



# Interactions and Covariation of Ecological Drivers Control CO<sub>2</sub> Fluxes in an Alpine Peatland

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## Abstract

Peatland ecosystems are a highly effective long-term carbon sink. However, the CO<sub>2</sub> fluxes could be substantially altered by climate changes and the fate of carbon stored in these ecosystems is still uncertain. Currently, most studies concerning the carbon fluxes in peatlands were performed at high latitude sites, where these ecosystems are more widely distributed compared to temperate regions, where peatlands are less frequent and, in addition to climate pressure, increasingly threatened by human activities. However, the information we have on these peatlands is very scarce. To fill this knowledge gap, we studied CO<sub>2</sub> fluxes in an alpine peatland, through light and dark incubations. Using the natural variation in ecological conditions, we identified the main drivers of CO<sub>2</sub> fluxes, considering in particular their interactions and covariation. Ecosystem respiration and gross primary production were primarily stimulated by the lowering of the water table and the amount of photosynthetic radiation, respectively, whereas net ecosystem CO<sub>2</sub> exchange showed greater variation along the growing season. The influence on CO<sub>2</sub> fluxes of the interactions between the drivers investigated, including soil temperature and moisture as well as vegetation type and plant functional diversity, was found to be of pivotal importance. Finally, a substantial part of the variation in CO<sub>2</sub> emission and uptake processes was regulated by the joint variation of atmospheric and edaphic factors. To understand and predict the CO<sub>2</sub> dynamics of alpine peatlands, it is necessary to consider the interplays among ecological factors, especially in relation to the expected changes in climate and vegetation.

**Keywords** Alpine peatland · Ecosystem respiration · Gross ecosystem production · Net ecosystem exchange · Plant functional diversity · Ecological drivers

## Introduction

Peatlands are ecosystems that store more carbon than any other terrestrial ecosystem (Dise 2009). Covering only about 3% of Earth's land area, they hold the equivalent of half the C that is in the atmosphere as CO<sub>2</sub> and store approximately one-third of the global soil C pool estimated as  $455 \times 10^{15}$  g C (Gorham 1991; Yu et al. 2010; Ciais et al. 2013), which is twice as much as all forest C storage on the Earth (Fekete et al. 2017).

C accumulation in the soil depends on the differences between C fixation through primary production, and losses resulting from biological, chemical or physical

decomposition of plant-derived C. Its accumulation in peatlands is primarily the result of slow decomposition rates of plant litter under standing water or saturated soil conditions (Freeman et al. 1996; Clymo et al. 1998).

Peatlands are well known to be a long-term sink for atmospheric CO<sub>2</sub>, but the CO<sub>2</sub> fluxes could be substantially altered in a changing climate, because emissions from peat soils are positively related to temperature and water-table depth, both of these likely affected by climate change (Strack et al. 2006; Gerdol et al. 2008). In particular, dryness determined by decreasing water table and/or eutrophication induced by increasing temperatures accelerating nutrient cycling are expected to reduce net C sequestration by accelerating C losses either as dissolved organic C (Strack et al. 2008) or as gaseous CO<sub>2</sub> emissions (Gallego-Sala et al. 2018). The latter, transforming peatlands from sinks into sources of atmospheric C, will presumably exert a positive feedback to the climate warming (Schneider et al. 2012).

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However, these predictions do not consider the spatial variability of C accumulation and emission rates and their relationships with temperature, water table position and vegetation composition between different microtopographic zones in peatlands (Belyea and Baird 2006; Strack et al. 2006). Furthermore, whereas the main ecological drivers of CO<sub>2</sub> fluxes in peatlands are relatively well known, the interactions between multiple ecological factors and the importance of their covariation are less understood. Non additive effects of ecological factors on C fluxes in peatlands may arise not only among abiotic variables, such as soil temperature and water table, but also between biotic and abiotic factors. For instance, a lowering of the water table can lead to vegetation-specific effects. In fact, although the general effect of lower water table is to increase the flows of C, some vegetation types have a degree of self-regulation (Dise 2009), giving the C cycle of some particular vegetation types a certain degree of resilience to ecological perturbation. Such ability to self-regulate ecosystem functions is strongly dependent on biodiversity, and plant functional diversity has been recently found to be a stronger driver of C fluxes compared to taxonomical one (Milcu et al. 2014).

Peatlands are extensively located at high latitudes of the Northern Hemisphere, especially in the boreal and subarctic regions, where they cover vast areas (Mitsch and Gosselink 2000). Peat-accumulating ecosystems exist also at mid-latitudes in Central and Southern Europe, where they are mostly concentrated on mountain areas and represent only a minor component of the landscape (Gerdol et al. 2011; Essl et al. 2012; Tomaselli et al. 2018; Brancaloni et al. 2022). These temperate peatlands are home to specialized endangered species and habitats and hold, therefore, a remarkable scientific and conservation interest (Bragazza 2009). However, they are often poorly documented and located in rather densely populated areas where they are increasingly threatened by human activities that include agriculture, forestry and peat extraction (Essl et al. 2012; Grzybowski and Glińska-Lewczuk 2020). In a possible scenario, characterized by a combination of increasing temperatures and possible decreasing summer precipitation for temperate Europe (Fronzek et al. 2012), these ecosystems could be subject to ground water levels decrease, and peat mineralization increase with feedback release of greenhouse gases (Succow and Joosten 2001). However, still little scientific evidence based on measurements of the CO<sub>2</sub> and CH<sub>4</sub> exchanges is presently available because information on peatland ecosystems of this part of Europe has been missing so far with only a few exceptions (Bortoluzzi et al. 2006; Gerdol et al. 2008; Drollinger et al. 2019; D'Angelo et al. 2021).

Although less studied and widespread than their Nordic counterpart, temperate peatlands offer interesting possibilities to better understand the functioning of peatland ecosystems globally. First, because mountain areas, where

peatlands are concentrated at mid-latitudes, are characterized both by a greater biological diversity and by greater fluctuations in space and time of climatic and soil conditions (e.g. light, temperature, soil moisture and water-table depth) compared to similar ecosystems occurring at higher latitude. Such strong variation in ecological factors naturally produces wider and more steep gradients of the main ecological drivers, both abiotic and biotic, and the analysis of this natural variation could provide useful information to predict what the future responses of these ecosystems will be in the face of the current climate crisis. Secondly, temperate zones are naturally characterized by warmer temperature regimes than arctic, subarctic, and boreal ones, and therefore can inform about how Nordic peatlands will function in a future, warmer climate. The comparative analysis of the functioning of different vegetation types, and their associated biodiversity, can also provide useful data from the perspective of the management of these environments, which are among the most threatened by current climatic changes, especially in the relict sites of mid-latitude mountains.

Here we present a study on a temperate peatland located in the Italian south-eastern Alps. The primary objective of this study was to investigate the seasonal dynamics of the CO<sub>2</sub> fluxes and to identify the principal ecological drivers, both biotic and abiotic, of the CO<sub>2</sub> exchange between the peatland and the atmosphere, with a special focus on interactions and covariation between ecologically relevant variables. To this aim we ask:

- 1) How many and which vegetation units occur in the peatland investigated?
- 2) What are the main ecological drivers and their significant interactions for Ecosystem Respiration (ER), Gross Ecosystem Exchange (GEE) and Net Ecosystem Exchange (NEE)?
- 3) How important is the covariation between biological, climatic and edaphic factors for CO<sub>2</sub> uptake and release processes?

## Methods

### Study Site

The study was conducted in a peatland lying on the bottom of “le Viote” plateau (46°01'07" N, 11°02'34" E), in the Mt. Bondone massif (south-eastern Prealps). The peatland, currently named “Torbiera delle Viote”, extends over an area with a roughly quadrangular shape of 24 ha at an average elevation of 1560 m a.s.l. (Fig. 1). The “Torbiera delle Viote” was designated as Special Area of Conservation with the Site Code IT3120050 in 2014.



**Fig. 1** Satellite image from Google Earth of the peatland studied

This peatland originated from the terrestrialization of an ancient lake basin dammed by morainic deposits mainly composed of calcareous and crystalline erratic pebbles embedded in a silt matrix accumulated after last glacial retreat (Cescatti et al. 1999). Peat depth is c. 4 m (Dalla Fior 1969). Mean annual temperature in the area is 5.5 °C and total annual precipitation is 1189 mm, with two peaks in June and October indicating a sub-equinoxial precipitation regime (Cescatti et al. 1999). Presently, the peatland consists of a complex mosaic of short-sedge fens, partly invaded by the tussocks of the grass *Molinia caerulea*, *Sphagnum* lawns and hummocks, hollows and pools (see also Bonomi and Buffa 2000).

## Field Work

### Plot Location

In 2012, 27 plots of 0.5 m × 0.5 m were positioned in all the vegetation types visually identifiable in the field based on their physiognomy. The plots were permanently delimited with 27 transparent, polycarbonate collars 10 cm high, half inserted in the soil. Floristic composition of the plots was assessed in the summer 2012 by frequency counting

of vascular species and bryophytes within 100 sub-plots of 5 cm × 5 cm of a portable grid placed on the upper border of each frame. The grid was also used to measure the distance between the top of the collar and the soil surface in 25 regularly spaced points, to correct the chamber volume used in CO<sub>2</sub> flux estimates.

### CO<sub>2</sub> Flux Measurements

The study of C fluxes was concentrated on CO<sub>2</sub>, which constitutes the main land to atmosphere exchange of C in peatlands (Moore et al. 2002).

Fluxes were measured in 12 sampling dates, from mid-May to mid-October 2013. In particular, flux estimates performed during the growing season were grouped in three periods based on seasonal dynamics of GEE (averaged across all the plots): (1) early-season (from 14 May to 3 June, 3 sampling dates with below average GEE), (2) mid-season (from 18 June to 18 August, 6 sampling dates with above average GEE), and (3) late-season (from 12 September to 18 October, 3 sampling dates with below average GEE).

At each sampling plot and date, NEE and ER were measured using the light and dark chamber technique (Ward et al. 2007). For the fluxes measurement, two cubic chambers

(125 dm<sup>3</sup> of volume) were used: a transparent, polymethyl-metacrylate chamber for NEE and an opaque polycarbonate chamber for ER. During measures, chambers were placed on a polycarbonate frame, that, in turn, was put on the plot collar. This frame was equipped with a water-filled groove around the top assuring watertight closure of the chamber. Each chamber was equipped with 2 sets of eutectic plates (each of 1.5 dm<sup>3</sup> of volume) to prevent temperature increase and three battery-operated fans to ensure mixing of the air during the incubation.

Instantaneous NEE and ER were measured using an EGM-4 portable infrared gas analyser (PP Systems, USA) with CO<sub>2</sub> (ppm) readings taken at about 5-second intervals over 1 minute. NEE was measured, whenever possible, in stable light conditions. In each plot and sampling date, 3 incubations were performed with both the chambers, and the linear change in CO<sub>2</sub> concentration over time was used to calculate NEE and ER rates. The average value of the 3 measures per plot was then used in the analyses. Positive NEE indicates peatland-to-atmosphere exchange dominates and negative indicates atmosphere-to-land, that is, the peat is a source and sink, respectively. GEE was calculated as the difference between NEE and ER rates.

### Ecological Variables

A variety of ecological variables were recorded to explore their relationships with CO<sub>2</sub> fluxes.

Photosynthetic Photon flux density (PPFD) was measured in  $\mu\text{mol m}^{-2} \text{s}^{-1}$  with a quantum sensor (Onset, USA) placed inside the chamber during the incubations. Synchronous with the flux measurements, air temperature at +5 cm over the soil and soil temperatures at the depths of 5 and 10 cm were measured with thermocouple thermometers (Onset, USA) within the chamber.

Water table depth was measured using a polyvinyl chloride pipe 1.6 m long and with a diameter of 1.5 cm, with perforations along its length (Fogli et al. 2014). The pipe was inserted into the peat adjacent to each plot and water-table depth was measured in each sampling date. Soil moisture was measured in each plot after incubation by means of a TDR 300 (Spectrum Technologies, USA) with 7.6 cm long rods.

Soil temperature, moisture and water table depth were considered as edaphic predictors of CO<sub>2</sub> fluxes, whereas the growing season period (3-level categorical variable), PPFD and air temperature were considered as climatic predictors.

The frequency count of plants in each plot was used to calculate the Shannon-Wiener index and, coupled with functional trait data, to compute the functional dispersion index (Laliberté and Legendre 2010) with the package FD (Laliberté and Legendre 2010) of R (R Core Team 2022). The functional traits considered included 2 categorical variables:

wide functional type (2 levels: vascular and bryophyte) and narrow functional type (10 levels: fern, forb, graminoid, deciduous shrub, evergreen shrub, acrocarpous moss turf (i.e. vertical stems with little or no branching), pleurocarpous moss turf, pleurocarpous moss weft (i.e. intertwining branched layers), *Sphagnum* tuft (i.e. forming loose cushions not dome-shaped), *Sphagnum* turf), plant height measured in the field for all the species (at least 5 replicates), and 4 numerical traits extracted from TRY database (Kattge et al. 2020): (1) specific leaf area, (2) leaf dry matter content, (3) leaf size and (4) leaf nitrogen (species and available traits in TRY are reported in Online Resource 1). These latter four traits were respectively available for 37, 37, 28 and 20 out of 49 species, respectively accounting for 81.8%, 81.7%, 80.9% and 61.9% of the total frequency of plant species in plots, or 99.9%, 99.8%, 98.9% and 69.2% excluding bryophytes.

### Data Analysis

#### Vegetation Analysis

The vegetation plots were classified with numerical procedures. The original species frequency values were transformed using the Hellinger distance (Legendre and Gallagher 2001). A cluster analysis was then performed with the Ward's minimum variance method on the transformed distance matrix. All computations concerning the numerical classification were performed in R with the 'vegan' and 'cluster' packages. The plot groups obtained by the classification corresponded to microhabitats within the peatland and represented the analysed vegetation units. The indicator species for each vegetation unity were individuated by calculating the Indicator Value (IndVal) for all the species occurring in the plots as proposed by Dufrêne and Legendre (1997). The index measures the association between a species and a plot group combining species mean abundance and its frequency of occurrence in the groups. A high indicator value is obtained by a combination of large mean abundance within a group compared to the other groups (specificity) and presence in most sites of that group (fidelity). We considered as significant indicator species those having an IndVal higher than 0.40 at  $P < 0.050$ .

#### CO<sub>2</sub> Flux Analysis

Mahalanobis distance was used to find outliers in the multivariate dataset containing the direct flux estimates of ER and NEE. Considering the Chi-square statistic of the Mahalanobis distance and a P value of 0.001 as the threshold, 5 out of 298 rows in the dataset were regarded as outliers and not included in the following analyses, which were based on 293 flux estimates for ER, GEE, and NEE.

To identify the ecological drivers of CO<sub>2</sub> fluxes and to detect their main non-additive effects, various alternative models containing different sets of fixed and random factors were fitted with the package nlme (Pinheiro et al. 2022) of R and selected following the Akaike Information Criterion (AIC). First, starting with multiple linear regression models (with REML estimation) containing all the predictors (i.e. period of the growing season, photosynthetic photon flux density, air temperature, taxonomical diversity index, functional diversity index, vegetation type, soil volumetric water content, water-table depth, and soil temperatures; during model selection, soil temperature at 10 cm depth and additional measures at depth of 15 cm (recorded with an EGM-4 temperature probe) were discarded because less related to CO<sub>2</sub> fluxes compared to 5 cm depth temperature), optimal random effect structure was selected, corresponding to a random intercept for sampling date (12-level categorical variable) for ER, GEE, and NEE models. Then, linear model assumptions were assessed by visual inspection of model residuals and homoscedasticity was achieved by including variance structures related to vegetation type (8-level categorical variable) and growing season period (3-level categorical variable) for ER, GEE, and NEE models; also in this case, different models (fitted with REML) including alternative variance components were compared by means of the AIC. Finally, minimal adequate model was selected by excluding collinear predictors (based on a threshold of the variance inflation factor of 5) and non-significant terms. Given the occurrence of correlation between fixed factors, alternative models (with ML estimation) including different sets of predictors were compared by means of the AIC. In these models, only two-way interactions between predictors were considered and, in order to obtain more parsimonious and general models, only highly significant interaction terms (with P value <0.010) were kept in the model structure.

The role of joint effects of variation in biological, climatic and edaphic factors on CO<sub>2</sub> fluxes was explored by means of the variation partitioning on CO<sub>2</sub> emission and uptake processes. To this aim, the variance (as adjusted R<sup>2</sup>) in ER and GEE explained by three sets of explanatory variables (biological, climatic and edaphic factors) was partitioned among components, and their significance tested, whenever possible, by means of partial redundancy analysis (RDA) with the package vegan (Oksanen et al. 2020) of R. With this partial canonical ordination, it is possible to test the influence on a response matrix, containing ER and GEE fluxes, of different matrices, containing alternative sets of explanatory variables, in the presence of covariables. In this way, partial RDAs allow to partition and test the amount of variance in CO<sub>2</sub> fluxes uniquely explained by different sets of predictors and to explore the contribution of the joint variation among them. Being the focus of this analysis the identification of the role of joint variation between classes of ecological

variables, forward selection of RDAs was carried out separately for biological, climatic and edaphic factors (Borcard et al. 2011). Among the biological variables we included vegetation type and plant taxonomical and functional diversity, whereas period of the growing season, air temperature, and PPFD were considered as climatic variables; finally, water-table depth and soil temperature and moisture represented the edaphic ones.

## Results

### Description of Vegetation Units

Eight plot groups were recognized in the classification dendrogram at a dissimilarity value of about 1.2 (Online Resource 2). These groups represented the vegetation units considered in the present research (Table 1). Each unit was named after the two species having the highest IndVal whenever it was possible or, in absence of indicator species, using the names of the two species exclusively occurring in the unit or having the maximum frequency within the plots of the unit. The frequency of the indicator species, as well as the frequency of all other species in each group, are shown in a synoptic table (Online Resource 3). The main features of the vegetation units are briefly described in Table 1 after having grouped them according to their habitat categories identified based on a combination of vegetation structure and ground morphology (see Gerdol et al. 2011).

### Main Drivers of CO<sub>2</sub> Fluxes

Based on the F-values of the main terms included in the models, ER, GEE and NEE are primarily controlled by different ecological factors. In particular, the depth of the water table is the main driver of ER (Table 2a), whereas GEE is mainly driven by the photosynthetic photon flux density (Table 2b). However, both the above mentioned ecological factors have a secondary role in controlling NEE, which showed the strongest variation along the growing season (Table 2c).

### Non-additive Effects of Drivers

Concerning the interplays between ecological factors, all the CO<sub>2</sub> fluxes depended on several non-additive effects of drivers (interaction terms in Table 2 and Online Resource 4).

In particular, the effect of lowering water table on ER (Table 2a) differed among vegetation types (Fig. 2a), with a strong increase of ER in fen pools and hollows (CC and EC) and a negligible effect on *Sphagnum* hummocks (SE and SC). For instance, considering air and soil temperatures of 15 °C and soil moisture of 61% during the mid-season,

**Table 1** Description of the vegetation units occurring in the peatland studied

<i>Shallow pools and fen hollows</i> : Shallow water bodies with a continuous cover of brown mosses and small sedges	
1) <i>Carex lasiocarpa-Carex limosa</i> group (CC) - 3 plots, 18 species (14 vascular plants, 4 bryophytes)	Constant and most frequent species: <i>Scorpidium cossonii</i> <i>Carex lasiocarpa</i> <i>Menyanthes trifoliata</i> <i>Valeriana dioica</i> <i>Campyllum stellatum</i>
Significant indicator species: <i>Carex lasiocarpa</i> <i>Carex limosa</i> <i>Parnassia palustris</i> <i>Menyanthes trifoliata</i>	Physiognomy: moderately species-rich fen pools whose appearance is given by small sedges (mainly <i>Carex lasiocarpa</i> and <i>C. limosa</i> ). Other common and abundant vascular species are <i>Menyanthes trifoliata</i> , and <i>Valeriana dioica</i> . <i>Molinia caerulea</i> , <i>Equisetum palustre</i> and <i>Carex rostrata</i> occur constantly, but with lower frequency. Among bryophytes, <i>Scorpidium cossonii</i> and <i>Campyllum stellatum</i> form a conspicuous carpet under the vascular plants
2) <i>Eriophorum latifolium-Carex rostrata</i> group (EC) - 3 plots, 18 species (16 vascular plants, 2 bryophytes)	Constant and most frequent species: <i>Scorpidium cossonii</i> <i>Carex rostrata</i>
Significant indicator species: <i>Eriophorum latifolium</i>	Physiognomy: moderately species-rich fen pools mostly characterized by the dominance of <i>Carex rostrata</i> . Other constant vascular species locally prominent are <i>Molinia caerulea</i> , <i>Trichophorum alpinum</i> , <i>Potentilla erecta</i> and <i>Eriophorum latifolium</i> . Also here bryophytes represent a conspicuous component of the vegetation, attaining high frequencies and forming extensive carpets with <i>Scorpidium cossonii</i> and <i>Campyllum stellatum</i>
3) <i>Aulacomnium palustre-Tomenthypnum nitens</i> group (AT) - 3 plots, 17 species (14 vascular plants, 3 bryophytes)	Constant and most frequent species: <i>Equisetum palustre</i> <i>Aulacomnium palustre</i> <i>Valeriana dioica</i>
Significant indicator species: <i>Aulacomnium palustre</i> <i>Tomenthypnum nitens</i> <i>Equisetum palustre</i> <i>Valeriana dioica</i>	Physiognomy: moderately species-rich fen hollows with extensive carpets of <i>Aulacomnium palustre</i> and <i>Tomenthypnum nitens</i> , from which most frequently emerge the culms of <i>Equisetum palustre</i> and the flowering stems of <i>Valeriana dioica</i> . Among the other vascular plants, there are with some frequency <i>Molinia caerulea</i> , <i>Menyanthes trifoliata</i> and small individuals of <i>Salix rosmarinifolia</i>
<i>Sphagnum lawns</i> : Open areas with a ground carpet of peat mosses and low herbaceous cover	
4) <i>Sphagnum subsecundum-Drosera rotundifolia</i> group (SD) - 3 plots, 14 species (12 vascular plants, 2 bryophytes)	Constant and most frequent species: <i>Trichophorum alpinum</i> <i>Molinia caerulea</i> <i>Sphagnum subsecundum</i>
Significant indicator species: <i>Sphagnum subsecundum</i> <i>Drosera rotundifolia</i> <i>Trichophorum alpinum</i> <i>Eriophorum angustifolium</i>	Physiognomy: species-poor wet <i>Sphagnum</i> lawns characterized by extensive <i>Sphagnum subsecundum</i> carpets. Among vascular species, the most frequent are <i>Trichophorum alpinum</i> and <i>Molinia caerulea</i> , that occurs with sparse tussocks. The other vascular species are represented only as scattered individuals, except <i>Drosera rotundifolia</i> and <i>Eriophorum angustifolium</i>
<i>Small-sedge fens</i> : Peatland vegetation fed by mineral-rich water with a mixture of sedges, short to medium-sized wetland herbs and a ground carpet of rich-fen bryophytes	
5) <i>Molinia caerulea-Carex davalliana</i> group (MC) - 5 plots, 21 species (20 vascular plants, 1 bryophyte)	Constant and most frequent species: <i>Molinia caerulea</i> <i>Carex nigra</i>
Significant indicator species: <i>Molinia caerulea</i>	Physiognomy: small-sedge fens with diverse composition whose general physiognomy is given by the tussocks of the grass <i>Molinia caerulea</i> , that invaded the original fen after a progressive drying of the peat. Three plots, having high frequency of <i>Carex nigra</i> , <i>C. panicea</i> , <i>Trichophorum alpinum</i> and <i>Valeriana dioica</i> and the occurrence of <i>Carex davalliana</i> and <i>C. hostiana</i> , likely preserved the original species richness and diversity of the small-sedge fen. The residual two plots are extremely species poor because the dense herbage and the thick litter of <i>Molinia caerulea</i> reduced the associated flora to very few species. Bryophytes are represented by occasional occurrences of <i>Tomenthypnum nitens</i>

**Table 1** (continued)

<i>Sphagnum hummocks</i> : Peatland microreliefs formed by <i>Sphagnum</i> mosses growing tightly packed together to form hummocks or cushions	
6) <i>Sphagnum compactum-Eriophorum vaginatum</i> group (SE) - 4 plots, 11 species (10 vascular plants, 1 bryophyte)	Physiognomy: species-poor microreliefs whose general physiognomy is given by sparse tussocks of <i>Molinia caerulea</i> intermixed with bushes of the sub-shrub <i>Calluna vulgaris</i> and most frequently accompanied by <i>Trichophorum alpinum</i> . Other vascular species occurring with some frequency are the small sedges <i>Carex nigra</i> , <i>C. echinata</i> and the forb <i>Potentilla erecta</i> . Two plots are differentiated by cushions of <i>Sphagnum compactum</i>
Significant indicator species: none; <i>Sphagnum compactum</i> occurs only in this group	Constant and most frequent species: <i>Molinia caerulea</i> <i>Calluna vulgaris</i> <i>Trichophorum alpinum</i>
7) <i>Sphagnum capillifolium-Calluna vulgaris</i> group (SC) - 3 plots, 15 species (13 vascular plants, 2 bryophytes)	Physiognomy: species-poor to moderately rich <i>Sphagnum</i> hummocks where <i>Sphagnum capillifolium</i> is accompanied by the ericaceous sub-shrub <i>Calluna vulgaris</i> . <i>Molinia caerulea</i> is constant also here, but with lower frequency values. The other species play a subordinate role, with only the ericaceous sub-shrub <i>Vaccinium uliginosum</i> subsp. <i>microphyllum</i> , and the moss <i>Polytrichum strictum</i> being occasionally frequent
Significant indicator species: <i>Sphagnum capillifolium</i> <i>Calluna vulgaris</i>	Constant and most frequent species: <i>Sphagnum capillifolium</i> <i>Calluna vulgaris</i>
Peripheral disturbed vegetation	
8) <i>Carex nigra-Deschampsia cespitosa</i> (CD) - 3 plots, 5 vascular species	Physiognomy: extremely species-poor fens lying at the border at the peatland and in the past subject to grazing. <i>Carex nigra</i> and <i>Deschampsia cespitosa</i> are alternatively dominant. Bryophytes lack at all
Significant indicator species: <i>Carex nigra</i>	Constant and most frequent species: <i>Carex nigra</i>

model estimates indicated that a similar lowering of 20 cm of the water table would be associated with a substantial increase of ER in fen pools (corresponding to +1.4 g CO<sub>2</sub> m<sup>-2</sup> h<sup>-1</sup> for CC), a slight increase of ER in peripheral disturbed vegetation (CD: +0.1 g CO<sub>2</sub> m<sup>-2</sup> h<sup>-1</sup>), and a slight decrease of ER in *Sphagnum* hummocks (SC: -0.1 g CO<sub>2</sub> m<sup>-2</sup> h<sup>-1</sup>). In addition, while increasing temperatures in waterlogged soils determined a limited increase in ER, warmer temperatures strongly stimulated ER if soil had lower moisture levels (Fig. 2b, left) and, on the other hand, decreasing soil moisture stimulated more ER with higher compared to lower temperatures (Fig. 2b, right). Moreover, the effects of warmer soils on ER depended on the vegetation type (Fig. 2c), with a marked differentiation even within the same habitat categories (e.g. *Sphagnum* hummocks: SE vs SC, fen pools: CC vs EC). Finally, the ER in diverse vegetation types showed different seasonal patterns (Fig. 2d), with the lowest changes along the growing season in *Sphagnum* lawns (SD) and the greatest differentiation in ER over time in peripheral disturbed vegetation (CD).

Concerning GEE (Table 2b), the variation in plant functional diversity had non-consistent effects among the different vegetation types (Fig. 3a), with higher functional diversity being associated with increasing gross assimilation (SE), no changes (MC) or decreasing CO<sub>2</sub> uptake (EC). In addition, the key role of PPFD was not constant along the growing season (Fig. 3b), with an increasing effect in the late growing period compared to the early one. Furthermore, the period of the growing season modulated the GEE levels among the vegetation types (Fig. 3c) and the responses to variation in plant functional diversity (Fig. 3d). In particular, among the most evident differences among vegetation types can be mentioned those between fen hollows (AT), maintaining high levels of gross CO<sub>2</sub> uptake throughout the growing season, and fen pools (CC), which showed a marked variation with an uptake peak in the mid-season (Fig. 3c). The early and late period of the growing season were associated with a positive effect of functional diversity on GEE, whereas in the central part of the growing season such trend was not kept (Fig. 3d).

In addition to the general role of seasonality on NEE (Table 2c), the growing period modulated both light and temperature responses. In particular, increasing level of PPFD stimulated greater net CO<sub>2</sub> uptake in the late part of the growing season in comparison with the early one (Fig. 4a), with an intermediate trend in the mid-season. In addition, the effects of warmer soil temperature differed along the growing season (Fig. 4b), with almost no influence in the early-season, decreasing net uptake in the mid-season and increasing uptake in the late one. Moreover, NEE of the diverse vegetation types differed along the growing season (Fig. 4c), with the lowest temporal changes in net CO<sub>2</sub> uptake in *Sphagnum* hummocks (SC)

**Table 2** Minimal adequate models on the relationships between CO<sub>2</sub> fluxes and ecological factors

	df (N,D)	F-value	P value
(a) Ecosystem Respiration			
Water-table depth (WTabD)	1241	46.91	<0.001
Growing season period (GSeaP)	2,9	8.86	0.008
Air temperature	1241	8.32	0.004
Soil temperature (STem)	1241	5.98	0.015
Vegetation type (VegT)	7241	2.09	0.045
Soil moisture (SMoi)	1241	0.63	0.428
WTabD × VegT	7241	14.61	<0.001
STem × SMoi	1241	8.81	0.003
STem × VegT	7241	4.12	<0.001
GSeaP × VegT	14,241	3.85	<0.001
(b) Gross Ecosystem Exchange			
Photosynthetic Photon Flux Density (PPFD)	1247	20.98	<0.001
Growing season period (GSeaP)	2,9	19.96	0.001
Vegetation type (VegT)	7247	18.63	<0.001
Plant functional diversity (PFunD)	1247	5.95	0.016
VegT × PFunD	7247	18.17	<0.001
PPFD × GSeaP	2247	10.51	<0.001
GSeaP × VegT	14,247	6.99	<0.001
GSeaP × PFunD	2247	5.00	0.007
(c) Net Ecosystem Exchange			
Growing season period (GSeaP)	2,9	22.23	<0.001
Photosynthetic Photon Flux Density (PPFD)	1247	6.50	0.011
Soil temperature (STem)	1247	3.59	0.059
Vegetation type (VegT)	7247	1.87	0.076
GSeaP × PPFD	2247	13.44	<0.001
GSeaP × STem	2247	8.74	<0.001
GSeaP × VegT	14,247	4.33	<0.001
STem × VegT	7247	3.36	0.002

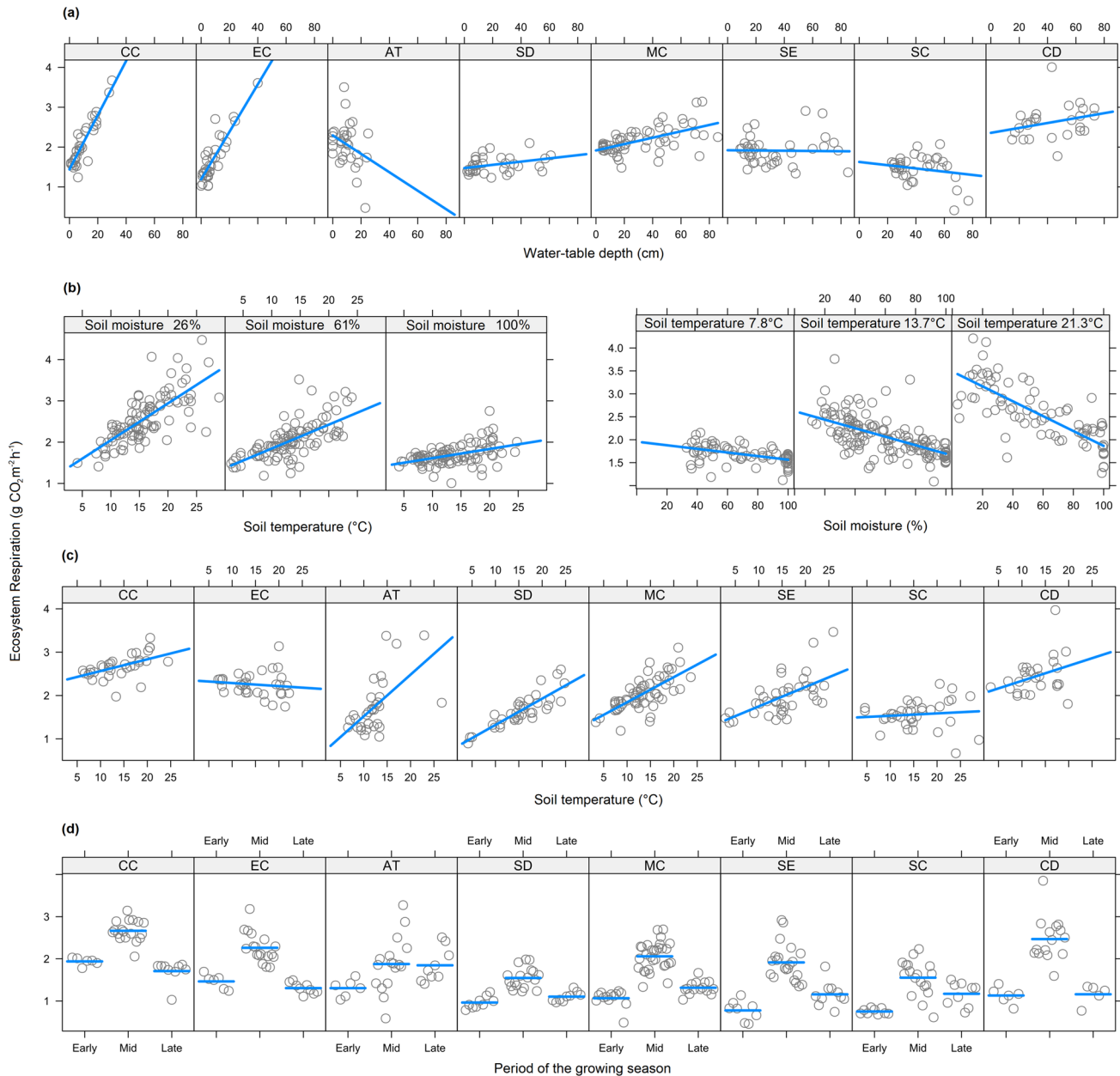
and a strong seasonal variation in peripheral disturbed vegetation (CD). In particular, the vegetation types with the highest and the lowest NEE were respectively fen hollows (AT:  $-0.88 \text{ g CO}_2 \text{ m}^{-2} \text{ h}^{-1}$ ) and peripheral disturbed vegetation (CD:  $-0.06 \text{ g CO}_2 \text{ m}^{-2} \text{ h}^{-1}$ ) in the early growing period, fen pools (EC:  $-1.79 \text{ g CO}_2 \text{ m}^{-2} \text{ h}^{-1}$ ) and *Sphagnum* lawns (SD:  $-0.72 \text{ g CO}_2 \text{ m}^{-2} \text{ h}^{-1}$ ) in the mid-season, and *Sphagnum* hummocks (SC:  $-1.05 \text{ g CO}_2 \text{ m}^{-2} \text{ h}^{-1}$ ) and peripheral disturbed vegetation (CD:  $+0.51 \text{ g CO}_2 \text{ m}^{-2} \text{ h}^{-1}$ ) in the late part of the growing period. Finally, the vegetation types showed different NEE response to increasing temperature (Fig. 4d), spanning from a low change in fen hollows (AT) to a strong reduction of net uptake in peripheral disturbed vegetation (CD). In particular, considering a soil temperature range from 5 °C to 25 °C and PPFD of  $1500 \mu\text{mol m}^{-2} \text{ s}^{-1}$ , model estimates indicated that *Sphagnum* hummocks (SC) have negative NEE (corresponding to net CO<sub>2</sub> sink) along all the growing season, fen pools (CC) could become net source of CO<sub>2</sub> with soil

temperature > 20 °C only in the early part of the growing season, whereas peripheral disturbed vegetation (CD) would be a net CO<sub>2</sub> source with temperature > 10 °C in the early season and > 20 °C both in mid- and late-season.

### The Role of Covariation of Ecological Factors

Variation partitioning on CO<sub>2</sub> uptake and release indicated that the most important fraction controlling these ecosystem processes is the joint variation in climatic and edaphic conditions (Fig. 5). Indeed, while the contributions solely due to climate and soil explained respectively 18.0% and 3.4% of the variation in ER and GEE, the variation explained jointly by climatic and edaphic factors turned out to be more than double, equal to 44.4%. In comparison with these abiotic factors, the variation in ER and GEE ascribable to the unique contribution of the biota seemed relatively low, being equal to 4.9%, and similar to the one attributable to the joint variation of biological and climatic factors (4.3%).





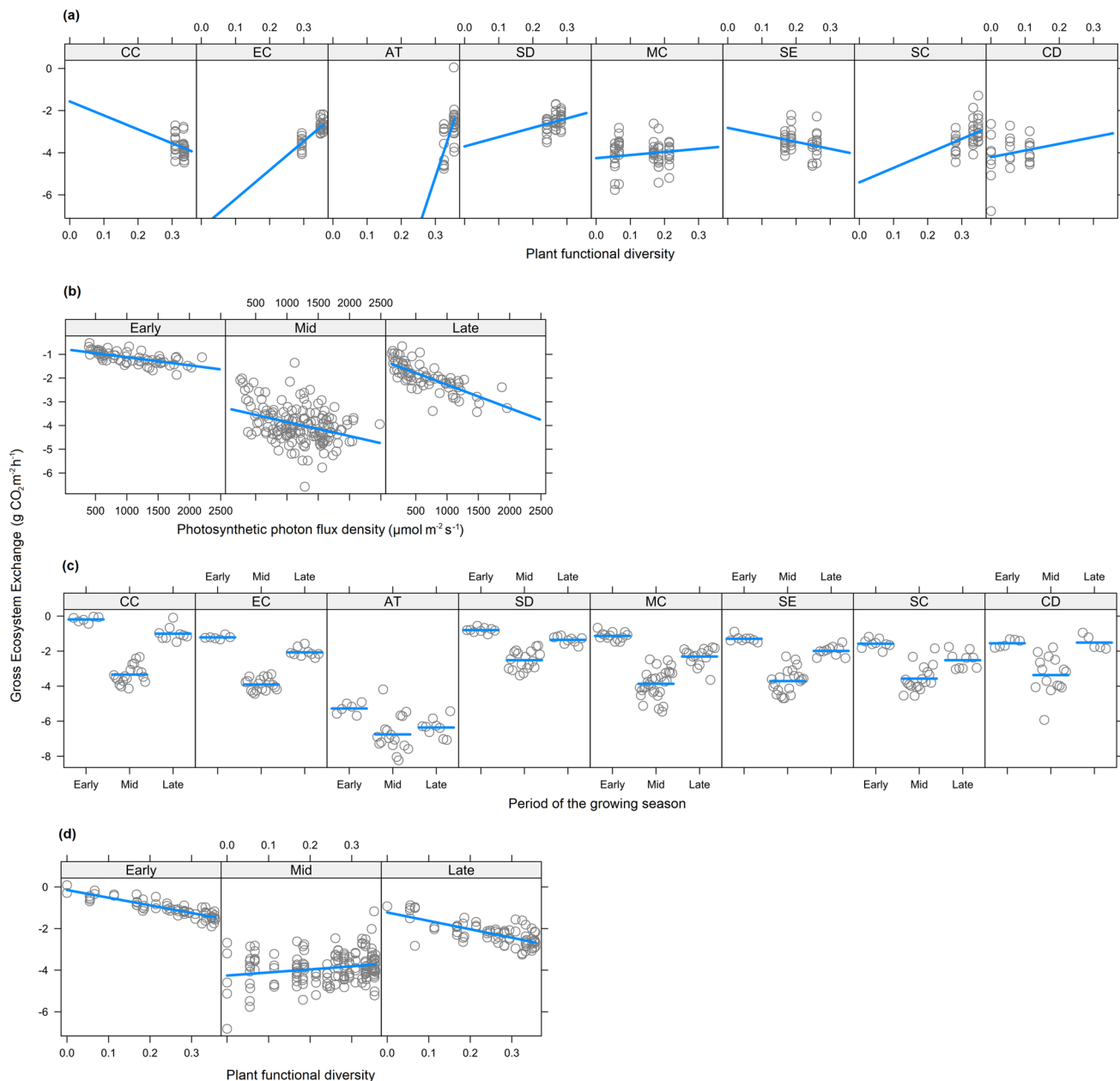
**Fig. 2** Responses of ecosystem respiration to interactions between: (a) vegetation type and water-table depth, (b) soil moisture and temperature, (c) vegetation type and soil temperature, and (d) vegetation

type and period of the growing season. Abbreviations for vegetation types are reported in Table 1

## Discussion

The estimates of CO<sub>2</sub> fluxes in a peatland from the alpine region revealed a high sensitivity to variation of the principal ecological drivers and highlighted the possible effects of future climatic changes on the C balance of these ecosystems in the Alps. Results demonstrated the high spatial-temporal variability of some key indicators of peatland functioning concerning C cycling (that is, ER, GEE and NEE) and that they are controlled by different

ecological factors. Our results also showed the pivotal importance of interactions between ecological variables, which should be considered in predicting the future functioning of these ecosystems under climate and land-use changes and associated vegetation dynamics. Furthermore, the intrinsic covariation between classes of ecological factors corresponds to a large proportion of CO<sub>2</sub> emission and uptake variability, showing the strong role of integration and coupling among different ecological features for C-cycle in peatland ecosystems.

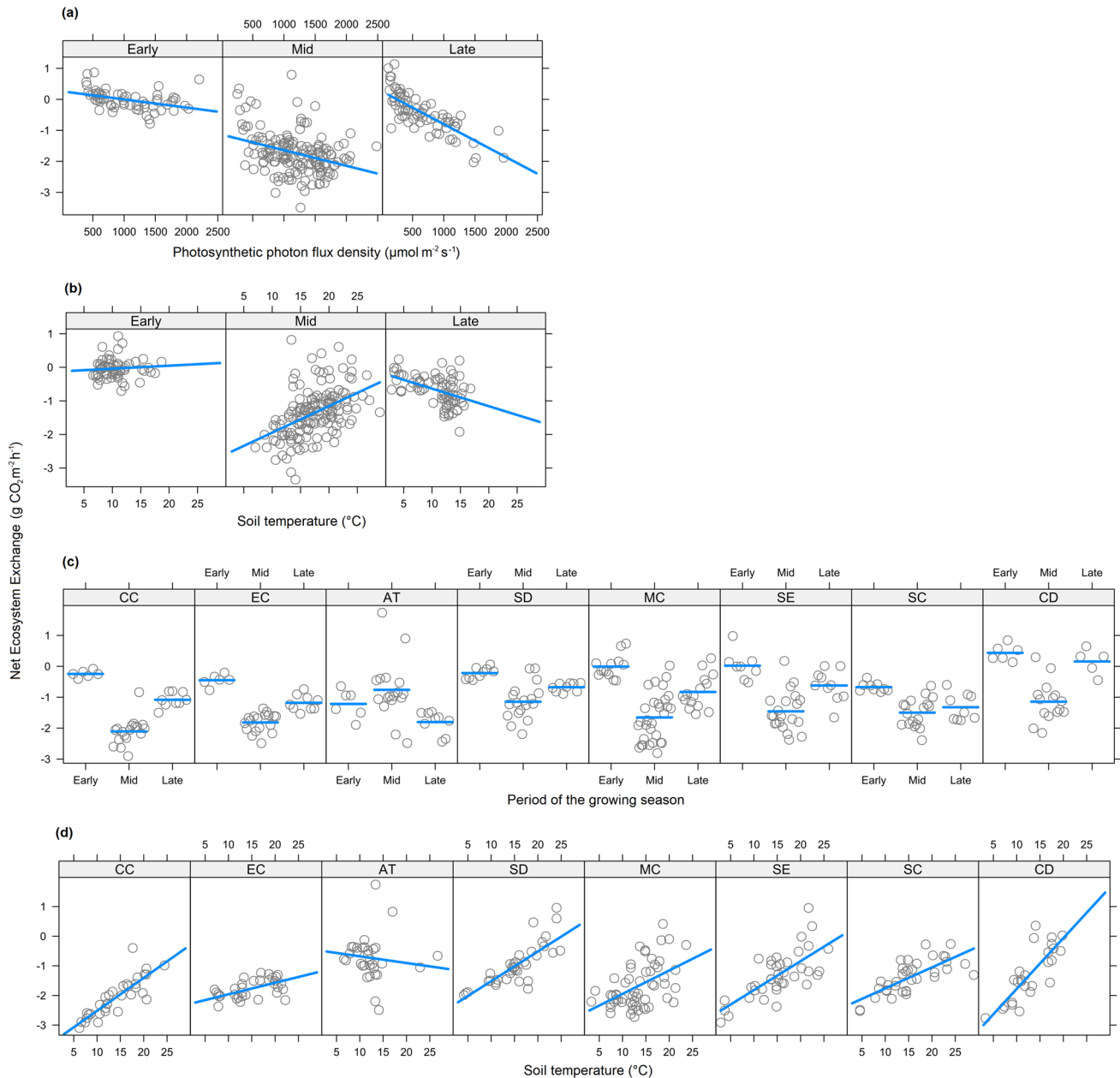


**Fig. 3** Responses of gross ecosystem exchange to interactions between: **(a)** vegetation type and plant functional diversity, **(b)** period of the growing season and photon flux density, **(c)** vegetation type

and period of the growing season, and **(d)** period of the growing season and plant functional diversity. Abbreviations for vegetation types are reported in Table 1

In particular, ER resulted primarily positively related to the depth of the water table. That this hydrological parameter could be the dominant causal driver controlling CO<sub>2</sub> emissions in peatlands was already reported by several authors from boreal (Flanagan and Syed 2011, Munir et al. 2015 and reference therein) and alpine peatlands (Gerdol et al. 2008). The water table drawdown implicates, in fact, a greater aerated portion of the peat profile (Belyea and Clymo 2001) leading to enhanced oxygen availability for microbial decomposition and root growth

and thus to higher respiration rates (Schneider et al. 2012). In the perspective of a global warming scenario, peatland hydrological models (see Roulet et al. 1992) predicted that lowering of water table in boreal peatlands may alter carbon storage and greenhouse gas emissions from these ecosystems (Strack and Waddington 2007). However, the lowering water table increased ER differently in diverse vegetation types, with greater CO<sub>2</sub> emission in plant communities with higher water table levels (pools and hollows: mean water-table depths <10 cm and coefficient

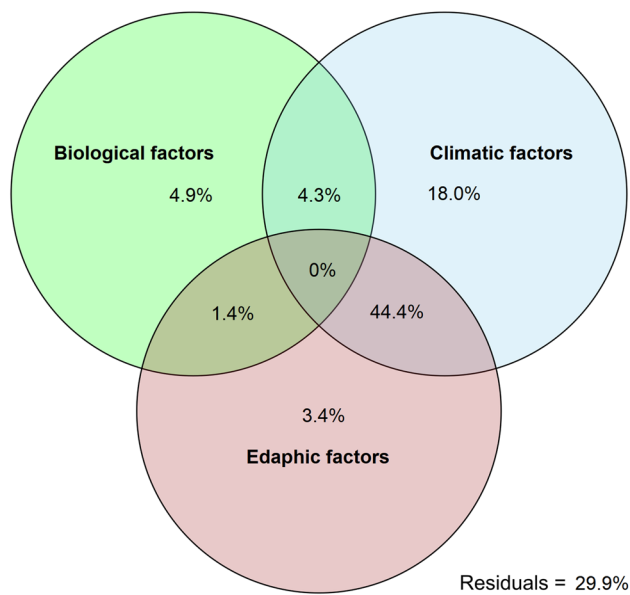


**Fig. 4** Responses of net ecosystem exchange to interactions between: (a) period of the growing season and photon flux density, (b) period of the growing season and soil temperature, (c) vegetation type and

period of the growing season, and (d) vegetation type and soil temperature. Abbreviations for vegetation types are reported in Table 1

of variation >70%) and a negligible effect on *Sphagnum* hummocks, where water table is lower (mean water-table depth of 41 cm) and relatively constant during the vegetative season (coefficient of variation <40%). In addition, the biological activity within *Sphagnum* hummocks could be less dependent on the water-table depth compared to other microhabitats, due both to the water-retention promoted by the density of capitula and to the capillarity rise of water supported by pore geometry and connectivity of *Sphagnum* species (McCarter and Price 2014).

Not surprisingly, our analysis indicated that the increase in GEE rates is mainly driven by increasing photosynthetic photon flux density (PPFD), as previously reported by Strack et al. (2006) for a boreal peatland and by Pullens et al. (2016) for the same alpine peatland here studied. In addition, it was also rather variable along the growing season and significantly influenced by the vegetation type, suggesting an important role of plant phenological development and physiological differences among plant species in controlling GEE. Differences in GEE fluxes among vegetation types



**Fig. 5** Venn diagram of variation partitioning between biological, climatic and edaphic factors influencing CO<sub>2</sub> uptake and release processes

were already shown for a boreal peatland by Schneider et al. (2012), who reported a lower GEE in hummocks compared to lawns and hollows. This finding was explained considering that surface dryness, occurring more often at hummocks, can lead to a reduction of vascular plants and *Sphagnum* species photosynthesis, whereas the water saturation characterising hollows during most of the growing season mainly resulted in reduced ER. Interestingly, our analyses indicated that the functional diversity is more important for CO<sub>2</sub> gross assimilation compared to the taxonomical one. This result highlights the fact that diversity in plant species, although vital for the conservation of species and habitats, plays a secondary role for ecosystem functioning compared to the diversity in plant functional traits (see also Milcu et al. 2014). However, to date, we know little about the role of functional traits in modulating the different components of the ecosystem-level C fluxes. Indeed, to our knowledge, this is the first study that demonstrates a significant role of plant functional diversity on a key component of CO<sub>2</sub> fluxes in peatland ecosystems.

Although NEE depends on the balance between CO<sub>2</sub> emission and uptake, its variation was not influenced by the depth of the water table—the main driver for ER. Differently, NEE was stimulated by increasing PFD—the main driver for GEE. However, NEE showed the strongest changes during the growing season, with the greatest net CO<sub>2</sub> uptake in the mid growing season and the lowest uptake in the early season, highlighting the role that vegetation development has in determining this ecosystem process. Seasonal patterns of NEE, clearly expressed by all the vegetation types,

were reported also by Schneider et al. (2012). Such temporal dynamics is most likely due to the phenological development of plants and soil microorganisms, but it may also be partly due to the combined action of variations in moisture and temperature during the snow-free period. Considering all the measures performed along the growing season, we did not find evidence of a significant difference in NEE among the different vegetation types, which indicates some compensation between the variations in ER and GEE in the plant communities investigated. Similarly, even soil temperature did not have a significant influence on NEE, probably because of the stimulating effects on both CO<sub>2</sub> emission and assimilation.

The early studies examining the effects of ecological changes on peatland C cycling were focused on single drivers (Freeman et al. 1992). Subsequently, the interactions between multiple drivers were investigated by taking into account more than one driver (Ellis et al. 2009). Nevertheless, knowledge of interactions between abiotic and biotic factors remains insufficiently investigated. This is a critical point, because the understanding of the role of biological, climatic and edaphic factors and their interactions in the functioning of peatland ecosystems could provide valuable insight into the implications of future ecological changes and a consistent basis for the inference of the effect of ecological changes on peatlands with different biotic and abiotic characteristics (Dise 2009; Armstrong et al. 2015). In the light of this, and with the aim at contributing to fill this knowledge gap, our research focussed also on the importance of the interactions between multiple ecological factors and the role of their covariation.

Concerning ER, the analysis of interaction between ecological drivers revealed that the simultaneous increase of temperature and decrease of soil moisture—the latter likely depending on lowering of water table and/or higher evapotranspiration rates—stimulated ER with a multiplicative effect. A similar result was obtained by Drollinger et al. (2019) from a pine peat bog in the Austrian Eastern Alps. Pullens et al. (2016), for the same alpine peatland investigated here, indicated increasing ER with decreasing soil moisture. Our results, even if collected in several locations of the peatland characterised by different vegetation types, are in agreement with the evidenced negative effect of soil moisture on CO<sub>2</sub> emissions. Furthermore, being able to also consider the influence of temperatures, the present study has revealed that this effect is more marked the higher the temperatures are. Water-table drawdown, reducing of soil moisture and rising of soil temperature are predicted as expected effects of climate change on peatlands (see, among others, Strack and Waddington 2007, Hájek et al. 2022). Their combined influence on ER may alter carbon storage and greenhouse gas emissions from these ecosystems inducing releasing of stored soil carbon to atmosphere as CO<sub>2</sub> acting a positive climatic feedback. Anyway, at a mid-term temporal scale, ER increase could be, on the one hand,

minimized by peat subsidence observed after water table drawdown that limited the increase in the size of the peat oxic zone lowering rates of soil respiration and, on the other hand, exacerbated by a trend to higher respiration rates and increased productivity coincident with a significant increase of vascular vegetation cover also this related to the lowering of water table (Strack and Waddington 2007).

The effects of warmer soils on ER differed substantially among vegetation types. In particular, most of the communities where vascular plants are prominent or dominant, especially those where the grass *M. caerulea* is particularly abundant, showed a relevant increase of ER related to the temperature increase. This result can be explained considering the phenological development of *M. caerulea*, whose vegetative peak occurs around midsummer, which could be a stimulating effect on soil organisms associated with this species as well. Also the marked differentiation between SE and SC within *Sphagnum* hummocks can be attributed to the different abundance of *M. caerulea* between the two vegetation types. The different seasonal patterns of ER in diverse vegetation types seems also to be related to the phenology of the vascular plants (the tall sedges *Carex lasiocarpa* and *C. rostrata* in CC, *Trichophorum alpinum* and *Eriophorum latifolium* in EC, *M. caerulea*, especially in MC and SE and *Carex nigra* in CD). Furthermore, the differences in the temporal dynamics of the vegetation cover, with wider variations in communities dominated by taller vascular compared to the ones dominated by bryophytes, can influence the microclimatic conditions, and therefore have an indirect and differential impact on ER.

Considering GEE, non-additive effects were found between vegetation types and plant functional diversity, with inconsistent effects of variation in functional diversity in different communities. However, such pattern could be interpreted with caution, since the variation in functional attributes of plants within the same vegetation type was rather low. In addition, results indicated other three significant interaction governing GEE, all including the period of the growing season, along which differential effects of PPFD, vegetation type and functional diversity were found. In particular, increasing PPFD enhanced GEE more in the late season than in the early one, probably due to the seasonal dynamics of plant development and the covariation between solar radiation and temperature, more limiting in fall compared to summer. In addition, variation in plant composition among communities resulted in different temporal patterns of gross CO<sub>2</sub> assimilation among vegetation types, with the lowest and the greatest variations respectively shown by *Sphagnum* lawns (SD) and fen pools (CC). Such differences, likely mainly related to different development and functionality between vascular

plants and bryophytes, were also evident considering the significant interaction between the growing period and the plant functional diversity. Indeed, the lowest functional diversity was found in a vegetation type (CD) dominated by one or few vascular species, whereas plots in which vascular species were associated with a bryophyte layer had higher functional diversity. Considering this variation among vegetation types, an increase in functional diversity enhanced GEE more at the beginning and at the end of the growing season, probably because bryophytes can have a relatively high photosynthetic activity both before the vascular plants have completed their leaf development and after they have begun the senescence phase. This result suggests a functional complementarity, with respect to the gross CO<sub>2</sub> uptake, between vascular plants and bryophytes, very different from the effects of the co-occurrence between graminoids and dwarf shrubs. In fact, through experimental removal of functional groups, strong increases in GEE were observed in a boreal peatland following the removal of ericoid dwarf-shrubs (Ward et al. 2009). In all the years of the period 2012–2014, the peatland studied, unlike others comparable ecosystems for which CO<sub>2</sub> flux monitoring exists, was a net source of CO<sub>2</sub> (Pullens et al. 2016), whereas gross primary productivity (g-CO<sub>2</sub> m<sup>-2</sup> d<sup>-1</sup>) was significantly higher than in other similar ecosystems. Pullens et al. (2016) explained this result with the large abundance of the graminoid *M. caerulea* in this peatland. Our results confirm the possible role of this plant on overall peatland GEE, given that the MC vegetation type, characterized by the dominance of the tussocky grass *M. caerulea*, had the highest GEE during the mid-part of the growing season.

Concerning NEE, the overwhelming role of seasonality is highlighted by the presence of the three interactions between the period of the growing season and PPFD, soil temperature, and vegetation type. This was consistent with the results of a recent study carried out in an alpine peatland from the Tibet Plateau showing that soil temperature was the main driver of seasonal variation of NEE (Yao et al. 2022).

In particular, the differential responses of NEE to seasonality were very similar to those shown by GEE, with a light-limitation of net CO<sub>2</sub> assimilation more marked in the late season. The hypothesis that this pattern could be linked, in addition to plant phenological development, also to thermal limitation, seems to be supported by the NEE dynamics in relation to temperature variation. In fact, warmer temperatures during the late season increased net CO<sub>2</sub> assimilation, while they have an opposite effect in the middle part of the season—when the temperature is probably not a limiting factor.

Furthermore, the type of vegetation also modulated the seasonal dynamics of NEE, with the smallest variation

in *Sphagnum* hummocks (SC) and the largest changes in disturbed peripheral vegetation (CD), in which NEE collapsed after the mid-season. Finally, warmer temperatures seemed to reduce, albeit with different intensities, the net assimilation of CO<sub>2</sub> in all types of vegetation with the exception of fen hollows (AT), for which a role of this ecological variable has not been highlighted. This result may depend both on different photosynthetic activity of the plant species occurring in diverse vegetation types and on differential temperature effects on organic matter stored into the soil. Such modulating effect of vegetation on warming was previously observed for a boreal peatland, where graminoid-dominated communities showed the greatest reduction in net CO<sub>2</sub> uptake following experimental warming (Ward et al. 2013).

Despite the great diversification of vegetation in the peatland investigated, and the obvious role of plants in CO<sub>2</sub> uptake, the variation of the biological characteristics explained only a small portion (about 5%) of ER and GEE variation. Surprisingly, almost half of the variance in these CO<sub>2</sub> fluxes explained by the ecological factors taken into consideration was attributable to the joint variation of climatic and edaphic factors. This fraction, which reflects the close interdependence between atmospheric and soil conditions, appeared to govern ER and GEE considerably. Furthermore, considering that climatic factors alone explained about one fifth in the variance in CO<sub>2</sub> fluxes, it is evident the importance of understanding the effects of ecological drivers to predict how the functionality of these ecosystems will change in the future. This is particularly pressing considering the current phase of climate warming, and the greater frequency of extreme events such as dry spells and heatwaves, which will have a decisive influence on the main factors that control CO<sub>2</sub> flux dynamics in the peatlands of the Alps.

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**Data Availability** The datasets analysed in the current study are available from the corresponding author on reasonable request.

## Declarations

**Competing Interests** The authors have no relevant financial or non-financial interests to disclose.

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