

Peatlands of Southern South America: a review

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SUMMARY

Southern South American peatlands (SSAP) play a key role in the ecological dynamics of Patagonia. They mostly comprise of undisturbed environments which provide important ecosystem services, including carbon sequestration, water reservoir and habitat for both widespread and endemic organisms. When compared with boreal peatlands, our knowledge of the functioning of SSAP is poor, and it is necessary to raise awareness about their scientific and ecological value and to ensure their conservation. This article examines a broad base of historical and contemporary published research literature on the peatlands of Chile and Argentina, from 1843 onwards, to identify gaps in knowledge, implications for the assessment of peatland functioning, and targets for peatland conservation and management. To achieve this goal, we reviewed a total of 196 research papers/reports from across the peer-reviewed and grey literature. We conclude that gaps in our knowledge and understanding of SSAP have deeply undermined the development of effective conservation strategies for these understudied ecosystems. To reverse this situation, we recommend that future research and management efforts should aim: (1) to build an inventory of the peatlands that exist in SSAP, including their location and area; (2) to ensure land use planning prioritises the maintenance of SSAP ecosystem services; (3) to improve existing legislation and protocols of good and sustainable practice for extractive activities; and (4) to carry out an extensive awareness campaign aimed at the local population and key decision makers.

KEY WORDS: Argentina, Chile, conservation, mires, Patagonia, wetlands

INTRODUCTION

Peatland ecosystems are efficient carbon sinks and represent one of the largest carbon pools in the biosphere. They store an estimated 550 GtC - twice the carbon stock of global forest biomass - in only 3 % of terrestrial land area (Joosten & Couwenberg 2008, Yu 2012). Peatlands are also central to the hydrological cycle, through water storage, regulation of water quality, groundwater recharge, and flood and drought mitigation. They also play a key role in the conservation of biodiversity, archaeological remains and palaeoenvironmental archives (Ramsar

2004). Peat and *Sphagnum* moss are recognised globally as a valuable economic resource, with peatland-derived products used as fuel, to absorb oil spills, and as a horticultural growing medium (Joosten *et al.* 2016). However, peat is a non-renewable resource.

In South America, temperate peatlands are concentrated in the Southern Cone of the continent, primarily in Chilean and Argentine Patagonia (Landry *et al.* 2010) (Figure 1). The distribution and variation in these ecosystems is also influenced by a longitudinal (east–west) gradient of humidity and altitude created by the Andes mountain range,

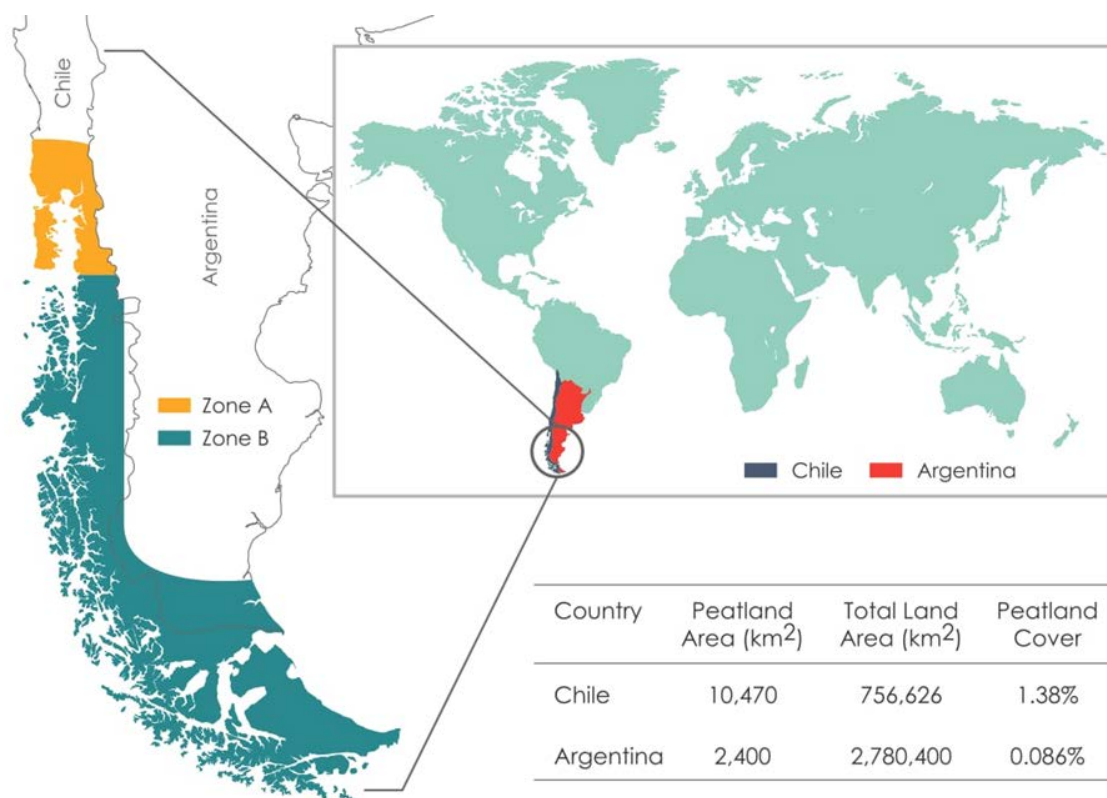


Figure 1. Main distribution of peatlands in Southern South America and area estimation in Chile and Argentina according to Rydin & Jeglum (2006). Zone A: scarce peatlands, located in depressions or high altitude areas, Zone B: abundant peatlands, located in varied reliefs.

producing a range of peatland functional types that reflect this (Kleinebecker *et al.* 2010).

Southern South American peatlands (SSAP) have historically been less studied than their counterparts in the Northern Hemisphere, most likely owing to a combination of factors: a low critical mass of researchers interested in these ecosystems; their comparatively limited spatial extent; and their remote and often inaccessible location (Saavedra & Figueroa 2015). The eastern and austral regions of southern South America present a fragmented mosaic of oceanic channels, fjords and continental islands, formed through extensive glacial activity and tectonic movement (Arroyo *et al.* 2005). Consequently, low population density and reduced connectivity ensures near-pristine conditions at many field sites, which are often only reachable after journeys lasting several days from urbanised regions, which are themselves only accessible by water or air.

Peatlands are recognised for their challenging environmental characteristics (e.g. high water tables, often acidic conditions), which limit the establishment of flora and fauna (Rydin & Jeglum 2006). Nevertheless, floristic studies of SSAP have described a high diversity of, often endemic, bryophyte and lichen species (Díaz *et al.* 2008, León *et al.* 2014,

Souto *et al.* 2015), further emphasising the importance of protecting these systems in order to maintain global biodiversity. Furthermore, the ecological role and cultural value of these endemic bryophyte and lichen species remains largely unknown.

Palynological studies undertaken in SSAP have made significant contributions to our understanding of the biogeography of southern South America by reconstructing past variability in ecosystem extent and composition (Villagrán 2001, Rabassa *et al.* 2006). These studies have also permitted the reconstruction of Quaternary climate variability, providing long-term context for current climatic changes and future scenarios (Villa-Martínez & Moreno 2007).

SSAP, like all peatlands, play a central role in a range of biogeochemical cycles. The functioning of SSAP in terms of carbon sequestration is strikingly similar to that of northern boreal peatlands, despite having developed under very different climatic boundary conditions (Loisel & Yu 2013a). It is estimated that these peatlands represent the main extratropical carbon sink in the Southern Hemisphere (Loisel & Yu 2013a, Iturraspe 2016, Holl *et al.* 2019). SSAP also hold large reserves of fresh water. *Sphagnum* moss present in these systems intercepts

runoff and stores rainwater, regulating basin-scale water flow (Holden 2005), and providing a steady supply of freshwater to local communities and surrounding ecosystems. Therefore, the degradation of these ecosystems could release greenhouse gases into the atmosphere (Veber *et al.* 2018, Valdés-Barrera *et al.* 2019), with clear implications for their contribution to climate change.

Despite the clear importance of these ecosystems, SSAP are under threat from a widespread peat and moss extraction industry across the region (Iturraspe 2016). There is an urgency to address the considerable gaps in knowledge and understanding of these unique peatlands, not least to raise an awareness of their value and ensure their conservation. We present a comprehensive and, to the best of our knowledge, exhaustive review of the literature on the peatlands of southern Chile and Argentina. The aims of this article are: i) to present an integrated and critical review of the current knowledge on peatlands of southern South America; ii) to identify the main gaps in knowledge to be addressed as research priorities in future studies; and, iii) to assess the issues in the degradation and conservation of these systems, and discuss tools for their sustainable management and protection. As far as we know, this study represents the first effort to synthesise all the existing information about SSAP.

DISTRIBUTION OF SOUTHERN SOUTH AMERICAN PEATLANDS

Peatlands are located at high latitudes in both hemispheres. In the Southern Hemisphere, temperate peatlands are found mainly in southern South America (Chile and Argentina) (Figure 1), New Zealand and the Falkland Islands (Rydin & Jeglum 2006). In Chile, these ecosystems possess a sizeable range from Cordillera Pelada in Valdivia (40 °S) to the far south (56 °S) (Schlatter & Schlatter 2004), becoming most prevalent south of the Guaitecas Archipelago (Pisano 1977, Schlatter & Schlatter 2004, Díaz *et al.* 2015). Considerable variability in estimates of the extent of temperate peatlands in Chile highlights a lack of understanding of these systems. Joosten (2010) estimates that Chile contains about 10,996 km² of peatlands, Rydin & Jeglum (2006) report 10,470 km², surveys of Chilean native forest (CONAF 2006, CONAF/UACH 2012, 2014) indicate an area of 32,296 km² of peatland, and Xu *et al.* (2018) report 2,276 km².

The northernmost Argentinean peatlands are found in the northeast portion of the Patagonian Andes (36 °S to 50 °S) and most are localised in

Andean foothill forest environments and their surroundings (Blanco & de la Balze 2004, Iturraspe 2016). There, they occur as scattered units, in hollows or in higher altitudinal areas. Instead, Tierra del Fuego concentrates most Argentinean peatlands (~ 2,700 km²) (Iturraspe 2016). Rydin and Jeglum (2006) estimated that Argentina contains about 2,400 km² of peatlands. In that country, the southwest–northeast precipitation gradient determines a transitional zone from the Fuegian Andes to the north, with mosaics of *Nothofagus* forests, grasslands, *Sphagnum* bogs and Cyperaceae fens. Away from the Andes, from eastern Patagonia to the north of Tierra del Fuego Island (36 °S to 54 °S) the windy and dry climate of the steppe produces a general water balance deficit that significantly limits the presence of peatlands and other wetlands.

NATURAL HISTORY OF PEATLANDS

Climate, geomorphology and origin

The climate in the western part of southern South America is characterised by strong and near constant westerly winds (the ‘southern westerlies’), cool summers due to the cold Humboldt Current and mean temperatures in the coldest month greater than 0 °C (Coronato *et al.* 2017). Precipitation is the determining factor for peatland vegetation (Arroyo *et al.* 2005, Kleinebecker 2007, Rodríguez 2015). In the wind-exposed hyper-oceanic belt, with precipitation > 2,000 mm yr⁻¹, cushion bogs prevail, dominated by the cushion plants *Astelia pumila* and *Donatia fascicularis* (Kleinebecker 2007, Iturraspe 2016). Ombrotrophic bogs dominated by *Sphagnum magellanicum* are found with precipitation between 500 and 1,500 mm yr⁻¹ on the lee side of the southern Andes (Loisel & Yu 2013a, Iturraspe 2016), although *S. magellanicum* dominated bogs are also occasionally found in areas with higher precipitation (e.g. 3,300 mm yr⁻¹; cf. Rodríguez 2015). The diminishing effect of nutrient inputs by sea-spray on the oceanic–continental gradient seems to be another crucial factor for the replacement of cushion plants by *S. magellanicum* as the dominant bog vegetation type (Kleinebecker 2007, Rodríguez 2015). In areas with precipitation of 500–2,000 mm yr⁻¹, minerotrophic peatlands (fens) also occur, dominated by rushes (e.g. *Marsippospermum grandiflorum*) and in wetter areas sedges (e.g. *Carex* spp.) (Loisel & Yu, 2013a, Iturraspe 2016).

Most SSAP have a post-glacial origin, forming in areas that became ice-free after the retreat of the ice sheet that covered southwestern South America during the Late Pleistocene (Rabassa *et al.* 2006). Yu

et al. (2010) indicate that most peatlands in South Patagonia initiated between 19,000–10,000 cal yr BP, with peaks around 17,000–14,500 cal yr BP and 13,500 cal yr BP (calibrated with IntCal04, cf. Reimer *et al.* 2004). This is in line with the deglaciation history of the region, although evidence also suggests that some peatlands formed at even earlier stages (ca. 6,500 cal yr BP, ca. 4,000 cal yr BP) (Holz *et al.* 2012, Loisel & Yu 2013b). The initiation peaks coincide with interstadial periods at the end of the Pleistocene, ca. 16,000–14,000 ¹⁴C yr BP and ca. 13,000–11,000 ¹⁴C yr BP (uncalibrated) (Heusser 1995). The first probably coincides with the temperature rise between 17,500–17,150 cal yr BP, which initiated the deglaciation of the Patagonian Ice sheet (McCulloch *et al.* 2000, Davies *et al.* 2020). Between 12,000–8,500 cal yr BP precipitation was higher than at any other point in the Holocene occurred (Lamy *et al.* 2010). The period between 11,500 cal yr BP and 9,000 cal yr BP was also exceptionally warm, with average temperatures ~ 3 °C above present (Fontana & Bennett 2012). Combined, the first millennia of the Holocene presented favourable conditions for mire formation. Warmer and moister conditions also occurred between 5,000 BP and 2,000 BP, most likely as a result of an increase in the intensity of the southern westerly winds (Loisel & Yu 2013a).

Three main pathways to peatland formation are terrestrialisation, paludification and primary peat formation (Rydin & Jeglum 2006). Terrestrialisation refers to the infilling of limnic systems (e.g. lakes) with organic sediments. A typical feature is a base layer of gyttja, under younger layers of peat (Succow & Joosten 2001). Peatlands which were initiated through terrestrialisation are reported across the full regional extent of SSAP. Paludification refers to a rise in water level that initiates peat formation on a former, less wet ground (Rydin & Jeglum 2006). The *pomponales* which are commonly found on the Isla Grande de Chiloé and in the continental areas of Los Lagos Region fall into this category, even though they are the result of recent anthropogenic activities and therefore possess a shallow peat layer under a peat-producing *Sphagnum* layer (León & Oliván 2014). The *pomponales* owe their origin to intense wood cutting and fire-mediated clearing activities that took place throughout the last two centuries in areas with poorly drained soils. Finally, primary peat formation refers to the accumulation of peat directly on top of wet mineral clay, primarily of glacial origin (till). This type is common on alluvial plains and typical of glacial forelands (Rydin & Jeglum 2006). Many SSAP formed through this pathway. Bogs which formed on alluvial plains are common in areas

with high precipitation. Peat formation can also take place in the drier parts of Patagonia in the so-called *mallines* (Mazzoni & Rabassa 2013), which correspond to a wetland type internationally known as ‘suo’ (Joosten & Clarke 2002, Roig & Roig 2004). In these ecosystems soil saturation is not permanent throughout the whole year. However, peat formation takes place when the organic matter content is more than 30 %, which can occur in the central parts of the ecosystem. They are typical of the Patagonian steppe in Argentina (Mazzoni & Rabassa 2013), but can also be found in the Chilean region of Aysén (Hauser 1984).

Classification of peatlands

Peatland classifications have generally been elaborated with specific foci in mind, and therefore differ considerably with respect to their purpose which can include, for example, support for decision-making on landscape uses, protection of biodiversity, and soil classification systems. In southern South America, one of the most used classification criteria is based on the dominant plant communities. Pisano (1977) describes mainly three groups: i) raised bog communities, dominated by hummocks and lawns of *Sphagnum magellanicum* moss; ii) non-raised bog communities or cushion plant bogs, dominated by *Donatia fascicularis* and *Astelia pumila*; and iii) graminoid tundra communities dominated by species of *Carex*, *Schoenus* and *Carpha*. Amigo *et al.* (2017) presented an update of the peatland plant-sociological nomenclature, defining four groups: i) cushion bogs; ii) *Sphagnum* bogs; iii) "montane tundra" bogs; and iv) sedge-grass bogs. Studies until 2010 mainly used the Soil Taxonomy (USDA 1999) as the classification tool, defining peatlands as Histosols and their associated subcategories. A disadvantage of the Soil Taxonomy system is its generalisation, which does not include descriptions of the peat forming process, the hydrological regime, the influential climatic factors, the nature of the substrate, and the peatland ecology. Studies exploring these aspects were performed in Tierra del Fuego (Iturraspe & Roig 2000, Köpke 2005, Iturraspe *et al.* 2013), using the “Bog-Fen” hydrological principle to differentiate peatlands according to their hydrological inputs, a principle widely used in Germany (AG-Boden 2005), Sweden (Rydin & Jeglum 2006) and the peatland regions of the USA (Chadde *et al.* 1998). Recently, studies in Chile have started to apply wetland and peatland classification systems with a focus on hydrogeomorphic and ecological principles (e.g. based on the classification systems of Spain, Sweden, Germany and South Africa), as well as on peatland ecosystem services. Díaz *et al.* (2008), León (2012)

and León *et al.* (2016) described botanical differences between *turberas* (geogenic and ombrogenic peatland) and *pomponales* (anthropogenic peatland). In the Baker and Pascua River basins (Aysén-Chile), Rodríguez (2015) developed a four-level classification system integrating: a) main relief and hydrology allowing peatland formation (five combinations); b) hydrogeomorphic peatland types (five types); c) peatland ecotypes based on dominant vegetation (eight types); and d) botanical composition of organic substrates forming peatland soils (eleven types).

Formation and carbon accumulation

The most extensive investigations into peat distribution in southern South America were undertaken by two Finnish expeditions in 1928–1929 and 1937–1938 (Auer 1942). Their mapping campaigns indicated that the average thickness of Fuegian peatlands is 3–4 m, although 7 m is reached frequently, and peats of up to nearly 12 m depth have been documented (Loisel & Yu 2013a). Peatlands in valleys of northern Patagonia more frequently reach depths of more than 10 m (Auer 1942).

Peatland formation takes place through the accumulation of organic carbon. Succession pathways have been described for: a) cushion bogs (Heusser 1995, Teltewskaja 2010, Grootjans *et al.* 2014, Rodríguez 2015); b) raised bogs (Heusser 1989, Sapkota *et al.* 2007, Holz *et al.* 2012, Loisel & Yu 2013a, Rodríguez 2015); and c) fens (Fesq-Martin *et al.* 2004, Markgraf *et al.* 2007, Villa-Martínez & Moreno 2007, Rodríguez 2015).

Loisel & Yu (2013a) studied carbon accumulation rates of four peatlands in the Chilean Magallanes region and reviewed carbon accumulation rates for 19 peatlands from the literature, with depths ranging between 1.7 m and 11.8 m. Their results revealed a mean annual carbon accumulation rate of 16 g m⁻² yr⁻¹. After the fen–bog transition, which occurred in at least 14 of the 23 peatlands (mostly after 4,200 cal yr BP), the rate of carbon accumulation increased by about 20 % (Loisel & Yu 2013a). These estimates are lower than those reported by Rodríguez (2015) for three peatlands in Aysén, with a mean of 27 g C m⁻² yr⁻¹. The latter, however, had lower mean depth of about 2 m, which is likely to account for the difference, as with increasing mire depth the typically slow rate of anaerobic peat decomposition increases (Clymo *et al.* 1998). Consequently, even higher rates of carbon accumulation were reported by León & Oliván (2014) for three shallow *pomponales* of around 30 cm depth and 100 years of age on the Isla Grande de Chiloé, with a mean of 47 g m⁻² yr⁻¹.

Auer (1942) observed a typical successional

pathway in SSAP in a gradient from El Chaltén to the southern coast of Tierra del Fuego in Argentina, characterised by peatland evolution/development from *Carex* peat, through to brown moss peat and then *Sphagnum magellanicum* peat. In the undisturbed peatlands of southern Patagonia, many sites previously colonised by *S. magellanicum* are now covered by cushion plants (Kleinebecker *et al.* 2007, Rodríguez 2015, Teltewskaja 2010). These plants, mainly *Astelia pumila*, are able to feed from and produce peat, colonising surfaces covered by *S. magellanicum*, where the addition of oceanic salt cations have generated conditions favourable for vascular plant development (Fritz *et al.* 2012). These bogs possess greater carbon sink potential compared to *Sphagnum* bogs (Holl *et al.* 2019). Teltewskaja (2010) also reported the presence of *Tetroncium magellanicum* peat, *Donatia fascicularis* peat, brown moss peat and fen peat forming during the peatland genesis. Recent studies report eleven organic substrate types in the region of Aysén, Chile, alone: a) *S. magellanicum* peat; b) amorphous peat; c) radicells peat; d) *Ericaceae* peat; e) cushion plant peat; f) *Oreobolus* peat; g) *S. fimbriatum* peat; h) cypress wood peat; i) brown moss peat; j) *Schoenoplectus* peat and k) organic gyttja (Rodríguez 2015). More information is provided in Table A1 in the Appendix.

Peatlands of Patagonia, from Chiloé to Cape Horn, are capable of high levels of carbon fixation, with C_{org} values ≥40 %. Estimates suggest low C accumulation in *pomponales* from Chiloé, of 12 kg m⁻² (Cabezas *et al.* 2015) or 13 kg m⁻³ (León & Oliván 2014), whereas in the peatlands of the Aysén and Magallanes regions values of 30 kg m⁻³ (Rodríguez 2015) and 53 kg m⁻³ (Rodríguez unpublished data) are reached. Summing the carbon stores for Chiloé (León 2012), Aysén (Rodríguez 2015) and Magallanes (Loisel 2015), the total carbon reserve of Chilean Patagonia may be at least 7.62 billion tonnes (1.4 % of the global estimate of peat C). The C/N quotient of slightly decomposed bog peat (C/N = 31–57; Biester *et al.* 2003, León & Oliván 2014, Rodríguez 2015) is usually higher than in fens or highly decomposed bog peat (C/N = 20–27 (Biester *et al.* 2003, Rodríguez 2015)). High C/N implies low availability of plant nutrients and hence low turnover, maintaining the peatland balance and avoiding its colonisation by invasive species.

Palaeoenvironmental and palaeoclimatic archives

Numerous peat-based palaeoenvironmental and palaeoclimatological reconstructions are available for the mid- and high-latitudes of the Northern Hemisphere. In contrast, palaeoenvironmental

studies from the corresponding latitudes of the Southern Hemisphere are far fewer (Van der Putten *et al.* 2012). Plant macrofossils have been used to reconstruct long-term records of climate change in SSAP (Mauquoy *et al.* 2010, Chambers *et al.* 2012, Chambers *et al.* 2014, Echeverría 2016) and are particularly useful in aiding understanding of the dynamics of long-term peatland development, given that they are preserved *in situ* and not affected by long distance dispersal (Barber 1993, Echeverría & Mancini 2018). The palaeofloristics of sub-fossil bryophyte remains have been extensively investigated in the Northern Hemisphere peatlands and identification guides are widely available (Mauquoy & van Geel 2007). In contrast, the palaeofloristics of Southern Hemisphere peat deposits do not currently approach this level of detail. Despite some limitations, raised peat bogs have the potential to record ecological competition and succession processes in peatland ecosystems and external (i.e. climate) forcing mechanisms driving changes in water table depths, or a combination of these processes (Mauquoy *et al.* 2008).

Currently only a single palaeobryofloristic record, spanning the early Holocene to the present, is available for southern South America (De Vleeschouwer *et al.* 2014), where peatland development and palaeoclimate changes were studied. Additional bryophyte and vascular plant macrofossil records have been published (Mauquoy *et al.* 2004, Chambers *et al.* 2007, Markgraf & Huber 2010, Loisel & Yu 2013a, Chambers *et al.* 2014). The information available in these publications is summarised in Table A2 (Appendix). Plant macrofossil analysis in Northern Hemisphere peat bogs is frequently employed as part of a multi-proxy approach to palaeoenvironmental reconstruction that can include several climate proxy techniques. Many of these techniques have also been pioneered in southern South America, including testate amoebae (Van Bellen *et al.* 2014, Van Bellen *et al.* 2016) and simultaneous δD , $\delta^{18}O$ and $\delta^{13}C$ analyses of alpha-cellulose from *Sphagnum* mosses (Daley *et al.* 2012, Loader *et al.* 2016).

In most of the mentioned cases, the authors used an indicator species approach to reconstruct wet/dry climatic conditions based upon modern-day ecology of bryophytes and macrofossils (Mauquoy *et al.* 2004, Markgraf & Huber 2010, Chambers *et al.* 2014). The diversity of *Sphagnum* species in the SSAP is lower compared to the Northern Hemisphere, with *Sphagnum magellanicum* occupying a broad ecological niche. However, *Sphagnum falcatulum*, a species largely restricted to the Southern Hemisphere - although it has also been

recorded in central Asia (Michaelis 2011) - is also present in wet hollows and fringing bog pools in the SSAP. It is a member of the *Sphagnum* section *Cuspidata* and is consistent with other species in the Northern Hemisphere that are indicators of wetter conditions (van Bellen *et al.* 2016). Mauquoy *et al.* (2004) inferred local water tables based upon the percentage of *Sphagnum magellanicum* leaves and stems, and *Empetrum*/Ericaceae macrofossils. Markgraf & Huber (2010) grouped peat macrofossils (both bryophyte and vascular plant remains) into dry and wet fen and bog indicators as proxies for effective moisture changes. Chambers *et al.* (2014), based upon variation of *Sphagnum magellanicum* and *Empetrum*/Ericaceae percentages, identified dry (low *Sphagnum* percentage) and wet (high *Sphagnum* percentage) episodes to indicate low and high local peatland water table depths, respectively. The bioclimatic envelope of these peatlands was also investigated, and the results suggest that they occupy a distinct niche, characterised by mild mean annual temperatures and weak temperature seasonality. Finally, a high-resolution record of peatland development spanning the fen–bog transition was presented by De Vleeschouwer *et al.* (2014).

Hydrology

Southern Patagonia has very steep gradients of continentality and moisture. As a result, peatlands here range from hyper-oceanic western peatlands to continental peat bogs and fens within 100 km of the eastern side of the Andes (Kleinebecker *et al.* 2007). Furthermore, the latitudinal extent of the region drives temperature and radiation gradients which have a strong effect on peatland water balance. Consequently, hydrological peatland features and processes vary substantially among SSAP.

Raised bogs require a stable water balance during the whole year and a high water table is a necessary condition for growth and maintenance of most peatlands. Results of hydrological studies on the raised bogs of Tierra del Fuego (Iturraspe & Roig 2000, Köpke 2005, Baumann 2006) confirm that water table fluctuations are low compared to those in mineral soils. Baumann (2006) attributes this to efficient hydrological self-regulation mechanisms (Joosten 1993, Van der Schaaf 1999) that keep water table fluctuations within a small range. Water table lowering results in decreased evapotranspiration and lateral runoff because of a reduction in the horizontal peat porosity at the lower level of the acrotelm. On the other hand, topographic variability at the mire surface induces changes in vegetation, micro-relief and increases surface water storage capacity. It is unclear whether SSAP dominated by vascular plants

possess this ecohydrological ability (Fritz *et al.* 2011).

It is also difficult to distinguish the acrotelm zone in most fens. Fens have low water table variation because of continuous groundwater supply, however, Pérez-Haase & Iturraspe (2005) reported high water level variation in María Behety Fen in Tierra del Fuego because of the particular characteristics of the hydrological system in which it is located. This study also remarks on the significant contrast between the hydrological and nutrient characteristics of fens from the different environments of Tierra del Fuego, although it is clear that these variations are due to mineral groundwater influence. There are very few references about water flow through cushion bogs of vascular plants in the region.

Water storage on the peatland surface can be considerable in patterned peatlands. Large macrotopes usually include shallow pool systems and endotelmic lagoons that are valuable water reservoirs. Pools are commonly found on cushion bogs. Roig & Collado (2004) described cushion bogs in Moat, Tierra del Fuego and distinguished *Astelia* bogs ‘with water’ from *Astelia* bogs ‘without water’; the former description corresponds to patterned peatlands with scattered pools elongated perpendicular to the slope.

Austral peatlands contribute to hydrological water basin regulation in a natural environment with highly contrasting climatic patterns and poor water distribution. They provide fresh water, enhance flood regulation capacity, improve water quality and diminish soil erosion (Joosten & Clarke 2002, Iturraspe 2016). However, the real significance of these hydrological services varies in each case. The influence of peatlands to flow regulation in a basin/sub-basin is heavily dependent on the peatland area in the catchment and the hydrological features of these wetlands, such as the regular depth of the water table.

Peatlands cover over 80 % of the total area in several river basins of eastern Tierra del Fuego, where they are the main water regulation system. However, flood events can be extreme when intense rainfall occurs under conditions of saturated peat. Like other hydrological regulation systems, peatland flood regulation capacity depends also on humidity conditions prior to the rainfall (Evans *et al.* 1999, Iturraspe *et al.* 2013). The river waters of this region also show typical features of peatland influence: high humic acid concentration, low pH and dark brownish colour.

Peatland hydrological regulation is sometimes evaluated by considering only the water exchange capacity of the peat matrix. However, surface

peatland reservoirs can produce significantly control hydrology. The peatland complex of Carbajal Valley, near the city of Ushuaia, comprises patterned raised bogs, pool systems and endotelmic lagoons linked to the surface drainage. Here, peatlands also intercept incoming water from the main course and tributaries which flow down from the hills, suppressing flooding further. Thus, these wetlands are able to both slow output flow and to reduce the normal annual maximum peak flow of the main river by 35 % (Iturraspe 2010).

Peatland hydrological regulation has a direct impact on the quality of life of local communities. For example, peatlands are key for freshwater supply on Chiloé Island. Compared to continental Chile, this island has mountain ranges of low altitude, and so it does not receive significant additional water inputs from snowmelt throughout the year, as is the case on the mainland. Freshwater is instead derived mainly from precipitation, with peatlands acting as ‘reservoirs’ (Zegers *et al.* 2006). Under future climate change scenarios reductions in rainfall, as experienced in recent years, means that availability of fresh water in the island is increasingly at risk and the conservation of peatlands is growing in importance, as a means of mitigating against this problem.

BIODIVERSITY

Peatland ecosystems are sites of great ecological relevance, since they play a fundamental role in biodiversity conservation as a refuge for some of the rarest and most unusual species of flora and fauna dependent on wetlands (Ramsar 2004).

Microbes

Peatlands are home to a variety of microbes, including viruses, bacteria, and protists. However, almost all the existing information for peatland-dwelling microbes comes from the Northern Hemisphere (e.g. Lara *et al.* 2011, Ballaud *et al.* 2016, Tian *et al.* 2019 and references therein). There, they exhibit diversities and abundances that exceed those exhibited by any plant or animal present in those ecosystems.

Data are comparatively limited for microbes dwelling in SSAP. In a recent exploratory survey, Fernández *et al.* (unpublished data) found that these peatlands have a remarkable number of viral (bacteriophage) hosts, i.e. bacteria. 25 bacterial phyla and over 3,000 operational species (~350,000 16S rDNA sequences) were recorded in just 50 g of wet peat collected from five near-pristine peatlands from the Aysén Region, Chile. Since viral (bacteriophage)

diversity and abundance often mirror that of bacteria (Breitbart & Rohwer 2005, Koonin *et al.* 2020), it is suspected that SSAP harbour an important but still unexplored diversity and abundance of viruses.

The study of SSAP bacteria is still in its infancy and all surveys have concentrated only on the southernmost peatlands, including those located on Tierra del Fuego (Argentine territory) (Kip *et al.* 2012, Quiroga *et al.* 2015) and Navarino Island (Chile) (Graham *et al.* 2017). There, bacteria exhibit high diversity and abundance. More than 890 operational taxonomic units (OTUs) were identified in 30,225 sequences collected along a transect (n=15 samples) in Tierra del Fuego (Quiroga *et al.* 2015), while more than 75 genera were identified in 50,000–84,000 sequences collected in just one peatland from Navarino Island (Graham *et al.* 2017). In Tierra del Fuego, Proteobacteria emerges as the dominant bacterial phylum representing 42–51 % of the 16S rDNA sequences recovered (Kip *et al.* 2012, Quiroga *et al.* 2015). Other major bacterial phyla are Acidobacteria (28 %) and Verrucomicrobia (13 %) (Kip *et al.* 2012), as well as Actinobacteria (22 %) and Bacteroidetes (15 %) (Quiroga *et al.* 2015). In Navarino Island, bacterial communities are also dominated by Proteobacteria (~80 %), Acidobacteria (~10 %) and Verrucomicrobia (~10 %) (Graham *et al.* 2017). However, bacteria from Navarino Island were studied using two genes (16S and 23S rDNA); therefore, these results cannot be directly compared with those from Tierra del Fuego. In Tierra del Fuego, the vast majority of the bacterial taxa found were rare, with 72 % of OTUs occurring in a single sample (Quiroga *et al.* 2015). In Navarino Island thousands of sequences could not be assigned to any known bacterial lineage (Graham *et al.* 2017). Therefore, bacterial communities in SSAP could be represented by several lineages so far unknown to science. It is not clear what role these bacteria play in these ecosystems, although experimental evidence suggests that Proteobacteria might be responsible for the bulk of methane oxidation, at least in peatlands of Tierra del Fuego (Kip *et al.* 2012).

Eukaryotic single-celled organisms or protists, particularly those referred to as testate amoebae, are the most studied microbial group in SSAP. Testate amoebae are a polyphyletic group of shelled (tested) protists composed of at least three major and phylogenetically unrelated taxonomic groups, including Arcellinida (Amoebozoa), Euglyphida (Cercozoa) and amoebae within Amphitremida (Kosakyan *et al.* 2020). The study of these protists in SSAP dates back to the 19th century, when Ehrenberg (1843) described testate amoeba species from Cape Horn, Chile. Since then, more than 100

testate amoeba species have been observed and described from SSAP, many of them endemic to Argentina and/or Chile (Fernández *et al.* 2015, and references therein). Indeed, SSAP exhibit testate amoeba compositions that differ from those found in peatlands from other regions (Fournier *et al.* 2016). Much of this endemic diversity may be the product of biogeographical processes, including the radiation of new testate amoeba lineages in SSAP via allopatric speciation events prompted by the southward expansion of peatlands and other subantarctic environments short after the retreat of the Patagonian Ice Sheet during the Late Pleistocene (Fernández *et al.* 2016). Testate amoebae inhabiting SSAP may be good bioindicators to monitor peatland pollution, restoration and management, since they are sensitive to changes in environmental conditions including UV-B radiation (Searles *et al.* 1999, Robson *et al.* 2005), pH, temperature, water level and nutrient content (Zapata 2005, Fernández & Zapata 2011). Testate amoeba shells can be preserved for thousands of years in peatlands and have been successfully employed as palaeohydrological proxies to reconstruct past climate variability from SSAP (Van Bellen *et al.* 2014). Many testate amoebae build shells by agglutinating sediment from the environment, including tephra in sites covered by volcanic ash. Thus, they have also been proposed as proxies to investigate the magnitude and impact of past and recent volcanic eruptions in Patagonian peatlands (Delaine *et al.* 2016).

Peatland microfungi are also important for biodiversity, as part of the food web of the *Sphagnum* mat, and as decomposers in the aerobic layer. Studies of fungal diversity and ecological functionality have been carried out in Fuegian peatlands (Robson *et al.* 2004, Paredes *et al.* 2014).

Flora and lichens

Plant communities are directly involved in the ecological functions and processes of peatlands (Rydin & Jeglum 2006). However, the floristic diversity of SSAP are little studied (San Martín *et al.* 1999, Schlatter & Schlatter 2004, Teneb & Dollenz 2004, Teneb *et al.* 2008, Kleinebecker *et al.* 2010, Domínguez *et al.* 2015a) compared to peatlands of the Northern Hemisphere. Information on the bryophytes and macro-lichens of these systems is even scarcer (Díaz *et al.* 2008, Villagra *et al.* 2009, León *et al.* 2013, León *et al.* 2014, Larraín 2015, León *et al.* 2016).

The vascular flora of peatlands includes 126 species classified in 89 genera and 57 families. At least 77 species are endemic to southern Patagonia (Domínguez *et al.* 2015a). Of particular note among

the endemic species are two orchids, *Chloraea gaudichaudii* and *Gavilea araucana* (Domínguez & Bahamonde 2013, Domínguez *et al.* 2015a), and two insectivorous plant species, *Pinguicula antarctica* and *Drosera uniflora*. There are no reports so far of the presence of exotic or introduced plants in undisturbed peatlands.

The biodiversity of bryophytes and lichens also distinguish the SSAP. In total, 195 species have been reported: 76 mosses, 68 liverworts and 51 macrolichens. The majority of identified taxa are endemic (more than 50 %) (Díaz *et al.* 2008, Villagra *et al.* 2009, León *et al.* 2013, León *et al.* 2014, Larraín 2015, Souto *et al.* 2015). The genus *Sphagnum* is the most abundant of the bryophytes, in terms of peat surface cover. However, the number of *Sphagnum* species in southern South America is much lower than the reported in other peat-rich regions, such as Canada (Vitt & Belland 1995) or Europe (Laine *et al.* 2018). Another contrasting finding is the high number of liverwort species present in the SSAP, in comparison to the Northern Hemisphere where, for instance, Vitt & Belland (1995) reported 20 species of liverworts in Canadian peatlands, and Wheeler (1993) mentioned 17 species of liverworts in British bogs.

Plant biodiversity in peatlands is largely a function of peatland type, pH and nutrient availability (Kleinebecker *et al.* 2010, León *et al.* 2018b). In *Sphagnum* peatlands, nutrient scarcity (especially nitrogen and phosphorous) limits the growth of

vascular plants, and bryophytes, graminoid species and small shrubs have the greatest diversity (Figure 2). *Sphagnum* peatlands are less diverse in terms of species richness than other types of peatlands, as *Sphagnum* bioengineers acidic conditions suitable for its own survival; but such peatlands are important for their role in C accumulation and their globally unique dominance of *Sphagnum magellanicum*. Graminoid peatlands have greater richness and diversity compared to *Sphagnum* peatlands, since roots have more access to the mineral substrate and/or they developed more nutrient-rich contexts (Domínguez *et al.* 2015a). Lower acidity also facilitates vascular species in this type of peatland. The main structuring species are members of Cyperaceae, *Schoenus antarcticus*, along with *Carpha schoenoides*; both are perennial herbs that grow in the shape of a tiller. Cushion peatlands are more diverse in vascular plants (Roig & Roig 2004); the structuring species in terms of coverage and richness are *Donatia fascicularis*, *Gaimardia australis* and *Astelia pumila*. All these species grow in the form of a cushion, and have a highly developed root system that allows nutrient uptake from greater depths (Fritz *et al.* 2011, Domínguez *et al.* 2015a).

Fauna

Although there is a general lack of information about fauna associated with peatlands, it is known that many animals inhabit or make sporadic visits to these ecosystems in diverse microhabitats such as ponds,

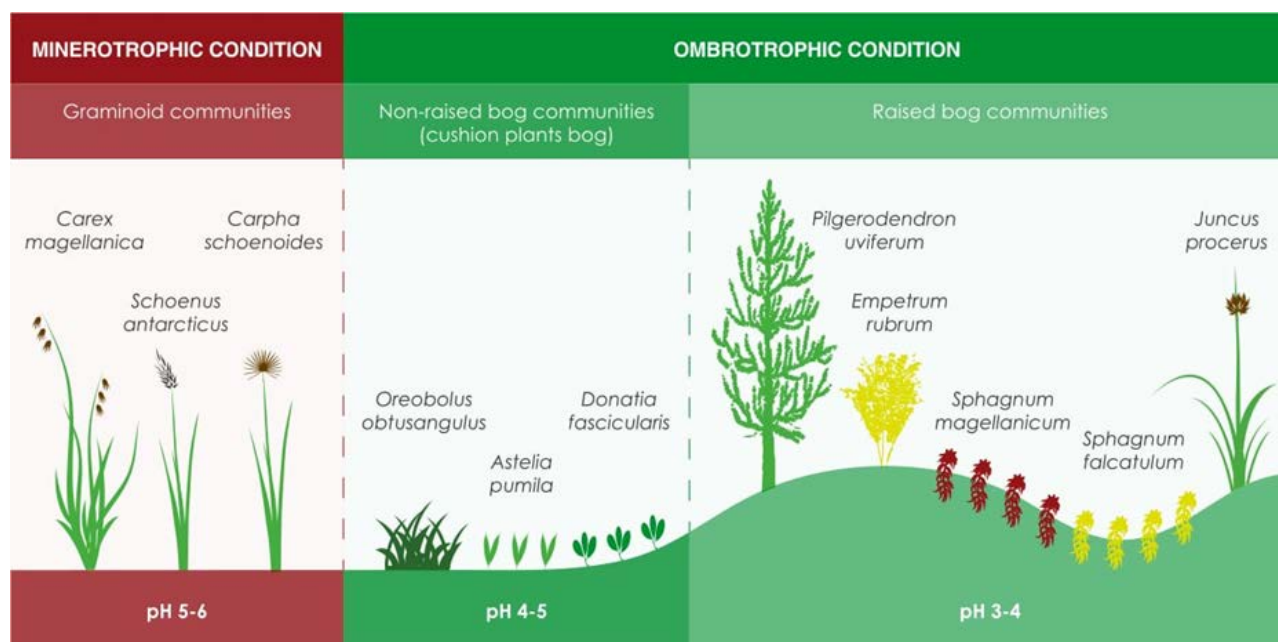


Figure 2. Schematic diagram showing the characteristic plant species along the gradient from minerotrophic to ombrotrophic condition in southern South America.

soil and vegetation (Rydin & Jeglum 2006). Studies of macroinvertebrate communities in Chilean and Argentine Patagonia are scarce. For Argentina, the works of Ringuet (1976–1981), Castellanos (1991–1995), Fernández & Domínguez (2001), and Domínguez & Fernández (2009), are all primarily focused on taxonomy. Studies in Chile about this type of peatland fauna are also limited. Mercado (2004) and Anderson (2004) present preliminary and qualitative studies that incorporate keys for taxonomic identification and determination of 21 taxa which include Diptera, Coleoptera and Trichoptera. Both studies discuss the need to conduct further research in these ecosystems. Subsequently, Jerez & Muñoz-Escobar (2015) conducted a study focused on the order Coleoptera associated with Magallanes peatlands, which reported a total diversity of 23 families, 105 genera and 173 species; Carabidae and Curculionidae were the most diverse. This paper also discusses the need to generate more studies in this type of ecosystem. Exploratory studies in two peatlands of Chiloé Island, Chile, show that the most abundant orders are Coleoptera, Diptera, Arachnida and Oligochaeta (Benítez-Mora, unpublished data). It should be noted that, although these ecosystems present conditions that could be considered inhospitable for many groups of invertebrates, the macroinvertebrate diversity found was high. Consequently, it is necessary to study further the diversity of this group, given the lack of specialised information on their diversity in Chilean peatlands.

Peatlands play an important role in the life cycle of many amphibians, as a refuge and source of food during summer droughts (Minayeva 2008). In Chile, several species of amphibians have been reported in peatlands (Celis-Diez *et al.* 2011, Ortiz 2015). Nevertheless, there is no specialised literature describing the diversity or biology of these organisms in this type of wetland.

Peatlands also support bird diversity (Minayeva 2008); but as in the previous cases, studies are scarce. Ruiz & Doberti Ltda. (2005) recorded 26 species of 7 different bird families in the peatlands of the Punta Arenas Region in Chile. Passeriformes and Falconiformes were those with the greatest number of species (11 and 5, respectively), while the most abundant species was the Upland Goose (*Chloephaga picta*), which frequently inhabits the lagoons formed in between the peatlands. Schlatter (2004) found a similar number of species, but specified that 13 species use peatlands as nesting sites. Ibarra *et al.* (2010) observe insectivorous birds to be the most dominant functional feeding group in

peatlands. These organisms require frequent feeding, therefore they must have a food source that allows them to feed at regular intervals. Consequently, the presence of a high proportion of small birds may further indicate that these environments have a reliable source of food (Ibarra *et al.* 2010). However, bird censuses conducted in peatlands are few in number (Schlatter 2004, Riveros *et al.* 2015). Accordingly, we do not yet have a clear understanding of bird diversity in these ecosystems.

Mammalians are the least understood group of peatland fauna. Ruiz & Doberti Ltda. (2005) recorded four mammalian orders: Artiodactyla, Carnivora, Rodentia and Lagomorpha, and Schlatter (2004) also reports Chiroptera and Xenarthra for the Magallanic peatland. The most abundant species were guanacos (*Lama guanicoe*), and three exotic, invasive species: North American beaver (*Castor canadensis*), European rabbit (*Oryctolagus cuniculus*) and Cape hare (*Lepus capensis*) (Ruiz & Doberti Ltda. 2005). Schlatter (2004) also reported several feral species: dogs, cats, cows and horses. Guzmán (2015) reported three rodent species. Most of the reported mammals make only occasional use of peatlands with exception of beavers, which not only inhabit peatland-forest mosaics, but are presumed to have had a significant but still unclear effect on peatlands in Tierra del Fuego by modifying water courses and raising local water tables. According to Schlatter (2004), the use of peatlands by guanacos could also be more than occasional. In summary, the fauna has been considerably less studied than the flora, and the challenge remains to fill these gaps in our knowledge and understanding.

THREATS

Due to their isolation, most SSAP are still in a relatively undisturbed state. However, increases in local population and peatland drainage associated with peat extraction or infrastructure projects might change this situation rapidly (Grootjans *et al.* 2010, Iturraspe 2016). The impact of peat extraction until now is not as intense as in many regions of the Northern Hemisphere, as the extraction is mostly done manually by small local enterprises (Grootjans *et al.* 2010, Vacarezza 2012). According to Domínguez *et al.* (2015b) only eight peatlands have been affected by peat extraction in the Magallanes region, with a total surface of 444 ha (0.16 % of the total area of peatlands in the region). In the Argentinian Tierra del Fuego 33 peat mining sites are recorded in an area of 4,600 ha, which is about one

percent of the Argentinian mires in Tierra del Fuego (Iturraspe & Urciuolo 2004, Cardone & Worman 2008). The peat extractors are small-scale enterprises who work manually, but still heavily affect mires within the mining areas (Iturraspe & Urciuolo 2004). For example, more than 6,200 tons of peat were extracted in 2018 from Chilean peatlands (SERNAGEOMIN 2019). The extraction of peat is 1 m deep, after removing 40–50 cm of vegetation cover. The exploitation is carried out in small pits from 14–20 m wide and 150–200 m long (Domínguez & Bahamonde 2012). No reports could be found about peat mining in other regions. Without appropriate protective legislation, the development of large-scale mechanised peat extraction industries, with the capacity to deplete local peat resources in a short time, remains a great threat to SSAP (Grootjans *et al.* 2010).

Peatlands have become quite important in Chile and Argentina due to the interest generated by the extraction and trade of *Sphagnum magellanicum* moss for horticultural purposes. The commercial interest in dry *Sphagnum* has grown progressively over the last 20 years. *Sphagnum* exportation from Chile increased by over 200 % between 2002 and 2017, during which time more than 3,500 tons of dried moss was exported (ODEPA 2019). The moss is mainly used in gardening and especially in horticulture (Oberpaur *et al.* 2010, Oberpaur *et al.* 2012, Arévalo *et al.* 2016). The unsustainable harvesting of *Sphagnum magellanicum* in the Los Lagos region of Chile has led to a depletion of this resource in many locations (Vacarezza 2012). Díaz *et al.* (2012) estimated that if the current rate of extraction of *Sphagnum* in Chiloé Island (Los Lagos region) continues without proper management, it would mean the extinction of the resource in less than 12 years. However, in the last ten years Chilean researchers have conducted studies that have made significant progress in the sustainable extraction of *Sphagnum* (Díaz *et al.* 2005a, Díaz *et al.* 2005b, Díaz 2008, Díaz *et al.* 2008, Díaz & Silva 2012, Díaz *et al.* 2012, Délano *et al.* 2013, Domínguez 2014). Manually harvesting by plot, removing only the first 12 cm of moss and replanting after harvest are some of the recommendations given for sustainable management and to transform moss into a renewable resource for farmers (Díaz 2008).

Another impact, both on peatlands and on other terrestrial ecosystems, was the introduction of 25 pairs of the North American beaver (*Castor canadensis*) to Tierra del Fuego in 1946 (Lizarralde *et al.* 2004, Arroyo *et al.* 2005). By 2004 they had multiplied to about 35,000–50,000 individuals, engineering landscapes by constructing dams

(Lizarralde *et al.* 2004). Even though their number is likely to be greater today, Henn *et al.* (2016) identified that the presence of peatlands in a given area was significantly related to the degree of beaver impact. Therefore, the ability of a peatland to maintain higher water tables could be critical to surviving the effects of beaver activity in drier areas. Moreover, Grootjans *et al.* (2014) reported that beavers also drain mires and pools by excavating channels to facilitate their own movements, and bursting of their dams may initiate erosion events that substantially lower the drainage base.

Cattle grazing can also lead to negative impacts on SSAP, and mainly occurs on minerotrophic peatland (Iturraspe 2016). Grootjans *et al.* (2014) reported peatland degradation in eastern Tierra del Fuego caused by excessive numbers of wild cows and horses. Moreover, logging of forested bogs also affects peatlands, especially those with *Pilgerodendron uviferum*, as the wood is highly prized (Holz 2009, Rodríguez 2015). The removal of trees changes the water balance of peatland, the penetration of the peatland with horses or carts disturbs peatland vegetation and therefore accumulation.

CLIMATE CHANGE

Peatlands are both a natural carbon sink and a methane (CH₄) emitter, with both processes dependent on the balance between peat accumulation and decomposition. Methane has a 28-fold higher greenhouse potential compared to carbon dioxide (CO₂) over a 100-year time frame (IPCC 2014). This is why peatlands are considered key components of the global carbon cycle and crucial in the planet's climate regulation (Yu *et al.* 2010). Carbon dynamics and budgets depend on the CO₂ exchange at the ecosystem level, controlled by fluxes of assimilation, respiration and emission of greenhouse gases, especially methane. Methanotrophic metabolism in the top layers of the *Sphagnum* bog act as a filter for methane, where carbon produced by the ecosystem is recycled, reducing the methane emissions (Kip *et al.* 2012). This balance is vulnerable to global warming, as an increase in temperature may diminish the carbon storage capacity of a peatland and enhance soil organic matter decomposition, having a significant cumulative effect on global atmospheric CO₂ contributions, and therefore increasing the overall greenhouse effect (Hopple *et al.* 2020).

In contrast to the extensively studied peatlands of the Northern Hemisphere, research on the atmospheric gas exchange in SSAP is scarce. In this

regard, Patagonian peatlands are natural, relatively pristine laboratories where the direct effect of global climate change on natural C flux balance can be studied, avoiding the collateral trace of human-impacted ecosystems. Studies on greenhouse gas emissions have been carried out in different types of Patagonian peatlands. Lehman *et al.* (2016) estimated CH₄ fluxes in different vegetation microforms in a raised *Sphagnum* bog, ranging between 49.04 and 10.49 mg m² d⁻¹ in *Sphagnum* lawns and hummocks, respectively; while the emission in drier microforms, such as those dominated by *Empetrum rubrum* heath averaged 3.97 mg m² d⁻¹. The microbial methanotrophic community that inhabits Patagonian *Sphagnum* mosses is comparable to that in peat mosses from the Northern Hemisphere, showing high abundance of methanotrophic *Methylocystis* species. In fact, the methane oxidising symbionts in *Sphagnum* hyaline cells are able to obtain 5–20 % of plant cell CO₂ by CH₄ oxidation (Kostka *et al.* 2016).

The exploitation of SSAP consists mainly of draining the wetlands for peat mining (see ‘Threats’ section), creating conditions where net methane contributions may decrease due to increasing methane oxidising activity. However, as long as the peat remains anoxic, the methane emissions could increase compared to undisturbed conditions. Veber *et al.* (2018) reported the methane emissions of a flooded managed fen being around 16.8 mg m² d⁻¹, in comparison to the 6 mg m² d⁻¹ assessed in control conditions.

On the other hand, cushion bogs are dominated by pulvinate-cushion plant communities, where the water table is near to the surface and several small pools are formed, and are considered to be a unique type of mire. The dominating plant species (i.e. *Donatia fascicularis* and *Astelia pumila*) are adapted to amphibious life, with highly developed root systems (around 2 m depth), transporting oxygen into the peat layer and creating oxic microzones (Fritz *et al.* 2011) at the rhizosphere. The reduction of the anoxic environment radically diminishes the total net CH₄ contributions from these bogs. High sea spray input in cushion bogs, high sulfate and reduced inorganic sulfur contents, also suggest a potential attenuation of methanogenesis by sulfate reduction (Broder *et al.* 2015). Even though little methane was detected in the peat rhizosphere of cushion plants, Münchberger *et al.* (2019) found high CH₄ concentrations in the peat below this zone. In equilibrium with the anoxic, deep methanogenic peat layers, at the surface of cushion bogs methane oxidation metabolism reduces the total methane contribution to the atmosphere.

Pools from cushion bogs are depleted in methane

CH₄ concentration and oxidising activity is low (Münchberger *et al.* 2019, Fritz *et al.* 2011), comparable to aerated habitats such as *Sphagnum* hummocks (Kip *et al.* 2012); however, *Sphagnum* bog pools are richer in methane and the oxidising activity is high, indicating a close association between the methane concentration in the pore water and the potential for methane oxidation.

Carbon dioxide dynamics are mainly controlled by radiation, temperature, water table and plant community composition. Carbon dioxide emissions generally respond positively to increased temperatures and negatively to oxygen-depleted (water saturated) soil conditions (Charman *et al.* 2013). Long-term peat accumulation is higher in peatlands dominated by *Sphagnum* in comparison to cushion peatbogs, and total ecosystem respiration (R_{eco}) and photosynthesis of both peatlands are promoted by warmer conditions, affecting the net ecosystem exchange (NEE) (Holl *et al.* 2019, Valdés-Barrera *et al.* 2019). However, R_{eco} is higher in cushion bogs in comparison to *Sphagnum* bogs, because cushion plant peat decomposes faster than the moss stems, leaves and branches (Mathijssen *et al.* 2019). In addition, plant-covered bogs are highly productive (regarding CO₂ sink) in comparison to *Sphagnum* peatlands (NEE: -122 and -27 g m⁻² y⁻¹, respectively) by 4.5 times higher CO₂ assimilation, approximately (Holl *et al.* 2019).

Although C assimilation continues throughout winter in both peatland types, cushion bogs increase their CO₂ sink function in spring, whereas net CO₂ uptake at *Sphagnum* bogs starts in summer. Similar to cushion bog, the NEE in a minerotrophic anthropogenic peatland is around -135 g m⁻² y⁻¹ which is largely depleted (-33 g m⁻² y⁻¹) when the site is disturbed by cattle grazing and moss extraction (Valdés-Barrera *et al.* 2019). The carbon balance in vascular-dominated and bryophyte-dominated peatlands may respond differently to warming and disturbing conditions, and could have a positive feedback to climate change (Gallego-Sala *et al.* 2018). Recently, Malhotra *et al.* (2020) reported a significant augmentation in fine-root system length of ericaceous shrubs in response to an experimental increase of up to 9 °C above ambient temperature, outcompeting the *Sphagnum* moss due to shading. In their experiment, dry peat increased aeration and nutrient availability leading to tree recruitment, creating a cascading effect on other species and, consequently, a rapid change in C balance in the peatland ecosystem.

Currently, global air temperature increases at 0.2 °C per decade, and in the near future, air temperature in the Southern Hemisphere is projected

to increase by 0.5–1 °C by the end of the 21st century (IPCC 2018). Holl *et al.* (2019) reported a reduction in annual NEE carbon uptake in a *Sphagnum* bog during a warmer year. A passive warming field experiment (1.2 to 3 °C air temperature increase during summer), detects differences in carbon dynamics in a cushion bog using close chamber incubations. Warming plots showed higher respiration fluxes and decreased net CO₂ uptake. During high temperature conditions, warming plots even turned from sinks into sources of atmospheric CO₂ (Castagnani 2019).

Patagonian peatlands are oligotrophic and receive low nutrient inputs from atmospheric deposition (Godoy *et al.* 2003, Broder *et al.* 2015). Sea spray and historical volcanic ash deposition has a limited effect on peatland plant composition, and is associated with increased decomposition in overlying peat layers (Mathijssen *et al.* 2019). Consistently, N₂O emissions remain close to zero (Veber *et al.* 2018). Field and mesocosm experiments reported that nutrient deposition changed the morphology of *Sphagnum* mosses, enhanced height increment (León *et al.* 2019) and decreased moss stem density. On the other hand, there was an increased susceptibility of *Sphagnum* moss to desiccation by nutrients, and nitrogen excess generated plant stress by declining the photosynthetic rate (Fritz *et al.* 2012).

SSAP are not exempt from the influence of the ozone hole that forms naturally over the Antarctic continent every austral spring-summer. The effects of UV-B radiation (UVBr) on the vegetation caused by the hole in the ozone layer have been reported thousands of kilometres from Antarctica, both in New Zealand (45 °S; Robson *et al.* 2005) and Tierra del Fuego (54 °S, Robson *et al.* 2003). However, given that Tierra del Fuego and its southern islands are the only terrestrial landmasses south of 55 °S latitude (Rozzi *et al.* 2008), they receive the highest levels of UVBr after the Antarctic continent. Increased UVBr reduces the height increment, morphology and stem density of *Sphagnum* moss, and also the growth of vascular plants (Searles *et al.* 2002, Robson *et al.* 2003). UVBr also reduces fungal community, rotifer, nematode and mite richness (Pancotto *et al.* 2003, Robson *et al.* 2004, Robson *et al.* 2005); and slightly increases the diversity of testate amoebae communities (Robson *et al.* 2005). These changes are associated with direct UVBr effects and changes in *Sphagnum* capitulum morphology and microenvironment produced by UVBr (Searles *et al.* 2001, Robson *et al.* 2004).

In summary, we highlight the knowledge gaps associated with SSAP locations and classification, and therefore the potential of these systems to

contribute to or mitigate against global climate change remains poorly studied. Comprehensive understanding of SSAP carbon dynamics is mandatory to accurately predict changes in their functioning and the ecosystem services they provide in response to global warming, including their contribution to global socio-environmental change mitigation strategies.

POLICIES

Policies in Chile

Peatlands were incorporated into Chilean environmental policy through the proclamation of the Ramsar convention (Amstein 2016), after which they were explicitly integrated into the associated regulation of the Environmental Impact Assessment System (SEIA), which in its most recent version stipulates that all drainage/desiccation of peatlands can only be carried out by obtaining a favourable rating in the SEIA. Peat is considered by the Chilean regulation as a concessionable fossil substance (i.e. non-renewable natural resource), regulated through the Mining Code (Law N° 18,248) (Ministerio de Minería 1983). Peat exploration or exploitation must be submitted to the SEIA. On the other hand, the water that composes peatlands is considered a national good for public use according to article 595 of the Civil Code (Amstein 2016). On this, property rights to exploitation can be acquired according to the Water Code (DFL N° 1,122) (Ministerio de Justicia 1981), and a 'water market' is established. Finally, the economic use of the living plants that make up peatlands, crucially the *Sphagnum* moss harvest, had no legal regulation in Chile until February 2018. The new policy regulation (DS N° 25) entered into force in February 2020, and established the obligation to have harvest plans approved prior to extraction (Ministerio de Agricultura 2017). Nevertheless, regulations on peatlands at an ecosystem unit (i.e. wetland) level coexist and sometimes conflict with regulations that address their essential components (i.e. peat, plants, water), demonstrating the ability of legislation to act without regard for the interconnected nature of peatland components and function within the ecosystem that sustains them.

The sectoral regulatory and institutional dispersion (Saavedra & Figueroa 2015), lack of information on biodiversity, and insufficient legal control are aspects that make effective management of peatland ecosystems difficult. The ecosystem services of peatlands present in protected areas of Chile have been valued at a minimum \$316 billion dollars per year (Figueroa 2010). These wetlands also

play a key role in mitigation of and adaptation to climate change (Joosten & Clarke 2002, Joosten *et al.* 2012, Parish *et al.* 2008). Nevertheless, both globally and nationally, climate change mitigation initiatives (e.g. REDD and REDD+) have focused on forests and plantations because of their visibility and capacity to capture carbon quickly when compared to peatlands, even though the latter are larger and more efficient carbon sinks. Consequently, it seems a priority for the country to develop regulations and policies that allow for the adequate protection and management of its peatlands. An indispensable step is the inclusion of peatlands in the National Inventory of Greenhouse Gases, for which there are already reference estimations by the Intergovernmental Panel on Climate Change (IPCC 2014). In 2020, Chile has advanced in this direction, peatlands have been included in the Nationally Determined Contribution (NDC) to the Paris Climate Agreement (Gobierno de Chile 2020).

Policies in Argentina

Peat extraction in Argentina is regulated by the National Mining Law. No other national regulation defines specific policies for peatland management. Nevertheless, in 1992 Argentina signed the RAMSAR Convention for wetlands conservation. RAMSAR recognises peatlands as wetlands, and in Argentina international treaties prevail over national laws. The environmental legal framework was improved in the 1990s. Argentina is a federal country whose constitution establishes that provinces are owners of their natural resources, and thus provinces can determine specific policies for their use and conservation, including peatlands.

The province of Tierra del Fuego, which includes most of the Argentinean peatlands, made important decisions in 2008 related to peatland management. About 100 requests for peat mining concessions were blocked and a 'Strategy and Action Plan for the wise use of the mires of Tierra del Fuego' was developed with the coordination of the Provincial Water Resources Agency and the support of both the *Fundación para la Conservación y Uso Sustentable de los Humedales* - Wetlands International, and the *Fundación Ambiente y Recursos Naturales*. The main topics of this action plan are: inventory; integral economic analysis; environmental planning; urgent protection of unique areas; peatland use regulation; development of technical norms and best practices; capacity building; community participation; education and research (Iturraspe & Urciuolo 2014).

In the framework of the action plan, the Andorra Valley was declared a RAMSAR site in 2009. This valley includes peat bogs, glaciers, rivers and lakes,

which provide water for Ushuaia city. The Secretary of Sustainable Development and Environment of Tierra del Fuego, by Resolution SDSyA401/2011, delimited a zone where all new peat mining activities will be installed under regulated conditions. It is located in the centre of the province close to Tolhuin town, where many peatlands are already affected. At least 40 % of the peatland area must be preserved in this zone to maintain the hydrological regulation. No peat concessions will be admitted outside this 'sacrificial area', and peatlands there must be preserved. This regulation does not harm rights of existing peat extractors (Iturraspe & Urciuolo 2014).

Finally, the law for water management in Tierra del Fuego, enacted in 2016 by the Provincial Parliament, recognises peatlands as wetlands, considers wetlands as water resources, and assigns attributions to the enforcement authority for wetland protection and conservation. The law considers regulations for wetland drainage and other activities that may produce their degradation (Urciuolo *et al.* 2017).

CHALLENGES FOR CONSERVATION: THE FUTURE OF SSAP

As shown in the different sections of this review, the SSAP fulfil important ecological functions and provide valuable services across local to global scales. Because their existence is threatened, conservation measures are needed. Knowledge is central to successful conservation. This review demonstrates the role that SSAP have as ecosystems (Figure 3), and also highlights that they are under-researched. Saavedra & Figueroa (2015) point out that scientific articles on peatlands published worldwide (years 2003–2007) show that most of research into these ecosystems was carried out in Europe (52 %), and that the contribution of South American studies was marginal (2 %). This further highlights the large information gaps that exist when compared to the peatlands of the Northern Hemisphere.

In recent years government and academic agencies have worked together to reduce these gaps in scientific research, management and education (Valdés-Barrera *et al.* 2012). In addition, information platforms have recently emerged, such as 'Mires of Chile' (Rodríguez & Gabriel 2018) and 'Turberas' (León *et al.* 2018a), which aim to being an awareness of the importance of SSAP to a wider audience. A working group composed of Chilean and Argentinian professionals has also been established to work on priority actions. These include:

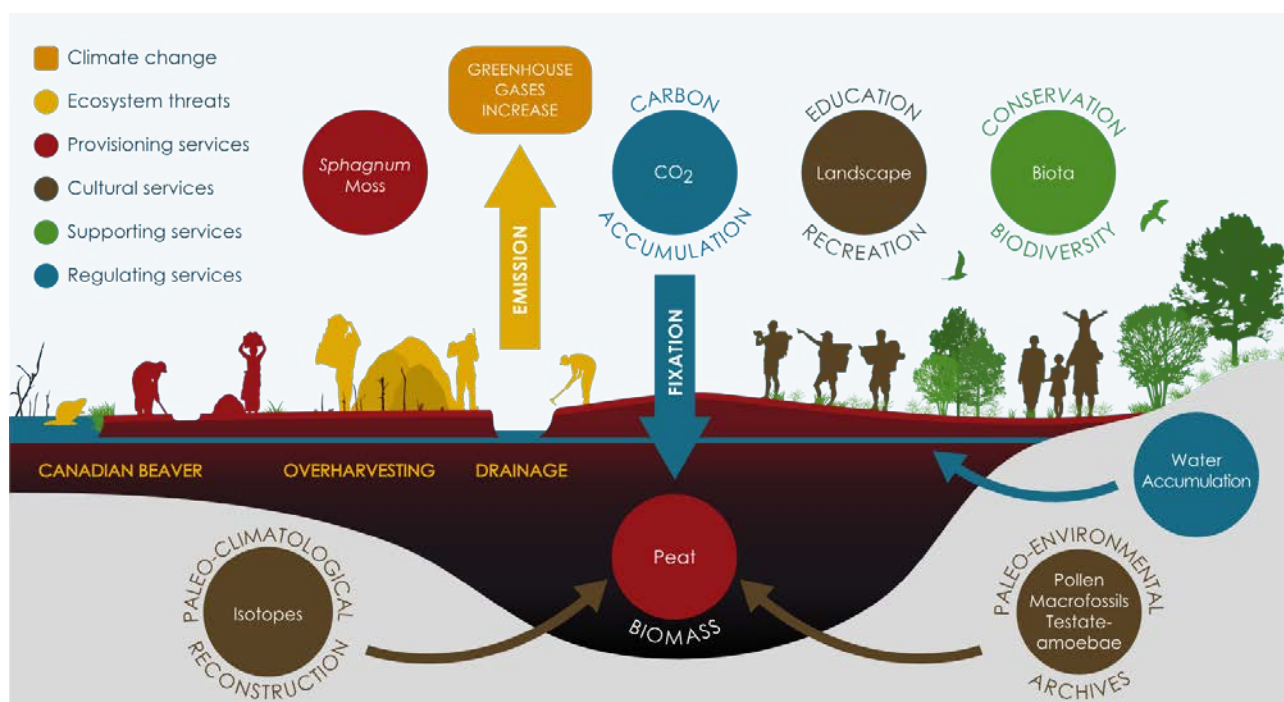


Figure 3. Ecosystem services and threats to peatlands of southern South America.

- i) Designing a strategy in both Chile and Argentina, which includes research, management and increasing awareness in the community.
- ii) Carrying out an inventory of peatlands and a proposal of land use planning, focused on the maintenance of priority ecosystem services (i.e. carbon, water, and biodiversity).
- iii) Developing collaborative work among public, academic and citizen organisations to improve the existing legislation, to carry out an evaluation that allows for the integrated management of these ecosystems and their components. Within this issue arises the need to challenge the perception of peat as a mining resource and apply other regulatory frameworks that seek sustainable management, as well as addressing the effects of *Sphagnum* extraction on the ecosystem.
- iv) Conducting studies of ecosystem processes, mainly focusing on the hydrological and carbon cycle dynamics, linking them with policies and regulations.
- v) Carrying out studies on restoration of disturbed peatlands, undertake a survey and develop an inventory of degraded peatlands to measure the impact of anthropogenic actions on these ecosystems.
- vi) Implementing protocols of good practice and sustainability for extractive activities and develop a system of environmental certification in order to encourage sellers and consumers to care for these ecosystems.
- vii) Carrying out an extensive public awareness campaign aimed at local populations, making these ecosystems and their value known and understood, as well as communicating the implications of the disturbance of peatlands and how this relates to the health of these rare and precious ecosystems.

ACKNOWLEDGMENTS

This article is an outcome of the workshop entitled “*Turberas: puesta al día y desafíos*” (14 Jun 2017). The workshop was supported by FONDECYT Grant N° 11150275 from the Comisión Nacional de Investigación Científica y Tecnológica (CONICYT). L.D.F. is funded by ANID (FONDECYT 11170927). We are very grateful to the reviewers and Dr Stephan Glatzel for their constructive suggestions.

AUTHOR CONTRIBUTIONS

CL developed the revision design; all authors managed the literature searches and contributed to writing the first draft of the manuscript; CL, VP, TR, and LF critically reviewed and edited drafts; AB

designed and made the figures; CL, VP, RM, LF, TR, AB, AS, and RI contributed to refinement and editing the final manuscript. All authors approved the final manuscript.

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Submitted 08 Jun 2020, final revision 09 Sep 2020

Editor: Stephan Glatzel

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Appendix

Table A1. Peatland substrate types and values for specific factors in Aysén and Southern Magallanes (Chile) sites. CHA-M = peatlands on islands of the Cape Horn Archipelago - Magallanes. PBR-A = peatlands in the Pascua & Baker Riverbasins - Aysén (Rodríguez unpublished data). ^aData from Kleinebecker (2007) for different mires of Magallanes and Tierra del Fuego. *No value available, **No standard deviation available.

Substrate	pH		Total pore volume (%)		Bulk-density (g cm ⁻³)		Organic carbon (TOM%)		Nitrogen (TOM%)	
	CHA-M (n=28)	PBR-A (n=470)	CHA-M (n=28)	PBR-A (n=189)	CHA-M (n=28)	PBR-A (n=46)	CHA-M (n=28)	PBR-A (n=46)	CHA-M (n=28)	PBR-A (n=46)
<i>S. magellanicum</i> peat	4.38 ± 0.49	3.85 ± 0.61	89.9 ± 1.6	91 ± 5	0.09 ± 0.02	0.06 ± 0.01	46.2 ± 0.23	45.5 ± 5.1	0.88 ± 0.07 ^a	1.11 ± 0.58
Amorphous peat	5.86 ± 0.60	4.42 ± 0.65	85.9 ± 1.3	90 ± 2	0.14 ± 0.01	0.10 ± 0.01	47.5 ± 1.05	45 ± 15.6	*	1.44 ± 0.71
Radicells peat	4.38 ± 0.78	4.2 ± 0.59	85.2 ± 2.3	89 ± 4	0.10 ± 0.02	0.09 ± 0.01	44.2 ± 0.20	51.2 ± 4.3	*	1.66 ± 0.51
Ericaceae peat	*	4.04 ± 0.46	*	92 ± 2	*	0.07 ± 0.01	*	54 ± 1.4	*	1.8 ± 0.63
Cushion plants peat	5.08 ± 0.57	3.7 ± 0.45	85.4 ± 2.3	91 ± 1	0.12 ± 0.01	0.09 ± 0.01	47.1 ± 0.23	41.8 ± 8.5	1.94 ± 0.15 ^a	1.51 ± 0.25
<i>Oreobolus</i> peat	*	3.72 ± 0.22	*	92 ± 1	*	0.09 ± 0.01	*	51.53 ± 4.75	*	1.3 ± 0.16
<i>S. fimbriatum</i> peat	4.31 ± 0	4.26 ± 0.79	82.7 ± 3.1	89 ± 1	0.08 ± 0.01	0.09 **	47.1 ± 0.23	26.27 **	*	0.76
Cypress wood peat	*	5.05 ± 0.92	*	92 ± 2	*	0.06 ± 0.01	*	47.81 ± 5.66	*	1 ± 0.12
Brown moss peat	4.2 ± 0	5.59 ± 0.97	83.7 ± 0.5	90 ± 4	0.15 ± 0.05	0.10 **	48.4 ± 0.2	31.40 **	*	1.47
<i>Schoenoplectus</i> peat	*	5.32 ± 0.80	*	94 ± 1	*	0.06 **	*	18.40 **	*	1.35
Organic gyttja	*	5.37 ± 0.89	*	81 ± 3	*	0.20 ± 0.03	*	39.89 ± 5.11	*	1.79 ± 0.73

Table A2. Studies of southern South American peatlands where bryophyte macrofossils were used to make palaeoenvironmental reconstructions. ESC: Escondido; CN: Cerro Negro; HB: Harberton, Tierra del Fuego, Argentina; PG: Paso Garibaldi, Tierra del Fuego, Argentina; RR: Río Rubens, Región de Magallanes, Chile; UAV: Upper Andorra Valley.

	Mauquoy <i>et al.</i> 2004	Chambers <i>et al.</i> 2007	Markgraf & Huber 2010	Loisel & Yu 2013	De Vleeschouwer <i>et al.</i> 2014b	Chambers <i>et al.</i> 2014
Study area	Andorra Valley, Tierra del Fuego, Argentina	Andorra Valley, Tierra del Fuego, Argentina	PG, Argentina HB, Argentina RR, Chile	UAV, ESC, HB, Tierra del Fuego, Argentina CN, Región de Magallanes, Chile	Karukinka Valley, Tierra del Fuego, Chile	Andorra Valley, Tierra del Fuego, Argentina
Peatland type	<i>Sphagnum magellanicum</i> bog	<i>Sphagnum magellanicum</i> bog	PG and HB: <i>Sphagnum magellanicum</i> bog RR: <i>Empetrum rubrum</i> / <i>Polytrichum strictum</i> bog	UAV, ESC, HB, CN: raised <i>Sphagnum magellanicum</i> bogs	<i>Sphagnum magellanicum</i> bog	<i>Sphagnum magellanicum</i> bog
Age of analysed peatland	1,400 cal yr BP	2,800 cal yr BP	PG: 14,000 cal yr BP HB: 16,000 cal yr BP RR: 17,000 cal yr BP	UAV: 11,060 cal yr BP ESC: 7,410 cal yr BP HB: 1,990 cal yr BP CN: 9,275 cal yr BP	7,800 cal yr BP	2,800 cal yr BP
Bryophyte macro-remains identified	<i>Sphagnum magellanicum</i> , <i>Campylopus</i> sp.	<i>Sphagnum magellanicum</i>	PG: <i>Sphagnum</i> sp. HB: <i>Drepanocladus</i> sp., <i>Sphagnum magellanicum</i> RR: <i>Sphagnum</i> sp.	<i>Sphagnum</i> spp., <i>Drepanocladus</i> spp.	<i>Sphagnum magellanicum</i> , <i>Dicranoloma</i> spp.	<i>Sphagnum magellanicum</i>
Proxies analysed	Percentages of <i>Sphagnum magellanicum</i> leaves and stems- <i>Empetrum</i> /Ericaceae roots	Percentages of <i>Sphagnum magellanicum</i> leaves (and <i>Sphagnum</i> stems)- <i>Empetrum</i> /Ericaceae roots	Relative abundances (ordinal scale) of major peat components (<i>Sphagnum</i> sp., <i>Drepanocladus</i> sp., <i>Polytrichum strictum</i> , Cyperaceae, Juncaceae)	CN and UAV: stratigraphic analysis of plant macrofossil samples	Palaeobryofloristic associations identifying minerotrophic and ombrotrophic peatland development stages	Percentages of <i>Sphagnum</i> leaves- <i>Empetrum</i> /Ericaceae roots
Other proxies investigated	Pollen, fungal spores, testate amebae and peat humification	Peat humification	Pollen and charcoal	Vascular macrofossils (herbaceous, ligneous and unidentifiable organic matter), peat stratigraphy, bulk density, organic matter content	Peatland geochemical (metal) composition, vascular macrofossils, charcoal	Peat humification