



1 **Annual and seasonal CO₂ flux in a temperate north-Patagonian peatland exposed to varying intensities**
2 **of commercial *Sphagnum* moss harvesting**

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30 **Abstract**

31 Peatlands hold the largest carbon (C) reserves worldwide and therefore play a fundamental role in climate
32 change mitigation. In the Southern Hemisphere, peatlands distributed in the Patagonia represent the
33 principal extratropical C sink. Nevertheless, increasing anthropogenic pressures, such as the commercial
34 harvesting of *Sphagnum* moss, threaten their capacity to regulate CO₂ fluxes, a situation that has been
35 scarcely studied.

36 We conducted a field study that quantified and analyzed the annual and seasonal CO₂ fluxes in a North
37 Patagonian peatland subjected to varying intensities of commercial *Sphagnum* harvesting: high, moderate,
38 and undisturbed. Using closed chamber techniques, we measured the components of the CO₂ flux over
39 the course of one year, while also identifying the predominant environmental drivers influencing these
40 fluxes.

41 The results showed that moss harvesting intensity was directly correlated with net ecosystem exchange
42 (NEE) fluxes. The high-intensity extraction site acted as a net CO₂ source (375.7 g CO₂-C m⁻² yr⁻¹), the
43 moderately harvested site was approximately carbon neutral (10.2 g CO₂-C m⁻² yr⁻¹), and the undisturbed
44 site functioned as an annual CO₂ sink (-167.1 g CO₂-C m⁻² yr⁻¹). Seasonal fluxes revealed that disturbed
45 sites emitted more CO₂ in summer and acted as sinks in spring, while the undisturbed site sequestered
46 CO₂ year-round. In winter, all three sites functioned as CO₂ sinks due to environmental conditions that
47 favored productivity and minimized respiration.

48 Photosynthetically active radiation was the key bioclimatic driver regulating gross primary production and
49 NEE, while air and soil temperature primarily influenced ecosystem respiration. These findings provide
50 relevant evidence for understanding carbon dynamics in peatlands affected by commercial *Sphagnum*
51 harvesting and underscore the need for sustainable management regulations to preserve their role as
52 carbon sinks in Chilean Patagonia.



53 **1. Introduction**

54 Peatlands are ecosystems that develop under conditions of water saturation and low oxygen availability
55 in the soil (Finlayson & Milton, 2016; Dickopp et al., 2018). They play a crucial role in climate change
56 mitigation due to their capacity to store large amounts of carbon (C) in the form of partially decomposed
57 organic matter (Blodau, 2002; Yu, 2012; Harenda et al., 2018; Strack et al., 2022; Li et al., 2024). This carbon
58 storage is essential for understanding global biogeochemical processes, as peatlands hold approximately
59 30% of the Earth's terrestrial carbon, equivalent to twice the carbon stored in forest biomass, despite
60 covering only 3% of the global land surface (Limpens et al., 2008; Yu et al., 2010; Joosten et al., 2016;
61 Leifeld & Menichetti, 2018; Leifeld et al., 2019).

62 Throughout the Holocene, peatlands have acted as carbon sinks by capturing atmospheric CO₂ that would
63 otherwise contribute to rising concentrations of this greenhouse gas in the Earth's atmosphere (Dunn &
64 Freeman, 2011; Sirin, 2022; Helbig et al., 2022; Strack et al., 2022). However, their fragility and
65 vulnerability to anthropogenic disturbances pose a significant risk to global climate stability (Frolking et
66 al., 2011; Harris et al., 2022; Loisel & Gallego-Sala, 2022). The release of stored carbon due to peatland
67 degradation represents a major source of CO₂ emissions, potentially undermining efforts to mitigate
68 climate change (Loisel et al., 2021; Strack et al., 2022; UNEP, 2022; Mattila, 2024).

69 The anthropogenic pressures exerted on peatlands differ markedly between the Northern and Southern
70 Hemispheres in terms of timing, intensity and type of disturbance. In this regard, Southern Hemisphere
71 peatlands have been less affected by direct human impacts and degradation processes (León et al., 2021;
72 UNEP, 2022). Nonetheless, temperate peatlands in the Southern Hemisphere, particularly those
73 distributed across Australasia and Patagonia, have increasingly been subjected to anthropogenic
74 pressures, mainly related to peat and *Sphagnum* moss extraction (Whinam & Buxton, 1997; Whinam et
75 al., 2003; León et al., 2021; Lopatin et al., 2022; Pacheco-Cancino et al., 2025).



76 Temperate peatlands located in the northern region of Chilean Patagonia (41°–45° S) have shown a
77 sustained increase in *Sphagnum* moss harvesting in recent decades, driven by strong commercial interest
78 and growing international demand, especially from Asian markets (Díaz et al., 2012; Díaz & Silva, 2018;
79 Blok et al., 2021). As a result, many peatlands in this region exhibit signs of unsustainable moss harvesting,
80 posing a threat to their ecological stability and functionality (León et al., 2012; Díaz & Silva, 2018). Despite
81 this, there is a notable lack of scientific evidence addressing the impacts of this disturbance on the
82 ecosystem services provided by these environments, particularly concerning CO₂ fluxes. This gap is
83 especially concerning given that Patagonian peatlands represent the primary extratropical carbon sink and
84 reservoir in the Southern Hemisphere (UNEP, 2022; Pérez-Quezada et al., 2023).

85 Recent studies suggest that disturbances associated with *Sphagnum* moss harvesting can significantly alter
86 the processes of CO₂ capture and release in peatlands (Silvan et al., 2017; Valdés-Barrera et al., 2019;
87 Karjalainen et al., 2025). However, few studies have examined how varying intensities of commercial
88 *Sphagnum* extraction influence annual and seasonal CO₂ flux dynamics, as most analyses are limited to the
89 vegetation growing season. Expanding the temporal scope of such studies is essential to better understand
90 flux dynamics and develop strategies for the conservation and sustainable management of these
91 ecosystems and their associated resources.

92 To address this knowledge gap, we performed in situ measurements of CO₂ flux components using
93 transparent and opaque closed chambers over the course of one year, including the seasonal dynamics, in
94 two sites subjected to different commercial extraction intensities of *Sphagnum magellanicum* and one
95 undisturbed site, located in a temperate peatland in northern Chilean Patagonia. In addition, we identified
96 the environmental drivers that most strongly influenced CO₂ fluxes at each study site. We hypothesized
97 that increasing *Sphagnum* harvesting intensity would lead to greater annual and seasonal CO₂ emissions
98 to the atmosphere. The specific objectives of this study were: i) to quantify annual and seasonal CO₂ fluxes
99 at two sites under different levels of *Sphagnum* moss harvesting and one undisturbed site in a North
100 Patagonian peatland, ii) to analyze and compare the components of annual and seasonal CO₂ fluxes among

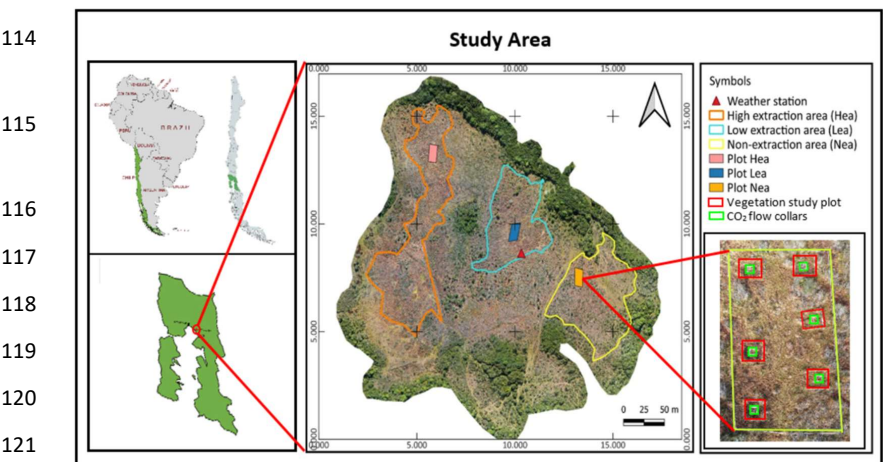


101 sites with varying harvesting intensities and an undisturbed area, and
102 iii) to identify the main environmental drivers influencing annual CO₂ fluxes at the different study sites.

103 **2. Materials and methods**

104 **2.1. Study area**

105 The study area is located in the province of Llanquihue, Los Lagos Region, approximately 28 km east of the
106 city of Puerto Montt (41°34'S, 72°42'W) (Fig. 1, Pacheco-Cancino et al. (2025)). It corresponds to a
107 transitional minerotrophic peatland formed as a result of human activity associated with forest fires and
108 intensive logging of native forests (Díaz et al., 2008; León et al., 2018), developed on volcanic ash-derived
109 soils locally known as “ñadis”. These soils feature a placic horizon, which leads to poor drainage and
110 waterlogging, particularly during the winter season (Carrasco et al., 2017). The climate in the area is
111 classified as temperate rainy with oceanic influence (Di Castri & Hajek, 1976), with a 30-year mean annual
112 temperature of 10.3° C and an average annual precipitation of 1560 mm (reference period 1991–2020,
113 Chilean Weather Service). The average depth of the peat layer in the study area is 0.66 m.



122 **Figure 1.** Location of the study area, sites with different intensities of commercial *Sphagnum* moss
123 harvesting, and undisturbed site; sampling areas within each site and distribution of point measurement
124 units for CO₂ fluxes. Obtained from Pacheco-Cancino et al. (2025).

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Two distinct areas with differing intensities of *Sphagnum* moss harvesting were identified within the study site. The first area covers approximately 1 ha and has been harvested using tools (hooks and forks) during successive seasons over the past eight years, following a high-intensity extraction scheme (H-ea). In the most recent moss harvesting season prior to the study, an area of approximately 850 m² was disturbed, leaving heterogeneously distributed undisturbed patches with a residual moss cover of less than 30%. The microtopography in H-ea is characterized by a predominance of lawns, along with fewer hollows and minor hummocks. The main vegetation species present at this site include *Sphagnum magellanicum* Brid., *Sphagnum fimbriatum* Wilson, *Juncus procerus* E. Mey., *Juncus stipulatus* Nees & Meyen, *Gaultheria pumila* (L.f.) D.J. Middleton, and *Myrteola nummularia* (Poir.) O. Berg. Among vascular plants, small shrub species represent the dominant functional group in terms of surface cover. The second area encompasses approximately 0.5 ha and, unlike H-ea, moss harvesting has been carried out manually under a less intensive extraction scheme (L-ea). In the most recent extraction period prior to the study, a ~350 m² section was disturbed, maintaining a residual moss cover of around 50%. The microtopography in L-ea features low hummocks, lawns, and some marginal hollows. The main vegetation species in this site include those already described for H-ea, along with *Gaultheria antarctica* Hook.f., *Rubus geoides* Sm., *Carex magellanica* Lam., *Ugni molinae* Turcz., *Empetrum rubrum* Vahl ex Willd., and *Eucryphia cordifolia* Cav. In this case, among vascular plants, herbaceous species represent the group with the greatest coverage. Additionally, a third undisturbed site of approximately 0.8 ha with 100% *Sphagnum* moss cover (N-ea) was included as a reference area. This site exhibits irregular microtopography composed of taller hummocks than those observed in L-ea, along with lawn zones. In addition to the species already described for the previous two sites, the vegetation at this location includes *Gaultheria mucronata* (L.f.) Hook. & Arn., *Baccharis concava* (Ruiz & Pav.) Pers., *Tepualia stipularis* (Hook. & Arn.) Griseb., *Amomyrtus meli* (Phil.) D. Legrand & Kausel, *Amomyrtus luma* (Molina) D. Legrand & Kausel, *Caldcluvia paniculata* (Cav.) D. Don, *Weinmannia trichosperma* Cav., and *Drimys winteri* J.R. Forst. & G. Forst. In this case, tree species exhibit the highest coverage among vascular plants.



151 **2.2. CO₂ flux measurements**

152 At each study site, a 200 m² plot (20 × 10 m) was delineated, within which six sampling units (SUs) were
153 randomly established for conducting point-based CO₂ flux measurements (Fig. 1). The SUs were located in
154 representative areas reflecting the conditions of the moss harvesting sites and the reference site,
155 maintaining a minimum distance of 2 m between the edges of each SU and the margins of the 200 m² plot.
156 A total of 18 SUs were established across the study area.

157 We conducted CO₂ flux measurements on two consecutive days approximately every 15 days during the
158 vegetation growing season, between 20 November 2021, and 14 April 2022. Outside of the growing
159 season, that is, between 15 April and 19 November 2022, measurements were carried out once or twice
160 per month, with reduced sampling intensity due to lower net CO₂ exchange between the ecosystem and
161 the atmosphere (Alm et al., 1999; Saarnio et al., 2007). This schedule resulted in a total of 32 field sampling
162 dates over the course of the study period. Eighteen PVC collars (six per plot at each site), measuring 60 ×
163 60 cm, were permanently installed to a depth of ~20 cm at the center of each SU (Fig. 1), which could be
164 accessed by installing boardwalks to avoid soil disturbances. Each collar had an upper groove that allowed
165 for the placement of a plexiglass closed chamber (60 × 60 × 50 cm, 95% transparency) used to record CO₂
166 fluxes (Heinemeyer & McNamara, 2011; Pavelka et al., 2018). The groove also enabled an airtight water
167 seal during measurement. To measure CO₂ fluxes, a custom-built device was installed in the chamber
168 headspace. The system was based on an Arduino™ microcontroller and included a non-dispersive infrared
169 CO₂ sensor (model 030–8–0010 K30 FR, SenseAir, Sweden) and a barometric pressure sensor (model BMP-
170 280, Bosch, Germany), similar to the setup described by Mecagga et al. (2024). The device was developed
171 by the Department of Electronic Engineering at Universidad de La Frontera. The K30 FR sensor was selected
172 for its proven accuracy and reliability in CO₂ flux studies in peatlands (Mecagga et al., 2024; Martin et al.,
173 2017). Calibration was performed using GasLab® 2.3.1.4 software by comparing CO₂ fluxes recorded with
174 the K30 FR to those from an EGM-4 IRGA (PP-Systems), with adjustments for temperature, pressure, and
175 relative humidity (Martin et al., 2017).



176 The chamber was also equipped with an air temperature and humidity sensor (Hobo U23 Pro v2, USA) and
177 two small fans (Sunon, MagLev, Taiwan) to ensure adequate air mixing inside the chamber headspace. A
178 vent tube was installed to equalize pressure during chamber placement and removal. Net ecosystem
179 exchange (NEE) was measured during daytime under full sunlight with the transparent chamber installed
180 for five minutes, recording CO₂ concentrations at one second intervals. Subsequently, the chamber was
181 covered with a reflective, insulating hood to simulate dark conditions and measure ecosystem respiration
182 (R_{eco}), which includes both autotrophic (R_a) and heterotrophic (R_h) respiration. R_{eco} measurements were
183 conducted at similar intervals and durations as those for NEE. Gross primary production (GPP) was
184 calculated as the difference between NEE and R_{eco} , following the expression proposed by Samaritani et al.
185 (2011), Beetz et al. (2013), and Eickenscheidt et al. (2015):

$$186 \quad NEE = GPP + R_{eco} \quad (1)$$

187 Between each measurement, the chamber was ventilated by gently shaking it to restore ambient CO₂
188 concentration. Two complete measurement cycles were conducted per extraction area and sampling day:
189 one between 9:00 and 13:00 h, and another between 14:00 and 18:00 h during the growing season; and
190 from 8:30 to 12:30 h and 13:00 to 17:00 h during the non-growing season. This schedule aimed to capture
191 the diurnal variation in environmental conditions. CO₂ flux rates were calculated based on the linear
192 change in CO₂ concentration over time (Brown et al., 2017; Pavelka et al., 2018; Laine et al., 2019),
193 considering the chamber volume, surface area, internal temperature, and atmospheric pressure, in
194 accordance with the ideal gas law (Wright et al., 2011; Järveoja et al., 2018). Fluxes were derived by fitting
195 a linear regression, following methods described in previous studies (Riutta et al., 2007; Juszczak et al.,
196 2012; Murray et al., 2017; D'Angelo et al., 2021). Only measurements with regression R² values ≥ 0.90
197 were considered. The atmospheric sign convention was used to interpret CO₂ exchange, whereby positive
198 fluxes indicate net CO₂ emissions from the ecosystem, and negative fluxes represent net CO₂ uptake by
199 the ecosystem (Elsgaard et al., 2012; Järveoja et al., 2018).



200 **2.3. Environmental variable data recording**

201 During CO₂ flux measurements at each site, we recorded environmental variables considered relevant for
202 evaluating their relationship (positive, negative, or neutral) with the components of annual and seasonal
203 CO₂ fluxes (GPP, R_{eco}, and NEE). In this context, the water table level (WT) was measured using perforated
204 PVC piezometers (1 m depth, 75 mm diameter), with holes every 10 cm, installed 0.5 m from the edges of
205 each sampling unit. WT depth was recorded using a pressure transducer (Keller model DCX-22,
206 Switzerland). Additionally, during each chamber installation, the following variables were recorded:
207 incident photosynthetically active radiation (PAR) using a quantum sensor (Apogee model MQ-200, Utah,
208 USA); soil temperature and volumetric moisture content at depths of 5 and 10 cm (ST₅, ST₁₀, SMC₅, SMC₁₀)
209 using a stainless-steel probe (RK520-01 sensor, Rika Electronics Tech, China); and air temperature and
210 relative humidity outside the chamber using a thermohygrometer (Extech model 444703, Taiwan).

211 An automated weather station (model UC-NCR-VIA-10-S100-HOBO U30, USA) was installed in the study
212 area to continuously record various environmental variables. The weather station was placed 30 m south
213 of the L-ea site and was programmed to record data every 30 minutes for the following variables: air
214 temperature (T_{air}), relative humidity (RH), precipitation (Pp), solar radiation (SR), atmospheric pressure
215 (AP), photosynthetically active radiation, water table level, and soil temperature and moisture at depths
216 of 5 and 10 cm.

217 **2.4. Modelling of CO₂ flux components (GPP, R_{eco}, and NEE)**

218 Ecosystem respiration in peatlands is primarily influenced by air and soil temperature (Updegraff et al.,
219 2001; Lafleur et al., 2005; Juszczak et al., 2013; Swails et al., 2022; Rankin et al., 2023). Therefore, R_{eco} is
220 commonly modeled as an exponential or polynomial function of temperature (Kelly et al., 2021; Swails et
221 al., 2022). In this context, Lloyd & Taylor (1994) proposed that the relationship between R_{eco} and
222 temperature can be accurately described by an Arrhenius type equation, in which the effective activation
223 energy for respiration varies inversely with temperature. The exponential regression model suggested by



Lloyd and Taylor (1994) has demonstrated high reliability in various studies assessing CO₂ fluxes in different types of peatlands (Elsgaard et al., 2012; Beetz et al., 2013; Eickenscheidt et al., 2015; D'Angelo et al., 2021), and was selected in this study to model R_{eco}:

$$R_{eco} = R_{ref} \times \exp \left[E_0 \left(\frac{1}{T_{ref} - T_0} - \frac{1}{T_{soil} - T_0} \right) \right] \quad (2)$$

Where R_{eco} is the measured ecosystem respiration rate, R_{ref} is respiration at the reference temperature, E_0 is the activation energy (K), T_{ref} is the reference temperature (283.15 K), T_0 is the constant baseline temperature for the onset of biological processes (227.13 K), and T_{soil} is the best fit temperature variable among those recorded in the study, i.e., T_{air} , ST_5 , or ST_{10} .

R_{ref} and E_0 were calculated using field measured R_{eco} data through the Microsoft Excel® Solver add-in (Beyer & Höper, 2015; Baird et al., 2019). In this case, the objective function was to minimize model error (Eq. 2), obtained by summing the squared differences between observed and modeled R_{eco} values (Baird et al., 2019). The selected R_{ref} and E_0 values were those generated by a model adjusted according to the temperature variable (T_{air} , ST_5 , or ST_{10}) that produced the highest coefficient of determination (R^2) from a linear regression between modeled and observed data. Linear interpolation was used to estimate R_{ref} and E_0 values between successive field campaigns. R_{eco} fluxes were then calculated at 30-minute intervals using temperature data recorded by the weather station (Beyer & Höper, 2015; Eickenscheidt et al., 2015), which allowed the calculation of daily, seasonal, and annual R_{eco} fluxes.

On the other hand, light availability, expressed as irradiance (PAR), plays a crucial role in estimating GPP in peatlands, due to its influence on species specific photosynthetic rates under non-limiting light conditions (Peichl et al., 2018). In general, the relationship between PAR and GPP can be described by a rectangular hyperbolic function of the Michaelis-Menten type (Michaelis & Menten, 1913; Johnson & Godoy, 2011; Laine et al., 2016). Therefore, this approach was adopted in the present study, given its



246 widespread use in research on various types of peatlands (Baird et al., 2019). The model used was the
247 following:

$$248 \quad GPP = \frac{GPP_{max} \times \alpha \times PAR}{GPP_{max} + \alpha \times PAR} \quad (3)$$

249 Where PAR is the photon flux density of photosynthetically active radiation, α is the initial slope of the
250 regression curve associated with light use efficiency, and GPP_{max} is the upper limit of production rate as
251 PAR approaches infinity (Beetz et al., 2013).

252 The same methodological approach used to determine R_{eco} model parameters was applied here, using the
253 Excel Solver add in to estimate α and GPP_{max} . Values for both parameters between successive field
254 campaigns were obtained through linear interpolation. Daily, seasonal, and annual accumulated GPP
255 fluxes were calculated from the modeled α and GPP_{max} values in combination with the PAR records stored
256 by the weather station at 30-minute intervals. To account for the reflection and absorption of incoming
257 radiation by the transparent chamber, PAR values were reduced by 5% for GPP modeling, following
258 Eickenscheidt et al. (2015).

259 Additionally, seasonal NEE records were reconstructed at 30-minute intervals for each study site using Eq.
260 (1). In this calculation, modeled GPP values were treated as negative (indicating CO_2 uptake), while R_{eco}
261 values were treated as positive (representing CO_2 release to the atmosphere), in accordance with the
262 atmospheric sign convention (Baird et al., 2019).

263 **2.5. Statistical analyses**

264 Data for the CO_2 flux components obtained from the sampling units (SUs) at each site were averaged to
265 avoid pseudoreplication (Järveoja et al., 2016; Peichl et al., 2018). Consequently, site level means were
266 calculated by averaging the values from the six SUs per site (Swails et al., 2022). The normality of GPP, R_{eco} ,
267 and NEE datasets was assessed with the Kolmogorov–Smirnov test; because the data deviated from



normality, non-parametric tests were applied. We used the Kruskal–Wallis analysis of variance (ANOVA) followed by Dunn’s multiple comparison test with Bonferroni correction to evaluate the significance of differences in CO₂ fluxes (GPP, R_{eco}, and NEE) among sites (Heinemeyer et al., 2018; Viru et al., 2020; Swails et al., 2022). In all cases, *p*-values < 0.05 were considered statistically significant. To identify the main environmental drivers of CO₂ fluxes, we performed partial least squares regression (PLS-R) analysis (Bayer et al., 2012; Peichl et al., 2014). PLS-R transforms predictor variables into orthogonal components, providing a solution to multicollinearity in multiple linear regression and reducing data dimensionality (Vega-Vilca & Guzmán, 2011). This method was selected because several environmental variables were highly correlated. It reduced the set of predictors to a smaller number of uncorrelated principal components, thereby preventing instability in regression coefficients. The PLS-R analyses used the nonlinear iterative partial least squares (NIPALS) algorithm, Jackknife cross validation, and variable importance in projection (VIP) scores to evaluate the influence of each environmental factor. All statistical analyses were carried out with XLSTAT software.

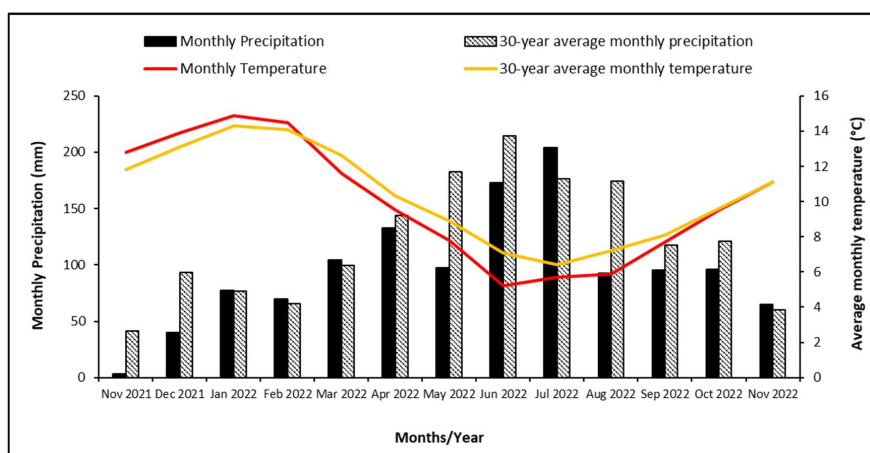
3. Results

3.1. Meteorological conditions

Total precipitation recorded during the study period was 1250 mm, representing a 20.2% deficit compared to the 30-year historical annual average (1567 mm; 1991–2020). The months with the greatest rainfall deficits relative to the historical average were December, August, and May, with deficits of 57%, 47%, and 46%, respectively. Conversely, the months with the highest surplus compared to historical values were July and February, with surpluses of 15% and 6%, respectively. During the study period, the highest monthly precipitation was recorded in June and July, with 172 mm and 204 mm, respectively. The driest months were November and December, with 67 mm and 40 mm, respectively (Fig. 2). The average air temperature during the study period was 10.1 °C, which was 0.4 °C lower than the 30-year historical mean (1991–2020). However, the months of November, December, January, and February recorded monthly



mean temperatures above historical averages. In contrast, May and June exhibited the lowest deviations below the historical mean (Fig. 2). The highest monthly mean air temperature was observed in January (14.9 °C), and the lowest in June (5.2 °C).



295

296 **Figure 2.** Records of monthly total precipitation and monthly mean temperature during the study period,
297 and their comparison with 30-year historical records (1991–2020).

298

299 3.2. Annual behavior of environmental variables

300 Annual analysis of SMC₅ revealed significant differences among the three sites ($H = 213.9$; $p < 0.0001$), with
301 H-ea recording the highest values and N-ea the lowest. Dunn's pairwise multiple comparison test also
302 indicated statistically significant differences among all sites ($p < 0.0001$). The annual mean SMC₅ across the
303 sites was 0.389 ± 0.066 , 0.340 ± 0.047 , and $0.320 \pm 0.037 \text{ m}^3 \text{ m}^{-3}$ for H-ea, L-ea, and N-ea, respectively (Fig.
304 S1). Seasonal analysis also showed significant differences among sites within each season (summer: $H =$
305 151.1 ; $p < 0.0001$; autumn: $H = 93.7$; $p < 0.0001$; winter: $H = 196.6$; $p < 0.0001$; spring: $H = 60.2$; $p < 0.0001$).
306 Annual analysis of SMC₁₀ also exhibited significant differences among sites ($H = 38.2$; $p < 0.0001$), although
307 pairwise comparisons indicated significant differences only between N-ea and the other two sites ($p <$
308 0.0001). The annual mean SMC₁₀ values were 0.390 ± 0.036 , 0.386 ± 0.036 , and $0.402 \pm 0.048 \text{ m}^3 \text{ m}^{-3}$ for
309 H-ea, L-ea, and N-ea, respectively (Fig. S2). At the seasonal level, SMC₁₀ differed significantly among sites



in autumn ($H = 22.1$; $p < 0.0001$), winter ($H = 52.1$; $p < 0.0001$), and spring ($H = 15.6$; $p < 0.0001$), but not in summer ($H = 3.9$; $p = 0.14$). Both variables exhibited annual peaks in early July 2022, due to elevated cumulative rainfall over the preceding two days (53.6 mm), and the lowest values in late November, associated with low precipitation during the first 23 days of the month (41 mm). All three study sites recorded the highest seasonal averages of SMC_5 and SMC_{10} in winter and the lowest in summer (Table 1).

Table 1. Mean, minimum, and maximum values of seasonal daily average records of environmental variables for each study site.

Sites	Environmental Variables	Summer			Autumn			Winter			Spring		
		Min	Max	$\bar{X}$	Min	Max	$\bar{X}$	Min	Max	$\bar{X}$	Min	Max	$\bar{X}$
H-ea	SMC_5 (m^3/m^3)	0.290	0.365	0.325	0.318	0.545	0.392	0.410	0.541	0.455	0.265	0.487	0.361
	SMC_{10} (m^3/m^3)	0.326	0.396	0.359	0.359	0.533	0.403	0.385	0.572	0.418	0.302	0.425	0.366
	ST_5 ($^{\circ}C$)	16.2	24.5	20.6	4.8	19.1	13.4	5.5	16.2	13.4	10.7	22.1	17.1
	ST_{10} ($^{\circ}C$)	15.2	21.6	18.6	6.5	17.4	13.2	6.7	16.3	11.7	11.8	19.6	15.9
	WT (cm)	-2.6	-20.6	-14.4	1.7	-13.3	-7.4	2.4	-13.4	-6.1	-0.8	-20.1	-10.9
L-ea	SMC_5 (m^3/m^3)	0.270	0.322	0.294	0.289	0.450	0.342	0.355	0.448	0.386	0.332	0.406	0.320
	SMC_{10} (m^3/m^3)	0.323	0.393	0.356	0.356	0.528	0.399	0.382	0.567	0.415	0.300	0.421	0.363
	ST_5 ($^{\circ}C$)	16.3	22.6	19.6	7.5	18.4	14.1	8.1	16.3	14.1	12.1	20.7	16.9
	ST_{10} ($^{\circ}C$)	14.2	22.8	18.8	4.2	17.1	11.6	4.3	15.8	9.6	9.9	20.2	15.2
	WT (cm)	-2.6	-24.8	-17.1	1.9	-15.8	-8.5	2.5	-15.9	-6.9	-0.4	-24.2	-12.9
N-ea	SMC_5 (m^3/m^3)	0.264	0.306	0.284	0.280	0.408	0.322	0.332	0.406	0.357	0.250	0.376	0.304
	SMC_{10} (m^3/m^3)	0.318	0.410	0.361	0.362	0.589	0.419	0.396	0.641	0.439	0.287	0.448	0.371
	ST_5 ($^{\circ}C$)	14.1	20.5	17.5	5.2	16.2	11.8	5.7	14.1	11.8	9.8	18.5	14.7
	ST_{10} ($^{\circ}C$)	12.1	20.3	16.5	3.5	14.9	9.8	3.6	13.6	7.9	8.2	17.9	13.1
	WT (cm)	-8.9	-31.1	-23.4	-3.5	-22.1	-14.7	-2.7	-22.2	-13.1	-6.6	-30.4	-19.2

In addition, annual records of ST_5 showed significant differences among the study sites ($H = 66.4$; $p < 0.0001$). However, pairwise comparisons revealed no significant difference between H-ea and L-ea ($p = 0.564$), but significant differences were observed between these two sites and N-ea ($p < 0.0001$). This condition may be associated with the higher vegetation cover at N-ea, which likely absorbed more solar radiation, thereby reducing direct soil heating. The annual mean ST_5 was 15.5 ± 4.6 , 15.6 ± 3.6 , and



323 13.4 ± 3.5 °C for H-ea, L-ea, and N-ea, respectively (Fig. S3). At the seasonal level, the Kruskal–Wallis test
324 indicated significant differences among sites within each season (summer: $H = 126.9$; $p < 0.0001$; autumn:
325 $H = 27.2$; $p < 0.0001$; winter: $H = 49.8$; $p < 0.0001$; spring: $H = 42.1$; $p < 0.0001$). Soil temperature at 10 cm
326 depth (ST_{10}) also showed significant differences among the three sites ($H = 91.9$; $p < 0.0001$), with annual
327 mean values of 14.8 ± 3.3 , 13.7 ± 4.4 , and 11.8 ± 4.1 °C for H-ea, L-ea, and N-ea, respectively (Fig. S4).
328 Significant differences among sites were also observed across all seasons (summer: $H = 78.1$; $p < 0.0001$;
329 autumn: $H = 46.1$; $p < 0.0001$; winter: $H = 112.5$; $p < 0.0001$; spring: $H = 42.8$; $p < 0.0001$). For both variables,
330 the highest annual values were recorded during the first third of January 2022 at all three sites. This peak
331 was associated with higher daily average solar radiation during that period (368.7 W m^{-2}), combined with
332 low soil moisture content (Fig. S1 and S2). In addition, ST_{10} showed elevated values at the beginning of
333 summer. Conversely, the lowest annual ST_5 and ST_{10} values were recorded between the last days of May
334 and early June, due to low average air temperatures (three-day mean = 1.4 °C) and subzero minimum
335 temperatures (three-day mean = -3.3 °C), which caused morning ground frosts. Seasonally, the highest
336 mean values for both temperature variables across all sites were recorded in summer, and the lowest in
337 winter (Table 1).

338 Annual WT data also showed significant differences among sites ($H = 227.3$; $p < 0.0001$), with H-ea
339 exhibiting the highest levels (i.e., WT closer to or above the peat surface) and N-ea the lowest. The annual
340 mean WT depth at each site was -9.6 ± 5.5 cm (H-ea), -11.3 ± 6.8 cm (L-ea), and -17.6 ± 6.8 cm (N-ea)
341 (Fig. 3). Seasonal WT data also revealed significant differences among the three sites in every season
342 (summer: $H = 80.4$; $p < 0.0001$; autumn: $H = 106.3$; $p < 0.0001$; winter: $H = 84.1$; $p < 0.0001$; spring: $H =$
343 61.5 ; $p < 0.0001$). All three sites recorded their highest WT levels in early July, associated with 70 mm of
344 cumulative rainfall over the preceding three days. This led to localized flooding in parts of H-ea and L-ea,
345 with water levels surpassing the peat surface. Conversely, the deepest WT levels were recorded at all sites
346 in early February, following a 10-day period without precipitation. Across the study sites, the shallowest



seasonal WT levels (i.e., closest to the surface) were observed during winter, and the deepest during summer (Table 1).

Figure 3. (a) Mean daily water table level at the three sites during the study period; (b) mean daily photosynthetically active radiation during the study period.

Daytime mean PAR values (i.e., $\text{PAR} \geq 20 \mu\text{mol m}^{-2} \text{s}^{-1}$) recorded over the annual period averaged $433.8 \pm 341.8 \mu\text{mol m}^{-2} \text{s}^{-1}$. The highest PAR values were reached in mid January, with an average of $1178.2 \pm 7.2 \mu\text{mol m}^{-2} \text{s}^{-1}$, while the lowest readings were recorded between late June and early July, with



358 an average of $31.6 \pm 7.1 \mu\text{mol m}^{-2} \text{s}^{-1}$ (Fig. 3). Seasonal average daily PAR values were 727.2 ± 279.2 ,
359 311.1 ± 195.4 , 126.7 ± 93.4 , and $584.4 \pm 353.2 \mu\text{mol m}^{-2} \text{s}^{-1}$ for summer, autumn, winter, and spring,
360 respectively. The lowest daily average PAR values for each season occurred in early January (summer),
361 early June (autumn), late June (winter), and early in the season during spring. Conversely, the highest daily
362 average PAR values were recorded in mid January (summer), late March (autumn), mid June (winter), and
363 mid December (spring).

364 3.3. Annual and seasonal CO₂ fluxes

365 The model used to estimate GPP fluxes showed a good fit across the three study sites, with R^2 values of
366 0.94, 0.96, and 0.98, and RMSE values of 0.55, 0.57, and 0.43 for H-ea, L-ea, and N-ea, respectively,
367 indicating a strong correspondence between observed and modeled data (Fig. S5). A similar pattern was
368 observed in the R_{eco} modeling, with R^2 values of 0.88, 0.87, and 0.95, and RMSE values of 0.56, 0.46, and
369 0.49 for H-ea, L-ea, and N-ea, respectively (Fig. S6). The specific model parameters for GPP (α and GPP_{max})
370 and R_{eco} (R_{ref} and E_0) are reported by campaign and site in Tables S1–S3.

371 When considering integrated GPP fluxes over the annual period, the Kruskal–Wallis test revealed
372 significant differences among sites ($H = 21.1$; $p < 0.0001$) (Fig. 4). During the study period, the highest mean
373 daily GPP was recorded at N-ea with a value of $-9.6 \pm 5.9 \text{ g CO}_2\text{-C m}^{-2} \text{d}^{-1}$ (most negative value), followed
374 by L-ea (-8.6 ± 4.1) and H-ea ($-6.8 \pm 2.6 \text{ g CO}_2\text{-C m}^{-2} \text{d}^{-1}$). The highest daily average GPP rates at all three
375 sites occurred in mid January (DOY 11), associated with high PAR levels. Additional GPP peaks were also
376 observed in early December at H-ea and N-ea, and in late November at L-ea. The lowest mean daily GPP
377 rates were recorded in early June (DOY 157), mid July (DOY 191), and mid June (DOY 171) for H-ea, L-ea,
378 and N-ea, respectively (Fig. 5). Total accumulated GPP fluxes during the study period were -2490.1 ,
379 -3159.1 , and $-3538.2 \text{ g CO}_2\text{-C m}^{-2}$ for H-ea, L-ea, and N-ea, respectively. At the seasonal scale, the highest
380 average daily GPP was recorded in summer for H-ea and N-ea (-8.9 ± 2.3 and $-16.6 \pm 2.5 \text{ g CO}_2\text{-C m}^{-2} \text{d}^{-1}$,
381 respectively), and in spring for L-ea ($-12.3 \pm 2.4 \text{ g CO}_2\text{-C m}^{-2} \text{d}^{-1}$). Conversely, the lowest seasonal daily GPP



382 values occurred in winter at H-ea and N-ea (-4.7 ± 0.7 and -4.3 ± 0.6 g CO₂-C m⁻² d⁻¹, respectively), and in
383 autumn at L-ea (-5.3 ± 2.1 g CO₂-C m⁻² d⁻¹) (Fig. 6). Compared to summer, winter GPP decreased by 47%,
384 52%, and 74% at H-ea, L-ea, and N-ea, respectively. The highest seasonal GPP accumulation occurred in
385 spring at H-ea (-800.5 g CO₂-C m⁻²) and L-ea (-1121.1 g CO₂-C m⁻²), accounting for 32% and 35% of their
386 respective annual totals. At N-ea, the greatest GPP accumulation was recorded in summer (-1497.1 g CO₂-
387 C m⁻²), representing 42% of the annual total. The lowest seasonal GPP accumulation occurred in winter
388 for H-ea (-430.8 g CO₂-C m⁻²) and N-ea (-394.5 g CO₂-C m⁻²), corresponding to 17% and 11% of their
389 respective annual GPP. In L-ea, the lowest accumulation was observed in autumn (-485.6 g CO₂-C m⁻²),
390 which represented 14% of the site's annual GPP. Overall, seasonal comparisons of average daily GPP
391 showed minor differences between autumn and winter at L-ea, and between spring and summer at H-ea.
392 In contrast, N-ea exhibited marked differences among all seasons.

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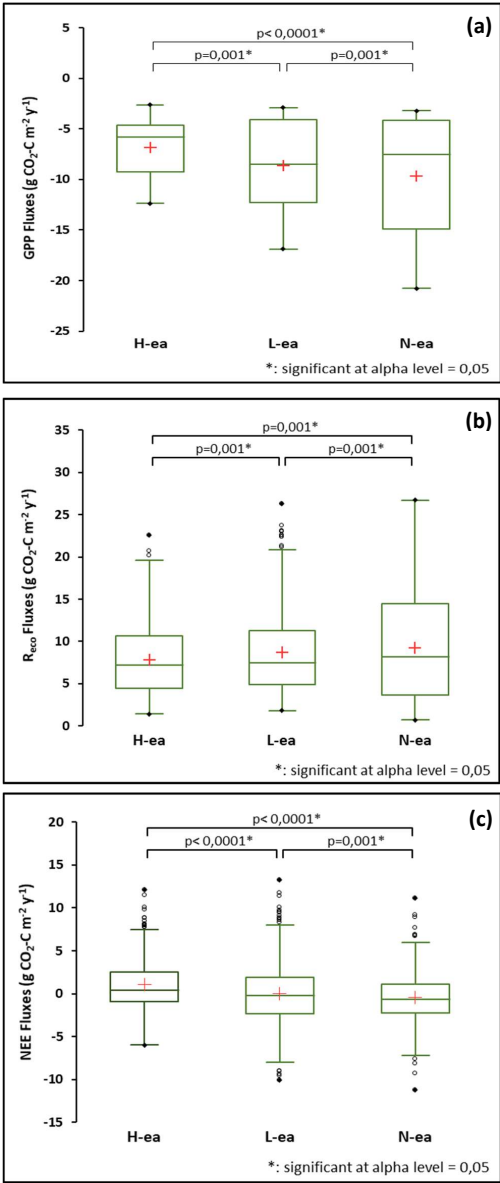
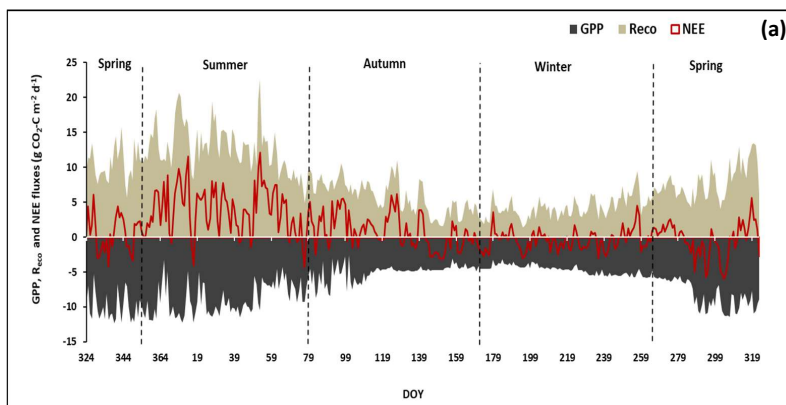


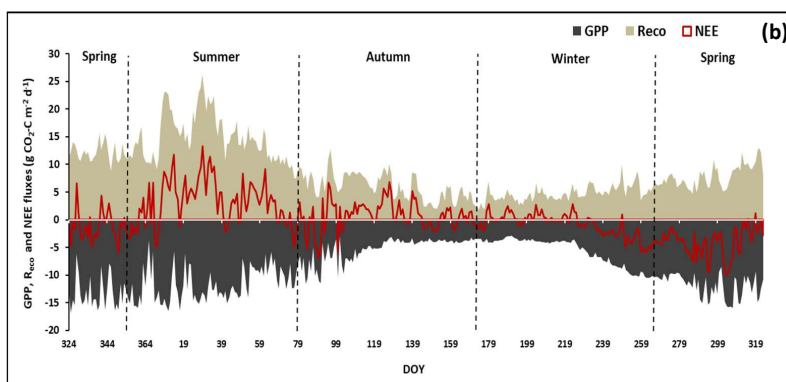
Figure 4. Boxplots of GPP (a), R_{eco} (b), and NEE (c) fluxes for each site. (Red crosses indicate mean values. Central horizontal bars represent medians. The lower and upper box edges correspond to the first and third quartiles, respectively. Black dots at the ends of the whiskers indicate the minimum and maximum values at each site. Points above or below the whisker limits may be considered outliers.)



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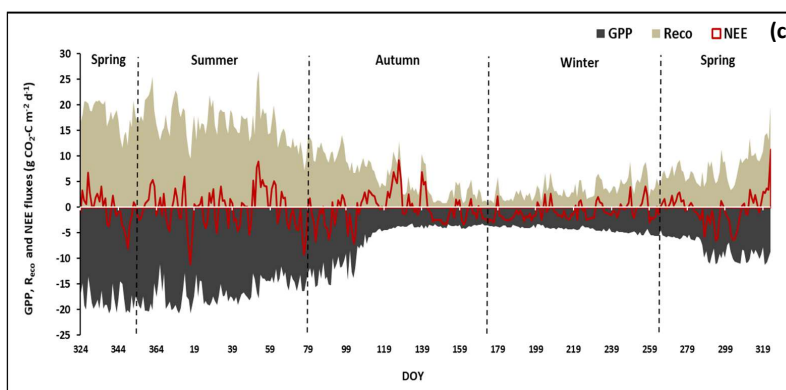
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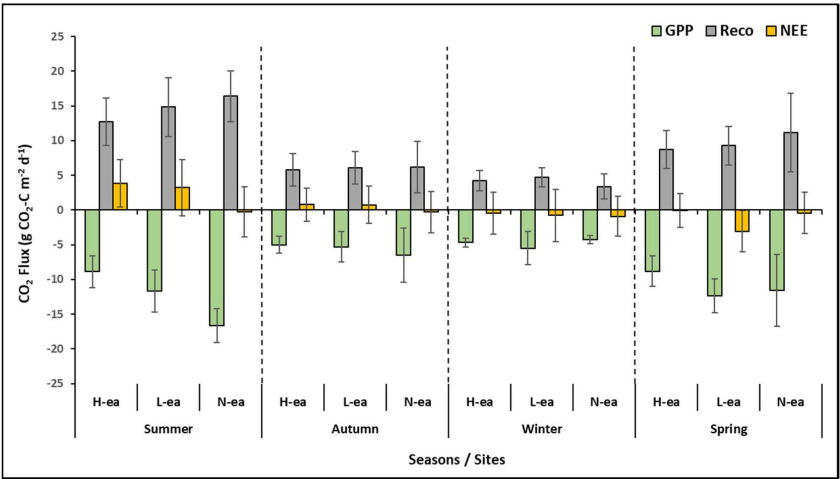
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Figure 5. Annual dynamics of GPP, R_{eco} , and NEE fluxes ($\text{g CO}_2\text{-C m}^{-2} \text{d}^{-1}$) at H-ea (a), L-ea (b), and N-ea (c).

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454

455 **Figure 6.** Seasonal GPP, R_{eco} , and NEE fluxes at the three study sites.

456

457 For annual integrated R_{eco} fluxes, the Kruskal–Wallis test revealed significant differences among sites ($H =$
458 200.7; $p = 0.001$) (Fig. 4). The highest daily mean R_{eco} fluxes were recorded in late February at H-ea and N-
459 ea (DOY 53), and in late January at L-ea (DOY 29). An additional prominent peak occurred in mid January
460 at H-ea and L-ea, and in late December at N-ea. Conversely, the lowest daily mean fluxes were observed
461 in mid July at H-ea (DOY 195), and in late June at L-ea and N-ea (DOY 174) (Fig. 5). Over the full study
462 period, the highest average daily R_{eco} was recorded at N-ea ($9.2 \pm 6.3 \text{ g CO}_2\text{-C m}^{-2} \text{ d}^{-1}$), followed by L-ea
463 (8.6 ± 4.8) and H-ea (7.8 ± 4.1) (Fig. 4). Total annual accumulated R_{eco} fluxes were 2865.7, 3169.2, and
464 3371.1 $\text{g CO}_2\text{-C m}^{-2}$ for H-ea, L-ea, and N-ea, respectively. At the seasonal scale, the highest and lowest
465 average daily R_{eco} values across all sites were recorded in summer (H-ea: 12.7 ± 3.4 ; L-ea: 14.9 ± 4.2 ; N-ea:
466 $16.4 \pm 3.7 \text{ g CO}_2\text{-C m}^{-2} \text{ d}^{-1}$) and in winter (H-ea: 4.2 ± 1.5 ; L-ea: 4.7 ± 1.4 ; N-ea: $3.4 \pm 1.8 \text{ g CO}_2\text{-C m}^{-2} \text{ d}^{-1}$),
467 respectively (Fig. 6). Compared to summer, average daily R_{eco} in winter decreased by 66%, 68%, and 79%
468 at H-ea, L-ea, and N-ea, respectively. Among all seasons, winter showed the lowest accumulated R_{eco} at all
469 three sites (H-ea: 389.2; L-ea: 433.8; N-ea: 312.2 $\text{g CO}_2\text{-C m}^{-2}$), accounting for 13%, 14%, and 9% of the



470 total annual R_{eco} , respectively. In contrast, summer recorded the highest seasonal R_{eco} fluxes (H-ea: 1145.9;
471 L-ea: 1336.4; N-ea: 1475.7 g CO₂-C m⁻²), representing 40%, 42%, and 44% of the respective annual totals.
472 Seasonal comparisons of daily average values showed marked differences between seasons at all three
473 sites.

474 Results for annual integrated NEE fluxes also showed significant differences among sites ($H = 390.4$; $p <$
475 0.0001) (Fig. 4). The annual average daily NEE values were 1.03 ± 3.04 , 0.03 ± 0.19 , and -0.46 ± 2.91 g CO₂-
476 C m⁻² d⁻¹ for H-ea, L-ea, and N-ea, respectively. Corresponding annual accumulated NEE fluxes were 375.6,
477 10.2, and -167.1 g CO₂-C m⁻², indicating that only N-ea functioned as a net CO₂ sink. L-ea was near neutral,
478 and H-ea acted as a net CO₂ source to the atmosphere (Fig. 7). Our results indicate that H-ea, L-ea, and N-
479 ea acted as CO₂ sinks for 150, 194, and 214 days of the year, respectively. The peak daily CO₂ emission at
480 each site occurred in late February at H-ea (DOY 53), late January at L-ea (DOY 29), and mid November at
481 N-ea (DOY 323). Conversely, the highest daily uptake (most negative NEE) was recorded in late October at
482 H-ea and L-ea (DOY 304), and in mid January at N-ea (DOY 17), indicating distinct seasonal patterns
483 influenced by vegetation cover and composition (Fig. 5). At the seasonal level, the highest average daily
484 emissions occurred during summer at H-ea and L-ea, with values of 3.8 ± 3.4 and 3.2 ± 4.1 g CO₂-C m⁻² d⁻¹,
485 respectively. In contrast, N-ea acted as a CO₂ sink throughout all four seasons. Notably, all three sites
486 functioned as CO₂ sinks during spring and winter; however, H-ea showed only a weak sink behavior during
487 spring. When comparing seasonal daily average NEE values, only N-ea exhibited consistent magnitudes
488 and behavior (emission or sink) between summer and autumn.

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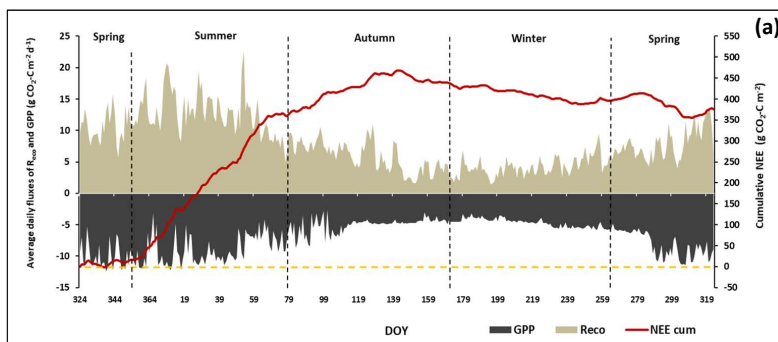
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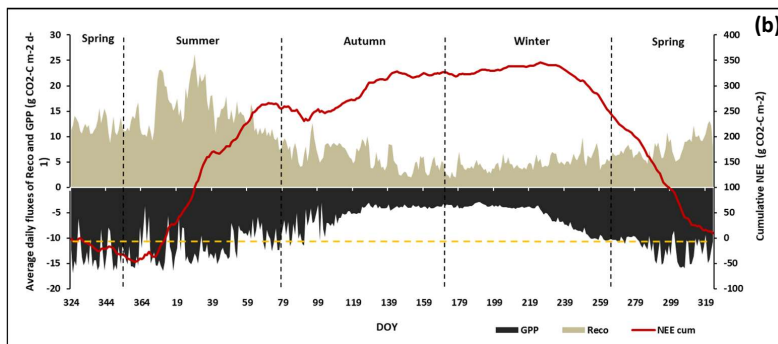
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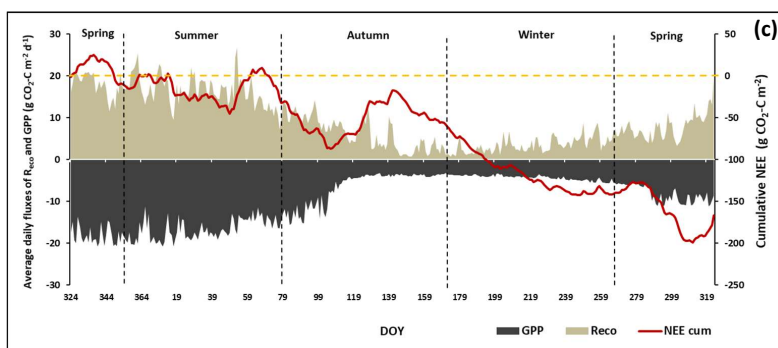
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Figure 7. Cumulative NEE fluxes (solid red line) for H-ea (a), L-ea (b), and N-ea (c). The horizontal yellow dashed line indicates the zero level of the secondary axis corresponding to cumulative fluxes

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3.4. Influence of environmental drivers on annual CO₂ fluxes

The results of the partial least squares regression (PLS-R) analysis for GPP across the different sites indicated a good model fit for H-ea and L-ea, with R^2 values of 0.73 and 0.77, respectively. In contrast, the model for N-ea showed a lower fit, with an R^2 value of 0.54. The PLS-R analysis identified PAR, T_{air} , ST_{10} and ST_5 as the most relevant drivers of GPP across all three sites. At H-ea and L-ea, only PAR surpassed the VIP threshold of 1, indicating a clearly dominant influence on GPP over the other environmental variables. At N-ea, both PAR and the temperature related variables (T_{air} , ST_{10} , and ST_5) exceeded the VIP = 1 threshold, indicating that they were the most influential on GPP at that site (Fig. 8).

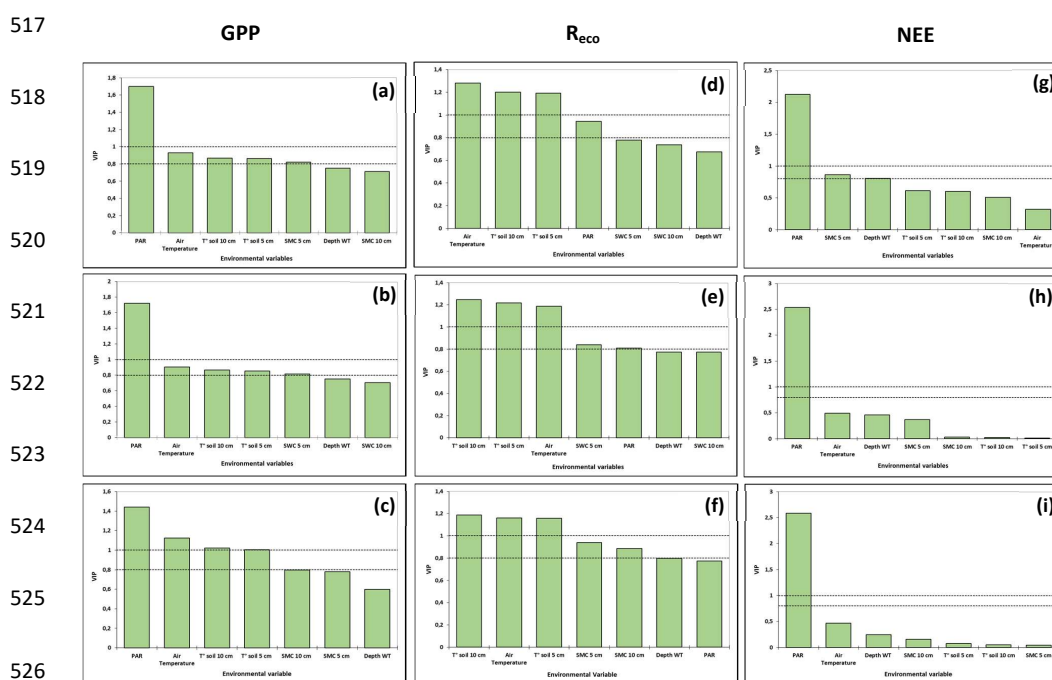


Figure 8. Variable importance in projection (VIP) scores obtained through partial least squares regression between GPP (a, b, c); Reco (d, e, f); NEE (g, h, i) fluxes and different environmental drivers. Panels (a), (d), and (g) correspond to fluxes from H-ea; (b), (e), and (h) to fluxes from L-ea; and (c), (f), and (i) to fluxes from N-ea.



532 For R_{eco} , the regression models showed good fit at all three sites, with R^2 values of 0.76, 0.75, and 0.85 for
533 H-ea, L-ea, and N-ea, respectively. The PLS-R analysis identified temperature related environmental
534 variables, either T_{air} or soil temperatures (ST_{10} and ST_5), as the most influential for R_{eco} fluxes at all sites.
535 ST_{10} was the predominant variable for R_{eco} at L-ea and N-ea, where both ST_5 and T_{air} also exceeded the VIP
536 = 1 threshold. At H-ea, the most influential variable was T_{air} , although both ST_5 and ST_{10} also surpassed the
537 VIP = 1 threshold. In addition to temperature, PAR and SMC_5 were also relevant variables for R_{eco} at the
538 sites (VIP > 0.8) (Fig. 8).

539 Finally, the PLS-R models for NEE showed the weakest fits, with R^2 values of 0.32, 0.49, and 0.33 for H-ea,
540 L-ea, and N-ea, respectively. The models clearly identified PAR as the dominant variable influencing NEE
541 fluxes across all three sites, with VIP scores exceeding 1. At H-ea, both SMC_5 and WT were also considered
542 important, with VIP scores above 0.8. In contrast, at L-ea and N-ea, no other variable exceeded a VIP of
543 0.5, indicating a predominant influence of PAR on NEE fluxes at those two sites (Fig. 8).

544 **4. Discussion**

545 **4.1. Annual CO_2 flux dynamics**

546 Analysis of the components of annual CO_2 fluxes revealed that both accumulated GPP and R_{eco} exhibited
547 high magnitudes across the three study sites. Although such high rates are not commonly reported in the
548 literature, studies on CO_2 fluxes in temperate warm peatlands in both hemispheres have yielded
549 comparable results (Campbell et al., 2014; Beyer & Höper, 2015; Valdés-Barrera et al., 2019; D'Angelo et
550 al., 2021; Gunawardhana et al., 2025), supporting our findings. Furthermore, the only previous study
551 addressing annual CO_2 fluxes in an anthropogenic peatland of northern Patagonia subject to commercial
552 *Sphagnum* harvesting (Valdés-Barrera et al., 2019) reported annual cumulative values for GPP and R_{eco} of
553 3599 ± 88 and 3567 ± 67 g CO_2 m⁻², respectively, similar to those observed in our study. The high annual
554 GPP and R_{eco} rates in this geographic region are likely associated with environmental variables such as
555 elevated PAR levels, warmer annual mean temperatures, longer photoperiods, and an extended growing



556 season (Frolking et al., 1998; Loisel et al., 2012; Helfter et al., 2015; Peichl et al., 2018). Additionally, our
557 study area receives substantial annual precipitation, favoring soil moisture conditions throughout much of
558 the year. In combination with these environmental factors, the presence of *Sphagnum* dominated
559 vegetation and perennial vascular plants, especially shrubs and trees with higher leaf area indices, helps
560 maintain year-round productivity. Similar patterns have been reported for peatlands in Australasia
561 (Campbell et al., 2014; Gunawardhana et al., 2025). The annual cumulative NEE for the undisturbed site
562 (N-ea), $-167.1 \text{ g CO}_2\text{-C m}^{-2}$, falls within the range of values reported for other undisturbed temperate
563 peatlands (Lafleur et al., 2001; Campbell et al., 2014; Helfter et al., 2015; Goodrich et al., 2017; Valdés-
564 Barrera et al., 2019).

565 Significant differences in annual GPP were observed among sites (Fig. 4), with N-ea showing the highest
566 mean daily GPP ($-9.6 \pm 5.9 \text{ g CO}_2\text{-C m}^{-2} \text{ d}^{-1}$), which was 1.4 and 1.1 times higher than values recorded at
567 H-ea and L-ea, respectively. This result can be attributed to a higher proportion of photosynthetically
568 active biomass associated with dense vascular vegetation cover, particularly juvenile and more developed
569 tree species, as well as small shrubs, both of which exhibit high leaf area indices and are composed entirely
570 of perennial species. Additionally, a continuous *Sphagnum* moss layer covered the soil surface at N-ea,
571 enhancing photosynthetic capacity (Korrensalo et al., 2016; Peichl et al., 2018; Kokkonen et al., 2022;
572 Hanson et al., 2025). Peichl et al. (2018) suggested that the coexistence and balanced proportion of
573 *Sphagnum* and vascular plant biomass are relevant to GPP in *Sphagnum* dominated peatlands. A lower
574 average WT at N-ea, particularly during the growing season, may have enhanced vascular plant
575 productivity (Sulman et al., 2010; Zhong et al., 2020), though it may also have reduced *Sphagnum*
576 productivity (Helbig et al., 2022; Kokkonen et al., 2024). Conversely, the reduced *Sphagnum* cover at H-ea,
577 resulting from commercial harvesting, and the unintended removal of vascular plants during repeated
578 moss extraction using hooks and forks (Oberpaur et al., 2018), impaired photosynthetic performance. H-
579 ea showed the lowest diversity of plant functional types, which likely limited its GPP (Ward et al., 2009;
580 Kuiper et al., 2014; Laine et al., 2022). In addition, the open site conditions at H-ea, lacking protective



581 vascular vegetation, may have compromised *Sphagnum* photosynthetic efficiency, especially during the
582 growing season (Hájek et al., 2009; Kokkonen et al., 2022).

583 In contrast, L-ea exhibited the presence of tree and shrub species, which likely facilitated *Sphagnum*
584 establishment and productivity by providing protective cover against desiccation. Furthermore, the less
585 intensive harvesting approach at L-ea allowed the site to maintain GPP levels close to those observed at
586 the undisturbed area, demonstrating that maintaining $\geq 50\%$ residual moss cover can contribute positively
587 to productivity in the short term after harvesting (Pacheco-Cancino et al., 2023). Several studies have
588 shown that in *Sphagnum* dominated peatlands, mosses play a key role in regulating GPP and the ecosystem
589 C cycle. Despite having lower photosynthetic capacity than vascular plants, they contribute the majority
590 of green biomass (Kuiper et al., 2014; Korrensalo et al., 2016; Voigt et al., 2024).

591 In peatland ecosystems, several studies have indicated that R_{eco} dynamics are primarily governed by
592 thermal and hydrological regimes (Lafleur et al., 2005; Juszczak et al., 2013; Liu et al., 2024). However, it
593 has also been noted that R_{eco} rates may be linked to vegetation photosynthetic activity and the subsequent
594 release of root exudates that stimulate microbial decomposition of peat (Bubier et al., 2003; Basiliko et
595 al., 2012; Bragazza et al., 2015; Korrensalo et al., 2020). Based on these insights, we can hypothesize that
596 differences in R_{eco} fluxes among study sites (Fig. 4) may be associated with such drivers. R_{eco} dynamics were
597 likely influenced by the soil thermal regime (ST_5 and ST_{10}), particularly during the growing season, a pattern
598 consistent with findings from northern hemisphere temperate peatlands (Updegraff et al., 2001; Lafleur
599 et al., 2005; Juszczak et al., 2013). Nevertheless, the lower soil temperature averages (ST_5 and ST_{10})
600 observed at N-ea would have been expected to reduce R_{eco} by limiting microbial activity, but this was not
601 the case. On the contrary, N-ea exhibited the highest R_{eco} rates during the study period, which is
602 inconsistent with the typically reported effects of soil temperature on R_{eco} . Differences in R_{eco} among sites
603 may instead be linked to WT behavior. In this case, the higher respiration rates observed at N-ea may have
604 been associated with a consistently deeper WT throughout the year (Fig. 3), which likely promoted aerobic
605 decomposition of organic matter (Strack et al., 2014; Wilson et al., 2016; Górecki et al., 2021). Conversely,



shallower WT levels at H-ea and L-ea may have helped to reduce annual R_{eco} rates. Thus, at N-ea, the WT may have been a stronger driver of R_{eco} than the soil thermal regime, a condition also experimentally supported by previous studies (Munir et al., 2015; Pearson et al., 2015; Laine et al., 2019). Additionally, higher photosynthetic rates at N-ea, associated with greater biomass of *Sphagnum* and vascular plants, may have enhanced microbial activity and R_{eco} through the release of root exudates. In this regard, Crow & Wieder (2005) reported that vascular plants can contribute between 35% and 57% of the total surface peat respiration, mainly through rhizosphere processes, including root respiration and microbial mineralization of root exudates. With regard to NEE, H-ea functioned as a strong annual CO_2 source ($375.6 \text{ g } CO_2\text{-C m}^{-2} \text{ yr}^{-1}$) (Fig. 7), as GPP was not sufficient to offset site level R_{eco} , especially during the growing season. This condition was driven by reduced *Sphagnum* cover due to intensive harvesting and lower vascular plant biomass (Kuiper et al., 2014). In contrast, L-ea approached CO_2 neutrality ($10.2 \text{ g } CO_2\text{-C m}^{-2} \text{ yr}^{-1}$) (Fig. 7), likely due to greater *Sphagnum* cover after harvesting and a higher proportion of herbaceous and small shrub species, which contributed to increased GPP. This suggests that maintaining >50% residual moss cover after harvest may help mitigate the impacts of this anthropogenic disturbance on annual CO_2 fluxes. Similar values have been reported by Valdés-Barrera et al. (2019) for a peatland in northern Chiloé Island subject to commercial moss harvesting and livestock grazing, with an annual NEE of $-35 \text{ g } CO_2\text{-C m}^{-2} \text{ yr}^{-1}$. Finally, N-ea acted as a significant CO_2 sink during the year ($-167.1 \text{ g } CO_2\text{-C m}^{-2} \text{ yr}^{-1}$) (Fig. 7), due to continuous *Sphagnum* cover and a high proportion of perennial arboreal and shrubby vascular vegetation, which supported increased GPP, particularly during the growing season, exceeding R_{eco} (Zhong et al., 2020). Similar values were reported by Valdés-Barrera et al. (2019) for a section of anthropogenic peatland that had remained undisturbed for more than 40 years ($-135 \text{ g } CO_2\text{-C m}^{-2} \text{ yr}^{-1}$). Likewise, studies in undisturbed temperate *Sphagnum* dominated peatlands in Australasia indicate these ecosystems act as significant net C sinks, with reported values of $-292.5 \text{ g C m}^{-2} \text{ yr}^{-1}$ (Gunawardhana et al., 2025) and $-234.3 \text{ g C m}^{-2} \text{ yr}^{-1}$ (Campbell et al., 2014). Previous research in Finland (Silvan et al., 2017; Karjalainen et al., 2025) also confirms that *Sphagnum* harvesting areas show a reduced CO_2 sink capacity compared to undisturbed areas. Therefore, maintaining continuous *Sphagnum* moss cover is essential for peatlands to sustain their



632 function as CO₂ sinks (Brown et al., 2017; Purre et al., 2019; Kasimir et al., 2021; Pacheco-Cancino et al.,
633 2023).

634 **4.2. Seasonal dynamics of ecosystem net exchange**

635 Annual NEE fluxes exhibited characteristic seasonal variations, with substantial daily fluctuations at all
636 three sites, particularly during summer and spring, moderate in autumn, and low during winter, except for
637 the final weeks of that season at the L-ea site (Fig. 5). Similar patterns have been observed in other studies
638 of temperate peatlands in the Southern Hemisphere (Gunawardhana et al., 2025).

639 Distinct patterns of CO₂ emission and uptake were observed across sites at the seasonal scale (Fig. 6). The
640 highest CO₂ emissions occurred during summer at H-ea and L-ea, with mean daily fluxes of 3.8 ± 3.4 and
641 3.2 ± 4.1 g CO₂-C m⁻² d⁻¹, respectively. This may be attributed to increased R_{eco} driven by enhanced
642 microbial activity associated with elevated air and soil temperatures and declining water table levels
643 (Chivers et al., 2009; Helfter et al., 2015; Ofiti et al., 2021; Nielsen et al., 2023). Additionally, at H-ea,
644 approximately 20% of the area consisted of bare peat patches resulting from repeated intensive
645 harvesting. Previous studies have indicated that bare peat surfaces tend to increase R_{eco} rates during
646 warmer periods compared to vegetated areas, as direct exposure to the atmosphere accelerates organic
647 matter oxidation and heterotrophic respiration (Waddington & Warner, 2001; Petrone et al., 2003; Purre
648 et al., 2019). Furthermore, lower moss and vascular plant cover at H-ea and L-ea meant that
649 photosynthetic activity was insufficient to offset R_{eco}, contrasting with the conditions at N-ea, as also noted
650 in other studies (McNeil & Waddington, 2003; Waddington et al., 2010; Kuiper et al., 2014). During
651 autumn, H-ea and L-ea remained CO₂ sources, though with lower average daily values than in summer (H-
652 ea: 0.8 ± 2.4 ; L-ea: 0.7 ± 2.6 g CO₂-C m⁻² d⁻¹), due to declining R_{eco} driven by cooler temperatures and
653 reduced photosynthetic activity associated with decreased PAR (AminiTabrizi et al., 2022; Antala et al.,
654 2022). In contrast, N-ea functioned as a CO₂ sink, a condition also reported for other undisturbed
655 temperate peatlands (Campbell et al., 2014), likely because *Sphagnum* mosses remain important



656 photosynthesizers during early spring and late autumn, when PAR is low (Korrensalo et al., 2017).
657 Surprisingly, all three sites acted as CO₂ sinks during winter, an uncommon observation in the literature,
658 as most evidence on this season derives from boreal and subarctic peatlands in the Northern Hemisphere
659 (Bubier et al., 1998; Alm et al., 1999; Aurela et al., 2001; Aurela et al., 2002; Bäckstrand et al., 2010). In
660 those ecosystems, CO₂ emissions tend to be high due to the cessation of photosynthesis under persistent
661 snow cover, frozen soils (temperatures < 0 °C), and the dormancy or senescence of vegetation under low
662 PAR (Alm et al., 1999; Aurela et al., 2001; Bubier et al., 2002). Northern temperate peatlands have also
663 shown low winter emissions (~11 µg CO₂ m⁻² s⁻¹) (Lafleur et al., 2001; Lund et al., 2007). In contrast,
664 meteorological conditions in our study area during winter (precipitation and temperature) were more
665 favorable for the continued productivity of *Sphagnum* and vascular plants, albeit at lower rates (Küttim et
666 al., 2019; Bengtsson et al., 2020). Küttim et al. (2019) noted that, under suitable conditions, moss
667 productivity during winter can account for 5–10% of annual totals, depending more on meteorological
668 conditions than on plant ecophysiology or microsite characteristics. In the North Patagonian winter, the
669 temperate oceanic climate (mean daily air temperature = 5.9 °C, with few frost days), sufficient PAR for
670 photosynthetic activity (mean = 126 µmol m⁻² s⁻¹, with > 200 µmol m⁻² s⁻¹ recorded during 10% of daytime
671 hours) (Haraguchi & Yamada, 2011), and high rainfall frequency and quantity (Krebs et al., 2016) likely
672 supported winter productivity at all study sites. These factors suggest that *Sphagnum* may have continued
673 to grow during winter, contributing to the CO₂ sink condition (Malmer et al., 2003; Chong et al., 2015), a
674 phenomenon also reported for a warm temperate peatland in Georgia (Transcaucasus) with similar
675 climatic conditions (Krebs et al., 2016). Moreover, the fact that all vascular plant species recorded at the
676 three sites were perennials may have further supported GPP. Similar findings were reported by Campbell
677 et al. (2014) for a temperate peatland in New Zealand. In addition, during winter, all three sites exhibited
678 the shallowest WT levels, which likely reduced R_{eco} rates by limiting aerobic oxidation of organic matter.
679 Finally, we acknowledge the possibility that the GPP model may have overestimated winter productivity,
680 as it does not account for reduced photosynthetic efficiency during this period (Shaefer et al., 2012).
681 During spring, all three sites acted as CO₂ sinks, a condition also documented in other temperate peatlands



682 in the Southern Hemisphere (Campbell et al., 2014; Gunawardhana et al., 2025). However, H-ea exhibited
683 a very weak daily mean uptake ($-0.05 \pm 2.5 \text{ g CO}_2\text{-C m}^{-2} \text{ d}^{-1}$) compared to L-ea (-3.1 ± 2.9), where the
684 highest seasonal cumulative NEE of the year was recorded. An early onset of the growing season,
685 facilitated by warmer air temperatures (Fig. 2), and greater moss, forbs, and shrub cover (compared to H-
686 ea), may have extended the photosynthetic period and enhanced spring sink strength (Peichl et al., 2015;
687 Antala et al., 2022).

688 **4.3. Environmental drivers of annual CO₂ fluxes**

689 The PLS-R models consistently identified PAR as the most influential variable for GPP across the three study
690 sites (VIP > 1), followed by variables associated with air and soil thermal regimes (T_{air} , ST_{10} , and ST_5), in
691 agreement with several studies conducted in temperate peatlands (Loisel et al., 2012; Järveoja et al., 2018;
692 Purre et al., 2019; Carbone et al., 2023). In the case of *Sphagnum* GPP, Loisel et al. (2012) found that
693 PAR was the primary predictor of moss growth based on a global dataset, reporting low productivity rates
694 in cold climates with short growing seasons and low light availability, consistent with earlier observations
695 by Hayward & Clymo (1983). Other studies have also reported that temperature positively influences moss
696 growth in late summer and autumn, particularly for *S. magellanicum*, the dominant species at our study
697 sites (Krebs et al., 2016; Walker et al., 2017; Bengtsson et al., 2020). Moore et al. (2006) indicated that soil
698 temperature, more so than air temperature, shows a strong correlation with increased GPP in temperate
699 peatlands. Meanwhile, photosynthesis in vascular vegetation is strongly driven by PAR and either air or
700 soil temperature in mid latitude peatlands, where both factors determine photosynthetic efficiency and
701 ecosystem scale carbon balance (Frolking et al., 1998; Strack et al., 2006; Riutta et al., 2007).

702 For R_{eco} , the PLS-R model identified T_{air} and soil temperatures (ST_{10} and ST_5) as the main environmental
703 drivers. Our results are consistent with previous studies that identified thermal regimes as the dominant
704 environmental controls on temporal variation in R_{eco} in peatlands (Lafleur et al., 2005; Mäkiranta et al.,
705 2009; Juszczak et al., 2012; Juszczak et al., 2013), as warmer temperatures stimulate microbial activity,



706 resulting in increased CO₂ emissions. Some studies have shown that temporal variation in R_{eco} is tightly
707 linked to peat temperature at 5 cm depth, explaining up to 94% of daily variation in some cases (Juszczak
708 et al., 2013). Additionally, research in southeastern U.S.A. peatlands found that soil respiration increases
709 with temperature, peaking at 25 °C, and that respiration sensitivity to temperature (Q₁₀) tends to increase
710 with greater mean annual water table depth (Swails et al., 2022), a pattern observed at the N-ea site.
711 These findings highlight the importance of surface air and soil temperatures as key drivers of R_{eco} in
712 temperate peatlands.

713 Finally, the PLS-R model identified PAR as the most influential driver of annual NEE at all three study sites
714 (VIP > 1). Soil temperature and SMC_s were ranked much lower, with VIP values < 0.5. Studies in boreal
715 peatlands confirm that NEE responds significantly to variations in PAR, especially during the growing
716 season (Bubier et al., 1998), as observed at N-ea. Similarly, in restored peatlands, increases in PAR have
717 been shown to enhance daytime CO₂ uptake (D’Acunha et al., 2019). Helbig et al. (2022), in a study of 20
718 Northern Hemisphere peatlands, found that mean site level annual CO₂ uptake increased with higher
719 mean incident radiation, highlighting light availability as an important control on annual NEE fluxes. PAR
720 exerted a decisive influence at all three sites, as evidenced by high daily NEE variability during the growing
721 season (November to April), when PAR levels peaked. In contrast, during winter and late autumn, NEE
722 variability decreased due to the more uniform behavior of PAR.

723 5. Conclusions

724 Our study successfully quantified annual and seasonal CO₂ fluxes using closed chambers in a temperate
725 peatland of northern Patagonia following commercial harvesting of *Sphagnum magellanicum* under
726 different extraction intensities, and compared them to an undisturbed reference site.

727 The annual cumulative GPP and R_{eco} fluxes were high across all three study sites compared to those
728 reported for temperate peatlands in the Northern Hemisphere. This condition was associated with
729 environmental variables that support greater productivity of mosses and dominant perennial vascular



730 vegetation. The cumulative NEE fluxes measured at the undisturbed site fell within the range reported for
731 intact temperate peatlands in the Southern Hemisphere.

732 The intensity of commercial *Sphagnum* harvesting was directly correlated with annual NEE fluxes: the high
733 intensity extraction site acted as a strong CO₂ source, the moderate intensity site exhibited near neutrality,
734 and the undisturbed site functioned as an annual net CO₂ sink.

735 Seasonal NEE fluxes showed significant daily variations at all three sites during summer and spring, which
736 stabilized by late autumn and throughout winter. The strongest CO₂ source behavior at disturbed sites
737 occurred during summer, while the largest sink activity was observed during spring. The undisturbed site
738 consistently captured CO₂ year-round. During winter, all three sites acted as CO₂ sinks due to less
739 restrictive meteorological conditions that favored productivity and minimized respiration losses.

740 Annual GPP and NEE fluxes were driven by PAR, while R_{eco} was primarily controlled by air and soil thermal
741 regimes, indicating that whether a peatland acts as a CO₂ source or sink is mainly determined by vegetation
742 composition and cover, and their interaction with bioclimatic variables that influence productivity.

743 Our study provides valuable insights to bridge existing knowledge gaps and advance the understanding of
744 CO₂ flux dynamics associated with commercial *Sphagnum* harvesting in temperate peatlands of the
745 Southern Hemisphere. Furthermore, our findings may inform new policy proposals related to the
746 conservation and sustainable management of peatlands in northern Patagonia.

747

748 **Data Availability.** All data presented in this study will be available at the time of publication.

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751



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