

# Conservation value of low-productivity forests measured as the amount and diversity of dead wood and saproxylic beetles

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**Abstract.** In many managed landscapes, low-productivity land comprises most of the remaining relatively untouched areas, and is often over-represented within protected areas. The relationship between the productivity and conservational value of a site is poorly known; however, it has been hypothesized that biodiversity increases with productivity due to higher resource abundance or heterogeneity, and that the species communities of low-productivity land are a nested subset of communities from more productive land. We tested these hypotheses for dead-wood-dependent beetles by comparing their species richness and composition, as well as the amount and diversity of dead wood, between low-productivity (potential forest growth  $<1 \text{ m}^3 \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$ ) and high-productivity Scots pine-dominated stands in Sweden. We included four stand types: stands situated on (1) thin soils and (2) mires (both low-productivity), (3) managed stands, and (4) unmanaged stands set aside for conservation purposes (both high-productivity). Beetle species richness and number of red-listed species were highest in the high-productivity set-asides. Species richness was positively correlated with the volume and diversity of dead wood, but volume appeared to be a better predictor than diversity for the higher species richness in set-asides. Beetle species composition was similar among stand types, and the assemblages in low-productivity stands were largely subsets of those in high-productivity set-asides. However, 11% of all species and 40% of red-listed species only occurred in high-productivity stands, while no species were unique to low-productivity stands. We conclude that low-productivity forests are less valuable for conservation than high-productivity forest land. Given the generally similar species composition among stand types, a comparable conservational effect could be obtained by setting aside a larger area of low-productivity forest in comparison to the high-productivity. In terms of dead wood volumes, 1.8–3.6 ha of low-productivity forest has the same value as 1 ha of unmanaged high-productivity forest. This figure can be used to estimate the conservation value of low-productivity forests; however, as high-productivity forests harbored some unique species, they are not completely exchangeable.

**Key words:** *dead wood; low-productivity forest; mire; Pinus sylvestris; productivity–diversity relationship; saproxylic.*

## INTRODUCTION

According to the Nagoya protocol, an international convention currently ratified by 96 countries, 17% of terrestrial habitats should be protected by year 2020 to improve the status of biodiversity, and the protected areas should be ecologically representative. The representativeness of protected areas can be affected by their productivity, as productivity and species diversity are often positively related (e.g., Waide et al. 1999, Gillman and Wright 2006). There is a tendency to preserve land of lower than average productivity (e.g., Fridman 2000, Scott et al. 2001, Juutinen et al. 2004), as it may be the only land that has been left unmanaged, but also because it constitutes a less expensive way to obtain a large area of set-asides. However, if biodiversity in general is higher in more productive land, there is a risk that an important part of diversity will remain unprotected if mainly low-productivity land is set aside (e.g., Honkanen et al. 2010).

The relationship between species richness and productivity varies depending on spatial scale and taxa, but generally, at least when measured over larger spatial scales, richness

tends to increase with increasing productivity (e.g., Chase and Leibold 2002, Gillman and Wright 2006). One possible explanation of this pattern is that resource availability increases with increasing productivity, leading to larger populations, which in turn results in lower extinction risk, and thus to higher species richness (Srivastava and Lawton 1998). Higher numbers of individuals can also lead to higher species richness through sampling effect: if a local species assemblage is a random sample of a regional species pool, more species will be found in larger samples (Evans et al. 2005). Alternatively, high-productivity environments may be more heterogeneous, and therefore provide a larger variety of different habitats, which facilitate coexistence and thereby increase species richness (Abrams 1995).

The effect of productivity on biodiversity has rarely been studied in forests, but higher productivity has been found to lead to higher species richness in some species groups, such as vascular plants, bryophytes, and polypores (e.g., Gjerde et al. 2005). This may be due to increased resource abundance or habitat heterogeneity, since also the amount and diversity of structures important for biodiversity, such as large trees and dead wood, generally increase with productivity (Sippola et al. 1998, Nilsson et al. 2002, Liira and Kohv 2010). Forests of low productivity are therefore generally considered to be of limited value for species of conservation concern (Cederberg 1997). Nevertheless, such forests

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might host special assemblages of species, e.g., certain insects and lichens associated with slow-growing trees in sun-exposed habitats that are not found on more productive stands (Cederberg 1997). Since forests with lower productivity are often less affected by forest management, e.g., logged less intensively (Storaunet et al. 2005), they may also be valuable for species requiring long habitat continuity.

Especially in countries where forests are intensively managed, low-productivity forests may constitute a large proportion of all remaining unmanaged forest land. For instance in Sweden, low-productivity forests (defined as land with an annual wood production rate  $<1 \text{ m}^3/\text{ha}$ ) cover 18% of the forested land (Swedish Forest Agency 2014) and should, according to the current forestry law, be left unmanaged. Thus, they constitute 72% of all forest land exempted from forestry (Swedish Forest Agency 2014). To our knowledge such general restrictions do not exist in other regions, but low-productivity forests are nevertheless often over-represented within protected areas (e.g., Finnish Forest Research Institute 2014) and less affected by forest management (e.g., Storaunet et al. 2005). Since low-productivity forests are managed less intensively, they have usually been given only little attention by conservation biologists and there is thus a lack of knowledge on the conservation value of these forests. There are no empirical studies specifically examining the species assemblages in low-productivity forests and it is not known whether low-productivity stands represent a similar habitat type as more high-productivity forests. It is thus not possible to determine whether they should be included in the area of protected forest land, or be considered as a separate, distinct habitat type when assessing conservation targets. Therefore, it is necessary to obtain more knowledge on the biodiversity in low-productivity forests and compare them to more productive forest land to properly assess their conservational value.

In this study, we examine the importance of low-productivity boreal forests for saproxylic (i.e., dead-wood-dependent) beetles. We survey beetle assemblages in two different types of low-productivity forests, stands on thin, rocky soils and mires (the main categories of low-productivity forest in Fennoscandia), and in two types of high-productivity forests, including older managed stands and unmanaged, voluntarily set-aside stands. This is done in four regions in a south-north gradient in Sweden. Along the south-north gradient, there is not only a difference in climate, but also a difference in management history, with a longer history of more intensive management in the south (Angelstam 1997).

We hypothesize that beetle species richness is higher in high-productivity forests due to higher resource abundance (volume of dead wood) or heterogeneity (diversity of dead wood). Due to a harsher climate and generally lower productivity, we expect the overall species richness to be lower in the north than in the south. Among the low-productivity forest types, we expect those on thin soils to be more species rich than those on mires, as they may be more variable in productivity and microclimate, i.e., more heterogeneous. Furthermore, we expect that the species composition will differ between high-productivity and low-productivity stands, as they at least in part represent different environment. For instance, certain species, due to their affinity for slow-growing trees, sun-exposed habitats, or requirement of long habitat

continuity, may occur predominantly in low-productivity forests. To test these hypotheses, we compare the beetle assemblages as well as dead wood volume and diversity in low-productivity and high-productivity stands. We assess whether species richness differs among high-productivity and low-productivity stands and whether the possible differences are explained by resource abundance or heterogeneity. Second, we examine whether the beetle assemblages in low-productivity stands are distinct or a subset of those in high-productivity stands. In addition, we estimate the standing volume and tree growth rate to validate the categorization of stands as high-productivity or low-productivity.

## METHODS

### Data collection

Saproxylic beetle assemblages and forest structure were surveyed in 192 Scots pine (*Pinus sylvestris*)-dominated forest stands located in four different vegetation zones in Sweden (Fig. 1; hemiboreal, southern boreal, middle boreal, and northern boreal vegetation zones (Ahti et al. 1968)). In all four zones, Norway spruce (*Picea abies*) and Scots pine are the two dominating tree species and, in low-productivity forests, Scots pine is always dominating. We included four different types of stands: two types of low-productivity stands (forested mires and stands on “thin soil,” i.e., on rocky outcrops, hilltops, or bare rocks) and two types of high-productivity stands (old managed stands and unmanaged set-asides). The stands were arranged in blocks of four, each

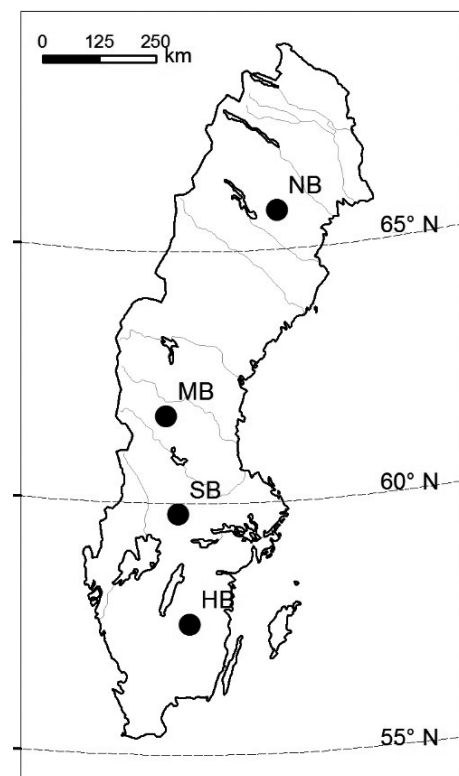


FIG. 1. Location of the study regions (HB, hemiboreal; SB, southern boreal; MB, middle boreal; NB, northern boreal) in Sweden.

block including all four stand types. Within each of the four regions, we had 12 blocks of stands, i.e., a total of 48 stands.

We selected study stands based on stand information provided by the landowner, the forest company Sveaskog AB. In each of the four regions included in our survey, we first selected 12 pine-dominated stands (pine basal area >60%) that were set aside from forestry based on their presumed conservational value (assessed indirectly by occurrence and availability of a number of structural indicators, such as old trees and standing and downed dead wood). Close to each of the 12 set-asides, we selected two low-productivity stands (one located in mire and one on thin soil) that, according to the information from the landowner, fulfilled the following criteria: pine-dominated stands with a tree cover >10% of the ground area but a potential annual timber productivity <1 m<sup>3</sup> per ha. Finally, to each of the triplets, we selected a mature (>80 yr old) high-productivity managed pine forest (pine basal area >60%). Since all chosen stands were pine-dominated, their average productivity was likely lower than the overall average in the studied regions.

The fieldwork was conducted during spring and autumn 2016, since the largest number of dead-wood-dependent beetle species occur as adults at that time (Wikars et al. 2005). The reason for this is that, for many species, the adults emerge in the autumn and hibernate and can thus be found both in spring and autumn. Eight study plots with a radius of 20 m were set up in each stand (i.e., the total area surveyed was 1.005 ha per stand). Within the plots, beetles were searched on standing and downed pine dead wood with a diameter of >10 cm and length of >2 m (including all dead trees that were completely inside the plots and every second of the downed dead trees that crossed the plot border). Diameter, length, proportion of bark left, type (standing or fallen tree), and age (died within last two years with needles still present or older) were recorded for all dead wood items, but to keep the survey effort reasonable, a maximum of five dead wood items per plot were surveyed for beetles. However, only a very small proportion of plots (14 out of the total of 1,536 plots) contained more than five dead wood items, which implies that nearly all dead wood items within the plots were included in the beetle survey. To obtain a comparable measure, we surveyed a constant area of 0.6 m<sup>2</sup> (equaling a tree with a diameter of 10 cm surveyed to the height of 2 m) per dead wood item. First, the trunks were searched visually to record all beetle galleries. Second, any loose bark and soft wood (to a depth of approximately 5 cm) was removed and sieved and all beetles (both adults and larvae) found this way were identified and recorded. Adults that could not be identified in the field were collected for a later laboratory identification. Many larvae and galleries were only identified to genus level as, in many cases, it is impossible to identify them to the species level. In addition to these measures, we also measured the basal area of all living trees (with a relascope), and the diameter, height (using a hypsometer), and age of one living Scots pine (randomly selected among the larger pines) at each plot.

#### *Statistical analyses*

The volume of intact dead trees was calculated using Laasasenaho's (1982) volume function for pine and of broken

trees using the geometric formula for a circular cylinder for broken trees. The diversity of dead wood was calculated as the number of different dead wood types present in each stand (Siitonen et al. 2000). The dead wood items were classified into 18 types based on three characteristics that are important for saproxylic organisms (Dahlberg and Stokland 2004): diameter (10–20, 20–29, or ≥30 cm), position (standing or downed) and decay stage (estimated on a three-point scale based on the age of the trees and presence of bark: fresh trees that had died within the last two years, older trees with bark still present, or older trees without bark).

To obtain an estimate of stand productivity, we calculated average tree growth rates by dividing the volume of living trees (assessed from tree height and basal area, Cernold [1981]) by the average tree age. Note that this method may underestimate the growth rates for managed stands if these have been thinned in the past, as well as for older stands since an increasing proportion of the accumulated growth will disappear due to tree mortality as the stand ages.

We used two-way analysis of variance to compare stand structure among stand types and regions; the tested variables were tree growth rate, stand volume, the average age and basal area of living trees, total dead wood volume, dead wood diversity, proportion of standing dead trees and mean diameter of dead wood items (in each of these stands considered as samples).

To compare the beetle species richness among the four stand types we used sample-based rarefaction curves with 95% confidence limits (Hsieh et al. 2016a). We constructed the rarefaction curves by considering stands as samples (stands constitute a standardized sample with a constant area surveyed and, with the exception of a few stands that contained extremely high amounts of dead wood, all dead wood items within the study plots surveyed) and using presence-absence data on the species' occurrence in the stands. The rarefaction curves were constructed independently for each of the four regions.

To examine the effect of stand-scale factors on beetle species richness, we modeled the number of species per stand using generalized linear mixed models (GLMMs) with Poisson distribution and logarithmic link function. Block (i.e., the group of four stands) was included as a random variable, while the potential explanatory variables were region and the volume and diversity of dead wood. Although the volume and diversity of dead wood were moderately correlated (Pearson's  $r = 0.52$ ), there was no apparent collinearity between these variables since the variable inflation factor (VIF) < 3 (Zuur et al. 2010) and both variables were kept in the model. To enable comparisons of effect sizes, we standardized the variables included (Gelman 2008). We generated a set of models including all possible combinations of the explanatory variables and compared these using Akaike's information criteria corrected for sample size (AIC<sub>c</sub>). Since we were unable to detect a single best model, we included all models with a difference of AIC<sub>c</sub> < 4, and performed model averaging over these models to estimate the effect sizes for each explanatory variable (Grueber et al. 2011). The models are presented in Appendix S1. In addition, we calculated relative importance of each of the explanatory variables (RVI) by summing the AIC<sub>c</sub> weights of all models in which the variables occurred.

Red-listed species were too few to be analyzed as a separate group. Therefore we only counted the numbers of red-listed species occurring in different stand types. We considered all species that have been included in the Swedish Red lists published during the period 2000–2015 (the Red lists are updated every five years; Swedish Species Information Centre 2015).

We used permutational multivariate analysis of variance (PERMANOVA; Anderson 2001) to test whether the composition of beetle communities differed between stand types. The PERMANOVAs were run separately for each region, performing 5,000 permutations, using the Bray-Curtis dissimilarity measure and data on species' abundances (number of observations per stand). Rare species that occurred in only one or two stands within the entire data set (a total of 18 species) were excluded from the analysis. To illustrate the community composition, we performed nonmetric multidimensional scaling (NMDS) separately for each region. The NMDS were run using Bray-Curtis dissimilarity measure, performing 500 runs with random starting configurations for the real data, and searching for two-dimensional solutions. In addition, we examined the nestedness of the species communities, i.e., whether the communities with lower species number were a subset of the more species-rich communities. This was done by calculating the proportion of the species found in a particular stand type that also occurred in the more species-rich stand types within the same region. Finally, we calculated the numbers of unique species for each stand type, as well as for high-productivity and low-productivity stand types within each region, again excluding rare species.

All statistical analyses were performed with R 3.3.1 (R Core Team 2016), using package iNEXT (Hsieh et al. 2016b) for the rarefaction curves, packages lme4 (Bates et al. 2015), MuMIn (Barton 2016), arm (Gelman and Su 2016), and car (Fox and Weisberg 2011) for the GLMMs, and packages vegan (Oksanen et al. 2016) and rvaIDEmem-oire (Hervé 2016) for the PERMANOVAs and NMDS.

## RESULTS

### Species richness

In total, we made 7,432 observations (on average 38.7 per stand; an observation refers to a species occurring on one dead wood item) of 90 species of saproxylic beetles. Of these, 22 had, at some point during the period 2000–2015, been Red-listed in Sweden, and 13 are Red-listed according to the most recent Red list (Swedish Species Information Centre 2015; Appendix S2). The species richness was overall higher in more productive forest types; in all regions, the species richness was highest in set-asides and lowest in stands on mires. Managed stands had similar species richness as stands on thin soils, except for the northernmost region where stands on thin soils were more species rich. Of the two low-productivity stand types, stands on thin soils had generally higher species richness than stands in mires (Fig. 2). The highest number of Red-listed species, 16, were found in the set-asides, while 13 were found in stands on thin soils, 10 in managed stands and 8 in stands in mires. This pattern was consistent also for the species included in the most recent Red list (11 species found in set-asides, 8 in stands on thin soils, 5 in managed stands, and 4 in mires).

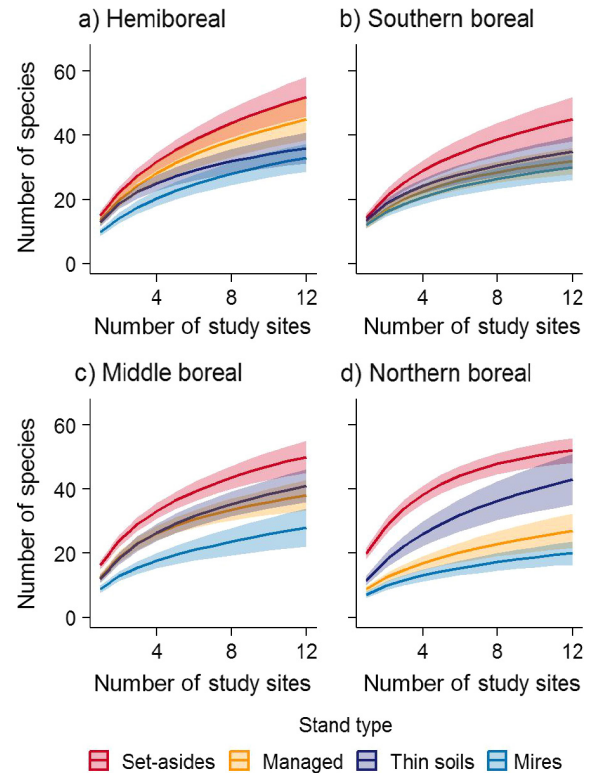


FIG. 2. Sample-based rarefaction curves (with 95% confidence limits) presenting the cumulative number of beetle species relative to the number of surveyed stands in the different stand types and regions.

At the stand level, species richness was positively correlated with both volume and diversity of dead wood (Table 1). After controlling for the effects of dead wood volume and diversity, region was less important; the only difference was slightly lower species richness in southern boreal than in hemiboreal stands.

### Species composition

The community composition differed among stand types in the hemiboreal and northern boreal regions (PERMANOVA  $P = 0.04$  and  $P < 0.001$ , respectively; Appendix S3), while no differences were observed in the other regions ( $P = 0.34$  and  $0.07$  for southern and middle boreal regions,

TABLE 1. The model-averaged parameter estimates (with 95% confidence intervals) for the GLMM of stand-scale beetle species richness (hemiboreal used as a reference level for the region).

Factor	Estimate	95% CI	RVI
Intercept	2.509	2.42, 2.59	
Region			0.26
Southern boreal	-0.137	-0.27, -0.01	
Middle boreal	-0.074	-0.20, 0.06	
Northern boreal	-0.053	-0.19, 0.08	
Dead wood volume	0.521	0.35, 0.69	1.00
Dead wood diversity	0.215	0.05, 0.38	1.00

Note: RVI, relative importance of explanatory variables.

TABLE 2. Numbers of unique species, i.e., species found from only one stand type or on only high-productivity or low-productivity stands within a region.

Stand type	Hemiboreal	Southern boreal	Middle boreal	Northern boreal	All regions
Set-asides	5 (2)	8 (2)	8 (2)	12 (3)	5 (4)
Managed forests	5 (0)	0 (0)	1 (0)	1 (0)	0 (0)
Thin soils	3 (0)	2 (0)	5 (1)	3 (0)	0 (0)
Mires	0 (0)	1 (0)	1 (0)	0 (0)	0 (0)
Productive stands	17 (2)	11 (2)	13 (2)	14 (3)	8 (4)
Low-productivity stands	3 (0)	5 (0)	6 (1)	4 (0)	0 (0)

Notes: Numbers are given for all species and species red-listed in Sweden in the latest assessment in 2015 (in parentheses). Species found on fewer than three stands within the whole data (18 out of 90 for all species, 3 out of 13 for red-listed species) are excluded.

respectively). These patterns are also illustrated in the NMDS graphs (Appendix S4). In the northern boreal region species composition differed among all stand types (pairwise comparisons:  $P < 0.05$ ), except for mires and stands on thin soils that had similar species communities (pairwise comparison:  $P = 0.13$ ). In the hemiboreal region, there were no differences among stand types (pairwise comparisons:  $P > 0.05$ ). Within each of the regions, forests on high-productivity land harbored more unique species than forests on low-productivity land (Table 2). When assessed across all regions, only set-asides hosted unique species, and the species communities on low-productivity land were nested subsets (measured as the percentage of shared species between stand types) of those found on more productive land (Table 3).

#### Stand structure

The characteristics of living trees and dead wood differed among stand types. The productivity (measured as growth

TABLE 3. Total numbers of beetle species observed in the different stand types within each region and the nestedness of species communities, here expressed as the proportion of species common to both stand types within a region.

Stand type	Species	Common species (% of all species) with		
		Set-asides	Thin soils	Managed
<b>Hemiboreal</b>				
Set-asides	55			
Thin soils	36	32 (86)		27 (75)
Managed forests	45	40 (89)		
Mires	33	32 (97)	25 (76)	29 (88)
<b>Southern boreal</b>				
Set-asides	45			
Thin soils	35	28 (80)		
Managed forests	32	26 (81)	24 (75)	
Mires	30	23 (77)	22 (73)	20 (67)
<b>Middle boreal</b>				
Set-asides	50			
Thin soils	41	35 (85)		
Managed forests	38	34 (90)	31 (82)	
Mires	28	25 (89)	23 (82)	21 (75)
<b>Northern boreal</b>				
Set-asides	52			
Thin soils	43	37 (86)		
Managed forests	27	25 (93)	25 (93)	
Mires	20	19 (95)	20 (100)	17 (85)

rate, standing volume, and basal area of living trees) was higher in high-productivity than low-productivity stands, thus validating the a priori categorization, and stands on thin soils had higher productivity than stands in mires (Fig. 3a–c, Table 4). Tree age was highest in set-asides followed by stands on thin soils (Fig. 3d, Table 4). The volume of dead wood was highest in set-asides and lowest in mires, but did not differ between stands on thin soils and managed stands (Fig. 4, Table 4). Mires had also the lowest dead wood diversity, whereas differences among the other three stand types depended on the region (Fig. 3e, Table 4).

## DISCUSSION

### Beetle species richness

This is, to our knowledge, the first study to examine how species richness and community composition differ between high-productivity and low-productivity forests. Our results show that forest on low-productivity land has lower beetle species richness and harbors fewer Red-listed species than set-asides situated on high-productivity land (Fig. 2). This is consistent with the previous observations that species richness generally increases with a productivity gradient within high-productivity boreal forests, for beetles (Stokland 1997, Sippola et al. 2002) as well as for other species groups such as polypores (Gjerde et al. 2005), birds (Stokland 1997, Honkanen et al. 2010), and vascular plants (Chen et al. 2004, Reich et al. 2012).

The positive correlation between species richness and productivity has been suggested to be derived from higher resource availability in more productive environments (e.g., Srivastava and Lawton 1998). Concurrently, we found a positive correlation between species richness and resource availability, here expressed as dead wood volume (Table 1). Furthermore, we also found that both species richness and dead wood volume were higher in the high-productivity set-asides than in low-productivity stands. This was expected, as dead wood volume generally correlates with the volume of living trees (Sippola et al. 1998, Ranius et al. 2004), which in turn increases with productivity. In addition, dead wood volume is known to be decreased by forest management (e.g., Siitonen 2001), which was evident also in our data: in high-productivity, managed stands, dead wood volumes as well as species richness were generally similar to those in low-productivity stands. This further emphasizes the importance of dead wood as a driver of beetle species richness. Our results are, thus, in accordance with the suggestion that

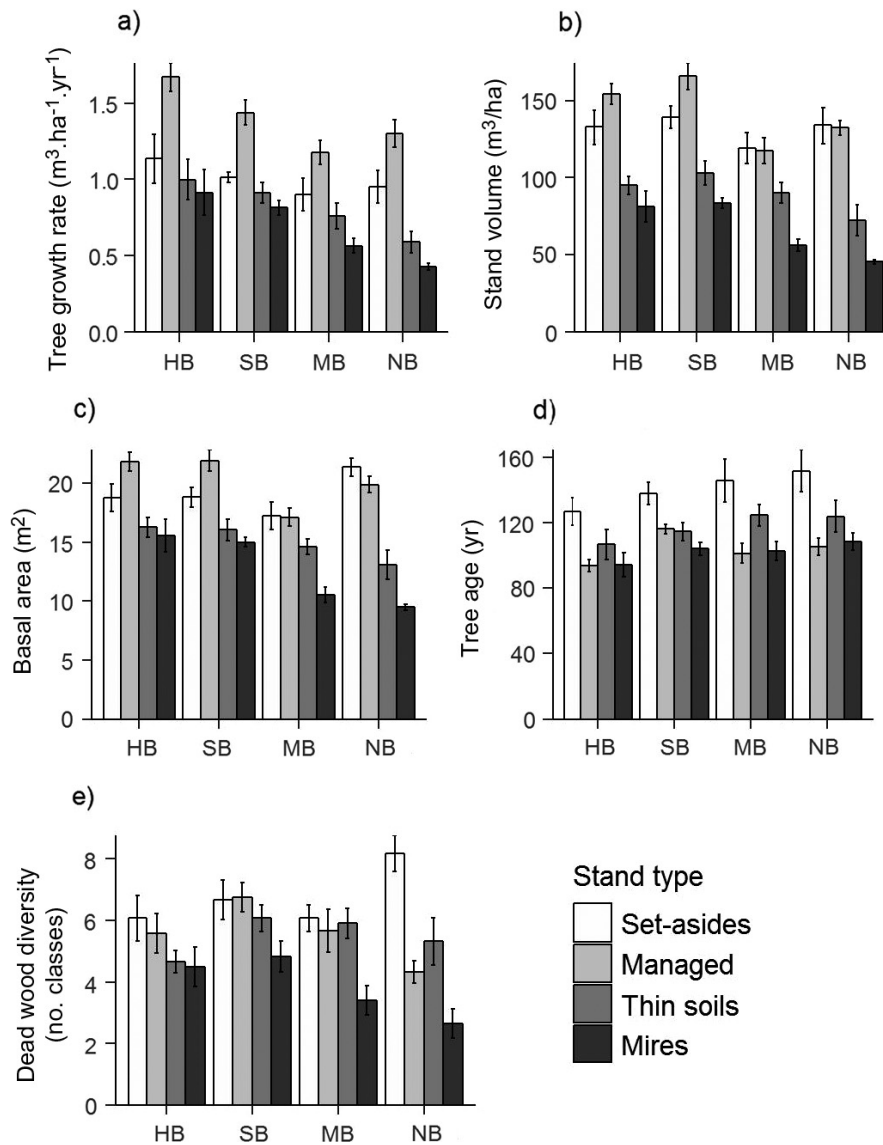


FIG. 3. Growth rate ( $\text{m}^3 \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$ ), volume ( $\text{m}^3/\text{ha}$ ), basal area ( $\text{m}^2$ ), and age of living trees and the diversity of dead wood in the different regions (HB, hemiboreal; SB, southern boreal; MB, middle boreal; NB, northern boreal) and stand types (means  $\pm$  SE).

TABLE 4. The effects of stand type and region on stand structural variables.

Variable	Stand type		Region		Stand type $\times$ region	
	$F_{3,176}$	$P$	$F_{3,176}$	$P$	$F_{9,176}$	$P$
<b>Living trees</b>						
Tree growth rate	44.88	<0.001	13.47	<0.001	–	–
Standing volume	78.32	<0.001	12.09	<0.001	–	–
Basal area	62.69	<0.001	12.62	<0.001	4.15	<0.001
Tree age	21.87	<0.001	3.91	<0.001	–	–
<b>Dead wood</b>						
Total volume	18.49	<0.001	1.91	0.129	–	–
Diversity	18.43	<0.001	2.57	0.056	2.77	0.047

Notes: Results are from two-way ANOVAs. The interaction term between stand type and region was included only when it was significant ( $P < 0.05$ ). Results of pairwise comparisons are provided in Appendix S5. Cells with dashes refer to cases where the interaction term was not included in the ANOVA.

higher species richness observed in more productive environments is generated by higher resource availability (for saproxylic species [Sippola et al. 2002, Gjerde et al. 2005, Svensson et al. 2016]; birds [Hurlbert 2004, Evans et al. 2008, Honkanen et al. 2010; vascular plants [Chen et al. 2004, Reich et al. 2012]).

In addition to the amount of resources, we found that also the diversity of dead wood (at the stand scale) correlated positively with beetle richness. This is in accordance with the hypothesis that higher species richness in more productive environments stems from higher habitat heterogeneity (Abrams 1995), and with previous studies reporting that dead wood diversity can be an important driver of saproxylic beetle diversity (e.g., Similä et al. 2003, Lassauce et al. 2011). However, in our study, the dead wood diversity did not vary among stand types as clearly as volume: in most regions, only stands on mires differed by having lower diversity of dead wood than other stand types, while dead wood diversity in

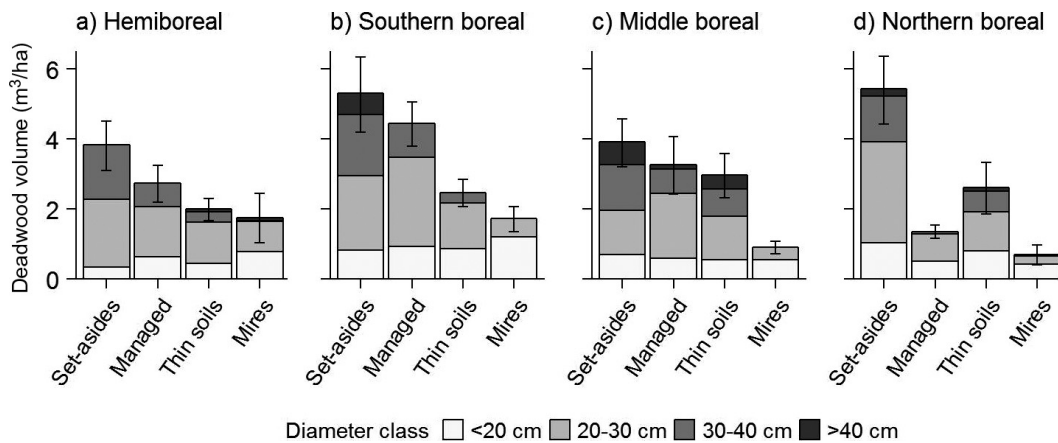


FIG. 4. Volume of dead wood ( $\text{m}^3/\text{ha}$ , means  $\pm$  SE) in different regions and stand types, divided into diameter classes.

both types of high-productivity stands and low-productivity stands on thin soils was approximately the same. Thus, although we found species richness to be positively correlated to both volume and diversity of dead wood, volume seemed to be more important than diversity in explaining the high richness in high-productivity set-asides. However, disentangling the effects of dead wood volume and diversity is generally difficult (e.g., Seibold et al. 2016) and these two variables were found to be correlated in our data. Thus, the conclusion of their importance should be regarded with some caution. In general, there appears to be little consensus regarding the relative importance of resource amount and heterogeneity in explaining the relationship between productivity and species diversity, as some studies report both to be important (Sipola et al. 2002, Chen et al. 2004, Reich et al. 2012), while others indicate that resource heterogeneity is unimportant (Evans et al. 2008, Honkanen et al. 2010).

Contrary to our hypothesis, we did not find the overall species richness decreasing toward the north. Instead, the regional differences appeared to depend on the stand type, and were best explained by dead wood volumes. The difference in species richness between set-asides and the other stand types was most pronounced in the north. Set-asides had higher dead wood volumes in the northern boreal region than elsewhere, which is possibly explained by differences in the history and intensity of forest use: the human impact has generally been larger in the southern parts of the boreal region (Angelstam 1997), and thus even the set-aside stands have likely often been subject to forestry. In northern regions, set-aside stands remain closer to natural state, with higher dead wood volumes and diversity.

#### Beetle species composition

The composition of beetle assemblages was generally similar among stand types, and the species occurring in the low-productivity stands appeared to be a subset of the species found in the more species-rich set-asides. Thus, we did not find support for the hypothesis that low-productivity stands would host a specific subset of beetle species. It has been hypothesized that certain species would prefer low-productivity stands due to their association with sun-exposed and slow-growing wood that can be common in such forests

(Cederberg 1997). We found higher basal area of living trees in high-productivity than low-productivity stands, suggesting that the sun exposure is indeed different, but apparently this did not affect the species composition. In contrast, many studies on saproxylic insects have reported an effect of sun exposure, but such studies have often compared habitats that show greater contrast in sun exposure compared to our study (e.g., between clearcuts and forests; McGeoch et al. 2007, Sahlin and Ranius 2009) or used sampling methods that measure flight activity rather than abundance (e.g., window traps), and thus may overestimate the positive effect of sun exposure (Sverdrup-Thygeson and Ims 2002, Koch Widerberg et al. 2012; see, however, Lindhe et al. 2005). Also the estimated tree growth rates and standing volumes differed among stand types, as expected. In managed stands, both growth rates and standing volume were much higher than those of low-productivity forests. In addition, the set-asides had high standing volume, even though the growth rates often were closer to those observed in low-productivity stands. Although we may have underestimated the growth rates in set-asides due to the high age of these stands, it is also possible that this reflects the general phenomenon that land of low productivity is overrepresented among set-asides (e.g., Fridman 2000, Scott et al. 2001). The small difference in growth rates may thus partly explain the similarity in species composition between low-productivity stands and set-asides.

Eight species were found only in high-productivity stands (Table 2; species found in fewer than three stands were excluded). Five of these were unique for set-asides, and four of these five species (*Dropephylla clavigera*, *Olisthaerus substriatus*, *Orchesia fasciata*, and *O. minor*) were Red-listed according the latest assessment (Swedish Species Information Centre 2015). This implies that 11% of all observed species and 40% of Red-listed species were confined to productive forests (including only species found in at least three stands). Thus, several of the species present in high-productivity forests are apparently rare or missing in low-productivity forests. One reason for this could be that high-productivity forests contain a higher density of dead wood and more large-diameter woody debris, which may both favor saproxylic species (Dahlberg and Stokland 2004, Sahlin and Schroeder 2010, Ranius et al. 2011). However, as all of these eight species were relatively infrequent (five or fewer

observations in the whole data), there may also be some random variation in their occurrence.

#### *Differences between low-productivity forest types*

Of the two types of low-productivity stands studied, stands on thin soils had higher species richness than mires. The composition of beetle assemblages was similar in both types of low-productivity forests, suggesting that these stand types are functionally similar habitats for saproxylic beetles. Thus, the difference in species richness is most likely explained by the lower volume and lower diversity of dead wood found in mires, especially in the northern regions. Stands on mires also appeared to have slightly lower productivity (due to lower observed tree growth rates), and lower standing tree volume than stands on thin soils, which likely has contributed to the observed differences in dead wood volume.

#### *Implications for conservation*

Low-productivity forests have a lower conservation value than high-productivity forests, as they contain less dead wood and thus have a lower beetle species richness. Moreover, low-productivity forests are not a distinct habitat with a specialized beetle fauna: although there were certain species that were only found in the high-productivity stands, a majority of the observed species still occurred in stands of both productivity classes. This implies that, by setting aside low-productivity forests, it is possible to obtain a relatively similar conservation effect as by setting aside high-productivity forest land if a larger area is set aside. If, for example, the volume of dead wood is used as a measure of the conservation value of an area, on average 1.8 and 3.6 times (1.3–2.0 and 2.0–8.0, depending on the region) larger area of stands on thin soils and mires, respectively, would be required to achieve the same conservation effect on saproxylic species in comparison to setting aside high-productivity land.

However, this comparison is reasonable only if species composition is similar among productivity classes. As several of the observed species, including several Red-listed species, were confined to the high-productivity stands, such forests seem to have an additional conservation value that cannot be fully compensated for by setting aside larger areas of low-productivity forests. Furthermore, in this study, both high-productivity and low-productivity stands were dominated by Scots pine, and consequently we only studied dead wood of Scots pine, which likely contributed to the similar beetle assemblages among stands. By selecting only pine-dominated stands for the study, we have also likely excluded the most productive stand types, which may have increased the similarity in species assemblages. If other tree species and other types of habitats, including the most productive forest types, are considered, different productivity classes may host more distinct beetle communities (e.g., Similä et al. 2002). In that case, setting aside low-productivity forests cannot compensate for loss of high-productivity land.

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