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RESEARCH ARTICLE

Surrounding landscape composition influences saproxylic beetle assemblages after prescribed burning

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Abstract

1. Biodiversity is affected by local and landscape factors, yet which of these is most important seems to vary depending on species group and context. Understanding how environmental factors affect species at different spatial scales is crucial for effective conservation planning. Here, we examine the influence of local and landscape characteristics on saproxylic and fire-favoured beetle populations after prescribed burning.
2. Beetles (*Coleoptera*) were collected using flight intercept traps at 23 sites across three regions in Sweden. Prescribed burning had been conducted on the sites 4–7 years earlier. We analysed the relationships between species richness, abundance and community composition, and environmental variables at both local (burn sites) and landscape scales (2, 5, 10 and 20 km radius around the burn sites). Local variables were deadwood volume, canopy cover and burn extent. Landscape variables included the area of forests that were protected, old (>120 years), clear-cut and burned, and the standing timber volume of Scots pine, Norway spruce and deciduous trees.
3. In total, we recorded 3094 saproxylic beetles, belonging to 188 species. Of these, 1153 individuals (37 species) were classified as fire-favoured. No local variables had a significant influence on beetle richness or abundance. For landscape relationships, 5 and 10 km scales were most relevant for analysing saproxylic beetle responses. At these scales, saproxylic beetle richness was positively associated with the protected forest area, whereas abundance showed a negative relationship. In contrast, richness of saproxylic beetles was negatively associated with the area of clear-cuts, while abundances of saproxylic and fire-favoured species were positively associated. Species richness was similar across regions, whereas species composition varied. The proportion of old forests was an important variable contributing to regional dissimilarity in species composition.
4. *Synthesis and applications.* Our study highlights the importance of the surrounding landscape for shaping saproxylic beetle communities after prescribed burning. Forest management and conservation measures within a 5–10 km radius of prescribed burns can influence beetle assemblages post-burn and should be

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considered when planning burns aimed at promoting saproxylic beetles. In addition, as species composition varied across regions, this indicates that prescribed burning in different regions complements each other.

KEYWORDS
boreal forest, landscape composition, prescribed burning, restoration planning, saproxylic beetles

1 | INTRODUCTION

In fire-prone forest ecosystems across the globe, prescribed fire is utilized as a management tool with a variety of applications (Burrows & McCaw, 2013; Lindberg et al., 2020; Ryan et al., 2013). The main application in many regions is fire hazard reduction through intentional burns to decrease fuel loads (Boer et al., 2009; Hunter & Robles, 2020). In the boreal forests of Fennoscandia, common applications are site preparation for forest regeneration within production forestry and within nature conservation as a restoration tool (Cogos et al., 2020; Lindberg et al., 2020; Ramberg et al., 2018).

Burning for conservation purposes in boreal forest aims to benefit biodiversity by restoring structures and dynamics that have been diminished or degraded due to intense forestry management practices and effective fire suppression (Granström, 2001; Lindberg et al., 2020). The extent and location of these prescribed burns are primarily determined by practical and safety considerations. However, to be effective, it is also crucial to identify areas in the landscape where restoration will provide the greatest benefit for targeted species and reduce negative impacts on fire-sensitive species.

An important aim of prescribed burning is to create deadwood, as a shortage of this substrate in production forests is a threat to many saproxylic (i.e. deadwood dependent) species (Siitonen, 2001). Saproxylic beetles are dependent on deadwood for their larval development (Stokland et al., 2012), and many of them are favoured by fires (Bell, 2023). Among the fire-favoured beetles, some are pyrophilic, that is, dependent on and adapted to fire, whilst others are more generally disturbance-adapted, with a preference for sunlit-open habitats (Bell, 2023; Wikars, 1997). Previous studies have confirmed that both wildfire and prescribed burning promote saproxylic and fire-favoured beetles (Hjältén et al., 2018; Johansson et al., 2011; Wikars, 1997). However, there is limited knowledge on how the surrounding landscape affects species occurrences after burning (see, however, Kouki et al., 2012; Ranius et al., 2014; Rubene et al., 2017).

An increase in the local (site) amount and heterogeneity of deadwood has been shown to increase saproxylic beetle abundance and richness, and influence species composition (Larsson Ekström et al., 2021; Ranius et al., 2014; Seibold et al., 2016). This is in accordance with the species-energy hypothesis, which links higher species richness and abundance with an increased habitat amount, as more energy is available (Wright, 1983), and with the habitat-heterogeneity hypothesis, which associates increased species richness with increased habitat diversity, as more niches are present (MacArthur & MacArthur, 1961; Seibold et al., 2016).

Increasingly, there is support for the habitat amount hypothesis (HAH), which states that the total habitat amount within a landscape is more important than its spatial configuration (Fahrig, 2013; Watling et al., 2020), but also see Gonçalves-Souza et al. (2025) and sources within. A landscape with more suitable habitat is predicted to support more species, resulting in higher species numbers at sites within it compared to sites in landscapes with less suitable habitat. For saproxylic beetles, the landscape habitat amount is at least as important as local habitat amount in explaining species composition and richness (Hallinger et al., 2018; Rubene et al., 2017; Seibold et al., 2017). Protected forests and old forests generally sustain larger volumes of deadwood than managed, younger forest (Kyaschenko et al., 2022; Siitonen, 2001) and on a landscape scale, these deadwood-rich forest types are commonly positively related to saproxylic species richness and abundance (Hämäläinen et al., 2023; Olsson et al., 2012; Stenbacka et al., 2010). The amount of clear-cut area might also be important, since clear-felling changes habitat conditions for saproxylic beetles, benefiting open-habitat specialists (Stenbacka et al., 2010). The amount of specific tree species in the landscape can also influence saproxylic species (Hallinger et al., 2018). For fire-favoured species, the area burned forest in the landscape is likely an important source habitat, as many of these species reproduce in fire-affected dying or dead trees (Wikars, 2006). Knowledge about the effects of landscape characteristics on saproxylic beetles following prescribed burning is limited, making it uncertain how important these are for beetle biodiversity, and which should be considered when planning the location of conservation burns.

In addition, to make informed conservation decisions on prescribed burning, it is essential to understand the spatial scale at which landscape variables influence targeted species. However, determining the appropriate scale for saproxylic beetles is challenging. For example, the spatial scale of effect of habitat amount varies widely among saproxylic beetles, ranging from <100 m (Ranius et al., 2011) to at least 30 km (Bell, 2023; Ranius et al., 2014). The scale of effect is the radius at which the landscape composition best predicts species responses (Jackson & Fahrig, 2012). Testing a range of scales will likely enhance the chances of identifying a relevant scale of effect.

At a larger scale, regional differences can limit species distributions, shaping regional species pools. In Sweden, regions vary greatly in climate (Ahti et al., 1968) and management history (Josefsson

& Östlund, 2011; Linder & Östlund, 1998), which also affect the current area of remnant natural forest (Svensson et al., 2019). In general, species richness is expected to decline with increasing latitude (Hillebrand, 2004). For saproxylic beetles, temperature may limit their distribution, creating regional differences (Gossmann et al., 2024). Differences in land use can also be important, and regions less influenced by forest management may harbour a larger number of red-listed and fire-favoured species (Kouki et al., 2012). In Sweden, northern regions have a shorter history of intense forest management and a higher share of near-natural and natural forests compared to the south. Thereby, northern sites are likely to possess rarer and fire-favoured species.

The aim of this study was to gain a deeper understanding of how local and landscape variables shape saproxylic beetle communities after burning. We sampled saproxylic beetles at 23 sites in Sweden that had been burned 4–7 years earlier. We expected species richness and abundance in burn sites to increase with: (1) local habitat amount (deadwood volume and burn extent) and (2) the area of protected forest, old forest (>120 years) and burned forests—these categories are not mutually exclusive—and volume of living trees per ha in the surrounding landscape. For clear-cuts, we expected a positive relationship with fire-favoured species, as they are adapted to disturbances, but not for saproxylic species in general. We compared three regions in Sweden differing in climate and land-use history. We predicted that saproxylic species richness and abundance would be higher in the southern regions, while abundance and richness of fire-favoured species would be higher in the north.

2 | MATERIALS AND METHODS

The study was conducted in 2022 in three regions in Sweden: south, central and north (Figure 1). Eight sites burned 4–7 years prior to the inventory were chosen per region. All sites were within protected areas (nature reserves, national park or Natura 2000) and ranged in

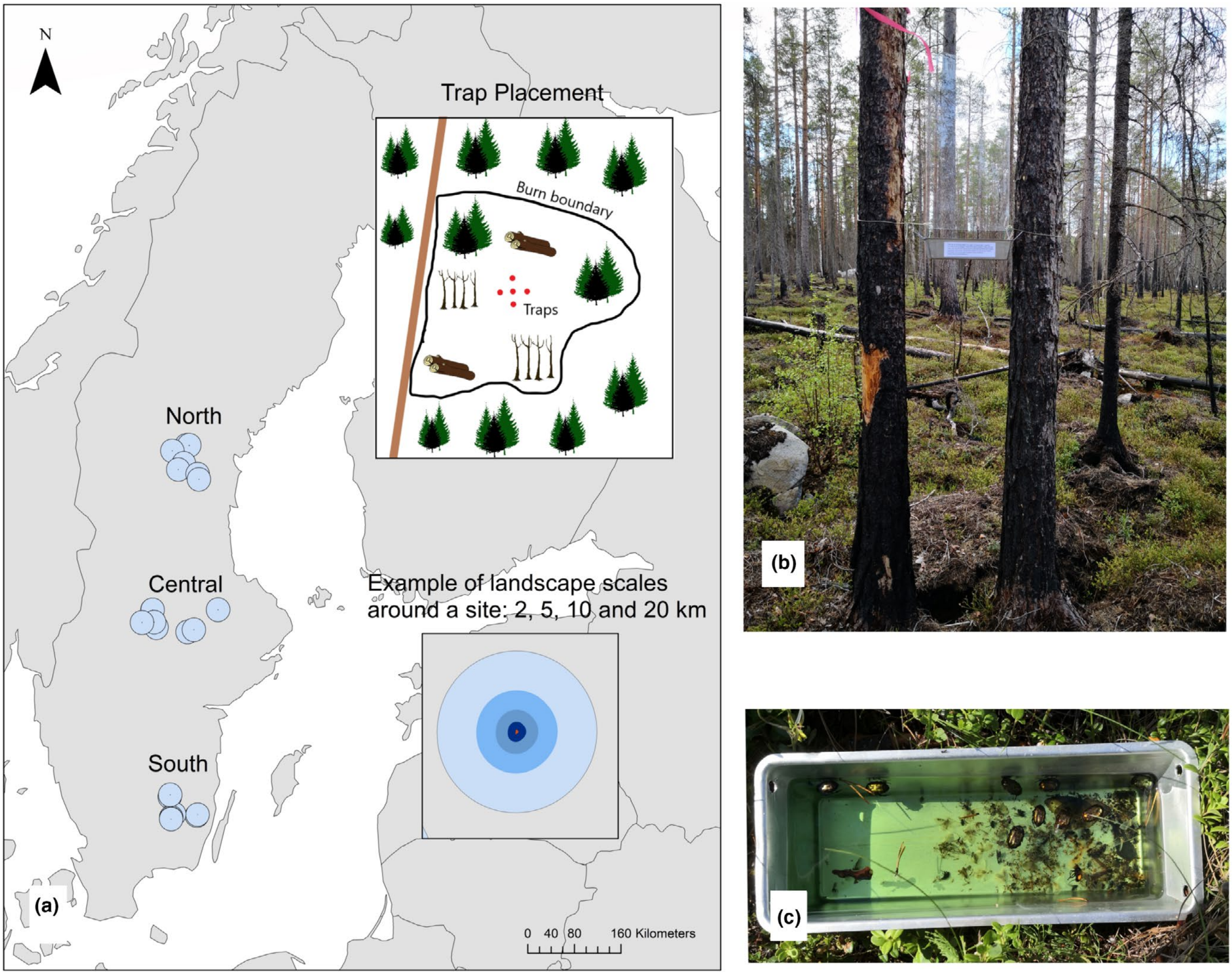

FIGURE 1 (a) Locations of the north, central and south sites within Sweden and the extent of the 20 km buffer, with insets exemplifying trap placement within a site and the four scales around a site used in landscape analysis. (b) Example of a trap on site. (c) Example of tray containing insects at collection; the greenish colour is from the propylene glycol.

size from 6 to 40 ha (see Table S1). One site in the north fell away during fieldwork leaving 23 sites.

2.1 | Species survey and identification

Flight intercept traps were used as they are appropriate for sampling saproxylic beetles, and they are particularly useful when the aim is to compare sites and not to study specific deadwood items (Ranius & Jansson, 2002; Wikars et al., 2005). Permits to place traps within nature reserves were granted by the respective County boards (Gävleborg, Kronoberg, Jönköping, Väster Norrland, Kalmar, Örebro and Västmanland). This study did not require ethical approval. Four to five traps were placed centrally in each burn, approximately 25 m apart and in different directions (Figure 1; Table S1). The traps consisted of a 30 × 60 cm plastic sheet with an aluminium tray (1.8 L) attached under the sheet. The tray was half-filled with propylene glycol and water (50:50) to preserve fallen insects. The traps were fastened at four points with rope to nearby trees at a height of approximately 1.5 m to avoid disturbance by wildlife (Figure 1).

The traps were up for approximately 6 weeks (end of May to beginning of July), coinciding with the peak activity season for saproxylic beetles (Wikars et al., 2005). We excluded traps that did not contain preservation liquid (and no insects) from the analysis, as such traps were considered to have malfunctioned, likely due to strong winds (Tables S2 and S3). Beetles were manually sorted from the rest of the trap contents standardized to 20-min per trap. The beetle expert Hans-Erik Wanntorp, Stockholm, identified the beetles to species level (Species list: Table S4). Beetle species (*Coleoptera*) were sorted as saproxylic based on an unpublished list by Mats Jonsell (based on Hansen, 1964; Koch, 1989; Palm, 1959) and confirmed by Lars-Ove Wikars. Fire-favoured classification was based on Rubene et al. (2017), and included species that have a statistically significant association with burned habitats or have been validated as fire-favoured by experts.

2.2 | Local variables

Data on local variables were collected in 2020. We measured standing and fallen coarse deadwood (diameter at breast height ≥10 cm) in 50-m transects, arranged 50 m apart in a grid pattern encompassing the site. The line transect method was used for fallen deadwood (Van Wagner, 1968), entailing measuring the diameter of deadwood that intersected with the transect line. The volume (in m^3/ha) of fallen deadwood was calculated using the equation:

$$V = \pi^2 \times \sum_{i=1}^{n} \left(\frac{\mathrm{DT}_i^{\,2}}{8L} \right),$$

where DT_i = diameter (in dm) of wood item i at transect crossing, and L = transect length (in m) (Van Wagner, 1968).

Standing deadwood diameter and height were measured within 2.5 m on each side of the same transects used for estimating fallen deadwood. The volume of standing deadwood was calculated using the equation for a cylinder. The volumes of total, standing and fallen deadwood were included as variables in statistical tests. Canopy cover (%) was measured above each trap using CanopyApp (For Apple iOS, Version 1.0.3, University of New Hampshire) as openness can influence saproxylic beetle assemblages (Seibold et al., 2016). The extent and year of the burn, as well as region, were also included in the analyses (Table S1).

2.3 | Landscape variables

At the landscape level, we collected data on the area of burned forest (wildfires and prescribed), protected forest, clear-cut forest, forest older than 120 years and standing volume per hectare of living trees. Overlaps in forest type occurred; for example, some old forests and burned forests were also protected.

Coordinates and extent of all reported wildfires were sourced from The Swedish Civil Contingencies Agency. Wildfire polygons (circular) were created using the coordinates and extent to attain an estimate of recent wildfire areas within buffers. Prescribed burn data was retrieved from county boards and Life Taiga (an EU funded project conducting prescribed burns), as well as the largest forest landowners in Sweden (Sveaskog, Holmen, SCA, and Stora Enso). Many fire-favoured beetles can be found on burn sites directly after burning, but generally decrease with time (Ranius et al., 2014; Wikars, 2006). We included data on burned forests for the years 2012–2021, since we considered that burns surrounding our sites (burned 2015–2018) could potentially constitute dispersal sources for insects.

The area of protected forests (national parks, nature reserves, Natura 2000 and woodland key habitats) was sourced from the Swedish Environmental Protection Agency and Swedish Forest Agency. The area of forest that had been clear-cut between 2012 and 2021 was obtained from the Swedish Forest Agency. The area of forest older than 120 years, and standing volume per hectare of Norway spruce (*Picea abies*), Scots pine (*Pinus sylvestris*) and deciduous trees (raster resolution 25 × 25 m) is based on a combination of satellite imagery and validation in the field by the Swedish National Forest Inventory program, and was downloaded from SLU Forest Map (2010).

To account for variations in both habitat amount and the spatial scale of effect, landscape variables were computed for circular landscapes at four spatial scales (2, 5, 10 and 20 km radius from the burn site perimeter; Figure 1). ArcGIS (ESRI, 2020) was used to synthesize and calculate data for each environmental variable at each scale. For raster layers (tree volumes per ha and forest age), the tool *zonal statistics as table* (ESRI, 2020) was used to calculate the mean per hectare for tree volumes and total area in hectares for age. For vector layers (burns, protected forest and clear-cut area), the tool *tabulate area* (ESRI, 2020) was used to calculate the area in hectares.

2.4 | Statistical analysis

The response variables species richness and abundance were calculated and analysed per site for both all saproxylic species and for fire-favoured species specifically. To address any issues with sampling effort and efficiency, abundance-based rarefaction (iNEXT package; Hsieh et al., 2024) was used to estimate the species richness of each site, using the site with the lowest abundance as the comparison point (saproxylic: 61, fire-favoured: 18). Abundance of each site was calculated as mean abundance per trap.

We examined the effect of local and landscape variables (Table S5) on species richness and abundance per site using generalized linear models (GLMs: Mass; Venables & Ripley, 2002). For species richness, we used Poisson models with a log-link function. Due to overdispersion, we used negative-binomial GLMs for species abundance. Diagnostic plots were used to assess model fit and assumptions (DHARMa package; Hartig, 2022). Correlations between some variables and scales made all-inclusive models unreliable (Figures S1–S4). Thereby, each variable and scale were modelled separately. In one site, the fire-favoured abundance was very high (Table S3), disproportionately affecting models, so all models for fire-favoured abundance were run both with and without this site to avoid misleading results. Model AIC was extracted for each model, and ΔAIC was calculated for models if several scales were significant at $p < 0.05$ to identify the scale of effect (Jackson & Fahrig, 2012). Models with $\Delta\text{AIC} < 2$ were considered equally plausible (Burnham & Anderson, 2002). Buffer extent overlapped especially at the 20 km scale (Table S6). Thereby, to test for spatial autocorrelation, Moran's I autocorrelation coefficient for model residuals was calculated (spdep package; Bivand & Wong, 2018). No autocorrelation was found (Table S7).

Patterns in species composition for all saproxylic species, and for fire-favoured species specifically, were explored using non-metric multidimensional scaling (NMDS: vegan package; Oksanen et al., 2020). NMDS is well suited for analyses where the focus is on the relative positioning of statistical individuals, rather than their absolute distances. Euclidean distances on Hellinger transformed data was used, which is appropriate for species abundance data and reduces the influence of rare species (Legendre & Gallagher, 2001). Assumptions of homogeneity of spread were tested (Vegan package; Oksanen et al., 2020). Goodness-of-fit was assessed using the 'stressplot' function (Vegan package; Oksanen et al., 2020). Permutational multivariate analyses of variance (PERMANOVA) was used to test differences between regions (Vegan package; Oksanen et al., 2020). Spatial autocorrelation was assessed using Moran's I on the NMDS axes and on the residuals of the PERMANOVA model. While NMDS axes showed significant spatial autocorrelation (Moran's I, $p < 0.05$), no spatial autocorrelation was detected in the PERMANOVA residuals, indicating that the model effectively captured the spatial variation (Table S7). As we also wanted to examine how local and landscape variables may affect species composition, these were fitted in NMDS as vectors and their significance assessed with permutation tests.

All statistical analyses were performed with R 4.3.3 (R Core Team, 2024).

3 | RESULTS

In total, we collected 3094 individuals belonging to 188 saproxylic beetle species (Tables S2 and S4). Out of these, 1153 individuals belonging to 37 species were classified as fire favoured (Tables S3 and S4). We recorded 12 species (39 individuals) that are red-listed in Sweden (SLU Artdatabanken, 2020) (Table S4). Four pyrophilic species were recorded (*Stephanopachys linearis* $N = 7$, *Stephanopachys substriatus* $N = 1$, *Euracmaeops septentrionis* $N = 7$ and *Denticollis borealis* $N = 1$).

3.1 | Local and landscape effects on richness and abundance

For all variables significantly related to response variables, the spatial scale of effect was either 5 or 10 km, with both scales receiving equivalent statistical support ($\Delta\text{AIC} < 2$; Table 1). Saproxylic abundance was positively associated with the area of clear-cut forest but negatively associated with the area of protected forests (Figure 2 (1a–d); Table 1). In contrast, the richness of saproxylic species was positively associated with the area of protected forests but negatively associated with the area of clear-cut forest (Figure 2 (2a–d); Table 1). The abundance of fire-favoured species was positively associated with the area of clear-cut forest, while there were no relationships between the richness of fire-favoured species and any of the environmental variables tested for. For local variables, no significant relationships (based on $\alpha = 0.05$) were detected (Table S8).

3.2 | Saproxylic species composition

Species composition of saproxylic beetles differed among regions (Figure 3; PERMANOVA $R^2 = 0.18$. $F_{2,22} = 2.24$ and $p = 0.001$). At the landscape scale, the area of forest older than 120 years was important for explaining site dissimilarity (Figure 3; Table 2). The landscape variables area of protected forest and volume of spruce were also influential. At the local scale, the amount of fallen deadwood was important.

3.3 | Fire-favoured species composition

The species composition of fire-favoured beetles differed among regions (Figure 4; PERMANOVA $R^2 = 0.18$. $F_{2,22} = 2.21$, $p = 0.009$). Forest older than 120 years was an important predictor of species

TABLE 1 Results of generalized linear model ANOVAs for the effects of local and landscape variables (single variable models) (2, 5, 10 and 20 km buffers) on saproxylic and fire-favoured beetle abundance (mean per trap) and species richness (rarefied).

Response variables	Environmental variables	df	Deviance	Residual DF	Residual deviance	*p* value	Model AIC (ΔAIC)
Saproxylic abundance	Protected forest 5 km	1	11.9	21	23.1	<0.001	176.5 (Δ1.7)
	Protected forest 10 km	1	14.9	21	23.2	<0.001	174.8 (Δ0)
	Protected forest 20 km	1	7.5	21	23.4	0.006	179.6 (Δ4.8)
	Clear-cut forest 5 km	1	3.9	21	23.4	0.05	182.3
Saproxylic richness	Protected forest 5 km	1	6.04	21	21.9	0.01	141.4 (Δ1.1)
	Protected forest 10 km	1	7.1	21	20.8	0.008	140.3 (Δ0)
	Clear-cut forest 5 km	1	4.6	21	22.1	0.03	142.6 (Δ0)
	Clear-cut forest 10 km	1	3.9	21	22.8	0.05	143.3 (Δ0.7)
Fire-favoured abundance	Clear-cut forest 5 km$^{*\text{with extreme}}$	1	11.3	21	20.9	<0.001	138.9
	Clear-cut forest 5 km$^{*\text{without extreme}}$	1	4.7	20	27.0	0.03	119.6

Note: Only results $p \leq 0.05$ are included. Landscape variables with marginal influence can be found in Table S9. Model AIC and ΔAIC are included to facilitate interpretations of scale of effect. Effect plots can be found in Figure 2.

composition, especially at 5 and 10 km scales (Table 3). The volume of standing spruce and the area of clear-cut forests also explained site dissimilarity.

4 | DISCUSSION

Our results show that landscape habitat amount seems to have a stronger effect on shaping saproxylic beetle communities after prescribed burning than the local habitat amount. This is in accordance with the habitat amount hypothesis (Fahrig, 2013), which has been supported in a study of saproxylic beetles (Seibold et al., 2017). There was a positive relationship between area of protected forests in the surrounding landscape and richness of saproxylic beetles at the burn sites. Protected, unmanaged forests host a greater richness and abundance of saproxylic species compared to production forests and clear-cuts (Paillet et al., 2010; Stenbacka et al., 2010), likely due to the larger volumes and diversity of deadwood present compared to the surrounding production-forest matrix (Kyaschenko et al., 2022; Siitonen, 2001). This highlights the importance of maintaining or increasing the amount of protected forest habitat in the landscape for saproxylic beetle conservation, as these areas may serve as source habitats for post-burn colonization.

In contrast to the positive effect of protected forest area on species richness, we found negative associations between clear-cuts and species richness. The opposite was true for abundance; the abundance of saproxylic beetles decreased with the area of protected forests but increased with increasing area of clear-cuts in the landscape. Also, for fire-favoured species, abundance was positively associated with clear-cut area. Clear-cuts are open, sun-lit environments with relatively high volumes of smaller diameter deadwood. Previous studies have found that clear-cuts have lower species richness than standing forest and harbour distinct communities dominated by disturbance adapted (including fire-favoured) and open-habitat specialists (Johansson et al., 2007; Stenbacka et al., 2010). The proportion of clear-cuts in our landscapes at 5 and 10 km scales ranged from 2% to 10%. A high proportion of recent clear-cuts may indicate an intensive production landscape, potentially leading to an impoverished species pool, which could explain the reduced richness in areas with more clear-cuts. The patterns in abundance are likely due to similarities in habitat between burn sites and clear-cuts, as they both may favour specific disturbance adapted species. For example, *Hylastes brunneus* is a disturbance adapted species that was abundant in our study. It feeds on roots of newly dead pines, which are abundant on clear-cuts and in some of our burn sites.

Though we studied the effects of landscape composition up to 20 km surrounding burn sites, the strongest effects were evident within 5 and 10 km, suggesting this is the range of spatial scales at which landscape structure best predicts the response of saproxylic beetle assemblages. However, as the spatial scale of response varies widely among saproxylic species (Ranius et al., 2011, 2014), this scale of effect should be viewed in terms of the community as a

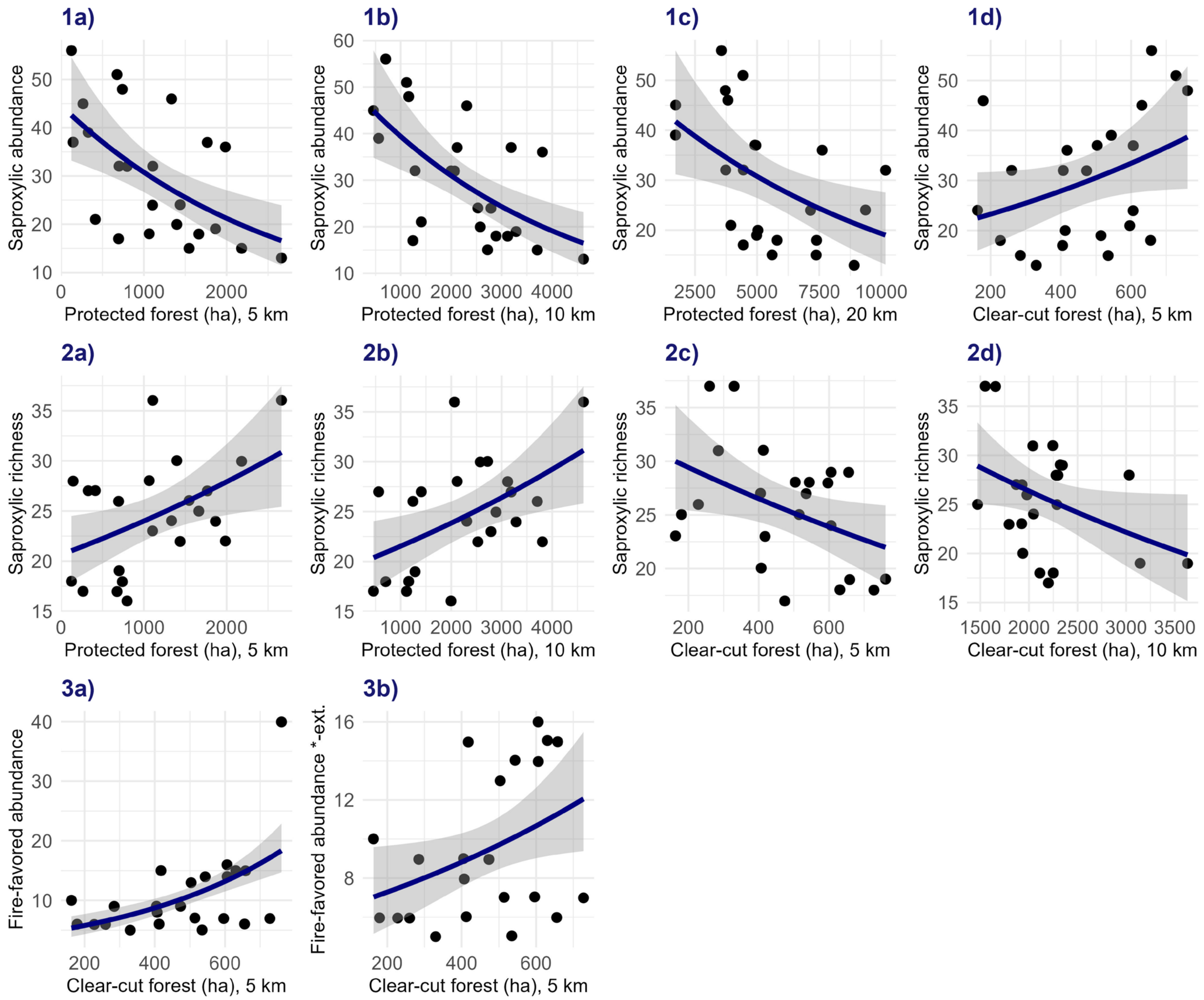

FIGURE 2 Effect plots for (1) the saproxylic abundance in relation to protected forest area at (1a) 5 km (1b) 10 km and (1c) 20 km and (1d) clear-cut forest area at 5 km; (2) the saproxylic richness in relation to protected forest area at (2a) 5 km and (2b) 10 km, and clear-cut forest area at (2c) at 5 km and (2d) 10 km; (3) the fire-favoured abundance in relation to clear-cut forest area at 5 km (3a) with an extreme value and (3b) without. Black dots are data points, the blue line shows the predicted value and the grey areas depict 95% confidence intervals. Generalized linear model ANOVA results can be found in Table 1.

whole and not for specific species. We suggest that landscapes with a radius of 5–10 km should be considered when planning prescribed burns in the context of saproxylic and fire-favoured beetles.

Counter to our expectations, we found no relationships between richness or abundance of saproxylic or fire-favoured beetles and the burned or old forest area. Within 10 km of our sites, the mean proportion of burned forests was 0.4% and for old forests 1%. Possibly, the lack of a relationship may be due to these forest types being too scarce in the landscape to significantly influence beetles at our burn sites. Other studies suggest that richness of saproxylic species in general is positively associated with the proportion of old forest (Hämäläinen et al., 2023; Olsson et al., 2012) within similar landscapes as ours. However, these studies focus on other species or interactions and not on saproxylic or fire-favoured beetles.

We found clear differences in species composition among regions, as expected, but no differences in species richness between regions, which was unexpected. In general, species richness is expected to be higher at lower latitudes, following the latitudinal diversity gradient (Hillebrand, 2004). Our results may indicate that differences in current and historic land use and beetle climatic ranges (Gossmann et al., 2024) are more important for shaping saproxylic beetle communities, resulting in different species composition but similar richness across regions.

We found that the area of old forests in the landscape, which was highest in the northern region, was an important variable explaining saproxylic and fire-favoured beetle composition. This supports the earlier findings that the proportion of old forest in the landscape is important for forming the species composition of saproxylic beetles

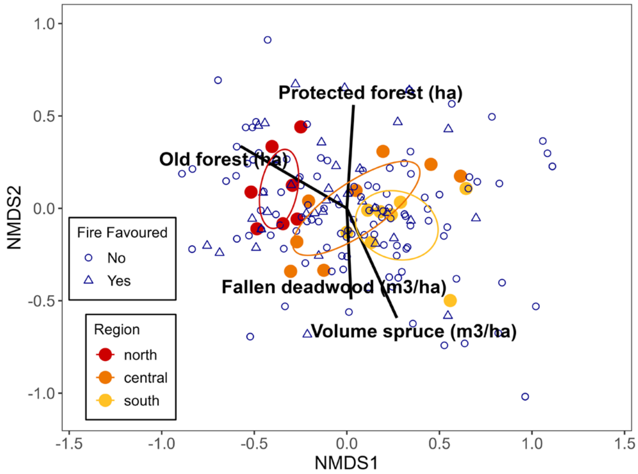

FIGURE 3 Nonmetric multidimensional scaling (NMDS) ordination plot showing differences in all saproxylic beetle species between three Swedish regions. Fire-favoured beetles are indicated with triangles, whereas other saproxylic beetles are represented by circles. Environmental variables are fitted as vectors, where the length of the vectors indicates their importance and their position indicates the direction of change. Vector details can be found in Table 2. The two-dimensional stress ratio is 0.14. Non-metric fit $R^2 = 0.979$ and Linear fit $R^2 = 0.895$.

TABLE 2 Results of multiple regression of environmental variables at different scales with ordination axes in the NMDS (Figure 3).

Scale	Environmental variables	NMDS1	NMDS2	R^2	*p* value
Local	Fallen deadwood (m^3/ha)	0.05	−0.99	0.25	0.05
2 km	Protected forest (ha)	0.06	0.99	0.32	0.02
5 km	Forest older than 120 years (ha)	−0.80	0.60	0.43	0.003
10 km	Forest older than 120 years (ha)	−0.86	0.50	0.50	0.001
20 km	Forest older than 120 years (ha)	−0.85	0.51	0.45	0.004
	Volume of spruce (m^3/ha)	0.40	−0.92	0.43	0.005

Note: Values in NMDS1 and NMDS2 columns represent the relationship of environmental variables to the first and second NMDS axes. *p* values are results of permutation tests. If an environmental variable was significant at several scales ($p \leq 0.05$), its mean was fitted in the NMDS plot (Figure 3).

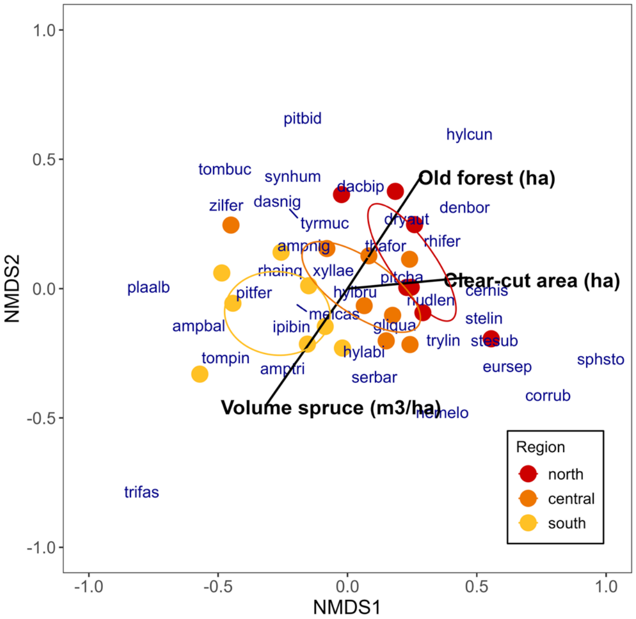

FIGURE 4 Nonmetric multidimensional scaling (NMDS) ordination plot showing differences in fire-favoured beetles between three Swedish regions. Environmental variables are fitted as vectors, where the length of the vector indicates their importance and position indicates the direction of change. The black text and lines indicate variables significant at $p \leq 0.05$. Vector details can be found in Table 3. Species abbreviation explanations can be found in Table S3. The two-dimensional stress ratio is 0.18. Non-metric fit $R^2 = 0.966$ and Linear fit $R^2 = 0.832$.

TABLE 3 Results of multiple regression of environmental variables at different scales with ordination axes in the NMDS (Figure 4).

Scale	Environmental variables	NMDS1	NMDS2	R^2	*p* value
5 km	Forest older than 120 years (ha)	0.51	0.85	0.40	0.005
10 km	Forest older than 120 years (ha)	0.55	0.83	0.41	0.004
	Volume of spruce (m^3/ha)	−0.70	−0.71	0.26	0.04
20 km	Forest older than 120 years (ha)	0.54	0.83	0.35	0.02
	Volume of spruce (m^3/ha)	−0.57	−0.82	0.38	0.008
	Clear-cut forest (ha)	0.99	0.09	0.27	0.04

Note: Values in NMDS1 and NMDS2 columns represent the relationship of environmental variables to the first and second NMDS axes. *p* values are results of permutation tests. If an environmental variable had a statistically significant effect at several scales, its mean was fitted in the NMDS plot (Figure 4).

(Olsson et al., 2012). The species composition at southern sites was associated with local high volumes of deadwood and high volumes of spruce in the landscape. This likely reflects the adaptation of the species pool to a higher proportion of spruce in the south compared to the north.

Land-use history may also have an effect on shaping our beetle communities, with the north having a shorter management history and thereby more intact natural forests (Svensson et al., 2019).

Kouki et al. (2012) found that decreasing species richness from eastern to western Finland was matched by increased management intensity. Though we found no differences in richness between regions, the majority of pyrophilic species were found in the northern region, while none were recorded in the southern region. Our south–north gradient encompasses climatic as well as current and historical land-use differences, all of which may influence community composition. As these factors co-vary along with the latitudinal gradient, their individual effects and respective contributions to the observed patterns are difficult to disentangle. It is, nevertheless, clear that regions host different species assemblages, demonstrating that a uniform effect from prescribed burning on community composition cannot be expected among regions, which is important to consider when planning where to conduct prescribed burning.

5 | CONCLUSIONS

Our study shows that the surrounding landscape plays a significant role in shaping saproxylic beetle communities after prescribed burning. Species richness and abundance, as well as community composition, varied depending on the extent of protected forests, old forests and clear-cuts in the surrounding landscape. This demonstrates that forest management and conservation measures in the surrounding landscape influence the biodiversity of burned forests and should be considered when planning burns aimed at promoting saproxylic beetles. As we found that landscapes with a 5–10 km radius were the most relevant scale for predicting saproxylic beetle assemblage responses, we suggest that at least this scale should be taken into account when planning prescribed burns. Prescribed burns in this study were conducted in protected forests, and surrounding protected forest influenced observed species richness and composition. Therefore, prescribed burning can be viewed as one tool among others in landscape-scale conservation, with, for example, preserving forests in reserves also being important. Finally, since species composition varied between regions but not richness, we found no clear evidence indicating that one region should be prioritized over another. The variation in species pools across regions instead indicates that prescribed burning in different regions complements each other.

AUTHOR CONTRIBUTIONS

Ellinor Ramberg, Joachim Strengbom, Lars-Ove Wikars and Thomas Ranius conceived the ideas and designed methodology; Ellinor Ramberg collected and analysed the data; all authors interpreted the data; and Ellinor Ramberg led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflicts of interest to declare.

DATA AVAILABILITY STATEMENT

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.k3j9kd5m4 (Ramberg et al., 2025).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Table S1: The 23 sites included in this study, the region, protection type, the burn extent (ha), the approximate radius (m) from center to site edge, burn year, canopy cover (mean % at trap locations, lower % indicates lighter conditions) and number of traps placed per site.

Table S2: Overview of saproxylic beetle total abundance, total richness, mean abundance per trap and rarefied richness in each site, including the region and viable number of traps per site.

Table S3: Overview of fire-favored beetle total abundance, total richness, mean abundance per trap and rarefied richness in each site, including the region and viable number of traps per site.

Table S4: Species list of all saproxylic beetles in this study, including their abbreviation and total abundance found.

Table S5: The local and landscape environmental variables used and their source.

Table S6: Overlap in km2 and distance in km for each buffer size per site with their nearest neighbor.

Table S7: Moran's I autocorrelation coefficient for model residuals and NMDS axes (Table 1, Fig 3 and Fig 4 in main document).

Table S8: Results of generalized linear model ANOVAs for the local variables: burn extent (ha) and year, canopy cover (%), region, and total, standing and fallen deadwood volume (m3/ha), effects on saproxylic and fire-favored beetle abundance (mean per trap) and species richness (rarefied).

Table S9: Results of generalized linear model ANOVAs for the effects of local and landscape variables (2, 5, 10, and 20 km buffers) on saproxylic and fire-favored beetle abundance (mean per trap) and species richness (rarefied).

Table S10: Results of multiple regression of environmental variables at different scales with ordination axes in the NMDS (All saproxylic species: Figure 3).

Figure S1: Correlations between landscape variables at 2 km.

Figure S2: Correlations between landscape variables at 5 km.

Figure S3: Correlations between landscape variables at 10 km.

Figure S4: Correlations between landscape variables at 20 km.

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