

Do conservation measures in forest work? A comparison of three area-based conservation tools for wood-living species in boreal forests



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ABSTRACT

Loss of natural forests and decline in forest biodiversity has led to several policy initiatives in recent years. Despite this, the importance of smaller set-asides vs forest reserves for conservation measures is poorly understood. We aimed to evaluate the importance of three different area-based conservation measures commonly used in north-European forests; retention patches, woodland key habitats and forest nature reserves. We did this for two contrasting ecological systems; *fungi in late-decay spruce logs* and *beetles in early-decay aspen snags*.

Eight replicated sites for each of the three conservation measures were investigated in a total of four boreal forest landscapes in south-Norway. Fungi were surveyed on existent late-decay spruce logs in two landscapes, and beetles trapped on experimentally added aspen dead-wood units in three landscapes. Richness and species composition were analyzed separately for specialist and generalist species.

We found larger differences in species composition between conservation measures for old-growth fungi specialists than generalists, although species richness patterns were less clear. The main contrast was found between nature reserves and retention patches. On the other hand, specialist beetles associated with early-decay aspen showed no difference between set-asides. The assemblage of aspen generalist beetles tended to be richest in the woodland key habitats and showed clear differences between the conservation measures. There was considerable variation in response to conservation measures between landscapes, related to quality of the set-asides.

Species specialized to an ephemeral, early-decay system were able to utilize such substrates in all of the conservation measures, while the smaller and more modified set-asides could not cater for the specialists dependent on stable, late-decay systems. Species with broader habitat demands in general responded to all conservation measures. We conclude that retention patches, woodland key habitats and forest reserves fill complementary functions for wood-living species in boreal forest and should all be part of future forest conservation strategies.

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1. Introduction

An increasing concern surrounding the loss of natural forests and the decline in forest biodiversity has led to a rise in research and policy initiatives in recent years. One important initiative is the Strategic Plan for Biodiversity 2011–2020, drawn up by the Convention on Biological Diversity and agreed upon by the governments of the world in Japan 2011. It states that by 2020, at least 17% of the areas of particular importance for biodiversity and ecosystem services are to be conserved through “ecologically representative and well-connected systems of protected areas and

other effective area-based conservation measures”. If we are to reach this target for the forest ecosystems of the world, we need a much better empirical understanding of the functioning and the relative importance of forest reserves and smaller set-asides than we have today.

1.1. Conservation measures in forestry

In the past 25 years, forest conservation measures have shifted from a strong emphasis on protected areas, toward a wider focus including also matrix management (e.g. Ricketts et al., 2001; Lindenmayer and Franklin, 2002; Debinski, 2006; Gustafsson et al., 2012). In the late 1980s, a new forest management model – retention forestry – was introduced in northwestern North

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America as a response to the need to better integrate wood production and biodiversity (Franklin, 1989), and spread rapidly to other regions of the world (Gustafsson et al., 2012). Retention forestry can be defined as an approach to forest management based on the long-term retention of structures and organisms, such as live and dead trees and small areas of intact forest, at the time of harvest (Lindenmayer et al., 2012). These structures are not removed in future forest management operations and hence undergo natural processes of growth and decay. The retention of different legacies such as dead and living trees on harvested areas is today a very important and widely applied conservation practice, especially in the boreal forest landscape (Heithecker and Halpern, 2006; Martinez Pastur et al., 2009; Gustafsson et al., 2010; Lindenmayer et al., 2012; Runnel et al., 2013).

Areas exempted from felling through protection or retained in cutting operations can be considered as a continuum of area set-asides, spanning across a range of spatial scales. At the smallest scale, single trees can be retained, dispersed in the harvesting unit. Retained trees can also be left aggregated in small groups (mainly <0.5 ha), e.g. in rocky outcrops, along waterways (riparian buffer zones) or toward the margins of the harvesting unit (Gustafsson et al., 2010). Woodland key habitats (WKH) can be considered the next step up on a spatial scale of area set-asides, with an average size in Fennoscandia and Baltic countries in the range of 0.7–4.6 ha (Timonen et al., 2010). Although exact definition and legal status might vary, a WKH is essentially a small habitat patch that is thought to be particularly valuable for maintaining landscape-level biodiversity and therefore exempted from logging. The concept originates from Sweden in 1992 (Nitare and Norén, 1992) and has subsequently been adopted in much of Northern Europe (Timonen et al., 2010).

1.2. Evaluating species responses to conservation measures

In order to evaluate the efficiency of protected areas and area-based conservation measures such as small-scale set-asides in forestry, we need to link the management tools to real-world ecology. In the present study we compared three categories of area-based conservation measures typical of North European forest: *Retention patches, woodland key habitats and forest reserves*.

All these conservation measures supply dead wood, which is a key substrate in forest and supports a large and unique biodiversity. The distribution and dynamics of the dead wood differ between tree species and decay, which also affects the associated biodiversity. We therefore compared the effect of different area-based conservation measures for two ecological systems: *fungi in late-decay spruce logs and beetles in early-decay aspen snags*.

The dynamics of these systems pose an interesting contrast in the boreal and hemiboreal forest of Northern Europe: on one hand, Norway spruce (*Picea abies*) occurs continuously across large stretches of forest, as spruce is a dominating species in this region. In addition, spruce has a maximum life span of 400–500 years and the decay of large trees can take up to 100 years (Storaunet and Rolstad, 2002). It is well established that many endangered species of fungi are associated with slowly decaying spruce logs in natural forest (Berg et al., 2002; Junninen and Komonen, 2011).

On the other hand, European aspen (*Populus tremula*) occurs dispersed in forests dominated by coniferous species. It is a pioneer species, regenerating after forest fire or similar large clearing events, and then gradually being replaced by Norway spruce. It is quite common to find single large senescent aspen trees interspersed in the mature coniferous forest. The lifespan of European aspen is rather short, 80–100 years, and once dead, the wood decays fast. Recently-dead aspen is a short-lived, but important insect habitat, with a number of associated saproxylic beetle species (Siitonen and Martikainen, 1994; Tikkanen et al., 2006).

Previous studies on both fungi and insects have shown that the response to fragmentation may differ between generalist (eurytopic) and specialist (stenotopic) species (Davies et al., 2004; Driscoll and Weir, 2005; Stokland and Larsson, 2011; Nordén et al., 2013). Therefore we analyzed the response of the species specialized to the habitats in question, separately from the response of generalist species with broad habitat preferences. In a combined observational and experimental setup in four landscapes in Southern Norway, we addressed the following questions for the two systems:

- (1) Do similar late-decay spruce logs support *the same species richness and assemblages* of fungi in retention set-asides, woodland key habitats and forest reserves? Is the response different between generalists and specialists?
- (2) Do replicated units of early decay aspen serve as habitat for *the same species richness and assemblages* of beetles, regardless of which area-based conservation measure they are placed in? Is the response different between generalists and specialists?

We expected more difference between set-aside categories for habitat specialists, as they are expected to be more sensitive to fragmentation than habitat generalists. If that is the case, retention set-asides should host fewer specialists than WKHs, and WKHs should house fewer than reserves. Finally, we predicted that the difference will be greater for specialized late-decay fungi in spruce than for specialized early-decay beetles in aspen, due to the larger need for stability in space and time of late decay systems.

2. Materials and methods

2.1. Study areas and site selection

The study was conducted in Southern Norway, in the southern or middle boreal vegetation zone (Moen, 1998), and consisted of forest dominated by spruce, with birch (*Betula pubescens*), aspen (*P. tremula*), and sometimes Scots pine (*Pinus sylvestris*) as subdominants.

The study was conducted in four different landscapes; Losby Bruk in Østmarka (mainly Lørenskog municipality, Lat. 59.89, Long. 10.97, 150–300 masl), Oslo municipal forests in Nordmarka (Lat. 60.00, Long. 10.71, 200–500 m), Selvik Bruk in Vestskogen (Drammen/Sande municipalities, Lat. 59.68, Long. 10.12, 130–200 masl) and Gran Almønning and Mathiesen/Eidsvold Værk in Hadelands østås (Gran/Hurdal municipalities, Lat. 60.36, Long. 10.75, 500–700 masl). The field work was conducted between 2006 and 2011.

All forest holdings were certified through the PEFC Norway, as is almost all forest in Norway <http://www.pefcnorway.org/>. This implies that important woodland key habitats for forest biodiversity (selected by the Complementary Hotspot Inventory method (Gjerde et al., 2007), average size 1 ha (Timonen et al., 2010), making up 1.5% of productive forest (Søgaard et al., 2012)) has been designated and set aside on all properties. Similarly, retention trees and retention patches have been left at final felling (4–6 years before onset of the study) both along mires, streams or lakes and in the felling area in general, measuring 0.5–1 tree per ha of clear-cutting and with a mean size less than 0.5 ha. All studied landscapes included a forest reserve, making up 3–7% of the study areas.

In each of the study landscapes we set up a block design representing three different area-based conservation measures typical of North European forest: retention set-asides (RET), woodland key habitats (WKH) and strict nature reserves (NAT). Each block was replicated 8 times within each landscape, giving a total

number of study sites (4 landscapes \times 3 management categories \times 8 replicates) of 96 (Fig. 1).

The WKH and RET sites were selected randomly from the forest holdings' forest management databases and the plot was placed in the center of the site. The NAT sites were selected by placing a grid across the reserve area and selecting points randomly, but no closer than 200 m to other points or to the edge of the reserve. The exact location of the plot was adjusted in field so that the center of all sites was placed in spruce-dominated *Myrtillus* site type forests and with a similar sun exposure.

2.2. Observational setup for fungi study

Fungi were recorded on five downed logs of spruce in each study site. Only logs in medium and high degree of decay (r3–5, as defined by Høiland and Bendiksen, 1996) were included. The decay stage of each log was recorded. The logs were randomly selected by sampling the first five logs >3 m long and DBH (diameter in breast height) >20 cm, within a 10 m wide transect. The transect started out eastward from plot center. If the transect crossed a boundary, either to another vegetation type, to young forest or the margin of the site itself, the line transect was angled 90° – first to the south, and if necessary further to the west, then to the north and so on. To enhance independence of log observations, minimum distance between two logs was set to five meters (not connected by a third log). The transect length from plot center to the fifth log was recorded as a measure of log quantity in each study site.

All discernible specimens of all species belonging to the large morphological groups of polyporaceous fungi and corticiaceous fungi, including heterobasidiomycetes, were recorded and identified in the field or collected for identification in lab.

The lack of ecological legacies in retention patches in some of the study landscapes represented a challenge in the fungi part of the study. In two of the study landscapes, it was not possible to find sufficient retention patches that actually contained at least five medium/large sized and medium/late decay spruce logs. The fungi part of the present comparison of all three set-aside

categories thus only includes the two landscapes above a certain minimum quality of retention set-asides.

2.3. Experimental setup for beetle study

For the study of early-successional beetles associated with aspen dead wood, a field experiment was set up in three of the landscapes: fresh aspen trees were cut down in a forest outside the study areas and the suitable part of the tree was cut into units of approx. 20 cm diameter and one meter length. The wood units were transported out to the study sites and placed upright, using a 60 cm long iron bar hammered half-way into the wood unit and half-way down into the ground to stabilize it. We placed two wood units in each study site, spaced ca. one meter apart. All wood units were produced in the same cutting operation to limit any confounding effects of wood quality, and wood units were assigned randomly to study sites. Sun exposure (using a relascope) was measured to ensure there were no differences in sun exposure at the trap locations in the three set-aside categories (ANOVA, $df = 2, p = 0.7$). We measured the amount of living and dead aspen around the trap locations, in a plot with radius = 30 m.

Flight interception traps (with windows 20 cm \times 40 cm, a funnel and a container underneath filled with ethylene glycol and detergent) were mounted on each wood unit by the use of wires. Sixteen traps were placed in each area-based conservation measures category, giving a total of 144 traps. The traps were operating for three summers (2007–2009). In the second and third year one of the dead wood units was closed in by a large net so the trap acted as an emergence trap, only sampling beetles having developed or overwintered in the unit. All trap data were pooled for the analyses.

2.4. Data analysis

Fungi not determinable in the field by EB were identified by experts in the lab. Nomenclature follows The Species Nomenclature Database (<http://www2.artsdatabanken.no/artsnavn/ContentPages/Hjem.aspx>). The fungi were grouped into two categories, based on information in the Norwegian Red List (Kålås et al., 2010) and in Stokland and Larsson (2011): one group contained species described as occurring mainly on large or late-decay logs of spruce and/or mainly in old natural spruce forest, including 9 red-listed species for which exact habitat demands are not known. These were denoted *old-growth specialists*. The other group contained the remaining species, for simplicity denoted *generalists* hereafter, although they can have specializations to other conditions than old-growth. One occurrence of a fruiting body was defined as presence on a log.

All beetle individuals were identified to species and grouped according to habitat association using the database from Dahlberg and Stokland (2004) and additional literature. *Aspen-specialist species* was the sub-group of saproxylic species preferring aspen dead wood, mainly in the early successional stages, while *aspen generalist species* included species that occur in aspen dead wood without having a preference for aspen.

We used generalized linear models (GLM; Poisson distribution, Log link) with set-aside categories nested within landscapes to analyze to what extent the variation in species richness of different functional groups could be explained by the different area-based conservation measures, and to assess the importance of the different study areas. We tested if adding environmental variables (decay stage and distance between sampled logs for fungi, number of dead or living aspens for beetles) improved the models. Landscapes and set-asides were coded as nominal variables, so that the parameter for each nominal level can be interpreted as the differences in the predicted response for that level from the average

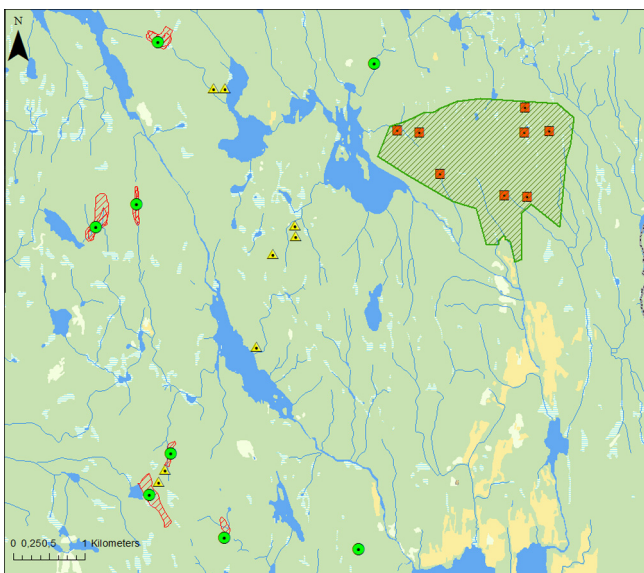


Fig. 1. Map of one of the study landscapes (Oslo) to illustrate the design. Hatched green is a nature reserve, while hatched red denotes a woodland key habitat. Squares are the 8 sites in nature reserves, circles are the 8 sites in woodland key habitats and triangles are the 8 sites in small retention patches. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

predicted response over all levels. We used Maximum Likelihood as the estimation method. The models were checked for overdispersion using Pearson ChiSquare/DF. These data analyses were conducted in JMP Pro 10.0.0.

A multi-response permutation procedure (MRPP) was used to test differences in species composition between landscapes and conservation categories. Species and sites with only one record (singletons) were removed prior to the analysis as needed to calculate within-group distances (Peck, 2010). All comparisons were based on a Sørensen (Bray-Curtis) index of dissimilarity. The effect is given as *A*-values (chance-corrected within-group agreement) with *A* = 1 representing equal groups and *A* = 0 represents heterogeneity within groups as expected by chance. The *p*-value represents the probability of a larger or equal delta. As a fungus species was only counted once per log, number of logs with a particular fungus at each site was used as a measure of abundance, ranging from 1 to 5. The MRPP analysis was calculated in PC-ORD 6.

3. Results

3.1. Fungi on spruce logs

In the two study landscapes we recorded 1566 occurrences of fungi, belonging to 160 different species; 134 corticoid and 26 poroid species (Supplementary material Appendix 1, Table A1). Forty-nine species occurred only on one log in this material, while the most abundant species, *Xylodon brevisetus*, occurred on 79 logs. Twenty-five species were categorized as old-growth specialists, with a total of 158 occurrences (Supplementary material Appendix 1, Table A1).

3.1.1. Species richness in categories of set-asides

In a nested GLM, the generalist fungi species differed in species richness both between landscapes, with Selvik being higher than Gran, and between categories, with the NAT-sites having a higher than mean species richness in Gran and WKH-sites having a lower than mean species richness in Selvik (Table 1).

Similarly, the species richness of specialized old-growth fungi also differed between landscapes and set-aside categories in a nested GLM (Table 1). The number of species was highest in Gran,

and the RET-sites in this landscape had a lower than mean species richness whereas the WKHs had a higher than mean species richness (Table 1).

Although the design variables were the basis of this study, the field work gave us reason to believe that there were differences in the dead wood quality between the two landscapes. The mean log decay was significantly different between the categories, and indicated larger variation in Gran than in Selvik (Gran mean: NAT = 4.0, WKH = 4.15, RET = 3.8; Selvik mean: NAT = 3.63, WKH = 3.60, RET = 3.50, ANOVA *p* = 0.002). The log decay seemed to have a different effect on the number of old-growth and generalist species (Fig. 2). The distance we had to walk to find five suitable logs differed between the categories in Gran (mean: NAT = 208 m, WKH = 157 m, RET = 506 m, ANOVA *p* = 0.047,) but not in Selvik although the trend of more dispersed logs in retention patches was similar (mean: NAT = 153 m, WKH = 180 m, RET = 280 m, ANOVA *p* = 0.3). Neither of these variables improved the models in Table 1 as evaluated by the AIC.

3.1.2. Species composition in categories of set-asides

The old-growth fungi species and the generalists differed in species composition between landscapes (MRPP, pairwise comparisons *p* < 0.001 in both analyses). Thus, tests between set-asides were performed within each landscape. As opposed to the species richness discussed above, there was no difference in species composition of generalist fungi between the three set-asides in any of the landscapes (Table 2). For the old-growth fungi on the other hand, the NAT differed in species composition from WKH and RET in Gran (Table 2).

3.2. Beetles in early-decay aspen

In the field experiment on early-decay aspen, we collected 15,900 beetle individuals (573 species), of which 13,437 were saproxylic (363 saproxylic species). Eleven species were categorized as aspen specialists and 153 species were categorized as aspen generalists. Twenty species were listed as threatened or near threatened in the Norwegian Red List (Kålås et al., 2010) (Supplementary material Appendix 1, Table A2). 11% of the saproxylic species were represented only by one individual while the most abundant species *Haploglossa villosula* made up 6% of the individuals.

Table 1

Parameter estimates from GLMs of species richness of Generalist fungi and of old-growth specialist fungi, in a model with the design variables landscape and set-aside (nested in landscape). *N* = 240. Significant *p*-values are in bold.

Term	Estimate	Std error	L-R ChiSq	Prob > ChiSq
<i>Generalist fungi (effect test: landscape: df = 1, p = 0.004, set-aside: df = 4, p = 0.009)</i>				
Intercept	1.761	0.027	2543.377	<.001
Landscape[Gran]	-0.077	0.027	8.314	0.004
Landscape[Selvik]	0.077	0.027	8.314	0.004
SetAside[RET]Gran	-0.021	0.056	0.143	0.706
SetAside[WKH]Gran	-0.095	0.057	2.816	0.093
SetAside[NAT]Gran	0.116	0.054	4.518	0.034
SetAside[RET]Selvik	0.093	0.050	3.342	0.068
SetAside[WKH]Selvik	-0.152	0.054	8.327	0.004
SetAside[NAT]Selvik	0.060	0.051	1.364	0.243
<i>Old-growth specialist fungi (effect test: landscape: df = 1, p = 0.003, set-aside: df = 4, p = 0.073)</i>				
Intercept	-0.477	0.084	38.349	<.001
Landscape[Gran]	0.250	0.084	9.039	0.003
Landscape[Selvik]	-0.250	0.084	9.039	0.003
SetAside[RET]Gran	-0.326	0.159	4.552	0.033
SetAside[WKH]Gran	0.322	0.136	5.511	0.019
SetAside[NAT]Gran	0.004	0.146	0.001	0.979
SetAside[RET]Selvik	0.082	0.183	0.198	0.656
SetAside[WKH]Selvik	-0.255	0.199	1.729	0.189
SetAside[NAT]Selvik	0.173	0.179	0.914	0.339

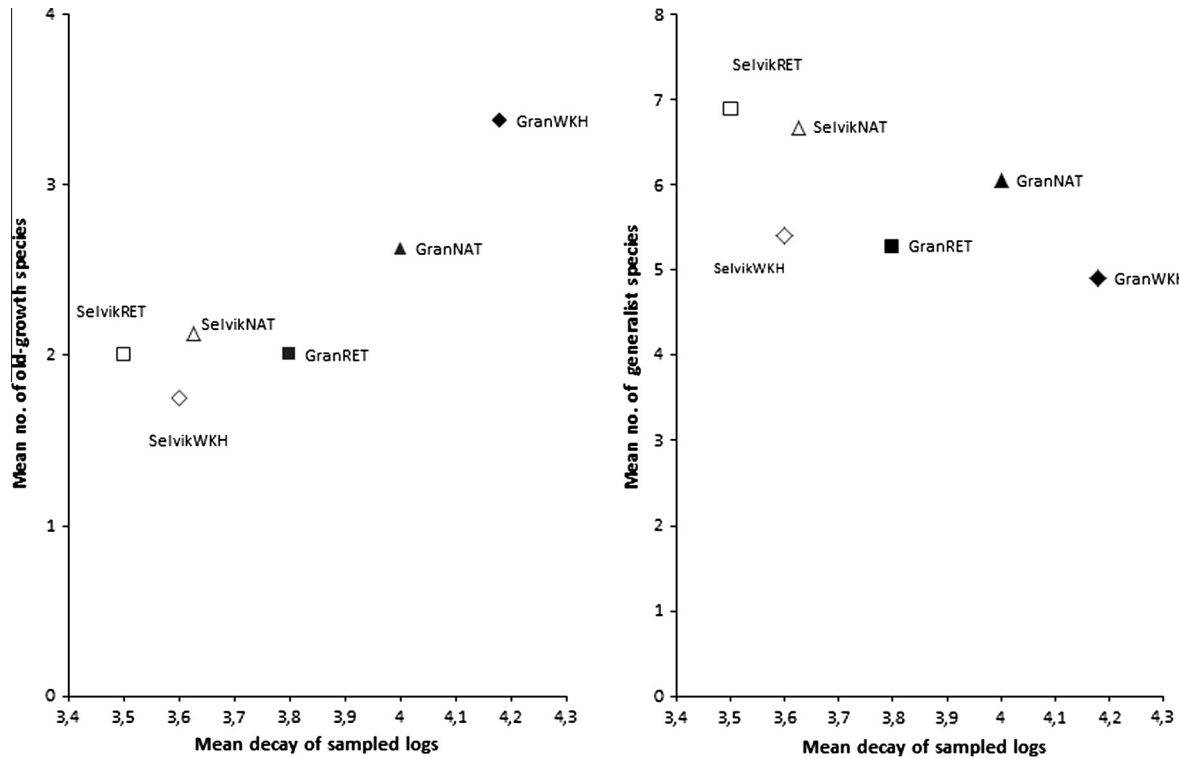


Fig. 2. Mean number of (a) old-growth fungi species and (b) fungi species not associated with old-growth, plotted by mean decay of the 40 sampled logs in each set-aside class within each landscape. Decay stage was rated on a scale from 3 to 5. Note the difference in scale at the y-axis.

Table 2
Multi-response permutation procedure (MRPP) analysis of generalist (upper part) and specialists (lower part) fungi on spruce logs in different forest set-asides. The effect size *A* (1 identify equal groups) with *p*-value in parenthesis is presented for each comparison. Significant *p*-values are marked in bold. NAT = nature reserve, WKH = woodland key habitat, RET = retention trees. The number of species and sites are reduced due to removal of singletons.

Landscape (No. of species)	Number of sites compared			WKH vs NAT	WKH vs RET	NAT vs RET
	WKH	RET	NAT	<i>A</i> (<i>p</i> -value)	<i>A</i> (<i>p</i> -value)	<i>A</i> (<i>p</i> -value)
<i>Generalist fungi</i>						
Gran (87)	8	8	8	0.003 (0.391)	0.013 (0.148)	0.003 (0.380)
Selvik (95)	8	8	8	-0.010 (0.802)	0.009 (0.170)	0.002 (0.389)
<i>Specialist fungi</i>						
Gran (9)	7	6	7	0.071 (0.039)	0.022 (0.233)	0.076 (0.034)
Selvik (9)	5	5	7	0.042 (0.146)	0.022 (0.284)	-0.019 (0.696)

3.2.1. Species richness in categories of set-asides

In a nested GLM, species richness of aspen generalist beetles differed between the landscapes and the set-asides (Table 3). Selvik was the most species rich landscape. WKHs had a higher than mean species richness in Losby (*p* = 0.061) and Selvik. The RET-sites had a higher than mean species richness in Losby whereas a lower than mean species richness in Selvik. No difference was found between landscape and set-aside categories for the specialized beetles (Table 3).

The amount of living or dead aspens nearby trap sites did not indicate any difference between categories (Losby mean living/dead: NAT = 2.13/0.38, WKH = 0.88/0, RET = 1.15/0, ANOVA both n.s.; Selvik mean living/dead: NAT = 0/0, WKH = 1.25/0.13, RET = 0/0, ANOVA both n.s.).

3.2.2. Species composition in categories of set-asides

The species composition of aspen generalist species differed significantly between landscapes (MRPP, pairwise comparisons, *p* < 0.001). Thus, tests between set-asides were performed within each landscape. Species composition in retention set-asides and

nature reserves differed most (i.e. had the highest *A*) and this difference was significant in all three landscapes. Further, WKHs differed from the RET set-asides in two landscapes. The WKHs also differed from the NAT-sites in Losby (Table 4).

Similar to the species richness discussed above, the species composition of aspen specialists did not differ between landscapes (MRPP; *A* = -0.006 *p* = 0.627, 9 species included in the analysis) or set-aside categories (MRPP; all landscapes, *A* = 0.013, *p* = 0.137, 9 species included in the analysis).

All main results are summed up in Table 5.

4. Discussion

4.1. Relationship between conservation measure category and ecological conditions

We designed the study to investigate the effect of conservation set-asides, and study sites were therefore chosen and grouped according to set-aside category. Although the process of setting aside retention patches and WKHs is based on legislation

Table 3

Parameter estimates from a GLM of species richness of Aspen generalist beetles, in a model with the design variables landscape and set-aside (nested in landscape). $N = 71$. Significant p -values are in bold.

Term	Estimate	Std error	L-R ChiSq	Prob > ChiSq
<i>Aspen generalists beetles: (effect test: landscape: $df = 2$, $p < 0.001$, set-aside: $df = 6$, $p < 0.001$)</i>				
Intercept	3.489	0.021	10100.352	<.001
Landscape[Losby]	-0.080	0.030	7.037	0.008
Landscape[Oslo]	-0.072	0.030	5.959	0.015
Landscape[Selvik]	0.152	0.028	28.418	<.001
SetAside[RET]Losby	0.133	0.053	6.154	0.013
SetAside[WKH]Losby	0.098	0.052	3.524	0.061
SetAside[NAT]Losby	-0.232	0.056	17.648	<.001
SetAside[RET]Oslo	-0.024	0.053	0.212	0.645
SetAside[WKH]Oslo	0.053	0.052	1.030	0.310
SetAside[NAT]Oslo	-0.028	0.053	0.292	0.589
SetAside[RET]Selvik	-0.097	0.048	4.178	0.041
SetAside[WKH]Selvik	0.108	0.046	5.516	0.019
SetAside[NAT]Selvik	-0.011	0.047	0.052	0.819
<i>Aspen specialists beetles: (effect test: landscape: $df = 2$, $p < 0.472$, set-aside: $df = 6$, $p = 0.976$)</i>				
Intercept	0.804	0.080	78.482	<.001
Landscape[Losby]	0.047	0.112	0.175	0.675
Landscape[Oslo]	-0.138	0.116	1.440	0.230
Landscape[Selvik]	0.091	0.110	0.670	0.413
SetAside[RET]Losby	0.025	0.199	0.015	0.901
SetAside[WKH]Losby	0.040	0.193	0.044	0.834
SetAside[NAT]Losby	0.065	0.188	0.118	0.731
SetAside[RET]Oslo	0.107	0.213	0.257	0.612
SetAside[WKH]Oslo	0.038	0.209	0.033	0.856
SetAside[NAT]Oslo	0.145	0.200	0.512	0.474
SetAside[RET]Selvik	0.070	0.182	0.149	0.700
SetAside[WKH]Selvik	0.070	0.182	0.149	0.700
SetAside[NAT]Selvik	0.141	0.192	0.556	0.456

Table 4

MRPP test between aspen associated beetle species without specialists in the three conservation categories. The effect size A ($A = 1$ identify equal groups) with p -value in parenthesis is presented for each comparison. Significant p -values are given in bold.

Landscape	No. of species	Number of sites compared			WKH vs NAT A (p -value)	WKH vs RET A (p -value)	NAT vs RET A (p -value)
		WKH	RET	NAT			
Losby	65	8	7	8	0.021 (0.049)	0.028 (0.031)	0.050 (0.001)
Oslo	59	8	8	8	0.021 (0.058)	0.026 (0.036)	0.039 (0.005)
Selvik	81	8	8	8	0.002 (0.394)	0.009 (0.217)	0.022 (0.050)

Table 5

Summary of trends for generalists and specialists of fungi and beetles, when considering main results with $p < 0.1$. For detailed test statistics, see other tables.

	Generalists species richness	Generalists species composition	Specialists species richness	Specialists species composition
Fungi	Difference WKH lowest. NAT highest in one landscape	No difference	Difference WKH highest and RET lowest in one landscape	Difference NAT different in one landscape
Beetles	Difference WKH highest	Difference RET different	No difference	No difference

(The Norwegian Forestry Act, 1995) and forest certification guidelines <http://www.pefcnorway.org/>, the real-life application will differ between forestry holdings. This means that the ecological characteristics within set-aside categories can show substantial variation between landscapes. This was illustrated by the difference in mean decay of the logs sampled for fungi in the two landscapes (Fig. 2) and the fact that two landscapes (Oslo and Losby) did not hold a sufficient number of logs in the retention patches to be included in the fungi study. Still, the results summarized in Table 5 underline the importance of all three conservation measures for different groups of wood-living species.

Also, because nature reserves cover one continuous area in each landscape, it was not possible to replicate individual reserves. Instead, sites were replicated within one reserve and therefore situated closer to each other than the sites in the other two categories

(Fig. 1). This could have resulted in a larger variation of ecological conditions and therefore of species, in the WKH and RET categories. Still, as this is the reality resulting from the landscape patterns of our conservation measures, we think it is a relevant sampling set-up in an evaluation of how these measures function. We did, however, restrict the extent of each study landscape, to limit the influence from geographical variation in the RET and WKH sites (Fahrig, 2013).

4.2. Old-growth fungi specialists reflect ecological conditions in set-asides

As the fungal communities observed in this study depended on the dead wood units present in the different categories at the onset of the study, they reflected a historical component. Communities

are shaped not only by the present environmental conditions in the plot and in the surroundings, but also by several factors of larger spatial and temporal scale (Kouki et al., 2012; Sverdrup-Thygeson et al., 2014). Today's nature reserves might be situated in landscapes less influenced by historical land use than average. The WKHs can be surrounded by old or young forest, with different times since cutting. Similarly, retention patches will differ in surroundings and time since cutting, but also in pre-cutting condition, ranging from old-growth conditions to thoroughly managed forest. If left to natural processes the dead wood qualities in all categories will improve with time, providing better conditions for demanding old-growth related species. Still, from studies on restoration effort in different European forests, there are indications that responses of the related biodiversity might lag behind (Bouget et al., 2014; Vandekerckhove et al., 2011).

We expected species richness and species composition of fungi to reflect both the qualities and microclimatic conditions (e.g. edge effects) of dead wood present, and the historical component of the surrounding species pool within dispersal distance (serving as dispersal sources). Based on this, we expected the old-growth species to exhibit a higher frequency of occurrence in the nature reserves and woodland key habitats than in the retention patches. This was also confirmed in one landscape. Moreover, the species composition differed between the nature reserve and the other two set-aside categories in this landscape. The long-term stability of the nature reserve vs woodland key habitats and retention patches might have served to retain more of the original species pool in this area. The importance of large areas in near-natural conditions for the species assemblage of fungi has been established in several previous studies (e.g. Junninen et al., 2006; Hottola et al., 2009). As for the generalist fungi, the nature reserve had the highest species richness in Gran, but there was no difference between the retention and woodland key habitats for this group. Moreover, the generalist fungi did not differ in species composition between either of the set-asides.

The high species richness of old-growth fungi species in woodland key habitats, but contrasting species composition from the nature reserve, place WKHs as an important set-aside with different qualities than nature reserves. This is in contrast to field studies in Finland, which found little support for the importance of WKHs in maintaining species diversity and red list species of polypores, most likely due to different definitions of WKHs (Junninen and Kouki, 2006; Hottola and Siitonen, 2008). For lichens and bryophytes in boreal Sweden, in a similar comparison as ours, WKHs proved important (Perhans et al., 2007). The functioning of WKHs in a longer time perspective is however not clear. Both edge effects (Snäll and Jonsson, 2001; Siitonen et al., 2005) and a possible extinction debt (Berglund and Jonsson, 2005, 2008) can reduce the future contribution from WKHs to the conservation of red-listed or specialized species.

No clear trends could be seen between the set-aside categories in Selvik, neither in species richness nor composition. This landscape showed less difference in the important environmental characteristic decay stage of dead wood, which influenced the species richness (Fig. 2). This is in line with other results: in their review of factors important for conservation of polypores, Junninen and Komonen (2011) concluded that at the substrate scale, the decay stage is the strongest determinant of species richness.

4.3. Early-decay aspen specialist beetles are not affected by set-aside type

The experimental part focusing on early-successional beetles controlled for any differences in dead wood decay and quality between set-aside classes, by supplying similar units of dead wood in all the set-aside classes. Contrary to our main prediction, we did

not find any difference for the aspen specialist beetles, neither in species richness nor in composition, between the categories. This can be due to one of several factors.

First, dead aspens are ephemeral substrates, with a fast turnover in associated insect fauna during the first years of decay. The species associated with early decay stages of dead wood are expected to have a high capacity to colonize new habitat patches (Ranius et al., 2011). Our results fitted this prediction as it seemed that the beetles specialized in colonizing early-decay aspen were able to reach the experimental dead wood units regardless of placement.

The ability to reach new aspen habitat will of course depend on whether the distribution pattern of dead aspen in space and time in the forest landscape is within the range of conditions that the species are adapted to. Ranius et al. (2011) studied experimental log-piles of aspen in managed forest and forest reserves in a part of Finland with a low amount of aspen dead wood outside forest reserves. Similar to our study, they found that the dead aspen wood attracted many aspen associated beetle species. Contrary to our results, however, they also found the highest level of species richness of aspen-specialists in areas with high levels of habitat connectivity, and from their text this must be interpreted as sites being within (or close to) reserves. A partly contrasting result is also found in Sahlin and Schroeder (2010). The discrepancy with our data could be related to differences in the extent of decline in large, dispersed aspens in Northern Europe (Kouki et al., 2004; Sahlin and Schroeder, 2010; Lankia et al., 2012).

Second, we might have failed to attract or trap the most demanding and/or dispersal-limited species among the aspen beetle specialists. If we assume that there is a segment of early-successional aspen specialists for which the experimental units were not suitable, we could have missed a potential signal from such species. By comparing with earlier datasets from the same area (Sverdrup-Thygeson and Ims, 2002; Sverdrup-Thygeson and Birkemoe, 2009), we noted only two such possible candidates (*Ampedus nigroflavus* or *Cucujus cinnaberinus*, both red-listed (Kälås et al., 2010)).

The aspen-associated but less specialized beetles showed a different pattern compared with the specialists, with a trend of higher species richness in experimental dead wood units placed in WKHs. This was in unison with results from a study of spruce dead wood in different set-asides, where WKHs had significantly more beetle species, as well as significantly more red-listed species, than the retention patches (Djupström et al., 2008).

Similar to Djupström et al.'s (2008) patterns for spruce beetles, we also found that the species composition of aspen generalist beetles in the reserves differed significantly from that of retention patches in all three landscapes. The fact that the assemblages of this large species group also differed between WKHs and RET (two landscapes) and between WKHs and NAT (one landscape), illustrates that all the set-aside categories contribute in a complementary way to the species pool in the landscape.

4.4. Conclusion

The forest certification guidelines were the same in all forest holdings in our study, but the outcome in terms of ecological quality of the different conservation measures was still heterogeneous, probably due to differences in past and present forestry practises.

In the observational study of fungi on late-decay spruce, one study-landscape exhibited clear differences in spruce dead wood between the set-aside categories. Here, the retention patches had the lowest species richness of fungi specialists associated with old-growth conditions. Also, species composition of old-growth specialist fungi was significantly different in nature reserves compared to either WKHs or retention patches. This emphasizes the importance of large, high-quality set-asides for the species

specialized to the conditions of high-connectivity old growth forest (Junninen and Komonen, 2011). In the landscape with similar dead wood quality across set-aside categories, the species patterns showed little difference.

In the landscape field experiment part of the study, we controlled for differences in microhabitat quality by creating units of dead aspen wood and then followed the early attraction and establishment of beetles. The beetles specialized in early-decay aspen showed no difference between set-aside categories, while the assemblage of aspen generalist beetles was most rich in WKHs and showed clear differences between the set-asides. One possible explanation is that the species' evolutionary adaptations to their ephemeral habitat still are efficient in today's changed forest landscape.

We conclude that retention patches, woodland key habitats and nature reserves all fill important and complementary functions for wood-living species in boreal forest and should be part of forest conservation strategies.

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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.2014.06.036>.

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