

Density-dependent vole damage in silviculture and associated economic losses at a nationwide scale

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ABSTRACT

Voles inflict damage to silviculture by debarking or severing tree seedlings. The large-scale impacts of vole damage to silviculture, both in terms of severity and financial losses are, however, poorly known. In autumn 2005, cyclically fluctuating vole populations were at their highest in Finland for over 15 years, which led to extensive damage to silviculture during the winter 2005/06. We carried out a nationwide assessment of the incidence, spatial extent and economic value of damage and its relation to vole abundance in privately owned forests during this winter. Damage data were obtained with a questionnaire addressed to the directors of all Forest Management Associations (FMAs) operating in Finland, and vole abundance data from 15 long-term monitoring projects across the country. Voles were confirmed to have destroyed ca. 4.7 million tree seedlings, covering a total effective damage area of ca. 2600 ha. The directors of the FMAs estimated that the actual level of damage was likely to exceed 8.5 million seedlings, or 5400 ha. Roughly 80% of all damage was inflicted on Norway spruce (*Picea abies*), ca. 10% on Scots pine (*Pinus sylvestris*) and ca. 10% on birch (*Betula* sp.) and other species. Considering costs of replanting alone, a most likely very conservative estimate of the financial impact of vole damage during the winter 2005/06 lies between 2.2 and 4.0 million €. The occurrence of damage during the winter was positively related to vole abundance in the previous autumn. This validates vole population monitoring as an effective tool for forecasting near-future damage to silviculture. Our results suggest that if vole populations continue to fluctuate as they currently do, levels of damage to Finnish forests will be great also in the future, far exceeding damage levels recorded in earlier decades.

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1. Introduction

Voles are considered serious pests in silviculture in many regions of the world (Gill, 1992a; Baxter and Hansson, 2001). Voles most often cause damage during the earliest phases of forest regeneration by gnawing bark and severing entire young seedlings (Gill, 1992a; Baxter and Hansson, 2001), which increases the risk of seedling mortality. Voles also have indirect negative effects on seedlings by predisposing them to wound-infecting pathogens (Bazzigher, 1973; Roll-Hansen and Roll-Hansen, 1980; Gill, 1992b;

Henttonen et al., 1994), which may increase mortality at later stages of tree development. Vole damage often also reduces the economic value of timber, e.g., through stem deformations (Heikkilä and Löyttyneemi, 1992). Increased seedling mortality due to vole damage must in many cases be compensated for by costly replanting measures. As the need for replanting postpones forest establishment, also harvesting measures are delayed, leading thus to further economic losses.

The impact of vole damage to silviculture, both in terms of severity and financial value is poorly known. This is partly due to the fact that voles were not identified as a major problem to silviculture until fairly recently, e.g., not before the 1960s in northern Europe (Myllymäki, 1977a). Also, comprehensive and systematic monitoring schemes to assess vole damage have rarely been implemented (but see Kaneko et al., 1998). Myllymäki (1977a) reviewed existing information on vole damage to

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silviculture in Europe following World War II; during approximately three decades, voles were reported to have destroyed ca. 80 million forest tree seedlings in northern Europe. In Finland, voles reportedly destroyed ca. 7.4 million forest tree seedlings on ca. 4000 ha during 1973–1980 (Teivainen, 1981). In Hokkaido, Japan, vole damage to seedlings was very severe in the 1950s and 1960s, with maximum annual losses accumulating to ca. 60 million destroyed seedlings (Kaneko et al., 1998).

In northern Europe, voles undergo multiannual population cycles, during which densities may fluctuate several hundred-fold between high and low density years (Hansson and Henttonen, 1985; Stenseth, 1999). Vole populations commonly attain their highest peak densities in late summer or early autumn, after which densities decline over the course of the winter due to food resource depletion (Stenseth, 1999; Huitu et al., 2003a). It is during these decline winters when voles cause the most extensive damage to silviculture and horticulture (Kanervo and Myllymäki, 1970; Larsson, 1973; Myllymäki, 1977a; Teivainen, 1981).

It has been shown that vole abundance and the degree of vole damage are positively correlated at small local scales (Hansson, 1986). However, considerable variation in the degree of damage commonly exists both within (Henttonen et al., 1995) and between different geographic locations (Hansson, 1986), which makes large-scale, e.g., nationwide, forecasting and prevention of damage very difficult. While both vole damage and vole abundances have been separately monitored at large scales with substantial effort (damage: e.g., Larsson, 1973; Myllymäki, 1977a; Hansson and Larsson, 1980; Teivainen, 1981; abundance: reviewed by Hansson and Henttonen, 1985; Turchin, 2003; see also Huitu et al., 2003), simultaneous information on the dynamics of voles and damage imposed by them at corresponding scales is conspicuously rare (but see Kaneko et al., 1998).

The cyclic fluctuations of voles are often spatially synchronous across large areas (Henttonen et al., 1977; Henttonen and Wallgren, 2001; Huitu et al., 2003b; Sundell et al., 2004). The areas in which vole populations fluctuate synchronously are not fixed geographically, but shift variably between population cycles, possibly due to variations in climatic conditions (Moran, 1953). For example, in the southern half of Finland, it was common in the 1980s and 1990s for western vole populations to fluctuate synchronously and precede population fluctuations in the east by approximately 1 year (monitoring scheme of the Finnish Forest Research Institute [Metla]). During the most recent vole cycles, however, both areas have been synchronized, coinciding with exceptionally high vole densities simultaneously in the entire southern part of Finland in autumn 2005. Meanwhile, northern Finnish populations were at very low densities. Following snowmelt in spring 2006, numerous reports were aired of extensive damage to forest seedlings throughout vast areas of southern Finland.

Our objectives in this study were to (1) assess the extent of damage to silviculture across Finland following the exceptionally high peak abundance of voles, (2) estimate the economic losses due to vole damage, and (3) determine the dependence of vole damage to silviculture on vole abundance on a national scale. Based on the known level of vole abundance in autumn 2005, we predicted that vole damage would rise to millions of tree seedling on thousands of hectares, accumulating in economic losses to millions of euros. We also predicted that levels of damage would be positively associated with vole abundance.

2. Methods

2.1. Vole damage data

We determined the incidence and spatial extent of vole damage to silviculture during the winter 2005/06 by use of a questionnaire

addressed in summer 2006 to the directors of all Forest Management Associations (FMAs) operating in Finland. Altogether 154 FMAs operated in 2006 across Finland to provide forestry services to non-industrial private forest owners. Collectively the FMAs operate on ca. 10.5 million hectares, which accounts for ca. 52% of all productive forest area and ca. 79% of privately owned forest area in Finland (Peltola, 2007). The corresponding values for areas in which vole damage was reported are ca. 8.5 million hectares, accounting for ca. 63% of total area and 81% of privately owned area (Peltola, 2007).

Private forest owners are eligible for state compensation for vole damage losses exceeding a given threshold. Restocking is compensated for when <1000 viable seedlings/ha, and total replanting when <600 viable seedlings remain following damage (recommended initial planting density for most forest trees is 1600–2000 seedlings/ha; Anon., 2001). Eligibility for compensation for vole damage is conditional on inspection by an FMA official. Through these inspections, FMAs obtain estimates of total vole damage in their area of operation and simultaneously also information on the coverage of inspections relative to the area of operation.

In the questionnaire, we requested the directors of the FMAs to calculate and report the following, separately for different tree species: (1) the verified total number of seedlings destroyed by voles, summing both compensation categories, (2) the verified total area in hectares in which vole damage required replanting, i.e., where <600 viable seedlings/ha remained post-damage, (3) the estimated true number of seedlings destroyed by voles, taking into account the coverage of damage inspections at the time of the questionnaire, and (4) the estimated total area in hectares in which vole damage required replanting, again considering inspection coverage. The directors were also requested to report the operational area of their FMA, as well as information on the species of vole responsible for the damage, if identified.

In a number of instances (18.5%), FMAs returned questionnaires containing only verified accounts of damage or estimates of damage, either for numbers of seedlings or damaged areas. In these instances, we extrapolated the missing data using the fully completed questionnaires. For example, where seedling numbers were not reported, the damaged area values were multiplied by the planting density of the given species (Norway spruce *Picea abies*: 1800/ha, Scots pine *Pinus sylvestris* 2000/ha, other species 1600/ha), and vice versa. In instances where verified numbers of damaged seedlings were provided while estimates of true damage were not, the latter were obtained by multiplying by the mean factor by which those FMAs that had provided both types of information had made their estimates. Questionnaires were not returned by two FMAs which were obviously situated within the core area of vole damage. Corresponding values of vole damage for these areas were obtained from respective regional forestry centres, which handle compensation claims. It should be noted that regional forestry centres do not compile statistics specifically on vole damages or compensations paid for these, but on biotic and abiotic damages collectively. However, in summer 2006, no other forms of claims other than those from vole damage were reported in this category to the regional forestry centres.

2.2. Vole abundance data

Vole abundance data were available from 15 sites across Finland from which also vole damage reports from the FMAs were obtained (Fig. 1). The abundance data has been collected either as part of Metla's national vole trapping surveys (8 sites) or by various research projects for other purposes (7 sites; see Huitu et al., 2003b; Korpimäki et al., 2005; Kontiainen et al., 2008; Kallio et al., 2009). The data consists of annual trapping series spanning 11–29

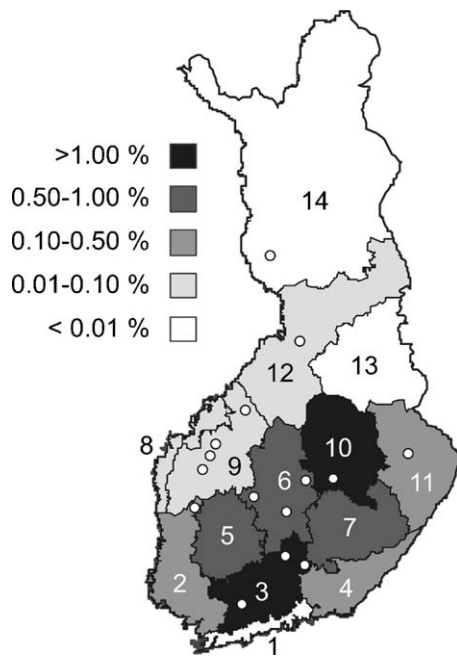


Fig. 1. Levels of vole damage in regional forestry centres, expressed as the percentage of verified effective vole damage area of the total area covered by young seedling stands (height of the dominant tree storey <1.3 m). Numbers refer to different regional forestry centres: (1) Rannikko South, (2) South-West Finland, (3) Häme-Uusimaa, (4) South-East Finland, (5) Pirkanmaa, (6) Central Finland, (7) Etelä-Savo, (8) Rannikko North, (9) South Ostrobothnia, (10) Pohjois-Savo, (11) North Karelia, (12) North Ostrobothnia, (13) Kainuu, (14) Lapland. Circles indicate vole trapping sites.

years, during which voles have been trapped by site-specific standard trapping methods involving either live or snap trapping. Trapping has been carried out every autumn in each of the 15 trapping sites with ca. 50–100 trap nights (number of traps set \times number of nights they were set) in forest and/or field habitats. For sites in which both habitat types were trapped regularly during the series, abundance indices were calculated from pooled numbers of field vole (*Microtus agrestis*) and bank vole (*Myodes glareolus*) catches in both habitats. In sites where only forests were trapped regularly, only bank vole catches were used for calculations. The use of different species should not bias estimations of relative vole abundance, since field vole and bank vole populations fluctuate synchronously through vole cycles (Korpimäki et al., 2005). Vole abundance indices are expressed as voles per 100 trap nights (total number of voles trapped/number of trap nights \times 100).

All vole trapping series included an abundance index for autumn 2005. Due to site-specific differences in trapping methods, possibly habitat quality, and species used for calculations, we chose to standardize each trapping series to mean = 0 and standard deviation = 1. From the standardized series, we used the autumn 2005 value from each site for our explanatory variable, index of local vole abundance. By using this protocol, each standardized value is comparable between sites and represents the magnitude of the vole abundance peak in autumn 2005 relative to the mean level of vole fluctuations within a given site.

2.3. Data analysis

For each FMA, we calculated effective damage areas for each tree species by dividing the verified number of seedlings destroyed by voles by the recommended planting density of the species in question (see above). By summing the effective damage areas of each species per FMA, we obtained values of the collective number

of hectares on which voles had destroyed all seedlings. Similar values were calculated also for the reported damage estimates.

To obtain an index of the severity of vole damage, we divided the effective vole damage area by the area covered by young seedling stands (height of the dominant tree storey <1.3 m; Peltola, 2007), separately for each FMA. The amount of young seedling stands in each FMA was derived from the ratio of young seedling stands to all forests within the municipalities in which the FMAs are based, by using municipality-wise forest resource data gathered for the 9th National Forest Inventory (Peltola, 2007). Calculations of FMA-wise vole damage indices were carried out for both verified and estimated damages and summarized per regional forestry centre.

Excluding the northernmost part of the country, Lapland, where no vole damage was reported, roughly two-thirds of all artificial regeneration in Finland is done by planting, predominantly with spruce (ca. 74% of all planting; Peltola, 2007). Vole damage is clearly most problematic in planted seedling stands, as opposed to those established by artificial or natural seeding, in which seedling densities are commonly high enough to buffer browsing damage. Estimates of the economic value of vole damage in this study were therefore based on the summed 2005 national mean estimated costs of mounding and replanting (260 €/ha and 594 €/ha, respectively; Peltola, 2007).

The relationship between vole abundance and vole damage to silviculture was analysed with a linear regression model, with the verified vole-damaged area for each FMA in which trapping was carried out as response variable (natural logarithm-transformed to meet assumptions of normality) and the standardized autumn 2005 vole abundance indices as explanatory variable (analysis carried out with PROC GLM, SAS statistical software).

3. Results

In total, 92 of 154 (60%) FMAs returned an answered questionnaire. During the winter 2005/06 voles were verifiably reported to have destroyed 4.69 million tree seedlings on an effective damage area of 2539 ha. Based on estimates by the FMA directors, the collective level of vole damage to silviculture most likely exceeded 8.5 million seedlings and 5400 ha (Table 1). No quantitative information regarding the extent of damage by different vole species was provided.

In those FMAs in which vole damage had occurred, the verified effective vole damage area encompassed $0.69 \pm 0.10\%$ (mean \pm SE) of all young seedling stands within the operational area of the association. The most severe instances of damage occurred in the central interior regions of the country, in Pohjois-Savo, where the area destroyed by voles in cases exceeded 3.5% of all young seedling stands. On a regional forestry centre-level, the verified effective vole damage area encompassed $0.50 \pm 0.13\%$ (mean \pm SE) of all young seedling stands (Table 1). Severe damage was reported throughout the southern and central parts of Finland, in the regional forestry centres of Häme-Uusimaa, Pohjois-Savo, Pirkanmaa, Central Finland and Etelä-Savo, while virtually no damage instances were reported from more northern parts of Finland (Fig. 1).

Voles caused damage to Norway spruce, Scots pine, birch (*Betula* sp.), larch (*Larix* sp.) and aspen (*Populus* sp.). 82% of all reported damage was inflicted on spruce, 11% on pine and 7% on birch and other species. The economic value of verified vole damage during the winter 2005/06 is ca. 2.2 million €. The corresponding value based on the damage estimates provided by the directors of the FMAs is 4.0 million €.

The degree of vole damage, expressed as the effective vole damage area relative to the total area of young seedling stands per FMA, was positively related to vole abundance (0.60 ± 0.26 [estimate \pm SE]; ANOVA, $P = 0.039$, $n = 15$; Fig. 2).

Table 1
Verified and estimated damage to forestry by voles in the winter 2005/06, expressed as the number of seedlings and hectares damaged and costs associated with the level of damage. All figures are regional forest center-wise sums (see Fig. 1). Regional centres are sorted according to the verified proportion of young seedling stands that suffered damage.

Regional forest centre	Damaged seedlings		Damaged hectares			Proportion of young stands damaged (%)		Costs (€)	
	Verified	Estimate ^a	Verified	Estimate ^a	Effective ^b	Verified	Estimate ^a	Verified	Estimate ^a
Häme-Uusimaa	703 770	1 066 432	392	640	391	1.12	1.84	334 078	505 364
Pohjois-Savo	1 040 474	1 560 267	540	827	572	1.04	1.50	488 065	733 281
Etelä-Savo	1 308 600	2 536 838	972	1763	725	0.96	2.33	619 541	1 204 377
Pirkanmaa	468 486	1 155 283	355	794	260	0.82	2.50	222 144	547 423
Central Finland	521 700	952 500	307	559	288	0.56	1.08	245 780	448 463
SE Finland	333 478	510 385	206	334	186	0.41	0.74	158 685	242 437
SW Finland	104 616	228 042	53	98	55	0.34	0.60	47 354	103 744
N Karelia	130 300	265 613	92	206	73	0.12	0.33	62 381	127 196
Rannikko N	16 000	50 000	7	21	8	0.06	0.16	6 879	21 587
S Ostrobothnia	57 341	137 638	39	132	31	0.05	0.21	26 056	62 579
N Ostrobothnia	8 015	17 692	4	10	4	0.02	0.05	3 805	8 437
Sum/mean	4 692 780	8 480 692	2967	5384	2593	0.50	1.03	2 214 769	4 004 888

^a Estimates provided by directors of the FMAs.

^b Verified number of damaged seedlings divided by their recommended species-specific planting density.

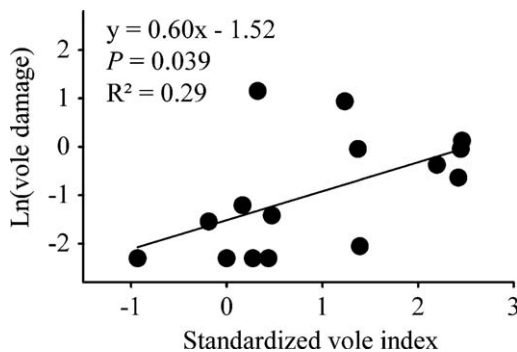


Fig. 2. Relationship between the relative abundance of voles in autumn 2005 at 15 vole trapping sites in Finland (see Fig. 1) and the verified effective vole damage area of the total area covered by young seedling stands (height of the dominant tree storey <1.3 m) within the operational areas of the same Forest Management Associations in which trappings were carried out.

4. Discussion

Roughly 25% of Finnish forests suffer at any given time from various sources of qualitative or quantitative damage (Peltola, 2007). In total, vertebrates are a cause of damage on ca. 3.4% of total forest land area (Peltola, 2007). While moose (*Alces alces*) are often suggested to be the most considerable vertebrate pest in northern boreal silviculture (Lavsund, 1987; Edenius et al., 2002; Tomppo and Joensuu, 2003), correspondence with regional forestry centre officials consistently indicates that in years of peak abundance voles are considered in many areas clearly more detrimental to forest health than moose. Voles can therefore be regarded as one of the most serious pests of silviculture in Northern Europe.

Vole populations in northern Fennoscandia fluctuate cyclically with a period of 3–5 years (Hansson and Henttonen, 1985, 1988; Hanski et al., 1991; Sundell et al., 2004; Korpimäki et al., 2005; Kallio et al., 2009). In peak phases of the cycle, field voles may attain densities exceeding 400–500, and bank voles densities exceeding 100 individuals/ha, while during low phases densities may remain well below one individual/ha (Myllymäki, 1977b). In the peak phase of a cycle, voles suffer from a lack of high quality food, namely overwintering green basal grass stems (Huitu et al., 2003a). This greatly increases the likelihood of voles resorting to food items of poorer quality than grasses, such as tree seedlings.

According to our prediction, the relative abundance of voles was positively associated with the degree of damage to silviculture on a nationwide scale (Fig. 2). This clearly demonstrates that vole population monitoring is a valid and effective tool for predicting near-future damage to silviculture. However, the observed relationship between the degree of damage and vole abundance was far from unequivocal. A considerable amount of variation exists in the degree of damage between areas that could not be accounted for by vole densities (Fig. 2; see also Henttonen et al., 1995).

Modern silvicultural practices involve a multitude of successive protocols which may influence the susceptibility of a given seedling or seedling stand to vole damage, independently of vole abundance. These may include, e.g., choice of seedling species (Gill, 1992a; Hjältén et al., 2004), seedling origin (Rousi, 1983; Rousi et al., 1997), fertilization (Roy and Bergeron, 1990; Rousi et al., 1993), site preparation (Löf et al., 2006), seedling protection (Löf et al., 2004) and ground vegetation control (Hytönen and Jylhä, 2005). Also weather conditions, especially in winter (Aars and Ims, 2002; Korslund and Steen, 2006), proximity of seedling stands to optimal vole habitat, as well as the relative abundance of natural enemies, such as predators or pathogens, may affect the magnitude of vole damage. It is evident that different combinations of the above mentioned factors may well generate great variation in how vole abundances translate into damage. What is therefore equally clear is that effective control programs against vole damage must be multifactorial in their approach, including, e.g., avoidance of planting in years with exceptionally high vole densities, controlling ground vegetation as effectively as possible, using tree shelters when feasible and even vole trapping or poison baiting.

Variation in our results may also stem from inter-areal differences in damage assessment. Results from the study questionnaire regarding verified numbers of destroyed tree seedlings are based on field inspections in damaged stands. Most often these inspections are carried out as circular point counts of viable seedlings using a radius of 3.99 m (50 m²) in spring or early summer. The reliability of inspections is at its best in early summer, before ground vegetation increases too much in height to prevent effective visual counting. However, early inspections may lead to an overestimation of mortality, as small seedlings often recover well from clipping damage (Vandenbergh et al., 2008). Severed seedlings commonly develop new leader shoots from adventitious buds or from lateral shoots located below the wound (Gill, 1992b), but these may not be visible from a distance of a few

meters until later in the summer. Hence viable seedlings may be falsely classified as destroyed by voles.

There are two reasons which suggest that such inspection biases do not compromise the general validity of our results. Firstly, it is apparent from the magnitude of estimations provided by the directors of the FMAs that only a portion of the actual damages had been verified at the time of the questionnaire. Furthermore, it is likely that a large proportion of forest owners never reported damage from their stands (Hänninen et al., 2001). Secondly, according to directors, verified numbers of seedlings destroyed were often derived from and directly proportional to the amounts of seedlings ordered from nurseries for restocking or replanting following vole damage. Therefore economic losses due to voles were unaffected by the potential subsequent recovery of inspected seedlings. Both factors lead us to believe that the figures presented here likely represent conservative estimates of vole damage to privately owned forests in the year in question.

Vole damage to forest tree seedlings may have both direct and/or indirect negative effects on seedling survival and tree quality. In addition to direct negative effects in the form of increased mortality, the effects of mammalian browsing, also by voles, may also be indirect. Damage may lead to growth losses over several years (Lavsund, 1987; Danell et al., 1994; Zamora et al., 2001; Edenius et al., 2002), which in turn may influence rotation times and financial returns on a temporal scale of decades. Vole-induced wounding may also increase the likelihood of pathogenic infections by e.g., rot- and stain-causing fungi, which may increase tree mortality with a substantial delay (Bazzigher, 1973; Roll-Hansen and Roll-Hansen, 1980; Gill, 1992b; Henttonen et al., 1994). The consumption of apical buds, particularly by bank voles, induces switching of leader shoots, which results in crookedness and malformations in the stem trunk, which may greatly reduce tree quality as sawtimber (Heikkilä and Löyttyniemi, 1992). Although potentially considerable, the indirect effects of vole damage in economic terms are impossible to estimate from our current data.

Our estimates of economic losses due to vole damage are based on the hectare-wise summed costs of soil preparation (i.e., mounding) and replanting (Peltola, 2007). In many cases, soil preparation may not be necessary prior to replanting, particularly in young clearcuts in which ground vegetation does not yet dominate. If this is the case, costs of re-establishing entire seedling stands may decrease by ca. 30% (Peltola, 2007). However, seedling performance tends to decrease as the time between soil preparation and planting increases (Nilsson and Örländer, 1995). Also, restocking stands in which vole damage is patchy and only partial is relatively more costly than replanting entire stands. Both factors increase the total estimate of the financial impact of vole damage correspondingly.

Recent trapping surveys in autumn 2008 indicated that vole population densities have in many areas of southern Finland reached higher levels than encountered during any earlier period during the ca. 30-year history of the vole monitoring scheme of Metla (see Metla's biannual vole abundance reports [in Finnish]: <http://www.metla.fi/tiedotteet/list/myyrat.htm>). Population fluctuations have been very regular in Finland after a lower-amplitude period of irregularity in the mid 1990s. This contrasts findings from elsewhere in Europe, where in many areas small rodent cyclicity appears to be disappearing (Ims et al., 2008). Vole population fluctuations in Finland have also been increasing steadily in amplitude during the past decade, nearing highest densities ever recorded. No consensus has emerged as to the cause of these changes in vole dynamics, but it is very likely that they are merely random long-term fluctuations that have also been documented in earlier decades. Nonetheless, observations from vole time series together with our present results suggest that vole damage to

silviculture has increased considerably after the turn of the century, currently far exceeding those recorded in earlier decades (Teivainen, 1981). If vole population fluctuations do not change radically, levels of damage to Finnish forests will continue to be great also in the near future. There is a clear need to allocate more research effort into the identification of those factors, which may most feasibly be manipulated to minimize vole damage to silviculture in the future.

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References

- Aars, J., Ims, R.A., 2002. Intrinsic and climatic determinants of population demography: the winter dynamics of tundra voles. *Ecology* 83, 3449–3456.
- Anon., 2001. Hyvän metsänhoidon suositukset. Metsätalouden kehittämiskeskus Tapio. Metsäkustannus Oy, Helsinki (in Finnish).
- Baxter, R., Hansson, L., 2001. Bark consumption by small rodents in the northern and southern hemispheres. *Mammal Review* 31, 47–59.
- Bazzigher, G., 1973. Wound rot in spruce stands after bark stripping. *European Journal of Forest Pathology* 3, 71–82.
- Danell, K., Bergström, R., Edenius, L., 1994. Effects of large mammalian browsers on architecture, biomass, and nutrients of woody plants. *Journal of Mammalogy* 75, 833–844.
- Edenius, L., Bergman, M., Ericsson, G., Danell, K., 2002. The role of moose as a disturbance factor in managed boreal forests. *Silva Fennica* 36, 57–67.
- Gill, R.M.A., 1992a. A review of damage by mammals in north temperature forests. 2. Small mammals. *Forestry* 65, 281–308.
- Gill, R.M.A., 1992b. A review of damage by mammals in north temperature forests. 3. Impact on trees and forests. *Forestry* 65, 363–388.
- Hanski, I., Hansson, L., Henttonen, H., 1991. Specialist predators, generalist predators, and the microtine rodent cycle. *Journal of Animal Ecology* 69, 353–367.
- Hansson, L., Henttonen, H., 1985. Gradients in density variations of small rodents: the importance of latitude and snow cover. *Oecologia* 67, 394–402.
- Hansson, L., Henttonen, H., 1988. Rodent dynamics as community processes. *Trends in Ecology and Evolution* 3, 195–200.
- Hansson, L., 1986. Bark consumption of voles in relation to snow cover, population density and grazing impact. *Holarctic Ecology* 9, 312–316.
- Hansson, L., Larsson, T.-B., 1980. Small rodent damage in Swedish forestry during 1971–1979. *Swedish Wildlife Research* 1, 1–64.
- Heikkilä, R., Löyttyniemi, K., 1992. Growth response of young Scots pines to artificial shoot breaking simulating moose damage. *Silva Fennica* 26, 19–26.
- Henttonen, H., Wallgren, H., 2001. Small rodent dynamics and communities in the birch forest zone of northern Fennoscandia. In: Wielgolaski, F.E. (Ed.), *Nordic Mountain Birch Forest Ecosystems*, 27. UNESCO Man and Biosphere Series, UNESCO, Paris and Parthenon Publishing Group, New York and London, Man and the Biosphere Series, pp. 261–278.
- Henttonen, H., Lilja, A., Niemimaa, J., 1994. Myyrien ja hyönteisten aiheuttamat sieni-infektioit koivun taimien uhkana. Metsäntutkimuslaitoksen tiedonantoja 496, 125–129 (in Finnish).
- Henttonen, H., Niemimaa, J., Kaikusalo, A., 1995. Myyrät ja pellonmetsitys. In: Hytönen, J., Polet, K. (Eds.), *Peltojen metsitysmenetelmä*, vol. 581. Metsäntutkimuslaitoksen tiedonantoja, pp. 97–117 (in Finnish).
- Henttonen, H., Kaikusalo, A., Tast, J., Viitala, J., 1977. Interspecific competition between small rodents in subarctic and boreal ecosystems. *Oikos* 29, 581–590.
- Hjältén, J., Danell, K., Ericson, L., 2004. Hare and vole food browsing preference during winter. *Acta Theriologica* 49, 53–62.
- Huitu, O., Koivula, M., Korpimäki, E., Klemola, T., Norrdahl, K., 2003a. Winter food supply limits growth of northern vole populations in the absence of predation. *Ecology* 84, 2108–2118.
- Huitu, O., Norrdahl, K., Korpimäki, E., 2003b. Landscape effects on temporal and spatial properties of vole population fluctuations. *Oecologia* 135, 209–220.
- Hytönen, J., Jylhä, P., 2005. Effects of competing vegetation and post-planting weed control on the mortality, growth and vole damages to *Betula pendula* planted on former agricultural land. *Silva Fennica* 39, 365–380.

- Hänninen, H., Karppinen, H., Ovaskainen, V., Ripatti, P., 2001. Metsänomistajan uudistamiskäyttötymien. Metsätieteen aikakauskirja 4, 615–629 (in Finnish).
- Ims, R.A., Henden, J.-A., Killengreen, S.T., 2008. Collapsing population cycles. *Trends in Ecology and Evolution* 23, 79–86.
- Kallio, E.R., Begon, M., Henttonen, H., Koskela, E., Mappes, T., Vaheri, A., Vapalahti, O., 2009. Cyclic hantavirus epidemics in humans—predicted by rodent host dynamics. *Epidemics* 1 (2009), 101–107.
- Kaneko, Y., Nakata, K., Saitoh, T., Stenseth, N.C., Bjørnstad, O.N., 1998. The biology of the vole *Clethrionomys rufocanus*: a review. *Researches on Population Ecology* 40, 21–37.
- Kanervo, V., Myllymäki, A., 1970. Problems caused by the field vole *Microtus agrestis* (L.) in Scandinavia. EPP0 Publications Series A 58, 11–26.
- Kontianen, P., Brommer, J.E., Karell, P., Pietiäinen, H., 2008. Heritability, plasticity and canalization of ural owl egg size in a cyclic environment. *Journal of Evolutionary Biology* 21, 88–96.
- Korpimäki, E., Norrdahl, K., Huitu, O., Klemola, T., 2005. Predator-induced synchrony in population oscillations of co-existing small mammal species. *Proceedings of the Royal Society of London B* 272, 193–202.
- Korslund, L., Steen, H., 2006. Small rodent winter survival: snow conditions limit access to food resources. *Journal of Animal Ecology* 75, 156–166.
- Larsson, T.-B., 1973. Smågnagarskador på skogskulturer i Sverige 1900–1970—small rodent damage in Swedish forestry during the period 1900–1970. Institutionen för Skogszoologi. Rapport och uppsatser 14. 26 p. (in Swedish with English summary).
- Lav Sund, S., 1987. Moose relationships to forestry in Finland, Norway and Sweden. *Swedish Wildlife Research (Suppl. 1)*, 229–244.
- Löf, M., Thomsen, A., Madsen, P., 2004. Sowing and transplanting of broadleaves (*Fagus sylvatica* L., *Quercus robur* L., *Prunus avium* L. and *Crataegus monogyna* Jacq.) for afforestation of farmland. *Forest Ecology and Management* 188, 113–123.
- Löf, M., Rydberg, D., Bolte, A., 2006. Mounding site preparation for forest restoration: survival and short term growth response in *Quercus robur* L. seedlings. *Forest Ecology and Management* 232, 19–25.
- Moran, P.A.P., 1953. The statistical analysis of the Canadian lynx cycle. I. Structure and prediction. *Australian Journal of Zoology* 1, 163–173.
- Myllymäki, A., 1977a. Outbreaks and damage by the field vole, *Microtus agrestis* (L.) since World War II in Europe. *EPP0 Bulletins* 7, 177–207.
- Myllymäki, A., 1977b. Demographic mechanisms in the fluctuating populations of the field vole *Microtus agrestis*. *Oikos* 29, 468–493.
- Nilsson, U., Örländer, G., 1995. Effects of regeneration methods on drought damage to newly planted Norway spruce seedlings. *Canadian Journal of Forest Research* 25, 790–802.
- Peltola, A. (Ed.), 2007. Finnish Statistical Yearbook of Forestry 2007. Finnish Forest Research Institute, (in Finnish with English summary), p. 434.
- Roll-Hansen, F., Roll-Hansen, H., 1980. Microorganisms which invade *Picea abies* in seasonal stem wounds. 2. Ascomycetes, fungi imperfecti, and bacteria—general discussion, hymenomycetes included. *European Journal of Forest Pathology* 10, 396–410.
- Rousi, M., 1983. Myyrien aiheuttamat vahingot Pohjois-Suomen puulajikoikeissa talvella 1981/82. *Folia Forestalia* 569, 1–10 (in Finnish).
- Rousi, M., Tahvanainen, J., Henttonen, H., Uotila, I., 1993. The effect of shading and fertilization on the resistance of winter-dormant European white birch (*Betula pendula*) to vole and hare feeding. *Ecology* 74, 30–38.
- Rousi, M., Tahvanainen, J., Henttonen, H., Herms, D.A., Uotila, I., 1997. Clonal variation in susceptibility of white birches (*Betula* spp.) to mammalian and insect herbivores. *Forest Science* 43, 396–402.
- Roy, J., Bergeron, J.-M., 1990. Role of phenolics of coniferous trees as deterrents against debarking behavior of meadow voles (*Microtus pennsylvanicus*). *Journal of Chemical Ecology* 16, 801–808.
- Stenseth, N.C., 1999. Population cycles in voles and lemmings: density dependence and phase dependence in a stochastic world. *Oikos* 87, 427–461.
- Sundell, J., Huitu, O., Henttonen, H., Kaikusalo, A., Korpimäki, E., Pietiäinen, H., Saurola, P., Hanski, I., 2004. Large-scale spatial dynamics of vole populations in Finland revealed by the breeding success of vole-eating avian predators. *Journal of Animal Ecology* 73, 167–178.
- Teivainen, T., 1981. Geographic trends in voles in Finland in the years 1973–1980. *Metsäntutkimuslaitoksen tiedonantoja* 21, 1–18.
- Tomppo, E., Joensuu, J., 2003. Hirvieläinten aiheuttamat metsätuhot Etelä-Suomessa valtakunnan metsien 8. ja 9. inventoinnin mukaan. *Metsätieteen aikakauskirja* 4, 507–535 (in Finnish).
- Turchin, P., 2003. *Complex Population Dynamics: A Theoretical/Empirical Synthesis*. Princeton University Press, Princeton and Oxford.
- Vandenberghe, C., Freléhoux, F., Buttler, A., 2008. The influence of competition from herbaceous vegetation and shade on simulated browsing tolerance of coniferous and deciduous saplings. *Oikos* 117, 415–423.
- Zamora, R., Gómez, J.M., Hódar, J.A., Castro, J., García, D., 2001. Effect of browsing by ungulates on sapling growth of Scots pine in a Mediterranean environment: consequences for forest regeneration. *Forest Ecology and Management* 144, 33–42.