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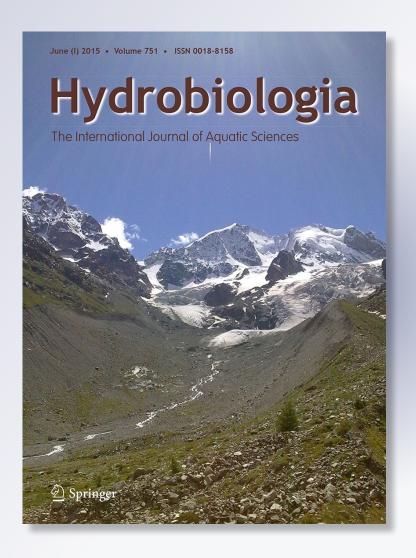
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PRIMARY RESEARCH PAPER

Landscape-driven environmental variability largely determines abiotic characteristics and phytoplankton patterns in peat bog pools (Tierra del Fuego, Argentina)

Gabriela Mataloni · Gabriela González Garraza · Alicia Vinocur

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Abstract Ombrotrophic peat bogs from Tierra del Fuego are characteristically raised, dome-shaped, fed by precipitation, and nutrient-poor. Their landscape pattern consists of a *Sphagnum magellanicum* matrix encompassing pools with different morphometric and trophic features. Within the framework of a 2-year limnological survey in five pools from Rancho Hambre peat bog, we analyzed phytoplankton communities under the hypothesis that taxonomic composition would show a spatial pattern driven by ultimately landscape-controlled environmental features such as

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Departamento de Biodiversidad y Biología Experimental, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, 1428 Buenos Aires, Argentina pH and trophic status, while temperature and weatherdependent features would account for seasonal changes in abundance and structure. Among the 305 taxa recorded, most were Conjugatophyceae and Bacillariophyceae, and were strongly associated to circumneutral pH and minerotrophic conditions, though limited superficial connectivity among pools accounted for dissimilar taxonomic compositions. Despite such differences, phytoplankton of pools with similar morphometry and trophic status showed similar dominant and richest taxonomic groups undergoing paralell changes over time. Seasonal temperature fluctuations were modulated by pool size and modified not only abiotic properties but also phytoplankton abundance, with different taxa showing strong summer peaks in different pools. An interpretative model is proposed which will be tested as a tool for predicting community strategy and temporal variation patterns as responses to different environmental templates.

Keywords Phytoplankton structure · Peat bog pools · Wetlands · Landscape · Interpretative model · Limnological characterization

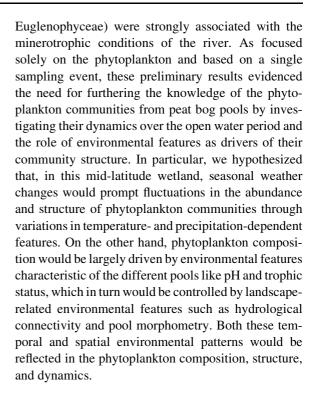
Introduction

Among wetland types, peatlands are globally relevant for both researchers and environmental managers due to their extension (3% of the total Earth surface) and high holding capacity of soil carbon and freshwater



(about one third and 10% of the total of the planet, respectively) (Joosten & Clarke, 2002). These characteristics arise from the accumulation of slowly decomposing organic matter (peat) under climatic conditions which favor waterlogging, mostly low temperatures and abundant, evenly distributed precipitation. Inside peatlands, mires are areas where peat is actively being accumulated resulting in raised, domeshaped peat bogs, fed by precipitation, and consequently very nutrient-poor (ombrotrophic) (Roig & Roig, 2004). The typical landscape pattern of such a peat bog consists of a matrix of terrestrial vegetation usually dominated by Sphagnum mosses encompassing patches of shallow, acid, humic water bodies. These display a range of abiotic features, from minerotrophic pools with slightly acidic, harder waters partially delivered by ground water to ombrotrophic pools with acidic, softer waters, fed only by precipitation and long submitted to the cation exchange action of Sphagnum plants, which take up base cations and liberate protons (Clymo, 1964).

While only 4% of peatlands are located in South America (Parish et al., 2008), the island of Tierra del Fuego encompasses the southernmost area of extensive peatland development (Lindsay et al., 1988). Peatlands cover 2,700 km², 12.5% of the total surface of Argentinean Tierra del Fuego province (Iturraspe, 2010), thereby constituting a key regulator of its hydrological resources. Rancho Hambre (54°47'S, 68°19'W) is a typical Sphagnum-dominated ombrotrophic peat bog (Roig & Roig, 2004) located among the ridges of the Andes in the Tierra Mayor Valley, about 50 km from Ushuaia City. Its domed central area is surrounded by a peripheral drainage network composed of two streams that flow into Lasifashaj River (Grootjans et al., 2010). The phytoplankton communities of the river and five pools (water hollows) were first studied by Mataloni & Tell (1996). Remarkable differences concerning abiotic features and phytoplankton structure evidenced the lack of connection among the river and the pools. These in turn differed in their phytoplankton structure, with pools of different sizes showing distinct taxonomic compositions and larger pools showing higher species richness. Surprisingly, Cyanobacteria—mainly Chroococcales—not only showed many species but also dominated two of the water hollows, and their abundance was negatively correlated with pH, while other groups of minor relevance in these environments (Tribophyceae,



Materials and methods

Field data acquisition and laboratory analyses

Five pools located along a transect crossing the dome of Rancho Hambre peat bog were selected to represent different morphometric features (Fig. 1; Table 1). Between October 2008 and April 2010, all were sampled on eight occasions during the annual ice-free period (October-April). One to four sampling sites were selected for limnological characterisation within each water body, according to its size. As RH1, RH2, and RH4 were large, deep water bodies, three sampling points (shore, water surface, and bottom) were established in RH1 and RH2, and four points (north and south shores, water surface, and bottom) in the largest RH4, while shallow (depth <50 cm), small (area <1,000 m²) pools RH3 and RH5 were only sampled from the shore. Field observations showed that the bog dome was divided into small catchments by lengths of Sphagnum hummocks colonized by lichens, vascular plants, and Nothofagus saplings. Among the pools studied, only RH1 and RH4 had superficial inflows and/or outflows, while the other evidenced the lack of subsurface connection through different heights of water level in



Fig. 1 Map of Rancho Hambre, showing the five pools studied (after González Garraza et al., 2012)

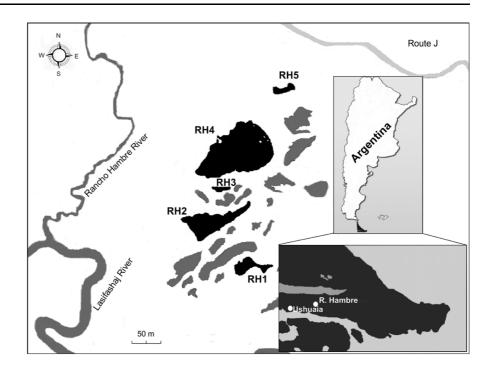


Table 1 Morphometric and abiotic features of the pools studied

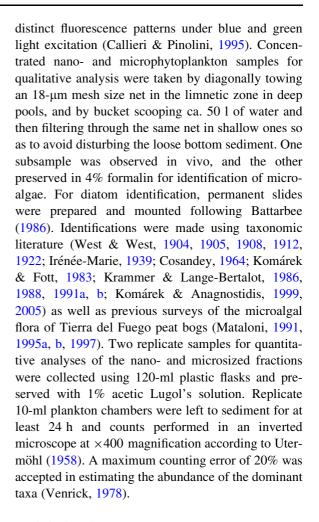
Pool	RH1	RH2	RH3	RH4	RH5
Latitude (S)	54°44′52.87″	54°44′48.61″	54°44′46.75″	54°44′41.51″	54°44′39.35″
Longitude (W)	67°49′29.44″	67°49′31.66″	67°49′31.69″	67°49′31.69″	67°49′26.7″
Maximum length (m)	81.9	162.9	50.7	195.7	34.5
Maximum width (m)	28.5	66.2	10.5	122.9	12.7
Maximum depth (cm)	95	150	33	150	33
Water temperature (°C)	8.8 (2.2–17.3)	8.6 (1.1–17.0)	11.8 (3.2–25.0)	8.5 (2.4–15.0)	10.6 (1.7-20.0)
pН	5.7 (5.0-7.1)	4.5 (3.8–5.5)	4.5 (3.6–5.4)	6.3 (5.8–7.0)	4.6 (4.1–5.4)
Electric conductivity (EC) (μS cm ⁻¹)	23.6 (13.6–50.0)	22.8 (8.7–40.0)	33.1 (10.0–82.0)	29.8 (16.0–60.0)	25.6(5.5–50.0)
Dissolved oxygen (mg l ⁻¹)	10.5 (8.2–14.0)	11.3 (7.6–14.4)	10.4 (8.7–12.9)	10.6 (7.6–12.2)	9.9 (8.6–11.5)
Oxygen saturation (%)	93 (65–114)	101 (63–135)	100 (73–134)	94 (63–118)	93 (71–112)
Suspended solids (mg l ⁻¹)	2.1 (0.7–3.7)	2.5 (0.9-8.3)	5.5 (0.4–20)	6.1 (1.6-23.9)	4.1 (0.3–10.9)
DIN ($\mu g l^{-1}$)	46 (7–102)	53 (7–239)	55 (10–103)	44 (19–107)	36 (0-73)
TN (μ g I^{-1})	5,317 (1,430–10,100)	6,293 (1,980–12,870)	7,305 (1,980–11,330)	6,859 (1,073–26,000)	9,479 (3,410–30,000)
PO_4 -P (µg 1^{-1})	62 (27–93)	58 (23–157)	61 (30–130)	34 (10-60)	31 (20–50)
TP (μ g l ⁻¹)	206 (113-477)	172 (92–330)	169 (90–308)	164 (88–290)	195 (77–420)
Total hardness (mg equivalent $CaCO_3 l^{-1}$)	25.6 (7–41.4)	24.2 (6.8–46.2)	22 (7.5–43.3)	30.5 (11.0–42.5)	22.3 (10.9–36.4)
DOC (mg 1^{-1})	7.3 (5.4–9.2)	7.5 (5.1–9.0)	10.4 (2.8–13.4)	5.4 (4.4–7.0)	8.4 (3.9–11.6)

For abiotic features, mean values over the sampling period are given together with the value range (between parentheses). Part of this information was published in González Garraza et al. (2012)



neighboring water bodies. The largest, well-connected pool (RH4) showed the least variation in water level over the study period [coefficient of variation (CV) = 7%, while hydrologically isolated RH2 varied most (CV = 29%) (González Garraza et al., 2012). According to these authors, continuous temperature monitoring showed that water of the smallest pool (RH3) had a much wider diurnal temperature variation and reached higher maximum temperatures than its counterpart RH4. Pools RH2, RH3, and RH5 showed their ombrotrophic status through lower, very stable pH values, as demonstrated by ANOVA significant differences for this parameter among minerotrophic (RH1-RH4) and ombrotrophic (RH2-RH3-RH5) pools (P < 0.001). All water bodies were well mixed and consequently well oxygenated throughout the sampling period due to constant, unrestricted wind action (González Garraza et al. 2012).

On the same dates, all planktonic communities were surveyed in order to characterize the entire food web structure of the pools and its variation over the open water period (Quiroga et al., 2013) For this purpose, heterotrophic bacteria and flagellates were quantitatively sampled, and both qualitative and quantitative samples were taken for the analysis of all other planktonic communities (phytoplankton, ciliates, and metazooplankton). Quiroga et al. (2013) give a detailed account of the methods employed for taxonomic identification, enumeration, and biovolume calculation for the different communities. Regarding phytoplankton, samples for chlorophyll a (Chl a) were collected in plastic bottles, filtered onto 0.7-µm pore size fiberglass filters (Whatman GF/F) and preserved at -20° C. Photosynthetic pigments were extracted with hot ethanol (60–70°C). Chlorophyll a concentrations corrected for phaeopigments were measured with a spectrophotometer and calculated following the equations given in Marker et al. (1980). For picophytoplankton enumeration, water samples were collected using 120-ml plastic flasks and fixed in situ with 2% glutaraldehyde. Subsamples (2-5 ml) were filtered onto 0.22-µm pore size black polycarbonate filters according to Porter & Feig (1980). Filters were mounted on a microscope slide with fluorescence-apt immersion oil. Counts of this fraction were performed using an epifluorescence microscope (Olympus BX40F4, Tokyo, Japan) at ×1,000 magnification; pico-sized pigmented prokaryotic and eukaryotic cells (Pcy and Peuk, respectively) were identified by



Statistical analyses

For each large pool, no significant differences between sampling points were revealed for any abiotic variable or phytoplankton descriptor (abundance, species richness, diversity, and chlorophyll a) through randomized complete block MANOVA employing sampling dates as blocks and sites of the pool as fixed effects factors, as well as individual randomized block model III twofactor ANOVA without within-cell replication (Zar, 2010). Therefore, sampling points within each large pool were considered as grab samples, and values of all variables averaged per sampling date. The floristic composition of pools on every sampling date were compared by means of a cluster analysis, and a similarity matrix was obtained for their species pools (total floristic list over the sampling period) using Jaccard similarity index (J) (Magurran, 2004). Shannon's diversity values were computed following



Magurran (2004). In order to assess the influence of the different biotic and abiotic factors on the overall diversity, as well as on the abundance and species richness of the different main taxonomic groups of the phytoplankton, a canonical correspondence analysis was performed taking into account all dates using CANOCO 4.5 software (ter Braak & Šmilauer, 1998). For this purpose, taxonomic groups with not more than one species in one given sample were excluded from species richness data, and those not reaching at least 3% relative frequency on one sampling date were excluded from abundance data. As picophytoplankton was solely composed of eukaryotic cells (Peuk), it was regarded as a single group in terms of abundance.

Results

A total number of 305 taxa belonging to the nano + microphytoplankton were recorded from the whole peat bog over the study period. Most of them were green algae (mainly Conjugatophyceae), Bacillariophyceae and Cyanobacteria (Table 2). Among these, the two former showed a much higher species richness in minerotrophic pools. In particular, RH1 had about 50% more species than larger, acidic RH2 (Table 3). On the other hand, just 38 *ubiquitous* taxa, most of them Chroococcales, were recorded in all sites, regardless of environmental differences. Similarity values of the Jaccard index (J) among the species pools (total species list over the study period) of the five water bodies were generally low, with highest values computed for pairs of environmentally similar pools $(J_{\text{RH1-RH4}} \text{ and } J_{\text{RH3-RH5}} = 0.54)$, while the smallest and the largest pools, located just 20 m apart, had the least similar species composition ($J_{RH3-RH4} = 0.31$).

With regard to changes in floristic composition over time, phytoplankton communities were both characteristic and constant in minerotrophic large pools RH1 and RH4, as shown by the clustering of all samples from each of these sites (Fig. 2). On the other hand, samples taken from RH3 in 2009/2010 seem to stand for another core of floristic identity, in which RH5 and RH2 samples joined in at higher linking distances. Dispersion of samples from RH2 showed a high species turnover at this site. Noticeably, although the floristic composition of shallow pools RH3 and RH5 was not highly similar (J = 0.54), their diversity values followed one and the same temporal pattern

over the study period (Fig. 3). Only five out of the ten taxonomic groups recorded met the criterion for inclusion in the analysis of the temporal changes in abundances (Fig. 4). Abundant groups did not coincide with the richest ones, thus excluding both diatoms and desmids. While a general trend toward increasing higher summer abundances was recorded at all sites, during summer 2008–2009 shallow RH3 and RH5 showed unusually high summer peaks of Cryptophyceae and Chrysophyceae.

A canonical correspondence analysis explained 84.7% of the species-environment relation through the two first axes with a high degree of significance (P < 0.002). Temperature and electric conductivity (EC) highly influenced the distribution of samples and phytoplankton descriptors over axis 1 (eigenv.0.79 and 0.72, respectively) thus reflecting temporal changes in environmental conditions, while pH ordinated them over axis 2 (eigenv. 0.50). The positions of samples and phytoplankton descriptors are plotted separately in Fig. 5a and b for clarity. All spring (October) samples are located close together on the left side of the diagram, with those belonging to minerotrophic pools RH1-RH4 showing higher scores on pH-driven axis 2. On the contrary, February samples are closely associated with high temperatures and EC values, particularly in small RH3 and RH5. High summer peaks of cryptophycean Plagioselmis sp. characterize both pools and, together with summer peaks of the chrysophycean *Ochromonas* spp. and the chlorococcalean Kirchneriella microscopica Nyg., result in a negative response of the Shannon-Weaver diversity index to temperature. As expected, minerotrophic pools RH1 and RH4 showed the highest species richness in relation to circumneutral pH values. Also the abundances of Chlorophyta pro parte, Dinophyceae, and Chrysophyceae are associated with a milder pH, while those of Cyanobacteria clearly identify acid pools, mainly RH2. A trial CCA which included the abundances of potential phytoplankton grazers (ciliates and metazooplankton) did not change significantly these results and therefore the model with less explanatory variables was retained. Table 4 compares the limnological characterization of the five water bodies based on key landscape-driven abiotic features together with the structure and temporal fluctuations of their phytoplankton communities. Clear differences among deep, minerotrophic and shalombrotrophic pools distinct result in



Table 2 List of all taxa identified from the phytoplankton in each pool over the study period

Taxa		RH1	RH2	RH3	RH4	RHS
Cyanobacteria						
Alternantia geitleri Schil.	*	•	•	•	•	•
Anabaena sp. 1		•			•	
Anabaena sp. 2		•	•		•	•
Aphanocapsa elachista W. et G. S. West	*	•	•	•	•	•
Aphanocapsa incerta (Lemm.) Cronberg et Kom.	*	•	•	•	•	•
Aphanocapsa planctonica (G. M. Smith) Kom. et Anag.		•		•	•	•
Aphanothece elabens (Bréb.) Elenkin		•		•	•	•
Aphanothece minutissima (W.West) Komárkova-Legnerová et Cronberg		•	•	•		•
Aphanothece nidulans Richter	*	•	•	•	•	•
Aphanothece stagnina (Sprengel) A. Braun	*	•	•	•	•	•
Calothrix sp.					•	
Chroococcus limneticus Lemm.	*	•	•	•	•	•
Chroococcus minimus (Keissler) Lemm.	*	•	•	•	•	•
Chroococcus minor (Kütz.) Näg.		•	•	•		•
Chroococcus minutus (Kütz.) Näg.	*	•	•	•	•	•
Chroococcus turgidus (Kütz.) Näg.	*	•	•	•	•	•
Chroococcus sp.			•	•		•
Cyanodictyon reticulatum (Lemm.) Geitler	*	•	•	•	•	•
Cyanosarcina burmensis (Skuja) Kovacik				•		•
Cyanothece aeruginosa (Näg.) Kom.						•
Cylindrospermum sp.					•	
Eucapsis minor (Skuja) Elenkin	*	•		•	•	
Geitlerinema splendidum (Greville) Anag.					•	
Gloeocapsopsis pleurocapsoides (Novacek) Kom. et Anag.	*			•	•	
Hapalosiphon cf. hibernicus W. et G. S. West		•	•	•	•	•
Leptolyngbya crassior (Skuja) Anag.		•	•	•		
Merismopedia elegans A.Braun	*	•	•		•	
Merismopedia punctata Meyen	*	•	•	•	•	•
Microcystis smithii Kom. et Anag.	*	•	•	•	•	•
	•	•	•	•	•	•
Nostoc sp. Phormidium chlorinum (Kütz.) Anag.		_			•	
Phormidium aff. chlorinum (Kütz.) Anag.		•			•	
		•	_		•	
Phormidium simplicissimum (Gom.) Anag. et Kom. Pseudanabaena catenata Lauterborn		•	•			
Pseudanabaena sp.		•		•	•	•
Rhabdoderma lineare Schmidle et Lauterborn	*	_	_	_	•	_
	*	•	•	•	•	•
Rhabdogloga smithii (P. et F. Chodet) Kom.	74"	•	•	•	•	•
Rhabdogloea smithii (R. et F. Chodat) Kom.	*		_	_	•	•
Rhabdogloea sp.	*	•	•	•	•	•
Scytonema sp.		•				
Bacillariophyceae						
Achnanthes sp.1		•			•	•
Achnanthes sp.2		•			•	



Table 2 continued

Taxa		RH1	RH2	RH3	RH4	RH5
Achnanthidium minutissimum (Kütz.) Czarnecki		•		•	•	•
Brachysira brebissonii Ross		•			•	
Brachysira cf. intermedia (Oestrup) LB.		•	•		•	
Cocconeis placentula var. lineata (Ehr.) V. H.		•	•		•	•
Cymbella cf. heteropleura (Ehr.) Kütz.		•			•	
Cymbopleura naviculiformis Auerswald			•		•	
Encyonema elginense (Krammer) D. G. Mann					•	
Encyonema neogracile Krammer		•	•		•	
Encyonema perpusillum var. chilense Krammer, Rumrich et LBert.		•	•		•	•
Eunotia bilunaris (Ehr.) Mills	*	•	•	•	•	•
Eunotia exigua (Bréb.) Rabenhorst	*	•	•	•	•	•
Eunotia flexuosa (Bréb.) Kütz.		•	•		•	•
Eunotia aff. gracillima (Krasske) Nörpel		•	•		•	
Eunotia intermedia (Krasske) Nörpel et LB.	*	•	•	•	•	•
Eunotia minor (Kütz.) Grun.	*	•	•	•	•	•
Eunotia monodon Ehr.		•	•		•	
Eunotia muscicola Krasske					•	
Eunotia naegelii Migula	*	•	•	•	•	•
Eunotia veneris (Kütz.) De Toni	*	•	•	•	•	•
Fragilaria capucina Desmazieres morpho 1		•			•	
Fragilaria capucina Desmazieres morpho 2		•			•	
Fragilaria exigua Grun.		•			•	
Fragilaria germainii Reichardt et LB.					•	
Frustulia rhomboides var. rhomboides (Ehr.) De Toni		•	•	•	•	
Frustulia rhomboides var. saxonica (Rabenh.) De Toni	*	•	•	•	•	•
Frustulia rhomboides var. saxonica fo. capitata (Mayer) Patrick	*	•	•	•	•	•
Frustulia rhomboides var. saxonica fo. undulata Hust.		•	•	•		
Gomphonema acuminatum var. coronatum (Ehr.) Smith					•	
Gomphonema exilissimum (Grun.) LB. et Reichardt		•			•	•
Gomphonema gracile Ehr.					•	
Gomphonema aff. subclavatum (Grun.) Grun.					•	
Gomphonema truncatum var. capitatum (Ehr.) Grun.		•			•	
Gomphonema sp.					•	
Kobayasiella sp.		•	•		•	•
Microstatus sp.		•			•	
Navicula cf. radiosa Kütz.			•			
Neidium cf. affine (Ehr.) Pfitzer		•			•	•
Neidium ampliatum (Ehr.) Krammer		•			•	
Neidium sp.		•	•			
Nitzschia aff. fonticola Grun.					•	
Nitzschia gracilis Hantzsch		•			•	•
Nitzschia palea (Kütz.) W. Smith		•	•		•	•
Pinnularia borealis Ehr.					•	•



Т	Ы	. 2	continued

Taxa		RH1	RH2	RH3	RH4	RH5
Pinnularia divergens var. decrescens (Grun.) Krammer		•	•		•	•
Pinnularia mesolepta (Ehr.) W. Smith morpho 1		•	•	•		•
Pinnularia microstauron (Ehr.) Cl.	*	•	•	•	•	•
Pinnularia neomajor Krammer		•	•		•	
Pinnularia obscura Krasske				•		
Pinnularia aff. subcapitata Gregory		•			•	
Pinnularia subgibba Krammer		•	•		•	•
Pinnularia viridiformis Krammer		•	•		•	
Sellaphora laevissima Kütz.					•	
Stauroneis phoenicenteron (Nitzsch) Ehr.		•	•	•	•	
Staurosira venter (Ehr.) Cl. et Möller					•	
Staurosirella aff. pinnata Ehr.		•			•	
Stenopterobia intermedia (Lewis) V. H.		•			•	
Surirella linearis var. linearis W. Sm.		•	•		•	
Surirella linearis var. constricta (Ehr.) Grun.			•		•	
Surirella cf. pseudolinearis Krasske					•	
Surirella sp.					•	
Synedra acus Kütz.					•	•
Tabellaria flocculosa (Roth) Kütz.		•	•		•	•
Chrysophyceae						
Dinobryon sertularia Ehr.	*	•	•	•	•	•
Mallomonas sp.1		•	•	•	•	
Mallomonas sp.2		•	•		•	
Salpingoeca sp.						•
Synura sp.		•	•	•		•
Chrysophyceae 1		•				•
Chrysophyceae 2		•			•	
Chrysophyceae 3		•				
Chrysophyceae 4		•		•		
Chrysophyceae 5		•	•			•
Chrysophyceae 6			•			
Chrysophyceae 7		•				
Chrysophyceae cysts		•	•	•	•	•
Dinophyceae						
Hemidinium nasutum Stein			•			
Peridinium centenniale (Playfair) Lefevré	*	•	•	•	•	•
Peridinium inconspicuum Lemm.	*	•	•	•	•	•
Peridinium wierzejskii Woloszynka	*	•	•	•	•	•
Peridinium willei Hutfeld-Kaas	*	•	•	•	•	•
cf. Amphidium sp.		•				
Tribophyceae						
Pseudostaurastrum cf. lobulatum (Pasch.) Fott		•	•		•	
Chlorophyta pro parte						
Actinochloris sphaerica Kors.		•		•	•	



Table 2 continued

Taxa		RH1	RH2	RH3	RH4	RH5
Ankistrodesmus falcatus (Corda) Ralfs					•	
Ankistrodesmus fasciculatus (Lundb.) KomLegn.					•	•
Ankistrodesmus fusiformis Corda		•	•	•	•	
Ankyra judayi (G. M. Smith) Fott		•				
Binuclearia cf. tectorum (Kütz.) Berger	*	•	•	•	•	•
Botryococcus braunii Kütz.	*	•	•	•	•	•
Chlamydomonas sp. 1			•			
Chlamydomonas sp. 2					•	
Chlamydomonas sp. 3		•				
Chlamydomonas sp. 4		•				
Chlamydomonas sp. 5		•				
Chlamydomonas sp. 6			•			
Chlamydomonas spp.			•	•	•	•
Chloromonas angustissima (Ettl) Gerloff		•	•			
Chloromonas sp.			•			
Coelastrum indicum Turn.		•	•		•	
Coenochloris planconvexa Hind.					•	
Coenochloris sphagnicola Hind.		•				
Coenocystis subcylindrica Kors.		•				
Dictyochlorella globosa (Kors.) Silva					•	
Dictyosphaerium ehrenbergianum Näg.					•	
Dictyosphaerium pulchellum Wood		•			•	
Dictyosphaerium sphagnale Hind.					•	
Enallax cf. alpinus Pasch.		•		•		•
Enallax coelastroides (Bohl.) Skuja						•
Eutetramorus fottii (Hind.) Kom.		•		•	•	
Fusola cf. viridis Snow			•			
Geminella sp.					•	
Kirchneriella irregularis var. Irregularis (G. M. Smith) Kors.				•	•	
Kirchneriella irregularis var. Spiralis Kors.					•	
Kirchneriella microscopica Nyg.	*	•	•	•	•	•
Korshikoviella michailovskoensis (Elenk.) Silva		•			•	
Lobocystis planctonica (Tiff. Et Ahlstr.) Fott					•	
Microspora palustris Wichm.	*	•	•	•	•	•
Monoraphidium griffithii (Berk.) KomLegn.		•			•	
Monoraphidium minutum (Näg.) KomLegn.					•	
Oocystis lacustris Chod.				•	•	•
Oocystis submarina Lagerh.				•	•	•
Pandorina morum (O.F.Müller) Bory		•				
Pediastrum angulosum (Ehr.) ex Menegh.					•	
Polyedriopsis cf. spinulosa (Schmidle) Schmidle		•				
Quadrigula closterioides (Bohl.) Printz			•	•	•	•
Quadrigula lacustris (Chod.) G. M. Smith		•	•			
Quadrigula sp.		•	•			



Table 2 continued

Taxa	RH1	RH2	RH3	RH4	RH5
Saturnella saturna (Steinecke) Fott			•		•
Scenedesmus brevispina (G. M. Smith) Chod.		•	•	•	•
Scenedesmus cf. dispar (Bréb.) Rabenh.			•		
Scenedesmus ecornis (Ehr.) Chod.	•	•	•		•
Scenedesmus heimii Bourr.	•	•		•	
Scenedesmus obliquus (Turp.) Kütz.				•	
Scenedesmus quadrispina Chod.	•	•		•	
Scenedesmus serratus (Corda) Bohl.	*	•	•	•	•
Scenedesmus cf. spinosus Chod.	•			•	
Scenedesmus sp.	•			•	
Schroederia sp.				•	
Sphaerellocystis sp.				•	
Sphaerocystis cf. bilobata Broady	•		•	•	
Stigeoclonium sp.		•		•	
Treubaria setigera (Arch.) G. M. Smith					•
Chlorophyceae 1	•				
Chlorophyceae 2					•
Chlorophyceae 3	•			•	•
Chlorophyceae 4				•	
Chlorophyceae 5				•	
Chlorophyceae 6	•				
Chlorophyceae 7	•				
Oedogoniales	•	•	•	•	•
Conjugatophyceae					
Actinotaenium cucurbita var. attenuatum (G. S. West) Teil.		•	•	•	•
Actinotaenium globosum (Bulnh.) Först.	* •	•	•	•	•
Arthrodesmus octocornis Ehr. ex Ralfs	•				•
Closterium acutum Bréb.	•	•	•		•
Closterium archerianum Cl. ex P. Lundell	•				
Closterium calosporum Wittrock	•				
Closterium cf. calosporum Wittrock	•				
Closterium cynthia De Not.	•	•			
Closterium cynthia var. cynthia Croasdale	•				
Closterium closterioides (Ralfs) Louis et Peeters	•	•	•		•
Closterium gracile Bréb. ex Ralfs	•				
Closterium gracile var. elongatum W. et G. S. West	•				
Closterium incurvum Bréb.	•			•	
Closterium intermedium Ralfs	•	•	•		
Closterium jenneri var. robustum (G. S. West) Krieger	•				
Closterium juncidum Ralfs	•				
Closterium kützingii var. vittatum Nordst	•	•		•	
Closterium pronum Bréb.	•				
Closterium striolatum fo. recta W. West	•				
Closterium striolatum Ehr.	* •	•	•	•	•



Table 2 continued

Taxa		RH1	RH2	RH3	RH4	RH5
Closterium toxon W. West		•	•		•	
Closterium venus Kütz.					•	
Cosmarium bioculatum var. canadense Krieger et Gerloff		•				
Cosmarium coarctatum W. West		•			•	
Cosmarium connatum Bréb. ex Ralfs			•			•
Cosmarium constrictum var. subdeplanatum (Schmidle) Krieger et Gerloff					•	
Cosmarium contractum var. ellipsoideum (Elfving) W. et G.S. West					•	
Cosmarium hammeri Reinsch.		•	•		•	
Cosmarium humile var. glabrum Gutwinski		•			•	
Cosmarium laeve var. rotundatum Messik.					•	
Cosmarium margaritiferum var. kirchneri (Borgesen) Föster		•	•		•	
Cosmarium phaseolus var. phaseolus fo. minus Boldt.					•	
Cosmarium cf. pseudobicuneatum Jao						•
Cosmarium pseudoprotuberans O. Kirchner		•			•	•
Cosmarium pseudoprotuberans var. alpinus Racib.		•				
Cosmarium pygmaeum Arch.			•		•	
Cosmarium quadratum var. willei (Schmidle) Krieger et Gerloff		•			•	
Cosmarium quadrifarium Lundeil		•	•		•	•
Cosmarium regnesii var. regnesii Reinsch.					•	
Cosmarium regulare Schmidle		•	•		•	
Cosmarium sinostegos var. obtusius Gutwinski		•		•	•	
Cosmarium subtumidum Nordst.		•			•	
Cosmarium trilobulatum fo. retusum Gutwinski					•	
Cosmarium truncatellum Perty					•	
Cosmarium venustum var. excavatum (Eichler et Gutwinski) W. et G.S. West		•	•			
Cosmarium cf. venustum fo. minor (Wille) W. et G.S. West		•	•			
Cosmarium sp. 1		•			•	
Cosmarium sp. 2					•	
Cylindrocystis brebissonii var. brebissonii Menegh.	*	•	•	•	•	•
Cylindrocystis brebissonii var. jenneri (Ralfs) Hansgirg			•			•
Euastrum attenuatum var. lithuanicum fo. pulchellum Prescott et Scott		•			•	
Euastrum binale (Turp.) Ehr.		•			•	
Euastrum insulare var. insulare (Wittr.) Roy	*	•	•	•	•	•
Euastrum obesum var. obesum Josh		•	•	•		•
Euastrum obesum var. trapezicum (Börg.) Krieger	*	•	•	•	•	•
Euastrum sphyroides Nordst.		•				
Euastrum sp.		•	•			
Gonatozygon pilosum Wolle		•			•	
Hyalotheca dissiliens var. dissiliens (Smith) Bréb.			•	•		•
Micrasterias radiosa Ralfs		•				
Mougeotia sp.		•		•	•	
Netrium digitus var. digitus (Ehr.) Hzigs et Rothe		•		•		
Netrium sp.		•				•
cf. Octacanthium bifidum (Bréb.) Compère					•	



Table 2 continued

Taxa		RH1	RH2	RH3	RH4	RH5
Penium cylindrus Bréb. ex Ralfs		•	•			
Penium phymatosporum Nordst.			•			•
Sphaerozosma vertebratum Bréb. ex Ralfs					•	
Staurastrum borgeanum fo. minus Schm.		•	•			
Staurastrum crenulatum (Näg.) Delp.		•	•	•	•	
Staurastrum floriferum W. et G. S. West					•	
Staurastrum cf. gracile var. coronulatum Boldt.					•	
Staurastrum inconspicuum Nordst.		•				
Staurastrum iotanum Wolle		•	•		•	•
Staurastrum laeve W. West		•	•		•	
Staurastrum lapponicum Grönbl.		•			•	
Staurastrum margaritaceum (Ehr.) Menegh.		•		•		•
Staurastrum muricatum Bréb. ex Ralfs			•	•		
Staurastrum paradoxum Meyen		•	•		•	•
Staurastrum polytrichum (Perty) Rabenh.	*	•	•	•	•	•
Staurastrum subavicula W. et G. S. West		•			•	
Staurastrum subnudibrachiatum W. et G. S. West		•	•	•	•	
Staurastrum tetracerum Ralfs		•			•	
Staurastrum sp. sensu Lenzenweger		•	•	•	•	
Staurodesmus connatus (Lundell) Thomasson		•			•	
Staurodesmus convergens var. convergens Teil.		•	•		•	
Staurodesmus crassus (W. et G.S. West) M.B. Florin	*	•	•	•	•	•
Staurodesmus cuspidatus var. cuspidatus (Bréb.) Teil.		•	•	•	•	
Staurodesmus dejectus (Bréb.) Teil.		•			•	
Staurodesmus dickiei (Ralfs) Lillieroth					•	
Staurodesmus extensus var. joshuae (Gutwinski) Teil.		•			•	•
Staurodesmus extensus var. vulgaris (Eichle et Racib.) Croasdale	*	•	•	•	•	•
Staurodesmus mamillatus (Nordst.) Teil.		•			•	
Staurodesmus aff. mamillatus (Nordst.) Teil.		•	•			
Staurodesmus patens (Nordst.) Croasdale	*	•	•	•	•	•
Staurodesmus phimus var. robustus Teil.					•	
Staurodesmus quiriferus Teil.		•			•	•
Staurodesmus triangularis (Largerheimi) Teil.		•	•		•	•
Staurodesmus sp.					•	
Teilingia excavata (Ralfs ex Ralfs) Bourr.		•	•		•	
Teilingia granulata (Roy et Biss.) Bourr.		•	•		•	•
Tetmemorus brebissonii (Menegh.) Ralfs		•	•	•		•
Tetmemorus granulatus (Bréb.) Ralfs		•	•			•
Xanthidium smithii Arch.	*	•	•	•	•	•
Euglenophyceae						
Euglena sp.				•		
Phacus onyx Pochm.		•			•	
Phacus polytrophos Pochm.		•			•	
Phacus pyrum (Ehr.) Stein					•	



Table 2 continued

Taxa	RH1	RH2	RH3	RH4	RH5
Phacus swirenkoi Skv.				•	
Trachelomonas lacustris var. ovalis Drez. emend. Defl.	•			•	
Trachelomonas volvocina var. punctata Playf.	•			•	
Cryptophyceae					
Cryptomonas sp.	•				
Plagioselmis sp.	•	•	•	•	•
Florideophyceae					
Batrachospermum sp.		•	•	•	•

^{*} Indicate taxa recorded from all five pools. Among Chlorophyta, Conjugatophyceae stand as a separate group on account of their particular traits, while other classes (Chlorophyceae + Ulvophyceae + Treubouxiophyceae) are grouped under Chlorophyta proparte

phytoplankton communities regarding every community structure descriptor dealt with in this study.

Discussion

The maritime, cold-temperate climate of Tierra del Fuego has provided the ideal setting for the development of mires for the past ca. 15,000 years until present (Coronato et al., 2006). Peat bogs in this region can display a wide range of topographical arrangements (Grootjans et al., 2010). In particular, the dome of Rancho Hambre is characteristically subdivided into small catchments by lengths of moss hummocks, therefore affecting the connectivity of water bodies, which in turn modulates changes in water level, as demonstrated by precipitation-fed, hydrologically isolated RH2 showing the strongest effects of precipitation events over the sampling period (González Garraza et al., 2012). Also pool morphometry ultimately influenced water level by dictating a temporal pattern of temperature variation characterized by higher mean and absolute maximum temperatures during summer in shallow RH3 and RH5, which in turn lowered water level through evaporation. This was reflected by higher mean values and wider ranges for conductivity, suspended solids (González Garraza et al., 2012), and DOC (Quiroga et al., 2013) in these pools. On the other hand, low connectivity lead individual pools to have distinctly different sets of physical and chemical features even when spread just a few meters apart. In particular, steadily lower pH values identified ombrotrophic pools.

The total amount of taxa identified in the nano + microphytoplankton from Rancho Hambre is in line with former surveys of Fuegian (Mataloni, 1997) and European mires (Nováková, 2002; Borics et al., 2003; Krivograd Klemenčič et al., 2010). Although most of them belong to the Conjugatophyceae (desmids), Bacillariophyceae (diatoms) and green algae (Chlorophyta pro parte), almost all these species were always present in low frequencies, as also pointed out by the above-mentioned authors. In particular, desmids represented one third of the recorded taxa, in accordance with the characteristic high richness of this group in mires around the world, and showed a marked preference for minerotrophic pools (Neustupa et al., 2009; Krivograd Klemenčič et al., 2010). Furthermore, Stepanková et al. (Štepánková et al. 2008) pointed out the strong relation between the distribution of desmids, pH, and conductivity in a recovering mire and the value of this group as indicator of environmental changes only later reflected by the macroflora. On the other hand, almost 50% of the Cyanobacteria (18 out of 40 taxa) were recorded from all five pools. Moreover, this group shared a significant proportion, and even occasionally dominated the phytoplankton biovolume in all pools but the most minerotrophic RH4 (González Garraza, 2012). This supports previous results from Rancho Hambre which challenged the idea that acid conditions disfavor cyanobacterial growth (Mataloni & Tell, 1996) but were later dismissed by Rauch et al. (2006). As in all diversity analyses based on morphological identification, there is a high probability that the diversity of mixotrophic nanoflagellates such as small



Table 3 Total species richness over the study period for each pool and main taxonomic group
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	RH1	RH2	RH3	RH4	RH5	All pools		
Number of taxa								
Cyanobacteria	32	25	26	32	28	40		
Bacillariophyceae	46	32	15	59	25	64		
Chrysophyceae	11	7	5	5	6	13		
Dinophyceae	5	5	4	4	4	6		
Tribophyceae	1	1	0	1	0	1		
Chlorophyta pro parte	35	22	20	43	19	68		
Conjugatophyceae	79	47	26	65	32	103		
Euglenophyceae	4	0	1	6	0	7		
Cryptophyceae	2	1	1	2	1	2		
Florideophyceae	0	1	1	1	1	1		
Total species richness	215	141	99	218	116	305		

Chlorophyta pro parte: classes Chlorophyceae + Ulvophyceae + Treubouxiophyceae

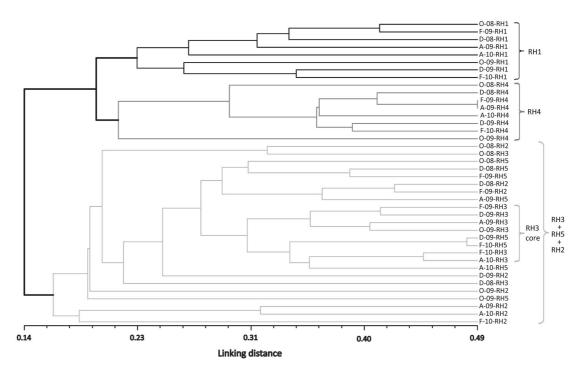


Fig. 2 Clustering of samples based on the floristic composition of the nano- and microphytoplankton. RH3 core stands for a group of RH3 samples clustered together

Chrysophyceae might have been underestimated. Further evidence provided by preliminary data on molecular environmental diversity (Illumina HiSeq) points in that direction (Lara et al., 2014) and will be the core subject of future research.

According to the dendrogram based on floristic composition, phytoplankton of the pools with steadier values of abiotic features was more constant over time, with samples clustering together in very definite groups. On the other hand, the smallest water body



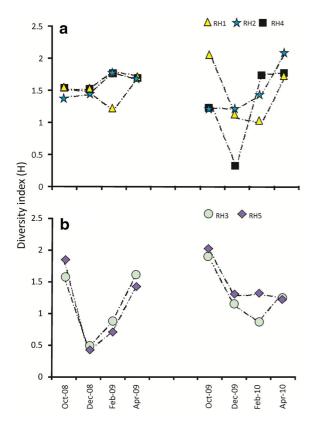


Fig. 3 Values of Shannon-Weaver diversity index (H) for a large pools and **b** small pools on each sampling date

(RH3) had the lowest species richness and its composition changed less over time than that of RH5 and RH2.

The positive correlation between pool area and species richness in other five pools from Rancho Hambre found by Mataloni & Tell (1996) was interpreted as a patch-size effect by these authors. Nevertheless, the environmental constraint imposed by pH seems to play a more important role in this sense, in agreement with Druvietis et al. (2010) observations from Latvian Sphagnum bogs, as species richness in RH2 was lower than in smaller, circumneutral RH1 and comparable to those of shallow, acidic RH3 and RH5. On the other hand, it was also RH2 which showed the highest species turnover, most probably due to the strong dilution/concentration effect in this pool caused by changes in water level. While low similarity of the phytoplankton composition among close yet distinct pools was caused by environmental variability, differences among similar water bodies should be ascribed to low dispersal ability of the species concerned, as Cerná (2010) proved that microalgae dispersal was hampered even by small-scale barriers in a peat bog. Nevertheless, the fact that the two shallower pools had one and the same diversity temporal pattern provides evidence that the same driving processes operate at one time. Indeed, overall similarities were recorded amongst the planktonic webs of all five pools in the spring post-thawing period, which resembled those of (sub)polar environments (Izaguirre et al., 1998; Vincent et al., 2008). Yet, as the season proceeded, structural differences arose among the planktonic trophic webs of large versus small pools, which are liable to affect phytoplankton structure (Quiroga et al., 2013). Phytoplankton showed different mean abundance, structure, and dynamics among water bodies, as pools with different features were numerically dominated by different taxonomic groups and even size fractions, with eukaryotic picophytoplankton playing a key role in RH2. Abundances also varied broadly over both open water periods, with summer temperatures triggering peaks of different species mainly in shallow RH3 and RH5, hence lowering summer diversity values, a fact well observed in Maritime Antarctic limnetic systems (Izaguirre et al., 1998; Mataloni et al., 2000).

Results of the canonical correspondence analysis (CCA) were both highly explanatory and highly significant. The positioning of samples over axis 1 clearly reflected a temporal source of environmental variation characterized by temperature and temperature/precipitation-driven EC. October samples from all pools are located close together, coincidently with the results of Quiroga et al. (2013), who found strong overall similarities among the spring trophic webs of all five pools. The influence of morphometry on the pattern of temperature variation is reflected in the high scores of summer samples from shallow RH3 and RH5 on this axis. These conditions favor the growth of the cryptophycean *Plagioselmis* sp., while the chlorophyte Kirchneriella microscopica dominated large, minerotrophic RH4. In turn, the particular combination of morphometric, trophic, and pH features of RH2 allowed for a characteristic picophytoplankton dominance. Though phytoplankton abundance was mainly temporally driven, axis 2 reflects the influence of pH on species richness, as hypothesized on the basis of preliminary results by Mataloni & Tell (1996). These authors ascribed the



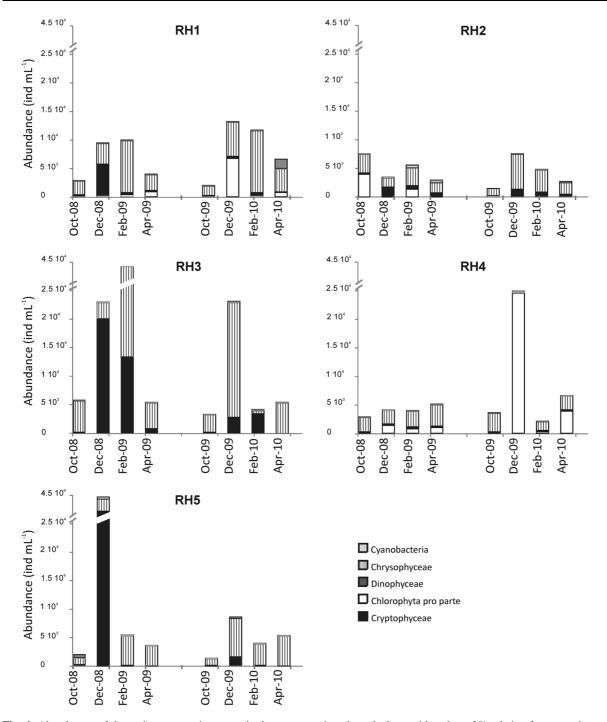


Fig. 4 Abundances of the major taxonomic groups in the nano + microphytoplankton with at least 3% relative frequency in one sample

strong association of Euglenophyta (Euglenophyceae in this paper) with Lasifashaj River to its minero-trophic character, an observation which is confirmed here by the high score of this group on axis 2. In

general, pH stands as a key feature in determining phytoplankton composition.

The characterization of pools displayed in Table 4 shows distinctly minerotrophic features for large,



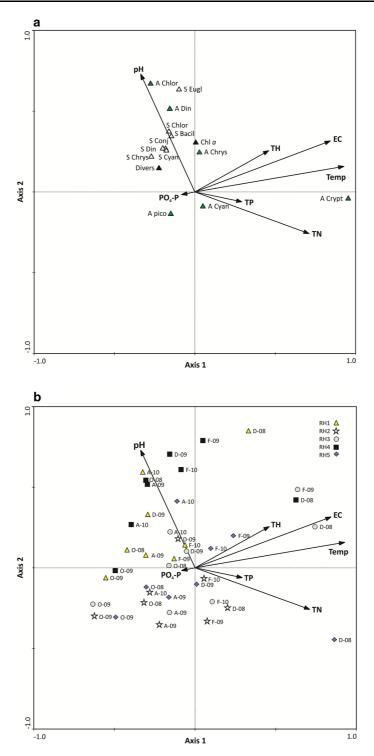


Fig. 5 a Ordination of the phytoplankton descriptors over the two first axes configured by abiotic features. *TH* total hardness, *EC* electrical conductivity, **a** abundance, e.g., A Chloro: abundance of Chlorophyta *pro parte* S: species richness, e.g., S

Eugl: species richness of Euglenophyceae **b** Ordination of all samples over the two first axes configured by abiotic features. Alphanumeric codes stand for sampling month—year, e.g., D-08: December 2008



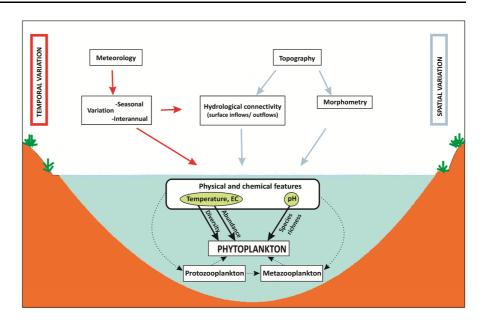
Table 4 Comparison of the studied pools on the basis of landscape- and weather-driven abiotic features, and structure and dynamics of the phytoplankton

Features	RH1	RH2	RH3	RH4	RH5
Morphometrical	Large, deep	Large, deep	Small, shallow	Large, deep	Small, shallow
Hydrological					
Superficial connectivity	Connected	Isolated	Isolated	Connected	Isolated
Water level variability	Medium	High	Medium	Low	Medium
Physical and chemical					
Temperature	Lower, constant	Lower, constant	Higher, variable	Lower, constant	Higher, variable
Hd	Mildly acid	Acid	Acid	Mildly acid	Acid
Phosphate	Higher	Higher	Lower	Higher	Lower
DOC	Lower	Lower	Higher	Lower	Higher
Trophic status	Minerotrophic	Minero/ombrotrophic	Ombrotrophic	Minerotrophic	Ombrotrophic
Phytoplankton					
Species richness	70 (57–98)	41 (27–61)	34 (20-43)	83 (47–112)	41 (25–55)
Richest taxonomic groups	Conjugatophyceae Bacillariophyceae Chlorophyta <i>pro parte</i>	Conjugatophyceae Bacillariophyceae Chlorophyta <i>pro parte</i>	Cyanobacteria Conjugatophyceae	Conjugatophyceae Bacillariophyceae Chlorophyta <i>pro parte</i>	Cyanobacteria Conjugatophyceae
Diversity index (H)	1.46 (0.98–1.99)	1.53 (1.20-2.11)	1.21 (0.45–1.84)	1.45 (0.30–1.78)	1.27 (0.40–1.99)
Picophytoplankton abundance $(10^3 \text{ ind mL}^{-1})$	3.3 (1.1–8.7)	50.6 (1.1–191.0)	4.2 (0.9–7.9)	9.3 (2.1–33.9)	3.7 (0.9–11.0)
Nano- and microphytoplankton abundance (10³ ind mL¹)	7.6 (3.0–13.2)	4.9 (2.8–7.5)	13.8 (3.4–39.7)	6.8 (2.2–25.0)	11.1 (2.0–44.5)
Dominant groups	Chrysophyceae (Cryptophyceae Chlorophyta pro parte)	Chrysophyceae (Chlorophyta <i>pro parte</i>)	Chrysophyceae (Cryptophyceae)	Chrysophyceae (Chlorophyta pro parte)	Chrysophyceae (Cryptophyceae)
Mean chlorophyll a	0.86 (0.39–1.31)	0.68 (0.23–1.26)	1.35 (nd-3.48)	2.31 (1.03-4.71)	1.38 (0.17–3.48)
Temporal variation pattern	Summer dominance by mixotrophic nanoflagellates	Summer dominance by autotrophic picoplankton	Summer dominance by mixotrophic nanoflagellates	Summer dominance by autotrophic picoplankton	Summer dominance by mixotrophic nanoflagellates

Higher values of measurable features are represented as Bold, intermediate ones as Italics and lowest as normal typeface. To ease comparison and characterization of phytoplankton communities, similar non-measurable features (e.g., taxonomic composition) have also been assigned similar typeface. Sub-dominant or only occasionally dominant groups are between parentheses



Fig. 6 Proposed interpretative model of the main environmental features driving the phytoplankton structure and dynamics in Rancho Hambre pools and their temporal and spatial variability sources. Red (dark gray) arrows stand for temporal variability. Light blue (light gray) arrows stand for spatial variability. Dotted arrows stand for trophic relationships likely contributing to structure phytoplankton communities in these systems, as shown in Quiroga et al. (2013)



connected RH1 and RH4 on one hand, ombrotrophic features for shallow, isolated RH3 and RH5, and an intermediate status for large, isolated RH2. Regarding phytoplankton features, those relating to community composition (species richness, diversity, and richest taxonomic groups) clearly reflect these spatial differences, whilst abundances and related features such as dominant groups and chlorophyll *a* concentrations involve more complex spatial and temporal patterns. Indeed, summer abundance peaks of nanoflagellates characterize shallow RH3 and RH5, while eukaryotic picophytoplankton dominates RH2 and, to a lesser extent, RH4. The high proportion of large cells in spring and autumn explains the higher mean chlorophyll *a* concentrations in the latter.

While different studies have attributed changes in the composition and richness of peat bog phytoplankton and phytobenthos microalgae to distinct environmental features (Nováková, 2002; Krivograd Klemenčič et al., 2010), an integrated view denotes environmental diversity as a key factor shaping the structure of Rancho Hambre phytoplankton, in accordance with Borics et al. (2003). Indeed, in this system, a complex interaction of topographic, morphometrical, and hydrological features results in a high environmental diversity in both space and time, the

first given by distinct pH and trophic status of pools, and the latter acting not only through temperaturedriven changes in physical and chemical parameters but also on community properties such as abundance, biomass, and composition. Such biotic effects were observed in Rancho Hambre by Quiroga et al. (2013) for metazoans, and are liable to affect phytoplankton features through trophic cascading effects, as formerly observed by Jürgens & Matz (2002). Our results allowed us to propose an interpretative model which sums up the basic limnological functioning of these peat bog pools and how it affects phytoplankton (Fig. 6). According to it, the microtopographic configuration plays a key role on the connectivity among water bodies, and hence in the species flux among them. This confers the Sphagnum matrix an unexpected resistance for this type of wetland landscape, revealed by the low similarity among the taxonomic composition of the different patches. Yet, phytoplankton communities of pools with similar morphometry and trophic status show similar overall structures undergoing parallel changes over time independently of the species composing them.

In sum, peat bogs are landscapes that, despite an apparently simple structure consisting of limnetic patches embedded in a peat matrix, are driven by a



complex set of interacting features that render seemingly alike pools environmentally diverse. Nevertheless, this research showed that though species composition of the phytoplankton in the studied pools is unpredictable on the basis of such features, the community strategy in terms of dominant and richest taxonomic groups as well as temporal variation patterns can be predicted with the help of the proposed interpretative model. This will be validated through the analysis of larger numbers of pools in peat bogs with different characteristics, with a view to use phytoplankton as a sentinel community of environmental changes in these wetland limnetic environments.

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