Habitat preference in terrestrial Tardigrades[1]

T H O R K I L E. H A L L A S

The habitat preferences of Tardigrades are correlated with the sequence of decay of the substrate. The commonest species are restricted to specific microhabitats in the samples and their presence is mutually exclusive. If two Tardigrade species occupy adjacent microhabitats in a breakdown sequence, they should be found together more frequently than would be expected by chance. On this basis a simple model of the spatial relationships of the eight commonest species in Finland is presented. The model is consistent with the known distribution of the species involved.

Thorkil E. Hallas, Statens Skadedyrlaboratorium, Skovbrynet 14, DK—2800 Lyngby, Denmark.

In most studies dealing with Tardigrades the samples have been described by the names of the plants with some notes about the locality. Yet, after following this custom, NELSON (1975), in common with most previous investigators, found no correlation between the various moss species and the species of Tardigrades. It has been assumed that Tardigrades puncture moss cells and feed on them. But, as pointed out by HALLAS & YEATES (1972), there is no conclusive evidence that Tardigrades feed on moss. Obviously, a better interpretation of the findings and more realistic ideas about the microhabitats are needed.

1. The fundamental idea

The moss cushion, a typical substrate of Tardigrades, contains numerous microhabitats. From the upper productive part, ageing and decay proceed to the bottom layers. Each Tardigrade species is restricted to a small range of microhabitats within this sequence of biodegradation (HALLAS & YEATES 1972, HALLAS 1975).

The breakdown processes, though complex, are the result of enzymes and mechanical factors acting in a certain order. This allows a crude generalization by which the habitat preferences of most Tardigrades can be indicated on a single scale. A given sample may comprise either the whole of the breakdown sequence or only a part, but even without a detailed knowledge of the nature of the samples it is possible to obtain some ecological information. This is demonstrated firstly for the frequencies of individual species and then for the coexistence of species. The mathematical treatment is based on the counts obtained by HALLAS (1977) in a study of 230 samples from Finland yielding 2692 Tardigrades belonging to 45 species.

2. Mutual exclusiveness

In samples collected in the traditional way the most common species are very abundant, the others being sparse. Only a few species belong to the intermediate category. The percentage of samples with Tardigrades is remarkably constant, usually 70—80 %. In my material (HALLAS 1977) it was 76.9 %, and in NEDERSTRÖM's (1919) material, also from Finland, 75.7 %. In both these studies the two most frequent species, *Macrobiotus hufelandii* Schultze and *Hypsibius dujardini* (Doyere), together ac-

counted for three-quarters of the positive samples, the other species together accounting for the remaining fourth. This allows us to conclude as follows:

Let the species be numbered 1, 2, ..., n, according to frequency rank. The chances of finding each of them are thus denoted as

(1) $P_1, P_2, ..., P_n$

The chances of not finding each of them are

(2) $(1-P_1), (1-P_2), ..., (1-P_n)$

Correspondingly, the change of finding none of them in a sample will be

(3) $(1-P_1) (1-P_2) ...... (1-P_n)$

The chance of finding at least one of the species is

(4) $1-(1-P_1) (1-P_2) ...... (1-P_n)$

This is another way to express the frequency of positive samples, which is almost constant. Consequently, the product of the first few brackets (each representing the most frequent species) must be almost constant, too. The most frequent species are thus mutually exclusive in the samples, because the microhabitats of the individual species are unevenly distributed. Let us consider what kinds of microhabitats we actually encounter when sampling moss cushions.

3. Quantity and diversity of microhabitats

The live green part of a moss cushion forms the "a" layer. The "b" layer consists mainly of the standing dead portion and litter, the "c" layer of the rhizoids and soil at the base of the cushion.

A moss cushion is a mosaic composed of patches of different ages. These all have an "a" layer and the older parts have a "b" layer too, the oldest parts possessing all three layers. This is why the "a" layer species (HALLAS 1975) *Macrobiotus hufelandii* is usually more frequent in moss samples than the "b" layer species (see HALLAS & YEATES) *Hypsibius dujardini*, and these both outnumber the "c" layer species *Hypsibius (Diphascon) scoticus* (J. Murray).

The proportions of these layers seem to follow certain rules. The "a" layer grows to a definite density and thickness. With further growth the lowermost part of the "a" layer dies

(partly because it is deprived of light) and so becomes the "b" layer. Thus, a sample taken from an older part of the cushion will contain proportionally more of the "b" layer. Similar relationships also exist between the "b" and "c" and between the "a" and "c" layers. In consequence, the individual Tardigrade species are bound to be mutually exclusive in their frequencies. Although the argument is based on moss cushions, it can be freely applied to the other kinds of samples that contain the same species (i.e. lichens, soils, litter). This is because the species in question may be expected to prefer similar parts of the breakdown sequence when inhabiting substrates other than moss.

The number of different microhabitats increases with the age of a substrate, and maximal diversity may be attained when the sequence includes every stage from primary production to humus mixed with minerals (complete sequence). Thus, older substrates generally provide suitable microhabitats for a larger number of species (0—8 species is the number expected in a sample). The number of individuals of a species depends on how long its particular microhabitat has been present in the sample, the spatial extent of the microhabitat, and not least the annual fluctuations in the microbial activity within this microhabitat (i.e. the amount of food available). In extremely dry sites lichens and mosses grow slowly, and therefore even in minute cushions tardigrade species may have been accumulating for decades.

4. How to predict the succession of Tardigrade species

In practice, the observer will be unable to see the diversity of microhabitats which a sample actually contains. Nor is it necessary for him to do so. Inevitably, the successive stages of breakdown form a sequence. Thus two Tardigrade species occurring in such a sequence are more likely to be found together if their preferred microhabitats overlap to some extent. With regard to the pairwise coexistence between the 8 most frequent species in my Finnish material, 76 % of the cases are as predicted by the simple products of their separate frequencies in the whole set of samples. The remaining 24 % of the cases are the most interesting, as they represent coexistence due to overlapping of microhabitats. The actual number of cases

may serve as a measure of the extent of the overlap between the microhabitats. This can be calculated from

$$(5) \quad (P_{1+2} - P_1 P_2) \, S$$

where P_{1+2} is the observed coexistence of two species in the samples and $P_1 P_2$ is their expected coexistence due to chance. S is the number of samples from which these frequencies were calculated.

The model (Fig. 1) is based on calculations from this formula and shows data for the 8 most frequent Finnish species of terrestrial Tardigrades. Only cases of overlap exceeding +1 are shown.

So far, the model conforms perfectly with our present knowledge of the distribution of *Macrobiotus harmsworthi* J. Murray and *Hypsibius*

(Diphascon) scoticus, which are genuine soil species, and for *H. (Isohypsibius) prosostomus* Thulin and *H. (s.str.) dujardini*, which are litters species (HALLAS & YEATES 1972). *M. hufelandii* seems to be confined to the topmost layer in mosses, the "a" layer described by HALLAS (1975). For the other species concerned the model seems to fit well with the observations. *Milnesium tardigradum* (Doyere) is a large predatory species and does not inhabit the soil interstices, where pore space is limiting.

About 10^3 two-species relations can be calculated from the data given by HALLAS (1977). Further data would be necessary, however, to improve their significance. For calculating overlapping coexistence, formula (5) has the advantage that the numbers of cases are additive and may be accumulated during several investigations.
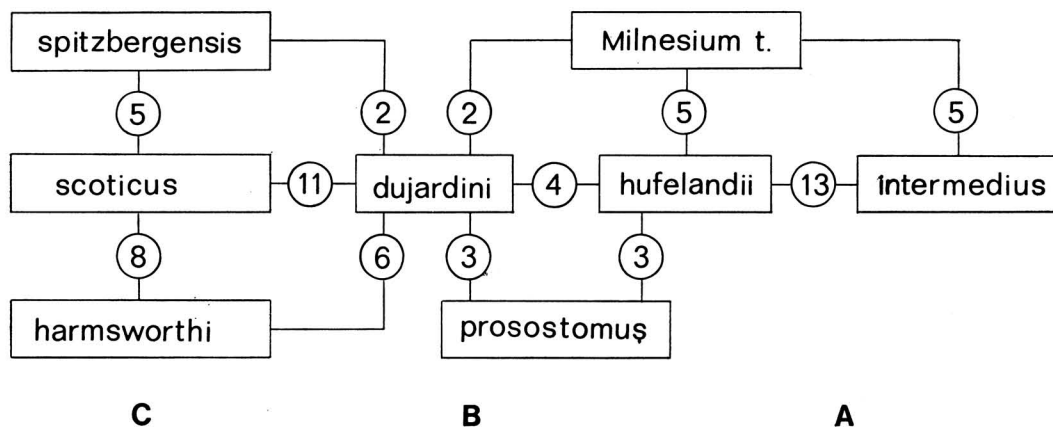

Fig. 1. A model of the ecological relations between the eight terrestrial Tardigrade species most frequent in Finland. The model is based on calculations from species frequencies observed in samples. The encircled digits are a measure of the overlap between the micro-niches of the species in question. A, B and C refer to the homology with the "a", "b" and "c" layers in moss cushions. The species to the left inhabit soil; *dujardini* and *prosostomus* are species of litter. The species to the right are confined to the green parts of the moss.

References

HALLAS, T. E. 1975: Interstitial water and Tardigrada in a moss cushion. — Ann. Zool. Fennici 12: 255—259.
—»— 1977: Survey of the Tardigrada of Finland. — Ann. Zool. Fennici 14:173—183.
HALLAS, T. E. & YEATES, G. W. 1972: Tardigrada of the soil and litter of a Danish beech forest. — Pedobiologia 12:287—304.

NEDERSTRÖM, P. 1919: Die bis jetzt aus Finnland bekannten Tardigraden. — Acta Soc. Fauna Flora Fennica 46:1—25.

NELSON, D. R. 1975: Ecological distribution of tardigrades on Roan Mountain, Tennessee — North Carolina. — Mem. Ist. tal. Idrobiol. 32, Suppl.: 225—276.