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Cyclic small rodents in boreal forests and the effects of even-aged forest management: Patterns and predictions from a long-term study in southeastern Norway

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ABSTRACT

Small mammals, especially microtine rodents, play an important role in the dynamics of boreal forest ecosystems. Even-aged forest management, in which old, semi-natural forests are converted to clear-cuts and culturally regenerated stands, is expected to have pronounced impact on the abundance and composition of this group of animals due to changes in the understory vegetation. During a 39 year-period we sampled autumn numbers of small mammals in uncut, semi-natural old forest and in recent clearcuts, supplemented by a 7-year sample from middle-aged plantations. Field voles *Microtus agrestis* were almost exclusively trapped in clearcuts. Bank voles *Myodes glareolus* dominated in the old forest, but reached equal or higher densities than field voles in clearcuts. Here, their combined abundance exceeded that of bank voles in old forest. Some years, wood lemmings *Myopus schisticolor* contributed significantly to vole abundance in old forest. Other rodents *Apodemus* spp. were rarely captured, mainly in clearcuts, and shrews *Sorex* spp. numbered < 15 percent of the total number of captured animals. Throughout the whole period we discerned 11 vole cycles, with highest peaks in bank voles in old forest. After high numbers during the 1980s, abundances of all species fell markedly during the 1990s, most distinctively in clearcuts, where the field vole almost totally disappeared. From the late 2000s, abundances of all species returned to pre-1990 levels and beyond. In the early and late periods, combined vole numbers were 26% higher in clearcuts compared to old forest, whereas the opposite was true in the middle period. In middle-aged plantations, bank voles numbered only one third of what it was in clearcuts and old forest, and other voles were rarely trapped. The results support the general notion that bank voles thrive in bilberry-rich, older forest and field voles in grass-dominated habitat. Contrary to general assertions, bank vole was abundant also in clearcuts, possibly due to invasion from surrounding old forest, but peak densities were lower than in old forest, possibly due to suppression by field voles. The variation of small mammals in forest age classes concurred closely with recent results reported from Finland. On a landscape scale, the results from these two and other studies predict that the total biomass of small rodents will be reduced by even-aged forest management, not because of conversion of older, semi-natural forest to clearcuts, but because of a decline in numbers in middle-aged and older, secondary forests.

1. Introduction

Small mammals are a key component of the boreal forest ecosystem. In Fennoscandia, this group consists of early-successional *Microtus* species and older forest *Myodes* species and wood lemmings *Myopus schisticolor*, besides wood mice *Apodemus* spp. and shrews *Sorex* spp. Microtine rodents are known to fluctuate in 3–5-year cycles with quite large amplitudes (e.g. Stenseth, 1999), thereby impacting small and medium-sized predators both numerically and functionally. For instance, ground-nesting forest grouse *Tetraoninae* suffer heavy mortality

from generalist predators when vole numbers decline after population peaks – a relationship referred to as the alternative prey hypothesis (Lack, 1954; Hagen, 1969; Angelstam et al., 1984). Similarly, both specialist mammalian predators like stoat *Mustela erminea* and least weasel *M. nivalis* and several species of raptors produce large litters and fledglings during "vole years".

The *Myodes* and *Microtus* voles differ in habitat and diet as well as in morphology and social organization. Studies in the 1970 s and 1980 s (Hansson, 1971; Myllymäki, 1977) showed that the field vole *Microtus agrestis* subsists almost exclusively on graminoids; the species is

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therefore restricted to grass-dominated habitats like old fields and clearcuts. The granivorous bank vole *Myodes glareolus* has a wider food niche and is distributed in forests with an understory of herbs and dwarf shrubs, especially bilberry *Vaccinium myrtillus*. Since field voles are larger than bank voles they are considered to be dominant over bank voles (Hansson, 1983; Henttonen and Hansson, 1984; Gurnell, 1985). Furthermore, their social structures differ; the field vole forms matrilineal clusters during the breeding season with territorial males living in large non-overlapping home ranges, whereas in bank vole, females are territorial with hierarchical, overlapping males inside their home ranges (Pusenius and Viitala, 1993; Ylönen et al., 1995; Pusenius et al., 1998). Presumably due to their different social structures, the field vole typically shows more pronounced annual fluctuations than the bank vole, with larger amplitudes between peak and low densities during the cycle (Hansson and Henttonen, 1985). The wood lemming may periodically contribute significantly to the overall biomass of microtine rodents in boreal forest. It belongs to the taiga fauna and mainly occurs in old spruce forests rich in mosses. In contrast to other boreal rodent species it is a specialized bryophage with a diet consisting of 75–90% mosses (Eskelinen, 2002). The population density periodically shows large fluctuations, but the peaks may not be as regular as in other microtine rodents (Eskelinen et al., 2004; Bobretsov and Lukyanova, 2017). During population peaks, however, its local distribution may cover larger continuous areas (Ims et al., 1993).

In a historical perspective – before commercial forestry - natural forest fires created early successions and presumably favorable habitat for *Microtus*, with surrounding non-burnt forest probably constituting optimal habitat for *Myodes* and wood lemming. However, pine forests burnt more often than richer spruce forests. Hence, larger landscape sections on more productive soils consisted of bilberry-rich, old spruce forests (Rolstad et al., 2017). With the onset of commercial forestry 2–3 centuries ago, the conifer forests were for a rather long period harvested by high-grading and selection cuttings, combined with extensive control of forest fires. By late 1800 s and early 1900s, this management regime had presumably reduced the areas of open, grass-rich fields and favored sparsely stocked coniferous forests with dense bilberry ground cover (Lie et al., 2012). *Microtus* was probably then less abundant than in earlier times. The present clearcutting harvesting method, with subsequent planting of Norway spruce *Picea abies* and natural regeneration of Scots pine *Pinus sylvestris* from retained seed trees – leading to even-aged forest management – started in Fennoscandia in the late 1940s and early 1950s. This recent increase in early successions from clearcuts presumably restored prime habitats for *Microtus*.

Despite the long-term pervasive transformation of the Fennoscandian boreal forest ecosystem, first by means of extensive high-grading and recently by clearcutting and even-aged plantations, surprisingly few studies have addressed how these changes in management regime might have affected the small rodents community and their dynamics (Bogdziewicz and Zwolak, 2014). In a comparative study in North America, Sullivan and Sullivan (2001) concluded that regeneration systems which leaves overstory trees either singly or in groups are less favorable for *Microtus* than treeless clearcuts. In another review article from the same continent, Kirkland (1990) found no consistent results on the effects of harvesting methods on small mammals, except that – in general – species richness was enhanced on clearfelled areas. In Fennoscandia, from early, general studies of diets and habitat use of small rodents (e.g. Hansson, 1971, 1983), some authors have predicted that clearcutting forestry will increase total vole abundances owing to the creation of prime *Microtus* habitat after clearfelling (Henttonen 1989; Rolstad and Wegge, 1989; Ims, 1991), and because this species has higher growth potential than *Myodes* (Henttonen and Hansson, 1984). Conversely, Gorini et al. (2011) predicted a decline in small rodents due to the harvesting of semi-natural old forest, since the loss of this prime *Myodes* habitat would not be compensated for by *Microtus* on the following grassy clearcuts. This view is partly supported by other Fennoscandian studies, which recorded low abundances of bank voles in middle-aged and older regenerated plantations (Ecke et al., 2002; Panzacchi et al., 2010; Savola et al., 2013). However, these field studies suffer from short temporal duration (2–5 years), besides being conducted during a period of remarkably low numbers of field voles.

As part of a long-term field study of forest grouse in southeastern Norway (Wegge and Rolstad, 2011, 2017) we measured the abundance of small mammals in a coniferous forest subjected to industrial, clearcutting forest management. Here, we report on their temporal variation pattern during 39 years (1979–2017), with particular focus on the two main vole species, i.e. the bank vole and the field vole. Besides contributing to the general understanding of small mammal dynamics in boreal Fennoscandia, we specifically address the above-mentioned predictions regarding the likely impacts of clearcutting and plantation forestry on this important animal group.

2. Study area

The study was carried out in Varald State Forest, located next to the Swedish border in southeast Norway (60°10′N, 12°30′E). The gently undulating terrain between 200 and 400 m a.s.l. consists of Norway spruce and Scots pine interspersed with scattered birch *Betula* spp. and aspen *Populus tremula*. Mixed pine and spruce forest – the *Vaccinio-Pinetum* vegetation type (Kielland-Lund, 1981) – covers > 50 percent. The remaining semi-natural forest of this type consists of an overstory dominated by pine, with spruce in the lower strata, and a dense field layer consisting of a mixture of bilberry, crowberry *Empetrum nigrum* and intermingling bog whortleberry *Vaccinium uliginosum* and cowberry *Vaccinium vitis-idaea*. These old forest stands originated after mixed-severity fires during the 18th and 19th centuries, of which the last fires occurred during the 1850–1870s (Bråthen, 2016). Thus, the age of the overstory pine trees today amounts to 150–200 years. Contiguous with other mixed conifer forests on all sides – only interspersed with small patches of small abandoned farmlands – the forest has been subjected to timber harvesting for several centuries. When clearcutting became the main harvesting regime in the early 1950s – replacing the selection method – cutting blocks were initially rather large (> 50 ha in the 1960–1970s), but have successively been reduced in size, today rarely exceeding 20 ha. During the last four decades, the coverage of semi-natural, old conifer forests has been more than halved from 50 to 20%, the remaining consisting of middle-aged (55%) and young (10%) silvicultural stands of pure and mixed plantations of spruce and pine. Today, clearcuts < 10 years of age cover 15%.

In addition to a dense population of moose *Alces alces*, fewer roe deer *Capreolus capreolus*, semi-resident wolves *Canis lupus* and lynx *Lynx lynx* and smaller herbivores, fluctuating numbers of stoat, least weasel and denser populations of red fox *Vulpes vulpes* and pine marten *Martes martes* are the main predators of small mammals, supplemented by different species of owls, goshawk *Accipiter gentilis* and common buzzard *Buteo buteo*. For more detail, see Wegge and Rolstad (2011, 2017).

3. Material and methods

3.1. Trapping

The small mammal guild consisted of bank voles *Myodes glareolus*, field voles *Microtus agrestis*, wood lemmings *Myopus schisticolor*, wood mice *Apodemus* spp., and shrews *Sorex* spp. We estimated the abundance of these species in the early successional stage after clearfelling (henceforth termed clearcuts) and in semi-natural old forest by the standardized snap trapping method (Hansson, 1967; Myllymäki et al., 1971). Baited with raw potato, the traps were placed along c. 250 m long transects for two days, spaced 5 paces apart and checked every day. The clearcuts were between 4 and 12 years old, dominated mainly by hairy wave-grass *Deschampsia flexuosa* and *Calamagrostis* spp. Other species – depending on site conditions – were various herbs like

fireweed *Epilobium augustifolium* and raspberry *Rubus idaeus*, besides remnant ericaceous shrubs, sprouting deciduous trees such as willows *Salix* spp.*,* aspen *Tremula tremuloides* and birch *Betula* spp., and small spruce and pine seedlings. The trapping sites in the old, semi-natural forest (150–200 yrs.) were in bilberry-dominated stands of the *Vaccinio-Pinetum* type; only a few transects (< 10%) were in the richer *Piceetum myrtillietosum* type (Kielland-Lund, 1981). In old forest, bilberry was the dominating dwarf shrub in all transects, with interspersing heather *Calluna vulgaris* and cowberry in drier sites and bog whortleberry *V. uliginosum* in moister sites. Most of the 39 years, we trapped at the same 2–4 sites in each of the two main forest age classes, but sites in clearcuts had to be relocated occasionally owing to successional development. Sampling was carried out in late August/first week of September each year.

During 7 years, we also sampled small mammals in middle-aged, culturally regenerated stands. This served to show the change in abundance and composition of small rodents as the conifer seedlings on the clearcuts developed with closing of canopies and subsequent changes in the field layer vegetation. In one of the years (2007), 6 such stands were sampled, in addition to clearcuts and old forests. In each of the other 6 years, 1 or 2 middle-aged conifer stands were also sampled. In total, 14 middle-aged stands were sampled – 7 in spruce and 7 in pine plantations – ranging in age between 18 and 40 years, with most between the ages of 25–35 years. Total sampling consisted of 15,000 trap-nights in the three forest age classes.

3.2. Analyses

The abundance index was expressed as number of animals trapped per 100 net trap-nights. The net number of trapping nights was defined as total traps set minus half of traps released without capture and/or number of unreleased traps with disappeared bait. Animals were assumed to be present in the sampling area even if no animals were trapped. To allow for parametrical statistical tests, we therefore added a figure $0 < x \leq 0.5$ to zero values according to the overall relative abundance of the respective species (Suppl. Table S.1). We used $\log_{10}$-ratios in one-sample "pairwise" tests and 1/3-power transformations in non-pairwise comparative tests. The 1/3-power function was preferred over log (x + 1), which typically is used in vole-trapping studies, because the power function performs slightly better at low numbers. For values 5–50, the power and log functions are practically similar.

In comparative studies using snap-trapping, few authors have considered inter-specific differences in trappability. Instead, trapping indices, like numbers captured/100 trap nights, have been used directly when comparing abundances among species. Not surprisingly, trappability varies with several factors (kind of bait being used, relative density, ranging behaviour and home range size). By comparing small mammal catches at extensive (small quadrat) and intensive (modified standard minimum grid) trapping designs in southern Sweden, Hansson (1975) showed that bank voles were 3–4.5 times more trappable than field voles (see also Stenseth and Hansson 1979). In a study from Finnish Lappland, Viitala (1977) reported that another *Myodes* species, the grey red-backed vole *M. rufocanus*, was 1.5–2 times more trappable than field voles. Savola et al. (2013) also acknowledged the differences in trappability between *Myodes* and *Microtus*, stating that higher trappability of the former probably was due to their larger ranging behavior.

Since the objective in our study was to examine how abundances of voles vary in different successional stages, a correction factor for different trappability was needed. From the inferences of the Swedish and Finnish studies, we chose to use a factor of ×3 for field voles. The trappability of wood lemmings is also known to be low, presumably even lower than field voles (Bondrup-Nielsen and Ims, 1988; Eskelinen et al., 2004; Bobretsov and Lukyanova, 2017). However, to be conservative, we applied the same factor of ×3 to this species. Most probably, the trappability of the other small mammals also varies, but

because their indices were quite low, adjustments for trappability would not have altered the general results in this study.

Another challenge of snap-trapping studies relates to trap saturation. Field studies employing traps that can capture only one individual at a time may underestimate true population abundance because, at high density, the estimated abundance approaches an upper value determined by the total number of traps. Xia and Boonstra (1992) pointed out that the number of voles caught per 100 trap nights therefore should be corrected. However, according to Hanski et al. (1994) this problem arises first at high population densities, demonstrating that for indices up to 35 catches per 100 trap nights the relationship with true population density is practically linear. In our study, total catches surpassed 30 per 100 trap nights in four of 39 years, and 40 in only one year. We therefore assumed trap saturation to be negligible and refrained from any corrections.

4. Results

A total of 1545 small mammals were captured in 15,000 trapping nights during the 39-year period. Bank vole was the most frequently captured vole, followed by field vole in grassy clearcuts. Together, these two species made up for 90% of all captured voles. Except for shrews, which amounted to18% of all small mammals, other species were rarely recorded (Fig. 1, Table 1). Like reported in other studies, bank voles dominated in the old, semi-natural forest, whereas field voles were restricted to clearcuts. Somewhat surprisingly, bank vole was almost equally abundant in clearcuts as in old forest. After adjusting for lower trappability of field voles (with a factor of 3×), the two species were about equally abundant in clearcuts (Fig. 1), and their combined abundance there exceeded that of bank voles in old forest (Table 1).

Throughout the whole period we discerned 11 vole cycles (Fig. 1). The abundances of most species were highly correlated (Table S.2). In spite of quite different diets – shrews correlated with both microtines both in clearcuts and in old forest, and wood mice correlated with both field vole and bank vole in clearcuts. Wood lemmings also correlated significantly with the other two microtines in both habitat types, although with markedly more irregular peak years.

Notably, abundances were markedly lower during the 19-year period from 1990 to 2008. In this period, high peaks disappeared in both species (except for bank voles in old forest in 2002), but the cyclic fluctuations were still evident. The decline from the 1979–1989 was most pronounced in clearcuts, where field vole and bank vole numbers dropped by 80 and 50%, respectively (field vole: $F_{2, 36} = 3.84$, P = 0.03; bank vole: $F_{2, 36} = 6.79$, P = 0.003). In comparison, bank vole in old forest declined insignificantly 23% ($F_{2, 36} = 1.15$, P = 0.33). In total, the abundance of small rodents in the middle period was about one-half of what it was in the 1980s (Fig. 2a and b). Following this low period, high peaks reappeared after 2008, and abundances of most species increased markedly, reaching even higher abundances than in the first period of 1980s (Fig. 1, Table 1). Again, the change was most pronounced in clearcuts, where especially bank voles increased to almost twice the abundances of the 1980s. Comparing clearcuts and old forest in the two high density periods, and including the more irregularly fluctuating wood lemming (also adjusted for low trappability), the total density of small rodents was 26% higher in clearcuts (P = 0.047, Fig. 2a, Table 2).

In middle-aged forest stands, field voles were more or less absent, being captured only once in a total of 1722 trap-nights (Table 3). Also, the abundance of bank vole was markedly lower, amounting to less than one-half of its abundance in old forest and clearcuts (ANOVA: P < 0.05, both, Table 4, Fig. 3). The patterns in the 7 years of comparative sampling were quite similar; only in year 2006 were bank voles more abundant in young forest than in clearcuts (Fig. 4). In the middle-aged plantations, more voles were trapped in the spruce stands than in pine stands; the indices were 2.41 versus 0.92 and 0.46 versus 0.03 for bank voles and field voles (after corrections) in the two types of stands,
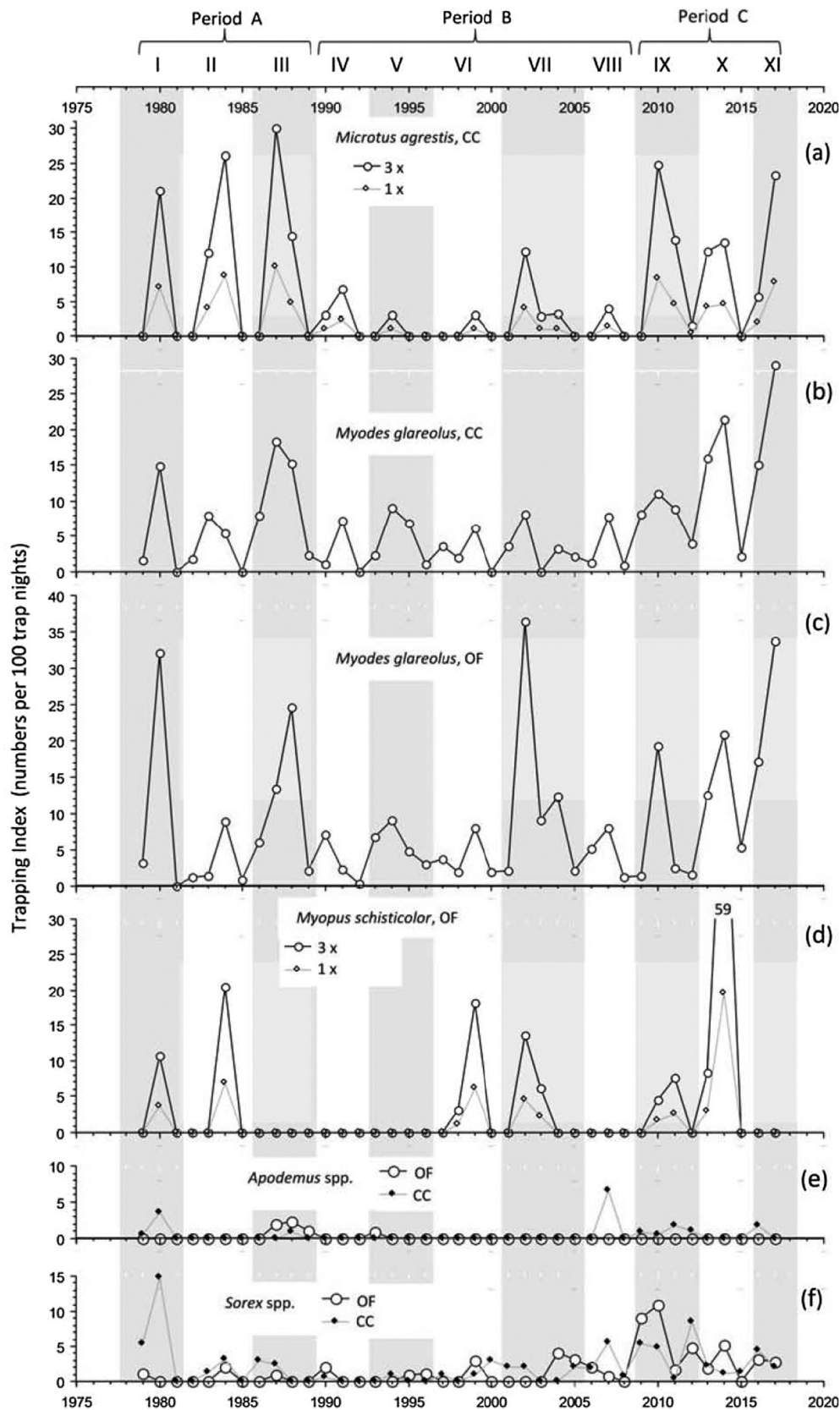
Fig. 1. Trapping indices (number og individuals trapped per 100 trap nights) shown for (a) field vole in clearcuts, (b) bank vole in clearcuts, (c) bank vole in old natural forest, (d) wood lemming in old natural forest, (e) wood mice in clearcuts and old natural forest, and (f) shrews in clearcuts and old natural forest. Field vole and wood lemming are also shown with corrected (3×) indices (see methods for explanation). Successive vole cycles are indicated by shadings and roman numerals, divided in three periods: (A) 1979–1989, 11 years, (B) 1990–2008, 19 years, and (C) 2009–2017, 9 years.

Table 1
Total number of captures and average yearly trapping indices in clearcuts and old semi-natural forest for the whole study period of 39 years. Field vole, wood lemming and total sum of rodents are corrected with ×3 for low trappability. Percentages are based on trapping index of all rodents, and for shrews on overall captures.

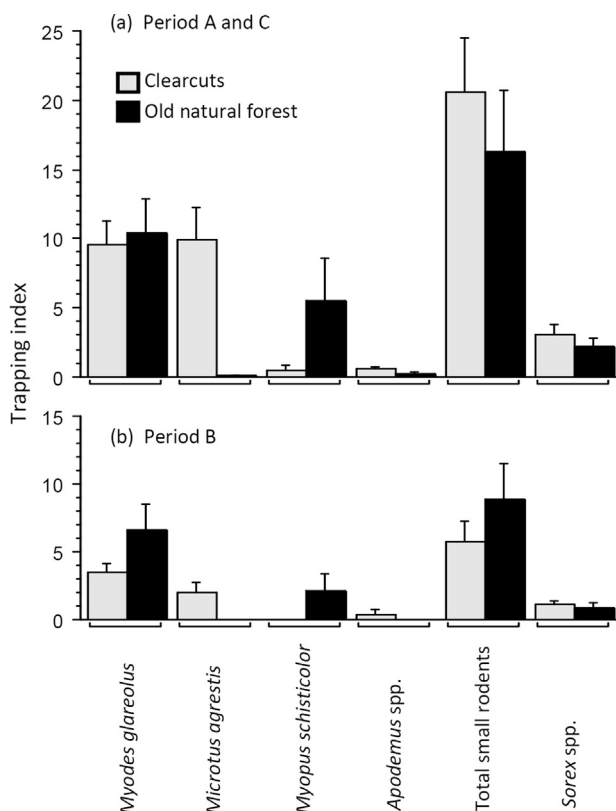|		Total no.	Per 100 t.n	%
Clearcuts: 7667 trap nights	Bank vole	501	6.59	49.3
	Field vole	181	(2.02) 6.07	45.3
	Wood lemming	8	(0.09) 0.27	2.1
	Wood mouse	41	0.45	3.3
	Sum rodents	731	(9.15) 13.38	100.0
	Shrews	169	2.09	13.5
Old natural forest 5611 trap nights	Bank vole	418	8.58	67.8
	Field vole	1	(0.01) 0.03	0.2
	Wood lemming	76	(1.29) 3.88	30.7
	Wood mice	7	0.16	1.3
	Sum rodents	502	(10.04) 12.66	100.0
	Shrews	100	1.55	10.9

Fig. 2. Average trapping indices in clearcuts and old natural forest (a) for period A and C combined (1979–1989 and 2009–2017: n = 20) and (b) for period B (1990–2008: n = 19). Bars denote SEs.

respectively. Owing to small sample sizes and uneven distribution of stand ages, no further analyses were performed.

5. Discussion

Our results concur with other studies on the general habitat associations of the two main vole species (Hansson, 1971; Myllymäki, 1977; Panzacchi et al., 2010; Gorini et al. 2011); the bank vole was most abundant in bilberry-rich, semi-natural old forest, while field voles were almost exclusively found in grass/forb-dominated habitat. In our

species comparison, after correcting for different trappability, we found that bank voles were about equally abundant as field voles in 4–12 year-old clearcuts, and that their combined abundance there exceeded that of bank voles in old forest. The abundance of bank voles on clearcuts was higher than expected from the literature. This could be because clearcuts do not consist of only graminoids; logging debris, regenerating woody perennials and a partly rocky substrate provide suitable – although not optimum – habitat also for bank voles; this variation in structural characteristics and composition has also been emphasized by Kirkland (1990) and Ecke et al. (2002). Another possible reason for rather high abundance of bank voles on clearcuts is that our clearcuts were relatively small (mostly < 10 ha), which facilitated invasion from surrounding older forest.

During the 39-year long sampling period, vole abundances, especially in clearcuts, were markedly lower during the 1990s and first part of 2000s. While cyclic-like fluctuations were discernible like in the preceding period, peak abundances, especially in field vole, were much reduced. Notably, field voles almost disappeared, for reasons that are not quite clear (see Korpela et al. 2013). The remarkable decline occurred across the whole of Fennoscandia, triggering speculations of far-reaching, cascading effects on ecosystem functioning (Hörnfeldt et al., 2005; Ims et al., 2008; Cornulier et al., 2013; Korpela et al., 2013; Ecke et al., 2017). However, like reported from different parts of their range (Brommer et al., 2010; Korpela et al., 2013), cycles with large amplitudes reappeared in our study area during the first decade of this century. The most pronounced increase was then recorded in field voles, but also bank voles increased; in clearcuts peak abundances of both species increased more than twofold compared to the previous low period. For bank voles in old forest the increase was less discernible and not statistically significant from the middle, low period.

Total densities of small rodents were markedly lower in culturally, regenerated stands than in clearcuts and semi-natural old forest. This pattern compares quite closely with the Finnish study of Savola et al. (2013), which recorded not only a disappearance of field voles but also that bank voles declined markedly from young (9–15 years) to middle-aged (24–30 years) plantations. Most of our plantations were of the same age interval as their middle-aged stands. Furthermore, Panzacchi et al. (2010) reported remarkably low densities of bank voles in older cultural stands between 40 and 90 years. Hence, all Fennoscandian studies imply that the abundance of bank voles is markedly lower not only in the middle-aged stands, but also in older cultural stands compared with the abundance in remnant, semi-natural old forest.

In spite of several experimental field studies (Hansson, 1975; Viitala, 1977; Stenseth and Hansson, 1979), which showed that *Microtus* are less trappable than *Myodes*, in nearly all inter-specific comparisons, the two species groups have been assumed equally trappable. Contrasting this, from capture-mark-recapture (CMR) analysis of live trapping data, (Panzacchi et al., 2010) reported that field voles had higher – not lower – trappability than bank voles. Furthermore, from successive snap-trapping captures, Korpimäki and Norrdahl (1989) reported no difference in trappability between *Myodes* and *Microtus* in another Finnish field study. In our study, we corrected the trapping index of field vole and wood lemming with a factor of ×3. According to Hansson (1975) and Stenseth and Hansson (1979) this may be a conservative correction. Because trappability is of paramount importance in comparative studies of small rodents when using conventional snap trapping or live capture, this question should be given more attention in future studies.

Across Fennoscandia, semi-natural conifer forests are harvested by the clearcutting method and replaced with dense plantations of genetically improved trees. In pine forest, the method of seed-tree retention after clearfelling, followed by natural regeneration, is now likely to be replaced by the same method as applied to spruce, using genetically improved planting stock (Jansson et al., 2017). Today, the age of final harvesting of spruce forests is 60–80 years, of pine forests a little higher. In such managed forests, an estimated 70% or more will

Table 2
Annual pairwise comparisons (one-sample log-ratio test) of trapping indices of different rodent groups in clearcut and old semi-natural forest, shown separately for four period categories: (A) 1979–1989, 11 years, (B) 1990–2008, 19 years, (C) 2009–2017, 9 years, (A + C) 20 years, and total period of 39 years. Statistically significant log-ratios ($P < 0.05$) are shaded.

Comparison	Group	Period	log-ratio	95% lower	95% upper	df	t-value	P-Value
Bank vs. field vole	Clearcuts	Total	0.270	0.104	0.435	38	3.30	0.002
		A	0.181	-0.196	0.558	10	1.07	0.309
		B	0.307	0.061	0.553	18	2.63	0.017
		C	0.299	-0.079	0.676	8	1.83	0.106
		A + C	0.234	-0.009	0.478	19	2.01	0.059
Clearcuts vs. old semi-natural forest	Bank vole	Total	-0.118	-0.256	0.020	38	-1.73	0.092
		A	-0.031	-0.252	0.190	10	-0.31	0.762
		B	-0.278	-0.494	-0.061	18	-2.70	0.015
		C	0.113	-0.175	0.402	8	0.91	0.392
		AC	0.034	-0.129	0.197	19	0.44	0.668
Clearcuts vs. old semi-natural forest	Bank and field vole	Total	0.121	0.002	0.240	38	2.06	0.046
		A	0.230	0.021	0.439	10	2.46	0.034
		B	-0.045	-0.202	0.112	18	-0.60	0.557
		C	0.338	0.047	0.628	8	2.68	0.028
		A + C	0.278	0.120	0.437	19	3.69	0.002
Clearcuts vs. old semi-natural forest	Total rodents	Total	0.014	-0.103	0.131	38	0.25	0.808
		A	0.121	-0.077	0.318	10	1.36	0.203
		B	-0.131	-0.302	0.040	18	-1.61	0.124
		C	0.191	-0.084	0.465	8	1.60	0.148
		A + C	0.152	0.004	0.300	19	2.15	0.045

Table 3
Total number of captures and average yearly trapping indices in clearcuts, middle-aged plantations and old semi-natural forest, shown for a subset of 7 years (1982, 1983, 1986, 1999, 2000, 2006 and 2007). Field vole, wood lemming and total sum of rodents are corrected with × 3 for low trappability. Percentages are based on trapping index of all rodents, and for shrews on overall captures.

		Total no.	Per 100 t.n	%
Clearcuts: 1655 trap nights	Bank vole	77	4.71	56.4
	Field vole	18	(0.90) 2.71	32.5
	Wood lemming	0	0	0
	Wood mouse	20	0.93	11.1
	Sum rodents	115	(6.54) 8.35	100.0
	Shrews	35	2.25	21.2
Middle-aged plantation: 1722 trap nights	Bank vole	29	2.06	82.7
	Field vole	1	(0.14) 0.43	17.3
	Wood lemming	0	0	0
	Wood mice	0	0	0
	Sum rodents	30	(2.20) 2.49	100.0
	Shrews	13	0.63	20.2
Old semi-natural forest: 1223 trap nights	Bank vole	52	4.59	62.2
	Field vole	1	(0.06) 0.19	2.6
	Wood lemming	6	(0.87) 2.60	35.2
	Wood mice	0	0	0
	Sum rodents	59	(5.52) 7.38	100.0
	Shrews	7	0.83	10.1

Table 4
ANOVA with Bonferrroni multiple comparisons of trapping indices of bank vole, field vole, and total rodents in clearcuts (Cc), middle-aged plantations (MaP), and old semi-natural forest (OnF), based on power-transformed values ($x^{1/3}$) as shown for bank vole in Fig. 4.

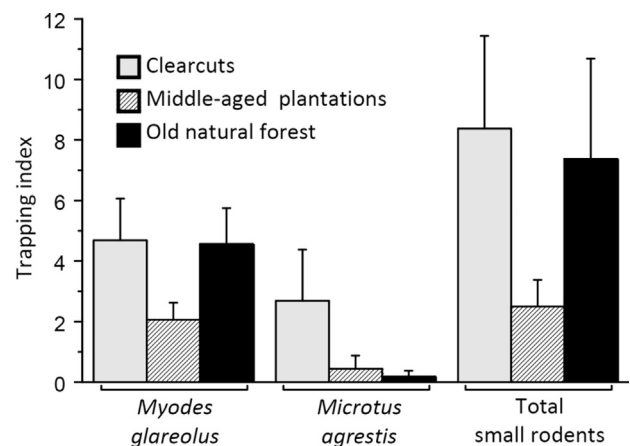|	Bank vole	Field vole	All rodents
Overall ANOVA: $F_{2, 6}/P$	3.98/0.05	11.97/0.002	4.59/0.03
Cc vs MaP: P	0.04	0.001	0.01
Cc vs OnF: P	0.86	0.002	0.45
MaP vs OnF: P	0.03	0.94	0.05

Fig. 3. Average trapping indices of bank vole, field vole, and all rodents combined, in clearcuts, middle-aged plantations, and old natural forest, compared for a subset of 7 years (1982, 1983, 1986, 1999, 2000, 2006 and 2007). Field vole and wood lemming are included with corrected (×3) indices (see methods for explanation). Bars denote SEs.

consist of plantations older than 20 years. As implied by recent studies – including ours – the abundance of voles in the middle-aged and older plantations is predicted to be markedly lower than in the former semi-natural, old forest. Once we enter the next epoch, when most of the
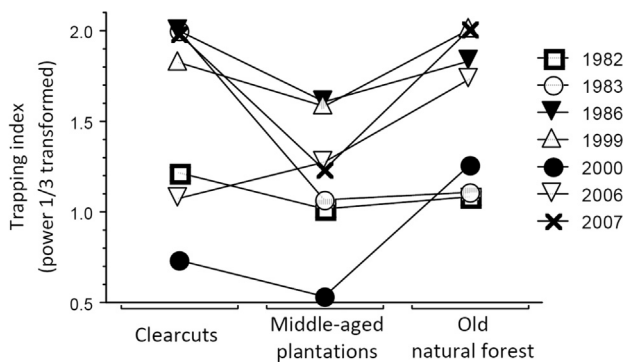
Fig. 4. Trapping indices of bank vole shown separately for 7 years of comparative sampling in clearcuts, middle-aged plantations, and old natural forest. Note: trapping index shown in power-transformed values ($x^{1/3}$).

forest landscape will consist of plantations, we predict that the total abundance of voles will be markedly lower than in the naturally regenerated forests of previous times. Patches of clearcuts and culturally rejuvenated stands up to 10–15 years will then function as vole "hotspots" in a forested matrix much impoverished of such species.

As suggested by Gorini et al. (2011), the overall abundance of bank vole is predicted to decline most markedly in landscapes originally dominated by bilberry-rich spruce forests. To some extent, high vole abundance in clearcuts and young plantations may compensate for the decline in older plantations. In such forest – mainly of the *Piceetum-myrtillietosum* type (Kielland-Lund, 1981) – the grassy and mixed field layer created on clearcuts changes markedly and rapidly after conifer canopy closure (Uotila and Kouki, 2005). Therefore, in spruce forests, less dense plantings followed by early thinning may retain the grassy field vegetation and stimulate regrowth of bilberry (Esseen et al., 1997; Bergstedt and Milberg, 2001; Uotila and Kouki, 2005; Widenfalk and Weslien, 2009), thereby providing suitable habitat for both vole species. Conversely, early planting with dense seedlings will shorten the period of favorable *Microtus* habitat, and retaining high tree density in older plantations will prevent the development of bilberry ground layer for *Myodes*. In pine-dominated landscapes, voles are predicted to be less influenced by the clearfelling practice and subsequent silvicultural treatments owing to more subtle changes in the ground vegetation following harvesting and regeneration (Uotila et al., 2005). However, since the overall abundance of small mammals is lower in pine forest, less reduction there will play a minor role in the total reduction of biomass of small rodents.

Small rodents, especially bank voles and field voles, constitute a main food source for many avian and mammalian predators (Hagen, 1969; Korpimäki, 1994; Lindström and Hörnfeldt, 1994; Leckie et al., 1998; Dell'Arte et al., 2007). Presumably, when even-aged forest management based on the clearcutting method was introduced in the 1950s, the biomass of field voles increased, thereby supporting more predators with subsequent higher predation pressure on small game species. This view has long persisted as a main explanation for long-term declines in tetraonid birds in Fennoscandia (Angelstam et al., 1984; Marcström et al., 1988; Henttonen, 1989; Lindström et al., 1994; Kurki et al., 2000; Wegge and Rolstad, 2011). However, the recent period of low vole numbers in the 1990s throws some doubt about this general understanding of vole-grouse relationships. During the 15–20 years when voles declined markedly across most of Fennoscandia (Brommer et al., 2010; Korpela et al., 2013; Magnusson et al., 2015; Ecke et al., 2017, this study) new clearcuts were created at a steady pace. During this period, forest grouse populations continued to decline (Sirkiä et al., 2010) or remained stable (Wegge and Rolstad, 2011).

On the other hand, the field vole – the main vole in grassy clearcuts – is bigger than bank voles, thus representing a higher food biomass/individual than bank voles. The former species has also been reported

to be more sluggish in movement and therefore easier to catch than bank voles, thus constituting a preferred prey species (MacDonald, 1977; Sundell et al., 2008). From our study area, Lundstadsveen (2011) provided evidence for this: in winter fox scats, the proportions of field voles and bank voles were equal, in spite of much lower abundance of the former in snap trapping the preceding autumn and the following spring (after index correction). Therefore, its short-term proliferation on clearcuts – although not reaching as high densities as previously – might have been sufficient to sustain a dense guild of both specialist and generalist predators. During the last decade, when vole abundances returned to pre-1990 levels with more field voles in clearcuts, this habitat provides more prey for both mammalian and avian predators, thus possibly again mediating a higher functional and numerical predation pressure on alternative prey, including forest grouse.

The red fox is a main predator on eggs, chicks and adults of boreal forest grouse (Marcström et al., 1988; Lindström et al., 1994; Kauhala et al., 2000; Wegge and Rolstad, 2011). Although this species may have benefitted from the creation of clearcuts with associated *Microtus* prey, other factors like less snowy winters (Selås and Vik, 2006) and food from remains of hunter and wolf-killed ungulates (Needham et al., 2014) have probably been equally or more influential for their general increase in recent years. In the future forested landscape, dominated by even-aged monocultures with low vole densities, fragments of clearcuts and young stands will continue to produce temporal pulses of vole food for predators. In the short-term, this might not alter the general relationship between predators and grouse; both red fox and other predators will respond both numerically and functionally to the cyclic voles. However, the predation pressure on grouse in the years between peaks will probably increase because of a lowered abundance of this food source in all other habitats. In the long-term, vole specialists like small mustelids and owls might be negatively affected by the lower biomass of bank voles in culturally regenerated monocultures, while generalists like red fox is likely to maintain high densities due to their flexible foraging behavior.

Acknowledgements

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2018.04.011.

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