Zero to moderate methane emissions in a densely rooted, pristine Patagonian bog - biogeochemical controls as revealed from isotopic evidence

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Abstract. Peatlands are significant global methane (CH_4) sources, but processes governing CH_4 dynamics have been predominantly studied on the northern hemisphere. Southern hemispheric and tropical bogs can be dominated by cushion-forming vascular plants (e.g. *Astelia pumila*, *Donatia fascicularis*). These cushion bogs are found in many (mostly southern) parts of the world but could also serve as extreme examples for densely rooted northern hemispheric bogs dominated by rushes and sedges. We report highly variable summer CH_4 emissions from different microforms in a Patagonian cushion bog as determined by chamber measurements. Driving biogeochemical processes were identified from pore water profiles and carbon isotopic signatures. An intensive root activity throughout a rhizosphere stretching over 2 m depth accompanied by molecular oxygen release created aerobic microsites in water-saturated peat leading to a thorough CH_4 oxidation (< 0.003 mmol L^{-1} pore water CH_4, enriched δ^{13}C-CH_4 by up to 10‰) and negligible emissions (0.09 ± 0.16 mmol CH_4 m^{-2} d^{-1}) from *Astelia* lawns. In sparsely or even non-rooted peat below adjacent pools similar pore water profile patterns as obtained under *Astelia* lawns were found which emitted very few amounts of CH_4 (0.23 ± 0.25 mmol m^{-2} d^{-1}). Below the *A. pumila* rhizosphere pore water concentrations increased sharply to 0.40 ± 0.25 mmol CH_4 L^{-1} and CH_4 was predominantly produced by hydrogenotrophic methanogenesis. Few *Sphagnum* lawns and – surprisingly – one lawn dominated by cushion-forming *D. fascicularis* were found to be local CH_4 emission hot spots with up to 1.52 ± 1.10 mmol CH_4 m^{-2} d^{-1} presumably as root density and molecular oxygen release dropped below a certain threshold. The spatial distribution of root characteristics supposedly causing such pronounced CH_4 emission pattern was evaluated on a conceptual level aiming to exemplify scenarios in densely rooted bogs. We conclude that presence of cushion vegetation as a proxy for negligible CH_4 emissions from cushion bogs needs to be

interpreted with caution. Nevertheless, overall ecosystem CH_4 emissions at our study site were probably minute compared to bog ecosystems worldwide and widely decoupled from environmental controls due intensive root activity of e.g. *A. pumila*.

1 Introduction

Peatland ecosystems are significant natural methane (CH_4) sources on the global scale responsible for about 10% of global annual CH4 emissions (Aselmann and Crutzen, 1989; Mikaloff Fletcher et al., 2004). CH_4 has a 28-fold higher global warming potential over a 100-year time horizon compared to carbon dioxide (CO_2) (IPCC, 2014) and, thus, processes governing CH_4 dynamics in peatlands receive much attention to estimate global greenhouse gas emissions.

The slowdown of decomposition and accumulation of C in rainwater-fed peatlands (bogs) results from e.g. a high water table, anoxic conditions, recalcitrant peat forming litter, low temperatures, inactivation of oxidative enzymes and an accumulation of decomposition end-products (Beer and Blodau, 2007; Limpens et al., 2008; Bonaiuti et al., 2017). Once methanogenic conditions are established, CH_4 production is mainly controlled by substrate supply of labile organic matter (Hornibrook et al., 1997; Whalen, 2005). Then, slow diffusive transport along the concentration gradient from deep anoxic peat layers to the atmosphere leads to CH_4 release. In upper, unsaturated and oxic peat zones that typically extent only about few decimetres (Whalen, 2005; Limpens et al., 2008), CH_4 might get consumed by methanotrophic microbes (Chasar et al., 2000; Whalen, 2005; Berger et al., 2018). Consequently, water table position and fluctuations strongly control the amount of emitted CH_4 (Blodau and Moore, 2003; Whalen, 2005). While CH_4 oxidation suppresses CH_4 emissions in diffusion dominated systems, ebullition by fast release of gas bubbles or plant-mediated transport by aerenchymatic roots can substantially increase CH_4 emissions (Fechner-Levy and Hemond, 1996; Joabsson et al., 1999 and references therein; Chasar et al., 2000; Colmer, 2003; Whalen, 2005; Knoblauch et al., 2015; Burger et al., 2016; Berger et al., 2018). With a high share of ebullitive fluxes, vegetated or open water pools in peatlands are considered as strong CH_4 emitters (Hamilton et al., 1994; Blodau 2002; Burger et al., 2016) that have, however, received less attention than the vegetated surfaces (Pelletier et al., 2014). Pools can even turn the peatlands' C balance into a source (Pelletier et al., 2014), but examples of low emission pools have been also reported (Knoblauch et al., 2015).

Carbon isotopic signatures ($\delta^{13}C$) are a valuable tool for identifying mechanisms and pathways of CH_4 dynamics. Carbon isotopic signatures in pore water of northern hemispheric bogs (hereafter termed northern bogs) vary typically between -80 to -50‰ and -25 to +10‰ for CH_4 and CO_2, respectively (e.g. Whiticar et al., 1986; Hornibrook et al., 1997; Chasar et al., 2000; Hornibrook et al., 2000; Beer et al., 2008; Steinmann et al., 2008; Corbett et al., 2013). Depending on the available substrate for methanogenesis, it was mostly observed that either the acetoclastic or hydrogenotrophic pathway predominates, resulting in distinctive carbon isotope signatures of CH_4 (acetate fermentation $\delta^{13}C$-CH_4 ~ -65 to -50‰, CO_2 reduction $\delta^{13}C$-CH_4 ~ -110 to -60‰) (Whiticar et al., 1986). Methane is prevailingly produced by acetoclastic methanogenesis when fresh, labile organic matter is available whereas the production pathway shifts towards hydrogenotrophic methanogenesis when organic matter becomes increasingly recalcitrant (Hornibrook et al., 1997; Popp et al., 1999; Chasar et al., 2000; Conrad, 2005). A predominance of the latter pathway is indicated by strong fractionation between $^{12}C/^{13}C$ resulting in relatively depleted $\delta^{13}C$-

CH_4 corresponding to a fractionation factor α_c between 1.055 and 1.090 (Whiticar et al., 1986) and a $\delta^{13}C$-CH_4 isotopic signature following that of $\delta^{13}C$-CO_2 (Hornibrook et al., 2000). Subsequent methanotrophy alters the isotopic signature of CH_4 by discriminating against ^{13}C and the residual CH_4 remains enriched while produced CO_2 becomes depleted in ^{13}C (Chasar et al., 2000; Popp et al., 1999). As both, acetoclastic methanogenesis and methanotrophy, result in a $\delta^{13}C$-CH_4 signature enriched

5 in ^{13}C and a small apparent fractionation factor (Whiticar et al., 1986; Conrad, 2005), the acetoclastic pathway cannot be clearly separated from methanotrophic conditions based on carbon isotopes only (Conrad, 2005).

The majority of studies elucidating CH_4 dynamics in peatlands have been conducted on the northern hemisphere (e.g. Blodau, 2002; Limpens et al., 2008; Yu, 2012 and references in these), whereas only little research deals with CH_4 dynamics in bogs on the southern hemisphere (hereafter termed southern bogs) (Broder et al., 2015). Contrary to northern bogs, southern bogs

10 are not only vegetated by *Sphagnum* mosses, dwarf shrubs or few graminoids such as the rush-like species *Tetroncium magellanicum*, but also by vascular plants (Kleinebecker et al., 2007) that can densely root upper peat layers (Fritz et al., 2011; Knorr et al., 2015). Another feature that can be found in both systems are pools with sparse or no vegetation (Fritz et al., 2011; González Garraza et al., 2018). The vascular plants, for instance of the genus *Astelia* (Asteliaceae), *Donatia* (Stylidiaceae) or *Oreobolus* (Cyperaceae), independently developed a cushion life form to protect from harsh climate in cold environments

15 (Gibson and Kirkpatrick, 1985; Boucher et al., 2016). Bogs dominated by cushion-forming vascular plants (hereafter termed cushion bogs) can be found in many (mostly southern) parts of the world, for instance all along the high Andes (Coombes and Ramsay, 2001; Benavides et al., 2013; Fonkén, 2014) down to southernmost Patagonia (Ruthsatz and Villagran, 1991; Heusser, 1995; Kleinebecker et al., 2007; Grootjans et al., 2014), in highlands of eastern Africa (Dullo et al., 2017) as well as in New Guinea (Hope, 2014), New Zealand and Tasmania (Gibson and Kirkpatrick, 1985; Ruthsatz and Villagran, 1991) and some

20 sub-Antarctic islands (Ruthsatz and Villagran, 1991). These cushion bogs could also be regarded as extreme examples for densely rooted northern bogs that are dominated by rushes and sedges.

To our knowledge, only two studies reported CH_4 emissions from southern vascular-plant dominated bogs with quite inconsistent results. Over a New Zealand bog dominated by the evergreen "wire rush" *Empodisma robustum*, CH_4 emissions exceeded those commonly reported from northern bogs (Goodrich et al., 2015), while emissions from a Patagonian cushion

25 bog dominated by *Astelia pumila* were negligible (Fritz et al., 2011). Both, high and negligible CH_4 emissions, were mainly explained by the extensive aerenchymous roots of the prevailing plant species: The aerenchyma might function as a conduit for CH_4 from deep peat layers to the atmosphere in the first case, whereas in the second case pronounced O_2 supply by roots might have resulted in a thorough oxidation of pore water CH_4 and enhanced organic matter decomposition. However, Fritz et al. (2011) were the first to investigate CH_4 dynamics below *Astelia* lawns and determined emissions only sporadically without

30 considering all predominant microforms and plant communities. Thus, general conclusions about CH_4 emissions from this type of ecosystem are so far restricted. Furthermore, more knowledge on biogeochemical processes throughout the peat column of *Astelia* lawns as a model plant for cushion-forming, aerenchymous plants and in other microforms is needed to extent our limited understanding of these first insights into CH_4 dynamics in cushion bogs. Despite the variety of bogs dominated by densely rooted, aerenchymous plants on the northern and southern hemisphere, there is some evidence from latest research

that very low CH_4 pore water concentrations could be a more common phenomenon in those ecosystems (Dullo et al., 2017; Agethen et al., 2018; Knorr et al., 2015). In general, promotion or suppression of CH_4 production should be determined by the ratio of root density and activity associated with O_2 release versus presence of labile root organic matter or exudates accompanied with O_2 consumption (Blodau, 2002; Agethen et al., 2018).

5 Here, we quantified austral summer CH_4 emissions from dominant microforms in a Patagonian cushion bog and examined possible environmental and biogeochemical controls. We hypothesized that (I) emissions from cushion plant vegetation dominated by *Astelia pumila* or *Donatia fascicularis* are negligible while pools and *Sphagnum* lawns emit CH_4 in considerable amounts, and that (II) pore water CH_4 and DIC concentration profiles and its carbon isotopic signatures below densely-rooted *Astelia* lawns reflect a distinct CH_4 oxidation effect contrary to sparsely- or even non-rooted peat below pools, and that (III)

10 besides by methanotrophy, isotopic composition of pore water CH_4 could also be affected by a predominance of acetoclastic methanogenesis throughout the rhizosphere of *Astelia* lawns shifting towards CO_2 reduction with peat depth and in sparsely- or even non-rooted peat below pools. Biogeochemical controls of CH_4 emissions from *Sphagnum* lawns were not subject of this study, as they have been intensively studied in northern bogs (e.g. Hornibrook et al., 1997; Beer and Blodau, 2007; Steinmann et al., 2008; Corbett et al., 2013) and even southern bogs with mixed vegetation in absence of notable cushion plant

15 coverage (Broder et al., 2015).

2 Material and Methods

2.1 Description of the study site

The study was conducted at a cushion bog on the Peninsula Mitre in southernmost Patagonia, Tierra del Fuego (Moat, 54°58'S, 66°44'W, Fig. 1). Peatlands of the Peninsula Mitre provide the nowadays rare opportunity to study carbon dynamics under

20 pristine conditions as they can be considered as largely undisturbed by human activities such as drainage, agriculture or elevated atmospheric nitrogen deposition (Kleinebecker et al., 2008; Fritz et al., 2011; Grootjans et al., 2014; Paredes et al., 2014). About 45% of this area are covered by peatlands (Iturraspe, 2012) while little is known about these ecosystems because of their poor accessibility (Iturraspe, 2012). The study site at Moat belongs to a complex system of sloping mires, blanket bogs, fens and – in coastal areas - cushion bogs (Iturraspe, 2012; Borromei et al., 2014). The studied cushion bog is located in

25 exposed proximity to the Beagle channel with harsh winds (Grootjans et al., 2014) resulting in an oceanic climate with average daily temperatures of 6°C and annual precipitation of 500 mm (Fritz, 2012).

Large areas of the cushion bogs in Moat are characterized by a comparatively flat micro-relief and covered by the cushion-forming plants *Astelia pumila* and *Donatia fascicularis*. The vegetation of the studied bog is composed of a mosaic of different plant communities characterized by specific plant species with lawns of *A. pumila* being the prevailing microform. *Sphagnum*

30 *magellanicum* or *D. fascicularis* grow in small lawns (patches of few square meters) at pool margins where *S. magellanicum* supposedly benefits from protection against desiccation. *Tetroncium magellanicum*, a rush-like herb that does not form cushions but presumably establishes aerenchymous roots as it tolerates inundation (von Mehring, 2013), is associated

predominantly with *Sphagnum* lawns but also with *Astelia* and *Donatia* lawns or sporadically inhabits pools. These sparsely vegetated pools of different size (< 0.5 m² - ~10 m²) and ~0.5 m depth are embedded in *Astelia* lawns. Pool sediments are inhabited by cyanobacteria (Arsenault et al., 2018; González Garraza et al., 2018) and submerged *Sphagnum* mosses such as *Sphagnum cuspidatum* (Kleinebecker et al., 2007; Kip et al., 2012). Peat formation started ~11000 years ago (Borromei et al.,

5   2014), and previously, the bog was dominated by *S. magellanicum* while *A. pumila* invaded the area around 2600 years before present as determined by pollen analyses (Heusser, 1995). The peat below *Astelia* lawns is densely rooted with on the average 2.15 g DW L of peat^{-1} down to 1.7 m (Fritz et al., 2011). Mean root lifetimes of *A. pumila* has been estimated to be ~3-4 years indicating a high root turnover (Knorr et al., 2015).

2.2 Sampling and analysis of solid peat and root biomass

10   Peat coring in *Astelia* and *Sphagnum* lawns (data not shown) was done using a Russian peat corer (Eijkelkamp Agrisearch Equipment, Giesbeek, the Netherlands) down to a maximum depth of 7.5 m in *Astelia* lawns. Roots of *A. pumila* in *Astelia* lawn cores were sorted out and treated separately. The density of *D. fascicularis* root biomass was determined by cutting three 0.1 x 0.1 m sods down to a depth of 0.4 m. Peat and root biomass samples were oven dried at 70°C until constant weight to calculate peat bulk density and porosity as well as *D. fascicularis* root density. Total C and N contents together with abundance

15   of ^{15}N and ^{13}C in the solid peat were determined using an elemental analyser (EA 3000, EuroVector, Redavalle, Italy) connected to an isotope ratio mass spectrometer (IRMS, NU instruments, Wrexham, UK).

2.3 Environmental variables

Environmental variables were determined during two measurement campaigns in 2015 and 2016 at half-hourly intervals. Photosynthetic active radiation (PAR, HOBO S-LIA-M003, Onset, USA, up to 2500 µmol m^{-2} s^{-1}) and air temperature (HOBO

20   S-TMB-M0x, Onset, USA) were recorded by a weather station (HOBO U30 NRC, Onset, USA) in both years during austral summer months. Water table fluctuations at two replicate sites in *Astelia* lawns (Levelogger Edge 3001 and Barologger Edge, Solinst, Canada; both installed in perforated PVC tubes) and soil temperature in four depths of 0.05, 0.1, 0.3 and 0.5 m (HOBO TMCx-HD and HOBO U-12-008, Onset, USA) were measured continuously.

2.4 Chamber measurements and analyses of soil-atmosphere CH$_4$ fluxes

25   **2.4.1 Field measurements**

The closed chamber technique was used to determine CH$_4$ fluxes during two measurement campaigns in austral summer from December 2014 to March 2015 and in February and March 2016. One week prior to measurements, PVC collars with a height of 0.2 m were permanently installed ~0.15 m into the peat of the dominant microforms characterized by a specific plant species

and a particular plant community (*Astelia* lawns: 2015 N = 3, 2016 N = 5; *Sphagnum* lawns: 2015 N = 3, 2016 N = 5; *Donatia* lawns: 2016 N = 3). The exact installation depth and the micro-relief of the surface within each collar was determined repeatedly to calculate the exact headspace volume for CH_4 flux estimation. The collars were equally arranged around three wooden platforms constructed in January 2014 to minimize disturbance during measurements and distributed over the study site to account for spatial variability. Different numbers of replicates between the two campaigns and the different microforms are the result of logistical constraints.

A cylindrical, transparent chamber with a basal area of 0.13 m^2 and a height of 0.4 m was used for soil-atmosphere flux measurements. The chamber was equipped with a fan to ensure mixing of the headspace air, a PAR sensor (HOBO S-LIA-M003, Onset, USA) and a temperature sensor (HOBO S-TMB-M0x, Onset, USA). A second temperature sensor recorded ambient temperature (HOBO S-TMB-M0x, Onset, USA) and all sensor data were logged in 1s-intervals to a data logger (HOBO U30 NRC, Onset, USA). This set-up allowed us to control air temperature inside the chamber within approximately 3°C deviation of the ambient air temperature. If necessary, ice packs were installed inside the chamber to avoid temperature increase. Due to strong wind conditions we decided against the installation of a vent tube. An opening in the top of the chamber avoided overpressure during chamber placement. This opening was closed immediately after the chamber was gently placed on a collar for at least 3 minutes to conduct measurements. Collars were equipped with a water-filled rim to ensure a gas-tight seal between chamber and collar during measurements. Pool fluxes were performed with a floating chamber of identical dimension and design on four pools located at each platform. The chamber wall extended approximately 0.04 m into the water during measurements.

All measurements were performed under a broad range of irradiance between 7:00 am to 22:00 pm (local time) to determine diurnal variations in CH_4 fluxes. At least once during each sampling period of two to three consecutive days, all selected microforms and pools were measured under dark conditions. Opaque, reflective material was used to cover the chamber for dark conditions. Measurements were taken every two weeks during the first campaign in 2015 (N = 405 measurements) and during two occasions in 2016 (N = 132 measurements). A more regular measurement routine throughout the whole season was constrained by harsh weather conditions and the remoteness of our study site.

The chamber was connected by a 2 mm inner diameter polyethylene tubing to a gas analyser (Los Gatos Ultraportable Greenhouse Gas Analyser 915-001, Los Gatos Research) to record the increase of CH_4 concentrations over time at a rate of 1 hz. Between measurements, atmospheric background concentrations were achieved inside the chamber. The gas analyser was equipped with an external pump providing a flow rate of 2 L min^{-1} and pumping the analysed gas back to chamber creating a closed system. Prior to each campaign, the instrument was recalibrated.

We estimated the cover of plant species within each collar to the nearest 5% and counted the number of *T. magellanicum* shoots to further characterize the different microforms (Table 1). In 2015, vegetation surveys were conducted at the beginning and at the end of the measurement campaign. Since no change in vegetation was observed, surveys were conducted only once during the campaign in 2016. For each collar, the position above the water table was determined once during each sampling

period of consecutive days to account for different positions in the micro-relief and to determine a specific water table position. Additionally, we determined the area of each individual microform patch in which a collar had been installed.

2.4.2 CH₄ flux calculation and statistical analyses

Soil-atmosphere CH_4 fluxes were calculated from the gas concentration increase over time within the chamber using the software package (MATLAB Release R2015a) routine described in Eckhardt and Kutzbach (2016) and Kutzbach et al. (2007). Gas concentration was modelled either as a linear or an exponential function of time. Models performance was compared using Akaike's Information Criterion (AIC) as a measure of goodness-of-fit. This routine resulted in 90% of cases in a linear function of time (N = 485) and in 10% of cases in an exponential function of time (N = 52).

We visually inspected all concentration increases over time and none of the measurements showed a stepwise concentration increase indicative of ebullient events. Of the 3 minutes measurement time, 50 - 180 s (mostly around 90 s) were selected for the CH_4 flux calculation to exclude unstable conditions due to e.g. chamber placement particularly at the beginning of the measurement. Fluxes with a slope not significantly different from 0 (tested with an F-Test, $p > 0.05$) were set to zero (20% of cases, N = 105).

Normal distributions of CH_4 flux datasets were checked by a Kolmogorov-Smirnov test. Due to non-normality, the Kruskal-Wallis analysis of variance followed by multiple comparison U-tests adjusted by the Bonferroni method were applied to determine significant differences between CH_4 fluxes of different microforms and collars. The relationships between CH_4 fluxes and environmental variables (soil temperature, water table depth fluctuations) as well as additional features of individual collars were evaluated by Spearman's rank correlation (Table 2). A response of CH_4 emissions to the investigated environmental variables was identified only for a few individual collars. Therefore, no seasonal or annual ecosystem emissions were calculated. Statistical analyses were performed using Matlab (MATLAB Statistics Toolbox Release R2017a). All flux data were reported as mean ± standard deviation.

2.5 Depth profiles of peat pore water concentrations

2.5.1 Sampling and field measurements

Multilevel piezometers (MLP), as described in Beer and Blodau (2007), were installed during both measurement campaigns in austral summer 2015 and 2016 to determine pore water concentrations in depth profiles. The MLPs provided a spatial sampling resolution of either 0.1 or 0.2 m and were equipped with diffusive equilibration samplers made of permeable silicone tubes providing 4 mL gas sample volume together with a 5 mL crimp-vial filled with deionized water and covered with a permeable membrane (Supor-200 0.2 μ, Pall corporation, Pall life sciences). To collect gas samples, MLPs were stepwise retrieved and the gas volume extracted from the equilibration sampler with a 3 mL syringe was transferred into nitrogen-flushed 5 mL crimp vials. The crimp vials were capped with a butyl stopper with an aluminium crimp seal. MLPs were installed in *Astelia* lawns and pools in three replicates at each platform where closed chamber measurements were performed.

In January 2015, MLPs were installed in *Astelia* lawns (0.2 m resolution, 2 m depth) and pools (0.1 m resolution 0-1 m, 0.2 m resolution below down to a maximum depth of 4 m) for five weeks equilibration time. From gas samples pore water concentrations of CH_4, dissolved inorganic carbon (DIC) and hydrogen (H_2) were determined. To measure sulfate concentrations, a potential electron acceptor originating from sea spray and affecting competitiveness of methanogenesis

5 (Broder et al., 2015), a pore water subsample obtained from each crimp-vial was transferred to a storage vial and stored frozen until analysis. An aliquot of each remaining pore water sample was measured in-situ with a pH/EC-meter (Combo HI 98129/130, Hannah instruments, Germany).

In January 2016, MLPs were installed to a depth of 3 m in pools (resolution as in 2015) for three weeks equilibration time and afterwards again in *Astelia* lawns (0.1 m resolution in transition zone from rooted to non-rooted peat in 1-2 m depth) for nine

10 weeks of equilibration time. In 2016, equilibration samplers were used to collect CH_4 and CO_2 samples and determine their carbon stable isotopic signatures. Pore water samples obtained from crimp-vials were used to measure O_2 concentrations in-situ with a planar trace oxygen minisensor (Fibox 3, Presens, Germany).

2.5.2 Analytical procedures

Gas samples were transported to Germany and analysed within four weeks. Gaseous CH_4 and CO_2 concentrations were

15 measured with a gas chromatograph (8610C, SRI Instruments, USA) equipped with a methaniser and flame ionization detector (FID). Hydrogen concentrations were analysed on a H_2-Analyzer (Ametek TA 3000 H_2 Analyser, Trace Analytical TA 3000r). Sulfate concentrations were obtained by ion chromatography (883 Basic IC plus, Metrohm, Herisau, Switzerland). Stable carbon isotopic signatures of CH_4 and CO_2 were simultaneously determined by Cavity Ring-Down Spectroscopy (CRDS; Picarro G2201-I connected to a small sample isotope module (SSIM, model A0314), Picarro Inc., USA). As this set-

20 up required a minimum sample volume of 20 mL, samples were diluted with nitrogen prior measurements. The instrument was calibrated in the beginning of every measurement day using two working standards of CH_4 (1000 ppm, -42.48‰) and CO_2 (1000 ppm, -31.07‰). Isotopic signatures are given in δ-notation relative to Vienna Peedee belemnite (VPDB). As samples were stored for several weeks and $\delta^{13}C$-CO_2 values were biased in case of high CH_4 concentrations in the sample, a correction procedure was applied following Berger et al. (2018).

25 ### 2.5.3 Calculations and statistical analyses

Pore water concentrations of CH_4, dissolved inorganic carbon (DIC) and H_2 were re-calculated from gaseous concentrations obtained from equilibration samplers by applying Henry's law following Eq. (1):

$$c = K_H * p \hspace{6cm} (1)$$

where c is the concentration in mol L^{-1}, p the pressure in atm and K_H the Henry-constant that was corrected according to Sander

30 (1999) for mean soil temperatures of 10°C in February 2015 and 2016 as well as 7°C in April at a depth of 0.5 m. DIC

concentrations at prevalent pH conditions were calculated with respect to carbonate speciation considering equilibrium constants following Stumm and Morgan (1996). All pore water data were reported as mean ± standard deviation (N = 3).

Zones of CH_4 production and consumption in the peat column were visually identified based on observed pore water concentration gradients. For a quantitative evaluation of pore water concentration gradients, steady-state conditions as well as a dominance of diffusive gas transport would have to be assumed; this may only partly apply to the system under study here, given the large root biomass. Nevertheless, we additionally applied a software routine using inverse modelling (PROFILE, Berg et al., 1998) for zone identification. This modelling approach supported the results obtained visually, but provided further rough estimates for production and consumption zones due to the complex diffusivity in the rhizosphere of highly rooted peat and, thus, results are presented in the appendix only.

An apparent isotopic fractionation factor α_c was determined (Whiticar et al., 1986; Hornibrook et al., 2000) to assess the predominant methanogenic pathway and / or methanotrophic activity following Eq. (2):

$$\alpha_c = \frac{\delta^{13}C_{CO_2} + 1000}{\delta^{13}C_{CH_4} + 1000} \tag{2}$$

3 Results

3.1 Characteristics of solid peat and root biomass

Roots of *A. pumila* were present in the upper profile down to a depth of 1.8 m (rhizosphere) in *Astelia* lawn cores. Throughout the rhizosphere, we observed a highly decomposed and amorphous peat supposedly originating from *A. pumila* that developed above *Sphagnum* peat. Peat below *Sphagnum* lawns was continuously formed predominantly by *Sphagnum*. Total C and N contents in the peat together with natural abundance of ^{15}N and ^{13}C are given in Table 3. Root density of *D. fascicularis* was 0.014 ± 0.010 g DW L of peat^{-1} at 0.35 m depth while root density of *A. pumila* was not determined once again as it has been already quantified with > 4 g DW L of peat^{-1} in around 0.5 m depth (Fritz et al., 2011).

3.2 Environmental conditions and potential controls on CH₄ fluxes

The study site was characterized by daily mean PAR values up to ~700 µmol m^{-2} s^{-1} with maximum values exceeding 2000 µmol m^{-2} s^{-1} and daily mean air temperatures ranging from -0.5°C to 17°C during the measurement campaigns in austral summer from January to April (Fig. 2). Soil temperature in summer reached maximum daily average values of 15°C and 12°C at 0.05 m depth and 0.5 m depth, respectively. Concurrently, the water table fluctuated close to the surface between -0.03 m and -0.23 m and differed consistently about few centimetres between the two water table measurement sites in *Astelia* lawns. CH_4 fluxes approached zero in many cases, but differed significantly from zero down to absolute values of 0.01 mmol CH_4 m^{-2} d^{-1}. Fluxes below absolute values of 0.01 mmol CH_4 m^{-2} d^{-1} did not differ significantly from zero and were therefore set to zero. For collars exhibiting low magnitude fluxes neither seasonal trends (data not shown) nor a relationship to water table and

soil temperature fluctuations could be identified (Table 2). Yet, significant relationships between water table fluctuations or variations in soil temperatures were established for those few lawns with considerable emissions (Table 2).

3.3 Soil-atmosphere CH$_4$ fluxes and features of microforms possibly affecting CH$_4$ emissions

Summer CH$_4$ emissions in a South Patagonian cushion bog were highly variable among the dominant microforms *Astelia* lawns, *Sphagnum* lawns and *Donatia* lawns characterized by specific plant species as well as pools and showed a pronounced spatial pattern even within microforms. Compared to all other microforms, only *Sphagnum* lawns showed considerable emissions with 1.52 ± 1.10 mmol CH$_4$ m^{-2} d^{-1} while *Astelia* lawns emitted nearly no CH$_4$ with 0.09 ± 0.16 mmol m^{-2} d^{-1} (Fig. 3). Methane emissions from pools were also low (0.23 ± 0.25 mmol m^{-2} d^{-1}) and not significantly different from intermediate *Donatia* lawn fluxes (0.66 ± 0.96 mmol CH$_4$ m^{-2} d^{-1}). During some occasions, we determined even significant, negative CH$_4$ fluxes, mainly from *Astelia* lawns (Fig. 3a, Table 2). Most of these negative fluxes as well as the majority of fluxes (41%) that were set to zero were obtained from one individual collar throughout the whole measurement campaigns precluding the possibility of a measurement artefact.

As indicated by high standard deviations, CH$_4$ emissions between replicates of all microforms were not consistent. Field observations suggested that CH$_4$ emissions of a microform were not only controlled by the predominant plant species, but might have been associated with additional features of the respective microform. Therefore additional microform features (i.e. number of *T. magellanicum* shoots, cover of *D. fascicularis*, extend of the microform in which a specific collar was installed) were assessed. However, as we did not expect such small-scale spatial variability between emissions of individual collars, the results of this survey given in Table 2 are of rather explorative, preliminary character as the low number of replicates (3 to 5 collars) in combination with several outliers barely allows any sound statistical analysis. Nevertheless, collars with elevated or comparatively high emissions had some features in common: Emissions from one *Astelia* lawn were with ~0.3 mmol CH$_4$ m^{-2} d^{-1} (significantly) higher in both sampling years compared to fluxes measured from the other *Astelia* lawns. This *Astelia* lawn collar with elevated emissions was characterized by (I) the presence of many *T. magellanicum* shoots together with a high share of *D. fascicularis* and (II) placed in a lawn with small extent surrounded by a mosaic of small pools and *D. fascicularis* patches (both smaller than 1 m^2). Surprisingly, also one *Donatia* lawn was a substantial CH$_4$ source of 2.10 ± 0.14 mmol m^{-2} d^{-1}, even exceeding the highest emissions observed from *Sphagnum* lawns on all measurement occasions in 2016. Similar to the *Astelia* lawn with elevated emissions, the collars of *Donatia* and *Sphagnum* lawns with high emissions were characterized by (I) a high amount of *T. magellanicum* shoots and (II) placed in lawns surrounded by small pools and other patches of *D. fascicularis* with no *A. pumila* nearby. Emissions obtained from one *Sphagnum* lawn were with less than 0.3 mmol CH$_4$ m^{-2} d^{-1} in both sampling years significantly lower compared to emissions from other *Sphagnum* lawns. Vice versa, this collar with low *Sphagnum* emissions was characterized by (I) the lowest number of *T. magellanicum* shoots among all *Sphagnum* lawn collars and (II) installed in a small *Sphagnum* lawn surrounded by *A. pumila*.

3.4 Pore water CH$_4$ and DIC concentration profiles

Pore water profiles in peat columns below *Astelia* lawns and pools showed similar trends in pore water concentrations and during both sampling years. CH$_4$ concentrations were almost zero in the upper pore water profile below *Astelia* lawns (< 0.003 mmol L^{-1}) down to a depth of around 1.5 m, which corresponds to the zone where the rhizosphere was most pronounced (Fig. 4a). Below this depth, CH$_4$ concentrations sharply increased up to 0.25 ± 0.08 mmol L^{-1} at 3 m depth. CH$_4$ concentrations in pore water profiles below pools resembled profiles obtained under *Astelia* lawns on elevated levels. Throughout the upper profile down to 1.5 m, CH$_4$ concentrations were ~0.03 mmol L^{-1} with a peak around 0.3 m depth (0.06 ± 0.06 mmol L^{-1}) and increased steeply to 0.40 ± 0.25 mmol L^{-1} in 3 m depth. Maximum concentrations in comparable depths reached similar levels in both sampling years below *Astelia* lawns, but maximum concentrations below pools were about 3times higher in 2015 compared to 2016.

DIC predominantly occurred as dissolved CO$_2$ because of the low pH ranging from 3.36 to 4.77. Contrary to CH$_4$, DIC concentrations increased constantly with depth from around 1 mmol L^{-1} near the surface to 2.60 ± 1.0 mmol L^{-1} in 2 m depth below *Astelia* lawns and 2.94 ± 1.1 mmol L^{-1} in 3 m depth below pools (Fig. 4b). With depth, DIC converged with CH$_4$ concentrations, which was reflected by DIC:CH$_4$ ratios that were extremely high in the rhizosphere below *Astelia* lawns exceeding 100 (Fig. 4c). Beneath the rhizosphere, ratios steeply approached values below 40. Under pools, ratios slightly decreased with depth but were mostly around 40 down to 1.5 m with two distinct peaks of very little CH$_4$ at the surface and around 0.8 m depth. In deep peat layers below the rhizosphere, DIC:CH$_4$ ratios detected under *Astelia* lawns and pools converged and reached lowest ratios of ~10 and ~5, respectively.

Visual inspection of concentration profiles but also modelling of CH$_4$ production and consumption rates indicated a predominance of CH$_4$ consumption throughout the whole rhizosphere below *Astelia* lawns and in roughly corresponding depths under pools (Fig. 4a, Fig. 6). Maximum CH$_4$ consumption was identified in the lower rhizosphere around 1.5-2 m where the increase in CH$_4$ concentration was most pronounced. Deep peat layers below the rhizosphere of *Astelia* lawns and similar depths below pools were considered as CH$_4$ sources. In these depths, the high concentration levels of CH$_4$ (up to 0.40 ± 0.25 mmol L^{-1}) sustain substantial upward diffusion of CH$_4$ following the concentration gradient into the consumption zone throughout the rhizosphere of *Astelia* lawns and in corresponding depths below pools.

3.5 Carbon isotopic values in pore water and apparent fractionation

Values of δ^{13}C in CH$_4$ did not show a clear depth trend below *Astelia* lawns and ranged in the upper profile down to 2 m depth between -87.2 ± 10.1 to -72.1 ± 10.3‰ (Fig. 4d). Isotopic δ^{13}C-CH$_4$ values below pools became less negative with depth from -93.4 ± 9.2 to -73.7 ± 1.2‰ with a minimum peak in upper peat layers around 0.3 m of -101.0 ± 5.6‰. In the upper meter of the profile, values of δ^{13}C-CH$_4$ were thus up to 25‰ more negative below pools compared to *Astelia* lawns while the isotopic values of both profiles converged in deep peat layers below 2 m at -80‰. Values of δ^{13}C in CO$_2$ below *Astelia* lawns became more negative with depth in the upper profile down to 1 m reaching values as low as -32.4 ± 0.8‰ and increased to $-19.5 \pm$

1.0‰ in 3 m depth. Below pools, values became less negative with depth throughout the whole profile from -21.2 ± 0.4 to -6.0 ± 1.5‰ (Fig. 4e).

Apparent fractionation factors varied only slightly and showed opposite trends below the two microforms. Values increased slightly from 1.060 to 1.066 below *Astelia* lawns, peaking at 1.045 in 0.5 m depth. Below pools, apparent fractionation factors

5   decreased with depth from 1.079 to 1.073 with a maximum of 1.091 around 0.3 m depth (Fig. 4f).

3.6 Hydrogen, oxygen and sulfate concentrations in pore water profiles

Hydrogen concentrations were mostly below 3 nmol L^{-1} below *Astelia* lawns while they were elevated below pools, ranging between 3 and 10 nmol L^{-1} (Fig. 5a). Maximum concentrations were reached in the upper profile of *Astelia* lawns with up to 11.83 ± 17.88 nmol L^{-1} and, besides a peak at the surface, below pools from 1 to 2 m depth with up to 41.61 ± 64.63 nmol L^{-1}

10 . Molecular oxygen concentrations were mostly below 5% saturation and tended to be higher in the upper profile down to 2 m below *Astelia* lawns compared to pools (Fig. 5b). Sulfate concentrations were similar below both, *Astelia* lawns and pools, and reached highest values near the surface with up to 16.43 ± 11.85 µmol L^{-1}. With depth, concentrations decreased and approached zero below 1 m (Fig. 5c).

4 Discussion

15   This study is among the first dealing with CH$_4$ dynamics in an austral, vascular-plant dominated cushion bog. We aimed to reveal patterns of CH$_4$ emissions and their environmental as well as potential belowground biogeochemical controls. We furthermore attempted to elucidate the CH$_4$ dynamics in the peat below the four predominant microforms on a conceptual level based on the results presented here and in previous studies.

4.1 Environmental controls on CH$_4$ emissions

20   Summer CH$_4$ emissions of a South Patagonian cushion bog dominated by *A. pumila* were low albeit spatial heterogeneity was pronounced with small patches of *Sphagnum* or *Donatia* lawns being local emission hot spots. The variation of CH$_4$ fluxes was mainly controlled by the dominant plant species of each lawn microform which emitted significantly different amounts of CH$_4$. We found only few significant responses of CH$_4$ fluxes to water table fluctuations or variations in soil temperatures (Table 2). Such weak coupling between environmental variables and CH$_4$ emissions is not surprising as fluxes from most

25   individual collars were relatively low. Furthermore, the water table fluctuated only slightly near the surface (Fig. 2) and may thus not serve as a primary control on CH$_4$ emissions. Stronger effects may only be expected when amplitude and duration of fluctuations affect peat redox conditions substantially (Blodau and Moore, 2003; Knorr et al., 2009). Under such stable moisture conditions and as long as methanogenesis is not limited by substrate supply, the sensitivity of methanogenic microbial consortia to temperature should become apparent (Whalen, 2005). Variations in landscape CH$_4$ fluxes have indeed been related

to soil temperature previously (Rinne et al., 2007; Jackowicz-Korczyński et al., 2010; Goodrich et al., 2015) which is in accordance with the present study. The temporal variability of CH_4 emissions over the two investigated seasons was rather low (data not shown) due to low seasonality in both, temperature and precipitation, in the study region. Measurement campaigns extending over shoulder seasons and comparing years of contrasting weather conditions would be necessary to reveal the impact of more pronounced water table fluctuations or temperature regimes on CH_4 fluxes in South Patagonian cushion bogs.

4.2 *Astelia* lawns – zero emission scenario

Emissions from *Astelia* lawns were minute (0.09 ± 0.16 mmol m^{-2} d^{-1}) and significantly lower than from all other microforms (Fig. 3) verifying our first hypothesis. The near-zero emissions were well explained by near-zero CH_4 concentrations (< 0.003 mmol L^{-1}) in the rhizosphere down to around 1.8 m. Only below, concentrations increased sharply to 0.2 mmol L^{-1} in 2 m depth (Fig. 4a). The low CH_4 concentrations even turned some *Astelia* lawns into a small sink for atmospheric CH_4 as shown by negative fluxes that were obtained sporadically throughout the whole measurement campaigns, confirming earlier results (Kip et al., 2012). These findings agree with previous research by Fritz et al. (2011) who observed CH_4 emissions from *Astelia* lawns in a comparably low magnitude as presented here and presented a similar CH_4 concentration depth profile. Extremely low CH_4 concentrations have also been obtained by Dullo et al. (2017) in upper peat layers of an Ethiopian cushion bog. Nevertheless, in deep peat layers below the rhizosphere, CH_4 concentrations of our study approached magnitudes reported for Chilean bogs with mixed vegetation consisting of *Sphagnum* mosses and *A. pumila* (Broder et al., 2015). This is in the lower range of concentrations described from northern bogs mostly around 0.5 mmol L^{-1} (e.g. Blodau and Moore, 2003; Beer and Blodau, 2007; Beer et al., 2008; Corbett et al., 2013) but even reaching up to 5 mmol L^{-1} in comparable depths (Steinmann et al., 2008).

A CH_4 concentration profile as observed at our site yet suggests that in deep peat layers below the rhizosphere (> 2 m) CH_4 was produced at substantial rates and comparably low oxidation, as indicated by DIC:CH_4 ratios notably smaller than 40 (Fig. 4c). Subsequently, CH_4 got almost completely oxidized on its diffusive way to the atmosphere as visualized on a conceptual level (Fig. 6). Ratios of DIC:CH_4 under methanogenic conditions in northern bogs are typically around 5 (e.g. Hornibrook et al., 1997; Blodau and Moore, 2003; Corbett et al., 2013), but can be as high as 30 (Steinmann et al., 2008). Notably higher ratios throughout the rhizosphere suggested methanotrophic activity and availability of either alternative electron acceptors or O_2 from aerenchymous roots suppressing methanogenesis (Colmer, 2003; Mainiero and Kazda, 2005; Knorr et al., 2008a, Fritz et al., 2011; Dullo et al., 2017). Diffusion and plant-mediated transport as pathways for upward CH_4 transport would have caused higher emissions and ebullition requires supersaturation of at least ~350 mmol CH_4 L^{-1} in the pore water (Fechner-Levy and Hemond, 1996; Beer et al., 2008). The sharp drop in CH_4 concentrations from -2 to -1.5 m depth characterized this peat layer as a zone of strongest methanotrophic activity, as supported by modelled consumption zones.

Carbon isotopic values obtained from pore water profiles reflected rhizosphere processes, although the δ^{13}C-CH$_4$ signature alone did not provide a clear indication for oxidative effects in the rhizosphere as proposed in our second hypothesis. A strong effect of only methanotrophy should result in a shift of the mean δ^{13}C-CH$_4$ signature to more enriched values and distinct changes in the fractionation factor from lower to upper horizons. Methane isotopic signatures were close to -80‰ in deep peat layers while above 2 m depth values ranged from -90 to -70‰ throughout the rhizosphere (Fig. 4d) while the fractionation factor increased slightly (Fig. 4f). These surprisingly negative δ^{13}C-CH$_4$ values throughout the rhizosphere along with a comparatively small shift and a wider standard variation of replicate samples are an unexpected result that needs further explanation.

We can only explain the pronounced variation in replicate δ^{13}C-CH$_4$ values to be associated with the presence of aerenchymous roots and the mean δ^{13}C-CH$_4$ depth pattern by a co-existence of aerobic and anaerobic microsites that would both support such strong variation within short spatial scales. The occurrence of small-scale aerobic microsites attached to roots releasing O$_2$ into water-saturated (peat) layers has been previously suggested (Colmer, 2003), also for peatlands on the northern hemisphere (Popp et al., 1999; Knorr et al., 2008a; Corbett et al., 2013). Life time and activity of *A. pumila* roots are highly dynamic (Knorr et al., 2015) and supposedly governed temporal and spatial expansion of microsites. Within these microsites, labile organic matter and CH$_4$ were rapidly consumed by aerobic respiration and methanotrophy resulting in CH$_4$ enriched in ^{13}C by up to 10‰ (Fig. 4d). This δ^{13}C-CH$_4$ signature and the apparently small ^{12}C/^{13}C fractionation observed throughout the rhizosphere (Fig 4f) revealed the influence of a strongly fractionating process such as CH$_4$ oxidation. Although based on ^{13}C isotope fractionation alone CH$_4$ oxidation cannot be clearly separated from acetoclastic methanogenesis (Whiticar et al., 1986; Conrad, 2005), oxidative effects in the rhizosphere were very likely since diffusion or plant-mediated transport were excluded as sinks for CH$_4$. Methanotrophy leaves CH$_4$ in the pore water enriched by ~10‰ while produced CO$_2$ becomes depleted (Chasar et al., 2000; Popp et al., 1999) as observed here throughout the rhizosphere with less negative signatures occurring only at greater depths (Fig. 4e). Also values of δ^{13}C-CO$_2$ of less than -30‰ that were substantially lower than the source organic matter material around -26‰ (Table 3) can only be explained by the influence of ^{13}C depleted carbon from oxidation of ^{13}C depleted CH$_4$. Substantial rates of root respiration were a further source for depleted CO$_2$ in the pore water (Corbett et al., 2013) as suggested by high DIC:CH$_4$ ratios mostly exceeding 100 throughout the prevailingly water-saturated rhizosphere (Fig. 4c). Nevertheless, O$_2$ release by roots still exceeded consumption, as demonstrated by O$_2$ saturation reaching up to 10% (Fig 5b). This O$_2$ supply may thus not only fuel CH$_4$ oxidation but also heterotrophic respiration using molecular oxygen or other electron acceptors regenerated by this O$_2$ input (Colmer, 2003; Mainiero and Kazda; 2005). Likely further sources of CO$_2$ could have been dissimilatory sulfate reduction in anaerobic microsites of surface peat layers down to 0.4 m (Fig. 5c) with sulfate originating e.g. from sea spray (Kleinebecker et al., 2008; Broder et al., 2015). Taking together these results obtained from CH$_4$ and DIC concentration profiles and its carbon isotopic signatures, the second hypothesis stating that pore water concentrations below *Astelia* lawns reflect a distinct CH$_4$ oxidation effect was confirmed.

Enriched CH$_4$ being only a leftover from CH$_4$ oxidation should result in a δ^{13}C-CH$_4$ depth pattern following that of the δ^{13}C-CO$_2$ profile (Hornibrook et al., 2000), but such pattern was not observed in our study (Fig. 4d and e). The surprisingly negative

$\delta^{13}C\text{-}CH_4$ signature throughout the rhizosphere is likely explained by production of few amounts of CH_4 in anaerobic microsites in absence of living roots. Either hydrogenotrophic or acetogenesis and subsequent acetoclastic methanogenesis cause large fractionation (Steinmann et al., 2008) and could add depleted CH_4 to the rhizosphere. As we did not quantify other parameters such as labile organic root matter or root exudates, acetate concentrations or its carbon isotopic signatures, we cannot clearly determine the relative importance of both pathways for our study. Elevated H_2 concentrations in surface peat layers (Fig. 5a) indicated high H_2 production by fermentation compared to consumption by e.g. sulfate reduction or hydrogenotrophic methanogenesis, presumably due to high root litter input and root exudates (Knorr et al., 2009; Estop-Aragonés et al., 2013). But as acetogens can outcompete hydrogenotrophic methanogens at low temperatures especially when H_2 is available, (Kotsyurbenko et al., 2001), we propose that acetoclastic methanogenesis was the more important pathway here. Together with the probably high amounts of labile organic matter available to serve as substrate for methanogenesis throughout 2 m of rhizosphere, this explanation would support our third hypothesis. With depth, root density presumably decreased (Fritz et al., 2011) and a slight increase in $^{12}C/^{13}C$ fractionation indicated a shift to a predominance of hydrogenotrophic methanogenesis and, below 2 m depth, absence of microsites (Fig. 4f) as α_c-values of replicate samples varied less and increased towards 1.065 (Whiticar et al., 1986; Conrad, 2005).

4.3 Pools – low emission scenario

Pools exhibited with 0.23 ± 0.25 mmol CH_4 m^{-2} d^{-1} second lowest emissions of the microforms under study (Fig. 3). Such low emissions were contrary to our first hypothesis and somewhat surprising since they have been previously reported to be similar to *Sphagnum* lawns (Fritz et al., 2011) and were expected to be relevant CH_4 sources because of prevailing anoxic conditions (Blodau, 2002). Moreover, other studies identified pools as hot-spots of CH_4 emissions from peatlands (Hamilton et al., 1994; Pelletier et al., 2014; Burger et al., 2016). This was clearly not the case here, as emissions were in the same order of magnitude as pool fluxes in South Patagonian *Sphagnum* bogs (Lehmann et al., 2016).

Low emissions were associated with CH_4 pore water concentrations surprisingly resembling those below *Astelia* lawns on slightly elevated levels (Fig. 4a). These low pore water concentrations in sparsely- or even non-rooted peat below pools were not supported by our second hypothesis and require another explanation. The $\delta^{13}C\text{-}CH_4$ signature was depleted compared to *Astelia* lawns down to 2 m depth, followed largely that of $\delta^{13}C\text{-}CO_2$ (Fig. 4d, e) and, thus, did not indicate a methanotrophic effect. As upward diffusion of CH_4 against the concentration gradient is impossible, we can only explain low pore water concentrations by lateral exchange of CH_4. We suggest that root O_2 release by *A. pumila* controlled even CH_4 dynamics below adjacent microforms as visualized on a conceptual level in Figure 6. The thorough CH_4 oxidation below *Astelia* lawns may establish a lateral concentration gradient of CH_4. Thereby, CH_4 from adjacent microforms may diffuse to the rhizosphere of *Astelia* lawns where it was consumed. As the micro-relief is not pronounced at our study site, we propose that there is a large depth zone throughout the 2 m rhizosphere of *Astelia* lawns and in corresponding depths below pools with negligible water flow and a predominance of diffusive transport. In this depth zone, we observed a highly decomposed and amorphous peat as

previously described for cushion bogs (Ruthsatz and Villagran, 1991; Fritz et al., 2011) indicating a very high water permeability that would together with a high water table position facilitate such lateral exchange (Baird et al., 2016). The assumption of lateral exchange was supported by a peak in DIC:CH_4 ratios accompanied by very low CH_4 concentrations around 0.8 m below pools (Fig. 4c) inhibiting upward diffusion. Lateral root ingrowth and O_2 supply from adjacent *Astelia* lawns could furthermore supress methanogenesis and keep CH_4 concentrations below pools low, in particular if pools are small.

Patterns of carbon isotopic signatures, levels of H_2 concentrations ~10 nmol L^{-1} sufficient to maintain hydrogenotrophic methanogenesis (Heimann et al., 2010), and low DIC:CH_4 ratios suggested methanogenic conditions over the whole profile (Fig. 4c, 5c). Methanogenesis was especially indicated by a slight peak of CH_4 concentrations associated with lower DIC:CH_4 ratios and elevated H_2 ratios around 0.3 m depth. However, even high activity of fermentation processes as indicated by peaking H_2 levels from 1 to 2 m depth did not translate to changes in fractionation factor (Fig. 4f, 5a), but suggest that CH_4 was produced only very locally if at all. Low substrate supply from highly decomposed organic matter and thus unfavourable thermodynamic conditions seemed to limit CH_4 production as suggested by very negative δ^{13}C-CH_4 signatures (Fig. 4d) accompanied with peaking α_c-values in the upper profile (Fig. 4f) (Knorr et al., 2008b; Hornibrook et al., 1997). Instead, methanogenesis might have been outcompeted by other electron accepting processes, such as sulfate reduction (Fig. 5c). If produced at all, CH_4 was rapidly consumed around 0.3 m depth by methanotrophic bacteria inhabiting submerged *Sphagnum* mosses that provided recalcitrant organic matter on pool bottoms (Kleinebecker et al., 2007; Kip et al., 2012; Knoblauch et al., 2015), or associated with cyanobacteria (Arsenault et al., 2018; González Garraza et al., 2018). Within the open water of pools which was well-mixed by strong winds, CH_4 production and excess of H_2 were diminished due to electron acceptor availability for consumption (e.g. O_2, sulfate). Thus, the pools at our study site belonged to examples of low emission pools as described in Knoblauch et al. (2015).

4.4 *Sphagnum* and *Donatia* lawns – low to moderate emission scenario

CH_4 emissions from *Sphagnum* and *Donatia* lawns were most variable among microforms ranging from near-zero to local emission hotspots. *Sphagnum* lawns showed significantly higher CH_4 emissions of 1.52 ± 1.10 mmol m^{-2} d^{-1} than all other microforms (Fig. 3). Substantially higher fluxes from *Sphagnum* lawns at our study site have been previously described by Fritz et al. (2011) and emissions reported here were in the same order of magnitude as determined for *Sphagnum* lawns in South Patagonian bogs dominated by *Sphagnum* mosses (Broder et al., 2015; Lehmann et al., 2016). Highest emissions obtained in the present study from *Sphagnum* and *Donatia* lawns were at intermediate levels compared to northern bogs (Blodau, 2002; Laine et al., 2007; Limpens et al., 2008).

We present the first CH_4 emission data obtained from *Donatia* lawns. Contrary to our expectations, *Donatia* lawns emitted 0.66 ± 0.96 mmol CH_4 m^{-2} d^{-1} and had thus second highest CH_4 emissions of our study. One lawn even exceeded emissions of the strongest *Sphagnum* lawn source (Fig. 3c, Table 2) on all measurement occasions. As these comparatively high emissions

could be well reproduced, we conclude that an artefact can be excluded. Therefore, our first hypothesis, that cushion plants emit negligible amounts of CH_4, could retrospectively only be partly confirmed, as it depends on the specific cushion-forming plant species. We conclude that the presence of cushion plants as a proxy for negligible CH_4 emissions from cushion bogs needs to be carefully interpreted.

5   The spatial distribution of vascular plant root characteristics and its oxidative effects apparently controlled CH_4 dynamics in the study site as suggested by the pronounced spatial variability of emissions associated with our preliminary observations of microform features (Table 2). *D. fascicularis* established a deep and aerenchymous, but with < 0.05 g DW L of peat^{-1} a substantially less dense rooting system compared to *A. pumila* with > 4 g DW L of peat^{-1} in around 0.5 m depth (Fritz et al., 2011). The lower root density of *D. fascicularis* was probably below a specific threshold at which O_2 release did not suppress

10   emissions any more. Instead, the roots might have accelerated CH_4 production by presence of labile organic matter while facilitating emissions (e.g. Joabsson et al., 1999; Blodau, 2002; Colmer, 2003; Whalen, 2005; Agethen et al., 2018). As root O_2 release promotes nutrient mobilization (Colmer, 2003), this assumption of little if any O_2 release by *D. fascicularis* is in line with Schmidt et al. (2010) who found nutrient concentrations in *D. fascicularis* to be almost as low as in *S. magellanicum* while *A. pumila* contained significantly higher amounts of nutrients.

15   *Sphagnum* and *Donatia* lawns that showed substantial CH_4 emissions were beyond the sphere of influence by *A. pumila* roots. Although not measured here, pore water CH_4 concentrations below *Sphagnum* and *Donatia* lawns with remarkably higher emissions probably increased steeply below the water table (Fig. 6), like common depth profiles in northern (e.g. Beer and Blodau, 2007; Limpens et al., 2008; Corbett et al., 2013) or southern bogs (Broder et al., 2015). This explanation implies that the pore water below those lawns was not well-connected to pore water influenced by *A. pumila* roots. A spatial variability of

20   peat physical properties on the ecosystem scale was suggested by water table records (Fig. 2) demonstrating that one site responded faster than the other to, for instance, precipitation events.

We speculate that the biogeochemistry below *Sphagnum* and *Donatia* lawns with near-zero emissions was, likewise to pools, influenced by root activity of nearby *A. pumila* (as visualized in Fig. 6). This assumption was supported by previous research in our study site. Fritz et al. (2011) showed that below *Sphagnum* lawns pore water CH_4 concentrations can be substantially

25   lowered throughout rhizosphere-influenced peat layers. Further research should be undertaken to investigate why CH_4 emissions from *Sphagnum* and *Donatia* lawns appear to be highly variable in order to understand CH_4 dynamics in under-researched cushion bogs.

4.5 Implications for ecosystem CH_4 emissions from Patagonian cushion bogs

Highest summer emissions in the present study were considerably lower compared to maximum austral summer fluxes of ~150

30   mg CH_4 m^{-2} d^{-1} (9.4 mmol m^{-2} d^{-1}) determined for a New Zealand bog dominated by the vascular evergreen "wire rush," *Empodisma robustum* (Goodrich et al., 2015). The authors explained such high CH_4 emissions by comparatively wet conditions and a high density of aerenchymous vegetation providing a gas conduit for CH_4 transport in their study site. Compared to CH_4

emissions of northern bogs ranging from 3 to 53 mg m^{-2} d^{-1} at intermediate levels in wet bogs to up to 80 mg m^{-2} d^{-1} (Blodau, 2002; Laine et al., 2007; Limpens et al., 2008; 0.2 to 2.2 and up to 5 mmol m^{-2} d^{-1}), highest summer emissions in the present study represent a pronounced CH_4 source. Nevertheless, overall ecosystem CH_4 emissions would probably be among the lowest described for pristine bog ecosystems worldwide when taking into account the high proportion of the surface area where *Astelia*

5   lawns prevailed.

While *Donatia* lawns covered only small parts of our study site, we observed other parts of the complex bog system in the whole study area to be widely dominated by *D. fascicularis* instead of *A. pumila* which is in line with previous studies (Heusser, 1995; Grootjans et al., 2014) who described the cushion bogs in the Moat landscape to be covered by both, *A. pumila* and *D. fascicularis*. Thus, amounts of emitted CH_4 could be significant also on the ecosystem scale once *D. fascicularis* dominates.

10   For instance, a predominance of *D. fascicularis* is typical for later vegetation succession stages in cushion bogs of Tierra del Fuego (Heusser, 1995) or Chile (Ruthsatz and Villagran, 1991; Kleinebecker et al., 2007).

5 Conclusion

We conclude from our study that the spatial distribution of cushion-forming *A. pumila* root density and activity and associated O_2 supply strongly controlled CH_4 production and consumption in a pristine Patagonian cushion bog. Thereby, CH_4 emission

15   were reduced to near-zero levels and largely decoupled from environmental controls. The high root density even regulated CH_4 dynamics below adjacent microforms with less or non-rooted peat such as pools, *Sphagnum* lawns or lawns dominated by cushion-forming *D. fascicularis* by maintaining lateral concentration gradients in upper peat layers. Nevertheless, when root density dropped below a certain threshold, CH_4 production might have been accelerated by presence of labile root organic matter or exudates accompanied with O_2 consumption along with facilitated CH_4 transport by aerenchymatic roots of e.g. *D.*

20   *fascicularis*. Under such circumstances, CH_4 emissions increased to intermediate levels compared to northern bogs. Therefore, the presence of cushion plants as a proxy for negligible CH_4 emissions from cushion bogs should be interpreted carefully. As cushion bogs can be found in many (mostly southern) parts of the world and only very limited knowledge about CH_4 dynamics from these systems exist, future research should take into account a possibly high spatial variability of CH_4 emission from bogs dominated by cushion plants. We demonstrated an extreme scenario for how a spatial distribution of root density in the

25   peat can lead to a pronounced pattern of CH_4 emissions. Yet, the underlying ratio between root characteristics and O_2 supply determining this emission pattern should be applicable to other densely rooted peatlands in general. Further research should be undertaken to prove relationships that have been developed here on a conceptual level in order to extend our knowledge on CH_4 dynamics in under-researched cushion bogs.

30   *Data availability.* The data can be accessed by email request to the corresponding authors.

Author contributions. CB, TK and WM designed the study. WM, CB, TK and VAP conducted field work and sample analyses with the help of KHK. WM performed data analyses and prepared the manuscript with contributions from KHK, TK and VAP.

Competing interests. The authors declare that they have no conflict of interest.

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Figures
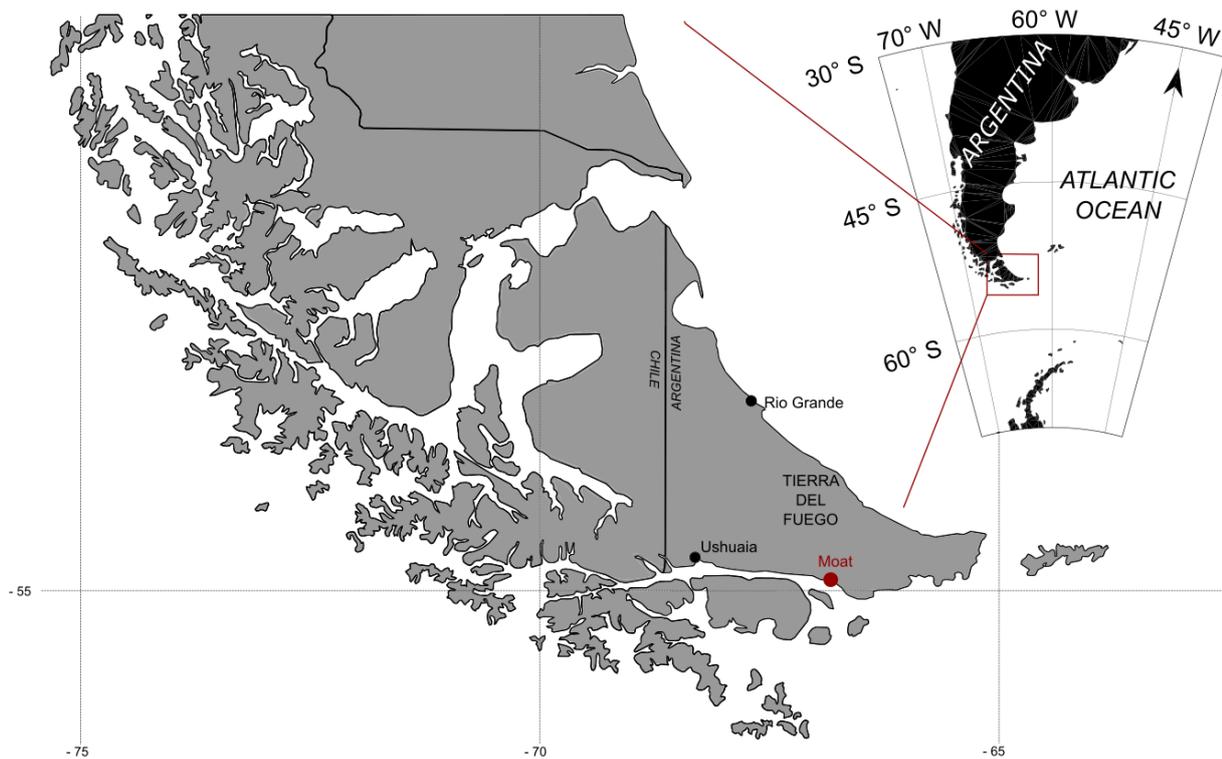
Figure 1. Location of the study area in southernmost Patagonia. The investigated cushion bog in Moat is located 130 km eastern of Ushuaia (Argentina). The map was created at http://www.simplemappr.net accessed on 11.12.2017 and in Matlab (MATLAB Mapping Toolbox Release R2017a).
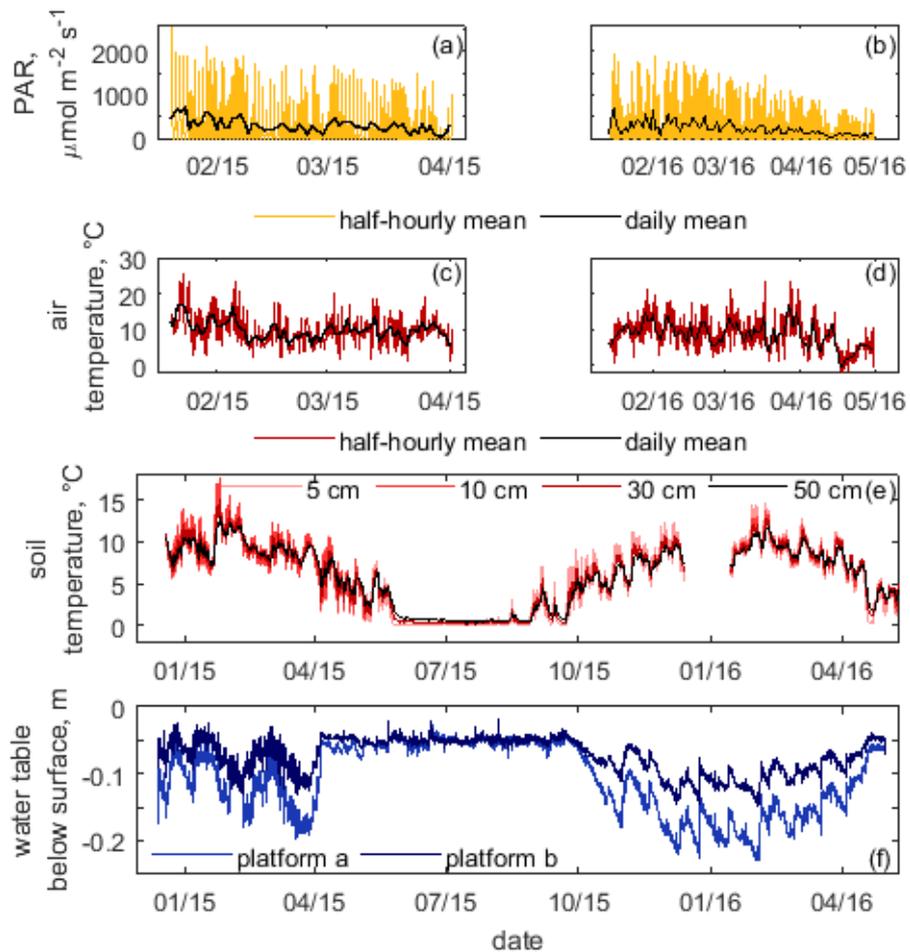
Figure 2. Time series of environmental variables during the study period. Photosynthetic active radiation (PAR, a, b) and air temperature (c, d) are presented as half-hourly and daily means during two austral summer periods. Soil temperature (e) and water table position below surface (f) were continuously recorded and are shown as half-hourly means. Note the difference in response time between platform a and platform b where water table fluctuations were recorded.
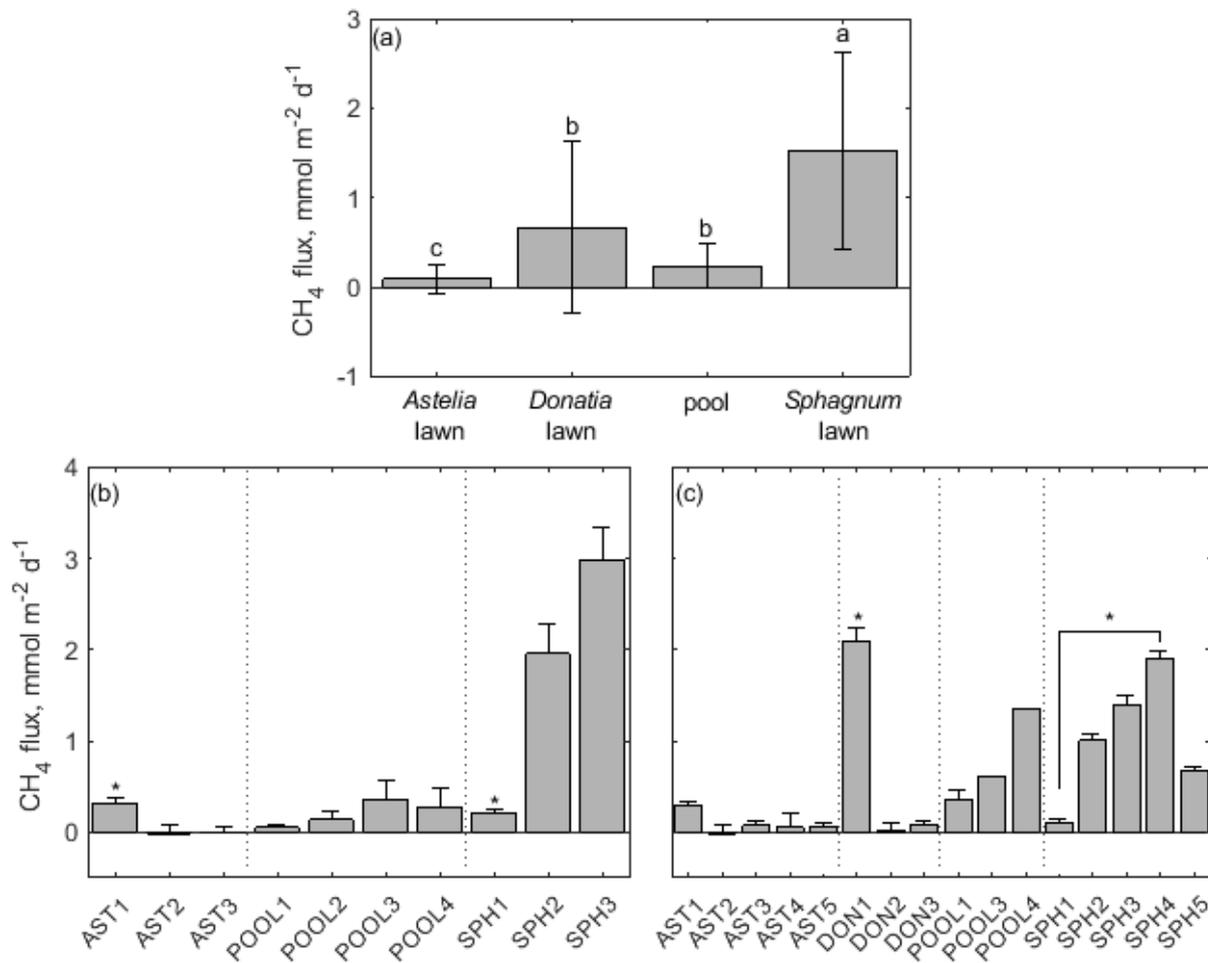
Figure 3 a-c. Mean CH_4 emissions and their standard deviation determined from dominant microforms (a) and individual collars during the two measurement campaigns (b, c) in a Patagonian cushion bog. Different letter superscripts denote significantly different amounts of emitted CH_4 between microforms despite variability within microforms was substantial (a) or from collars within one microform (b, c) that were identified by Kruskal-Wallis analysis of variance and multiple comparison U-tests with Bonferroni adjustment.
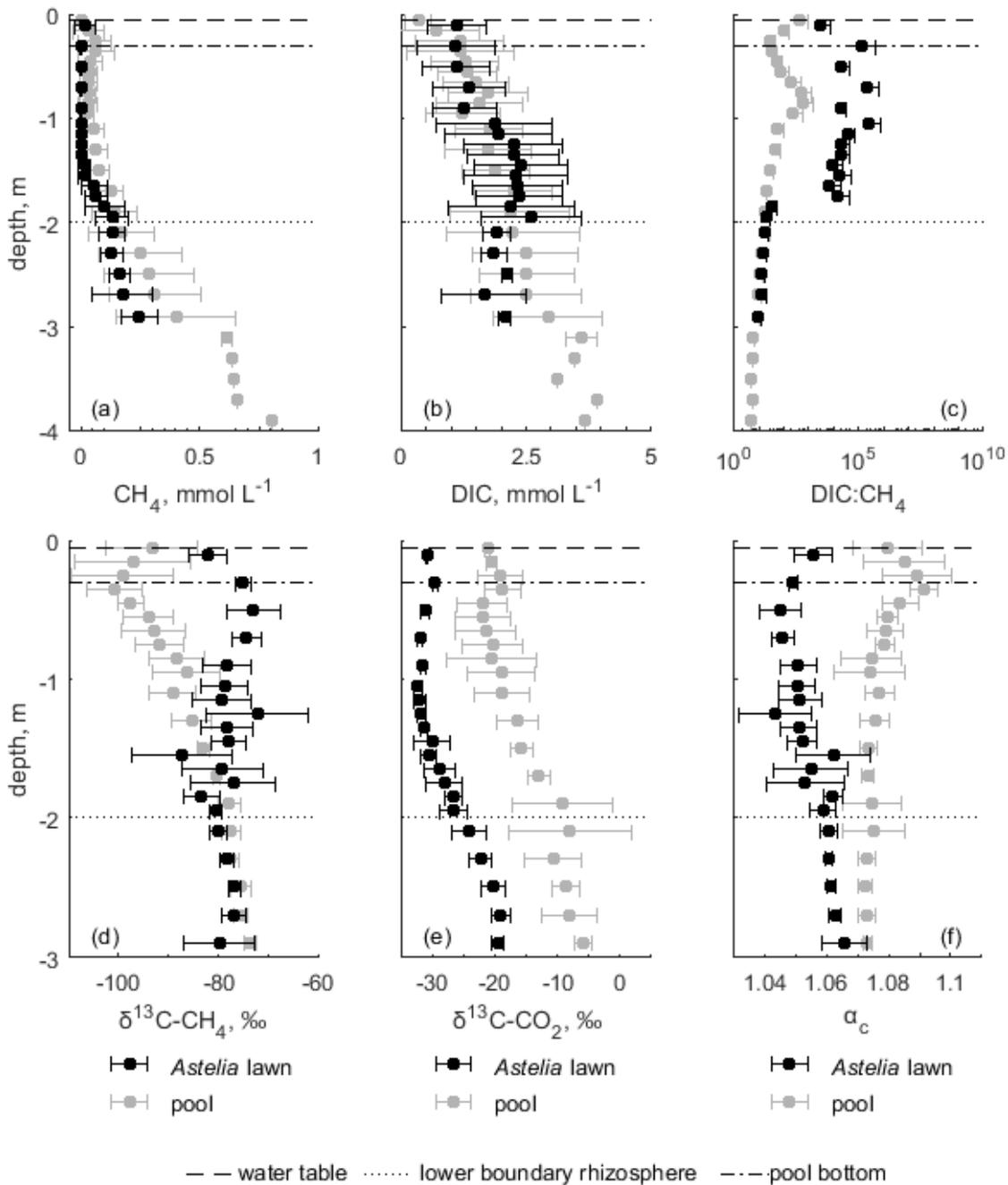
Figure 4 a-f. Pore water composition in depth profiles obtained from MLPS (N = 3) installed in *Astelia* lawns and pools during two sampling campaigns in austral summer 2015 and 2016. Mean values and their standard deviation are presented. CH₄ (a) and DIC (b) concentrations as well as related DIC:CH₄ (c) ratios were determined during both sampling events while carbon isotope values of CH₄ (d) and DIC (e) and corresponding fractionation factors (f) were investigated only during the second

campaign. DIC:CH$_4$ ratios are shown on a logarithmic scale without negative standard deviation for *Astelia* lawns and pools. Displayed depths represent the centre of a MLP segment and had to be standardized because of different sampling resolution in both years. The water table position and approximate maximum rooting depth (rhizosphere) refer to *Astelia* lawns only. Note the different scale of the y-axis in the upper and lower three panels.
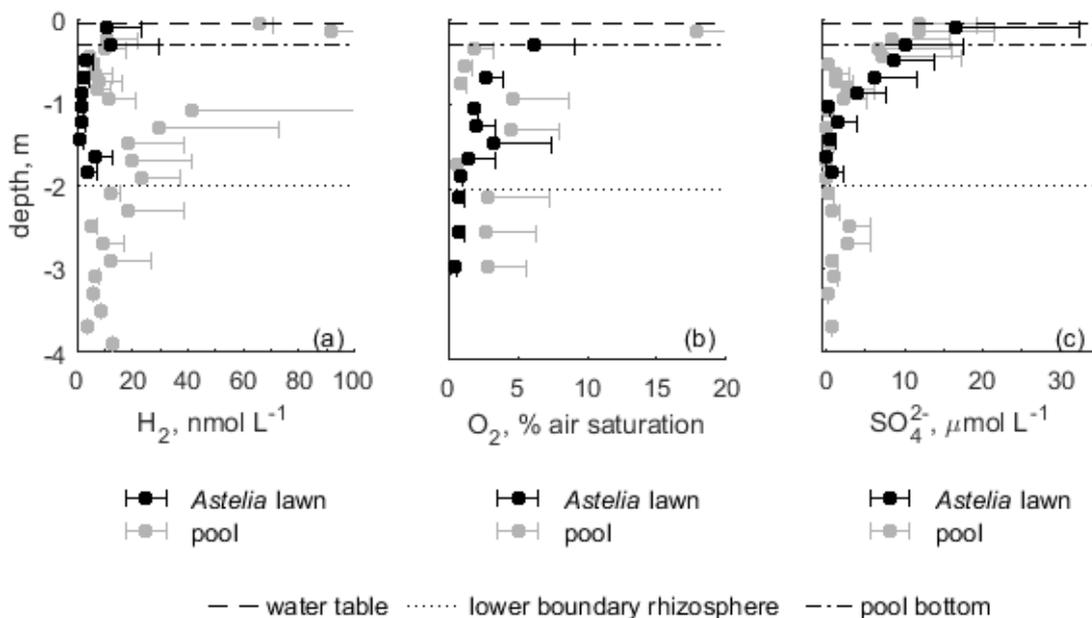
Figure 5 a-c. Profiles of H$_2$ (a), O$_2$ (b) and sulfate (c) pore water concentrations obtained from MLPs (N = 3) installed in *Astelia* lawns and pools during two sampling campaigns in austral summer 2015 and 2016. Mean values and their standard deviation are presented. Displayed depths represent the centre of a MLP segment and had to be standardized because of different sampling resolution in both years. The water table position and approximate maximum rooting depth (rhizosphere) refer to *Astelia* lawns only.
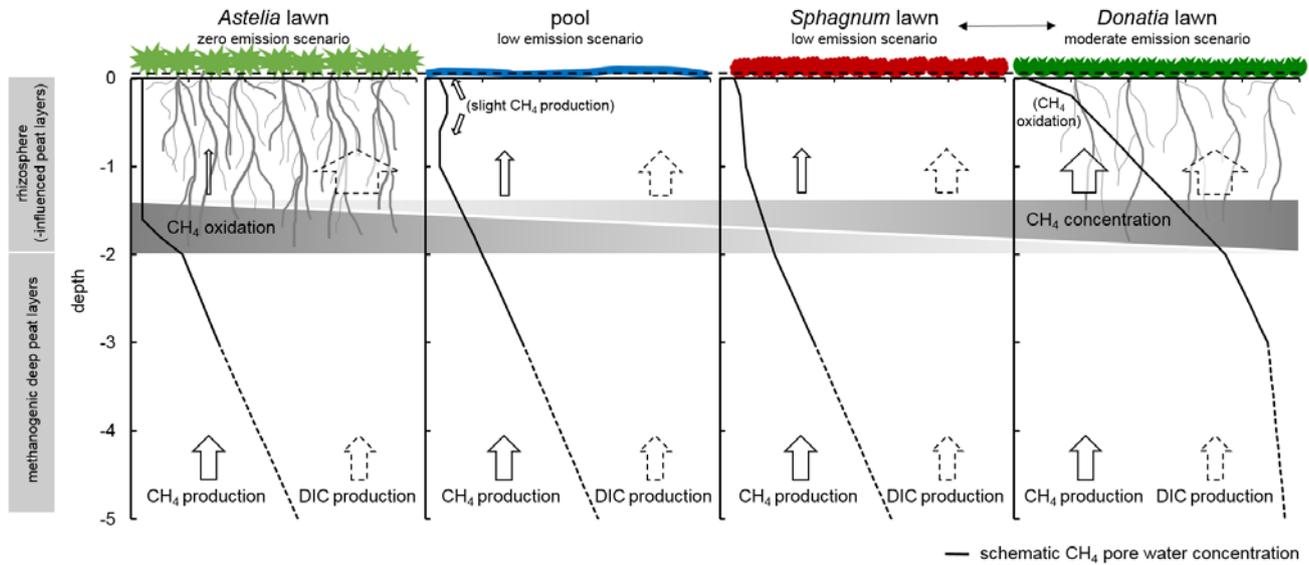
Figure 6. Schematic CH$_4$ concentration profiles below the four dominant microforms in a Patagonian cushion bog. The shape of profiles was derived from data obtained in the present study together with those by Limpens et al. (2008), Fritz et al. (2011) and Broder et al. (2015). The size of arrows represents the relative magnitude of either a CH$_4$ or CO$_2$ flux following the diffusion gradient. The water table position is displayed by a dashed line near the surface. CH$_4$ oxidation by root O$_2$ release resulted in near-zero CH$_4$ pore water concentrations in densely rooted peat below *Astelia* lawns. With increasing distance from densely rooted peat, CH$_4$ oxidation decreased while CH$_4$ concentration increased until reaching a depth profile typical for those of northern peatlands with less if any roots in water-saturated peat layers. Exemplary sequence of microforms, derived from observed amounts of emitted CH$_4$. Other sequences of microforms are reasonable as microforms occur in various combinations in the field.

Tables

Table 1. Characteristic plant species of dominant microforms in a Patagonian cushion bog. Species composition was determined during the second measurement campaign within collars where closed chamber measurements were conducted. Mean cover (%) and its standard deviation of characteristic were given and plant species with a mean cover < 5 % were listed with +.

species	*Astelia* lawn	*Sphagnum* lawn	*Donatia* lawn
		microform	
Astelia pumila	84 ± 16		
Donatia fascicularis	8 ± 10	+	90 ± 9
Sphagnum magellanicum		94 ± 4	
Tetroncium magellanicum	+	7 ± 2	+
Caltha dioneifolia	+	+	6 ± 5
Empetrum rubrum	+		
Gaultheria antarctica	+	+	+
Myrteola nummularia	+		

Table 2. CH$_4$ fluxes determined from individual collars installed in dominant microforms of a Patagonian cushion bog. Number of flux measurements, their mean and standard deviation are presented. Significantly different fluxes from collars within one microform were identified by Kruskal-Wallis analysis of variance and multiple comparison U-tests with Bonferroni adjustment. Results of computing Spearman's rank correlation coefficient rho for the relationships between CH$_4$ fluxes and possible environmental controls, namely water table depth determined separately for each collar and soil temperature in 0.05 m depth, are given. Furthermore, characteristics of collars and results of computing Spearman's rank correlation for the relationships between mean CH$_4$ fluxes during the second campaign and each feature are shown. Microform size refers to the extent of a microform in which a specific collar was installed. P-values < 0.05 indicate a correlation significantly different from zero.

year	micro-form		N	mean flux, mmol CH$_4$ m^{-2} d^{-1}	p	rho	p	rho	p	number of shoots	rho	p	cover, %	rho	p	size, m²	rho	p
				Kruskal-Wallis analysis		water table depth, m		soil temperature, °C		presence *T. magellanicum*			presence *D. fascicularis*			microform size		
2015	*Astelia* lawn	1	60	0.32 ± 0.05	< 0.05	-0.22	n.s.	n.d.	n.d.									
		2	64	-0.02 ± 0.09	n.s.	-0.21	n.s.	0.17	n.s.									
		3	55	-0.01 ± 0.07	n.s.	0.03	n.s.	-0.08	n.s.									
	Sphagnum lawn	1	62	0.21 ± 0.05	< 0.05	-0.21	n.s.	n.d.	n.d.									
		2	64	1.96 ± 0.33	n.s.	0.41	< 0.05	0.52	< 0.05									
		3	54	2.99 ± 0.35	n.s.	0.2	n.s.	0.6	< 0.05									
	pool	1	13	0.05 ± 0.03	n.s.			n.d.	n.d.									
		2	12	0.14 ± 0.08	n.s.			0.4	n.s.									
		3	10	0.36 ± 0.2	n.s.			0.64	< 0.05									
		4	11	0.28 ± 0.2	n.s.			-0.01	n.s.									
2016	*Astelia* lawn	1	7	0.29 ± 0.04	n.s.	0.27	n.s.	-0.13	n.s.	15			25			1.12		
		2	11	-0.02 ± 0.1	n.s.	-0.22	n.s.	-0.16	n.s.	0			4			4.45		
		3	8	0.07 ± 0.05	n.s.	-0.68	n.s.	-0.31	n.s.	0	0.67[a]	n.s.	0	0.01	n.s.	26.66	-0.10	n.s.
		4	11	0.06 ± 0.15	n.s.	-0.09	n.s.	0.13	n.s.	0			8			3.38		
		5	11	0.06 ± 0.04	n.s.	-0.44	n.s.	0.14	n.s.	6			2			4.55		
	Donatia lawn	1	9	2.1 ± 0.14	< 0.05	-0.82	< 0.05	0.74	< 0.05	30			80			0.26		
		2	11	0.01 ± 0.09	n.s.	0.29	n.s.	-0.64	< 0.05	9	1.00[a]	n.s.	97	-1.00[a]	n.s.	0.15	0.50	n.s.
		3	10	0.08 ± 0.04	n.s.	-0.46	n.s.	-0.2	n.s.	18			92			0.96		
	Sphagnum lawn	1	9	0.09 ± 0.05	< 0.05	0.68	n.s.	-0.78	< 0.05	66	0.40	n.s.	0	0.71[a]	n.s.	0.43	0.00	n.s.
		2	11	1.01 ± 0.06	n.s.	0.15	n.s.	-0.42	n.s.	165			0			2.38		

	3	11	1.39 ± 0.1	n.s.	-0.05	n.s.	-0.05	n.s.	175	0	2.7
	4	9	1.9 ± 0.08	< 0.05	-0.44	n.s.	0.25	n.s.	108	4	0.38
	5	10	0.68 ± 0.03	n.s.	0.17	n.s.	-0.22	n.s.	120	0	0.65
pool	1	2	0.35 ± 0.11	n.s.			n.d.	n.d.			
	3	1	0.6 ± 0	n.s.			n.d.	n.d.			
	4	1	1.35 ± 0	n.s.			n.d.	n.d.			

n.s. = not significant, n.d. = not determined, [a] = despite a (relative) high absolute value of Spearman's rho, p-values did not indicate a significant correlation, probably because of outliers.

Table 3. Summary of peat characteristics obtained from two peat cores taken in *Astelia* lawns in a Patagonian cushion bog. Data were averaged over the respective depths sampled in 0.1 m resolution.

peat characteristics	depth, m	bulk density, g cm^{-3}	N, %	C, %	CN	$\delta^{15}N$	$\delta^{13}C$
amorphous, highly decomposed cushion peat with many living *Astelia* roots, only close to the surface (0-0.4 m) with recognizable plant material	0-1	0.03	1.42	49.31	37.62	-1.24	-25.63
	1-2	0.06	1.83	52.45	28.69	1.24	-26.18
	2-3	0.06	1.52	51.37	34.38	1.12	-26.33
	3-4	0.06	1.22	50.49	41.98	0.22	-25.78
Sphagnum peat, with depth increasingly amorphous and decomposed	4-5	0.11	1.17	47.86	41.45	-1.59	-26.43
	5-6	0.10	1.18	47.56	40.67	-1.62	-26.77
	6-7	0.15	1.28	50.27	44.34	-1.97	-27.08