

Environmental Controls of Cryptogam Composition and Diversity in Anthropogenic and Natural Peatland Ecosystems of Chilean Patagonia

Carolina A. León,^{1*} Gisela Oliván Martínez,² and Aurora Gaxiola^{3,4}

¹Centro de Investigación en Recursos Naturales y Sustentabilidad, Universidad Bernardo OHiggins, Fábrica 1990, segundo piso, Santiago, Chile; ²Departamento de Biología Vegetal I, Facultad de Ciencias Biológicas, Universidad Complutense de Madrid, 28040 Madrid, Spain; ³Departamento de Ecología, Pontificia Universidad Católica de Chile, Alameda 340, Santiago, Chile; ⁴Instituto de Ecología y Biodiversidad, Santiago, Chile

ABSTRACT

Peatlands exhibit highly characteristic ecological traits and are unique complex ecosystems. Nevertheless, knowledge about southern South American peatlands is very limited. In this study, we analyzed species composition of bryophytes and lichens of Southern Hemisphere peatlands, specifically from eight peatlands of Isla Grande de Chiloé (Chiloé Island) in southern Chile (42°–43°S and 75°–73°W). Two kinds of *Sphagnum* peatlands were studied: natural and anthropogenic peatlands. Our results indicate the existence of clear environmental gradients affecting the structure of bryo-lichenic communities in the *Sphagnum* peatlands of Chiloé. Canonical correspondence analysis suggests that variation in bryophyte and lichen species composition mainly follows ombrotrophic–minerotrophic and lithotrophic–thalassotrophic gradients. Surface-water

chemistry is the most significant factor accounting for changes in floristic composition among our study sites. In contrast to our expectations, bog origin (natural or anthropic) was not the most significant factor accounting for changes in floristic composition among peatlands. Other elements, such as the water source supplying peatlands or the influence of sea spray, were more relevant in the bryo-lichenic flora species occurrence in the peatlands of Chiloé. We also observed clear differences in ecological niches among species in general additive model response curves. Therefore, our results show that despite the origin, the ecology of peatlands follows common rules with peatlands from the Northern Hemisphere.

Key words: bogs; wetlands; southern South America; Chiloé; CCA and GAM.

Received 12 September 2016; accepted 14 February 2017;
published online 10 April 2017

Electronic supplementary material: The online version of this article (doi:10.1007/s10021-017-0142-z) contains supplementary material, which is available to authorized users.

Author contributions C.A.L. designed the study, performed research, analyzed data and wrote the paper. A.G. analyzed results and wrote the paper. G.O.M. designed the study, contributed to field work and manuscript development.

*Corresponding author; e-mail: carolina.leon@ubo.cl

INTRODUCTION

Peatland ecosystems are characterized by a substantial accumulation of organic matter in soil (peat). They occupy around 3% of terrestrial ecosystems and have been shown to be important players in the global carbon (C) cycle in the recent past (Yu and others 2010). Peatlands are present from the tropics to high latitudes; however, it is in

the Northern Hemisphere where peatlands are most abundant (Charman 2002; Roulet and others 2007; Yu and others 2009). Southern peatlands (SP), on the other hand are less extensive and appeared after the last glaciation (that is, 13–17 ka) (Heusser 2003; Arroyo and others 2005), as well as in recent years as a product of soil degradation (for example, forest cover removal) (Whinam and others 2003; Díaz and others 2008). Indeed the majority of studies on nutrient and water dynamics in peatland ecosystems come from peatlands at high latitudes of the northern hemisphere (Vitt and Chee 1990; Vitt and others 1990; 1995a). In contrast, baseline knowledge of the structure and dynamics of austral peatland ecosystems is scarce (Whinam and others 2003; Kleinebecker and others 2008).

In southern South America (40–55°S), peatlands cover about 45,000 Km², roughly equivalent to 25% of the landmass (Yu and others 2010; Loisel and Yu 2013). The vast majority of these peatland ecosystems were formed via terrestrialization, which is peat accumulation in open water (Arroyo and others 2005), or via paludification, which occurs when peat accumulation starts directly over a paludifying mineral soil. Soil paludification, caused by human activities (for example, forest removal), has contributed to the presence of peatlands in the last centuries (Whinam and Buxton 1997; Whinam and others 2003; Díaz and others 2008). Forest cover removal, via fire or intense logging, promotes paludification because tree removal reduces evapotranspiration and increases wetness of the soil organic layer (Díaz and others 2008). Waterlogged soils hamper plant growth and establishment (Gaxiola and others 2010), as well as forest regeneration (Gaxiola and others 2010; Albornoz and others 2013). Hence, high precipitation combined with low evapotranspiration can hasten the establishment of peatlands over forests. Accordingly, reductions in forest cover, particularly of forests growing on poorly drained soils, have been linked to the formation of peatlands in southern Chile (Díaz and others 2008) and New Zealand (Whinam and Buxton 1997). However, due to its recent formation, peat accumulation of these “anthropogenic peatlands” is smaller compared to natural peatlands (Díaz and others 2008; León and Oliván 2014), and species diversity differs between them. Actually, León and others (2014) found that anthropogenic peatlands had twice the amount of bryophytes and lichens species than natural peatlands, whereas liverworts and mosses were more frequent in natural peatlands. Few studies, however, have analyzed the possible role of water

chemistry on floristic composition of “anthropogenic peatlands”; hence, we do not know the extent to which these peatlands follow those patterns described for natural peatlands and whether the origin of peatlands determines nutrient dynamics and species composition.

Water chemistry is considered to be the major factor controlling peatland ecology (du Rietz 1954; Rydin and Jeglum 2006), and the key driver behind changes in floristic elements and ecological processes throughout peatland development (Rydin and Jeglum 2006). Peatland development occurs along a successional gradient that goes from minerotrophic to ombrotrophic conditions (Granath and others 2010). During this “hydroseral succession,” peatland development begins on wet mineral soils, where the water in the peat has passed over or through mineral soils. These minerotrophic peatlands tend to be species-rich but tend to progress toward ombrotrophy as water decreases in base content and increases in acidity. Ombrotrophic peatlands tend to be species-poor with low mineral concentrations in the water (Bridgham and others 2001; Granath and others 2010). These changes are interpreted as being largely due to autogenic processes related to species replacement and reduced inputs of mineral soil water (van Breemen 1995; Hughes and Barber 2004). Accordingly, minerotrophic peatlands tend to be dominated by “brown mosses” (that is, an artificial group that includes *Drepanocladus*, *Brachythecium*, and so on) and sedges, while *Sphagnum* mosses and woody shrubs dominate acidic ombrotrophic peatlands (Rydin and Jeglum 2006; Vitt and Wieder 2008; Kleinebecker and others 2010). Furthermore, sea spray can also affect water chemistry, for example, via sodium and chloride water concentrations, and regulate water chemistry of coastal peatlands (Vitt and others 1990; Kleinebecker and others 2007; Martínez-Cortizas and others 2009). This thalassotrophic condition (that is, influence of oceanic water), present in some peatlands, can also have significant impacts on species composition (Wheeler and Proctor 2000). Such knowledge on soil chemistry and species composition in peatlands comes mainly from studies in natural peatlands (Vitt and Chee 1990; Vitt and others 1990; Vitt and others 1995a; Tuittila and others 2007), and it is not very clear whether these patterns are also present in anthropogenic peatlands.

The aims of this study are: (i) to understand whether the minero-ombrotrophic paradigm of Northern Hemisphere peatlands holds for peatlands in southern Chile and (ii) to understand differences

between natural and anthropogenic peatlands in floristic composition and water chemistry.

METHODS

Study Area

The study area is situated on Isla Grande de Chiloé (Chiloé Island) in southern Chile (42°–43° S and 73°–75°W). The climate in this area is wet temperate with a strong oceanic influence (di Castri and Hajek 1976), with a mean annual temperature of 9.6°C (4.0°C min.–19.1°C max.) (Carmona and others 2010) and an annual rainfall range between 1900 and 2300 mm (CONAF 2009), reaching 6000 mm in some areas (Pérez and others 2003). We selected two kinds of peatlands as defined according to their origin; the first type corresponded to natural peatlands that originated after the last glaciation, 10,000–12,000 years ago (Porter 1981; Hauser 1996). The second type corresponded to anthropogenic peatlands that were formed in flooded areas where *Sphagnum* moss colonized after forest cover was removed either by fires or logging (Díaz and others 2008). We chose three sites with natural peatlands and five with anthropogenic peatlands (Figure 1).

Sampling

To evaluate the extent to which origin determines species composition among peatlands, we sampled biotic and abiotic variables in each of the eight sites previously categorized according to their origin (for example, natural or anthropogenic peatland). In each peatland, we randomly established three 50-meter linear transects within each peatland, and in each of these, we established three plots at 0, 25 and 50 m points. Therefore, we had eight peatlands with nine sample points. To describe the habitat structure, we defined a set of variables that we considered relevant in the dynamics of these peatlands. We first evaluated those variables related to plot microtopography following the description of Vitt and others (1995b) and Rydin and Jeglum (2006). Additionally, we assigned a microtopographic category to each plot (Hummock: NAN1, Lawn: NAN2, Carpet: NAN3, *Tepualia stipularis* base: NAN4) and an indirect measure of soil moisture levels (MOI) estimated by touching the substrate (dry to touch: MOI1, wet to touch: MOI2, and saturated soils: MOI3). Indirect moisture measurements were taken at least 3 days after a rainfall event and at noon to reduce the probability of condensed water present in early mornings. Moreover, we assigned a vascular plant category

based on the dominant plant life form. In order to relate biotic and abiotic variables, we further evaluated variables associated with water chemistry at each plot. In the austral summer of 2009 and within a 20-day window, we took water-table samples from surface water collected from shallow pits dug in the soil at least 1 day before collection. We used acid-washed (10% HCl) polyethylene bottles and measured in situ conductivity (EC) and pH (HI 98129 Combo meter, Hanna Instruments Inc., Rhode Island, USA). Finally, samples were kept at 5°C in a plastic cooler with ice and taken to the laboratory for chemical analyses of water minerals: calcium (Ca²⁺), magnesium (Mg), sodium (Na), and chloride (Cl), as well as total nitrogen (total N), ammonium (N–NH₄), nitrites (N–NO₂), nitrate (N–NO₃) and potassium (K). Chemical analyses were performed at the *Instituto de Investigaciones Agropecuarias - Laboratorio de Suelo* (soils laboratory) in Chillán, Chile, following Sadzawka and others (2006). Finally, we georeferenced each sample plot and measured distance from the Pacific Ocean using Google Earth. This was made to evaluate a potential thalassotrophic effect.

Considering that our study area is an island with high oceanic influence and rainfall, we used the Ionic Ratio (IR) as an indicator of water type in relation to relative Ca and Cl concentrations. The IR indicates, on a scale from 0 to 1, the proportion of groundwater vs. rain and seawater. Because minerotrophic groundwater contains high Ca²⁺ concentrations associated with mineral soils, it has a higher IR than rainwater. Moreover, seawater, as well as rainfall water, is characterized by low IR due to high Cl concentrations. Intermediate values represent a mixture of ground water and rainwater (Hedenäs 2003). The IR was calculated as $2[Ca]/(1[Ca] + [Cl])$.

Species Composition

To characterize species composition across peatlands, at each site we extracted nine blocks of the superficial layer of soil (that is, 20 × 20 × 10 cm). We followed Bullock's harvest method (Bullock 1997) for biomass and species richness. Plant and lichen species were carefully determined according to morphological characters, and their characteristics were compared with data from the literature, type or other herbarium specimens. Additionally, for lichens, we also used chemical compounds that were identified using thin layer chromatography (TLC), following the protocol of White and James (1985). Specimens were deposited in the herbari-



Figure 1. Location of eight peatland sites on Chiloé Island. Natural peatlands: PL, Púlpito; CA, Caulles; and RN, Rio Negro. Anthropogenic peatlands: SD, Senda Darwin; CH, Chepu; PM, Pumanzano; LC, Lecam; and TG, Teguel.

ums of the Universidad Complutense de Madrid, Spain (MACB) and of Universidad de Concepción, Chile (CONC). Although *Drosera uniflora* is a vascular plant, we registered it due to its great significance as an indicator of natural peatland species (Díaz and others 2008). Due to their tiny size, liv-

erworts species such as *Calypogeia sphagnicola*, *Cephalozia skottsbergii* and *Hyalolepidozia bicuspidata* were grouped as a single functional group called Tin hep. Likewise, lichen species such as *Cladonia pycnoclada*, *Cladonia mitis*, and *Cladonia arbuscula* subsp. *squarrosa* were all considered as the sub-

genus *Cladina* because chemical tests are required for correct determination (tests were applied in the lab). Table 1 provides a list of species and functional groups collected. Dry biomass per species was used to estimate species abundance for each sample plot.

Data Analysis

To test for significant differences in surface-water chemical variables across peatlands (for example, natural and anthropogenic), we used the non-parametric Kruskal–Wallis H and Mann–Whitney U tests, respectively. Categorical variables (origin of peatland, microtopography, soil moisture, dominant vascular plant life form, and harvesting) were transformed into dummy variables and represented by centroids. We used K levels = K *dummy* variables. Redundant dummy variables were included to facilitate visualization of the results in the ordination diagrams (Lepš and Šmilauer 2003). To

avoid the influence of rare species in the analysis, we only included species present in at least three sampling points (ter Braak and Šmilauer 2002) in the analysis.

To describe the effects of ecological gradients by which species were sorted, we used ordination techniques: the detrended correspondence analysis (DCA) and the canonical correspondence analysis (CCA). For these analyses, 19 environmental variables (see the Supplemental Material) and 24 species were used. In the first step, we performed a DCA without data transformation to estimate the species gradient length (Lepš and Šmilauer 2003). The DCA revealed a gradient length of the first axis of 4.034 SD. This suggests that the use of a unimodal ordination method was appropriate for this data analysis because the long gradient of first axis was larger than 4.0 SD (ter Braak and Šmilauer 2002; Lepš and Šmilauer 2003). Accordingly, we subsequently used a CCA to graphically display the

Table 1. Differences in the Relative Abundance (%) of Non-vascular Plant and Lichen Species Between Natural and Anthropogenic Peatlands from Chiloé Island in Southern Chile

Species	Code	Natural peatlands	Anthropogenic peatlands
Mosses			
<i>Sphagnum magellanicum</i>	Sph mag	80.8 ± 17.8	67.3 ± 34.1
<i>Campylopus acuminatus</i>	Cam acu	21.7 ± 24.1	
<i>Dicranoloma imponens</i>	Dic imp	9.3 ± 11.3	16.7 ± 18.4
<i>Dicranoloma billardierei</i>	Dic bil	0.2 ± 0.0	9.8 ± 16.3
<i>Campylopus introflexus</i>	Cam int		4.3 ± 7.3
<i>Polytrichastrum longisetum</i>	Pol lon		27.4 ± 27.6
<i>Sphagnum falciculatum</i>	Sph fal		33.3 ± 36.5
<i>Sphagnum fimbriatum</i>	Sph fim		36.3 ± 31.3
<i>Sphagnum capillifolium</i>	Sph cap		7.7 ± 14.5
Liverworts			
<i>Riccardia rivularis</i>	Ric riv	29.1 ± 31.3	18.4 ± 14.9
<i>Riccardia floribunda</i>	Ric flo	9.1 ± 12.5	14.9 ± 10.4
<i>Kurzia setiformis</i>	Kur set	4.3 ± 4.2	2.6 ± 3.4
<i>Lepicolea ochroleuca</i>	Lep och	3.0 ± 4.3	19.2 ± 28.9
<i>Herbertus runcinatus</i>	Her run	2.7 ± 2.8	
<i>Jamesoniella colorata</i>	Jam col	0.3 ± 0.3	11.1 ± 16.2
<i>Frullania</i> cf. <i>boveana</i>	Fru bov	0.1 ± 0.1	0.7 ± 0.2
<i>Hyalolepidozia bicuspidata</i> - <i>Calypogeia sphagnicola</i> - <i>Cephalozia skottsbergii</i>	Tin hep	0.1 ± 0.1	0.6 ± 1.4
<i>Saccogynidium australe</i>	Sac aus		0.1 ± 0.1
<i>Telaranea blepharostoma</i>	Tel ble		0.4 ± 0.6
Lichens			
<i>Cladonia arbuscula</i> subsp. <i>squarrosa</i> - <i>Cladonia mitis</i> - <i>Cladonia pycnoclada</i>	Cla Cla	9.3 ± 13.8	8.0 ± 6.7
<i>Cladonia gracilis</i> subsp. <i>elongata</i>	Cla gra	1.4 ± 0.0	9.5 ± 9.0
<i>Cladonia squamosa</i>	Cla squ	0.3 ± 0.4	3.7 ± 3.4
<i>Usnea</i> sp.	Usn		0.2 ± 0.2
Insectivorous plant			
<i>Drosera uniflora</i>	Dro uni	0.5 ± 1.0	

Species are listed in decreasing order in relation to natural peatlands.

environmental gradients. Significance of the canonical axes was contrasted with a Monte Carlo permutation test (999 permutations). Furthermore, we applied forward selection regression to identify the relevant explanatory variables (Scarlett and O'Hare 2006). Marginal and conditional effects were tested (Lepš and Šmilauer 2003). The statistical significance of Lambda A was assessed by means of Monte Carlo tests. In order to assess the niche breadth of different species based on the set of variables grouped in axes 1 and 2 of CCA, we generated response curves of species abundance as a function of values of CCA axes 1 and 2. For this, we used generalized additive models (GAM) (Zuur and others 2007) assuming a Poisson distribution. The fitted model was compared with a null model, and a fit function complexity was selected using the Akaike information criterion (AIC) (Lepš and Šmilauer 2003; Kleinebecker and others 2010).

The Kruskal–Wallis H test was run in STATISTICA 7.0 (StatSoft 2004), and ordination analyses and GAM modeling were conducted with CANOCO for Windows 4.5 (ter Braak and Šmilauer 2002). We employed PAST (Hammer and others 2001) for the diversity index.

Finally, to evaluate the potential role of *Sphagnum* as an ecosystem engineer of peatland ecosystems (Jones and others 1994), we evaluated the effect of *Sphagnum* abundance on water pH on bryo-lichenic species diversity. For this, we first calculated the Shannon diversity index (H') (Magurran 2004) for each plot, and then we used a generalized linear model to examine the effects of *Sphagnum* abundance, water pH, and origin (that is, natural and anthropogenic), on bryo-lichenic diversity (\hat{H}). We also evaluated the interaction effects of these explanatory variables on \hat{H} . We used R the command `glm` in R v. 2.7.1 (R Development Core Team 2011).

RESULTS

Characterization of Surface-water Chemistry

In contrast to expectations, water chemical parameters did not differ as a function of peatland origin (Table 2). We found, however, significant differences in chemical parameters among localities, but only K differed as a function of origin (Table 2). In contrast to expectations, we found that the most acidic and least acidic sites were of anthropogenic origin (that is, 3.79 and 4.85), and the two highest EC values were also observed in anthropogenic peatland water. Finally, natural

peatlands tended to have lower IR compared to anthropogenic peatlands; this suggests that the latter have more contact with groundwater.

Relationships Among Species Composition and Environmental Parameters

CCA analysis suggests that there are clear environmental gradients that separate species; the first axis is related to water biochemistry and the second axis to distance from the Pacific Ocean (Figure 2). The last result is evidence of the oceanic influence in the structure of these peatlands. We found that eigenvalues for the first two axes were 0.450 and 0.370. The correlations between environmental variables and species were 0.815 (axis 1) and 0.763 (axis 2). The first axis is associated with variables such as (i) IR and NH_4 , and (ii) Ca and pH. The second axis is mainly associated with distance from the Pacific Ocean (Figure 2). The Monte Carlo test gave a p value of 0.003 for the first canonical axis and 0.002 for all canonical axes, indicating that species were significantly related to environmental variables. Forward selection of environmental parameters in the CCA revealed that IR, microtopography (for example, base of the *Tepualia stipularis* trunk), distance to the Pacific Ocean, and Na were the four variables in the dataset that influence most community structure (Table 3).

Out of the 24 bryophyte and lichen species, only 12 had significant response curves with Axis 1 of the CCA (Figure 3 A–D) and 13 species with Axis 2 (Figure 3 E–H). Such differential species response curves confirm differentiation according to the ecological niches suggested by our CCA results. On Axis 1, which is the one associated with environmental variables such as IR and Ca, we found that abundance of mosses changed along the axis, where *Sphagnum falcatulum* and *Dicranoloma imponens* were more abundant to the left of the axis (Figure 4A, B), whereas *Polytrichastrum longisetum* showed greater abundance to the right of the axis (Figure 3B). On the other hand, liverworts showed different trends (Figure 3C) where lichens exhibited greater abundance at the center of the axis (Figure 3D). These results suggest that species have different nutrient and pH requirements. On Axis 2, which is mainly associated with longitude and distance from the Pacific Ocean, we found differences in abundance of moss species (Figure 3E, F), especially for *Sphagnum* species. *Sphagnum falcatulum* and *Sphagnum fimbriatum* increased to the left of the axis, and *Sphagnum magellanicum* increased toward the center of the axis. This showed clear

Table 2. Differences in Water Chemical Variables Measured on Surface Water from Eight Peatland Sites with Contrasting Origin Along Chiloé Island in Southern Chile

	Anthropogenic peatlands	Natural peatlands	P
pH	4.26 ± 0.42	4.23 ± 0.33	0.86
EC (µS/cm)	153.7 ± 97.2	127.4 ± 87.1	0.19
Mg (mg/L)	1.4 ± 0.7	1.6 ± 1.5	0.58
K (mg/L)	2.9 ± 2.7	5.3 ± 3.7	0.03*
Ca (mg/L)	2.9 ± 1.9	3.3 ± 3.4	0.69
Cl (mg/L)	15.3 ± 8.8	19.3 ± 15.7	0.99
Total N (mg/L)	2.8 ± 1.5	3.8 ± 1.6	0.05*
IR	0.27 ± 0.17	0.20 ± 0.07	0.59

Values are means (±1 SD) of 45 samples for the anthropogenic and 27 for the natural sites.

*Values for significant differences after nonparametric Mann–Whitney U test.

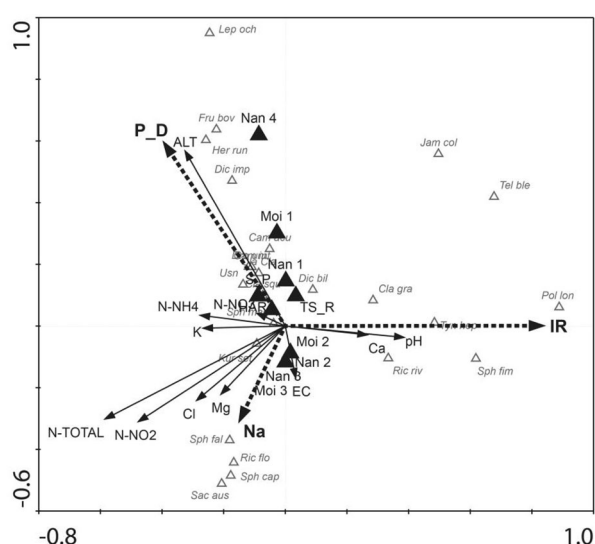


Figure 2. CCA biplot of bryophyte and lichen species by all environmental variables. Species are shown as shaded triangles. Environmental variables are shown as continuous vectors, dummy variables as large unshaded triangles, and selected variables by forward stepwise as dashed vectors. Species codes are explained in Table 1. Environmental variables codes: S_P. origin of peatland; HAR. *Sphagnum* moss harvesting; P_D. distance from Pacific Ocean; ALT. altitude; NAN. microtopography (NAN1: Hummock. NAN2: Lawn. NAN3: Carpet. NAN4: *Tepualia stipularis* base); Moisture. MOI (MOI1: Dry. MOI2: moderately wet. MOI3: saturated); TS_R. accompanying vascular plants; IR. ionic ratio.

differences in the response of species to changing conditions such as sea spray and humidity. Liverworts on the other hand were concentrated at the extreme end of the axis (Figure 3G), abundance of *Riccardia floribunda*, and *Riccardia rivularis* showed increases to the left of the axis. This also suggests a specific response of each species to nutrients and pH. Finally, distribution of lichens, *Cladonia* subgen

cladina and *Cladonia squamosa* concentrated toward the center of the axis (Figure 3H), suggesting that these organisms prefer transitional peatlands.

Finally, we found that irrespective of origin, pH significantly predicts H' ($F_{1,66} = 31.2$, $P < 0.0001$), actually pH alone explained 72% of model deviance. Additionally, we found that for a given pH species, diversity tended to be higher in anthropogenic than in natural peatlands (Figure 4A); hence, there was a significant covarying effect of peatland origin and H' ($F_{1,65} = 4.2$, $P < 0.04$), and the interaction term “pH:origin” was barely significant and $F_{1,64} = 4.1$, $P < 0.04$, respectively (Figure 4A). Overall there was a negative relationship between the percentage of *Sphagnum* abundance and species diversity (Figure 4B); however, the strength of this relationship did not vary as function of peatland origin ($F_{1,64} = 0.2$, $P = 0.70$). Therefore, *Sphagnum* abundance was the key predictor of species diversity ($F_{1,66} = 178$, $P < 0.0001$), and alone it explained 28% of model deviance. When all peatlands were analyzed together, we found a significant effect of *Sphagnum* abundance on water pH ($F_{1,70} = 35.6$, $P < 0.0001$); however, this effect was only significant in anthropogenic peatlands ($F_{1,43} = 40.9$, $P < 0.0001$; Figure 5). Natural peatlands did not show this trend ($F_{1,25} = 2.9$, $P < 0.09$).

DISCUSSION

Chemical characteristics of surface water showed that despite differences in origin and factors that promoted the establishment of peatland ecosystems in Chiloé Island, physicochemical parameters did not differ (that is, natural and anthropogenic) (Table 2). Although water chemistry is considered a key factor for plant composition of peatland

Table 3. Marginal and Conditional Effects of Environmental Factors from the Canonical Correspondence Analysis (CCA) on Species Composition Across Eight Peatland Sites with Contrasting Origin Along Chiloe Island in Southern Chile

	Marginal effects		Conditional effects		
	Lambda 1	Lambda A	<i>p</i>	<i>F</i>	
IR	0.33	0.33	0.001	4.99	
Nan 4	0.24	0.24	0.002	3.71	
P_D	0.26	0.22	0.001	3.62	
Na	0.11	0.14	0.003	2.27	

Only significant variables are shown in the table.

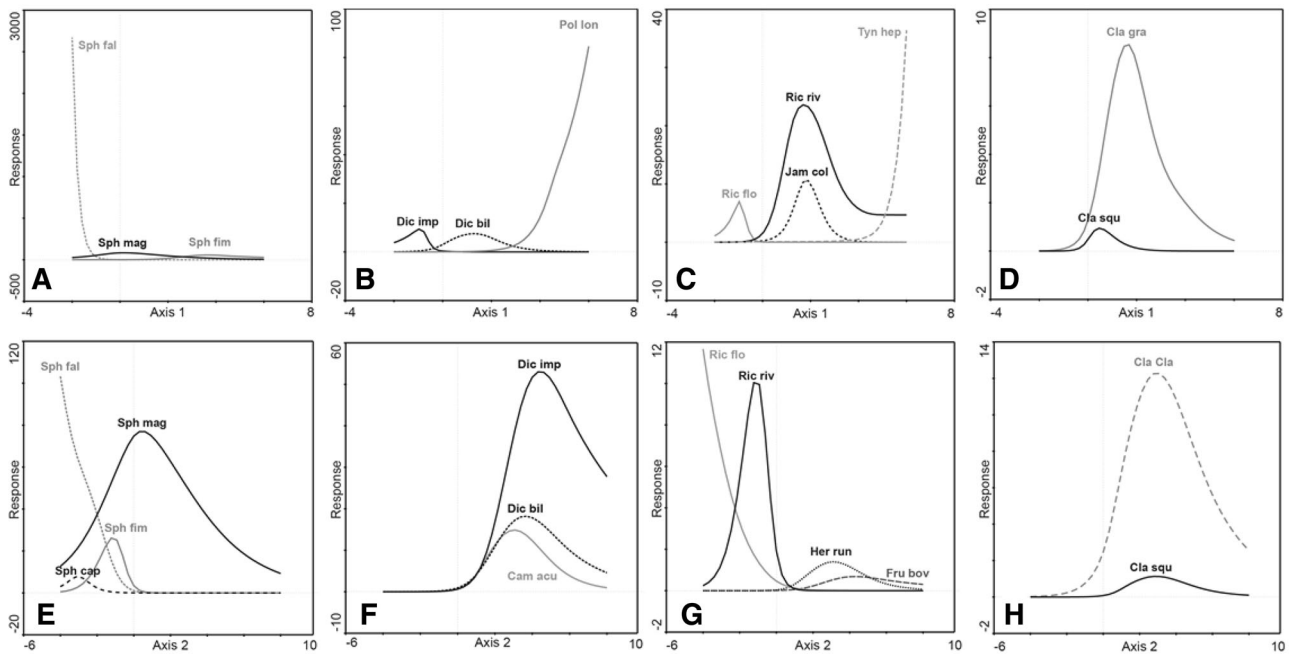


Figure 3. Response curves of generalized additive models (GAM) to Axis 1 (A–D) and Axis 2 (E–H) of canonical correspondence analysis (CCA) in *Sphagnum* species (A and E), moss species (except *Sphagnum*) (B and F), liverwort species (C and G), and *Cladonia* species (D and H). We only considered species with significant responses and that were not eliminated by the Akaike information criterion (AIC). The response is presented as dry biomass per sample plot. For species codes, see Table 1.

ecosystems, we found that the abundance of *Sphagnum* has also played a key role. As previously suggested by van Breemen (1995), *Sphagnum* has the ability to outcompete other plants by creating acidic, nutrient-poor, and anoxic conditions, hence is considered an ecosystem engineer of these peatland ecosystems (Jones and others 1994). In particular, in our study sites, we can see that water pH decreased as a function of *Sphagnum* abundance (Figure 5), and this trend was highly significant in anthropogenic peatlands. Therefore, a biotic factor such as *Sphagnum* abundance is driving water

chemistry and species diversity in several of our studied peatlands. These results are in agreement with previous studies that have found that increasing *Sphagnum* abundance strongly reduces the performance of lichens and liverworts (Lang and others 2009).

Surface-water chemistry is the most significant factor accounting for changes in floristic composition among our study sites. In contrast to our expectations, bog origin (natural or anthropic) was not the most significant factor accounting for changes in floristic composition among peatlands.

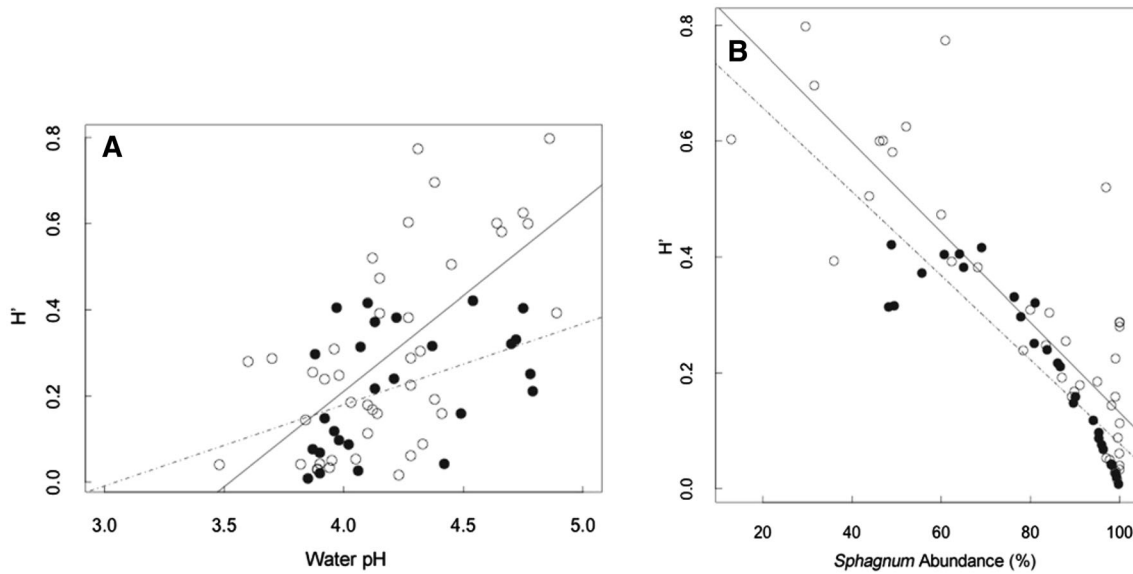


Figure 4. **A** Relationship between water pH and bryo-lichenic diversity index (H') anthropogenic (*open circles*) and natural (*solid circles*) peatlands of southern temperate Chile. *Solid line* is the fit for anthropogenic peatlands where $H' = 0.44\text{pH} - 1.56$, $R^2 = 0.39$, $P < 0.0001$. *Dashed line* is the fit for natural peatlands where $H' = 0.18\text{pH}$, $R^2 = 0.15$, $P < 0.02$. **B** Decreasing species diversity index (H') with increasing *Sphagnum* abundance in eight peatland ecosystems in southern Chile; *solid line* is the fit for anthropogenic peatlands where $H' = -0.007x + 0.84$, $R^2 = 0.72$, $P < 0.0001$, *dashed line* is the fit for natural peatlands where $H' = -0.007x + 0.74$, $R^2 = 0.71$, $P < 0.0001$.

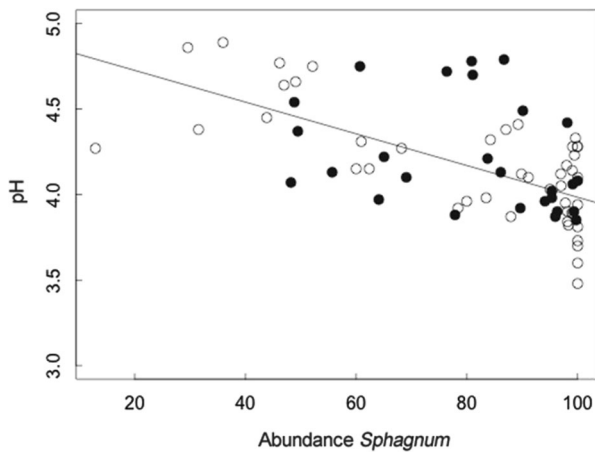


Figure 5. Decreasing water pH with increasing *Sphagnum* abundance. *Solid line* is the fit for anthropogenic peatlands where $\text{pH} = -0.009x + 4.91$, $R^2 = 0.47$, $P < 0.0001$. *Open circles* denote anthropogenic peatlands, and *solid circles* correspond to natural ones.

Other elements, such as the water source supplying peatlands or the influence of sea spray, were more significant for the occurrence of bryo-lichenic species of in the studied peatlands of Chiloé. Indeed, our results are consistent with Nicholson and others (1996) and Gignac and others (1991), who also found that biogeochemical variables related to water chemistry largely explained variation in the

floristic composition of Canadian peatlands. Similarly, Kleinebecker and others (2008) highlighted the importance of biogeochemical variables in peatland vegetation in southern Patagonia. Furthermore, based on the differences in ions and elements among our sites we can identify rainfall water as the main source of water and nutrients for these peatlands on Chiloé Island. Nonetheless, in two of the sites (anthropogenic), we found high IR values, which may indicate a mixture of groundwater and rainfall. In these localities with transitional conditions, there may still be a connection to the groundwater, but further studies are required to test this. Our results corroborate the findings of Daniels and Eddy (1985) in European peatlands that suggested that water chemical characteristics (amount of dissolved ions and degree of acidity) in peatlands is one of the main factors influencing the distribution of species, and potentially of peatland floristic composition and dynamics.

Based on the results of our CCA, we were able to identify two sets of variables that best describe the structure of bryo-lichenic communities as well as the ecosystem dynamic of peatlands with contrasting origin on Chiloé Island. One set of variables (that is, Axis 1 in the CCA) reflects an ombrotrophic to transitional (that is, minerotrophic) condition and the second set, which is Axis 2 of the CCA, rather reflects a thalassotrophic-transitional lithotrophic

gradient (Figure 2). Accordingly, Axis 1 reflects the influence of water chemistry on species occurrence and can be interpreted as a gradient from ombrotrophic to transitional conditions associated with IR in the first place, and Ca and pH in the second place. IR is related to the source of water and nutrient inputs, hence water. The consideration of an ombrotrophic-transitional gradient in Chiloé peatlands is reinforced by the fact that Ca concentrations and pH values increased from ombrotrophic to transitional peatlands (see CCA diagram; Figure 2). These results are similar to those reported for natural peatlands in Canada where Gignac and Vitt (1990) also found that pH values and Ca concentrations increased from ombrotrophic to minerotrophic conditions. The explanation for this is that in ombrotrophic peatlands, where water is not in contact with mineral soils, rainfall is the only source of Ca. Finally, in ombrotrophic peatlands the high abundance of *Sphagnum* mosses increases the concentration of organic acids that further increase cationic exchange; hence water pH becomes more acidic (Clymo 1964; Rydin and Jeglum 2006). This explanation can also be applied in the case of Chiloé peatlands for the ombrotrophic to transitional gradient that we found. In accordance with previous studies, we found that NH_4^+ levels in peatland surface water were higher in ombrotrophic compared to transitional peatlands (Figure 2) (Vitt and others 1995a). We argue that lower levels in NH_4 found in transitional/minerotrophic peatlands could be related to the higher plant NH_4 consumption associated with higher species diversity and abundance common to these types of peatlands (Rydin and Jeglum 2006). Nevertheless, further studies on plant nutrient use and consumption are required to better understand nutrient fluxes and biogeochemistry of peatland ecosystems in Chile.

Biogeochemistry of peatland ecosystems on Chiloé Island is clearly affected by proximity to the Pacific Ocean, sea spray, and sea water, hence the origin of what we called a “thalassotrophic-transitional lithotrophic gradient” sensu Wheeler and Proctor (2000). This ordination reveals the influence of sea spray on water chemistry and the role of distance from the Pacific Ocean in driving species diversity in our study sites. Our results are in agreement with previous studies in the Northern Hemisphere where ocean spray also played a significant role on vegetation structure and composition of peatlands of Europe (Wheeler and Proctor 2000; Martínez Cortizas and others 2009), Canada (Comeau and Bellamy 1986), and Southern Patagonia (Kleinebecker and others 2008). Hence, distance to the ocean in ombrotrophic-prone peatlands should not only be considered as a geographic or climatic element, but also as a variable that regulates peatland chemistry via inputs of Ca, Mg, and Na.

We found that bryophyte and lichen species show distinctive ecological niches in relation to water chemical conditions (Figure 3). Here we tested whether environmental parameters related to the set of variables from axes 1 and 2 of the CCA affected the niche breadth of the most dominant species at our study sites (Rydin 1986; Rydin 1993). As expected, we found that ombrotrophic-transitional curves show a distinct species separation. Accordingly, different groups (mosses, liverworts or lichens) occupied different ecological niches along the ombrotrophic-transitional gradient (Figure 3). Nevertheless, we suggest that species also respond to nutrient availability in different ways; some species, such as *Sphagnum falcatum*, *Riccardia floribunda* (a liverwort), and *Dicranoloma imponens*, were more abundant under ombrotrophic condi-

Table 4. Comparisons Among Chemical Variables of Surface Water from Natural and Anthropogenic Peatlands from Chiloé Island in Southern Chile, and Peatlands from the Northern Hemisphere

	Chiloé Island, Chile	Coastal peatlands, Canada ^{1*}	Inland peatlands, Canada ^{2*}	Coastal peatlands, Spain ^{3*}
Water pH	3.7–4.8	4.1–4.8	3.9–4.2	3.9–4.9
EC ($\mu\text{S}/\text{cm}$)	35.3–253.1	6.7–82.3	28–50	39–48
Ca (mg/L)	0.29–7.9	0.16–0.38	3–4.3	0.3–0.6
Cl (mg/L)	4.5–40.5	3.5–23.3	–	7–11.8
Na (mg/L)	3.41–18.58	0.54–13.90	1.54–1.63	4–4.6
Mg (mg/L)	0.29–3.63	0.22–1.6	0.74–1.39	0.6–0.7
K (mg/L)	0.17–11.79	0.02–0.14	0.54–0.78	0.3–0.4

*Published data.

¹British Columbia (Vitt and others 1990), ²Central Alberta (Vitt and others 1995a) and ³Galicia (Martínez-Cortizas and others 2009).

tions while *Sphagnum fimbriatum* and *Polytrichum longisetum* preferred transitional conditions (Figure 3). Until now, differences in bryo-lichenic composition between natural and anthropogenic peatlands were considered to be related to the origin, but our study shows that water chemistry is the key driver. In relation to differences in bryo-lichenic composition between northern and southern peatlands, we found that peatlands in Chiloé have higher diversity of liverworts (that is, 30 species) than peatlands of Northern Hemisphere (20 species—Canada, 17 species—British bogs) (Wheeler 1993; Vitt and Belland 1995; León and others 2014). In contrast, the diversity of *Sphagnum* is lower in Chiloé peatlands (that is, six species) than in Europe or Canada, where more than 20 *Sphagnum* species have been reported (Wheeler 1993; Vitt and Belland 1995).

Peatlands from Chiloé Island tend to fit within chemical and ecological ranges described for ombrotrophic peatlands in the Northern Hemisphere (Table 4) as we did not find any peatland that could be described as minerotrophic. Therefore, succession in young (that is, less than 200 year old, anthropogenic peatlands) does not seem to start with species-rich, mineral-rich, low pH water (Zobel 1988; Granath and others 2010). Further studies are required to learn about biogeochemical cycles in these peatlands to assess how human activities can cause alterations of these cycles and affect the structure and dynamics of peatland ecosystems.

Finally, despite the great ecological importance of peatlands, we know very little about the dynamics of species composition and the main environmental factors driving these ecosystems in the Southern Hemisphere, and the geological history, biological adaptation, and community structure has received little attention in the scientific literature. However, our results show that despite different origins, the ecology of peatlands follows common rules with peatlands from the Northern Hemisphere, where water chemistry is the key factor on species composition and vegetation structure.

ACKNOWLEDGEMENTS

This research was supported by grants AECID A/025081/2009, Cooperación al Desarrollo UCM 4138114 and AECID A/030011/2011. We are very grateful to Dr. Alfonso Benítez-Mora for his assistance in the field. We wish to thank the Fundación Senda Darwin, Aserradero A.R.P., Chepu adventures, I. Municipalidad de Dalcahue and CONAF

Chiloé for their logistic support during fieldwork. Lic. Elena Araujo for her help with TLC, Dra. Jara Vassallo for her assistance with the data analysis. C. A. León acknowledges the support of the doctoral fellowship provided by CONICYT-Gobierno de Chile. This is a contribution to the Research Program of LTSER-Chile network at Senda Darwin Biological Station, Chiloé, Chile.

REFERENCES

- Albornoz F, Gaxiola A, Seaman BJ, Pugnaire F, Armesto J. 2013. Nucleation-driven regeneration promotes post-fire recovery in a Chilean temperate forest. *Plant Ecol.* 214:765–76.
- Arroyo MT, Plissock P, Mihoc M, Arroyo-Kalin M. 2005. The Magallanic moorland. In: Fraser LH, Keddy PA, Eds. *The world's largest wetlands. Ecology and conservation.* New York: Cambridge University Press. p 424–45.
- Bridgman SD, Updegraff K, Pastor J. 2001. A comparison of nutrient availability indices along an ombrotrophic–minerotrophic gradient in Minnesota wetlands. *Soil Sci Soc Am J* 65.
- Bullock J. 1997. *Plants.* In: Sutherland WJ, Ed. *Ecological census techniques: a handbook.* UK: Cambridge University Press. p 111–38.
- Carmona MR, Aravena JC, Bustamante-Sanchez MA, Celis-Diez JL, Charrier A, Díaz IA, Díaz-Forestier J, Díaz MF, Gaxiola A, Gutiérrez AG, Hernandez-Pellicer C, Ippí S, Jaña-Prado R, Jara-Arancio P, Jimenez J, Manushevich D, Necochea P, Nuñez-Avila M, Papic C, Pérez C, Pérez F, Reid S, Rojas L, Salgado B, Smith-Ramírez C, Troncoso A, Vásquez RA, Willson MF, Rozzi R, Armesto JJ. 2010. Estación Biológica Senda Darwin: investigación ecológica de largo plazo en la interfase ciencia-sociedad. *Rev Chil de Hist Nat* 83:113–42.
- Clymo RS. 1964. The Origin of Acidity in *Sphagnum* Bogs. *The Bryol* 67:427–31.
- Comeau PL, Bellamy DJ. 1986. An ecological interpretation of the chemistry of mire waters from selected sites in eastern Canada. *Can J Bot* 64:2576–81.
- CONAF. 2009. Plan de Acción Provincial Chiloé—Plan de Gestión Territorial. Castro: Oficina Provincial Chiloé - Corporación Nacional Forestal. p 49.
- Charman D. 2002. *Peatlands and environmental change.* New York: Wiley. p 301.
- Daniels RE, Eddy A. 1985. *Handbook of European sphagna.* Great Britain: Institute of Terrestrial Ecology, Natural Environment Research Council. p 262.
- di Castri F, Hajek ER. 1976. *Bioclimatología de Chile.* Santiago: Editorial Universidad Católica de Chile. p 128.
- Díaz MF, Larraín J, Zegers G, Tapia C. 2008. Caracterización florística e hidrológica de turberas de la Isla Grande de Chiloé, Chile. *Rev Chil de Hist Nat* 81:445–68.
- du Rietz GE. 1954. Die Mineralbodenwasserzeigergerenze als grundlage einer natürlichen zweigliederung der nord- und mitteleuropäischen moore. *Vegetatio* 5:571–85.
- Gaxiola A, McNeill SM, Coomes DA. 2010. What drives retrogressive succession? Plant strategies to tolerate infertile and poorly drained soils. *Funct Ecol* 24:714–22.

- Gignac LD, Vitt DH. 1990. Habitat limitations of *Sphagnum* along climatic, chemical, and physical gradients in mires of western Canada. *Bryol* 93:7–22.
- Gignac LD, Vitt DH, Zoltai SC, Bayley SE. 1991. Bryophyte response surfaces along climatic, chemical and physical gradients in peatlands of western Canada. *Nova Hedwig* 53:27–71.
- Granath G, Strengbom J, Rydin H. 2010. Rapid ecosystem shifts in peatlands: linking plant physiology and succession. *Ecology* 91:3047–56.
- Hammer Ø, Harper DAT, Ryan PD. 2001. PAST: paleontological statistics software package for education and data analysis. *Palaeontol Electron* 4:9.
- Hauser A. 1996. Los depósitos de turba en Chile y sus perspectivas de utilización. *Rev Geol de Chile* 23:217–29.
- Hedenäs L. 2003. The European species of the *Calliergon-Scorpidium-Drepanocladus* complex, including some related or similar species. *Meylania* 28:1–116.
- Heusser CJ. 2003. Preface. In: Heusser CJ, Ed. *Developments in Quaternary Sciences—Ice Age Southern Andes A Chronicle of Paleocological Events*. Amsterdam: Elsevier. p 7–8.
- Hughes PDM, Barber KE. 2004. Contrasting pathways to ombrotrophy in three raised bogs from Ireland and Cumbria, England. *The Holocene* 14:65–77.
- Jones CG, Lawton JH, Shachak M. 1994. Organisms as ecosystem engineers. *Oikos* 69:373–86.
- Kleinebecker T, Holzel N, Andreas V. 2008. South Patagonian ombrotrophic bog vegetation reflects biogeochemical gradients at the landscape level. *J Veg Sci* 19:151–60.
- Kleinebecker T, Holzel N, Vogel A. 2007. Gradients of continentality and moisture in South Patagonian ombrotrophic peatland vegetation. *Folia Geobot* 42:363–82.
- Kleinebecker T, Hölzel N, Vogel A. 2010. Patterns and gradients of diversity in South Patagonian ombrotrophic peat bogs. *Austral Ecol* 35:1–12.
- Lang SI, Cornelissen JHC, Hölzer A, Ter Braak CJF, Ahrens M, Callaghan TV, Aerts R. 2009. Determinants of cryptogam composition and diversity in *Sphagnum*-dominated peatlands: the importance of temporal, spatial and functional scales. *J Ecol* 97:299–310.
- León CA, Oliván G. 2014. Recent rates of carbon and nitrogen accumulation in peatlands of Isla Grande de Chiloé-Chile. *Rev Chil de Hist Nat* 87.
- León CA, Oliván G, Larraín J, Vargas R, Fuertes E. 2014. Bryophytes and lichens in peatlands and *Tepualia stipularis* forest of Isla Grande de Chiloé-Chile. *Anales del Jardín Botánico de Madrid* 71:e003.
- Lepš J, Šmilauer P. 2003. Multivariate analysis of ecological data using CANOCO. p 283.
- Loisel J, Yu Z. 2013. Holocene peatland carbon dynamics in Patagonia. *Quat Sci Rev* 69:125–41.
- Magurran AE. 2004. *Measuring biological diversity*. Oxford: Blackwell.
- Martínez-Cortizas A, Pontevedra Pombal X, Nóvoa Muñoz JC, Rodríguez Fernández R, López-Sáez JA. 2009. Turberas ácidas de esfagnos. In: Martínez Cortizas A, Ed. *Bases ecológicas preliminares para la conservación de los tipos de hábitat de interés comunitario en España*. Madrid: Ministerio de Medio Ambiente, y Medio Rural y Marino. p 1–64.
- Nicholson BJ, Gignac LD, Bayley SE. 1996. Peatland distribution along a north-south transect in the mackenzie river basin in relation to climatic and environmental gradients. *Vegetatio* 126:119–33.
- Pérez CA, Armesto JJ, Torrealba C, Carmona MR. 2003. Litterfall dynamics and nitrogen use efficiency in two evergreen temperate rainforests of southern Chile. *Austral Ecol* 28:591–600.
- Porter SC. 1981. Pleistocene glaciation in the southern Lake District of Chile. *Quat Res* 16:263–92.
- R Development Core Team. 2011. *R: a language and environment for statistical computing*: Vienna, Austria.
- Roulet N, Lafleur P, Richard P, Moore T, Humphreys E, Bubier J. 2007. Contemporary carbon balance and late Holocene carbon accumulation in a northern peatland. *Glob Change Biol* 13:397–411.
- Rydin H. 1986. Competition and niche separation in *Sphagnum*. *Can J Bot* 64:1817–24.
- Rydin H. 1993. Mechanism of interactions among *Sphagnum* species along water level gradients. *Adv Bryol* 5:153–85.
- Rydin H, Jeglum JK. 2006. *The Biology of Peatlands*. London: Oxford University Press. p 343.
- Sadzawka A, Carrasco MA, Grez R, Mora ML, Flores P, Neaman A. 2006. Métodos de análisis de suelos recomendados para los suelos de Chile. Serie Actas INIA N° 34. Santiago, Chile: Instituto de Investigaciones Agropecuarias. p 164.
- Scarlett P, O'Hare M. 2006. Community structure of in-stream bryophytes in English and Welsh Rivers. *Hydrobiologia* 553:143–52.
- StatSoft. 2004. *STATISTICA for Windows, user's guide (version 7.0)* Tulsa: StatSoft Incp.
- ter Braak CJF, Šmilauer P. 2002. *CANOCO reference manual and CanoDraw for windows user's guide: Software for Canonical Community Ordination (version 4.5)*. Ithaca NY: Microcomputer Power. p 500.
- Tuittila ES, Väliaranta M, Laine J, Korhola A. 2007. Quantifying patterns and controls of mire vegetation succession in a southern boreal bog in Finland using partial ordinations. *J Veg Sci* 18:891–902.
- van Breemen N. 1995. How *Sphagnum* bogs down other plants. *Trends Ecol Evol* 10:270–5.
- Vitt DH, Bayley SE, Jin T-L. 1995a. Seasonal variation in water chemistry over a bog-rich fen gradient in continental western Canada. *Can J Fish Aquat Sci* 52:587–606.
- Vitt DH, Belland RJ. 1995. The bryophytes of peatlands in continental western Canada. *Fragm Florist et Geobot* 40:339–48.
- Vitt DH, Chee W-L. 1990. The relationships of vegetation to surface water chemistry and peat chemistry in fens of Alberta, Canada. *Vegetatio* 89:87–106.
- Vitt DH, Horton DG, Slack NG, Malmer N. 1990. *Sphagnum*-dominated peatlands of the hyperoceanic British Columbia coast: patterns in surface water chemistry and vegetation. *Can J For Res* 20:696–711.
- Vitt DH, Li Y, Belland RJ. 1995b. Patterns of bryophyte diversity in peatlands of continental western Canada. *Bryologist* 98:218–27.
- Vitt DH, Wieder K. 2008. The structure and function of bryophyte-dominated peatlands. Goffinet B, Shaw AJ, editors. *Bryophyte Biology*: Cambridge University Press. p357–391.
- Wheeler BD. 1993. Botanical diversity in British mires. *Biodivers Conserv* 2:490–512.
- Wheeler BD, Proctor MCF. 2000. Ecological gradients, subdivisions and terminology of north-west European mires. *J Ecol* 88:187–203.
- Whinam J, Buxton R. 1997. *Sphagnum* peatlands of Australasia: an assessment of harvesting sustainability. *Biol Conserv* 82:21–9.

- Whinam J, Hope GS, Clarkson BR, Buxton RP, Alspach PA, Adam P. 2003. *Sphagnum* in peatlands of Australasia: their distribution, utilization and management. *Wetlands Ecol Manage* 11:37–49.
- White J, James PW. 1985. A new guide to microchemical techniques for the identification of lichen substances. *Bull Brit Lichen Soc* 57:1–41.
- Yu Z, Beilman DW, Jones MC. 2009. Sensitivity of northern peatland carbon dynamics to holocene climate change. *Carbon Cycling in Northern Peatlands: American Geophysical Union*. p55-69.
- Yu Z, Loisel J, Brosseau DP, Beilman DW, Hunt SJ. 2010. Global peatland dynamics since the last glacial maximum. *Geophys Res Lett* 37:L13402.
- Zobel M. 1988. Autogenic succession in boreal mires—a review. *Folia Geobotanica et Phytotaxonomica* 23:417–45.
- Zuur A, Ieno EN, Smith GM. 2007. *Analysing ecological data*. New York: Springer Press. p 672.