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Small mammal abundance in relation to environmental variables in three Swedish forest phases

Smådäggdjurens talrikhet i förhållande till omvärlds-faktorer i olika skogsstadier

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Abstract

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The distribution of the most common small mammal species was examined with regard to the main forest phases ('afforestations', mature forests and 'reforestations'), plant communities, basic habitat variables and management techniques in a southern, a central and a northern Swedish region. The density indices from trapping with standard methods showed different patterns of population fluctuation in these regions. There were many clear differences in the distribution of the various species in the different plant communities. For example, field voles Microtus agrestis *and shrews* Sorex araneus *appeared in highest numbers in luxuriant communities on peaty soil in the autumn, and wood mice* Apodemus sylvaticus *appeared in greatest numbers in areas with plant colonization on recently abandoned fields. In several instances such habitats could be identified as potential surplus areas for the small mammals. Habitat factors especially germane to the abundance of small mammals were depth of litter and humus, amount of boulders, vertical cover and soil moisture. Significant management techniques in this connection were ditching, cleaning in forest and reforestations and burning. Possible causal relations behind the distributions are discussed.*

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Contents

1 Introduction

Small mammals are economically important to Swedish forestry. The damage caused by them is well known, but in some respects (e.g. by eating pest insects) they may have a beneficial influence. The field vole, *Microtus agrestis* (L.) debarks tree seedlings on abandoned farm land ("afforestations") and on replanted forest land ("reforestations"). This is perhaps the most important small mammal damage in Nordic forestry (Myllymäki 1977a). Similar damage is done by the bank vole, *Clethrionomys glareolus* Schr., although presumably to a smaller extent (Hansson and Zejda 1977). Both bank voles and mice (viz. the wood mouse, *Apodemus sylvaticus* L. and the yellow-necked mouse, *Apodemus flavicollis* Melch.) devour sown tree seeds (Hansson 1975a). Such seeds have also been found to be eaten by the otherwise insectivorous shrew, *Sorex araneus* L. (Myllymäki and Paasikallio 1972).

The occurrence of the small mammal species in the various habitats is known in a very general way. But there have been surprisingly few quantitative studies on differences between habitats and, similarly, little analysis of the habitat factors determining the densities of the various small mammal species. This study was primarily intended to ascertain variations in numbers of small mammals between distinct forest types. A second aim was to elucidate general habitat variables correlated with the abundance of the various species. Finally, the abundance would be analysed in relation to management practices.

It was thus intended to make a survey of relative densities of the small mammal species in various forest environments. Such a description may be of practical value to foresters wishing to avoid undue damage from these animals. Causal relations behind the distribution of the animals will be treated in other contexts.

2 Methods

Small mammals were sampled in 1971—75 with standard methods in a southern, a central and a northern Swedish region as well as in Norway and Finland (Myllymäki *et al.* 1977). Trapping was performed in abandoned fields, often planted with forest seedlings, in mature spruce (or, in one locality, beech) forest and in reforestations. Sampling was performed in spring (May—June) and autumn (mainly October) in all eight localities (Fig. 1), but less regularly in high summer (July—August). Each locality comprised some 500 km^2.

Small quadrats (SQ) according to Myllymäki *et al.* (1971) were used as sampling units. Three snap-traps were placed within a 1.5 m radius in each of the four corners of a 15×15 m quadrat. The traps were baited with dried apples and Polish wicks (Grodzinski *et al.* 1966). The traps were examined for trapped animals during two consecutive days. This two-day catch was used as an index of the small mammal density. However, the relations between index and density values vary between different rodent species and is obscure for the shrews (Hansson 1975b). Thus, the indices of various species cannot be compared. Water voles, *Arvicola terrestris* (L.) are generally too big for the traps used so no evaluation will be made for the few individuals of this species caught. Other species caught in small numbers included wood lemming, *Myopus schisticolor* (Lillj.), pygmy shrew, *Sorex minutus* L. and watershrew, *Neomys fodiens* L. The total number of animals examined was approx. 8500 (1723 *M. agrestis,* 4267 *C. glareolus,* 65 *C. rufocanus,* 543 *A. flavicollis,* 1137 *A. sylvaticus* and 754 *S. araneus*).

In each locality and for each sampling period, three to six starting points were selected at random. From there SQ:s were

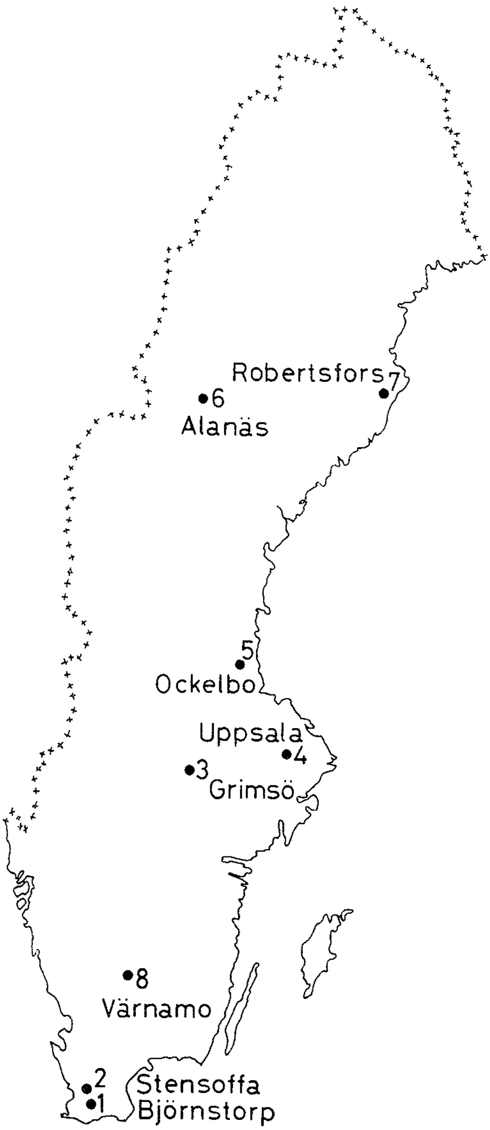


Figure 1. Trapping localities during the 1971—75 survey. They are pooled into three regions with localities 1, 2, and 8 forming South Sweden, 3, 4, and 5 Central Sweden and 6 and 7 North Sweden.

distributed at intervals of 100 m. They were laid out in the most extensive direction in the different plots of the three forest phases. Care was taken to ensure that no systematic pattern in the habitats coincided with the distribution of the quadrats.

For each SQ a number of variables were examined and denoted. They constituted three groups:

A. Classification of the forest phase and plant community. The latter was mainly recognized according to Kielland-Lund (1971) as regards mature forest vegetation and according to Hansson and Myllymäki (1974) for unstable and ecologically poorly studied vegetation in abandoned fields and reforestations.

B. Soil conditions and physical factors. In principle the terminology and definitions of the Swedish Forest Survey (Riksskogstaxeringen 1971) were used.

C. Forest management. In this case division was also made largely according to the definitions of the Swedish Forest Survey. The classifications are shown in connection with certain analyses presented in "Results".

Differences in index values between habitats, physical factors, or types of management were examined by one-way analysis of variance with the two-day catch of each SQ being the sampling unit. However, owing to great seasonal and/or annual variations in rodent numbers the material had to be split into certain regions, years and seasons. Physical factors were examined for all habitats jointly in order to discover (if possible) basic and predictive characteristics for the occurrence of the various species. Effects of management were examined separately for each forest phase, but certain practices appeared in two or three of them.

3 Results

3.1 Density variations during 1971—75

The annual and seasonal variations in density indices are shown in Figs. 2—4. The variations were examined with respect to abandoned farm land, mature forests and reforestations for the commonest species in these forest phases. The various localities were pooled into the three geographical regions. Mid-summer and autumn indices from the same year were generally similar and were also pooled.

In southern Sweden there were pronounced seasonal variations in density for all species with low abundance in spring and yearly peaks in summer—autumn. The annual variations were small or random, there being no evidence of cyclic changes in density. In central Sweden there was a pronounced peak in autumn, 1973, in the vole species. The abundance of *C. glareolus* was high as early as in the autumn, 1972. The spring densities in 1973 and 1974 were fairly high, while remaining springs and autumns showed low values. In northern Sweden the peak lasted between autumn, 1972, and autumn, 1974, with relatively high numbers also during intervening springs. In 1971 and 1975 there were very few animals. The mice, *Apodemus* spp. were common only in southern Sweden. Shrews, *S. araneus,* were found all over Sweden but did not show such violent fluctuations in numbers as did the voles. However, there was a small peak in shrew numbers in the autumn, 1972, and a slight increase in 1975.

Because of the density variations, the material was divided into regions and seasons, which had to be analysed separately. The data from southern Sweden were divided into the two groups of spring and summer—autumn catches for the whole of the period, 1971—75. For central Sweden two groups were also distinguished: for the autumns of 1972 and 1973 and the springs of 1973 and 1974. For northern Sweden corresponding groups comprised the autumns of 1972, 1973 and 1974 and the springs of 1973 and 1974. The remaining material for central and northern Sweden was very sparse, so the data from the "low" years had to be disregarded.

3.2 Density variations between forest phases and plant communities

First, differences in densities were examined for the three major forest phases. The results are shown in Fig. 5. Abandoned fields in southern Sweden were divided into those of peat and those of mineral soil. A smaller number of samples were also taken on mires and in mature pine forests (on sandy sediments). Results from the two latter habitats will only be discussed briefly.

In southern Sweden (Fig. 5A) almost all species showed significant differences in numbers between forest phases. *M. agrestis* was absent from mature forests. It was considerably more common in abandoned fields on peat soil than in fields on mineral soil or in reforestations in autumn, the reverse being true for spring. *C. glareolus* was a little more common in reforestations than in mature forest, both in spring and summer—autumn. Few animals appeared in any of the seasons in abandoned fields. *S. araneus* showed small variations between habitats in spring, with the lowest numbers recorded in forests, while in autumn it showed a high abundance in abandoned fields on peat soil. *A. flavicollis* occurred in mature forests and few animals were caught in abandoned fields, which was especially true in summer—autumn. For *A. sylvaticus* there was no significant difference between the phases in spring, while in summer—autumn the species was most common in reforestations and rather scarce in abandoned fields on peat soil.

In central Sweden (Fig. 5B) *M. agrestis* did not show any difference between phases in spring but was clearly over-represented in abandoned fields in summer-autumn. It appeared in very small numbers on mires. *C. glareolus* was most common in mature forests but also showed high density indices in reforestations. It was considerably less common in mature pine forests and abandoned fields. *S. araneus* and *A. flavicollis* did not show any significant differences; *A. sylvaticus* did so in summer—autumn with the highest numbers observed in reforestations. However, only limited numbers of the last three species were trapped.

In northern Sweden (Fig. 5C) *M. agrestis* was most common in abandoned fields, especially in the autumn. As in central Sweden a few animals were caught in mature forests. Here, too, *C. glareolus* mainly occurred in the mature forests. In this region a fair number of bank voles were caught in abandoned fields, especially in the autumn. Samples from dry pine forests contained few bank voles. In the autumn, *S. araneus* was most common in abandoned fields, the northern species *C. rufocanus* at this time mainly occurring in reforestation areas.

M. agrestis was the most common species in the abandoned fields. It did not show any significant density variations between various plant communities in the spring (Fig. 6A), and in the autumn it was most common in *Carex*-tall forb communities on peat soil in southern and central Sweden. In northern Sweden no difference was detected between communities even in the autumn. *A. sylvaticus* (Fig. 6B) was most common

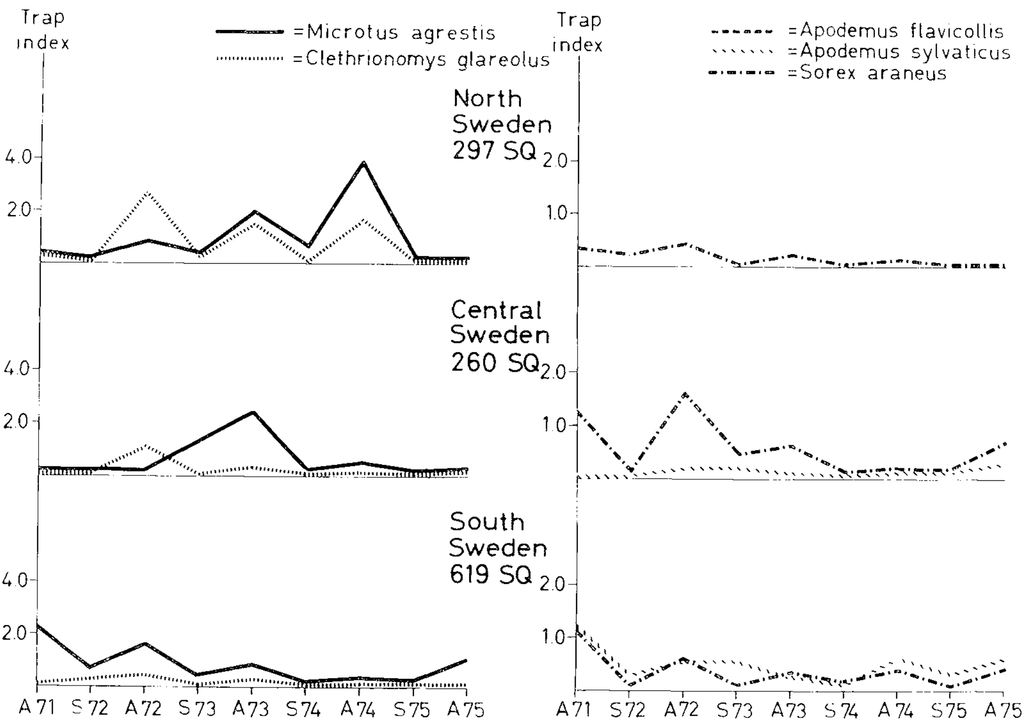


Figure 2. Annual and seasonal variations in density of the most common small mammals in afforestations. The mean number of animals caught during two days per Small Quadrat (SQ) has been used as an index ("Trap index") of density. The total number of SQ is given for each region sampled. A71 refers to (high summer—) autumn 1971, S72 to spring 1972, etc.

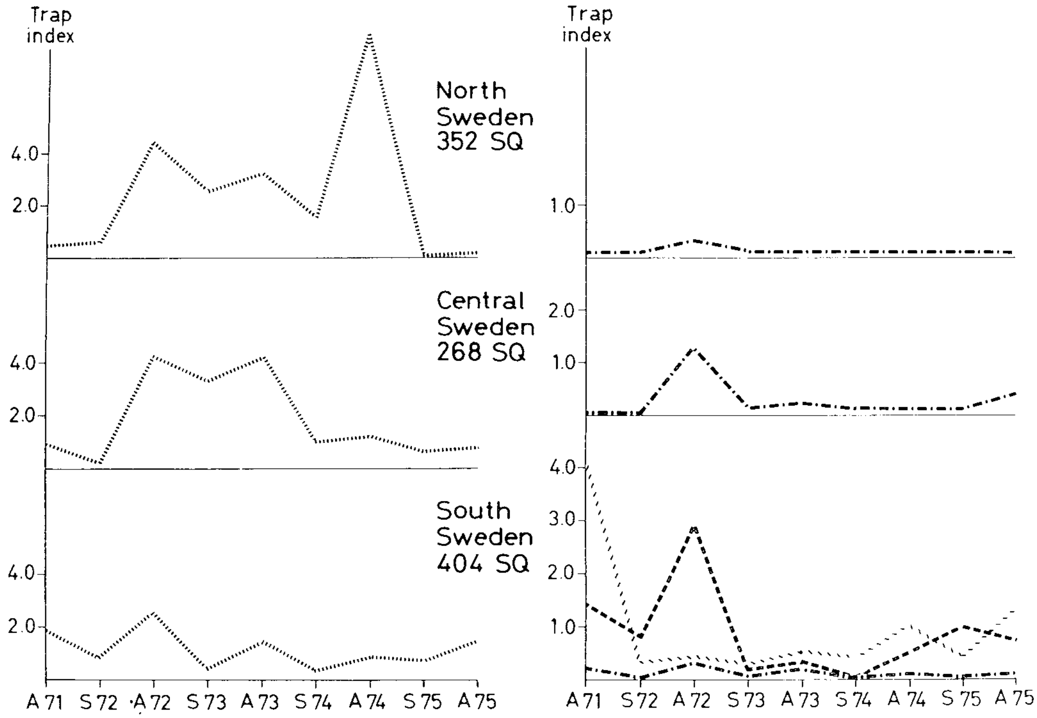


Figure 3. Annual and seasonal variations in density of the most common small mammals in mature forests. Other explanations as for Figure 2.

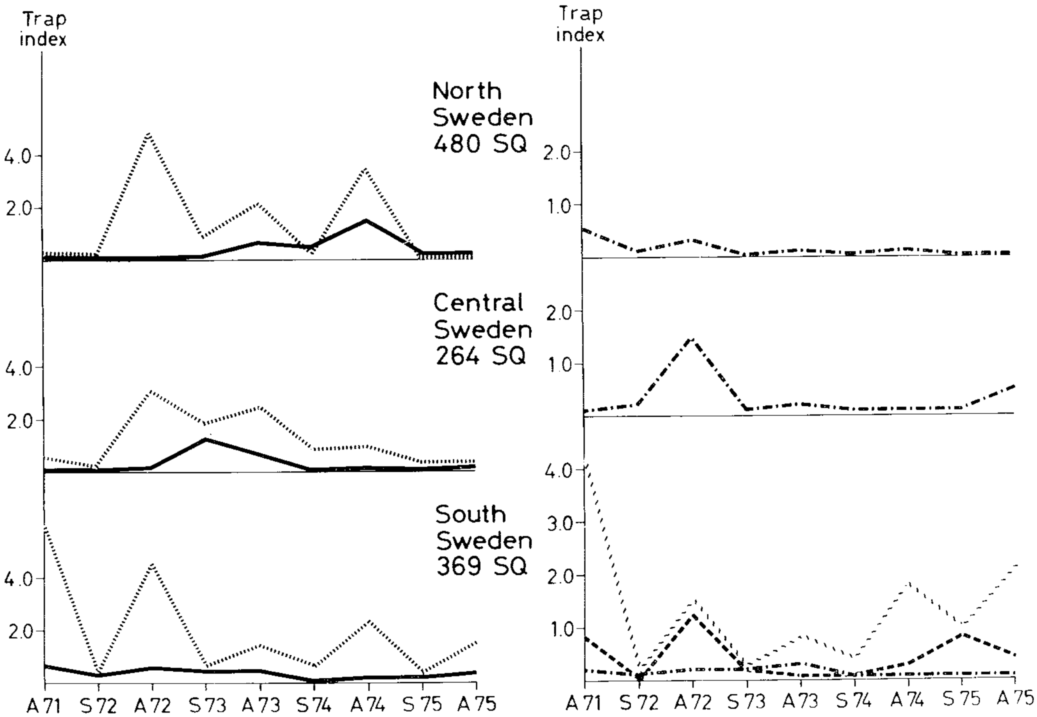


Figure 4. Annual and seasonal variations in density of the most common small mammals in reforestation areas. Other explanations as for Figure 2.

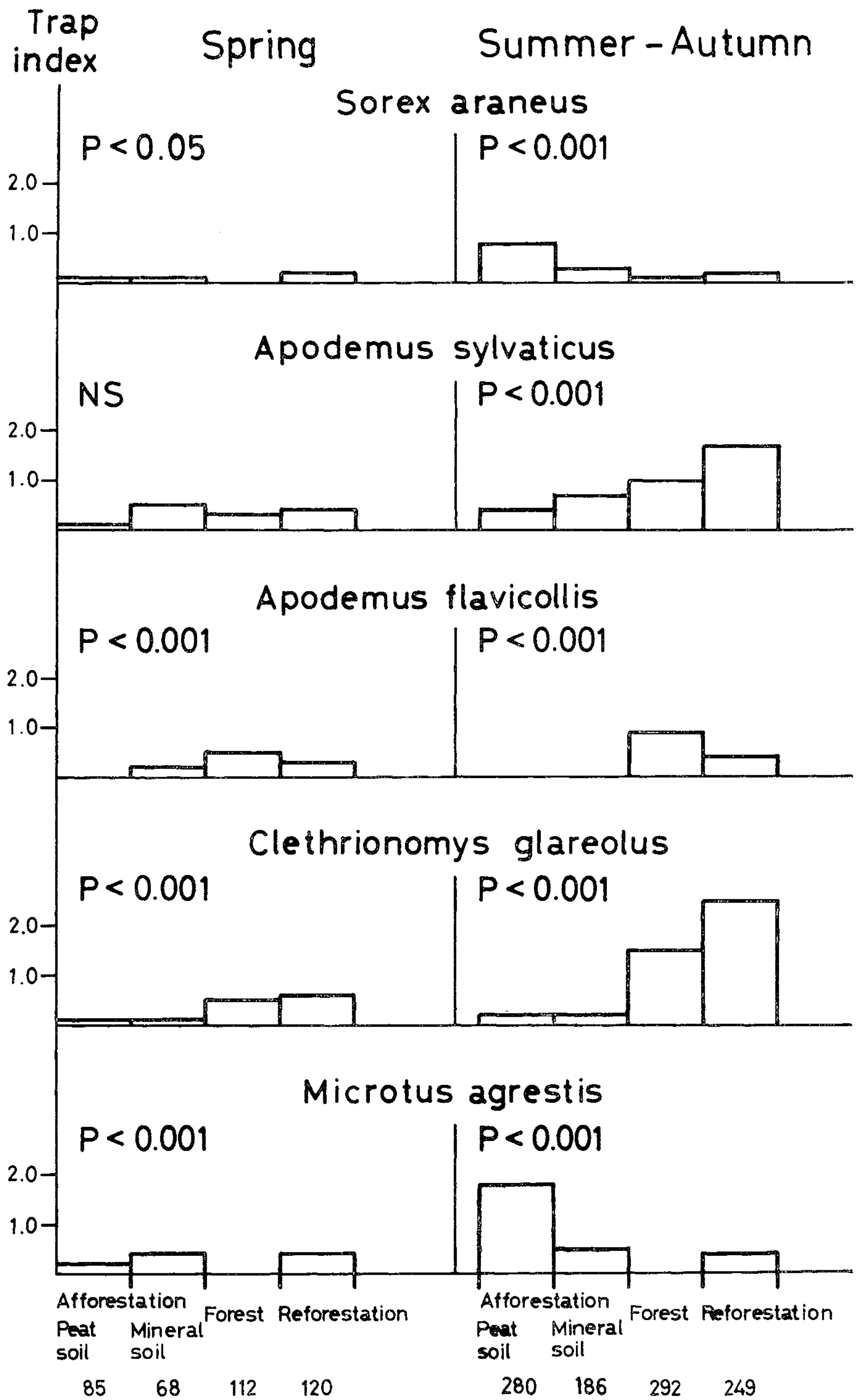
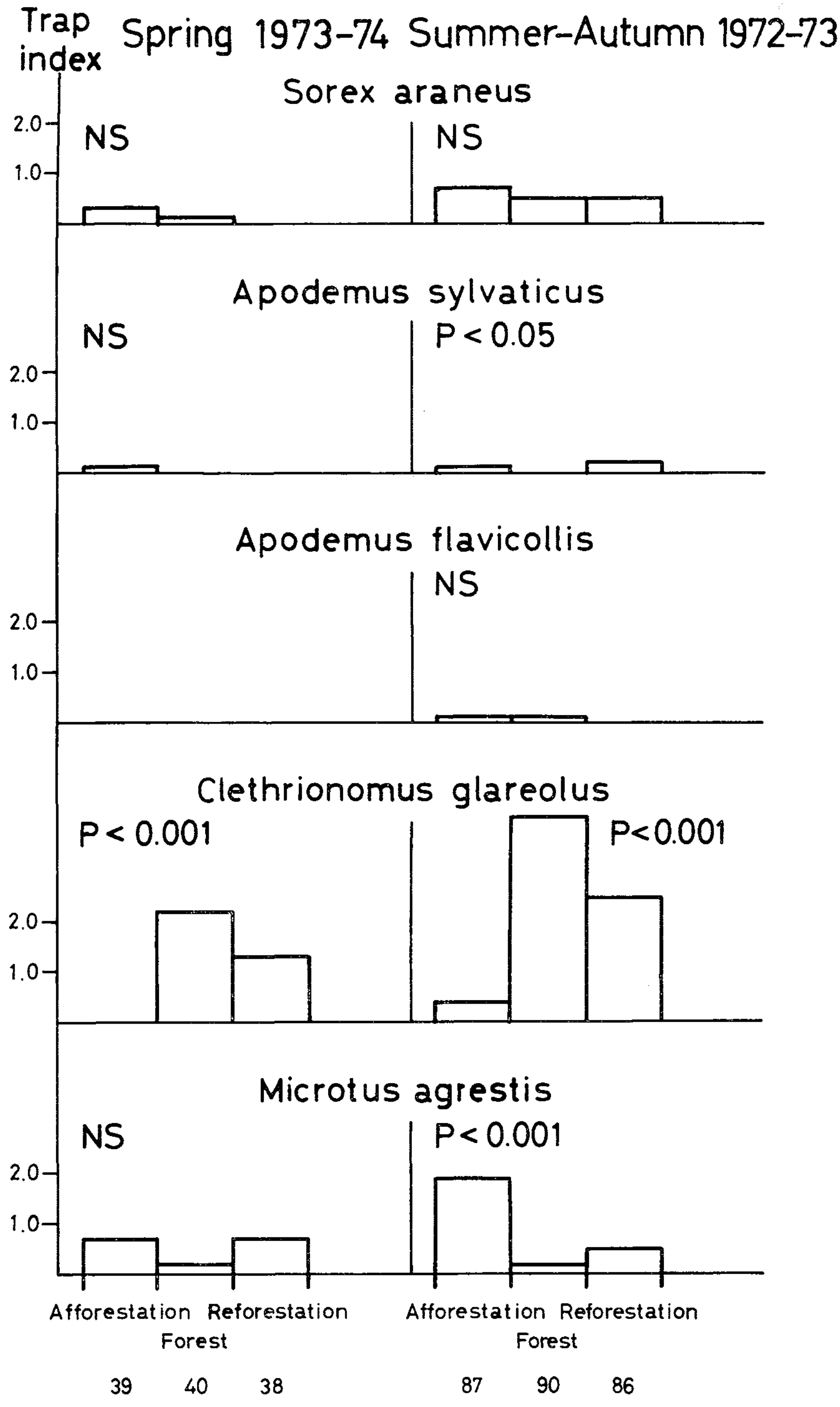
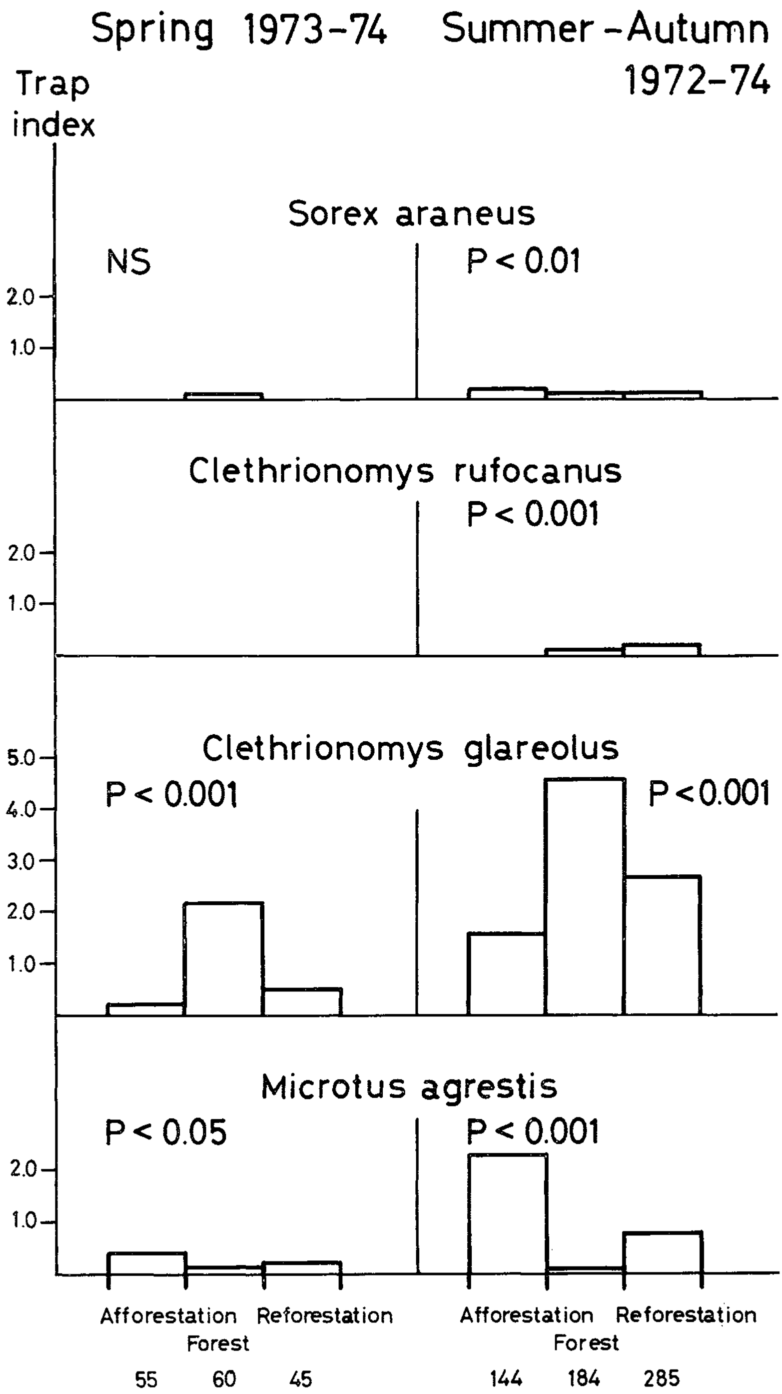


Figure 5. Differences in abundance of various small mammal species between forest phases as estimated by trap indices (explained in Figure 2).

5A. South Sweden generally. Samples from afforestations on peat soil and mineral soil have been distinguished but the significance levels (P-values) refer to comparisons between the three major phases. NS = no significant difference. The number of SQ:s is given below forestry phase.



5B. Central Sweden during peak years. Explanations as for 5A.



5C. North Sweden during peak years. Explanations as for 5A.

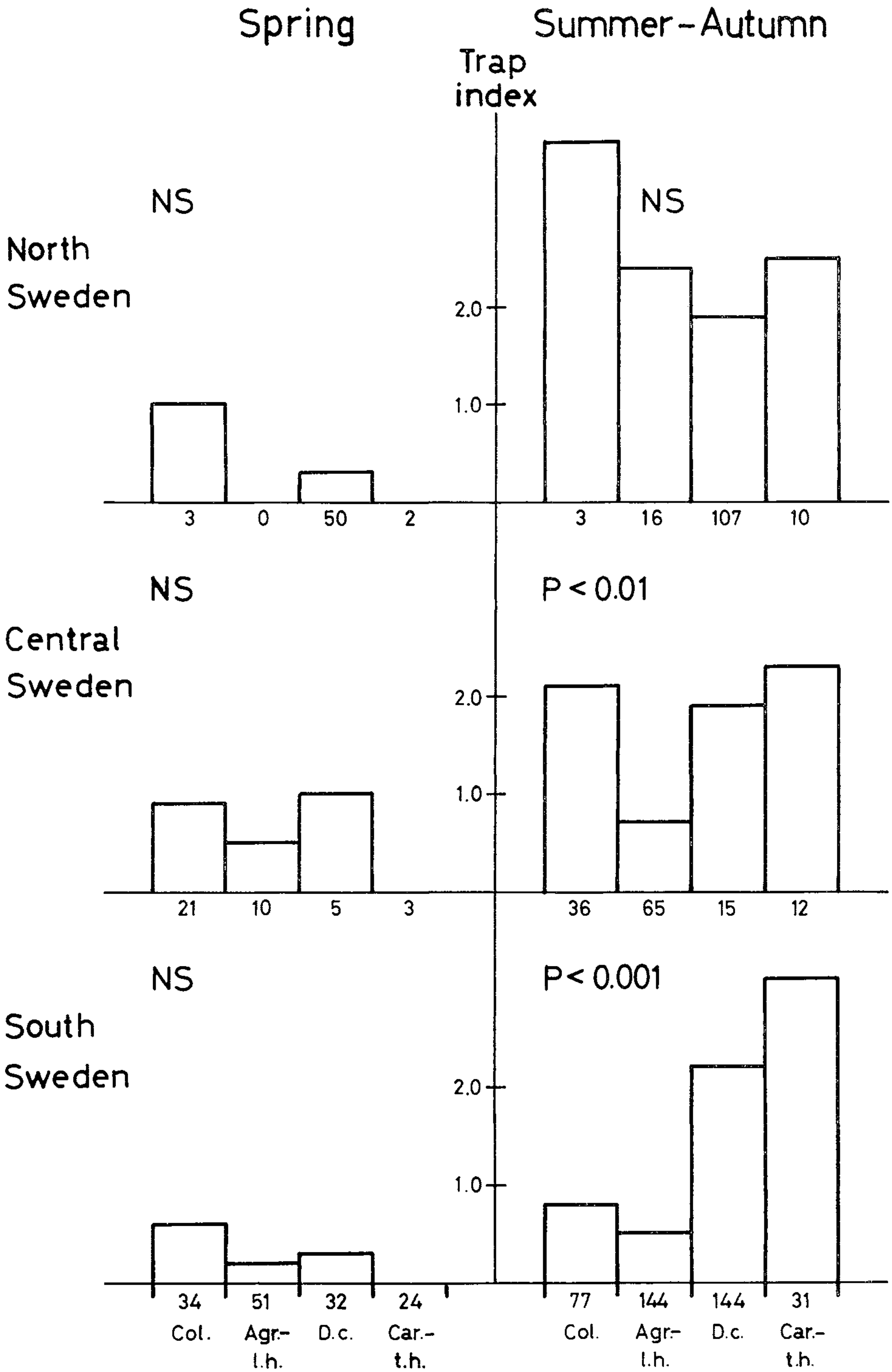
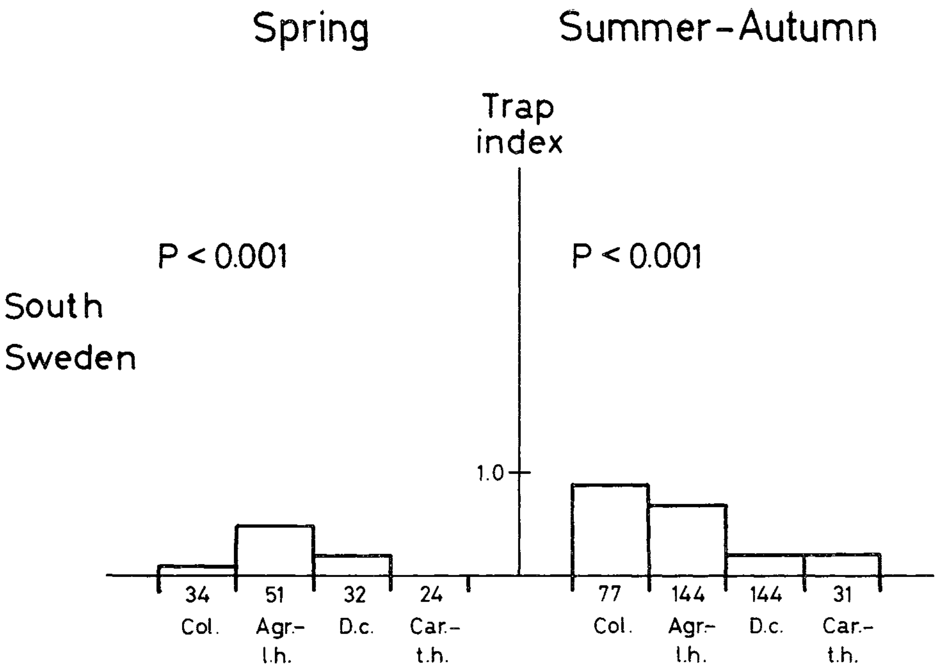


Figure 6. Variations in abundance, owing to type of plant community, of the small mammal species most common in afforestations. The following plant communities were distinguished:

Col. = the colonization phase (annuals and early grasses).
Agr.-l.h. = the *Agrostis tenuis*-low herb stage in dry fields.
D.c. = the *Deschampsia caespitosa* stage with moderate moisture.



6B. *Apodemus sylvaticus.*

in communities on dry or sandy soil, i.e. with colonizing forbs (in autumn) or in the *Agrostis*-low forb community. *S. araneus* (Fig. 6C) only showed significant differences in southern Sweden in summer—autumn and was then most common in *D. caespitosa* and *Carex*-tall forb communities on peat or moist soil. The few bank voles that appeared in abandoned fields did not show a preference for any particular plant community.

In forest communities *C. glareolus* (Fig. 7A) was the most common small mammal species. In southern Sweden it was most abundant in the rich "meadow" type of beech forest but was also numerous in the *Myrtillus* type of spruce forest. In central Sweden no differences were found between communities, although in northern Sweden the species was most common in the *Myrtillus* type in the spring and in fern-forb types in the autumn. However, no fern-forb types were sampled in spring. In spring and summer—autumn *A. flavicollis* (Fig. 7B) was most common in the meadow type of beech forests in southern Sweden. In the same region *A. sylvaticus* (Fig. 7B) was predominantly caught in summer—autumn in the mixed coniferous forest. *S. araneus* (Fig. 7C) in summer—autumn occurred in greatest numbers in the *Myrtillus* type, but was almost absent from beech forests.

Both *M. agrestis* and *C. glareolus* are common on reforestations. For *M. agrestis* (Fig. 8A) the significant differences between plant communities only occurred in northern Sweden in summer—autumn. This species was most common in the later successional stages with *Chamaenerion-Rubus idaeus* and *Betula* bushes. Also for *C. glareolus* (Fig. 8B) there were small differences be-

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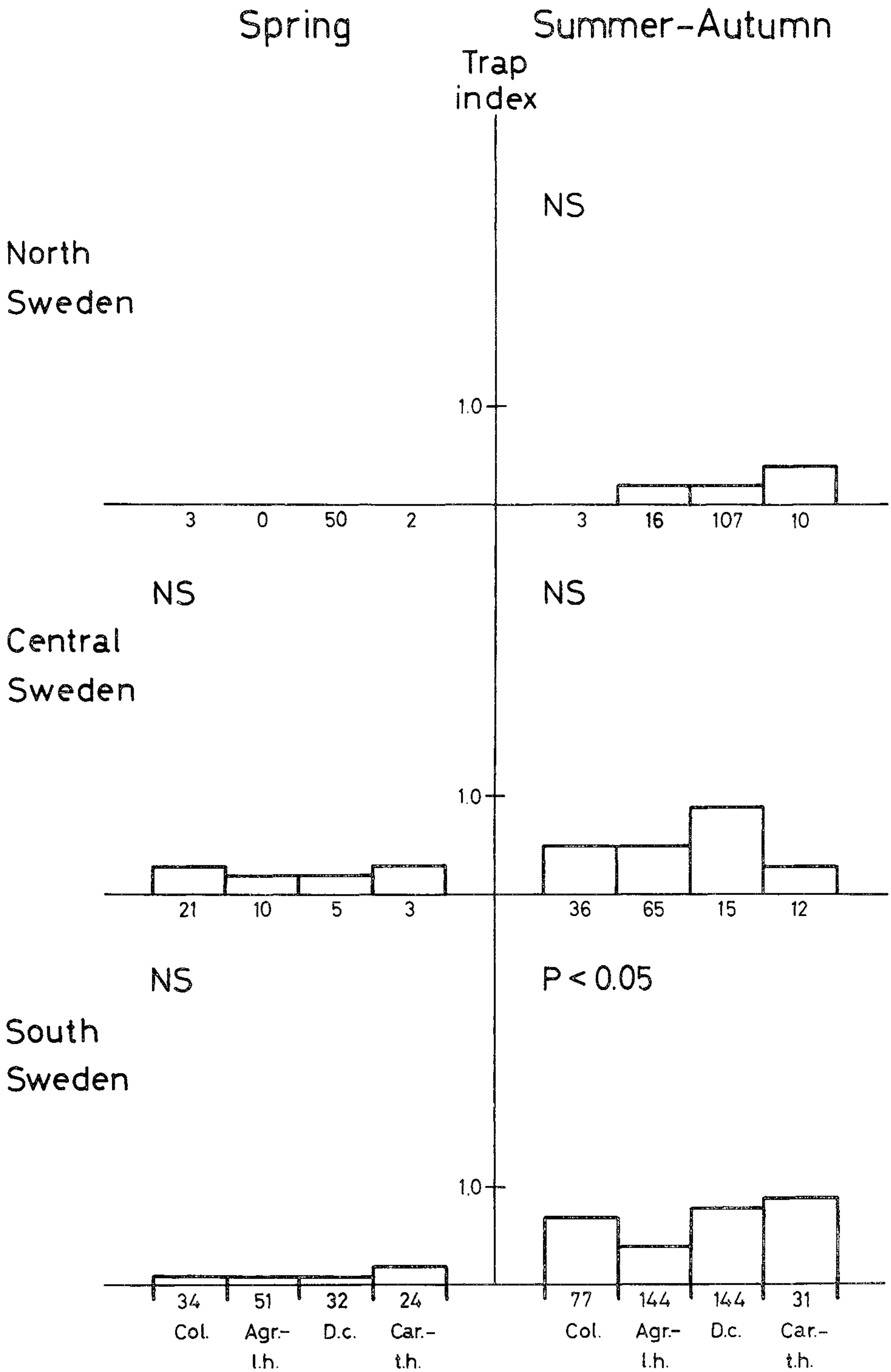
Car.-t.h. = the *Carex* spp.-tall herb stage in wet fields.
The number of SQ:s in each community is given at the base lines.
6A. *Microtus agrestis.*



6C. *Sorex araneus.*

tween communities. In the spring in central Sweden the species was most common in two communities: in the first colonization phase of the vegetation on reforestation areas; and in the latest stages e.g. with *Betula* bushes or small trees. The same distribution was observed in northern Sweden in summer—autumn. Although at insignificant levels, similar differences were found in other seasons and other regions. In southern Sweden *A. flavicollis* (Fig. 8C) was most common in the late brushwood stage of the reforestations, while in the spring, *A. sylvaticus* (Fig. 8C) appeared in largest numbers in the intermediate *Chamanaerion-Rubus idaeus* stage. *S. araneus* (Fig. 8D) did not show any differences between communities except during summer—autumn in northern Sweden, where it was most common in the *Chamaenerion-Rubus idaeus* and brushwood stages.

Potential surplus areas are indicated by the relative changes in density from spring to autumn. If, for example, a certain plant community shows a higher rate of increase and a higher autumn density level than others, this particular community may be a source from which animals invade neighbouring areas in the autumn-winter. Certain such habitats were found in this study. *M. agrestis* increased much more rapidly in afforestation areas (especially on peat soil) than in reforestation areas or forests (Fig. 5). When we turn to the plant communities (Fig. 6A) it is obvious that the moist afforestation habitats (i.e. the *Carex*-tall herb and *D. caespitosa* communities) in particular are potential surplus areas. These latter conditions were especially pronounced in southern Sweden. There were some indications of similar circumstances for *S. araneus*. *C. glareolus* increased rapidly during the summer in mixed spruce-pine forests and showed a much better recruitment in "meadow" than in "heath" beech forests (Fig. 7A). However, for this species, it was not possible clearly to define any surplus habitats. *A. flavicollis* (Fig. 7B) increased more rapidly in beech than in spruce forests and the former may represent surplus areas. The converse may be true for *A. sylvaticus* (Fig. 7B). For this latter species the colonization phase of abandoned fields apparently constitutes a surplus habitat (Fig. 6B).

3.3 **Influences of some basic factors**

The abundance of a species in various habitats may be greatly affected by a single factor. Such factors will be very important for predicting places were high densities of various rodent species will occur. However, in many cases several factors will interact, perhaps in different ways at different places or at different densities. Such factors will have a low predictive value. Yet other factors may only be correlated with decisive variables. Furthermore, if a species changes habitats seasonally, e.g. as a result of flooding, the importance of given factors in various seasons may be inverted.

In the present context we are looking for predictive factors and more complicated relationships will be disregarded. Thus, from the large number of factors examined only those showing a fairly consistant relationship with the small mammal densities will be tabulated. Other factors studied, the effect of which varied between seasons or regions or which did not show any significant effect, will only be briefly mentioned. In the following treatment all habitats are thus pooled. The same regions and seasons are delimited as in Sect. 3.2, except that spring samples from central and northern Sweden are pooled owing to the limited number of animals caught in each region.

Litter depth was an important factor for all species (Tab. 1). *M. agrestis* showed the consistently highest densities in deep litter, while *C. glareolus* appeared in places with no or little litter. *S. araneus* showed the same pattern as *M. agrestis*. The highest numbers of the two *Apodemus* species were found in litter of moderate depth.

The depth of humus was also important (Tab. 2). *M. agrestis* was found on highly humic soils (e.g. peat soils), while *C. glareolus* preferred areas with a thin to medium humus-layer. As in the previous case *S. araneus* was most similar to *M. agrestis*,

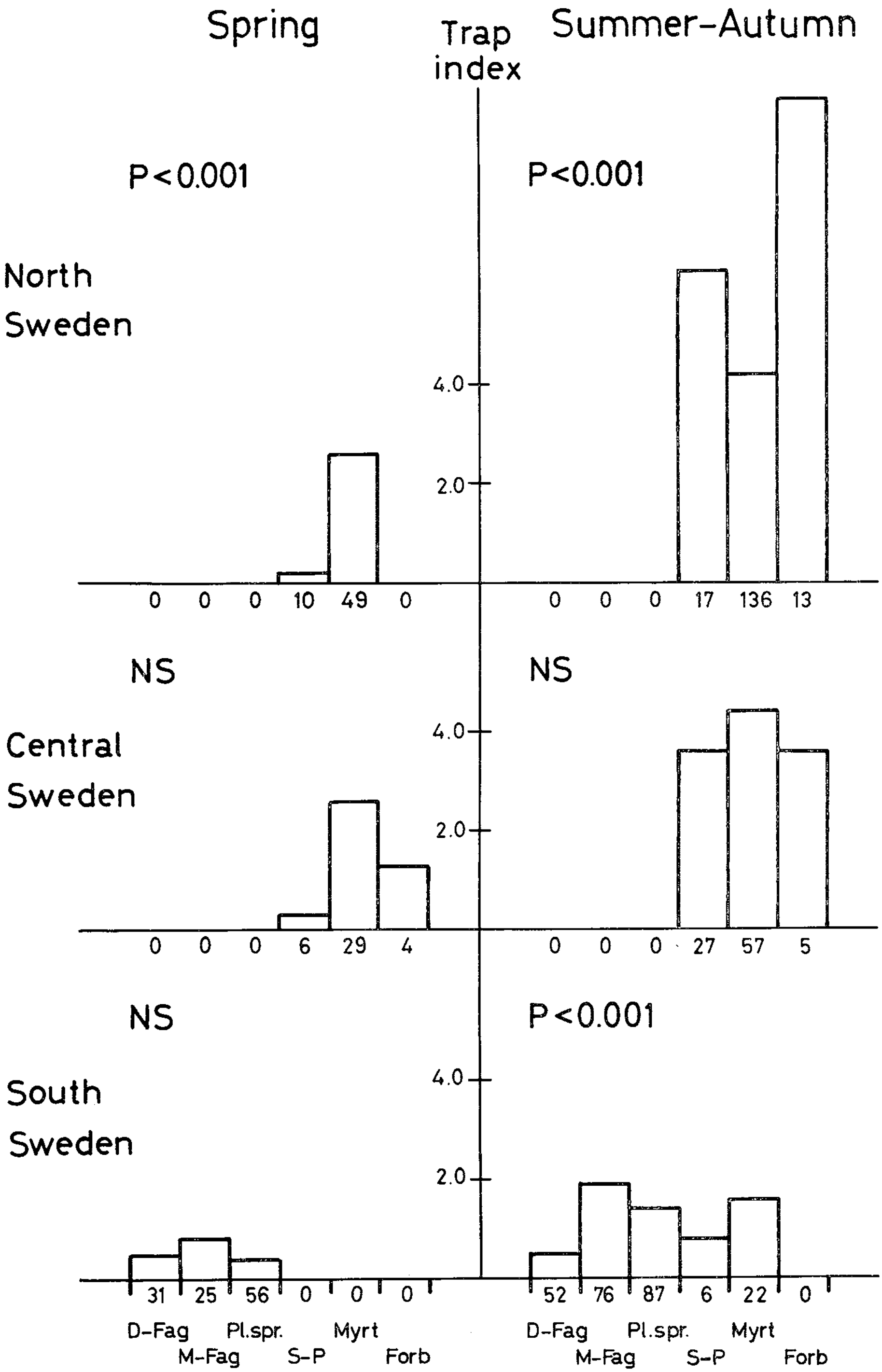
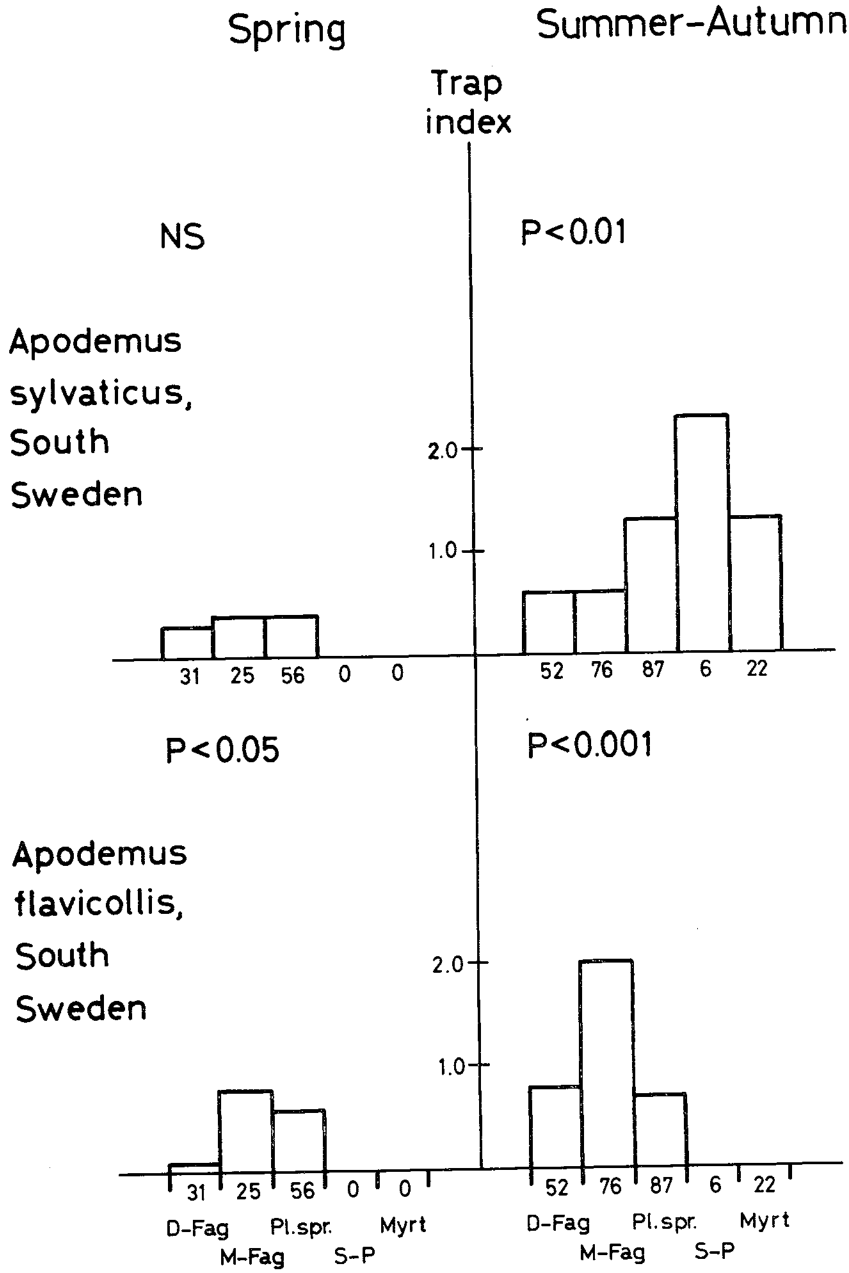


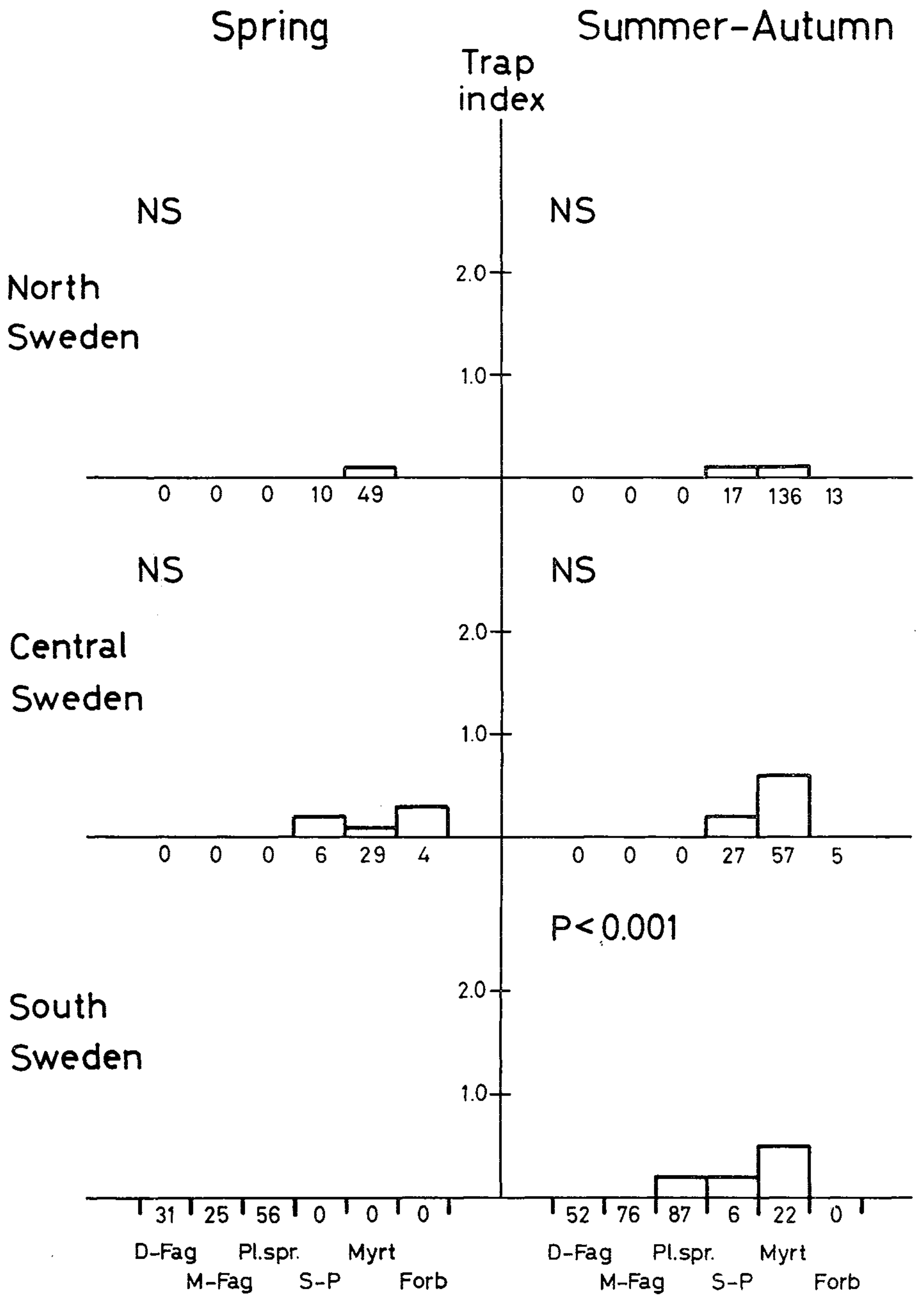
Figure 7. Variations in abundance, owing to type of plant community, of the small mammal species most common in mature forests. The following forest types were distinguished:

D-Fag. = "heath" beech forest *(Deschampsia-Fagetum).*
M-Fag. = "meadow" beech forest *(Melico-Fagetum + Fraxino-Fagetum).*
Pl. spr. = spruce forest planted in earlier cultivated fields (in southern Sweden).
S-P = mixed spruce-pine forest *(Vaccinium-Pinetum).*



7B. *Apodemus flavicollis* and *Apodemus sylvaticus*.

Myrt = blueberry spruce forest (*Eu-Piceetum*, *Myrtillus*-type).
Forb = forb-rich spruce forest (*Eu-Piceetum Dryopteris*-type + *Melico-Piceetum*).
The number of SQ:s in each community is given at the base lines.
7A. *Clethrionomys glareolus*.



7C. *Sorex araneus.*

while the two *Apodemus* species avoided areas rich in humus.

The incidence of boulders could also be seen to be a basic factor (Tab. 3). *M. agrestis* and *S. araneus* were common when there were no or very few boulders. *C. glareolus* and the *Apodemus* spp. mainly appeared where there was a moderate or large number of boulders or where the boulders were very large (i.e. the only significant effect for *A. flavicollis*). Boulders are usually covered with moss, at least in central and northern Sweden. *C. glareolus* seemed to prefer moss-covered boulders but this was not the case with *A. sylvaticus*.

The degree of cover had a pronounced effect (Tab. 4). *M. agrestis* appeared only where there was an extensive soil cover, while *C. glareolus* and the *Apodemus* species preferred an intermediate condition. The latter species appeared in smaller numbers in extreme conditions with regard to degree of cover. This factor had no pronounced effect on *S. araneus*.

With regard to soil moisture (Tab. 5), conditions become still less clear-cut. *M. agrestis* appears in moist and also wet areas and the *Apodemus* species mainly in mesic environments. However, for *C. glareolus* and *S. araneus* there were no clear relationships.

In relation to the remaining factors examined, the *Apodemus* spp. was found in the smallest numbers on peat soil, as compared with all textural soil types defined. The majority of maximum numbers of *C. glareolus* were found on morainic soils. From various soil profiles *M. agrestis* and *S. araneus* were most numerous in gley areas, while few *Apodemus* individuals were found there. Some *C. glareolus* maxima appeared on podzols but this was not consistent. With regard to soil particle size only *C. glareolus* showed a consistent pattern with most animals being caught on sand or fine sand soils.

3.4 **Management effects**

Distinct effects resulting from different management practices were also looked for. The basic factors (3.3) vary considerably in the three forest phases and some practices are mainly applied in certain environmental conditions, e.g. ditching in wet areas. Therefore, high numbers of animals in connection with ditching may only indicate that these animals prefer moist or wet areas. Nevertheless, ditching may be a good indicator of high abundance of the species. But it cannot be used as such when applied to completely new conditions. Thus, significant effects of management, as occurred during the period, 1971—75, can be used as indicators of animal abundance but, on cautious examination, may also be tentatively evaluated as causal agents.

In general, there were few significant variations in small mammal numbers as a result of different management techniques. Only a few fairly clear examples are shown in the tables, the remaining cases being discussed and interpreted in the text.

3.4.1 *Afforestations*

In southern Sweden there were more *M. agrestis* in fields that had been previously ploughed than in unploughed areas (Tab. 6). No such significant variations were found for *M. agrestis,* nor for any other species, in central or northern Sweden. In all regions *M. agrestis* was more common in ditched than unditched fields (Tab. 6), whereas no such consistent relation was found for the other species. *C. glareolus* and the *Apodemus* spp. were more common in fields planted with forest seedlings than in unplanted fields. *M. agrestis* and *S. araneus* showed no consistent relation in this respect. Neither tree species nor tree age had any clear influence.

M. agrestis preferred ditched fields probably because such fields have moderate moisture and a thick layer of old grass. Uncultivated meadows on former forest ground are normally not ploughed, often have a low and sparse vegetation and are not attractive to field voles. It seems obvious that the individuals of the forest species *C. glareolus* and *A. flavicollis,* that move into abandoned fields should prefer

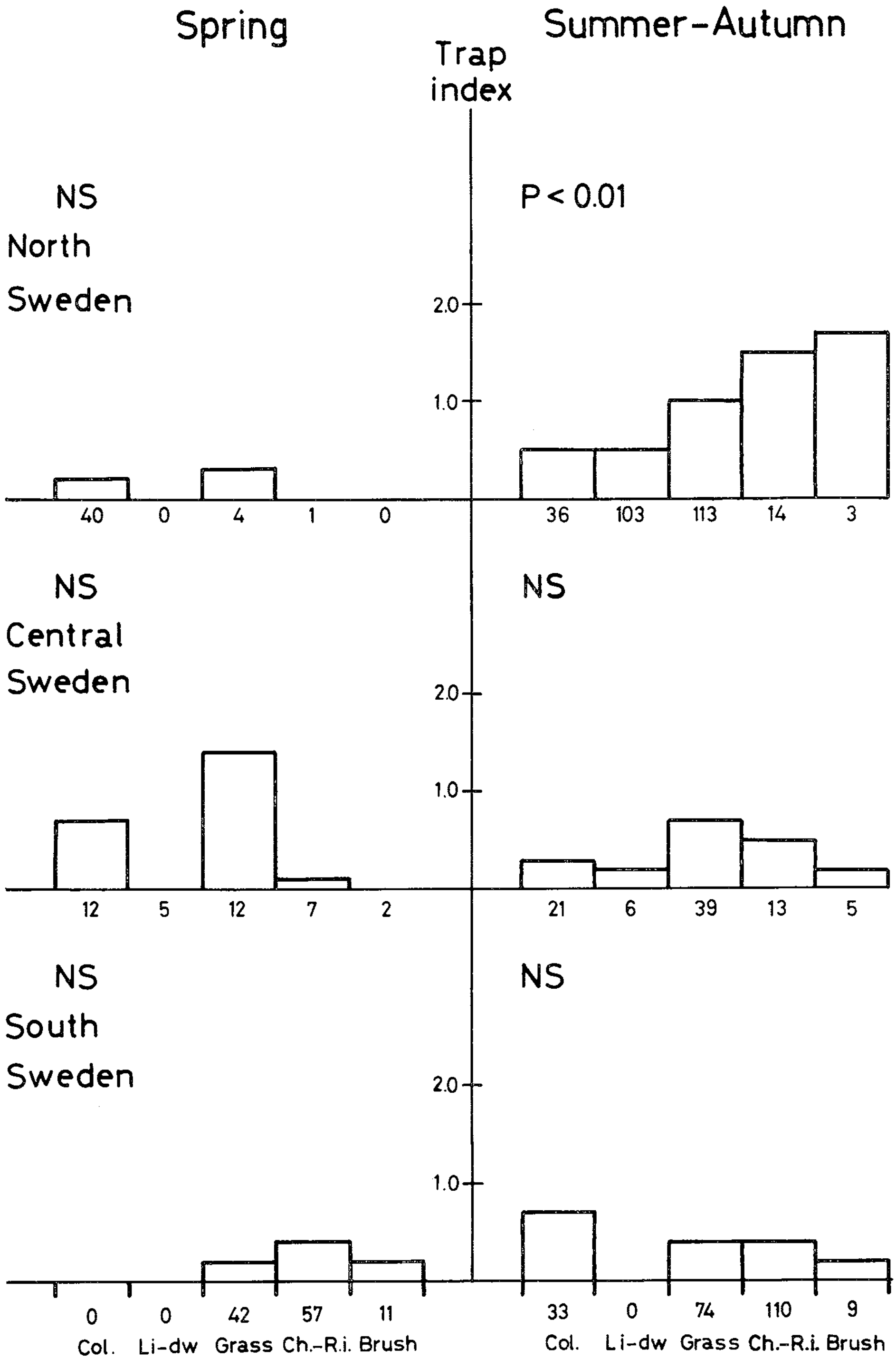
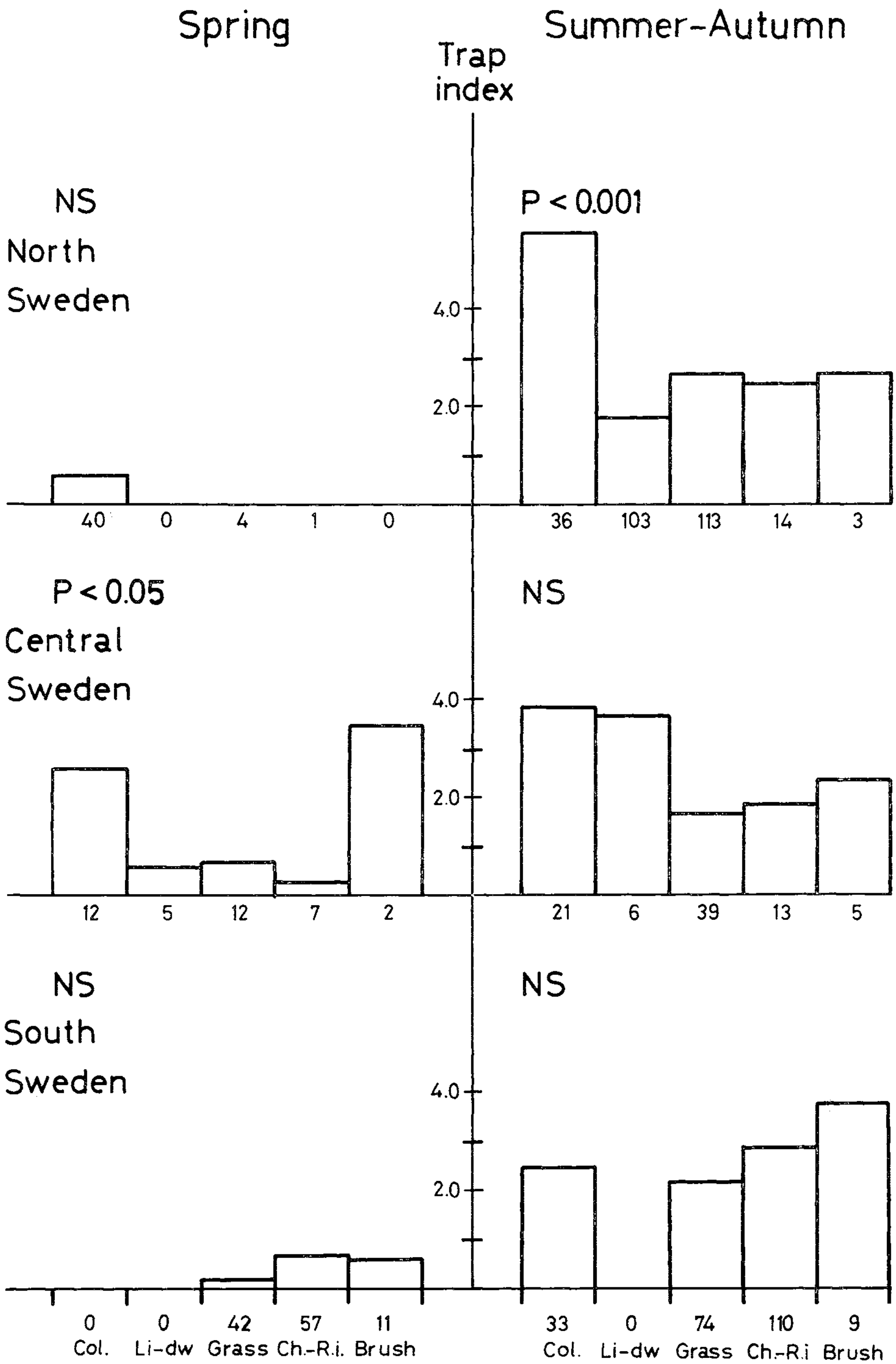


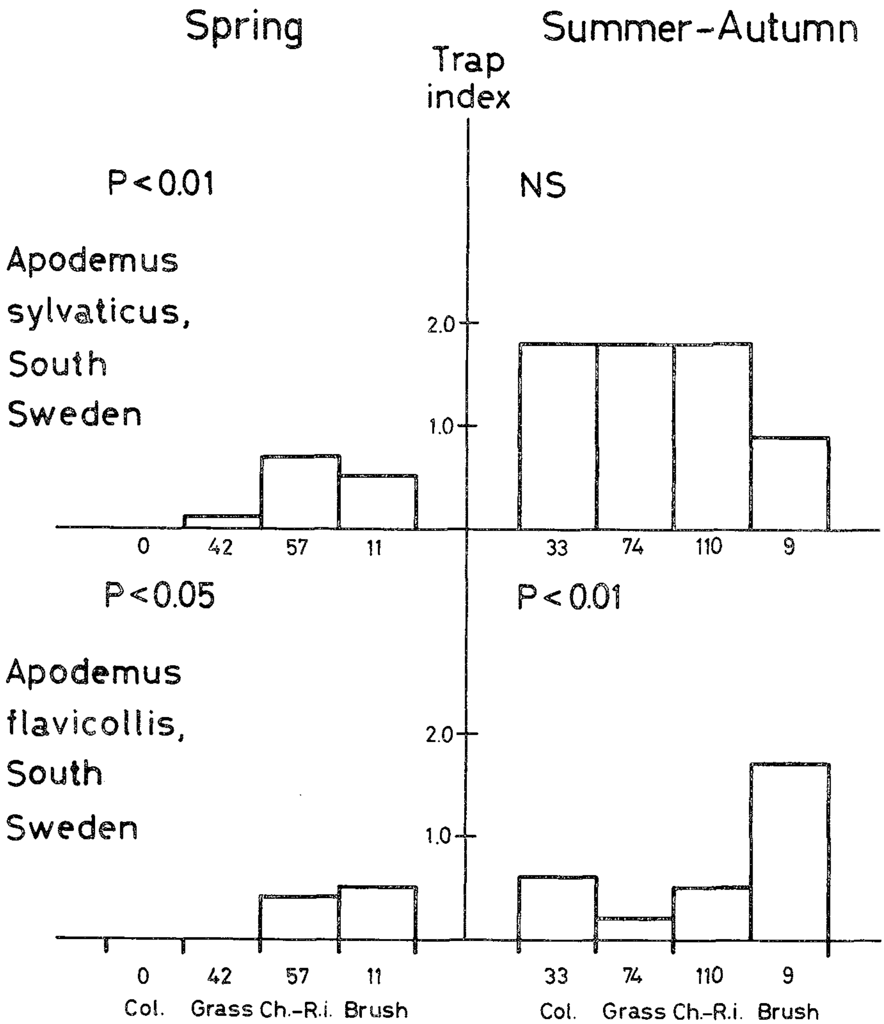
Figure 8. Variations in abundance, owing to type of plant community, of the small mammal species most common in reforestatitons. The following plant communities were distinguished:

Col. = the colonization phase (just after felling).
Li-Dw = the lichen-dwarf shrub (e.g. *Calluna*) stage in dry/poor areas.
Grass = the grass (mainly *Deschampsia flexuosa*) stage in intermediate areas.
Ch.-R.i. = the *Chamaenerion-Rubus idaeus* stage in moist/rich areas.



8B. *Clethrionomys glareolus.*

Br = the brushwood (e.g. *Betula, Salix, Sorbus*) late stage.
The number of SQ:s in each community is given at the base line.
8A. *Microtus agrestis.*



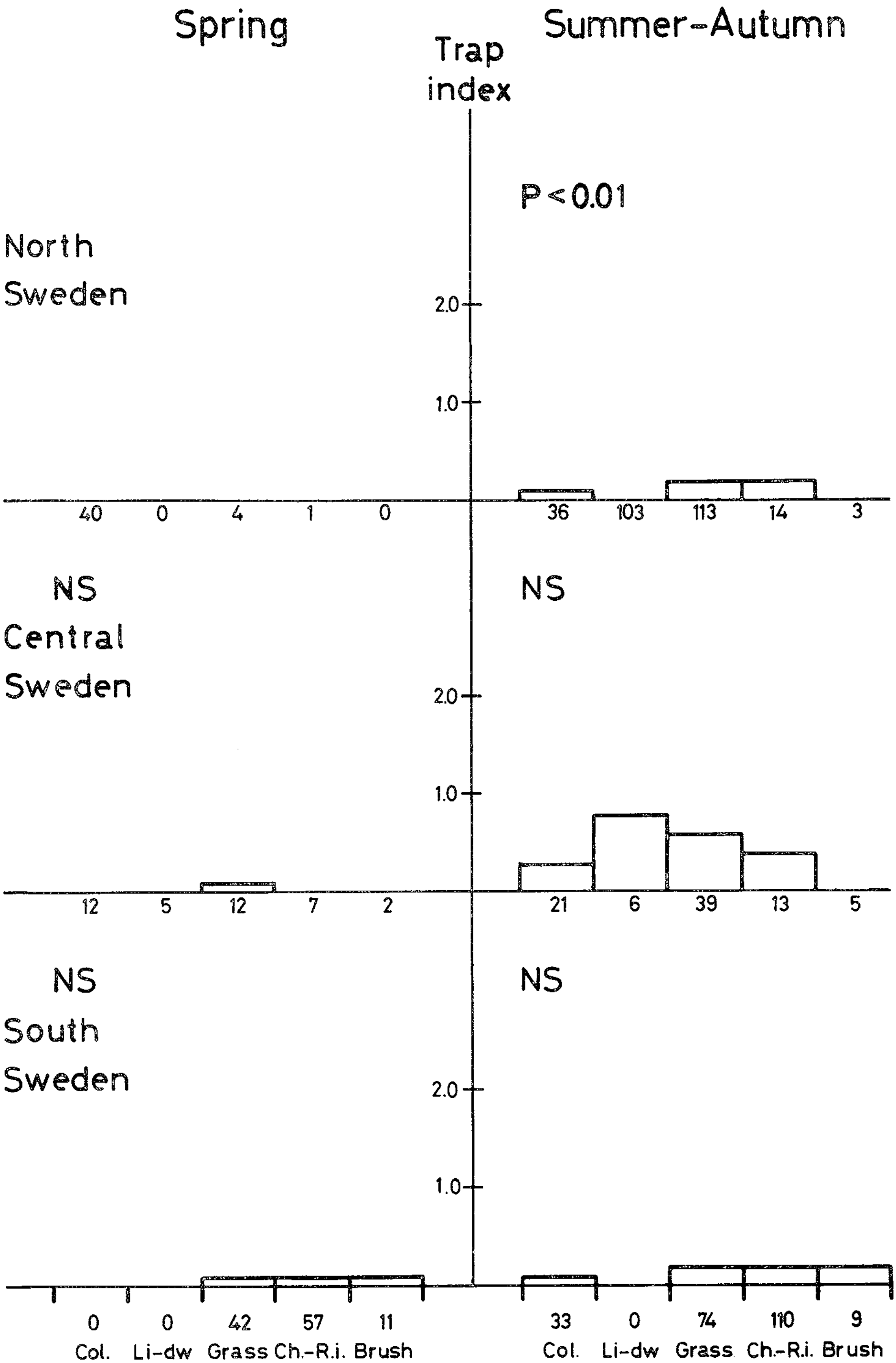
8C. *Apodemus flavicollis* and *Apodemus sylvaticus.*

to settle in areas with some kind of forest vegetation.

3.4.2 *Mature forests*

The few catches of *M. agrestis* and *S. araneus* in mature forests were mainly obtained after cleaning; *C. glareolus* did not show any consistent correlation to this factor (Tab. 7). Similarly, *M. agrestis* and *S. araneus* preferred a moderate level of canopy closure, while *A. flavicollis* appeared in the most closed forests. *C. glareolus* and *A. sylvaticus* did not show any significant variation in this respect. In central and northern Sweden most *C. glareolus* were caught in forests that were 30—60 years old and were less abundant in older forests. Thinning or selective felling did not have any clear effect on small mammal abundance and the same was the case in time after cleaning or thinning.

C. glareolus was previously found to occur mainly at moderate cover, whereas *M. agrestis* and *S. araneus* preferred better cover. The latter species were probably attracted by the slash in cleaned forests. It is more difficult to find a reason for the abundance of *C. glareolus* in fairly young forests.



8D. *Sorex araneus.*

Table 1. Small mammal abundance as affected by the depth of litter. Classification of litter depth: 0, 1, 1—5 and >5 cm.

Region and season	*M. agrestis*	*C. glareolus*	*A. flavicollis*	*A. sylvaticus*	*S. araneus*
Southern Sweden, spring	P<0.01 Max: >5 Min: 0—1	NS	NS	NS	NS
Southern Sweden, summer—autumn	P<0.001 Max: >5 Min: 0	P<0.01 Max: 0—1 Min: >5	P<0.01 Max: 1—5 Min: 0—1	P<0.001 Max: 0—5 Min: >5	P<0.001 Max: >5 Min: 0—5
Central and northern Sweden, spring	P<0.01 Max: >5 Min: 0	P<0.001 Max: 1 Min: 0	—	—	P<0.05 Max: >5 Min: 0
Central Sweden, summer—autumn	P<0.001 Max: >5 Min: 0—1	P<0.001 Max: 0—1 Min: >5	NS	P<0.01 Max: 1—5 Min: 0—1 and >5	P<0.001 Max: >5 Min: 0—5
Northern Sweden, summer—autumn	P<0.001 Max: 1—>5 Min: 0—1	P<0.001 Max: 0—1 Min: >5	—	—	NS

Table 2. Small mammal abundance as affected by the depth of humus. Classification of humus depth: 0—3, 3—10, 10—20 and >20 cm.

Region and season	*M. agrestis*	*C. glareolus*	*A. flavicollis*	*A. sylvaticus*	*S. araneus*
Southern Sweden, spring	NS	NS	P<0.05 Max: 0—10 Min: >10	NS	P<0.01 Max: >20 Min: 0—10
Southern Sweden, summer—autumn	P<0.001 Max: >20 Min: 0—10	P<0.001 Max: 0—20 Min: >20	P<0.01 Max: 0—20 Min: >20	P<0.001 Max: 0—20 Min: >20	P<0.001 Max: >20 Min: 0—3
Central and northern Sweden, spring	P<0.05 Max: >10 Min: 0—3	P~0.05 Max: 3—20 Min: >20	—	—	NS
Central Sweden, summer—autumn	P<0.001 Max: 10—20 Min: 0—3	P<0.001 Max: 0—10 Min: >10	NS	NS	P<0.05 Max: 10—20 Min: >20
Northern Sweden, summer—autumn	P<0.001 Max: >10 Min: 0—10	P<0.001 Max: 0—10 Min: >10	—	—	NS

Table 3. Small mammal abundance as affected by the amount of boulders. Classification: 0 %, 1—10 % of the area, normal occurrence without moss, normal occurrence with moss, rich occurrence with and without moss and large boulders.

Region and season	*M. agrestis*	*C. glareolus*	*A. flavicollis*	*A. sylvaticus*	*S. araneus*
Southern Sweden, spring	$P < 0.05$ Max: 1—10 % Min: Remaining	NS	NS	NS	NS
Southern Sweden, summer—autumn	$P < 0.001$ Max: 0 % Min: Remaining	$P < 0.05$ Max: Normal-rich Min: < 10 %	NS	$P < 0.05$ Max: Normal Min: Remaining	NS
Central and northern Sweden, spring	$P < 0.01$ Max: 0—10 % Min: Rich-large boulders	$P < 0.001$ Max: Normal Min: 0 %	—	—	$P < 0.01$ Max: 0 % Min: Remaining
Central Sweden, summer—autumn	$P < 0.001$ Max: 0—10 % Min: Moss cover	$P < 0.001$ Max: Moss cover + large boulders Min: 0 %	$P < 0.05$ Max: Large boulders Min: Remaining	$P < 0.001$ Max: Rich without moss Min: Remaining	NS
Northern Sweden, summer—autumn	$P < 0.001$ Max: 0 % Min: > 10 %	$P < 0.001$ Max: Normal with moss cover Min: Remaining	—	—	$P < 0.001$ Max: 0—10 % Min: Remaining

Table 4. Small mammal abundance as affected by the cover. Classification: Vertical soil cover by vegetation, slash and litter 0—10, 10—30, 30—50, 50—70, 70—90 and 90—100 %.

Region and season	*M. agrestis*	*C. glareolus*	*A. flavicollis*	*A. sylvaticus*	*S. araneus*
Southern Sweden, spring	$P < 0.05$ Max: 70—100 Min: < 70	$P < 0.01$ Max: 50—70 Min: < 50	NS	NS	$P < 0.05$ Max: 30—50 Min: Remaining
Southern Sweden, summer—autumn	$P < 0.001$ Max: 90—100 Min: 0—50	$P < 0.001$ Max: 50—70 Min: 90—100	$P < 0.001$ Max: 50—70 Min: 70—100	$P < 0.001$ Max: 30—70 Min: 0—30, 90—100	$P < 0.001$ Max: 70—100 Min: 0—30
Central and northern Sweden, spring	$P < 0.001$ Max: 70—100 Min: 0—30	$P < 0.05$ Max: < 90 Min: 90—100	—	—	NS
Central Sweden, summer—autumn	$P < 0.001$ Max: 70—100 Min: < 70	$P < 0.001$ Max: < 90 Min: 90—100	NS	NS	NS
Northern Sweden, summer—autumn	$P < 0.001$ Max: 90—100 Min: 0—50	$P < 0.001$ Max: 30—70 Min: 90—100	—	—	NS

Table 5. Small mammal abundance as affected by soil moisture. Classification: Dry, mesic, moist and wet soil.

Region and season	*M. agrestis*	*C. glareolus*	*A. flavicollis*	*A. sylvaticus*	*S. araneus*
Southern Sweden, spring	NS	NS	P < 0.05 Max: Mesic Min: Remaining	NS	NS
Southern Sweden, summer—autumn	P < 0.001 Max: Moist-wet Min: Dry-mesic	P < 0.001 Max: Mesic Min: Moist-wet	P < 0.001 Max: Mesic Min: Remaining	P < 0.001 Max: Dry-mesic Min: Moist-wet	P < 0.001 Max: Moist Min: Remaining
Central and northern Sweden, spring	NS	P < 0.05 Max: Remaining Min: Dry	—	—	NS
Central Sweden, summer—autumn	NS	P < 0.05 Max: Mesic-moist Min: Wet	NS	NS	P < 0.01 Max: Mesic Min: Wet
Northern Sweden, summer—autumn	P < 0.01 Max: Moist Min: Dry	NS	—	—	NS

Table 6. Small mammal abundance as affected by ploughing and ditching in abandoned fields. Classifications are ploughing or ditching at any previous time or not at all.

Region and season	Ploughing	Ditching		
	M. agrestis	*M. agrestis*	*A. sylvaticus*	*S. araneus*
Southern Sweden, spring	P < 0.05 Max: Ploughed Min: Unploughed	NS	NS	NS
Southern Sweden, summer—autumn	P < 0.01 Max: Ploughed Min: Unploughed	P < 0.001 Max: Ditched Min: Unditched	NS	P < 0.001 Max: Ditched Min: Unditched
Central and northern Sweden, spring	NS	P < 0.05 Max: Ditched Min: Unditched	—	NS
Central Sweden, summer—autumn	NS	P < 0.05 Max: Ditched Min: Unditched	NS	P < 0.05 Max: Unditched Min: Ditched
Northern Sweden, summer—autumn	— (no unploughed areas)	NS	—	NS

Table 7. Small mammal abundance as affected by cleaning in mature forests. This management was classified as obvious cleaning at any previous time or not at all.

Region and season	*M. agrestis*	*C. glareolus*	*A. flavicollis*	*A. sylvaticus*	*S. araneus*
Southern Sweden, spring	NS	$P < 0.05$ Max: No cleaning Min: Cleaning	NS	NS	NS
Southern Sweden, summer—autumn	NS	NS	NS	NS	$P < 0.01$ Max: Cleaning Min: No cleaning
Central and northern Sweden, spring	$P < 0.05$ Max: Cleaning Min: No cleaning	NS	—	—	NS
Central Sweden, summer—autumn	NS	NS	NS	NS	NS
Northern Sweden, summer—autumn	$P < 0.05$ Max: Cleaning Min: No cleaning	$P < 0.01$ Max: Cleaning Min: No cleaning	—	—	NS

Table 8. Small mammal abundance as affected by felling operations. Classification: Clear-cutting and seed trees. Seed trees were not used in southern Sweden.

Region and season	*M. agrestis*	*C. glareolus*	*C. rufocanus*	*S. araneus*
Central and northern Sweden, spring	NS	NS	—	NS
Central Sweden, summer—autumn	NS	NS	—	NS
Northern Sweden, summer—autumn	$P < 0.01$ Max: Clear-cutting Min: Seed trees	$P < 0.001$ Max: Clear-cutting Min: Seed trees	NS	$P < 0.001$ Max: Clear-cutting Min: Seed trees

3.4.3 *Reforestations*

In northern Sweden *M. agrestis, C. glareolus* and *S. araneus* were less common in areas with natural regeneration by seed trees than in clear-felled areas (Tab. 8). For most species examined the highest densities were found in cleaned reforestations (Tab. 9). Only *S. araneus* did not show any consistent relation. The effects of soil management in northern Sweden were fairly consistent (Tab. 10). In the case of *M. agrestis, C. glareolus* and *S. araneus* fewer animals were caught when burning or soil scarification had been performed than when there had been no soil treatment. For *C. rufocanus* in northern Sweden, however, many more animals were caught in burned than in untreated reforestations. *M. agrestis* and *S. araneus* were found in the highest numbers

Table 9. Small mammal abundance as affected by cleaning in reforestations. Classification: Cleaning at any time after felling or not at all.

Region and season	*M. agrestis*	*C. glareolus*	*C. rufocanus*	*A. flavicollis*	*A. sylvaticus*	*S. araneus*
Southern Sweden, spring	NS	NS	—	P < 0.05 Max: Cleaning Min: No cleaning	P < 0.05 Max: Cleaning Min: No cleaning	NS
Southern Sweden, summer—autumn	NS	NS	—	P < 0.05 Max: Cleaning Min: No cleaning	NS	NS
Central and northern Sweden, spring	NS	NS	—	—	—	NS
Central Sweden, summer—autumn	NS	NS	—	NS	NS	P < 0.01 Max: No cleaning Min: Cleaning
Northern Sweden, summer—autumn	P < 0.001 Max: Cleaning Min: No cleaning	P < 0.001 Max: Cleaning Min: No cleaning	NS	—	—	P < 0.01 Max: Cleaning Min: No cleaning

Table 10. Small mammal abundance as affected by ground treatment. Classification: Burning, soil scarification and no treatment. Burning was not performed in southern Sweden.

Region and season	*M. agrestis*	*C. glareolus*	*C. rufocanus*	*A. flavicollis*	*A. sylvaticus*	*S. araneus*
Southern Sweden, spring	NS	NS	—	NS	NS	NS
Southern Sweden, summer—autumn	NS	P < 0.01 Max: No treatment Min: Scarification	—	NS	NS	NS
Central and northern Sweden, spring	NS	NS	—	—	—	NS
Central Sweden, summer—autumn	NS	NS	—	NS	NS	NS
Northern Sweden, summer—autumn	P < 0.001 Max: No treatment Min: Burned	P < 0.001 Max: No treatment Min: Burned and scarified	P < 0.001 Max: Burned Min: No treatment	—	—	P < 0.001 Max: No treatment Min: Burned and scarified

in the ditched areas. *M. agrestis* and *C. rufocanus* were most common in reforestation areas 3—10 years old, whereas the *Apodemus* spp. appeared mainly just after felling. *M. agrestis* and *S. araneus* were less common in reforestations planted with pine than in those with spruce or in unplanted areas.

Ditching, cleaning and a certain age of the reforestation areas indicate good ground shelter; and such shelter is necessary for the occurrence of *M. agrestis* and *S. araneus,* in particular. Pine seedlings are usually planted on rather unproductive forest soil, which is also unfavourable for these species. The same situation exists in areas of natural regeneration.

4 Discussion

Most of the variables shown to affect small mammal abundance can be included in the term "shelter". This may include vegetative cover, forest slash, litter, boulders, porous soil, etc. The way in which the abundance of various species is influenced by the various factors apparently depends on the ability of the species to escape predators, which includes their burrowing capabilities. However, the very different abundance of *M. agrestis* and *S. araneus* on peat soils in the spring and in summer—autumn may reflect the flooding of these areas in winter, which forces the animals to move up to mineral soil in the late autumn and recolonize the peat soil habitats in summer.

An attempt is made in Fig. 9 to summarize the effects of forest phase and shelter on the commonest small mammals. A sere from an abandoned field, through a closed forest to a reforestation is imagined. The multilayered cover of the soil by vegetation, litter, boulders, etc., is suggested as an easily recognizable element for the discussion of small mammal occurrence. In view of different possible adaptations to escape predators, various small mammal species are more or less favoured by dense cover. *M. agrestis* and *S. araneus* have very similar demands but *S. araneus* is relatively more common in closed forests. *M. agrestis,* in particular, needs abundant cover close to the ground. It is only able to burrow in peat or very porous soils and has its nest at ground level if there is enough vegetation. As less shelter can usually be expected in reforestation areas than in abandoned fields, the species will be more restricted in the former habitat. *C. glareolus* is very common in all forest types except the poorest ones. It appears sometimes on late afforestations and often on reforestations, especially in the early and late stages. In northern Sweden it also moves into cultivated fields, gardens and houses during population peaks (Hansson and Zejda 1977). In southern Sweden it is most abundant in reforestation areas but, in central and northern Sweden, in closed forests. This is explained by the poor vegetation cover existing in forests in southern Sweden, especially in planted spruce forests (cf. Hansson 1974). On the other hand, reforestation areas in southern Sweden usually have a more luxuriant vegetation (especially the *Chamaenerion—R. idaeus* type and later stages) than those in the north. *C. rufocanus* shows similar habitat distribution to that of *C. glareolus* but seems to be more common in areas with relatively less cover. *A. flavicollis* is closely bound to the old deciduous forest, where it climbs in the trees (Hoffmeyer 1973). It ventures only rarely into reforestations and even less frequently into afforestations. It needs considerably more overall cover than *A. sylvaticus* (Hoffmeyer 1973), a species characteristic of open landscapes. This latter species is very cautious and agile and is well equipped for exploiting open areas at night. It also burrows in soil with hardly any cover.

These observations are in general agreement with the results of the few, similar, quantitative habitat surveys carried out in Europe. Artimo (1963) in southern Finland found that *C. glareolus* and *S. araneus* were considerably more common in spruce than in pine forests, although both forests had a field layer of mainly *Vaccinium myrtillus. M. agrestis* occurred fairly regularly in both types of forest but achieved highest abundance in the spruce forest. In eastern Finland (Sotkamo), Kalela *et al.* (1971) observed most *C. glareolus* in moist forests with tall trees. However, the abundance of this species varied little between the forest

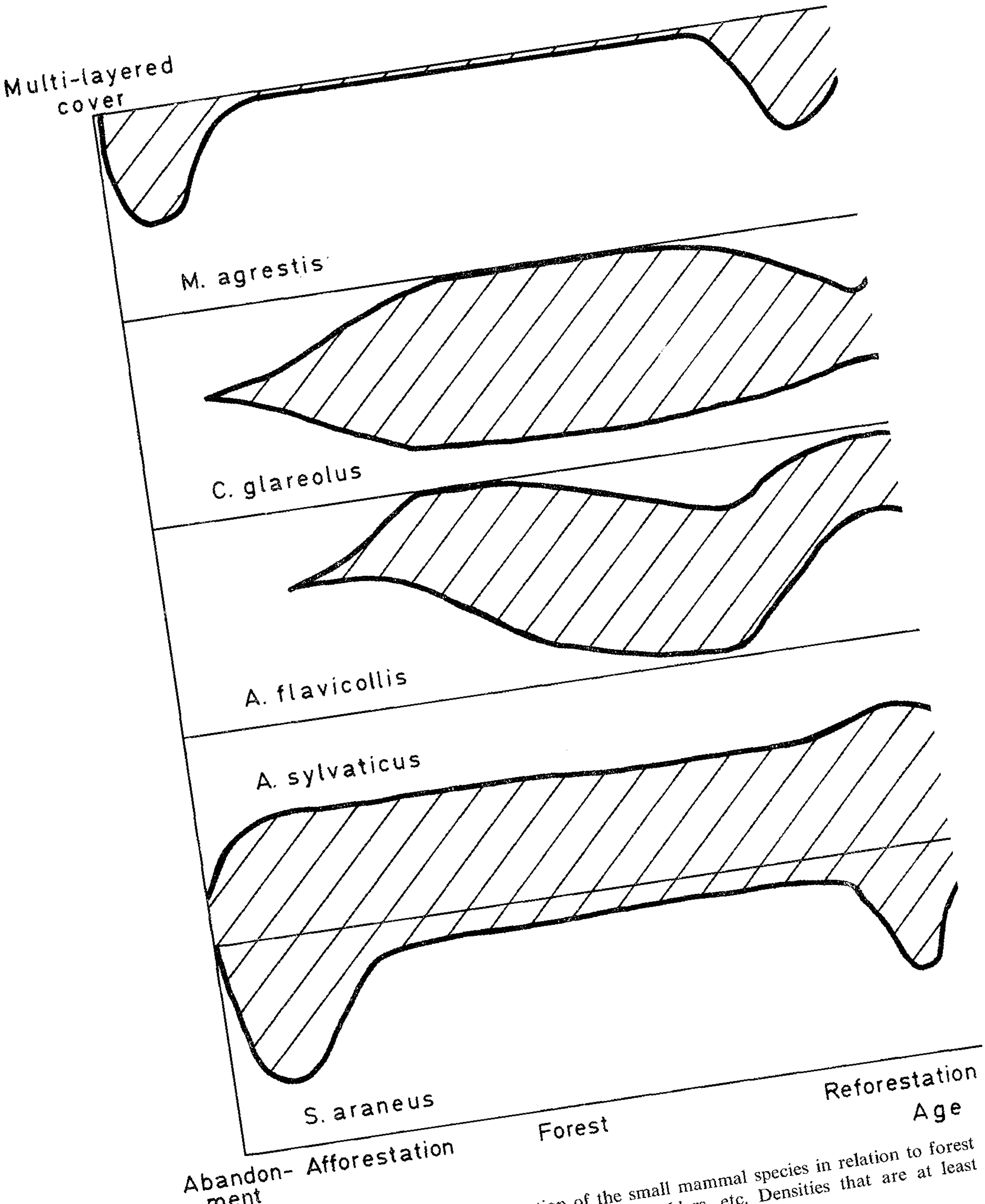


Figure 9. General pictures of the distribution of the small mammal species in relation to forest phase and the cover provided by vegetation, litter, boulders, etc. Densities that are at least moderate are considered to appear within the hatched zones.

types. In that area *M. agrestis* was common on mires and appeared only in wet or moist types of forests. In Poland, Ryszkowski (1971) found higher numbers of bank voles in mixed pine-deciduous forests than in pure pine forests. Also Bock (1972) in the same country found that bank voles preferred moist rather than dry forest associations. From European parts of the Sovjet Union, Tupikova and Korenberg (1965) report that after clear-felling *A. sylvaticus* increased heavily in numbers while the population of *C. glareolus* decreased. *S. araneus* was found to be somewhat more common in mature forests than in the following reforestations, a finding that conflicts with the Swedish observations. In North America, Miller and Getz (1977) tried to determine what factors influenced the distribution of small mammals in forests. They found cover, especially herbaceous vegetation, to be the main factor affecting the abundance of most species. A few species showed a stronger relation to soil moisture but moisture and vegetative cover may also be related.

The overall picture of small mammal occurrence given in the text and in Fig. 9 may be used in a general way to predict under what circumstances various species will occur at population peaks. However, the findings here are based on the conditions during 1971—75 and may not be applicable in the future should forestry practices change. At present there are suggestions of new radical methods of forest management, such as the utilization of stumps and branches, mini-rotation silviculture and ditching and the afforestation of mires. In order to predict what species will abound under such new conditions, the causal relationships behind habitat selection must be known. Behaviouristic experiments are needed with varying types of soil, vegetation, moisture, darkness, etc. Such studies are in progress.

The distribution of one species may be affected by the presence of another through interspecific competition. In an outbreak year *A. flavicollis* drove *A. sylvaticus* away from forest habitats (Hoffmeyer and Hansson 1974). Larsson (1977) found that *M. agrestis* and *C. glareolus* showed inverse relations in occurrence, indicating competition between the two species and Henttonen *et al.* (1977) gave some support to the idea that the occurrence of *C. glareolus* in afforestation and reforestation areas is partly determined by the number of *M. agrestis.* Myllymäki (1977b) showed, in turn, that the presence of *M. agrestis* may be affected by *A. terrestris.* Thus, if a dominant species is favoured by certain environmental conditions this may have consequences for other species and their abundance. Such interspecific relations ought to be studied more closely. Some general mathematical models have been proposed for such relations by Stenseth *et al.* (1977).

The occurrence of surplus areas is another complicating factor. As a possible example some small grassy areas on peat soil in a large reforestation may produce a surplus of *M. agrestis* which will invade nearby poorer areas. This means that the unsheltered reforestation habitat cannot be regarded separately but that the whole landscape must be considered (Hansson 1977a, b). General mathematical models have been developed for such cases (Stenseth *et al.* 1977) and field studies on this problem are in progress.

The few clear variations caused by the type of management suggest that it might be difficult to reduce the small mammal populations by cultural methods. Only soil management and cleaning can be discussed in this respect, as both may be readily modified. In conjunction with burning, soil scarification and the omission of cleaning, low densities of most species were found. Larsson (1977) also found a correlation between burning and low rodent densities in an intensive study in a selected region in northern Sweden. However, these relations may be due to the use of these methods in areas which originally supported low numbers. Only experiments can determine if densities and forestry practice were causally related. Larsson (1975) performed such experiments, e.g. with burning, and found indications of a certain depressant effect on small rodent numbers and damage. In northern Sweden a fairly sparse and low vegetation develops after burning, which might explain these relations. It is more difficult to find an explanation for the correlation between soil scarification and low numbers of *C. glareolus* and *S. araneus*. Perhaps this method is employed to less extent in the early or late reforestation areas, in which *C. glareolus*, at least, is very abundant. Cleaning in mature forests and reforestations increases ground cover. It might be possible to avoid cleaning just before population peaks in order to protect susceptible seedlings. However, before such a recommendation is made, it should be determined whether or not cleaning is being undertaken in areas with a high degree of other cover, or if there is a direct relation involved.

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6 Sammanfattning

Alla vanligare arter av smådäggdjur kan vara ekonomiskt betydelsefulla i det svenska skogsbruket. Sorkarna ringbarkar plantor i skogskulturer och ympar i fröplantager. Skogssorken, skogsmössen och ibland även näbbmössen tar utsådda frön. Man föreslår i Sverige numera oftast att dessa problem skall åtgärdas genom modifikationer i skogsskötselmetoderna. En sådan inriktning förutsätter att de betydelsefulla arterna uppvisar distinkta skillnader i täthet mellan olika biotoper eller i relation till olika omvärldsfaktorer. Deras fördelningsmönster har tidigare varit känt i mycket grova drag men detta är ett första försök till en skogligt sett heltäckande och landsomfattande analys.

Smådäggdjur fångades med indexmetoder på utvalda lokaler över hela Sverige under 1971—75. Fångstytorna fördelades på övergiven åkermark, som ofta skogsplanterats, i mogen granskog och på hyggen. Samtidigt noterades relevanta biotop- och andra omgivningsfaktorer.

Smådäggdjursbestånden uppvisade olika fluktuationsmönster i olika regioner. I Sydsverige förekom en tämligen regelbunden rytm med låga vår- och höga höstbestånd, i Mellansverige en beståndstopp hos skogs- och åkersork under 1972—73 och i Nordsverige under 1972—74. Av detta skäl måste materialet vid analyserna delas upp i homogena tids- och regiongrupper.

Inom varje grupp studerades först skillnader i talrikhet mellan de tre huvudstadierna och vardera av dessa analyserades därefter med avseende på olika växtsamhällen. För grundläggande omgivningsfaktorer som förnadjup, blockighet etc. fastställdes endast om de totalt sett var betydelsefulla för de olika arterna utan att hänsyn togs till eventuellt samspel. För skötselåtgärder gjordes motsvarande analyser inom de separata skogsstadierna. Möjligheten av att observerade effekter av grundläggande faktorer eller skötselåtgärder berott på samspelseffekter eller någon bakomliggande korrelation diskuteras emellertid.

Följande observationer torde vara av störst betydelse för skogsbruket:

Åkersorken *(Microtus agrestis)* var under vårarna ungefär lika talrik på hyggen som på f.d. åkermark men nådde under hösten högst tätheter i växtsamhällen på fuktig åkermark. Det fanns färre skillnader mellan växtsamhällen på hyggen och arten var ej påtagligt vanligare på gräsrika hyggen. Den är starkt bunden till fuktigare marker med tjockt förna- och humusskikt och med god marktäckning men liten blockighet. Den var vanligast på dikade och röjda marker och på hyggen vanligare vid fullständig kalhuggning än vid fröträdställningar. Den var mindre vanlig på brända hyggen.

Skogssorken *(Clethrionomys glareolus)* var vanligare på hyggen än i mogen skog i Sydsverige men visade den omvända relationen i mellersta och norra Sverige. I samband med beståndstoppar kan den även gå ut på åkermark. Högsta tätheter konstaterades i örtrik granskog. Det fanns ganska små skillnader mellan växtsamhällen på hyggen men arten nådde störst tätheter på helt färska hyggen och i föryngringsytornas senare stadier. Den fanns i områden med föga förna och måttlig humustjocklek, med måttlig marktäckning men med viss blockighet. Den var vanlig på röjda hyggen och vanligare vid fullständig kalhuggning än vid fröträdställningar samt mindre vanlig på brända hyggen.

Den gråsidiga sorken *(Clethrionomys glareolus)* förekommer sparsamt i skogsmark i norra Sverige. Den synes vanligast på hyggen och speciellt brända sådana.

Mindre skogsmusen *(Apodemus sylvati-*

cus) var vanligast på hyggen men är talrik enbart i södra Sverige. Den förekom också i stort antal på åkermark kort efter det jordbruket lagts ner. De grundläggande faktorerna visade ungefär samma relationer som hos skogssorken.

Större skogsmusen *(Apodemus flavicollis)* är vanlig i södra Sverige men var där starkt bunden till den mogna (bok- och ek-) skogen.

Den vanliga näbbmusen *(Sorex araneus)* var mycket generaliserad i sin fördelning mellan olika biotoper och var endast sällsynt i den sydsvenska lövskogen. Dess fördelning i förhållande till grundläggande faktorer och skötselåtgärder liknade starkt åkersorkens.

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