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Research article

Wildfire influences species assemblage and habitat utilisation of boreal wildlife after more than a decade in northern Sweden

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Fires can strongly change the vegetation structure and the availability of resources for wildlife, but fire suppression has long affected the natural role of fire in shaping boreal ecosystems in northern Europe. Recently, wildfires have increased in frequency, possibly due to global warming. In contrast to the boreal systems in North America, there have been few studies on responses of wildlife to wildfires in northern Europe. Based on the findings from North America, we predict that responses of wildlife to wildfire vary among wildlife species: where mammalian herbivores, such as moose *Alces alces* and mountain hare *Lepus timidus*, will be attracted to burnt areas following an increase in food availability, other species, such as reindeer *Rangifer tarandus*, are negatively impacted due to fire reducing their preferred food. We then tested our predictions by contrasting wildlife utilization of sites that burnt by wildfire in 2006 with nearby unburnt control sites in three areas in northern Sweden. To measure wildlife utilization, we used 72 camera traps, equally divided between the burnt and control sites, with two placement strategies: random and on wildlife trails. The cameras recorded 27 mammal and bird species during summer 2018. Species assemblage differed between burnt and control sites. Fieldfare *Turdus pilaris* used burnt sites more than control sites, while pine marten *Martes martes* and western capercaillie *Tetrao urogallus* used control sites more than burnt sites. We however did not find support for a positive effect of past forest fires on any of the observed wild mammals. We discuss how, due to the impact of forestry, forage-rich habitat may not be as limiting in Scandinavia as in the North-American context, potentially leading to recently burnt sites being less attractive to herbivores such as moose.

Keywords: birds, fire disturbance, forest fire, forest management, habitat use, mammals



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Introduction

Wildfire is a crucial component of the boreal forest and alters its structure by opening up the canopy, creating coarse woody debris, changing the species composition of the field layer, adding charred wood, and reducing litter depth (Zackrisson 1977, Schimmel and Granström 1996, Eriksson et al. 2013, Berglund and Kuuluvainen 2021). These changes will be different depending on several factors such as burn severity, time since fire, latitude, and ecosystem productivity (Fang et al. 2018). One common long-term effect of fire in boreal forests is an increase in the cover of primary successional tree species, such as birch *Betula* spp., in the field layer (den Herder et al. 2009). Through these effects on the vegetation structure and composition, fires can affect the availability of food and shelter for wildlife in boreal forests (Engelmark 1999).

Fire as a natural disturbance in the boreal forest has been effectively suppressed in Fennoscandia during the last century (Pinto et al. 2020) but is now predicted to increase due to climate change (de Groot et al. 2013). However, the expansion of large-scale timber production and associated expansion of the road network and active fire suppression through creation of fire breaks have reduced the average annual area burned in Fennoscandia to less than 0.01% of the forested land (Granström 2001). The role of wildfire in shaping ecosystems has received increasing attention in terms of its role in biodiversity restoration as well as the interactions between fire and climate change (Masson-Delmotte et al. 2021).

A substantial number of studies have looked at the impact of fire suppression on certain taxa in the boreal forests of Fennoscandia. Specific examples from Fennoscandia include several studies that showed that wildfire affects bird community composition (Edenius 2011, Versluijs et al. 2017, Žmihorski et al. 2019) as well as certain specific bird species (Versluijs et al. 2019, 2020). However, studies on wildfire impacts on mammals are largely lacking from Fennoscandia (see Ecke et al. 2019 for a study on small mammals). As a result, there remain critical gaps in our understanding of the broader effects of fire on wildlife in general, i.e. the whole assemblage of larger mammals and birds. An improved understanding of the effects of fire on wildlife assemblages is especially important because of the predicted changes to fire regimes in northern boreal forests due to climate change (de Groot et al. 2013, Masson-Delmotte et al. 2021). Due to the limited knowledge about how fire regimes affect wildlife communities in Fennoscandia, we looked at other biomes and continents to further understand the mechanisms behind wildlife responses to fire.

Habitat requirements and traits (e.g. home range size or feeding type) influence how different species respond to fire (Eby et al. 2014). Fisher and Wilkinson (2005) reviewed the North American literature on wildlife responses to forest fire, including the effect of the time since fire. They found that insectivores had varied responses but generally increased in abundance in burnt areas a decade or two after the fire. Additionally, they found that large mammalian herbivores varied in their responses to fire, with caribou

Rangifer tarandus being less abundant in recently burnt areas while moose *Alces alces* increased in abundance in those areas (Fisher and Wilkinson 2005). Here, the fact that caribou avoided burnt patches is likely due to increased predation risk due to low cover and a lack of forage in terms of low lichen abundance (Joly et al. 2010), while moose are attracted to the burnt areas due to increased forage availability (Davis and Franzmann 1979). In a more recent review, Volkmann et al. (2020) highlight that most North American studies have focussed on ungulate and large-carnivore responses to past fires. They stressed a large knowledge gap for responses of medium-sized to small mammal species to forest fires, as well as for the impact of fires on species interactions (Fisher and Wilkinson 2005, Volkmann et al. 2020). Furthermore, we need to carefully consider habitat preferences of species, as well as the spatial scale of fires compared to species' home ranges, when evaluating the responses of wildlife communities to fire (Månsson et al. 2007).

In this study, we examined the difference in habitat utilization of wildlife assemblages, as measured with camera traps, between paired burnt and unburnt control sites in three areas in northern Sweden twelve years after wildfires occurred. Based on North American studies, we predicted that 10–15 years after a fire, forage availability for herbivores foraging on dwarf shrubs and young trees would be high relative to unburnt sites, leading to increased utilization of burnt sites by these herbivores, such as moose and roe deer *Capreolus capreolus* (den Herder et al. 2009, Zwolak 2009, Brown et al. 2018, Fredriksson et al. 2023). In contrast, lichen forage generally decreases after fire for a prolonged period of time (up to 58 years after burning, Joly et al. 2010), hence we predicted semi-domesticated reindeer *Rangifer tarandus* to instead utilize such burnt sites less than control sites. The utilization of forest sites by small mammalian herbivores, such as hares, is often higher in areas with a well-developed field layer found in later successional stages after fire (Fisher and Wilkinson 2005, Hutchen and Hodges 2019, Olson et al. 2023). Hence, we predicted utilization by hares to be higher in burnt sites compared to control sites. Finally, the increased presence of larger- and smaller-sized herbivores in burnt sites might attract carnivores as secondary consumers (Fisher and Wilkinson 2005, Olson et al. 2023), although smaller species such as the pine marten *Martes martes* might avoid burnt areas where canopy cover is missing (Volkmann and Hodges 2022). We thus predicted higher utilization of the burnt sites by carnivores in general, but lower use by pine marten.

Material and methods

Study area

Three large (> 300 ha) wildfires took place during the summer of 2006 in Norrbotten, northern Sweden. The areas are located on the south slope next to the Lule river in Muddus National Park (66°46'02.6"N, 20°09'36.4"E), 18 km north of the village of Lainio (67°54'26.7"N, 22°10'13.0"E) and

on the elevated Klusåberget in Bodträskfors (66°09'01.6"N, 20°49'43.0"E, Fig. 1). Due to the rareness of large natural wildfires in Fennoscandia since the implementation of effective fire suppression, these areas present a unique replicated opportunity to study the effects of wildfires on Fennoscandian wildlife communities. All three areas are characterized as boreal forest. However, they differ in their tree species composition with Lainio being dominated by Norway spruce *Picea abies* while the other two are dominated by Scots pine *Pinus sylvestris*. Bodträskfors is the most heavily managed area for timber production while Muddus and Lainio have semi-natural forests. The three wildfires also differed in their characteristics, where the wildfire in Bodträskfors was a mixed

ground and crown fire, the wildfire in Muddus was a ground fire, and the wildfire in Lainio a crown fire.

The study areas' productivity is generally very low due to their northern latitude, with Lainio and Muddus on the lowest range with 2.3 and 2.5 m³ forest growing per hectare per year while Bodträskfors at 3.1 m³ was slightly higher (calculated using unpublished data from the study sites). In each of the three study areas, we selected a control site of similar size and topography close to the burnt site (Fig. 1). Sites ranged in size from 216 to 422 ha (mean: 292 ha). Neither burnt nor control sites included stands that were harvested for forestry (either pre- or post-burn) in Muddus and Lainio, while the Bodträskfors study area contained some patches

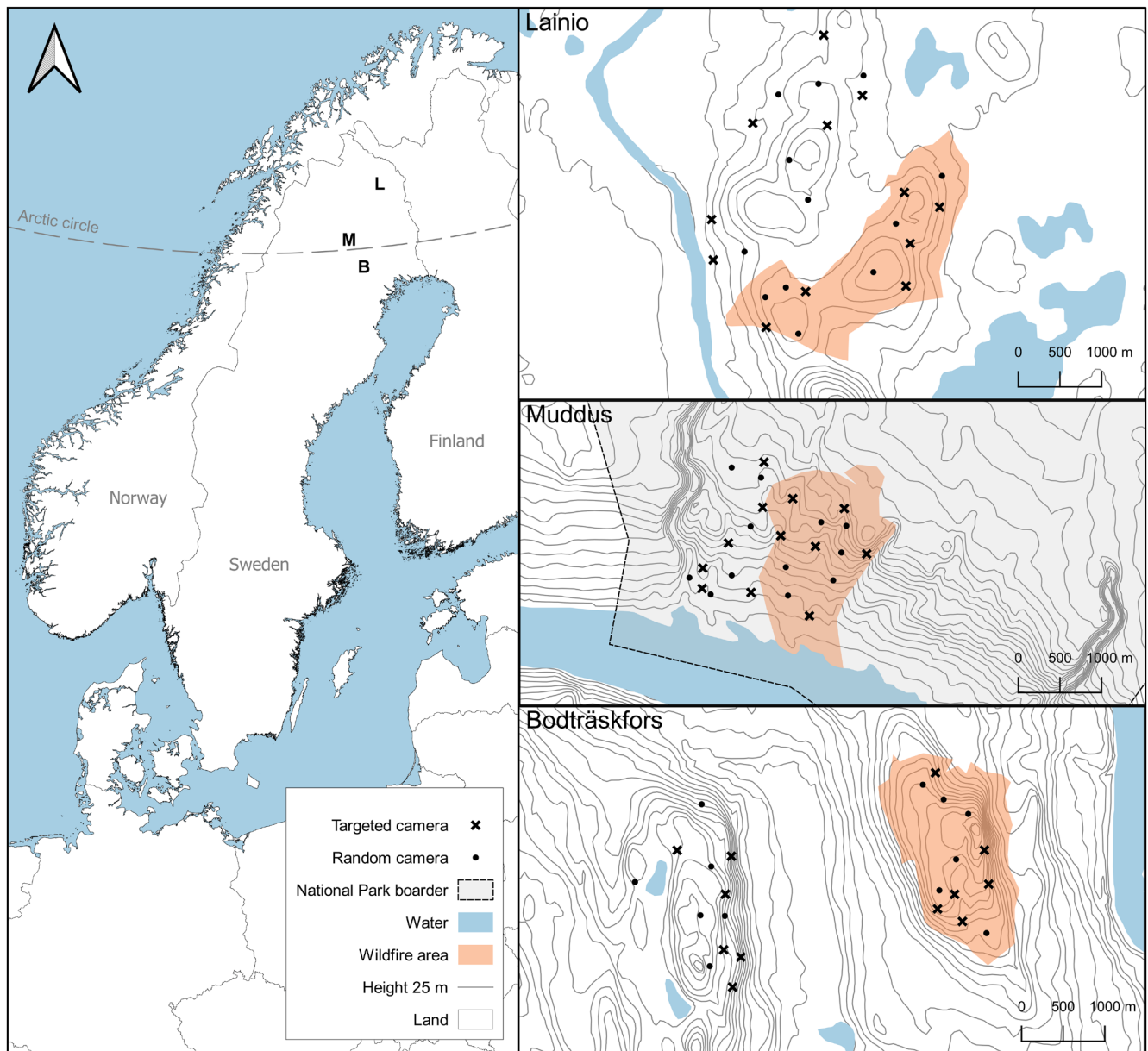


Figure 1. Map showing the locations of the tree wildfire areas; Lainio (L), Bodträskfors (B), and Muddus National Park (M) and the positions of the cameras denoted with black circles and crosses depending on placement type.

where harvest occurred around the year 2000 in the direct surroundings of the burnt site and on the western side of the control site.

Data collection

In each of the six sites, we deployed twelve camera traps (Reconyx Hyperfire HC 500) during June–September 2018 to quantify the utilization by wildlife. Because we were interested in the responses of both herbivores and carnivores, we used two different camera-trap placement strategies, based on previous studies that showed limited success of capturing large carnivores on randomly placed cameras (Bubnicki et al. 2019, Hofmeester 2021). We generated random locations within a shape-file (Fig. 1 for the burnt sites) delineating the study site in QGIS (ver. 3.14.0; QGIS Development Team 2009) for six of the twelve camera traps per site (from hereon referred to as random cameras). For the control sites, we selected an area of the same size and with similar topography directly next to the burnt site, within 2 km. The locations of the other six, targeted, camera traps (from hereon referred to as targeted cameras) were selected based on topographical maps of the study sites and patches that we expected carnivores to visit. We selected locations along ridges in the landscape characterized by a high terrain ruggedness index as these are often selected for by the two main large carnivores present in northern Sweden, Eurasian lynx *Lynx lynx* and wolverine *Gulo gulo* (Rauset et al. 2013). The average minimum distance between camera traps was 327 m (\pm 111 SD; range: 125–631 m).

In the field, we placed random cameras on the tree closest to the randomly generated location (< 30 m, but mostly within 10 m) with a good visibility (> 5 m without obstructions) towards the north to prevent issues due to direct sunlight into the camera lens. For targeted cameras, we walked along the ridge close to the selected location until we found a wildlife trail or clear feature in the topography, which would be channelling animal movement, at which we could aim the camera. We placed all cameras at a height of 20–50 cm from the base of the tree and angled them such that, at 3 m in front of the camera, the middle of their view was at approximately 30 cm from the ground surface and parallel to the ground. We did this to circumvent issues with steep or rocky terrain blocking the field of view of the camera, while ensuring that the cameras were placed low enough to capture small wildlife species. To correct for differences in detectability between species and camera locations, we placed distance markers at 2 m intervals and up to 18 m away from the camera in the centre of the camera view and had the camera take a picture of these markers during camera installation (Hofmeester et al. 2017), after which we immediately removed the markers. Cameras were set to take a series of ten images when triggered by the passive-infrared sensor at the highest sensitivity on 'rapid-fire' with no delay between triggers. We also set the cameras to take a time-lapse image at noon to monitor camera functioning. We installed the cameras in the field between 28 May and 7 June 2018 and collected them approximately

three months later between 5 and 25 September 2018. We thus monitored animal utilization during the peak of summer in this northern area. When collecting the cameras, we measured the visibility in front of each camera by aiming a laser range finder at camera height in three directions (-45° , 0° , and 45° from the middle of the camera view). We took images of ourselves when deploying and picking up the cameras, so we could use the first and last image taken by each camera to calculate the number of days the camera had been active. When a camera stopped working before we picked it up ($n = 5$), we used the time of the last (time-lapse) image as the end of the deployment.

All camera trap images were classified using the Trapper software – an open source camera-trap data management platform (Bubnicki et al. 2016). Trapper automatically grouped images into sequences when taken within 15 min of each other. For each sequence, we identified the species, and counted the number of individuals present in the images. Where possible we used sex and age to separate individuals to derive better counts. For example, when within one sequence an adult female moose would walk through the frame followed by several pictures of two moose calves, we would count these as two observations of three animals. We thus treated the combination of sequence, species, sex, and age as independent observations that could include more than one individual. If the animal or animals walked through the middle of the camera view, we estimated the distance interval at which they crossed the midline using the reference image with distance markers. We only determined one distance per observation, as the first distance at which any animal in that observation crossed the midline. For the example above, that would be one measurement for the female moose, and one for the first of the two calves crossing the midline. For each species and camera trap location, we summed the counts of all observations. Out of the 72 camera traps, two were not included in the analysis: one camera from the burnt site in Muddus, which accidentally was deployed with the wrong settings, and one camera from the burnt site in Bodträskfors site where the SD-card was filled up with images of moving vegetation within two days.

Correcting for detectability

All study sites were smaller than the average home range of most of the studied wildlife species, and burnt and control sites were situated close enough to each other for individual animals to utilise both sites. We were thus interested in comparing the 3rd order of habitat selection (sensu Johnson 1980), or within-habitat patch use, of the wildlife community between burnt and control sites rather than potential differences in density. This resulted in the need to correct for potential detection biases of camera traps at the 4th order (microsite) to 6th order (image) scale (sensu Hofmeester et al. 2019). We corrected for 4th and 6th order biases by our standardized camera-trap set-up with two placement strategies.

To correct for potential 5th order (camera trap-scale) biases in our estimation of patch use, we estimated the effective

detection distance (EDD) for each combination of species and camera location (Hofmeester et al. 2017). We fitted a hazard-rate detection probability function for point counts to the frequency of measured distance intervals using the 'mrds' package (ver. 2.2.4; Laake et al. (2020)). We used the log10-transformed body mass of captured species as derived from the EltonTraits database (Wilman et al. 2014) and the average visibility measurement (from our range finders) per camera as covariates. To accommodate for differences in body insulation between taxa, we ran two separate models for birds and mammals.

Differences in wildlife habitat between burnt and control sites

The effects of wildfire on wildlife habitat, both in terms of structural habitat and food availability for herbivores, likely differ among sites at small spatial scales due to differences in topography, fire severity, and other factors. Therefore, we measured two habitat characteristics at each camera-trap location that we could use to potentially explain differences between burnt and control sites. We collected data on the number of lying dead trees in a radius of 10 m around each camera location, as a measure of structural cover for smaller species and movement impediments for larger species. After that, we counted the number of young broad-leaved and Scots pine trees (< 80 cm) in a radius of 5 m around the camera location, as a measure of food availability for herbivores. We also included terrain ruggedness as a covariate in our models as this was one of the topography features that varied a lot between different camera locations, partially because we used it to select our targeted camera-trap locations. Moreover, ruggedness affects landscape use of many wildlife species (Rauset et al. 2013, Angoh et al. 2023).

Statistics

To test for differences in community assemblage as well as utilization of the different species between the burnt and control sites, we used a multivariate generalized linear model (multivariate GLM) with a negative binomial error distribution (Warton et al. 2012) as implemented in the 'mvabund' package (ver. 4.0.1; Wang et al. 2012). Multivariate GLMs were developed specifically for multivariate abundance data and thus are a promising way of analysing visitation frequencies of wildlife communities as measured with camera traps. An added advantage is that we could obtain estimates for both the whole community as well as univariate results for each species. Another advantage is that the univariate results for each individual species are automatically corrected for the fact that you run many models on the same dataset, reducing type I errors.

Because of a large number of zeroes and overdispersion in the data, we compared the fit of models using a negative binomial and Poisson error distribution and log link function using residual plots that showed a better fit for the negative binomial model. We ran two different models on

the number of observations per species and camera location. First, we ran a model where we added treatment (burnt versus control sites) and study area plus their interaction to the models to test for differences between burnt and control sites while accounting for the sampling strategy of multiple cameras per study area. This model also included placement type (targeted versus random) as a variable. Second, we ran a model with the three habitat variables as covariates: the logarithm of the number of dead trees, the logarithm of the number of young trees, and the terrain-ruggedness index value. Both models included the natural logarithm of the number of days the camera was active multiplied by the effective detection distance as an offset to correct for differences in sampling effort among locations and species. This second model did not include treatment, study area, or placement as variables, as these were correlated with the three habitat covariates (as tested with a generalized linear model with negative binomial distribution and log link for the count data and a linear model for the terrain ruggedness index).

We calculated adjusted p-values for each of the included parameters using residual permutation resampling as implemented in the 'mvabund' package. Apart from an overall assemblage analysis, we also were interested in the responses of individual species, so we performed a univariate analysis for all of the species using the anova function on the results from the multivariate GLM. Here, we also calculated adjusted p-values using residual permutation resampling. We interpret p-values as a continuous variable, where statistical significance does not strictly shift from significant to insignificant at the 0.05 p-value threshold (following Muff et al. 2022). Instead, we use the 'language of evidence' approach suggested by Muff et al. 2022, where one interprets findings with a p-value < 0.1 and refers to findings with p-values closer to 0 as presenting stronger evidence for a pattern versus findings with p-values closer to 0.1 presenting weak evidence for a pattern.

Results

On average, the cameras were active for 99 days (± 16 SD), resulting in a total effort of 6924 camera trapping days. In total, we observed 27 mammal and bird species, 17 of which were found at both control and burnt sites. The species that were found at most camera trap locations were: western capercaillie *Tetrao urogallus* (112 observations at 38 out of 72 locations), moose (96 observations at 33 locations) and semi-domesticated reindeer (388 observations at 30 locations) (Table 1). Six species, common raven *Corvus corax*, European pied flycatcher *Ficedula hypoleuca*, hooded crow *C. cornix*, northern wheatear *Oenanthe oenanthe*, stoat *Mustela erminea*, and yellow-necked mouse *Apodemus flavicollis*, were only detected in the burnt sites; while four species, bank vole *Clethrionomys glareolus*, brambling *Fringilla montifringilla*, European pine marten *Martes martes*, and roe deer, were only detected in the control sites (Table 1).

Table 1. The number of observations and camera trap locations with a minimum of one confirmed observation (within brackets) for all species divided between unburnt control site and burnt sites as well as among the three different areas: 'B' = Bodträskfors, 'L' = Lainio, 'M' = Muddus. Feeding types were based on Wilman et al. (2014).

Species name	Control				Burn				Traits	
	Total	B	L	M	Total	B	L	M	Trophic level/ feeding type	Taxonomic group
Bank vole <i>Clethrionomys glareolus</i>	1 (1)	0	0	1 (1)	0	0	0	0	Omnivore	Mammal
Black grouse <i>Lyrurus tetrix</i>	3 (3)	2 (2)	1 (1)	0	3 (3)	2 (2)	0	1 (1)	Herbivore	Bird
Brambling <i>Fringilla montifringilla</i>	1 (1)	0	0	1 (1)	0	0	0	0	Omnivore	Bird
Brown bear <i>Ursus arctos</i>	3 (3)	0	2 (2)	1 (1)	10 (4)	4 (2)	6 (2)	0	Omnivore	Mammal
Common raven <i>Corvus corax</i>	0	0	0	0	2 (1)	0	2 (1)	0	Carnivore	Bird
Eurasian lynx <i>Lynx lynx</i>	2 (2)	0	0	2 (2)	3 (3)	1 (1)	0	2 (2)	Carnivore	Mammal
Eurasian red squirrel <i>Sciurus vulgaris</i>	12 (4)	11 (3)	0	1 (1)	3 (2)	0	0	3 (2)	Herbivore	Mammal
European badger <i>Meles meles</i>	1 (1)	1 (1)	0	0	2 (2)	2 (2)	0	0	Omnivore	Mammal
European pied flycatcher <i>Ficedula hypoleuca</i>	0	0	0	0	1 (1)	0	0	1 (1)	Insectivore	Bird
European pine marten <i>Martes martes</i>	33 (12)	18 (6)	11 (3)	4 (3)	0	0	0	0	Omnivore	Mammal
Fieldfare <i>Turdus pilaris</i>	6 (5)	2 (2)	4 (3)	0	27 (14)	3 (3)	23 (10)	1 (1)	Insectivore	Bird
Hazel grouse <i>Tetrastes bonasia</i>	10 (3)	10 (3)	0	0	4 (2)	0	0	4 (2)	Herbivore	Bird
Hooded crow <i>Corvus cornix</i>	0	0	0	0	2 (1)	0	2 (1)	0	Carnivore	Bird
Meadow pipit <i>Anthus pratensis</i>	1 (1)	0	1 (1)	0	1 (1)	0	0	1 (1)	Insectivore	Bird
Mistle thrush <i>Turdus viscivorus</i>	8 (5)	3 (2)	0	5 (3)	28 (10)	3 (3)	12 (5)	13 (2)	Omnivore	Bird
Moose <i>Alces alces</i>	35 (18)	10 (7)	20 (8)	5 (3)	61 (15)	21 (2)	31 (8)	9 (5)	Herbivore	Mammal
Mountain hare <i>Lepus timidus</i>	26 (9)	16 (3)	7 (3)	3 (3)	43 (12)	14 (5)	3 (2)	26 (5)	Herbivore	Mammal
Northern wheatear <i>Oenanthe oenanthe</i>	0	0	0	0	2 (1)	2 (1)	0	0	Insectivore	Bird
Red fox <i>Vulpes vulpes</i>	7 (4)	0	7 (4)	0	10 (7)	2 (2)	8 (5)	0	Carnivore	Mammal
Redwing <i>Turdus iliacus</i>	4 (3)	0	4 (3)	0	13 (7)	4 (3)	8 (3)	1 (1)	Omnivore	Bird
Reindeer <i>Rangifer tarandus</i>	307 (15)	1 (1)	301 (12)	5 (2)	81 (15)	4 (3)	72 (9)	5 (3)	Herbivore	Mammal
Roe deer <i>Capreolus capreolus</i>	2 (2)	1 (1)	0	1 (1)	0	0	0	0	Herbivore	Mammal
Siberian jay <i>Perisoreus infaustus</i>	9 (7)	2 (2)	4 (3)	3 (2)	1 (1)	0	0	1 (1)	Omnivore	Bird
Song thrush <i>Turdus philomelos</i>	23 (11)	8 (4)	5 (3)	10 (4)	20 (11)	9 (3)	7 (5)	4 (3)	Omnivore	Bird
Stoat <i>Mustela erminea</i>	0	0	0	0	2 (1)	0	0	2 (1)	Carnivore	Mammal
Western capercaillie <i>Tetrao urogallus</i>	88 (26)	48 (9)	16 (11)	24 (6)	24 (12)	2 (2)	5 (2)	17 (8)	Herbivore	Bird
Yellow-necked mouse <i>Apodemus flavicollis</i>	0	0	0	0	1 (1)	0	0	1 (1)	Omnivore	Mammal
Number of camera-trap locations	36	12	12	12	34	11	12	11		

Table 2. Univariate results from a multivariate GLM on utilization of species with more than 10 cameras where the species was detected for a model including the experimental set-up as covariates. p-values < 0.05 are shown in bold type, and p-values < 0.10 in italic type. None of the less frequent species displayed p-values lower than 0.05 in the univariate results (not shown).

Species names	Explanatory variables	Deviance	p-value
European pine marten	Study area	2.0	1.00
	Treatment	18.6	0.001
	Treatment × Study area	2.4	0.87
	Placement	0	1.00
Fieldfare	Study area	20.6	0.002
	Treatment	9.3	0.07
	Treatment × Study area	7.7	0.11
	Placement	1.5	0.90
Mistle thrush	Study area	1.8	1.00
	Treatment	4.3	0.52
	Treatment × Study area	0.30	0.99
	Placement	4.5	0.61
Moose	Study area	5.8	0.67
	Treatment	2.6	0.77
	Treatment × Study area	0.89	0.98
	Placement	0.13	0.97
Mountain hare	Study area	2.9	1.00
	Treatment	0.46	0.99
	Treatment × Study area	2.2	0.87
	Placement	4.7	0.61
Reindeer	Study area	17.6	0.005
	Treatment	0.49	0.99
	Treatment × Study area	0.27	0.99
	Placement	2.7	0.69
Red fox	Study area	54.6	0.001
	Treatment	3.9	0.60
	Treatment × Study area	3.3	0.75
	Placement	9.7	0.11
Song thrush	Study area	0.46	1.00
	Treatment	0	1.00
	Treatment × Study area	1.5	0.94
	Placement	1.4	0.90
Western capercaillie	Study area	3.9	0.90
	Treatment	10.7	0.03
	Treatment × Study area	0.91	0.98
	Placement	9.9	0.11

We found strong evidence for differences in the wildlife assemblages (based on the multivariate GLM) of control and burnt sites (deviance (dev) = 77.1, $p = 0.001$), as well as differences among study areas (dev = 166.5, $p = 0.001$). The differences between control and burnt sites were not the same at all study areas (interaction term: dev = 63.5, $p = 0.001$). Furthermore, there was a clear difference in the number of observations between targeted and random camera trap locations (dev = 45.3, $p = 0.003$). As these differences were multidimensional, we used univariate analyses per species to see what patterns caused these community-level differences.

At a species level, we found moderate to strong evidence that western capercaillie and European pine marten utilized the control sites more than the burnt sites, while fieldfare *Turdus pilaris* utilized the burnt sites more than the control (Table 2, Fig. 2). Furthermore, reindeer, fieldfare, and red fox showed differences in utilization among the three study areas

with Lainio being the area with highest utilization (Fig. 2). None of the species showed a clear difference in number of detections between targeted and random camera traps.

The number of lying dead trees around camera trap locations was higher in burnt than in control sites ($\beta = 0.53$, $p = 0.003$). It also differed among study areas, with the largest numbers in Burträskfors and the lowest numbers in Muddus ($\beta = -0.60$, $p = 0.008$). Similarly, the number of young trees around camera trap locations was higher in burnt sites compared to controls ($\beta = 0.75$, $p = 0.007$), and higher in Burträskfors compared to Muddus ($\beta = -0.83$, $p = 0.02$). Terrain ruggedness index at camera trap locations was higher at targeted cameras compared to random cameras ($\beta = -0.38$, $p < 0.001$), as expected. It was also lower in Lainio compared to the other two areas ($\beta = -0.28$, $p = 0.005$).

We found strong evidence that utilization by wildlife assemblages (based on the multivariate GLM) changed multidimensionally with terrain ruggedness index (dev = 75.0, $p = 0.002$) as well as weak evidence that the number of lying dead trees influenced wildlife utilization (dev = 48.3, $p = 0.06$). The univariate results did not show many associations of wildlife visitation frequency with the three habitat covariates. We found moderate to weak evidence that visitation frequency of moose and reindeer decreased with terrain ruggedness index at the camera trap location (Table 3).

Discussion

Based on findings from North America, we expected the presence or suppression of wildfires to have a large impact on wildlife assemblages in boreal forests. However, we have limited knowledge on how fire influences wildlife in the heavily managed forests of Fennoscandia. Here, we present the responses of wildlife assemblages in three areas in northern Sweden to habitat changes a decade after wildfire. We found a shift in habitat utilization by the wildlife assemblage between burnt and control sites. The three study areas were also different from each other, highlighting the importance of local habitat conditions and spatial location in determining the habitat utilization of wildlife assemblages. Fieldfares had higher visitation frequencies in the burnt wildfire sites compared to the unburnt control sites. In contrast, we found higher visitation frequencies of western capercaillie and European pine marten in the control sites. This is in line with studies on small mammals and birds, which showed that habitat preferences of specific species drive their use of forest habitats after a wildfire, where some species were attracted to burnt patches while other species avoided these patches (Ecke et al. 2019, Žmihorski et al. 2019). In contrast to our expectations, we did not find increased utilization of burnt sites by herbivores and carnivores, nor did we find avoidance of burnt sites by reindeer.

None of our studied herbivore mammals showed a difference in utilization between treatments. Our observations that reindeer did not avoid burnt sites was in contrast with previous studies on caribou from North America (Fisher and

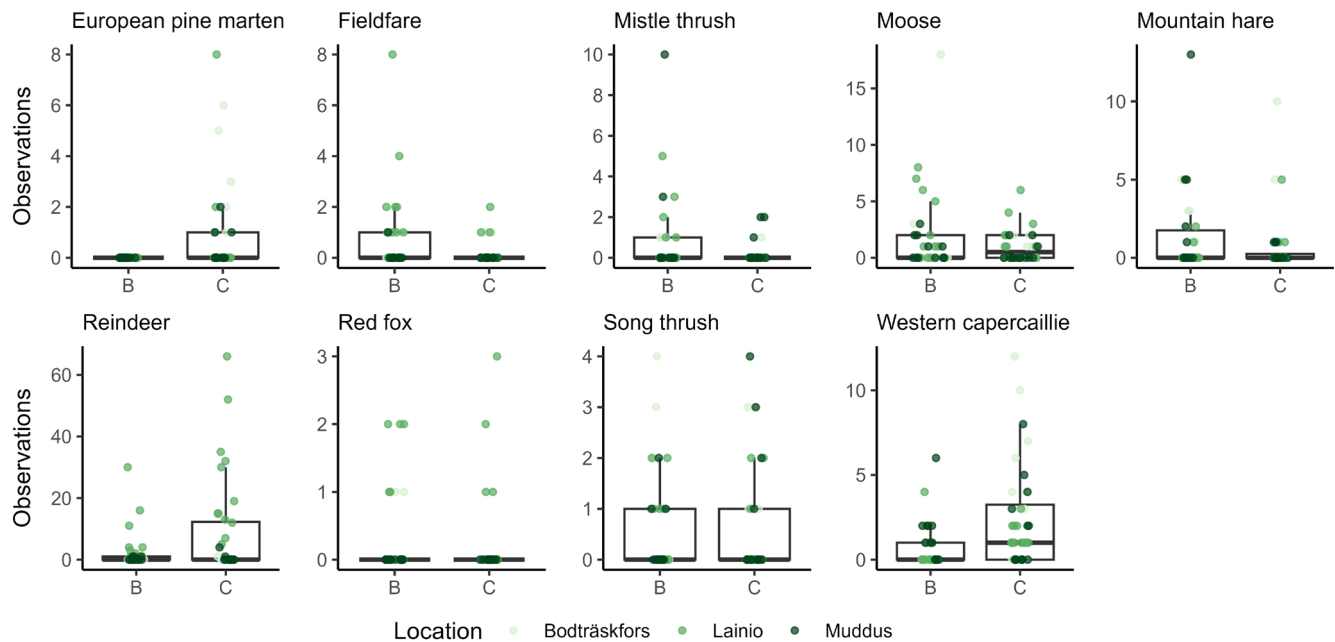


Figure 2. Number of observations for the species with observations at more than ten different camera trap locations split between the treatments where C=control and B=burnt. The y axis represents the number of observations without correction for the number of days that the camera was active or differences in effective detection distance among cameras, which were included as offset in the statistical models. Note the different scales on the y axis. The three different study areas are presented by different colours.

Wilkinson 2005, Joly et al. 2010). Reindeer is a lichen specialist and lichen cover can be negatively affected by fire and take a long time to recover (Joly et al. 2010, Lafontaine et al. 2019). However, most of our reindeer observations were from Lainio, where there was no ground fire but only a crown fire with likely limited effects on ground lichen, potentially explaining why we did not find a difference in reindeer utilization between burnt and unburnt sites. Our lack of response by moose to burnt areas contrasted with studies from North America showing that moose had higher abundance in sites at a similar successional stage after fire (Davis and Franzmann 1979, Fisher and Wilkinson 2005). Similarly, the lack of response by mountain hares is in contrast with studies on snowshoe hare *Lepus americanus* that generally have higher abundance a decade after fire (Fisher and Wilkinson 2005, Hutchen and Hodges 2019, Olson et al. 2023). The lack of response in these three herbivore species could potentially be a result of the relatively small size of our burnt and unburnt sites. This limits the possibility for a functional response in the smaller species (hares) and could cause the larger species to utilize the non-preferred site (unburnt for moose, burnt for reindeer) for a function other than foraging (e.g. thermal shelter) while still having access to a foraging site nearby. Furthermore, the different fire characteristics at the three sites (crown fire in Lainio versus ground fires in the other sites) might explain a lack of consistent patterns across sites.

We found that the burnt sites contained higher numbers of young trees, which are an important forage resource for mountain hares (Pulliainen and Tunkkari 1987) and moose (Milligan and Koricheva 2013, Felton et al. 2020)

in Fennoscandia. However, we did not find any associations between the number of young trees at a camera trap location and the utilization of that location by herbivores. Deer and hares have been found to use unburnt reference areas in North America, but shifted to the post-burnt sites when the understory vegetation regenerated enough to provide forage and cover from predators (Cave et al. 2021). The lack of a distinct difference in moose utilization stands out when comparing our findings to those of Fredriksson et al. (2023). While they observed higher utilization (in terms of pellet counts) in the same study areas during winter to be higher in the burnt areas, our study highlights these local seasonal differences in utilization. This indicates that the additional forage in the burnt sites might be more important for vertebrate herbivores in times of food scarcity (winter) compared to when food is abundant all over the landscape (summer). These findings highlight the importance of temporal aspects when it comes to wildlife responses to wildfire.

In contrast to our expectation, we did not find differences in utilization between burnt and control sites for most carnivores. The only exception was the pine marten, which we did not observe at all in burnt sites. One explanation for this is that we also did not find any large differences for most prey species. Our finding that pine martens seemingly avoided burnt sites is in line with studies in North America (Fisher and Wilkinson 2005) where American marten *M. americana* and Pacific marten *M. caurina* only rarely used burnt sites during the establishing phase, likely as a result of lack of prey and cover from aerial predators (Paragi et al. 1996, Volkmann and Hodges 2021, Volkmann and Hodges 2022). We did not find any associations between habitat characteristics and

Table 3. Univariate results from a multivariate GLM on utilization of species with more than 10 cameras where the species was detected for a model including habitat characteristics as covariates. p-values < 0.05 are shown in bold type, and p-values < 0.10 in italic type. None of the less frequent species displayed p-values lower than 0.05 in the univariate results (not shown).

Species names	Explanatory variables	Deviance	p-value
European pine marten	Ruggedness	1.7	0.99
	Lying dead wood	1.3	1.00
	Number of young trees	0.31	1.00
Fieldfare	Ruggedness	8.9	0.12
	Lying dead wood	3.0	0.95
	Number of young trees	1.3	1.00
Mistle thrush	Ruggedness	0.19	1.00
	Lying dead wood	0.26	1.00
	Number of young trees	0.88	1.00
Moose	Ruggedness	10.1	0.08
	Lying dead wood	0.12	1.00
	Number of young trees	1.9	1.00
Mountain hare	Ruggedness	1.3	0.99
	Lying dead wood	0.091	1.00
	Number of young trees	0.079	1.00
Red fox	Ruggedness	5.8	0.45
	Lying dead wood	3.2	0.93
	Number of young trees	1.2	1.00
Reindeer	Ruggedness	12.3	0.02
	Lying dead wood	0.029	1.00
	Number of young trees	0.051	1.00
Song thrush	Ruggedness	0.94	1.00
	Lying dead wood	0.45	1.00
	Number of young trees	0.77	1.00
Western capercaillie	Ruggedness	0.16	1.00
	Lying dead wood	2.6	0.97
	Number of young trees	1.3	1.00

carnivore utilization of camera trap sites, despite the expectation that several of the observed carnivores would likely select a location with a high terrain ruggedness index (Rauset et al. 2013, Angoh et al. 2023). A larger effort, e.g. by leaving the cameras in the field for multiple seasons or even years, might help to uncover patterns for species that showed less strong responses. Such studies would be needed to test for a related response of carnivores and their prey to past forest fires.

Fieldfares showed a higher utilization of the burnt sites over the control sites, while western capercaillie showed the opposite pattern. This is in line with previous studies showing that some bird species showed a preference for burnt sites after wildfire while others avoided these (Edenius 2011, Versluijs et al. 2017, Žmihorski et al. 2019). In a study three years after the wildfire, surveying birds in the same burnt sites in Muddus and Lainio, Edenius (2011) observed that ground-feeding insectivores (such as thrushes) were common in burnt sites. Previous studies in Fennoscandia showed that western capercaillie preferentially selected older forest (> 90 years; Swenson and Angelstam 1993), which would explain the higher utilization of control sites. None of the observed bird species showed associations with the measured habitat characteristics. Most bird species that we observed were observed only a few times, making inference about their habitat utilization difficult.

Despite our relatively high camera-trapping effort in terms of density and number of cameras, we still obtained relatively few observations for several of the species in our study. This was likely due to overall low abundance of these species in our system, resulting in low statistical power for those species. This was especially true for most carnivore species in this study, likely due to the fact that they occur at very low density in these landscapes, making it difficult to detect patterns in utilization among sites. This is an issue inherent to studies in low-density systems such as the boreal forest. Increased sampling effort, in the form of an extended study period, might help to increase the number of observations needed to disentangle utilization patterns of rarer wildlife species. This would inherently also mean that such a study would need to include multiple seasons or years, allowing for the study of seasonal differences in utilization of burnt sites by the different species. Furthermore, although ground-foraging birds are captured by camera traps, there might be many bird species that do not spend a large amount of time on the ground that we have missed. Due to their vocal activity, birds can be surveyed using passive acoustic monitoring (Ross et al. 2023), which might result in a higher statistical power to show differences in species utilization between burnt and control sites, for especially songbirds. Thus, a combination of methods might help in getting a better understanding of how the terrestrial vertebrate community responds to past wildfire.

Wildfire has been an important factor shaping the boreal forest in Fennoscandia and has impacts on the heterogeneity of whole landscapes. However, one could argue that important foraging habitat (initiation and establishment phase forest) for species such as mountain hare and moose is already provided by the Swedish forestry model (with extensive clearcutting), making burnt sites less important for these herbivores in the Swedish context. This would mean that burnt sites in this landscape do not necessarily add as much heterogeneity for wildlife in terms of early successional stages compared to other less managed boreal forests. Although wildfire and forestry affect forest composition differently, e.g. by promoting different species to regenerate after disturbance (Bouchard and Pothier 2011), we argue that these differences are relatively minor compared to the provisioning of otherwise absent young successional forest at the landscape scale. However, other habitat structures created by wildfire, for example lying deadwood that could provide cover for smaller wildlife species, could still be an important contribution of wildfire to habitat that would otherwise not exist. Furthermore, the difference in responses we found compared to the North American context might also be explained by the differences in scale of wildfire and forestry between continents, with large fires and forestry blocks in North America versus smaller-scale fires and forestry blocks in Fennoscandia (Burton et al. 2008, Rolstad et al. 2017). A landscape-level study focused on the site utilization of wildfire sites relative to early successional forest created by forestry, as well as mature forest, would help elucidate these potential differences. The decadal response of our study areas also needs to be considered in the context of their high latitude (above 66°N) in

combination with their relatively low productivity where the succession is slower compared to warmer and higher productivity sites. Three replicates of large wildfires in northern Sweden provided a unique opportunity to study the effects of wildfire on an assemblage of boreal wildlife after a decade and complement the growing knowledge from other ecosystems and continents. In an already heavily managed and disturbed landscape such as Fennoscandia our results show that the wildfire sites were avoided by some species, while one of the studied species utilized the wildfire sites to a larger degree compared to control sites. This suggest that heterogeneous landscapes, where old forests coexist with early successional habitats created by wildfire or forestry, are of utmost importance for wildlife inhabiting boreal ecosystems.

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Permits – All camera trapping was performed confirming to Swedish legislation, meaning that images of people were not stored or used in the analyses. Furthermore, we made sure to obtain the proper permissions from landowners and the County Administrative Board of Norrbotten to perform camera trapping.

Author contributions

Emelie Fredriksson: Conceptualization (equal); Formal analysis (equal); Investigation (lead); Methodology (supporting); Software (lead); Visualization (lead); Writing – original draft (lead); Writing – review and editing (supporting). **Joris P. G. M. Cromsigt:** Conceptualization (equal); Funding acquisition (supporting); Methodology (supporting); Validation (supporting); Writing – review and editing (supporting). **Tim R. Hofmeester:** Conceptualization (equal); Data curation (lead); Formal analysis (equal); Funding acquisition (supporting); Investigation (supporting); Methodology (lead); Project administration (lead); Software (supporting); Visualization (supporting); Writing – original draft (supporting); Writing – review and editing (lead).

Transparent peer review

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Data availability statement

All data and code used for the analyses of this manuscript are available at GitHub: <https://github.com/Tim-Hofmeester/wildfire>. An archived version of this repository can be found

on Zenodo: <https://doi.org/10.5281/zenodo.12743387> (Fredriksson et al. 2024).

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