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Effects of canopy gap disturbance on forest birds in boreal forests

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We studied the effects of small-scale disturbance on breeding, forest passerine birds in an old-growth and managed boreal forests in northern Finland. Small-scale disturbance (< 2 ha) in an old-growth and managed forests originated from wind falls and small clear cuts. Continuous forest without gaps was used as a control for both management types (old-growth and managed forests). Passerines' response to disturbance was examined by estimating species richness and abundance of different ecological groups. Species richness and the total abundance of birds did not differ between gap and non-gap plots, neither did the abundance of most ecological groups. Management type or study year were the most important factors explaining abundances. Our results differ from studies conducted in temperate forests, mainly in North America, where small-scale disturbance have been found to increase avian diversity and abundance. Differences between boreal and temperate forests or in avian assemblages between continents may explain observed differences.

Introduction

Disturbance is an omnipresent factor shaping the environment and species assemblages (Huston 1994, Brawn *et al*. 2001). Disturbances such as fire, pathogens, wind falls and herbivory have long been shown to affect tree species composition, age structure of trees and seedling performance in tropics (e.g., Schnitzer & Carson 2001), in temperate forests (e.g., Bormann & Likens 1979, Brokaw & Busing 2000), and in boreal forests (Zackrisson 1977, Spies & Franklin 1989, Kuuluvainen 1994). Particularly in temperate and tropical forests the role of small-scale disturbance has been emphasized (Hallé *et al*. 1978, Bormann & Likens 1979), whereas in boreal forests large-scale disturbance by fire has been thought to be the major disturbance factor (Zackrisson 1977, Niklasson & Granström 2000, *see* also Kuuluvainen 1994). There is a growing body of evidence suggesting that small-scale wind-breaks or canopy gaps are important elements in the boreal forest dynamics (e.g., Steijlen & Zackrisson 1986, Kuuluvainen *et al*. 1998). Syrjänen *et al*. (1994), for example, demonstrated that wind-fall gaps of 0.01–0.5 ha in a pristine taiga forest were common and, hence, wind disturbance creates substantial heterogeneity to a landscape.

Despite the vast literature on gap dynamics in forest succession and tree regeneration, much less attention has been paid to the effects of gaps on animals inhabiting forest biomes. The effects of small-scale canopy gap disturbance on species richness can be predicted from the intermediate disturbance hypothesis (Connell 1978). According to that hypothesis, species richness peaks at intermediate levels of disturbance. At lower levels of disturbance, competition limits species coexistence, whereas at higher levels of disturbance increased mortality due to disturbance restricts species numbers. Spatial and temporal frequency of disturbance may also affect species abundance if it affects the amount of available resources. In boreal forests, fire clearly represents large-scale disturbance, while gap formation within continuous forest stands for intermediate disturbance (given that it is not too frequent in time or space). Therefore, we should expect higher diversity of animals at those sites as compared with that in undisturbed or highly disturbed forest.

Forest birds are a species group that is directly dependent on the forest structure and habitat diversity in a forest (Hildén 1965, Chalfoun & Martin 2007) and, therefore, provides an excellent model to examine the effects of small-scale disturbance. A recent meta-analysis on the effects of small-scale logging (group selection harvesting) on forest bird species richness and abundance in North America suggested that in forests logged to mimic natural gap formation, small-scale disturbance generally increased bird species diversity and abundance by providing breeding habitat for early-successional birds without notably negatively affecting species inhabiting mature forests (Forsman *et al*. 2010). The only Eurasian study (Fuller 2000), conducted in a pristine temperate forest, also reported higher species number and abundance in tree-fall gaps than within an undisturbed forest. However, natural disturbance and human-caused disturbance, such as clear-cutting, may differ in their ecological effects (Niemelä 1999) and, therefore, it is possible that small-scale cuttings are not a substitute for natural disturbances in forest ecosystems (Bengtsson *et al*. 2000).

Most studies that stress effects of small-scale disturbance on birds were made in temperate forests and compared the effects of disturbance between logged and continuous forests (but *see* Fuller 2000), while very little is known whether man-made and natural small-scale disturbances have similar effects (but *see* Fuller 2000, Greenberg & Lanham 2001, Faccio 2003). Taking into account the need to maintain forest biodiversity by mimicking natural disturbance dynamics in managed forests (Hunter 1990, Hansen *et al*. 1991, Haila 1994, Angelstam 1998, Mönkkönen 1999) it is of utmost importance to know whether species respond similarly to natural and mimicked processes in natural and managed environments.

Our objective in this study is to address the relationship between breeding bird diversity and abundance and gap disturbances in boreal forests of northern Finland. We examine how gaps created by wind falls and gap harvesting affect species richness and abundance of different guilds in boreal coniferous forests. According to the intermediate disturbance hypothesis, we predicted that species richness is higher at the gap sites. Because wind falls and cuttings create new, open habitat pocket within a continuous forest, we predict that it attracts species preferring such habitat, such as tropical migrants (Helle & Fuller 1988) and edge-preferring species (Helle & Järvinen 1986, Virkkala 1987) and their density is higher at gap sites than in the continuous forest. In addition, by comparing observed species richness and abundance between gap-dominated and continuous forests we can examine whether the effects of small-scale disturbance are parallel in old-growth and managed forests.

Methods

Study areas and study design

We carried out the study in 1998 and 1999 in two separate areas in northern Finland. Old-growth forest plots were in the Pisavaara Nature Reserve (66°20´N, 25°E) and managed forest plots were in Kivalo (66°25´N, 27°E) at the Finnish Forest Research Institute experimental research area.

The areas are ca. 70 km apart. The Pisavaara Nature Reserve (ca. 50 km^2) is located on a hill (100–200 m a.s.l), on the border between a coastal plain and a northern highland, whereas managed forest plots were in the highland area. Southern slopes in Pisavaara, where study plots were situated, are dominated by Norway spruce (*Picea abies*) with scattered aspen (*Populus tremulus*) stands and Scots pine (*Pinus sylvestris*) (Penttilä *et al*. 2001). In Kivalo, plots were situated at somewhat higher altitudes (200–300 m a.s.l.) than in Pisavaara, but the dominating tree species is also spruce with scattered birch (*Betula* spp.) (Vuopio *et al*. 2001). In both management types (old-growth and managed forest), shrub layers are weak consisting mainly of single saplings.

In Pisavaara, the average canopy-gap size was 0.4 ha (range: 0.2–0.5 ha). Gaps originated from wind falls caused by the *Mauri* storm in 1982, and were located in the lower parts of the spruce-dominated forests (100–140 m a.s.l.). In managed forest, gaps were rectangle-shaped clear cuts within a continuous forest (180–320 m a.s.l.). The average clear-cut area was 1.3 ha (range: 0.2–1.97 ha); two areas were logged in 1987 and the rest in 1982. There was thus a difference in average size of a gap between management types, but this was unavoidable as no other experimental research forests or old-growth forests were available. Control plots, which were in continuous forest stands, were located in the same forest area as the corresponding gap plots.

Our sampling unit was a square plot of 4 ha (200 × 200 m) within which breeding bird densities were surveyed. In Pisavaara, we had five gap plots and four undisturbed forest control plots. In Kivalo, we had four gap plots and five control plots censused over two years. We placed a survey plot so that the gap located in the middle of the plot included also the surrounding forest. This design allowed us to observe birds breeding in the gap, and those breeding in the forest in the vicinity of the gap, which may have been attracted there because of the gap. The forests surrounding the gap and control plots were undisturbed and their characteristics did not differ between the gap and control plots within management types (*see* below). Gap and control plots had no distinctive edges, bogs or other open areas in the immediate vicinity of the plots. To ensure the independence of the observations, all study plots were at least 200 m apart.

Bird surveys

We conducted bird surveys in June, which is the main breeding season in the area. All plots were surveyed in both study years. We used a single-visit study plot method, which detects about 60% of breeding pairs and 90% of breeding species in forested areas in Finland (Järvinen & Lokki 1978). Because of a short breeding season and simple habitat structure, the census efficiency is probably even greater in the north (Järvinen *et al*. 1978). We surveyed each plot thoroughly by walking slowly through the plot along parallel lines 50 m apart. We flagged the corners of the plot and the walking route. A fixed time of 90 minutes was used to survey each plot and we marked all observed birds and their movements onto schematic study maps. While surveying, care was taken to simultaneously identify singing males, since the interpretation of the territorial birds was done on the basis of one census. We recorded only birds observed within the study plot. We conducted surveys between 04:00–10:00 in fair weather.

Since in northern Fennoscandia the density of forest birds is low, we conducted analyses at the guild or ecological group level. Gaps enhance seedling growth and the presence of deciduous trees (Kuuluvainen 1994, Syrjänen *et al*. 1994, Kuuluvainen & Juntunen 1998) which in turn create feeding and nesting opportunities for birds. Fallen trees may also create secure nest sites for ground-nesting species and dead wood may provide food resources to some species. We, therefore, pooled species according to their nesting microhabitats and foraging habits. Gaps also incorporate elements of early successional stages and increase edge habitat within the continuous forest. This may attract or repel birds with preference to edges or intact forest, respectively. It has been shown that in Europe, tropical migrants are relatively more abundant in forest of younger successional stages than in older ones (Helle & Fuller 1988), hence one can assume that tropical migrants are more abundant in gaps than in continuous forest (cf. Fuller 2000). To examine this, we classified species according to their preference to edge and migratory status. Bird species were classified into ecological groups according to their migratory status, edge preference, nesting microhabitat and foraging habits after von Haartman *et al*. (1967), Helle and Järvinen (1986), Cramp (1992), Jokimäki and Huhta (1996) and Imbeau *et al*. (2003).

The redstart (*Phoenicurus phoenicurus*), the spotted flycatcher (*Muscicapa striata*), the treecreeper (*Certhia familiaris*) and the bullfinch (*Pyrrhula pyrrhula*) were not classified into any of the foraging groups because they would have been the sole representatives of their guilds. Only passerine species were included into analyses because abundances of other bird groups, such as woodpeckers, were too low for statistical analyses. The siberian jay (*Perisoreus infaustus*) was excluded from all analyses because its territory size is larger than the size of our study plot (*see* Appendix 1 for details).

Vegetation measurements

Study plot vegetation was described for every plot from systematically assigned sampling sites (circles with a radius of 9.77 m). Sampling sites were located along three lines 100 m apart, two lines being at the sides of the census square and one in the middle. In the continuous forest plots, there were six, and in the gap plots, 7–8 sampling sites on the lines systematically 50 m apart. In the gap plots, four sites were located in forested areas around the gap, and 3–4 sites in the gap depending on the size and shape of the gap.

Vegetation data consisted of average age of trees, basal area of trees, height of dominant trees, and canopy cover which was measured in the field by experienced forest technicians. Also numbers of dead ground logs, standing snags (> 1.5 m), numbers of saplings (< 1 m in height) and small trees (< 10 cm dbh) were counted. Spruce and birch saplings overwhelmingly dominated the shrub layer and, therefore, we present the results only for them. Average age of trees was extracted from the database of Finnish Forest Research Institute. Basal area of trees (m^2) was measured using a angle-count method. Average height of dominant trees (meters) was measured using a hypsometer. Canopy cover of trees (%) was estimated through a sighting tube (10 cm long by 4 cm in diameter).

Statistical methods

We used repeated measures ANOVA to test for the effects of small-scale gaps on total bird abundance, species number and the abundance of different ecological species groups. Management type (old-growth forest and managed forest) and disturbance (gap present or not) were included into analyses as fixed factors, and study years as repeated measures. We included into the model all the main effects of the factors, year and all the interactions. This enabled us to examine simultaneously the effect of the gap in two different management types and also take into account potential annual differences in bird abundances. As repeated ANOVA was conducted in similar manner in all cases, we report only results for those factors that were statistically significant.

Vegetation characteristics of the forest structures were compared between gap (measures taken from the forested area of the plot) and non-gap plots within and between management types using a *t*-test. From this comparison, we excluded the data from the gaps because differences between gaps and forest are self-evident. However, we also compare vegetation characteristics of gaps between the management types. We conducted the analyses using the SPSS 11.5 software.

Results

Except for older trees in continuous forest compared with those in the gap plots ($t_7 = 3.23$, $p = 0.014$) in managed forest, there were no differences in measured forest characteristics between the gap (in the forested areas of the gap plots) and continuous forest plots within management types for any of the measured variable (all other $p > 0.091$; *see* Table 1), implying that potential differences in avian assemblages are not due to differences in forest characteristics. There were statistically significant differences in forest characteristics between management types in the forested areas of the plots. Trees were higher ($t_{16} = 3.72$, $p = 0.002$), tree volume ($t_{16} = 3.84$, $p = 0.002$), basal area of trees ($t_{16} = 2.72$, $p = 0.015$) and canopy cover were greater ($t_{16} = 2.64$, $p = 0.018$) in old-growth forest than in managed forest. Also numbers of small spruces, snags, ground logs and spruce saplings were higher in the old-growth forest than in the managed forest (Table 1). Only the average age of dominant trees ($t_{16} = 1.25$, $p = 0.238$) and the number of birch saplings ($t_{16} = 0.341$, $p = 0.737$) did not differ between management types (Table 1).

The vegetation characteristics in the actual gaps differed clearly between management types (Table 2). Age ($t_7 = 1.74$, $p = 0.126$) and height ($t_7 = 1.91$, $p = 0.098$) of the dominant trees (saplings) and the number of birch saplings ($t_7 = 0.54$, $p = 0.604$) were the only variables that did not differ between the old-growth and managed forest, while all the other characteristics showed higher values in the old-growth forests ($p < 0.048$). Because gaps in the managed forest were created by removing the trees, they included less decaying wood than in the old-growth forest (Table 2). Gaps in the managed forest were also about five years younger than in the old-growth forest, which may explain why the sapling layer was so much weaker than in the old-growth forest. Even though the average tree height in the gaps in the old-growth forest was only 2.13 m, the density of tree saplings was high, which is reflected in high tree volume per unit area (Table 2).

In total, we observed 24 passerine forest bird species in our study plots. The average number of bird species in a plot (Fig. 1a) or average total

Table 1. Variables (mean ± SD) describing characteristics of the forest in the study plots. Values are calculated from the data collected from sampling sites (four in gaps, and six in continuous forest) in forested areas of the plot (data from gaps are excluded). Age refers to the age of the dominant trees.

Variable	Old-growth forest		Managed forest	
	Forest	Gap	Forest	Gap
Age (years)	177 ± 21	168 ± 13	220 ± 0	156 ± 45
Basal area (m^2)	18.7 ± 3.16	19.3 ± 2.7	16.75 ± 2.9	13.8 ± 1.8
Canopy cover (%)	37.1 ± 10.4	33.0 ± 11.9	21.12 ± 13.4	22.1 ± 7.45
Height (m)	18.2 ± 2.8	18.1 ± 1.6	14.8 ± 2.4	14.0 ± 2.2
Tree volume (m^3 ha^{-1})	168.0 ± 50.3	172.0 ± 28.4	120.9 ± 33.6	96.1 ± 18.2
Number of spruce (< 10 cm dbh)	20.5 ± 11.7	33.85 ± 13.16	7.2 ± 2.9	15.9 ± 16.8
Number of snags (> 1.5 m)	3.1 ± 1.7	3.15 ± 0.74	1.7 ± 0.8	0.75 ± 0.6
Number of ground logs	10.6 ± 1.6	12.5 ± 3.47	4.1 ± 1.3	3.43 ± 4.3
Number of spruce sapling	8.3 ± 5.5	16.1 ± 10.38	1.1 ± 0.6	1.18 ± 1.0
Number of birch sapling	2.6 ± 2.4	1.5 ± 0.7	2.2 ± 1.9	1.44 ± 0.4

Table 2. Variables (mean ± SD) describing vegetation characteristics of the gaps in the old-growth and managed forests.

Variable	Old-growth forest	Managed forest
Age (years)	11.65 ± 5.01	6.88 ± 2.39
Basal area (m^2)	9.65 ± 2.79	0
Height (m)	2.13 ± 1.54	0.64 ± 0.16
Tree volume (m^3 ha^{-1})	92.35 ± 26.83	0.06 ± 0.01
Number of spruce (< 10 cm dbh)	29.07 ± 15.80	0.94 ± 1.20
Number of snags (> 1.5 m)	2.32 ± 1.16	0.25 ± 0.20
Number of ground logs	24.27 ± 6.54	3.00 ± 4.24
Number of spruce sapling	23.72 ± 17.00	8.50 ± 4.78
Number of birch sapling	11.20 ± 10.71	15.06 ± 10.49

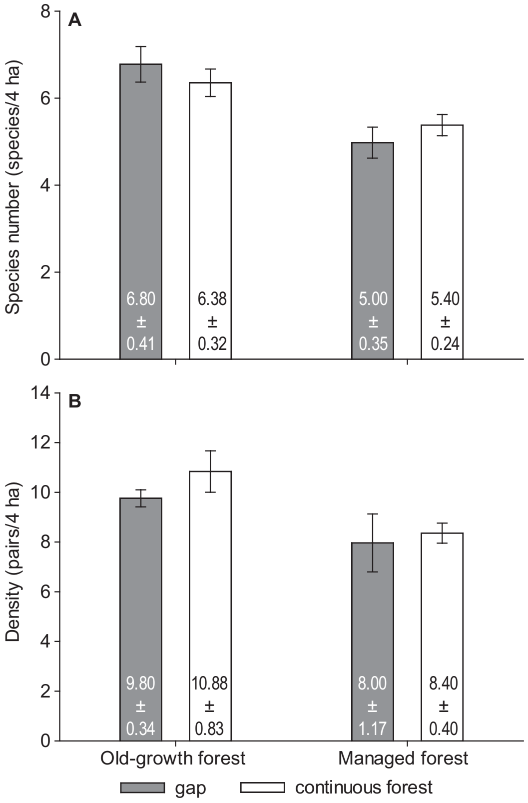

Fig. 1. (**A**) Mean ± SE number of species, and (**B**) total ± SE density of breeding birds per 4 ha in gaps and continuous forest in the old-growth and managed forests. Mean ± SE values are also shown in the columns.

density of birds (Fig. 1b) did not differ between the gap and continuous forest plots. The average number of species (6.60 species/4 ha) and their average density (10.28 pairs/4 ha) in the old-growth forest were higher than the corresponding estimates in the managed forest (5.20 species and 8.22 pairs/4 ha; Table 3).

In the old-growth forest, we observed altogether 18 and 15 passerine species in the continuous and gap-dominated plots, respectively. The three species observed only in the gap plots were: the tree pipit (*Anthus trivialis*), the wren (*Troglodytes troglodytes*) and the mistle thrush (*Turdus viscivorus*), while the fieldfare (*T. pilaris*), the dunnock (*Prunella modularis*), the coal tit (*Parus ater*), the greenish warbler (*Phylloscopus trochiloides*) and the common chiffchaff (*P. collybita*) were observed only in the continuous forest. In the managed forest, we observed 17 and 16 species in the continuous and gap-dominated plots, respectively. The continuous-forest plots included the great (*Parus major*) and the coal tits and the treecreeper (*Certhia familiaris*) that were not observed in the gap plots, while the yellow wagtail (*Motacilla flava*) and the mistle thrush were observed only in the gap plots.

The presence of a gap had no effect on densities of most nesting or foraging guilds (*see* Table 4). The most important factor for cavity and ground nesters and foliage gleaners was

Table 3. Compilation of repeated measures ANOVA for species number and total density, and density of different bird groups divided by nesting and foraging guilds, migratory status and preference for edge or forest interior. For each analysed dependent variable the results of only statistically significant factors are shown. All the statistical models were similar consisting of gaps (present or not) and management type (old-growth and managed forest) as fixed factors, and census year as repeated measures.

Source of variation	df	MS	*F*	*p*
Species number				
Management type	1	8.56	16.67	0.001
Error	14	0.51		
Total density				
Management type	1	19.14	8.31	0.012
Error	14	2.30		
Cavity nesters				
Year	1	10.5	7.19	0.012
Error	14	1.67		
Ground nesters				
Year	1	36.90	30.08	< 0.001
Error	14	3.32		
Foliage gleaners				
Year	1	63.34	11.26	0.005
Error	14	5.63		
Tropical migrants				
Management type	1	20.67	5.64	0.032
Error	14	3.67		
Short-distance migrants				
Management type	1	5.87	3.71	0.075
Error	14	1.58		
Residents				
Year	1	4.05	4.93	0.043
Error	14	0.43		
Edge species				
Year	1	28.00	8.57	0.011
Management type	1	29.61	8.10	0.013
Error	14	3.65		
Forest interior				
Year	1	16.50	4.51	0.052
Error	14	2.15		

the effect of year whereas management type or gap did not have any effect (Table 3). The model did not explain density of off-ground nesters at all. In ground foragers, there was a statistically significant interaction between year and gap (MS = 3.76, $F_{1,14} = 6.96$, $p = 0.019$) suggesting a divergent effect of gaps between years. This was due to the lack of any ground foraging species inthe gap plots in managed forests in 1998, which resulted in contradicting trends between years, which prevented us from using the results of repeated ANOVA any further. Therefore, we analysed the abundance of ground foragers separately for both years using 2 × 2 factorial ANOVA with management type and gap *vs*. non-gap as factors, and an interaction term between these factors.

In 1998, the model explained statistically significantly the observed variation in the abundance of ground foragers (MS = 3.45, $F_{3,14} = 4.50$, $p = 0.021$), but gap was not of importance whereas management type was the best explaining factor (MS = 8.40, $F_{1,14} = 10.94$, $p = 0.005$). In 1999, the model explained significantly the variation (MS = 2.38, $F_{3,14} = 3.57$, $p = 0.042$) and the presence of gap was the most important factor in the model affecting positively density of ground foragers in both management types (MS = 3.80, $F_{1,14} = 5.69$, $p = 0.032$). In the old-growth forest, the densities of ground foragers in the gaps and in the continuous forest were 1.8 and 0.50 pairs/4 ha, respectively; and in the managed forest, 0.75 and 0.20 pairs/4 ha, respectively. Management type was of no significance in 1999.

Management type was the strongest explaining factor for densities of tropical and short-distance migrants with higher densities in the old-growth forests (Tables 3 and 4). In both management types, tropical migrants seemed to be somewhat more abundant in the continuous forest than in the gaps (Table 3) but the presence of a gap did not have any statistical significance (Table 4). Annual differences were the most governing factor for density of residents (Table 4) while management type or gap did not have a significant effect. The presence of gaps did not have any significant effect either on density of forest interior or on species preferring edge, management type and year being the strongest factors (Tables 3 and 4).

Discussion

Small-scale gap disturbance by tree falls or small clear-cuts did not increase the average species number or their abundance. At the species-group level, the presence of a gap had only negligible effects on passerine-bird densities. Only ground foragers showed positive density response to the presence of gaps in both management types

Table 4. Mean ± SE densities (pairs/4 ha) of species groups in four different types of forest plots.

Species group	Old-growth forest		Managed forest	
	Gap	Continuous forest	Gap	Continuous forest
Nest site				
Cavity	1.5 ± 0.50	2.4 ± 0.52	1.5 ± 0.32	1.5 ± 0.22
Ground	3.3 ± 0.37	3.3 ± 0.63	2.4 ± 1.05	2.5 ± 0.35
Off-ground	5.0 ± 0.27	5.3 ± 1.11	4.1 ± 0.31	4.4 ± 0.19
Foraging guild				
Ground foragers	1.9 ± 0.43	1.1 ± 0.31	0.4 ± 0.24	0.6 ± 0.19
Foliage gleaners	5.2 ± 0.46	6.3 ± 0.75	5.9 ± 0.85	5.8 ± 0.46
Migratory status				
Residents	0.40 ± 0.19	1.0 ± 0.20	1.0 ± 0.20	0.8 ± 0.25
Short-distance migrants	4.6 ± 0.53	4.0 ± 0.46	3.4 ± 0.31	3.6 ± 0.29
Tropical migrants	4.8 ± 0.41	5.9 ± 0.52	3.6 ± 1.14	4.0 ± 0.42
Edge preference				
Edge	6.0 ± 0.16	6.1 ± 0.90	3.9 ± 1.05	4.6 ± 0.33
Forest interior	3.8 ± 0.46	4.8 ± 0.43	4.1 ± 0.72	3.8 ± 0.34

(old-growth and managed forest) in one of the study years, whereas other nesting and feeding guilds showed no response. Also, birds' migratory status or preference for edge did not show any responses to gap. In general, management type and study year had the strongest impact on bird densities. Nevertheless, in the old-growth forest in the Pisavaara Nature Park, some species preferring open habitats (the tree pipit) or fallen trees (nest-sites for the wren) were observed only in gap plots. Therefore, even though at the plot level gap disturbance did not increase species numbers or their densities, gaps may contribute to species diversity at larger scales.

Characteristics of the forest structure in the forested parts of the plot did not differ between the gap and the continuous forest within management type, which may partly explain similar avian community composition in gaps and continuous forest. Differences in the forest structure between management types are partly due to the somewhat different geographic locations. In contrast, the vegetation structure in the gaps differed clearly between management types. In the old-growth forest, the number of ground logs was higher and also the schrub layer (consisting mainly of spruce and birch saplings) was better developed than in the managed forest. This result suggest that if management aims to mimic natural processes, creating small-scale gaps is not enough, and more attention should also be paid to what is left in the gap.

The results of this study were both qualitatively and quantitatively different from studies conducted in temperate areas (mainly in North America) where species numbers and/or their abundances increased in managed gaps as compared with those in continuous forests (Forsman *et al.* 2010), or by natural processes creating gaps within continuous forests (Fuller 2000, Greenberg & Lanham 2001, Faccio 2003). Other studies have shown that even though the species number and their density did not considerably differ between small gaps and undisturbed forests, species responded differently to mimicked disturbance depending on whether they were early- or late-successional birds (Keller & Anderson 1992, Lent & Capen 1995, Dellasala *et al.* 1996, Annand & Thompson 1997, Chambers *et al.* 1999). Increased species diversity in gaps has usually been attributed to new habitat type (open habitat), emergence of early succession vegetation, increased shrub vegetation and increased amount of edge habitat. However, in this and Fuller's (2000) study, gaps did not affect the density of tropical migrants even though in Europe they have been shown to prefer early succession vegetation (Helle & Fuller 1988, Mönkkönen & Helle 1989, Helle & Niemi 1996).

Gaps also create edges between the forest and an open area, which are important habitats for some birds or increase their feeding opportunities. There is evidence that food is more plentiful in gaps than within an undisturbed forest (Blake & Hoppes 1986; *see* also Helle & Muona 1985, Martin & Karr 1986, Jokimäki *et al.* 1998). However, we did not find any consistent effects among examined bird groups.

What might explain the qualitatively different results between our study and those conducted in temperate areas (*see* above)? First, due to our limited sample size, we must interpret our results with care. However, because small-scale disturbance is frequent and a plausibly important factor affecting the dynamics of boreal ecosystem (Syrjälä *et al.* 1994), it is important to lay out hypotheses for future studies. We suggest that three explanations are most likely. First, undisturbed temperate deciduous forests usually have more closed canopies as compared with boreal forests. For example, in Fuller's study (2000), canopy cover at non-gap sites was 90% whereas in our study it was only between 20% and 37%. Therefore, the contrast between the continuous forest and the gap-dominated forest is not as striking in boreal as it is in temperate areas. In addition, shrub layer is not well developed in Fennoscandian boreal forests, possibly explaining the lack of effect of gaps on bird richness.

The second explanation is the age of the gap. The meta-analysis by Forsman *et al.* (2010) suggested that the positive effect of gaps on bird abundance decreases with time elapsed from the disturbance. At our study sites, time from the origin of the gap varied between 11 and 16 years. It is possible that effect of gap is apparent only shortly after disturbance.

Thirdly, differences in the ecology of North American and Eurasian birds may also explain the contrasting results. In North America, mature forests are predominantly inhabited by tropical migrants, whereas in Eurasia residents and short-distance migrants are dominating bird groups there, and tropical migrants are associated with early stages of forest succession (Helle & Fuller 1988, Helle & Niemi 1996). Moreover, there are also more habitat specialists among North American birds than in Europe (Mönkkönen 1994), that can utilize ephemeral space and resources provided by gaps. Indeed, even though Fuller (2000) observed higher species numbers and abundances in gaps than in continuous forests, he concluded that only a few species showed strong responses to gap formation. In North America, however, species response to gaps was positive across nearly all species (Forsman *et al*. 2010).

The major factor affecting bird densities was the annual variation in bird numbers. Annual variation in avian occurrence and densities can be high in northern populations (Haila *et al*. 1996). Variation in population densities may affect occupancy of habitats, such as gaps *vs*. continuous forests, which may explain the divergent response of ground foragers to the presence of gaps between years in our study. Wide temporal fluctuation in species numbers may easily obscure even moderate responses to changes in habitat characteristics.

Management of boreal forests in Finland has so far mimicked almost exclusively large-scale disturbances since mature stands at the end of rotation are normally clear-cut, but several novel management alternatives, including gap harvesting, have been proposed (Hunter 1990, Angelstam 1998, Mönkkönen 1999). In forest landscapes where large-scale forestry is inappropriate and where sensitive forest management is required, such as in moist forests, riparian stands or in the vicinity of conservation areas, small-scale gaps created by selective harvesting is a feasible method (Angelstam 1998, Bergeron & Harvey 1997). Our results imply that management by creating small-scale openings in the continuous forest may provide a meaningful way to manage forests and maintain passerine species diversity during the breeding period. However, our vegetation analyses suggest that more attention should be paid to how much dead wood is left in the gap. The amount of dead wood may be particularly important for many woodpecker species that were not considered in this study. Furthermore, differences in bird assemblages between gaps and continuous forests need to be examined more rigorously with a larger sample of gaps and bird species than in the present study. Ideally, temporal variation in avian densities within and across years should also be examined in order to get a more thorough view on the effects of small-scale disturbance on avian populations.

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Appendix 1. Observed species and their classification into ecological groups (Migratory behaviour: resident, tropical or short-distance migrant; Preference for forest edge *vs.* forest interior; Nest-site location: cavity, ground nest or off-ground; Foraging habit: foliage gleaner, ground forager). *P. phoenicurus*, *M. striata*, *C. familiaris* and *P. pyrrhula* were not classified into any of the foraging groups because their foraging habits were not considered in the analyses.

Species	Migratory behaviour	Preference	Nest-site location	Foraging habit
Anthus trivialis	Tropical	Edge	Ground nest	Ground forager
Troglodytes troglodytes	Short-distance	Interior	Ground nest	Ground forager
Prunella modularis	Short-distance	Edge	Off-ground	Foliage gleaner
Erithacus rubecula	Short-distance	Edge	Cavity	Ground forager
Phoenicurus phoenicurus	Tropical	Interior	Cavity	–
Turdus pilaris	Short-distance	Edge	Off-ground	Ground forager
Turdus iliacus	Short-distance	Edge	Off-ground	Ground forager
Turdus philomelos	Short-distance	Interior	Off-ground	Ground forager
Turdus viscivorus	Short-distance	Interior	Off-ground	Ground forager
Phylloscopus trochilus	Tropical	Edge	Ground nest	Foliage gleaner
Phylloscopus collybita	Tropical	Interior	Ground nest	Foliage gleaner
Phylloscopus trochiloides	Tropical	Edge	Ground nest	Foliage gleaner
Regulus regulus	Short-distance	Interior	Off-ground	Foliage gleaner
Ficedula hypoleuca	Tropical	Interior	Cavity	Foliage gleaner
Muscicapa striata	Tropical	Edge	Off-ground	–
Parus montanus	Resident	Interior	Cavity	Foliage gleaner
Parus ater	Resident	Interior	Cavity	Foliage gleaner
Parus major	Resident	Edge	Cavity	Foliage gleaner
Certhia familiaris	Resident	Interior	Cavity	–
Fringilla coelebs	Short-distance	Edge	Off-ground	Foliage gleaner
Fringilla montifringilla	Short-distance	Interior	Off-ground	Foliage gleaner
Pyrrhula pyrrhula	Resident	Interior	Off-ground	–
Motacilla flava	Tropical	Edge	Ground	Ground forager
Emberiza rustica	Short-distance	Edge	Ground nest	Ground forager