



Effectiveness of local conservation management is affected by landscape properties: Species richness and composition of saproxylic beetles in boreal forest clearcuts



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ABSTRACT

Landscape context is known to affect species diversity patterns and can even influence the effectiveness of local conservation management in agricultural landscapes. For other land uses, like forestry, landscape effects are poorly known. We aimed to determine whether landscape composition modifies the response of saproxylic beetle species to local habitat and conservation management, with focus on dead wood and prescribed fire, in managed boreal forest landscapes. We surveyed beetles on 32 clearcuts in central Sweden. We measured local (fire, dead wood, flower resources, patch size) and landscape factors (fire, dead wood within 1–2 km radius), and analysed interactions between these in mixed models. The response was species richness of beetles with different habitat specialization – conifer specialists, deciduous specialists, flower visitor and pyrophilous species, and abundance of a red-listed species, *Tragosoma depsarium*. Local and landscape factors, as well as interactions between them, affected species richness patterns. Prescribed fire and amount of dead wood, both on local and landscape scale, affected species richness and composition of several groups. There were interactions between local and landscape factors in five models out of six. Locally, we observed a positive response to flower richness for several groups, while the response to prescribed fire and dead wood amounts typically was affected by landscape factors. The results suggest that effectiveness of local conservation management is affected by landscape properties; the positive effects of local dead wood amounts and burning occurred on clearcuts in landscapes with large amounts of dead wood, but not in landscapes with small amounts of dead wood.

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1. Introduction

Understanding landscape effects on local diversity patterns and ecological processes is fundamental for developing successful approaches for biodiversity conservation (Tschardt et al., 2012). One reason for this is that landscape composition can influence the effectiveness of local conservation management (Tschardt et al., 2005; Batáry et al., 2011). Habitat improvement actions (e.g., agri-environment schemes, AES) appear to be most effective in simple landscapes (with 1–20% non-crop habitats) (Rundlöf and Smith, 2006; Rundlöf et al., 2008; Batáry et al., 2010; Concepción et al., 2012; Smith et al., 2010). This is because in more complex landscapes (>20% non-crop habitats), organisms move between habitats and therefore biodiversity is high everywhere, while in cleared landscapes (<1% non-crop habitats) the

species pool is so small that the local species richness does not respond to conservation management. So far, landscape effects on local conservation effectiveness have been studied in agricultural systems, but rarely in other managed habitats, such as forests.

Wide regions of boreal Europe and North America are dominated by managed forest land harvested by clearcutting. In such forests, conservation actions to mitigate negative effects of clearcutting are often applied in form of green tree and dead wood retention (Franklin et al., 1997; Gustafsson et al., 2012). Prescribed fire is also used in some regions, commonly in Fennoscandia, to promote species that suffer from loss of natural disturbance dynamics due to fire-suppression (Granström, 2001; Vanha-Majamaa et al., 2007). Local effects of these actions have been studied on many taxa (tree retention: Rosenvald and Löhmus, 2008; Gustafsson et al., 2010; fire: Martikainen et al., 2006; Toivanen and Kotiaho, 2007), while the importance of landscape composition for the effectiveness of living-tree and dead wood retention, and prescribed fire, in promoting species diversity is largely unknown. However, it has been suggested that the species richness

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of fire-dependent insects after habitat restoration depends on the regional context, with more species colonising burned forests where the management history is shorter (Kouki et al., 2012).

A large proportion of forest species are saproxylic, i.e. dead wood dependent (for instance, about 25% in Finland; Siitonen, 2001), and many of them are today declining or threatened (Stokland et al., 2013). This is because dead wood amount and diversity decreases when forests are managed (Siitonen, 2001; Similä et al., 2003). Saproxylic beetles are dependent on dead wood for their larval development. Other requirements on the habitat are less known, but some species visit flowers to feed on pollen and nectar as adults (Palm, 1959). Beetles are known to respond to flower density or species richness in grassland (Hegland and Boeke, 2006) and deciduous forest habitats (Cerambycidae, Fayt et al., 2006; Müller et al., 2008). However, to what extent flowers constitute a limiting factor for saproxylic beetles in boreal forests is not known. Forest fires create large amounts of dead and dying trees, which benefit many saproxylic organisms. There are also certain species that are specifically associated with burned habitats (Boucher et al., 2012; Toivanen and Kotiaho, 2007). Despite well studied local effects, few studies have addressed the importance of surrounding landscape for saproxylic diversity (Sverdrup-Thygeson et al., 2014). Thus, the knowledge is still limited on the relationship between saproxylic species diversity and distribution of dead wood on different spatial scales, recent fire history in the landscape, and interactions between local and landscape effects.

We studied saproxylic beetles on clearcuts in managed boreal forests and assessed effects of local management and landscape context on the species richness and species composition of all saproxylic beetles and within ecological groups connected to specific resources: (i) coniferous wood specialists, (ii) deciduous wood specialists, (iii) pyrophilous species, and (iv) flower visitors. Moreover, we analysed abundance of the most frequently occurring red-listed species. For species richness, interactions between local and landscape factors were tested in order to assess the importance of landscape context for local conservation management. We posed the following question: is species richness and composition affected by local habitat characteristics and landscape composition

and if so, are the local effects different depending on the landscape context? We expected that species richness would respond positively to high dead wood amount and to resources associated with their habitat specialisation locally. We also hypothesized that resources on landscape scale would be prerequisite for a positive local response to dead wood amount and burning.

2. Methods

2.1. Site selection

The study was carried out in a boreal forest region in south-central Sweden, approximately 22,500 km², dominated by managed forests with even-aged stands of Scots pine *Pinus sylvestris* and Norway spruce *Picea abies*. Green tree retention is applied (according to the certification standards at least 10 live trees per hectare) and dead wood is created during harvesting as artificial snags, felled logs, tree-tops and branches. The average amount of dead wood in managed forests in Sweden is about 6 m³ ha⁻¹ (Fridman and Walheim, 2000).

We initially located all burned clearcuts in the region, using data from the Swedish Forest Agency and the two main forest companies in the region, Bergvik Skog and Sveaskog. Based on locations of burned clearcuts, we selected eight landscapes (approximately 10 × 10 km) within the region, with at least 20 km distance between them (Fig. 1). Within each landscape, we selected 3–5 clearcuts separated by at least 500 m; in total 32 clearcuts were surveyed in the region. Where possible, two clearcuts with prescribed fire and two without were selected per landscape, but if only one burned clearcut was available, an additional burned clearcut was added in another landscape in order to balance the number of both types on the regional level. Some of the burned sites were salvage-logged after wildfires and some were clearcut first and then subjected to prescribed burning.

The selected clearcuts had been cut/burned 3–5 years ago. This age interval was chosen because of higher probability to collect species that actually reproduce on the sites, as studies on more recently disturbed sites may predominantly collect individuals

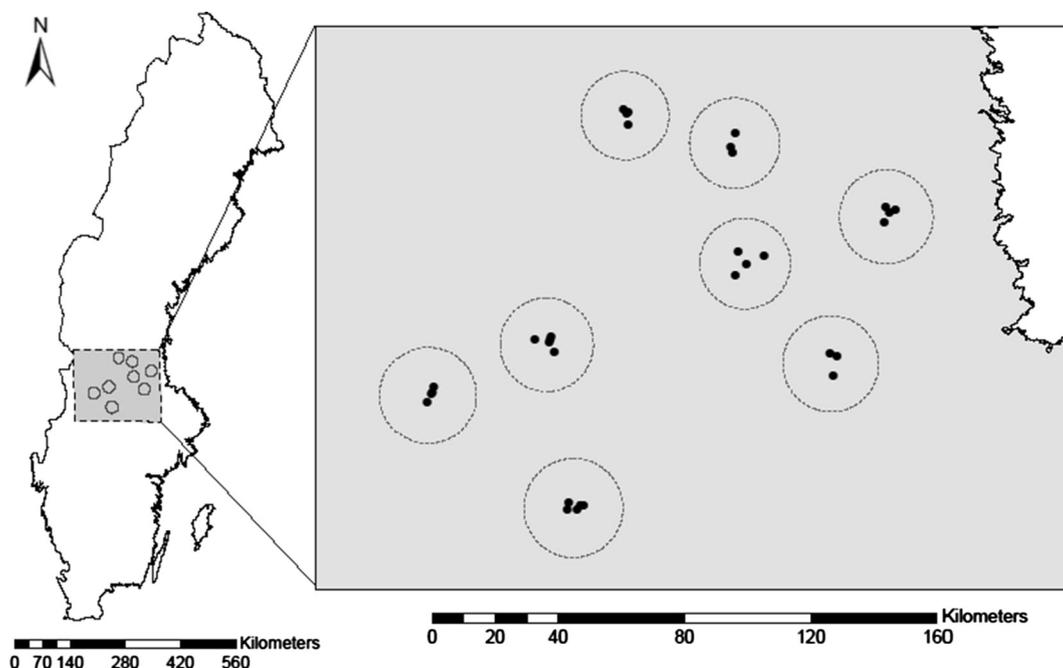


Fig. 1. Map of the study region in central Sweden; locations of the eight landscapes are marked with open circles and the 32 individual sites are marked with filled black circles.

from other sites that were attracted to the disturbance (Saint-Germain et al., 2004). Dead wood created at the disturbance are then in a phase suitable for many species living under the bark and in moderately decayed wood (Stokland et al., 2013).

Within each clearcut, a trapping area was selected, based on abundance of snags; at least seven were required in order to set up all traps. Where possible, the trapping areas were at least 50 m from any forest or water edge. We aimed at surveying areas of approximately the same size in all clearcuts, irrespective of clearcut size. The study site area (hereafter site) was defined by the trapping area plus a 50 m buffer measured by GPS (Garmin) from the outermost trap locations. The site area had an average size (\pm S.D.) of 2.3 (\pm 0.5) ha.

2.2. Beetle sampling

Beetles were collected with window traps and coloured pan traps from all clearcuts during summer 2011, from 1st of June until 22nd of August. On each clearcut, three window traps (0.2×0.2 m) were set on snags 1.5 m above ground and two clusters of three pan traps (white, yellow, blue; diameter 0.15 m) were set on wooden poles 0.5 m above ground. The distance between window traps and between window and pan traps was at least 10 m, and the clusters of pan traps were separated from each other by 50 m (for details on trap construction, see Rubene et al., 2015). The window traps were emptied three times during the summer and the pan traps four times.

Saproxylic beetles were sorted and identified to species level by a taxonomy expert (Olof Hedgren), with a few exceptions where only identification to genus was possible (Table S1, Supplementary Material). Species data from all traps and collection events were pooled for each clearcut prior to analyses. We used available literature (Ehnström and Axelsson, 2002) and expert knowledge (see acknowledgements) to assign saproxylic species to the following ecological groups: coniferous specialists, deciduous specialists, pyrophilous species and flower visitors (Table S1, Supplementary Material).

Previous studies have shown that it can be difficult to use old literature sources to separate species that are attracted to burned forest from those that are drawn to increased dead wood amounts (which can occur after clearcutting and other disturbances) (Johansson et al., 2011). Therefore, we compiled a new list of pyrophilous species based on recent studies which have surveyed beetles in burned and unburned habitats (see Table S2, Supplementary Material for species list and literature list). All species assessed by the selected studies are included in the list, not only the species collected in the current study. Species assignment was based on three types of data: (i) statistical analyses showing significant association with burned forest habitats, (ii) differences in species abundance between burned and unburned sites and (iii) expert reports on species being fire-dependent or strongly associated with fire (see Supplementary Material for details).

2.3. Local factors

Local habitat factors were estimated within each site area. Clearcut size was mapped using ArcMap 10.1 (ArcGIS, ESRI, Redland, CA, USA), by defining each clearcut as the total contiguous area of cut forest at each location. We recorded presence/absence of prescribed fire, measured the total amount of dead wood (i.e. sum of downed and standing dead wood), the number of flowering plant species and flower abundance (Table 1). The total volume of downed dead wood per hectare was calculated by measuring length and diameter of all logs with diameter >15 cm and summing their volume to the site level. The volume of standing dead wood per hectare was calculated from measurements of all high-stumps and all dead standing trees that were at least 5 cm diameter at base and with height >1 m. Dead wood was divided into three categories: (i) conifer wood (sum of Scots pine and Norway spruce), (ii) deciduous wood and (iii) lying pine wood (logs of Scots pine > 15 cm in diameter). We looked at lying pine wood separately because it is the predominant habitat of *T. depsarium*. Flower richness was estimated by counting all flower producing plant species encountered while systematically walking through the site

Table 1
Measured factors on local and landscape scale. Median values and ranges are given separately for burned clearcuts (n = 15) and unburned clearcuts (n = 17). For factors which were only used for specific species groups, the response groups are given in parentheses.

Habitat factors	Units	Scale	Unburned (median, range)	Burned (median, range)
Clearcut area (all groups)	ha	Local	8.83 (3.19–39.5)	21.5 (4.1–115)
Total dead wood (all species, flower visitors, pyrophilous)	m ³ ha ⁻¹	Local	5.24 (1.65–9.64)	6.78 (2.87–25.43)
Conifer dead wood (conifer specialists)	m ³ ha ⁻¹	Local	4.77 (1.59–9.17)	4.99 (2.26–25.08)
Deciduous dead wood (deciduous specialists)	m ³ ha ⁻¹	Local	0.12 (0–1.36)	1.04 (0.12–5.71)
Downed pine dead wood (<i>T. depsarium</i>)	m ³ ha ⁻¹	Local	3.22 (0.33–14.17)	4.03 (0.46–14.22)
Burned (all groups)	1/0	Local	–	–
Flower richness (all groups)	# of species	Local	9 (5–14)	9 (4–14)
Flower abundance (all groups)	Proportion occurrence	Local	0.32 (0.22–0.86)	0.36(0.13–0.99)
Dead wood amount (all groups)	m ³ ha ⁻¹	Land	7.1 (2.97–9.53)	7.9 (2.97–9.53)
		1 km		
		Land	6.79 (2.97–9.53)	7.75 (2.97–9.53)
		2 km		
Coniferous rich (conifer specialists) [*]	Proportion of area (Reserves + coniferous WKH)	Land	0 (0–0.09)	0 (0–0.009)
		2 km		
Deciduous rich (deciduous specialists)	(Reserves + deciduous WKH + deciduous forest)	Land	0.015 (0.0002–0.24)	0.018 (0.0005–0.048)
		1 km		
		Land	0.015 (0.001–0.047)	0.014 (0.002–0.048)
		2 km		
Dead wood rich (other groups)	(Reserves + all WKH + deciduous forest)	Land	0.015 (0.0002–0.24)	0.018 (0.0005–0.048)
		1 km		
		Land	0.019 (0.001–0.098)	0.013 (0.002–0.048)
		2 km		
Burned forest land (all groups)	Proportion of area (Wildfires + prescribed fire + burned WKH)	Land	0.057 (0–0.54)	0.022 (0–0.33)
		1 km		
		Land	0.015 (0–0.28)	0.015 (0–0.22)
		2 km		

during the four visits. Abundance of each species was visually estimated and assigned to one of three abundance classes: 1 – occurs on 1–10% of site area, 2 – occurs on 10–50% of the site area, and 3 – occurs on $\geq 50\%$ of the site area. The abundance classes were transformed into coverage values of 0.01, 0.1 and 0.5, respectively. The coverage values were summed for all species per site to obtain a measure of total flower abundance.

2.4. Landscape factors

We estimated landscape components which reflect the amount of habitats potentially important for dead wood dependent beetle diversity. They were (i) amount of dead wood, (ii) proportion of habitats rich in dead wood (forest reserves and woodland key habitats) and (iii) proportion of burned forest land (Table 1). The landscape factors were measured on two spatial scales: in a radius of 1 km and 2 km surrounding each surveyed site. All landscape factors were estimated with GIS ArcMap 10.5 (ArcGIS, ESRI, Redland, CA, USA).

The amount of dead wood was assessed using Swedish National Forest Inventory data (2012), which is based on sample plots on productive forest land ($>1 \text{ m}^3 \text{ ha}^{-1}$) in managed as well as protected areas. Average values of dead wood volume are calculated in polygons based on at least 20 sample plots. All dead wood with diameter $>10 \text{ cm}$ is included, except stumps from tree harvest.

Burned forest land included all areas burned during the last 3–10 years. These contained all burned sites of the same age as the surveyed clearcuts (3–5 years) and also 6–10 years old burned forest land, because such areas may act as dispersal sources. We estimated the proportion of burned forest land in the landscape by combining data on forest wildfires (from the Swedish Civil Contingencies Agency), prescribed fires conducted mainly on clearcuts by forest managing companies (Bergvik Skog and Sveaskog), prescribed fires mainly in protected forests ordered by administrative county boards, and woodland key habitats (WKH) classified as burned forest”.

We estimated the proportion of habitats rich in dead wood separately for conifer specialists, deciduous specialists and combined other groups (all species, flower visitors, pyrophilous species). For conifer wood specialists we combined areas of forest nature reserves and coniferous forest WKH, except burned forest. This is because WKH and nature reserves have been shown to contain more dead wood than surrounding managed forests (Ekblom et al., 2006; Jönsson and Jonsson, 2007). For deciduous wood specialists we included: woodland key habitats rich in deciduous trees, forest nature reserves and forest with high volume of deciduous trees. The last was assessed from kNN maps of forest land in Sweden with $25 \times 25 \text{ m}$ resolution, which combine data from ground surveys (Swedish National Forest Inventory) and satellite images (Landsat ETM) (Reese et al., 2003). We included forest with $\geq 50 \text{ m}^3/\text{ha}$ deciduous trees. For all species, pyrophilous, and flower visiting species, we combined all coniferous and deciduous-rich habitats described above, i.e., forest nature reserves, all WKH (except burned forest) and deciduous-rich forest. Deciduous-rich forest was included because such forests may have originated after fires and thus may indicate historically fire-affected areas and because deciduous forests are more sunlit/open, which may favour flowering plants.

3. Analyses

3.1. Species richness estimation

To address sampling efficiency we used rarefaction in EstimateS 9.1.0 (Colwell, 2013), which showed that the sampling was insuffi-

cient for direct comparison of observed species richness. We therefore estimated species richness per site by calculating non-parametric richness estimators (ACE, ICE, Chao1 and 2, Jackknife 1 and 2) to account for unsampled species (Magurran and McGill, 2011). For each group, we chose the estimator which appeared most stable (leveled off or approached an asymptote) at present sample size, produced none or few extreme (outlier) values and had low variation (SD). The chosen richness estimators were ACE (abundance based coverage estimator, Chao et al., 2000; Chazdon et al., 1998) for all dead wood living beetles, conifer specialists, flower visitors and pyrophilous species, and ICE and Chao2 (incidence based estimators, Chao, 1984; Chao et al., 2000; Chazdon et al., 1998) for deciduous specialists. We collected a relatively large number of individuals of a red-listed species, *Tragosoma depsarium* (NT, Swedish Species Information Centre 2015), so we analysed number of individuals of this species individually. *Tragosoma depsarium* is a longhorn beetle (Cerambycidae), which mainly reproduces in large logs of old pines in open habitats and is therefore threatened by forest management, which reduces the amount of large dead wood (Wikars, 2004).

3.2. Model composition

We analysed the response of estimated species richness and number of collected individuals of *T. depsarium* per site to the predictors on the local scale: patch size, dead wood amount, occurrence of prescribed fire, flower species richness and abundance, and on the landscape scale: dead wood amount, proportion of dead wood-rich habitats and proportion of burned forest land. To assess the effects of local and landscape factors on species richness, we used linear mixed models (Bunnefeld and Phillimore, 2012) in R (R Core Team, 2013), package *nlme* (Pinheiro et al., 2013). We chose to use linear models, i.e. Gaussian distribution instead of Poisson, because the estimated species richness are continuous data and at relatively large mean values ($>5-10$) of the response variable the Poisson distribution approaches the shape and properties of a Gaussian distribution. We used histograms and QQ-plots of residuals to assess assumption of normality of species richness models (Zuur et al., 2010). Abundance of *T. depsarium* was analysed with mixed models in *lme4* (Bates et al., 2011), using Poisson distribution. Landscape identity was included as random factor in all species richness models, to account for the spatial nested structure of sites within landscapes. We used logarithmic transformation for local dead wood amount and patch size and square-root transformation for landscape proportion data and flower abundance prior to analyses. All predictor variables were checked for collinearity and only one spatial scale of each landscape factor was included in any model at a time, as the scales are correlated. The scales included in the main effects models determined the scales of factors tested in interactions. All continuous explanatory variables were centered to a mean of zero prior to analyses, to ease the interpretation of interactions and reduce collinearity between factors included in the interaction and the interaction term (Schielzeth, 2010).

3.3. Model selection

The models were built by forward selection using AIC (Akaike, 1974) corrected for small sample sizes (AICc), starting from a model with only the intercept and the random factor. First, we built a main effects model, by adding explanatory variables one at a time, based on which variable lowered AICc the most. In each following step, all remaining variables were tested and the procedure was stopped when adding variables no longer decreased the AICc. We then added one interaction at a time to the main effects model and retained it in the model if AICc decreased. We tested

interactions between (i) local dead wood amount and local burning, (ii) local fire and proportion burned forest land in the landscape, (iii) local dead wood amount and landscape dead wood amount or proportion dead wood rich habitats, (iv) local burning and landscape dead wood amount or proportion dead wood rich habitats, and (v) local dead wood amount and proportion burned forest land in the landscape. The first interaction was tested because burning may modify the quality of the dead wood. The other four interactions were tested because resources on landscape scale may be a prerequisite for a positive local response to dead wood amount and burning.

3.4. Species composition

We used non-metric multi-dimensional scaling (NMDS) in R package *vegan* (Oksanen et al., 2013) to study differences in species composition of all beetle groups. The same explanatory variables that were used in species richness analyses were also fitted in NMDS and their significance was assessed with a permutation test using the *env* function in *vegan* (Oksanen et al., 2013). We used Bray-Curtis index of dissimilarity, no data transformation, and species abundance data in the analyses, because we wanted to retain information about potential differences in individual abundances between clearcuts with different properties.

4. Results

We collected a total of 6239 individuals, belonging to 149 saproxylic beetle species, of which three were red-listed (Swedish Species Information Centre 2015, Table S1, Supplementary Material). Additional four species were red-listed according to the previous Swedish Red-List (Swedish Species Information Centre 2010). On average, about 30 species per site were collected, with the largest proportions belonging to flower visitors and conifer specialists. Average species richness values (estimated and observed) and individual abundances are summarised for burned and unburned clearcuts in Table 2.

4.1. Species richness

Both local and landscape scale factors influenced species richness patterns of saproxylic beetles on clearcuts (Table 3). Prescribed fire and amount of dead wood, both on local and landscape scale, affected species richness of several groups. In the final models, there were totally six significant interactions between local and landscape variables (Table 3). Four of them implied that positive effects of local dead wood and prescribed burning occurred in landscapes with large amounts of dead wood, but not in landscapes with little dead wood. Specifically, two of the interactions (for pyrophilous species and *T. depsarium*) implied that in landscapes with large amounts of dead wood, the effect of local burning was positive, while it was negative in landscapes with little dead wood (Figs. 2 and 3). Furthermore, for conifer specialists

and all species, the local amount of dead wood had a strong positive on species richness in landscapes with large amounts of dead wood, while in landscapes with little dead wood this relationship was slightly negative. Finally, for flower visitors and all species, the effect of local burning was clearly negative in landscapes with large burned areas, which was not the case in landscapes with less burned areas.

4.2. Species composition

Community composition varied among sites and the most important explanatory factors were consistent with those affecting species richness (Table 4). Species composition was relatively more affected by landscape factors than species richness. Burning on local and landscape scale, flower richness and dead wood amount in the landscape were important factors affecting site dissimilarity for all species combined (Fig. 4; $k = 2$, stress = 0.12), and similar results were obtained for conifer specialists ($k = 2$, stress = 0.12), flower visitors ($k = 3$, stress = 0.11) and pyrophilous species ($k = 3$, stress = 0.15). Deciduous wood specialists were the only group for which species composition was not affected by fire or any other environmental factor ($k = 2$, stress = 0.15).

5. Discussion

5.1. Local effects

Local habitat characteristics, measured on a scale of a few hectares, influenced species richness and species composition. We found significant effects of dead wood amount, prescribed fire and flower richness. The size of the clearcut, however, did not influence beetle species richness. Note that the sampling effort was standardized, i.e. independent on clear cut size (cf. Fahrig, 2013). One possible explanation for this pattern is that saproxylic beetles on clearcuts are strong dispersers and therefore move without constraint between clearcuts. Another is that the sampled beetles are a mixture of generalists and specialist species developing in clear-cuts, forest-edges and mature forests, and therefore the relationship between total species richness and clear-cut size becomes complex, as clear-cuts may only constitute habitat patches surrounded by non-habitat for species dependent on sun-exposed dead wood. The few studies on saproxylic beetles that have found an effect of patch size have considered species specialised to rare habitats (e.g., tree hollows, Ranius, 2002; aspen specialists, Sahlin and Schroeder, 2010) and such populations may be more strongly dependent on the size of the local patches than generalist species. Since we studied dead wood dependent organisms, a positive effect of dead wood amount was expected, and we found that for all species and for pyrophilous species. Higher species richness can be due to that populations are more persistent if more habitat is available (Gaggiotti and Hanski, 2004). Moreover, many saproxylic beetle species are associated with certain dead wood qualities (Palm, 1959), and more dead

Table 2

Estimated average species richness per site, observed number of species and individual abundance (\pm SD) of the studied species groups.

	Estimated richness		Observed richness		Abundance	
	Burned	Unburned	Burned	Unburned	Burned	Unburned
All species	51.1 (10.42)	50.3 (12.63)	31.6 (7.06)	34.3 (8.61)	161.93 (103.57)	224.12 (151.94)
Conifer specialists	18.82 (6.25)	20.99 (6.94)	10.53 (2.75)	13.35 (4.23)	67.8 (46.51)	72.82 (45.88)
Deciduous specialists	19.58 (11.19)	11.78 (4.74)	8.8 (2.78)	7.53 (2.71)	35.47 (25.07)	29.12 (25.98)
Pyrophilous species	16.03 (6.2)	15.35 (5.49)	9.6 (1.96)	10.12 (3.02)	60.8 (40.21)	56.94 (37.81)
Flower visitors	16.81 (4.78)	20.55 (5.61)	13.2 (3.99)	15.88 (4.36)	123.8 (95.55)	178.29 (142.85)
<i>Tragosoma depsarium</i>	–	–	–	–	4.07 (4.71)	2.24 (2.7)

Table 3

Mixed model results for species richness of all saproxylic beetles, conifer and deciduous specialists, pyrophilous species, and abundance of *Tragosoma deparium*. The spatial scale for the landscape factors is given in parentheses. SE and t values are given for species richness models, SD and z values for *T.depsarium* abundance model; DF: residual degrees of freedom, Δ AICc: difference from intercept- and random factor-only model.

Model	Estimate	SE (SD)	t (z)	p	DF
<i>All species</i>					
Dead wood (local)	3.89	2.99	1.3	0.2	18
Dead wood (land 1 km)	-2.47	0.82	-2.99	0.008	18
Dead wood (local) × Dead wood (land 1 km)	3.46	1.58	2.19	0.04	18
Burned (local)	-1.87	5.68	-0.3	0.7	18
Burned (land 1 km)	48.8	20.05	2.43	0.02	18
Burned (local) × Burned (land 1 km)	-88.9	25.38	-3.5	0.002	18
Random landscape (Intercept; residual)		0.0011; 8.8			
<i>Conifer specialists</i>					
Dead wood (local)	1.08	1.67	0.65	0.52	21
Dead wood (land 1 km)	-1.53	0.53	-2.87	0.009	21
Dead wood (local) × Dead wood (land 1 km)	2.32	0.93	2.49	0.02	21
Random landscape (Intercept; residual)		0.0002; 5.78			
<i>Deciduous specialists</i>					
Burned (local)	9.2	2.65	3.47	0.002	21
Flower richness (local)	1.84	0.55	3.32	0.003	21
Deciduous rich (land 2 km)	-52.15	27.3	-1.9	0.07	21
Random landscape (Intercept; residual)		0.0003; 6.87			
<i>Flower visitors</i>					
Flower richness (local)	0.55	0.3	1.75	0.09	20
Burned (local)	-6.5	2.3	-2.8	0.01	20
Burned (land 2 km)	36.9	13.66	2.7	0.01	20
Burned (local) × Burned (land 2 km)	-41.03	16.7	-2.45	0.02	20
Random landscape (Intercept; residual)		1.22; 4.5			
<i>Pyrophilous species</i>					
Dead wood (local)	2.56	1.61	1.59	0.12	20
Burned (local)	-0.15	1.9	-0.08	0.9	20
Dead wood (land 1 km)	-2.1	0.59	-3.6	0.002	20
Burned (land 2 km)	9.17	5.76	1.59	0.1	20
Burned (local) × Dead wood (land 1 km)	2.33	0.89	2.6	0.02	20
Random landscape (Intercept; residual)		0.0002; 4.8			
<i>Tragosoma deparium</i>					
Burned (local)	0.48	0.21	1.97	0.048	24
Flower richness (local)	0.28	0.07	4.03	<0.001	24
Dead wood (local)	0.87	0.27	3.2	0.001	24
Dead wood (land 2 km)	-0.07	0.18	-0.4	0.69	24
Burned (local) × Dead wood (land 2 km)	0.54	0.21	2.59	0.009	24
Random landscape (Variance; StDev)		0.2; 0.45			

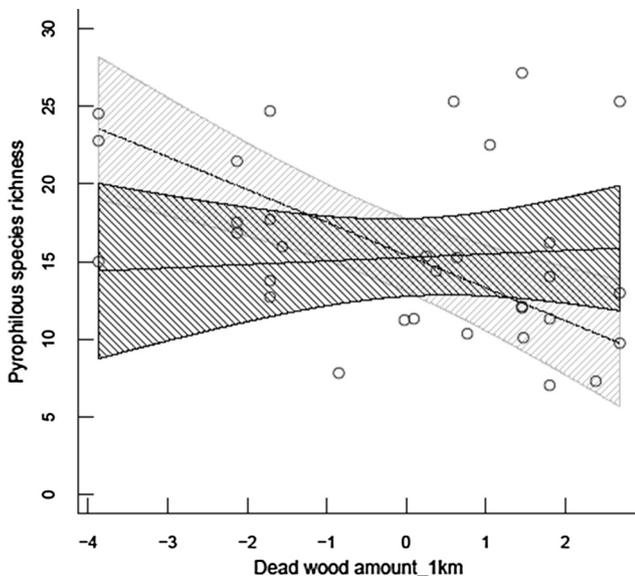


Fig. 2. Relationship between dead wood amount in the landscape within 1 km radius (centered values) and pyrophilous species richness on unburned (grey) and burned (black) clearcuts. The model residuals are shown as black dots, the estimated slopes as lines and the 95% confidence intervals as polygons.

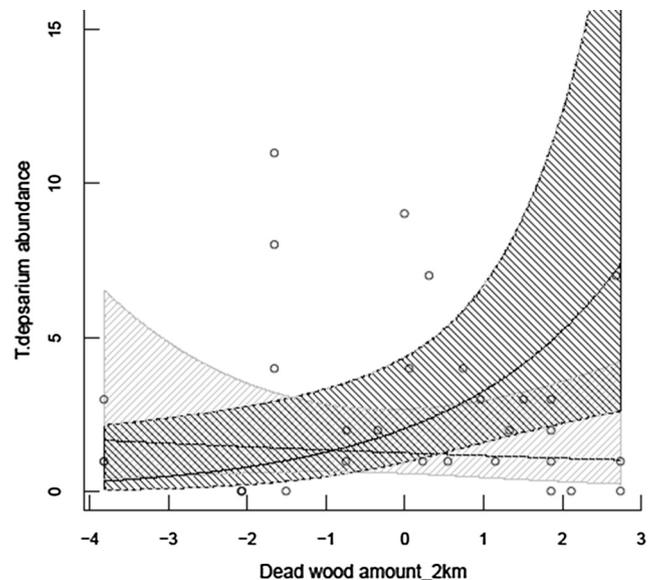


Fig. 3. Relationship between dead wood amount in the landscape within 2 km radius (centered values) and abundance of *T. deparium* on unburned (grey) and burned (black) clearcuts. The model estimated slopes are shown as lines and the 95% confidence intervals as polygons.

Table 4
NMDS results from species composition analyses, r^2 values of significant explanatory variables shown; significance levels: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

Species group	Burning (local)	Burning (landscape)	Flower richness	Dead wood (landscape)
All species	0.12*	0.23* (1 km)	0.39**	0.35** (1 km)
Conifer specialists	0.17**	0.39** (1 km)	0.32**	0.26* (1 km)
Flower visitors	0.13*	0.21* (1 km)	0.44***	0.23* (1 km)
Pyrophilous species	0.16**	0.34** (2 km)	0.21*	0.28** (1 km)

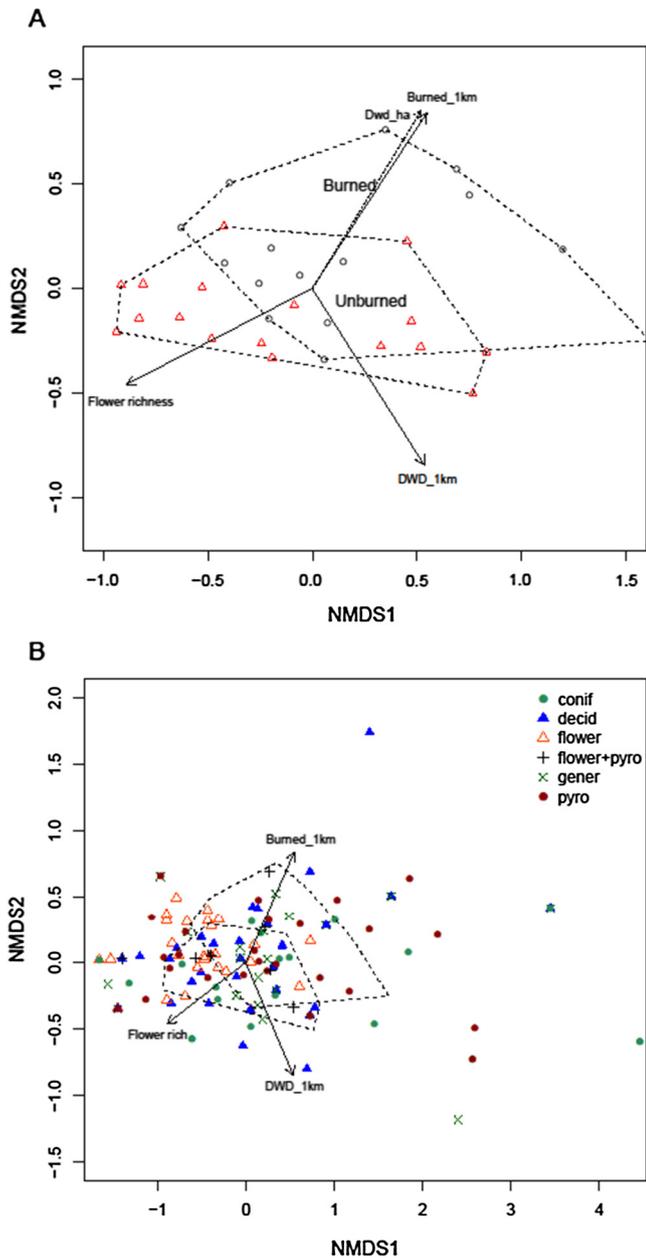


Fig. 4. NMDS plots illustrating species composition of all species; environmental variables shown with arrows, arrow length shows importance of a variable and arrow direction shows steepest change in variable values; group boundaries for burned and unburned sites drawn with *ordihull* function in R package *vegan* (Oksanen 2013). A -sites, burned - black circles, unburned - red triangles; dashed arrow shows non-significant local dead wood amount with effect in same direction as burned area. B -species, groups with different specialisation shown with different symbols (legend). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

wood likely means higher diversity of dead wood types and thereby habitat for more species. Dead wood amount has been found important for local species richness (McGeoch et al., 2007;

Seibold et al., 2016), but the strength of this relationship varies (e.g., Gibb et al., 2006).

Prescribed fire on clearcuts increased species richness of deciduous specialists, while for all species, flower visitors, pyrophilous species, and abundance of *T. depsarium*, the effect of prescribed fire was dependent on landscape characteristics. Also, species composition differed significantly between burned and unburned sites. A fire in a forest may have large positive effects on saproxylic diversity because much dead wood is created (Drapeau et al., 2002; DellaSala et al., 2006; Boucher et al., 2012). On clearcuts, the effect of fires is probably smaller, since the potential for dead wood creation is limited and some dead wood may even be destroyed. Thus, it is not certain what effect of clearcut burning should be expected. It has been found, however, that burned areas that resemble forest after natural fires, e.g. through a higher level of tree retention, have, on average, a higher species richness of saproxylic beetles (Toivanen and Kotiaho, 2007; Hyvärinen et al., 2009). The positive affect on deciduous specialist richness might be due to that the amount of deciduous dead wood was somewhat higher on burned sites, however, the amount was usually so low that it is to a high extent a matter of chance to what extent dead deciduous trees were within the sampled sites (Table 1). Therefore, burning may correlate to the dead wood availability in the surrounding parts of the clearcut better than the dead wood amount measured on the local scale, which may explain why deciduous specialists responded positively to fire. Interestingly, only in landscapes with large amounts of dead wood, we observed a positive response of pyrophilous species to burning. We based our definition of pyrophilous species on published field data in order to avoid common problems of outdated and too broad definitions (Johansson et al., 2011); yet we observed a similar average species richness on burned and unburned sites (Table 2). Thus, our results suggest that it is a challenge to understand and define species preferences, since species occurrence patterns may depend on the context of each study. However, three of the observed species have previously been defined as strictly fire dependent (Wikars, 1992) - *Cryptophagus corticinus*, *Sphaeriestes stockmanni* and *Stephanopachys linearis* - and they were all exclusively found on burned sites.

Flower richness had a positive effect on flower visitor and deciduous specialist richness and *T. depsarium* abundance, and was an important factor determining species composition, particularly for flower visitors (Tables 3 and 4). Many species of saproxylic beetles forage on pollen and nectar as adults (Palm, 1959), and ensuring an adequate supply of suitable nectar plants has been suggested as a measure to favour saproxylic beetles (Alexander, 1998). We found no effect of flower abundance on species richness of any group, which may be due to that the most abundant flowering plants on clearcuts, *Vaccinium* dwarf shrubs, provide pollen and nectar during a limited time in the season. Thus, flower abundance may be a poor measure of continuity in pollen and nectar abundance. Higher richness of flowering plants likely indicates that the resources are spread out more evenly over the season, and can consequently support higher beetle species richness. Studies in other habitats have reported positive associations between flower-visiting insects and flower abundance (Müller et al., 2008), flower species richness (Potts et al., 2003), or both (Hegland and Boeke, 2006). Adults of *T. depsarium* are not known

to feed at all or to visit flowers (Ehnström and Holmer, 2007), yet it showed a positive response to flower richness. Flower richness may have a positive direct effect on saproxylic beetles, but may also be correlated to some unmeasured habitat properties, e.g. moisture or large proportion of deciduous trees before clearcutting, which may be important for species richness and abundance.

5.2. Landscape effects

We found that all studied landscape components and spatial scales were important for at least some species groups. The tested effects of landscape composition within 1–2 km are within the range in which effects of habitat amount on saproxylic beetles have often been found (Gibb et al., 2006; Götmark et al., 2011; Olsson et al., 2012; Ranius et al., 2011). Most relationships between landscape components and species richness were affected by interactions with local factors, which means that several of them at least sometimes are negative. Negative relationships may be caused by a dilution effect, when migrants are too few to fill all habitats in landscapes with high habitat availability (Bowman et al., 2002; Otway et al., 2005). Thus, in landscapes with little new habitat created, clearcuts may attract dispersing beetles to a larger extent, since the “competition” for the dispersing individuals from higher-quality sites is smaller. Another explanation is that the dead wood-rich habitats were predominantly late-successional forest. Thus, in landscapes with a high proportion of such habitat, populations of early-successional species which mostly colonise clearcuts may indeed be smaller.

5.3. Landscape effects on local conservation management

We observed six interactions between local and landscape factors. Two of the interactions were related to the landscape-level burned area, and suggested that fewer species are present on burned than unburned clearcuts in landscapes with large burned area. These results should however be treated with caution due to limitations in the range of data, specifically lack of data points representing unburned clearcuts in landscapes with large burned areas and burned clearcuts in landscapes with low burned area. The other four interactions implied that the positive effect of local dead wood and burning occurred in landscapes with large amounts of dead wood, but not in landscapes with little dead wood. Thus, our results support the idea that resources on landscape scale is a prerequisite for a positive local response to local resource availability. There are at least two factors that can contribute to this pattern. First, it may be due to that a larger species pool is present when there is more dead wood at a landscape scale, which allows colonization of more species in sites with more dead wood (Kouki et al., 2012). Second, it may be that the “competition” for dispersing individuals increases with increased amounts of dead wood, which decreases the number of species in sites with little dead wood.

This outcome is consistent with many studies in agricultural systems that have found that the effects of local factors are influenced by the landscape context (Tscharntke et al., 2012), but to our knowledge this is the first time this has been tested in forest habitats. In agricultural systems, habitat improvement actions (e.g., agri-environment schemes, AES) appear to be most effective in simple landscapes (with 1–20% non-crop habitats) (Rundlöf and Smith, 2006; Rundlöf et al., 2008; Batáry et al., 2010; Concepción et al., 2012; Smith et al., 2010). Also our study landscape could be described as simple, since it was dominated by managed habitat. This means, for instance, that dead wood-rich habitats constituted on average 2% (and a maximum 24%) of the landscape. Also, the observed average amount of dead wood on landscape scale was low (3–9 m³ ha⁻¹), which is typical for managed boreal forests and similar to the Swedish average (Fridman

and Walheim, 2000). Thus, our results reflect the situation in landscapes with long forest management history, which is the current reality in most of Fennoscandia.

The observed interactions with landscape-level dead wood amounts have consequences when formulating strategies for conservation efforts in managed forests. In landscapes rich in dead wood, the retention level strongly affects species richness of saproxylic beetles, while in landscapes with little dead wood, the retention level will have little effect. This means that instead of keeping retention level constant at every clearcut, it is better with a variable retention. Previous studies of individual saproxylic beetle species have also given support to variable retention, since it means that retained dead wood will to a higher degree be used by specialized species (Rubene et al., 2014; Schroeder et al., 2006). Also theoretical studies have suggested that the amount of dead wood created at retention forestry is too low to efficiently decrease extinction risks of species (Hanski, 2000; Ranius and Roberge, 2011). However, this is the first time variable retention adapted to landscape properties is supported by species richness assessments of larger groups of saproxylic beetles.

5.4. Conservation and management implications

In this study, we assessed the importance of the landscape context for local conservation actions taken at clearcutting in managed forests. The response group, saproxylic beetles, includes a variety of life history strategies; however, the study was designed to focus on species associated with early successional forest stages, e.g., burned habitats, with open canopy conditions and abundance of fresh dead wood (Heikkala et al., 2016). The sampled species pool is representative of Swedish managed forest landscapes with high proportion of clearcuts. Such landscapes are also the targets of the two conservation management actions we have studied, dead wood retention at clearcutting and prescribed fire. The red-listed *T. depsarium*, which is not known to be associated with clearcuts, was collected rather abundantly from many sites. With our approach we evaluated conservation actions that create early-successional habitats with a high species richness of saproxylic beetles, and it is likely that among the benefiting species, there are some rare species as well.

Saproxylic beetles are dependent on dead wood as larvae, yet many feed on nectar and pollen as adults. This study shows that dead wood and flowers are important for saproxylic beetle diversity on clearcuts. Consequently, increasing dead wood amounts on clearcuts can increase saproxylic beetle richness. Flower richness on clearcuts has obtained little interest, but can probably be promoted by maintaining habitat openness through e.g., delayed planting of conifers. Prescribed burning has varying effects, and since prescribed burning increases the variability in habitat quality at a landscape scale, it probably has a positive effect on overall species diversity at a landscape level.

In landscapes rich in dead wood, the amount of dead wood in clearcuts strongly affects species richness of saproxylic beetles, while in landscapes with little dead wood, dead wood amounts in clearcuts have little effect. This means that the level of retention should be variable among clearcuts and adapted to the amount of dead wood in surrounding landscape. Our study reflects the conditions in boreal forest landscapes with long history of intensive management, which dominate in Northern Europe, while in regions with more natural forests, the conditions and biodiversity patterns may be different.

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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.2017.05.025>.

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