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Temporary shallow pools in high-Andes 'bofedal' peatlands:

a limnological characterization at different spatial scales

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Abstract

This study is the first to characterize the limnological features of high-altitude peatland pools in the Andes cordillera (>4000 m). Data were collected at two different spatial scales: the scale of individual patches of peatland (bofedales; areas ranging between 0.01 and 10 ha) and the scale of 'localities' (areas of approximately 7 km^2). Patterns of variable associations were similar at the different spatial scales. The major gradient of variation appeared to represent a productivity gradient. Water plant cover and richness were associated with alkalinity

Keywords: *Andean temporary pools, physico-chemistry of bofedales, high-altitude peatlands, Limnology.*

Résumé

Les mares temporaires peu profondes des tourbières «bofedales» des Hautes-Andes: une caractérisation limnologique à différentes échelles spatiales

Cette étude est la première à décrire les caractéristiques limnologiques de mares de tourbières de haute altitude situées dans la Cordillère des Andes (>4000 m). Pour la récolte des données, deux échelles spatiales ont été considérées: l'échelle de la tourbière (bofedales: surface entre 0.01 et 10 ha) et l'échelle de la «localité» (surfaces de environ 7 km^2). Les associations entre les variables apparaissent similaires pour les deux échelles spatiales. Le principal gradient de variation correspond à un gradient de productivité. La couverture et la richesse des plantes aquatiques sont associées à l'alcalinité.

Mots-clés: *Mares temporaires des Andes, physico-chimie des bofedales, tourbières de haute altitude, limnologie*

Introduction

"Bofedales", also known as "turberas", "vegas andinas", "cenegales" or "oconales" (Alzérreca 1988; Seibert 1993), are peatlands that occur in the valley bottoms of the Andes cordillera at altitudes ranging from 4000 to 4400 m a.s.l. Bofedales are mires that are often subject to harsh climatic conditions, such as strong annual water level fluctuations, intense solar radiation, high-velocity winds, and daily frosts (Alzérreca 2001; Navarro and Maldonado 2002; Earle et al. 2003). Unlike many peatlands in the northern hemisphere, bofedales are not formed by *Sphagnum*, but by low cushion-forming vegetation. They are not ombrotrophic but fed by small rivulets, precipitation and ground water. Bofedales have been shown to be recent and dynamic systems, with a high capacity for carbon accumulation (Earle et al. 2003). In addition, they are increasingly recognized as important regulators of the local water balance (Van Damme 2002). As grazing pastures for llama and alpaca, they are very important for the local economy (De la Barra and Bilbao 2003). Many, however, are being threatened by an unsustainable use, such as land conversion, cattle overstocking, and peat cutting (Alzérreca 2001; JS Coronel personal observation). Despite the abundance and economic importance of bofedales, there is only limited num-

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ber of studies on their ecology, typology, history or agronomical use (Wilcox 1986; Alzérreca 1988; Ruthsatz 1993; Seibert 1993; Alzérreca 2001; Navarro and Maldonado 2002, Earle et al. 2003; De la Barra and Bilbao 2003).

Clusters of small and shallow pools typically characterize the bofedal landscape. These pools are subject to pronounced seasonal water level fluctuations (Fig. 1). Many are temporal and fall dry during the dry period of the year (Alzérreca 2001). The pools show a high variation in connectivity: pools can be hydrologically isolated while others are interconnected with local rivulets. Some are located along the margins of small streams. With the exception of

Figure 1. Photographs of a characteristic bofedal system and associated pools in the Tunari cordillera (Cochabamba, Bolivia): a) and b) show a bofedal peatland during the winter and summer, respectively; c) vegetated pool; d) pool devoid of vegetation and with thick layer of organic mud on bottom; e) relatively large pool; f) relatively small pool.

the latter, the temporal pools are typically fishless. So far, the limnological features and biological communities of these characteristic pools remained unstudied.

Aquatic ecosystems in highland regions are increasingly considered important because of their unique plant and animal communities and because of their potential as indicators for the effects of atmospheric pollution and global change (Marchetto et al. 2004). The bofedal systems of the Tunari cordillera are located close to Cochabamba, one of Bolivia's largest cities. In recent years, this region has known a rapid economic and urban development. This undoubtedly coincides with an increased pressure on the surrounding mountain ecosystems through changes in land use, increased air pollution and associated deposition of nutrients and pollutants. For a future evaluation of human induced environmental alterations, there is a clear need for baseline data on physical, chemical and biological ecosystem characteristics (Hamilton et al. 2001; Michelutti et al. 2002). Furthermore, such data are essential for further studies on the biodiversity, functioning and sustainable use of these unique ecosystems.

This study is the first that provides a large-scale dataset on the limnological features of pools in bofedal peatlands. The study is part of a larger study on patterns of biodiversity in these ecosystems. The specific objectives of this paper were: (1) to characterise limnological features of a large number of bofedal pools, (2) to assess variation in these features across different localities, and (3) to explore for associations between ecologically relevant variables at different spatial scales.

Experimental procedures

Study area

The bofedales we studied are situated in the region of the Tunari cordillera (Cordillera Oriental, Bolivia). These bofedales are generally small in surface area and numerous. They are located in the biogeographical province "Peruvian Puna" (Navarro and Maldonado 2002). The characteristic vegetation of the bofedales in the Tunari region consist of the species *Plantago tubulosa, Deyeuxia rigescens, Werneria pygmaea, Gentianella primuloides, and Distichia muscoides* (Navarro and Maldonado 2002). The bofedales show a patchy distribution and can be found in the larger valleys, along rivulets or in small pockets and depressions of the mountain landscape. In this landscape, pools are almost exclusively confined to the peatlands. The pools are typically very small and shallow and almost exclusively temporal and fishless. They lack water input from long-distance drainage and fill from snow melt via rivulets, underground springs, or from precipitation during the period October-March. During the dry season (April to September) the pools dry out gradually (see Fig. 1).

Sampling

During February 2004, we sampled 61 peat bog pools in the Tunari Cordillera (Fig. 2). We made use of the particular hierarchical spatial organization of the pools to study the limnological characteristics at two different spatial scales: (1) the scale of 'localities', where localities are defined as areas with a radius of approximately 1.5 km. In total, pools of four different localities were sampled: Taquiña, San Ignacio, Saito, and Toro (Fig. 2). In each locality we randomly sampled one pool per bofedal with 4 to 15 bofedales per locality (a total number of 31 bofedales; see Table 1); (2) the scale of bofedales: for a selection of six bofedales (two in Taquiña and Toro, and one in Saito and San Ignacio), we sampled the entire set of pools, which corresponds to 5 to 8 pools per bofedal (a total number of 36 pools). In conclusion, we thus generated two independent datasets corresponding with two different levels of spatial scale (a 'LOC dataset', corresponding to the scale of localities, and a 'BOF dataset', corresponding to the scale of bofedales).

Table 1. Number of peatlands ('bofedales') and pools sampled at the localities Taquiña, San Ignacio, Saito and Toro in the Tunari cordillera (Cochabamba, Bolivia). The table also gives the range in altitudes, latitudes and longitudes per locality.

	Taquiña	**San Ignacio**	**Saito**	**Toro**
Code	T	SI	S	TR
Total bofedal number	15	4	5	7
Entirely sampled bofedales	2	1	1	2
Total pool number	27	9	9	16
Altitude range (m)	4067 - 4335	4311 - 4333	4331 - 4429	4382 - 4416
Latitude range (S)	17°15'84'' - 17°17'19''	17°10'56'' - 17°10'89''	17°13'10'' - 17°13'67''	17°14'80'' - 17°15'72''
Longitude range (W)	66°07'62'' - 66°08'92''	66°22'43'' - 66°22'79''	66°22'73'' - 66°22'99''	66°11'55'' - 66°11'96''

From each pool, we assessed physical, chemical, morphometric, and biotic variables (Table 2). Sampling was carried out during the day. Water temperature, dissolved oxygen, pH, and conductivity were measured using sensors. Pool depth and the thickness of the organic mud layer on the bottom were recorded with a graduated stick. Water transparency was measured using a cylindrical Snell's tube (length: 0.6 m; diameter 60 mm; disc diameter: 55 mm). Water samples for nutrients (nitrates and total phosphorus), major ions (chloride, sulfate, sodium, potassium, calcium, magnesium, bicarbonates and carbonates) and chlorophyll a were collected with a 2 L bottle at the mid water column depth of each pool. For chlorophyll a a measured volume of water was filtered through a Whatman GF/F filter and stored on ice. Quantitative samples of zooplankton were collected with a zooplankton tube sampler and filtered through a 30-μm mesh. Samples were preserved in a 5% sucrose-formaldehyde solution (final concentration). Water plants were identified to species level *in situ* and water plant cover was estimated as the percentage of plants covering the pool's surface area. For each pool the shortest distance to the nearest rivulet was measured. Altitude and geographic position were recorded using the geographical positioning system (GPS).

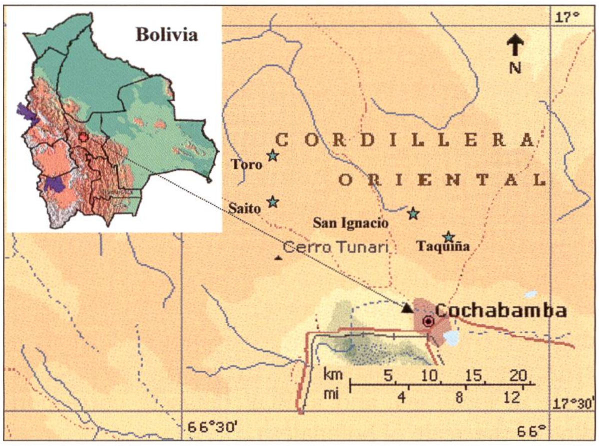


Fig. 2. Map of part of the Tunari cordillera (Cochabamba, Bolivia) with the location of the sampled localities (indicated by asterisks). Insert: map of Bolivia with an indication of the study area.

Sample analysis

Chemical analysis for nutrients and major ions was carried out by the "Centro de Aguas y Saneamiento Ambiental" of the Universidad Mayor de San Simón (Bolivia) following standard methods of the American Public Health Association (APHA; Eaton et al. 1998). Chlorophyll a was quantified after extraction with 90% acetone (Nusch 1980). Zooplankton density estimates were based on counts of at least 300 specimens per sample. Total zooplankton biomass was estimated from the density data and published length-dry weight relationships.

Data analysis

All variables, except pH, were logarithmically transformed prior to any statistical analysis. The variables alkalinity, water plant cover and water plant species richness were log(x+1) transformed because of the occurrence of zero-values.

We first tested whether pools from different localities differ in characteristics. For this we followed a multivariate approach. Permutation tests (999 permutations) were applied on redundancy analysis models (RDA) in which 'locality' was specified as nominal explanatory variable. The tests were performed for three groups of dependent variables: morphometric, physico-chemical and biotic variables (see Table 2). RDA was applied rather than canonical correspondence analysis (CCA) because a detrended correspondence analysis (DCA) had indicated a predominance of linear rather than of unimodally shaped associations between variables (length of gradients: < 0.25; Leps and Smilauer 2003). Variation partitioning (Borcard et al. 1992) was applied to estimate the fraction of variation explained by 'locality'.

For all of the variables, variation within each of the four localities and within each of the entirely sampled bofedales was assessed by calculating the standard deviation. Mann-Whitney U-tests were applied to test for differences in variation between the set of localities and the set of bofedales.

Associations between variables were explored with product-moment correlation analyses and standardized principal components analyses (PCA). This was separately done for the LOC- and BOF-datasets. To avoid distortions in associations because of systematic differences between localities in the LOC-dataset, 'locality' was specified as co-variable in the PCA-analyses. For the same reason, each variable was adjusted for differences between localities prior to correlation analysis. For pools from a given locality this was done by subtracting the calculated locality average from the original data. The same approach was followed for the BOF-dataset. All significant correlations were visually checked with scatter plots. Some correlations were distorted because of inadequate distributional properties. In such case, associations between variables were additionally evaluated with the non-parametric Spearman rank correlation. Patterns of associations between ecologically relevant variables on the scale of bofedales were formally compared with those on the scale of entire localities following the approach of Clarke and Ainsworth (1993). Both adjusted data sets were first standardized (minus the average and divided by the standard deviation) to account for the difference in units between variables. Subsequently, for each dataset, one triangular matrix was constructed from the Euclidian distances between each possible pair of variables. Finally, the degree of association between the two matrices was calculated with a Spearman's rank correlation coefficient (ρ). The significance level of the correlation coefficient ρ was determined by a permutation test (999 random permutations). This test was performed by the routine 'RELATE' in the statistical software program PRIMERv5 (Clarke and Gorley 2001).

Associations between variables should be interpreted with care and do not necessarily indicate causal relationships. It can nevertheless be useful to evaluate alternative hypotheses by assessing how well hypothesis-based expectations agree with patterns of associations that emerge from descriptive field data. Phytoplankton biomass, water plant cover and water plant species richness are three fundamental ecosystem characteristics. Phytoplankton and water plants represent the most important primary producers in pool systems, in addition to periphyton. In addition, phytoplankton may strongly affect the light climate that may be of determining importance for water plants. Water plant cover and species richness are also of major importance because they create structural heterogeneity and mediate many ecosystem functions. With multiple regression analysis we explored for the sets of variables that potentially affect phytoplankton biomass, water plant cover and water plant species richness via known ecological mechanisms. For each of these variables, a forward selection was performed on a list of a priori chosen explanatory variables (see Table 2).

Table 2. The physico-chemical, morphometric and biotic variables that were assessed in this study for 61 peatland pools in the Tunari cordillera (Cochabamba, Bolivia). The table also gives the codes of the variables that are used in other tables and graphs. Crosses (+) indicate the variables that were used in the PCA analyses. Asterisks (*) in the three most right columns indicate which variables were subjected to a forward selection procedure for the construction of multiple regression models (see text for more details, see also Table 5) in order to explain the dependent variables chlorophyll a concentration (CHLa), water plant cover (WPCOV) and water plant species richness (WPSPR). Thickness of organic mud layer (ORGMUD): 1: pools with less than 0.05 m of organic mud layer, 2: pools with mud layer between 0.05 and 0.20 m thickness, and 3: pools with mud layer thicker than 0.20m.

Variable	Code	Units	Median	Min	25%perc	75%perc	Max	Multiple regressions		
								CHLa	WPCOV	WPSPR
Physico-chemical										
Total phosphorus^{+}	TP	mg P L^{-1}	0.01	0.01	0.01	0.01	0.63	*	*	*
Nitrate^{+}	NO3	mg N L^{-1}	0.1	0	0.1	0.1	0.4	*	*	*
Sulfates	SO4	mg S L^{-1}	0.9	0.6	0.9	0.9	114.6			
Chlorides	Cl	mg L^{-1}	0.5	0.3	0.4	0.8	7.1			
Calcium	Ca	mg L^{-1}	3.2	0.5	2.4	4.1	9.6			
Magnesium	Mg	mg L^{-1}	1.1	0	0.9	1.6	6.3			
Sodium	Na	mg L^{-1}	1.1	0.1	0.7	1.6	5.3			
Potasium	K	mg L^{-1}	0.4	0.1	0.3	0.6	1.5			
PH+	pH		7.5	4.9	6.8	8.0	9.7	*	*	*
Conductivity^{+}	COND	µS cm^{-1}	15	5.3	12.2	19.2	238			
Alkalinity^{+}	ALK	mg CaCO3 L^{-1}	9.1	0	6.2	12.9	31.2	*	*	*
Transparency^{+}	TRANSP	m	0.4	0.1	0.3	0.4	0.5		*	*
Oxygen^{+}	O2	mg L^{-1}	6.1	3.4	5.4	7.1	11.6			
Distance to the nearest rivulet	DNR	m	4.5	0.3	2	20	100	*	*	*
Altitude^{+}	ALT	m a.s.l.	4327	4067	4252	4383	4429			
Organic mud^{+}	ORGMUD		1	1	1	2	3		*	*
Morphometric										
Depth^{+}	DEPTH	m	0.2	0.03	0.13	0.3	0.5	*	*	*
Area^{+}	AREA	m^{2}	23	1.5	8.7	78.3	532		*	*
Biotic										
Chlorophyll a^{+}	CHLa	µg L^{-1}	10.8	1.8	5.4	18.2	153.5		*	*
Water plant cover^{+}	WPCOV	%	70	0	50	90	100	*		
Water plant species richness^{+}	WPSPR		3	0	2	4	6			
Zooplankton biomass^{+}	ZOOPB	µg L^{-1}	43.1	0	10.4	88	541	*		

Results and discussion

Limnological features

One major aim of the study was to characterize the limnology of the bofedal pools. The studied pools were small and shallow (Table 2). Surface area ranged between 1.5 and 532 m^2. Depth ranged between 0.03 and 0.5 m. Most physico-chemical and biotic variables showed very high variation between pools and often differed with more than one or two orders of magnitude. Concentrations of ions like sulphates (SO_4^{2-}), chlorides (Cl^-), calcium (Ca^{2+}), magnesium (Mg^{2+}) and sodium (Na^+) ranged between values of 0.6 mg L^{-1} and less to values higher than 5 mg L^{-1} (Table 2). Conductivities ranged between 5 and 238 µS cm^{-1}. The water in the pools showed a relatively low buffer capacity (alkalinity < 31.2 mg $CaCO_3$ L^{-1}). The pH ranged from acid to alkaline. The frequency distribution of alkalinity showed a bimodal pattern, with a low number of pools (n = 9) of very low alkalinity (0 mg $CaCO_3$ L^{-1}) and the majority of pools ranging between 6.2 and 20.5 mg $CaCO_3$ L^{-1}. Concentrations of nutrients that potentially limit primary production (e.g., total phosphorus and nitrates) were very low and in many cases below the detection limit (lower than 0.01 mg L^{-1} in 81% of the cases for total phosphorus and in 11% of the cases for nitrates; Table 2). Water transparency varied between 0.1 and 0.4 m Snell's depth and the bottom of the pools was always visible. With some exceptions, phytoplankton biomass was generally low: chlorophyll a levels were lower than 18.2 µg L^{-1} in 75% of the cases. Part of the pools was highly covered by submerged and floating leaved vegetation, while other pools had only sparse or no vegetation (Table 2; Fig. 1).

According to our physico-chemical data, the majority of bofedal pools can be considered as minerotrophic mires (Heinselman 1970; Verhoeven et al. 1990; Miserere et al. 2003). A minority of the pools were, nevertheless, characterized by a very low pH and alkalinity which may indicate that some pools are to a large extent hydrologically isolated and fed by rain water or carbonate poor ground water.

Spatial heterogeneity between and within localities

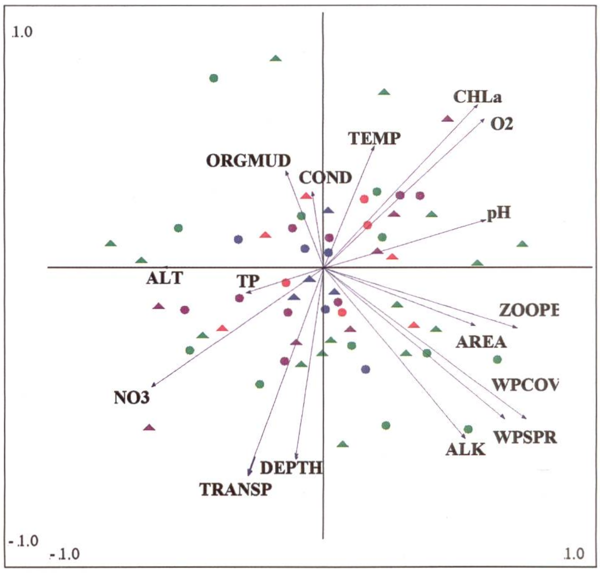
Pools were studied at different localities in order to assess the degree of spatial heterogeneity in limnological features. According to the RDA-analyses, pools belonging to different localities differed in physico-chemical characteristics, but not in morphometrics and only marginally significant in biotic variables. Locality explained about 23 % of the variation in the physico-chemical dataset (Table 3). Nitrates, chlorides, sodium, alkalinity, and thickness of the organic matter layer were the variables that showed the most pronounced differences between localities (ANOVA, p-values <0.05).

Table 3. Results of variation partitioning on standardized RDA-models, quantifying the amount of variation that is explained by the variable 'locality'. Variation partitioning was separately carried out for physico-chemical, morphometric, and biotic variables (see Table 2). Trace: total amount of variation explained by 'locality'.

Variable	Trace	F-ratio	p-value
Physico-chemical	0.23	2.56	0.001
Morphometric	0.11	1.59	0.164
Biotic	0.18	1.88	0.080

Depending on the biogeographical context and local climatic, geologic and hydrologic conditions, bofedales show high variation in physico-chemical and biological features (Navarro and Maldonado 2002). Conductivity of bofedal pools in the Sajama region (Bolivia), for example, has been found to be considerably higher than in the Tunari region (JS

Figure 3. Biplot of a standardized PCA-analysis performed on the LOC-dataset (the within locality level). The plot illustrates the relationships between environmental variables and sampling sites. The pools of the BOF-dataset (within bofedal level) are represented as supplementary samples and did not influence the ordination pattern. Arrows represent variables, triangles represent LOC-pools, and circles represent the supplementary BOF-pools. Colors represent the localities sampled: green: Taquiña, purple: Toro, red: Saito, and blue: San Ignacio. See Table 2 for an explanation of the variable codes.



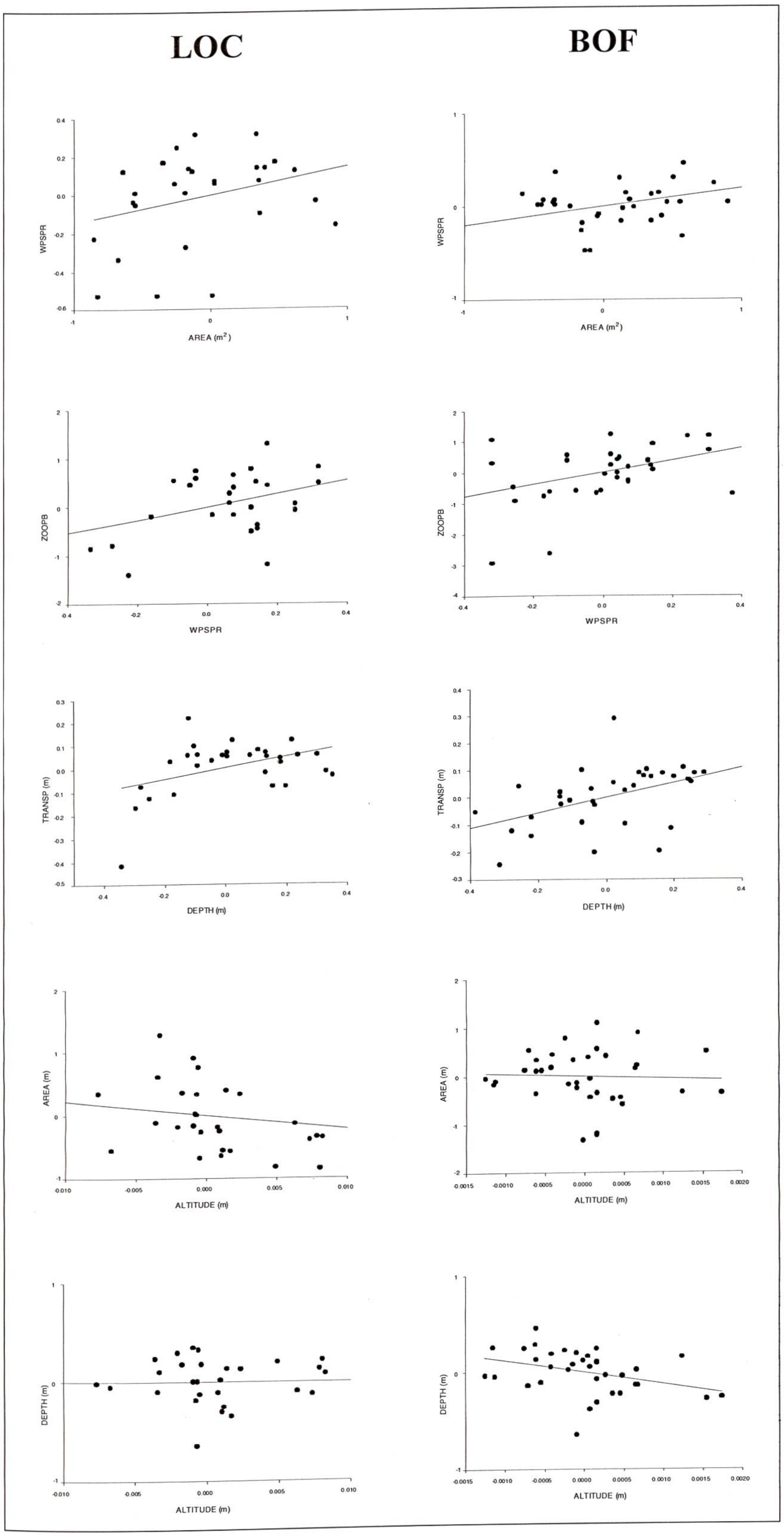


Figure 4. Scatter plots showing the associations between ecological relevant variables at different spatial scales: the within-locality scale (LOC) and the within-bofedal scale (BOF). The graphs present data that were adjusted for differences between localities upon log-transformation (see Materials and Methods). See Table 4 for the corresponding r- and p-values. WPSPR: water plant species richness; ZOOPB: zooplankton biomass; TRANSP: water transparency; AREA: pool surface area; DEPTH: pool depth.

Coronel et al. unpublished results). Vegetations may also differ to a large extent. In contrast to the bofedales in the Tunari region, bofedales in the southern margin of the Andean Altiplano are dominated by species of the rush *Oxychloe* (Ruthsatz 1993; Navarro and Maldonado 2002; Earle et al. 2003). Our results may therefore only be representative for the Tunari cordillera, and extrapolations to conditions in bofedales from other parts of the Andes should be done with prudence. Differences in physico-chemical characteristics between localities within the Tunari region, as revealed by our analyses, undoubtedly reflect inter-locality differences in atmospheric deposition, surface sediment and bedrock geochemistry (Hamilton et al. 2001; Navarro and Maldonado 2002).

Variation between pools on the small scale of single bofedales was also very high and about of the same order of magnitude as the variation found between pools on a locality scale. According to Mann-Whitney U-tests applied on the standard deviations of bofedales and localities, none of the pool characteristics showed a significant difference in variation between the two levels of scale. The relatively high variation between pools within bofedales is also exemplified in the biplot of the standardized PCA analysis on the LOC dataset (Fig. 3). This implies that bofedales of the Tunari region can contain a highly diverse set of pool habitats despite their relatively small surface area.

Association patterns for ecologically relevant variables: PCA- and correlation analyses

We tested if association patterns between limnological variables can be reproduced at different spatial scales. The correlation between the Euclidean distance matrices of the LOC- and the BOF-datasets was significant (r_{Sp}: 0.43, $P < 0.001$), indicating that there indeed was a correspondence between the patterns of variable associations at the two different spatial scales. This observation was confirmed by high correlation coefficients between the first and second PCA-axes of the LOC- and BOF-datasets, respectively (PCA1: $r = 0.70$, $P < 0.001$; PCA2: $r = 0.68$, $P < 0.001$). The high degree of concordance between the LOC and BOF datasets indicates that associations between variables are robust and shows that they are to a large degree scale independent, at least within the considered geographical region.

Patterns of association between variables were studied in more detail with standardized PCA and correlation analysis. The first two axes of the partial standardized PCA-analysis on the LOC-dataset explained in total 44.8% of the variation in the dataset (Eigenvalue PCA1; 24.2; Eigenvalue of PCA2: 20.6). The first axis of the PCA on the LOC-dataset was positively associated with surface area, the abundance of the studied biota (water plant cover, chlorophyll a concentration and zooplankton biomass), water plant species richness, alkalinity, pH and oxygen, and tended to be negatively correlated with altitude and nitrates. The second axis of the PCA was positively associated with chlorophyll a, oxygen and the thickness of the organic mud layer and negatively with depth, water transparency, alkalinity, water plant cover and water plant species richness (Fig. 3).

Detailed correlation analysis (Table 4) also confirmed associations between variables that were significant in both the BOF- and LOC- datasets, e.g. positive correlations between the coverage degree of macrophytes, macrophyte species richness, and zooplankton biomass; positive correlations between area, and macrophytes coverage and species richness; positive correlations between depth and water transparency, and positive correlations between pool surface area and pH (Table 4; Fig. 4). In the LOC-dataset, chlorophyll a was positively correlated to pH and O2, and negatively with depth. These tendencies were also found in the BOF-dataset, but not significant (Table 4).

There were, however, also differences in the patterns of variable associations between the LOC- and BOF-datasets. For example, associations of variables with altitude differed markedly between the datasets. Within localities, the average altitude range was 103 m and there was a negative association between altitude and pool surface area (Spearman rank correlation: $r_{SP} = -0.43$; $p = 0.017$), while no association was found between altitude and depth (Fig. 4). Within bofedales, the average altitude range was only 17 m and there was a negative association between altitude and depth, while no association was found between altitude and surface area (Fig. 4). In the LOC dataset, distance to the nearest rivulet was also positively correlated with surface area ($r = 0.50$; $p = 0.004$).

According to the PCA-results, the major gradient in pool characteristics was associated to variables that are typically associated to primary productivity in oligotrophic and poorly buffered freshwater systems, like alkalinity, pH and oxygen concentration. Indeed, biomass of the major biotic groups appeared to follow this gradient and suggest being bottom-up controlled. The productivity-associated gradient tended to decrease with increasing altitude within localities. Nitrates were negatively associated with this productivity gradient, suggesting that nitrate concentration is determined by the uptake from primary producers rather than that it limits the growth of these primary producers. Total phosphorus is difficult to evaluate as a potential limiting nutrient because the majority of

*Table 4. Matrix of product-moment correlation coefficients between some ecologically relevant variables. Correlations were separately calculated for two independent datasets: a dataset on the scale of localities (the LOC-dataset; down diagonal) and a dataset on the scale of individual bofedal peatlands (the BOF-dataset; above diagonal). See Table 2 for an explanation of the variable codes. *: P< 0.05; **: P<0.01; ***: P<0.001.*

	pH	TRANSP	ALTITUDE	DEPTH	AREA	WPCOV	WPSPR	ZOOPB
PH		0.13	0.16	0.08	0.66***	0.31	0.56***	0.21
TRANSP	-0.27		-0.19	0.54**	0.26	0.22	0.13	-0.04
ALTITUDE	-0.25	0.06		-0.38*	-0.06	0.25	0.33*	0.25
DEPTH	-0.14	0.56**	-0.01		0.15	0.30	0.32	0.00
AREA	0.47**	0.00	-0.23	0.21		0.34*	0.46**	0.01
WPCOV	0.11	0.20	-0.38*	0.17	0.35*		0.88***	0.34*
WPSPR	0.12	0.18	-0.19	0.17	0.35*	0.87***		0.48**
ZOOPB	0.46*	-0.21	-0.38*	0.14	0.37*	0.50**	0.47**	

the measurements were below the detection limit. In the following subsections, we discuss the results of regression analyses performed on the phytoplankton and water plant data collected at the LOC-scale.

Phytoplankton biomass

For chlorophyll a, depth and zooplankton biomass explained a total of 38 % of the variation. Associations with chlorophyll a were negative for depth and positive for zooplankton biomass (Table 5). Apart from the possibility of P-limitation, no other variables could be identified as possible determinants of phytoplankton biomass. Chlorophyll a concentration was positively instead of negatively associated with zooplankton biomass, which indicates that zooplankton is bottom-up controlled rather than that zooplankton grazing limits phytoplankton biomass through top-down control. Furthermore, there was no evidence for negative interactions between phytoplankton and water plant vegetations. Many studies in lake and pools of the temperate region have revealed negative associations between phytoplankton biomass and water plant cover (Scheffer 1998). Such negative associations have been explained by a variety of mechanisms, such as competition for nutrients and light or allelopathy. Compared to water plants phytoplankton is generally the weakest competitor for nutrients because phytoplankton entirely depends on nutrient concentrations in the water column, while plants can also rely on nutrients in the sediments. Especially under nutrient poor conditions, this is a major disadvantage for phytoplankton. Indeed, chlorophyll a concentrations were generally very low (75% of the observations below 18.2 $\mu g\ L^{-1}$), while water plants often covered the entire surface of pools. Nevertheless, there were no indications in the dataset for negative associations between phytoplankton and water plants. The negative relation between chlorophyll a and pool depth may be the result of lower resuspension rates of sedimented algae in the deeper pools.

Table 5. Results of multiple regression analyses performed for the dependent variables chlorophyll a, water plant cover and water plant species richness. The models were constructed with the explanatory variables that were retained with a forward selection procedure. See Table 2 for the explanation of the variable codes and for the lists of the variables that were originally subjected to the selection procedures. R^2: Coefficient of determination; β: standardized regression coefficient; Std.Err.: Standard error of β.

Chlorophyll a; R^2: 0.38; $p<0.001$

	β	Std.Err.	T(28)	p-level
Intercept		0.04	0.00	1.000
DEPTH	-0.53	0.19	-3.60	0.001
ZOOPB	0.39	0.06	2.63	0.013

Water plant cover; R^2: 0.73; $p<0.001$

	β	Std.Err.	t(26)	p-level
Intercept		0.08	1.95	0.061
ALK	0.71	0.19	6.61	<0.001
ORGMUD	-0.14	0.32	-1.42	0.164
DNR	-0.30	0.10	-2.54	0.017
AREA	0.27	0.12	2.24	0.033

Water plant species richness; R^2: 0.52; $p<0.0001$

	β	Std.Err.	t(25)	p-level
Intercept		0.03	0.00	1.000
ALK	0.58	0.10	4.38	<0.001
ORGMUD	-0.32	0.17	-2.46	0.020
NO_3	-0.25	0.10	-1.92	0.064

Water plant cover and water plant species richness

For water plant cover, a model constructed of alkalinity, pool surface area, distance to the nearest rivulet, and thickness of the organic mud layer explained 73% of the variation (Table 5). Alkalinity explained a relatively very high portion of the variation (Beta-coefficient = 0.71; $p < 0.001$). Alkalinity and area were positively associated with water plant cover. Water plant cover tended to decrease with increasing distance to the rivulets and with an increasing layer of mud on the sediments (Table 5; Fig. 5). Potentially important variables for water plants, like total phosphorus, nitrates or water transparency were not important in explaining water plant cover variation. Water plant species richness was strongly correlated with water plant cover ($r = 0.65$; $p = <0.001$). Water plant species richness was well explained by a model built on alkalinity, thickness of the organic mud layer and nitrates (total fraction of explained variation: 52%; Table 5). Water plant species richness showed positive associations with alkalinity and a negative association with organic mud and the nitrate concentration.

Macrophyte cover and diversity contribute to the structural heterogeneity of the aquatic environment (Scheffer 1998) and may therefore be steering factors for the functioning of the system (Jeppesen et al. 1997) and the abundance and diversity of higher trophic levels (Declerck et al. 2005). The strong positive associations between both variables and zooplankton biomass in our study exemplify this.

Pools with high degree of macrophyte coverage tended to be rich in macrophyte species. Ordinary correlation analysis revealed only a weak associa-

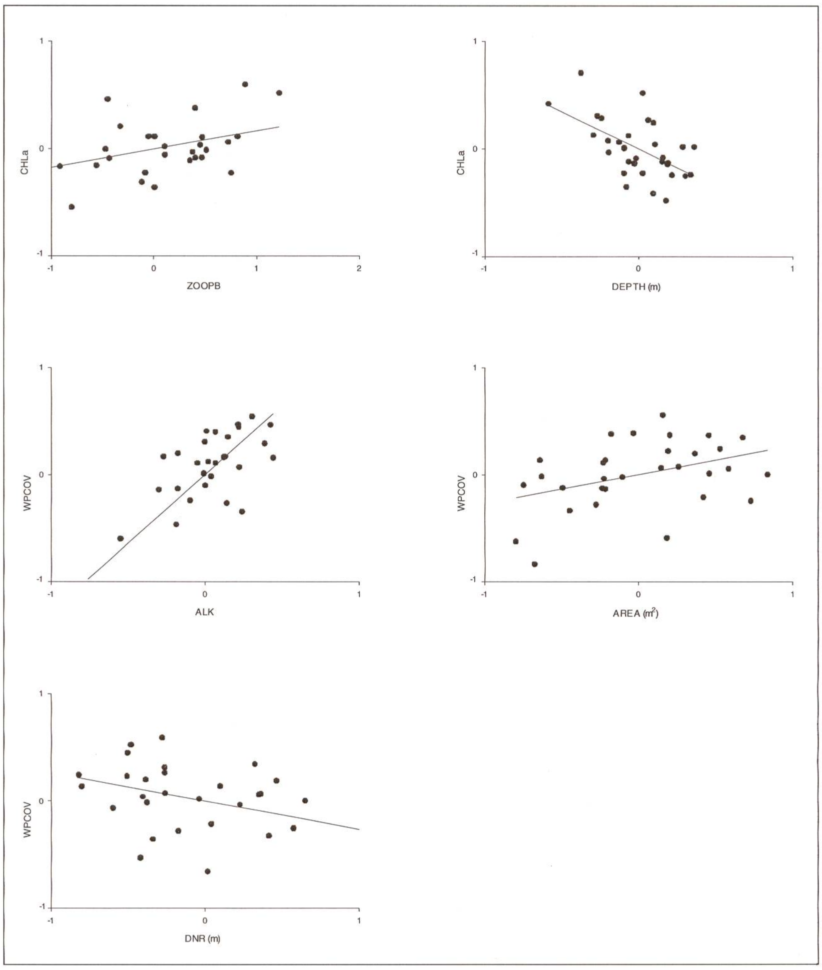


Figure 5. Scatter plots showing the associations of chlorophyll a concentrations and water plant cover with important explanatory variables. The plots represent partial correlation analyses as the variables in the plots are represented by residuals. These residuals were obtained from regression of the variables on the remaining variables in the multiple regression models specified in Table 5. See Table 5 for the detailed regression results. CHLa: chlorophyll a; ZOOPB: zooplankton biomass; WPCOV: water plant cover; DNR: distance to nearest rivulet; ALK: alkalinity.

tion between alkalinity and these variables. A minority of pools with very low alkalinity values tended to have no or only very sparse vegetation compared to pools with higher alkalinity, and there were exceptions to this pattern. However, upon adjustment of the data for locality specific differences and upon correction for variables like area and distance to the nearest rivulet through multiple regression analysis alkalinity was revealed as the most important variable in explaining variation in water plant cover and water plant species richness. The strong positive correlation between water plants and alkalinity may be indicative for carbon limitation of water plants in this type of poorly buffered systems. This result is in line with several other studies on temperate lakes in which alkalinity has been shown to be the main determinant of the richness of water plant species (Vestergaard and Sand-Jensen 2000).

There was also a negative association between water plant cover and distance to the nearest rivulets. Possibly, there exists a nutrient gradient as a function of the distance to rivulets: pools that are located close to rivulets may receive higher amounts of nutrients (like phosphorus) from rivulets than pools that are located at larger distances. Our nutrient analyses were based on water samples and may yield poor estimates of the total amount of nutrients that are present in the pool systems. We may have missed associations between nutrients and water plant cover because incoming nutrients from rivulets are probably immediately incorporated by vegetation.

The positive association between water plant cover and pool surface area may be related to trampling by cattle and llama. Trampling by large animals can be very destructive to water plant vegetations (Declerck et al. in prep.). Trampling is most intensive in small pools, whereas the central part of larger pools is probably less impacted. In addition to a positive effect of alkalinity, macrophyte species richness appeared to be negatively associated with the thickness of the organic mud layer on the sediments. Mud layers are often instable and anoxic and may form substrates that are unsuitable for water plant growth. The negative association with water plant species richness may indicate that only few water plants may cope with these suboptimal conditions.

Nitrates showed the tendency to be negatively correlated to water plant cover and water plant species richness, indicating that the concentrations of this nutrient seemed to be determined by water plants, rather than that the nutrient itself limited the growth of vegetation. In the area, llama herds are fairly abundant and it is possible that llama enrich the pools with nitrogen, leading to a relaxation of nitrogen limitation.

Conclusion

Our results show a high degree of variability for most limnological characteristics in the high-altitude peatland pools. Locality can explain part of this variation for physico-chemical variables but less for morphometric and biotic variables. Limnological variables also show pronounced differences between pools within localities as well as at the small spatial scale of individual bofedales. Patterns of variable associations are, nevertheless, to a large degree similar at the different spatial scales. PCA-analysis revealed a major gradient of variation for the biomass of different biota (macrophytes, phytoplankton, zooplankton) and for several physico-chemical variables that may reflect a gradient in primary productivity (pH, oxygen). Water plant cover and water plant species richness were positively associated with alkalinity, which may indicate an important degree of carbon limitation.

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