Relationships between aquatic invertebrates, water quality and vegetation in an Andean peatland system

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SUMMARY

Peatlands (known as *bofedales* in the Peruvian Andes) provide important social and environmental services in the Peruvian Puna ecoregion, especially as sources of water and forage for domestic livestock. In biological terms, these peatlands are key habitats with their own community structure, dynamics and interactions; and they serve as biodiversity hotspots within the High Andes. In this article we assess the relationships between: (i) physical structure, (ii) water quality, (iii) plant communities and (iv) the assemblages of aquatic invertebrates (benthic macroinvertebrates) in three peatlands located in Cuzco Region, southern Peru. The results suggest that the benthic macroinvertebrate assemblage is a good indicator of the trophic status of the small pools that are typically present in bofedales. Trophic status is, in turn, primarily related to spatial and seasonal water availability and the types of plant communities present in each peatland.

KEY WORDS: benthic invertebrates, bofedal, eutrophic processes, macroinvertebrate, seasonal fluctuation

INTRODUCTION

In comparison with complex forests and coastal mangrove swamps, inland peatlands are often regarded as species-poor habitats. However, their structural diversity and the associated variation in wetness can make them more diverse than the surrounding habitats (Desrochers & Duinen 2006). In fact, peatlands are complex ecosystems hosting many species that are found only or mainly in peatland habitats (Minayeva *et al.* 2008), as also reported by several authors for high-altitude peatlands in the Tropical Andes (Alzecarra *et al*. 2006, Squeo *et al*. 2006, Telleria *et al*. 2006, Maldonado Fonkén 2014).

The characteristic self-generated spatial heterogeneity of a peatland provides the environmental factors that define its biodiversity and species distribution at microtope and microform scale. For vegetation, microenvironments are distinguished on the basis of their typical plant species (Ruthsatz 2012); whose distribution is, in turn, associated with the availability of water throughout the year, livestock grazing, soil characteristics, water chemistry, *etc*. (Squeo *et al*. 2006, Cooper *et al*. 2010, Maldonado Fonkén 2014, Salvador *et al*. 2014). Thus, these environmental factors determine the distribution of plant communities and influence biodiversity indices.

In peatlands the influence of vegetation on aquatic invertebrates is related to the physical "building" arising from peat formation and the resulting microtopographical (pool-flat-hummock) features, accumulation of organic matter, and access to/influence over water sources (Verberk *et al*. 2006).

Smits *et al*. (2002) show clearly that the relative position of a pool affects diverse environmental conditions such as direct or indirect contact with minerotrophic surface water or groundwater, pH, nutrient availability, and the components and structure of the vegetation. These differences can lead to differentiation in the composition and structure of invertebrate assemblages, to the point that some species are found only in pools and hollows at the centre of a raised bog while others are found only in the transitional mire at its edges. Verberk *et al*. (2006) identify spatial heterogeneity as the most important defining factor for the diversity of aquatic invertebrates in bogs, and a key target for restoration efforts.

The use of aquatic organisms to assess water quality is a century-old approach (Kolkwitz & Marsson 1909). Microalgae (Rumeau & Coste 1988, O'Sullivan & Reynolds 2005, Stevenson & Rollins 2007), macrophytes (Gregg & Rose 1982) and fish (Karr 1981) have been used as indicators of ecological status in freshwater habitats; but of all the freshwater organisms that have been considered for use in biological monitoring, benthic macro-invertebrates (mainly aquatic insects, mites, molluscs, crustaceans and annelids) are most often recommended (Hellawell 1988, Bonada *et al*. 2006, Carter *et al*. 2007). Their utility is based on a series

of attributes (Rosenberg & Resh 1993): (i) being ubiquitous, they are affected by perturbations in all habitat and water body types; (ii) the large number of species offers a spectrum of responses to perturbations; (iii) the sedentary nature of many species allows spatial analysis of disturbance effects; (iv) their relatively long life cycles often exceed, and thus allow examination of, the temporally integrated effects of regular or intermittent perturbations, variable concentrations, *etc*.; (v) the taxonomy of many groups is well known and identification keys are available; (vi) many data analysis methods are available for macroinvertebrate assemblages; *etc*.

Despite their demonstrated utility as biological indicators, benthic macroinvertebrates have seldom been used as indicators of ecological quality or conservation status in wetlands and, especially, Neotropical peatlands. Only a few methods have been developed for wetlands (Doherty *et al*. 2000, Lane *et al*. 2003, Pilarczyk *et al*. 2007, Stewart *et al*. 2007). These methods are usually based on the Biotic Integrity Paradigm (Karr 1981, Karr & Chu 1997), which assumes the existence of a "typical community" defining the natural (ideal) condition. This paradigm ignores natural variability as well as the effect of naturally limiting harsh conditions, to which few species are adapted, that configure relatively species-poor habitats even if these habitats are not altered or of low quality. The applicability of traditional approaches to using macroinvertebrates as ecological indicators is also limited in (especially Andean) peatlands by the remarkable variability of water availability, which is responsible for clear differences in trophic status, nutrient availability, *etc*. (Siegel & Glaser 2006, Squeo *et al*. 2006).

In this research, we conduct a preliminary assessment of the relationships between the composition and structure of macroinvertebrate assemblages, water quality characteristics, physical features of peatland pools and vegetation characteristics, during two seasons (dry and wet) on three small Andean peatlands (bofedales) in the Cuzco Region of Peru.

METHODS

Site description

In the central Andes, bofedales are mostly confined to an altitude range of 3,200–5,000 m a.s.l. (Squeo *et al.* 2006). Our work was conducted at three typical sites in the Province of Chumbivilcas (Cuzco Region), with two (Sites 1 and 2) in the District of Chamaca and the third (Site 3) in the District of Velille (Figure 1, Table 1). Site 1 (S1; Figure 2) is a small (4 ha) peatland located on moderately sloping

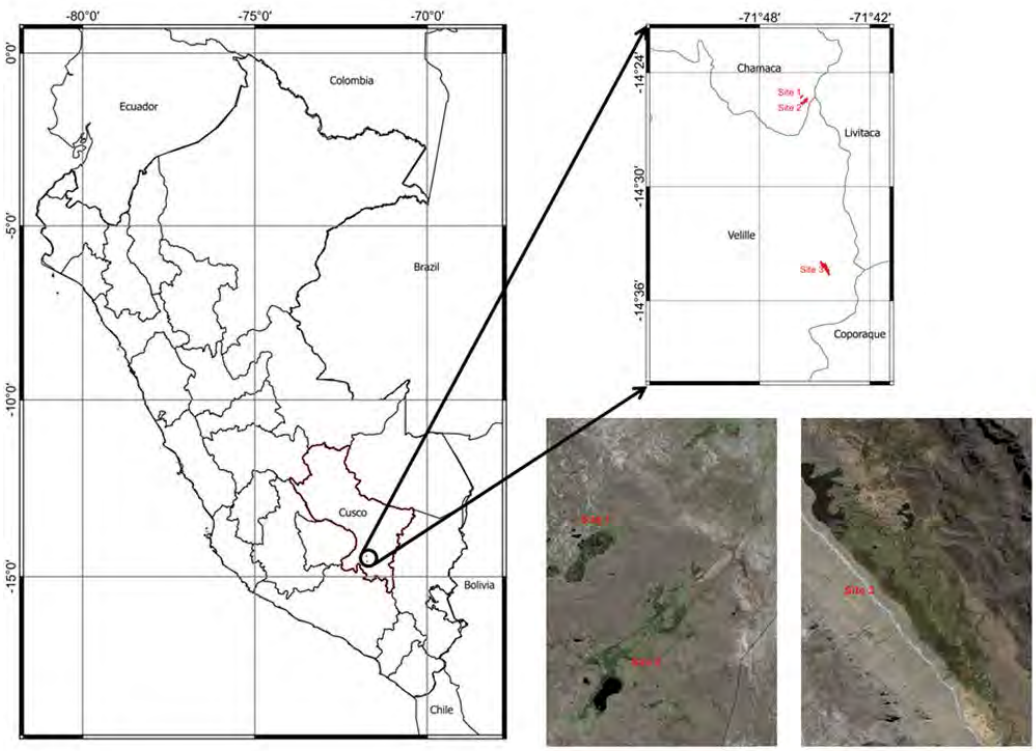

Figure 1. Maps showing (left) the location of Cuzco Region within Peru and (top right) the locations of the study sites in relation to local administrative boundaries; and aerial views (bottom right) of Sites 1, 2 and 3.

terrain, its altitude range is 4,652–4,667 m a.s.l., its length is 360 m (slope approximately 4.16 %), and it is dominated by a stream grassland plant community with small patches of *Distichia muscoides* Nees & Meyen (Maldonado Fonkén 2014). Site 2 (S2; Figure 3) is a steeply sloping peatland, approximately 10.45 ha in area, with an altitude range of 4,559–4,675 m a.s.l. and a length of 710 m (slope 16.34 %); the dominant plant community is *Distichia* peatland with small patches of stream grassland (Maldonado Fonkén 2014). Site 3 (S3) is the largest (29.87 ha; altitude 4,301–4,323 m a.s.l.; slope 1.08 %) and most distinctive of the three peatlands. Its dominant plant community is peaty meadow, but patches of *Distichia* peatland occur in a flatter area and it is crossed by a small stream. This site presents large, deep, unconnected or little-connected pools with slow water exchange rates (Figure 3).

Table 1. Locations (central points) of the three study sites.

District	**Peatland**	**Coordinates (UTM)** [Zone 18 South - WGS84]		**Altitude** (m a.s.l.)
Chamaca	Site 1 (S1)	202132	8403864	4,652 – 4,667
	Site 2 (S2)	202488	8403595	4,559 – 4,675
Velille	Site 3 (S3)	204590	8387398	4,301 – 4,323

Figure 2. Photograph showing a view across Site 1.

Figure 3. Photographs showing the situations and surface characteristics of Site 2 (above) and Site 3 (below).

Field sampling and data collection

The climate of the whole of Peru, and particularly of its southern parts, is characterised by alternating wet and dry seasons with five rainy months (December to April) and seven dry months (May to November) *per* year (Viparelli & Napoli 1982). For this reason, our field visits took place in July 2011 (dry season) and March 2012 (wet season).

Aquatic habitat and macroinvertebrates

Samples were collected from 18 sampling units during each visit (five at Site 1, eight at Site 2 and five at Site 3). Each sampling unit was a 25 × 25 m square (i.e. an area of 625 m²) of peatland where it was possible to identify a series of pool-hummock features. Within each sampling unit we collected:

- water quality data;
- benthic macroinvertebrate samples, by sweeping an aquatic D-frame-net over 1 m^2 of pool-bottom surface (four sub-samples of 0.25 m^3 each); and
- information about the physical quality of the pools as aquatic habitat, following an approach suggested by Doherty *et al.* (2000) (Table 2).

Vegetation

In each bofedal, eight (Site 2) or three (Sites 1 and 3) transects of length 50 m were evaluated using the repeated cover method (a type of point transect) recommended by Mateucci & Colma (1982) for grasslands. Species were identified in the field if possible, and otherwise by collecting specimens for later examination by a specialist at the National University of San Marcos. Ground cover was assigned to one of the following categories: bare soil, water, ice, litter, moss and (other) plants (total vegetation cover). Mosses were distinguished from other plants because they are relatively rare in bofedales at this latitude (Maldonado Fonkén 2015). The data were converted to percentage cover values for analysis.

Several attributes of the plant communities of each site were assessed. The plant species recorded were grouped into four categories, on the basis of our own field observations and published sources (León 1993, Tovar 1993, León & Young 1996, Salvador *et al*. 2006, Salvador *et al.* 2009). The categories were: aquatic plants (A), occasionally (intermittently) aquatic plants (O), species that develop in soils with high or constant humidity (Ws), and other plants. The abundance (percentage cover) of each of these four 'hydric' groups was calculated. We also computed the following diversity indices: Margalef richness (d), Pielou's evenness (J), Shannon-Wiener (log_2) (H) and Simpson's index of diversity (1-D) (Krebs 1989, Magurran 2004).

Table 2. Physical habitat survey protocol (attributes and scores) used to assess the characteristics and conditions of pool microhabitats. Based on Doherty *et al*. (2000) and Lane *et al.* (2003).

Attributes	Description	Score (points)
Peatland zone (or sector)	upper	1
	middle	2
	lower	4
General slope of the peatland zone	flat (< 2.5%)	1
	sloping (> 2.5%)	2
Pool size	small (< 2 m²)	1
	medium (2–5 m²)	2
	large (> 5 m²)	4
Pool connectivity	isolated	1
	connected, without flow	2
	connected, with flow	4
Pool depth	shallow (≤ 50 cm)	1
	deep (> 50 cm)	2
Substratum and vegetation	vegetation absent	1
	dominated by cyanobacteria	2
	dominated by filamentous algae	4
	macrophyte/moss dominated	8

Data analyses

For the data analyses, two numerical approaches were employed.

- First, to discriminate between sites and identify any seasonal or spatial trends in the macroinvertebrate data (only), a similarity analysis was performed by Non-Metric Multidimensional Scaling (NMDS) (Kruskal 1964, Rabinowitz 1975), and the groups thus identified were represented using convex hulls to differentiate the association patterns reflecting season, peat type, water availability, *etc*.
- The second analysis identified relationships between the composition of macroinvertebrate communities and environmental variables (e.g., physical habitat structure, water quality and plant

community). For this, a Canonical Correspondence Analysis (Ter-Braak 1995) was performed and the most important variables were identified by their correlations with the Canonical Axes 1 and 2.

RESULTS

The full results of the physical habitat survey can be found in Table A1 (Appendix). In terms of the physical characteristics recorded, there are only modest differences among the study sites and these characteristics can vary between wet and dry seasons, especially in the upper parts of Sites 1 and 2, where the reduction in water availability during the dry season causes the water table to retreat well below the mire surface. This significantly affects the depth of water in the pools and, consequently, their connectivity and water exchange rates (between pools and with the nearest streams). The differences in the measured chemical variables between sampling times (wet *versus* dry season) and sites (Sites 1 and 2 *versus* Site 3) were compared using a t-test (Table 3). Ten of the 12 chemical variables (Table A2) differed significantly between the two seasons, but only pH differed significantly between sites, with a higher mean value for Sites 1 and 2 (7.75) than for Site 3 (7.18). Comparing values obtained for the field-measured variables pH, electrical conductivity (EC) and dissolved oxygen (DO) concentration in the dry and wet seasons, pH and DO showed no significant differences. Only EC changed significantly between our two field visits, with average values of 76.24 µS cm^{-1} during the wet season and 102.71 µS cm^{-1} during the dry season. The increase can be related to the lower water exchange rate in the dry season, which is expected as a consequence of the reduction in water table levels and surface connectivity affecting the concentration of solutes. EC is clearly related to the NO_3^- concentration (measured in the laboratory), for which the mean value was also significantly higher during the dry season (0.093 mg L^{-1}) than during the wet season (0.043 mg L^{-1}).

Variation of macroinvertebrate assemblages among bofedales

The benthic macroinvertebrate fauna varied significantly with peatland vegetation type and water availability. The Non-Metric Multidimensional Scaling (NMDS) analysis demonstrates that the composition and structure of the assemblages present at Sites 1 and 2 were similar, and very different from those at Site 3 (Figure 4). The differences in taxon

Table 3. Results obtained from the t-tests comparing water quality variables between seasons and sites.

	Comparison between seasons (dry *versus* wet)		**Comparison between sites (S1 and S2 *versus* S3)**	
Water quality variables	**p-value**	**significance**	**p-value**	**Significance**
pH	0.34	n.s.	4.49E-06	**
Electrical conductivity (EC)	4.76E-07	**	0.57	n.s.
Dissolved Oxygen (DO)	0.25	n.s.	0.13	n.s.
Total alkalinity	1.03E-06	**	0.64	n.s.
Total hardness	0.007	**	0.65	n.s.
NO_3^-	6.66E-05	**	0.50	n.s.
Dissolved Phosphorus (P)	0.034	*	0.23	n.s.
Dissolved Potassium (K)	1.84E-10	**	0.83	n.s.
Total Phosphorus (TP)	0.0006	**	0.89	n.s.
Total Potassium (TK)	2.09E-10	**	0.79	n.s.
Biochemical O_2 Demand (BOD)	6.04E-12	**	0.37	n.s.
Chemical O_2 Demand (COD)	4.44E-05	**	0.90	n.s.

Significance codes: n.s. = not significant; *: significant at $\alpha = 0.05$; **: significant at $\alpha = 0.01$.

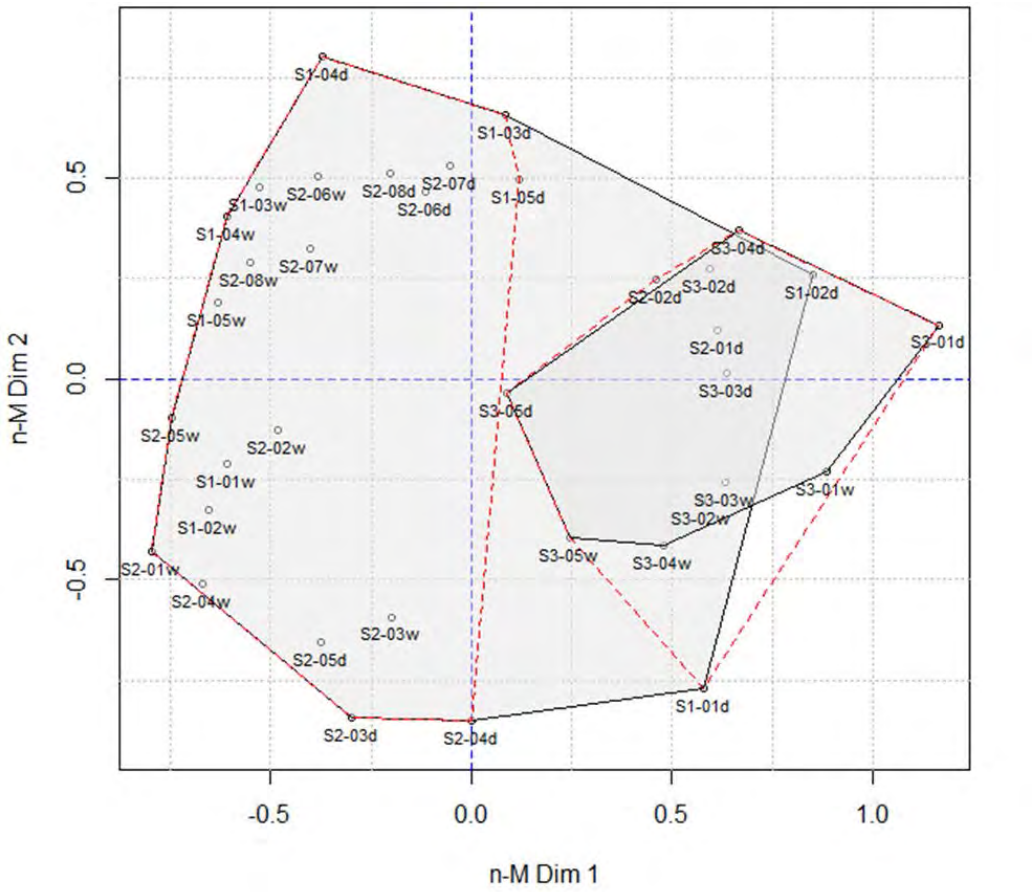

Figure 4. Scatter plot resulting from the NMDS analysis of macroinvertebrates assemblage composition. Grey convex hulls are based on a simple grouping method: Group 1 includes samples from Sites 1 and 2, and Group 2 contains samples from Site 3. Red convex hulls (dashed margins) are also based on a simple grouping: Group 1 includes almost all of the samples from Sites 1 and 2, and Group 2 contains samples from Site 3 plus samples collected from the upper and middle parts of Sites 1 and 2 during the dry season.

composition between stations located within Sites 1 and 2 (stream grassland and *Distichia* peatland) and the stations on Site 3 (peaty meadow in association with *Distichia* peatland) clearly differentiate the samples into two principal groups, with almost all of the samples from Sites 1 and 2 on the left-hand side and Site 3 samples, plus samples S1-01d, S1-02d, S2-01d and S2-02d, on the right, with an important overlap between the two groups. A detailed analysis demonstrated that this comprises four samples (S1-01d, S1-02d, S2-01d and S2-02d), all collected in the upper parts of the respective peatlands during the dry season. The occurrence of taxa by site and season is provided in Table A3.

Environmental variables *versus* macro-invertebrates community

Two Canonical Correspondence Analyses (CCA) were conducted using the family composition (presence and abundance) of the benthic invertebrates assemblage; the first with water quality variables and the second with physical habitat factors.

For the first CCA, which examined family composition (presence and abundance) of the benthic invertebrates assemblage and water quality variables (Figure 5), the first and second Canonical Axes represent 53 % of the total variability observed (eigenvalues). The correlation values (Pearson's r) between the water quality environmental variables (WQ) and the resultant first and second Canonical Axes (CA1 and CA2) are shown in Table 4. The most influential environmental variables (water quality) were Dissolved Oxygen (DO) and Chemical Oxygen Demand (COD). DO gave correlation values (Pearson's r) of 0.55 and 0.43 units with CA1 and CA2, respectively, while COD showed the strongest correlation with CA2 (r = -0.74 units). A detailed analysis of the samples ordination plot (Figure 6) reveals an organisation similar to that observed in the

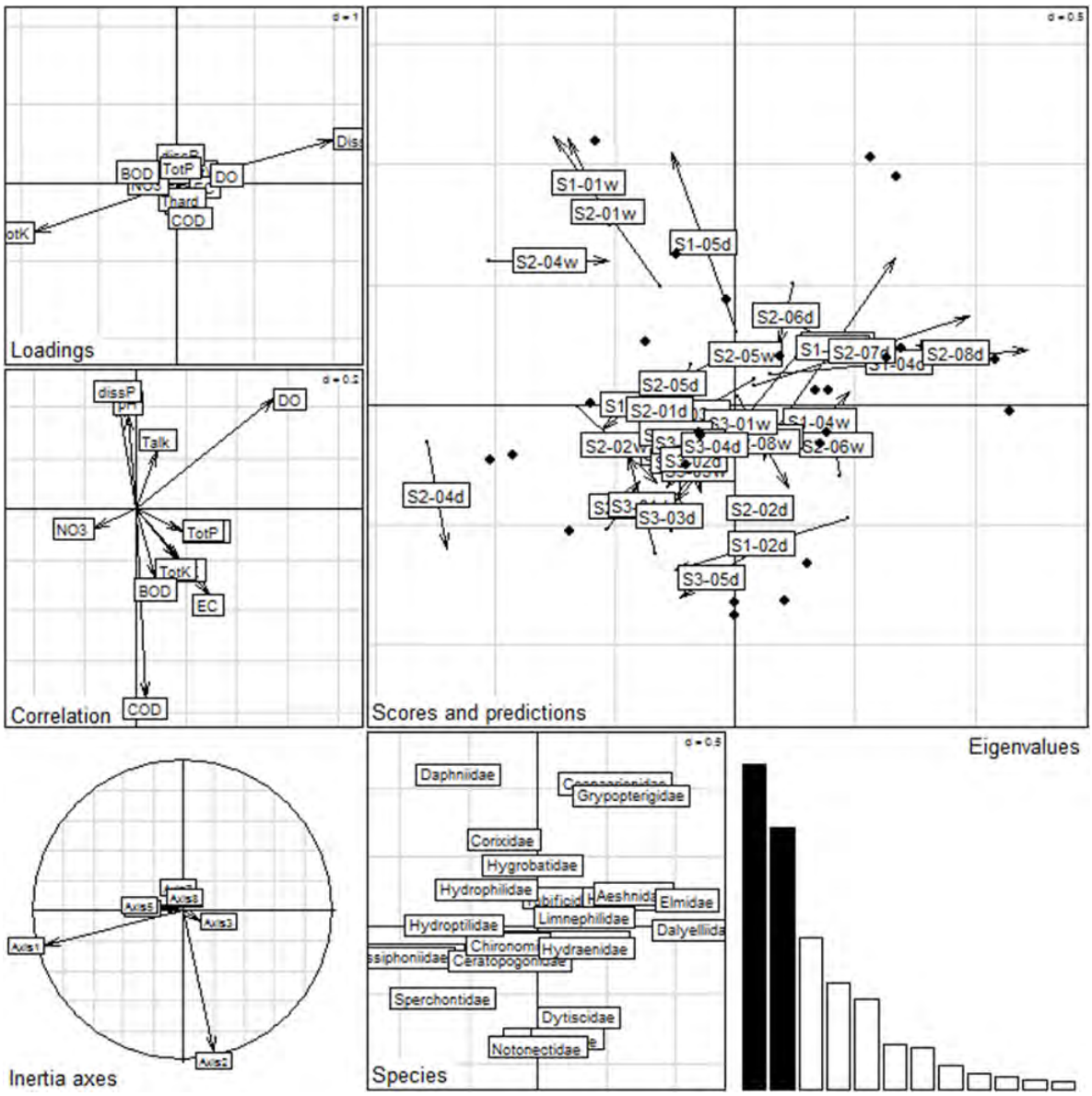

Figure 5. Canonical Correspondence Analysis (CCA) between water quality variables and benthic macroinvertebrate families.

Table 4. Correlation values (Pearson's r) between water quality variables and the first and second canonical axes. Grey cells: significant non-directional correlation at $\alpha = 0.05$.

Water quality variables	**CA1**	**CA2**	**Water quality variables**	**CA1**	**CA2**
pH	-0.03	0.37	Dissolved phosphorus	-0.07	0.42
Conductivity	0.29	-0.33	Dissolved potassium	0.18	-0.20
Dissolved oxygen	0.55	0.43	Total phosphorous	0.19	-0.09
Total alkalinity	0.09	0.23	Total potassium	0.16	-0.20
Total hardness	0.19	-0.09	Biochemical oxygen demand	0.08	-0.27
Nitrate (NO_3^-)	-0.16	-0.08	Chemical oxygen demand	0.04	-0.74

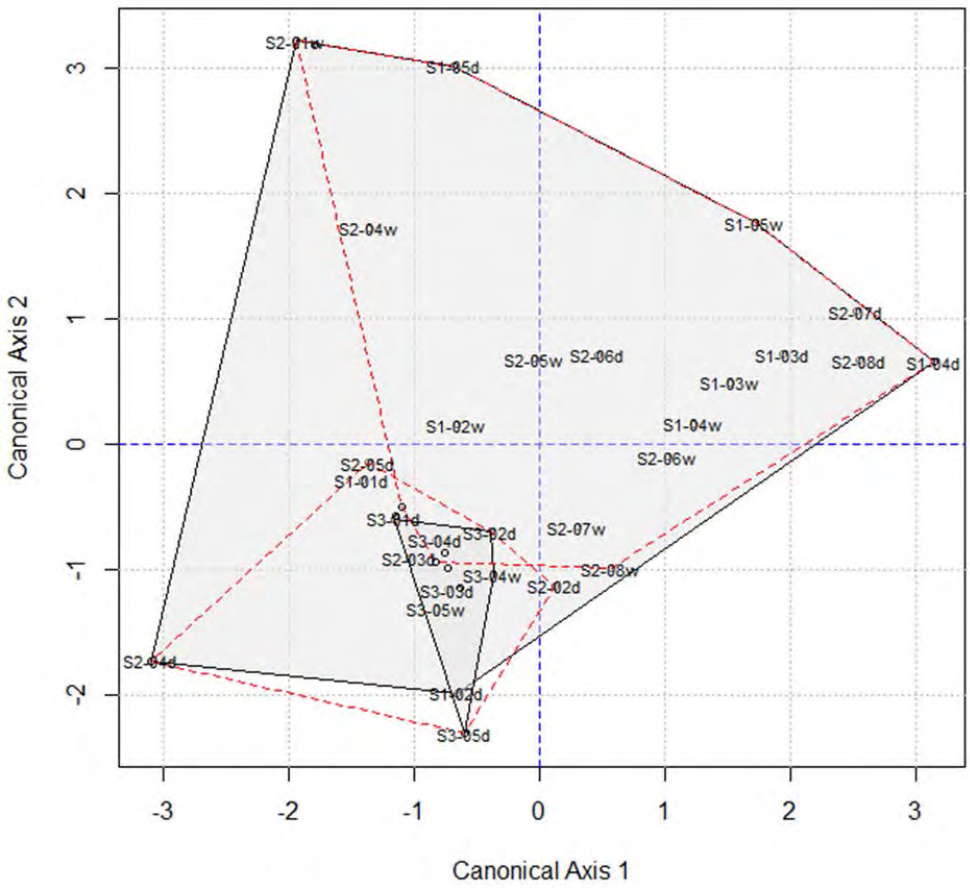

Figure 6. Sample scatter plot from the water quality *versus* macroinvertebrate families CCA. Grey convex hulls are based on a simple grouping method: Group 1 includes samples from Sites 1 and 2, and Group 2 contains samples from Site 3. Red convex hulls (dashed margins) are also based on a simple grouping: Group 1 includes almost all of the samples from Sites 1 and 2, and Group 2 contains samples from Site 3 plus samples collected from the upper and middle parts of Sites 1 and 2 during the dry season.

segregation analysis developed from the species composition data, with two very clear groups: (i) the first with a strong and very stable association between seasons, composed of samples collected at Site 3. The clustering patterns appear to reflect oxygen availability. The group composed of S3 samples plus selected S1 and S2 dry-season samples is located at the lower left-hand side of the ordination space, yielding negative values on CAs 1 and 2, axes with which DO is positively correlated. By contrast, almost all of the samples collected at Sites 1 and 2 during the wet season, and in the lower parts of these peatlands during the dry season, are placed in the positive range of at least one of CAs 1 and 2, in direct relation with the increase of DO concentrations. The remaining variables have the potential to determine differences in specific cases or within each of the groups, but are less important for the total dataset.

For the second CCA, examining family composition (presence and abundance) of the benthic invertebrates assemblage and physical habitat features (Figure 7), the first and second Canonical Axes represented 76 % of the total variability observed (eigenvalues). The correlation values (Pearson's r) between the environmental variables and the resultant first and second canonical axes (CA1and CA2) are shown in Table 5. The most influential habitat features were the relative location of the sample within the peatland site, with correlation values of -0.80 and 0.39 for CA1 and CA2 respectively, and the pool substrate cover (r = -0.86 for CA1). The samples are organised along CA1with relatively clear segregation patterns (Figure 8). At the left-hand side of CA1 (negative region) an important group of samples collected from Sites 1 and 2 are clustered without clear distinction between dry and wet seasons. On the opposite side (upper right of the ordination space), the samples collected at Site 3

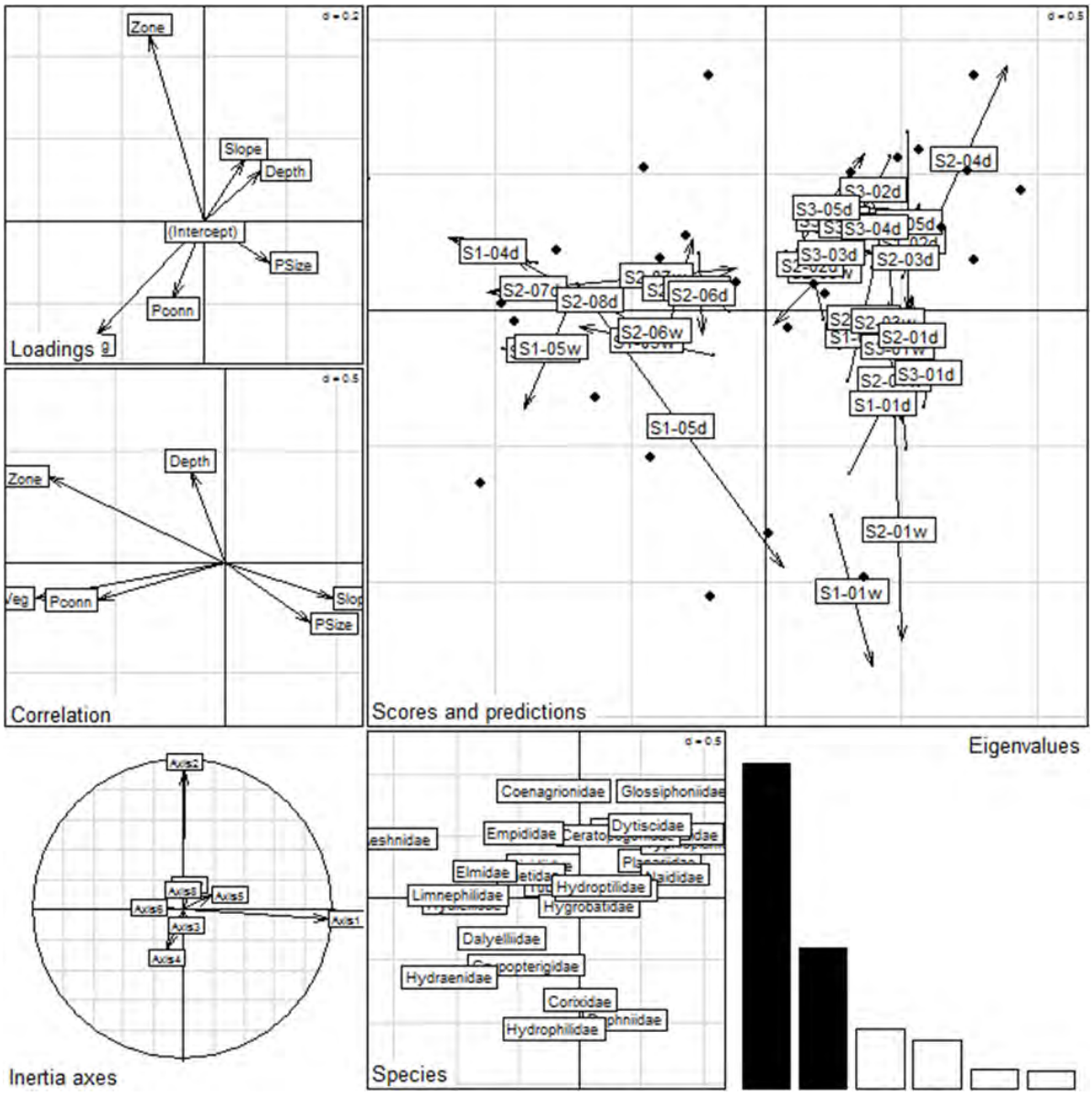

Figure 7. Canonical Correspondence Analysis (CCA) between physical habitat features and benthic macroinvertebrate families.

constitute a more compact group with very similar biological composition and stable environmental characteristics in both seasons. It is noteworthy that samples from Sites 1 and 2 (dry season) are strongly associated with the samples collected at Site 3 (dry and wet seasons). Samples from Sites 1 and 2 were collected in the upper and middle parts of the more typical steeply sloping peatlands (Sites 1 and 2), where the reduction in water availability during the dry season is more intense. This pattern is very similar to that observed in the previous analyses, and reinforces our appreciation of the importance of water availability and its relationship with nutrient availability and trophic levels in the pools.

Table 5. Correlation values (Pearson's r) between physical habitat features and the first and second Canonical Axes. Shaded cells indicate significant non-directional correlations at $\alpha = 0.05$.

Physical habitat features	CA1	CA2
Peatland zone	-0.80	0.39
General slope	0.48	-0.16
Pool size	0.38	-0.27
Pool connectivity	-0.57	-0.17
Pool depth	-0.16	0.41
Substratum/vegetation	-0.86	-0.16

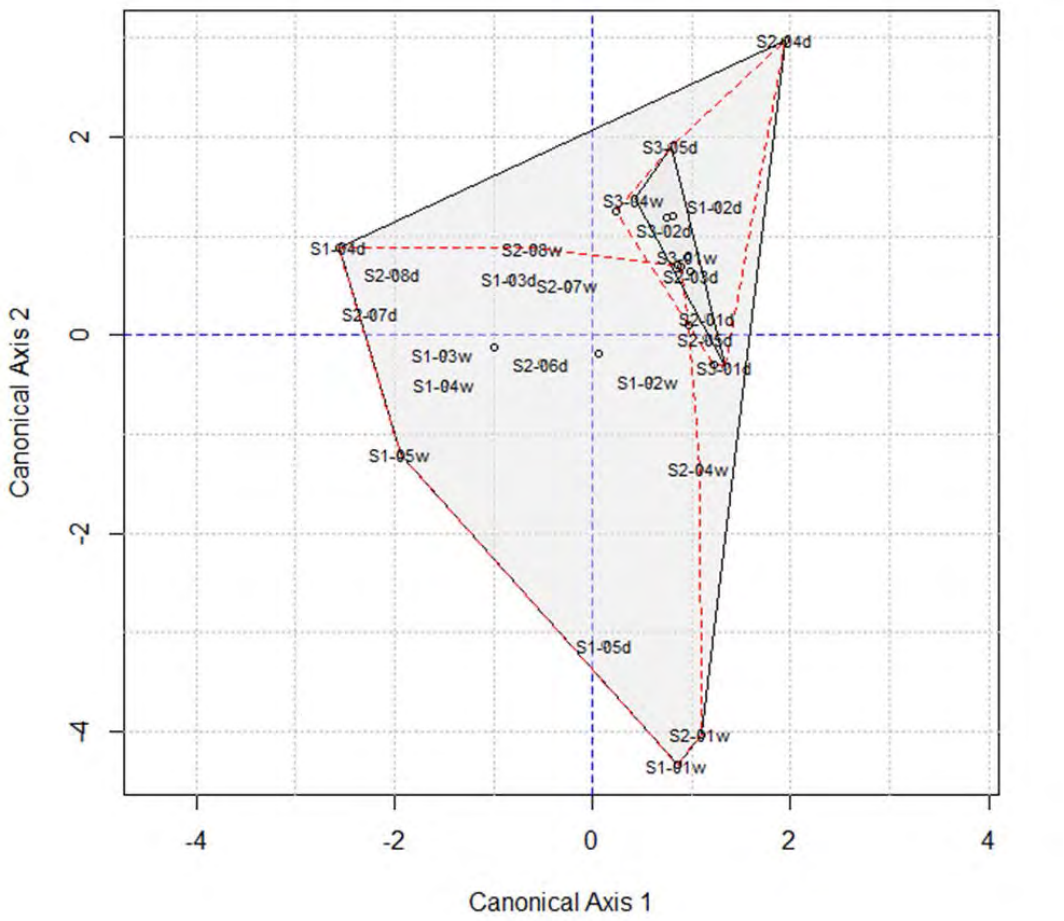

Figure 8. Sample scatter plot from the physical habitat *versus* macroinvertebrate families CCA. Grey convex hulls are based on a simple grouping method: Group 1 includes samples from Sites 1 and 2, and Group 2 contains samples from Site 3. Red convex hulls (dashed margins) are also based on a simple grouping: Group 1 includes almost all of the samples from Sites 1 and 2, and Group 2 contains samples from Site 3 plus samples collected from the upper and middle parts of Sites 1 and 2 during the dry season.

Plant community *versus* invertebrates assemblage

The CCA comparing all of the assessed attributes of the plant communities (Table A4) with the family composition (presence and abundance) of the benthic invertebrate assemblages is presented in Figure 9. In this analysis the first and second Canonical Axes represent 50.8 % of the total variability observed (eigenvalues). The vegetation attributes with the highest correlation values (Pearson´s r, Table 6) with Canonical Axes 1 and 2 are: percentage cover of aquatic plants (r = 0.39 and r = -0.31), water (r = -0.27 and r = 0.34), ice (r = 0.23 and r = 0.36), total vegetation cover (r = -0.04 and r = -0.49) and litter (r = -0.28 and r = -0.37). The samples ordination plot (Figure 10) exhibits a similar pattern to that observed in the previous analyses, with two main groups. The first is a very stable group composed of vegetation and macroinvertebrate samples from S3 in both seasons. This group is located mostly within the lower-left sector of the plot. The second group contains samples from S1 and S2, and shows more variability between samples than the first group; but, as observed in the previous analyses, the presence of samples collected in the upper and middle parts of S1 and S2 leads to an overlap between the two convex hulls (related with the spatial grouping factors). If Samples S2-01d and/or S2-02d are removed from the analysis, the segregation between the groups emerges more clearly, defined by the observed differences in composition and environmental characteristics.

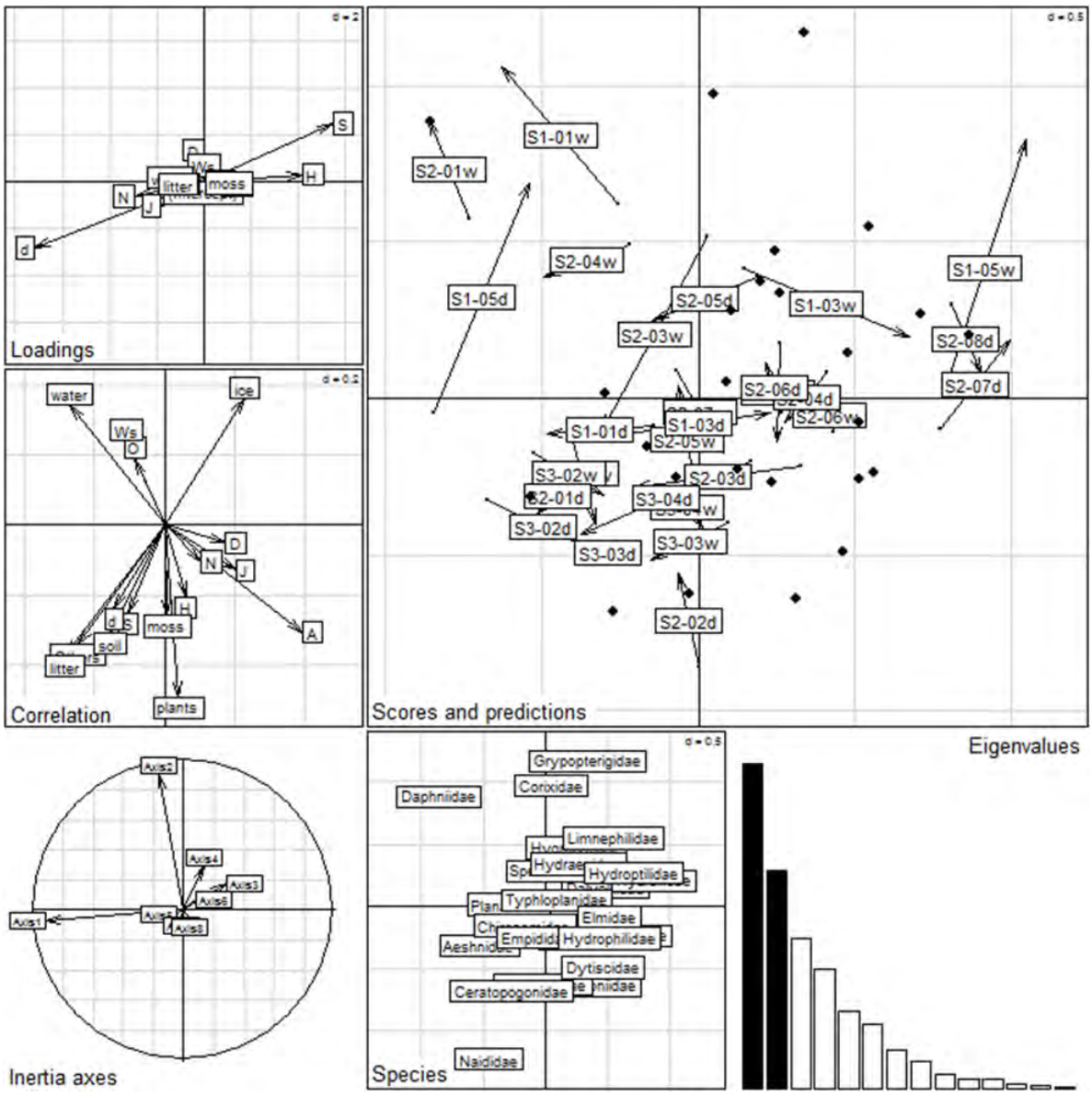

Figure 9. Canonical Correspondence Analysis (CCA) between plant community parameters and benthic macroinvertebrate families.

Table 6. Correlation values (Pearson's r) between plant community parameters and the first and second canonical axes. Grey cells: significant non-directional correlation at α = 0.05.

Plant community attributes	CA1	CA2	Plant community attributes	CA1	CA2
Number of species (S)	-0.10	-0.25	High humidity species (Ws)	-0.11	0.24
Abundance (N)	0.10	-0.10	Others	-0.25	-0.34
Margalef richness (d)	-0.15	-0.24	Bare soil	-0.16	-0.31
Pielou's evenness (J)	0.20	-0.13	Water	-0.27	0.34
Shannon-Wiener index (H)	0.06	-0.20	Ice	0.23	0.36
Simpson's index of diversity (1-D)	0.17	-0.05	Litter	-0.28	-0.37
Aquatic species (A)	0.39	-0.31	Moss	0.01	-0.26
Occasionally aquatic species (O)	-0.08	0.19	Plants	0.04	-0.49

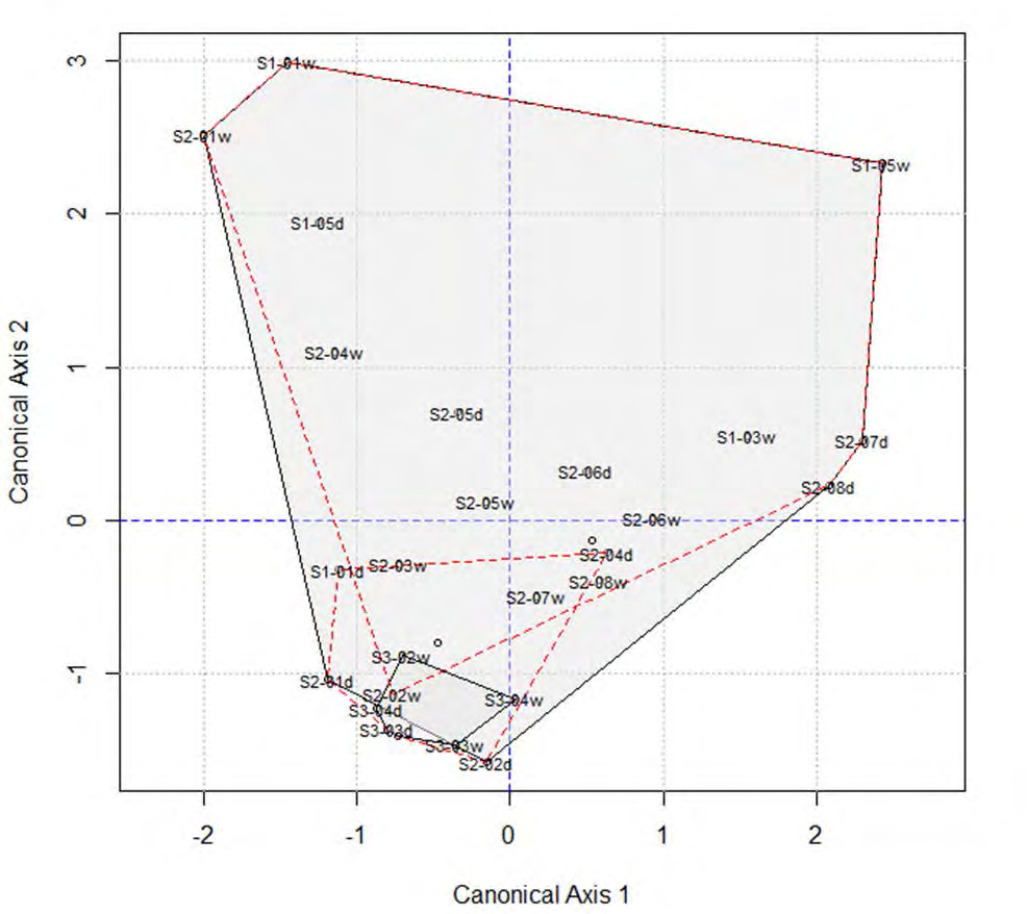

Figure 10. Sample scatter plot from the plant community *versus* macroinvertebrates families CCA. Grey convex hulls are based on a simple grouping method: Group 1 includes samples from Sites 1 and 2, and Group 2 contains samples from Site 3. Red convex hulls (dashed margins) are also based on a simple grouping: Group 1 includes almost all of the samples from Sites 1 and 2, and Group 2 contains samples from Site 3 plus samples collected from the upper and middle parts of Sites 1 and 2 during the dry season.

DISCUSSION

The relationships of physical structure, water quality and plant communities with aquatic invertebrates (benthic macroinvertebrates) assemblages all showed similar patterns, with samples from Site 3 forming a stable group and samples from Sites 1 and 2 forming a separate and more variable group. The variability in the three sites that we studied was associated with the spatial heterogeneity between peatlands and within each peatland. Seasonality usually increased the variability, especially because water availability/ presence was one of the key elements for the biological groups (plants and macroinvertebrates) assessed. High or low oxygen availability is also an important factor in defining the trophic status of aquatic habitats and usually influences the composition of the aquatic community (Wetzel 2001, O'Sullivan & Reynolds 2004, Lampert & Sommer 2007).

Pool water depth is a critical factor for the assemblages of macroinvertebrates in bofedales. It affects microhabitat availability, water quality, connectivity and water exchange rate, and thus influences the abundance and composition of species. Nevertheless, even though bofedal vegetation requires high water levels through the year (Alzerreca *et al*. 2006, Squeo *et al*. 2006, Maldonado Fonkén 2014), maintenance of the water table is not necessarily related to pool water depth.

Each of the three bofedales had a particular spatial heterogeneity, with differences between the sites in slope, vegetation composition, plant species abundance, micro-topographical features, and the presence of water bodies (small lakes, streams and pools). This heterogeneity was reflected in the

seasonal composition and abundance of the macroinvertebrate assemblages. Water availability was also strongly correlated with seasonality, especially in those peatlands (like Site 2) or zones of the peatlands (S1-01 and S1-02) that are isolated (because of slope or microtopography) without a permanent source of water. This was shown in the CCA analysis, where the relative location (zone of the peatland) of the sample was the most influential habitat feature. It is important to note that physical habitat features had a stronger influence than water quality variables on the macroinvertebrate assemblage.

Bofedales are usually complexes of different plant communities (Ruthsatz 2012, Maldonado Fonkén 2014) whose composition and abundance are related to water quantity and availability through the year, location, altitude, topography, exposure, latitude and livestock influence. Vegetation is directly related to macroinvertebrate micro-environments. According to the CCA, the most important habitat factors for invertebrates are the abundance of aquatic plants, water, ice, litter and vegetation cover. Again, seasonal and spatial water availability directly influences all of these elements. In this case, ground cover was a more useful indicator than diversity indices or plant community composition based on water requirements. The information that this simple metric provided as a habitat descriptor often provided a stronger correlation with the macroinvertebrate assemblage. Thus, it could be used as a 'fast and friendly' method to describe the micro-environmental characteristics of bofedales. A similar method was used successfully by Naoki *et al*. (2014) to quantify vegetation types and abiotic habitats in bofedales in Bolivia.

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Appendix

Table A1. Physical habitat data for pools within the 18 sampling units at Sites 1, 2 and 3 (S1, S2 and S3) in March 2012 (wet season) and July 2011 (dry season).

Season	Physical habitat features	Site-Sampling Unit																
		S1-01	**S1-02**	**S1-03**	**S1-04**	**S1-05**	**S2-01**	**S2-02**	**S2-03**	**S2-04**	**S2-05**	**S2-06**	**S2-07**	**S2-08**	**S3-01**	**S3-02**	**S3-03**	**S3-04**	**S3-05**
wet	Peatland zone	1	2	2	4	4	1	1	2	2	2	4	4	4	1	2	2	4	4
	General slope	1	1	1	1	1	2	2	2	2	2	1	1	1	1	1	1	1	1
	Pool size	4	4	2	2	2	4	2	4	4	2	4	2	4	4	2	2	4	4
	Pool connectivity	2	2	2	4	4	2	4	4	4	4	4	4	4	2	2	2	2	2
	Pool depth	1	1	1	1	2	1	2	1	1	2	2	2	2	2	2	2	2	2
	Substratum/vegetation	4	1	4	8	8	4	4	2	2	2	8	8	8	4	1	2	4	4
	Total Score	**13**	**11**	**12**	**20**	**21**	**14**	**15**	**15**	**15**	**14**	**23**	**21**	**23**	**14**	**10**	**11**	**17**	**17**
dry	Peatland zone	1	2	2	4	4	1	1	2	2	2	4	4	4	1	2	2	4	4
	General slope	1	1	1	1	1	2	2	2	2	2	1	1	1	1	1	1	1	1
	Pool size	4	4	2	2	2	4	2	4	4	2	4	2	4	4	2	2	4	4
	Pool connectivity	1	1	1	2	4	1	1	2	2	2	2	4	4	1	1	1	1	1
	Pool depth	1	1	1	1	2	1	1	1	1	2	2	2	2	2	2	1	2	1
	Substratum/vegetation	4	1	4	8	8	4	4	2	2	2	8	8	8	4	1	2	4	4
	Total Score	**12**	**10**	**11**	**18**	**21**	**13**	**11**	**13**	**13**	**12**	**21**	**21**	**23**	**13**	**9**	**9**	**16**	**15**

Table A2. Values of water quality variables recorded for the sampling locations. BOD = Biochemical Oxygen Demand; COD = Chemical Oxygen Demand.

Season	Variable	Units	S1-01	S1-02	S1-03	S1-04	S1-05	S2-01	S2-02	S2-03	S2-04	S2-05	S2-06	S2-07	S2-08	S3-01	S3-02	S3-03	S3-04	S3-05
wet	pH	Standard unit	8.02	8.25	8.01	7.78	7.52	7.48	8.08	8.01	7.86	7.58	7.52	7.76	7.68	6.85	7.46	7.51	7.28	7.15
	Conductivity	µS cm^{-1}	72.1	91.9	76.3	79.8	69.4	70.0	69.5	83.5	63.4	71.5	85.0	87.2	96.2	73.3	61.9	78.2	59.5	83.7
	Dissolved oxygen	mg L^{-1}	6.23	6.38	7.15	6.81	7.26	6.95	6.48	7.22	5.18	7.48	7.51	7.22	7.41	6.86	6.38	6.41	7.02	5.86
	Total alkalinity	mg $CaCO_3$ L^{-1}	16.1	21.7	28.1	26.6	24.7	28.2	18.5	29.8	23.3	21.1	21.0	29.5	15.2	26.1	26.3	20.9	22.7	18.5
	Total hardness	mg $CaCO_3$ L^{-1}	26.9	17.9	18.3	25.8	18.6	16.7	28.1	15.6	19.8	27.3	28.2	22.5	21.9	25.7	22.8	28.3	18.8	21.7
	Nitrate (NO_3^-)	mg L^{-1}	0.047	0.003	0.003	0.050	0.010	0.070	0.080	0.060	0.010	0.080	0.030	0.070	0.080	0.040	0.050	0.020	0.050	0.020
	Dissolved phosphorus	mg L^{-1}	0.06	0.02	0.06	0.06	0.02	0.04	0.03	0.05	0.05	0.03	0.00	0.03	0.02	0.05	0.06	0.00	0.00	0.01
	Dissolved potassium	mg L^{-1}	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.000	0.001	0.001
	Total phosphorus	mg L^{-1}	0.09	0.05	0.09	0.05	0.04	0.06	0.06	0.05	0.08	0.09	0.11	0.07	0.07	0.04	0.04	0.09	0.04	0.10
	Total potassium	mg L^{-1}	0.002	0.002	0.002	0.002	0.002	0.002	0.002	0.002	0.002	0.002	0.002	0.002	0.002	0.002	0.002	0.010	0.002	0.002
	BOD	mg L^{-1}	3	4	2	3	3	4	5	2	5	3	4	3	5	3	4	3	2	2
	COD	mg L^{-1}	6	14	9	13	10	5	11	9	6	8	11	8	11	6	11	7	5	8
dry	pH	Standard unit	8.54	8.52	7.81	7.25	7.51	8.02	7.51	7.23	7.48	7.15	7.89	7.41	7.50	7.17	7.25	6.88	7.02	7.21
	Conductivity	µS cm^{-1}	125.1	113.2	107.8	126.8	104.8	92.9	97.7	104.2	109.8	80.6	79.6	89.0	109.5	89.2	98.7	89.8	125.1	104.9
	Dissolved oxygen	mg L^{-1}	4.11	6.44	7.07	5.51	7.40	7.43	7.12	4.54	3.47	8.22	8.56	7.07	8.52	7.54	4.59	3.20	6.24	5.68
	Total alkalinity	mg $CaCO_3$ L^{-1}	18.4	18.4	12.0	17.1	11.7	10.5	11.7	19.2	17.1	17.2	17.6	14.5	20.0	11.7	15.0	12.8	18.9	13.4
	Total hardness	mg $CaCO_3$ L^{-1}	24.6	25.2	29.5	29.5	31.8	16.9	34.9	28.1	23.3	25.6	29.6	22.4	28.9	23.9	29.2	25.3	39.4	20.1
	Nitrate (NO_3^-)	mg L^{-1}	0.061	0.058	0.040	0.060	0.130	0.060	0.070	0.080	0.140	0.080	0.100	0.110	0.090	0.140	0.120	0.140	0.150	0.040
	Dissolved phosphorus	mg L^{-1}	0.05	0.04	0.05	0.07	0.06	0.04	0.05	0.06	0.08	0.06	0.06	0.02	0.03	0.03	0.05	0.02	0.08	0.02
	Dissolved potassium	mg L^{-1}	2.628	3.135	4.965	1.985	1.960	3.650	2.290	2.650	1.840	3.200	3.080	3.810	2.040	4.080	2.150	4.330	3.150	2.010
	Total phosphorus	mg L^{-1}	0.08	0.08	0.08	0.11	0.11	0.11	0.10	0.08	0.08	0.10	0.08	0.09	0.09	0.08	0.11	0.09	0.09	0.11
	Total potassium	mg L^{-1}	2.687	3.643	5.892	2.641	2.900	5.110	3.270	3.780	2.740	4.890	4.180	5.020	2.550	6.440	2.580	5.100	4.500	2.770
	BOD	mg L^{-1}	7	8	8	9	7	8	11	9	8	9	7	6	7	5	7	6	9	8
	COD	mg L^{-1}	11	19	13	13	11	14	21	17	15	12	9	9	9	14	15	14	12	19

Table A3. Species and morphospecies of benthic macroinvertebrates recorded at the sampling locations.

PHYLUM	CLASS	ORDER	FAMILY	Taxon (species or morphospecies)	wet season			dry season		
					S1	S2	S3	S1	S2	S3
PLATYHELMINTHES	TURBELLARIA	TRICLADIDA	Planariidae	*Girardia festae* (Borelli, 1898)	X	X	X		X	
PLATYHELMINTHES	TURBELLARIA	TRICLADIDA	Planariidae	*Dugesia* sp.1	X	X	X			X
PLATYHELMINTHES	TURBELLARIA	NEORHABDOCOELA	Dalyelliidae	*Gieysztoria* sp.1	X	X		X		
PLATYHELMINTHES	TURBELLARIA	NEORHABDOCOELA	Typhloplanidae	*Mesostoma* sp.1		X			X	
ANNELIDA	CLITELLATA	HAPLOTAXIDA	Tubificidae	*Epirodrilus antipodum* Cernosvitov, 1939	X	X	X			
ANNELIDA	CLITELLATA	HAPLOTAXIDA	Tubificidae	*Pristinella* sp.1	X		X	X	X	
ANNELIDA	CLITELLATA	HAPLOTAXIDA	Naididae	*Nais* sp.1	X	X	X	X	X	X
ANNELIDA	CLITELLATA	RHYNCHOBDELLIDA	Glossiphoniidae	*Helobdella* sp.1			X		X	
MOLLUSCA	BIVALVIA	VENEROIDA	Pisidiidae	*Pisidium meierbrooki* Kuiper & Hinz, 1984		X	X	X	X	X
ARTHROPODA	BRANCHIOPODA	DIPLOSTRACA	Daphniidae	*Ceriodaphnia quadrangula* (Müller, 1785)	X	X		X	X	X
ARTHROPODA	BRANCHIOPODA	DIPLOSTRACA	Daphniidae	*Daphnia* sp.1	X	X				
ARTHROPODA	BRANCHIOPODA	DIPLOSTRACA	Daphniidae	*Scapholeberis* sp.1	X					X
ARTHROPODA	MALACOSTRACA	AMPHIPODA	Hyalellidae	*Hyalella simplex* Schellenberg, 1943	X	X	X	X	X	
ARTHROPODA	MALACOSTRACA	AMPHIPODA	Hyalellidae	*Hyalella jelskii* (Wrzesniowski, 1879)	X	X			X	
ARTHROPODA	MALACOSTRACA	AMPHIPODA	Hyalellidae	*Hyalella pteropus* Schellenberg, 1943		X				
ARTHROPODA	MALACOSTRACA	AMPHIPODA	Hyalellidae	*Hyalella* sp.1	X	X		X	X	X
ARTHROPODA	MALACOSTRACA	AMPHIPODA	Hyalellidae	*Hyalella* sp.2			X		X	X
ARTHROPODA	ARACHNIDA	ACARI	Hygrobatidae	*Hygrobatella* sp.1	X		X	X	X	X
ARTHROPODA	ARACHNIDA	ACARI	Hygrobatidae	*Hygrobatella* sp.2	X	X		X	X	
ARTHROPODA	ARACHNIDA	ACARI	Sperchontidae	*Sperchonopsis* sp.1		X	X	X	X	X
ARTHROPODA	INSECTA	ODONATA	Coenagrionidae	*Protallagma titicacae* (Calvert, 1909)					X	X
ARTHROPODA	INSECTA	ODONATA	Aeshnidae	*Rhionaeschna* sp.1				X		X
ARTHROPODA	INSECTA	EPHEMEROPTERA	Baetidae	*Andesiops peruvianus* (Ulmer, 1920)	X	X		X	X	
ARTHROPODA	INSECTA	EPHEMEROPTERA	Baetidae	*Baetodes* sp.1			X	X	X	X
ARTHROPODA	INSECTA	PLECOPTERA	Grypopterigidae	*Claudioperla tigrina* (Klapalek, 1904)	X					
ARTHROPODA	INSECTA	HEMIPTERA	Corixidae	*Ectemnostega quechua* (Bachman, 1961)	X			X		

PHYLUM	CLASS	ORDER	FAMILY	Taxon (species or morphospecies)	wet season			dry season		
					S1	S2	S3	S1	S2	S3
ARTHROPODA	INSECTA	HEMIPTERA	Corixidae	*Ectemnostegella* sp.1	X	X				
ARTHROPODA	INSECTA	HEMIPTERA	Corixidae	*Dasycorixa* sp.1	X	X			X	
ARTHROPODA	INSECTA	HEMIPTERA	Notonectidae	*Notonecta* sp.1			X	X		X
ARTHROPODA	INSECTA	DIPTERA	Ceratopogonidae	*Atrichopogon* sp.1		X	X		X	X
ARTHROPODA	INSECTA	DIPTERA	Ceratopogonidae	*Bezzia* sp.1		X			X	
ARTHROPODA	INSECTA	DIPTERA	Chironomidae	*Alotanypus* sp.1	X	X	X			
ARTHROPODA	INSECTA	DIPTERA	Chironomidae	*Cardiocladius* sp.1				X	X	X
ARTHROPODA	INSECTA	DIPTERA	Chironomidae	*Cricotopus* sp.1			X	X		X
ARTHROPODA	INSECTA	DIPTERA	Chironomidae	*Cricotopus* sp.2	X	X			X	
ARTHROPODA	INSECTA	DIPTERA	Chironomidae	*Cricotopus* sp.3	X	X	X	X	X	X
ARTHROPODA	INSECTA	DIPTERA	Chironomidae	*Limnohyphes* sp.1					X	
ARTHROPODA	INSECTA	DIPTERA	Chironomidae	*Parametriocnemus* sp.1		X	X			
ARTHROPODA	INSECTA	DIPTERA	Chironomidae	*Pentaneura* sp.1			X	X	X	X
ARTHROPODA	INSECTA	DIPTERA	Chironomidae	*Polypedilum* sp.1	X	X		X	X	
ARTHROPODA	INSECTA	DIPTERA	Chironomidae	*Podonomus* sp.1				X	X	X
ARTHROPODA	INSECTA	DIPTERA	Chironomidae	*Podonomus* sp.2				X	X	
ARTHROPODA	INSECTA	DIPTERA	Chironomidae	*Podonomus* sp.3					X	
ARTHROPODA	INSECTA	DIPTERA	Chironomidae	*Tanytarsus* sp.1	X	X				
ARTHROPODA	INSECTA	DIPTERA	Chironomidae	Chironiminae undet.1			X		X	X
ARTHROPODA	INSECTA	DIPTERA	Empididae	*Neoplasta* sp.1				X	X	X
ARTHROPODA	INSECTA	COLEOPTERA	Dytiscidae	*Rhantus signatus* (Fabricius, 1775)					X	
ARTHROPODA	INSECTA	COLEOPTERA	Dytiscidae	*Lancetes praemorsa* (Erichson, 1834)				X	X	X
ARTHROPODA	INSECTA	COLEOPTERA	Elmidae	*Austrelmis consors* Hinton, 1940	X	X		X	X	X
ARTHROPODA	INSECTA	COLEOPTERA	Hydraenidae	*Hydraena* sp.1	X	X				
ARTHROPODA	INSECTA	COLEOPTERA	Hydrophilidae	*Tropisternus* sp.1				X	X	
ARTHROPODA	INSECTA	TRICHOPTERA	Hydroptilidae	*Leucotrichia* sp.1			X	X	X	X
ARTHROPODA	INSECTA	TRICHOPTERA	Hydroptilidae	*Metrichia* sp.1	X	X		X	X	
ARTHROPODA	INSECTA	TRICHOPTERA	Limnephilidae	*Antarctoecia* sp.1	X	X	X	X		

Table A4. Vegetation data. Key to abbreviated column headings: A = aquatic species; d = Margalef richness index; H = Shannon-Wiener index (log_2); J = Pielou's evenness; N = abundance (percentage cover) of all vegetation; O = occasionally aquatic species; others = plant species without specific hydric requirements; S = number of species; Ws = plant species that grow in soils with high or constant humidity;1-D = Simpson's index of diversity.

Season	Transect	S	N (%)	Diversity indices				% cover of hydric groups				Ground cover (%)					
				d	J	H	1-D	A	O	Ws	others	bare	water	ice	litter	moss	plants
wet	S2-01	11	86	2.24	0.74	2.57	0.74	14	70	0	2	2	78	0	0	0	20
	S2-02	15	100	3.04	0.85	3.31	0.87	20	74	4	2	0	56	0	2	2	40
	S2-03	12	140	2.23	0.88	3.17	0.87	10	112	18	0	6	36	0	0	0	58
	S2-04	15	154	2.78	0.76	2.96	0.83	0	140	10	4	2	14	0	0	0	84
	S2-05	15	174	2.71	0.80	3.13	0.84	6	152	8	8	6	4	0	0	0	90
	S2-06	14	158	2.57	0.80	3.05	0.84	44	112	2	0	0	22	72	2	0	4
	S2-07	15	168	2.73	0.78	3.05	0.83	58	102	6	2	0	18	76	0	0	6
	S2-08	14	168	2.54	0.81	3.09	0.84	34	122	12	0	2	10	76	0	0	12
	S1-01	12	154	2.18	0.75	2.69	0.79	6	134	8	6	0	22	62	0	0	16
	S1-03	12	114	2.32	0.80	2.85	0.81	10	92	2	10	2	38	30	0	0	30
	S1-05	15	140	2.83	0.89	3.49	0.89	10	120	10	0	2	38	2	0	0	58
	S3-02	13	178	2.32	0.74	2.75	0.77	24	148	6	0	0	22	0	0	0	78
	S3-03	16	132	3.07	0.83	3.32	0.87	24	98	2	8	8	38	0	0	4	50
	S3-04	13	160	2.36	0.86	3.18	0.87	38	118	4	0	8	44	0	0	0	48
dry	S2-01	10	94	1.98	0.45	1.51	0.41	10	84	0	0	10	28	0	12	2	48
	S2-02	16	116	3.16	0.88	3.53	0.88	38	66	2	10	6	28	0	6	0	60
	S2-03	11	102	2.16	0.85	2.95	0.83	12	78	4	8	2	20	6	10	0	62
	S2-04	12	110	2.34	0.80	2.88	0.82	4	92	4	10	12	12	0	0	0	76
	S2-05	11	106	2.14	0.84	2.92	0.84	0	76	14	16	8	2	20	4	2	64
	S2-06	8	116	1.47	0.77	2.30	0.74	50	62	0	4	10	10	16	0	0	64
	S2-07	9	126	1.65	0.74	2.34	0.72	60	66	0	0	0	12	2	0	2	84
	S2-08	10	106	1.93	0.79	2.62	0.79	16	84	6	0	4	14	14	4	2	62
	S1-01	8	118	1.47	0.76	2.27	0.75	2	110	2	4	8	0	2	12	0	78
	S1-03	12	118	2.31	0.81	2.89	0.81	8	92	12	6	26	0	0	6	0	68
	S1-05	15	110	2.98	0.86	3.36	0.88	16	68	22	4	16	12	0	12	4	56
	S3-02	8	116	1.47	0.71	2.14	0.67	0	96	2	18	8	0	0	14	0	78
	S3-03	15	154	2.78	0.87	3.41	0.89	22	92	6	34	6	2	0	2	2	88
	S3-04	12	114	2.32	0.75	2.68	0.76	54	58	0	2	16	20	2	0	0	62