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Spatial Variation in Carbon Effluxes Mediated by Grazing–Soil Interactions in a Semi-Natural Floodplain Grassland of North-Eastern Belgium

Robin Tersago[1] | Camille Van Eupen[1] | Jeroen Meersmans[2] | Ben Aernouts[3] | Ellen Truyers[4] | Gert Verstraeten[5] | Ellen Desie[1] | Karen Vancampenhout[1]

[1]Department of Earth and Environmental Sciences, KU Leuven, Geel, Belgium | [2]TERRA Teaching and Research Centre, University of Liege, Gembloux Agro-Bio Tech, Gembloux, Belgium | [3]Department of Biosystems, KU Leuven, Geel, Belgium | [4]Hooibeekhoeve, Provincie Antwerpen, Geel, Belgium | [5]Department of Earth and Environmental Sciences, KU Leuven, Leuven, Belgium

Correspondence: Robin Tersago (robin.tersago@kuleuven.be)

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ABSTRACT

Permanent grasslands play a vital role in terrestrial carbon sequestration. However, their function as carbon sinks or sources is influenced by environmental factors—such as edaphic properties—and by management practices, notably grazing. Because direct measurement of management effects on soil carbon stocks is challenging, efflux data offer valuable insights into soil carbon dynamics. Yet, the spatial density of such measurements is often insufficient to capture in-field variability, particularly in heterogeneous landscapes like floodplains. This study investigates how short-distance variation in edaphic conditions modulates the response of CO_2 and CH_4 effluxes to changes in grazing intensity in a temperate floodplain grassland in the Grote Nete valley, North-Eastern Belgium. The site is characterised by rapid transitions in vegetation and soil properties over short distances. We conducted tri-weekly measurements of CO_2 and CH_4 effluxes across 14 plots using a portable closed-chamber system. These measurements were paired with grazing intensity data derived from GPS tracking, as well as assessments of soil temperature, moisture, texture, carbon stocks, pH and nutrient levels. Our findings reveal pronounced spatial variability in carbon effluxes, both between plots and within individual plots. While soil temperature consistently influenced both CO_2 and CH_4 emissions, the impact of grazing intensity was significantly modulated by local edaphic conditions. For example, CH_4 efflux was more sensitive to grazing in finer-textured soils. These results underscore the importance of accounting for local heterogeneity and enhancing spatial replication in future studies to develop more precise and site-specific management recommendations.

1 | Introduction

Permanent grasslands represent a vital ecosystem within European agricultural landscapes, encompassing over 30% of agricultural land (Eurostat 2020; Schils et al. 2022). Although these systems, classified as agricultural land, are primarily used for feed production and livestock grazing, they often have a multifunctional role in providing a range of ecosystem services, including flood control, climate regulation, biodiversity conservation and cultural benefits (Bengtsson et al. 2019). A particularly critical service is carbon (C) sequestration, as grasslands globally are estimated to store approximately 34% of total soil organic carbon (SOC) stocks (Smith et al. 2007; Lal 2008; Bai and Cotrufo 2022). Floodplain grasslands in North-Western Europe offer especially promising conditions for carbon sequestration due to their elevated water tables and frequent flooding (Whiting and Chanton 2001), promoting slow carbon decomposition while also limiting suitability for arable farming or urban development (Rommens et al. 2006; Crabbé and Coppens 2019; Swinnen et al. 2020).

However, SOC stocks in grasslands are highly sensitive to environmental and management changes, and these systems can shift from net carbon sinks to sources (Smith 2014; Conant et al. 2017). Despite their potential, practical management recommendations for enhancing carbon stocks in permanent grasslands remain limited—particularly in unimproved or semi-natural floodplain grasslands where legislation, biodiversity objectives, or environmental constraints restrict the use of carbon-rich soil amendments (Boone et al. 2020; Rodrigues et al. 2021). Adjusting grazing regimes has been proposed as a promising strategy for increasing carbon capture and storage (CCS; Bai and Cotrufo 2022), yet findings in the literature are inconclusive. For instance, several studies report reductions in SOC under more intensive grazing (Zhou et al. 2017; Abdalla et al. 2018), while others suggest that grazing can enhance soil carbon storage (Li et al. 2011).

A major limitation in assessing the effects of management on soil carbon sequestration is the difficulty of detecting changes through direct measurements of SOC stocks (Smith 2004; Smith, Soussana, et al. 2020). Moreover, grasslands are underrepresented in decision-support tools for soil carbon management, such as RothC (Coleman et al. 1996), CENTURY (Parton 1996) and PaSim (Riedo et al. 1998), which often fail to capture the complexity of these systems due to low data density (Conant and Paustian 2004; Ciais et al. 2010; Rolinski et al. 2018; Smith, Soussana, et al. 2020; Smith, Bagchi, et al. 2020). In-field greenhouse gas efflux measurements, which quantify soil-atmosphere gas exchange, have become increasingly valuable for understanding soil carbon dynamics, particularly by capturing short-term responses to management changes (Allaire et al. 2012; Vidon et al. 2015; Smith, Soussana, et al. 2020). While significant progress has been made in improving the temporal resolution of efflux measurements—for example, through flux towers and permanent chambers—the spatial resolution remains insufficient to reflect the environmental and edaphic heterogeneity typical of floodplain grasslands.

This limitation contributes to persistent uncertainty regarding the influence of environmental and edaphic variability on greenhouse gas effluxes and, by extension, on the development of best practices for carbon sequestration in floodplain grasslands (Ciais et al. 2010; Imer et al. 2013; Wohl and Pfeiffer 2018; Bengtsson et al. 2019; Godde et al. 2020; Bai and Cotrufo 2022; Wohl and Knox 2022). While regional patterns of carbon distribution in grasslands are increasingly well documented (e.g., Ottoy et al. 2022), the extent to which fine-scale heterogeneity within fields modulates the effectiveness of management interventions remains poorly understood (Conant and Paustian 2002; Carozzi et al. 2022). Given that management decisions are typically implemented at the field scale, accounting for spatial variability is essential to enable site-specific and adaptive strategies in floodplain grasslands (Imer et al. 2013; Wohl and Knox 2022). This need is further underscored by the growing availability of precision grazing technologies (Bretas et al. 2024), which offer new opportunities to modulate grazing intensity in response to environmental gradients (Maestre and Cortina 2003; Wang et al. 2016).

This issue is particularly salient in Flanders, a key region in Europe for grassland carbon dynamics, where SOC stocks have declined markedly over the past three decades. More than half of the region's grasslands currently fall below SOC thresholds considered necessary for maintaining soil health and productive capacity (Lettens, Van Orshoven, van Wesemael, et al. 2005; Tits et al. 2020). This trend is especially pronounced in the Campine region, characterised by sandy soils with suboptimal carbon levels across nearly all grassland sites (Lettens, Van Orshoven, van Wesemael, et al. 2005; Lettens, Van Orshoven, Van Wesemael, et al. 2005; Meersmans et al. 2011). In many cases, Flemish grasslands—particularly those situated in floodplains—have transitioned from net carbon sinks to sources (e.g., due to changes in land-use and management, including more frequent renewals or deeper ploughing, lower use of carbon-rich soil amendments, biodiversity losses, drainage or climate change effects; Mestdagh et al. 2009; Meersmans et al. 2011; Carozzi et al. 2022; Spohn et al. 2023; De Rosa et al. 2024; Segrestin et al. 2025) despite their formally acknowledged role in the Flemish climate strategy, which emphasises the conservation of grassland carbon stocks as a priority for regional climate policy (Flemish Government 2019).

The objective of this study is to examine if fine-scale spatial variation in driving factors influences the dynamics of carbon effluxes in floodplain grasslands, both across space and in time throughout one growing season. Specifically, we investigate whether such local soil heterogeneity modulates the response of CO_2 and CH_4 effluxes to varying levels of grazing intensity. The study was conducted in a representative floodplain grassland located in the Grote Nete valley, North-Eastern Belgium, characterised by over 250 years of continuous grassland management (AGIV and KBR 2009) and currently subject to extensive grazing.

We hypothesize that (1) spatial variability in greenhouse gas effluxes is substantial due to pronounced heterogeneity in driving factors within the study area, and (2) the response of CO_2 and CH_4 emissions to a change in grazing intensity is modulated by these local-scale differences (Allaire et al. 2012; Yang et al. 2019; Bai and Cotrufo 2022).

2 | Materials & Methods

2.1 | Study Area

The study area is located in the valley of the Grote Nete river in the Campine area in North-East Belgium. The average annual minimum temperature is 8.6°C and the total annual maximum temperature amounts to 15.8°C. The mean annual temperature amounted to 12.1°C. The average total annual precipitation amounts to 820.7 mm (RMI 2023).

The Grote Nete catchment drains the Campine plateau, consisting of gravel and sand deposits formed by alluvial and aeolian processes during the middle Pleistocene (Gullentops et al. 2001; Beerten et al. 2018; Swinnen et al. 2020). The Grote Nete valley is a drift sand landscape in the South of the European sand belt, typified by broad valleys with limited discharge gradients (Beerten et al. 2018). The major drifts were situated between

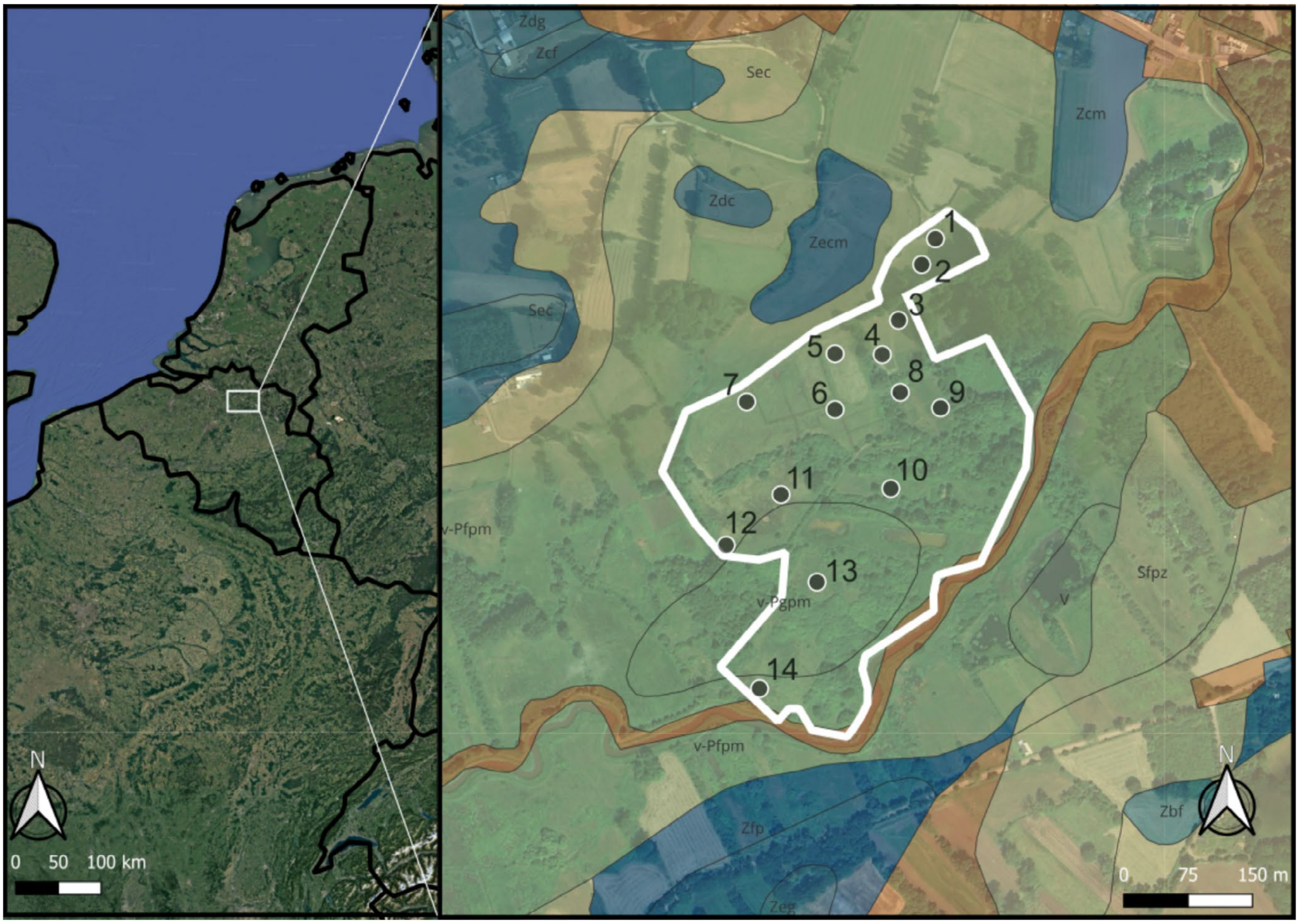

FIGURE 1 | Location of study area (13.29 ha) within Belgium, with the location of the plots within the study area. The Belgian soil map is shown as a background layer on the right panel (Ameryckx et al. 1995).

1500 and 1800 AD and they stopped as they reached the groundwater table. Pioneering vegetation then stabilised the landscape where the ground was not covered by new aeolian sand (Beerten and Leterme 2015). The Pleistocene niveo-aeolian cover sands rest on Pliocene glauconitic sands and are locally overlain by Holocene alluvia and a build-up of peat (Beerten et al. 2018).

The studied plots lie in between Grote Nete and a tributary, Molenlaak, ca. 1.5 km upstream of their convolution (Baeyens 1969; Jacobs et al. 1993). Groundwater levels were manipulated in the past as valley sections were managed as water-meadows for hay production or drained to allow grazing. Ditches and canals can still be observed in the microrelief of the study area. The elevation in the study area was on average 15.9 m a.s.l, and local differences in elevation were never larger than 2 m.

Soils of the studied area were mapped in the 1950's-60's and classified as vPfpm and vPgpm in the Belgian soil classification system (Figure 1). The letter in the third position reflects drainage class, and a higher prevalence of 'g' over 'f' reflects poorer drainage in the South-West of the study area. The soil series are indicative of soils formed in Holocene valley deposits, with an important influence of the Pliocene glauconitic deposits and often overlying older peaty deposits at shallow depth (20–125 cm, indicated by 'v'). The second letter 'P' indicates sandy loam as the dominant texture, with up to 12% clay, 32.5%–50% silt (2–50 μm) and 50%–67.5% sand. By the time of the publication of the soil map (1968), the groundwater table in summer rarely dropped below 80 cm and in winter was not deeper than 20 cm, with frequent inundations (Baeyens 1969). Since that time, the water table has dropped due to widening of ditches and drainage structures, as well as changes in river morphology downstream (Beerten 2010; Beerten and Leterme 2015). Measurements in 2008 and 2012 estimate the current groundwater table to fluctuate between 15 and 114 cm depth (INBO 2014). Profile development in these fairly young, low-lying soils is limited and soil processes are dominated by the high groundwater level. Most prominent features are a strongly organic A horizon, redoximorphic features, and local accumulations of buried peat, bog iron, and vivianite. According to WRB, the dominant soils of the Grote Nete floodplain key out as Fluvic Gleyic Umbrisols (Loamic, Fluvic, Thaptohistic) and Fluvic Reductigleyic Umbric Gleysols (Loamic, Thaptohistic), with local inclusions of Dystric Rheic Sapric Histosols (Dondeyne et al. 2014).

2.2 | Setup and Sampling

In the study area of 13.29 ha depicted in Figure 1, 14 plots of 3 × 3 m were selected based on preliminary field observations and discussions with the site managers. For each plot, vegetation was characterised in May 2023. Plant species were determined and their abundance was noted using the Londo scale (Appendix B), which was converted to a decimal scale afterwards (Londo 1976). After recording vegetation characteristics, plots were sampled for soil properties and carbon effluxes (vide infra).

2.3 | Greenhouse Gas Efflux Measurements

As our study focuses on the influence of short-distance spatial variation, we opted for a technique that provided a high spatial resolution (Dannoura et al. 2006; Savage et al. 2014; Görres et al. 2016). We therefore chose a portable automatic measuring chamber and an analyser. This enabled us to study SOC dynamics at the appropriate spatial scale in order to detect differences in C-effluxes as a result of management practices such as grazing (Figure 3). Measurements were repeated every 3 weeks across 14 plots to account for spatio-temporal variability (Phillips et al. 2009).

Opaque PVC rings were placed in the 3 × 3 m plots where the vegetation was characterised to measure greenhouse gas effluxes. The rings were 11 cm high and 20 cm in diameter and were sharpened on one end. The rings were inserted into the ground until approximately 3 cm remained above the surface. A minimum of three PVC rings were placed in each plot (two were added in the grazed plots to anticipate that some rings might be damaged by cattle).

Greenhouse gas effluxes were measured every 3 weeks during the growing season (June 2023—October 2023 & March 2024—July 2024), using the LI-COR 7810 with Smart Chamber (Lincoln, NA USA). No measurements were carried out during winter as the study area was often submerged and the majority of greenhouse gas effluxes occur during the growing season (Peterson et al. 2021; Stewart et al. 2024). The gas analyser works using Optical Feedback—Cavity Enhanced Absorption Spectroscopy (OF-CEAS) and has a precision of 3.5 ppm CO_2 at 400 ppm with 1 s averaging with a range of 0 to 10,000 ppm. For CH_4, the precision amounts to 0.60 ppb CH_4 at 2 ppm with 1 s averaging in a range of 0 to 100 ppm. The smart chamber was placed on top of the PVC ring and the seal was maintained using a gasket. The system worked in a closed loop when operative measuring CO_2 and CH_4. The system measured CO_2 and CH_4 concentrations at a frequency of 1 Hz for on average 45 s. These measurements are consequently fitted on a linear regression to calculate the flux. The measurements were always conducted between 9:30 and 16:30 in a randomised order to avoid interference of the diurnal pattern of respiration. The standing biomass in the PVC ring was clipped to 2 cm before the efflux measurement to minimise potential interference in the gas measurement (Borchard et al. 2015; Fóti et al. 2016; Hou et al. 2016). Soil moisture and soil temperature were measured simultaneously at 5 cm depth using a Stevens HydraProbe (Portland, OR USA). Respiration is measured as the raw efflux rate by the system in μmol CO_2 $m^{-2} s^{-1}$. However, as soil respiration is dependent on the amount of available C in the soil (Q. Chen et al. 2010), the raw efflux rate was converted to mg C from CO_2 per g SOC (top 60 cm) per hour following Kovacs et al. (2024). A similar protocol was used to convert the raw efflux of CH_4 to mg C from CH_4 per g SOC. This standardised respiration measure was calculated using the following equation:

$$R_s\left(\mathrm{mgC - CO_2\ gSOC^{-1}\ h^{-1}}\right) = \frac{\mathrm{dC}}{\mathrm{dT}}.\ 12.10^{-3}.\ 3600.\mathrm{SOC_{mass}}^{-1}.10^{-3} \tag{1}$$

$$R_s\left(m\mathrm{gC - CH_4\ gSOC^{-1}\ h^{-1}}\right) = \frac{\mathrm{dC}}{\mathrm{dT}}.\ 12.10^{-6}.\ 3600.\mathrm{SOC_{mass}}^{-1}.10^{-3} \tag{2}$$

where R_s is the soil respiration, $\frac{dC}{dT}$ is the raw efflux rate (μmol CO_2 $m^{-2} s^{-1}$ or nmol CH_4 $m^{-2} s^{-1}$ respectively) and SOC is the Soil Organic Carbon stock up to 60 cm depth (kg SOC m^{-2}).

2.4 | Grassland Management

A comparative analysis of historic maps (AGIV and KBR 2009) reveals that the site has known a consistent historic land-use of meadows and hayfields, with local thickets of wood- and shrubland. During the experiment, the studied fields were mowed once (beginning of August 2023) and extensively grazed by 13 cows (of which 4 calves) from the beginning of May to the end of October 2023. The farmer uses a virtual fencing system (NoFence) that facilitates a grazing regime in which the cows are frequently moved and tracked by GPS trackers in the collars. The collar data include the GPS location of each cow every 15 min and an index for the activity of the cattle. Locations for which the activity index was 0 (inactive cattle, e.g., sleeping) were removed from the analysis, as well as the data from 10 PM at night till 6 AM in the morning when the cattle were likely not grazing. Activity data were no longer supported by the virtual fencing provider from 2024 onwards, which limits the analysis of grazing intensity to the first year of measurements. Other analyses where grazing intensity was not included in the calculations did utilise the complete dataset.

To study the effect of grazing on soil carbon efflux, we quantified grazing intensity as the number of active cattle during the 10-day period before a gas flux measurement. We used these active cattle data to create heatmaps of the number of cow locations, with a pixel size matching an area of 11.5 × 11.5 m. Data were extracted from this heatmap to determine the grazing intensity for each plot (Paz-Kagan et al. 2016). This led to a grazing intensity indicator of the last 10 days for each plot, which was further used in the GAMM. The study area has been subjected to a wide range of grazing intensities as shown in Figure 3. High grazing intensities were mostly observed in the western part of the study area. The north-western part received a particularly high grazing intensity as the drinking water for the cattle was located here. The northernmost plots were not grazed during the duration of the study as the cattle did not have access to this part of the study area.

2.5 | Soil Sampling and Laboratory Analysis

Soil samples were taken during the summer of 2023 in each plot at four depths (0–10, 10–30, 30–60 and 60–100 cm). These depths were based on the protocol of the Flemish carbon monitoring incentive (Lettens et al. 2024). The sampling technique consisted of 3 samples (consisting of 2 mixed augerings each) per plot. Only the first sample of each plot was augered to 100 cm depth, as variation is limited at this depth. The other samples were augered up to 60 cm. Bulk density samples were taken using both a Kopecky ring and a root auger (Eijkelkamp).

All soil samples were air dried (50°C for 48 h; Franzluebbers 2022), ground and sieved to 2 mm. They were analysed for total C and total N using dry combustion (Dumas 1831) with a Thermo Scientific Flash 2000 Organic Elemental Analyser (Waltham, MA, USA) and stocks were calculated according to the following formula:

$$\mathrm{SOC}_{\mathrm{stock}} = \rho_{\mathrm{s}} \times \frac{\mathrm{SOC}}{100} \times \mathrm{Th} \tag{3}$$

where $\mathrm{SOC}_{\mathrm{stock}}$ is the SOC stock per square meter (kg SOC m^{-2}), ρ_s is the soil bulk density of each layer (kg m^{-3}), SOC is the SOC content of that layer (g C/100 g soil) and Th is the layer's thickness (m). We analysed the soil samples for pH by weighing 8 g of dried soil and mixing with demineralized water in a 50 mL tube (1:5 ratio soil: liquid) The sample was subsequently shaken for 2 h and centrifuged for 10 min at 3000G. Afterwards, the pH of the supernatans was measured using a pH meter (ATI Orion model 370) (Waltham, MA, USA) (Thomas 1996). The top samples (0–30 cm) were analysed for nitrate (NO_3^-), nitrite (NO_2^-) and ammonium (NH_4^+) by an extraction of 2.500 g of fresh soil with 25.0 mL of 1 M KCl solution (Dorich and Nelson 1984). They were subsequently all measured using a continuous flow analyser (Skalar SAN++ (Breda, The Netherlands)) coupled with an autosampler. The results were obtained as a concentration of the samples (mg kg^{-1}). Nitrate and nitrite were measured using the reduction method with cadmium. Ammonium was measured using a modified Berthelot reaction (Rhine et al. 1998). The phosphate (PO_4^-) content of the sample was subsequently measured using the ascorbic acid method. To determine the phosphate content of the samples, 5 g of fresh soil sample was weighed and extracted by 25.0 mL of demineralized water (Watanabe and Olsen 1965). We also measured soil texture using a laser diffraction method (Mastersizer 3000 [Malvern, UK]) to determine particle size, using the following fractions: clay (0–8 μm), silt (8–50 μm) and sand (50–2000 μm) (Taubner et al. 2009).

2.6 | Statistical Analysis

The vegetation in the study area was assessed by making a Non-metric multidimensional scaling (NMDS) diagram of species abundance in each plot. This analysis was conducted using the package 'vegan' in R (Oksanen et al. 2025). Soil properties were quantified by conducting a Principal Component Analysis (PCA) on the chemical variables of the soil samples (nitrate, nitrite, phosphate, ammonium), soil texture, and pH. The first principal component (PC1) was then further used as a metric for quantifying variability in edaphic conditions.

All efflux measurements were first uploaded into the SoilFluxPro software, which adjusts the deadband and post-purge time to ensure an optimal fit to the linear regression to calculate the greenhouse gas efflux. Measurement data (including efflux, soil temperature and SWC) were consequently filtered, using R (R Core Team 2024), where we removed outliers of the linear efflux values (based on the interquantile range (IQR) method; Tukey 1977) and entries with a SWC below 0.05 $m^3 m^{-3}$ as this is the typical permanent wilting point for a sandy soil (Pardossi et al. 2009).

Generalised additive mixed models (GAMMs) were used to assess the impact of soil type, soil temperature, soil moisture and grazing intensity on soil CO_2 and CH_4 effluxes (R_S). This data only included measurements of 2023 as the activity data of the cattle was not present in data of 2024. The model included smooth terms for soil temperature (soilTemp), the first principal component of soil properties (soilType), soil moisture (SWC) and grazing intensity (grzInt), using cubic regression splines to account for nonlinear relationships. Additionally, a tensor product smooth term was included to capture the interaction between soil properties (soilType) and grazing intensity (grzInt) allowing us to assess whether the effect of management differs within the study area. Plot identity (plotID) was modelled as a random effect using a spline-based random effect term. The model structure was as follows:

$$\begin{aligned} Rs \sim\ & s(\mathrm{soilTemp}, k=3) + s(\mathrm{soilType}, k=3) \\ & + s(\mathrm{grzInt}, k=3) + te(\mathrm{soilType}, \mathrm{grzInt}, k=3) \\ & + s(\mathrm{SWC}, k=3) + s(\mathrm{plotID}) \end{aligned} \tag{4}$$

Partitioning the variance explained by the GAMMs was calculated using the gam.hp package (Lai 2024) in R. This package calculates the R^2 for each individual term of the model, based on the concept of 'average shared variance' (Lai et al. 2022). This made it possible to estimate the relative importance of each factor. The tests used to compare results were a *t*-test when results were normally distributed and a Wilcoxon rank sum test when results were not normally distributed. Every analysis was conducted in R version 4.3.1 (R Core Team 2024).

The Q10 and R10 functions were fitted using the nls function (a non-linear solver) in R to fit the respiration measurements to the following function (Schindlbacher et al. 2009):

$$R_s = R_{10} \times Q_{10}^{(T_s - 10)/10} \tag{5}$$

In this function, R_s is the measured respiration (mg CO_2-C g^{-1} C h^{-1}), R_{10} is the basal respiration rate at 10°C (which corresponds roughly to the annual mean temperature in Belgium) and Q_{10} is the temperature sensitivity, representing the amount that R_s would increase for every 10°C increase in soil temperature (T_s) (Kovacs et al. 2024).

3 | Results

3.1 | Characterisation of Vegetation Composition and Edaphic Properties

A full species list is available in Appendix C. Species encountered are indicative for nutrient-rich grasslands (i.e., *Festuca pratensis* and *Poa trivialis*; Van Meerbeek 2024), and for grasslands starting a transition from an agricultural monoculture of perennial rye grass (*Lolium perenne*) into more species-rich associations (the so called 'transformation stage 2' according to the Dutch grassland classification system; Schippers et al. 2012). Plot scores of the NMDS analysis (Figure 2, left panel) are converging in two distinct clusters. Low scores on NMDS 1 correspond with plots found in the north of the study area, with a higher dominance of a.o. *Holcus lanatus and Festuca pratensis*, species indicative for stage 2 grasslands on coarser-textured soils (Prosser et al. 2023). High scores on NMDS 1 were found for plots in the south of the study area (except for plot 8), where the higher abundance of *Poa trivialis* and *Alopecurus pratensis* is indicative for stage 2 grasslands on finer-textured soils (Harasimiuk and Cyrczak 2004). A full representation of NMDS loadings of present species can be found in Appendix C.

The clustering in vegetation concurs with a contrast in soil properties as depicted in Figure 2 (right panel), Table 1 and Appendices A and B. The multivariate analysis in this figure

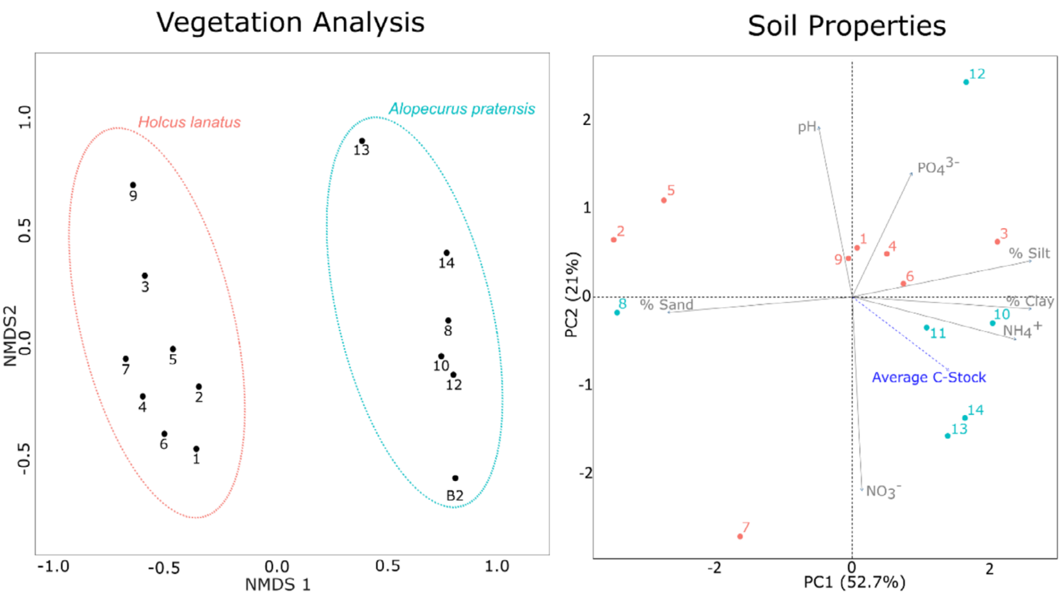

FIGURE 2 | (left) NMDS of the vegetation in the plots of the study area, with scores representing plots in the Northern zone in red and plots in the Southern zone in blue. Loadings (species) can be found in Appendix C; (right) Principal component analysis (PCA) of chemical soil variables and texture, with symbols denoting plot scores from the Northern zone (typified by *Alopecurus pratensis*) noted in red and from the Southern zone (typified by *Holcus lanatus*) noted in blue. Principal component 1 (PC1) of the PCA explains 52.7% of variation and principal component 2 (PC2) explains 21% of variation. PC loadings are represented by grey vectors. C-stock is represented by a dotted line, indicating that it was not included in the analysis for creating the PCA, but is solely there as additional information.

TABLE 1 | Average and standard deviation of soil conditions of plots in both zones and *p*-values for significance differences (Wilcoxon rank sum test or *t*-test). Significance codes: ***$p<0.001$, **$p<0.01$, *$p<0.05$, (*) $p<0.1$.

	Zone A (North) (plot 1–9)	Zone B (South) (plot 10–14)	*p*-value
Bulk samples	$n=9$	$n=5$	
% Sand	50.28 ± 32.18	14.11 ± 7.68	0.03*
% Silt	29.74 ± 20.80	45.90 ± 1.63	0.11
% Clay	19.98 ± 11.73	39.99 ± 6.49	4.48e-03**
pH	5.72 ± 0.14	5.55 ± 0.30	0.17
% OC (0–60 cm)	6.16 ± 2.65	9.91 ± 5.04	0.09 (*)
% N (0–60 cm)	0.47 ± 0.21	0.74 ± 0.40	0.11
NO_3^- [mg N kg^{-1}]	6.74e-07 ± 1.21e-06	1.18e-06 ± 1.31e-06	0.30
NH_4^+ [mg N kg^{-1}]	2.37e-06 ± 9.63e-07	3.05e-06 ± 3.16e-07	0.16
PO_4^{3-} [mg P kg^{-1}]	1.69e-06 ± 4.79e-07	2.47e-06 ± 1.19e-06	0.10
Field measurements	$n=238$	$n=136$	
Soil temperature [°C]	20.7 ± 3.83	23.3 ± 3.65	2.13e-09***
Soil water content [m^3 m^{-3}]	0.33 ± 0.19	0.29 ± 0.19	0.04*

confirms the difference in texture between the plots typified by *A. pratensis* and *H. lanatus* in the northern part of the study area (lower scores on PC1) and the plots typified by *P. trivialis* and *F. pratensis* to the south of the study area (higher scores on PC1, accounting for 52.7% of the variance in soil properties), which concurs with differences in C stocks and NH_4^+ concentrations. The second principal component (PC2) reflects a gradient in pH and available nutrients, explaining an additional 21% of the variance.

Combined, the vegetation and soil data show a notable difference in site conditions between the northern (zone A) and southern part of the study area (zone B; Figure 3). Due to the contrasting vegetation communities and edaphic properties, we chose to divide the study area into a Northern zone A and a Southern zone B. The differences in texture between the zones are statistically significant (sand and clay, Table 1), and zone B has a higher carbon content (i.e., 9.91 ± 5.0 vs. 6.16 ± 2.7; marginally significant, $p = 0.09$). Zone A classifies as a loamy soil, while zone B is a silty clay loam soil according to the USDA texture triangle. Zone A has a significantly lower soil temperature, corresponding to its significantly higher soil water as compared to zone B.

The left panel in Figure 3 represents variation in grazing pressure as derived from the GPS collar data, reflecting similar spatial contrasts in both zones.

3.2 | Variation in Efflux

There is a marginally significant difference ($p = 0.05$) in mean cumulative CO_2 efflux between zone A (0.23 μmol m^{-2} s^{-1}) and zone B (0.16 μmol m^{-2} s^{-1}, Table 2). The cumulative CH_4 efflux does not show a significant difference between the two zones ($p = 0.22$).

Figure 4 depicts the change in CO_2 efflux with increasing soil temperature. Basal respiration (R10) is similar for both zones, while efflux increases stronger with soil temperature for zone A as compared to zone B. This indicates a higher temperature

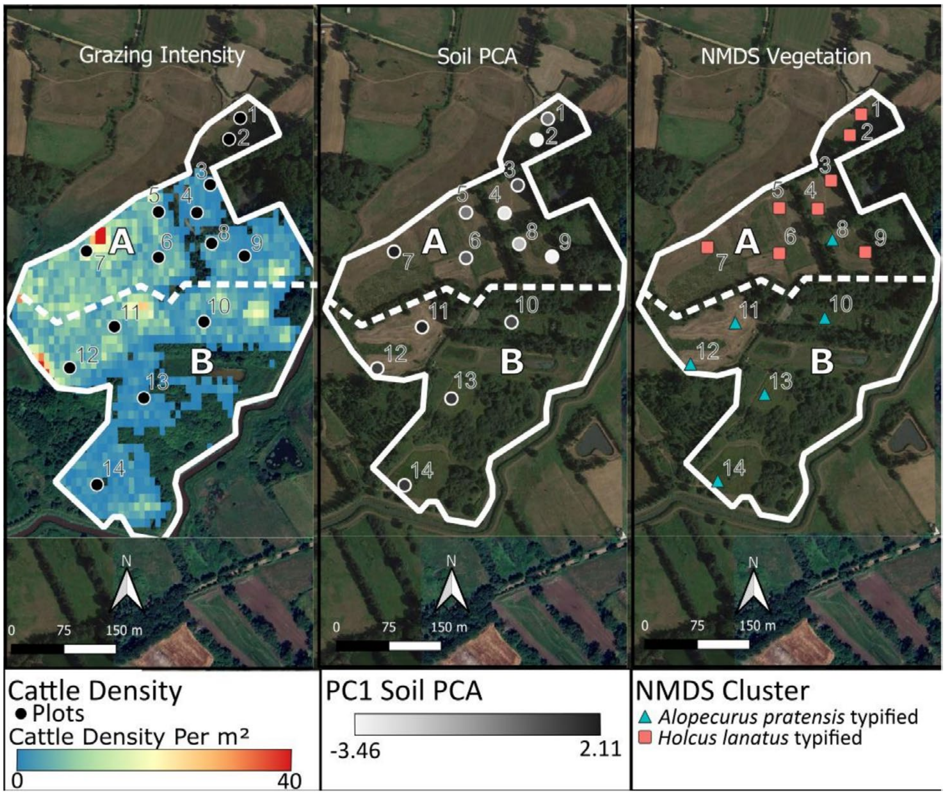

FIGURE 3 | Map of the study area and zones A and B, with the grazing intensity (left), scores on dimension 1 of the PCA of soil variables (middle), and the two clusters on the NMDS diagram (right). The grazing intensity was calculated based on the sum of all cattle location registrations (1 per 15 min from June 2023 to October 2023) in one pixel (11.5 × 11.5 m), normalised to cattle per square meter.

TABLE 2 | The median of the cumulative efflux over time and the median carbon stock. Dates where not every plot was measured were excluded from the calculation. The third column shows *p*-values of a test between the plots of the two zones.

	Zone A	Zone B	*p*-value
Cumulative CO_2 efflux [mg CO_2–C g^{-1}C h^{-1}]	0.23 ± 7.43e-04	0.16 ± 1.15e-03	0.05 (*)
Cumulative CH_4 efflux [mg CH_4–C g^{-1}C h^{-1}]	1.79e-07 ± 4.76e-07	−1.74e-05 ± 3.26e-07	0.22
C-Stock (0-60 cm) [kg SOC m^{-2}]	6.00 ± 2.01	7.77 ± 7.61	0.05 (*)

sensitivity of CO_2 efflux in zone A in comparison to zone B, although this difference is not significant. Note that the intra-plot variability in efflux (i.e., the variation in efflux on the same measuring date between the rings of the same plot, represented by the vertical whiskers in Figure 4) is very high and sometimes larger than the inter-plot variability or than the average effect-size of a 10-degree temperature increase.

Figure 5 shows the variability within a plot and between plots in the study area at the start, in the middle, and at the end of a growing season. The maximum variability within one plot is shown in dark grey, while the overall variability on that day is shown in light grey. This graph shows that the maximum variability within one plot is comparable over multiple measurement dates. In addition, it shows that the variability within one plot can be relatively large compared to the overall variability.

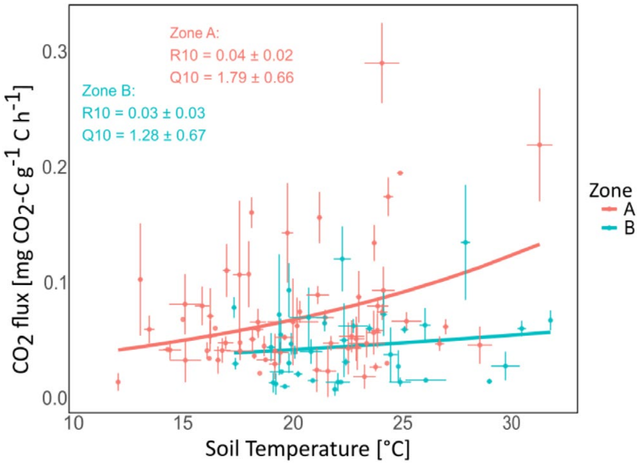

FIGURE 4 | Change in CO_2 efflux per increase in soil temperature. Points represent tri-weekly measurement averages per plot, obtained by averaging all replicate-rings within one plot. Whiskers represent the standard error of efflux (*Y*-axis) and temperature (*X*-axis) of the measurements within one plot. Lines indicate the Q_{10} model fit for zone A (red) and zone B (blue). The mean Q_{10} and R_{10} value is calculated as the mean Q_{10} or R_{10} of all individual Q_{10} values per plot and noted with a ±95% confidence interval.

3.3 | Impact of Context & Management on Efflux

Predictors for the Generalised additive mixed model (GAMM) were not correlated, as shown in the correlation plot in Appendix D. The vegetation diversity was excluded from this model as this factor did not contribute to a better model fit. All smooth terms in the GAMM were included with 3 possible nodes.

For the CO_2 model, soil temperature had a significant positive effect ($p < 0.01$), and the interaction between soil conditions and grazing intensity also had a significant positive effect ($p = 0.02$). The figures of the effect of this interaction are shown in Appendix E. Soil water content alone did not have significant effects. The random effect of plot identity was significant ($p < 0.01$), indicating considerable variation among plots not captured by the fixed effects and interaction. The adjusted R^2 was 0.69, with 70.6% of the deviance explained, suggesting a strong model fit.

For the CH_4 model, soil temperature also showed a significant positive effect ($p = 0.04$), and the interaction between soil conditions and grazing intensity was also positively significant ($p = 0.03$). However, individual effects of soil conditions and soil moisture were not significant. The plot identity effect remained highly significant ($p < 0.01$). The adjusted R^2 was lower at 0.41, with 44.4% of the variation explained, indicating a moderate model fit.

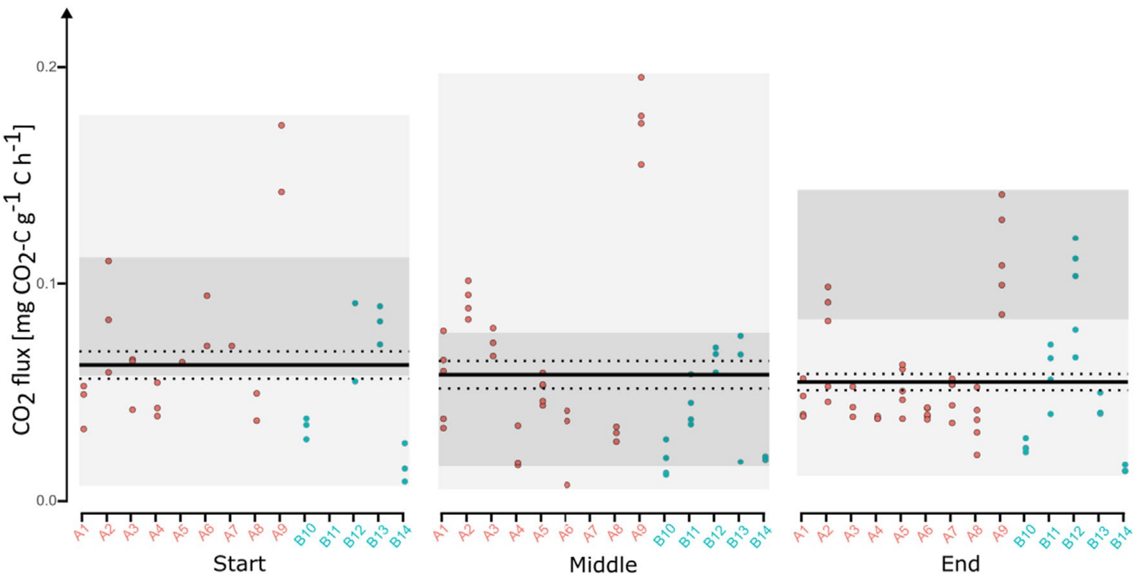

FIGURE 5 | Repeated CO_2 efflux measurements of all collars in all plots in the two zones A and B in the study area at the start (12th of June 2024), the middle (7th of August 2023) and the end of a growing season (9th of October 2023). CO_2 efflux is shown as the relative CO_2 efflux compared to the soil organic carbon (0–60 cm). The dark grey areas represent the maximal variance measured within a plot, and the light grey areas represent the total range in efflux measurements of that day. The thick black line represents the mean efflux of that day, while the dotted lines represent the standard error of that measurement day.

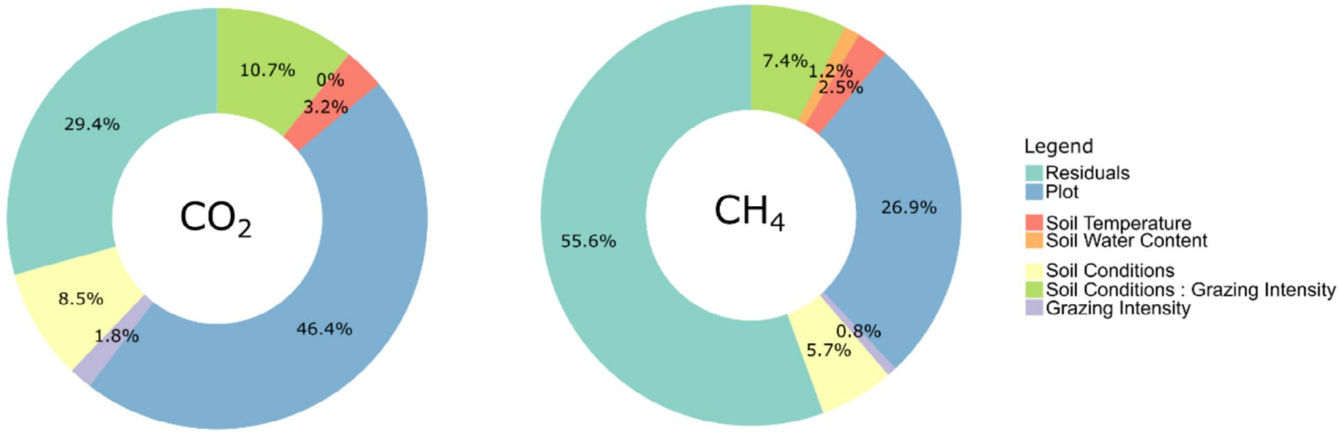

FIGURE 6 | Variance partitioning for both CO_2 and CH_4 efflux GAMMs.

In the variance partitioning analysis, residual variance was higher in the CH_4 efflux model (55.6%) compared to the CO_2 efflux model (29.3%), indicating a greater proportion of unexplained variability in CH_4 effluxes. The largest share of explained variance was attributed to plot identity, followed by the interaction between soil conditions and grazing intensity. Soil conditions, grazing intensity and their interaction combined explained 21% and 13,9% of the variance of the CH_4 and CO_2 effluxes, respectively.

4 | Discussion

4.1 | Effect of Context on Carbon Efflux

Our study, covering two distinct zones with differing edaphic properties, emphasises that both soil conditions and management have an effect on carbon efflux, with these effects varying across fine spatial scales. The plots in the northern zone (zone A) are sandier (loamy; USDA 1999) while samples from the southern zone (zone B) have more silt and clay (silty clay loam; USDA 1999). This reflects a typical process in floodplains in Flanders, where the formation of levees deposits coarser material, while finer particles settle in backswamps (Vandenberghe et al. 1984). Such differences in soil texture influence other processes, including moisture retention properties, aeration and oxygen availability (Singh et al. 2024). These can in turn contribute to short-distance variability in carbon effluxes, even under similar soil temperature and moisture conditions (Vidon et al. 2015).

Measured edaphic variables (primarily soil texture) explained 5.7% of CH_4 efflux variation and 8.5% of CO_2 efflux variation respectively (Figure 6), on top of a much larger plot effect (46.4% and 26.9%, respectively). Soil texture also interacts with the effects of soil moisture and temperature, potentially modifying their impact on soil gas effluxes (Figure 4). Further adding to the complexity which influences carbon effluxes is bulk density. Bulk densities which we measured ($0.92 \pm 0.21\,g^{-1}\,cm^{-3}$ for 0–10 cm, $1.17 \pm 0.27\,g^{-1}\,cm^{-3}$ for 10–30 cm and $1.10 \pm 0.42\,g^{-1}\,cm^{-3}$ for 30–60 cm respectively) were rather low for the region ($1.35 \pm 0.28\,g^{-1}\,cm^{-3}$ for 0–10 cm, $1.38 \pm 0.25\,g^{-1}\,cm^{-3}$ for 10–30 cm and $1.60 \pm 0.03\,g^{-1}\,cm^{-3}$ for 30–60 cm, respectively) (Mestdagh et al. 2009). This deviation can be explained by the peaty substrate at a limited depth, which generally has a lower bulk density (Swinnen et al. 2020). These factors affect diffusion of gases into the soil (Qiu et al. 2005; Ball 2013; Vidon et al. 2015; Martins et al. 2017) and the stabilisation of soil carbon through aggregation or organo-mineral interactions (Lehmann and Kleber 2015).

Given the important role of SOC in driving microbial respiration and associated efflux, we standardised all measurements for total SOC stock to better isolate other effects (e.g., temperature) in further analysis. The Q10 plots illustrate this, indicating that the sandier zone A is more susceptible to changes in temperature than zone B, likely as sandy soils tend to heat up more quickly than loamy soils (Figure 4). This dependency of temperature effects on soil conditions has also previously been described in other studies (Chen et al. 2010; Ma et al. 2021), increasing the complexity of predicting greenhouse gas effluxes, as both physical and biological parameters of the soil contribute to the rate of microbial processes (Blagodatsky and Smith 2012).

4.2 | Effect of Climate on Carbon Efflux

CO_2 efflux in grasslands is widely recognised as being primarily driven by climatic factors such as temperature and moisture (Hörtnagl et al. 2018; Feigenwinter et al. 2023). In our study, we observed a significant nonlinear effect of soil temperature on CO_2 efflux, primarily driven by the sandier plots (zone A), as illustrated in Figure 4. In contrast, soil moisture had no significant influence (Table 3). This absence of a soil moisture effect is likely due to the consistently higher groundwater table in the study area, as soil moisture typically influences CO_2 efflux only when its fluctuation is large (e.g., flooding events or droughts; Lindenberger et al. 2025). The promoting effect of temperature on mineralization processes is well documented (Yvon-Durocher et al. 2014) yet depends on adequate soil moisture availability (Su et al. 2020). When sufficient soil moisture is present, respiration becomes primarily temperature-dependent (Qiu et al. 2005). However, at excessively high moisture levels, respiration rates decline due to restricted microbial mineralization processes (Yang et al. 2002; Qiu et al. 2005), which was not the case in the measured period of our study. As times of extreme moisture

TABLE 3 | Comparative summary of Generalised Additive Mixed Models (GAMMs) for standardised linear CO_2 and CH_4 effluxes, respectively. Parametric coefficients are reported as estimates (standard errors). Smooth terms are represented by effective degrees of freedom.

Term	$edfCO_2$	FCO_2	pCO_2	$edfCH_4$	FCH_4	pCH_4
Parametric coefficients						
Intercept	—	0.06 ± (0.04)	0.09.	—	−0.14 ± (0.04)	< 0.01***
Smooth terms (fixed)						
s(Soil temperature)	1.27	921.17	< 0.01***	1.83	6.96	0.04*
s(Soil conditions)	1.97	3160.62	0.86	1.60	46.38	0.11
s(Grazing intensity)	5.41e-07	0.00	0.99	4.79e-09	0.00	0.51
te(Soil conditions, grazing intensity)	1.87	162.63	0.02*	0.96	2.13	0.03*
s(Soil water content)	5.41e-08	0.00	0.80	0.17	0.19	0.23
Smooth terms (random)						
s(Plot)	11.01	28.87	< 0.01***	10.54	7.36	< 0.01***

Note: Significance codes: *** $p<0.001$; ** $p<0.01$; * $p<0.05$; * $p<0.1$.

may suppress respiration rates, we did not take any measurements when plots were inundated. Additionally, measuring greenhouse gas effluxes under flooded conditions poses some technical challenges, as soils which are saturated have a fragile structure which may complicate the placement of a manual chamber (Zaman et al. 2021).

Similarly, soil temperature also significantly influenced CH_4 efflux, while soil moisture showed no significant impact. This result is somewhat unexpected, as methane efflux has traditionally been linked to groundwater table fluctuations in the study area (Zhao et al. 2020; Rafalska et al. 2023; Tian et al. 2023; Xu et al. 2024). However, recent research suggests that this relationship holds only up to a critical groundwater level, depending on the context, beyond which methane efflux variability increases (Calabrese et al. 2021; Cui et al. 2024). Additionally, geochemical processes involved in methane production may respond more rapidly to temperature changes than to shifts in groundwater levels, particularly at higher latitudes (Bloom et al. 2010). This means that the effects of temperature may be more visible in the short-term measurements of this research, and that the long-term effects of changes in groundwater table (and therefore soil moisture) may not be detected as clearly.

The consistently high groundwater table in our study area may have created a predominantly anoxic environment, favouring methane production over oxidation, thereby explaining the strong influence of soil temperature on CH_4 efflux.

This hypothesis is supported by the presence of the letter *v* in the soil series of the Belgian soil classification (Figure 1), which denotes the presence of a peaty substrate. The complexity of methane dynamics originates from the interplay between two opposing processes: methane production and oxidation (Schaufler et al. 2010). On the one hand, methane oxidation occurs when the groundwater table is low enough to allow oxygen diffusion into the soil, enabling methanotrophic bacteria to consume CH_4 (Chen et al. 2011). On the other hand, CH_4 production is possible at higher groundwater levels, where anaerobic conditions promote methanogenesis (Zhao et al. 2020).

4.3 | Variability in Carbon Efflux

We found considerable spatial heterogeneity in our study area, beyond what was indicated on the Belgian soil map (Figures 1, 4, and 5). A variance partitioning analysis was executed on the resulting models to compare the variation explained by individual variables for both CO_2 and CH_4 effluxes. This analysis concluded that a very large proportion of variation is attributed to the random factor 'plot', with a larger proportion for CO_2 efflux compared to CH_4 efflux (46.4% for and 26.9%, respectively), highlighting an overarching importance of location-specific variables like soil microbial composition, root respiration for CO_2, small differences in bulk density, profile characteristics and so on (Wang et al. 2009). In contrast, CH_4 efflux is more strongly governed by hydrological conditions, such as groundwater table depth, which is more uniform across the study area (Rafalska et al. 2023).

The high variation between sampling plots, even within the same meadow, indicates that sampling designs for carbon efflux measurements in floodplain grasslands should consider sufficient spatially distributed sampling locations across the study area, even if soil and vegetation conditions may seem similar.

Based on our results, increasing the number of sampling plots should yield better results than increasing the number of repetitions per plot. Figure 5, for instance, shows that the within-plot variance is relatively limited compared to the between-plot variance, illustrating the importance of plot-level differences in shaping carbon efflux variability. This implies that while temporal fluctuations occur, site-specific characteristics play a more important role in steering effluxes, strengthening the need for a spatially explicit sampling design (McDaniel et al. 2017). As a proof of concept, we also evaluated this variation for an agricultural grassland in the same time period (Appendix F) and found similar trends: although the effluxes on this agricultural grassland were larger, the variability was similar to the floodplain grassland presented here. This illustrates that the effluxes of chamber-based methods cannot be extrapolated to field-scale, even when the context may seem relatively similar.

4.4 | Context-Dependent Effects of Grazing

The effects of grazing on soil carbon effluxes and SOC have previously led to mixed results in international literature, with general trends still largely unclear (McSherry and Ritchie 2013; Hou et al. 2016; Tang et al. 2019). For example, some articles report that a higher grazing intensity decreases soil CO_2 effluxes (Tang et al. 2019), while others illustrate the opposite (Shi et al. 2017; Ma et al. 2021). However, both perspectives acknowledge that the impact of grazing on soil CO_2 effluxes is strongly influenced by local soil conditions, (including temperature and moisture), highlighting the need for site-specific grazing management. Our results align with these earlier observations, indicating that the impact of grazing intensity depends on interactions with edaphic conditions and that variables such as soil texture and nutrients play a critical role in shaping both CH_4 and CO_2 emissions. We also found that the interaction of grazing intensity with soil conditions accounts for a substantial variance (10.7% and 7.4%, respectively; Figure 6). Consequently, studies that examine grazing in isolation—without considering these interactions—may overlook key dynamics governing greenhouse gas effluxes in grasslands. This result also means that offering general suggestions for management in temperate grasslands may prove to be difficult, as they are located on a variety of soil types (Baldock et al. 2012). However, virtual fencing offers potential to optimise grassland management at a very local scale when land managers have access to detailed local soil information. It can therefore be applied to achieve a greater ecological impact.

4.5 | Limitations and Scope for Future Research

This study is subject to some constraints, including its duration (one growing season), measurement frequency and sampling density (12 plots is limited to account for spatial autocorrelation (Mathiba and Awuah-Offei 2015)). Our case study, moreover, suggests that a higher sampling density can improve the sampling design in other research setups with a similar context throughout Flanders.

Additionally, we chose to measure the effluxes manually instead of using automated chambers, which reduces the temporal resolution but increases the spatial resolution. The high costs of automated chambers limit the number of plots that can be measured, and therefore the representativeness. Moreover, permanent automated chambers can have a limiting effect on local vegetation growth (Wang et al. 2013), on the amount of rain reaching the soil, and are hard to combine with grazing animals (Görres et al. 2016).

Measuring grassland ecosystems more intensively to investigate the effects of grazing management on the carbon cycle can be an opportunity for further research. Grazing is a complex management practice to assess as it influences bulk density, net primary production, and fertilisation, all at the same time (Lai and Kumar 2020). In addition, it is a management practice which is widely employed all over the world, with research reporting mixed results on the effect on SOC (Bai and Cotrufo 2022). It would therefore be interesting to include regular measurements of soil chemical composition, greenhouse gases, plant growth, and other biotic parameters for a longer timeframe to keep track of how grazing influences different parts of a grassland ecosystem. These more extensive measurements would also allow us to investigate the influence (and interplay) of biotic and abiotic parameters on the carbon balance, whereas we only studied the effects on effluxes in this study. A more controlled setup would also enable us to investigate the effect of management on specific mechanisms and processes.

5 | Conclusion

This study demonstrates the high spatial variability in soil carbon effluxes across short spatial distances in floodplain grasslands, driven by interactions between soil properties, climatic variables and grazing intensity. Our results indicate that plot-associated heterogeneity explains a substantial portion of variation in both CO_2 and CH_4 emissions. This variability must be considered when scaling up from plot-level measurements to ecosystem-level estimates (Imer et al. 2013) and when designing sampling strategies in these ecosystems, especially for chamber-based carbon efflux measurements. A robust sampling design should include a higher sampling density and consider soil heterogeneity to capture a result which is representative for the study area.

Importantly, our results indicate that soil conditions and grazing intensity interact to influence carbon effluxes in temperate floodplain grasslands. For instance, CH_4 efflux increases with grazing intensity on a loamier soil, whereas this effect is not noticeable on a sandier soil. These context-dependent findings highlight the importance of accounting for both soil characteristics and grazing pressure when developing management plans. Optimal stocking densities may vary between locations and even within a location. They should therefore be tailored to site-specific soil conditions to maximise carbon sequestration potential.

Given the complexity of these management effects, future studies should focus on longer-term monitoring of multiple parameters. Integrating biotic and abiotic parameters will be essential to further improve our understanding of the carbon balance in these ecosystems.

Overall, understanding these dynamics will be essential for developing more effective management practices for temperate floodplain grasslands. By adapting management to local soil conditions, land managers can contribute to both ecological goals and climate mitigation efforts.

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Ethics Statement

This research was conducted in accordance with ethical standards for scientific integrity and transparency. All procedures involving animals and environmental measurements complied with institutional guidelines.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data used for this study are available from the corresponding author upon reasonable request.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Data S1:** sum70159-sup-0001-Supinfo.docx.