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Research article

Long-term decline and local extinction of *Clethrionomys rufocanus* in boreal Sweden

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Abstract

Over the past three decades in boreal Sweden, there has been a long-term decline of cyclic sympatric voles, leading to local extinctions of the most affected species, the grey-sided vole (*Clethrionomys rufocanus*). We monitored this decline by snap-trapping on 58 permanent plots spread over 100 km^2 in spring and fall from fall 1971–2003. The reason for the decline is largely unknown, although a common major factor is likely to be involved in the decline of *C. rufocanus* and of the coexisting voles. However, here we deal with the reasonability of one complementary hypothesis, the habitat fragmentation hypothesis, which assumes that part of the decline of *C. rufocanus* is caused by habitat (forest) destruction. There was considerable local variation in the decline among the 58 1-ha sampling plots, with respect to both density and timing of the decline; however, all declines ended up with local extinction almost without exception. Local declines were not associated with habitat destruction by clear-cutting within sampling-plots, as declines started about equally often before as after clear-cutting, which suggested that habitat destruction outside sampling plots could be involved. In a multiple regression analysis, local habitat preference (LHP; expressed as a ratio of observed to expected number of voles trapped per habitat) together with two habitat variables in the surrounding (2.5×2.5 km^2) landscape matrix explained 56% of the variation among local cumulated densities of *C. rufocanus* and hence of local time-series. LHP was positively correlated and explained 31% of the variation, while connectivity among clear-cuts was negatively correlated and proximity among xeric-mesic mires was positively correlated and explained additional 16% and 9%, respectively. Even if the overall decline cannot be connected to local clear-cutting on sampling-plots, clear-cutting and hence habitat fragmentation/destruction in the surrounding landscapes potentially influenced grey-sided vole numbers negatively.

Introduction

Northern vole and lemming populations, as in Fennoscandia, often exhibit short-term (3–5 years) population cycles, and there are a number of hypotheses on the causes of these cycles (reviewed by Stenseth 1999; Batzli 2001). In Fennoscandia there is a north–south gradient with respect to vole population fluctuation patterns, with cycles in the north, non-cyclic populations in the south and semi-cyclic populations in between (Hansson and Henttonen 1985, 1988). There are similar geographical gradients on Hokkaido, Japan and in central Europe (Björnstad et al. 1998; Tkadlec and Stenseth 2001). In addition to short-term cycles and geographical gradients, there has been an overarching long-term decline in the size of different cyclic vole populations in Fennoscandia during the last 20 years. Generally, this decline has been characterised by an increased frequency and severity of winter declines, and has shown up as a drop in spring densities (e.g. Hörnfeldt 1991, 1994, 1995, 2004; Hanski and Henttonen 1996; Hansen et al. 1999; Hansson 1999; Henttonen 2000; Ekerholm et al. 2001), suggesting some common underlying and major cause to the decline. In our study-area in boreal Sweden the decline became apparent in the early 1980s, and has been especially pronounced in the grey-sided vole (*Clethrionomys rufocanus* Sund.) as this species has also shown a collapse in fall densities, in contrast to the sympatric bank vole (*C. glareolus*) and field vole (*Microtus agrestis*) (Hörnfeldt 2004). A number of hypotheses concerning possible causes of the long-term decline have also been proposed (Hörnfeldt 1991, 1995, 1998, 2004). We have tested and refuted the destructive sampling hypothesis, which suggested that the collapse was driven by our recurrent snap-trapping on our permanent plots (Christensen and Hörnfeldt 2003). The major hypothesis assumes that the negative effects have arisen from adverse winter conditions caused by changes in the winter climate. However, the decline, not only of spring but also of fall densities, in *C. rufocanus* suggests that some additional factor is involved in the current decline of this species and that habitat fragmentation caused by forestry is a likely such candidate (Hörnfeldt 1995, 2004).

For mammalian populations it has been proposed that habitat fragmentation initially has a negative effect on population levels purely because of habitat loss. If fragmentation continues and only a low proportion of suitable habitat is left in the landscape, population size is reduced in relation to the size and isolation of the habitat patches, i.e. because of true fragmentation (Andrén 1994, 1996). Landscape quality must be defined in relation to each species' dispersal abilities, and a species with good dispersal ability in its pristine environment can be a poor disperser in a fragmented landscape (Fahrig 2001). However, corridors, which enhance connectivity, might improve dispersal through otherwise hostile landscapes (Henein and Merriam 1990; van Apeldoorn et al. 1992; LaPolla and Barrett 1993; Bennett et al. 1994). With a higher degree of fragmentation in an area the amount of edge zones increase. Generalist predators might benefit from this, resulting in higher predation rates in edge zones and smaller patches (Wilcove 1985; Andrén and Angelstam 1988; Andrén 1992).

Traditionally, studies of relationships between vole density and habitat have focused on local habitat characteristics (e.g. Kalela 1957; Larsson and Hansson 1986; Johannesen and Mauritzen 1999; Ecke et al. 2001, 2002, 2003; Christensen and Hörnfeldt in press), although it has frequently been pointed out that landscape habitat composition is also likely to influence animal numbers (Hansson 1977, 1999; Lidicker 1988, 2000; Wiens 1989; Kareiva and Wennergren 1995; Hargis et al. 1999). Only recently have differences in densities and dynamics of vole populations been analysed in relation to landscape properties (Martinsson et al. 1993; Delattre et al. 1996; Oksanen and Henttonen 1996; Oksanen et al. 1999; Huitu et al. 2003; Ecke et al. in press), which probably reflects how difficult it was to obtain relevant habitat data on the landscape level before satellite images became available (Ecke et al. in press). Similarly, the simultaneous consideration of effects on density of both local and landscape properties has been delayed (Angelstam et al. 1987; Mönkkönen et al. 1997; Hambäck et al. 1998; Moilanen and Hanski 1998; Mazerolle and Villard 1999; Orrock et al. 2000; Reunanen et al. 2000; Fedriani et al. 2002).

The present study was based on long-term monitoring of vole populations on permanent sampling plots, using an extensive, landscape-based grid of uniformly distributed plots. Here we show that *C. rufocanus* has declined in a multitude of patterns usually ending up in local extinction, as represented by the time-series of individual sampling-plots. We also show that the local cumulated densities of *C. rufocanus* were positively correlated with the vole's preference for local habitat and negatively or positively correlated with habitat characteristics in the surrounding landscape matrix (matrix as used by Forman and Godron 1986). The negative correlation with occurrence of clear-cuts is a strong indication that habitat fragmentation may indeed be involved in the long-term decline of *C. rufocanus*, and stresses the importance of carefully testing the habitat fragmentation hypothesis.

Methods

Study area

This study was carried out in a 100×100 km^2 large area, in the middle and northern boreal zone (Ahti et al. 1968) in northern Sweden (≈64°N, 20°E) (Figure 1), which is dominated by coniferous forests (Norway spruce and Scots pine) and mires (Lundmark 1986). In 1994 the study area included 34% mixed forests, 21% clear-cuts, 19% pine forests, 9% xeric-mesic mires, 6% water, 6% agricultural land, 3% spruce forests and 2% broadleaved forest according to the topographic map (Swedish National Land Survey) and forest parameters (Ecke et al. in press).

Trapping methods

Long-term monitoring of cyclic vole populations was based on snap-trapping on permanent 1-ha sampling plots and has been performed in the study area (Figure 1a) in spring and fall from fall 1971 to 2005 (e.g. Hörnfeldt 1978, 1994, 2004, 2005). Since 1979 the trapping has been part of the National Environmental Monitoring Programme. The study area can be divided into four different areas (NW, NE, SW and SE; Figure 1b), each with four 5×5 km^2 sub-areas (Figure 1b), in each of which we usually performed trapping on four 1-ha permanent sampling plots (Figure 1c; see also Figure 2). In all, trapping has been carried out on 58 of 64 initially selected permanent plots, uniformly distributed according to the Swedish National Grid, with no pre-assessment of habitat or geographic elements occurring in the landscape. Each sampling plot contained ten trap stations, centred and spaced 10 m apart along the diagonal of the 1-ha square. The ten trap stations represented one to four different habitat patches; each patch defined according to main- and sub-habitat type (Figure 1d, see also Christensen and Hörnfeldt in press). The plots or trap-stations not used (Figure 2a, b, Appendix Table A1 and A2) were located at untrappable sites, such as lakes. Five snap traps were set per station and hence 50 traps were normally used per sampling plot. The traps operated during three consecutive nights, corresponding to a total trapping effort of 150 trap nights per sampling plot during each sampling period (spring and fall) (for details see Hörnfeldt 1978, 1994, 2004).

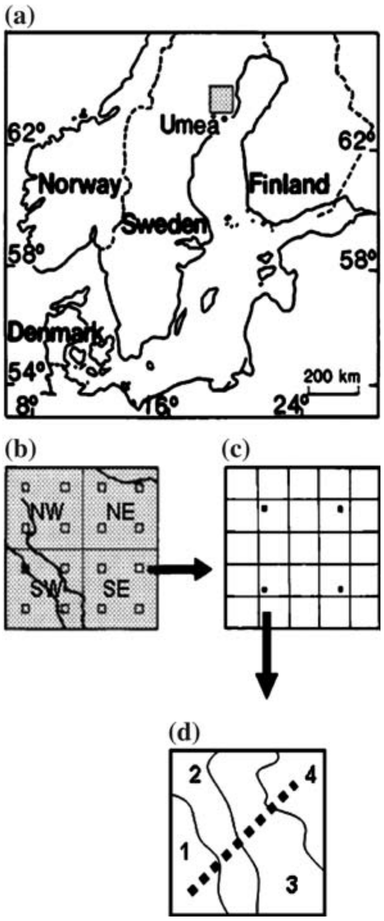

Figure 1. (a) Location of the 100×100 km^2 study area (shaded) in northern Sweden, (b) the study area is divided into 4 different areas; NW and SW (inland) and NE and SE (coastal), each with four 5×5 km^2 sub-areas, (c) each of these sub-areas contains four 1-ha plots where trappings took place (unless plots were on untrappable sites; see text), and (d) each 1-ha plot with 10 trap-stations, representing 1–4 different habitat patches.

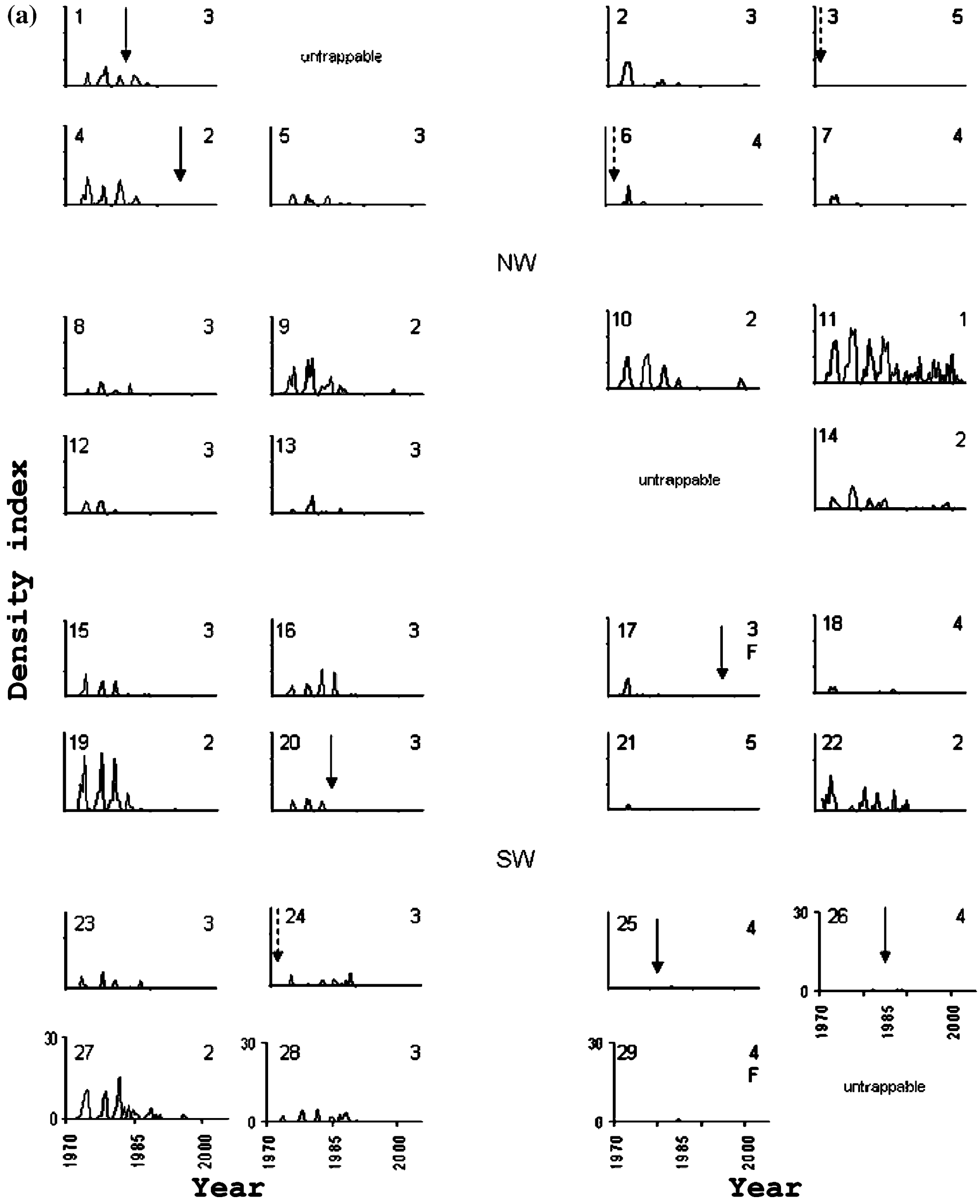

Figure 2. Local time-series for *Clethrionomys rufocanus* density indices, expressed as number of individuals trapped per 100 trap-nights, in spring and fall from fall 1971–2003 for (a) inland (NW, SW) and (b) coastal areas (NE, SE); series positioned to match the geographical location of the 58 1-ha sampling plots as explained in Figure 1. Site number in upper left corner refers to habitat descriptions in Appendix Table A1 A2. Number in upper right corner refers to the time-series' cluster-group, and F to series with voles trapped in fall only. Solid arrows denote time of clear-cutting of sampling plots, and broken arrows denote sampling plots that were clear-cut before trapping started in 1971. Note that Y-scales and X-scales are the same as in bottom row of graphs.

Statistical analysis

Density indices (number of grey-sided voles trapped per 100 trap-nights) were calculated for each 1-ha sampling plot for every year and season separately, so that individual time-series were obtained for the 58 sampling-plots. We used cluster-analysis (Euclidean distance, Ward's method; MINITAB 1998) to group the 58 time-series based on three variables (a) total cumulated density

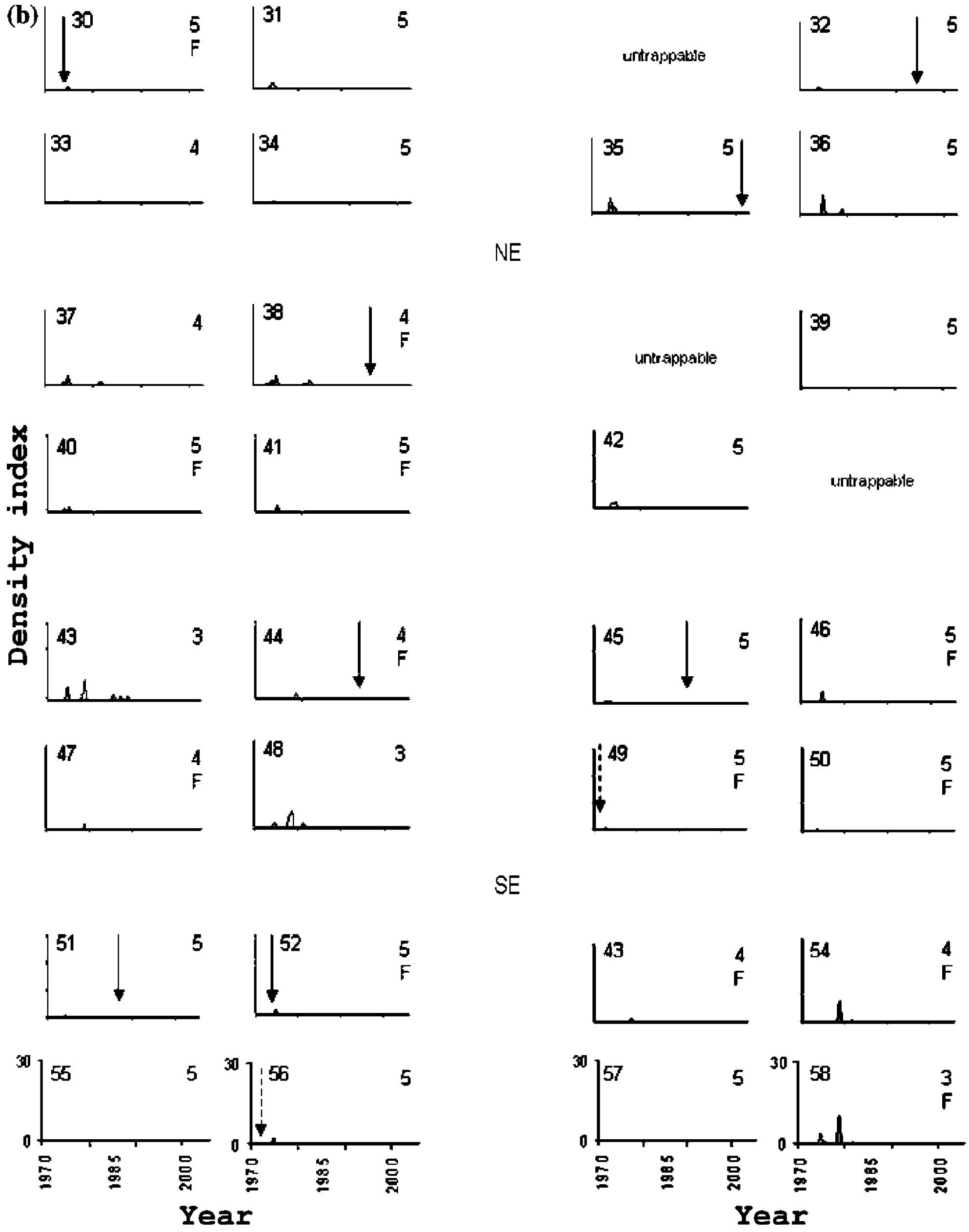

Figure 2. Continued.

indices, (b) number of seasons before local extinction, and (c) number of seasons with no voles trapped. To reveal any differences in dynamics related to local habitat, we also calculated density indices per habitat (patches with the same habitat were aggregated together) for high-density (see below), inland areas and for low-density (see below), coastal areas.

The main habitats on the 58 1-ha sampling plots were determined at the start of trapping in 1971, and sub-habitat types were classified in 1973–74 according to the forest type classification system (Arnborg 1990) and to that of the International Biological Programme (1971) for mires/swamps (Appendix Table A1 and A2; see also Christensen and Hörnfeldt in press). Major habitat changes within the sampling plots, like clear-cutting were noted when they occurred.

Based on data from Christensen and Hörnfeldt (in press), we calculated a local habitat preference index as the ratio of observed to expected number of trapped reproductive *C. rufocanus* females in spring 1971–1978 in that particular habitat, assuming the expected number of females to be proportional to the number of traps in that habitat. Males and immatures showed similar relative densities as females in different habitats and the patterns were similar in spring and autumn (Christensen and Hörnfeldt in press). For sampling plots consisting of >1 type of habitat patch, the local habitat preference (LHP), was calculated as the weighted mean for the different patch types (see Appendix Table A1 and A2). As the grey-sided vole seemed to avoid clear-cuts in our study area (Christensen and Hörnfeldt in press) we weighted the LHP of sampling-plots that were clear-cut or became clear-cut in the course of the study by first multiplying LHP with the number of years that the plots were defined as forested (trees ≥2 m of height) and then dividing the product by the length (number of years) of the time-series. Habitat preference indices >1 indicated a preference for that specific habitat.

We also used a set of 20 landscape parameters, derived from satellite images and a 2.5×2.5 km^2 area surrounding each sampling plot, that were previously found to differ significantly among low and high density sites, based on the cumulated density indices of *C. rufocanus* specimens trapped on the individual sampling plots in 1980–99 (Appendix Table A3; for details, see Ecke et al. in press). Dependence of local cumulated density of *C. rufocanus* (or CRCD) on local habitat (LHP for each sampling-plot), and on the 20 landscape parameters, was analysed in a step-wise multiple regression using square root transformed CRCD values (SPSS 11.5.1, 2001). Correlation coefficients among the 21 predictor variables ranged from −0.788 to 0.798.

Results

The previously reported long-term decline of *C. rufocanus* in the study area (e.g. Hörnfeldt 1991, 1994, 2004; Christensen and Hörnfeldt 2003; Ecke et al. in press), is the sum of a multitude of patterns of decline on the 58 1-ha sampling plots, with respect to local densities and timing of the decline, all ending up with local extinction, almost without exception (Figure 2a, b; see also Table 1). With respect to both spring and fall densities, the average decline was 100% from the highest density in 1974 to the latest

Table 1. Descriptive statistics for 5 cluster-groups representing 58 local time-series of *Clethrionomys rufocanus* trapped in spring and fall from fall 1971–2003 (65 seasons in total); *n* denotes number of sampling plots.

	Cluster group					Kruskal Wallis, *df* = 4
	1 (*n* = 1)	2 (*n* = 7)	3 (*n* = 16)	4 (*n* = 13)	5 (*n* = 21)	*p*
Fall occupancy[a] (%)	87.9	36.8 ± 7.7	17.8 ± 6.5	5.6 ± 3.0	3.6 ± 3.3	0.000
Cumulated density index, fall	231.3	61.1 ± 22.9	17.3 ± 6.9	3.9 ± 3.4	2.4 ± 2.9	0.000
Spring occupancy[a] (%)	40.6	29.5 ± 7.2	10.7 ± 4.8	3.1 ± 3.1	0.9 ± 1.4	0.000
Cumulated density index, spring	80.7	28.9 ± 9.4	7.8 ± 4.0	0.8 ± 0.9	0.3 ± 0.6	0.000
Mean index before local extinction	4.8	2.1 ± 0.6	0.8 ± 0.2	0.2 ± 0.1	0.4 ± 0.4	0.000
Cumulated density index, fall + spring[b]	312	89.9 ± 22.6	25.1 ± 8.8	4.7 ± 3.8	2.8 ± 3.0	0.000
No. of seasons before local extinction[b]	65	44.6 ± 12.0	31.2 ± 9.4	21.9 ± 8.6	5.7 ± 4.1	0.000
Number of seasons with no voles trapped[b]	23	43.0 ± 3.6	55.6 ± 2.9	62.2 ± 1.7	63.5 ± 1.3	0.000
Seasons with no voles trapped 1971–1979	7	7.7 ± 1.4	12.1 ± 1.4	15.1 ± 1.6	15.6 ± 1.0	0.000
Seasons with no voles trapped 1980–1989	3	9.3 ± 1.8	14.7 ± 2.6	17.9 ± 1.1	19.0 ± 0	0.000
Seasons with no voles trapped 1990–2003	12	25.1 ± 3.3	27.9 ± 0.3	28.0 ± 0	28.0 ± 0	0.000
Year of extinction (median)	Not extinct	1995	1987	1981	1974[c]	Not tested

[a] Occupancy means ≥1 individual trapped.

[b] Parameters used in the cluster analysis.

[c] As 4 of the plots in cluster group 5 where extinct already in 1971 they were excluded when calculating year of extinction.

comparable cyclic stage in 2002; cyclic stage judged according to Hörnfeldt (1994, 2004). However, 1–2 of the sampling plots, but mainly Ekträskkludden (no. 11 in Figure 2a) occasionally still yield a few *C. rufocanus* specimen, as in the latest still ongoing cycle starting in 2003 (Hörnfeldt 2005 and unpublished data).

There was a clear division between in land (western) and coastal (eastern) sites with generally higher abundances in the inland (Figure 2a and 2b; see also Figures 3 and 4). Cluster analysis revealed two clear clusters, C1 and C2, of high quality. These were characterised by high vole occupancy both in spring and fall, high cumulated and mean density indices, high number of seasons with vole occupancy before local extinction, and a low number of seasons with no voles trapped (Table 1). C3 was of intermediate quality, while C4 and C5 were low quality clusters with low cumulated density indices and persistence (Table 1). Inland areas had more high-quality and intermediate quality time-series (C1–C3) than coastal areas (Appendix Table A4). Only 10% of the time-series in inland areas yielded no voles or only voles in fall compared with as many as 55% of the coastal areas, suggesting that either coastal plots comprised more sink habitats (sensu Pulliam 1988) or that they were located outside the *C. rufocanus* distribution range (see Discussion). Also, declines started earlier and persistence was lower in coastal compared with inland areas in both low and high quality habitats. Persistence was generally higher and densities appeared higher in high than in low quality habitats in inland areas (Figures 3 and 4).

Local habitat destruction, by clear-cutting, on the 1-ha sampling plot as such was not conclusively associated with the local declines, since 63% of the clear-cut ha-plots ($N = 18$) in inland and coastal areas became clear-cuts after and only 37% of these ha-plots became clear-cuts before the major decline starting in the 1980s. Plots unaffected by clear-cutting also showed local declines (Figure 2a, b). However, trapping results indicated that the clear-cuts on the ha-plots were almost completely avoided and rarely used by reproductive males and females in spring as well as in fall (Christensen and Hörnfeldt in press).

As vole densities in the coastal area were rather low, and this area had no plots belonging to the high quality cluster group (see above), we restricted the analysis of dependence of local cumulated density of *C. rufocanus* (CRCD) on local habitat and landscape habitat parameters to the 29 sampling plots in the inland area. In a stepwise multiple regression, LHP together with two habitat variables at the landscape level explained 56% of the CRCD variation among sites and hence local time-series (Table 2). The relative contribution was 31% and positive for the LHP index, 16% and negative for clear-cut connectivity (sensu McGarigal and Marks 1995; connectance index, i.e. proportion of clear-cut patches within ≤ 200 m from another clear-cut) and 9% and negative for distance among xeric-mesic mires in the surrounding landscape. These three independent variables showed low (<0.31) and non-significant inter-correlations. As CRCD was correlated with several other independent variables (range of r: -0.56 to 0.53), in addition to LHP, we also tested some alternative models. We did this by letting each of the next highest correlated variables (-0.56, 0.53 and -0.45) enter the multiple regression in the first step by suppressing the other "candidates". However, the alternative models explained 16–42% less of the CRCD variation than the adopted model did. The predictor variables in the adopted model were weakly to moderately correlated with other predictor variables in Appendix Table A3. Thus, we considered any masking effects of the selected variables on correlated variables left out of the model to be of minor importance. LHP and distance among xeric-mesic mires were strongest correlated with variable 2, among the other variables in Appendix Table A3 ($r = 0.53$ and -0.53, respectively). Clear-cut connectivity was correlated with several other landscape variables, but strongest correalted ($r = 0.74$) with the related clear-cut variable 8 in Appendix Table A3.

Discussion

C. rufocanus ranges from Japan through Siberia to its western limits in Fennoscandia (Kaneko et al. 1998). In Sweden *C. rufocanus* is distributed throughout the mountain region and into the boreal zone, and according to the distribution map by Hansson (1974), our study area lies at the border of the species' distribution range in the boreal zone; see also Ecke et al. (in press). Species at the edge of their distribution range are generally more vulnerable to habitat changes than in centre of the range as, at the edge, their most suitable habitat is more patchily distributed and animals then depend on continuous immigration from larger source areas for persistence (Angelstam

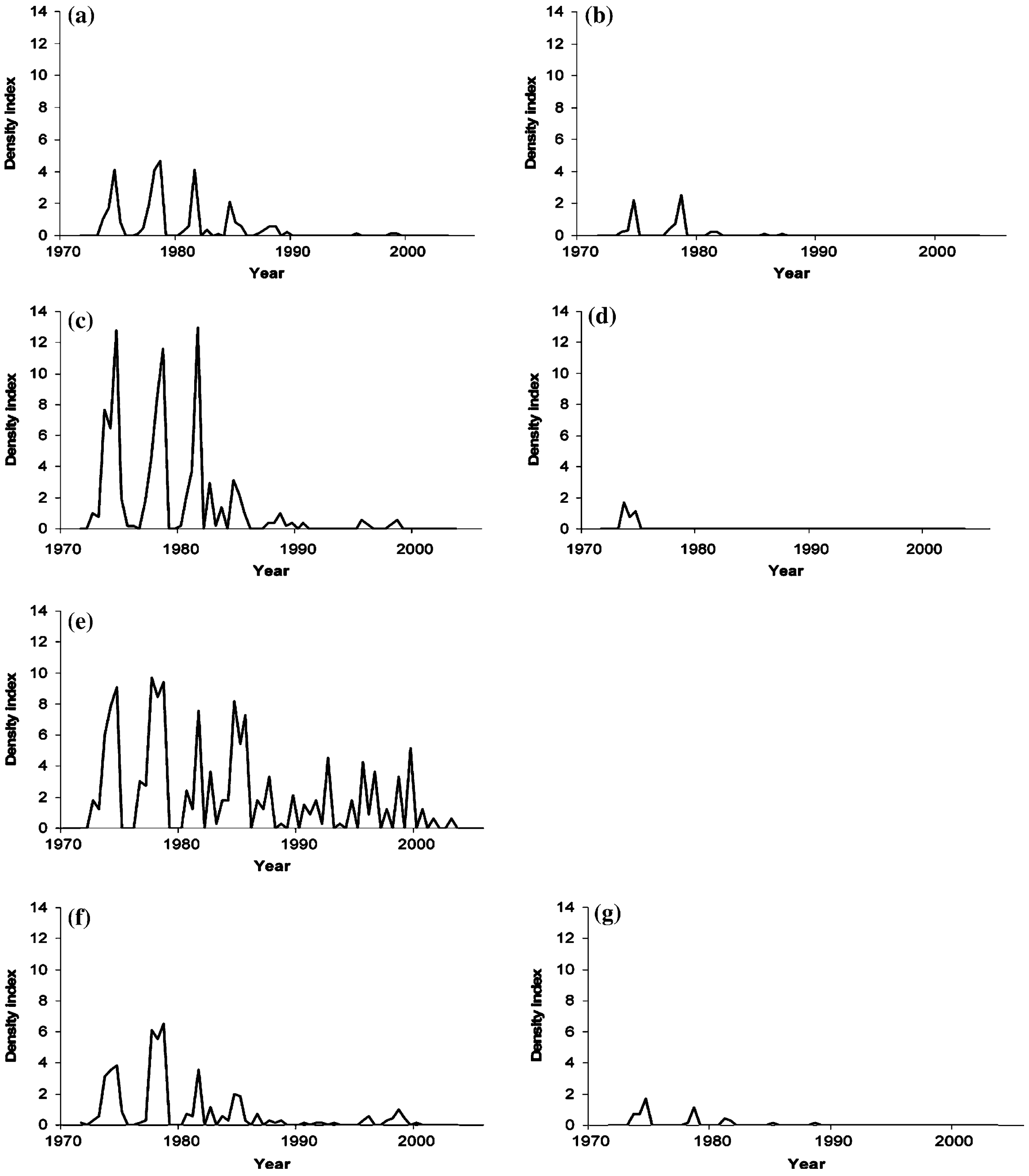

Figure 3. Average *Clethrionomys rufocanus* density indices, expressed as number of individuals trapped per 100 trap-nights, in spring and fall from fall 1971–2003 in inland (left) and coastland (right) high quality habitats (sensu Christensen and Hörnfeldt in press): (a–b) dry, (c–d) moist, (e) wet/hydric dwarf-shrub type forests, and (f–g) forest/swamp complex rich with dwarf-shrubs.

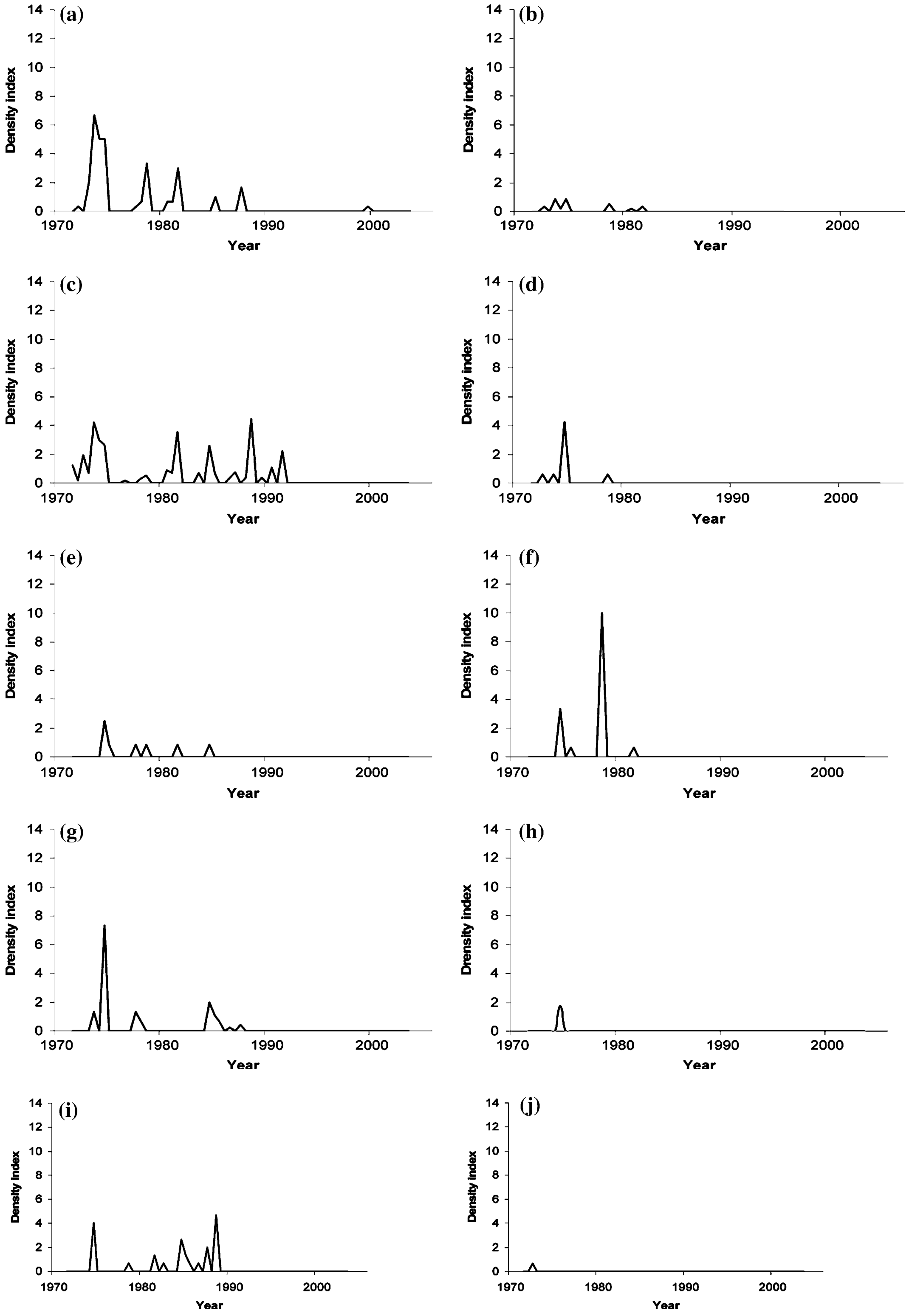

Figure 4. Average *Clethrionomys rufocanus* density indices, expressed as number of individuals trapped per 100 trap-nights, in spring and fall from fall 1971–2003 in inland (left) and coastland (right) low quality habitats (sensu Christensen and Hörnfeldt in press): (a–b) mesic *Dryopteris*, (c–d) *Myrtillus*, (e–f) xeric dwarf-shrub type forests, (g–h) dry, and (i–j) moist dwarf-shrub type clear-cuts.

Table 2. Regression coefficients for statistically significant ($p < 0.05$) independent variables in a multiple regression model ($p = 0.000$) of cumulated density indices (CRCD) for 29 local western (inland) time-series of *C. rufocanus* trapped on permanent 1-ha sampling-plots in 1971–2003.

Constant	Statistics	Independent variables			
		Preference index for local habitat	Connectivity among clear-cut areas	Distance among xeric-mesic mires	Adjusted R^2
9.706	Regression coefficient	0.454	−0.347	−0.343	–
	t-value	3.466	−2.712	−2.557	–
	Entry order	1	2	3	–
	Relative contribution	0.31	0.16	0.09	0.56

et al. 1987). The grey-sided vole is a habitat specialist that prefers pine boulder terrains (Siivonen 1968), dry to moist forests with dwarf-shrubs, and forest/swamp complexes (Ims 1987; Christensen and Hörnfeldt in press). In a study of habitat preferences based on data collected prior to the main population decline, we trapped no reproductive *C. rufocanus* females and only a few reproductive males in clear-cuts in spring close to the start of the reproductive season, thus suggesting that clear-cuts were avoided (Christensen and Hörnfeldt in press). Consequently we considered clear-cuts as sink habitats (sensu Pulliam 1988). Thus, for a habitat specialist (at the border of its distribution range) like *C. rufocanus* that avoids clear-cuts, it is reasonable to predict that habitat fragmentation resulting in increased occurrence of clear-cut areas will have negative effects on average abundance. Such negative effects may arise from both the removal of suitable habitat, i.e. habitat loss (Andrén 1994, 1996), and from true fragmentation leading to increased occurrence of edge zones and increased predation (Wilcove 1985; Andrén and Angelstam 1988; Andrén 1992), thereby contributing to decreased colonisation of preferred habitat patches by dispersing voles (cf. Andreassen and Ims 1998). In the long run, extensive habitat fragmentation will affect population viability and lead to extinction (Lande 1987; Andrén 1994, 1996).

There was much variation among sampling plots in densities and timing of the decline of *C. rufocanus*, ending up with local extinctions at different times (Figure 2a, b; Table 1), which in itself suggests that conditions such as local habitat or surrounding landscape composition/patterns may be involved in causing the observed patterns. However, local habitat destruction by clear-cutting on the individual 1-ha plots as such was not conclusively connected to the local declines, as clear-cutting occurred as much before the actual decline as after, and plots that were not affected by clear-cutting also showed local declines (Figure 2a, b). This suggested that the important habitat changes might be occurring in the surrounding landscape matrix, which would then influence the dynamics on the 1-ha plots. This was supported by the multiple linear regression showing that cumulated densities on the local 1-ha plots were explained by a combination of local habitat preference (LHP) and matrix characteristics. Three variables, LHP together with two landscape variables, explained 56% of the CRCD variation among sites (Table 2), and hence of the variation in densities and dynamics on the individual sampling plots in the inland area (Figure 2a). The positive importance of high quality habitats at the local scale (mainly some types of forest or forest/swamp complex rich with dwarf-shrubs; see above and Appendix Table A1) was supported by the correlation of the LHP-index with the CRCD explaining 31% of its variation (Table 2). Also, *C. rufocanus* generally appeared to have a higher persistence and higher densities in high quality than in low quality habitats (Figures 3 and 4). Among the landscape variables, distance among xeric-mesic mires (either fens or bogs and usually with grasses, sedges, herbs and/or dwarf-shrubs) was negatively correlated with and explained 9% of the CRCD site variation (Table 2). This relationship implied a positive effect on CRCD when xeric-mesic mires were distributed close to each other. Unfortunately, we have not yet been able to derive the same habitat classification from satellite images at the landscape level as previously adopted for studying habitat selection and preference at the sampling plot scale. However, the importance of proximity among xeric-mesic mires at the landscape scale is supporting earlier findings on habitat selection at the local scale, where forest/swamp complexes rich in dwarf-shrubs, in addition to forests of dry, moist or wet/hydric dwarf-shrub type (see Arnborg 1990 for forest type definitions), belong to the habitats preferred by *C. rufocanus* (Ims 1987; Christensen and Hörnfeldt in press). The connectivity of clear-cut areas in the surrounding landscape was negatively correlated with and explained 16% of the CRCD variation (Table 2), implying that clear-cuts negatively affect densities of grey-sided voles. It is evident that clear-cutting of old-growth forest has been intense at the regional level during the 20th century and especially so in the 1970s (Östlund et al. 1997). The connectivity of clear-cut areas in the landscape is probably the temporally most variable of the variables included in the multiple regression model. This result really suggests that habitat destruction might be involved in the long-term decline of *C. rufocanus*. The negative effect of habitat destruction was also suggested in a previous study (Ecke et al. in press), finding that low cumulated *C. rufocanus* densities were associated with a high amount (percentage area) and connectivity of clear-cuts and also with a high fragmentation of old-growth pine forest in the surrounding landscape.

Our study is the first one attempting to simultaneously consider influence of both local and landscape habitat properties on the long-term decline in density of a truly cyclic vole population (sensu Hörnfeldt 1994, 2004). The results in this study were in line with the habitat fragmentation hypothesis (sensu Hörnfeldt 2004), but the hypothesis needs further evaluation, also with respect to the possible mechanisms (cf. Ecke et al. in press). Most important is to establish time-series data for important landscape variables that are not currently available (see also Ecke et al. in press), to explore whether different timing of the declines of *C. rufocanus* on individual plots can be linked to local processes of habitat changes at the levels of the plots and their surrounding landscape matrix. Although the habitat fragmentation hypothesis received support here, it is clear that habitat fragmentation cannot be the only and major cause behind the long-term vole decline (Hörnfeldt 2004). This is especially true in some declining northern vole populations in areas where no forest cutting occurs in the Fennoscandian mountains (Hanski and Henttonen 1996; Hansen et al. 1999). Since decreased wintering success has been identified as the most important component in the long-term decline of *C. rufocanus*, and of its sympatric species *C. glareolus* and *Microtus agrestis* as well, it is reasonable to assume that a change in the winter climate is the most important factor behind the long-term decline in vole densities in boreal Sweden (Hörnfeldt 2004).

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Appendix A1. Habitat composition in the early 1970s of individual 1-ha plots in the inland, western part of the study area, and preferences for local habitat by *Clethrionomys rufocanus* females (according to data in Christensen and Hörnfeldt (in press); see Methods for details).

Sequence number of individual 1-ha-plots	Habitat																
	Anthro-pogenic	Forest									Clear-cut			Mire			
	Farmland and roadsides	Xeric dwarf-shrub	Mesic dwarf-shrub	Dry dwarf-shrub	Myrtillus	Moist dwarf-shrub	Wet/hydric dwarf-shrub	Wet Dryopteris dwarf-shrub	Mesic Dryopteris dwarf-shrub	Mesic herb dwarf-shrub	Dry dwarf-shrub	Myrtillus	Moist dwarf-shrub	Normal dwarf-shrub	Forest/swamp complex rich with dwarf-shrubs	Open poor swamp complex	Local habitat preference index
1				100													0.83
2									100								0.77
3												100					0
4						100											2.24
5		80													20		0.28
6											100						0
7							20	80									0.34
8				100													0.83
9				30											70		1.23
10				30		50									20		1.65
11							100										1.69
12				20											80		1.29
13				10											90		1.34
14				70											30		1.00
15				80						20							0.66
16				100													0.83
17					80	20											0.69
18															100		1.40
19						100											2.24
20				100													0.83
21							100										1.69
22					100												0.69
23									100								0.77
24													100				0
25					100												0.69
26					100												0.69
27				30		70											1.81
28				30											70		1.23
29				100													0.83

Sequence number refers to corresponding number in Figure 2a. Numbers in the habitat columns refer to % of that habitat within individual 1-ha-plots. (Note that clear-cutting has occurred in some sites and succession has progressively converted some early clear-cuts into forests (see Figure 2a, for clear-cutting information)).

Appendix A2. Habitat composition in the early 1970s of individual 1-ha plots in the coastal, eastern part of the study area, and preferences for local habitat by *Clethrionomys rufocanus* females (according to data in Christensen and Hörnfeldt (in press); see Methods for details).

Sequence number of individual 1-ha-plots	Habitat																
	Anthro-pogenic	Forest									Clear-cut				Mire		
	Farmland and roadsides	Xeric dwarf-shrub	Mesic dwarf-shrub	Dry dwarf-shrub	Myrtillus	Moist dwarf-shrub	Wet/hydric dwarf-shrub	Wet Dryopteris dwarf-shrub	Mesic Dryopteris/ dwarf-shrub	Mesic herb dwarf-shrub	Dry dwarf-shrub	Myrtillus	Moist dwarf-shrub	Normal dwarf-shrub	Forest/swamp complex rich with dwarf-shrubs	Open poor swamp complex	Local habitat preference index
30											100						0
31															100		1.40
32									100								0.77
33															100		1.40
34						100											2.24
35						100											2.24
36				100													0.83
37															100		1.40
38									100								0.77
39	100																0 [a]
40															100		1.40
41				30		70											1.82
42				100													0.83
43				80											20		0.94
44									100								0.77
45									100								0.77
46				90	10												0.82
47				100													0.83
48				60		40											1.39
49													100				0
50					60	40											1.31
51			100														0[a]
52											90				10		0.14
53				100													0.83
54				50											50		1.12
55	100																0[a]
56														100			0[a]
57																100	0[a]
58		100															0

Sequence number refers to corresponding number in Figure 2b.

Numbers in habitat columns refer to % of that habitat within individual 1-ha-plots. (Note that clear-cutting has occurred in some sites and succession has progressively converted some early clear-cuts into forests (see Figure 2b, for clear-cutting information)).

[a] As these habitats only were represented in the coastal area, calculations were based on unpublished coastal data for expected and observed numbers of trapped voles.

Appendix A3. Landscape parameters (according to McGarigal and Marks 1995, except for standing volume) that were previously found to differ significantly among low and high density sites (based on the cumulated densities of *Clethrionomys rufocanus* in spring 1980–99 on the 1-ha sampling plots), and derived from 2.5×2.5 km^2 areas surrounding individual 1-ha sampling plots ($n = 22$) in inland areas (for details, see Ecke et al. in press).

Landscape parameters	Sign of relationship
1. Simpson's diversity index of elevation classes	–
2. Simpson's diversity index of different cover classes of exposed cobbles	+
3. Percentage area of landscape with low content of exposed cobbles on moraine soils	–
4. Core percentage area (at least 200 m from edge) of landscape with low content of exposed cobbles on moraine soils	–
5. Fragmentation index of landscape with low content of exposed cobbles on moraine soils	+
6. Intermixing of areas with a low content of exposed cobbles on non-moraine soils among other cover classes of exposed cobbles	+
7. Intermixing of peat deposits among other land use types	+
8. Percentage area of clear-cuts in the landscape	–
9. Core percentage area (at least 200 m from edge) of clear-cuts in the landscape	–
10. Fragmentation index of clear-cuts	+
11. Connectance index (threshold distance 200 m) of clear-cuts	–[a]
12. Euclidean nearest neighbour distance among water systems	–
13. Euclidean nearest neighbour distance among xeric-mesic mires[b]	–[a]
14. Intermixing of xeric-mesic mires[b] among other land use types	+
15. Intermixing of broad-leaved forest among other land use types	+
16. Intermixing of spruce forest among other land use types	+
17. Connectance index of old-growth mixed forest	–
18. Fragmentation index of old-growth pine forest	–
19. Standing volume (m^3/ha) of non-birch broadleaved trees	–
20. Patch richness of pine productivity class	+

[a] Significant landscape parameters in a multiple regression of local density on individual 1- ha sampling plots in relation to local habitat preference and surrounding landscape parameters (see text).

[b] Either fens or bogs and usually with grass, sedges, herbs and/or dwarf-shrubs.

Appendix A4. Number of sampling plots in different cluster-groups in inland and coastal areas.

Cluster group	No. (%) of sampling-plots		
	Inland	Coastal	Total
1	1 (100)	0 (0)	1
2	7 (100)	0 (0)	7
3	13 (81)	3 (19)	16
4	6 (46)	7 (54)	13
5	2 (10)	19 (90)	21

Proportions in different cluster groups differed significantly between inland and coastal areas ($\chi^2_4 = 28.1$, $p = 0.000$).

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