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Short-term effects of wildfire on bird assemblages in old pine- and spruce-dominated forests in northern Sweden

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Effects of wildfire on forest birds have rarely been studied in Fennoscandia. Hence, birds were surveyed three years after fire at two large areas that were not subjected to salvage logging, in northern Sweden. The 300- and 440-ha burns and surrounding forests were dominated by Scots pine and Norway spruce, respectively. Closed-nest breeders and ground-feeding insectivores were more abundant within the burns than in the surrounding forests, whereas ground- and shrub-breeders were nearly equally abundant in the burns and in unburned forests. Redpoll and Tree Pipit were more common within than outside the burns. Birds feeding on insects in the air and the Redstart were more abundant in burned than in unburned spruce-dominated forest but no such difference was found in pine-dominated forest, suggesting that the short-term effects of wildfire on these birds were stronger in spruce-dominated forest than in pine-dominated forest. A contributing factor might be that crown fire killed most trees in the spruce-dominated burn, but most of the large trees survived the ground fire in the pine-dominated burn.

1. Introduction

Wildfires can strongly affect the structure and functioning of boreal forests (Goldammer & Furyaev 1996, Shorohova *et al*. 2009). They used to be relatively common and cover vast areas in Swedish boreal forests (Niklasson & Granström 2000), but today the prolonged, effective fire suppression has practically eliminated them (Zackrisson 1977). Not surprisingly, therefore, data on forest bird-fire relationships are scant from this part of the boreal forest biome. In comparison, much more work has been done in North America (Saab & Powell 2005). However, more knowledge of the ecological impacts of fire in general, and of the relationship between fire and birds in particular, is needed as there is a growing interest in Fennoscandia in using fire as a management tool to emulate natural disturbances (Korpilahti & Kuuluvainen 2002). A further motivation is that wildfires may become more common and more extensive following anticipated climate changes (Flannigan *et al*. 2009).

Since wildfires vary in frequency, intensity and size, it is difficult to generalize about their effects. However, with increasing numbers of studies, data are accumulating, thus allowing meta-analyses and syntheses of bird responses to fire (Saab & Powell 2005). Our understanding has also been advanced by addressing fire-bird relationships from the perspective of ecological theory, such as disturbance theory, foliage-height diversity and

life-history traits (Lindenmayer *et al*. 2008). However, although possibilities for deriving generalisations are improving, we still have limited knowledge of the magnitude of avian responses to fire. Comparisons between recent burns and unburned, surrounding areas provide a powerful yet underutilized approach to increase such knowledge (Saab & Powell 2005).

In the summer of 2006, three large (≥3 km^2) wildfire events occurred in northernmost Sweden. Two of these areas, viz. Muddus National Park (66°46' N/ 20°10' E) and Lainio (67°54' N/ 22°10' E), did not face subsequent salvage logging, offering rare opportunities to study the effects of fire in intact burns and surrounding forests under Fennoscandian conditions. This paper presents the first systematic survey of breeding birds at these two areas three years after the fire, and discusses the findings with reference to ecological theory.

The effects of fire on birds at the two areas were examined at the guild and species levels. Species selected to study were typical forest species for northern Fennoscandia, and the guild delineation was in accordance with ecological groups defined in earlier studies (e.g., Haapanen 1965, Helle & Mönkkönen 1990). Synthesising findings reported in different ecosystem types in North America, Saab & Powell (2005) concluded that arboreal and ground-feeding insectivores, and birds breeding in closed nests or on ground generally favour burned habitat, whereas birds breeding in shrubs are less affected. To test whether these patterns apply to Fennoscandian boreal forests, birds were categorised to Saab & Powell's (2005) feeding and breeding niche guilds a priori. Birds feeding on insects in the air, ground-feeding insectivores and birds breeding in closed nests or on ground were predicted to be more abundant within than outside the burns, whereas the abundance of shrub-nesting birds was predicted to be approximately the same. Furthermore, the magnitude of these responses was expected to vary between the two areas, as the effects of fire depend on local conditions, weather, and forest structure and composition (Shorohova *et al*. 2009).

2. Material and methods

2.1. Study areas

In mid-August 2006, lightning initiated a fire in the southern part of Muddus National Park. About 300 ha of rocky terrain at 165–325 m a.s.l., intersected by deep ravines connected to the Lule River in the south, was affected. This part of the national park is dominated by mid-aged to mature (ca. 100–140 years old) Scots pine (*Pinus sylvestris*) forests of low productivity. The thin field-layer vegetation is dominated by lichens and evergreen Ericaceae, mostly cowberry (*Vaccinum vitis-idaea*) and black crowberry (*Empetrum nigrum* ssp. *hermaphroditum*). The Muddus burn was a ground fire, and most of the larger trees survived.

The Lainio fire occurred in June 2006 and originated from prescribed regeneration burning in a managed forest. The fire became uncontrolled and spread into the adjacent ca. 200 years old forest stands. Approximately 440 ha of the forest on the hill Temminkivaara, 340–400 m a.s.l., burned over the subsequent days. The Lainio fire was a crown fire that killed most trees and left just a few scattered patches of unburned forest. Compared with Muddus, the terrain in Lainio is less steep and rocky. Forests are dominated by Norway spruce (*Picea abies*), with a significant amount of birch (*Betula pubescens*) and a small portion of Scots pine. Field-layer vegetation is more luxuriant and thicker than in Muddus and is dominated by

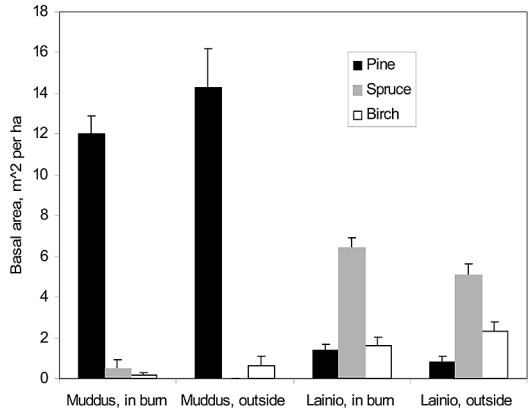

Fig. 1. Basal area of standing living and dead trees (>1.3 m) at the bird-survey points. Mean ±1 SE are shown.

Fig. 2. Forest structure in the Muddus (above) and Lainio (below) burned study forests.

mosses and dwarf shrubs, predominantly bilberry (*Vaccinium myrtillus*).

Besides being strikingly different in tree-species composition, the areas also differed in basal area of standing live and dead trees (Fig. 1). In 2009, the basal area was very similar in the burns and adjacent unburned forests at both areas (Fig. 1), reflecting the fact that very few trees had fallen three years after the fires. However, there was a stronger contrast in the field-layer vegetation in the burned parts of the two areas, since the layer was very thin and dominated by lichens and Ericaceae in Muddus, but grasses (especially *Deschampsia flexuosa*) dominated in Lainio (Fig. 2).

2.2. Bird surveys

Survey points were systematically distributed using 1:50,000 maps of the study areas on which the fire boundaries had been delineated, at the inter-

Table 1. The abundance of species with ≥20 individuals (in descending order of abundance) and observer-induced variability.

Species	Scientific name	Abundance	Variance
Brambling	*Fringilla montifringilla*	301	10
Redpoll	*Carduelis flammea*	225	25
Siskin	*Carduelis spinus*	212	16
Redstart	*Phoenicurus phoenicurus*	170	13
Willow Warbler	*Phylloscopus trochilus*	107	7
Redwing	*Turdus iliacus*	96	11
Spotted Flycatcher	*Muscicapa striata*	75	7
Song Thrush	*Turdus philomelos*	68	10
Crossbill	*Loxia curvirostra*	63	2
Tree Pipit	*Anthus trivialis*	51	2
Chaffinch	*Fringilla coelebs*	41	4
Pied Flycatcher	*Ficedula hypoleuca*	22	1
Mistle Thrush	*Turdus viscivorus*	22	3
Three-toed Woodpecker	*Picoides tridactylus*	20	2

sections of 250 m (E–W) × 500 m (N–S) grids covering the burns and adjacent unburned forests. Survey points were distributed so that 60% were in burned forests and 40% were in unburned forests. All survey points in unburned forests were within 750 m from the fire perimeter. Point coordinates were transferred to a GPS unit prior to field visits. In a few instances in the field, points were moved up to 30 m if their locations were in steep ravines or in non-forest habitat. A total of 44 points were visited in Muddus and 49 in Lainio. At each point, the basal area (m^2 ha^{-1}) of standing live and dead trees was estimated using a relascope, an optical sighting gauge used for standard forest inventories.

Bird surveys were 5-min point counts for all birds seen and heard, both stationary and over-flying. A pilot study showed that it was difficult to accurately determine the distance between survey points and birds, and that these estimates varied among observers. No distance limitation for the point counts was therefore applied, but as the same pilot study revealed that >90% of the observations were done <100 m from the survey points, 250 m between points was deemed sufficient to ensure independence of most observations. However, the Cuckoo (*Cuculus canorus*) was excluded from the analysis as its song carries over considerably longer distances. Two observers (the author and Christer Olsson) worked simultaneously but independently of each other in the surveys. The double-count survey method was chosen to enable estimates of detection probability (Nichols *et al*. 2000) to be obtained and to assess the precision of abundance estimates. The surveys were conducted between 02.30–10.30 AM, on 8–14 June 2009. The temperature varied between 1 °C in early mornings to 15 °C at around 10 AM, winds were weak (<4 m/s) and the skies were clear to moderately overcast.

2.3. Analysis

For each species, total abundance was estimated as (Magnusson *et al*. 1978):

$$I = |((C+O_1+1)(C+O_2+1))/(C+1)|-1 \quad (1)$$

and the associated variance was estimated as

$$Var = (O_1O_2(C+O_1+1)(C+O_2+1))/((C+1)^2(C+2)) \quad (2)$$

where C = minimum number of individuals observed by both observers summed over all observation points; O_1 = difference between the number of individuals observed by observer 1: and O_2 = difference between the number of individuals observed by observer 2 and C.

Life-history and guild-assignment data were obtained from Alerstam (1982) and Snow & Perrins (1998). For many of the rarer species, the

Table 2. The abundance of bird guilds and species in burned and unburned forests of Muddus and Lainio areas (individuals observed per survey point), and a summary of GLM results for the significance of study area, habitat type (burned vs. unburned forest) and study area vs. habitat type in determining these. Area = the effect of study area (Muddus or Lainio), Habitat = the effect of habitat type (burned or unburned), and Area × Habitat = interaction between these two factors. + = "more common in". Entries for response patterns are presented where $p < 0.05$ (GLM results adjusted for spatial autocorrelation). CN = Closed-nest breeders, GN = Ground-nest breeders, SN = Shrub-nest breeders, IaF = Arboreal insectivores, IgF = Ground-feeding insectivores.

		Muddus		Lainio		GLM summary		
Species	Guild	Burned (26)	Unburned (18)	Burned (29)	Unburned (20)	Area	Habitat	Area × Habitat
	CN	3.1	2.5	5.9	3.4	Lainio +	Burned +	
	GN	1.9	1.4	5.5	4.6	Lainio +		
	SN	4.2	4.3	4.0	3.2			
	IaF	4.8	4.6	5.8	3.2	Lainio +	Burned +	Lanio: Burned +
	IgF	3.4	2.8	3.9	2.2		Burned +	
Brambling		2.5	2.4	3.3	4.5			
Redpoll	SN	2.4	1.9	2.9	1.6		Burned +	
Siskin		3.1	3.2	1.1	1.7	Muddus +		
Redstart	CN/IgF	1.3	1.7	2.3	1.4			Lainio: Burned +
Willow Warbler	GN	0.1	0.1	1.7	2.4			
Redwing	SN/IgF	0.2	0.1	2.2	1.0	Lainio +		
Spotted Flycatcher	IaF	1.0	0.8	0.8	0.4			
Song Thrush	IgF	0.6	0.4	0.8	0.8			
Crossbill		1.4	0.6	0.1	0.6	Muddus +		
Tree Pipit	GN/IgF	0.7	0.5	0.7	0.2		Burned +	
Chaffinch		1.0	0.7	0.1	0.1			
Pied Flycatcher	CN/IaF	0.2	0.5	0.1	0.3			
Mistle Thrush	IgF	0.2	0.1	0.2	0.3			
Three-toed Woodpecker	CN	0.2	0.2	0.3	0.1			

raw data consisted of numerous counts of zero. Therefore, a lower limit of 20 individuals in total was set for an inclusion in the analyses at the species level. The variance:mean ratio for the remaining species and the five species guilds was approximately 1 in all cases except for the Crossbill (*Loxia curvirostra*; ca. 11). The effects of study area (Muddus vs. Lainio) and habitat type (burned vs. unburned forest) were analysed with a Generalized Linear Model (GLM) using a Poisson error distribution and log link function, except for the Crossbill for which a negative binomial error distribution was used. GLM residuals were tested with Moran's *I* at 250-m distance intervals from 0 to 2,000 m for spatial auto-correlation. Bonferroni-adjusted *p* values were used to account for spatial autocorrelation at each distance class, and if found significant a spatial regression model (Simultaneous Autoregression Model, SAM; Rangel *et al*. 2006) was fitted to the data to evaluate the significance of the area and habitat type together with space. R statistical software (R Development Core Team 2008) was used for the GLM-analysis and SAM v. 3.0 (Rangel *et al*. 2010) software for the Moran's *I* analysis and the spatial regression modelling.

3. Results

In total, 1593 individuals of 33 species were recorded at the 93 survey points. Five species produced more than 100 observations each: Brambling (*Fringilla montifringilla*), Redpoll (*Carduelis flammea*), Siskin (*Carduelis spinus*), Redstart (*Phoenicurus phoenicurus*) and Willow Warbler (*Phylloscopus trochilus*) and together accounted for 64% of the total abundance. Fourteen

species were sufficiently abundant for ≥ 20 individuals to be recorded (Table 1).

GLM revealed remarkable differences in the bird fauna between the two fires, between burned and unburned forests, and some interactions between these two factors (Table 2). Closed-nest and ground breeders, arboreal insectivores and the Redwing (*Turdus iliacus*) were more abundant in Lainio, whereas Siskin and Crossbill were more abundant in Muddus. Burned forests generally hosted more closed-nest breeders, arboreal insectivores and ground-feeding insectivores. Moreover, Redpoll and Tree Pipit were also significantly more common within than outside the burns. Finally, arboreal insectivores and Redstart appeared particularly abundant in the burned forests of Lainio. The rest of the comparisons or interactions were non-significant (Table 2). When the spatial autocorrelation was accounted for, the effect of habitat type (burned vs. unburned forest) in the GLM analysis remained the same.

4. Discussion

The present study contrasted two kinds of Fennoscandian boreal forests with distinct variation in vegetation and natural disturbance regime. The Muddus fire area consists of xeric, low-productivity forest that would be subject to recurrent, low-intensity ground fires with short fire-return intervals in the absence of fire suppression (Engelmark 1984). In contrast, Lainio represents a richer, spruce-dominated forest type, which in natural conditions would be affected by high-intensity crown fires with longer fire intervals (Shorohova *et al*. 2009). Tree dynamics at such sites are different, with cohort dynamics dominating at low productivity and xeric sites, while fine-scale gap dynamics are more important at richer, spruce-dominated sites (Shorohova *et al*. 2009).

At the guild level, arboreal and ground-feeding insectivores and closed-nest and ground breeders were expected to be more abundant within than outside the burns, whereas shrub-nesting birds were predicted to be less affected. These predictions were all supported by the present data, with the exception of ground breeders. Since there was only one replicate of each forest type, this result cannot be attributed solely to the effect of fire, as the study areas may have differed in other ways as well, such as soil quality and/or weather conditions. Due to the lack of data it is not possible to determine, for example, whether fire had a significant impact on the amount and/or availability of flying insects, or whether the en masse creation of substrates for perching and breeding, in terms of dead standing trees, facilitated arboreal insectivore birds in Lainio. The result for ground-feeding insectivores was also in agreement with the predictions, and indicates a general positive effect of fire across forest types on this guild. Ground-layer predatory and non-predatory beetle species increase after fire (Muona & Rutanen 1994), which may benefit birds searching for insects on the ground.

Regarding closed-nest breeders, fire often creates abundant dead wood and consequently potential cavity trees. Interestingly, Redstarts responded to fire as did the arboreal insectivore guild, i.e., both were most abundant in the spruce-dominated Lainio burn. This finding may conflict with expectations based on Redstart's designation as a mature-forest species (Helle 1985). Since Redstarts mostly nest in tree cavities one would not expect habitat suitability for Redstarts to substantially differ between burned and adjacent unburned forests, since very few trees were downed by the fire. Furthermore, the Three-toed Woodpecker (*Picoides tridactylus*), the most prominent excavator of natural tree cavities in both study areas, did not differ in abundance between burned and unburned forests. Hence it seems reasonable to assume that the differences in availability of tree holes for breeding were minor for these species. However, the Redstarts also occasionally use hollows and cavities on the ground for nesting (author's pers. obs.). The Lainio fire exposed tree roots previously embedded in thick mosses and dwarf shrubs, potentially creating abundant micro-habitats for Redstart breeding. Hence, in addition to potential area-specific differences in habitat characteristics, one explanation for the higher abundance of Redstarts in the spruce-dominated Lainio burn is that fire may have increased the number of breeding niches for this species. The higher abundance of Redstarts in Lainio, where almost all trees were killed by the fire, is in line with Virkkala (1987) and Virkkala & Rajasärkkä (2006) who found that Redstarts prefer particularly open forest.

While the response of shrub-nesting birds to fire was as expected, the non-significant effect on the abundance of ground breeders was unexpected. The basal area of standing trees between burned and unburned forests within study areas did not significantly differ, and the visual impression was that these forests were also very similar with respect to openness and structure. This might help to explain why ground-nesting birds did not significantly respond to fire. The significant effect of study area on ground-breeding birds, Siskin and Redwing may be related to differences in tree-species composition and general openness between the two areas. Ground-nesting birds might find suitable breeding habitats more easily in the more open Lainio spruce forests than in the denser pine forests of Muddus. The greater abundance of birch in Lainio may also generally provide more breeding sites for Redwing (cf. Virkkala 1987), and as the tree bases had often been severely burned they too may provide nesting places for this species that commonly nests near ground.

In 2009, three years after the fire, very few burned trees had fallen at the two areas. The rate of tree fall in the future will probably increase more in the spruce-dominated Lainio burn than in the pine-dominated Muddus burn, since most trees had been killed in the former. This process may take long, as indicated by the ca. 200-ha Reivo wildfire (65°46' N, 19°07' E): in a spruce-dominated area similar to Lainio, many dead trees were still standing 13 years after the fire (Boström 1988). Natural succession is slow at these northern latitudes, and the abundance of birds with closed nests may be very low in the early phases of succession in managed Fennoscandian forests (Haapanen 1965, Helle 1985, Helle & Mönkkönen 1990). However, the present study showed that the abundance of such birds can be considerably higher during the initial stages of succession following natural disturbance.

The future development of bird assemblages in pine and spruce forests following disturbance by fire is difficult to predict, since many interacting factors may affect them. For example, the pace of change in the shrub layer may strongly depend on the browsing by mammalian herbivores, such as mountain hare (*Lepus timidus*), reindeer (*Rangifer tarandus*) and moose (*Alces alces*). During the bird surveys in 2009, there was a high density of faeces of these mammals, and direct observations of hare and reindeer were made within the burns, indicating common use of these burned forests by these mammals. In Reivo, birch regrowth was suppressed by intense browsing by Reindeer long after the fire (author's pers. obs.), and at high latitudes spruce regenerates in the shade of birch. Thus, intense browsing on birch may retard succession and even lead to replacement of spruce by light-demanding pine (Engelmark 1993), thus altering the course of succession. Elsewhere in Muddus National Park and in Reivo, deciduous trees primarily regenerate in piles of fallen trees, protected from herbivory (author's pers. obs.). Hence, once trees start to fall, birch regeneration may increase, particularly in the spruce-dominated Lainio burn. Judging by the vegetation structure in older burns in the pine-dominated Muddus National Park, the changes in forest composition and structure are likely to be smaller in the pine-dominated Muddus than in the spruce-dominated Lainio burn, and to have less dynamic effects on bird assemblages.

In conclusion, the follow-up of three years after fire did not demonstrate negative effects by fire on the abundance of bird guilds or of individual species. On the contrary, the present results indicate positive population responses particularly in the spruce-dominated Lainio area. As stated earlier, these conclusions should be interpreted with caution, since the study was based on only two fire sites. However, most forest-bird species encountered are habitat generalists that are probably evolutionary adapted to large scale disturbances caused by fire. Thus, some specialist responses might have been negative too. The results suggest that isolated wildfires positively affect populations of many species by increasing habitat heterogeneity at the landscape scale. The results also highlight several issues that need to be explored in more detail. Most urgently, information about the demographic consequences of wildfire is required (e.g., Nappi & Drapeau 2009), as the true avian responses to fire probably deviate from expectations based on knowledge about bird responses to habitat transformation in managed forests (Wyshynski & Nudds 2009). For example, experimental studies using nest boxes could be used to contrast reproductive success and chick survival between burned and undisturbed forests (Huhta *et al.*

1999). It would also be desirable to replicate large tracts of burnt forest, which is presently difficult to achieve in managed forest landscapes. Finally, given the limited data currently available, and the slow pace of natural succession in northern forests, long-term monitoring programmes are needed.

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Sammanfattning

På grund av långvarig och effektiv brandbekämpning är effekterna av brand på fågelfaunan i fennoskandiska boreala skogar dåligt kända. Vi vet särskilt lite om effekterna av storskaliga bränder. Här rapporteras resultaten av en inventering av fågelfaunan i 300 respektive 440 ha stora brännor i Norrbotten, Sverige, tre år efter brand. Skogarna dominerades av tall (Muddus nationalpark) respektive gran (Lainio).

Hålhäckande fåglar och fåglar som letar insekter på marken var vanligare i brännorna än utanför, medan markhäckande och buskhäckande fåglar förekom i samma mängd i bränd och obränd skog. Gråsiska och trädpiplärka var vanligare i bränd skog. Arter som fångar insekter i luften samt rödstjärt var vanligare i brännan i grandominerad skog än i talldominerad skog, vilket indikerar att inverkan av brand var större på dessa arter i grandominerad skog. En sannolik förklaring är att kronbranden i det grandominerade området dödade de flesta träden, medan merparten av träden överlevde markbranden i det talldominerade området.

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