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# Patterns of carabid diversity in Finnish mature taiga

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We studied the variation in carabid assemblages on mature Finnish taiga on three spatial scales: (1) among eight geographical areas in southern and central Finland, (2) on a regional scale among sampling sites within a 450-km$^2$ study area, and (3) on a local scale among sampling sites within a 4-km$^2$ study area. The total carabid sample included 21079 individuals of 49 species. Significantly more individuals and species were captured in the southern study areas than in the more northern ones. A positive correlation existed between species distribution and their abundance among study areas. Five species (ranked in descending order: *Calathus micropterus, Pterostichus oblongopunctatus, Amara brunnea, Notiophilus biguttatus, Cychrus caraboides*) were found in all the eight study areas. *C. micropterus* was the numerically dominant species, consisting 8–83% of the sample in the study areas. The second most abundant species, *P. oblongopunctatus*, constituted 6–36% of the sample. Our study provides baseline information about the composition of carabid assemblages in mature, coniferous boreal forest. This knowledge can be used in assessing effects of forestry practices upon the boreal biota.

## 1. Introduction

Intensive utilization of forest resources has, during the 20th century, caused profound changes in the structure of Finnish forests. For instance, in southern Finland, stands >140 years constitute today only 0.9% of forest land, whereas forests <60 years make up over 50% (Aarne 1992). In Sweden, the proportion of old growth has decreased from 44% to 7% in the last 80 years in state forests (Linder & Östlund 1992).

These changes have demonstrably affected populations in Finland of certain old forest specialists, including invertebrates (e.g. Mikkola 1991, Rassi & Väisänen 1987, Väisänen et al. 1993). However, there is still ridiculously little quantitative data available about species assemblages of invertebrates in mature boreal forest let alone about community changes following forest management practices (Väisänen 1988, Danks & Foottit 1989). Successful assessment of the impact of forest management on the flora and fauna requires knowledge about species assemblages in the intact boreal forest as baseline data. Thus, collections of survey data from different parts and types of the boreal forest are urgently needed

(Haila et al. 1994). Our paper is based on such survey data of carabid beetles from eight study areas in southern and central Finland. We seek to examine the composition of carabid assemblages in mature coniferous forest on three spatial scales: (1) among geographical areas, (2) on a regional scale among sampling sites within a 450-km$^2$ study area in central Finland, and (3) on a local scale among sampling sites within a 4-km$^2$ study area in southern Finland. The results are discussed in the light of the potential effects of forestry practices on the carabid fauna of the boreal zone.

## 2. Study areas and sampling procedure

Carabids were collected in eight study areas from southern to central Finland:

1) The Åland Islands (ca. 60°N, 20°E), 20 sites in 1983 (Niemelä et al. 1986, 1990b);
2) Helsinki (60°N, 25°E), 8 sites in 1988 (Niemelä et al. 1990b);
3) Espoo (60°N, 25°E), 22 sites (10 in 1983 and 12 different sites in 1984) (Halme & Niemelä 1993);
4) Luukki (60°N, 25°E), one site (0.25 ha) in 1991;
5) Vaskijärvi (61°N, 22°E), 27 sites in 1993;
6) Musturi (62°N, 24°E), one site (1.3 ha) in 1985 (Niemelä et al. 1992);
7) Häme (62°N, 23°E) 25 sites in 1985 (Niemelä et al. 1988, 1990a);
8) Talaskangas (64°N, 27°E), 10 sites in 1989.

Study areas 1–3 belong to the hemiboreal phytogeographical zone or are right on the border between the hemiboreal and southern boreal zones (Ahti et al. 1968). Study areas 4–6 belong to the southern boreal zone, and study area 7 is located on the border between southern boreal and mid-boreal zones. Talaskangas (study area 8) is located in the middle boreal zone. All the forests studied were mature (trees >100 yrs), spruce (*Picea abies*) or spruce and pine (*Pinus silvestris*) dominated stands. Naturally, the forest vegetation varies among the study areas because of differences in soils and topography, and due to a gradual change in climate. The mean annual temperature is 5.5°C on the Åland Islands, 4.5–5°C in Helsinki and Espoo, 3–4°C in Häme, and lowest in Talaskangas (2–2.5°C) (Alalammi 1987). Concomitantly, the duration of the growing season decreases gradually from ca. 180 days on Åland to 145–150 days in Talaskangas (Alalammi 1987).

Carabids were collected by pitfall traps (plastic cups, diameter 65 mm, volume 170 ml) partly filled with a preservative (usually ethylene glycol). The traps were in operation throughout the growing season (May through September or October) in Helsinki, Luukki, Musturi and Talaskangas, and from May through July in Vaskijärvi. In Åland and Espoo the sampling period was 5 days in June and 5 days in August, and in Häme 21 days in June and 15 days in August. The number of traps used is given in Table 1.

As the sampling efforts differed among the study areas, we used rarefaction (Simberloff 1978) in computing species richness in samples of the same size. The Czekanowski index of percentage similarity was used to compare the samples among study sites and within sampling sites. The software was provided by Baer and Penev (1993). Hurlbert's (1971) index $\Delta_1$ was used to study species diversity:

$$\Delta_1 = \frac{N}{N-1}\left(1 - \sum_{i=1}^{S} \Pi_i^2\right)$$

where $N$ = total number of individuals in the sample, $N_i$ = the number of individuals of the $i$th species in the sample, $\Pi_i = N_i/N$, $S$ = the number of species in the sample. Index values range from 0 (low diversity) to 1 (high diversity).

## 3. Results

### 3.1. Variation in carabid assemblages among the study areas

The carabid sample from the eight study areas included 21079 individuals of 49 species (Table 1). As trapping effort varied between the study areas, we used numbers of individuals per one trapping day for comparisons. The catch was higher in Åland, Helsinki and Espoo than in the other study areas. Luukki is geographically close to Helsinki and Espoo but is located 75 meters above sea level and corresponds climatically to somewhat more northern areas. The value of the diversity index $\Delta_1$ decreased slightly towards the north, being somewhat higher among the three southernmost areas (Åland, Helsinki, Espoo, mean = 0.84, *SD* = 0.03) than among the other study areas (mean = 0.69, *SD* = 0.22) (Table 1).

Rarefaction estimates of species richness showed that study areas in the hemiboreal zone (Åland, Espoo and Helsinki) hosted the highest numbers of species (Fig. 1). The differences between these three areas and the remaining ones was statistically significant at 650 individuals (catch from Åland and Häme). The most northern area, Talaskangas, had the lowest species richness.

The species-abundance distribution of the samples resembled log-series distribution, in that the proportion of scarce species (1–8 individuals) was high (Fig. 2). Towards the north, species-abundance distribution become more extreme as the proportion of very scarce species (1–2 individuals) and that of the numerically dominant species increased (Fig. 2).

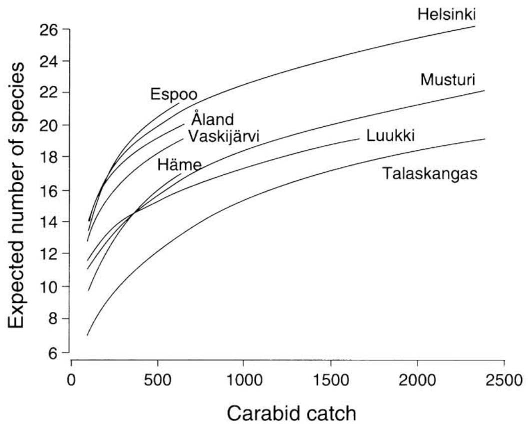


Fig. 1. Rarefaction estimates of species richness as a function of carabid catch in the eight study areas.

Table 1. Catches of the 13 most abundant carabid species, and of *Carabus violaceus* and *Notiophilus reitteri*.

| | Åland | Hels. | Espoo | Luukki | Vaskij. | Häme | Must. | Talask. | Total |
|---|---|---|---|---|---|---|---|---|---|
| *Calathus micropterus* (Dft.) | 50 | 3463 | 127 | 627 | 309 | 265 | 553 | 3727 | 9121 |
| *Pterostichus oblongopunctatus* (F ) | 42 | 1545 | 74 | 217 | 283 | 66 | 853 | 321 | 3401 |
| *Amara brunnea* (Gyll.) | 1 | 1135 | 22 | 299 | 40 | 49 | 48 | 55 | 1649 |
| *Patrobus atrorufus* (Ström) | 15 | 1285 | 1 | 0 | 1 | 0 | 3 | 0 | 1305 |
| *Trechus secalis* (Payk.) | 202 | 531 | 144 | 75 | 16 | 22 | 1 | 0 | 991 |
| *Notiophilus biguttatus* (F ) | 8 | 76 | 7 | 50 | 61 | 92 | 285 | 175 | 754 |
| *Carabus hortensis* L. | 59 | 320 | 56 | 96 | 16 | 67 | 22 | 0 | 636 |
| *Cychrus caraboides* (L.) | 22 | 73 | 32 | 86 | 22 | 28 | 256 | 33 | 552 |
| *Pterostichus melanarius* (Ill.) | 112 | 373 | 8 | 0 | 0 | 0 | 0 | 0 | 493 |
| *P. niger* (Schall.) | 81 | 125 | 118 | 124 | 16 | 0 | 5 | 0 | 469 |
| *Leistus terminatus* (Hellw. in Pz.) | 11 | 65 | 3 | 0 | 18 | 28 | 287 | 25 | 437 |
| *Carabus glabratus* Payk. | 0 | 16 | 47 | 43 | 66 | 19 | 31 | 72 | 294 |
| *C. nemoralis* Müller | 0 | 214 | 0 | 2 | 0 | 0 | 0 | 0 | 216 |
| *C. violaceus* L. | 13 | 0 | 8 | 0 | 0 | 0 | 0 | 0 | 21 |
| *Notiophilus reitteri* Spaeth | 0 | 0 | 0 | 0 | 0 | 5 | 20 | 8 | 33 |
| Other species | 41 | 411 | 44 | 54 | 46 | 9 | 41 | 59 | 705 |
| Total | 657 | 9632 | 691 | 1673 | 894 | 650 | 2405 | 4475 | 21079 |
| Individuals/trapping day | 0.22 | 0.48 | 0.21 | 0.03 | 0.06 | 0.03 | 0.04 | 0.09 | |
| Number of species | 20 | 32 | 21 | 19 | 20 | 17 | 22 | 21 | 49 |
| Species not found elsewhere | 1 | 6 | 0 | 0 | 1 | 3 | 0 | 5 | 16 |
| $\Delta_1$ | 0.84 | 0.81 | 0.87 | 0.80 | 0.77 | 0.78 | 0.78 | 0.30 | |
| Number of sites | 20 | 8 | 22 | 1 | 27 | 25 | 1 | 10 | |
| Number of traps per site | 15 | 15 | 15 | 288 | 7 | 30 | 300 | 52 | |

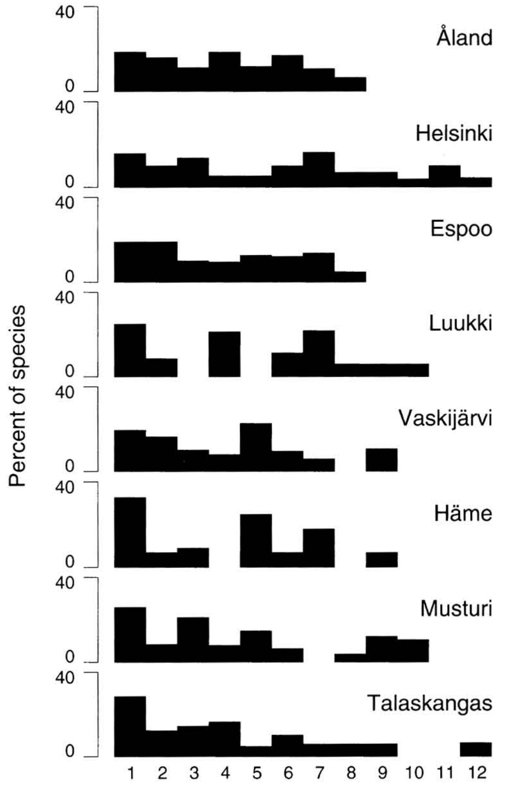


Fig. 2. Proportion of species plotted against number of individuals arranged in abundance classes with $\log_2$ base (octaves) in the eight study areas.

## 3.2. Species turnover across the geographical gradient

Among the 49 species, there was a positive correlation between the number of study areas occupied and the total catch (Spearman rank correlation $r_s$ = 0.89, $P < 0.001$) (Fig. 3). Five species occurred in all of the eight study areas, making up 19% (in Åland) to 96.4% (in Talaskangas) of the sample (Table 1). Overall, the most abundant species was *Calathus micropterus,* making up 43% of the total catch. However, its proportion varied greatly among the study areas. In Åland it constituted a mere 7.6% of the catch, whereas in Talaskangas its proportion ranged as high as 83.3%. In Helsinki, Luukki, Vaskijärvi and Häme its proportion was more than one third of the sample, and in five study areas it was the most abundant species.

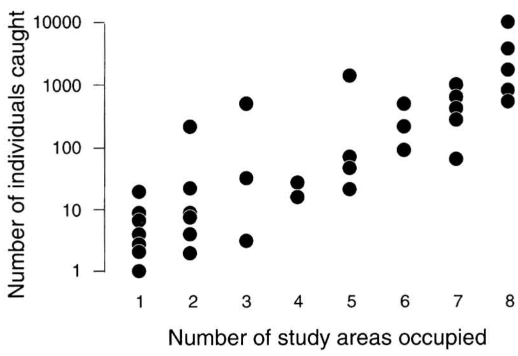


Fig. 3. Number of individuals as a function of the number of study areas collected from for the 49 species.

About one third of the species (16) occurred in only one study area (Table 1). All these species were scarce, and in total they constituted only 0.3% of the catch (59 individuals). Furthermore, no unique species were collected in Espoo, Luukki or Musturi. Thus, of the 49 species in total, about two-thirds (33 species) occurred in 2–8 study areas. A minority of these species occurred only in the north (*Notiophilus reitteri, Pterostichus adstrictus*) or in the south (*Pterostichus melanarius, P. niger, Carabus nemoralis, C. violaceus*). Most species were found throughout the geographical gradient, although they may have been absent from some study areas (Table 1).

The average percentage similarity of the carabid assemblages among the study areas was 34% (Table 2). There was no clear trend of decreasing similarity with increasing geographical distance between study areas. The average similarity among the four southern study areas (Åland,

Table 2. Values for the Czekanowski index of percentage similarity among the eight study areas.

| | He | Es | Lu | Va | Mu | Hä | Ta |
|---|---|---|---|---|---|---|---|
| Åland | 13 | 66 | 30 | 27 | 11 | 33 | 6 |
| Helsinki | | 12 | 28 | 16 | 29 | 12 | 57 |
| Espoo | | | 49 | 46 | 22 | 52 | 13 |
| Luukki | | | | 58 | 51 | 49 | 34 |
| Vaskijärvi | | | | | 48 | 68 | 30 |
| Musturi | | | | | | 38 | 35 |
| Häme | | | | | | | 22 |

Espoo, Helsinki, Luukki) was 33% and among the four northern areas (Vaskijärvi, Häme, Musturi, Talaskangas) 40%. The average similarity between the southern and northern areas was 32%.

### 3.3. Regional and local variation in carabid assemblages

We used the ten sampling sites from Talaskangas located within an area of 30 × 15 km (450 km$^2$, the longest intersite distance being 25 km) to study regional variation in carabid assemblages. Among the ten sampling sites, there was a six-fold difference between the smallest and largest catch (180–1140 individuals/site) and species richness ranged from 3 to 14 species (mean = 7.6 species/site). The value of the diversity index $\Delta_1$ ranged from 0.08 to 0.68 (mean = 0.29). Species composition varied greatly as well. Of the 22 species collected in Talaskangas, 11 occurred in one or two sampling sites, and only two (*C. micropterus, Notiophilus biguttatus*) in all sampling sites. However, the numerical dominance of *C. micropterus* was clear, and it made up 47–96% of the catch in the sites.

In spite of the fairly high species turnover among the sites, the average similarity among the sampling sites in Talaskangas was as high as 60% (range 27–93), probably due to the dominance of *C. micropterus*. There was no clear trend of decreasing similarity with increasing distance between the sites.

The eight sites (intersite distance 100–700 m) in Helsinki, located in a 4-km$^2$ forest area, were used to study local variation in carabid assemblages. Among the eight sampling sites, the degree of variation was lower than among the ten more dispersed site in Talaskangas. In Helsinki, the largest catch was only 1.6 times that of the lowest one (986–1592 individuals/site), and species richness ranged from 16 to 26 (mean = 20.3 species/site). The value of the diversity index $\Delta_1$ was much higher and varied less than in Talaskangas, ranging from 0.72 to 0.82 (mean = 0.78). Furthermore, species composition among the eight sites varied little. Of the total of 32 species collected, 13 (41%) were found in all sampling sites, and seven species were collected in one sampling site only. *C. micropterus* was the most abundant species in seven of the eight sites, thus making up 12–48% of the catch. In Helsinki, the average value of the similarity index was 75% (range 45–91).

## 4. Discussion

Our study showed that carabid species richness, overall abundance and diversity were higher in the southern study areas than in the more northern ones. These patterns may depend on habitat differences on the one hand, and on species' geographical distributions on the other. Due to different methods and accuracies of describing the vegetation in our study areas, it is virtually impossible to directly compare the vegetation among them. However, there is a general trend of decreasing species richness towards the north in Finland. For instance, according to the literature, our southern study areas have in general a milder climate and harbour a higher number of herbaceous plant species (Kalliola 1973, Tuhkanen 1984, Alalammi 1987). In addition, geographical zonations of other animal taxa correspond relatively well with the phytogeographical ones (Järvinen & Väisänen 1973, 1980).

For some carabid species (notably *P. melanarius, P. niger* and *T. secalis*), absence or scarcity in the northern areas was probably due to the combined effect of an unfavourable forest environment and their geographical distribution (see also Niemelä et al. 1990a). Although regarded as forest species, they are known to be rather 'demanding' in their habitat selection (Lindroth 1986). In our northern study areas (62–64°N) they approach the limit of their distribution at 65–66°N and may thus occur only in the most favourable forest habitats and not in the relatively barren coniferous forests we studied. For instance, *P. melanarius* has been collected in low numbers in cultivated habitats in Häme (Niemelä, unpublished data). On the other hand, some species (e.g. *Amara brunnea, N. biguttatus*) were scarcer in the southern study areas which are located well within their geographical ranges.

Species turnover among the study areas was considerable, but five species were collected in all the eight study areas. Thus, it appears that there is a set of common forest species that are widely distributed in the western palaearctic taiga (see also Niemelä 1993). In our southern study areas this set of species is complemented by species requiring more 'luxurious' forests, e.g., *Patrobus atrorufus, P. melanarius* and *C. nemoralis* (Lindroth 1985, 1986). In the more northern areas, however, no additional abundant species were found.

It is worth noting that many of the abundant species in our data occur widely in the coniferous forests of central and northern Europe. For instance, in a spruce forest in Denmark, *C. micropterus* was clearly the most abundant species (81% of the sample) and *P. oblongopunctatus* the second most abundant (8%) (Reddersen & Jensen 1991). In a pine stand in northern Poland, *P. oblongopunctatus* was the numerically dominant species and *C. micropterus* was the fourth one (Szyszko 1974). Further south, in a pine forest in Bohemia, *P. oblongopunctatus* was among the most frequently caught carabids, but *C. micropterus* was absent (Šustek 1981). In the coniferous forests in western Russia (Mari ASSR), the carabid assemblage was very similar to those of our study areas. There, the three most abundant species were, in descending order, *P. oblongopunctatus, Trechus secalis* and *C. micropterus* (Arnoldi & Matveev 1973).

The variation in carabid assemblages decreased with decreasing size of geographical area studied. Similarity among samples was lowest among study areas representing different geographical locations in southern and central Finland. On a regional scale (Talaskangas) similarity among sites was higher and on a local scale (Helsinki) yet higher. Interestingly, there was no clear trend toward decreasing similarity with increasing geographical distance between the study areas. These results indicate that there is a high degree of continuous species turnover across the southern-central Finnish boreal forest. Only a few species are generalists, whereas most species have a more restricted geographical distribution resulting in high variation among study areas.

To conclude, our results provide a quantitative assessment of the carabid fauna of mature boreal forest across southern and central Finland. The numerically dominant forest generalists, especially *C. micropterus*, are widely distributed and locally abundant in different kinds of forest types and age classes (see also Niemelä et al. 1988). However, many species of average abundance were restricted to the southernmost study areas. On the other hand, they may in the north occur in some distinct forest types not included in our study. It would seem profitable to investigate in more detail the distribution and habitat occurrence of these species. It is conceivable that changes in forest structure due to forestry practices affect these species, in addition to the rare specialists, more profoundly than it does the widely distributed generalists.

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