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The Importance of Small-Scale Heterogeneity in Boreal Forests: Variation in Diversity in Forest-Floor Invertebrates across the Succession Gradient

Author(s): Jari Niemelä, Yrjö Haila and Pekka Punttila

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The importance of small-scale heterogeneity in boreal forests: variation in diversity in forest-floor invertebrates across the succession gradient

Jari Niemelä, Yrjö Haila and Pekka Punttila

Heterogeneity in species assemblages of forest-floor arthropods – carabid beetles,
ants and spiders – within and between different forest age classes was studied in the
southern Finnish taiga. The importance of processes operating on the local scale
(within the movement radius of the species) vs on the regional scale (among forest
stands) in determining the observed variation was assessed. Four data sets with
different spatial resolutions in mesic forests in the same general study area were used.
The material consists of 18 283 carabids of 51 species, 48 769 spiders of 212 species,
and 126 718 worker ants of 23 species. Analyses of abundance variation and species
complementarity among successional stages revealed that in all the three taxa species
occurring in the mature forest were prevalent in the younger successional stages as
well, constituting more than half of the catch in any age class. A great majority of
carabid and spider species were widely distributed across the forest age-classes,
whereas ants include a higher proportion of species with a narrower amplitude across
the succession gradient. Comparisons of similarity between samples at increasing
distance from one another on the local scale within forest stands (a few tens of meters
to a few hundreds of meters) showed a quite consistent pattern in carabids and
spiders: there was more variation between sampling sites in young successional forests
than in the mature forest. Furthermore, only in the mature forest a slight, albeit
statistically not significant, negative relationship between similarity of samples and
distance between sampling sites was detected. In carabids and spiders, comparisons
between samples located at a distance of 10–15 m from each other showed consider-
able heterogeneity, the mean percentage similarity being c. 0.6 (in ants c. 0.8). On the
regional scale, systematic variation between young and mature forest stands is a
major element increasing the total diversity (species turnover c. 50% in carabids and
spiders; compositional similarity c. 0.3–0.4 in carabids, 0.2–0.3 in spiders), but
variation within forest stands on a spatial scale of 10–15 meters is another important
component in the total heterogeneity. The results suggest that regional abundance
variation is a primary factor influencing the composition of local assemblages; a set
of hypotheses elaborating this conclusion is formulated. The result implies that
maintenance of habitat heterogeneity on a small scale (10–15 m) is needed to
preserve biodiversity in managed forests.

J. Niemelä (correspondence) and P. Punttila, Dept of Ecology and Systematics, P.O.
Box 17, FIN-00014 Univ. of Helsinki, Finland. – Y. Haila, Satakunta Environmental
Research Centre, Univ. of Turku, FIN-28900 Pori, Finland. (Present address: Dept of
Regional Studies, Environmental Policy, Univ. of Tampere, P.O. Box 607, FIN-33101
Tampere, Finland).

'Biodiversity' has in recent years become a shorthand for heterogeneity and variation in nature. Three levels of biodiversity are usually distinguished from each other: diversity of genes in populations, diversity of species in communities, and diversity of ecosystems in landscapes and regions (e.g. Wilson 1988, Solbrig 1991). These are patterns which are produced and reproduced by a variety of processes operating on different spatial and temporal scales. Thus, biodiversity is a 'descriptively complex' term (Wimsatt 1974) in the sense that different alternative criteria can be used for its characterization, and the patterns discerned using alternative criteria do not necessarily coincide. In every particular instance the aspect of biodiversity that is considered, and the criteria that are used in quantification need to be defined (Huston 1994, Haila and Kouki 1994, Harper and Hawksworth 1994).

Our focus in this paper is on variation in species assemblages of forest-floor arthropods – carabid beetles, ants and spiders – within and among different forest age classes in the southern Finnish taiga on the local scale, that is, in an area that is well within the dispersal radius of all the species included in the study. In particular, we evaluate the relative importance of processes operating on the local vs on the regional scale in determining the variation observed. This has been recognized as a major problem in understanding ecological variation well before the recent upsurge of the 'biodiversity' issue (see, for instance, Preston 1960, Williams 1964, MacArthur 1972, Wiens 1981, Ricklefs 1987, and Ricklefs and Schluter 1993).

Operational definitions of local vs regional scale vary greatly among taxa according to the characteristic area and length of time over which individuals of each taxa interact with the physical environment and individuals of other taxa. This multiplicity of scales creates the problem of defining an adequate 'observation window', i.e. securing a sampling design that allows relevant types of heterogeneity to be detected and not be hidden behind averages (Rosen 1977, Wiens 1989).

Our sampling design covered three different scales which can be conceptualized using the scheme of alpha-, beta- and gamma-diversity proposed by Whittaker (1972): 'alpha' refers to individual samples, 'beta' to comparisons among samples either within or between different successional forest stages, and 'gamma' to the overall species richness in the whole data set. We pursue the following question: How is total diversity in these taxa in the whole set of data 'built up' from local assemblages distributed across the succession gradient? In particular, we compare variation in assemblage composition within vs among stands representing different successional stages. This comparison allows us to estimate the degree of complementarity in samples taken across the succession gradient (Colwell and Coddington 1994).

Two mutually exclusive extreme alternatives for the formation of regional diversity from local samples would

be (Ricklefs 1987, Holt 1993): 1) lack of regional structure, local assemblages being comparable to random samples 'drawn' from a regional 'pool', or 2) differentiation into locally saturated communities, with great variation in species composition in local samples representing different communities. However, both of these extremes are unrealistic as local assemblages vary everywhere systematically with environment and are 'structured' in this sense, but also comprise widely distributed species with a broad environmental amplitude. Our aim is to quantify this relationship in the ground arthropods in the taiga.

Our previous analyses on bird and carabid distributions suggest that species assemblages in the taiga may be relatively close to the first extreme (Haila et al. 1994). This is quite plausible considering the huge fluctuations in environmental conditions that have occurred in the present boreal areas during the Pleistocene, particularly in regions intermittently covered by continental ice (Birks 1986, Delcourt and Delcourt 1991, Shugart et al. 1992, Haila 1994, Pastor et al. 1996) as well as the year-to-year unpredictability in local conditions due to seasonal variation. It is also quite obvious that there are no tightly structured 'communities' in the taiga but, rather, species in most taxa are distributed mainly independently of each other along gradients in the environmental space (Whittaker 1967, Austin 1985, 1986, 1990; see Tonteri et al. 1990, Tonteri 1994, Haila et al. 1994).

In addition to differentiation among forest types, the degree of differentiation according to 'microsite' variation (Whittaker and Levin 1977) within forest types is important. It is not 'average forest' that most species require but some particular elements within the forest are needed. 'Microsites' are certainly important for organisms that require a specific habitat element such as decaying wood of particular species and age, or a given species of bracket fungus (Esseen et al. 1992, Kaila et al. 1994). However, population numbers of even such generalized species as carabid beetles correlate with, and are possibly locally determined by, fairly subtle, small-scale variation in ground cover (Niemelä et al. 1992).

These observations may be generalizable: if small-scale heterogeneity within forest stands considerably enhances local species richness and supports viable populations of specialized species, then this should be a major focus both in biodiversity assessment and in management. Indeed, a consensus has been reached among ecologists that an adequate strategy for diversity preservation is to secure heterogeneity of the environment on different scales simultaneously (e.g. Hunter 1990, Noss 1990, Hansen et al. 1991, Niemelä et al. 1993). This recommendation, however, remains toothless without specification as to what elements of environmental variation actually are important, and how they translate into square meters and hectares in management plans. Managers should be given detailed advice on what the relevant scales of heterogeneity are.

Material and methods

Study area

Our sampling sites were located in southern Finland at the border between south- and mid-boreal zones (Ahti et al. 1968, Järvinen and Väisänen 1973, 1980) in three study areas: Seitseminen National Park, Helvetinjärvi National Park, and the surroundings of Hyytiälä Forestry Station; the areas are ca 50 km apart from each other (ca 62°N, 23°E). Studied forests are mostly mesic, conifer-dominated and relatively barren; general descriptions are in Haila et al. (1987) and Niemelä et al. (1988).

The separation between local and regional scales is itself conventional and depends on the scale of the study. In our study the 'regional scale' was constituted by all the study areas together. This gives a comprehensive picture of the composition of forest fauna in the three taxa as well as the relative abundances of the species. The 'local scale' was constituted by sampling sites within each one of the three study areas (Seitseminen, Helvetinjärvi, Hyytiälä), where linear distances among the sites were between 1–10 km. Thus, the 'region' consisted of three 'localities' in our sampling design. For the smallest spatial units in the analyses we use the term 'study site'; each study site was constituted by several single 'samples'. Depending on sample size we used either single samples or pooled data of 'study sites' in the analyses that follow.

The data sets

We used pitfall trapping to collect the samples (Niemelä et al. 1986, 1990b, Spence and Niemelä 1994). The traps were plastic cups ($\varnothing$ 65 mm, vol. 170 ml) which were half-filled with water, preservative (NaOH or ethylene glycol) and detergent. The numbers and configurations of traps varied in the different data sets (see below).

Samples of the three taxa were collected from the same traps, i.e. the sampling design was identical for each one of the taxa. In analyses concerning ants we used the capture frequency ('rate of occurrence' or incidence) instead of worker number as a measure of abundance because of their social mode of life. This helps to scale the abundance of species with different colony size. The data we use originated from four sampling schemes:

1) Regional survey (referred to as 'regional survey'). In 1984 and 1985 we made a survey of ground-living arthropods in 60 sites in the three study areas (see above) including 19 spruce-dominated mature stands (trees > 120 yr), 14 pine-dominated mature stands (> 100 yr), 12 mature but managed stands (60–100 yr), three medium-tall managed stands (20–60 yr), and 12 young pine-dominated, regenerating stands (<20 yr).

For habitat details in each stand class, see Niemelä et al. (1988). In 1984, we had fifteen traps in each study site, placed in a 3 × 5 grid with 5 m distances between the traps; the traps were in operation for five days between 3–10 June, and between 19–26 August. In 1985, we had thirty traps in each study site, placed in a 5 × 6 grid with 5 m distances between the traps; the traps were in operation for 21 d (3–26 June) plus 15 d (5–21 August). Carabids were analyzed from all of the sites, while ants and spiders were analyzed from 31 of them (12 spruce-dominated mature stands, 7 pine-dominated mature stands, 8 managed mature stands, 1 medium-tall managed stands, 3 young pine-dominated stands); the sampling design and original data are described in Niemelä et al. (1988), Punttila et al. (1994) and Pajunen et al. (1995). Because of the small size of single samples in this data set, we used it only for general comparisons as specified below.

2) Mature forest [referred to as 'mature forest (Musturi 1985)']. In 1985, we conducted an intensive sampling using a grid of 300 traps in Musturi State Forest (20 ha, spruce-dominated forest mostly > 140 yr) near Hyytiälä Forestry Station. Traps in the grid were 5 m apart and arranged in 12 'rows' of 25 traps. The traps were operated between 11 May and 23 November 1985. The area, sampling scheme and carabid data are described in Niemelä et al. (1992). In the analyses of this study, however, we include only 100 traps (4 'rows' of 25 traps), because it was logistically impossible to collect spiders from all the traps. In the following analyses the whole grid was regarded as a single study site, and the pooled data of four neighbouring traps across the 'rows' of 25 traps were used as single 'samples'. In ants, we used incidence data from the four neighbouring traps of each of the 25 trap-rows summed over the 26 sampling periods, i.e. an incidence range of 0–104.

3) 14/20 yr cutover [referred to as '14/20-yr cutover (Seitseminen 1987)']. In 1987, we conducted a survey within a large and relatively homogeneous sapling area (total area 80 ha, cut in two halves 14 and 20 yr prior to our sampling) in Seitseminen National Park, using 800 traps arranged in 16 grids of 50 traps each. The distances between the traps were 7 m within each grid of 50 traps, and the sets of 50 traps were placed in four groups of four sets, the distances within groups being 100–600 m and between groups c. 250–2 000 m. The pooled data of each 50-trap set was regarded as a sample, and the four groups of 50-trap sets were separate study sites. Two of the study sites were in the 14 yr and the other two in the 20 yr half of the area. The four 'study sites' will be labeled '14 yr A', '14 yr B', '20 yr A' and '20 yr B'. The traps were operated from 3 May through 20 September (ants and spiders collected in a shorter period; spiders collected from 29 traps; for ants see Punttila et al. 1996). The habitats, sampling scheme and ant data are described in Punttila et al. (1996) (for carabids, see Tukia 1991).

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4) Early succession [referred to as 'early succession (Hyytiälä 1989)']. In 1989, we conducted a survey that covered three classes of young forest, viz., 0 yr, (cut the winter prior to our sampling), 2 yr, and 10 yr old, near Hyytiälä Forestry Station. Each forest class was represented by two sampling areas, 1–8 km apart; one of the 2 yr old areas and both 10 yr old sites had been treated by prescribed burning after cutting. In each sampling area we had a total of 208 traps, operated from 9 May through 10 October (ants collected in a shorter period, see Punttila et al. 1991). The traps were arranged in sets of 13 traps with 1–2 m distances among them; each set represented a sample. The 13-trap sets in each sampling area were organized into four 15 × 15 m quadrates 50 m apart, a 13-trap set being located in each corner of each quadrate. Each quadrate was a study site. We collected carabids and ants from all the 13 traps but spiders from 7 traps in each set. However, this difference does not influence the spatial configuration because single traps within the sets were not independent of each other. In addition, the survey included four mature forest reference sites, where we had one set of 13 traps (i.e. took one sample) in each. The habitats, sampling design and the ant data are described in Punttila et al. (1991). The 'study sites' are labeled '0 yr (1) A through D', '0 yr (2) A through D', '2 yr (1) A through D', '2 yr (2) A through D', '10 yr (1) A through D', and '10 yr (2) A through D', and the reference data 'mature forest (1989)'.

Study questions and analyses

We focus on studying two types of variation in species composition and richness in our data:

1) How much does species composition change across the succession gradient? We examine the degree of habitat specialism vs generalism of species relative to the range of habitat variation across the succession gradient. Our purpose is a) to get an idea of the overall variation in the composition of species assemblages across the gradient, and b) to assess the habitat amplitude of individual species.

The following approaches were used: a) For evaluating variation in assemblage composition we calculated the proportion that individuals of mature forest species formed of total samples from younger forest classes; the data set 'mature forest (1989)' served as a reference in this comparison. These proportions indicate the colonization of or persistence in young successional stages by species occurring in the mature forest. b) For evaluating the breadth of the habitat amplitude of single species we calculated 'incidence functions' (see Diamond 1975) across different forest age classes. The functions show the number of study sites in a given forest age class in which a given species was recorded and, thus, the constancy of presence of each individual

species across the succession gradient. Because of the uneven distribution of our sampling sites across the gradient, the results are representative of the early stages only.

In addition, we estimated complementarity in species lists across the early stages of succession in the data set 'early succession (Hyytiälä 1989)', using the formulae given by Colwell and Coddington (1994):

$$C_{jk} = \frac{\sum\limits_{i=1}^{S_{jk}} |X_{ij} - X_{ik}|}{\sum\limits_{i=1}^{S_{jk}} \max(X_{ij}, X_{ik})},$$

where X_{ij} and X_{ik} are the presence-absence values for species i in species list j and k. The value of the complementarity index varies from 0 (species lists identical) to 1 (no species shared). This comparison was standardized by sampling effort (pooled sample of 52 traps from each age class).

2) How much does variation within vs complementarity among forest stands contribute to the overall variation across the succession gradient? We examine the significance of 'micro-site' variation for the small-scale distribution of forest-floor arthropods. Our purpose is to estimate the increase in beta-diversity in pairwise comparisons between samples when the distance of the samples increases, 'distance' here meaning both the geographical distance of sampling points within study areas and their ecological distance along the succession gradient. If variation among samples close to each other within the same study area is large compared with variation among samples from different study areas, this implies that small-scale habitat heterogeneity is important for the distribution of the species. Conceptually, the analysis is analogous to an analysis of variance, namely, partitioning of the total variation in species assemblages to variation within vs between successional stands; for a similar methodological point see Underwood (1994).

For this analysis we used the data sets 'mature forest (Musturi 1985)', '14/20 yr cutover (Seitseminen 1987)' and 'early succession (Hyytiälä 1989)'. As the basic unit of comparison we used single samples, as described for each one of the data sets above. The relevance of the comparisons depends on how adequately samples, study sites and study areas were defined in our sampling design. This question lacks an unambiguous answer because single samples taken with pitfall traps operated for a long period of time are never really 'point samples' but rather include individuals from an unknown area in the surroundings of the actual trapping sites.

The samples were compared pairwise by Czekanowski index of percentage similarity using the software package BIODIV (Baev and Penev 1993). This is a useful index for two reasons: First, the meaning of 'percentage similarity' is intuitively clear. Second, as shown by studies using constructed data, the value of

Czekanowski index is a linear function of the actual difference in composition between the samples that are compared with each other, provided sample sizes are adequate (Wolda 1981, Pesenko 1982, Kohn and Riggs 1982). Unfortunately, however, estimates of percentage similarity are biased by sampling error: no two samples taken from the same community are identical, and thus comparison of any ecological assemblage with itself, based on samples, would yield percentage similarity <100%. Furthermore, this bias increases with increasing heterogeneity of the assemblages compared (Venrick 1983). Thus, a direct comparison of percentage similarity values across taxa with different levels of assemblage heterogeneity is not legitimate. To evaluate the degree of this bias, we used the graphs given in Venrick (1983).

It was not logistically possible for us to make habitat descriptions on the scale of single sampling points in the 'early succession (Hyytiälä 1989)' study. Consequently, it was not possible to assess directly whether the samples varied systematically with, for instance, ground-layer vegetation.

Identifying scales of heterogeneity relevant for management, and answers to the question of the relative importance of within-stand vs between-stand variation for maintenance of the diversity of forest-floor arthropods are eagerly awaited by managers. No realistic a priori hypotheses can be formulated about this question as the necessary background data are lacking (as forcefully emphasized for instance by Schluter and Ricklefs 1993). We aim at a thorough description of patterns in our data in such a way that the plausibility of alternative explanatory hypotheses can be assessed (Haila 1988, 1992).

The total sample includes a fair number of species represented by only a few individuals as is always the case in 'blind' sampling (Fisher et al. 1943, Preston 1960, Williams 1964), but it is highly unlikely that any numerous forest species would be missing.

The proportion that individuals of species included in the data set 'mature forest (1989)' formed of the samples from other successional stages is shown in Fig. 1. Qualitatively the pattern is clear and quite similar in the three taxa: the proportion was high in the '0 yr' samples, dropped to ca 65% in the '2 yr' samples, and increased thereafter reaching 85–98% in the '60 yr' sample. A critical stage is presumably tree-canopy closure (Haila 1994, Haila et al. 1994). The more rapid decline in the proportion of mature-forest spiders than in that of carabids and ants after cutting suggests that among spiders species favouring open habitats have a better colonization ability and/or mature-forest species have lower persistence in the recently cut sites than the other two taxa. In each taxon, however, species occurring in the mature forests had a strong hold in the assemblage of all successional stages, making up ≥50% of the total catch. Note that the standardized catches were larger in young than in old successional stages for spiders and carabids (see also Niemelä et al. 1988, Punttila et al. 1991, 1994, Pajunen et al. 1995).

Similarly, an analysis of complementarity in the species lists across young successional stages showed for both carabids and spiders that the '0 yr' samples had more similar species lists with the mature forest than did the '2 yr' or '10 yr' samples (Table 2). We excluded ants from this comparison because of their low species numbers; for another analysis with similar results, see Punttila et al. (1991).

Results

Change in species composition across the succession gradient

Samples obtained from the four different data sets are presented in Table 1. Our pooled sample represents fairly well the regional 'gamma-diversity' of forest species as there was considerable overlap among the data sets in species identities. The representativeness of the sample was also checked by inspecting the distribution maps of the handbooks by Lindroth (1945) for carabids and Collingwood (1979) for ants. No obvious missing species were detected, given that habitat affinities particularly relative to successional stages are quite ambiguous. For forest-floor spiders a comparable handbook is missing. However, for spiders as well as for the other taxa our confidence in the representativeness of the species list is supported by the very small proportion of species with a low incidence (Tables 3, 4 and 5 and Appendices 1 and 2).
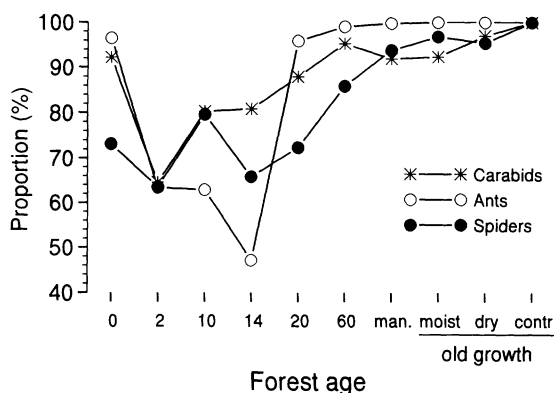

Fig. 1. Proportion of those carabid, ant, and spider species in the younger forest age classes that were found in the old-growth forest ('control', 100%). The 'control' is the 'mature forest (1989)' from the 'early succession (Hyytiälä 1989)' data set. Man. is mature managed forest.

Table 1. Number of individuals (ind.) and species (spp.) of carabids, spiders and ants (workers) from the different data sets used in this study.

| | Carabids | | Spiders | | Ants | |
	ind.	spp.	ind.	spp.	ind.	spp.
Regional survey	1438	40	3074	83	50185	14
Mature forest (Musturi 1985)	898	22	7471	101	6847	12
14/20 yr cutover (Seitseminen 1987)	1488	26	3239	99	37479	22
Early succession (Hyytiälä 1989)	14414	47	34985	192	32205	22
Total	18238	51	48769	212	126716	23

The distribution of single species across the succession gradient

A great majority of the species were widely distributed across the forest age classes, and the number of species restricted to a particular successional stage was low (Tables 3, 4 and 5; scarce species are listed in Appendices 1 and 2). In carabids, two species (of 29 numerous ones), Agonum quadripunctatum and Cicindela campestris, were found with a high incidence in the '2 yr' samples but were missing from the other age classes (Table 3). Synuchus vivalis, was found only in '2 yr' and '10 yr' samples, and a few more species occurred in three age classes in the range between age classes 0 yr and 20 yr. On the other hand, none of the species found with a high incidence in the mature forests were restricted to that type of forest. Of the 21 scarce species, seven were found only in one age class: four in '2 yr', one in '10 yr', and 2 in 'mature forest' (Appendix 1).

In spiders, five species (of 94 numerous ones) were found with a high incidence in only one forest age class but were missing from the others: Araneus omoedus in 'mature forest', Tuberta arietina in '0 yr', and Erigone dentipalpis, Oedothorax apicatus, and O. apicatus/retusus in '2 yr' samples (Table 4). All these species were relatively scarce (5–22 individuals). Additional four species were found in only two age classes, viz., Pityhyophantes phrygianus, Walckenaeria clavicornis and Zornella subterraneus in the 'mature forest' and '0 yr' samples, and Zelotes pusillus in the '0 yr' and '10 yr' samples. Another five species occurred only in three age

Table 2. Complementarity of species lists in the different forest age classes in the 'early succession (Hyytiälä 1989)' data set for carabids and for spiders. For calculation of the complementarity see text.

	Carabids	Spiders
Complementarity		
0–2 yr	0.49	0.47
2–10 yr	0.44	0.52
10 yr–mature	0.52	0.63
0–mature	0.52	0.45
2–mature	0.64	0.58
No. of species		
0 yr	19	65
2 yr	34	74
10 yr	22	81
mature	15	62

classes. Overall, similar to the carabids, most of the spiders were broadly distributed across the succession gradient. Of the 118 scarce species, 52 were caught in only one age class (31 species represented with one individual): eight in '0 yr', 16 in '2 yr', nine in '10 yr', six in '14/20 yr', and 13 in 'mature forest', i.e. the occasional species were not concentrated in any particular forest age class (Appendix 2).

In ants, the four species found in all the three mature-forest data sets, i.e. C. herculeanus, F. aquilonia, F. lugubris and M. ruginodis (Table 5) were also numerous in these forests. These species are capable of inhabiting mature forests with closed tree canopy, and they occurred at varying numbers also in the younger successional stages. The rest of the species found in the mature forests were mostly occasional observations of workers originating presumably from colonies located in more open sites, e.g. windfall openings and forest edges. Also among the rest of the high-incidence species, occasional workers were commonly recorded from many successional stages, but when judged by their numbers in these data sets, a list of high-incidence open-country species can be generated. Such species in these data were F. lemani, F. fusca, F. sanguinea, L. niger, M. sulcinodis and L. acervorum. These species were numerous especially in the 10 yr and 14/20 yr sites, whereas in most cases only occasional workers were recorded from younger or older sites. The colonies of these species are dependent on direct sunlight and thus, require open tree canopy.

Variation within sampling areas

We present the values of the percentage similarity index calculated for the three taxa separately among single samples in the data sets 'mature forest (Musturi 1985)', '14/20 yr cutover (Seitseminen 1987)', and 'early succession (Hyytiälä 1989)'. The variation in the index values is shown as a function of the distance between 'sampling sites' within each 'study area'.

In the data set 'mature forest (Musturi 1985)' the similarity between neighbouring samples was c. 0.8 in every taxon and declined monotonously with distance, although the differences reached were not statistically significant (Fig. 2). The curves of carabids and spiders

Table 3. Incidence of individual carabid species in data sets across the forest succession gradient. The figures show the number of sampling units (maximum number of units in brackets under the site code) in which each species was found in 'early succession (Hyytiälä 1989)' data (two 0 yr, two 2 yr, and two 10 yr sites), '14/20 yr cutover (Seitseminen 1987)' and in all mature forest data sets 'regional survey' (years 1984 and 1985 separated), 'mature forest (Musturi 1985)' and 'early succession (Hyytiälä 1989)'. The total number of individuals in all the data sets included in this comparison is in brackets after each species name. Only the species that occurred in all the sampling units in at least one age class are included.

	Sampling area							
	0/1 (4)	0/2 (4)	2/1 (4)	2/2 (4)	10/1 (4)	10/2 (4)	14–20 (4)	mature (4)
Agonum fuliginosum (235)	0	4	4	3	2	3	2	0
Agonum quadripunctatum (196)	0	0	4	0	0	0	0	0
Agonum sexpunctatum (597)	1	3	4	4	1	1	2	0
Amara brunnea (243)	0	2	4	4	1	3	3	4
Amara lunicollis (608)	4	4	4	4	4	3	4	0
Bembidion bruxellense (155)	1	0	4	2	0	1	0	0
Bembidion lampros (325)	1	0	4	4	4	4	1	0
Calathus micropterus (5006)	4	4	4	4	4	4	4	4
Carabus cancellatus (19)	1	1	4	4	0	1	2	0
Carabus glabratus (174)	3	3	3	4	4	1	4	4
Carabus hortensis (96)	0	0	1	0	0	1	3	4
Carabus nitens (56)	1	0	4	4	0	4	0	1
Cicindela campestris (50)	0	0	4	1	0	0	0	0
Cychrus caraboides (198)	3	4	3	4	4	2	4	4
Harpalus quadripunctatus (764)	4	3	4	4	4	4	4	3
Leistus ferrugineus (50)	0	0	2	4	3	1	2	3
Leistus terminatus (156)	2	3	4	4	1	2	4	3
Miscodera arctica (83)	0	0	2	2	3	4	4	0
Notiophilus biguttatus (371)	3	2	4	4	4	4	4	4
Notiophilus palustris (305)	2	2	4	4	4	4	0	2
Patrobus assimilis (61)	1	4	2	4	1	0	1	1
Pt. adstrictus (391)	4	4	4	4	2	4	0	2
Pt. cupreus (585)	3	1	4	4	4	4	0	1
Pterostichus niger (411)	0	4	4	4	0	4	0	2
Pterostichus nigrita (133)	0	4	4	3	3	2	0	2
Pt. oblongopunctatus (3982)	4	4	4	4	4	4	4	4
Pt. strenuus (367)	4	3	4	4	4	4	4	1
Synuchus vivalis (139)	0	0	3	0	4	4	0	0
Trechus rubens (40)	2	0	4	1	1	0	1	0
Trechus secalis (860)	4	4	4	4	4	4	4	3

had identical shapes, but that of ants dropped more steeply at 15–20 m distance; this can be expected on the basis of interspecific territoriality of Formica aquilonia and F. lugubris, that dominate the ant community of mature forests (Punttila et al. 1991, 1994, 1996) and also Musturi (Niemelä et al. 1992).

Figure 3 shows these analyses for the data set '14/20 yr cutover (Seitseminen 1987)'. The shortest distance was between groups of traps in the corners of each 50 trap grid; we used nine traps for carabids and ants, and 6 traps for spiders. Then we calculated the similarities separately for samples from 'study sites' 100–200 m from each other, and >200 m from each other. In ants the similarity was c. 0.8 irrespective of distance, i.e. similar to that in the mature forest but without the decline found there. The lack of the decline in similarity with increasing distance is probably because wood ants are only a minor element in the communities of young forests (Punttila et al. 1994, 1996).

In both carabids and spiders, in contrast, the level of similarity was considerably lower than in 'mature forest', c. 0.5–0.6 in both taxa, and there was no statistically significant relationship with distance. In spiders, interestingly, the smallest similarity was between sites that were close to each other.

Figure 4 shows the analysis for the data set 'early succession (Hyytiälä 1989)'. The sampling areas were analysed separately, i.e. two areas for each one of the age classes ('0 yr', '2 yr', '10 yr'). The general patterns for all six sampling areas were similar: there was no discernible relationship between similarity of samples and distance between sites. The level of similarity was again somewhat higher in ants than in the other groups, particularly in the '0 yr' sampling areas where the ant communities were still in the first summer following cutting dominated by the wood ants Formica aquilonia and F. lugubris (Punttila et al. 1991). In carabids and spiders the level of similarity was c. 0.5–0.6, i.e. clearly lower than in the 'mature forest' and quite similar to that in the data set '14/20 yr cutover (Seitseminen 1987)'.

In conclusion, these comparisons show quite a consistent pattern: there was more variation between sampling sites in young successional stages than in the mature forest, but only in 'mature forest (Musturi

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Table 4. Incidence of individual spider species in data sets across the forest succession gradient. The figures show the number of sampling units (maximum number of units in brackets under the site code) in which each species was found in 'early succession (Hyytiälä 1989)' data (two 0 yr, two 2 yr, and two 10 yr sites), '14/20 yr cutover (Seitseminen 1987)' and in mature forest data sets 'regional survey' (year 1984), 'mature forest (Musturi 1985)' and 'early succession (Hyytiälä 1989)'. The total number of individuals in all the data sets included in this comparison is in brackets after each species name. Only the species that occurred in all the sampling units in at least one age class are included.

	Sampling area							
	0/1 (4)	0/2 (4)	2/1 (4)	2/2 (4)	10/1 (4)	10/2 (4)	14–20 (4)	mature (3)
Acantholycosa lignaria (186)	2	2	4	3	3	4	1	2
Agroeca brunnea (237)	4	2	2	4	4	4	3	3
Agroeca proxima (67)	3	3	1	4	4	4	0	2
Agyneta cauta (859)	2	2	2	3	4	4	4	3
Agyneta conigera (450)	3	4	4	4	1	4	4	3
Agyneta olivaceus (62)	4	3	0	0	2	1	4	1
Agyneta ramosa (618)	4	4	0	3	1	3	3	3
Agyneta subtilis (658)	4	4	4	4	1	3	3	3
Allomengea scopigera (196)	1	4	2	3	0	0	0	2
Alopecosa aculeata (387)	4	3	4	4	3	4	2	3
Alopecosa pinetorum (83)	2	3	2	1	0	0	0	3
Alopecosa pulverulenta (857)	2	4	4	4	4	4	4	0
Araneus omoedus (5)	0	0	0	0	0	0	0	3
Bathyphantes gracilis (1022)	3	3	4	4	4	4	3	3
Bianor aurocinctus (14)	0	0	1	1	4	3	1	0
Centromerus arcanus (1794)	4	4	4	4	4	4	4	3
Centromerus incilius (49)	0	0	2	1	4	4	3	1
Clubiona kulczynskii (28)	0	2	0	3	4	3	1	1
Clubiona subsultans (60)	3	3	0	1	1	0	0	3
Cnephalocotes obscurus (216)	2	3	3	4	4	4	4	2
Crustulina guttata (33)	1	0	2	1	4	3	4	0
Cryphoeca silvicola (778)	4	4	1	4	0	0	0	3
Dicymbium tibiale (2410)	4	4	4	4	4	4	4	3
Diplocentria bidentata (878)	4	4	4	4	4	4	2	3
Diplostyla concolor (1023)	3	3	4	4	4	4	4	3
Drassodes pubescens (119)	2	2	4	4	4	4	3	2
Erigone atra (446)	1	1	4	4	1	1	0	0
Erigone dentipalpis (22)	0	0	4	3	0	0	0	0
Erigonella hiemalis (137)	2	0	2	3	4	4	2	0
Eryopis flavomaculata (65)	1	0	0	1	4	4	4	1
Evarcha falcata (45)	2	0	0	1	3	4	4	2
Gnaphosa bicolor (1225)	4	3	4	4	4	4	4	1
Gnaphosa montana (32)	0	0	4	0	2	4	3	0
Haplodrassus signifer (551)	3	2	4	4	4	4	4	3
Haplodrassus soerensenii (693)	2	4	2	4	4	4	4	3
Latithorax faustus (299)	2	4	2	4	2	0	0	3
Lephyphantes tenebricola (768)	4	2	3	4	2	1	0	3
Lepthyphantes alacris (4763)	4	4	4	4	2	2	3	3
Lepthyphantes angulatus (220)	2	4	1	0	4	4	4	2
Lepthyphantes antroniensis (455)	4	4	4	2	1	1	0	3
Lepthyphantes mengei (47)	0	1	3	3	4	4	2	1
Macrargus carpenteri (27)	0	0	3	4	2	3	3	0
Macrargus rufus (1781)	4	4	4	4	4	3	0	3
Maso sundevalli (67)	2	4	0	2	1	0	0	3
Meioneta beata (89)	1	0	3	4	2	4	4	0
Meioneta gulosa (198)	0	1	4	4	1	4	0	0
Micaria aenea (84)	1	1	0	1	3	3	4	1
Micaria pulicaria (90)	2	1	1	3	4	4	1	0
Micaria silesiaca (25)	1	0	3	4	2	1	0	0
Micrargus apertus (159)	4	4	1	1	4	4	0	2
Micrargus herbigradus (449)	2	2	4	3	4	4	3	1
Microneta viaria (152)	2	2	0	0	2	3	4	2
Minyriolus pusillus (92)	4	1	3	3	2	2	4	3
Oedothorax apicatus/retusus (21)	0	0	4	0	0	0	0	0
Oedothorax apicatus (22)	0	0	4	2	0	0	0	0
Oreonetides vaginatus (102)	1	3	4	1	1	3	1	3
Oxyptila trux (83)	1	3	4	4	3	3	3	2
Pardosa amentata (628)	1	1	4	3	0	2	2	0
Pardosa fulvipes (773)	4	4	4	3	0	0	0	0
Pardosa hyperborea (26)	1	0	2	4	0	4	1	0
Pardosa lugubris (1992)	4	4	4	4	4	4	4	3
Pardosa palustris (79)	2	2	4	2	0	2	0	0
Pardosa pullata (1929)	4	4	4	4	4	4	3	0
Pardosa riparia (8743)	4	4	4	4	4	4	4	3

Table 4 (continued).

	Sampling area							
	0/1 (4)	0/2 (4)	2/1 (4)	2/2 (4)	10/1 (4)	10/2 (4)	14–20 (4)	mature (3)
Pardosa sphagnicola (716)	4	4	4	4	3	3	3	0
Phrurolithus festivus (28)	0	0	1	0	1	2	4	0
Pirata hygrophilus (55)	0	4	1	0	0	1	0	1
Pityhyophantes phrygianus (13)	3	0	0	0	0	0	0	3
Pocadicnemis pumila (344)	2	3	3	2	4	4	4	2
Porrhomma pallidum (195)	4	4	4	4	4	2	0	3
Robertus lividus (280)	3	4	4	4	4	4	2	3
Robertus scoticus (89)	2	4	3	3	3	1	2	3
Tapinocyba pallens (737)	4	4	4	4	4	4	4	3
Trichopterna mengei (173)	0	4	3	0	0	2	0	3
Trochosa spinipalpis (71)	1	3	0	1	0	2	4	2
Trochosa terricola (748)	4	4	4	4	4	4	4	2
Tuberta arietina (7)	4	1	0	0	0	0	0	0
Walckenaeria antica (499)	4	4	4	4	4	4	4	3
Walckenaeria clavicornis (33)	1	2	0	0	0	0	0	3
Walckenaeria cucullata (187)	4	2	0	3	2	2	4	3
Walckenaeria cuspidata (203)	4	4	2	1	4	4	1	3
Walckenaeria dysteroides (223)	3	3	4	4	4	4	4	3
Walckenaeria melanocephala (132)	3	4	4	3	4	4	1	3
Walckenaeria obtusa (146)	3	0	2	1	4	4	3	3
Xerolycosa nemoralis (476)	3	3	4	3	3	4	4	1
Xysticus audax (58)	4	4	4	4	3	2	1	2
Xysticus lineatus (25)	1	0	0	1	3	2	4	0
Xysticus luctuosus (25)	0	1	0	0	4	4	1	2
Zelotes latreillei (92)	3	0	1	4	4	4	4	0
Zelotes pusillus (17)	2	0	0	0	4	0	0	0
Zelotes subterraneus (339)	4	1	2	4	4	4	4	2
Zora nemoralis (239)	4	4	0	3	4	4	4	3
Zora spinimana (193)	3	4	1	4	4	4	3	3
Zornella cultrigera (23)	1	1	0	0	0	0	3	3

1985)' data set did we detect a slight, albeit statistically not significant negative relationship between similarity of samples and distance between sampling sites. This accords with a slight elevation gradient across the site (see Niemelä et al. 1992). Note, particularly, that the shortest distances between sites in both '14/20-year cutover' and 'early succession' were only some 10–15 m, i.e. well within the distances covered in the 'mature forest' study area. The difference in heterogeneity between mature forest and younger successional stages in our data seems thus real. On the other hand, the lack of a systematic relationship between similarity and distance indicates that the heterogeneity between the samples within 'study areas' is due to factors operating on the smallest scale of our sampling design, that is, on the scale of 10–15 m.

Complementarity between sampling sites

Table 6 shows the values of percentage similarity among pooled data sets from different sampling sites; the data sets '14/20 yr cutover (Seitseminen 1987)' and 'early succession (Hyytiälä 1989)' (with the mature forest reference) were included in these comparisons. Each row in Table 6 represents one comparison. We used the pooled data from each of the sampling sites for these comparisons because it is the overall difference between the sampling

sites we were interested in, not variation among single samples.

The '0 yr', '2 yr' and '10 yr' age classes in the 'early succession (Hyytiälä 1989)' data set were represented with two sampling areas. Comparisons within age classes yielded similarity index values in the range of 0.59–0.68 (carabids) and 0.44–0.76 (spiders), i.e. most of the values were similar to those obtained in comparisons within the respective sampling areas (Fig. 4). The only exception was recorded in spiders in the '2 yr' age class: their similarity between the areas '2 yr (1)' and '2 yr (2)' was 0.44 (Table 6) but values within both areas were c. 0.6. This difference is presumably because of the difference in treatment history between the areas: '2 yr (1)' had been burned after cutting in the summer preceding our sampling.

Values of the similarity index between study areas representing different forest age classes were consistently lower than those derived from comparisons within the study areas in spiders, and lower in some of the comparisons in carabids (Table 6). According to Figs 3 and 4, and Table 6, 0.6 is a rough average for similarity among sites within the young forest classes. In carabids, six of the thirteen comparisons between age classes shown in Table 6 ('neighbouring age' and 'remote age') yielded a difference of >0.1 similarity units (with rounding errors) compared with the average of 0.6 among similar-age sites.

Table 5. Incidence of individual ant species in data sets across the succession gradient. The figures show the number of sampling units (maximum number of units in brackets under the site code) in which each species was found in 'early succession (Hyytiälä 1989)' data (two 0 yr, two 2 yr, and two 10 yr sites), '14/20 yr cutover (Seitseminen 1987)' and in mature forest data sets 'regional survey' (year 1984), 'mature forest (Musturi 1985)' and 'early succession (Hyytiälä 1989)'. The total number of workers in all the data sets included in this comparison is in brackets after each species name.

	Sampling area							
	0/1 (4)	0/2 (4)	2/1 (4)	2/2 (4)	10/1 (4)	10/2 (4)	14–20 (4)	mature (3)
Camponotus herculeanus (2719)	3	4	4	4	4	4	4	3
Formica aquilonia (82264)	4	4	4	4	4	3	1	3
Formica exsecta (358)	0	0	1	0	1	2	4	0
Formica fusca (1076)	1	4	3	4	4	4	4	2
Formica lemani (4923)	3	3	4	4	4	4	4	2
Formica lugubris (8857)	1	4	3	3	1	2	4	3
Formica pratensis (5)	0	0	0	1	0	1	2	1
Formica pressilabris (7)	0	0	0	0	0	0	1	0
Formica rufa (6)	0	1	0	0	0	0	1	2
Formica sanguinea (8464)	0	2	4	4	4	4	4	1
Formica truncorum (7)	0	2	0	0	0	0	2	0
Formica uralensis (11)	0	1	0	0	1	0	4	2
Formicoxenus nitidulus (13)	1	0	0	0	0	0	1	1
Harpagoxenus sublaevis (29)	0	0	0	0	3	0	4	0
Lasius niger (1764)	0	2	2	3	4	4	4	2
Leptothorax acervorum (1682)	0	1	0	0	4	4	4	2
Leptothorax muscorum (7)	0	0	0	0	1	1	1	0
Myrmica lobicornis (410)	0	0	0	0	4	3	4	2
Myrmica rubra (6)	0	0	0	0	1	1	2	0
Myrmica ruginodis (7100)	4	4	4	4	4	4	4	3
Myrmica sabuleti (1)	0	0	0	0	1	0	0	0
Myrmica scabrinodis (33)	0	0	0	0	1	2	4	0
Myrmica sulcinodis (2867)	0	3	1	1	4	4	4	1

Thus, in carabids, our data showed an element of complementarity of c. 0.1–0.3 similarity units in about one half of the comparisons across age classes compared with comparisons within age classes.

Taking the same 0.6 as a rough average for similarity among sites within young successional stages in spiders (Figs 3 and 4), ten of the thirteen comparisons between age classes in Table 6 yielded a difference of >0.1 similarity units (with rounding errors) compared with this average. In one case the difference was 0.5 units, and in all the other cases 0.3–0.4 units. Thus, in spiders our data showed a larger element of complementarity in the comparisons across age classes compared with comparisons within age classes than in carabids.
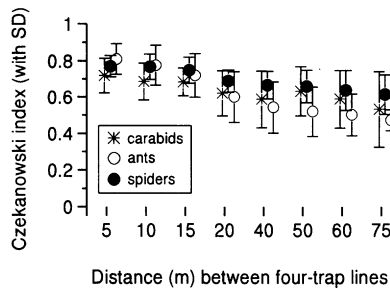

Fig. 2. The average Czekanowski percentage similarity (with SD) between pooled samples from 'columns' of four traps at different distances from each other in the 'mature forest (Musturi 1985)' data set. The values are calculated separately for carabids, ants and spiders.

Discussion

Heterogeneity within and among successional stages

Carabids and spiders are predators, i.e. they can be expected to depend more upon such habitat characteristics that determine availability and abundance of prey and facilitate successful hunting than on particular plant species. For wood ants honeydew excreted by aphids is an important source of nutrition but the availability of aphid trees is not primarily determined by other plant species. Single species of these arthropods show a varying degree of affinity with particular structural characteristics of the micro-habitat, particularly in web-building spiders (Pajunen et al. 1995), and moisture and tree-canopy variation in ants of young forests (Punttila et al. 1991, 1996). As a group, forest-floor arthropods reflect the condition of the soil food web. A few habitat specialists have been included in the Red Data Book of Finland as requiring special monitoring (Rassi et al. 1992).

We elaborate on two general patterns emerging from our analyses. First, in all three groups of arthropods we recorded a clear difference in both species list and assemblage composition between young, open successional stages and older stages with taller trees and closed canopy. The ground-arthropod fauna of clear-
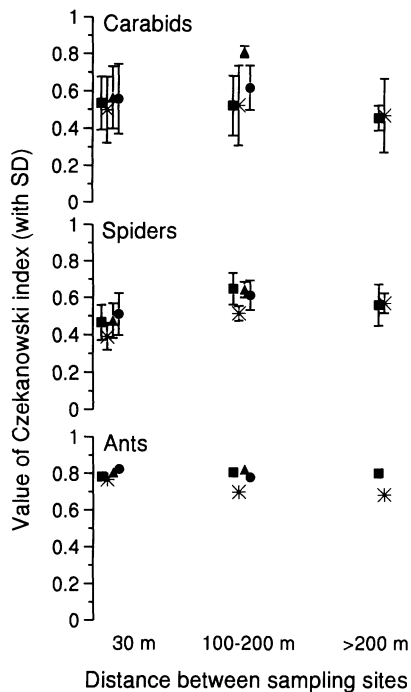
Fig. 3. The average Czekanowski percentage similarity (with SD) for carabids, spiders and ants among trap sets at different distances apart in the '14/20 yr cutover (Seitseminen 1987)' data set (24 comparisons among sets of nine traps for carabids and ants [six traps for spiders] at the 30 m distance, three comparisons among sets of 50 traps for all groups in the 100–200 m distance, and two comparisons among 50 traps for all groups in the >200 distance). Symbols: ■ '14 yr A', ∗ '14 yr B', ▲ '20 yr A', ● '20 yr B'.

cut forests received new species very rapidly, beginning in the first summer following cutting, which indicates a remarkable dispersal ability of the species (see also Punttila et al. 1991, Niemelä et al. 1993). Compositional similarity of assemblages in cutovers compared with mature forest dropped to ca 0.3 in carabids and 0.2 in spiders during the first years, but started to increase again with time. However, species occurring in mature forests apparently maintained viable populations in younger successional stages as well. They comprised >50% of the total assemblage in all forest age classes, and the level of complementarity in species composition in pairwise comparisons between different forest age classes was not >ca 50%.

Second, in all young stands we observed a high level of compositional heterogeneity between samples on a spatial scale of 10–15 m; this was c. 0.5 similarity units in both carabids and spiders. There was no increase in heterogeneity with increasing distance within the study areas, and pairwise comparisons between study areas of similar forest age ('0 yr', '2 yr', and '10 yr') revealed a similar level of heterogeneity. This level of heterogeneity is much higher than can be expected as a result of sampling bias alone. Expected similarity with the bias

would be >0.8 in samples that have comparable species richness and number of individuals (Venrick 1983: Fig. 1).

In principle, high complementarity between samples might be due to three different types of factors operating on different scales, namely, 1) sampling variation, 2) 'micro-site' variation within stands that are homogeneous in structural characteristics, and 3) variation between different stands (see also Colwell and Coddington 1994). Note that the first factor, 'sampling variation', is not only produced by the procedure of taking samples, it is also an inherent feature of ecological assemblages which are in a constant flux due to the contingent movements of individuals of different species. These two aspects of sampling variation cannot be distinguished from each other. As a matter of fact, 'sampling variation' grades smoothly into 'micro-site' variation, because the sample in every single pitfall trap is derived from an unknown area in the surroundings of the trap, and micro-site heterogeneity within this area can be expected to increase heterogeneity of the sample.

From above it follows that we can distinguish two levels of diversity in our data. On a higher level, the
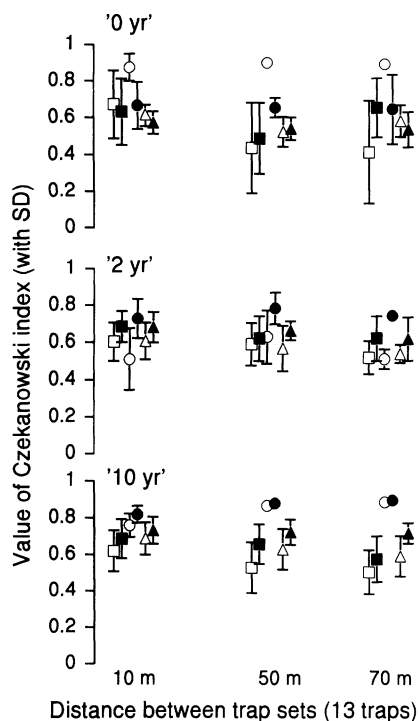
Fig. 4. The average Czekanowski percentage similarity (with SD) among trap sets at different distances from each other in the 'early succession (Hyytiälä 1989)' data set. The three forest age classes are separated: '0 yr', '2 yr' and '10 yr'. Symbols: □ carabids in '0 yr(1)', '2 yr(1)', '10 yr(1)', ■ carabids in '0 yr(2)', '2 yr(2)', '10 yr(2)', ○ ants in '0 yr(1)', '2 yr(1)', '10 yr(1)', ● ants in '0 yr(2)', '2 yr(2)', '10 yr(2)', △ spiders in '0 yr(1)', '2 yr(1)', '10 yr(1)', ▲ spiders in '0 yr(2)', '2 yr(2)', '10 yr(2)'. The average Czekanowski value is based on eight comparisons among sets of 13 traps.

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Table 6. The average value of Czekanowski similarity index and standard deviation between study sites of the same age, 'neighbouring age' (age classes next to each other) or 'remote age' (at least one age class between) for carabids and spiders. The number of comparisons with which the average is calculated is in brackets after the age.

	Carabids simil.	SD	Spiders simil.	SD
same age				
0 yr (1)	0.62	–	0.69	–
2 yr (1)	0.59	–	0.44	–
10 yr (1)	0.68	–	0.76	–
'neighbouring' age				
0 yr vs 2 yr (4)	0.52	0.10	0.32	0.05
2 yr vs 10 yr (4)	0.51	0.07	0.46	0.15
10 yr vs 14 yr (2)	0.34	0.00	0.27	0.04
14 yr vs 20 yr (1)	0.58	–	0.63	–
20 yr vs old growth (1)	0.74	–	0.19	–
'remote' age				
0 yr vs 10 yr (4)	0.52	0.10	0.22	0.03
0 yr vs 14 yr (2)	0.36	0.08	0.28	0.00
0 yr vs 20 yr (2)	0.45	0.05	0.25	0.03
0 yr vs contr. (4)	0.47	0.01	0.49	0.01
2 yr vs contr. (4)	0.27	0.03	0.20	0.07
2 yr vs 14 yr (2)	0.26	0.02	0.22	0.03
2 yr vs 20 yr (2)	0.31	0.06	0.20	0.01
10 yr vs contr. (4)	0.40	0.08	0.12	0.02

general physiognomy and composition of forest stands, determined by age, is a major deterministic factor: different species show different responses to forest structure, which creates population-level differentiation between forest age classes. Measured by percentage similarity (Table 6), differences among forest age classes were greater than when only species lists or proportions of total samples were used as a criterion (Table 2 and Fig. 1, respectively). In other words, relative abundances of the species varied more than species composition or total proportions would have predicted. This can be attributed to differential habitat selection and reproductive success of different species across the succession gradient.

On a lower level, we recorded considerable within-stand variation particularly in the young successional stages (Figs 3 and 4). This variation has two, not mutually excluding explanations: systematic variation on the 'micro-site' scale in environmental conditions, and/or chance. Explorative survey data cannot distinguish between these alternatives. On the other hand, different species may systematically favour particular spots with a certain type of ground cover (as observed in Musturi for carabids, Niemelä et al. 1992, see also Niemelä 1990, Niemelä et al. 1990a, Niemelä and Spence 1994; in Seitseminen cut-overs for ants, Punttila et al. 1996; and in our regional survey for spiders, Pajunen et al. 1995).

In view of these micro-habitat preferences the lack of a systematic relationship between percentage similarity and distance between the samples is quite unexpected, as one would expect spatial autocorrelation in environmental attributes within the sampling sites. This observation suggests that carabids and spiders (in distinction from ants which are tied to their colony locations and

are affected by strong species interactions) disperse actively all over the open young stands which they inhabit. If this is true, all species are potentially 'present' all over the stands but between-sample heterogeneity is produced by the tendency of different species to gather at different types of litter and vegetation, i.e. through preferential movement patterns on the individual scale (Niemelä et al. 1992).

Comparisons across taxa have often proven fruitful in tracing continent-wide geographic patterns in diversity variation. Although the general abundance-variation patterns in carabids and spiders were similar across the succession gradient, our earlier results suggest that their small-scale diversity variation is caused by different factors. We propose that particular habitat elements, such as structures of the vegetation created by different plant species, are relatively more important for spiders than for carabids, which are primarily influenced by quite coarse characteristics of the ground cover, such as litter quality (see Pajunen et al. 1995, and Niemelä et al. 1992, respectively). For ants, soil moisture and tree-canopy variation appear to be important.

The interplay between regional and local sources of variation

Our results suggest that local population size is primarily determined by abundance of the species on the regional level. Two features of the forest environment lend support to this conclusion: First, the environmental gradients in the study area are short as topographic variation is slight, soils are young and uniform (mixed glacial moraine), and both tree and understory vegetation are relatively species-poor and uniform, i.e. the dominant plant species are shared across a large por-

tion of the gradient. This relatively small variation in physical conditions across the environmental space implies that all species can potentially occur in a large part of the total environmental space. Changes in this space are driven by the vegetation, particularly trees (Holling 1992). Second, because of the pronounced seasonality of the northern environment, both resources and ground arthropod assemblages are essentially reproduced anew every growing season. This creates a strong element of small-scale stochasticity in the system. The availability of resources is unpredictable on the small scale, and carabids and spiders must move a lot to find them, whereas the coloniality in ants is a strong buffer against small-scale capriciousness of the environment (Oinonen 1956, Rosengren et al. 1979, Hölldobler and Wilson 1990). These features of the environment, together with active dispersal in most of the species, imply that the ambiguities in defining 'local' assemblages may be analogous to those in, for instance, the intertidal, although the relevant time-scales may vary (see Underwood and Petraitis 1993).

We specify this general conclusion with the following set of hypotheses:

1) A major element creating systematic variation in local assemblages is the contrast between mature and young forests. Both forest physiognomy, through its effect on microclimate, and the composition of undergrowth, through its effect on micro-habitats and litter, are presumably important determinants of this difference. Successional change in forest structure is relatively rapid in the first years and decades following cutting but slows down later on (Lindholm and Vasander 1987, and references therein). The favourable period for species of young successional stages is, accordingly, shorter than for species of mature forests; the former stage lasts until the canopy close, c. 20–30 yr, and the latter until the forest is cut again, i.e. >50 yr.

2) Local ground-arthropod assemblages are open: an assemblage at any moment in time at a particular site is a contingent collection of individuals representing those species that are around. Most of the abundant species occur over a broad amplitude of successional stages, albeit in varying numbers. Small-scale structure in the assemblage is created through the gathering of individuals of different species to preferred resources. Such small-scale heterogeneity in the environment tends to broaden the occurrence of the species across the succession gradient (for an analogous observation on plants, see Palmer and Dixon 1990). As suggested above, canopy closure is probably a threshold stage at which conditions on the ground change and the arthropod species assemblage changes accordingly.

3) The availability of suitable habitat on the regional scale determines the local abundance of the species, i.e. 'mass effects', or movements of individuals from suitable habitats to less suitable ones are important (An-

drewartha and Birch 1954). This corresponds to a 'source-sink' population structure (Wiens and Rotenberry 1981, Pulliam 1988) with the modification that the positions of 'sources' and 'sinks' may vary from year to year. Consequently, it is prohibitively difficult to discern any 'metapopulation' structure in this system (see also Harrison 1994).

4) The species richness of local assemblages is greatly increased by small-scale habitat heterogeneity, analogous to the 'micro-site' variation of Whittaker and Levin (1977). However, this variation of the environment seems to be 'fine-grained' relative to ground arthropods (see also Haila et al. 1994), i.e. the variation is well within their activity radius. Habitat heterogeneity on this scale may increase species richness by providing a more uniform resource distribution in time than is available in a homogeneous habitat. Such heterogeneity is essentially statistical in character and provides buffers against environmental fluctuations (Levins 1968). In an analogous fashion, several species of songbirds seem to favour heterogeneous locations in their territory selection in Seitseminen National Park (Haila et al. 1996).

These hypotheses imply that local assemblages of forest-floor arthropods, indeed, resemble 'samples' from a regional pool but with three major constraints. First, the species pool from which the samples are 'drawn' is constrained by general forest features, in other words, mature forest specialists do not belong to the pool 'sampled' in open areas, and vice versa. Second, the 'sampling efficiency' of a particular site is determined by small-scale habitat heterogeneity. Analogous points about the 'sampling' hypothesis were discussed by Preston (1960) and Haila (1983). Third, local ant assemblages are structured by species interactions (Punttila et al. 1991, 1996 and references therein), and large colonies of wood ants influence also other taxa (Punttila 1994 and references therein). On the other hand, there is an element of stochasticity in the establishment of ant colonies, that is, an element of 'sampling' albeit on a longer time scale than in the other taxa (Punttila et al. 1991, 1996). Overall, this suggestion corresponds to the process of 'proportional sampling' (Cornell 1993).

Concerning forest management two implications, corresponding to two different levels of forestry planning (Haila 1994), follow from these hypotheses. First, as efficient dispersal and 'mass effects' appear to be characteristic of the forest-floor arthropod fauna of the taiga, forests should be managed and monitored on the regional scale as a background factor affecting the composition of the regional species pool. Second, as habitat heterogeneity appears to have such a critical role for the heterogeneity of local assemblages, the maintenance of small-scale heterogeneity should be adopted as a golden rule in management operations within forest stands; the relevant scale is some tens of meters for forest-floor arthropods.

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Appendix 1. Less commonly caught carabid species. The figures show the number of sampling units (maximum number of units in brackets under the site code) in which each species was found. For the data sets see Table 3.

	Sampling area							
	0(1) (4)	0(2) (4)	2(1) (4)	2(2) (4)	10(1) (4)	10(2) (4)	14–20 (4)	mature (4)
Agonum ericeti (15)	0	0	0	0	0	0	2	0
Agonum mannerheimii (6)	0	0	2	0	0	0	0	1
Amara apricaria (2)	0	0	1	1	0	0	0	0

Amara communis (21)	0	0	2	3	2	2	1	0
Amara spp. (4)	1	0	1	1	0	1	0	0
Anisodactylus binotatus (1)	0	0	0	0	0	0	0	1
Bembidion quadrimaculatum (3)	0	0	1	1	0	0	0	0
Bembidion spp. (1)	0	0	1	0	0	0	0	0
Bradycellus caucasicus (4)	0	0	0	0	2	0	0	0
Calathus melanocephalus (5)	0	0	1	2	0	1	1	0
Clivina fossor (7)	0	0	2	0	2	0	0	0
Cymindis vaporariorum (17)	1	0	0	0	1	0	3	0
Dyschirius globosus (3)	0	0	1	0	1	0	0	1
Loricera pilicornis (5)	0	0	1	2	0	0	0	0
Notiophilus reitteri (5)	0	0	0	0	1	0	0	2
Notiphilus germinyi (1)	0	0	0	0	0	0	0	1
Patrobus atrorufus (3)	0	0	0	0	0	0	2	1
Pterostichus diligens (5)	0	0	0	0	0	0	1	1
Pterostichus vernalis (13)	0	0	3	0	1	0	0	0
Trechus quadripunctatum (2)	0	1	1	0	0	0	0	0
Trichocellus placidus (11)	0	0	2	0	3	2	0	0

Appendix 2. Less commonly caught spider species. The figures show the number of sampling units (maximum number of units in brackets under the site code) in which each species was found. For the data sets see Table 3.

	Sampling area							
	0(1) (4)	0(2) (4)	2(1) (4)	2(2) (4)	10(1) (4)	10(2) (4)	14–20 (4)	mature (3)
Abacoproeces saltuum (12)	0	1	0	0	0	1	3	2
Aelurillus v-insignitus (1)	0	0	1	0	0	0	0	0
Agyneta suecica (6)	0	0	0	0	0	1	3	0
Alopecosa cuneata (1)	0	0	0	0	1	0	0	0
Alopecosa fabrilis (4)	0	0	0	1	1	2	0	0
Alopecosa inquilina (11)	0	0	2	3	1	0	0	0
Alopecosa trabalis (2)	0	0	2	0	0	0	0	0
Aranues diatematus (1)	0	0	0	0	0	0	0	1
Astenargus paganus (2)	0	1	0	0	0	0	0	1
Bathyphantes parvulus (7)	0	1	1	1	1	1	0	0
Bathyphantes setiger (1)	0	0	0	1	0	0	0	0
Bolyphantes alticeps (8)	0	0	0	2	0	0	0	1
Bolyphantes index (2)	0	0	0	0	0	0	1	0
Caledonia evansi (19)	0	0	0	1	0	1	0	2
Centromerita bicolor (3)	0	0	1	1	0	0	1	0
Centromerus expertus (5)	0	1	0	0	0	2	0	0
Centromerus sylvaticus (9)	0	0	0	1	1	0	0	1
Ceratinella brevis (3)	0	0	0	0	0	0	0	1
Ceratinella scabrosa (2)	0	0	0	0	0	0	0	1
Ceratinops pectinata (5)	0	0	0	0	2	1	0	0
Cercidia prominens (2)	0	1	0	0	0	0	1	0
Clubiona frutetorum (1)	0	0	0	0	0	1	0	0
Clubiona trivialis (4)	0	0	1	0	1	2	0	0
Dicymbium nigrum (3)	1	0	0	1	1	0	0	0
Dismoticus bifrons (3)	0	1	0	0	0	1	0	0
Dolomedes fimbriatus (2)	0	1	1	0	0	0	0	0
Drapetisca socialis (31)	0	0	0	0	0	0	0	1
Drepanotylus borealis (1)	0	1	0	0	0	0	0	0
Entelecara congenera (2)	1	0	0	0	0	1	0	0
Episinus angulatus (1)	0	0	0	0	1	0	0	0
Ero cambridgei (13)	0	1	0	0	1	0	0	1
Ero furcata (75)	3	3	2	3	1	2	1	2
Euophrys aequipes (12)	0	0	0	0	2	3	1	0
Evansia maerens (2)	0	0	0	0	0	0	1	1
Gnaphosa holmii (3)	0	1	0	0	1	0	0	0
Gnaphosa muscorum (1)	0	0	0	1	0	0	0	0
Gonatium rubellum (2)	0	1	0	0	0	0	0	1
Gonatium rubens (1)	0	0	0	0	1	0	0	0
Gongylidielllum latebricola (1)	0	0	0	0	1	0	0	0
Gongylidiellum murcidum (5)	0	1	1	1	1	0	0	0
Hahnia onodinum (12)	0	2	0	1	0	0	3	2
Haplodrassus cognatus (3)	0	0	0	0	1	0	0	1
Haplodrassus moderatus (3)	0	0	0	0	1	0	2	0
Helophora insignis (35)	0	0	0	0	0	0	0	2

Hilaira herniosa (1)	0	1	0	0	0	0	0	0
Hygrolycosa rubrofasciata (1)	0	1	0	0	0	0	0	0
Lathys humilis (1)	0	0	0	0	0	0	0	1
Lepthyphantes angulipalpis (4)	0	0	0	0	0	0	0	1
Lepthyphantes cristatus (26)	0	3	0	0	0	3	3	1
Lepthyphant esericaceus (2)	0	1	0	0	0	0	0	0
Lepthyphantes flavipes (1)	0	0	0	0	0	0	1	0
Lepthyphantes nigriventris (1)	0	0	0	0	0	0	0	1
Lepthyphantes obscurus (3)	0	0	0	0	0	0	0	2
Lepthyphantes pallidus (12)	0	2	2	1	1	2	0	1
Linyphia coll. (7)	0	0	3	2	0	0	2	0
Linyphia triangularis (3)	1	0	0	0	1	0	0	0
Macrargus boreus (1)	0	0	0	0	0	0	0	1
Meioneta rurestris (4)	0	0	2	0	0	0	1	0
Meta mengei (13)	0	0	0	0	0	0	0	2
Micaria decorata (1)	0	0	0	1	0	0	0	0
Micaria formicaria (2)	0	0	1	1	0	0	0	0
Micrargus subaequalis (1)	0	0	0	1	0	0	0	0
Microlinyphia pusilla (3)	0	0	1	1	0	0	1	0
Minicia marginella (12)	0	0	1	1	3	1	3	0
Moebelia penicillata (5)	1	0	0	0	0	0	1	2
Neon reticulatus (3)	1	0	0	1	0	0	0	1
Neriene clathrata (5)	0	1	0	1	2	0	0	0
Notioscopus sarcinatus (1)	0	0	0	0	0	0	1	0
Oedothorax gibbosus (3)	0	2	0	0	0	0	0	1
Oedothorax gibbosus/tuberosus (5)	0	1	1	1	1	1	0	0
Oedothorax retusus (1)	0	0	0	0	0	1	0	0
Oedothorax tuberosus (5)	0	1	2	0	0	0	0	0
Oreonetides abnormis (1)	0	0	0	0	0	0	0	1
Oxyptila atomaria (15)	1	1	0	0	3	1	3	0
Pachygnatha degerii (3)	0	0	3	0	0	0	0	0
Pachygnatha listeri (6)	0	1	2	1	0	0	0	1
Pardosa bifasciata (7)	0	0	1	1	0	0	0	0
Pardosa monticola (1)	0	0	0	1	0	0	0	0
Pardosa prativaga (16)	0	0	0	0	0	0	2	1
Pelecopsis elongata (8)	0	0	1	1	0	0	1	2
Pellenes lapponicus (1)	0	0	1	0	0	0	0	0
Philodromus aureolus (3)	0	0	1	0	0	1	0	1
Pirata piraticus (8)	0	0	2	0	1	1	0	0
Pirata uligonosus (6)	1	2	0	0	0	0	0	2
Poeciloneta globosa (7)	0	3	0	0	0	1	0	1
Porrhomma pygmaeum (2)	0	0	1	0	1	0	0	0
Pseudophrys callida (1)	0	1	0	0	0	0	0	0
Robertus neglectus (1)	0	0	1	0	0	0	0	0
Savignya frontata (2)	0	0	1	0	0	0	0	0
Scotina palliardi (2)	0	0	0	0	0	0	2	0
Silomatopus phalerata (1)	0	0	0	0	0	0	1	0
Silometopus reussi (1)	1	0	0	0	0	0	0	0
Singa albovittata (2)	0	0	0	2	0	0	0	0
Singa pygmaea (1)	0	0	0	0	0	1	0	0
Singa sanguinea (3)	0	0	0	2	0	0	0	1
Steatoda bipunctata (6)	0	0	0	0	0	0	1	1
Stemonyphantes lineatus (8)	0	0	1	0	2	2	0	0
Tapinoba longidens (8)	0	0	0	2	0	0	0	1
Thanatus formicinus (10)	0	0	1	1	1	2	2	0
Theridion bimaculatum (11)	0	0	1	3	2	2	0	0
Theridion varians (2)	1	1	0	0	0	0	0	0
Thyreostenius parasiticus (14)	1	2	0	0	2	3	2	1
Tibellus oblongus (7)	0	0	1	2	0	1	0	0
Tibioplus arcuatus (12)	1	1	0	0	2	0	1	0
Tibioplus diversus (23)	1	1	1	0	0	0	0	1
Troxochrus nasutus (8)	1	2	1	0	0	0	0	2
Walckenaeria alticeps (1)	0	0	0	0	0	0	1	0
Walckenaeria lepida (3)	0	0	0	0	0	0	0	1
Walckenaeria mitrata (10)	0	0	0	0	2	2	0	1
Walckenaeria nudipalpis (4)	0	0	0	0	0	1	1	2
Walckenaeria vigilax (1)	0	0	1	0	0	0	0	0
Xysticus bifasciatus (3)	0	0	2	0	0	0	1	0
Xysticus cristatus (8)	0	0	0	1	0	0	2	1
Xysticus obscurus (7)	0	2	0	3	0	0	0	1
Xysticus ulmi (3)	0	0	1	0	1	0	1	0
Zelotes petrensis (21)	2	0	1	1	3	2	0	0
Zelotes serotinus (2)	0	0	0	0	1	0	0	0
Zora silvestris (1)	0	0	0	1	0	0	0	0