in areas about to receive such status.

Beetles were identified to species and categorized as saproxylic (including both facultative and obligative saproxylic species) according to The Saproxylic Database compiled by Dahlberg and Stokland (2004). Species were also categorized as red-listed according to the Norwegian Red List (Henriksen and Hilmo, 2015), and as indicator species for forest with natural characteristics (Dahlberg, 2011), as appropriate.

Several landscape-scale environmental covariates were included in our analyses: average age of the forest, volume of living spruce trees, and volume of living deciduous trees. These values, which were obtained for circular areas with a 1 km radius centered on each window trap, are available from SATSKOG and were derived from satellite images of the landscape (Gjertsen, 2007; Gjertsen and Nilsen, 2012). We chose to focus on these large-scale environmental variables as they could be obtained with the same precision for all sites (while environmental data collected in the separate projects differed in type and resolution). Forest characteristics at the landscape scale, in addition to the stand level, are relevant for beetle habitat selection (Bergman et al., 2012; Sverdrup-Thygeson et al., 2014a; Jacobsen et al., 2015; Sverdrup-Thygeson et al., 2017). Our choice of a 1 km radius is somewhat arbitrary, but we found covariates at this scale to be highly correlated with those at the 10 km scale (unpublished data) and so we are confident that our covariates are a good reflection of the landscape at multiple spatial scales. Mean age and volume values and variance for each forest category are shown in Table S1.

### 2.2. Analyses

We used generalized linear mixed models (GLMM) to explain variation in number of species between sites for saproxylic, natural-forest indicator, and red-listed species, while accounting for important sources of random variation. We used negative binomial GLMMs (Zuur et al., 2013) to account for overdispersion in species counts. Residual plots were inspected to assess model fit (Zuur et al., 2013). Fixed effects in these models included forest management category (managed, clear-cut or near-natural), average forest age within a 1 km radius of trap sites (“forest age 1 km”), average volume of spruce wood within a 1 km radius (“volume spruce 1 km”) and average volume of deciduous wood



**Fig. 1.** Map of window-trap trap locations for Beetles in Norway. Sites were located in clear-cuts ( $n = 105$ ), near-natural forests ( $n = 106$ ), and mature managed forests ( $n = 195$ ).

within a 1 km radius (“volume deciduous 1 km”). These landscape-level covariates were not highly correlated ( $VIF < 1.5$ ), so all were included in the models. Forest age and volume were log-transformed to improve model fit. All covariates were standardized prior to model fitting.

Random effects in our models included substrate to which the window trap was attached (none, spruce, birch, aspen, oak), sample year (1997, 1998, 2001, 2004, 2007) and region in which the sample site was located (Aust-Agder, Akershus, Buskerud, Hedmark, Oppland, Oslo, Telemark, Vest-Agder, Vestfold). Including region as a random effect helps to avoid any biases due to effects of spatial autocorrelation or latitude in the dataset.

Additionally, we used linear models to test whether our fixed effect covariates (average forest age, volume of spruce, and volume of

deciduous wood within a 1 km radius of the trap sites) differed depending on the location of the sites, i.e. forest category and region, and whether age and volume were correlated at this scale.

To compare beetle communities among sites, we used redundancy analysis (RDA) to analyze species composition as Hellinger-transformed abundance data (Borcard et al., 2018). Trap substrate, year, and region were added as conditional variables to focus on effects of the surrounding forest (1 km radius), i.e. forest management category, forest age, and volume of living trees. Significance of the ordination axes and the variables was assessed by permutation tests using the “anova.cca” function from the vegan package v. 2.4-6 (Oksanen et al., 2017). All analyses were performed in R version 3.4.3 (Hijmans, 2019).

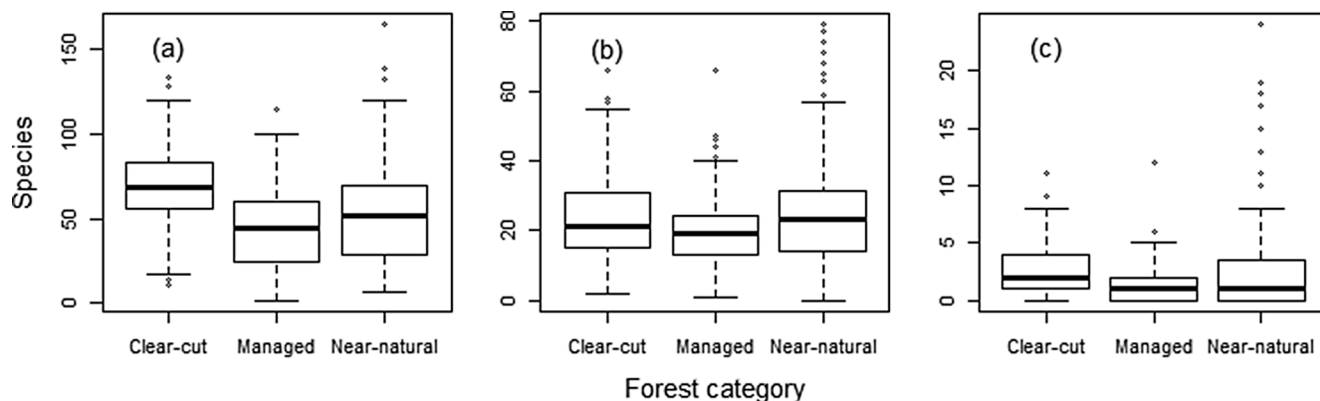


Fig. 2. Boxplots of number of saproxylic (a), indicator (b), and red-listed (c) beetle species captured per site by forest category in Norway. Sites were located in clear-cuts (n = 105), near-natural forests (n = 106), and mature managed forests (n = 195). Note the differences in y-axis scale.

### 3. Results

#### 3.1. Species richness

The dataset included 1267 beetle species (more than 35 percent of the approximately 3600 known beetle species from Norway) and 158,070 individuals in total, of which 680 species (84.5% of the individuals) were categorized as saproxylic. The 387 natural-forest indicator species (36 096 individuals) included 334 saproxylic species. There were 128 red-listed species (3542 individuals), of which 116 species (3254 individuals) were saproxylic and 95 species (2901 individuals) were indicator species. Raw number of each group of species caught from sites in each forest category are shown in Fig. 2.

Species richness of saproxylic, natural-forest indicator, and red-listed beetle species was significantly higher in ‘near-natural’ forest relative to closed canopy managed forest (Tables 1–3). Richness of these three groups was also significantly higher at sites located in clear-cuts relative to sites in closed canopy managed forest. Of sixteen sites with ten or more red-listed species, fourteen were in near-natural forests.

Average age of the forest surrounding the trap sites (1 km radius) was significantly and negatively correlated with richness of natural-forest indicator and red-listed beetle species, but the size of this effect was relatively small (Tables 2 and 3). Volumes of spruce and deciduous trees (1 km radius) were not significant in models for any of the species groups.

#### 3.2. Species composition

Explanatory variables describing the forest surrounding the trap sites (forest category, landscape forest age, and landscape volumes of

**Table 1**  
Generalized linear mixed model with negative binomial distribution for number of saproxylic beetle species sampled per site.

Saproxylic species	Estimate	SE	t-value	p-value
Intercept	3.56	0.47	7.5	<0.001
Category: (Managed)				
Near-natural	0.18	0.06	2.83	<b>0.005</b>
Clear-cut	0.32	0.05	6.28	< <b>0.001</b>
Forest age 1 km (log)	-0.03	0.02	-1.45	0.147
Volume deciduous 1 km (log)	0.02	0.02	1.03	0.305
Volume spruce 1 km (log)	0.03	0.02	1.29	0.196
Random effects	Variance	SD		
Region	0.47	0.69		
Year	0.16	0.4		
Trap substrate	0.68	0.83		

Negative binomial dispersion parameter: 10.37 (SE: 0.92).  
Log-likelihood: -1744.2.

**Table 2**  
Generalized linear mixed model with negative binomial distribution for number of natural-forest indicator beetle species sampled per site.

Indicator species	Estimate	SE	t-value	p-value
Intercept	2.74	0.45	6.05	<0.001
Category: (Managed)				
Near-natural	0.20	0.07	2.8	<b>0.005</b>
Clear-cut	0.23	0.06	3.95	< <b>0.001</b>
Forest age 1 km (log)	-0.05	0.02	-2.12	<b>0.034</b>
Volume deciduous 1 km (log)	0.03	0.02	1.35	0.179
Volume spruce 1 km (log)	0.04	0.03	1.56	0.118
Random effects	Variance	SD		
Region	0.3	0.54		
Year	0.14	0.37		
Trap substrate	0.7	0.84		

Negative binomial dispersion parameter: 10.84 (SE: 1.20).  
Log-likelihood: -1426.0.

**Table 3**  
Generalized linear mixed model with negative binomial distribution for number of red-listed beetle species sampled per site.

Red-listed species	Estimate	SE	t-value	p-value
Intercept	-0.23	0.56	-0.41	0.680
Category: (Managed)				
Near-natural	0.44	0.18	2.52	<b>0.012</b>
Clear-cut	0.76	0.14	5.62	< <b>0.001</b>
Forest age 1 km (log)	-0.13	0.06	-2.33	<b>0.020</b>
Volume deciduous 1 km (log)	-0.03	0.06	-0.61	0.545
Volume spruce 1 km (log)	-0.03	0.06	-0.43	0.664
Random effects	Variance	SD		
Region	0.24	0.49		
Year	0.28	0.53		
Trap substrate	0.99	1		

Negative binomial dispersion parameter: 5.05 (SE: 1.29).  
Log-likelihood: -697.3.

deciduous wood and of spruce wood) explained a small proportion of the variation in species composition of saproxylic (3.6%) and natural-forest indicator species of beetles (3.8%). Region, year and trap substrate were included as conditional variables, and explained a larger proportion of the variation for both species groups (41.2% explained for saproxylics and 30.1% for indicator species; region, year and trap substrate each contributed roughly the same amount to this explanatory power). Despite the low proportion of explained variation, forest category and landscape volume of spruce wood were significant in all ordination analyses (Table 4). Forest age significantly affected composition of saproxylic species, while volume of deciduous wood within a 1 km radius had a nearly significant effect on composition of indicator

**Table 4**

Permutation tests ( $n = 999$ ) of variance explained by forest category (managed, clear-cut or near-natural) and other covariates in RDA of community composition (Hellinger-transformed abundance) of saproxylic and natural-forest indicator species. Region, year and trap substrate are included in the RDAs as conditional variables.

	Variance	F-value	p-value
<i>Saproxylic species</i>			
Forest category	0.020	9.94	<b>0.001</b>
Forest age 1 km	0.002	1.52	<b>0.020</b>
Volume deciduous 1 km	0.001	1.17	0.148
Volume spruce 1 km	0.002	2.37	<b>0.001</b>
Residual	0.40		
<i>Indicator species</i>			
Forest category	0.022	9.04	<b>0.001</b>
Forest age 1 km	0.001	0.91	0.631
Volume deciduous 1 km	0.002	1.26	0.089
Volume spruce 1 km	0.002	1.72	<b>0.007</b>
Residual	0.46		

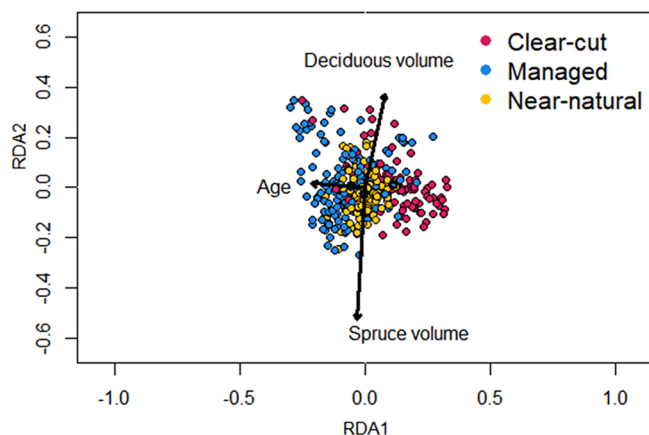
species (Table 4). Red-listed species were not analyzed separately due to the very low mean number of species at each site.

For saproxylic species, two ordination axes were significant, meaning that variation in community composition could not be reduced to a single dimension (RDA1 p-value = 0.001, variance = 0.019; RDA2 p-value = 0.001, variance = 0.002). Clusters of points from the three management categories overlapped considerably (Fig. 3), reflecting the low proportion of variation in species composition explained by these categories. Only the first axis was significant in ordination of indicator species community composition (RDA1 p-value = 0.001, variance = 0.020; RDA2 p-value = 0.249, variance = 0.002).

Volume of deciduous wood was significantly higher within a 1 km radius of trap sites in clear-cuts relative to sites in managed forest (Table S2). Volume of spruce wood and average forest age within a 1 km radius was significantly higher for sites in near-natural forest and significantly lower for sites in clear-cuts, relative to sites in closed-canopy managed forest (Table S3-S4). Nevertheless, landscape volume of spruce wood and volume of the forest in general were weakly but negatively correlated with forest age (Table S3-S4).

#### 4. Discussion

We found that fewer beetle species occurred in managed forests



**Fig. 3.** RDA of Hellinger-transformed abundance saproxylic beetles, explained by forest category and three landscape level covariates (1 km radius): volume of spruce wood, volume of deciduous wood, and average age of the forest. Both axes and all variables are significant ( $p < 0.05$ ) in the ordination. Centroids for each category are shown as squares. Region, year and trap substrate are included as conditional variables and therefore are not shown on the plot.

than in the other forest types, and community composition differed significantly as well. This was true for both saproxylic, natural-forest indicator, and red-listed species. Differences in forest age and tree volume at the landscape level did not account for these differences in community composition; rather, a suite of forest compositional and structural changes resulting from different management practices (Bouget et al., 2012) among forest categories are likely causes. In particular, levels of standing and lying deadwood, present but ephemeral in clear-cuts (Jonzell and Schroeder, 2014), are highest in more natural forests (Bouget et al., 2012). This resource, important for so many saproxylic species (and other taxa that depend on them), is much less common in intensively managed stands.

Clear-cuts, as well as near-natural forests, supported higher beetle species richness than closed-canopy intensively managed forests. This is not surprising, given that sun-exposed, coarse woody debris (CWD)-rich areas occur in and are important to the dynamics of natural forests (Sverdrup-Thygeson and Ims, 2002; Junninen et al., 2006; Tikkanen et al., 2006; Hedgren, 2007; Swanson et al., 2011). Many species, including natural-forest-dependent and red-listed species, are likely adapted to these open areas. Clear-cuts do contain more CWD than older age classes of managed forests (Lassauce et al., 2011; Jonzell and Schroeder, 2014), but contain less CWD than do open areas in natural forest, which often result from tree falls or other disturbances (Bouget et al., 2012).

In spite of being similar in species richness, clear-cuts cannot take the place of near-natural forests for a number of reasons. They host a different set of species, and we have shown through an ordination that community composition differs among these three forest types. This distinction between species richness and community composition is important, because richness patterns are often driven by common species (Lennon et al., 2011), whereas from a conservation perspective rare species are often of more interest. Furthermore, the relatively high species richness found in clear-cuts in our study is ephemeral and will pass as the canopy closes and little new dead wood is generated: the managed forests in our study, significantly less species-rich than either near-natural forest or clear-cuts, have developed from previous clear-cuts. In near-natural forests, on the other hand, species richness remains high over time, probably due to ongoing natural dynamics that continue to supply deadwood in various decay stages through time (Nascimbene et al., 2013).

It is widely recognized that landscape-scale, as well as local-scale, environmental characteristics affect forest communities (Sverdrup-Thygeson et al., 2014a; Sverdrup-Thygeson et al., 2017; Nordén et al., 2018). For our study sites, near-natural forests were on average surrounded by older forest, and forest with higher spruce volume, than were managed forests. Clear-cuts, on the other hand, were surrounded by younger forest with higher deciduous volume. Nevertheless, mean forest age within 1 km of a site was negatively correlated with spruce volume in that same radius. This may be because land with the highest site index has been the most intensively managed, resulting in higher volume, whereas stands on suboptimal sites have been allowed to grow older (Stokland, 1997) and develop near-natural characteristics.

It is at first puzzling why we found richness of red-listed species to be negatively correlated with forest age at the landscape scale. However, upon further examination we found that a subset of our species-rich near-natural and clear-cut sites happen to be located in an area with young forests in the surrounding landscape, and a subset of our species-poor managed forests were located in a landscape with very old forest. These relatively few but extreme points appear to be driving the relatively weak negative correlation between richness of this group and forest age. This highlights the difficulty in separating local and landscape scale effects using observational data in the absence of sampling that was specifically designed to do so. When community composition (rather than simply species richness) was considered using the ordination analyses, landscape-level covariates were significant (with the exception of deciduous volume) and showed stronger effects

in our analyses. This importance of landscape, as well as local, forest characteristics provides evidence that managers must consider how actions at larger spatial scales, as well as at the stand level, impact biodiversity (Sverdrup-Thygeson and Lindenmayer, 2003).

We found clear differences in both species richness and community composition between near-natural and intensively managed mature forests. These differences were apparent in spite of our mixed dataset, which combines beetle community data from a number of separate projects with varying study design, trap placement, and sampling effort. Additionally, it is possible that potential differences in capture rates among habitats (for example, increased flight of adult beetles in open and sunny clear-cuts) could have affected our results. Finally, the SATSKOG data that were used to estimate forest covariates in our 1 km radius plots can be less precise than ground measurements (Gjertsen, 2007; Gjertsen and Nilsen, 2012), making more detailed landscape analyses infeasible. The effects of region in our models make it likely either that unknown additional covariates, for which region is a surrogate, are important in determining beetle diversity, or that there is spatial autocorrelation among sites. Nevertheless, the consistent patterns found in our dataset give us confidence that our data are revealing real patterns of species occurrence.

In summary, beetle species richness and community composition in near-natural forests differ from those in intensively managed stands. This can likely be partially explained by increased deadwood volume and variety, increased forest age, and the presence of trees in multiple age classes in near-natural forests. These differences are likely to be important both in a given stand, and at the landscape level. Given the lack of the old-growth forest in Norway, and the potential for near-natural forests to increasingly resemble old-growth through time, these near-natural forests are likely to be of high importance for species dependent on old-growth habitats. Forest management strategies that attempt to balance species conservation with the economics of forest products have been shown to be most efficient when unmanaged forests are distributed across the land productivity gradient rather than being placed exclusively in locations with a low site index (Stokland, 1997). Conservation of these near-natural forests, including those in highly productive sites, should therefore be prioritized.

#### CRedit authorship contribution statement

**Rannveig M. Jacobsen:** Conceptualization, Methodology, Formal analysis, Writing - original draft. **Ryan C. Burner:** Methodology, Formal analysis, Writing - original draft. **Siri Lie Olsen:** Conceptualization, Methodology, Formal analysis, Writing - review & editing. **Olav Skarpaas:** Methodology, Writing - review & editing, Funding acquisition. **Anne Sverdrup-Thygeson:** Conceptualization, Writing - review & editing, Supervision, Funding acquisition.

#### Declaration of Competing Interest

The authors have no conflict of interest to declare.

#### Acknowledgements

We thank the Research Council of Norway for funding the projects "Ecosystem services in forests – biodiversity, climate mitigation and economy resources" (grant no. 160022/F40), and "ECOSERVICE - Approaches for integrated assessment of forest ecosystem services under large scale bio-energy utilization" (grant no. 233641/E50), as well as EU BiodivERsA for "BioESSHealth: Scenarios for biodiversity and ecosystem services acknowledging health" (grant no. 295621). Thanks also to Sindre Ligaard for identifying the beetle species, and to numerous field assistants who set and maintained traps.

#### Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foreco.2020.118124>.

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