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The moss dwelling testacean fauna of Île de la Possession

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Abstract An ecological study of the moss dwelling testacean fauna (Protozoa, Rhizopoda) on Île de la Possession (Crozet Archipelago, sub-Antarctica) revealed 83 taxa, belonging to 21 genera. The moss flora was dominated by cosmopolitan and ubiquitous taxa, such as *Trinema lineare*, *T. enchelys*, *Euglypha laevis* and *E. rotunda.* A cluster analysis and a correspondence analysis identified three communities: (1) a *Corythion dubium* assemblage found in a drier, slightly acidic terrestrial moss vegetation, (2) the *Arcella arenaria*, and (3) the *Difflugiella crenulata* assemblages, both characteristic of wetter, circumneutral habitats. The latter typified submerged mosses growing in running water, while the *A. arenaria* assemblage seemed to prefer mosses in standing waterbodies. Moisture conditions appeared to play a key role in determining the distribution pattern of testacean communities, while pH was only a secondary factor. A logistic regression emphasised the effect of the habitat type in controlling the variance in testacean assemblages. Moreover, the close relationship between bryophyte species and habitat type had a significant influence on the distribution pattern of the testate amoebae. Weighted averaging and calibration were used to estimate moisture optima and tolerances of the testate amoebae.

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Introduction

Testate amoebae (Protozoa: Sarcodina: Rhizopodea) have a world-wide distribution and inhabit a wide range of moist substrates. They are especially abundant in peaty soils and wet mosses (Smith 1992). Mainly in Europe, researchers have focussed on the diverse testate amoebae communities inhabiting the water films on the stems and leaves of *Sphagnum*-mosses (e.g. Beyens and Chardez 1984; Chardez et al. 1987; Corbet 1973; Foissner 1987; Heal 1962, 1964; Meisterfeld 1977; Mitchell et al. 1999, 2000a, 2000b; Tolonen 1986; Warner 1987).

Île de la Possession (Îles Crozet, sub-Antarctic region) provides an excellent environment to study the moss dwelling testate amoebae fauna since the vegetation on the island is mainly dominated by grasses and mosses. Although there are no *Sphagnum* species present (Frenot 1986), over 200 other moss species and liverworts have been recorded from Île de la Possession (Hébrard 1970). The ecological niche of *Sphagnum* is filled by *Sanionia* and *Racomitrium* moss species (N. Gremmen, personal observation). The earliest records of moss inhabiting testate amoebae on the island are by Richters (1907), who recorded eight species belonging to the genera *Arcella*, *Difflugia*, *Euglypha*, *Nebela* and *Trinema*. Smith (1975) found nine species of testate amoebae in soil samples. It is obvious that these preliminary studies on the terrestrial testate amoebae fauna on Île de la Possession are far from being complete.

Numerous studies (summarised in Mitchell et al. 1999) stressed the fact that moisture is the most important factor in controlling the distribution of testate amoebae species in microhabitats. The moisture regime of the habitat also has a significant influence on the activity of the testate amoebae fauna and its population fluctuations (Smith 1992). Besides moisture, there is a whole range of other factors contributing (in)directly to the distribution pattern of the testacean fauna. Some authors indicate a relationship between pH and testacean community structure studies (Beyens et al. 1995; Costan and Planas 1986; Ellison 1995). Schönborn (1962) stated that testate amoebae densities are being influenced by the eutrophication degree of lakes. Even temperature can co-determine the distribution pattern of the testacean fauna since testate amoebae require a minimum temperature at a specific time of the year to reproduce successfully (Medioli and Scott 1988). In addition, factors such as light, oxygen and food availability may also affect testate amoebae communities (Charman et al. 2000). Together with moisture and pH, this study will focus on the influence of the habitat type and bryophyte species on the distribution pattern of the moss dwelling communities. Do testate amoebae communities show a specific preference for certain habitats and/or specific moss species? Or is their occurrence only influenced by the moisture content of the environment?

The present paper is the third in a series of papers describing the actual living testate amoebae fauna in soil (Vincke et al. 2004a), freshwater (Vincke et al. 2004b) and moss habitats on Île de la Possession. The aims of this study are: (1) to examine the diversity and ecology of the moss dwelling testate amoebae fauna on Île de la Possession, (2) to improve the understanding of factors affecting the distribution of moss testate amoebae communities, and (3) to specify the preferences of testate amoebae with respect to moisture, habitat type and bryophyte flora.

Materials and methods

Study site

The Crozet Archipelago (45°48′–46°26′S, 50°14′–52°15′E) (Fig. 1) is situated in the southern Indian Ocean, 2,400 km north of the Antarctic continent and 2,600 km south-east from the South African coast. The archipelago lies about 300 km north of the Antarctic convergence and consists of five small volcanic islands, of which Île de la Possession is the largest (156 km^2). The Crozet archipelago belongs to the cold temperate province (Stonehouse 1982), characterised by an oceanic and cool climate. More information regarding climate, topography and vegetation of the island is given in Van de Vijver and Beyens (1999).

Sampling

During the austral summer of 1997–1998, over 400 moss samples were collected on Île de la Possession. A total of 109 samples from different locations spread over the entire island were selected for analysis. For each locality, different samples were chosen along a moisture gradient. Water was squeezed out of the sampled moss vegetation and stored in 50-ml PVC bottles, after adding 3% formaldehyde for fixation. A few moss plants were included as well in the same PVC bottle to ensure that the whole testate amoebae fauna of the moss had been sampled. The driest mosses were collected in plastic bags and further desiccated for 24 h at 40°C to avoid mould development. Dehydration may cause the collapsing of tests of some genera, especially genera *Corythion* and *Trachelocorythion* (S. Vincke, personal observation), but morphological identification of the testate amoeba species remained possible. All samples are stored at the University of Antwerp (UA), Department of Biology, Polar Ecology, Limnology and Paleobiology Unit.

The moisture content of the sampled mosses was determined with reference to the F-classification of Jung (1936). Table 1 shows the eight moisture classes of Jung (1936) together with the moisture content according to Meisterfeld (1977). When possible, pH was measured with a Hanna probe. Habitat type was determined using the following classes: running waters (R: rivers and brooklets), standing waters (S: pools and lakes), terrestrial mosses (T). Mosses were identified to the species level using a binocular microscope. Identifications are based on Van Zanten (1971), Hébrard (1970), Ochyra (1998) and Putzke and Pereira (2001). The majority of the samples were taken from *Breutelia integrifolia* (Tayl.) Jeag., *Brachytecium rutabulum* (L) Br. and Sch., *B. subplicatum* (Hamp.) Jeag. and *Sanionia uncinata* (Hedw.) Loeske. Moss species such as *Jamesoniella grandiflora* (Lindenb. and Gott.) Steph., *Schistidium falcatum* (Hook. f. and Wilson) B. Bremer were also encountered on more than one occasion.

Slide preparation and counting

All 109 moss samples were thoroughly shaken and stirred for 5 min in an indefinite amount of distilled water. The suspension was passed through a sieve with a mesh diameter of 595 μm and concentrated by centrifugation (10 min at 2,500 rpm). Afterwards rose bengal was added to distinguish dead from living tests (at the moment of sampling). Encysted testate amoebae were considered as being alive. In each moss sample, 150 tests were counted using a Leitz Wetzlar microscope. This number of counted tests should record most taxa present (Woodland et al. 1998), as long as an increase of 10% in sample size does not exceed a 10% increase of taxa (Müller-Dombois and Ellenberg 1974).

Morphological identifications of the testate amoebae are mainly based on works by Deflandre (1928, 1929, 1936), Grospietsch (1964), Decloître (1962, 1978, 1979, 1981), Ogden and Hedley (1980), Ogden (1983) and Hoogenraad and de Groot (1940).

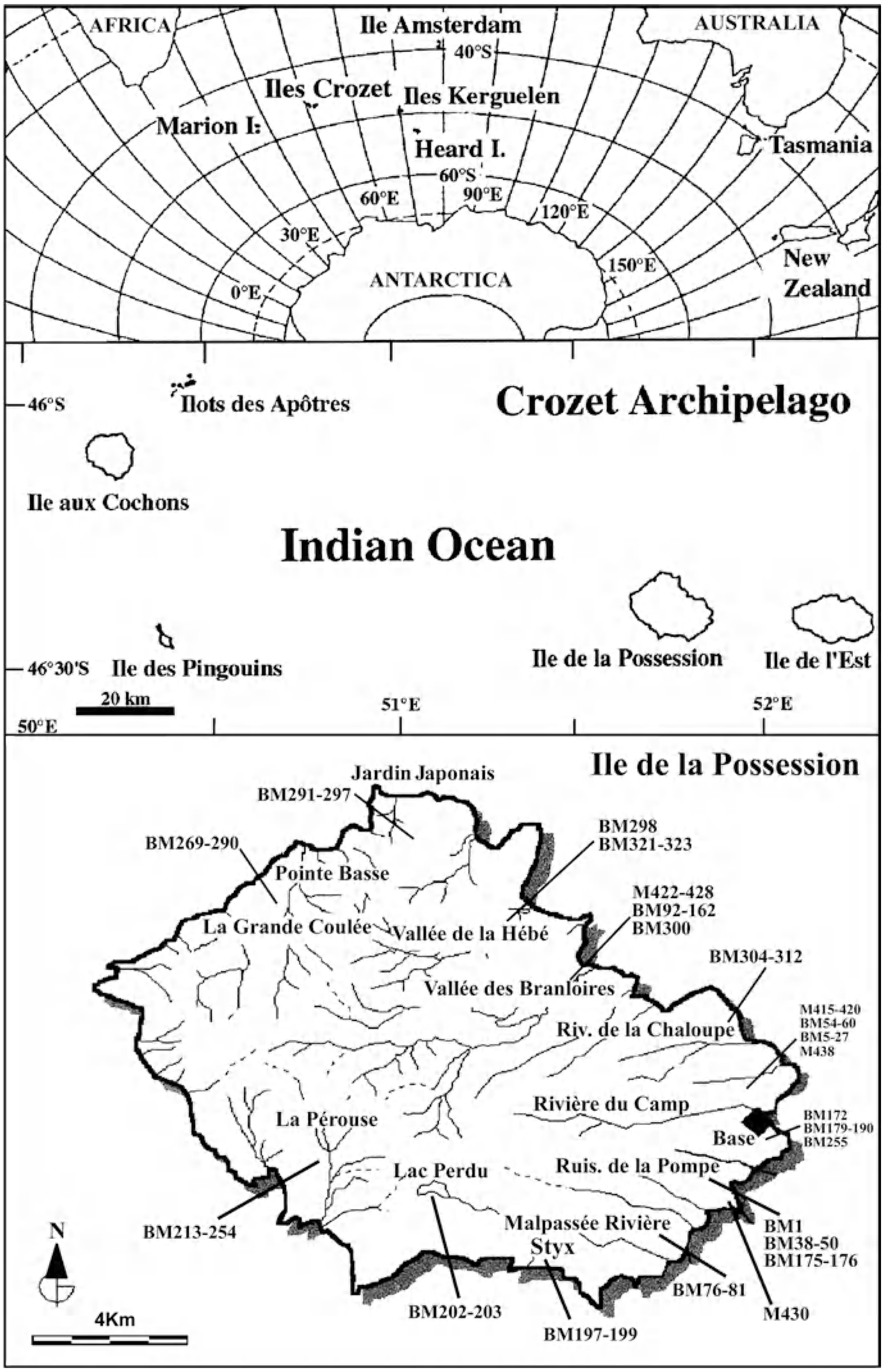

Fig. 1 Sketch map of Antarctica, the Crozet Archipelago and Île de la Possession, showing the locations of the different sampling sites (only first and last sample numbers are shown)

Table 1 Classification of moisture values according to Jung (1936) and Meisterfeld (1977)

Moisture class (Jung 1936)	Relative water content (Jung 1936)	Moisture content (Meisterfeld 1977) (%)
I	Open water or submerged vegetation	> 95
II	Floating vegetation—partly submerged, partly at the surface	> 95
III	Emerged vegetation—very wet—water drops out without pressure	> 95
IV	Wet—water drops out with moderate pressure	~95
V	Semi-wet—water drops out with moderate pressure	85–95
VI	Moist—water drops out with strong pressure	85–90
VII	Semi-dry—a few drops with strong pressure	< 80
VIII	Dry—no water drops with strong pressure	< 50

Data analysis

Diversity analysis

Diversity analysis [Shannon-Wiener diversity index ($\log_{10}$-based)] was performed using the multivariate statistical package MVSP (Kovach Computing Services 2002). The Gini evenness measure was calculated because of the independence of the number of taxa per sample and therefore allowing a better comparison between the samples (Nijssen et al. 1998).

In order to calculate the degree of turnover in species composition along the humidity gradient (FI–FVIII), Cody's (1975) β-diversity measure (β_c) was used : $\beta_c = (G+L)/2$, where G is the number of species gained and L is the number of species lost along the humidity gradient. Low values of β_c indicate low species turnover and hence no or only a limited influence of this parameter on the species composition.

Community analysis

A hierarchic-agglomerative cluster analysis, based on a minimum variance strategy with the Squared Euclidian Distance as a dissimilarity measure, was carried out to classify the species data (MVSP, Kovach Computing Services 2002). Species data were square root transformed.

Ordination techniques were performed to explore the relationships between the moss dwelling testate amoebae fauna and the measured environmental variables (F-value, habitat type, pH, moss species). A correspondence analysis (CA), carried out with the computer program CANOCO version 4.0 (ter Braak and Smilauer 1998), revealed that the total gradient length was larger than 3SD, indicating a non-linear relationship between parameters and the species abundance data (ter Braak and Prentice 1988). Species data were square root transformed in order to downweight dominant taxa. The statistical techniques used are described in full detail by Jongman et al. (1987). The sample outlier BM60 [the only sample dominated by *Centropyxis aerophila* (relative abundance of 66%)] was omitted from both CA and CCA analysis.

Logistic regression

To test statistically if the distribution pattern of the testacean fauna was determined by either the habitat type, the bryophyte flora or a combination of both parameters, a logistic model was used (data did not follow a normal distribution) (SAS, v. 8). The dependent variable was the abundance of a testate amoeba taxon in a certain sample (with a specific bryophyte flora in a certain habitat). The abundance data can be seen as discrete variables since there were always a fixed number of individuals (150) counted per sample. The independent variables were: testate amoebae species, moss species and habitat type. Therefore 15 frequently occurring discriminating testate amoebae taxa were selected (ARCARE–ASSMUS–ASSSP1–CENAER–CORDUB–DIFPRI–DLACRE–DLAOVF–EUGCIG– EUGCIL–EUGPOL–EUGSTR–HELSYL–MICPAT–PSEUFUL) (abbreviations, see Appendix). Only moss species (*Brachytecium*, *Breutelia*, *Sanionia*) which occurred frequently (at least 5 times) in the three different habitats (Running–Standing–Terrestrial) were used in the logistic model. Logistic regression results pointed out that all variables and their interactions were highly significant (χ^2; $p < 0.01$; except habitat × moss $p = 0.04$). Therefore a logistic model for each testate amoebae taxon was applied. In this case, the independent variables (moss and habitat) and their interaction were not always significant. The estimates of the least squares means were used to calculate the proportion of a certain testate amoebae taxon per habitat and per moss species.

Weighted averaging modelling

Weighted averaging (WA) regression and calibration were performed using C^2 (Juggings 2003) version 1.3. WA regression provides a computationally simple and reliable estimate of the optimal moisture (F-value) value of a testate amoeba taxon. WA calibration performs the reverse function, using the optima and abundances of the testate amoebae in the moss samples to estimate the F-value of a given sample.

Prior to the construction of the WA models, species–environment relationships were explored by a CCA-analysis. Inferring variable x from the species assemblage by WA modelling is considered justified as λ_1 (eigenvalue of first axis) is sufficiently large compared to λ_2 (eigenvalue of first unconstrained CCA axis) when running a CCA with x as the sole environmental value. However, since in literature no indication is given on the minimum acceptance value of the λ_1/λ_2 ratio, this step was ignored in this analysis.

Using the tolerance down-weighting approach (ter Braak and Van Dam 1989), the tolerance values of individual taxa are used to develop the WA. Taxa with a narrow tolerance are given more weight in a WA than those with a large tolerance. Also, shrinkage in the range of inferred values occurs, corrected either by classical deshrinking or inverse deshrinking methods (ter Braak and Van Dam 1989). The analysis was performed on all samples with F-value ranging from FIII to FVIII. Bryophyte vegetation with moisture values lower than FIII were considered too much influenced by the surrounding water and omitted from the analysis. Abundance data have not been transformed. Taxa occurring in less than three samples were also omitted from the calculations.

The predictive ability of the various calibration models was tested in terms of: (1) the apparent root mean square error (RMSE) of prediction, (2) the correlation coefficients between observed and inferred

F-values (r^2), (3) the bootstrap RMSE of prediction (Birks et al. 1990), and (4) the distribution of the residual values (observed minus inferred F-value) (Birks et al. 1990). A more complete discussion of WA theory and methods can be found in Jongman et al. (1995), ter Braak and Van Dam (1989) and Birks et al. (1990).

Results

Species composition

A total of 109 moss samples from Île de la Possession have been analysed, from which ten samples were withdrawn since they contained few (< 10 tests per slide) or no testate amoebae. The remaining 99 moss samples revealed a moss dwelling testate amoebae fauna of 83 taxa (including species, varieties and forms) belonging to 21 genera. The number of taxa per genus and the relative abundance of the different genera are presented in Fig. 2. The genera *Difflugia* and *Euglypha* are most species rich, respectively 20 and 17 taxa encountered. Their relative abundance of individuals is, however, much lower (5.1 and 13.2%, respectively). Instead, an overall dominance in abundance of the genus *Trinema* is observed (42%), due to the taxa *Trinema lineare* Penard (30%) and *T. enchelys* Leidy (12%). Other important taxa in this study are *Difflugiella crenulata* Playfair (9%), *Corythion dubium* Taranek (8%) and *Euglypha rotunda* Wailes (5.4%). The remaining 78 testate amoebae taxa have mean frequencies smaller than 5% (67 taxa: frequency < 1%). Diversity analysis revealed a mean Shannon–Wiener diversity index of 0.81 ± 0.02 and a mean Gini evenness measure of 0.36 ± 0.01. Mean number of taxa per sample was 15 ± 0.4.

An alphabetical list of all observed testate amoebae taxa together with their frequency of appearance (%) is given in the Appendix. This list contains 24 unidentified species (4.3% of all counted tests). Further morphological analysis, using scanning electron microscopy (SEM), is in progress.

Moss dwelling communities

A cluster analysis revealed three sample groups, which were confirmed by a CA (Fig. 3a). The three assemblages are named after their most characteristic taxon:

1. *Corythion dubium* assemblage
2. *Difflugiella crenulata* assemblage
3. *Arcella arenaria* assemblage.

Table 2 lists the main characteristics and taxa of the different assemblages. Sample sites on the CA-diagram have been labelled according to their F-moisture value (Fig. 3b), pH-value (when measured) (Fig. 3c), habitat type (Fig. 3d) and bryophyte species (Fig. 3e).

The *C. dubium* assemblage groups were all samples with relatively high F-moisture values (low moisture content). All samples taken from FVII and FVIII (very dry mosses) are situated in this cluster. Mean pH (6.1 ± 0.1) of this community is slightly acidic (Table 2). Samples from the *C. dubium* assemblage have been taken in standing pools or terrestrial habitats (Fig. 3d), where bryophyte species *S. uncinata* (Hedw.) Loeske and liverwort *J. grandiflora* (Lindenb. and Gott.) Steph. were frequently observed (Fig. 2e). Other characteristic taxa in the *C. dubium* assemblage are *Assulina muscorum* Greeff, *A.* sp. 1, *Cryptodifflugia compressa* Penard, *C. aerophila* Deflandre, *C. aerophila* var. *sphagnicola* Deflandre, *D. oviformis* var. *fusca* (Penard) Bonnet and

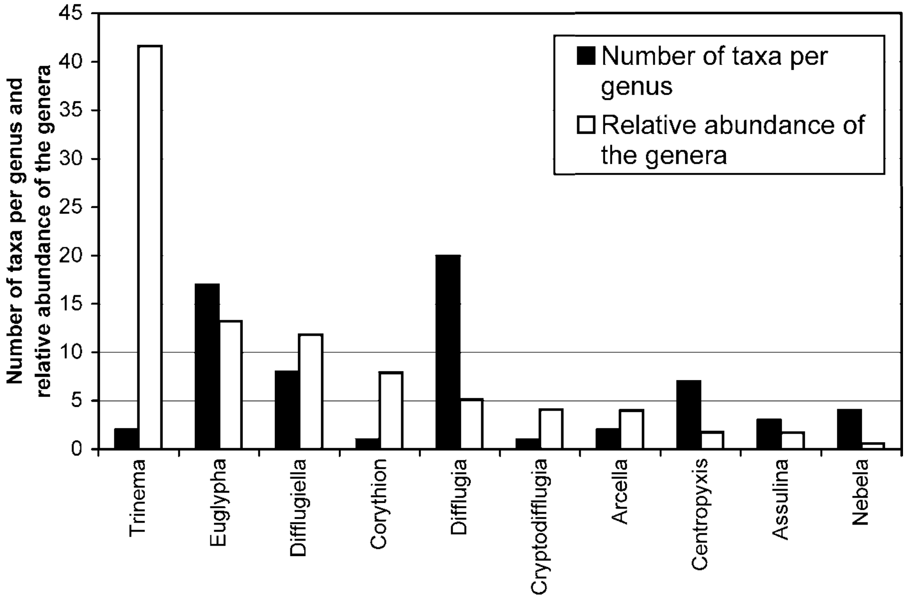

Fig. 2 The number of taxa per genus and the relative abundance of the different genera

Fig. 3a–e Correspondence analysis (*CA*): **a** CA-diagram showing clusters and most important testate amoebae taxa; **b** CA-diagram presenting moisture values (F-values) of the samples; **c** CA-diagram showing the pH of the samples (when measured); **d** CA-diagram showing the habitat type were the samples were taken; **e** CA-diagram representing the bryophyte flora of the samples. Taxon codes are explained in the Appendix

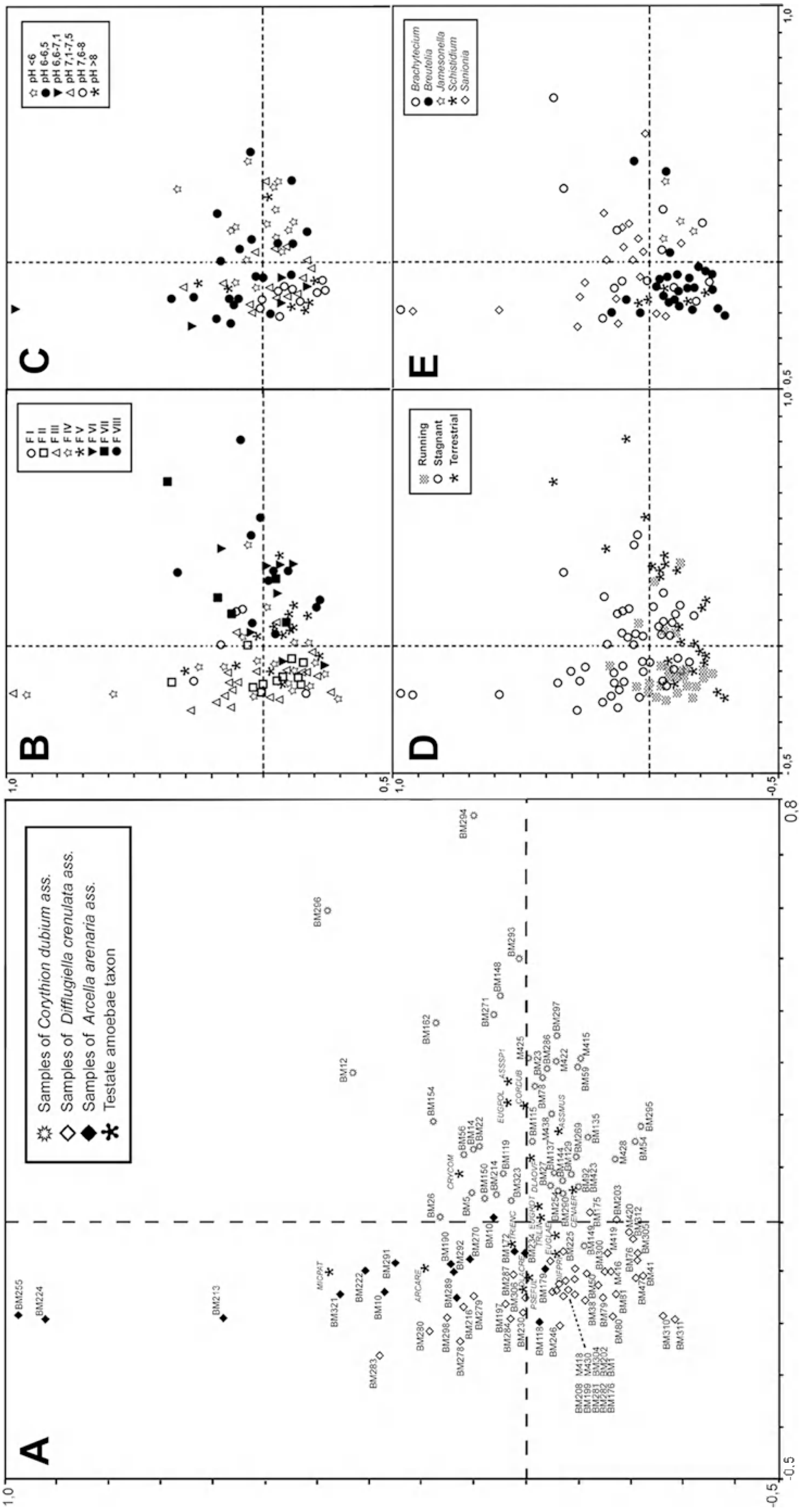

Table 2 Overview of the main characteristics of the three assemblages

	Corythion dubium assemblage	*Difflugiella crenulata* assemblage	*Arcella arenaria* assemblage
Number of samples	42	41	16
Number of species	58	73	46
Mean S.-W. diversity	0.76 ± 0.02	0.87 ± 0.02	0.72 ± 0.03
Mean gini evenness measure	0.36 ± 0.01	0.36 ± 0.01	0.34 ± 0.02
Mean species richness	13.7 ± 0.6	17.1 ± 0.5	12.4 ± 0.8
Mean F-value	Between V and VI	Between III and IV	Between III and IV
Mean pH	6.1 ± 0.1	7.3 ± 0.1	6.9 ± 0.4
Frequency of appearance in samples (%) × relative abundance in these samples (%)			
Arcella arenaria	43 × 2	49 × 6	100 × 15
Assulina muscorum	60 × 4	24 × 1	6 × 1
A. sp1	33 × 4	2 × 1	6 × 1
Centropyxis aerophila	29 × 10	49 × 2	0 × 0
C. aerophila var. *sphagnicola*	5 × 5	0 × 0	0 × 0
Corythion dubium	95 × 19	37 × 1	38 × 2
Cryptodifflugia compressa	74 × 10	27 × 2	88 × 5
Difflugia bryophila	0 × 0	22 × 1	0 × 0
D. pristis	40 × 2	78 × 3	44 × 2
Difflugiella crenulata	14 × 1	98 × 19	75 × 9
D. oviformis var. *fusca*	26 × 7	12 × 1	19 × 2
Genus *Difflugia*	64 × 3	98 × 9	81 × 6
Euglypha ciliata	21 × 4	2 × 1	0 × 0
E. ciliata var. *glabra*	14 × 5	0 × 0	0 × 0
E. laevis	67 × 6	98 × 7	81 × 3
E. polylepis	48 × 3	5 × 1	13 × 1
E. rotunda	93 × 7	90 × 6	56 × 4
E. strigosa	31 × 4	2 × 1	0 × 0
Heleopera sylvatica	19 × 2	7 × 1	6 × 1
Microchlamys patella	17 × 3	24 × 2	44 × 16
Pseudodifflugia fulva	29 × 2	76 × 5	56 × 4
Tracheleuglypha dentata	36 × 10	37 × 1	19 × 4
Trinema enchelys	81 × 9	100 × 11	100 × 26
T. lineare	100 × 30	100 × 33	100 × 22

Thomas, *E. polylepis* Bonnet and Thomas, *E. strigosa* Leidy, *E. ciliata* (Ehrenberg) Penard, *E. ciliata* var. *glabra* Wailes and Heleopera sylvatica Penard.

The *D. crenulata* assemblage has an F-value between III and IV, thereby indicating wetter moss samples and habitats compared to the *C. dubium* assemblage. Most samples with moisture values FI and FII (aquatic moss samples) are located in this cluster. The majority of the samples from the *D. crenulata* community have been taken from rivers and brooklets (Fig. 3d) with a mean circumneutral pH of 7.3 ± 0.1. The testacean fauna of this assemblage mainly inhabits *Breutelia* and *Schistidium* mosses (Fig. 3e) growing in running waters. The rather diverse *D. crenulata* community is also characterised by the testate amoeba taxon *Pseudodifflugia fulva* Penard and all observed taxa of the genus *Difflugia*, in particular *D. pristis* Penard and *D. bryophila* Jung.

The *A. arenaria* assemblage has an F-value between III and IV, and a mean pH of 6.9. A co-dominant taxon in this assemblage is *Microchlamys patella* (Claparede and Lachmann) Cockerell. Both *A. arenaria* and *M. patella* seem to prefer mosses growing in stagnant pools (Fig. 3d).

Testate amoebae taxa such as *T. lineare*, *T. enchelys*, *E. rotunda* Wailes, *E. laevis* Perty and *D. oviformis* Bonnet and Thomas are situated in the centre of the CA-diagram (Fig. 3a) and appear abundantly in all three assemblages (Table 2). These ubiquitous taxa do not seem to be selected for a particular pH or moisture content in a certain habitat, although *T. enchelys* appears to have a slight preference for wetter mosses.

The separation between the *C. dubium* assemblage on one hand and the *A. arenaria* and *D. crenulata* assemblages on the other hand is primarily based on the humidity (F-values) of the samples. The β-diversity along the moisture gradient (Fig. 4) shows an increased turnover rate at the transition from mosses with moisture values FIV–FV or from rather wet mosses to rather dry mosses, which emphasises again the importance of moisture in determining species composition.

Globally, turnover rates are relatively low, indicating the influence of other environmental variables on the distribution pattern of the testacean moss fauna. To define whether the presence of a testate rhizopod was also influenced by the habitat type, by the specific bryophyte flora or by both parameters, a logistic regression was carried out. For the majority of selected taxa, habitat type, bryophyte species and the interaction habitat × bryophyte, appeared highly significant (χ^2; $p < 0.0001$). This means that both parameters, and especially their interaction, contribute significantly to the distribution pattern of the majority of the tested taxa.

Figure 5 shows the proportion of some testate amoebae taxa for each habitat and each bryophyte flora, and indicates also the significance level of the tested independent variables.

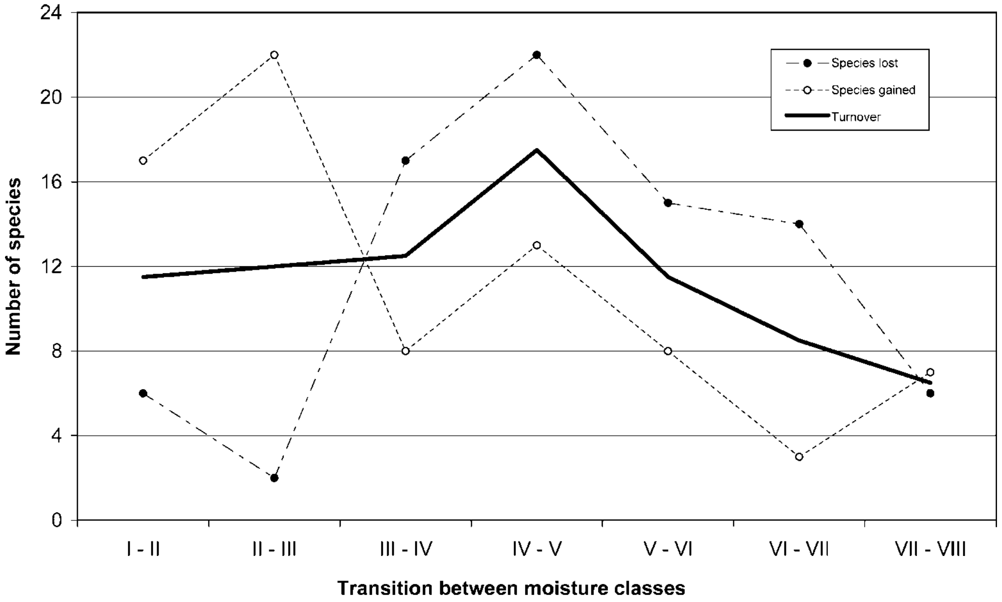

Fig. 4 Turnover rates (or β-diversity) along the moisture gradient (*thick black line*). With each transition to a higher moisture class, the number of species that are lost (*filled circle*) or gained (*open circle*) are shown

WA bryophyte inference models

Considering the importance of moisture for the moss dwelling testacean fauna, the relationship between testate amoebae communities and bryophyte moisture provides a good basis for the construction of a transfer function for the F-values.

Weighted averaging (WA) regression and calibration models are widely used in paleo-ecological studies for quantitative reconstruction of past environmental conditions. Several sets of WA models were developed to infer moss moisture values (Fig. 6, Table 3). There was no clear difference between the tested WA models in terms of correlation between observed versus inferred F-value, nor in terms of RMSE of prediction within the training set.

The apparent RMSE for the F-value calibrations is 1.17 (F-value) using classical deshrinking and 0.96 (F-value) using inverse deshrinking. Although WA calibration using inverse deshrinking seems to produce lower RMSE of prediction and higher correlation values as compared to classical deshrinking, it tends to underestimate values at the high end of the F-value gradient, displaying a significant trend in the residuals ($r^2 = 0.563$; $p < 0.001$; $df = 80$; $n = 82$). Classical deshrinking did not produce this significant trend ($r^2 = 0.001$; $p > 0.05$; $df = 80$; $n = 82$). Therefore, classical deshrinking provides the most reliable inferences of bryophyte moisture values.

To develop robust and reliable WA inference models, realistic optima of testate amoebae taxa must be estimated along the F-value gradient. To assess the ecological reliability of the optima, a comparison of goodness of fit (i.e. r^2 and RMSE of prediction) between observed versus WA-inferred estimates with and without bootstrapping was made. If the goodness-of-fit between observed and inferred values is much weaker when estimated using bootstrapping, the species optima are not clearly defined by WA techniques (Hall and Smol 1996). Table 3 summarises the data.

The used calibration set reliably estimated optima of the testate amoebae taxa along a moisture gradient (expressed by the F-value) as indicated by the relatively small differences between correlations (0.68 vs 0.63) and root mean square errors (1.17 vs 1.22) derived from WA models constructed with and without bootstrapping. Based all these results, we consider the $\mathrm{WA}_{\mathrm{boot}}$ model as our best testate amoebae F-value inference model. Since in the bootstrapping procedure, the r^2_{boot} of the tolerance down-weighted models (Table 3) are somewhat lower than the r^2, it is not considered appropriate to choose this model as being the most reliable.

In general, the testate amoebae inference model provides a relatively close estimate of the observed bryophyte moisture value. The model is accurate to within ±1 F-value on the basis of the $\mathrm{RMSE}_{\mathrm{boot}}$. This model provides a good basis for realistic error estimates of past moisture values reconstructions of the terrestrial bryophyte vegetation on Île de la Possession. Table 4 lists estimates of WA F-value optima and tolerances for the most common testate amoebae taxa and their effective number of occurrences (cf. Hill's N2: ter Braak 1990). Classical deshrinking regression equation is as follows for the bryophyte moisture: $y = 0.33x + 3.3$.

Discussion

The moss dwelling testate amoebae fauna on Île de la Possession is dominated by testacean taxa that are best adapted to the sub-Antarctic environment, such as *T. lineare*. *T. enchelys*, *E. rotunda* and *E. laevis*. These cosmopolitan species were also abundantly present in the aquatic habitats (Vincke et al. 2004b) and soils (Vincke et al. 2004a) on Île de la Possession.

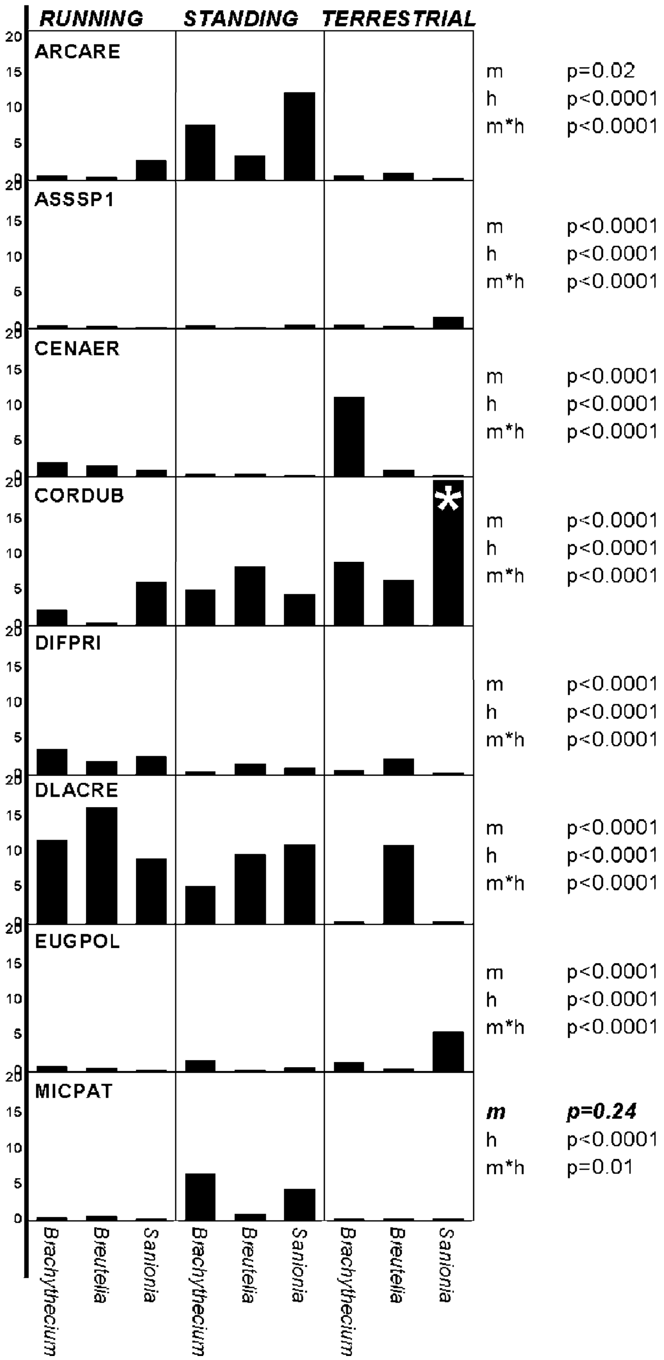

Fig. 5 Proportion (%) of some testate amoebae taxa per habitat (Running–Standing–Terrestrial) and per bryophyte flora (*Brachytecium–Breutelia–Sanionia*). The significance level of the tested independent variables are indicated with *m* moss, *h* habitat and *m* × *h* interaction between moss and habitat. The ☆ mark with *C. dubium* indicates that its proportion is 71.7%. Taxon codes are explained in the Appendix

Species richness of moss inhabiting testate amoebae is rather high compared to other sub-Antarctic islands [Marion Island: 53 taxa in 12 samples (Grospietsch 1971); Kerguelen Archipelago: 50 taxa in 53 samples (Bonnet 1981)]. Whether these dissimilarities are due to artefacts of sampling (methods and intensity), due to a better taxonomic resolution or due to real ecological differences between these island groups, will be determined in a later phase of this research when a complete biogeographical zonation of the testate amoebae fauna in the sub-Antarctic region can be given.

The trend of decreasing species richness towards the South Pole in the southern hemisphere (Smith 1982) is reaffirmed for the moss dwelling testacean fauna: 83 taxa on Île de la Possession versus 26 taxa in mosses on the Antarctic continent (Smith 1992).

Warner (1987) found an increase in species diversity with an increase of the moisture content of the habitat. Leaving the aquatic moss samples (FI and FII) aside, Warner's theory was confirmed in this study. Species diversity was highest in moss samples with FIII moisture values and decreased towards FVIII mosses. It needs to be mentioned that F-moisture values only become important when moisture is the limiting factor. FI and FII mosses are submerged and floating mosses taken from rivers and brooklets, where moisture conditions are rather stable and therefore never the limiting factor. The lower diversity of aquatic moss samples (FI and FII) is explained by the floating away of many testate rhizopods with the drift of the current. The same observation has been made by Schönborn (1981, 1982, 1992), who stated that testate amoebae contribute insignificantly to the flow of energy and the cycling of nutrients in running waters.

The key role of moisture, in determining the distribution pattern of testacean communities, reaffirms previous work on testate amoebae (Charman and Warner 1992; Mitchell 1999; Tolonen et al. 1994; Warner 1987; Warner and Charman 1994). However, pH was only a secondary factor affecting the species assemblages. Similar results were found by Charman and Warner (1992).

The three different assemblages in this study each define a specific ecological environment. The *C. dubium* assemblage was found in a drier, slightly acidic, terrestrial moss vegetation. *C. dubium* has frequently been reported as an indicator taxon of drier acidic moss habitats (Beyens et al. 1986, 1990, 1992; Opravilova and Zahradkova 2003; Tolonen et al. 1994; Van Kerckvoorde et al. 2000). Moreover, *A. muscorum* is generally regarded as an acidophilous species with xerophilous tendencies (Beyens et al. 1986, 1990; Tolonen 1986). On the neighbouring Kerguelen Islands, *A. muscorum* was characteristic for "mousses squelettiques" (Bonnet 1981), mosses with a mean moisture content of about 50% (i.e. FVII–FVIII) growing on lithosols.

The testate rhizopods of the *D. crenulata* and the *A. arenaria* assemblages were characteristic for wetter (circumneutral) habitats. The *D. crenulata* community typified submerged mosses growing in running waters, while the *A. arenaria* assemblage seemed to prefer mosses in standing pools. Genera such as *Difflugia* (most abundant in the *D. crenulata* assemblage) and are more restricted to the aquatic environment. Many *Difflugia* taxa were found in the aquatic habitats of South

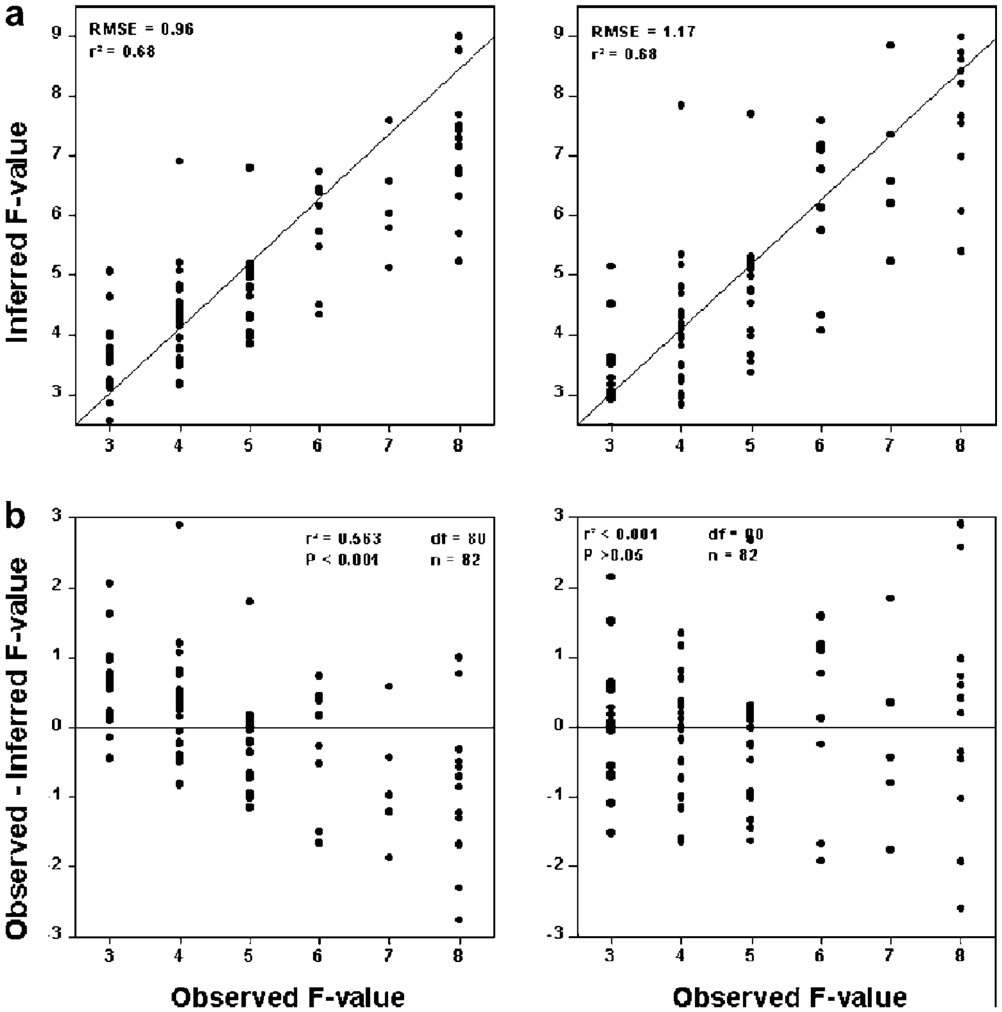

Fig. 6a, b Relationships between observed and inferred F-values (*up*) and observed versus residual F-value (*bottom*) in the training set for: **a** WA model with inverse deshrinking; **b** WA model with classical deshrinking. The *diagonal lines* in (**a**) represent 1:1 lines

Georgia (Beyens et al. 1995) and were also commonly observed in the freshwater habitats from the temperate and boreal zones in the northern hemisphere (Schönborn 1966). Smith (1992) classified *D. lucida* and *D. pulex* as hydrophylic species, associated with mosses and algae in less acid meltwater streams. Both species were most abundantly observed in circumneutral rivers and brooklets on Île de la Possession.

Many testate amoebae showed a preference for a certain habitat and/or a specific bryophyte species. However, the moss preference of the testacean fauna should be treated with caution. The moisture regime of a habitat does not only influence the distribution pattern of the testate rhizopods, but it is also the major determinant of the vegetation. Frenot (1986) stated that some bryophyte species were good indicators of the hydrological state of the soil, with, e.g., *B. integrifolia* (Tayl.) Jaeg. typically present in very wet environments, on the edge of lakes and rivers. Gremmen (1981) described a *Bryum laevigatum–B. integrifolia* association found in the water tracks in the mires on Marion Island. Hygrophytic bryophyte species of the genus *Schistidium* occur particularly by waterfalls (Longton 1988). On the contrary, *S. uncinata* (Hedw.) Loeske, one of the most common moss species in Antarctica (Putzke and Pereira 2001), prefers less humid environments (Frenot 1986). The abundance of this bryophyte species increases with the successional terrestrialisation process of pools (Gremmen 1981). Very often it is associated with the liverwort *J. grandiflora* (Lindenb. and Gott.) Steph. (Gremmen 1981).

Table 3 Correlation (r^2) and RMSE of prediction for the different WA methods

Method	Deshrinking	r^2	RMSE	r^2_{boot}	$\text{RMSE}_{\text{boot}}$
WA	Inverse	0.68	1.0	0.62	1.1
	Classical	0.68	1.2	0.63	1.2
WA_{boot}	Inverse	0.68	1.0	0.60	1.1
	Classical	0.68	1.2	0.61	1.2

In this study, *Breutelia* and *Schistidium* mosses have indeed been found in very wet environments, whereas *Sanionia* and *Jamesoniella* mosses were typical for rather dry, terrestrial habitats, as indicated by the CA-diagram. The relationship between testate amoebae assemblages

Table 4 Effective number of occurrence (Hill's N2), WA optima and tolerances of all taxa observed in ten or more samples from the training set. Taxon codes are explained in the Appendix

Taxon	Optimum	Tolerance	N2
DIFSP6	3.39	0.62	8.7
PSEFUL	3.44	0.78	17.6
DLACRE	3.57	0.74	27.2
EUGSP4	3.58	1.03	5.4
DIFPUL	3.62	1.07	12.6
ARCARE	3.78	1.02	16.8
MICPAT	3.78	1.10	5.1
CYPSP1	3.98	0.94	19.1
DIFGUS	4.04	1.06	7.2
EDACAM	4.10	1.05	10.5
DIFSP3	4.17	1.14	11.7
TRIENC	4.29	1.41	43.6
DLAOVI	4.37	1.28	19.9
EUGCRI	4.42	1.27	17.9
DIFPRI	4.45	1.64	24.0
DIFTEN	4.46	1.65	7.1
EUGLAE	4.57	1.28	41.9
TRILIN	4.78	1.56	63.5
EUGTUB	4.86	1.74	11.5
EUGROT	4.98	1.54	36.4
NEBVAS	4.99	1.31	4.7
TRACOR	5.24	1.61	23.5
ASSMUS	5.31	1.36	14.5
EUGSTR	5.59	1.69	4.9
HELPET	5.82	1.61	5.1
CRYCOM	6.19	1.81	11.8
ASSSP1	6.21	0.86	3.2
DLAOVF	6.27	1.39	2.6
CORDUB	6.44	1.67	19.3
TRADEN	6.88	1.75	6.8
EUGPOL	6.96	1.42	11.0
CENAER	7.15	2.06	4.0
EUGCIL	7.42	1.40	5.3

and bryophyte species does not necessarily imply a direct ecological link between the two types of organisms, but is explained by the fact that the moisture conditions of the environment primarily define the niches of the bryophyte species (Charman and Warner 1992). Therefore, it is not surprising that the interaction between habitat type and moss species has always been found significant in determining testacean distribution patterns. Nevertheless, the significant relationship between testate amoebae assemblages and the habitat × moss interaction will enhance the effectiveness and quality of further paleo-ecological studies, particularly of those based on a multiproxy approach. It will then be possible to link independent signals from both testate amoebae and mosses in fossil peat cores in a more appropriate way.

To study the direct relationship between testate amoebae assemblages and different bryophytes, the habitat type should remain constant. Most likely, specific characteristics of a bryophyte species (e.g. the branching degree of the moss, the angle of inclination of the leaves on the stem, age of the leaves) determine well-defined testacean communities. More attention will be given to the specific relationship between testate rhizopods assemblages and bryophyte species during future sampling programmes on Île de la Possession.

The significance of the habitat type in determining the distribution pattern of testacean taxa cannot be doubted, however. Metcalfe (1988) stated that when the chemistry varies little between sampling sites, the effect of the habitat structure should be emphasised. Indeed, there were only small differences in chemistry between the *D. crenulata* and *A. arenaria* assemblages (both circumneutral pH-values and moisture values around FIII), but the first community seemed to prefer running waters, while the latter one preferred standing pools. Previous studies already recognised the role of the physical habitat as an important factor in determining species composition of testate amoebae (Beyens et al. 1995), tardigrades (Dastych 1988; Kinchin 1994), rotifers (Jersabek 1995; Pejler 1995) and diatoms (Van de Vijver and Beyens 1999; Van de Vijver et al. 2001).

Considering the importance of the habitat's moisture regime in determining the distribution pattern of the testacean fauna, a transfer function for moisture (F-values) can provide a useful tool in later paleo-ecological research. Previous studies have used transfer functions to assess the relationships between testate amoebae and water tables (e.g. Warner and Charman 1994; Woodland et al. 1998).

Since moisture preference data for moss-inhabiting testate amoebae are scarce, it is difficult to test the effectiveness of our model with data of other studies. It is, however, possible to assess the optima of certain testate amoebae taxa. *H. sylvatica* Penard and *C. dubium* (optimum around FVI) have been reported earlier to be restricted to drier mosses (Jung 1936; Meisterfeld 1977). On the other hand, *A. arenaria* and *D. pristis*, present in the wetter samples (F-value optimum below FV), are known to be present in the wetter parts of the soils (Warner and Charman 1994; Woodland et al. 1998). Species that normally prefer intermediate conditions, such as *E. strigosa*, produce intermediate moisture values (optimum around FV) (Charman et al. 2000). These comparisons confirm the usefulness of the inferred model.

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Appendix

List of all observed testate amoebae taxa, including abbreviations used in text and figures. The taxon's frequency of appearance (%) is also added

ARCARE	*Arcella arenaria* Greeff	3.99
ARCDIS	*Arcella discoides* Ehrenberg	0.01
ARCHS1	*Archerella* sp1	0.08
ASSMUS	*Assulina muscorum* Greeff	1.06
ASSSEM	*Assulina seminulum* Penard	0.03
ASSSP1	*Assulina* sp1	0.63
CENACT	*Centropyxis aculeata* Stein	0.01
CENAER	*Centropyxis aerophila* Deflandre	1.55
CENASP	*Centropyxis aerophila* vas *sphagnicola* Deflandre	0.11
CENASY	*Centropyxis aerophila* vas *sylvatica* Deflandre	0.05
CENCAS	*Centropyxis cassis* Deflandre	0.01
CENDEF	*Centropyxis deflandriana* Bonnet	0.01
CENHIR	*Centropyxis hirsuta* Deflandre	0.01
CORDUB	*Corythion dubium* Taranek	7.89
CRYCOM	*Cryptodifflugia compressa* Penard	4.08
CYCSP1	*Cyclopyxis* sp1	0.05
CYCSP2	*Cyclopyxis* sp2	0.01
CYPSP1	*Cyphoderia* sp1	0.95
DIFAMP	*Difflugia ampullula* Playfair	0.01
DIFBAC	*Difflugia bacillifera* Penard	0.07
DIFBRY	*Difflugia bryophila* Jung	0.11
DIFCLU	*Difflugia* cfr. *lucida*	0.01
DIFGLA	*Difflugia globulosa* Dujardin	0.08
DIFGLO	*Difflugia globulus* Hopkinson	0.28
DIFLUC	*Difflugia lucida* Penard	0.14
DIFMIN	*Difflugia minutissima* Penard	0.02
DIFPRI	*Difflugia pristis* Penard	1.31
DIFPUL	*Difflugia pulex* Penard	0.73
DIFSP3	*Difflugia* sp3	0.10
DIFSP4	*Difflugia* sp4	0.02
DIFSP5	*Difflugia* sp5	0.48
DIFSP6	*Difflugia* sp6	0.01
DIFSP7	*Difflugia* sp7	0.01
DIFSP8	*Difflugia* sp8	1.15
DIFSP9	*Difflugia* sp9	0.09
DIFSP10	*Difflugia* sp10	0.01
DIFSP11	*Difflugia* sp11	0.07
DIFTEN	*Difflugia tenuis* (Penard) Chardez	0.42
DLACRE	*Difflugiella crenulata* Playfair	8.79
DLACRG	*Difflugiella crenulata* var. *globosa* Playfair	0.04
DLAMIN	*Difflugiella minuta* Playfair	0.05
DLAOVI	*Difflugiella oviformis* (Penard) Bonnet and Thomas	1.91
DLAOVF	*Difflugiella oviformis* var. *fusca* (Penard) Bonnet and Thomas	0.94
DLAPUS	*Difflugiella pusilla* Playfair	0.04
DLASAC	*Difflugiella sacculus* (Penard) Deflandre	0.03
DLASP3	*Difflugiella* sp3	0.03
EDACAM	*Edaphonobiotus campascoides* Schönborn. Foissner and Meisterfeld	0.18
EUGBRY	*Euglypha bryophila* Brown	0.01
EUGCIL	*Euglypha ciliata* (Ehrenberg) Perty	0.35
EUGCIG	*Euglypha ciliata* var. *glabra* Wailes	0.30
EUGCOM	*Euglypha compressa* Carter	0.05
EUGCOG	*Euglypha compressa* var. *glabra* Cash	0.03
EUGCRI	*Euglypha cristata* Leidy	0.38
EUGFIL	*Euglypha filifera* Penard	0.32
EUGLAE	*Euglypha laevis* Perty	0.03
EUGPOL	*Euglypha polylepis* Bonnet	4.78
EUGROT	*Euglypha rotunda* Wailes	0.59
EUGSP1	*Euglypha* sp1	5.44
EUGSP2	*Euglypha* sp2	0.01
EUGSP3	*Euglypha* sp3	0.12
EUGSP4	*Euglypha* sp4	0.01
EUGSTR	*Euglypha strigosa* Leidy	0.56
EUGTUB	*Euglypha tuberculata* Dujardin	0.16
EUGTUM	*Euglypha tuberculata* var. *minor* Taranek	0.01
HELSYL	*Heleopera sylvatica* Penard	0.20
HYASP1	*Hyalosphenia* sp1	0.06
HYASP2	*Hyalosphenia* sp2	0.03
HYASP3	*Hyalosphenia* sp3	0.02
HYASP4	*Hyalosphenia* sp4	0.01
MICPAT	*Microchlamys patella* (Claparede and Lachmann) Cockerell	1.58
NEBDEN	*Nebela dentistoma* Penard	0.07

NEBTUB	*Nebela tubulata* Brown	0.03
NEBVAS	*Nebela vas* Certes	0.46
NEBWAI	*Nebela wailesi* Deflandre	0.04
PARIRR	*Paraquadrula irregularis* Deflandre	0.13
PHRPAR	*Phryganella paradoxa* Penard	0.02
PSEFUL	*Pseudodifflugia fulva* Penard	2.07
PSEGRA	*Pseudodifflugia gracilis* Schlumberger	0.04
TRAACO	*Tracheleuglypha acolla* Bonnet and Thomas	0.02
TRADEN	*Tracheleuglypha dentata* (Vejdovsky) Deflandre	1.87
TRACOR	*Trachelocorythion pulchellum* (Penard) Bonnet	0.96
TRIENC	*Trinema enchelys* Leidy	11.79
TRILIN	*Trinema lineare* Penard	29.79

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