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Commentary

Mystery of the missing species: species-abundance distribution of boreal ground-beetles

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A recurring pattern in community samples is that a few species are abundant, while the great majority are scarce (e.g. Preston 1962). Many mathematical models have been developed fitting these species-abundance distributions, but the biological interpretation of the models is often contradictory (Magurran 1988). Consequently, Gray (1987) proposed that instead of trying to fit a model one could study community organization by comparing species-abundance distributions. Here, I use this approach to demonstrate a peculiarity in the structure of carabid assemblages in boreal forests.

The carabid data were collected from coniferous boreal forest in Finland using pitfall trapping during all of or most of the growing season (Table 1). The number of species in the samples was plotted against $\log_2$-based abundance classes or 'octaves' (Preston 1948).

Carabid species-abundance distribution in the taiga

In the boreal forest, carabid species-abundance distributions often resemble the log series model with the mode in the first octave (Niemelä et al. 1987, 1990). Furthermore, the dominant species are distinctly separate from the scarce ones (Fig. 1, Table 1). According to the commonly held view, the log normal distribution is the commonest one in nature (e.g. Preston 1948, 1962, Hughes 1986), and, as sample size is increased in time or space log series grades into log normal (Magurran 1988). In carabid samples from the boreal forest, however, species-abundance distributions do not change in this way with increasing sample size. I demonstrate this by first pooling samples from different sites within the same study area. Nine of ten samples from a large, mature forest area had at least two octaves with no species falling between the abundant and the scarce species. Pooling these samples did not change the pattern (Fig. 1a). Combining as many as 20 or 33 samples from different forest patches still produced a distribution with the mode in the first octave and a 'gap' between the scarce and abundant species (Fig. 1b, c).

I increased sample size in time by dividing a long sampling period (May through November) in a mature forest patch into three periods of about two months each. The species-abundance distributions in the early and mid-season (Table 1a) had the same shape as did the whole season sample (Fig. 1f), although the dominant species changed, as expected, during the season.

Examining yearly samples collected in that same coniferous forest patch during 1985–1990, I found a 'gap' in most samples between the abundant and scarce species (Table 1b).

In mature forest, thinned forest and recently cut forest the 'gap' in the species-abundance distribution was clear, whereas in the intermediate age classes (2–20 years since cutting) such a 'gap' was not present (Fig. 1c–e, Table 1d).

I have detected the 'gap' in assemblages from other geographical areas as well: in Belgian forests (data in Loreau 1992) and in some mature forest types in boreal North America (Niemelä et al. 1992b, 1993). In samples from agricultural areas the species-abundance distribution differed (Table 1e).

Why the missing species?

Boreal carabid assemblages appear to have a peculiar composition, with essentially two kinds of species: the scarce ones and the very few abundant ones with almost no intermediate species. This pattern seems to be typical for mature coniferous taiga forest, whereas in the cut forest the distribution was quite different. A few years after logging the 'gap' between the scarce and abundant species was filled, because forest species decreased and species of open habitat increased (Fig. 1c–e). When the trees reached the age of 20–30 years, species of open habitat started to decrease, and the structure of the carabid assemblage approached that of the mature forest.

Why then are only a few carabid species numerous in the mature coniferous forest? There are but tentative explanations. My favourite one is that coniferous forest is a less perfect environ-

Table 1. Number of species in different abundance classes with $\log_2$ base (octaves) of data sets. A: whole-season sample from one forest patch in central Finland divided into three periods (Niemelä et al. 1989). B: samples taken in 1985–90 in same forest patch as in A (Tukia unpubl.). C: sample from one coniferous forest patch in Åland Islands, southern Finland (Niemelä 1990). D: samples collected in different forest age-classes with years indicating time since cutting (Tukia unpubl.). E: samples collected in cultivations in southern Finland (Espoo, Halme & Niemelä 1993) and in central Finland (Lammi, Tukia unpubl.).

						Octaves							Total
	1	2	3	4	5	6	7	8	9	10	11	12	spp. / ind.
A													
May–June	4.5	3.5	3	1	1	–	2	1	–	1	–	–	17 / 973
July–August	5	3	1.5	2.5	–	1	1	3	1	–	–	–	18 / 1067
August–November	3	–	3	1	0.5	1.5	2	–	–	–	–	–	11 / 341
B													
1985	3	1	4	2	–	1	3	–	1	–	–	–	15 / 626
1986	3.5	1.5	1.5	3	1.5	–	1.5	0.5	1	–	–	–	14 / 569
1987	3	2	1	2	–	1	–	2	–	–	–	–	11 / 428
1988	4	1	–	–	2	2	1	–	1	1	–	–	12 / 1086
1989	3.5	3.5	1.5	2.5	1	2	–	–	–	1	1	–	16 / 2161
1990	3.5	1.5	1	2	1	1	1	1	–	–	–	–	12 / 346
1985–90	1.5	4.5	3.5	1.5	–	2.5	1.5	2	1	–	1	1	20 / 5216
C													
Åland	4.5	1.5	–	1	1	–	–	2	–	–	–	–	10 / 389
D													
1. yr.	7.5	2.5	2	2	3	4.5	3.5	1	–	–	2	–	28 / 3859
2. yr.	4.5	5.5	4	3	3	5	8	4	4	1	2	–	44 / 6583
10. yr.	7.5	3.5	2	3.5	4.5	4	2	3	2	3	–	–	35 / 4026
20–30 yr.	7	2	1.5	2.5	3	2	4	1	–	1	–	–	24 / 1435
Mature	7	1	1	2	2	–	–	1	1	–	–	–	15 / 650
E													
Espoo	14.5	10	6.5	5.5	7.5	2	2	–	–	–	–	–	48 / 611
Lammi	11	7.5	10	6.5	5	5	5	4	1	–	–	–	55 / 2305
Lammi	13	7.5	10	9.5	4	5	4	1	1	–	–	–	55 / 1328

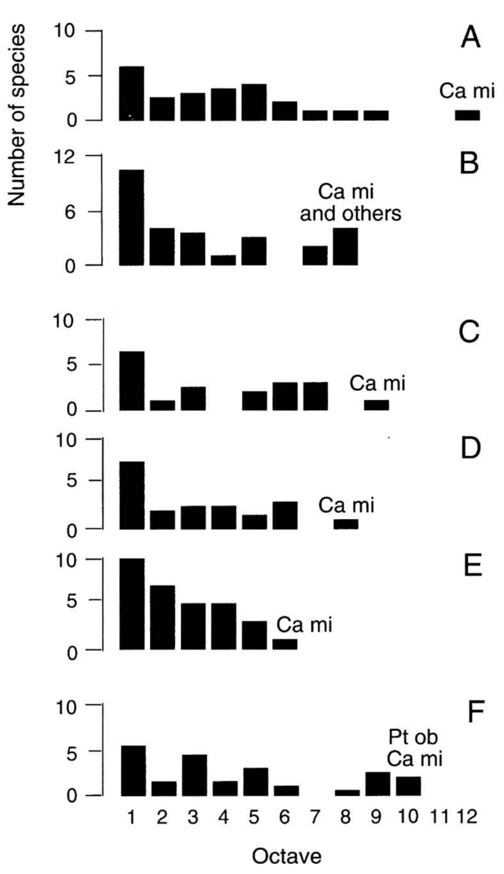

Fig. 1. Number of species (vertical axis) plotted against number of individuals arranged in abundance classes with $\log_2$ base (horizontal axis, octaves). — A: pooled sample from ten mature forest sites in eastern Finland (Tukia unpubl.). B: 20 mature forest sites in southern Finland (Halme & Niemelä 1993). C: 33 sites mature forest in central Finland (Niemelä et al. 1988). D: 12 thinned forest sites in central Finland (Niemelä et al. 1988). E: 12 young (< 20 yrs) forest sites in central Finland (Niemelä et al. 1988). F: one mature forest site in central Finland (Niemelä et al. 1992a). Ca mi = *Calathus micropterus* and Pt ob = *Pterostichus oblongopunctatus*.

ment for carabids than, for instance, the warmer and more open grasslands in recently cut sites. Overall carabid species richness is higher in the latter type of habitat than in boreal forest (Erwin 1979; see also Table 1). Thus, it appears that only a few species have adapted well enough to the boreal forest to be able to maintain high population numbers there (see also Loreau 1992). *Calathus micropterus*, the dominant species in most samples, appears to be one of the few such species (Fig. 1).

A correlate of this explanation is the availability of food. Many species occurring in the young forests feed on grass seeds, but grasses are rare in the mature forest. In addition, the scarcity of herbaceous plants in the mature forest may lead to a lack of the herbivorous arthropods and decomposers forming the primary prey for predatory carabids (Hengeveld 1980).

Among other factors possibly contributing to the peculiar structure of boreal carabid assemblages is interference by *Formica*-ants. Whereas most carabid species are adversely affected by the ants, the dominant *C. micropterus* is one of the few exceptions (Niemelä et al. 1992a).

Overall, for carabids, boreal coniferous forest may be an adversity or A-selected environment (Greenslade 1983). These environments tend to have low community diversity (but not necessarily low densities) and to harbour species with a generalist way of life. This is because an A-selected habitat is predictably unfavourable, which allows species to become closely adapted to it, while its severity keeps out competitors. According to Greenslade (1983), in regulating A-selected populations, physical factors are of greater importance than competition.

Another explanation for the organization of forest carabid communities was provided by Loreau (1992). Like Greenslade (1983), he suggested that only the dominant species are well enough adapted to the environment to be able to maintain high population numbers there. However, Loreau proposed that the dominant species may more often be regulated by competition than are the scarcer species which are mainly governed by the physical environment. Clearly, additional research is needed to reveal the mechanisms of the maintenance of the peculiar carabid community organization in the harsh boreal environment.

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References

Erwin, T. 1979: Thoughts on the evolutionary history of ground beetles: hypotheses generated from comparative faunal analyses of lowland forest sites in temperate and tropical regions. – In: Erwin, T. L., Ball, G. E. & Whitehead, D. R. (eds), Carabid beetles: their evolution, natural history, and classification: 539–587. W. Junk, Den Haag.

Gray, J. S. 1987: Species-abundance patterns. — In: Gee, J. H. R. & Giller, P. S. (eds), Organization of communities, past and present. 27th Symp. British Ecol. Soc.: 53–67. Blackwell Scientific Publications, Oxford.

Greenslade, P. J. M. 1983: Adversity selection and the habitat templet. — Amer. Nat. 122:352–365.

Halme, E. & Niemelä, J. 1993: Carabid beetles in fragments of coniferous forest. — Ann. Zool. Fennici 30:17–30.

Hengeveld, R. 1980: Polyphagy, oligophagy and food specialization in ground beetles (Coleoptera, Carabidae). — Neth. J. Zool. 30:564–584.

Hughes, R. G. 1986: Theories and models of species abundance. — Amer. Nat. 128:879–899.

Loreau, M. 1992: Species abundance patterns and the structure of ground-beetle communities. — Ann. Zool. Fennici 28:49–56.

Magurran, A. E. 1988: Ecological diversity and its measurement. — Princeton Univ. Press, Princeton. 179 pp.

Niemelä, J. 1990: Effect of changes in the habitat on carabid assemblages in a wooded meadow on the Åland Islands. — Notulae Entomol. 69:169–174.

Niemelä, J., Haila, Y. & Halme, E. 1987: Carabid assemblages in southern Finland, a forest-field comparison. — Acta Phytopatol. Entomol. Hungarica 22:415–422.

Niemelä, J., Haila, Y., Halme, E., Lahti, T., Pajunen, T. & Punttila, P. 1988: The distribution of carabid beetles in fragments of old coniferous taiga and adjacent managed forest. — Ann. Zool. Fennici 25:107–119.

Niemelä, J., Haila, Y., Halme, E., Pajunen, T. & Punttila, P. 1989: The annual activity cycle of carabid beetles in the southern Finnish taiga. — Ann. Zool. Fennici 26: 35–41.

— 1990: Diversity variation in carabid beetle assemblages in the southern Finnish taiga. — Pedobiologia 34:1–10.

— 1992a: Small-scale heterogeneity in the spatial distribution of carabid beetles in the southern Finnish taiga. — J. Biogeography 19:173–181.

Niemelä, J., Spence, J. R. & Langor, D. 1993: Logging and boreal ground-beetle assemblages on two continents: implications for conservation. — In: Gaston, K., Samways, M. & New, T. (eds), Perspectives in insect conservation. Intercept Publications, Andover, in press.

Niemelä, J., Spence, J. R. & Spence, D. H. 1992b: Habitat associations and seasonal activity of ground-beetles (Coleoptera, Carabidae) in central Alberta. — Can. Entomol. 124:521–540.

Preston, F. W. 1948: The commonness and rarity of species. — Ecology 29:254–283.

— 1962: The canonical distribution of commonness and rarity. — Ecology 43:185–215, 410–432.