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Full title

Macroclimate and local hydrological regime as drivers of fen vegetation patterns in Tierra del Fuego (Argentina)

Short title

Fen vegetation patterns in Tierra del Fuego (Argentina)

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Data availability

The data that support the findings of this study are openly available in OSF at https://osf.io/ghrv3/quickfiles, reference code

Perez-Haase_et_al_Tierra_del_Fuego_data.tsv.

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Abstract

In southern South America a sharp macroclimatic gradient is found, triggered by the Pacific oceanic influence through the Andes. Mires are substantial landscape units along the gradient, where they play varying roles through the area and include varying plant communities. In this study we analysed the relationship between vegetation and main abiotic factors in the minerotrophic mires (fens) at two different scales.

We chose three fens in Isla Grande from Cordillera and Magellanic Steppe zones, and their ecotone. There we characterized the distinct habitats by means of monitoring the water table fluctuations, the peat and the groundwater chemistry, and the vascular plant species composition.

The main floristic patterns were revealed by means of classification and ordination of 75 vegetation plots. Thus, we classified the relevés through multivariate analyses into six plant community types, two of which found in each fen. Behind the floristic distinctiveness of each site and each community type, structural vegetation descriptors such as species richness were similar. Overall, water table variables and groundwater chemistry showed the most important environmental differences between fens.

Our data point that the main environmental force driving vegetation patterns was the macroclimatic gradient, which shapes the regional floristic pools. This gradient would be also responsible for modifying the local conditions of the fen habitats, mostly in the form of broadening the hydrological conditions within the fens of the Steppe. At each fen, the hydrological regime is the main factor in the distribution of vascular plants, particularly through the varying water table depths.

Keywords: ecological gradients; biogeographic shifts; hydrological regime; mires; South America



Introduction

In Tierra del Fuego, at the southern part of South America, the Andes range triggers a strong precipitation gradient that follows the SW-NE direction. Humid southern winds blow in southernmost Tierra del Fuego, while dry western winds determine the precipitation regime northwards. Consequently, climate is rainy oceanic in the south coast, which promotes the *Nothofagus* forests, while it becomes dryer and thermally more contrasting (continental) northeastwards, where the landscape is a cold steppe (Collantes, Anchorena, Stoffella, Escartín, & Rauber, 2009; Frederiksen, 1988). In Isla Grande at Tierra del Fuego, sharp vegetation shifts are evidence for the distinction of two contrasting biogeographic regions, namely the forested Cordillera and the grassy Magellanic Steppe (Auer, 1965; Blanco & de la Balze, 2004), tied by a narrow transition zone or ecotone (Fig. 1). Both regions show clear differences in distinct bioclimatic variables, the most remarkable referring to rainfall decrease and rising west winds. This leads to a water deficit in the Magellanic Steppe, while the Cordillera experiences water surplus; and the balance is roughly zero in the ecotone zone. These climatic gradients entail contrasting shifts in the structure and composition of mires and in the vegetation matrix (Collantes et al., 2009; Grootjans, Iturraspe, Lanting, Fritz, & Joosten, 2010). In addition to water-related factors, growing thermal continentality northeastwards also affects the vegetation patterns (Kleinebecker, Hoelzel, & Vogel, 2007).

Mires are substantial landscape units all over Tierra del Fuego, although they play varying roles through the area. At the rainiest south areas mires and forests are the two main landscape units (Blanco & de la Balze, 2004; Pisano, 1977), while in the Magellanic Steppe mires cover much smaller areas, inside grassland landscapes (Collantes et al., 2009). Within the mire systems, ombrotrophic *Sphagnum* bogs only develop where precipitation exceeds evapotranspiration. Thus they thrive in the Andean Cordillera, vanish through the ecotone zone, and do not occur in the Steppe, where mires are entirely minerotrophic (Blanco & de la Balze, 2004; Collantes & Faggi, 1999; Grootjans et al., 2010). This vegetation gradient strongly drives the distribution of mire biota from landscape to regional scales, given the strong differences in structure and functioning between minerotrophic and ombrotrophic vegetation units (Bragazza, Rydin, & Gerdol, 2005; Malmer, 1986; Sjörs & Gunnarsson, 2002).

Studies aimed at mire vegetation in Tierra del Fuego are scarce. After the first descriptive attempts (Pisano, 1977; Roig, Anchorena, Dollenz, Faggi, & Méndez, 1985) a few papers have been produced from 2000 onwards focusing on relationships between vegetation and measured environmental variables. They have been devoted to ombrotrophic sphagnum bogs (Kleinebecker et al., 2007; Kleinebecker, Hoelzel, & Vogel, 2010), but also to the minerotrophic fens in the Magellanic Steppe (Collantes et al., 2009; Filipová, Hédl, & Dančák, 2013; Filipová, Hedl, & Covacevich, 2010), and to the mixed mire complexes which cover the most part of Eastern Tierra del Fuego (Iturraspe, Urciuolo, & Iturraspe, 2012). This helps to understand the mire species distribution along the environmental gradients operating at the regional scale. These gradients roughly coincide with those thoroughly studied in the temperate and cold regions of the northern hemisphere. Here, the vegetation distribution is strongly driven by the gradients poor-rich (which involves alkalinity, acidity, base saturation, etc.), fertility, salinity and water table depth (Økland, 1990; Økland, Økland, & Rydgren, 2001; Sjörs & Gunnarsson, 2002; Wheeler & Proctor, 2000). Moreover, macroclimatic gradients are significant determinants of vegetation patterns when studied at continental scale (Wheeler & Proctor, 2000; Peterka et al., 2017).

However, the studies made in Tierra del Fuego do not include information on the fen vegetation of the Cordillera region and very rarely of the ecotone zone (from where a single report from Roig (2001) is available). These studies (Grootjans, Iturraspe, Fritz, Moen, & Joosten, 2014; Grootjans et al., 2010) report on the fens occurring abundantly in slope springs and at the river banks. They evaluate the relationship between environmental variables and mire vegetation at the region scale (over tens of kilometres), but do not include accurate analyses at the mire scale. Thus, they did not analyse possible shifts in the relationship between environmental variables and vegetation along the pronounced bioclimatic gradients found in Tierra del Fuego. Such shifts have been evidenced in the European and North American mires, where the relevance of the environmental variables driving vegetation patterns varies from one biogeographic region to other, and at different scales (Belland & Vitt, 1995; Bragazza et al., 2005; Økland et al., 2001).

In this study we aimed: i) to describe the main ecological features driving the variation in the Tierra del Fuego fens and to evaluate the relationship between fen vegetation and main abiotic factors; and ii) to understand the patterns observed in the distribution, diversity and singularity of vascular plants at two complementary scales, that is at landscape and regional levels, namely within fen mosaics and between biogeographic regions. To do so, we characterized the visually distinct habitats by means of monitoring the hydrological regime through the growing season, and analysing the table water, the peat substrata and the species composition of the vascular vegetation at the optimal development period. This was done in three study sites set along a sharp climatic gradient in Isla Grande, Tierra del Fuego, where the fen vegetation plays varying ecological roles. Based on previous studies, we expected macroclimatic differences to be the main regional driver of vegetation shifts, and the poor-rich gradient to drive floristic change at local scale.

Material and methods

Study sites

We chose three medium-sized wetland areas along the climatic gradient going from wet oceanic to dry continental. These study sites were good examples of the two contrasting biogeographic regions recognised and their ecotone (Fig. 1), and were characterized in ecohydrological terms by Grootjans et al. (2010). The sites are:

Ushuaia: the site lies in Andorra Valley (54°45'40"S, 68°18'8"W; 190-200 m a.s.l.), a RAMSAR site in a suburban area of the city. Climate is oceanic boreal, with average annual temperature: 3.5 °C; average summer temperature: 7.6 °C; average annual precipitation: 600 mm (Iturraspe, Sottini, Schroder, & Escobar, 1989). It belongs to the Andean Cordillera biogeographic region. The most abundant species in the fen were *Carex curta, C. vallis-pulchrae* and *Juncus scheuchzerioides*. Main bedrock is sandstone (and slate) of lower Cretaceous. The fen is fed of drainage waters coming from a spring system located upslope, bordering the woodland. The surrounding landscape is made of *Nothofagus* (mainly, *N. pumilio*) forests and of ombrotrophic bogs of *Sphagnum magellanicum*. Ushuaia fen is used sporadically as extensive pasture for cattle. At the fen the peat reaches about 2.5 m depth.

Tolhuin: the second site was found in the central-southern part of Isla Grande, in the Estancia María Cristina (54°23'44"S, 67°14'32"W; 165-170 m a.s.l.), close to the Tolhuin village. Climate is also oceanic boreal (average annual temperature: 5.3 °C; average summer temperature: 9.6 °C; average annual precipitation: 500 mm). It is at the northern biogeographic limit of the ombrotrophic bogs of *Sphagnum magellanicum*, in the transition area between the regions of Andean Cordillera and Magellanic Steppe. Main bedrock is sandstone (and marine mudstone) from mid Eocene. The fen, fed by small rivulets, consisted in a wide sector dominated by *Carex gayana* and another area where *Sphagnum magellanicum* carpets and low hummocks have recently expanded. The fen is the result of the infilling of a lacustrine system, and includes a thick (about 2.5 m) level of blackish Cyperaceae peat. It is surrounded of *Nothofagus antarctica* forests and other wetland systems, mostly minerotrophic. Fens in this area are used sporadically as pastureland for sheep.

Río Grande: This site is in the Magellanic Steppe region, in the Estancia María Behety (53°47'40"S, 67°49'13"W; 15-20 m a.s.l.), next to the Río Grande city. General climate is still oceanic boreal, although precipitation is scarcer (average annual temperature: 5.5 °C; average summer temperature: 10.3 °C; average annual precipitation: 330 mm). Bedrock is mostly Oligocene-Miocene sandstone (and marine mudstone). Hygrophilous vegetation was dominated by *Caltha sagittata, Carex gayana* and *Hordeum lechleri* communities, which were best developed next to a small spring and a rivulet. Thus, this fen was secluded to a small depression within a landscape of *Festuca gracillima* grassland. Río Grande steppes and fens are grazed by sheep. According to Grootjans et al. (2010), the fen lies on a deep (about 3 m) bed of darkish Cyperaceae peat.

Field sampling

Sampling took place in the 2004-2005 summer, from December to March. At each site we set a system of sampling points which included at least three examples of each physiognomic vegetation unit, according to the dominant plant species; and also the main hydrological type, which was soligenous or topogenous (Damman & French, 1987). This consisted in 29 sampling points at Ushuaia, 30 at Tolhuin and 16 at Río Grande. In order to monitor the hydrological conditions, each sampling point

was equipped with a PVC pipe of 1.5 m in length with lateral holes at 5 cm intervals to allow water inflow, vertically sunk in the soil. We recorded the water table depth with respect to the topsoil every 15 (\pm 5) days, and estimated daily values by means of linear interpolation of the fortnight measures. Then we characterized each point by means of different variables related to the table depth (Table 1), namely the mean, minimum and maximum depth, and oscillation (maximum - minimum). Also, by linear interpolation we calculated the percentage of time when the water table was above ground (and so can cause stress through flood) and percentage of time when it was deep enough to allow oxygenation of the soils (depth between 50 and 100 cm).

At each sampling point we performed a vegetation relevé of a square area of 1×1 m centred on the pipe. Each relevé included all vascular plants, evaluated in terms of cover according to the Domin scale (van der Maarel, 1979). The relatively small size and the square shape were aimed to avoid relevant ecological gradients within each plot, which was characterized by the groundwater conditions measured at the central point. This floristic sampling was carried out in the third week of January 2005, at the optimal vegetation development. We also recorded the moss cover according to three functional categories, sphagnum moss (only *S. magellanicum* was present), brown (pleurocarpic) mosses, and other (mainly acrocarpic) mosses. Plant names and taxonomy followed Moore (1985).

Chemical analyses

At early February 2005 we measured the pH and electric conductivity of the water in each pipe, with a portable WTW TetraCon 325 sensor. At the same time, we took water and peat samples in a wide selection of the sampling points, stratified according to their situation in the water table gradient. This resulted in 22 water samples from Ushuaia, 20 from Tolhuin and 9 from Río Grande; and in 10 peat samples from Ushuaia, 14 from Tolhuin and 10 from Río Grande. Water samples, taken from the pipes, were filtered (through 0.20 µm pore filters) and acidulated, to be analysed for their total relevant ionic contents (see the ions analysed in Table 1) by means of inductively coupled plasma mass spectrometry (ICP-MS). Peat samples were the uppermost 15 cm of cores obtained with a soil drill. They were analysed in terms of pH (in dilution 1:2.5 between soil and distilled water), total carbon percentage, total nitrogen percentage (through the Kjeldahl method), and the

concentration of Ca, Mg, K and Na (by means of an acid digestion, followed by inductively coupled plasma mass spectrometry).

Statistical analyses

We performed a classification of the 75 vegetation relevés based on their species composition, to evaluate their floristic relationships. To do so, we previously transformed the Domin values to cover percent values, and then these to their logarithms. We then set a Hellinger distance matrix to produce a beta flexible hierarchical classification (with $\beta = -0.25$, according to Borcard, Gillet, & Legendre, 2011). We pruned the classification tree progressively to obtain clustering levels going from two to 15 groups (or vegetation types). We followed the Mantel criterion (Borcard et al., 2011) and chose the clustering level that kept the best distance relationships of the original matrix. However, we rejected those classifications with vegetation groups with less than three relevés in order to have enough samples per group. For each of the resulting group and for each site we calculated the phi fidelity index of all plant species (Chytrý, Tichý, Holt, & Botta-Dukát, 2002). Then, to compare the distribution of environmental variables between vegetation groups we performed pairwise multiple comparisons through Kruskal-Wallis tests.

To obtain the main floristic patterns we ordinated the vegetation relevés through a Principal Component Analysis (PCA) based on the species matrix, where species cover values were standardized emulating Hellinger distances (Legendre & Gallagher, 2001). After that, we produced three Detrended Canonical Analyses (DCA; Borcard et al., 2011), each for each study site, to reveal their particular floristic patterns and their main axis of variation. The relationships between the vegetation ordination and the habitat conditions were analysed by means of vector fitting the environmental variables (Borcard et al., 2011). We also calculated the Pearson correlation coefficient between the environmental variables, and between them and the first axis of the DCA.

We obtained and compared the species accumulation function at the different study sites according to the proposal of Cayuela, Gotelli, & Colwell (2015). The accumulation curves (based on the vegetation plots) were created through rarefaction and were used to contrast two null hypotheses: ecological (H0eco) and biogeographical (H0biog). Agreement with H0eco would mean that the vegetation

samples corresponded to a sole plant community, thus that any difference between them (concerning species richness, composition, or relative abundance) was due to sampling bias. Contrarily, agreement with H0biog would mean that the samples corresponded to distinct plant communities differing in their species composition, even if sharing similar species richness and species abundance distribution. Moreover, we evaluated the species β -diversity for each study site. We used the Hellinger distance matrix of the relevés to calculate, for each relevé group, the average distance between each relevé and the centroid of the group, which is a measure of its β -diversity (Anderson, Ellingsen, & McArdle, 2006).

All the statistical analyses were performed through R 3.0.2 (R Core Team, 2013). The hierarchical classification was performed with the Cluster package version 1.14.4 (Maechler, Rousseeuw, Struyf, Hubert, & Hornik, 2015); the Kruskal-Wallis tests with the Agricolae package version 1.2-1 (de Mendiburu, 2014); the ordinations, fitting of variables and β -diversity with the Vegan package version 2.2-1 (Oksanen et al., 2015); and the contrast of the ecological and biogeographical hypotheses with the rareNMtests package version 1.1 (Cayuela & Gotelli, 2014).

Results

Vegetation types and study sites

Following the Mantel criterion, we chose the classification of the 75 vegetation relevés into six vegetation types (Fig. A-1). Both six- and seven-cluster classifications had equivalent Pearson *r* correlation (0.640 and 0.642 respectively), but the seven-cluster classification created a group with only two samples, which we considered not acceptable. The types resulted equally distributed among the three sites, namely two types per site (Fig. 2). Concretely, types 1 and 2 were found in Ushuaia (except for one relevé of type 1 taken in Tolhuin); types 3 and 4 corresponded to Tolhuin (but one relevé came from Río Grande); and types 5 and 6 corresponded exclusively to Río Grande. All vegetation types corresponded to minerotrophic mires, where dominant plants were generally different Cyperaceae (or Poaceae) species (Annex, Table A-1), and locally the moss *Sphagnum magellanicum* (type 4, at Tolhuin).

Correspondingly, each study site was characterized by a fair number of faithful species (with phi fidelity values higher than 0.3 and p value lower than 0.01) and exclusive species (only found at a given study site; Table 2). However, the three study sites gave very similar figures in terms of total species richness, and faithful and exclusive species. Indeed, the diversity patterns were rather uniform between sites, as revealed by almost coincident numbers of species in 16 plots (calculated through cumulative curves after rarefaction of vegetation plots) and species density per area (Fig. 3). Only the ß-diversity gave significant differences between Tolhuin – with higher floristic dispersion among plots– and the other two sites. In relation to biodiversity structure, we rejected the null ecological hypothesis (p = 0.002) whereas we accepted the null biogeographical hypothesis (p = 0.387).

Ecological variation at regional scale

The sites studied exhibited noticeable differences in most of the environmental variables (Table 3). Soil variables contributed the less to distinguish the study sites, compared to water chemistry and hydrological regime. Almost all hydrological variables were significantly different between sites, and most of them were strongly correlated (Annex, Tables A-2 and A-3). The two vegetation types within each site differed in less environmental variables, i.e. seven in Ushuaia and eight in Río Grande and Tolhuin (Table 4). Globally, the hydrological variables gave the highest differences between vegetation types (and lower p-values) in the Kruskal-Wallis test (Table 4). Only three variables gave neither significant difference between sites nor between types: flood, the carbon nitrogen ratio (pCOt/pNt) of the peat, and the peat pH (ppH).

Referring to the hydrological regime, the water table depth was clearly different between sites (cf. maximum, minimum and mean depths in Table 4), although differences within sites were also noticeable. Río Grande included the most contrasting sampling points in this aspect, namely the difference between the highest and the lowest average position of the water table depth reached 100.8 cm, while it was 26.4 cm in Ushuaia and 40.5 cm in Tolhuin.

Ecological variation at local scale

The main floristic gradient in each study site was evidenced as the first axe in each of the corresponding DCA (Fig. 4). In Ushuaia six variables proved to be significant in the vector fitting (Annex, Table A-4): Min, Osc, Mean, Flood, EC and pH (cf. Table 1). Clearly, the highest correlation values to DCA axis 1 were shown by variables related to water table, which were strongly correlated to each other (Annex, Table A-5). So, we plotted in the Fig. 4 only the one most correlated to the first axis. Following the same criterion that in Ushuaia, the number of significant variables (Annex, Tables A-6 and A-8) was ten in Tolhuin (Max, ppH, , Mean, 50_100, pNt, pH, Min, EC, Na and Mn) and seven in Río Grande (Max, Mitj, pCOt, Na, Min, 50_100 and EC). In any case, many of these variables remained strongly correlated to each other (Annex, Tables A-7 and A9), and the one most correlated to the first axis in each DCA corresponded to the hydrological regime (Min in Ushuaia, and Max in Tolhuin and in Río Grande).

Discussion

Environmental variables driving fen vegetation patterns

The hydrological regime was the most contrasting in the fen of the Steppe area, where the water table depth achieved the lowest values in some of the plant community types (coinciding with Collantes et al., 2009 and Filipová et al., 2013). The sampling points more distant to the springs shifted to drier conditions in Río Grande than in the other two fens under rainier conditions. In fact, the table depth reached more than one meter depth in the marginal areas of the Río Grande fen. Drying off the fen surface released the plants of those communities from the flooding stress during part of the growth period. This is most probably a key factor in shaping the local plant communities, according to a number of studies (Kleinebecker et al., 2007; Vitt, 2006). As a result, the fen of the Steppe is more contrasting through the local landscape, since the plant communities bordering springs and rivulets were kept flooded or nearly to through summer.

The pH values and the Ca contents measured in peat and water correspond to fens from slightly acidic to slightly alkaline (Sjörs & Gunnarsson, 2002; Wheeler & Proctor, 2000). Our sampling points fit well with the intermediate category in the poor-rich gradient of fens (Chee & Vitt, 1989; Sjörs, 1952; Tahvanainen, 2004). This classification is based on the intermediate levels of Ca –ranging from 18 to 28 ppm, with no significant differences between sites- and the moderately acidic pH values from 5.6 to 6.2– through the study sites. However, the values indicated more acidity in Río Grande than in Ushuaia and Tolhuin. The higher levels of sulphur in Río Grande might be the cause of this moderate decrease in pH (Gunnarson, 2000). The high values of electric conductivity -from 197 to 290 µS/cm² – are evidence of the strong geogenous influence in all three fens. This also includes the sphagnum low hummocks (vegetation type 4), which are clearly non-ombrotrophic. Fertility was higher in Río Grande than in the other systems, as indicated by the soil and water contents of P and K –but not by the total N. This regional difference in fertility is likely related to higher grazing use at the Río Grande steppe than in the other two systems. Moreover, the Na content increases northwards along the regional gradient. Beyond the distance to the see, this may be partly due to an increasing influence of air-borne marine NaCl deposited by the prevailing western winds. In addition, the fen of Río Grande incorporates Na from a nearby salty pond following strong rains (Grootjans et al., 2010). The Na levels measured do not result into the occurrence of halotolerant plant species (Collantes et al., 2009; Filipová et al., 2013), but they help at understanding the differences in electric conductivity between study sites.

Most soils sampled are in accordance with the hemic histic soils documented by Collantes et al. (2009), which gave a C:N relationship around 20. Only the sphagnum low hummocks of type 4 yielded much higher values, near to 50, as a result of the low N content in the moss tissues (Rydin & Jeglum, 2006). Our values of soil pH showed only small variations, and were similar to that of the tall *Carex* marshes of Collantes et al. (2009), a community type very similar to most of our relevés in species composition. The other fen community types studied by Collantes et al. (2009) and by Filipová et al. (2013) in the Magellanic Steppe had soil pH values fair higher than our samples taken at the same fen.

Flora and vegetation types, and the singularity of the sphagnum low hummocks

The six vegetation types found evidenced varying similarity levels among them, as shows Fig. 2 (see also Fig. A-1 and Table A-1). The PCA ordination showed higher similarities within the couples of types from the same location; excluding Tolhuin, where the sphagnum low hummocks (type 4) were clearly different from the nearby fens of type 3. Thus, the higher distances between types were found between the sphagnum low hummocks and any other vegetation type; indeed, the Carex gayana fen of Tolhuin (type 3) was less like the neighbouring type 4 than to any other type, found in distant locations. Therefore, the development of sphagnum carpets and low hummocks promotes deep changes in plant species composition from the surrounding fens. This would be driven by raising the active soil layer from the water table and by soil and water acidification, as evidenced in other case studies (Bragazza et al., 2005; Grootjans et al., 2014; Tahvanainen, 2004). Moreover, the PCA ordination of vegetation types and sites do not follow the macroclimatic gradient. In addition to the singularity of the sphagnum low hummocks, this should be mostly due to the similarity between the fens of type 1 (Ushuaia) and type 5 (Río Grande).

The ecological singularity of the sphagnum low hummocks also affects their local diversity (Table 4), which results into lower α - and γ -diversities (total and rarefied values) with respect to the other vegetation types. This comes from the stressing conditions for vascular plants enhanced by the sphagnum hummocks (Kleinebecker et al., 2010), as is also known from the mires in the northern hemisphere (Hájková & Hájek, 2004; Malmer, 1986).

The macroclimatic or regional gradient

The chief floristic differences found between vegetation types were due to the site factor. A fair percentage (around 25%; Table 2) of the flora in each fen was exclusive of that site, a notable finding given the proximity between the sites in geographic terms. This local singularity is evidenced in the PCA ordination, where the sites appeared as three clouds, and in the classification of relevés, since the vegetation types obtained where consistent with the sites –two types from each site– with the only exception of two of the 75 relevés.

This regional pattern might respond to physical and chemical variables or to the continentality and moisture gradients. The measured environmental variables are

known to promote or to hamper distinct mire species. This refers mostly to the acidity (pH), the electric conductivity (and Ca and base content), the fertility, and the water table depth (Filipová et al., 2013; Økland et al., 2001; Wheeler & Proctor, 2000). Among these variables, the most influencing to the plant species variation in our study were the mean water table depth and the variation in the fertility indicators. The site Río Grande stands out in both variables, namely for lower water table (Table 3) and for the highest fertility (K, pK, P, and pNt variables), most probably related to persistent sheep grazing, which do not occur in the other sites. In this regard, the short pH gradient is likely to be related to a rather homogenous bedrock composition. The other variables are fair less determinant to mire vegetation according to most studies, except for the Na content. However, Na is a major vegetation driver at higher concentrations than those found in our study, even at Río Grande (cf. Collantes et al., 2009; Filipová et al., 2013).

The continentality and moisture gradients affect the regional distribution of most ecosystems in Tierra del Fuego through macroclimatic shifts, particularly forests and grasslands (Collantes & Faggi, 1999; Frederiksen, 1988; Pisano, 1977; Roig et al., 1985). According to that, the harsher bioclimate in the Magellanic Steppe would hamper the occurrence of several plant species, including most apparently trees. The main bioclimatic factor driving the vegetation patterns is the relationship between potential evapotranspiration and precipitation, according to Grootjans et al. (2010). In the case of mires, the fundamental border between water surplus and deficit is the key for understanding the distribution of ombrotrophic peatlands, and may be also relevant in the particular patterns found within minerotrophic systems. Thus, in fens under drier bioclimates the seasonal drying out of the superficial peat enhances its oxygenation and mineralization, which strongly influences soil chemistry. Therefore, drier bioclimatic conditions promote both the seasonal variation in the water table depth and, within a given fen, higher contrast among different fen points. This may be the case in our steppic fen system, where the soil in marginal areas dries out through summer. However, local factors, such as belowground drainage, can alter hydrological regimes elsewhere, and may be also contributing to water drawdown in the Río Grande fen.

In addition to ecological factors, the historical influence of strong bioclimatic differences between cold steppic landscapes in the north and more temperate

woodlands in the south has shaped the evolution, diversification and establishment of particular flora and vegetation in the two biogeographic regions (Collantes et al., 2009; Pisano, 1977; Roig et al., 1985). Distinct regional floristic pools would affect the species composition of the mires, even though if mire vegetation is mostly considered azonal at the landscape level (van der Maarel & Franklin, 2012).

Contrasting with the differences in species composition between fens in the different study sites, the structural parameters remained very similar through the macroclimatic gradient. The vegetation types of the three study sites had neither difference in α - nor in γ -diversity. However, higher β -diversity values differenced the Tolhuin system, due to the occurrence of low sphagnum hummocks including poor – though particular– vascular flora. The floristic pattern found in the three mire systems would fit with the proposal of Cayuela et al. (2015), where different floristic pools would produce similar vegetation patterns in terms of species richness and species relative abundances. This could occur if the flora and vegetation in the three biogeographic areas studied had been evolving under similar environmental pressures on different primeval floristic pools (Cayuela et al., 2015). Tierra del Fuego may have been place for this process, since the different biogeographic areas harbour different regional floristic pools.

The landscape (local) gradients

The DCA ordinations of the plant relevés express that most of the species variation responds to the varying water table depth and to its dynamics across study sites (Fig. 4). This is also expressed by the cluster distribution of two plant community types in each fen, from which one thrives in habitats with significantly deeper water table than the other does. Therefore, the hydrological regime stands out as the first ecological gradient at the fen scale. As far as we know, our data are the first evidence of the protruding role played by the water table depth and its dynamics in the distribution patterns of vascular plants in the fens of Tierra del Fuego (Collantes et al., 2009; Filipová et al., 2013). In the Northern Hemisphere, some studies proved the water table gradient to be the main driver of fen vegetation (Pérez-Haase & Ninot, 2017; Schenková et al., 2014). The relative weight of the hydrological variables seems to vary depending of the space scale considered in different

studies, and this may be related to the controversy generated when different areas have been compared (Økland et al., 2001; Wheeler & Proctor, 2000).

Beyond the preponderance of the hydrology, the ecological gradients in Tolhuin and Río Grande are more complex than in Ushuaia. The occurrence of the sphagnum hummocks in Tolhuin is cause for lengthening the pH, pNt and maximum water level depth gradients (Fig. 4). Once initiated, sometimes by colonization of locally thicker peat, sphagnum hummocks have a strong influence on habitat characteristics, which result in more acidity, deeper water table, and lower fertility (Sjörs & Gunnarsson, 2002). In Río Grande the soil contents of carbon and sodium are the most correlated variables with axis 1 of the DCA, together with the hydrological variables. Given the relatively lower content of sodium in our samples, the low ecological relevance of soil carbon, and the importance of the water table depth in the species distribution in mires (Kleinebecker et al., 2007; Økland, 1990; Vitt, 2006), the latter factor stands out as the main driver of species variation also in the Río Grande fen. Indeed, the total percentage of carbon in the peat is most probably driven by the dynamics of the water table, which strongly influences the organic matter mineralization (Moore & Basiliko, 2006; Rydin & Jeglum, 2006).

Concluding remarks

Our data points that macroclimate variation at regional scale leads to complex responses in mires, whereas variations in the water table depth are the main drivers of vegetation patterns at the landscape scale. The poor-rich gradient, which many authors found to be the most important driver of vegetation, is here correlated to the macroclimatic gradient, and against our expectation, it is a secondary driver at local scale. The short pH gradient measured in our three fens may have contributed to the leading role of water table dynamics.

On the one hand, the macroclimatic gradient driving the zonal vegetation in Tierra del Fuego influences the vegetation patterns of the fens –even if this vegetation category is chiefly azonal. From the last Quaternary glaciation onwards, the macroclimatic gradient has shaped the regional floristic pools, and hence the local pools. The gradient of increasing water deficit northwards would filter the plant species able to settle on the different mires (Boelcke, Moore, & Roig, 1985; Collantes et al., 2009; Grootjans et al., 2010). Moreover, the same macroclimatic

gradient modifies the local conditions of the distinct vegetation community types, mostly in the form of broadening the hydrological conditions in the fens of the Magellanic Steppe. There, lower rainfall and windier conditions bring drier conditions to the patches located further from water sources. Fens in the ecotone are not intermediate between those of Cordillera and Steppe, but showed own vegetation patterns and functioning.

On the other hand, the hydrological regime is the main factor in the distribution of vascular plants within the fens. Concretely, the extreme water table depths – maximum and minimum water depths– are the most correlated variables to the floristic variation. In addition, other gradients significantly affect the vascular plant patterns, and particularly the development of sphagnum hummocks caused the most evident vegetation shifts in these fens.

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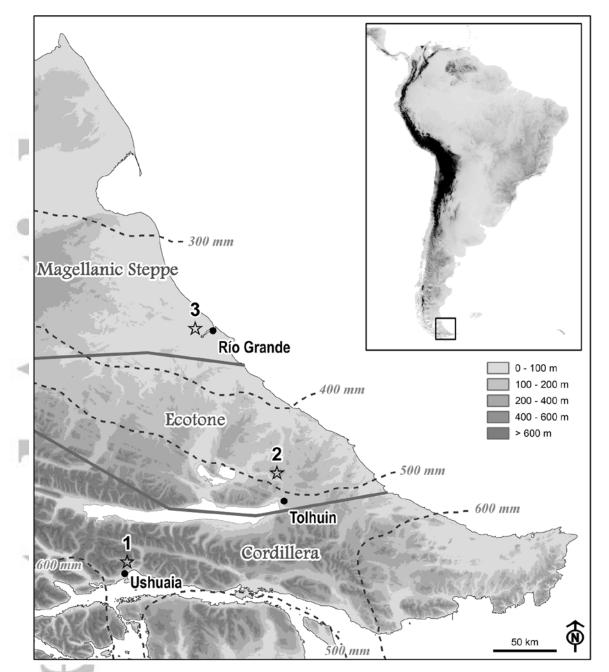
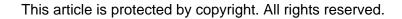


Figure 1. Location of the three study sites (**1**, Ushuaia; **2**, Tolhuin; **3**, Río Grande) in the Tierra del Fuego area, each in one of the three biogeographic regions recognised.



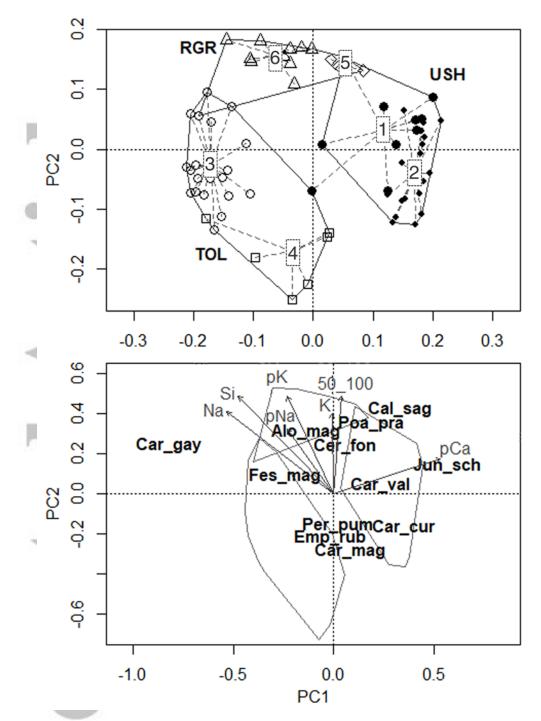
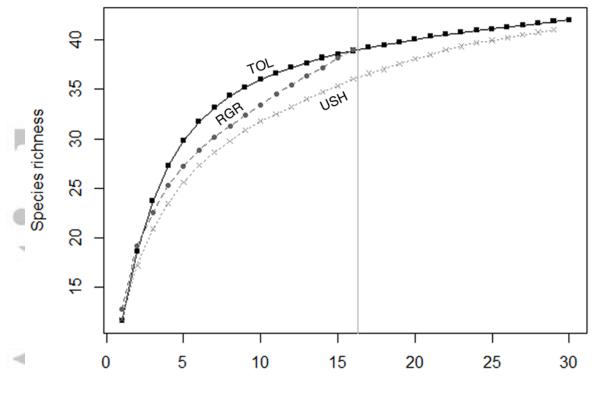


Figure 2. Ordination of the vegetation relevés on the space defined by the two first axes of the PCA, where the first axis stands for 0.148, and the second for 0.076 of the total variance. In the top graph, the relevés (symbols) of each study site are contoured of solid lines, and united with dotted lines to the centroid (numbers in discontinuous boxes) of the vegetation type where they belong. In the top graph sites are abbreviated as follows: RGR, Río Grande; TOL, Tolhuin; and USH, Ushuaia. In the bottom graph the arrows represent the best fitted (p-value < 0.01) environmental

variables, codified as in Table 1; and name abbreviations correspond to the 12 best fitted plant species, namely: Alo_mag, *Alopecurus magellanicus*; Cal_sag, *Caltha sagittata*; Car_cur, *Carex curta*; Car_gay, *Carex gayana*; Car_mag, *Carex magellanica*; Car_val, *Carex vallis-pulchrae*, Cer_fon, *Cerastium fontanum*; Emp_rub, *Empetrum rubrum*; Fes_mag, *Festuca magellanica*; Jun_sch, *Juncus scheuchzeroides*; Per_pum, *Pernettya pumila*; Poa_pra, *Poa pratensis*.

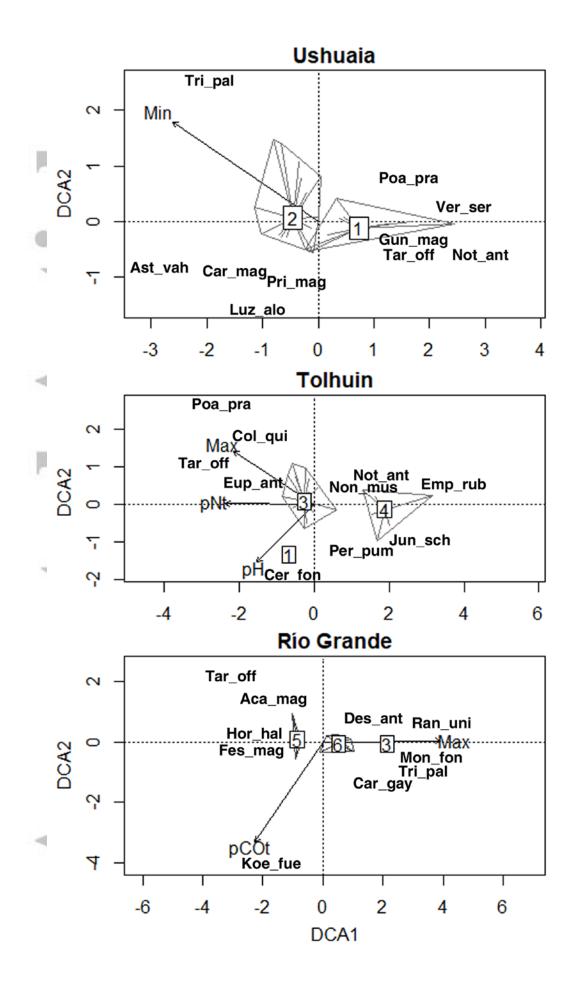
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Figure 3. Cumulative curves of species richness per growing number of relevés (samples), calculated through rarefaction. Site abbreviations: RGR, Río Grande; TOL, Tolhuin; and USH, Ushuaia. The vertical grey line designs the higher number of 16 relevés of Río Grande.

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Figure 4. Ordination of the vegetation relevés on the space defined by the two first axes of the DCAs made for each study site (the first axis stands for 0.455 in Ushuaia, 0.500 in Tolhuin and 0.451 in Río Grande). In each graph (site) the solid lines contour the relevés of each vegetation type; the corresponding centroids are identified as numbers in boxes, and the relevés are located at the tip of the radial lines. Arrows indicate the direction and strength of the environmental variables (abbreviated as in Table 1) with p-value lower than 0.01 and Pearson correlation coefficient with axis 1 higher than 0.5 in the DCA. In the case that two or more variables were highly correlated (> 0.75 or < -0.75) only the most correlated with the first axis is shown. The position of the ten most significant plant species (best fitted to axis 1, and found at least in 10% relevés in each site) are indicated by the following abbreviations: Aca_mag, Acaena magellanica; Ast_vah, Aster vahlii; Carex gayana; Car_mag, Carex magellanica; Cer_fon, Cerastium Car gay, fontanum; Col_qui, Colobanthus quitensis; Des_ant, Deschampsia antarctica; Emp_rub, Empetrum rubrum; Eup_ant, Euphrasia antarctica; Fes_mag, Festuca magellanica; Gun mag, Gunnera magellanica; Hor hal, Hordeum halophilum; Jun_sch, Juncus scheuchzeroides; Koe_fue, Koeleria fueguina; Luz_alo, Luzula alopecuroides; Non_mus, Nonadea muscosa; Not_ant, Nothofagus antarctica; Mon_fon, Montia fontana; Per_pum, Pernettya pumila; Poa_pra, Poa pratensis; Pri_mag, Primula magellanica; Ran_uni, Ranunculus uniflorus; Tar_off, Taraxacum officinale agg.; Tri_pal, Triglochin palustris; Ver_ser, Veronica serpyllifolia.

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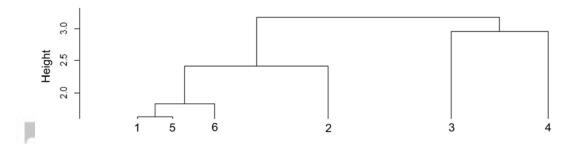


Figure A-1. Dendrogram resulting from the beta flexible clustering pruned to six groups. Numbers stand for the vegetation types.

Acc

Table 1. Environmental variables analysed, following the abbreviations used in the text and figures

	5
Water table depth	
Flood	Percentage of time when the water table was above ground (flooding)
50_100	Percentage of time when the water table was between -50 and -100 cm
Mean	Mean depth of the water table level (cm)
Max	Higher position of the water table (cm)
Min	Lower position of the water table (cm)
Osc	Oscillation (Max-Min) of the water table level (cm)
Water chemistry	
Ca, Mg, K, Na, P,	Concentration of these elements (ppm)
S, Si, Fe, Mn	
pН	pH
EC	Corrected electric conductivity (µS/cm)
Peat chemistry	
pCOt	Percentage of total organic carbon
pNt	Percentage of total nitrogen
pNt	Ratio of total carbon per total nitrogen
pCa	Calcium concentration (ppm)
pNa	Sodium concentration (ppm)
pMg	Magnesium concentration (ppm)
pK	Potassium concentration (ppm)
ррН	Soil pH

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Table 2. Species richness and singularity found in the three study sites through vegetation relevés. The number of species in 15 relevés was calculated by means of rarefaction, and beta-diversity was evaluated as the average dispersion of the samples from the centroid of the study site; different letters in the same row indicate significant differences in the Kruskal-Wallis test ($p < 0.001^{**}$). Phi-fidelity values are given for the ecologically most significant species (phi > 0.3, and p-value < 0.01; ** p 0.01 – 0.001, *** p < 0.001).

- -

	Ushuaia	Tolhuin	Río Grande
Number of samples (relevés)	29	30	16
Total number of species	41	42	39
Total number of faithful species	11	13	12
Total number of exclusive species	10	9	12
Number of species in 15 samples	35.2	38.4	39
Number of species/m ²	11.86	11.96	13
Beta-diversity**	0.66 a	0.77 b	0.64 a
Carex curta	0.73 ***	•	
Carex vallis-pulchrae	0.39 **		
Epilobium australe	0.43 **		
Gunnera magellanica	0.43 ***		
Juncus scheuchzeroides	0.57 ***		
Luzula alopecurus	0.38 **		
Veronica serpyllifolia	0.38 **		
Aster vahlii		0.38 **	
Carex fuscula		0.53 ***	
Carex gayana		0.44 ***	
Empetrum rubrum		0.37 **	
Galium antarcticum		0.43 **	
Gentianella magellanica		0.45 ***	
Nothofagus antarctica		0.35 **	
Primula magellanica		0.35 **	
Rostkovia magellanica		0.449 ***	
Alopecurus magellanicus			0.65 ***
Caltha saggitata			0.51 ***
Cerastium fontanum			0.59 ***
Deschampsia antarctica			0.61 ***
Euphrasia antarctica			0.41 **
Hordeum lechleri			0.41 **
Phleum alpinum			0.35 **
Pratia repens			0.73 ***
Ranunculus uniflorus			0.33 **
Stellaria debilis			0.53 ***

Table 3. Average values (and standard error) of the environmental variables at each study site. Different letters following the values in the same row (variable) mean significant differences after the Kruskal-Wallis test, at different levels according to the asterisks (p $0.05-0.01^*$, $0.01-0.001^{**}$, < 0.001^{***}). Variables are abbreviated as in Table 1.

50_100*** Mean*** Max*** Min***	0.08 (0.03) 0.01 (0.00) b -11.81 (1.25) a -1.72 (0.62) a -30.40 (2.52) a 28.67 (2.18)	Tolhuin 0.02 (0.01) 0.03 (0.01) b -19.91 (1.79) b -7.08 (1.54) b -37.00 (2.15) a 29.92 (1.19)	Río Grande 0.05 (0.05) 0.48 (0.11) a -53.05 (5.86) c -32.5 (6.87) c -65.5 (7.78) b
Flood 50_100*** Mean*** Max*** Min*** Osc Water chemistr	0.08 (0.03) 0.01 (0.00) b -11.81 (1.25) a -1.72 (0.62) a -30.40 (2.52) a 28.67 (2.18)	0.03 (0.01) b -19.91 (1.79) b -7.08 (1.54) b -37.00 (2.15) a	0.48 (0.11) a -53.05 (5.86) c -32.5 (6.87) c -65.5 (7.78) b
50_100*** Mean*** Max*** Min*** Osc Water chemistr	0.01 (0.00) b -11.81 (1.25) a -1.72 (0.62) a -30.40 (2.52) a 28.67 (2.18)	0.03 (0.01) b -19.91 (1.79) b -7.08 (1.54) b -37.00 (2.15) a	0.48 (0.11) a -53.05 (5.86) c -32.5 (6.87) c -65.5 (7.78) b
Mean*** Max ^{***} Min*** Osc Water chemistr	-11.81 (1.25) a -1.72 (0.62) a -30.40 (2.52) a 28.67 (2.18)	-19.91 (1.79) b -7.08 (1.54) b -37.00 (2.15) a	-53.05 (5.86) c -32.5 (6.87) c -65.5 (7.78) b
Max*** Min*** Osc Water chemistr	-1.72 (0.62) a -30.40 (2.52) a 28.67 (2.18)	-7.08 (1.54) b -37.00 (2.15) a	-32.5 (6.87) c -65.5 (7.78) b
Min*** Osc Water chemistr	-30.40 (2.52) a 28.67 (2.18)	-37.00 (2.15) a	-65.5 (7.78) b
Osc Water chemistr	28.67 (2.18)		
Water chemistr		29.92(1.19)	
	~ -		33.00 (3.53)
	y 21.35 (2.32) ab	18.17 (2.38) b	28.41 (2.82) a
Mg***	1.15 (0.20) c	2.71 (0.35) b	6.67 (0.78) a
K***	<2.50 b	<2.50 b	3.83 (1.25) a
Na***			. ,
P*	3.62 (0.80) c 0.05 (0.00) b	30.73 (4.91) b 0.08 (0.01) ab	46.55 (5.68) a 0.44 (0.35) a
P S***	0.03 (0.00) b 0.23 (0.04) c	0.58 (0.08) b	0.44 (0.35) a 3.66 (1.56) a
Si***	, ,	, ,	. ,
Fe*	1.66 (0.33) c	5.24 (0.70) b	9.25 (0.98) a
pH**	3.06 (2.39) b 6.19 (0.06) a	2.45 (0.84) ab	5.89 (4.44) a 5.88 (0.08) b
рп ЕС***	()	6.16 (0.09) a	· · · · ·
Sec. 1	209.90 (13.08) b	196.90 (12.02) b	289.36 (16.21) a
Peat chemistry pCOt	41.68 (0.53) a	38.50 (2.13) a	39.89 (0.89) a
pCOL	2.25 (0.10) a	1.90 (0.21) a	2.12 (0.10) a
pNt pCOt/pNt	18.85 (0.80) a	25.35 (4.27) a	19.03 (0.61) a
· · · · · · · · · · · · · · · · · · ·	312.20 (1248.03) a	3295.00 (699.17) b	4576.00 (888.68) k
	456.60 (71.83) b	555.64 (48.46) b	996.67 (123.26) a
	180.50 (30.66) b	323.79 (60.27) ab	533.33 (84.99) a
	283.60 (36.98) c	500.86 (61.96) b	1281.78 (222.83) a
·	5.64 (0.12) a	5.27 (0.12) a	5.32 (0.04) a
ррН	5.04 (0.12) a	5.27 (0.12) a	5.32 (0.04) a

Table 4. Characterisation of the six vegetation groups in terms of species richness and average values (and standard error) in the environmental variables showing significant differences (see table 3 for the total values referred to the study sites). Species number was calculated after rarefaction for each site (each couple of vegetation groups) for the lowest number of samples. Different letters following the values in the same row and within the same site mean significant differences after the Kruskal-Wallis test, at different levels according to the asterisks (p 0.05–0.01*, 0.01–0.001**, < 0.001***). Variables are abbreviated as in Table 1.

	Ush	uaia	Toll	huin	Río G	rande
	Veg. type 1	Veg. type 2	Veg. type 3	Veg. type 4	Veg. type 5	Veg. type 6
Species richness						
Number of samples						
(relevés)	10	20	23	7	5	10
Total number of						
species	39	33	44	12	26	34
Number of species	20	20.00	24 50	40	20	
(rarefaction)	39 13.97	28.09 10.70	34.58 13.48	12 5.26	26 14.77	25.66 12.94
Number of species/m ²	(1.10) a	(0.92) a	(0.64) a***	5.26 (0.97) b***	(0.86) a	(0.77) a
Water table level	(1.10) a	(0.02) u	(0.04) u	(0.07) 0	(0.00) u	(0.17) u
	0.02	0.00	0.00	0.11	0.92	0.25
50_100	0.02 (0.01) a**	0.00 (0.00) b**	0.00 (0.00) b**	0.11 (0.06) a**	0.83 (0.15) a*	0.35 (0.12) b*
	-19.44	-8.42	-14.85	-33.38	-89.98	-40.07
Mean	(1.50) b***	-0.42 (0.91) a***	(1.43) a***	-33.36 (2.92) b***	-09.90 (2.77) b**	(6.01) a*
	-5.20	-0.33	-2.63	-19.64	-65,90	(0.01) a 19,65
Max	(1.27) b**	(0.39) a**	(0.84) a***	(2.75) b***	(2,24) a**	(4,48) b*
and the second se	-44.58	-23.54	-31.37	-50.79	-97.90	-55.65
Min	(2.93) b***	(1.96) a***	(2.37) a***	(2.79) b***	(2.25) b**	(6.82) a*
	39.38	23.21	(2.07) a	(2.10)0	(2.20) 0	(0.02) u
Osc	(2.87) a***	(1.92) b***	·	•	·	•
Water chemistry						
					65.49	39.14
Na	•	•	•	•	(6.74) a*	(3.92) b*
S	0.47	0.20			8.67	<u>1.2</u> 4
	(0.19) a*	(0.05) b*	•		(3.19) a*	(0.23) b*
Mn			0.37	0.04		
	•	•	(0.14) a*	(0.03) b*	•	•
рН			6.27	5.68		
	•	•	(0.05) a*	(0.27) b*		
Peat chemistry						
oCOt			36.86	44.94		
	•	•	(2.45) b*	(0.65) a*	•	•
pNt			2.14	0.88		
prit	•	•	(0.19) a*	(0.07) b*	•	•
pCa					8409.00	3336.50
pou	•	•	•	•	(797.10) a*	(751.32) b
pNa					842.50	438.00
priu	•				(146.50) a*	(87.42) b
рК	501.25	247.57			_	
	(153.08) a*	(24.75) b*	•	•	•	•

ANNEX

AL 2	Ush	uaia	Tol	huin	Río Grande		
	Veg. type 1	Veg. type 2	Veg. type 3	Veg. type 4	Veg. type 5	Veg. type 6	
Mean WTD (cm)	-19.44	-8.42	-14.85	-33.38	-89.98	-40.07	
Faithful species	04.0	(0.0				10 5	
Carex vallis-pulchrae	24.0	10.9	0.8		2.4	12.5	
Veronica serpyllifolia	1.8						
Gunnera magellanica	6.9	0.8	0.5			0.2	
Juncus scheuchzeroides	13.0	22.9	0.3	1.4	10.0	10.5	
Carex magellanica	0.4	10.3	2.4	1.7			
Triglochin palustris	0.2	3.8	1.5			0.8	
Carex curta	5.9	14.9	2.0			0.5	
Carex fuscula	0.2		1.7				
Gentianella magellanica	0.4	0.2	1.2		0.8	0.2	
Carex gayana	0.2		60.0	5.0		66.3	
Nothofagus antarctica	9.0	0.7	3.1	6.0			
Empetrum rubrum				17.7			
Pernettya pumila	0.8	1.7	0.7	7.4			
Koeleria fuegiana	1.7	0.7	2.8		10.0	0.4	
Caltha saggitata	6.7	7.3	0.4		82.5	22.1	
Taraxacum officinale agg.	2.2	0.2	0.5		10.0	0.4	
Hordeum halophilum	0.5		1.3		14.5	0.4	
Hordeum lechleri					8.0	0.2	
Festuca magellanica	1.0	0.1	6.8		21.5	1.4	
Euphrasia antarctica			0.5		2.0	2.8	
Deschampsia antarctica		0.2	0.1		0.8	2.1	
Pratia repens					4.0	4.9	
Stellaria debilis			0.1		0.4	1.2	
Other species							
Acaena magellanica	6.8	4.1	3.2	0.9	5.4	0.7	
Agrostis alba	2.2	0.8	0.7		•••	0.2	
Alopecurus magellanicus	1.2		1.1	0.3	5.4	4.9	
Aster vahlii	0.2	0.3	1.3	0.0	0.1		
Calamagrostis stricta	0.2	0.0	0.7	0.7	1.0	0.7	
Cardamine glacialis		0.2	0.1	0.1	1.0	0.1	
Carex decidua		0.2	0.6				
Carex microglochin		0.1	1.8				
Cerastium fontanum	3.4	0.1	0.3		4.8	3.5	
		0.4 1.6	0.3 2.0		4.8 0.8		
Colobanthus quitensis	0.8				0.0	0.6	
Cotula scariosa	0.9	0.1	0.2				
Epilobium australe	1.6	0.4					
Galium antarcticum	0.2		0.9		• ·		
Gentiana prostrata	0.2		0.5		0.4	0.5	
Geum magellanicum	1.2		0.1				

Table A-1. Mean percentage cover in each vegetation group of the plant species found in more than one relevé and moss functional categories. Grey shadows indicate species fidelity (phi) index higher than 0.3 to a given vegetation-type.

Luzula alopecurus	1.2	0.9				
Montia fontana			0.1			0.2
Nonadea muscosa	1.0	0.3	0.4	0.9		
Osmorrhiza chilensis			0.2			
Phleum alpinum	3.2	0.6	1.0		4.8	3.0
Poa pratensis	12.7	2.5	0.8		11.4	3.7
Primula magellanica	0.4	0.5	0.9			
Ranunculus fuegianus		0.1				0.2
Ranunculus minutiflorus	0.4					
Ranunculus uniflorus			0.4			0.4
Rostkovia magellanica			2.5	5.0		
Sagina procumbens	2.0					
Schizeilema ranunculus	1.0	1.1	1.1	0.6	1.0	
Trifolium repens	0.2					0.2
Viola tridentata		0.2				
Mosses						
Sphagnum	0	0	0.1	85	0	0
Pleurocarpic mosses	17	26	13	1	1	16
Acrocarpic mosses	5	25	25	1	1	16

Accepted

_	Ca	Mg	к	Na	Р	S	Si	Fe	Zn	Mn	рН	EC	pCOt	pNt	pCa	рМg	pNa	рΚ	ррН	flood	50_100	Mean	Min	Max
Са	1																							
Mg	0.95	1																						
к	0.31	0.46	1																					
Na	0.87	0.94	0.35	1																				
P	0.1	0.2	0.76	0.08	1																			
S	0.94	0.95	0.3	0.92	0.02	1																		
Si	0.31	0.42	0.4	0.51	0.13	0.23	1																	
Fe	0.06	0.1	0.43	0.04	0.59	0	0.01	1																
Zn	0.22	0.27	0.3			0.21		0.04	1															
Mn	0.13		-0.02	0.04	0.06		0.09	0.04	-0.09	1														
pH	0.1			0.03					-0.13		1													
EC		0.94	0.25						0.17			1												
pCOt	-0.41			-0.13			-0.31			-0.47		0.02	1											
pNt									-0.14			0.26	-0.17	1	4									
pCa									-0.21			0.3	0.29	0.32	1	4								
pMg pNa		0.63		0.65				-0.18	0.1	-0.06		0.54 0.44	0.07	0 0.14	0.09	1 0.8	1							
	-												-0.15			0.8	0.63	1						
pK ppH	-								0.19				-0.13		-0.10			-0.15	1					
flood	-0.08								-0.19				-0.01		0.36			0.01	0.36	1				
50 100				0.54					0.39						-0.17				-0.29	-0.13	1			
Mean	-		-						-0.44					0.13		-0.69		-0.6	0.3	0.13	-0.87	1		
Min	-0.39												-0.26						0.33	0.35	-0.79	0.95	1	
Max									-0.46		0.23		-0.28	0.13		-0.67		-0.57		0.24	-0.87	0.97	0.88	
Osc		0.08	0.24		0.27	-0	0.09		-0.01			0.01			-0.17				-0.32		0.19		-0.61	-0.1

 Table A-2. Pearson r correlation coefficients between all the variables used. In bold, values > 0.75 or < -0.75.</th>

nung on u	ie PCA orunation (p 0.0
	Vector fitting r ²
Si	0.500***
pCa	0.419***
pK	0.389***
pMg	0.298**
50_100	0.215***
pNa	0.210*
K	0.194***
	Vector fitting r ²
Na	0.185***
Mean	0.170***
Mg	0.162**
Min	0.156**
Max	0.134**
Ca	0.103*
EC	0.078**

Table A-3. Variance explained (r^2) by those variables with significant vector fitting on the PCA ordination (p 0.05–0.01*, 0.01–0.001**, < 0.001***).

Table A-4. Variance explained (r^2) by those variables with significant vector fitting on the Ushuaia DCA ordination (p 0.05–0.01*, 0.01–0.001**, < 0.001***). Their correlation to DCA axis 1 is given in the last column.

	Vector fitting r ²	Pearson r correlation with DCA axis 1
Min	0.496***	-0.625
Osc	0.505***	0.617
Mean	0.385**	-0.515
Flood	0.317*	-0.274
CEc	0.408***	-0.252
рН	0.253*	-0.216

Table A-5. Pearson r correlation between those variables with significant vector fitting on the Ushuaia DCA ordination.

	рН	EC	flood	Mean	Min
рН	41				
EC	0.57	1			
flood	0.45	0.25	1		
Mean	0.64	0.31	0.52	1	
Min	0.51	0.21	0.34	0.92	1
Osc	-0.40	-0.19	-0.25	-0.83	-0.98

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Table A-6. Variance explained (r^2) by those variables with significant vector fitting on the Tolhuin DCA ordination (p 0.05–0.01*, 0.01–0.001**, < 0.001***). Their correlation to DCA axis 1 is given in the last column.

\sim		Pearson r
		correlation with
	Vector fitting r ²	DCA axis 1
Max	0.595***	-0.850
ppH	0.578*	-0.786
Mean	0.418***	-0.763
50_100	0.375***	0.756
pNt	0.697***	-0.741
рН	0.413***	-0.719
Min	0.210*	-0.601
EC	0.294**	-0.426
Na	0.403*	-0.343
Mn	0.381*	-0.340

Table A-7. Pearson r correlation between those variables with significant vector fitting on the Tolhuin DCA ordination.

	Na	Mn	pNt	ррН	рН	EC	e50_100	Mitj	Min
Na	1								
Mn	0.03	1							
pNt	0.14	0.02	1						
ррН	0.43	0.34	0.43	1					
рН	0.26	0.35	0.53	0.80	1				
EC	0.60	-0.07	0.40	0.62	0.42	1			
e50_100	-0.28	-0.18	-0.64	-0.76	-0.66	-0.40	1		
Mitj	0.35	0.11	0.70	0.64	0.49	0.40	-0.73	1	
Min	0.35	0.09	0.60	0.53	0.38	0.31	-0.62	0.95	1
Max	0.31	0.11	0.73	0.63	0.54	0.37	-0.76	0.95	0.84
<u> </u>	1								
	1								

Table A-8. Variance explained (r^2) by those variables with significant vector fitting on the Río Grande DCA ordination (p 0.05–0.01*, 0.01–0.001**, < 0.001***). Their correlation to DCA axis 1 is given in the last column.

	Vector fitting r ²	Pearson r correlation with DCA axis 1			
Max	0.817***	0.894			
Mean	0.791***	0.884			
pCOt	0.843**	-0.857			
Na	0.728*	-0.827			
Min	0.688***	0.817			
50_100	0.387*	-0.649			
EC	0.495*	-0.505			
	S				
	2				

Table A-9. Pearson r correlation between those variables with significant vector fitting on the Río Grande DCA ordination.

	Na	pCOt	EC	50_100	Mean	Min	Max
Na	1						
pCOt	0.81	1					
EC	0.37	0.70	1				
50_100	0.27	0.66	0.25	1			
Mean	-0.72	-0.78	-0.56	-0.80	1		
Min	-0.67	-0.76	-0.61	-0.78	0.97	1	
Max	-0.72	-0.75	-0.45	-0.80	0.97	0.89	1
	-						