Wildlife Community Patterns in Relation to Landscape Structure and Environmental Gradients in a Swedish Boreal Ecosystem

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Original article

Wildlife community patterns in relation to landscape structure and environmental gradients in a Swedish boreal ecosystem

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Many environmental patterns that may have profound effects on wildlife communities occur at the landscape scale, e.g. habitat fragmentation, human demography and distribution of various resources. In order to understand how alterations of such patterns could influence e.g. wildlife species occurrences and community composition, it is important to first study these relationships empirically and at the appropriate scale. We surveyed the wildlife community in a boreal ecosystem in central Sweden using pellet group counts, while walking 'wildlife triangles'. Our main aim was to investigate how the distribution of medium- and large-sized wild mammals and large-sized forest birds were affected by environmental variables at the landscape scale. In 2001-2003, pellet groups of mammals and forest birds were counted on 211 triangular routes with a perimeter of 4+4+4 km. The pellet groups which had accumulated after leaf fall were counted in spring. The environmental properties of each triangle, including information on latitude, altitude, infrastructure, land cover, forest type and forest stage, were determined using GIS maps. Statistical analyses involved mainly ordination (Principal Component Analysis, PCA). Significant environmental variables explaining the wildlife community composition and distribution in the boreal ecosystem were altitude, clear-felling and infrastructure. Our conclusion, however, is that most boreal mammal and forest bird species are habitat generalists and show little spatial pattern in distributions at the landscape scale. This indicates that habitat selectiveness probably occurs at a local scale in the boreal forest. Ultimately, our conclusion provides important direction for e.g. conservation measures and wildlife management.

Key words: forest grouse, landscape, mammals, pellet count, Principal Component Analysis, species richness, wildlife triangle

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Primary productivity in boreal ecosystems is often related to latitude, altitude, temperature and precipitation (Zheng et al. 2004), and resources for animals are determined by factors such as vegetation type and structure, human land use and habitat heterogeneity (Hansson 2002, Nikula et al. 2004). Food resources for herbivorous mammals depend directly on vegetation composition and, in many areas, on management-related stage of forest development (Mysterud et al. 1997, Danell et al. 2006), whereas many carnivores are habitat generalists and feed opportunistically on available prey (Hörnfeldt 1978, Kurki et al. 1998). Protective cover, which is found in e.g. dense understory vegetation and evergreen forests, is especially important for small-sized prey (Hansson 2002).

Natural disturbances in boreal forest systems are e.g. fires, insect out-breaks and windthrows (Niemelä 1999, Gromtsev 2002). More recently, significant disturbances mainly involve fragmentation and change of habitats by clear-cutting, spreading of human settlements and road networks (Niemelä 1999, Nelleman et al. 2001, Hytteborn et al. 2005).

Patterns of animal community composition and species richness are highly scale dependent and it is crucial to apply an appropriate scale for studying the effects of different factors on communities (Huston 1999, Kurki et al. 2000, Nikula et al. 2004). Empirical studies of mammal communities across large spatial scales continue to be rare in ecological research (however, see e.g. Hansson 2002, Fisher & Wilkinson 2005). Nevertheless, a considerable proportion of human impact on the environment takes place at the landscape scale (for definition see Willis & Whittaker 2002), e.g. fragmentation, deforestation, nature protection, forestry and human demography (Hansson 1992, Kurki et al. 1998, Nelleman et al. 2001). Disturbances may also be caused by the animals themselves, typically through feeding, trampling, defecation and urination (Persson et al. 2000). In order to understand the landscape scale distribution patterns of and interactions between wildlife species it is important to learn how communities are affected by environmental heterogeneity at that particular scale (although e.g. local processes may also greatly influence animal landscape distributions). Such information may guide conservation and management actions, the success and efficiency of which depend in part on targeting the right patterns and processes.

Faecal pellet counts have long been used for monitoring populations, primarily of cervids (Neff 1968) but also of e.g. mountain hare *Lepus timidus* (Angelstam et al. 1985). The method has the advantage of being less costly than animal counts from aircraft, and is potentially more reliable in areas with dense vegetation (Jordan et al. 1993). It is a convenient way of collecting information on and monitoring many species simultaneously. Average defecation rates needed for calculating corresponding densities from pellet counts are available for numerous species (Härkönen & Heikkilä 1999, Kindberg 2003) and areas (Persson et al. 2000, Forsyth et al. 2007).

The general aim of our study was to investigate large-scale patterns of wildlife community composition, in relation to environmental gradients in boreal forest in central Sweden. The focus was set at the landscape scale, covering two Swedish counties which together comprise approximately 26,000 km^2. Our main question was: How does the boreal wildlife community, including species distributions and relative abundances, relate to environmental variation at the landscape scale in Sweden?

Material and methods

Study area

In total, 222 equilateral triangular routes, i.e. wildlife triangles (Lindén et al. 1996), were positioned in the counties of Värmland and Örebro in central Sweden between ca 58°50'N and 60°N, within an area of approximately 26,000 km^2 (Fig. 1). Average precipitation is 600-900 mm/year with the higher amounts in the west and southwest (Swedish Meteorological and Hydrological Institute, SMHI, unpubl. data). The number of days with snow ranges from ca 75/year in the south to ca 200/year in the north (SMHI unpubl. data).

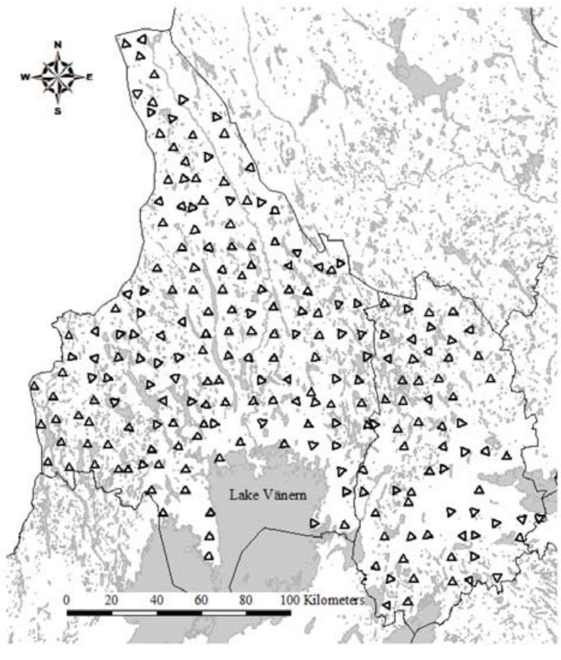

Figure 1. Arrangement of the 211 wildlife triangles in the counties of Värmland and Örebro in Sweden, which were used for pellet counts.

The study area is dominated by boreal forest in the north and agricultural land in the south-southeast. The boreal zones encompassed are (from north to south) the northern boreal, middle boreal, southern boreal and hemiboreal zones (Ahti et al. 1968). About 74% of the total land area of Värmland and 67% of Örebro is forested (Swedish Statistical Yearbook of Forestry, SSYF, 2007). Both counties are subjected to intensive forestry, with 63% of the total forest land area being younger than 50 years and the dominant tree species being Scots pine *Pinus sylvestris*, Norway spruce *Picea abies* and birch *Betula* spp., accounting for 90-95% of the total standing volume (SSYF 2007). About 6% of Värmland and 16% of Örebro is covered by arable land (SSYF 2007). The predominant agricultural crops in both counties are temporary grass/ley (52% of the agricultural land area in Värmland and 28% in Örebro) and cereals (23% in Värmland and 39% in Örebro; Yearbook of Agricultural Statistics 2007). The variation in climate, vegetation and land use within the study area is thus fairly large with a strong gradient from north (or northwest) to south (or southeast). Also, numerous lakes, rivers and mires contribute to a more variable landscape than is found in many other areas within the boreal forest zone. This variation was an important reason for our choice of these counties for the study.

Data collection

Each side of the wildlife triangles was 4 km, resulting in a 12 km perimeter. The triangles were placed at predetermined positions on a 10 km square grid covering the counties. The positions of the triangles were sometimes fine-tuned subjectively (not passing animal feeding stations or large agricultural fields, rivers and lakes), but preferably always with 10 km between triangles. GPS positions were registered and visible markers, such as sticks and coloured bands, were placed along the sides of the triangles.

Faecal pellets of 11 preselected species of mammals and large forest birds (species common in the area and whose pellets are easily recognised; Table 1) were counted in a total of 211 triangles (56 triangles were counted in each of the three years, 105 in two of the three years and 50 in one of the three years) between 19 March and 14 June of 2001-2003 (see Table 1). Circular plots for pellet counts (100 m^2 for moose *Alces alces* and 10 m^2 for remaining species) were placed at every 100 m along the triangle sides, giving a total of 120 plots/triangle. Depending on the species, either single pellets (e.g. hare *L. timidus* and *L. europaeus* and forest grouse) or pellet groups (e.g. moose and roe deer *Capreolus capreolus*, with a minimum number of 20 and 10 pellets/group, respectively) were counted. Only pellets dropped after leaf fall, estimated to 15 October, were counted, thus giving a measurement index of relative abundance of animals during the previous winter.

Table 1. Species list and average relative densities of birds and mammals in the study area in mid-Sweden. Densities are pooled for the years 2001-2003 and include average number of pellets or pellet groups in all triangles/year.

Species	Average number of pellets/pellet groups
Black grouse *Tetrao tetrix*	1141
Capercaillie *T. urogallus*	2122
Hazel grouse *Bonasa bonasia*	801
Hare spp. *Lepus timidus & L. europaeus*	7640
Wolf *Canis lupus*	3
Red fox *Vulpes vulpes*	69
Brown bear *Ursus arctos*	2
Badger *Meles meles*	13
Lynx *Lynx lynx*	0
Roe deer *Capreolus capreolus*	1189
Moose *Alces alces*	4936

Map data

Environmental properties were assigned to each triangle using ArcMap 9.1 (ESRI Corporation, Redlands, CA). GIS maps used included the Road map (i.e. Vägkartan), Swedish land cover data (i.e. Svenskt marktäcke-data) and, for Värmland only, the Vegetation map (i.e. Vegetationskartan). All maps are distributed by National Land Survey (Lantmäteriet) of Sweden (available at: http://www.lantmateriet.se/, also in English). The Road map contains information on e.g. road and rail networks and urban areas. Swedish land cover data is an overview of land use and vegetation, comprising 57 classes. It is similar to the European Union classification system CORINE land cover. The Vegetation map is based on Infra Red Photography (from 4,600 m) and is a detailed map of vegetation, including separate layers for composition (ca 70 classes plus additional information, giving > 300 variants), and forest phase (seven classes).

The triangles, each one surrounded by a 1-km wide buffer zone, were imported into the GIS maps and the landscape structures within and around them were examined (Fig. 2). More specifically, each triangle with its buffer zone was classified by absolute area of different types of land cover, including forest, arable land/pasture, clear-felling, lake and wetland, total length of water courses and infra-

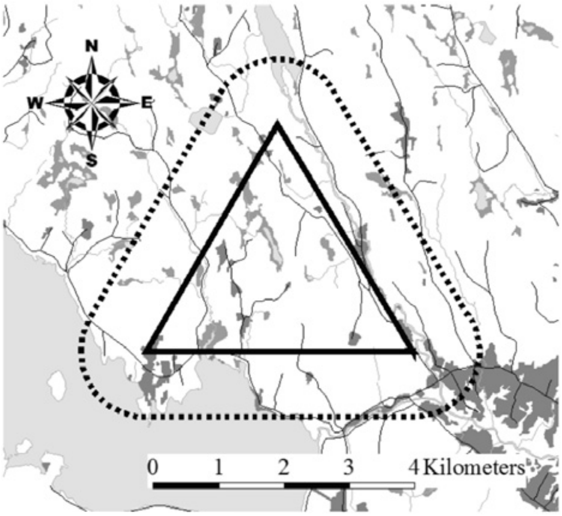

Figure 2. Close-up of one wildlife triangle (solid line) surrounded by its 1 km buffer zone (dashed line) in Värmland, Sweden.

structure, including all roads and railways, and mean altitude. Latitude, summed edge (i.e. the perimeter of all features) and detailed vegetation data, including the area of different forest types and development stages, were also used as environmental variables. Some vegetation variables comprised data from several classes: coniferous forest (different types and moisture levels), deciduous forest (different types and moisture levels), mire (all types of mire and marsh), thicket (deciduous thicket with remnant coniferous and deciduous trees) and rich vegetation (moist meadow and deciduous vegetation on mire and marsh). Thicket and rich vegetation are two types of habitats which are known to be important for many mammals and birds within the boreal forests of Fennoscandia (e.g. Essen et al. 1992).

Statistical methods

Data on infrastructure and land cover were available for both counties and the corresponding analyses included all the surveyed triangles. The detailed vegetation data were available only for Värmland and therefore the analyses on forest type and forest stage were performed only for this county. The data were analysed using multivariate methods in Canoco for Windows 4.5 (Ter Braak & Šmilauer 1998). Ordination biplots of common species (i.e. > 10 pellets or pellet groups) and environmental variables were constructed using Principal Component Analysis (PCA). PCA arranges sampling entities, most often species or sites, along continuous linear gradients of variation (i.e. principal components) thereby reducing the number of dimensions. In PCA the arrangement of sampling entities is not constrained by relationships to measured environmental variables. The variables are associated afterwards according to best fit. In our present study, the triangles were ordinated according to their animal species compositions (i.e. relative abundances based on pellet counts). The first and second principal components were used in the ordination biplots. Additional statistical analyses were made in SAS 8.02 (SAS 1990). The data were not normally distributed (Kolmogorov-Smirnov statistic D).

The significance of the selected environmental variables for explaining the variation in species pellet distributions were tested using Monte-Carlo Permutation test in Canoco, using unrestricted permutation type and 499 permutations. Statistically significant variables were marked in the biplots. Pearson correlations of the environmental variables were used as a complement to the multiple regressions to examine the degree of multicollinearity among the environmental variables.

Results

During the course of the study 51,482 plots (19,354 in 2001, 22,130 in 2002 and 10,000 in 2003) were sampled and 53,747 pellets or pellet groups from 10 species were encountered (compare with Table 1). The most common species were hare, moose and capercaillie *Tetrao urogallus*; pellets from brown bear *Ursus artos*, wolf *Canis lupus* and badger *Meles meles* were rare.

In the PCA biplot for both counties combined (Fig. 3, see test statistics in Table 2), there were two obvious species axes, one comprising capercaillie and moose and the second hare and roe deer. Remaining species were comparatively centrally located in the biplot. Among the environmental variables from the Road map and Swedish land cover data, altitude (Monte-Carlo Permutation Test: F-ratio = 14.83, $P < 0.002$), infrastructure (F-ratio = 6.69, $P < 0.002$) and clear-felling (F-ratio = 3.76, $P < 0.05$) explained statistically significantly parts of the species distribution data (see Fig. 3). However, the degree of explanation was low, merely 7% (for altitude), 3% (for infrastructure) and 2% (for clear-felling) of the variation in species pellet distributions. The cumulative percentage variance in the species data explained by the species axes 1 and 2 in the ordination was 74.7% and the correlations be-

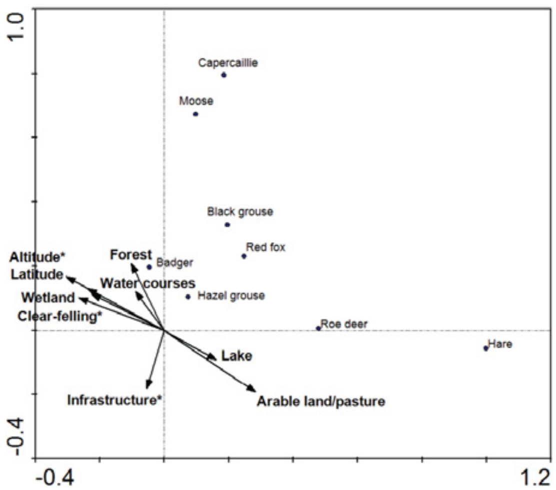

Figure 3. PCA ordination diagram based on pellet data of mammal and forest bird species in the counties of Värmland and Örebro, Sweden. Environmental variables include infrastructure from the Road map and different features of land cover from Swedish land cover data (both available for Värmland and Örebro). Cumulative percentage of the variation in the species data explained: axis 1: 59.8%, and axis 2: 74.7%. The environmental variables are represented by arrows. Variables which are statistically significant (Monte-Carlo Permutation Test: $P < 0.050$) for explaining the variation in animal species data are marked with an asterisk. Cumulative percentage of the variation in the species-environment relation explained: axis 1: 74.6%, and axis 2: 84.7%.

tween the axes and the environmental variables were low, always <0.10. According to the ordination diagram all wildlife species avoided infrastructure (see Fig. 3). The abundance of moose, capercaillie and badger were positively related to altitude and clear-felling. Roe deer and hare were positively related to arable land/pasture (not a significant variable; F-ratio $= 2.22$, $P < 0.084$).

Only latitude explained a significant proportion of the variation in species composition (16%; Monte-Carlo Permutation Test: F-ratio $= 27.09$, $P < 0.002$), and no forest type or stage variables were statistically significant when testing the variables from the Vegetation map (Fig. 4A-B) for the Värmland pellet data set separately. Roe deer and hare were negatively related to latitude, but the pattern was weak for the remaining species. The cumulative percentage variance in the species data explained by the

Table 2. Ordination statistics summary for the Principal Component Analysis diagrams illustrated in Figures 3, 4A and B.

Diagram	Ordination statistics	Axis 1	Axis 2	Axis 3	Axis 4
Figure 3	Eigenvalues	0.60	0.15	0.11	0.08
	Species-environment correlations	0.42	0.31	0.23	0.29
	Cumulative percentage variance of species data explained	59.80	74.70	85.80	93.40
Figure 4A	Eigenvalues	0.60	0.16	0.11	0.07
	Species-environment correlations	0.52	0.34	0.10	0.23
	Cumulative percentage variance of species data explained	59.80	75.60	86.30	93.60
Figure 4B	Eigenvalues	0.60	0.16	0.11	0.07
	Species-environment correlations	0.52	0.21	0.07	0.17
	Cumulative percentage variance of species data explained	59.80	75.60	86.30	93.60

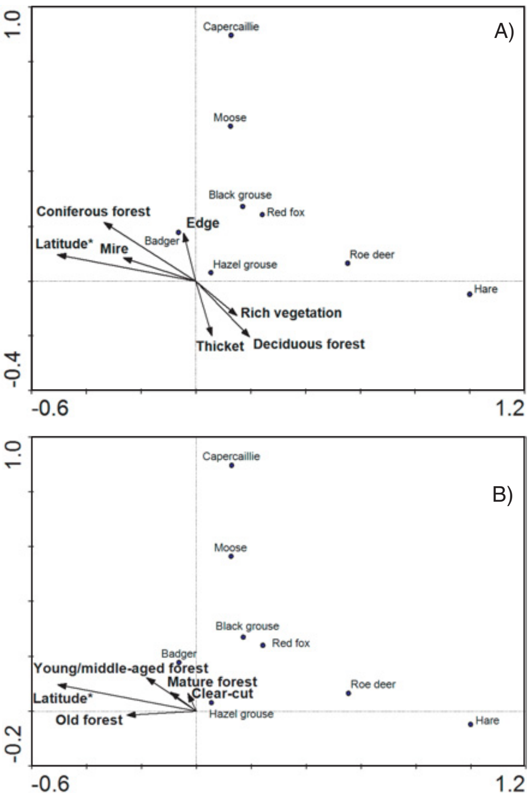

Figure 4. PCA ordination diagrams based on pellet data of mammal and forest bird species in Värmland, Sweden. Environmental variables include forest characteristics derived from the Vegetation map (available only for Värmland). Cumulative percentage of the variation in the species data explained: axis 1: 59.8%, and axis 2: 75.6%. The environmental variables are represented by arrows. Variables which are statistically significant (Monte-Carlo Permutation Test: $P < 0.050$) for explaining the variation in animal species data are marked with an asterisk. In A) the environmental variables include forest types. Cumulative percentage of the variation in the species-environment relation explained: axis 1: 82.9%, and axis 2: 91.2%. In B) the environmental variables include forest stages. Cumulative percentage of the variation in the species-environment relation explained: axis 1: 90.9%, and axis 2: 94.9%.

species axes 1 and 2 was 75.6% and the correlations between the axes and the environmental variables were low, up to 0.25. Several environmental variables correlated strongly with each other (Appendix IA and B), which may result in erroneous exclusion of significant variables (Graham 2003).

Discussion

Spatial patterns of animal occurrences

We found little relationship between species richness and the tested environmental gradients, especially those composed by different forest types and stages, nor did we find any real separation of species into subcommunities. One reasonable interpretation is that our scale of measurement is too large to detect some of the patterns in wildlife occurrences. The triangles are 4+4+4 km and it is possible that much of the variation in mammal and forest bird species distributions lies at a smaller scale (Danell et al. 1991, Åberg et al. 2000).

Another interpretation could be that the mammals of the boreal zone are in fact generalists and thus tolerate habitats of varying environmental characteristics. Large parts of the environmental gradients are acceptable for generalist species and their distributions will typically show little responses to slight and medium variation in environmental properties. Further, the positions of the triangles in the landscape were fine-tuned subjectively before data collection, which in essence meant excluding, for instance, some large open areas, lakes, and roads heavily used by traffic, and therefore the triangles were probably rather similar to each other in the eyes of forest-living wildlife.

The factors driving the wildlife community composition and distribution are: 1) lower temperatures and food availability, e.g. deciduous browse in the northern part of the study area which is dominated by coniferous forest, and 2) avoidance of infrastructure and for some species also open landscape, i.e. arable land and pastures, in the southern part of the area. Infrastructure may be associated with increased disturbance from humans (Nelleman et al. 2001) and open areas with predators (Kurki et al. 1998). We believe that the forest type and forest stage variables, which here were of little importance, may have significant effects on small-scale patterns of occurrence in wildlife species. Therefore, at a landscape scale, the occurrence of boreal wildlife species is described by only a fairly generalised, inter-related set of factors, i.e. those contributing to resource availability and those contributing to disturbance.

Effects of environmental resources

When investigating possible effects on individual species, much of the variation in pellet distributions seem to relate to roe deer and hare separating from the other species. Indeed, roe deer have different habitat requirements, with specialised dietary tolerances, compared to most of the other herbivores (Danell et al. 2006) and frequently inhabit agricultural areas (Cederlund & Liberg 1995). Although roe deer can dig for food underneath the snow (Mysterud et al. 1997), their ranges may also be restricted by snow cover, which often increases with altitude and latitude (SMHI, unpubl. data). Our study supports this through the close relationship between roe deer and one of the most important environmental variables in the Swedish land cover data, arable land/pasture, as well as decreasing altitude and latitude.

Moose is the only mammalian herbivore which is (weakly) positively related to clear-felled areas. It has long been known that moose in Sweden prefer to browse in young coniferous forests during winter (e.g. Bergström & Hjeljord 1987, Ball & Dahlgren 2002). However, due to the problem with multicollinearity among the environmental variables, it is hazardous to isolate the attractiveness of clear-felled areas for moose distribution. It may be that the combination of clear-felled areas with forested areas, wetlands and low density of infrastructure is the real key to distribution patterns in moose as well as in capercaillie, which show similar distribution patterns to moose.

Effects of disturbance

Our data confirm a negative impact of infrastructure on the boreal wildlife community, including most species monitored by the pellet counts. For many boreal wildlife species this is by no means a new result (Ball & Dahlgren 2002). However, different types of infrastructure were tested for significance in the same manner as is described for environmental variables in the Methods section. The results showed that public roads, as well as railways and streets, significantly explained variation in species data, whereas small private roads were insignificant (M. Wallgren, R. Bergström, K. Danell and C. Skarpe, unpubl. data). Accordingly, there seems to be a threshold of size and amount of traffic, below which roads do not constitute a disturbance to large and medium-sized wildlife.

Roe deer and hare pellets were negatively related to clear-felled areas. Several additional species, including both forest grouse and mammals, are also known to suffer from different degrees of forest fragmentation (Kurki et al. 2000, Fisher & Wilkinson 2005). However, in our data, most species seemed little affected by amounts of clear-cut. This could be due to multicollinearlity among and erroneous exclusion of significant environmental variables (see above). However, it may also be an effect of our level of resolution. Since the sampling quantities, i.e. the triangle buffers, are fairly large, it is possible that most of them include, on average, similar amounts of clear-cuts, even though different species may differentiate their habitat use within the triangle depending on their specific requirements and sensitivity.

Implications and concluding remarks

We suggest that common mammal and large-sized forest bird species distributions within the boreal forest ecosystem are little affected by environmental variation, particularly forest type and stage turnovers, at the landscape scale. Each one of our wildlife triangles with buffer zones encompasses ca 6.9 km^2 and, although more research is needed, we believe that smaller-scale differences in environmental properties have larger impacts on the animal community composition, than does variation at this scale. For example, in a study by Helle & Nikula (1996), based on Finnish wildlife triangles, the critical area of capercaillie habitat selection (when there were most significant differences between the same sets of forest classes) was between 0.8 and 3.1 km^2. A similar study encompassing more species would be of great value, not least for determining what the respective impacts of scale and general animal habitat demands are on patterns of species spatial distributions within the boreal forest.

Our findings may have important implications for research as well as for strategic interferences with wildlife populations. If species habitat selection and the way that animals interact with their environment does not occur at the greater landscape scale, then this suggests that the main focus of planning for conservation and population management, should be at the smaller scale. Our study forms one piece of the puzzle, which in the future may provide us with the full picture of boreal wildlife spatial ecology.

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Appendix I

Pearson correlation coefficients showing the amount of multicollinearity between the environmental variables derived from the Road map and Swedish land cover data (A) and from the vegetation data (B).

A)	Altitude	Arable land/ pasture	Clear-felled area	Forest	Infrastructure	Lake	Latitude	Water courses	Wetland
Altitude	1.00								
Arable land/pasture	-0.66	1.00							
Clear-felled area	0.31	-0.26	1.00						
Forest	0.27	-0.37	0.08	1.00					
Infrastructure	-0.43	0.32	0.06	-0.08	1.00				
Lake	-0.26	0.20	-0.13	-0.18	0.02	1.00			
Latitude	0.82	-0.41	0.24	0.11	-0.38	-0.21	1.00		
Water courses	0.04	-0.02	0.22	0.13	0.04	0.02	0.07	1.00	
Wetland	0.44	-0.24	0.30	0.03	-0.15	-0.10	0.38	-0.02	1.00

		Forest									
B)	Clear-cut	Coniferous	Deciduous	Edge	Latitude	Mature forest	Mire	Old forest	Rich vegetation	Thicket	Young/ middle-aged forest
Clear-cut	1.00										
Coniferous forest	0.18	1.00									
Deciduous forest	-0.11	-0.50	1.00								
Edge	-0.21	-0.08	-0.02	1.00							
Latitude	-0.10	0.53	-0.40	0.14	1.00						
Mature forest	-0.04	0.09	-0.11	0.06	0.02	1.00					
Mire	-0.08	0.05	-0.29	0.46	0.49	0.10	1.00				
Old forest	-0.25	0.13	-0.30	0.42	0.52	0.16	0.55	1.00			
Rich vegetation	-0.15	-0.46	0.75	0.20	-0.30	-0.06	-0.10	-0.06	1.00		
Thicket	0.26	< -0.01	0.23	-0.29	-0.03	-0.18	-0.17	-0.19	0.16	1.00	
Young/middle-aged forest	< 0.00	0.75	-0.19	-0.13	0.36	-0.53	-0.12	-0.14	-0.24	0.10	1.00