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Can landscape properties predict occurrence of grey-sided voles?

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Abstract There has been a long-term decline in spring and fall numbers of *Clethrionomys rufocanus* in boreal Sweden in 1971–2005. Previous studies on permanent sampling plots in the centre of 2.5 × 2.5 km landscapes suggested that habitat fragmentation (sensu destruction) could have contributed to the decline. Therefore, we tested these findings in a field study and compared trapping results on the central sampling plots of landscapes with a low degree of fragmentation (LDF) and of "hot spot" type with trapping results in managed forest landscapes with a high degree of fragmentation (HDF). We predicted that *C. rufocanus* would be more common on the LDF plots. We used our permanent plots supplemented with a new sample of plots, mainly of the rare LDF type, inside or just outside the long-term study area. Very few voles were trapped on both plot types, and no difference was found. However, a subsequent pilot study with trapping in a national park with large areas of pristine, unfragmented forest yielded more voles than in the managed, more fragmented, areas. Consequently, the initial field study data and some other recent data were also re-analysed from a "local patch quality" perspective. This alternative approach revealed the positive importance of large focal patches of forest >60 years old and their content of old-growth (pine) forest (>100 years). Interestingly, at the landscape level, the frequency distribution of patches of forest >60 years old, old-growth (>100 years), and especially of old-growth pine forest (>100 years), relative to the properties of plots with *C. rufocanus*, suggested that there are few forest patches left that are suitable for *C. rufocanus*. Our current results suggest that habitat fragmentation cannot be excluded as a contributing cause to the long-term decline of *C. rufocanus* in boreal Sweden.

Keywords Grey-sided vole · Habitat fragmentation hypothesis · Long-term decline · Managed forest landscape · Old-growth forest · Pristine forest landscape

Introduction

Long-term declines of cyclic vole populations have been observed at several localities in Fennoscandia during recent years (e.g., Hörnfeldt 1991, 1994, 1998, 2004; Hanski and Henttonen 1996; Hansen et al. 1999; Hansson 1999; Henttonen 2000) but similar changes in the dynamics have also been observed elsewhere in Europe and on Hokkaido in Japan (Saitoh and Nakatsu 1997; Bierman et al. 2006; Saitoh et al. 2006; Ims et al. 2008). In boreal Sweden vole numbers started to decline markedly in the early 1980s and have been revealed as a drop in spring densities for all predominant species, viz. the bank vole (*Clethrionomys glareolus*), grey-sided vole (*C. rufocanus*), and field vole (*Microtus agrestis*). This was accompanied by a gradually

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increased frequency and severity of winter declines of all species (Hörnfeldt 2004). Changes in the overwinter dynamics are a more or less common, basic feature also in most of the other above studies reporting temporal changes in vole dynamics. This indicates that there may be a common underlying factor, a likely candidate being weather and climate changes related to global warming (Hörnfeldt 2004; Bierman et al. 2006; Ims et al. 2008). The common factor in boreal Sweden has been suggested to be a warmer winter climate leading to less stable winters with adverse effects on voles, e.g., by reduction of the period with protective snow cover (Hörnfeldt 2004). The decline has been especially pronounced in *C. rufocanus*, which also shows much lower autumn densities. This has now brought the population to <5% of its highest density in the early 1970s and apparently to local extinctions on most of the permanent sampling plots in the early 2000s (Hörnfeldt 1998, 2004; Hörnfeldt et al. 2006). Understanding the causes of the decline of this and other vole species is important, as the decline has potentially far-reaching consequences for other organisms. Above all, several predators are also likely to decrease, as has recently been reported for Tengmalm's owl (*Aegolius funereus*) (Hörnfeldt 2004; Hörnfeldt et al. 2005; see also Ims et al. 2008).

The extreme decline, also in autumn, of *C. rufocanus* indicates some additional disturbance to this species. As local extinctions have not occurred simultaneously, habitat fragmentation has been suggested as a contributing cause to the decline of this species (Hörnfeldt 1998, 2004; Hörnfeldt et al. 2006). Habitat fragmentation (sensu destruction; Forman 1995; Hanski 1999) is a process including habitat loss, true fragmentation (resulting in decreased patch size and increased isolation of patches) and habitat degradation (Harris 1984; Andrén 1994, 1996; Hanski 1999; Fahrig 2003). Several other hypotheses have also been suggested and were reviewed by Hörnfeldt (2004). We previously tested the "destructive sampling hypothesis" and refuted it, as trapping results did not differ between permanent long-term trapping plots and previously untrapped plots (Christensen and Hörnfeldt 2003). In a series of papers we are currently focussing on exploring whether habitat destruction of forests can partly explain the decline of *C. rufocanus*. Ecke et al. (2006) found that cumulated spring density indices in 1980–1999 on the permanent sampling plots in the centre of 2.5 × 2.5 km landscapes were negatively related to fragmentation of old-growth pine forest and to occurrence of clear-cuts. Densities were higher in forest landscapes with a low degree of fragmentation (LDF) than in landscapes with a high degree of fragmentation (HDF). In northern Sweden, forestry has changed the landscape structure towards a decreased amount of old-growth pine forest and increased clear-cut areas (Östlund et al. 1997). This observed change in landscape structure and our previous results suggested that habitat destruction processes should be considered as possibly contributing to the decline of *C. rufocanus* in boreal Sweden.

This study was done in three successive steps. First, we carried out a field study aiming to test the above findings in Ecke et al. (2006). We predicted that if the sample of permanent LDFs and HDFs was supplemented with a new sample of mainly LDFs, LDF central sampling plots should yield *C. rufocanus* more frequently than plots in the centre of the temporary and permanent HDFs. However, we found few voles in both plot types. Second, in a subsequent pilot study, we therefore sampled a pristine forest landscape, characterized by a single large patch of forest >60 years old that also had a high proportion of old-growth forest (>100 years); this yielded more *C. rufocanus* individuals with much less effort. Third, and as a consequence, we re-analysed data from the initial field study and from temporary and permanent plots within the long-term study area. In this re-analysis we focussed on the importance of the focal forest patch instead of the structure of the surrounding landscape. Re-analysing data suggested that the occurrence of *C. rufocanus* was positively related to focal forest patch size and quality.

Methods

Study area

Long-term monitoring of cyclic vole populations in northern Sweden has been carried out by snap-trapping every spring and autumn since autumn 1971 on permanent sampling plots, as part of the ongoing national environmental monitoring programme (NEMP) (e.g., Hörnfeldt 1978, 1994, 2004, 2007). Monitoring is performed in a 100 × 100 km large area selected from the Swedish National Grid (≈64°N, 20°E; Fig. 1, see also Fig. 1 in Hörnfeldt 1994), and belongs to the middle and northern boreal zone (Ahti et al. 1968), which is dominated by a managed forest landscape. Sampling is carried out in 16 subareas of 5 × 5 km with clusters of (usually) four 1-ha sampling plots (Fig. 1 and Fig. 1 in Hörnfeldt 1994), so that each 1-ha plot is placed in the centre of a unique 2.5 × 2.5 km plot landscape.

C. rufocanus has declined tremendously in the study area, in spring as well as autumn, and has disappeared from most sampling plots (Hörnfeldt 2004; Hörnfeldt et al. 2006; Fig. 2).

In step 1 of this study, we used the permanent LDF and HDF plots in the western 100 × 50 km part of the long-term study area, as *C. rufocanus* has mainly been found there (Christensen and Hörnfeldt 2006), supplemented with temporary plots mainly in LDF landscapes within

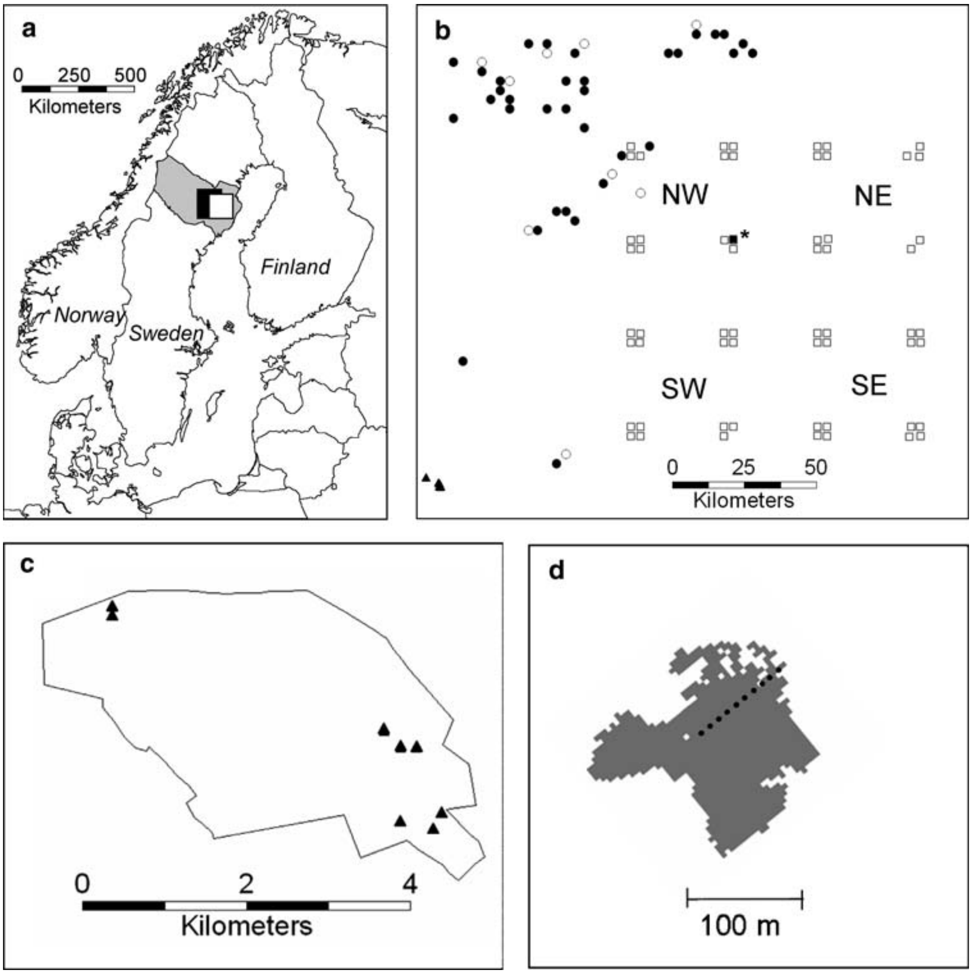

Fig. 1 **a** Location of the long-term study area (*white*) and the temporary field study area (*black*) in the county of Västerbotten (*grey*) in northern Sweden. **b**, **c** Schematic illustration of the study design. **b** The permanent long-term monitoring study area comprises 1-ha sampling plots marked by *squares*, normally in clusters of four plots (see also Fig. 1 in Hörnfeldt 1994). The field study comprised 1-ha sampling plots in the centre of 2.5 × 2.5 km forest landscapes with a low (LDF; *closed circles*) or high (HDF; *open circles*) degree of fragmentation; *C. rufocanus* was predicted to be more common on LDF than HDF plots (see Methods). The 72 1-ha sampling plots used in the field study were located in managed forest landscapes; 29 permanent plots in the western part of a long-term monitoring area (*squares*: one LDF, *closed* = Ekträskkludden, marked with an *asterisk*, and 28 HDF, *open*), and 43 temporary plots (*circles*: 34 LDF, *closed* and nine HDF, *open*). Eight additional plots in a subsequent pilot study were located in a pristine forest landscape (*closed triangles*) in Björnlandet National Park (**b**, lower left, and **c**). **d** Illustration of one focal habitat patch (*shaded*) intersecting the 1-ha sampling plot, represented by the ten stations (*filled circles*) along the diagonal trapping line

25 × 100 km to the north and 100 × 50 km to the west of the long-term study area (Fig. 1a). In step 2, we used a minor number of sampling plots within the pristine forest landscape of the 1,100 ha Björnlandet National Park, situated approx. 40 km south of the long-term study area (Fig. 1b, c). Finally, in step 3, we used data from the field study in step 1 supplemented with other recent data from temporary and permanent plots within the long-term study area.

Step 1, field study in managed forest landscapes

C. rufocanus is still regularly caught on one permanent sampling plot, the forested Ekträskkludden (Fig. 1b), among the 29 plots within the western 100 × 50 km part of the permanent study area (Hörnfeldt et al. 2006). This suggests that Ekträskkludden and its surroundings still have habitat properties suitable for the occurrence of *C. rufocanus* (Christensen and Hörnfeldt 2006; Ecke et al. 2006). Either local habitat or habitat properties of the surrounding landscape could be critical. However, Christensen and Hörnfeldt (2006) previously showed that even if the local habitat of the permanent sampling plots was preferred, this was not sufficient for *C. rufocanus* to occur there in the 1970s. Thus, we reasoned that *C. rufocanus* should occur on the central sampling plots in 2.5 × 2.5 km landscapes with properties similar to those of the "hot-spot" landscape around Ekträskkludden. Ecke et al. (2006) showed that, in

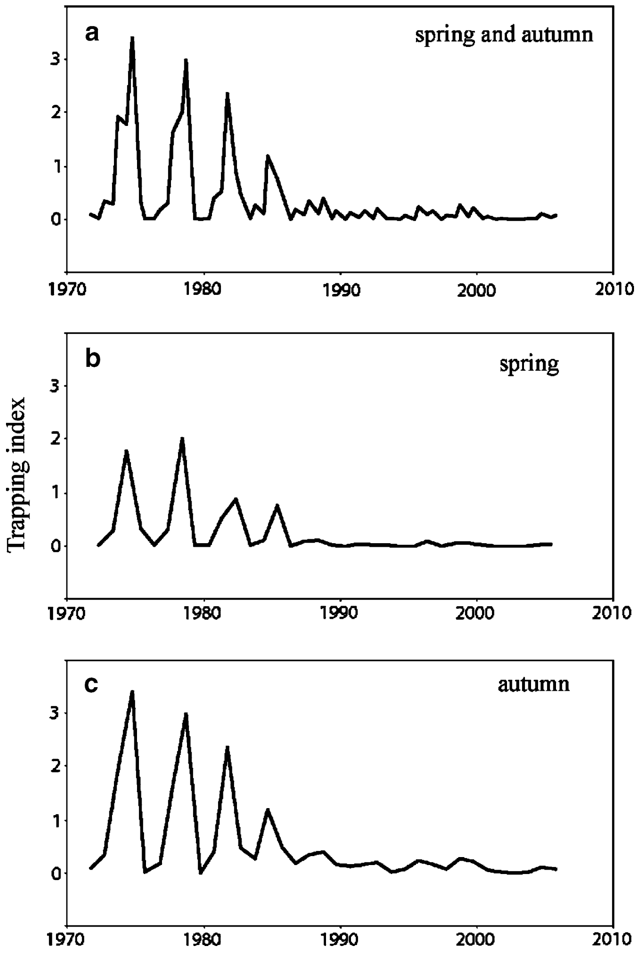

Fig. 2 Trapping indices (number of trapped individuals per 100 trap-nights) for *Clethrionomys rufocanus* in the long-term monitoring area (see Fig. 1b) in **a** spring and autumn, **b** spring, and **c** autumn, from autumn 1971 to 2005

the 2.5 × 2.5 km plot landscapes centred on the central permanent sampling plots, the degree of fragmentation of old-growth pine forest, and proportion of clear-cut area were important variables for explaining cumulated local densities of *C. rufocanus* in spring 1980–1999. Even if the long-term decline has made *C. rufocanus* rare, considering the frequency of occurrence of *C. rufocanus* on the permanent sampling plots (1:29, i.e., approx. 3%), we would expect to find approximately 24 "hot-spot" plots with *C. rufocanus* among the total of 800 potential plot landscapes within the western part of our long-term study area. The likelihood of discovering hot spots would increase further by extending the area, provided that we also managed to define the correct habitat criteria for Ekträskkludden to be used as a selection tool.

LDF and HDF landscapes

Based on the findings by Ecke et al. (2006), we started searching for additional hot-spot landscapes similar to Ekträskkludden, by analysing the landscape properties of a total of 2,000 potential 2.5 × 2.5 km plot landscapes within the Swedish National Grid that belonged to the western part of the permanent study area and adjacent areas to the north and west (Fig. 1a, b). We classified the 2.5 × 2.5 km plot landscapes as representing either a lower (LDF) or higher degree of forest fragmentation (HDF) (Table 1). Note that the temporary LDF landscapes were defined to have higher habitat quality than that surrounding Ekträskkludden with respect to all selection criteria, as they contained less fragmented and more old-growth pine forest and also less clear-cut areas (Table 1). Other landscapes were defined as HDF landscapes, each differing in ≥1 of the three criteria from the LDFs (Table 1). Thus, this necessarily resulted in some overlap between the LDF and HDF groups, but the groups differed according to all three selection criteria ($P < 0.001$, two-sample *t* test). The proportion of old-growth pine forest was included as a complementary variable to the fragmentation index of old-growth pine forest (see general recommendation by MacGarigal and Marks 1995).

The values of the landscape variables were calculated from *k*NN data derived from satellite images from 1999/2000, in a manner similar to that explained by Ecke et al. (2006). The *k*NN data used were estimates of volumes for

Table 1 Criteria for categorizing temporary 2.5 × 2.5 km plot landscapes into LDF and HDF types in managed forest landscapes and number and properties of investigated plot landscapes for the centred permanent and temporary sampling plots

Landscape habitat properties (see Ecke et al. 2006)	Criteria	LDF temporary sampling set	HDF sampling sets	
	LDF	Temporary ($n = 34$)	Permanent ($n = 28$)	Temporary ($n = 9$)
Fragmentation index of old-growth pine forest (%)	≤55	40.2 ± 3.8	64.9 ± 12.8	54.5 ± 19.4
Proportion area old-growth pine forest (%)	≥10	18.7 ± 4.9	4.8 ± 4.1	9.9 ± 7.1
Proportion area clear-cut (%)	≤17	11.8 ± 3.0	23.5 ± 9.2	18.7 ± 9.6

Note that properties of the single permanent LDF plot landscape, around the "hot spot" Ekträskkludden, were used as cut-off values for the LDF landscapes. Other landscapes were defined as HDF landscapes and differed relative to LDF landscapes in ≥1 of the habitat properties. The overall LDF ($n = 35$) and HDF ($n = 37$) groups differed according to all the three landscape properties used as selection criteria ($P < 0.001$, two-sample *t* test) different tree species and of forest age. These data are based on a k-nearest neighbour interpolation algorithm (kNN) between a Landsat ETM+ scene and field data from the Swedish National Forest Inventory (e.g., Reese et al. 2003). Estimates of forest variables (resolution 25 m) were available for all forest land and forested wetland according to a 1:100,000 scale map produced by the Swedish Land Survey. ArcGIS 8.2 was used for the GIS analyses (ESRI 2002). Landscape variables were calculated from raster files using Fragstat 3.3 applying the 8-cell neighbour rule (MacGarigal and Marks 1995). The fragmentation index (synonymous to percentage of like adjacencies) of old-growth pine forest was calculated according to MacGarigal and Marks (1995):

$$\text{Fragmentation index} = \frac{g_{ii}}{\sum_{k=1}^{m} g_{ik}} \times 100,$$

where g_{ii} is the number of like adjacencies among pixels of old-growth pine forest and g_{ik} is the number of adjacencies among pixels of old-growth pine forest and other land-use types. However, we converted and used the converted index (100 − Fragmentation index) throughout, so that a low converted fragmentation index means low fragmentation and a high index means high fragmentation (Ecke et al. 2006). A converted fragmentation index <0.5 but >0 thus indicates habitat loss. An index >0.5 indicates breaking apart of habitat and thus corresponds to habitat fragmentation per se, in the sense referred to by Fahrig (2003). Since the resolution of 1 pixel (25 × 25 m) is not reliable enough to secure further interpretation of the data, for less common habitats (e.g., old-growth pine forest) we only considered patches of $\geq$4 pixels.

Within the western part of the permanent study area there was one central permanent sampling plot in an LDF landscape (Ekträskkludden) and 28 central permanent plots in HDF landscapes. As the LDF landscapes were in such short supply among the central permanent sampling plots, the screening procedure above mainly served to locate more LDF landscapes for comparison of *C. rufocanus* occurrence on the central plots in LDF and HDF landscapes. For logistic reasons, all temporary plots had to be reasonably accessible. Therefore, 34 temporary out of a total of 38 identified LDF landscapes were chosen for this study. In addition to the LDF landscapes, nine neighbouring and temporary HDF landscapes were chosen (Table 2). Comparing contemporary trapping results in samples of central plots in LDF and HDF landscapes is critical. This would test the prediction derived from Ecke et al. (2006) that *C. rufocanus* individuals would be more common on the central plots in LDF than in HDF landscapes.

Table 2 Number of central permanent and temporary sampling plots in managed forest landscapes with a high (HDF) and low degree of forest fragmentation (LDF) in the field study

Landscape fragmentation category	Sampling plots in:		
	Managed forest landscapes		Total
	Permanent	Temporary	
HDF	28	9	37
LDF	1	34	35
Total	29	43	72

The 1-ha sampling plots within temporary LDF and HDF landscapes

Usually, the temporary 1-ha sampling plots were placed at the centre of the 2.5 × 2.5 km plot landscape. We only moved the 1-ha sampling plot to the nearest forested position (trees at least 2 m high) within the Swedish National Grid if the central position was not forested, but for example had been clear-cut. To check for similarity of local habitat between LDF and HDF 1-ha plots, we compared the local habitat preference (LHP) index for all temporary and permanent plots. Necessary calculations were based on the findings by Christensen and Hörnfeldt (2006), who expressed indices as the ratio of observed to expected numbers of *C. rufocanus* individuals trapped in different habitats in the 1970s (see also Hörnfeldt et al. 2006). As expected from the sampling design, there was no difference in the average LHP index of central sampling plots between LDF ($n = 35$) and HDF ($n = 37$) landscapes (0.62 ± 0.58 vs. 0.83 ± 0.60; $P = 0.13$, two sample t test). Similarly, altitude did not differ between the central sampling plots of LDF (range 210–370, mean 269 m) and HDF (range 170–348, mean 259 m) landscapes ($P = 0.31$; two sample t test); a check for the western, permanent sampling plots ($n = 29$, mean ± SD: 255 ± 49 m; with the hot spot Ekträskkludden at 257 m) revealed no significant correlation between the cumulated *C. rufocanus* index in spring 1980–1999 (see also Ecke et al. 2006) and altitude ($r_s = -0.05$, NS).

Trappings

All trapping was carried out within a three-week period at the shift of September/October in autumn 2004. Since *C. glareolus*, *C. rufocanus* and *M. agrestis* had synchronous population density peaks in the mountains in both Ammarnäs (approx. 200 km to NW and Vålådalen/Ljungdalen (approx. 350 km to WSW) in autumn 2004 and also in the permanent study area (although with only approximately 1/300 of the densities in the mountains for *C. rufocanus*)

(Hörnfeldt 2007), it is very likely that vole populations were also in the peak phase on the temporary sampling plots in the current field study. Permanent sampling plots comprised 1 LDF and 28 HDF central plots, and temporary plots comprised 34 LDF and 9 HDF central plots (Table 2). Within both permanent and temporary 1-ha sampling plots, the traps were centred along the diagonal in ten trap stations at 10 m intervals (Fig. 1d) and five snap-traps per station. The traps were set for three consecutive nights, giving a total trapping effort of 150 trap-nights per sampling plot (see Hörnfeldt 1978, 1994, 2004 for further details). Trapping indices were calculated as number of voles trapped per 100 trap-nights, to illustrate the long-term decline of *C. rufocanus* in the long-term study area as seen in Fig. 2.

Table 3 Number of trapped *C. rufocanus* and number of central permanent and temporary sampling plots with and without voles in managed forest landscapes with a high (HDF) and low degree of forest fragmentation (LDF) in the field study (see Methods)

Landscape categories	No. of trapped *C. rufocanus*	No. of sampling plots	
		With *C. rufocanus* ($n = 3$)	Without *C. rufocanus* ($n = 69$)
Permanent			
HDF	4	1	27
LDF	5	1	0
Temporary			
HDF	0	0	9
LDF	1	1	33

Step 2, trapping in a pristine forest landscape

Because of very low and similar numbers of voles trapped in both LDF and HDF plots, we also trapped voles on eight additional temporary sampling plots in the 1,144 ha Björnlandet National Park (Fig. 1c). This park comprises 3% lakes, 10% mires, and 87% forests. Old-growth forest constitutes 33% and old-growth pine forest 10% of the park area. All sampling plots belonged to the same 1,932 ha forest patch ≥60 years, also extending outside the national park. The plots in Björnlandet were selected subjectively and did not conform to the LDF criteria above, but were mainly selected to increase the chance of catching *C. rufocanus*, i.e., the objective was to place most plots in habitats that were as high-quality as possible, based on the findings in Christensen and Hörnfeldt (2006). Trapping on these 1-ha sampling plots were also carried out at the shift of September/October in 2004 and as outlined above.

Step 3, re-analysis of the trapping data: dependence on forest patch size and quality

As the trapping in Björnlandet yielded several *C. rufocanus* individuals, we shifted the focus to the importance of the focal forest patch properties. Therefore, we re-analysed the habitat properties of sampling plots with and without voles (see "Results") in the field study of autumn 2004. In the re-analysis we focused on focal forest patch size and quality; a focal forest patch intersected the sampling plot (see Fig. 1d). Three such central sampling plots with voles were available and used; one temporary LDF, one permanent LDF, and one permanent HDF sampling plot (Table 3). Note that in the group of sampling plots without *C. rufocanus*, we only used the remaining, central permanent plots ($n = 27$), as we know their trapping history, and that all but one (96%) of these western plots had previously harboured *C. rufocanus* before this species successively disappeared from these (Hörnfeldt et al. 2006).

When re-analysing the dependence of *C. rufocanus* occurrence on habitat properties using the focal forest patch perspective, we did not adopt the previous quadratic landscape limitations. Thus, properties of the whole focal patch were analysed, i.e., also parts that exceeded the 2.5 × 2.5 km scale. We somewhat arbitrarily chose and analysed the importance of size of patches representing: "young" (>15 years, i.e., older than clear-cut and with trees >2 m) and "medium-aged" (>60 years) forest and their content of old growth (>100 years) forest, especially of pine.

Finally, we also re-analysed the data on the occurrence of *C. rufocanus* obtained in the most recent years (1999–2005) in the whole permanent study area from the focal patch perspective, also including data from a field study testing for any effect of "destructive sampling" in autumn 1999. That field study was based on comparing sets of the regularly distributed permanent ($n = 58$) and temporary ($n = 58$) plots in the same sixteen 5 × 5 km subareas, with temporary plots located in between the permanent plots and 1 km apart from these (see Fig. 1 in Christensen and Hörnfeldt 2003 for further details).

Results

Within 3 out of 72 permanent and temporary sampling plots, we caught a total of ten *C. rufocanus* individuals in the field study in managed LDF and HDF forest landscapes.

The proportion of central LDF plots with voles was no greater than that of HDF plots (Table 3; Fisher's exact test, one-sided, $df = 1$, $P = 0.479$). This led us to reject the initial hypothesis, which predicted voles would be more common on plots in LDF than HDF landscapes, as insufficient to explain the occurrence of *C. rufocanus*. However, we realized that we might have used inappropriate selection criteria when searching for new hot-spot areas, viz. by characterizing habitat properties of the 2.5 × 2.5 km plot landscapes. We decided to adopt the alternative "patch quality perspective" (see "Methods"). We therefore first carried out a pilot study trapping at additional sampling plots in the more pristine forest landscape of Björnlandet National Park. In Björnlandet National Park we trapped a total of 11 *C. rufocanus* individuals on four out of the eight plots there. This was as many voles as in the original field study, albeit with a less strict sampling design in Björnlandet. Our intuitive feeling from this was that it would be necessary to proceed and explore the dependence of *C. rufocanus* on patch quality more carefully.

The sampling plots in Björnlandet National Park, where most *C. rufocanus* were trapped, belonged to a considerably larger patch of forest >60 years old (1,932 ha; Fig. 3a) than the plots in the initial field study.

Also, the 1-ha sampling plots that yielded *C. rufocanus* in the field study (step 1) had a larger focal patch of forest >60 years old than plots that yielded no voles (Fig. 4b; see also Fig. 3a). Notably, the frequency distribution of patches of forest ≥60 years and ≥1 ha in the western part of the permanent study area showed that 75% of the patches were <10 ha in 1999/2000 at the landscape level and considerably smaller than those yielding voles (Fig. 3a).

The focal forest patches (>60 years) of the sampling plots that yielded *C. rufocanus* also contained both more old-growth forest (Fig. 4d) and old-growth pine forest (Fig. 4f) than those that yielded no voles during the field study. Overall, the frequency distribution of size of old-growth forest (≥100 years) patches showed that larger patch sizes were rare at the landscape level (Fig. 3b). Especially, there were few large patches of old-growth pine forest (≥100 years), and none of >11 ha (Fig. 3c). Including young focal forest, as in the patches of forest >15 years, revealed fewer clear differences between plots with and without voles (Fig. 4a, c, e), than the comparison of patches with forest >60 years did. Only the content of old-growth forest within patches of forest >15 years was higher on plots with voles (Fig. 4e).

On the permanent sampling plots in 1999–2005 and on additional sampling plots in a field study in the same subareas in 1999 (above; see Christensen and Hörnfeldt 2003 for details), we trapped *C. rufocanus* on four out of five plots (80%) in the subarea containing the Ekträskkludden sampling plot, while only on one out of the other 111 plots (<1%). Patch analysis showed that all five plots with voles belonged to the same >3 × 10^5 ha patch of forest >15 years old. This forest patch also contained four of the remaining 25 permanent plots in the western part of the permanent study area. Also, applying a 25 m buffer, the three best plots with voles (including Ekträskkludden) with 94% ($n = 49$) of the voles trapped in 1999–2005 belonged to the same approx. 270 ha patch of forest >60 years old. That patch contained >40 ha (15%) old-growth pine forest. Note also that the HDF landscape that yielded four *C. rufocanus* belonged to the same forest patch >60 years old as Ekträskkludden.

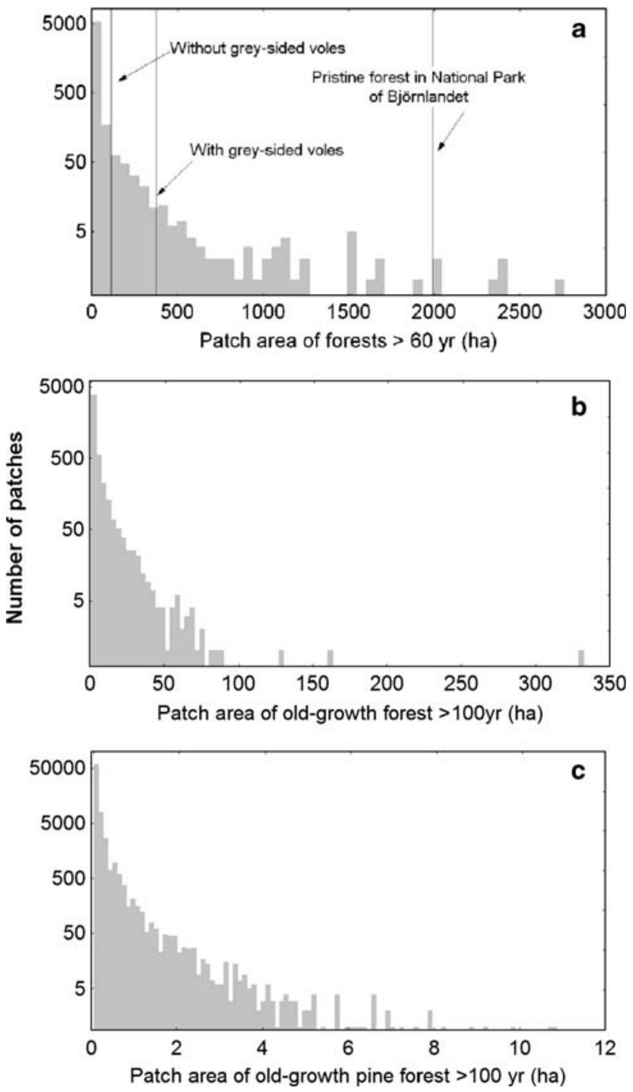

Fig. 3 Frequency distribution of patch sizes of **a** forest >60 years and ≥1 ha, of **b** old-growth forest >100 years, and of **c** old-growth pine forest >100 years, in all cases within the western 50 × 100 km part of the long-term environmental monitoring study area (cf. Fig. 1b). As a reference in **a** the mean area of the focal forest patches of sampling plots that yielded and did not yield *C. rufocanus* in the current field study are given, as is the size of the single forest patch within Björnlandet National Park that yielded most *C. rufocanus*

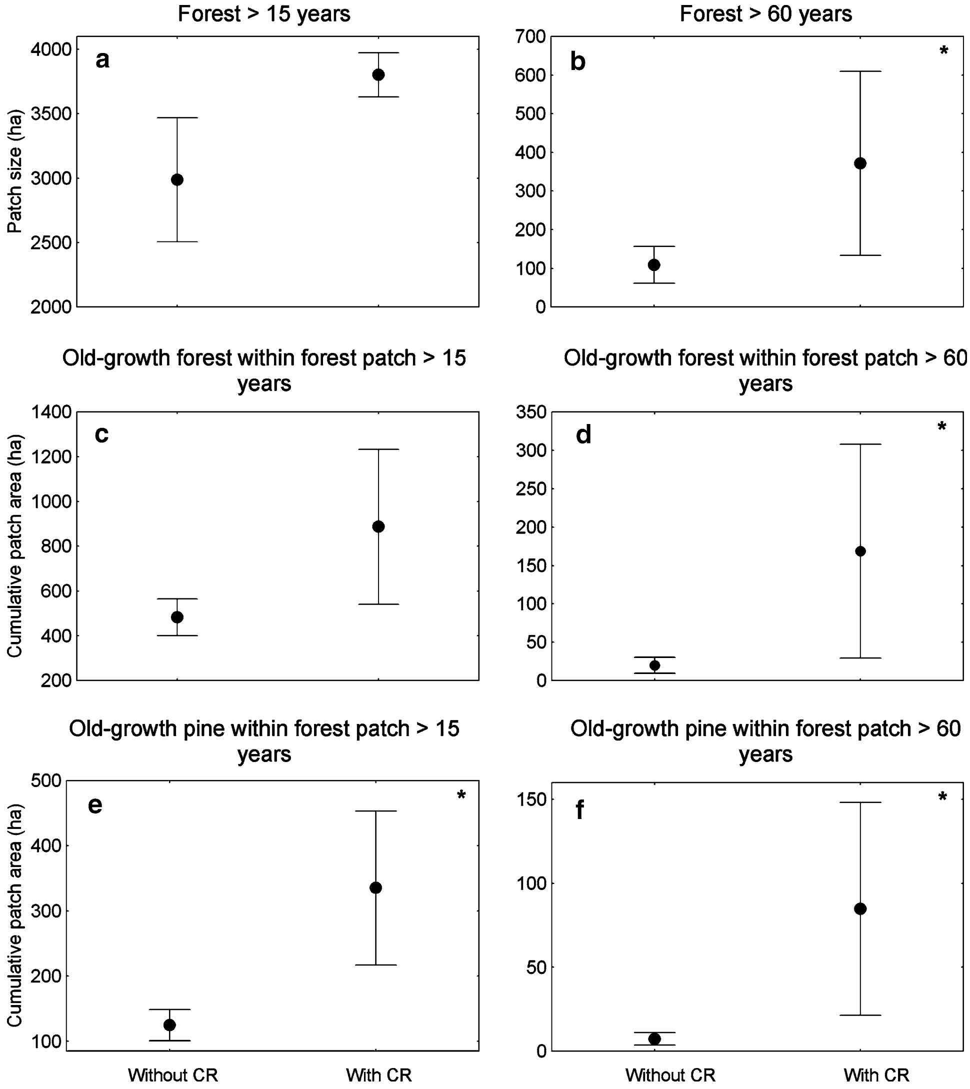

Fig. 4 Properties of focal forest patches (mean values ± 1 SE) intersecting the diagonal trapping line of 1-ha sampling plots (cf. Fig. 1d) where *C. rufocanus* were trapped (with CR, $n = 3$) and not trapped (without CR, $n = 27$); note that these data refer to permanent plots without *C. rufocanus* and permanent and temporary plots with *C. rufocanus* in the field study. **a** Patch size of forest >15 years old (i.e., with standing volume >25 m^3/ha), and **b** >60 years old. **c** Cumulative patch area of old-growth forest within the focal patch of forest >15 years, and **d** within the focal patch of forest >60 years. **e** Cumulative patch area of old-growth pine forest (>100 years) within the focal patch of forest >15 years, and **f** within the focal patch of forest >60 years. *Asterisks* denote significant differences ($P < 0.05$) between 1-ha sampling plots with and without *C. rufocanus* as tested with the Mann–Whitney *U* test

Discussion

The LDF landscape properties used for classification were insufficient for predicting the occurrence of *C. rufocanus* on the central plots. This was evident since there were few *C. rufocanus* individuals trapped on the central plots in the LDF landscapes, despite their assumed "hot spot" characteristics, and not even more than on the central plots in the HDF landscapes. However, this conclusion does not imply that *C. rufocanus* does not occur elsewhere in these landscapes. Elucidating this would have required a quite different approach from that we adopted for our aim (see below). The fact that several voles were fairly easily trapped in the subsequent pilot study in the pristine forest landscape of Björnlandet National Park, indicated that focal patch size could be an important characteristic that we had overlooked and not accounted for in the quadratic 2.5 × 2.5 landscape design of the initial field study. Thus, this motivated re-analysis of the data from the focal forest patch size and quality perspective.

Mean area of the focal patch of forest >60 years belonging to sampling plots with voles was larger (371 ha) than that for plots without voles (109 ha) in the field study. Further analyses showed that the focal forest patch of plots with *C. rufocanus* contained more old-growth and old-growth pine forest than plots without *C. rufocanus*. Thus, our results supported the importance of old-growth pine forest for occurrence of *C. rufocanus*, as was reported by Ecke et al. (2006).

In the permanent study area, the sampling plot Ekträskkludden is exceptional in the sense that it has yielded much higher numbers of *C. rufocanus* individuals, and that this species has shown higher persistence there than on the other sampling plots (Hörnfeldt et al. 2006). This "hot spot" has led us to assume that the key to understanding much of the decline of *C. rufocanus* could be found by comparing habitat properties of this sampling plot or its matrix with corresponding properties of other sampling plots.

The outstanding feature of Ekträskkludden and adjacent permanent and previously sampled temporary plots within the same 5 × 5 km subarea was emphasized by the fact that on four of these five (80%) sampling plots we trapped *C. rufocanus* in 1999–2005. In contrast, we only trapped *C. rufocanus* on one (<1%) of the remaining 111 plots outside this "hot spot" subarea. When re-analysing these trapping results from the patch perspective, the importance of focal forest patch size and quality was strengthened further, as the five plots with voles all belonged to the same patch of forest >15 years old. Furthermore, the three "best" plots of these yielded 94% of the total catch and belonged to the same patch of forest >60 years old that also contained >40 ha (15%) old-growth pine forest. Patch size analysis at the landscape level showed that there were few large patches of forest >60 years old in the western part of the long-term study area (Fig. 3a), and that there were even fewer large old-growth, especially old-growth pine forest patches (Fig. 3b, c), relative to the properties of plots with *C. rufocanus* (Fig. 4).

All the above lines of evidence, although partly based on small sample sizes, resulted from re-analysis of data from the field study and other recent trapping data in the long-term monitoring study area, and they point in the same direction. Together they suggest that focal forest patch size and quality are of major importance in determining occurrence and persistence of *C. rufocanus* in our study area.

Although, we cannot refute the hypothesis that the decline of *C. rufocanus* in boreal Sweden has partly been caused by destruction of forest habitat, we want to emphasize that this is not thought to be the main reason. And it is self-evident that it cannot be a cause at all in remote areas in the absence of logging, such as in Pallasjärvi and Kilpisjärvi in northern Finland, where *C. rufocanus* has still declined markedly (cf. Hanski and Henttonen 1996; Hansen et al. 1999; Henttonen 2000). On the contrary, the large similarities regarding the characteristics of the temporal changes of dynamics in sympatric vole species and different areas mainly refer to the winter dynamics with:

1. increased density dependence;
2. increased frequency of over winter declines; and
3. decreased delayed density dependence coinciding with a decline of spring densities and of the cyclic amplitude.

As also stated in the Introduction, these similarities altogether speak in favour of a common underlying factor in these cases (Hörnfeldt 2004; Bierman et al. 2006; Ims et al. 2008). This is accentuated further by the relatively similar timing of these events in different areas and by a recent review by Ims et al. (2008), showing that fading out of cycles has been observed not only in voles and their predators but also in forest grouse and Lepidoptera. The underlying factor suggested as being common to all these changes is the warmer weather/climate in recent years caused by global warming. In the cases of voles it is the warmer winter weather shortening the snow period and reducing the quality of the snow cover as protection to the voles that has been pointed out (Hörnfeldt 2004; Hörnfeldt et al. 2005; Bierman et al. 2006; Ims et al. 2008), although we agree with Ims et al. (2008) that this does not imply that the causal mechanisms need to be the same everywhere. The early and outstanding decline of *C. rufocanus* in boreal Sweden, being quite evident already in the early 1980s, may be related to the fact that in our study areas the species is at its distribution border (cf. Hansson 1974). Therefore the species is likely to be more sensitive to any kind of disturbance than other sympatric voles, and also than other *C. rufocanus* populations that are not so close to their distribution border (Hörnfeldt 1991, 1994, 2004). Negative effects from increased forestry, via habitat destruction, on population numbers of *C. rufocanus* could be reinforced by the negative effects of climate change, and vice versa.

Generally, increased patch size increases the probability of survival of species, populations, and individuals (MacArthur and Wilson 1967), and large patches outweigh the negative effects of long distances among patches (Harrison and Fahrig 1995). However, species respond differently to true habitat fragmentation depending on whether they are habitat specialists or generalists, or have high or low dispersal ability (Andrén 1996; Henein et al. 1998; Fahrig 2001; Franklin et al. 2002). The success of a species with a high dispersal ability in a pristine environment may be drastically reduced as true habitat fragmentation increases (Gibbs 1998; Fahrig 2001). However, such species may manage to persist by including several smaller patches in their home range when the landscape becomes fragmented into more and smaller patches. In contrast, poor dispersers are confined to and constrained by the current patch size, i.e., whether it is large enough or not for the species' survival and persistence (Ims et al. 1993). In our study area *C. rufocanus* is rarely found on clear-cuts and seems to avoid these (Christensen and Hörnfeldt 2006; Hörnfeldt et al. 2006), which suggests that an increased amount of clear-cuts makes it difficult for this species to disperse, and is likely to make it dependant on large forest patch sizes. In general, rare species show a positive relationship between population densities and patch size, and therefore it is particularly important to preserve and maintain large patches for enhancing survival and persistence of such species (Connor et al. 2000). In analogy with this, it is reasonable that this also holds true for strongly cyclic species such as the northern voles, which in the phase of low numbers are also very rare. Moreover, this may make them more vulnerable to habitat destruction than less fluctuating species.

Our re-analysis of the current field study data and other recent data from permanent and temporary sampling plots within the long-term monitoring area, and of current landscape structure from a patch perspective, are in line with the hypothesis by Hörnfeldt (2004) that habitat fragmentation (sensu destruction; Forman 1995; Hanski 1999) is a probable contributing cause to the current decline of *C. rufocanus* (Fig. 2). On the other hand, before this can be firmly concluded and before the relative role of habitat loss and true habitat fragmentation can be disentangled, as is desirable but rarely done according to Trzcinski et al. (1999) and Fahrig (2003), it is clear that more work has to be carried out (see below). Trzcinski et al. (1999) found habitat loss to be the by far most important factor affecting the distribution of birds, although we believe that this does not necessarily hold true for other less mobile species.

Our previous results suggested local extinction of *C. rufocanus* on most of our permanent sampling plots (Hörnfeldt et al. 2006). The current results on the importance of patch size and quality add to the evidence that populations in small isolated patches are most likely to go extinct (Hanski 1999). We hypothesize that a large forest patch, with large amounts of old-growth (pine) forest is important for the persistence of *C. rufocanus*. This could be tested by extended studies of pristine landscapes such as national parks and nature reserves of different size and forest composition, focussing on the dependence of occurrence and density of *C. rufocanus* on patch size and forest composition and on matrix composition. Finally, it is important to reconstruct time-series over local landscape changes, to make the critical evaluation whether such changes are temporally associated with local declines and extinctions of *C. rufocanus* on the current long-term monitoring sampling plots, and whether habitat loss, true habitat fragmentation, or both have been influential.

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