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Micro- and Macroscale Changes in Density and Diversity of Testate Amoebae of Tropical Montane Rain Forests of Southern Ecuador

Valentyna KRASHEVSKA, Mark MARAUN and Stefan SCHEU

J.F. Blumenbach Institute of Zoology and Anthropology, Animal Ecology, Georg-August-University Goettingen, Goettingen, Germany

Summary. We investigated changes in diversity and density of testate amoebae in epiphytes of trees in tropical montane rain forests of southern Ecuador. Local – microscale [height on tree trunk of 0 (base of tree trunk), 1 and 2 m; TH I, TH II and TH III, respectively] and regional – macroscale (forests at 1000, 2000 and 3000 m) changes were investigated. At the macroscale diversity and density of testate amoebae peaked at 2000 m. At the microscale diversity reached a maximum at TH I, whereas density reached a maximum at TH III. The percentage of empty shells at the macroscale was at a maximum at 2000 m and at the microscale at TH I, whereas the percentage of live cells was at a maximum at 3000 m and at TH III. The diversity of testate amoebae in epiphytes found in the present study was high (113 species). However, only two to nine species were dominant representing 54–85 percent of total living testate amoebae. The results suggest significant variations in density and diversity of testate amoebae at both the micro- and macroscale. However, for testate amoebae density the macroscale appears most important whereas changes in diversity are more pronounced at the microscale.

Key words: Altitude, epiphyte, live cells, moss, protist.

INTRODUCTION

Tropical montane rain forests are typically wet forests (Vance and Nadkarni 1990) with a high abundance and diversity of plants and animals that change with altitude (Brehm *et al*. 2006, Liede-Schumann and Breckle 2008). Altitudinal gradients recently attracted much interest in ecology (Körner 2000, Lomolino 2001, Rahbek 2005, Beck *et al*. 2008). Abiotic conditions, such as temperature, precipitation, humidity and soil factors, change profoundly with altitude (Tanner 1977, Marrs *et al*. 1988, Grieve *et al*. 1990, Flenley 1995). As a consequence, species richness of most organisms also change, but the changes often are not in parallel to altitude and vary among taxonomic groups (Gentry 1988, Lomolino 2001, Rahbek 2005, Gradstein 2008).

Due to the high precipitation and humidity in particular epiphytes are abundant and diverse in tropical montane rain forests and this also applies to montane rain forests in southern Ecuador (Gradstein 2008). Epiphyte mats attract a variety of animal taxa (Nadkarni and Longino 1990, Yanoviak *et al*. 2007), especially small

Address for correspondence: Valentyna Krashevska, J.F. Blumenbach Institute of Zoology and Anthropology, Animal Ecology, Georg-August-University Goettingen, Berliner Str. 28, 37073 Goettingen, Germany; Fax +49 (0) 551 395448; E-mail vkrashe@gwdg.de

species that live in water films, such as testate amoebae (Bonnet 1973, Meisterfeld 1978, Bamforth 2007). Moisture plays an important role for the density and diversity of testate amoebae (Bonnet 1973, Coûteaux 1976) and epiphyte habitats receive enough water and provide sufficient resources to support semi-aquatic life (Maguire 1971). Testate amoebae are widespread and an ecologically important group of unicellular organism (Clarke 2003) that have been shown to be good indicators of environmental conditions, such as humidity and acidity (Bonnet 1961, Bonnet 1978a, Warner and Chmielewski 1992). Regarding the diversity and density of testate amoebae in epiphyte microhabitats we addressed two fundamental questions: how do they respond to (1) altitudinal changes (macroscale) and (2) the location of epiphytes on trees (height on tree trunk; microscale)?

Recent studies in tropical montane rain forests of Ecuador suggest that the diversity and density of plants and animals (testate amoebae, geometrid moths, birds) peaks at intermediate altitude probably because of favourable abiotic conditions (Krashevska *et al*. 2007, Beck *et al*. 2008, Krashevska *et al*. 2008). Therefore, we hypothesised that total diversity and density of testate amoebae in epiphytes also peak at intermediate altitude irrespective of tree microhabitat (macroscale hypothesis, H 1).

Existing studies on testate amoebae in epiphytes focused on biogeographical issues and the structure of communities in different habitats (Nair and Mukherjee 1969, Chardez *et al*. 1972, Smith 1974, Smith 1978, Bonnet 1978b, Meisterfeld 1979, Beyens *et al*. 1992, Mitchell *et al*. 2004). Generally, however, compared to soil habitats testate amoebae in epiphytes on trees received little attention and this applies in particular to epiphytes of montane rain forests, e.g. no information is available on changes in diversity and density of testate amoebae in epiphytes with trunk height. Bonnet (1973) investigated epiphytes growing on trees and found them to be colonized predominantly by ubiquitous species. Therefore, we hypothesised that diversity and density of testate amoebae vary little with trunk height thereby contributing little to testate amoeba diversity (microscale hypothesis, H 2).

We quantified separately empty shells and live organisms to investigate factors that affect the turnover of testate amoebae. Low pH supports the conservation of empty shells (Schönborn 1973, Geltzer *et al*. 1985) and soil pH decreases with increasing altitude in the studied montane rain forests (Moser *et al*. 2007). Further, low temperature slows down the turnover of testate amoebae shells (Meisterfeld and Heisterbaum 1986) and temperature decreases with increasing altitude (Röderstein *et al*. 2005, Moser *et al*. 2007). In addition, the turnover of testate amoebae increases with increasing stress and stress conditions, such as variations in humidity, are likely to be more pronounced higher up in trees (Bonnet 1973, Meisterfeld 1978, Bohlman *et al*. 1995). Therefore, we hypothesised that the percentages of living cells decreases and that of empty shells increases with altitude and height of epiphyte location on tree trunks (H 3).

MATERIALS AND METHODS

Study sites

The study area is located in southern Ecuador within the Eastern Cordillera of the Andes in the province of Zamora-Chinchipe. Along an altitudinal transect three study sites at 1000, 2000 and 3000 m a.s.l. were investigated. The study site at 1000 m was located in Bombuscaro near the province capital Zamora (04°06′ S, 78°58′ W), the one at 2000 m in the Reserva Biologica San Francisco (RBSF) in the valley of the Rio San Francisco (03°58′ S, 79°4″ W) and the one at 3000 m in the Cajanuma area at the north-west gate of Podocarpus National Park south of Loja (04°06′ S, 79°10″ W).

The sites are covered with mostly undisturbed montane rain forest (Homeier *et al*. 2002). The climate is semihumid with 8 to 10 humid months per year. Accordingly, annual rainfall is high with ca. 2200, 3500 and 4500 mm at 1000, 2000 and 3000 m, respectively. The mean annual air temperature is decreasing with altitude from 14.9 to 12.3 to 8.9°C at 1000, 2000 and 3000 m, respectively. The coldest month is August, the warmest November (Röderstein *et al*. 2005); more details are given in Beck *et al*. (2008).

In the RBSF, a montane forest reserve of approximately 1000 ha in southern Ecuador, almost 2400 species of flowering plants, ferns, bryophytes and lichens have been recorded (Liede-Schumann and Breckle 2008), about every second species is an epiphyte (for more details see Kürschner and Parolly 2007). The RBSF harbours more than 500 species of bryophytes, probably the highest number ever recorded from such a small area in the tropics (Gradstein *et al*. 2007, Kürschner and Parolly 2007). In spermatophytes orchids, mostly growing as epiphytes, are the most specious family with a total of ca. 340 species. This is the highest number recorded for a neotropical forest site. Lauraceae, Melastomataceae and Rubiaceae are most species rich and most frequent throughout the study site (for details see Homeier *et al*. 2002).

Sampling

At each altitude a sampling area of 100–200 m^2 was selected and six trees with epiphytes were randomly chosen (macroscale). From each tree, three epiphyte samples at different height on tree trunks were taken (microscale): (1) at the bottom of the tree trunk (trunk height 0 m, TH I), (2) at a trunk height of 1 m (TH II) and (3) at a trunk height of ca. 2 m (TH III). Therefore, a total of 54 samples were analysed. The samples included epiphytes (mainly crypto-

gams) and decomposing organic materials, such as abscised parts of epiphytes and bark of host trees; epiphytes at TH I and II consisted mainly of mosses and other cryptogams, whereas at TH III they consisted of a variety of cryptogams. Cryptogam species composition varies markedly along tree trunks (Gradstein *et al*. 2007, Kürschner and Parolly 2007); the samples therefore consisted of a variety species which were not identified. Also, tree species vary strongly even on small spacial scales and therefore samples originated from different species on both the small and large scale. Samples were taken in March 2007.

Testate amoebae

Testate amoebae extraction was done by washing samples over filters of 500 µm and 250 µm mesh size, and then back-sieving the filtrate over a 20 µm mesh filter. The sieving over 500 and 250 µm was done with high water flow to maximize the extraction of tests (see Mitchell *et al*. 2004). Testate amoebae were investigated from the fraction between 250 and 20 µm and small forms were recovered from the filtrate on a 20 µm mesh filter. Microscopic slides were prepared and shells were identified and counted at 200 × or 400 × magnification with an upright Leitz Ortholux II. Testate amoebae were divided into live cells (live organisms and organism in cyst) and empty shells after staining with aniline blue (Merck, Darmstadt). For staining testate amoebae on microscopic slides one drop of aniline blue solution (2%) was added (see Schönborn 1968). Testate amoebae were determined to species (morphospecies) level and numbers were expressed per gram of air dry material (see Krashevska *et al*. 2007). The full names of species are listed in Appendix S1.

Statistical analyses

Data on diversity and density of testate amoebae taxa were analyzed by MANOVA to evaluate the effects of the factors Altitude and Trunk height. If significant protected ANOVAs were carried out for individual taxa to evaluate which of the taxa contributed to the significant MANOVA effect. Statistical analyses were performed using SAS 9.13 (SAS Institute Inc., Cary, USA). Data of density were log-transformed to improve homoscedasticity. Percentage data of live cells and empty shells were arcsine square-root transformed.

RESULTS

Species diversity

A total of 113 testate amoebae taxa were identified and counted (see Appendix S1). Generally, the number of species was at a maximum at 2000 m (Fig. 1), at a minimum at 3000 m and intermediate at 1000 m ($F_{2,45}$ = 21.0, $P < 0.0001$), and varied with trunk height with a maximum at TH I, a minimum at TH II and intermediate diversity at TH III ($F_{2,45}$ = 33.6, $P < 0.0001$). However, species number at TH II varied less than at TH I and TH III with the number at 1000 and 2000 m being similar (significant Altitude × Trunk height interaction $F_{2,45}$ = 5.2, $P = 0.0015$).

Dominance

Live forms: At 1000 m nine (TH I) and seven (TH II and TH III) species dominated (contributing > 5% to total abundance) and accounted for 70, 80 and 71% of the total abundance, respectively (Figs 2 A, B, C). At 2000 m six (TH I and TH II) and seven species (TH III) dominated and accounted for 83, 85 and 54% of the total abundance, respectively. At 3000 m six (TH I), two (TH II) and seven species (TH III) dominated and accounted for 81, 69 and 81% of the total abundance. *Euglypha strigosa* (Ehrenberg) was the most dominant species at eight sites, *Assulina muscorum* Greef at seven sites and *Cyclopyxis eurystoma* v. *parvula* Bonnet, Thomas at six.

Empty shells: The dominance of empty shells generally resembled that of live cells but with *Cyclopyxis eurystoma* v. *parvula* Bonnet, Thomas dominating at eight sites, *Euglypha strigosa* (Ehrenberg) at six sites and *Assulina muscorum* Greef at only five sites (Figs 2 D, E, F).

Density

MANOVA suggested that the density of testate amoebae significantly responded to changes in altitude (Wilks' Lambda 0.1033, $F_{6,86}$=30.3, $P < 0.0001$) and trunk height (Wilks' Lambda 0.5011, $F_{6,86}$ = 5.9, $P < 0.0001$) and the interaction of both (Wilks' Lambda 0.4049, $F_{12,114}$ = 3.9, $P < 0.0001$). The density of live cells increased in the order 1000 < 3000 < 2000 m ($F_{2,45}$ = 31.3, $P < 0.0001$; Fig. 3), and that of empty shells in the order 3000 < 1000 < 2000 m ($F_{2,45}$ = 58.6,

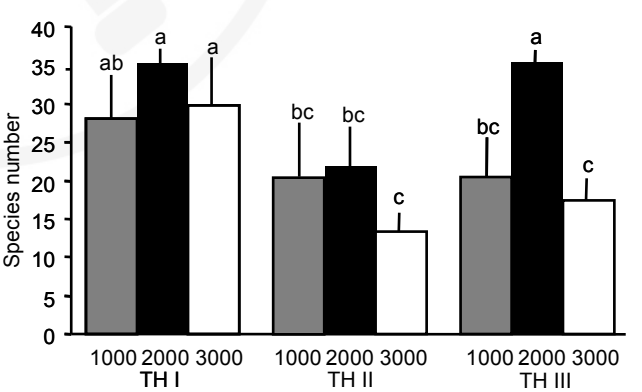

Fig. 1. Average species number of testate amoebae in epiphytes at three altitudes (1000, 2000 and 3000 m) and three trunk heights (0, 1, and 2 m labelled TH I, TH II and TH III, respectively). Means with standard errors. Bars with different letters vary significantly (Tukey's HSD test, $\alpha < 0.05$).

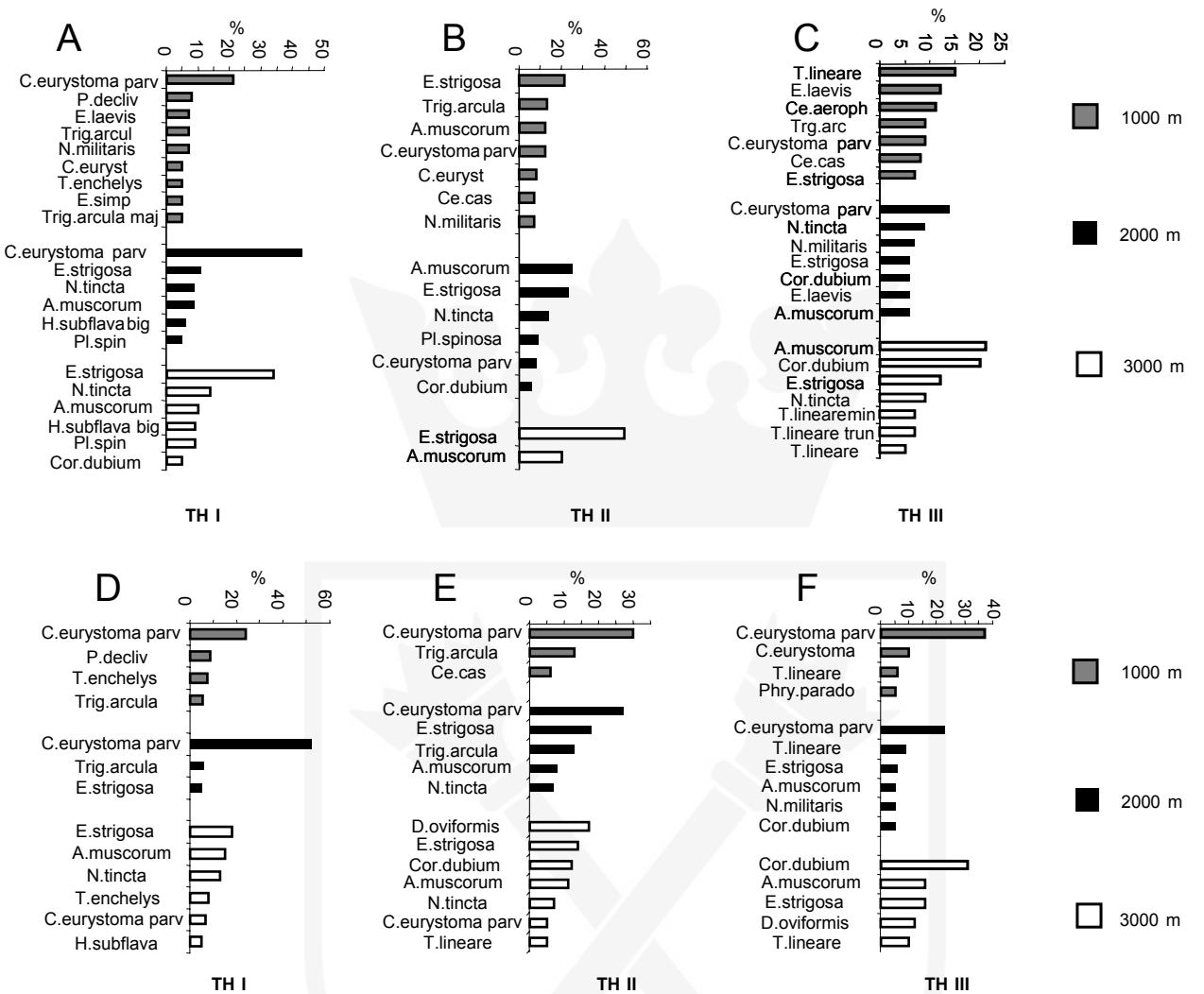

Fig. 2. Dominance of live cells (**A**, **B**, **C**) and empty shells (**D**, **E**, **F**) of testate amoebae in epiphytes at three altitudes (1000, 2000 and 3000 m) and three trunk heights (0, 1, and 2 m labelled TH I, TH II and TH III, respectively). Full names of species are listed in Appendix S1.

$P < 0.0001$; Fig. 4). At each of the altitudes the density of live cells significantly increased from TH I to TH II to TH III ($F_{2,45} = 16.2$, $P < 0.0001$ for Trunk height). The interaction between Altitude and Trunk height was significant for empty shells, reflecting the strong increase in the number of empty shells in the order TH II < TH I < TH III at 2000 m ($F_{2,45} = 5.0$, $P = 0.002$; Fig. 4).

Percentage of live cells and empty shells

Percentage of live cells was not similar to density and decreased in the order 3000 > 1000 > 2000 m ($F_{2,45} = 53.1$, $P < 0.0001$). However, changes in the percentage of empty shells resembled that in density increasing in the order 3000 < 1000 < 2000 m ($F_{2,45} = 53.8$, $P < 0.0001$). With trunk height the percentage of live cells increased in the order TH I < TH II ≤ TH III ($F_{2,45} = 12.1$, $P < 0.0001$), whereas the percentage of empty shells increased in the order TH III ≤ TH II < TH I ($F_{2,45} = 12.1$, $P < 0.0001$). The percentage of live cells was at a maximum (74%) whereas that of empty shells was at a minimum (26%) in TH III at 3000 m, and the percentage of empty shells was at a maximum (85%) and that of live cells at a minimum (15%) in TH I at 2000 m (for the Altitude × Trunk height interaction of live cells $F_{2,45} = 9.8$, $P < 0.0001$, of empty shells $F_{2,45} = 9.6$, $P < 0.0001$, respectively).

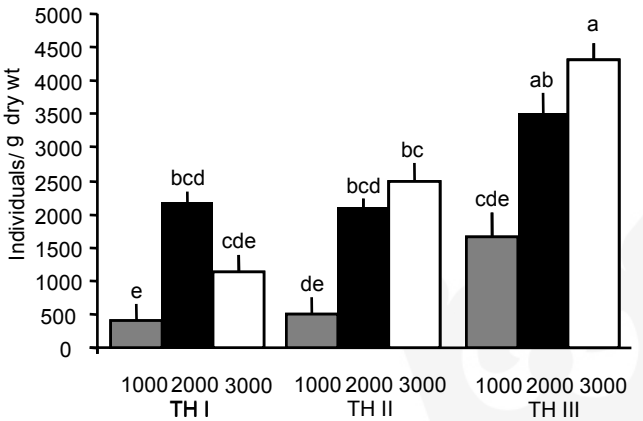

Fig. 3. Density of live cells of testate amoebae in epiphytes at three altitudes (1000, 2000 and 3000 m) and three trunk heights (0, 1, and 2 m labelled TH I, TH II and TH III, respectively). Means with standard errors. Bars with different letters vary significantly (Tukey's HSD test, $\alpha < 0.05$).

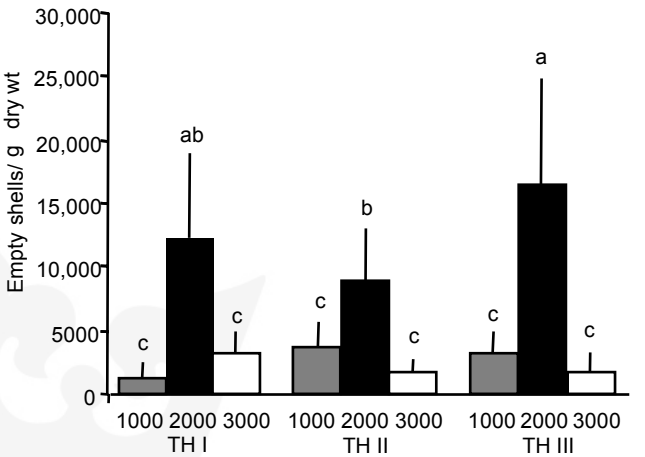

Fig. 4. Density of empty shells of testate amoebae in epiphytes at three altitudes (1000, 2000 and 3000 m) and three trunk heights (0, 1, and 2 m labelled TH I, TH II and TH III, respectively). Means with standard errors. Bars with different letters vary significantly (Tukey's HSD test, $\alpha < 0.05$).

DISCUSSION

Abiotic factors in particular acidity and humidity of the habitat are assumed to be the main determinants of the diversity and density of testate amoebae (Bonnet 1973, Coûteax 1976, Searles *et al*. 2001). In addition, testate amoebae have been assumed to be sensitive to stress, e.g. as induced by variations in humidity (Bonnet 1973, Meisterfeld 1978). Further, testate amoebae are likely to depend on the availability and diversity of resources and therefore may respond parallel to that of other organisms in particular plants (Lousier and Parkinson 1984, Schönborn 1992, Coûteaux and Darbyshire 1998) that provide the basal resources for decomposer systems, plant litter material. Along the studied altitudinal gradient in tropical rain forests of Ecuador acidity, humidity and UV-radiation increase, and temperature and tree height decrease. With tree height the variability of humidity and temperature increases likely resulting in increased stress for testate amoebae. In contrast to abiotic conditions, the diversity of plants and animals does not uniformly change with altitude but often peaks at intermediate altitude, i.e. at 2000 m (Beck *et al*. 2008, Liede-Schumann and Breckle 2008). Investigating testate amoebae in epiphytes at the microscale (trunk height of 0, 1 and 2 m) and macroscale (altitudes of 1000, 2000 and 3000 m) we expected their density and diversity to peak at 2000 m (parallel to plants and other animals; H 1) and to decline with trunk height (due to increased variability of abiotic factors; H 2).

A total of 113 testate amoebae taxa were found with the mean species richness of 25 per sampling location. Other studies investigating species richness of testate amoebae in epiphytes reported a maximum of ca. 80 species (Bartoš 1963, Bonnet 1973, Beyens and Chardez 1994, Bamforth 2007). By comparison, a total of 135 species of testate amoebae were found in litter and soil of the studied montane tropical rain forests in Ecuador (Krashevska *et al*. 2007). Therefore, the diversity of testate amoebae in epiphytes found in the present study is high. However, only two to nine species were dominant representing 54–85% of total living testate amoebae. Notably, these consisted predominantly of cosmopolitan species occurring in humid habitats of low pH, such as *Assulina muscorum* Greef and *Euglypha strigosa* (Ehrenberg) confirming earlier findings (Bonnet 1964, Schönborn 1973).

In agreement to our expectation (H 1) diversity and density of testate amoebae peaked at intermediate altitude (2000 m) with an average richness of 53 taxa and average density of 15,165 individuals/g dry wt. Remarkably, the density of testate amoebae in epiphytes exceeded that in litter and soil (Krashevska *et al*. 2007).

We expected that diversity and density of testate amoebae in epiphytes decline with increasing trunk

height (H 2). The results supported this hypothesis for testate amoebae diversity but not for density. Irrespective of altitude the diversity of testate amoebae indeed reached a maximum at TH I, whereas density of testate amoebae reached a maximum at TH III. High density at TH III at least in part may be due to the combined effect of favourable microclimatic conditions, e.g. high humidity combined with high UV-radiation (Beck *et al*. 2008) both are known to beneficially affect testate amoebae (Bonnet 1973, Coûteaux 1976, Searles *et al*. 2001). High frequency of species with acrostomy, e.g. species of the genera *Euglypha*, *Assulina* and *Nebela,* supports the conclusion that humidity is a major structuring force for testate amoebae at TH III. Aboveground species experience greater extremes in temperature, wetting and drying cycles than species on the forest floor (Bohlman *et al*. 1995). Therefore, only species adapted to variable environmental conditions are able to survive, e.g. species with short life cycles such as *Trinema complanatum* Penard and *Trinema enchelys* Leidy which already start to reproduce after ca.1–3 days (Schönborn 1975). Maximum diversity at TH I presumably results from the close vicinity to the forest floor where the number of species is even higher (Krashevska *et al*. 2007) and some of these species presumably colonize epiphytes at the base of trees, e.g. species of the genus *Plagiopyxis*. Furthermore, more constant abiotic conditions at the base of trees as compared to TH II and TH III presumably contributed to the high diversity of species at TH I.

Increasing acidity and decreasing temperature along the altitudinal gradient and more pronounced stress conditions higher up in trees led us to expect that percentages of live cells decreases and empty shells increases with altitude and height of epiphyte on tree trunks (H 3). In contrast to this expectation, the percentage of empty shells along the altitudinal gradient was at a maximum at 2000 m and on trees at TH I. With the data available, these patterns are difficult to explain but suggest caution of relating the turnover of empty shells to environmental conditions such as pH. Further, in contrast to our expectations, the percentage of live cells was at a maximum at 3000 m and at TH III. Potentially, high precipitation at this altitude (4500 mm/yr; Röderstein *et al*. 2005) results in high density of testate amoebae. Furthermore, lower density of empty shells was most pronounced higher up on tree trunks were the physical forces of raindrops presumably are most pronounced.

Results of the present study suggest significant changes in density and diversity of testate amoebae along both the micro- and macroscale. However, for testate amoebae density the macroscale appears most important whereas changes in diversity of testate amoebae are more pronounced at the microscale. The decline in diversity with increasing trunk height suggests that the diversity of testate amoebae predominantly depends on abiotic factors, in particular on the water regime of the habitat, i.e. constant moisture conditions; and distance from the more diverse forest floor. Maximum density at 2000 m along the studied altitudinal gradient suggests that testate amoebae density benefits from high diversity of other organisms in particular that of plants (Beck *et al*. 2008, Liede-Schumann and Breckle 2008). Maximum number of species at 2000 m suggests that this also applies to testate amoebae diversity indicating that at given abiotic conditions testate amoebae diversity is modulated by biotic factors such as the diversity and quality (e.g. carbon-to-nitrogen ratio) of plants driving the community composition of microorganisms, potential food resources for testate amoebae. To prove these assumptions experimental manipulations of major abiotic factors, such as the moisture regime, and biotic factors, such as the diversity of litter materials, are necessary. These investigations are currently under way at our study site.

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Appendix 1. List of testate amoebae given as individuals per gram of air dry material.

Species name	Tree trunk at 0 m						Tree trunk at 1 m						Tree trunk at 2 m					
	1000 m		2000 m		3000 m		1000 m		2000 m		3000 m		1000 m		2000 m		3000 m	
	mean	SD	mean	SD	mean	SD	mean	SD	mean	SD	mean	SD	mean	SD	mean	SD	mean	SD
Apodera vas Certes, 1889	7	4	7	2	12	8	23	15	0	0	13	4	0	0	0	0	0	0
Arcella arenaria Greeff, 1866	0	0	6	2	0	0	20	13	19	9	0	0	0	0	0	0	15	5
Archerella flavum Archer, 1877	2	1	0	0	0	0	13	8	0	0	8	3	0	0	0	0	0	0
Argynnia caudata Leidy, 1879	20	11	105	26	9	6	0	0	0	0	0	0	0	0	0	0	0	0
Argynnia dentistoma Penard, 1890	3	2	11	3	14	10	11	7	0	0	0	0	0	0	44	11	0	0
Assulina muscorum Greef, 1888	1	1	388	95	275	182	217	140	1231	596	799	278	44	22	1050	251	945	324
Assulina scandinavica Penard, 1890	0	0	0	0	16	11	0	0	0	0	0	0	0	0	0	0	0	0
Assulina seminulum (Ehrenberg, 1848) Leidy, 1879	2	1	10	2	7	5	0	0	61	30	40	14	0	0	192	46	7	2
Awerintzewia cyclostoma (Penard, 1902) Schouteden, 1906	6	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Centropyxis aculeata (Ehrenberg, 1838) Stein, 1857	4	2	0	0	0	0	0	0	11	5	0	0	24	12	0	0	0	0
Centropyxis aerophila Deflandre, 1929	0	0	0	0	22	14	101	65	112	54	92	32	218	111	146	35	0	0
Centropyxis aerophila var. *sphagnicola* Deflandre, 1929	0	0	0	0	0	0	0	0	43	21	12	4	0	0	0	0	0	0
Centropyxis cassis (Wallich, 1864) Deflandre, 1929	36	20	0	0	0	0	244	157	0	0	13	4	200	101	42	10	0	0
Centropyxis constricta (Ehrenberg, 1841) Deflandre, 1929	40	22	28	7	0	0	49	32	33	16	27	10	152	77	46	11	0	0
Centropyxis constricta var. *minima* Decloitre, 1954	0	0	0	0	0	0	0	0	0	0	0	0	12	6	0	0	0	0
Centropyxis laevigata Penard, 1890	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Centropyxis orbicularis Deflandre, 1929	0	0	0	0	0	0	0	0	0	0	0	0	8	4	0	0	0	0
Centropyxis plagiostoma Bonnet, Thomas, 1955	2	1	0	0	0	0	0	0	0	0	18	6	0	0	0	0	0	0
Certesella certesi Penard, 1911	0	0	0	0	3	2	0	0	0	0	0	0	0	0	0	0	0	0
Certesella martiali Certes, 1889	0	0	25	6	91	60	65	42	0	0	104	36	16	8	84	20	9	3
Certesella sp.	0	0	0	0	14	10	0	0	0	0	0	0	0	0	0	0	0	0
Corythion asperulum Schonborn, 1988	0	0	0	0	0	0	0	0	0	0	67	23	0	0	0	0	0	0
Corythion dubium Taranek, 1871	0	0	92	23	80	53	16	10	216	104	98	34	25	13	928	222	1415	486
Cryptodifflugia oviformis Penard, 1890	0	0	12	3	0	0	0	0	25	12	14	5	12	6	98	23	734	252
Cyclopyxis eurystoma Deflandre, 1929	43	24	182	45	59	39	195	126	423	205	94	33	426	216	514	123	79	27
Cyclopyxis eurystoma var. *parvula* Bonnet, Thomas, 1960	383	209	7237	1773	428	282	904	583	2521	1220	205	71	1550	787	4149	992	0	0
Cyclopyxis kahli Deflandre, 1929	13	7	40	10	4	3	68	44	240	116	0	0	187	95	289	69	0	0
Cyclopyxis lithostoma Bonnet, 1974	14	8	12	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Difflugia lucida Penard, 1890	0	0	5	1	0	0	0	0	0	0	0	0	16	8	0	0	0	0

Difflugia oblonga Ehrenberg, 1838	0	0	0	0	0	0	0	0	0	0	14	5	0	0	0	0	0	0
Distomatopyxis sp.	39	21	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Euglypha anodonta Bonnet, 1960	0	0	19	5	14	9	0	0	0	0	0	0	87	44	0	0	0	0
Euglypha anodonta var. *magna* Schonborn, 1964	39	21	0	0	0	0	27	17	46	22	0	0	0	0	157	37	0	0
Euglypha bryophila Brown, 1911	0	0	23	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Euglypha capsiosa Couteaux, 1978	34	19	6	1	0	0	11	7	0	0	0	0	0	0	237	57	0	0
Euglypha ciliata (Ehrenber, 1848) Leidy, 1878	0	0	58	14	38	25	0	0	218	105	30	10	24	12	480	115	21	7
Euglypha ciliata f. *glabra* Wailes, 1915	8	4	0	0	6	4	0	0	43	21	29	10	0	0	333	80	37	13
Euglypha compressa Carter, 1864	0	0	66	16	7	5	0	0	74	36	0	0	0	0	36	9	10	4
Euglypha compressa f. *glabra* Wailes, 1915	0	0	11	3	0	0	0	0	48	23	0	0	8	4	0	0	0	0
Euglypha cristata Leidy, 1874	13	7	48	12	10	7	0	0	0	0	0	0	44	22	126	30	70	24
Euglypha cristata f. *decora* Jung, 1942	5	2	0	0	0	0	0	0	17	8	0	0	0	0	53	13	0	0
Euglypha cuspidata Bonnet, 1959	0	0	0	0	0	0	0	0	0	0	0	0	0	0	62	15	0	0
Euglypha denticulata Brown, 1912	3	2	0	0	0	0	0	0	0	0	22	8	0	0	471	113	71	24
Euglypha filifera Penard, 1890	2	1	0	0	3	2	0	0	0	0	0	0	8	4	0	0	0	0
Euglypha laevis (Ehrenberg, 1832) Perty, 1849	50	28	38	9	0	0	41	27	9	4	0	0	234	119	573	137	113	39
Euglypha polylepis Bonnet, Thomas, 1960	0	0	0	0	7	5	0	0	0	0	0	0	0	0	70	17	9	3
Euglypha rotunda Wailes, 1915	5	3	22	5	9	6	0	0	0	0	0	0	0	0	297	71	73	25
Euglypha simplex Decloitre, 1965	60	33	12	3	3	2	53	34	0	0	0	0	0	0	0	0	0	0
Euglypha sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	74	18	0	0
Euglypha sp1	0	0	0	0	17	11	0	0	0	0	0	0	0	0	0	0	0	0
Euglypha strigosa (Ehrenberg, 1871) Leidy, 1878	6	3	854	209	688	454	297	191	2028	981	1431	499	109	55	1212	290	720	247
Euglypha strigosa var. *muscorum* Wailes, 1911	0	0	0	0	0	0	0	0	0	0	59	21	0	0	0	0	0	0
Euglypha tuberculata Dujardin, 1841	4	2	0	0	0	0	0	0	0	0	0	0	8	4	46	11	0	0
Euglypha tuberculata var. *minor* Taranek, 1882	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	21	7
Heleopera penardi Bonnet and Thomas	0	0	22	5	13	9	38	25	0	0	0	0	0	0	0	0	0	0
Heleopera petricola Leidy, 1879	29	16	25	6	94	62	0	0	45	22	0	0	49	25	338	81	0	0
Heleopera petricola var. *amethystea* Penard, 1902	0	0	12	3	20	13	0	0	0	0	0	0	8	4	0	0	0	0
Heleopera rosea Penard, 1890	0	0	0	0	18	12	0	0	0	0	0	0	0	0	0	0	0	0
Heleopera sphagni Leidy, 1874	0	0	14	3	10	7	0	0	0	0	0	0	0	0	0	0	0	0
Heleopera sylvatica Penard, 1890	21	11	26	6	0	0	117	75	0	0	0	0	28	14	0	0	0	0
Hyalosphenia elegans Leidy, 1879	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	7	2
Hyalosphenia minuta Cash, 1892	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	59	20
Hyalosphenia subflava (big; 90–100 µm)	3	2	277	68	298	197	0	0	0	0	0	0	0	0	0	0	7	2
Hyalosphenia subflava Cash, 1909	11	6	352	86	36	24	4	3	7	3	0	0	20	10	0	0	14	5

Lamtopyxis travei Bonnet, 1977	6	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Nebela barbata Leidy, 1874	0	0	5	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Nebela bohemica Taranek, 1882	0	0	0	0	0	0	0	0	7	3	0	0	0	0	0	0	0	0
Nebela collaris (Ehrenberg, 1848) Leidy, 1879	11	6	190	46	63	41	0	0	43	21	0	0	56	29	0	0	0	0
Nebela flabellulum Leidy, 1874	0	0	21	5	0	0	0	0	0	0	0	0	0	0	0	0	9	3
Nebela galeata Penard, 1902	0	0	26	6	0	0	17	11	0	0	0	0	0	0	0	0	0	0
Nebela gracilis Penard, 1910	7	4	395	97	23	15	91	58	7	3	0	0	0	0	37	9	0	0
Nebela lageniformis Penard, 1902	3	2	12	3	6	4	4	3	0	0	0	0	0	0	0	0	22	8
Nebela militaris Penard, 1890	52	28	355	87	202	133	149	96	434	210	21	7	68	35	1079	258	10	4
Nebela parvula Cash, 1909	0	0	0	0	0	0	0	0	0	0	0	0	0	0	20	5	0	0
Nebela penardiana Deflandre, 1936	0	0	42	10	33	22	0	0	7	3	0	0	36	18	61	15	0	0
Nebela tincta (Leidy, 1879) Awerintzew, 1906	3	2	570	140	364	240	41	26	891	431	344	120	0	0	517	124	236	81
Nebela tubulata Brown, 1911	40	22	25	6	111	73	7	5	0	0	13	4	12	6	87	21	0	0
Nebela tubulosa Penard, 1902	0	0	17	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Nebela wailesi Deflandre, 1936	1	1	87	21	14	9	0	0	0	0	0	0	12	6	12	3	0	0
Phryganella acropodia (Hertwig, Lesser, 1874) Hopkinson, 1909	0	0	0	0	0	0	0	0	0	0	0	0	0	0	71	17	0	0
Phryganella hemisphaerica Penard, 1902	0	0	0	0	14	10	0	0	36	17	0	0	0	0	14	3	0	0
Phryganella paradoxa Penard, 1902	0	0	87	21	90	60	61	39	236	114	40	14	191	97	0	0	0	0
Placocista spinosa (Carter, 1865) Leidy, 1879	6	3	235	58	140	92	0	0	302	146	47	16	0	0	83	20	42	15
Plagiopyxis declivis Thomas, 1958	138	75	493	121	9	6	55	36	58	28	8	3	24	12	28	7	0	0
Plagiopyxis labiata Penard, 1910	2	1	0	0	0	0	0	0	0	0	42	15	0	0	31	7	0	0
Planhoogenraadia acuta Bonnet, 1977	6	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Playfairina valkanovi Golemansky, 1966	2	1	13	3	0	0	0	0	0	0	0	0	0	0	310	74	17	6
Porosia bigibbosa Jung, 1942	0	0	10	2	0	0	0	0	0	0	0	0	0	0	110	26	0	0
Pseudodifflugia gracilis Schlumberger, 1845	5	3	0	0	0	0	66	43	0	0	0	0	0	0	0	0	0	0
Puytoracia bergeri Bonnet, 1970	0	0	0	0	0	0	0	0	0	0	0	0	0	0	194	46	0	0
Quadrulella quadrigera Deflandre, 1936	7	4	0	0	0	0	60	39	0	0	0	0	8	4	0	0	0	0
Quadrulella symmetrica (Wallich, 1863) Schulze, 1875	0	0	0	0	0	0	11	7	0	0	0	0	0	0	0	0	0	0
Sphenoderia fissirostris Penard, 1890	0	0	28	7	59	39	0	0	0	0	0	0	0	0	0	0	0	0
Sphenoderia lenta Schlumberger, 1845	0	0	5	1	0	0	0	0	0	0	0	0	0	0	0	0	8	3
Sphenoderia minuta Deflandre, 1931	0	0	6	1	14	9	0	0	0	0	0	0	0	0	0	0	0	0
Sphenoderia rhombophora Bonnet, 1966	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	9	3
Sphenoderia splendida (Playfair) Deflandre	0	0	97	24	10	7	0	0	0	0	0	0	0	0	0	0	0	0
Tracheleuglypha acolla Bonnet, Thomas, 1955	14	8	17	4	15	10	26	17	0	0	0	0	33	17	32	8	0	0

Tracheleuglypha dentata Deflandre, 1928	0	0	0	0	0	0	5	3	0	0	0	0	0	0	0	0	0	0
Trachelocorythion pulchellum (Penard, 1890) Bonnet, 1979	2	1	6	2	9	6	0	0	18	9	37	13	0	0	613	147	59	20
Trigonopyxis arcula Penard, 1912	93	51	748	183	184	121	479	309	1134	549	131	46	225	114	742	178	125	43
Trigonopyxis arcula var. *major* Chardez, 1960	39	21	230	56	59	39	115	74	213	103	0	0	0	0	0	0	0	0
Trinema clipelina Rauenbusch, 1987	0	0	0	0	0	0	0	0	0	0	0	0	0	0	123	29	0	0
Trinema complanatum Penard, 1890	30	16	52	13	16	10	51	33	0	0	0	0	48	24	696	166	13	5
Trinema complanatum var. *elongata* Decloitre, 1973	7	4	0	0	28	18	9	6	0	0	0	0	0	0	23	5	9	3
Trinema enchelys Leidy, 1878	111	60	147	36	288	190	28	18	38	18	23	8	56	28	167	40	23	8
Trinema galeata (Penard, 1890) Jung, 1942	0	0	12	3	0	0	172	111	17	8	296	103	8	4	23	5	0	0
Trinema grandis (Chardez, 1960) Golemansky, 1963	21	11	143	35	82	54	0	0	0	0	0	0	0	0	0	0	0	0
Trinema lineare Penard, 1890	64	35	313	77	142	94	112	72	19	9	0	0	341	173	1504	360	251	86
Trinema lineare var. *minuscula* Chardez, 1968	36	20	0	0	0	0	22	14	0	0	0	0	68	34	655	157	489	168
Trinema lineare var. *truncatum* Chardez, 1964	0	0	49	12	16	11	8	5	0	0	0	0	16	8	559	134	198	68
Trinema penardi Thomas, Chardez, 1958	23	13	0	0	4	3	18	11	87	42	21	7	32	16	63	15	0	0
Gen. nov.	33	18	7	2	0	0	0	0	0	0	0	0	20	10	0	0	0	0

SD – Standard Deviation.