

Population density and species composition of moss-living tardigrades in a boreo-nemoral forest

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This study investigates for the first time the tardigrade fauna in a variety of different mosses from a coniferous forest and an adjacent clear-cut area in southern Sweden. Tardigrades were found in a majority of the samples. Sixteen species were recorded, of which the cosmopolitan species *Macrobotus hufelandi* was the far most common. Some mosses, particularly species with “wefts” growth form, contained more tardigrades than other mosses, indicating that growth form may have an impact on tardigrade abundance. Mosses of the same species collected from a forest and from a clear-cut, respectively, did not show a general trend in the overall abundance of tardigrades, but the forest tended to contain more species. Five species of tardigrades (*Murrayon diana*, *Isohypsibius sattleri*, *Platicrista angustata*, *Diphascion belgicae* and *Diphascion pingue*) never previously reported from Sweden were recorded.

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Tardigrades (phylum Tardigrada) represent an important component of the aquatic meiofauna in many ecosystems, including terrestrial, limnic, and marine environments (Ramazzotti and Maucci 1983, Kinchin 1994). Particularly common are tardigrades in mosses, and due to the capacity of many species to survive complete desiccation (anhydrobiosis) high densities are often found in mosses inhabiting dry habitats.

Faunistic studies on eu- and heterotardigrades have indicated that different substrates (e.g., mosses, lichens, leaf litter, turf, soil, fresh water sediment) usually contain very different species associations (Bertolani 1982, Dastych 1988, Bertolani and Rebecchi 1996, Guidetti et al. 1999, Guidetti and Bertolani 2001). These studies, together with several ecological studies on tardigrades in terrestrial habitats such as mosses (Marcus 1929, Franceschi et al. 1962–63, Morgan 1977), lichens (Schuetz 1987), leaf litter (Hallas and Yeates 1972, Guidetti et al. 1999) and turf (Fleeger and Hummon 1975) suggest species-specific preference of substrate among tardigrades.

The factors limiting the distribution and occurrence of tardigrade species have not been extensively studied, but may relate to factors such as humidity conditions of the substrate, food sources, and predation. Wright (1991, 2001) refers to the evaporation rate of the substrate as one of the main factors. For tardigrades inhabiting mosses the structure and exposure of the moss will then be important factors influencing the rate of evaporation. The structure of the moss determines the degree of water retention, the thermal properties, and the substratum drainage (Wright 1991), all of which influence the humidity conditions within the moss. The environment in which the moss grows will determine the exposure to abiotic factors such as insolation, ambient relative humidity, temperature, and wind speed. Clear-cutting has a dramatic effect on the temperature and humidity conditions of soil and plant communities (Gimingham and Birse 1957). These changes are expected to influence the tardigrade communities towards more desiccation-tolerant species, and perhaps lower diversity. Tardigrade abundance may

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also be influenced by predation, as documented by Hyvönen and Persson (1996) who showed that tardigrade numbers in soils were reduced by artificial arthropod additions.

Few studies on semi-terrestrial and freshwater tardigrades in Sweden have been reported, and several of the available studies are from early of the last century (Richters 1903, Carlzon 1909, Thulin 1911, 1928, Miheľič 1971, Durante Pasa and Maucci 1979, Sohlenius et al. 1997). Also, with few exceptions these studies have been more faunistic than ecological, therefore providing little information about the structure of tardigrade communities.

The aim of this study is to provide a quantitative and qualitative estimate of the moss-dwelling tardigrade community in a south-Swedish boreo-nemoral forest, and the association between tardigrade populations and different moss species. I also compare the tardigrade communities of two habitats (70-yr-old spruce forest and a clear-cut) with different environmental conditions within the forest area.

Material and methods

In total, 101 moss samples from 24 different moss species were collected from a boreo-nemoral forest area near the village of Tranemåla (56°21.568'N, 14°45.760'E), south-eastern Sweden. All collection was done on the 5 July 2000. Two different but adjacent sites within the forest area were sampled.

Spruce forest

This site was a 70-yr-old managed 4 ha coniferous forest stand, with Norway spruce (*Picea abies*, 90%) and Scots pine (*Pinus silvestris*, 10%) as the only tree species. Mosses almost completely cover the ground (including boulders), with the dominating moss genera being *Hylocomium*, *Pleurozium*, *Hypnum*, *Dicranum*, *Ptilium*, and *Polytrichum*. Within this site, 74 samples from 18 different moss species were collected on the ground and on rocks (Appendix 1).

Clear-cut

This site was a 2.6 ha clear-cut with high field layer vegetation except for planted spruce (<1 m height) and a sparse stand of mature pine left for the purpose of natural rejuvenation. The previous spruce forest at this site (similar to the forest at the forest site) was cut in 1995, at an age of 75 yr. At the time of collection, other spruce stands, partially including our forest site, surrounded the clear-cut. The main field layer vegetation in the clear-cut was different species of grass

(mainly Poaceae). A few tree trunks, rocks and dead wood were also found. Compared to the spruce forest, mosses were very sparse in the clear-cut, with *Dicranum*, *Pleurozium* and *Hypnum* constituting the most common genera. Within this site 27 samples from 10 different moss species were collected (Appendix 1).

Moss species were determined in the field at collection and the samples were kept dry in paper bags at room temperature until extraction (1 week–2 months later). Only a part of each of these collected samples were used to extract animals. Tardigrades were extracted from the mosses using a modified Baermann's funnel design. The design consisted of a plastic funnel with a steel net (mesh size 1 mm) inserted at about half the depth of the main cone, and a plastic tube ending in an Eppendorf tube at the other end of the funnel. The moss was placed on the net and the funnel was filled with water until it covered the entire moss. Light was not used to promote downward motion. This set-up was left overnight (ca 12 h). By their natural movements, the animals (together with a few eggs) fall through the funnel and end up in the Eppendorf tube. From this extraction, tardigrades and their eggs were collected using a micro-pipette under a stereomicroscope. To collect any remaining animals and eggs, the moss was also rinsed over sieves (mesh sizes 0.25 mm and 0.04 mm). After extraction, the moss samples were dried at 40°C for one week, and the dry weight was then determined (these estimates are given in Appendix 1). No attempts were made to determine the living vs dead organic portion of the moss samples.

After collection, the total number of tardigrades in each sample was counted. A proportion, ranging from 20 to 100%, of the total amount of tardigrades and eggs was then mounted on slides in Hoyer's mounting medium. The slides were observed by a light microscope with phase contrast and differential interference contrast under oil immersion (100×), to determine the species.

Statistical analyses (ANOVA, Kruskal-Wallis Analysis of Variance, Pearson's correlation) were performed using SYSTAT. In the statistical analyses of associations between mosses and tardigrades only moss species including at least five sub-samples (replicates) were used. Eleven moss species satisfied this criterion in the forest site, and 4 species in the clear-cut.

Results

Tardigrades were found in 96% (27 out of 28) of the analysed mosses, and in 86% (87 out of 101) of all collected subsamples. Only in the single samples of *Dicranum montanum* and *Bryum* sp. were tardigrades absent. Sixteen tardigrade species were found, 5 of which (*Murrayon diana*, *Isohypsibius sattleri*, *Platicrista angustata*, *Diphascion belgicæ* and *Diphascion*

pingue) represent new records for Sweden. Of these species, *M. diana* is considered rare and is previously known only from Greenland (Kristensen 1982). Preparations with these new national records will be deposited at the Swedish Museum of Natural History, Dept of Invertebrate Zoology, Stockholm. The number of species observed in a given sub-sample did not depend on the amount of moss examined ($r = -0.13$, $p = 0.25$, $N = 81$), suggesting that also small moss samples appropriately captured the species composition. A summarizing table of the moss samples examined and the tardigrades found is given in Appendix 1.

Forest Site

All 16 tardigrade species recorded in this study were found within the forest site. The species most widely distributed among different mosses were *Macrobiotus hufelandi* (found in 89% of the moss species and 74% of all subsamples from the forest site), *Diphascon oculatum* (56 and 22%, resp.), *Mesocrista spitzbergensis* (56 and 32%, resp.), *Diphascon cf. scoticum* (50 and 24%, resp.), *Diphascon pingue* (50 and 28%, resp.), and *Milnesium tardigradum* (50 and 24%, resp.). Five species were found in only one sub-sample (Appendix 1). The number of tardigrade species found in a particular moss increased significantly with number of replicates ($r = 0.61$, $p = 0.007$, $N = 18$). Above three samples, however there was no increase in species number ($r = -0.44$, $p = 0.18$, $N = 11$).

The 11 moss species in which at least 5 sub-samples were collected differed significantly in the density ($H_{10} = 39.162$, $p < 0.001$, Fig. 1a) and mean species number ($H_{10} = 40.262$, $p < 0.001$, Fig. 2a) of tardigrades. The mosses *Hylocomium splendens* and *Ptilium crista-castrensis* were those with most different tardigrade species as well as the highest density of tardigrades, followed by *P. schreberi* and *Plagiothecium undulatum* (Fig. 1, 2). *Polytrichum formosum* had much fewer specimens but still including 10 different species. There was also an overall positive relationship between tardigrade density and species number ($r = 0.58$, $p < 0.001$, $N = 60$).

The tardigrade *M. hufelandi* was found in all except one (*Dicranum montanum*) of the moss species examined, and was by far the most common species, found in 76% (56 out of 74) of all samples.

Clear-cut

In the clear-cut samples, 11 species of tardigrades were recorded. *Macrobiotus hufelandi* was the only common species, found in 80% of the moss species, and in 70% of all sub-samples. No other tardigrade species was found in more than 3 of the 10 mosses. Several tardi-

grades (e.g., *D. cf. scoticum*, *M. tardigradum*, *D. oculatum*) that were widespread among mosses in the forest were absent or rare in the clear-cut. It must be remembered, however, that only four of the 10 mosses in the clear-cut were collected in replicates (due to scarcity of mosses in this habitat), which reduces the likelihood of finding rare species. A single and very small sample of *Orthotrichum* sp. contained the highest density of tardigrades among all investigated samples.

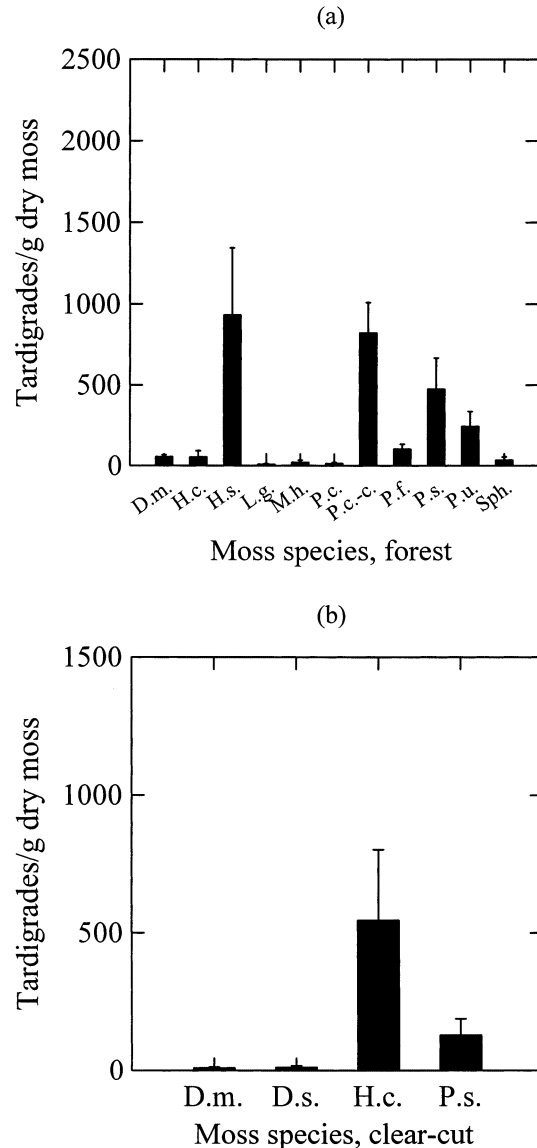


Fig. 1. Relative abundance of tardigrades (animals g⁻¹ dry moss) in different mosses of the (a) spruce forest habitat and of the (b) clear-cut. Standard errors are also indicated. D.m. = *Dicranum majus*, H.c. = *Hypnum cupressiforme*, H.s. = *Hylocomium splendens*, L.g. = *Leukobryum glaucum*, M.h. = *Mnium hornum*, P.c. = *Polytrichum commune*, P.c.-c. = *Ptilium crista-castrensis*, P.f. = *Polytrichum formosum*, P.s. = *Pleurozium schreberi*, P.u. = *Plagiothecium undulatum*, Sph. = *Sphagnum* sp. 2.

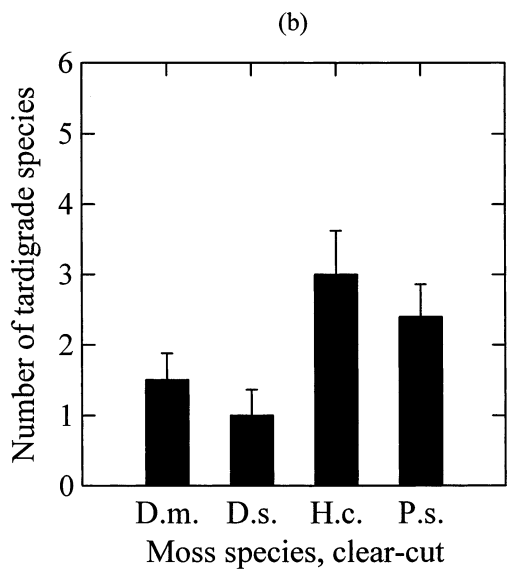
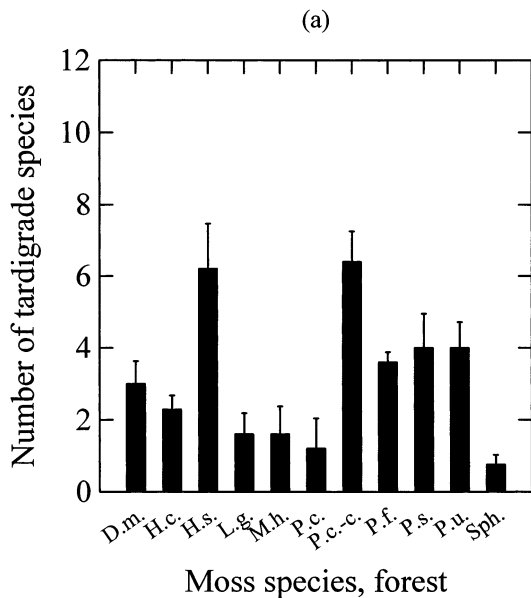


Fig. 2. Mean number of tardigrade species found in different mosses of the (a) spruce forest habitat and of the (b) clear-cut. Standard errors are also indicated. For explanations of moss species abbreviations, see Fig. 1.

Also in mosses from the clear-cut the density ($H_3 = 14.73$, $p = 0.002$) and mean number of tardigrade species ($H_3 = 10.27$, $p = 0.016$) differed among the 4 analysed moss species. *Hylocomium cupressiforme* contained the highest densities of tardigrades, followed by *Pleurozium schreberi* (Fig. 1b). These mosses also contained the highest mean number of different tardigrade species (Fig. 2b). As in the forest material, there was an overall positive relationship between tardigrade density and species number ($r = 0.74$, $p < 0.001$, $N = 21$).

Comparison of the forest vs clear-cut

Excluding an outlier with a density of 4600 tardigrades g^{-1} there was no significant difference in tardigrade density between the forest (mean = 200.1, SD = 376.0, $N = 74$) and clear-cut (mean = 135.2, SD = 294.2, $N = 26$; $F_{1,98} = 0.65$, $p = 0.42$). However, there was a marginally significant tendency towards higher mean number of species in the forest (forest: mean = 2.6, SD = 2.2, $N = 74$; clear-cut: mean = 1.7, SD = 1.2, $N = 26$; $F_{1,98} = 3.34$, $p = 0.071$).

Hylocomium cupressiforme and *P. schreberi* were the only mosses collected in both sites (forest and clear-cut) with sufficient number of sub-samples to allow statistical comparisons of tardigrade abundance and species number when moss species was controlled for. In *H. cupressiforme*, the overall density of tardigrades tended to be higher in the clear-cut compared to the forest ($U = 5.50$, $p = 0.051$, Fig. 3a). The mean value was dramatically higher in the clear-cut area, and the marginal significance is therefore due to a high variance among samples within site. In *P. schreberi*, no difference in the total density of tardigrades between the forest and clear-cut was found ($U = 19.0$, $p > 0.10$, Fig. 3a), although the mean value was considerable higher in the forest samples. The mean number of tardigrade

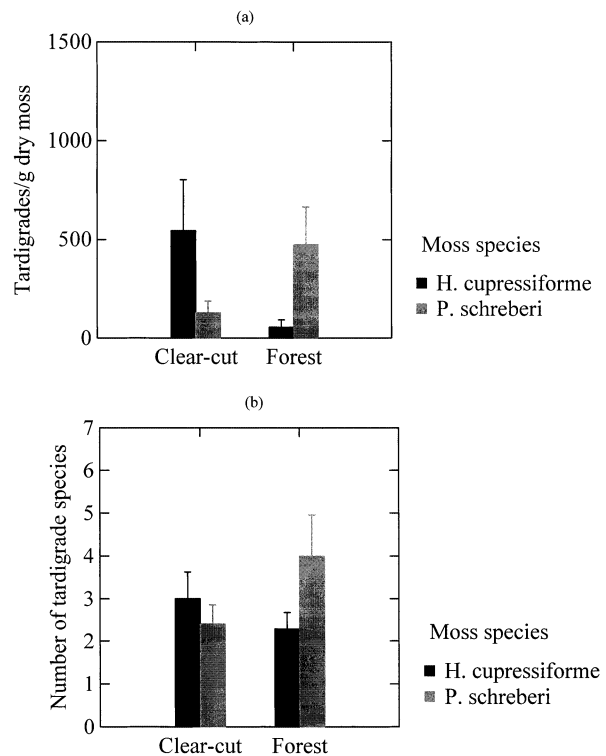


Fig. 3. Comparison between the spruce forest and the clear-cut with respect to (a) relative abundance and (b) mean number of tardigrade species in the moss species *H. cupressiforme* and *P. schreberi*.

species did not differ significantly among the forest and clear-cut samples in *H. cupressiforme* ($H_1 = 24.0$, $p = 0.26$, Fig. 3b), while in *P. schreberi* mean number of species was marginally significant higher in the forest ($H_1 = 4.5$, $p = 0.089$, Fig. 3b).

Discussion

General results

Tardigrades were found in a high proportion of the investigated moss samples. This is in accordance with Hallas (1978), who reported that 70–80% of all mosses investigated in previous studies were inhabited by tardigrades. Dastych (1988), however, found the lowest value of tardigrade-positive samples (TPS) in coniferous forests of Poland. Although most samples and moss species in our study contained tardigrades, only a few moss species had high densities. Consequently, while a majority of all mosses allow the life of tardigrades, only a few of them seem to provide suitable conditions for development and maintenance of large populations. The total number of species recorded in this study is identical to that reported by Dastych (1988) from Polish coniferous forests, although the species composition in the two studies was slightly different.

According to the zoogeographical and ecological classification of Sweden by Durante Pasa and Maucci (1979), our study sites are situated within their Group VII, representing “Inlands of southern Sweden, from Stockholm to Hälsingborg.... Forest with coniferae and broadleaves, with beech woods in the last part.” (p. 83). These authors report for Group VII the presence of *Pseudechiniscus suillus*, *M. hufelandi*, *Minibiotus intermedius*, *Macrobotus montanus*, and *Macrobotus richtersi*. Considering that *M. harmsworthi* and *M. richtersi* are species often found in the same substratum (Bertolani and Rebecchi 1996, Guidetti et al. 1999, Guidetti and Bertolani 2001), and probably have similar ecological needs, the present results have a quite good correspondence with those of Durante Pasa and Maucci (1979). The most common species found in this study were *M. hufelandi*, *Minibiotus intermedius*, and *M. harmsworthi*, which are cosmopolitan species or species with a wide distribution.

Ramazzotti and Maucci (1983) considered most *Diphascion* species to be hygrophilic. Also *M. spitzbergensis* and *P. angustata* may be considered hygrophilic (these species were still inserted within *Diphascion* by Ramazzotti and Maucci (1983)). Therefore, the species found in this study (apart from the xerophilic species *Milnesium tardigradum*) were mainly eurytopic or hygrophilic.

Macrobotus hufelandi was the only tardigrade found in all of the 24 analysed moss species, and was also

found in a majority of all sub-samples. This species is a well-known cosmopolitan tardigrade, found in a variety of habitats. The wide distribution of *M. hufelandi* among the current samples could relate to the eurytopic capacity of this species, and to the probably parthenogenetic mode of reproduction of this population (no males were found). Parthenogenesis is frequent in *M. hufelandi* (Biserov 1990) and may allow a high rate of successful colonization compared to other eurytopic species with amphimictic reproduction. An example of a eurytopic and amphimictic species in this study is *M. harmsworthi*, which in contrast to *M. hufelandi* was found in only 22% of all analysed moss species and in only 10% of all collected sub-samples.

Notable in the analysed samples is the complete absence of species from the class Heterotardigrada. This is in line with the results of Dastych (1988), see Table IV) who did not find any Heterotardigrades from coniferous forests in Poland.

Effects of moss species and growth form

Mosses with high density of tardigrades generally also had high species abundance. In particular the pleurocarps *H. splendens*, *P. schreberi*, *P. crista-castrensis* and *P. formosum*, seemed to present more favorable conditions for tardigrades than others. The above four moss species have a widespread distribution in the Scandinavian forests, although *P. crista-castrensis* has a more limited association with older spruce forests. Interestingly, three of these species are classified as having a “wefts” growth form, while *P. formosum* forms “turfs” (see Gimingham and Birse (1957) and Birse (1958) for classifications of bryological growth forms). Several factors relating to growth form (influencing, e.g., the water-retention capacity) and/or general life history (e.g. life span) of the moss should influence its suitability as a host for tardigrades, but analyses of the functional link between growth form and tardigrade abundance are scarce. Such analyses would be of great interest to understand the distribution of tardigrades in moss communities. Hallas (1978) suggested that the relative representation of the three layers constituting a moss (the green a-layer, the standing dead b-layer, the rhizoid and soil c-layer) will strongly influence the species diversity found in a given moss sample. Older mosses have a higher proportion of the b- and c-layers, and therefore provide suitable microhabitats for more tardigrade species. In light of the current findings it would be interesting to investigate whether mosses with the “wefts” growth form are also long-lived, with a potential to build up a high variety of microhabitats for tardigrades. The proportions of the three layers discussed by Hallas (1978) are also likely to vary among different species of moss. In the current study, I essentially ignored such variation by using dry mass of

mosses without distinguishing different moss layers. Future studies will hopefully reveal the extent to which variation in the proportions of growth layers affects the species diversity and population density of tardigrades.

Clear-cut effects

Clear-cutting has a dramatic effect on the bottom and field layer vegetation, including the moss community. Removal of the trees strongly influences both the climatic and nutritional conditions (Huhta 1976). The most pronounced microclimatic changes are increases in the mean and variance of microhabitat temperature and humidity (Gimingham and Birse 1957, Huhta 1971). These changes have strong negative effects on the moss community, and most mosses die after deforestation (Gimingham and Birse 1957, Bråkenhielm and Persson 1980). This strong impact was evident in the current study by the general scarcity of mosses in the clear-cut site. Obviously, therefore, clear-cutting has a strong negative impact on moss-living tardigrade communities in managed forests. For those mosses that survive or establish in the clear-cut, the changed environmental conditions should also have indirect influences on the associated tardigrade populations. The change towards drier conditions should favor tardigrade species more tolerant to xeric conditions and rapid desiccation, such as *Milnesium tardigradum*, *Ramazzottius oberhaeuseri*, and *Echiniscus testudo*. However, the two latter species were not found in any of our samples (although the two *Ramazzottius* sp. specimens could have been *R. oberhaeuseri*), and only one specimen of *M. tardigradum* was found in the clear-cut samples. Whether this was due to otherwise unsuitable conditions in the clear-cut for desiccation-tolerant species, limited possibilities of dispersal to the clear-cut area, or other factors remains unclear. Both in the total material and in the case of the moss *P. schreberi* the mean number of tardigrade species was higher in the forest site, suggesting that clear-cutting reduced the overall niche space for tardigrade populations.

In the current investigation I found no obvious tendency towards lower abundance of tardigrades in the clear-cut mosses when the total material was analysed. Also, in *H. cupressiforme* tardigrade densities tended to be higher in the clear-cut. Due to the high variance among sub-samples it is difficult to draw any firm conclusions about the effect of clear-cutting on tardigrade populations from the present material, although it does suggest a tendency towards lower species numbers and similar or higher densities in clear-cuts.

I have found no previous studies where the effects of clear-cutting on moss living tardigrades have been investigated. Some studies on the effect of clear-cutting on tardigrade abundance in forest soils have been reported, but results are rather inconclusive. For instance,

Sohlenius (1982) reported a tendency towards lower numbers of tardigrades in the first year after clear-cutting of a Scots pine forest compared to a control stand, but in the subsequent two years the abundance was variable. A similar study by Huhta (1976) in Finnish spruce forests also gave variable results, although there was a slight tendency towards higher abundances of tardigrades in the first years after clear-cutting. Effect of clear-cutting in soils and mosses are not readily comparable because most moss populations are in fact removed by clear-cutting, while soils remain, although in a qualitatively modified (improved) nutritional state.

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References

- Bertolani, R. 1982. Tardigradi (Tardigrada). Guide per il riconoscimento delle specie animali delle acque interne italiane. – Quaderni C.N.R., AQ/1/168, 15: 1–104.
- Bertolani, R. and Rebecchi, L. 1996. The tardigrades of Emilia (Italy). II. Monte Rondinaio. A multihabitat study on a high altitude valley of the northern Apennines. – Zool. J. Linn. Soc. 116: 3–12.
- Birse, E. M. 1958. Ecological studies on growth-form in bryophytes. III. The relationship between the growth-form of mosses and ground-water supply. – J. Ecol. 46: 9–27.
- Biserov, V. I. 1990. On the revision of the genus *Macrobotus*. The subgenus *Microbotus* s. str.: a new systematic status of the group *hufelandi* (Tardigrada, Macrobiotidae). Communication 1. – Zool. Zhurnal 69: 5–17, in Russian.
- Bråkenhielm, S. and Persson, H. 1980. Vegetation dynamics in developing Scots pine stands in central Sweden. – Ecol. Bull. 32: 139–152.
- Carlzon, C. 1909. Schwedische Tardigraden. – Zool. Anz. 34: 137–142.
- Dastych, H. 1988. The Tardigrada of Poland. – Monografie Fauny Polski 16. Państwowe Wydawnictwo Naukowe, Warszawa.
- Durante Pasa, M. V. and Maucci, W. 1979. Moss Tardigrada from the Scandinavian Peninsula. – Zeszyty Naukowe Uniwersytetu Jagiellońskiego 529: 47–85.
- Fleeger, J. W. and Hummon, W. D. 1975. Distribution and abundance of soil Tardigrada in cultivated and uncultivated plots of an old field pasture. – Mem. Ist. Ital. Idrobiol. 32 Suppl.: 93–112.
- Franceschi, T., Loi, M. L. and Pierantoni, R. 1962–63. Risultati di una prima indagine ecologica condotta su popolazioni di Tardigrada. – Boll. Mus. Ist. Biol. Univ. Genova 32: 69–93.
- Gimingham, C. H. and Birse, E. M. 1957. Ecological studies on growth-form in bryophytes. I. Correlations between growth-form and habitat. – J. Ecol. 45: 533–545.
- Guidetti, R. and Bertolani, R. 2001. The tardigrades of Emilia (Italy). III. Piane di Mocogno (northern Apennines). – Zool. Anz. 240: 377–383.
- Guidetti, R., Bertolani, R. and Nelson, D. R. 1999. Ecological and faunistic studies on tardigrades in leaf litter of beech forest. – Zool. Anz. 238: 215–223.
- Hallas, T. E. 1978. Habitat preference in terrestrial tardigrades. – Ann. Zool. Fenn. 15: 66–68.

- Hallas, T. E. and Yeates, G. W. 1972. Tardigrades of the soil and litter of a Danish beech forest. – *Pedobiologia* 12: 287–304.
- Huhta, V. 1971. Succession in the spider communities of the forest floor after clear-cutting and prescribed burning. – *Ann. Zool. Fenn.* 8: 483–542.
- Huhta, V. 1976. Effects of clear-cutting on numbers, biomass and community respiration of soil invertebrates. – *Ann. Zool. Fenn.* 13: 63–80.
- Hyvönen, R. and Persson, T. 1996. Effects of fungivorous and predatory arthropods on nematodes and tardigrades in microcosms with coniferous forest soil. – *Biol. Fertil. Soils* 21: 121–127.
- Kinchin, I. M. 1994. *The biology of Tardigrades*. – Portland Press, London.
- Kristensen, R. M. 1982. New aberrant eutardigrades from homothermic springs on Disko Island, west Greenland. – In: Nelson, D. R. (ed.), *Proc. of the Third Int. Symp. on Tardigrada*. East Tennessee State Univ. Press, pp. 203–220.
- Marcus, E. 1929. Tardigrada. – In: Bronn, H. G. (ed.), *Klassen und Ordnungen des Tierreichs*. Vol. 5, Abt. 4, Buch 3. Akad. Verlagsges., Leipzig.
- Mihelčič, F. 1971. Süßwassertardigraden aus Nordeuropa. – *Entomol. Scand.* 2: 205–214.
- Morgan, C. I. 1977. Population dynamics of two species of Tardigrada, *Macrobotus hufelandi* (Schultze) and *Echiniscus* (*Echiniscus*) *testudo* (Doyère), in roof moss from Swansea. – *J. Anim. Ecol.* 46: 236–279.
- Ramazzotti, G. and Maucci, W. 1983. *Il Phylum Tardigrada*. Terza edizione riveduta e corretta. – *Mem. Ist. Ital. Idrobiol.* 41: 1–1012.
- Richters, F. 1903. Nordische Tardigraden. – *Zool. Anz.* 28: 168–172.
- Schuetz, G. 1987. A one-year study on the population dynamics of *Milnesium tardigradum* Doyère in the lichen *Xanthoria parietina* (L.) Th. Fr. – In: Bertolani, R. (ed.), *Biology of Tardigrada, Selected Symposia and Monographs*. U.Z.I. 1, Mucchi Editore, Modena, pp. 217–228.
- Sohlenius, B. 1982. Short-term influence of clear-cutting on abundance of soil-microfauna (Nematoda, Rotifera and Tardigrada) in a Swedish pine forest soil. – *J. Appl. Ecol.* 19: 349–359.
- Sohlenius, B., Boström, S. and Ekeboom, A. 1997. Metazoan microfauna in an ombrotrophic mire at Abisko, northern Sweden. – *Eur. J. Soil Biol.* 33: 31–39.
- Thulin, G. 1911. Beiträge zur Kenntnis des tardigradenfauna Schwedens. – *Arkiv för Zoologi*, Band 7, No. 16: 1–60.
- Thulin, G. 1928. Über die Phylogenie und das System der Tardigraden. – *Hereditas* 11: 207–266.
- Wright, J. C. 1991. The significance of four xeric parameters in the ecology of terrestrial Tardigrada. – *J. Zool.* 224: 59–77.
- Wright, J. C. 2001. Cryptobiosis 300 years on from van Leeuwenhoek: what have we learned about tardigrades? – *Zool. Anz.* 240: 563–582.

Appendix 1. Summarizing data for analyzed samples in this study. The table gives the number of sub-samples collected for each moss species, moss species, habitat in which the moss was collected, dry weight of moss samples (mean and SD), number of tardigrades g⁻¹ dry weight of moss (mean and SD), proportion of extracted animals put on slides), inclusive number of tardigrade species found for each moss species, and total number of animals of specific tardigrade species found in the samples, with the number of sub-samples in which the species was found given in parentheses.

Sample	Sub-samples	Moss species	Habitat	Moss d.w., g		Tardigrades g ⁻¹ dw		Prop. in slides	Number of species	<i>Macrobiotus hufelandi</i>	<i>Macrobiotus harmsworthi</i>	<i>Minibiotus intermedius</i>	<i>Murrayon dianee</i>
				Mean	SD	Mean	SD						
1	5	<i>Pleurozium schreberi</i>	Forest	0.485	0.531	474.7	372.3	0.4	10	203 (4)	1 (1)	7 (2)	0
2	5	<i>Dicranum majus</i>	Forest	0.246	0.113	56.0	24.3	0.8	6	34 (5)	0	0	0
3	5	<i>Mnium hornum</i>	Forest	0.302	0.126	21.7	27.9	0.3	6	29 (3)	0	1 (1)	0
4	5	<i>Hylocomium splendens</i>	Forest	0.391	0.205	932.2	801.1	0.2	11	144 (5)	23 (2)	18 (4)	0
5	5	<i>Plagiothecium undulatum</i>	Forest	0.543	0.380	244.5	182.8	0.4	8	125 (5)	0	0	2 (1)
6	5	<i>Polytrichum formosum</i>	Forest	0.764	1.050	103.0	62.7	0.6	10	96 (5)	0	2 (1)	0
7	7	<i>Hypnum cupressiforme</i>	Forest	0.306	0.143	54.7	92.6	0.7	7	19 (4)	13 (4)	10 (1)	0
8	5	<i>Leukobryum glaucum</i>	Forest	0.214	0.122	9.3	8.2	0.8	4	7 (3)	0	0	0
9	5	<i>Ptilium crista-castrensis</i>	Forest	0.125	0.016	820.1	370.3	0.6	11	190 (5)	6 (1)	6 (2)	0
10	3	<i>Sphagnum</i> sp. 1	Forest	0.085	0.020	107.0	167.5	0.8	2	14 (2)	0	0	0
11	3	<i>Rhytidiadelphus loreus</i>	Forest	0.232	0.068	161.2	152.3	0.5	2	127 (3)	0	0	0
12	8	<i>Sphagnum</i> sp. 2	Forest	0.291	0.077	35.1	52.7	0.8	3	58 (4)	0	0	0
13	5	<i>Polytrichum commune</i>	Forest	0.439	0.072	13.9	15.1	0.8	4	21 (3)	0	1 (1)	0
14	2	<i>Aulacomnium androgynum</i>	Forest	0.410	0.300	7.5	10.6	1.0	2	3 (1)	0	0	0
15	2	<i>Lepidozia reptans</i>	Forest	0.620	0.540	1.0	1.4	1.0	1	2 (1)	0	0	0
16	1	<i>Dicranum montanum</i>	Forest	0.160	–	0.0	–	–	0	0	0	0	0
17	2	<i>Lophocolea heterophylla</i>	Forest	0.163	0.081	39.9	24.3	0.9	2	11 (2)	0	0	0
18	1	<i>Lophozia silvicola</i>	Forest	0.080	–	12.5	–	1.0	1	0	0	0	0
19	5	<i>Hypnum cupressiforme</i>	Clear-cut	0.240	0.096	545.7	502.5	0.7	6	376 (5)	3 (1)	40 (4)	0
20	5	<i>Dicranum scoparium</i>	Clear-cut	0.626	0.189	11.3	12.2	0.5	3	16 (3)	0	0	0
21	5	<i>Pleurozium schreberi</i>	Clear-cut	0.365	0.141	129.0	116.9	0.6	6	146 (5)	2 (1)	1 (1)	0
22	6	<i>Dicranum montanum</i>	Clear-cut	0.782	0.142	9.3	8.0	0.9	4	18 (4)	0	0	0
23	1	<i>Pogonatum aloides</i>	Clear-cut	1.100	–	2.7	–	0.3	1	1.0	0	0	0
24	1	<i>Polytrichum formosum</i>	Clear-cut	1.305	–	1.5	–	1.0	1	2.0	0	0	0
25	1	<i>Bryum</i> sp.	Clear-cut	0.285	–	0.0	–	–	0	0.0	0	0	0
26	1	<i>Dicranum spurium</i>	Clear-cut	0.335	–	17.9	–	0.5	1	0.0	0	0	0
27	1	<i>Orthotrichum</i> sp.	Clear-cut	0.025	–	4600.0	–	0.4	4	24.0	0	14	0
28	1	<i>Cynodontium strumiferum</i>	Clear-cut	0.265	–	7.6	–	1.0	1	2.0	0	0	0

Appendix 1. Continued.

Sample	<i>Diphascon belgicae</i>	<i>Diphascon cf. scoticum</i>	<i>Diphascon pingue</i>	<i>Diphascon oculatum</i>	<i>Diphascon cf. proroirostre</i>	<i>Platicrista angustata</i>	<i>Mesocrista spitzbergensis</i>	<i>Astatumen sp.</i>	<i>Milnesium tardigradum</i>	<i>Ramazzottius sp.</i>	<i>Isohypsibius prosostomus</i>	<i>Isohypsibius sattleri</i>
1	1 (1)	1 (1)	10 (3)	2 (1)	0	4 (2)	4 (3)	0	3 (2)	0	0	0
2	0	1 (1)	1 (1)	4 (2)	0	2 (2)	12 (4)	0	0	0	0	0
3	0	1 (1)	2 (2)	1 (1)	0	0	0	0	1 (1)	0	0	0
4	0	9 (4)	9 (4)	3 (2)	2 (1)	6 (3)	6 (2)	0	15 (4)	1 (1)	0	0
5	0	6 (3)	2 (2)	1 (1)	0	3 (2)	18 (4)	0	8 (2)	0	0	0
6	0	2 (2)	5 (3)	7 (2)	4 (1)	1 (1)	4 (2)	1 (1)	2 (1)	0	0	0
7	0	1 (1)	0	1 (1)	0	0	4 (2)	0	6 (3)	0	0	0
8	0	0	0	1 (1)	0	0	0	0	2 (2)	0	1 (1)	0
9	0	40 (4)	11 (4)	13 (4)	3 (2)	3 (3)	12 (4)	0	3 (2)	0	0	1 (1)
10	0	0	0	0	0	0	1 (1)	0	0	0	0	0
11	0	0	2 (1)	0	0	0	0	0	0	0	0	0
12	0	0	0	0	0	0	1 (1)	0	1 (1)	0	0	0
13	0	1 (1)	0	1 (1)	0	0	0	0	0	0	0	0
14	0	0	0	0	0	0	0	1 (1)	0	0	0	0
15	0	0	0	0	0	0	0	0	0	0	0	0
16	0	0	0	0	0	0	0	0	0	0	0	0
17	0	0	3 (1)	0	0	0	0	0	0	0	0	0
18	0	0	0	0	0	0	1	0	0	0	0	0
19	0	0	10 (3)	0	4 (1)	0	0	0	0	1 (1)	0	0
20	0	0	0	1 (1)	0	0	0	1 (1)	0	0	0	0
21	0	2 (2)	0	0	1 (1)	0	2 (2)	0	0	0	0	0
22	0	0	2 (1)	0	0	0	13 (3)	1 (1)	0	0	0	0
23	0	0	0	0	0	0	0	0	0	0	0	0
24	0	0	0	0	0	0	0	0	0	0	0	0
25	0	0	0	0	0	0	0	0	0	0	0	0
26	0	0	0	0	0	0	3	0	0	0	0	0
27	0	0	0	1	0	0	0	0	1	0	0	0
28	0	0	0	0	0	0	0	0	0	0	0	0