Control of carbon and nitrogen accumulation by vegetation in pristine bogs of southern Patagonia

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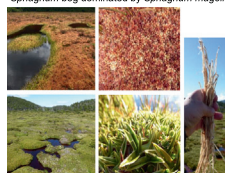
HIGHLIGHTS

- Patagonian peatlands are important long-term terrestrial C sinks in the Southern Hemisphere.
- Long term C storage of the cushion bog is similar to the *Sphagnum* bog, presumably due to high decomposition rates
- Low N accumulation rates in the *Sphagnum* bog prove the pristine character of Patagonian bogs
- Cushion bogs store higher amounts of N compared to *Sphagnum* bogs
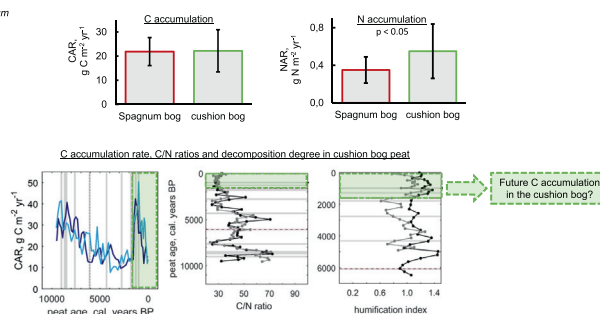
GRAPHICAL ABSTRACT

ARTICLE INFO

ABSTRACT

Peatlands are long-term sinks of carbon (C) and nitrogen (N) that are exposed to anthropogenic pressure. This has often induced a vegetation shift from peat mosses towards increasing presence of vascular plants. However, the impact of this vegetation shift on the sink function of peatlands remains unclear. To address this research gap, we studied C and N accumulation in a Patagonian cushion bog where a shift to the predominance of vascular cushion plants is a natural phenomenon since millennia. For comparison, long-term accumulation and decomposition patterns in a pristine Patagonian *Sphagnum* bog were studied. Thereto, we determined recent and long-term rates of C and N accumulation, their within-site variability, and studied plant-macrofossils. These results were related to decomposition indicators (C/N ratio, humification index, stable isotopes) of the bog types.
Despite differences in decomposition indicators, long-term rates of C accumulation were of similar magnitude in the *Sphagnum* (21.9 g C m^{-2} yr^{-1}) and in the cushion bog (22.2 g C m^{-2} yr^{-1}). N accumulation was significantly lower in the *Sphagnum* bog (0.35 g N m^{-2} yr^{-1}) compared to the surprisingly high accumulation in the cushion bog (0.55 g N m^{-2} yr^{-1}). Tephra depositions in the cushion bog about 1600 cal. Years ago presumably triggered the vegetation shift towards dominance of cushion plants by a fertilization effect. C accumulation rates during past decades in the upper decimeters of peat were four times higher in the cushion bog (245 g C m^{-2} yr^{-1}) compared to the *Sphagnum* bog (64 g C m^{-2} yr^{-1}), but substantially decreased since the appearance of cushion

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plants. High decomposition rates as indicated by decomposition indicators thus apparently offset the higher productivity of cushion plants in the long term. While cushion bogs appear to be effective N sinks, their C sink function may therefore be equal to *Sphagnum* bogs.

1. Introduction

Boreal and subarctic peatlands are crucial players in the global carbon (C) cycle that have accumulated approximately 500 gigatons (Gt) C during the Holocene over the last ~12,000 years (Gorham, 1991; Yu, 2012). Only a small imbalance of 2–16% (Tolonen and Turunen, 1996) between C uptake by plant photosynthesis and incomplete microbial decomposition and associated C release formed this giant, stable C reservoir in living, undisturbed peatlands over millennia (Clymo, 1984; Charman et al., 2013). Both processes are slowed-down in peatlands, since a scarce nutrient availability limits primary productivity (Aerts et al., 1992; Wang et al., 2014) and waterlogged peat hampers decomposition (Beer and Blodau, 2007; Bonaiuti et al., 2017). Due to its small magnitude, the imbalance between these opposing processes is sensitive to changes in the controls of primary productivity and decomposition, as a result affecting C accumulation and carbon dioxide (CO_2) release. Moreover, peatlands are also major potential GHG sources in the form of methane (CH_4) (Limpens et al., 2008; Yu et al., 2010; Frolking et al., 2011).

The rate of C accumulation in peatlands varies with time as the controls on C accumulation change. The local climate and hydrology or the surface microtopography determine the long-term C accumulation to a large extent (Belyea and Malmer, 2004; Charman et al., 2013; Loisel and Yu, 2013). The prevalent vegetation and its succession exert a further major control on a peatlands' C balance (Clymo, 1984; Belyea and Malmer, 2004; Loisel and Yu, 2013). For example, vascular plants have a higher productivity (Olid et al., 2014; Gavazov et al., 2017), but also more labile litter compared to peat-forming *Sphagnum* mosses (Dorrepaal et al., 2005; Moore et al., 2007) or may enhance peat decomposition by root exudates and rhizosphere oxygenation (Fritz et al., 2011; Gavazov et al., 2017; Agethen et al., 2018; Münchberger et al., 2019). Thus, primary productivity has even been identified as a more important control than decomposition throughout the past 1000 years of peatland C accumulation in the Northern Hemisphere (Charman et al., 2013). The vegetation furthermore tightly couples the accumulation of C to the accumulation of nitrogen (N). Plant growth requires a permanent supply of N which may in exclusively rainwater-fed peatlands (bogs) only be covered by N fixation or other atmospheric sources (Limpens et al., 2006; Vile et al., 2014; Knorr et al., 2015). During senescence, vascular plants effectively recycle nutrients leaving only nutrient-depleted litter, which is also more resistant to decomposition (Wang et al., 2014). Thus, the availability of N and other nutrients for plants and microbes strongly drives the incomplete decomposition i.e. accumulation of organic C in plant residues in peatlands (Olid et al., 2014; Wang et al., 2014; Knorr et al., 2015). Nevertheless, research of peat N accumulation has received much less attention than C accumulation (Loisel et al., 2014; Wang et al., 2014). Moreover, phosphorus (P) availability and recycling has been proposed to be a critical factor in N fixation and C accumulation (Wang et al., 2014).

Human impacts have strongly altered living peatlands, impairing their important natural C sink function. Past and present land use activities such as drainage, peat harvest and agriculture disturb the C accumulation of peatlands worldwide (Basiliko et al., 2007; Tiemeyer et al., 2016; Veber et al., 2018; León et al., 2021). Restoration efforts to reactivate the C sink function of peatlands often resulted in a high cover of vascular plants instead of the former *Sphagnum* dominance (Pfadenhauer and Klötzli, 1996; Tuittila et al., 1999; Limpens et al., 2008). While *Sphagnum* mosses usually outcompete vascular plants in wet and nutrient-poor conditions (van Breemen, 1995), a warmer and drier climate, fluctuating water levels, as well as the nowadays high rates of N deposition (up to 1.4 g m^{-1} yr^{-1}, Limpens et al., 2006) favour the growth of vascular plants and could likewise induce a vegetation shift in the plant community structure of peatlands (Berendse et al., 2001; Gavazov et al., 2017; Moore et al., 2019). The higher vascular plant presence may accelerate not only biomass production, but also litter decomposition rates (Dorrepaal et al., 2005; Moore et al., 2007; Gavazov et al., 2017), both processes that determine the direction of the imbalance needed for C accumulation. Hence, anthropogenic climate change and human release of reactive N exert a further pressure on peatlands. Long-term effects of this vegetation shift remain unclear and research is needed about the potential of peatlands to sustain their long-term C accumulation and C sink function.

While most of the research in peatlands has been undertaken in the Northern Hemisphere, peatlands also cover a substantial part of the land surface area in the Southern Hemisphere (Yu et al., 2010). In South Patagonia, peatlands have remained largely preserved from human impacts (Kleinebecker et al., 2008; Grootjans et al., 2010; Paredes et al., 2014). Therefore, these peatlands sustained – unlike many Northern Hemisphere counterparts – a pristine character and provide the nowadays rare opportunity to study undisturbed C and N accumulation over millennia (Loisel and Yu, 2013; León et al., 2021). Even atmospheric N deposition remains low (0.1–0.2 g N m^{-2} yr^{-1}; Fritz et al., 2012) and only comparatively little effects of anthropogenic climate warming change are expected (Middleton and Kleinebecker, 2012). Nevertheless, effects of tephra deposition have been described for these sites (Broder et al., 2012; Mathijssen et al., 2019), as observed elsewhere in areas with volcanic influence (Hughes et al., 2013; Ratcliffe et al., 2020), including more decomposed peat around tephra layers (Biester et al., 2003; Hughes et al., 2013; Mathijssen et al., 2019), fertilization effects and changes in vegetation (Hughes et al., 2013) or C accumulation rates (Ratcliffe et al., 2020).

Ombrotrophic Patagonian peatlands can be either dominated by raised, peat-forming *Sphagnum* mosses (hereafter termed *Sphagnum* bogs) or cushion-forming vascular plants (hereafter termed cushion bogs). These cushion bogs also occur in other parts of the Southern Hemisphere (Gibson and Kirkpatrick, 1985; Ruthsatz and Villagran, 1991; Benavides et al., 2013; Fonkén, 2014) and in tropical regions (Hope, 2014; Dullo et al., 2017). Interestingly, natural shifts from *Sphagnum*-dominated to vascular plant-dominated systems have also occurred in the pristine cushion bogs of Southern Patagonia, though (Heusser, 1995). A further unique feature of Patagonian bogs is their simple vegetation composition (Loisel and Yu, 2013) with only one dominant *Sphagnum* species, *Sphagnum magellanicum*, in *Sphagnum* bogs (Kleinebecker et al., 2007; Fritz et al., 2012; Loisel and Yu, 2013) or dense, extensive lawns of cushion-forming *Astelia pumila* or *Donatia fascicularis* in cushion bogs (Heusser, 1995; Kleinebecker et al., 2007; Borromei et al., 2014). The rhizosphere of these *Astelia* lawns is characterized by a root density four times larger than in Northern Hemisphere raised bogs (Fritz et al., 2011), and primary productivity of cushion bogs can be substantially higher compared to the moss-dominated bogs (Holl et al., 2019). The simple vegetation composition allows for investigations of C and N accumulation with comparatively few interacting effects between plant species and, due to the atmosphere as the only source of elements, without any catchment effects. As South Patagonia provides an ideal framework to extend our knowledge on biogeochemical processes in peatlands, more research attention is needed in this

important peatland region in the Southern Hemisphere with the highest share of the land surface covered by peatlands (Yu et al., 2010).

Long-term decomposition patterns in the peat profile reflect past changes in the controls on C accumulation and are a key to understanding variations in C and N accumulation over time. Plant macrofossil residues (e.g. Vitt et al., 2009; Hughes et al., 2013; Gałka et al., 2017), natural abundance of stable C and N isotopes (Alewell et al., 2011; Biester et al., 2014; Drollinger et al., 2020) and the decomposition degree as indicated by C/N ratios or an FTIR-derived humification index (Broder et al., 2012; Biester et al., 2014) are important peat characteristics that have been shown to provide information about past controls on decomposition. However, to date only few studies in southern Patagonia have been carried out addressing decomposition and C accumulation (e.g. Broder et al., 2012; Loisel and Yu, 2013; Knorr et al., 2015; Mathijssen et al., 2019) and long-term rates of N accumulation have not yet been determined for Patagonian peatlands to the best of our knowledge.

This study aims to compare C and N accumulation as well as decomposition in a South Patagonian cushion and a Sphagnum bog together with the within-site variability of typical microforms, each characterized by a distinct plant community. We hypothesized that (I) C and N accumulation rates in a Patagonian cushion bog are currently higher in lawns of Astelia pumila than in lawns of Sphagnum as cushion plants occur there alreday since several thousand years, while (II) long-term C and N accumulation rates and decomposition patterns do not yet differ between a cushion and a Sphagnum bog, and that (III) a shift in the vegetation composition from Sphagnum-dominated to cushion plant-dominated vegetation is also reflected in peat decomposition patterns.

The selected Sphagnum bog represents a typical South Patagonian peat bog developed in a mountain valley. At the studied cushion bog, the first cushion plants appeared about 2600 ^{14}C yrs. BP (years before present), as a result of which the vegetation composition in the cushion bog shifted from Sphagnum-dominated to vascular plant-dominated, probably accompanied by a change in climate (Heusser, 1995). Thus, this site provided an ideal location to investigate the millennial impact of vascular plants on C and N accumulation and decomposition patterns.

2. Material and methods

2.1. Description of the study site

The study was conducted in a raised Sphagnum-dominated bog (hereafter termed Sphagnum bog) and a cushion plant-dominated bog (hereafter termed cushion bog) located on Isla Grande de Tierra del Fuego close to the Beagle Channel in southernmost Patagonia,

Argentina (Fig. 1a). Cushion bogs are a typical feature of coastal areas in Tierra del Fuego (Iturraspe, 2012; Grootjans et al., 2010) that are gradually replaced by Sphagnum bogs with increasing distance from the coast (Kleinebecker et al., 2007). Intense winds and mild winters with an oceanic climate are typical for the region (Kleinebecker et al., 2008). In the Sphagnum and cushion bog, mean annual temperatures reach 5 °C and 6 °C and mean annual precipitation amount to 487 mm and 500 mm (Servico Meterológico Nacional; for the period between 1981 and 1990; Fritz, 2012; Iturraspe, 2012), respectively.

Detailed site descriptions can be found in previous studies (Lehmann et al., 2016; Münchberger et al., 2019; Holl et al., 2019) and are presented here only briefly: The surface in the Sphagnum bog (Valle de Pipo, 54°49′36.1″S 68°27′15.5″W, Parque Nacional Tierra del Fuego) shows a pronounced micro-relief and is composed of alternating stripes of dry hummocks elevated up to 50 cm above the water table and wet lawns with pools. As typical for Patagonian bogs (Kleinebecker et al., 2007; Fritz et al., 2012; Loisel and Yu, 2013), the vegetation is with >40% cover (Lehmann et al., 2016) dominated by one single peat-forming moss, Sphagnum magellanicum, growing in all habitats along the entire microtopographical moisture gradient, except for pools. Vascular plants such as the dwarf-shrub Empetrum rubrum and the rush Marsippospermum grandiflorum reach notable surface cover only at elevated, drier sites. Other frequently occurring vascular plants such as Tetroncium magellanicum, Gaultheria antarctica, Nothofagus antarctica, Carex magellanica, Rostkovia magellanica, Nanodea muscosa, and Pernettya pumila are present with low cover. Small patches of the surface are covered by lichens or showed bare peat without any vegetation, likely from former pools that have now dried up. Peat thickness can reach at least 678 cm with a peat age of 13,500 cal. yrs. BP at this site (Borromei et al., 2016).

The micro-relief at the cushion bog (close Bahía Moat, 54°58′04.0″S 66°44′05.7″W) is flat compared to the Sphagnum bog with a water table fluctuating close to the surface, which is largely covered by lawns of the cushion-forming plant Astelia pumila. A mosaic of pools and small lawns (patches of few square meters) dominated by S. magellanicum or cushion-forming Donatia fascicularis are embedded in these Astelia lawns. The bog's vegetation was previously dominated by S. magellanicum while A. pumila invaded around 2600 ^{14}C yrs. BP and the occurrence of the cushion plant D. fascicularis was dated to 1500 ^{14}C yrs. BP (Heusser, 1995). A. pumila establishes a dense, aerenchymous rooting system (Münchberger et al., 2019) with on the average 2.15 g dry root biomass L^{-1} (of peat) down to 1.7 m (Fritz et al., 2011) and a high root turnover as indicated by low root lifetimes of ~3–4 years (Knorr et al., 2015).
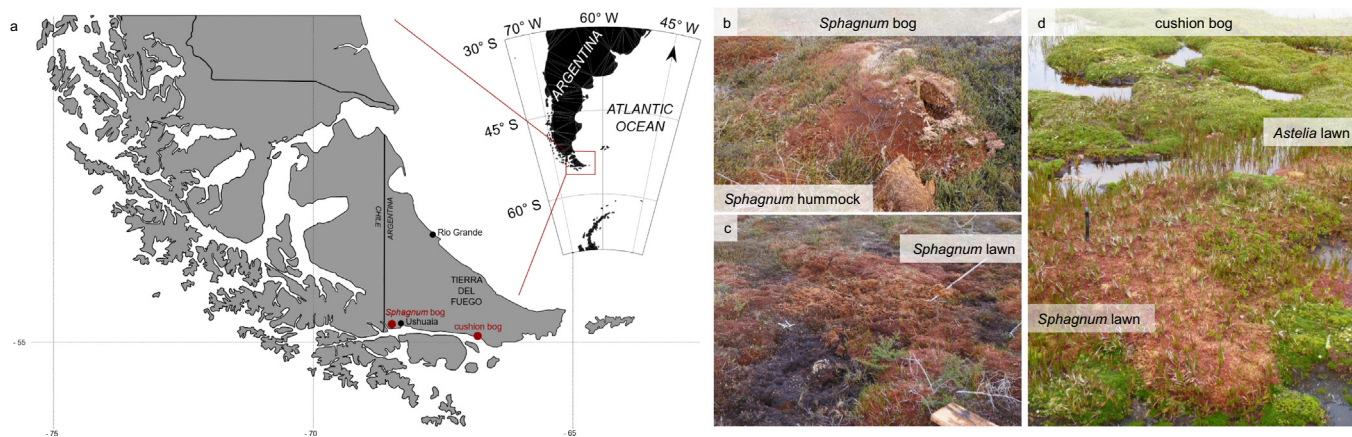

Fig. 1. a: Location of the study sites near Ushuaia in Tierra del Fuego, southernmost Patagonia (Argentina). The map was created at http://www.simplemapp.com accessed on 11.12.2017 and in Matlab (MATLAB Mapping Toolbox Release R2017a). b-d: Pictures showing the investigated microforms characterized by distinct plant communities and their specific plant species in the two contrasting Patagonian bog types. SB_HMK and SB_LWN profiles were sampled in hummocks (b) and lawns (c) of a Sphagnum bog, CB_SPH_LWN and CB_AST_LWN profiles were sampled in Sphagnum and Astelia lawns of a cushion bog (d). Note the dominance of S. magellanicum in Sphagnum hummocks and Sphagnum lawns and A. pumila in Astelia lawns.

2.2. Sampling of peat cores in the field

We selected four different microforms each characterized by a distinct plant community and its specific plant species (Fig. 1b-d) to obtain continuous peat profiles from the surface to the underlying mineral material in austral summer (February/March) 2014 and 2015. The most dominant microforms, *Sphagnum* lawn (SB_LWN) and *Sphagnum* hummock (SB_HMK), were sampled in the *Sphagnum* bog. *Astelia* lawns (CB_AST_LWN) and *Sphagnum* lawns (CB_SPH_LWN) were selected in the cushion bog. Although covering only small areas in the cushion bogs' surface, we assessed *Sphagnum* lawns as a relevant microform for carbon and nutrient dynamics due to the presumably higher cover of *S. magellanicum* in the past as previously described for this study site (Heusser, 1995; Borromei et al., 2014). All four microforms were sampled with a replicate of two to account for within-site differences. The selected microforms were carefully cored to avoid peat compaction using a Russian peat corer (Eijkelkamp Agrisearch Equipment, Giesbeek, Netherlands) and segmented into 10 cm slices.

In addition, surface peat cores were collected from one *Sphagnum* lawn in the *Sphagnum* bog and one *Astelia* lawn in the cushion bog to determine the age of recently accumulated peat. Hereto, 10 × 10 cm sods were cut with a knife in 3 cm slices down to 20 cm depth and below in 5 cm slices down to 50 cm depth. All slices were wrapped in sealed plastic bags and stored cool until laboratory analyses.

2.3. Analyses of solid peat characteristics from continuous peat profiles

All peat slices were oven dried at 70 °C until constant mass. Plant macrofossils were analysed to reconstruct the locally dominant vegetation and to identify the vegetation shift towards a dominance of cushion plant vegetation in CB_AST_LWN profiles. Samples of one *Astelia* lawn profile (CB_AST_LWN-2) and two *Sphagnum* lawn profiles, SB_LWN-2, CB_SPH_LWN-2, obtained in the *Sphagnum* bog and in the cushion bog, respectively, were chosen. About one-third of each samples' peat material was selected to obtain volume percentages of individual subfossils of vascular plants and mosses. The samples were washed and sieved under a gentle water current using a 0.2 mm sieve. The material was then examined under a stereomicroscope. The vascular plant composition was determined based on carpological remains and vegetative fragments (leaves, rootlets, epidermis). Volumetric percentages were estimated to the nearest of 5% for different moss and vegetative remains (rootlets and epidermis) of vascular plant species, or plant types, e.g. herbs or dwarf shrubs, where species level identification was not possible. Plant macrofossils of *Sphagnum* were identified using the identification key of Hölzer (2010) and macrofossils of vascular plants were compared to recent plants collected from this region. The percentages of amorphous organic matter and tephra, as well as macrocharcoal pieces in the peat samples, were also documented.

Before milling using a tungsten carbide insert, macroscopic, recently formed plant biomass i.e. mostly living aerenchymatic roots of *A. pumila* in CB_AST_LWN profiles were removed. Total C and N contents and natural abundance of $\delta^{15}N$ and $\delta^{13}C$ stable isotopes in homogenized peat were determined using an elemental analyser (EA 3000, EuroVector, Redavalle, Italy) connected to a stable isotope ratio mass spectrometer (IRMS, NU instruments, Wrexham, UK). To assess the influence of sea spray on peat decomposition in the upper meter of the peat and to identify tephra layers, further elemental composition was determined by wavelength-dispersive X-ray fluorescence spectroscopy (ZSX Primus II, Rigaku, Tokyo, Japan). Fourier-transformed infrared spectroscopy (FTIR) was applied to characterize peat organic matter quality down to 4 m as described in detail in Broder et al. (2012). Spectra were recorded on a FTIR spectrometer in the wavenumber range from 600 cm^{-1} to 4000 cm^{-1} (Varian 660; Palo Alto, USA).

2.4. ^{14}C and ^{210}Pb dating

A total of 34 samples from continuous peat profiles were dated by radiocarbon dating (^{14}C) (Table A.1) to determine long-term peat, C and N accumulation rates. Four slices from each of the eight profiles were selected in comparable depth intervals from surface peat (45 cm depth, slice from 40 to 50 cm depth, only the centre of a slice is given in the following) to the basal sample of the respective profile. Uppermost peat down to a depth of ~30 cm was in most cases too wet (Heusser, 1995) to be collected without altering the volume of the peat and thus bulk density calculations. Therefore, these peat layers were excluded from ^{14}C analyses. Two more slices were selected from both CB_AST_LWN profiles at the transition zone of *Sphagnum* to cushion plant peat identified based on macroscopic changes in the peat composition. Radiocarbon signatures of fossil bulk peat material was determined by accelerator mass spectrometry (AMS) at the Keck-CCAMS facility of the University of California, Irvine. The sample preparation routine conducted at the Department of Soil Ecology at the University of Bayreuth as well as further methodological details are described in Schulze et al. (2009). Peat slices of surface cores oven dried at 70 °C until constant mass and milled were sent to Flett Research Ltd. (Winnipeg, Canada) for radioactive lead (^{210}Pb) dating further confirmed by radioactive caesium (^{137}Cs) analyses to determine recent accumulation rates. In this approach, peat age was determined applying a constant-rate-of-supply (CRS) model (Appleby, 2001).

2.5. Calculations and statistical analyses

FTIR spectra were baseline corrected for further evaluation using a software routine (R package "irpeat", Teickner and Hodgkins, 2020; Hodgkins et al., 2018). Spectral FTIR absorption peaks at specific wavelengths (average location ±25 cm^{-1}) were attributed to recalcitrant functional groups of organic matter (1420 cm^{-1}: phenolic and aliphatic structures, 1510 cm^{-1}: amides, 1630 cm^{-1}: aromatics and aromatic or aliphatic carboxylates, 1720 cm^{-1}: carboxylic acids and aromatic esters; Niemeyer et al., 1992). These peaks of recalcitrant functional groups were then expressed relative to peaks of labile polysaccharides (indicated by a spectral absorption peak at 950–1170 cm^{-1}) to compute humification indices of continuous profiles (Broder et al., 2012 and references therein; R package "ir", Teickner, 2020). Higher values of these humification indices imply a decrease of labile polysaccharides relative to presence of recalcitrant functional groups in the organic matter and, thus, an increase in the decomposition stage.

To estimate the age of non-^{14}C dated peat slices of continuous profiles, age-depth modelling was conducted with a software routine (package rbacon 2.3.4, R version 3.5.2, Blaauw and Christen, 2011) using Bayesian statistics. The ^{14}C ages of radiocarbon dated samples were calibrated applying a calibration curve for Southern Hemisphere dates (SHcal13, Hogg et al., 2013) and, if necessary, a Southern Hemisphere postbomb curve (SH1-2, Hua et al., 2013), both implemented in the rbacon routine, and expressed as calibrated calendar years before present (cal. BP = before 1950). The age of peat layers was estimated at the 10 cm sampling intervals in continuous peat profiles.

Bulk density (dry mass per wet volume, g cm^{-3}) as well as total C and N contents (as C density and N density, g cm^{-3}) were calculated excluding the dry mass of aerenchymatic *A. pumila* roots (~4–20% of the total dry mass, if present) for every 10 cm peat slice. For each continuous peat profile, peat height increments as well as carbon and nitrogen density of each peat slice were divided by the respective time increment derived from modelled weighted mean ages to obtain apparent peat, C and N accumulation rates (PAR in mm yr^{-1}, CAR and NAR in g C m^{-2} yr^{-1} and g N m^{-2} yr^{-1}, respectively). Major changes in PAR corresponded to age intervals between ^{14}C dated peat slices, though. To assess differences in the peat development over time, three time periods spanning the first ~1200 and ~ 4200 years of peat development ("initial time period" with old peat, but at early stage of the bog) in

Fig. 2. Plant macrofossils determined in three continuous peat profiles sampled in a *Sphagnum* lawn (SB_LWN-2 profile, a) of a *Sphagnum* bog and in a *Sphagnum* lawn (CB_SPH_LWN-2 profile, b) and an *Astelia* lawn (CB_AST_LWN-2 profile, c) of a cushion bog.

the *Sphagnum* and cushion bog, respectively, and the last ~1600 years of peat development ("young time period" with young peat, but in late stage of the bog) were defined (Table A.2). The "intermediate time period" spans the time between end of "initial" and beginning of "young". These periods were specified according to three major changes in the vegetation composition derived from plant macrofossils (Fig. 2a-c) and the time periods uniformly transferred to all continuous peat profiles. Time-weighted means of PAR, CAR and NAR were calculated over the lifespan of both bogs and for each time period to estimate respective accumulation rates. Due to the difficulties named above, uppermost peat layers could not be sampled from all eight continuous profiles. Therefore, available data from peat layers above 30 cm depth were excluded and only data from peat layers below were included in calculations. Basal samples of old peat from the bottom of the bog with highest bulk densities (>0.09 g cm^{-3}) but presumably low organic matter content (<10%, Heusser, 1995) were excluded.

The activity of supported ^{210}Pb obtained from surface peat cores achieved background levels (i.e. levels of unsupported ^{210}Pb) at 24 cm depth in the *Sphagnum* bog and at 50 cm in the cushion bog. Deeper peat layers showed a ^{210}Pb signal below the detection limit. These peat layers at the detection limit were 80 and 55 years old. Recent accumulation rates of C and N during the last 50 years (RERCA, RERNA) were calculated likewise as accumulation rates of continuous peat profiles, but with time intervals derived from CRS modelled ages. The share of *A. pumila* aerenchymatic root dry mass for a specific height increment was inferred from respective peat slices of the continuous CB_AST_LWN-2 peat profile for which data above 0.40 m depth were available. Surface peat C and N contents were assumed to correspond to these peat slices as well, while for the C and N contents of roots 43.1% and 0.45% ($n = 5$), respectively, were assumed from available unpublished data of *A. pumila* roots. Surface C and N contents in the *Sphagnum* bog were estimated from uppermost ($n = 3$) mean C and N contents of the SB_HMK-2 profile for which data above 0.40 m depth were available with 45.5% and 0.30%, respectively.

Normal distributions of the data were checked by Kolmogorov-Smirnov tests. Due to non-normality, relationships between peat characteristics were evaluated pairwise for each microform by Spearman's rank correlation (MATLAB Statistics Toolbox Release R2020a). Log-transformation resulted in normality of accumulation rates data and an analyses of variances was applied to determine significant differences between accumulation rates in the two studied bogs. All results were evaluated at the 0.05 significance level and values are reported as mean ± standard deviation.

3. Results

3.1. Plant macrofossils and identification of peatland development time periods

Peat thickness at the cored locations in the *Sphagnum* bog reached a maximum of 455 cm in SB_HMK profiles while a maximum peat thickness of 735 cm was reached in the cushion bog in the CB_AST_LWN-2 profile (Table A.1). Plant macrofossil (Fig. 2a) records from the SB_LWN-2 profile were uniform and remained to ~80% from one single peat moss species, *Sphagnum magellanicum*. Only throughout the first ~1200 cal. yrs. BP of the peat development, a higher percentage of shrub residuals was identified with up to 50% combined with a high content of amorphous organic matter in the very beginning of peat accumulation. This time span was defined as the initial time period in the *Sphagnum* bog. Above a 20 cm thick layer of amorphous organic matter, presence of shrubs substantially decreased while remains of *S. magellanicum* associated with the rush *Tetronicum magellanicum* became more abundant. Plant macrofossil records from the CB_SPH_LWN-2 profile (Fig. 2b) also consisted mainly of *S. magellanicum* remains but were more diverse with residuals from herbs, shrubs and other mosses between 5 and 85% being present throughout the whole core.

The CB_AST_LWN-2 profile (Fig. 2c) showed the highest diversity of identified plant species and most variability in the proportions of plant macrofossils. Similar to the other two profiles, *S. magellanicum* was the dominant peat moss throughout the core, confirming our selection of microforms for this study. But *S. magellanicum* reached a maximum contribution to plant macrofossil residuals of only 60%. If present, remains of *S. magellanicum* were associated with high presence of *T. magellanicum* which was the most dominant species throughout the profile. Three zones were distinguished whose change corresponded to presence of charcoal and tephra layers; layers of tephra were characterized by elevated concentrations of e.g. strontium, titanium, aluminium, silicon, sodium, potassium and notably also P (Table A.4). From the first ~4200 cal. yrs. BP since peatland initiation mainly amorphous organic matter and residuals of herbs and woody species remained. This time span was defined as the initial time period in the cushion bog. These oldest peat layers were overlain by peat consisting mainly of *S. magellanicum* and *T. magellanicum* residuals abruptly changing at 1600 cal. yrs. BP to peat dominated by vascular plant remains without any further presence of *S. magellanicum* or *T. magellanicum*. This vascular plant peat consisted in deeper layers of unidentified herbs and amorphous organic matter that was replaced by a predominance of *A. pumila* residuals towards surface peat layers. Down to a depth of 1.8 m (rhizosphere) living roots of *A. pumila* were present and we observed a highly decomposed and amorphous peat. The vegetation shift at 1600 cal. yrs. BP was macroscopically visible also in the CB_AST_LWN-1 profile. Though this vegetation shift was only recognizable in CB_AST_LWN profiles, these last 1600 years of peat accumulation since the appearance of cushion plants in the cushion bog were defined as the "young time period" for all peat profiles at both bogs.

3.2. Peat, carbon and nitrogen accumulation in the Sphagnum bog

Peat accumulation at the cored locations in the *Sphagnum* bog was initiated ~6100 cal. yrs. BP (Table A.1). Bulk density of the peat had a mean of 0.06 ± 0.02 g cm^{-3} and was slightly higher in SB_HMK peat compared to SB_LWN peat during all three time periods (Fig. 3a, b, Table 1). With peat age and depth, bulk density increased significantly and was positively correlated with the humification index and negatively correlated with the δ^{13}C signature (Table A.3). Peat accumulated at a mean rate of 0.71 ± 0.05 mm yr^{-1}, substantially increased after the initial time period and reached highest PAR values during the young time period (Table 1). Furthermore, PAR tended to be higher in SB_LWN profile compared to SB_HMK profiles. Carbon accumulated at a mean CAR of 21.9 ± 5.8 g C m^{-2} yr^{-1} with, contrary to PAR, ~23% higher CAR in SB_HMK profiles compared to SB_LWN profiles throughout all time periods (Fig. 3i, j). SB_HMK and SB_LWN profiles also showed different patterns of CAR over time. CAR gradually decreased from the initial to the intermediate time period in SB_HMK profiles but C was thereafter accumulated at changing rates with a relatively constant mean until present. In SB_LWN profiles, CAR abruptly decreased at the end of the initial time period, but afterwards CAR gradually increased until C accumulation seemed to end at ~1100 cal. yrs. BP in the SB_LWN-2 profile while it substantially decreased during the young time period in the SB_LWN-1 profile associated with a minimum in bulk density at the same time (Fig. 3b). Similar patterns over time were observed for NAR (Fig. 3m-p) as indicated by a highly significant correlation between CAR and NAR (Table A.3). On average, N accumulated at NAR of 0.35 ± 0.14 g N m^{-2} yr^{-1}. During the last 50 years of peat development, accumulation rates of the *Sphagnum* lawn reached on the average a PAR of 5.4 ± 2.9 mm yr^{-1}, a RERCA of 63.8 ± 19.7 g C m^{-2} yr^{-1} and a RERNA of 0.40 ± 0.12 g N m^{-2} yr^{-1}.

3.3. Peat, carbon and nitrogen accumulation in the cushion bog

Peat at the cored points in the cushion bog accumulated for almost twice the time period compared to the *Sphagnum* bog since
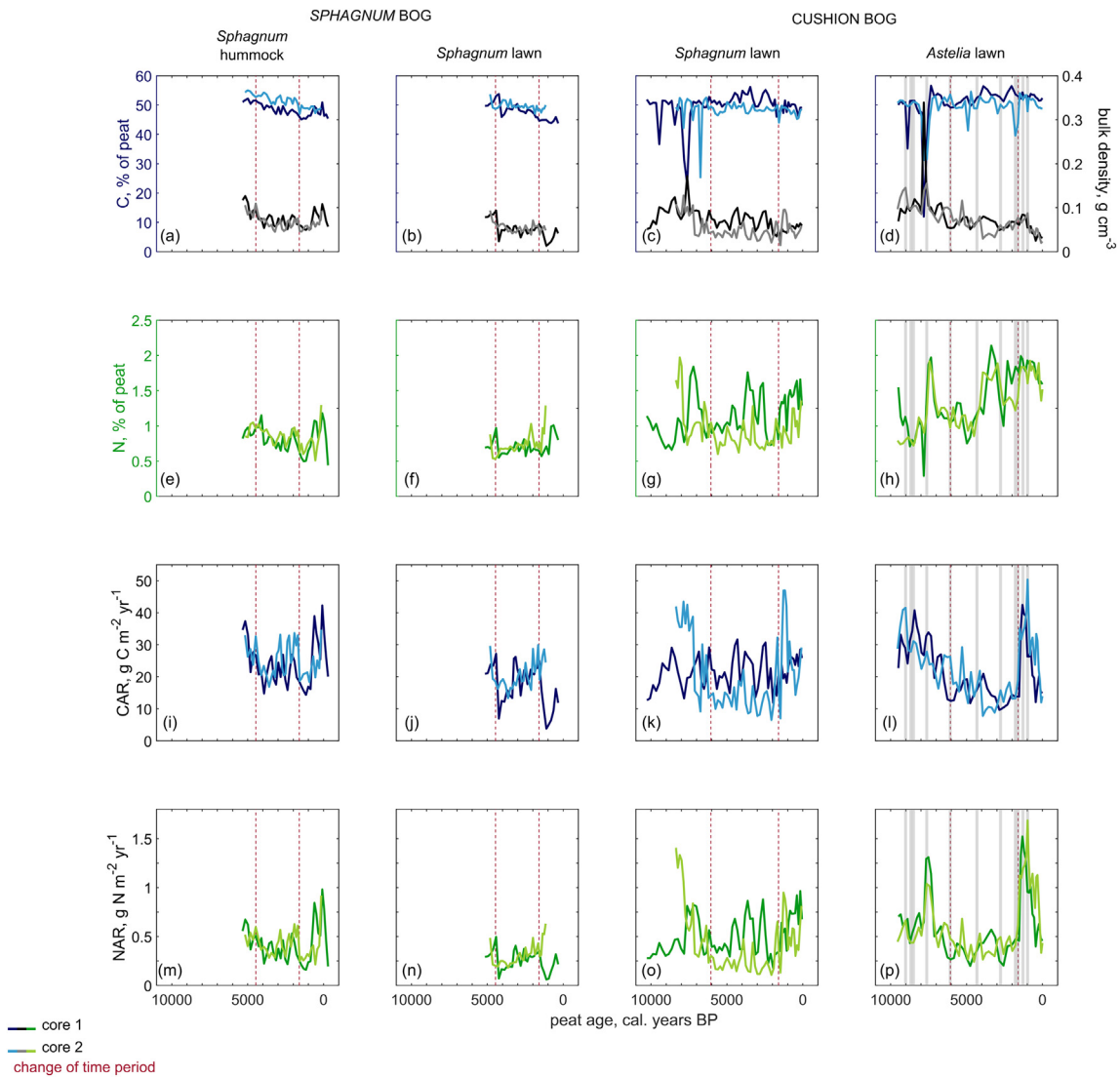
Fig. 3. Temporal variations in bulk densities, C and N contents as well as apparent long-term C and N accumulation (CAR and NAR) of continuous peat profiles obtained in different microforms in two Patagonian peat bogs. SB_HMK and SB_LWN profiles were sampled in hummocks and lawns of a *Sphagnum* bog, CB_SPH_LWN and CB_AST_LWN profiles were sampled in *Sphagnum* and *Astelia* lawns of a cushion bog. "Change of time period" refers to three time periods defined according to major changes in the vegetation composition derived from plant macrofossil analyses. Vertical grey lines denote tephra layers and charcoal identified in the CB_AST_LWN peat profile, and horizontal red dashed lines indicate change of time period. The vegetation shift towards a dominance of cushion-forming *A. pumila* was identified at 1600 cal. yrs. BP in the *Astelia* lawn profiles.

Table 1

Means of bulk density (BD) as well as peat, C and N accumulation (PAR, CAR, NAR) and their standard deviation of continuous peat profiles of different microforms in two Patagonian peat bogs. SB_HMK and SB_LWN profiles were sampled in hummocks and lawns of a *Sphagnum* bog, CB_SPH_LWN and CB_AST_LWN profiles were sampled in *Sphagnum* and *Astelia* lawns of a cushion bog. "Young" includes the time span of the last ~1600 years of peat development, "initial" includes the first ~1200 and ~ 4200 years of peat development in the *Sphagnum* and cushion bog, respectively. Intermediate defines the time period between end of "initial" and beginning of "young".

	Time period	BD, g cm^{-3}	PAR, mm yr^{-1}	CAR, g C m^{-2} yr^{-1}	NAR, g N m^{-2} yr^{-1}
SB_HMK	Young	0.066 ± 0.016	0.76 ± 0.05	23.88 ± 6.81	0.41 ± 0.23
	Intermediate	0.065 ± 0.011	0.72 ± 0.08	23.31 ± 4.66	0.38 ± 0.11
	Initial	0.091 ± 0.018	0.57 ± 0.01	27.24 ± 5.52	0.49 ± 0.29
SB_LWN	Young	0.044 ± 0.012	0.84 ± 0.05	18.39 ± 5.30	0.32 ± 0.12
	Intermediate	0.050 ± 0.008	0.82 ± 0.11	20.05 ± 4.32	0.29 ± 0.07
	Initial	0.066 ± 0.019	0.57 ± 0.01	18.77 ± 5.91	0.26 ± 0.12
CB_SPH_LWN	Young	0.053 ± 0.016	0.95 ± 0.01	24.45 ± 7.73	0.58 ± 0.21
	Intermediate	0.055 ± 0.016	0.66 ± 0.10	18.08 ± 5.94	0.36 ± 0.17
	Initial	0.074 ± 0.028	0.62 ± 0.06	21.51 ± 8.51	0.48 ± 0.29
CB_AST_LWN	Young	0.075 ± 0.037	0.99 ± 0.16	26.97 ± 9.83	0.93 ± 0.36
	Intermediate	0.054 ± 0.020	0.47 ± 0.03	14.85 ± 4.21	0.39 ± 0.11
	Initial	0.062 ± 0.015	0.56 ± 0.06	26.28 ± 7.44	0.60 ± 0.23

Table 2

Means of peat characteristics and their standard deviation of continuous peat profiles of different microforms in two Patagonian peat bogs. SB_HMK and SB_LWN profiles were sampled in hummocks and lawns of a *Sphagnum* bog, CB_SPH_LWN and CB_AST_LWN profiles were sampled in *Sphagnum* and *Astelia* lawns of a cushion bog. "Young" includes the time span of the last ~1600 years of peat development, "initial" includes the first ~1200 and ~ 4200 years of peat development in the *Sphagnum* and cushion bog, respectively. Intermediate defines the time period between end of "initial" and beginning of "young". N.d. = not determined.

	Time period	C, %	N, %	C/N ratio	$\delta^{13}C$, ‰	$\delta^{15}N$, ‰
SB_HMK	Young	47.83 ± 1.27	0.78 ± 0.22	66.00 ± 16.61	n.d.	n.d.
	Intermediate	49.90 ± 1.45	0.81 ± 0.11	62.35 ± 7.18	n.d.	n.d.
	Initial	52.52 ± 0.72	0.95 ± 0.09	55.72 ± 5.48	n.d.	n.d.
SB_LWN	Young	46.60 ± 0.76	0.82 ± 0.21	59.92 ± 13.21	−24.99 ± 0.46	−2.04 ± 0.67
	Intermediate	48.63 ± 1.20	0.71 ± 0.08	69.09 ± 6.69	−25.53 ± 0.61	−2.92 ± 0.87
	Initial	50.25 ± 2.23	0.68 ± 0.12	75.87 ± 11.33	−26.28 ± 0.51	−3.52 ± 0.76
CB_SPH_LWN	Young	48.31 ± 1.55	1.16 ± 0.22	44.19 ± 9.07	−25.36 ± 0.62	−1.20 ± 1.27
	Intermediate	50.05 ± 1.86	0.96 ± 0.23	55.00 ± 10.82	−25.68 ± 0.56	−1.83 ± 1.04
	Initial	47.98 ± 6.17	1.03 ± 0.33	50.60 ± 14.76	−26.19 ± 0.54	−1.91 ± 1.02
CB_AST_LWN	Young	51.75 ± 1.67	1.76 ± 0.15	29.56 ± 2.06	−25.95 ± 0.44	0.89 ± 0.86
	Intermediate	51.18 ± 2.85	1.39 ± 0.36	39.22 ± 10.40	−26.19 ± 0.82	0.73 ± 1.23
	Initial	48.19 ± 7.47	1.10 ± 0.33	46.54 ± 12.73	−26.41 ± 0.63	−1.71 ± 1.29

~11,100 cal. yrs. BP (Table A.1). Bulk density of the peat revealed a mean of 0.07 ± 0.03 g cm^{-3} (Fig. 3c, d, Table 1) and was higher in CB_AST_LWN profiles compared to CB_SPH_LWN profiles. Compared to the *Sphagnum* bog, mean bulk density decreased in the order SB_HMK > CB_AST_LWN > CB_SPH_LWN > SB_LWN throughout all time periods. Bulk density increased significantly with peat age and depth in the cushion bog and was negatively correlated with the C/N ratio and the $\delta^{13}C$ signature (Fig. 3c, d, Table 1).

Peat accumulated with a mean rate of 0.71 ± 0.07 mm yr^{-1} and, thus, at similar rates compared to the *Sphagnum* bog, but maximum PAR was distinctly higher with up to 0.99 ± 0.16 mm yr^{-1} observed in CB_AST_LWN profiles during the young time period (Table 1). During this period, PAR almost doubled not only in CB_AST_LWN profiles, but also CB_SPH_LWN profiles. Carbon accumulated at a mean CAR of 22.2 ± 8.8 g C m^{-2} yr^{-1} with lowest CAR during the intermediate time period (Fig. 3k, l). CB_AST_LWN profiles resembled each other with most pronounced changes over time compared to the other

microforms (Fig. 3l) and coincided with the vegetation shifts identified from plant macrofossil analyses in the CB_AST_LWN-2 profile. Since the beginning of peat development, CAR gradually decreased from ~40 g C m^{-2} yr^{-1} to ~10 g C m^{-2} yr^{-1} until rapidly increasing again to peaking accumulation rates >40 g C m^{-2} yr^{-1} at the time of the vegetation shift at 1600 cal. yr. BP and gradually decreased afterwards again down to ~10 g C m^{-2} yr^{-1}. Highest CAR among all microforms in the young period was also reached in CB_AST_LWN profiles with 27.0 ± 9.8 g C m^{-2} yr^{-1} albeit not being distinctly elevated compared to rates obtained from other microforms. While in the CB_SPH_LWN-2 profile CAR followed the pattern of both CB_AST_LWN profiles, CAR fluctuated at a relatively stable mean in peat of the CB_SPH_LWN-1 profile. Like in the *Sphagnum* bog, NAR patterns over time were similar to CAR patterns (Fig. 3i-p) as indicated by a highly significant correlation between CAR and NAR (Table A.3). Nitrogen accumulated with 0.55 ± 0.29 g N m^{-2} yr^{-1} at a significantly ($p < 0.05$) higher mean NAR compared to the *Sphagnum* bog and the maximum, distinctly higher NAR among all
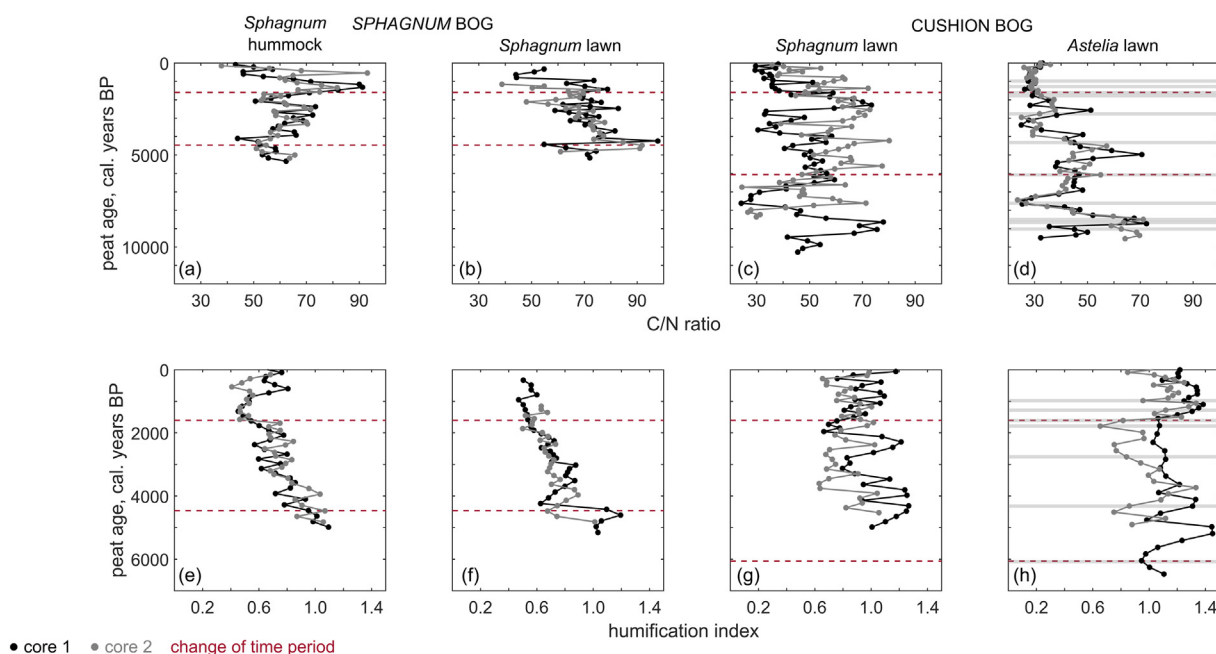

Fig. 4. Temporal variations in decomposition indicators (C/N ratio, FTIR-derived humification index) of continuous peat profiles obtained in different microforms in two Patagonian peat bogs. SB_HMK and SB_LWN profiles were sampled in hummocks and lawns of a *Sphagnum* bog, CB_SPH_LWN and CB_AST_LWN profiles were sampled in *Sphagnum* and *Astelia* lawns of a cushion bog. "Change of time period" refers to three time periods defined according to major changes in the vegetation composition derived from plant macrofossil analyses. Horizontal grey lines denote tephra layers and charcoal identified in the CB_AST_LWN peat profile, and horizontal red dashed lines indicate change of time period. The vegetation shift towards a dominance of cushion-forming *A. pumila* was identified at 1600 cal. yrs. BP in the *Astelia* lawn profiles.
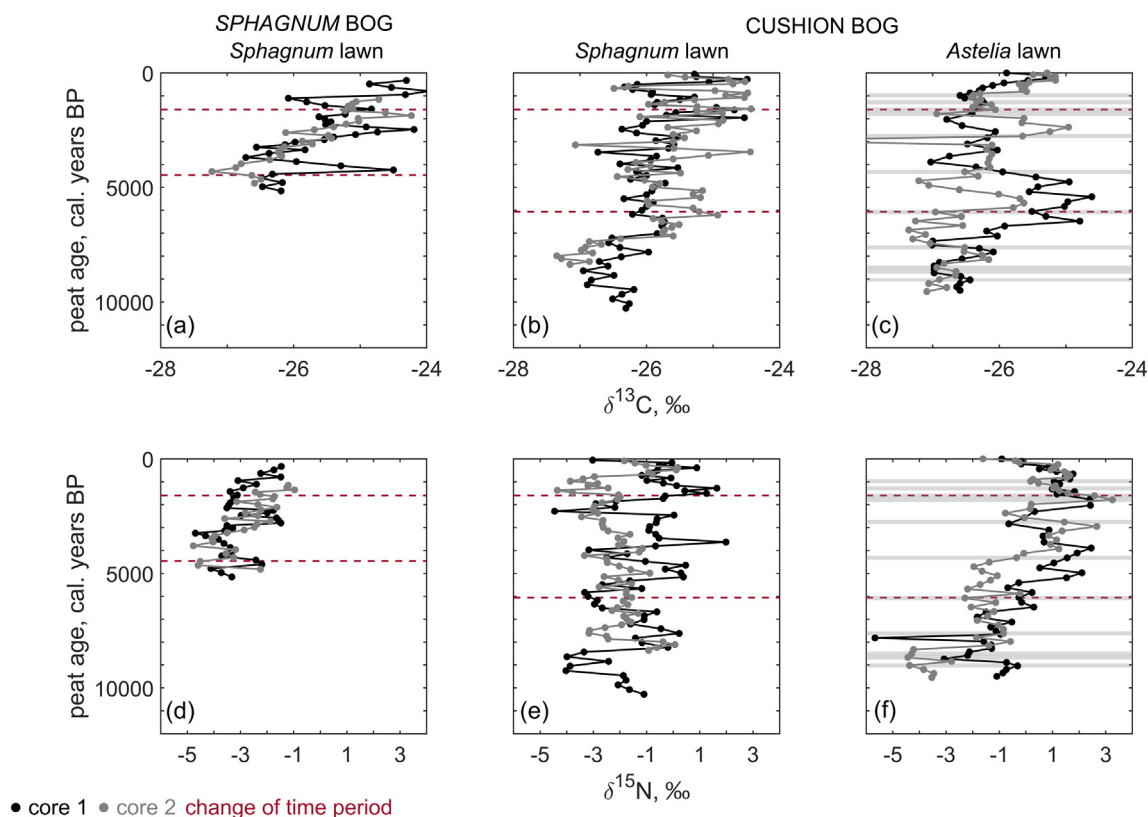
Fig. 5. Temporal variations in stable C and N isotopes of continuous peat profiles obtained in different microforms in two Patagonian peat bogs. SB_HMK and SB_LWN profiles were sampled in hummocks and lawns of a *Sphagnum* bog, CB_SPH_LWN and CB_AST_LWN profiles were sampled in *Sphagnum* and *Astelia* lawns of a cushion bog. "Change of time period" refers to three time periods defined according to major changes in the vegetation composition derived from plant macrofossil analyses. Horizontal grey lines denote tephra layers and charcoal identified in the CB_AST_LWN peat profile, and horizontal red dashed lines indicate change of time period. The vegetation shift towards a dominance of cushion-forming *A. pumila* was identified at 1600 cal. yrs. BP in the *Astelia* lawn profiles.

microforms of 0.93 ± 0.36 g N m^{-2} yr^{-1} was reached in CB_AST_LWN peat during the young time period. Accumulation rates during the recent period reached a mean PAR of 7.16 ± 1.26 mm yr^{-1}, a RERCA of 245.4 ± 55.4 g C m^{-2} yr^{-1} and a RERNA of 4.69 ± 0.26 g N m^{-2} yr^{-1}.

3.4. Elemental composition, peat organic matter quality and stable isotopes

The C content in the peat significantly increased with peat age except in CB_AST_LWN profiles (Fig. 3a-d, Table A.3) and had a mean of $49.2 \pm 2.0\%$ and $49.6 \pm 4.9\%$ in the *Sphagnum* and cushion bog, respectively. The N content did not show a consistent trend with peat age among the microforms (Fig. 3e-h), significantly decreased with peat age in CB_AST_LWN profiles (Table A.3) and was with a mean of $0.78 \pm 0.15\%$ lower in the *Sphagnum* bog throughout all time periods (Table 2) compared to the cushion bog with a mean of $1.21 \pm 0.35\%$. Mean C/N ratios were with 65.4 ± 11.4 higher in the *Sphagnum* bog compared to 44.9 ± 12.6 in the cushion bog and decreased in the order SB_LWN > SB_HMK > CB_SPH_LWN > CB_AST_LWN throughout all time periods (Table 2). While SB_HMK and especially CB_SPH_LWN profiles showed a pronounced variability in C/N ratios with peat age

(Fig. 4a, c), C/N ratios significantly increased with peat age in SB_LWN and CB_AST_LWN profiles (Fig. 4a, c, Table A.3). Peat accumulated during the young time period in CB_AST_LWN profiles composed of *A. pumila* macrofossils and had lowest C/N ratios of 29.6 ± 2.1 accompanied with a low variability (Fig. 4d, Table 2).

Humification indices of each profile (highly) correlated with each other ($R > 0.78$, $p < 0.00$ for all relationships; $R > 0.95$, p < 0.00 for all except four relationships) and, thus, only the 1630/1090 ratio indicative for presence of aromatics and aromatic or aliphatic carboxylates relative to carbohydrates is interpreted in the following. The humification index of peat sampled in the *Sphagnum* bog increased significantly with peat age (Fig. 4e, f, Table A.3). In contrast, the index in peat profiles in the cushion bog was more variable without a peat age trend, but was overall on a distinctly higher level (Fig. 4g, h). Especially, peat accumulated during the young time period in CB_AST_LWN profiles showed relatively high values pointing to presence of comparatively high amounts of recalcitrant functional groups (Fig. 4h). Except for SB_LWN profiles, the humification index was negatively correlated with C/N ratios (Table A.3).

Surface peat layers were enriched in $\delta^{13}C$ with values ~-25‰ and became significantly depleted with peat age down to ~-27‰ (Fig. 5a-c,

Table 3
Elemental concentrations in surface peat (35–100 cm depth) of continuous profiles of different microforms in two Patagonian peat bogs. Means and their standard deviation are given in ppm. SB_HMK and SB_LWN profiles were sampled in hummocks and lawns of a *Sphagnum* bog, CB_SPH_LWN and CB_AST_LWN profiles were sampled in *Sphagnum* and *Astelia* lawns of a cushion bog.

	Sulfate	Chloride	Rubidium	Strontium
SB_HMK	1149.64 ± 418.62	269.98 ± 110.49	6.36 ± 1.34	26.99 ± 4.01
SB_LWN	1250.86 ± 279.45	226.88 ± 133.92	7.19 ± 2.23	17.91 ± 3.02
CB_SPH_LWN	2874.64 ± 645.98	1701.52 ± 221.03	14.79 ± 2.33	40.59 ± 9.59
CB_AST_LWN	2455.64 ± 507.53	3068.49 ± 771.74	18.82 ± 3.20	58.56 ± 13.57

Table A.3). Stable C isotopic signatures had a mean of $-25.6 \pm 0.8‰$ and $-26.0 \pm 0.7‰$ in the *Sphagnum* and cushion bog, respectively. Carbon isotopic signatures of peat accumulated during young time period (since appearance of cushion plants) in CB_AST_LWN profiles became substantially depleted in $\delta^{13}C$ with peat age and reached values almost as low as basal peat layers (Fig. 5c). The change in the dominant plant macrofossils in peat of CB_AST_LWN profiles older than ~1600 cal. yrs. BP was furthermore associated with a more pronounced fluctuation in the $\delta^{13}C$ signature of older peat layers compared to younger layers above. Stable N isotopic signatures were with a mean of $-2.87 \pm 0.97‰$ notably depleted in $\delta^{15}N$ in the *Sphagnum* bog compared to the cushion bog with a mean of $-0.95 \pm 1.45‰$. Mean $\delta^{15}N$ signatures also became more depleted in the order CB_AST_LWN > CB_SPH_LWN > SB_LWN throughout all time periods (Table 2) and decreased significantly with peat age in SB_LWN and CB_AST_LWN profiles, but not CB_SPH_LWN profiles that showed a pronounced variability with peat age (Fig. 5d–f). As described for other peat characteristics, $\delta^{15}N$ values reflected the change in plant macrofossils in CB_AST_LWN profiles towards dominance of *A. pumila* remains. The signatures increased substantially by 4‰ from depleted values at the surface of ~-2‰ throughout peat layers accumulated during the young period (Fig. 5f), reaching ~2‰. In peat older than ~1600 cal. yrs. BP, $\delta^{15}N$ values became again depleted in ^{15}N with peat age. Stable isotopic signatures of C did not show a consistent relationship with the C/N ratio and were negatively correlated with the humification index in SB_LWN and CB_SPH_LWN profiles (Table A.3). Stable isotopic signatures of N were negatively correlated with the C/N ratio and did not show a consistent relationship with the humification index.

Sulfur and chloride concentrations in surface peat layers were 2- and 10-times higher in the cushion bog than in the *Sphagnum* bog (Table 3). Within the cushion bog, chloride concentrations in CB_AST_LWN profiles were almost twice as high as in CB_SPH_LWN profiles. Rubidium and strontium concentrations in surface peat of the cushion bog were on the average also twice as high as in the *Sphagnum* bog. All tephra layers in the CB_AST_LWN-2 profile and especially that layer deposited around 1600 cal. yrs. BP marking the shift towards *Astelia*-dominated peat corresponded with peaks of strontium, titanium, aluminium, silicon, sodium, potassium and also P concentrations compared to adjacent peat layers (Table A.4). For P, concentrations in cushion plant peat in the upper two meters of the CB_AST_LWN-2 profile were at a mean of 280 ppm (130–494 ppm), while levels in Sphagnum-derived peat below were at a mean of 133 ppm (112–149 ppm, Table A.4). No tephra layers, however, were evident from plant macrofossil analyses and metal concentrations obtained from SB_HMK, SB_LWN and CB_SPH_LWN profiles.

4. Discussion

4.1. The impact of cushion plant vegetation on C and N accumulation

Overall, the strong correlation between CAR and NAR across all peat profiles showed the crucial importance of N and thus of the vegetation in driving C accumulation (Wang et al., 2014; Ratcliffe et al., 2020). As postulated by our first hypothesis, the vegetation shift towards a dominance of *A. pumila* in the cushion bog resulted in substantially higher mean CAR and NAR of CB_AST_LWN profiles throughout the young time period (Table 1). The vegetation shift coincided with peaking CAR and NAR (Fig. 3k, l, o, p), indicating that primary productivity was initially promoted (Hughes et al., 2013; Ratcliffe et al., 2020). However, bulk density as well as CAR and NAR sharply dropped down again to low values ~10 g C m^{-2} yr^{-1} and < 0.5 g N m^{-2} yr^{-1} since the appearance of cushion plants (Fig. 3d, l, p). Such low CAR of ~10 g C m^{-2} yr^{-1} agreed well with CAR determined for an *A. pumila*-dominated Chilean bog (<10 g C m^{-2} yr^{-1}, Mathijssen et al., 2019).

The sudden disappearance of *T. magellanicum* in the plant macrofossils (Fig. 2c) as an indicator for wet conditions favourable for growth of *S. magellanicum* (Borromei et al., 2014) and occurrence of *A. pumila* was

associated with repeated deposition of tephra layers suggesting that the vegetation change towards a dominance of cushion plants might have been induced by volcano eruptions. Volcanic eruptions are a source of nutrients, especially for ombrotrophic bog ecosystems (Biester et al., 2003; Broder et al., 2012; Hughes et al., 2013; Mathijssen et al., 2019; Ratcliffe et al., 2020). Such a fertilization effect by tephra deposition was also suggested by our elemental analyses of selected profiles, in particular P, which stimulates plant productivity and C accumulation (Ratcliffe et al., 2020), as also observed here, but also promotes decomposition (Broder et al., 2012), thereby again favouring vascular plants (Hughes et al., 2013).

Interpretation of tephra layers in the CB_AST_LWN-2 profile is in general difficult due to great numbers of fall events and potential sources (Rabassa et al., 2006). Charcoal particles at ~4200 cal. yrs. BP could be related to fire ignited by the eruption of the Mt. Burney volcano (Stern, 2008) and tephra layers and charcoal particles at ~7750 cal. yrs. BP might originate from the H1 eruption of the Hudson volcano (Stern, 2008). Presence of macro-charcoal pieces in peat of the cushion bog in Moat has been also related to human settlements and burning (Heusser, 1995).

Very low C/N ratios of ~29 and a comparatively high FTIR-derived humification index in peat formed since ~1600 cal. yrs. BP in CB_AST_LWN profiles (Fig. 4d, h) agree with our third hypothesis and suggested high decomposition rates in peat originating from cushion plants, as described by previous authors (Ruthsatz and Villagran, 1991; Kleinebecker et al., 2007; Fritz et al., 2011; Mathijssen et al., 2019; Münchberger et al., 2019). High decomposition rates would explain the low accumulation rates and presumably originated from the nutrient-rich (Schmidt et al., 2010) and labile litter of vascular cushion plants (Dorrepaal et al., 2005; Moore et al., 2007). Decomposition was presumably also accelerated in the densely rooted rhizosphere of *Astelia* lawns (Fritz et al., 2011) by high root biomass turnover (Knorr et al., 2015) and oxygenation of the rhizosphere (Fritz et al., 2011; Münchberger et al., 2019) stimulating microbial and fungal decomposition (Paredes et al., 2014). The clear enrichment of P throughout the upper peat layers formed by *Astelia* (´Table A.4) suggests an intense recycling of nutrients through a dense and deep rooting system (Münchberger et al., 2019) along with more labile litter (Dorrepaal et al., 2005; Moore et al., 2007). The relation of P with the occurrence of tephra has been described before and points to tephra as a significant source of inputs of P (Ratcliffe et al., 2020). It appears that the higher primary productivity at this site (Holl et al., 2019) may not be able to compensate for the effective N recycling in the peat (Fritz, 2012) and the high decomposition rates of the litter in the rhizosphere on a longer time scale. Thus, the sharp decrease in bulk density associated with drops in CAR and NAR towards the present time opens the question whether cushion plants will succeed in accumulating peat and maintain long-term rates of C accumulation of similar magnitude as in the *Sphagnum* bog.

4.2. The impact of vegetation other than cushion plants on C and N accumulation

As revealed from plant macrofossil analyses, the vegetation in both bogs shifted from a dominance of vascular plants other than cushion plants (e.g. dwarf shrubs, grasses) to a dominance of *S. magellanicum* after the first ~1200 cal. yrs. BP of peat accumulation in the *Sphagnum* bog and ~4200 cal. yrs. BP of peat accumulation in the cushion bog. These early vegetation shifts induced an abrupt or gradual decrease in CAR and NAR in all peat profiles (Fig. 3i-p), probably related to decreasing bulk densities (Fig. 3a-d) in peat formed by recalcitrant *Sphagnum* litter (Dorrepaal et al., 2005; Moore et al., 2007). These early vegetation shifts could be interpreted as a fen-to-bog transition that has been observed in many Patagonian bogs (Loisel and Yu, 2013; Loisel and Bunsen, 2020). This transition is typically associated with a shift from highly decomposed, herbaceous basal fen peat to *Sphagnum*-

dominated bog peat (Loisel and Yu, 2013) around 4200 years ago (Loisel and Bunsen, 2020) as observed here (Fig. 2).

SB_HMK and SB_LWN profiles in the *Sphagnum* bog revealed different patterns of CAR and NAR over most of the peatland history. The increase in CAR observed in SB_LWN profiles (Fig. 3j) agreed well with Yu et al. (2010), who reported a gradual increase of C accumulation rates in Patagonian peatlands during the Holocene from ~15 to 28–40 g C m^{-2} yr^{-1}. Such pattern was not observed in SB_HMK profiles despite SB_LWN and SB_HMK profiles showing similar temporal patterns in their peat characteristics. This suggests that both SB_HMK coring sites were apparently characterized by similar local conditions, for example microtopography and hydrology or small vegetation changes, that differed from those at both SB_LWN sites, as it has been described before for different microforms (Belyea and Clymo, 2001; Turunen et al., 2004). Differing local conditions can furthermore explain why bulk density and CAR were higher in SB_HMK profiles compared to SB_LWN profiles throughout all time periods (Table 1). The 30% higher CAR and NAR in SB_HMK profiles compared to SB_LWN profiles were contrary to Belyea and Clymo (2001), who found that the peat accumulation rate is greatest for intermediate microforms (i.e. lawns) and least for microforms at the extremes of the water table gradient (i.e. hummocks, pools). Thus, we would have expected that at least youngest accumulation rates in SB_LWN profiles exceed those of SB_HMK profiles.

Interestingly, CAR and NAR in SB_LWN profile substantially decreased down to <10 g C m^{-2} yr^{-1} around 1000 cal. yrs. BP and even indicated a near-zero C and N accumulation since that time in one SB_LWN profile (Fig. 3j). Such low accumulation might originate from locally and temporarily different plant growth. For example, presence of lichens as occurring on the surface of our study site (Lehmann et al., 2016) could substantially reduce peat accumulation (Harris et al., 2018). In accordance to this, drier conditions explaining notably lower CAR were inferred from *E. rubrum* remains in peat profiles of Tierra del Fuego (Heusser, 1989; Björck et al., 2012) as observed at ~1100 cal. yrs. BP in the plant macrofossil analyses of the SB_LWN profile (Fig. 2a). Nevertheless, the near-zero CAR was probably a temporary phenomenon as we found living *Sphagnum* mosses at the surface of this profile.

4.3. Long-term accumulation of carbon, nitrogen and peat

CAR determined for the *Sphagnum* bog (21.9 g C m^{-2} yr^{-1}) corresponded well with that of the cushion bog (22.2 g C m^{-2} yr^{-1}), verifying our second hypothesis. The accumulation rates of both bogs fell in the range reported from other southern (22–23 g C m^{-2} yr^{-1}; Yu et al., 2010; Loisel and Yu, 2013; Ratcliffe et al., 2020) or northern peatlands (22.9 g C m^{-2} yr^{-1}, 45° to 69°N; Loisel et al., 2014). Compared with cushion bogs of the tropical high Andes with a CAR of 9–37 g C m^{-2} yr^{-1} (Hribljan et al., 2014; Hribljan et al., 2016), the cushion bog CAR reached a similar magnitude.

NAR has not yet been quantified for Patagonian peatlands to the best of our knowledge. NAR in the *Sphagnum* bog (0.35 g N m^{-2} yr^{-1}) was significantly lower compared to NAR in the cushion bog (0.55 g N m^{-2} yr^{-1}, $p < 0.05$), contradicting to our second hypothesis. Also, the *Sphagnum* bog NAR was remarkably lower compared with northern peatlands (0.5 g N m^{-2} yr^{-1}; Loisel et al., 2014), possibly due to low N deposition rates in Patagonia (0.1–0.2 g N m^{-2} yr^{-1}; Fritz et al., 2012). We attribute the difference between N accumulation and N deposition to biological N$_2$ fixation. Laboratory incubation of *Sphagnum* peat suggest great potential of biological N$_2$ fixation in Patagonian peatlands (Knorr et al., 2015). The rough NAR estimates of 1 g N m^{-2} yr^{-1} by the latter study were not confirmed, though. Higher NAR in the cushion bog can be explained by the higher N contents of *A. pumila* (Schmidt et al., 2010; Loisel et al., 2014) and correspond to higher N concentration in the upper peat below cushion plants (Kleinebecker et al., 2010).

The *Sphagnum* bog was, at ~6100 cal. yrs. BP, relatively young compared to the cushion bog, where peat growth initiated ~11,100 cal. yrs.

BP typical for Patagonian peatlands (Yu et al., 2010; Borromei et al., 2014). However, other parts of the *Sphagnum* bog have been shown to be deeper with peat accumulation starting 13,500 cal. yrs. BP (Borromei et al., 2016). Mean PAR reported here for both bogs was with 0.71 mm yr^{-1} high compared to the range of magnitude reported from Chilean *Sphagnum* bogs with 0.45–0.13 mm yr^{-1} (Biester et al., 2003; Mathijssen et al., 2019), from a Patagonian cushion bog with 0.31–0.77 mm yr^{-1} (Björck et al., 2012) or compared to northern peatlands with <0.5 mm yr^{-1} (Turunen et al., 2001).

4.4. Recent accumulation of peat, carbon and nitrogen

RERCA in the *Sphagnum* bog (63.8 g C m^{-2} yr^{-1}) was substantially higher compared to CAR and comparable to rates reported from Chilean *Sphagnum* bogs (up to 87.1 g C m^{-2} yr^{-1}, León and Oliván, 2014; Bunsen and Loisel, 2020). RERNA (0.40 g N m^{-2} yr^{-1}) was similar to NAR and was at the lower end of the range reported from the Chilean bog of the latter study (0.15–2.37 g N m^{-2} yr^{-1}, León and Oliván, 2014). Compared to a Canadian bog (1.4–3.2 g N m^{-2} yr^{-1}; Turunen et al., 2004), RERNA was notably lower, possibly due to the lower N deposition rates.

RERCA and RERNA in the cushion bog (245.4 g C m^{-2} yr^{-1} and 4.69 g N m^{-2} yr^{-1}) highly exceeded CAR and NAR, were higher than those rates reported from northern and southern *Sphagnum* bogs (Turunen et al., 2004; León and Oliván, 2014) and agreed with previous findings in cushion bogs (RERCA: 219 g C m^{-2} yr^{-1}; Hribljan et al., 2016). An about four-times higher cushion bog RERCA compared to the *Sphagnum* bog agrees well with findings of present-day net ecosystem exchange determined by eddy covariance measurements at these sites (Holl et al., 2019). The higher RERCA and RERNA compared to the *Sphagnum* bog can be explained by differences in the elemental concentrations between mosses and vascular plants, in particular regarding N and P, as well as the higher productivity of vascular plants (Olid et al., 2014; Gavazov et al., 2017). In addition to high mineralization rates, the biological N$_2$ fixation potential in peat below *A. pumila* (Knorr et al., 2015) provides another explanation for the notably higher RERNA, also compared to NAR in the cushion bog.

4.5. Within-site variability of decomposition patterns as compared between Sphagnum bogs and cushion bogs: C/N ratios and humification index

As expected, C/N ratios were generally negatively correlated with the humification index (Table A.3) indicating ongoing decomposition of the peat. The range of C/N ratios (Table 2) was comparable to those values reported previously for Patagonian bogs (Biester et al., 2003; Kleinebecker et al., 2008; Broder et al., 2012; Mathijssen et al., 2019). The consistent decrease in C/N ratios throughout all time periods in the order SB_LWN > SB_HMK > CB_SPH_LWN > CB_AST_LWN, except for the young time period with higher C/N ratios in SB_HMK compared to SB_LWN profiles (Table 2), pointed to very local factors effective for the decomposition rate over long periods of time. Overall, the difference in C/N ratios between both bogs rather reflected higher long-term decomposition rates in the cushion bog than differences in the peat source material as throughout most of the time the vegetation in both bogs was dominated by one peat moss species, *S. magellanicum*, as typical for Patagonian bogs (Kleinebecker et al., 2007; Fritz et al., 2012; Loisel and Yu, 2013, Fig. 2). However, the pronounced variability in C/N ratios and the humification index in cushion bog profiles, might be explained by the generally more diverse plant macrofossil records compared to the *Sphagnum* bog (Fig. 2).

Apart from vegetation effects, the local climate affected decomposition and therefore peat, C and N accumulation in both bogs. Due to its more coastal setting compared to the *Sphagnum* bog, the cushion bog was supposedly exposed to more rapid changes in precipitation and wind force patterns and thus nutrient input through sea spray or water table fluctuations affecting decomposition (Biester et al., 2004)

and may also have led to discontinuous tephra layers (Watson et al., 2015). Nutrient input through sea spray, in addition to tephra, was indicated by elemental concentrations in the peat (Table 3). Sea spray deposition may have resulted in higher long-term average decomposition rates as already hypothesized for oceanic cushion bogs in Chile (Kleinebecker et al., 2008; Broder et al., 2012) and as suggested by lower C/N ratios (Table 2), a higher FTIR-derived humification index and the pronounced temporal variations in these decomposition indicators (Fig. 4) compared to the *Sphagnum* bog. However, higher decomposition rates in the cushion bog did not result in generally lower accumulation rates. Therefore, parts of our second hypothesis, that long-term decomposition patterns in both bog types are similar, could not be confirmed.

4.6. Within-site variability of decomposition patterns as compared between Sphagnum bogs and cushion bogs: stable isotopes of C and N

Carbon isotopic signatures were in a narrow range comparable to other Patagonian bogs (Fig. 5a-c, Broder et al., 2012), and differed only slightly among the *Sphagnum* and cushion bog. In contrast, N isotopic signatures varied more pronounced (Fig. 5d-f), also compared to the Patagonian bogs studied by Broder et al. (2012). With a mean of −2.87‰ N istopic signatures were substantially more depleted in $\delta^{15}N$ in the *Sphagnum* bog compared to the cushion bog (mean of −0.95‰) pointing to a notable contribution of biological nitrogen fixation to N supply (Knorr et al., 2015). Mean $\delta^{15}N$ signatures also became more depleted in the order CB_AST_LWN > CB_SPH_LWN > SB_LWN throughout all time periods (Table 2). This pattern may partly reflect past dominant plant species as the intermediate time period with high presence of *T. magellanicum* in the CB_AST_LWN-2 profile (Fig. 2c) showed even a slightly positive $\delta^{15}N$ signature. Other plant functional types, except for grasses such as *T. magellanicum*, have a negative ^{15}N signature in their biomass (Kleinebecker et al., 2009).

Peat deposited during the young time period in CB_AST_LWN profiles showed a rapid decrease in the $\delta^{13}C$ and increase in the $\delta^{15}N$ signature (Fig. 5c, f). Such pattern was expected for an increasing degree of decomposition with increasing peat age (Asada et al., 2005; Krüger et al., 2017) and points to the intense decomposition in the rhizosphere of *A. pumila*. Stable C isotopic signatures obtained from peat under anaerobic conditions are expected to decrease with peat age due to an enrichment of recalcitrant organic matter which is depleted in [13]C (Alewell et al., 2011; Krüger et al., 2017; Drollinger et al., 2020). However, decomposition affected by root oxygen release to the rhizosphere as observed in *A. pumila* peat (Fritz et al., 2011; Münchberger et al., 2019) should result in stable C signatures increasing with peat age (Krüger et al., 2017; Drollinger et al., 2020). But such oxygenation effect on decomposition was not visible in the $\delta^{13}C$ signatures.

Contrary to the $\delta^{13}C$ signature, decomposition should result in an enrichment of the heavier ^{15}N isotopes in the isotopic signature, as microbes prefer to take up lighter ^{14}N isotopes while heavier isotopes remain in the peat (Broder et al., 2012). As the $\delta^{15}N$ signature did not show this expected pattern, except for the peat deposited during the young time period in CB_AST_LWN profiles, it may reflect fractionation processes more related to N-mineralization and recycling instead of solely decomposition processes (Biester et al., 2014). The enrichment in the $\delta^{15}N$ signature throughout the young period in peat of CB_AST_LWN profiles caused by intense decomposition (Asada et al., 2005; Krüger et al., 2017) together with the dominance of *T. magellanicum* throughout the intermediate time period might explain $\delta^{15}N$ enrichment of CB_AST_LWN profiles compared to CB_SPH_LWN and SB_LWN profiles. Apart from this well-recognizable effect of the dominant plant species (i.e. *A. pumila*) on the isotopic signatures that confirmed our third hypothesis, we did not observe any clear indications of the vegetation shifts in the isotopic signatures. Furthermore, relationships between isotopic signatures and decomposition indicators were not straightforward. From this it can be concluded that the $\delta^{15}N$

signature can be interpreted as a proxy for decomposition only if the effect of decomposition is very pronounced, such as in our example with accelerated decompositon due to intensive root activity of *A. pumila* (Fritz et al., 2011; Münchberger et al., 2019).

Right below the *A. pumila* rooting boundary, which coincided with the age of the vegetation change at 1600 cal. yrs. BP, the $\delta^{13}C$ signatures become less negative (Fig. 5c), $\delta^{15}N$ signatures become more negative (Fig. 5f) and the C/N ratios increase (Fig. 4d). These trends of the decomposition indicators point to less decomposed peat with depth right below the *A. pumila* rooting boundary. So, there is even some evidence that the deepest *A. pumila* roots penetrated and decomposed the older, underlying *Sphagnum* peat.

5. Conclusion

The vegetation composition had a crucial importance in driving C accumulation at both study sites. However, the shift from a fen to a bog system at both sites was not recognizable from decomposition indicators, as ongoing peat decomposition masked the effects of the various plant communities on the decomposition indicators. Contrary to this, the shift towards a dominance of cushion plants affected all investigated peat characteristics. This vegetation shift was presumably triggered by tephra deposition enhancing nutrient supply, in particular of P. Despite average RERCA during the past decades being distinctly higher in the cushion bog compared to the *Sphagnum* bog, CAR substantially decreased since the appearance of the cushion plants. The higher primary productivity of cushion plants may not be able to compensate for the extremely high decomposition rates of litter and peat in the rhizosphere on a longer time scale. So, while vascular cushion plants do not reduce the C sink strength of bogs, they store high amounts of N despite their high decomposition rates. Our study confirms the relevance of Patagonian peatlands as important long-term carbon sinks in the Southern Hemisphere and reveals a high N sink capacity of cushion bogs.

Data availability

The data can be accessed by email request to the corresponding authors.

CRediT authorship contribution statement

CB, TK, KHK and WS designed the study. WS, CB, TK and VAP conducted field work and sample analyses with the help of KHK. MG provided plant macrofossil analyses and WB performed the sample preparation routine for radiocarbon dating. WS performed data analyses and prepared the manuscript with contributions from KHK, TK, MG, WB and VAP.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2021.151293.

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