

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

3
4 Märtha Wallgren, Roger Bergström, Kjell Danell, Christina Skarpe

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6 Corresponding author: Märtha Wallgren, Department of Wildlife, Fish and Environmental
7 Studies, Swedish University of Agricultural Sciences, SE-901 83 Umeå, Sweden.

8 Telephone +46 90 786 86 56, Fax +46 90 786 81 62, Martha.Wallgren@vfm.slu.se

9
10 Roger Bergström, Forestry Research Institute of Sweden, Uppsala Science Park, SE-751 83
11 Uppsala, Sweden. Department of Wildlife, Fish and Environmental Studies, Swedish
12 University of Agricultural Sciences, SE-901 83 Umeå, Sweden. Telephone +46 18 18 85
13 59, Fax +46 18 18 86 00, Roger.Bergstrom@skogforsk.se

14
15 Kjell Danell, Department of Wildlife, Fish and Environmental Studies, Swedish University
16 of Agricultural Sciences, SE-901 83 Umeå, Sweden. Telephone +46 70 374 79 79, Fax +46
17 90 786 81 62, Kjell.Danell@vfm.slu.se

18
19 Christina Skarpe, Department of Forestry and Wildlife Management, Hedmark University
20 College, NO-2480 Koppang, Norway. Norwegian Institute for Nature Research (NINA),
21 Tungasletta 2, NO-7485 Trondheim, Norway. Telephone + 47 62 43 08 35, Fax + 47 62 43
22 08 51, Christina.Skarpe@hihm.no

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1 ABSTRACT

2
3 Many environmental patterns that may have profound effects on wildlife communities
4 occur at the landscape scale, e.g. habitat fragmentation, human demography and
5 distribution of various resources. In order to understand how alterations of such patterns
6 could influence e.g. wildlife species occurrences and community composition it is
7 important to first study these relationships empirically and on the appropriate scale. We
8 surveyed the wildlife community in a Mid-Swedish boreal ecosystem using pellet group
9 counts, while walking so called wildlife triangles. Our main aim was to investigate how the
10 distribution of medium- and large-sized wild mammals and large-sized forest birds were
11 affected by environmental variables at the landscape scale. In 2001-2003, pellet groups of
12 mammals and forest birds were counted on 211 triangular routes with a perimeter of 4+4+4
13 km. The pellet groups were accumulated over winter and counted in spring. The
14 environmental properties of each triangle, including information on latitude, altitude,
15 infrastructure, land cover, forest type and forest stage, were determined using GIS maps.
16 Statistical analyses involved mainly ordination (Principal Component Analysis). Significant
17 environmental variables explaining the wildlife community composition and distribution in
18 the boreal ecosystem were altitude, clear-felling and infrastructure. Our conclusion
19 however is that most boreal mammal and forest bird species are habitat generalists and
20 show little spatial pattern in distributions on landscape scale. This is important knowledge,
21 indicating that habitat selectiveness and structuring animal interactions probably occur on a
22 local scale in the boreal forest. Ultimately it provides important directions for e.g.
23 conservation measures and wildlife management.

INTRODUCTION

1
2
3 Primary productivity in boreal ecosystems is often related to latitude, altitude, temperature
4 and precipitation (Zheng et al. 2004) and resources for animals are determined by e.g.
5 vegetation type and structure, human land use and habitat heterogeneity (Hansson 2002,
6 Nikula et al. 2004). Food resources for herbivorous mammals depend directly on vegetation
7 composition and in many areas management-related stage of forest development (Myserud
8 et al. 1997, Danell et al. 2006), while many carnivores are habitat generalists and feed
9 opportunistically on available prey (Hörnfeldt 1978, Kurki et al. 1998). Protective cover,
10 which is found in e.g. dense understory vegetation and evergreen forests, is especially
11 important for small-sized prey (Hansson 2002).

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

16 Patterns of animal community composition and species richness are highly scale
17 dependent and it is crucial to apply an appropriate scale for studying the effects of different
18 factors on communities (Huston 1999, Kurki et al. 2000, Nikula et al. 2004). Empirical
19 studies of mammal communities across large spatial scales continue to be rare in ecological
20 research (however, see e.g. Hansson 2002, Fisher & Wilkinson 2005). Nevertheless, a
21 considerable proportion of human impact on the environment takes place on landscape
22 scale (for definition see Willis & Whittaker 2002), e.g. fragmentation, deforestation, nature
23 protection, forestry, human demography etc. (Hansson 1992, Kurki et al. 1998, Nelleman et

1 al. 2001). Disturbances may also be caused by the animals themselves, typically through
2 feeding, trampling, defecation and urination (Persson et al. 2000). In order to understand the
3 landscape scale distribution patterns of and interactions between wildlife species it is
4 important to learn how communities are affected by environmental heterogeneity on that
5 particular scale (although e.g. local processes may also greatly influence animal landscape
6 distributions). Such information may guide conservation and management actions, for
7 which success and efficiency depend on that the right patterns and processes are targeted.

8 Faecal pellet counts have long been used for monitoring primarily cervid populations
9 (Neff 1968) and e.g. mountain hare *Lepus timidus* (Angelstam et al. 1985). The method has
10 the advantage of being less costly than animal counts from aircraft and potentially more
11 reliable in areas with dense vegetation (Jordan et al. 1993). It is a convenient way of
12 collecting information on and monitoring many species simultaneously. Average defecation
13 rates needed for calculating corresponding densities from pellet counts are available for
14 numerous species (Härkönen & Heikkilä 1999, Kindberg 2003) and areas (Persson et al.
15 2000, Forsyth et al. 2007).

16 The general aim of this study was to investigate large-scale patterns of wildlife
17 community composition, in relation to environmental gradients in the Mid-Swedish boreal
18 forest. The focus was set at the landscape scale, covering two Swedish counties together
19 comprising approximately 26 000 km². Our main question was: How does the boreal
20 wildlife community, including species distributions and relative abundances, relate to
21 environmental variation at the landscape scale in Sweden?

22

23

METHODS

1

2 *Study area*

3 In total, 222 equilateral triangular routes, i.e. wildlife triangles, were positioned in the Mid-
4 Swedish counties of Värmland and Örebro between ca. 58° 50' N and 60° N and over an
5 area of approximately 26 000 km² (Figure 1). Average precipitation is 600-900 mm/year
6 with the higher amounts in the west and southwest (Swedish Meteorological and
7 Hydrological Institute, SMHI, unpublished data). The number of days with snow ranges
8 from ca. 75/year in the south to ca. 200/year in the north (SMHI unpublished data).

9 The study area is dominated by boreal forest in the north and agricultural land in the
10 south-southeast. The boreal zones encompassed are (from north to south) the northern
11 boreal, middle boreal, southern boreal and hemiboreal zones (Ahti et al. 1968). About 74%
12 of the total land area of Värmland and 67% of Örebro is forested (Swedish Statistical
13 Yearbook of Forestry, SSYF, 2007). Both counties are subjected to intensive forestry, with
14 63% of the total forest land area being younger than 50 years and the dominant tree species
15 being Scots pine *Pinus sylvestris*, Norway spruce *Picea abies* and birch *Betula* spp.,
16 accounting to 90-95% of the total standing volume (SSYF 2007). About 6% of Värmland
17 and 16% of Örebro is covered by arable land (SSYF 2007). Dominating agricultural crops
18 in both counties are temporary grass/ley (52% of the agricultural land area in Värmland and
19 28% in Örebro) and cereals (23% in Värmland and 39% in Örebro) (Yearbook of
20 Agricultural Statistics 2007). The variation in climate, vegetation and land use within the
21 study area is thus fairly large with a strong gradient from north (or northwest) to south (or
22 southeast). Also, numerous lakes, rivers and mires contribute to a more variable landscape

1 than found in many other areas within the boreal forest zone. This variation was an
2 important reason for why these counties were chosen for the study.

3

4 *Data collection*

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

11 Fecal pellets of 11 preselected species of mammals and large forest birds (species
12 common in the area and whose pellets are easily recognized, Table 1) were counted in
13 altogether 211 triangles (56 triangles were counted all three years, 105 two years and 50
14 one year) between March 19 and June 14 of 2001-2003 (Table 1). Circular plots for pellet
15 counts (100 m² for moose *Alces alces* and 10 m² for remaining species) were placed at
16 every 100 m along the triangle sides, giving a total of 120 plots/triangle. Depending on the
17 species either single pellets (e.g. hare *L. timidus* and *L. europaeus* and forest grouse) or
18 pellet groups (e.g. moose and roe deer *Capreolus capreolus*, with minimum number of 20
19 and 10 pellets/group, respectively) were counted. Only pellets dropped after leaf fall,
20 estimated to October 15, were counted, thus giving a measurement index of relative
21 abundance of animals during the previous winter.

22

23 *Map data*

1 Environmental properties were assigned to each triangle using ArcMap 9.1 (ESRI
2 Corporation, Redlands, CA). GIS maps used included the Road map (i.e. Vägkartan),
3 Swedish land cover data (i.e. Svenskt marktäckedata) and, for Värmland only, the
4 Vegetation map (i.e. Vegetationskartan). All maps are distributed by National Land Survey
5 (Lantmäteriet) of Sweden (<http://www.lantmateriet.se/>, homepage available in English).
6 The Road map holds information on road and railroad networks, urban areas etc. Swedish
7 land cover data is an overview of land use and vegetation, comprising 57 classes. It is
8 similar to the European Union classification system CORINE land cover. The Vegetation
9 map is based on Infra Red Photography (from 4 600 m) and is a detailed map of vegetation,
10 including separate layers for composition (ca. 70 classes plus additional information, giving
11 >300 variants) and forest phase (7 classes).

12 The triangles, each one surrounded by a 1 km wide buffer zone, were imported into
13 the GIS maps and the landscape structures within and around them were examined (Figure
14 2). More specifically, each triangle with its buffer zone was attributed by absolute area of
15 different types of land cover, including forest, arable land/pasture, clear-felling, lake and
16 wetland, total length of water courses and infrastructure, including all roads and railways,
17 and mean altitude. Latitude, summed edge (i.e. the perimeter of all features) and detailed
18 vegetation data, including the area of different forest types and development stages, were
19 also used as environmental variables. Some vegetation variables composed data from
20 several classes: coniferous forest (different types and moisture levels), deciduous forest
21 (different types and moisture levels), mire (all types of mire and marsh), thicket (deciduous
22 thicket with remnant coniferous and deciduous trees) and rich vegetation (moist meadow
23 and deciduous vegetation on mire and marsh). Thicket and rich vegetation are two types of

1 habitats which are known to be important for many mammals and birds within the boreal
2 forests of Fennoscandia (e.g. Essen et al. 1992).

3

4 *Statistical methods*

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

20 The significances of the selected environmental variables for explaining the variation
21 in species pellet distributions were tested with Monte-Carlo Permutation test in Canoco,
22 using unrestricted permutation type and 499 permutations. Statistically significant variables
23 were marked in the biplots. Pearson correlations of the environmental variables were used

1 as a complement to the multiple regressions to examine the degree of multicollinearity
2 among the environmental variables.

3 We also calculated the densities of four common species, including moose, roe deer,
4 hare and capercaillie *Tetrao urogallus*, using the formula $\text{no. of animals/km}^2 = N / (A \times T \times D)$,
5 where N is number of pellets or pellet groups found, A total area sampled (km^2), T number
6 of days of pellet accumulation (days between October 15 and the date of sampling) and D
7 the species-specific defecation rate (number of defecations/day). Average defecation rates
8 used were: 14 pellet groups/day for moose (references in Persson et al. 2000), 22 pellet
9 groups/day for roe deer (Cederlund & Liberg 1995), 115 pellets/day for capercaillie (Hjort
10 1994) and 475 pellets/day for hare (Pehrson 1996).

11

12

RESULTS

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14 During the course of the study 51 482 plots (19 354 in 2001, 22 130 in 2002 and 10 000 in
15 2003) were sampled and 53 747 pellets or pellet groups from 10 species were encountered
16 (Table 1). The most common species were hare, moose and capercaillie, while pellets from
17 brown bear *Ursus arctos*, wolf *Canis lupus* and badger *Meles meles* were rare.

18

19 In the PCA biplot for both counties combined (Figure 3, test statistics in Table 2),
20 there were two obvious species axes, one comprising capercaillie and moose and the second
21 hare and roe deer. Remaining species were comparatively centrally located in the biplot.

21

22

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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

1 significantly parts of the species distribution data (Figure 3). However, the degree of
2 explanation was low, merely 7% (altitude), 3% (infrastructure) and 2% (clear-felling) of the
3 variation in species pellet distributions. The cumulative percentage variance in the species
4 data explained by the species axes 1 and 2 in the ordination was 74.7% and the correlations
5 between the axes and the environmental variables were low, always <0.10 . According to
6 the ordination diagram all wildlife species avoided infrastructure (Figure 3). The abundance
7 of moose, capercaillie and badger were positively related to altitude and clear-felling. Roe
8 deer and hare were positively related to arable land/pasture (not a significant variable, F-
9 ratio=2.22, $p<0.084$).

10 Only latitude explained a significant proportion of the variation in species
11 composition (16% : Monte-Carlo Permutation Test, F-ratio=27.09, $p<0.002$), and no forest
12 type or stage variables, were statistically significant when testing the variables from the
13 Vegetation map (Figure 4a-b) for the Värmland pellet data set separately. Roe deer and
14 hare were negatively related to latitude, but the pattern was weak for remaining species.
15 The cumulative percentage variance in the species data explained by the species axes 1 and
16 2 was 75.6% and the correlations between the axes and the environmental variables were
17 low, up to 0.25. Several environmental variables correlated strongly with each other
18 (Appendix 1a and b, electronic version only), which may result in erroneous exclusion of
19 significant variables (Graham, 2003).

20

21

DISCUSSION

22

23 *Spatial patterns of animal occurrences*

1 We have found little relationship between species richness and the tested environmental
2 gradients, especially those composed by different forest types and stages, as well as no real
3 separation of species into subcommunities. One reasonable interpretation is that our scale
4 of measurement is too large to detect some of the patterns in wildlife occurrences. The
5 triangles are 4+4+4 km and it is possible that much of the variation in mammal and forest
6 bird species distributions lies on a smaller scale (Danell et al. 1991, Åberg et al. 2000).

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

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

1 inter-related set of factors: those contributing to resource availability and those contributing
2 to disturbance.

3

4 *Effects of environmental resources*

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

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

23

1 *Effects of disturbance*

2 The data confirms a negative impact of infrastructure on the boreal wildlife community,
3 including most species monitored by the pellet counts. For many boreal wildlife species
4 this is by no means a new result (Ball & Dahlgren 2002). However, different types of
5 infrastructure were tested for significance in the same manner as is described for
6 environmental variables in the Methods section. The results showed that public roads, as
7 well as railways and streets, significantly explained variation in species data, while small
8 private roads were insignificant (unpublished). Accordingly there seems to be a threshold
9 of size and amount of traffic, below which roads do not constitute a disturbance to large
10 and medium-sized wildlife.

11 Roe deer and hare pellets were negatively related to clear-felled areas. Several
12 additional species, including both forest grouse and mammals, are also known to suffer
13 from different degrees of forest fragmentation (Kurki et al. 2000, Fisher & Wilkinson
14 2005). However, in our data most species seemed little affected by amounts of clear-cut.
15 This could be due to multicollinearity among and erroneous exclusion of significant
16 environmental variables (see above). However, it may also be an effect of our level of
17 resolution. Since the sampling quantities, i.e. the triangle buffers, are fairly large, it is
18 possible that most of them include, on average, similar amounts of clear-cuts, even though
19 different species may differentiate their habitat use within the triangle depending on their
20 specific requirements and sensitivity.

21

22 *Implications and concluding remarks*

1 We suggest that common mammal and large-sized forest bird species distributions within
2 the boreal forest ecosystem are little affected by environmental variation, particularly forest
3 type and stage turnovers, at the landscape scale. Each one of our wildlife triangles with
4 buffer zones encompasses ca 6.9 km² and although more research is needed, we believe that
5 smaller-scale differences in environmental properties have larger impacts on the animal
6 community composition, than does variation at this scale. For example, in a study by Helle
7 and Nikula (1996), based on Finnish wildlife triangles, the critical area of capercaillie
8 habitat selection (when there were most significant differences between the same sets of
9 forest classes) was between 0.8 and 3.1 km². A similar study encompassing more species
10 would be of great value, not least for determining what the respective impacts of scale and
11 general animal habitat demands are on patterns of species spatial distributions within the
12 boreal forest.

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

20

21

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1

2

TABLES

3

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

English	Latin	Pellets/ pellet groups
Badger	<i>Meles meles</i>	13
Black grouse	<i>Tetrao tetrix</i>	1 169
Brown bear	<i>Ursus arctos</i>	2
Capercaillie	<i>Tetrao urogallus</i>	2 182
Hare spp.	<i>Lepus timidus & L. europaeus</i>	7 976
Hazel grouse	<i>Bonasa bonasia</i>	820
Lynx	<i>Lynx lynx</i>	0
Moose	<i>Alces alces</i>	5 131
Red fox	<i>Vulpes vulpes</i>	76
Roe deer	<i>Capreolus capreolus</i>	1 296
Wolf	<i>Canis lupus</i>	3

7

1 Table 2. Ordination statistics summary for the Principal Component Analysis diagrams
 2 illustrated in Figure 3 and 4 a and b. Highlighted lines are suspiciously similar. Are they
 3 correct?

Diagram	Ordination statistics	Axis1	Axis2	Axis3	Axis4
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	59.8	74.7	85.8	93.4
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	59.8	75.6	86.3	93.6
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	59.8	75.6	86.3	93.6

4

- 1 Table 3. Summary of densities of capercaillie, hare, moose and roe deer in Värmland and
- 2 Örebro, Sweden, given as number of individuals/km². Calculations are based on pellet
- 3 counts and are done individually for each triangle and the years 2001, 2002 and 2003.

(No./km ²)	Capercaillie	Hare	Moose	Roe deer
Mean	0.55	0.50	1.05	1.69
Maximum	10.81	5.32	4.52	12.78
Minimum	0	0	0	0
Median	0.077	0.30	0.93	1.01

1 Figure legends

2

3 Figure 1.

4 Map showing the arrangement of the wildlife triangles in the counties of Värmland and
5 Örebro in Sweden. 211 triangles were used for pellet counts.

6

7 Figure 2.

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

10

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

20

21 Figure 4.

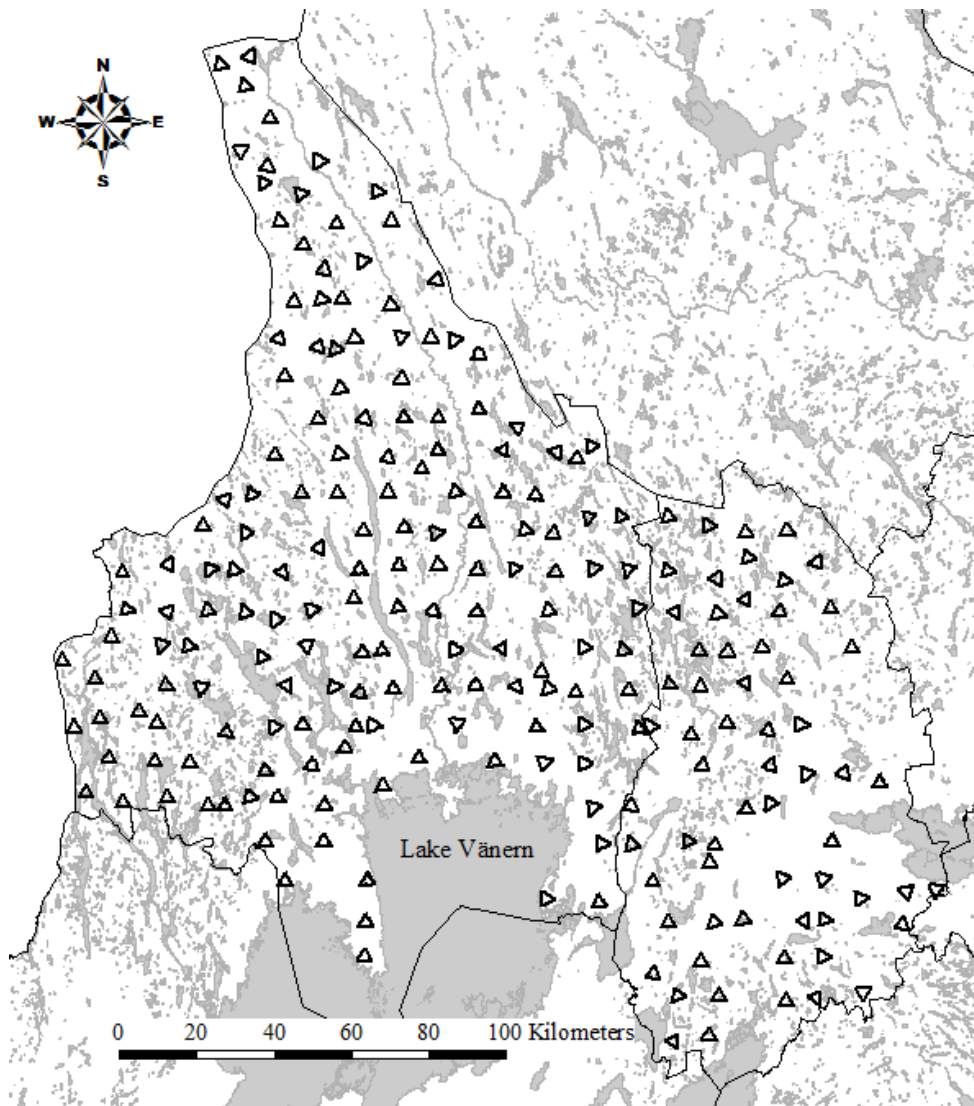
22 PCA ordination diagrams based on pellet data of mammal and forest bird species in
23 Värmland, Sweden. Environmental variables include forest characteristics derived from the

1 Vegetation map (available only for Värmland). Cumulative percentage of the variation in
2 the species data explained: axis 1: 59.8% and axis 2: 75.6%. The environmental variables
3 are represented by arrows. Variables which are statistically significant (Monte-Carlo
4 Permutation Test, $p < 0.050$) for explaining the variation in animal species data are marked
5 with *.

6 a) Environmental variables include forest types. Cumulative percentage of the variation in
7 the species-environment relation explained: axis 1: 82.9% and axis 2: 91.2%.

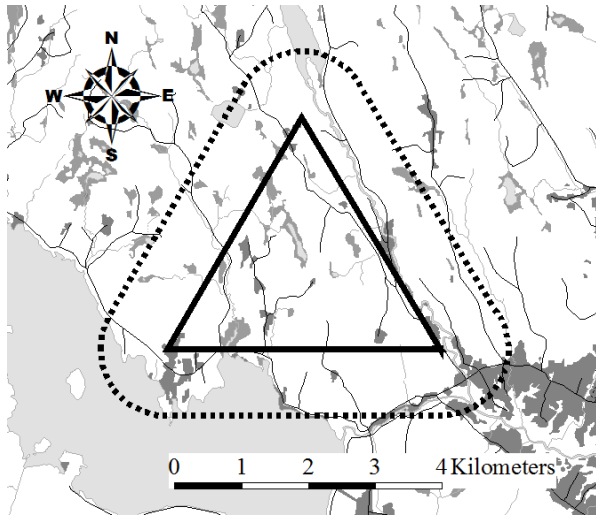
8 b) Environmental variables include forest stages. Cumulative percentage of the variation in
9 the species-environment relation explained: axis 1: 90.9% and axis 2: 94.9%.

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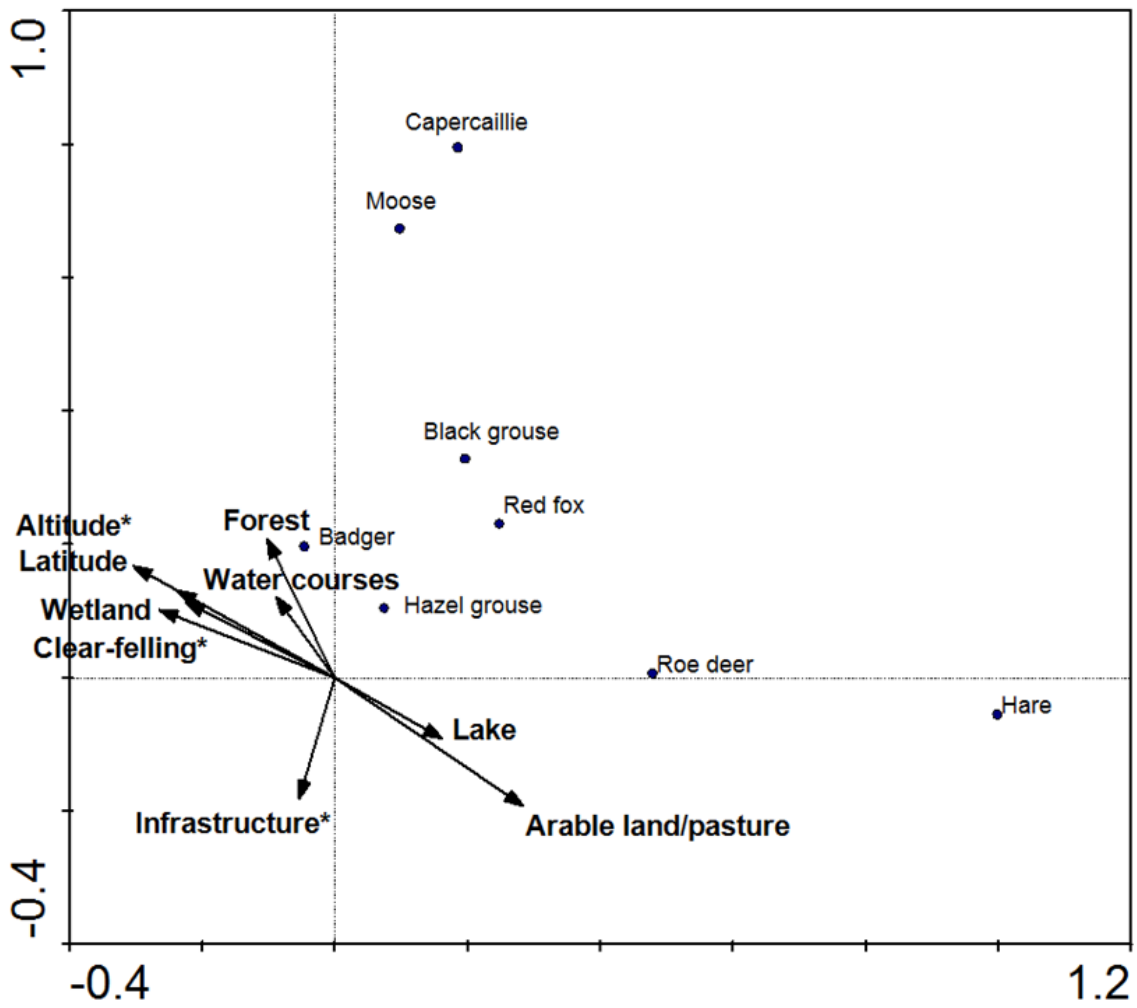
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2 Figure 1.



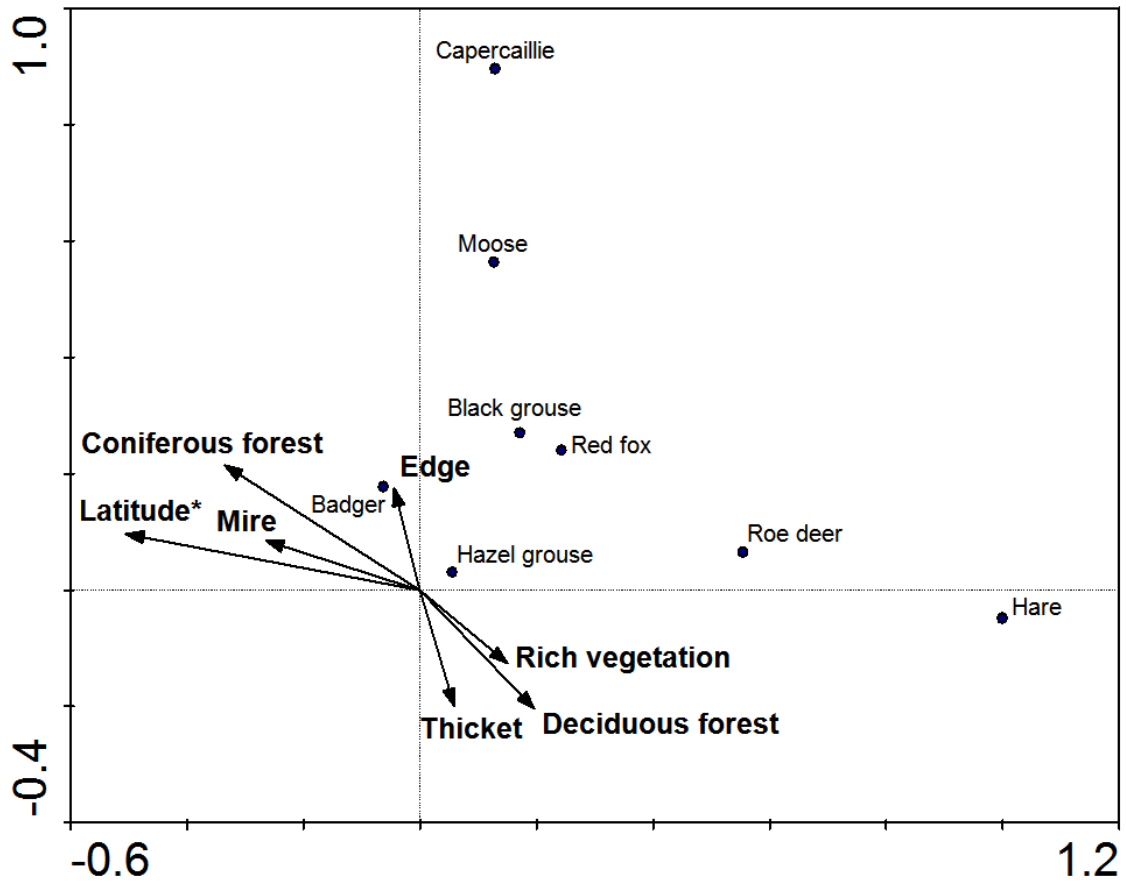
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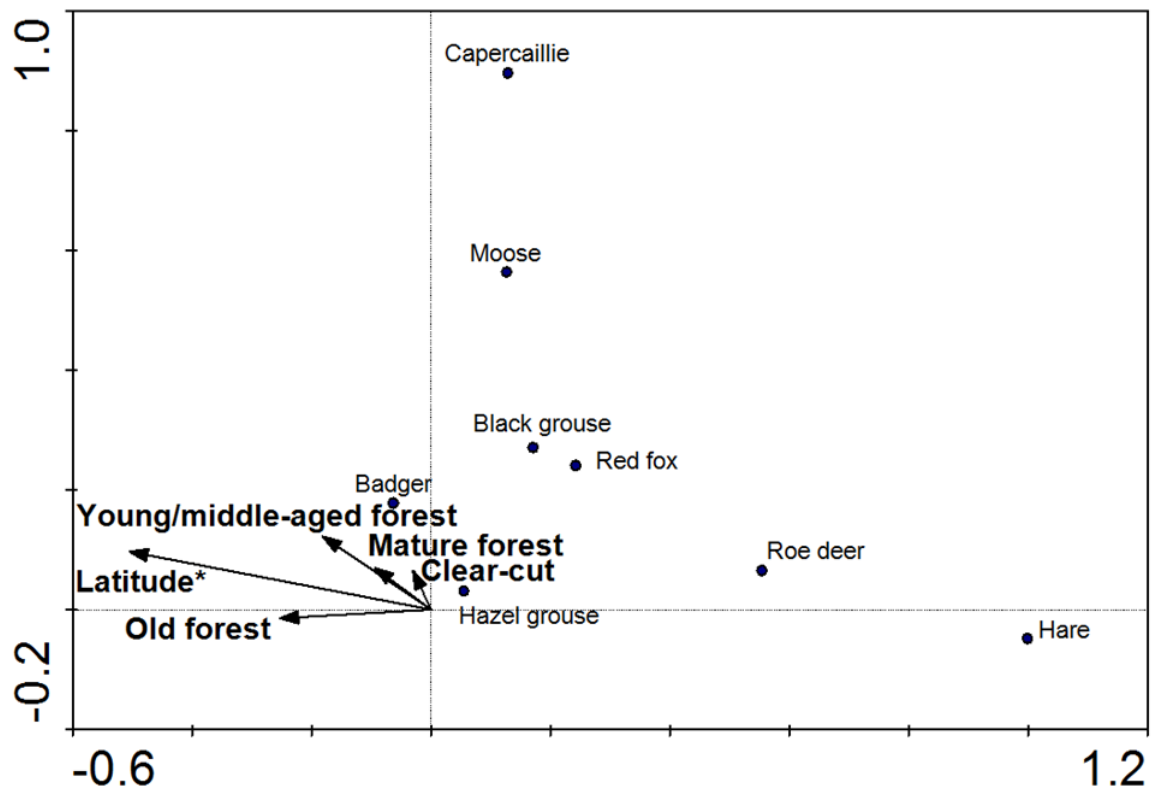
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Figure 3.



1

2 Figure 4a.



1

2 Figure 4b.

Appendix 1a. Pearson correlation coefficients showing the amount of multicollinearity between the environmental variables derived from the Road map and Swedish land cover data.

	Altitude	Arable land/pasture	Clear-felled area	Forest	Infrastructure	Lake	Latitude	Water courses	Wetland
Altitude	1								
Arable land/pasture	-0.66	1							
Clear-felled area	0.31	-0.26	1						
Forest	0.27	-0.37	0.08	1					
Infrastructure	-0.43	0.32	0.06	-0.08	1				
Lake	-0.26	0.20	-0.13	-0.18	0.02	1			
Latitude	0.82	-0.41	0.24	0.11	-0.38	-0.21	1		
Water courses	0.04	-0.02	0.22	0.13	0.04	0.02	0.07	1	
Wetland	0.44	-0.24	0.30	0.03	-0.15	-0.10	0.38	-0.02	1

Appendix 1b. Pearson correlation coefficients showing the amount of multicollinearity between the environmental variables derived from the Vegetation map.

	Clear-cut	Coniferous forest	Deciduous forest	Edge	Latitude	Mature forest	Mire	Old forest	Rich vegetation	Thicket	Young/middle-aged forest
Clear-cut	1										
Coniferous forest	0.18	1									
Deciduous forest	-0.11	-0.50	1								
Edge	-0.21	-0.08	-0.02	1							
Latitude	-0.10	0.53	-0.40	0.14	1						
Mature forest	-0.04	0.09	-0.11	0.06	0.02	1					
Mire	-0.08	0.05	-0.29	0.46	0.49	0.10	1				
Old forest	-0.25	0.13	-0.30	0.42	0.52	0.16	0.55	1			
Rich vegetation	-0.15	-0.46	0.75	0.20	-0.30	-0.06	-0.10	-0.06	1		
Thicket	0.26	<-0.01	0.23	-0.29	-0.03	-0.18	-0.17	-0.19	0.16	1	
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