



RESEARCH ARTICLE

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Key Points:

- Land use and seasonality rather than soil type and slope strongly influenced soil greenhouse gas (GHG) fluxes at a landscape-scale
- The minimum number of chamber locations required for robust landscape-scale flux estimates depends on the season, land use, and GHG type
- Chamber locations required to reduce uncertainties of landscape flux estimates declined as follows $N_2O > CO_2 > CH_4$

Supporting Information:

Supporting Information may be found in the online version of this article.

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Number of Chamber Measurement Locations for Accurate Quantification of Landscape-Scale Greenhouse Gas Fluxes: Importance of Land Use, Seasonality, and Greenhouse Gas Type

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Abstract Accurate quantification of landscape soil greenhouse gas (GHG) exchange from chamber measurements is challenging due to the high spatial-temporal variability of fluxes, which results in large uncertainties in upscaled regional and global flux estimates. We quantified landscape-scale (6 km² in central Germany) soil/ecosystem respiration (SR/ER-CO₂), methane (CH₄), and nitrous oxide (N₂O) fluxes at stratified sites with contrasting landscape characteristics using the fast-box chamber technique. We assessed the influence of land use (forest, arable, and grassland), seasonality (spring, summer, and autumn), soil types, and slope on the fluxes. We also evaluated the number of chamber measurement locations required to estimate landscape fluxes within globally significant uncertainty thresholds. The GHG fluxes were strongly influenced by seasonality and land use rather than soil type and slope. The number of chamber measurement locations required for robust landscape-scale flux estimates depended on the magnitude of fluxes, which varied with season, land use, and GHG type. Significant N₂O-N flux uncertainties greater than the global mean flux (0.67 kg ha⁻¹ yr⁻¹) occurred if landscape measurements were done at <4 and <22 chamber locations (per km²) in forest and arable ecosystems, respectively, in summer. For CO₂ and CH₄ fluxes, uncertainties greater than the global median CO₂-C flux (7,500 kg ha⁻¹ yr⁻¹) and the global mean forest CH₄-C uptake rate (2.81 kg ha⁻¹ yr⁻¹) occurred at <2 forest and <6 arable chamber locations. This finding suggests that more chamber measurement locations are required to assess landscape-scale N₂O fluxes than CO₂ and CH₄, based on these GHG-specific uncertainty thresholds.

Plain Language Summary Greenhouse gas emissions are subject to high spatial and temporal variability, leading to large uncertainties in regional and global estimates. We quantified fluxes of soil and ecosystem respiration (SR/ER-CO₂), methane (CH₄) and nitrous oxide (N₂O) at the landscape scale (6 km² in central Germany). We determine the number of measurement chambers required to estimate landscape fluxes within globally significant uncertainty thresholds. Our results show a stronger influence of season and land use, as opposed to soil type and topography. The number of chambers required for robust landscape-wide flux estimates depended on the size of the fluxes, which varied by season, land use and GHG type. An increase in the number of monitoring sites significantly reduced the uncertainties estimation on the whole landscape. Significant uncertainties in N₂O fluxes above the global annual mean was found when landscape measurements were made at <4 monitoring sites in forests and <22 monitoring sites (per km²) in cropland ecosystems during the summer period. For SR/ER-CO₂ fluxes, as few as <2 was sufficient in forest ecosystems and under <6 in cropland ecosystems. This result implies that in general more monitoring sites are needed to assess landscape-scale N₂O fluxes than for CO₂ and CH₄ fluxes.

1. Introduction

Carbon dioxide (CO₂), methane (CH₄), and nitrous oxide (N₂O) are potent greenhouse gases (GHGs) driving global climate change. The atmospheric concentrations of these GHGs have increased by approximately 40%, 150%, and 20%, respectively, since the pre-industrial era (IPCC, 2013). This increase has been primarily attributed to anthropogenic activities, including agriculture expansion and intensification and other land use

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changes (IPCC, 2019). Soils are crucial contributors of these GHGs, with land use changes from natural to agricultural lands having been shown to alter the contributions of soil CO₂ (Raich & Tufekcioglu, 2000), CH₄ (McDaniel et al., 2019), and N₂O (McDaniel et al., 2019; Syakila & Kroeze, 2011) fluxes to global atmospheric GHG budgets. Despite the importance of soils as sinks and sources of atmospheric GHGs and the influence of land use change and land management on flux directions and magnitudes, large uncertainties in soil flux estimates still exist. For instance, the global N₂O emissions from agricultural and natural soils range from 2.5 to 6.5 Tg yr⁻¹ N₂O-N (Tian et al., 2020). Higher uncertainties have also been reported for the global soil CH₄ sink (12–60 Tg yr⁻¹; Dutaur & Verchot, 2007) and global soil respiration (68–101 Pg C yr⁻¹; Raich & Potter, 1995; Raich et al., 2002; Jian et al., 2018).

The uncertainties in the global GHG fluxes are mostly associated with the upscaling procedure of flux estimates from eddy covariance (EC) tower measurements for CO₂ and by chamber techniques for N₂O and CH₄. In comparison with the EC technique, measurements of GHG fluxes with chambers allow the capturing of fine-scale flux variabilities, which enable the direct investigation of fine-scale land use and land management effects, and the partitioning of respiratory and gross primary production fluxes of CO₂, that is, information used for example, for gap filling EC data (Pavelka et al., 2018). However, it should be noted that the chamber technique cannot be used to quantify fluxes from large above-ground vegetation, such as forest canopies. In addition, most chamber measurements are usually limited to plot scales (e.g., Butterbach-Bahl et al., 2002; Nkongolo et al., 2010; Saiz et al., 2006) and that only a few studies tried to use chambers for assessing landscape-scale fluxes (e.g., Holst et al., 2007; Liu et al., 2009).

Several studies have shown that high spatial variations (beyond 100%) in soil surface fluxes can occur within a few meters (e.g., Arias-Navarro et al., 2017; Breuer et al., 2000; Dasselaar et al., 1998; Parkin & Venterea, 2010; Röver et al., 1999). The magnitudes of the soil GHG fluxes can also change significantly with seasons (Gütlein et al., 2018; Houska et al., 2017; Luo et al., 2013; Saiz et al., 2006). However, the main drivers of these spatial-temporal variations in soil GHG fluxes are still only partially understood, with previous studies broadly associating them with small-scale variabilities in biogeochemical production and consumption processes and soil and vegetation properties (Butterbach-Bahl et al., 2013; Röver et al., 1999; Saiz et al., 2006).

In soils, CO₂ is produced by microbial and root respiration. The CO₂ production at the soil surface can be measured with chambers as soil respiration (SR) as no significant CO₂ uptake processes are usually relevant within the soils. However, if chambers include above-ground biomass, for example, when measuring grasslands or arable land with opaque chambers, then the CO₂ production is ecosystem respiration (ER) (Oertel et al., 2016). CH₄ is produced in soils through methanogenesis under anaerobic conditions and consumed by methanotrophic microorganisms under aerobic conditions (Cicerone & Oremland, 1988). N₂O is mainly produced as a by-product in the nitrification process or as an intermediate in the denitrification process. However, other production processes such as dissimilatory nitrate reduction to ammonium (DNRA) and nitrifier-denitrification may also be responsible for the N₂O emissions (Butterbach-Bahl et al., 2013). All the aforementioned microbial processes are directly regulated by soil properties such as soil moisture, temperature, pH, and the availability of oxygen and substrates (Stehfest & Bouwman, 2006; Butterbach-Bahl et al., 2013; Table 1). At a higher level, these factors are further influenced by land use/land cover, land management practices, slope positions, soil type, and seasonal variations in weather patterns (Schaufler et al., 2010; Vilain et al., 2010; Arias-Navarro et al., 2017; Table 1).

Agricultural land use alters soil GHG fluxes through fertilizer inputs that are used to fuel crop growth. Nitrogen fertilizers can positively or negatively affect soil respiration due to their effects on below-ground biomass development and activity and plant-microbe interactions (Averill & Waring, 2017; Kuzyakov et al., 2000). The increased availability of soil inorganic nitrogen associated with fertilizer application has been found to lower the uptake rates of atmospheric CH₄ in arable soils by around 60% (Dobbie et al., 1996) and by about 20% in grassland soils (Täumer et al., 2020). Organic-based fertilizers such as livestock manure can also reduce soil CH₄ uptake rates indirectly by increasing the availability of carbon substrate for CH₄ production and directly through CH₄ emissions from the manure (e.g., Wang et al., 2013; Zhu et al., 2018). In contrast to CO₂ and CH₄, fertilizer inputs largely enhance N₂O emissions from agricultural soils (Tian et al., 2020), with fertilized soils contributing around 60% to total anthropogenic N₂O emissions (Syakila & Kroeze, 2011).

Land management practices such as regular tillage can cause changes in soil structure and bulk densities, affecting soil gas diffusivity and thereby the atmospheric CH₄ uptake of soils (Hütsch, 2001; Butterbach-Bahl & Papen, 2002, Table 1). Soil physical characteristics such as soil texture are also known to influence GHG

Table 1
A Summary of the Effects of Landscape Characteristics Such as Soil Properties, Land Use/Land Cover, Land Management, and Slope on Soil Greenhouse Gas Fluxes

Landscape features	Parameter	Influence on soil GHG fluxes	References
Soil	Moisture	Increase in GHG production at higher moisture content	Castro et al. (1995)
	Temperature	Enhanced microbial production rates with temperature increase	Castro et al. (1995), Ball. (2013), and Luo et al. (2013)
	pH	Decrease in CH ₄ uptake and N ₂ O emissions with an increase in pH	Borken and Brumme (1997) and Hütsch. (2001)
		No change in CO ₂ emissions with soil pH	Borken and Brumme (1997)
	Substrates (nutrients and carbon)	Enhanced soil respiration and reduced respiration rates after prolonged addition of nitrogen Increased N ₂ O emissions	Bowden et al. (2004) and Contosta et al. (2011) Schaufler et al. (2010) and Schelde et al. (2012)
Land use	Forest	Higher CH ₄ uptake in forest soils	Boeckx and Cleemput (2001)
	Arable and grassland	Lower N ₂ O fluxes compared to arable and grassland soils	Vilain et al. (2010)
		Lower CH ₄ uptake due to fertilizer application and disturbance of soil structure due to cultivation	Mosier et al. (1991), Hütsch. (2001), and Täumer et al. (2020)
		Higher N ₂ O fluxes due to fertilizer inputs	Syakila and Kroeze (2011)
		Higher soil ecosystem respiration in grassland compared to forest	Raich and Tufekcioglu (2000)
Land management	Tillage/ploughing	Increased CO ₂ emission and N ₂ O production	Mosier et al. (1991) and Krištof et al. (2014)
		Reduced CH ₄ uptake capacity of soils by disturbing the soil structure	Mosier et al. (1991), Hütsch. (2001), and Butterbach-Bahl and Papen (2002)
	Fertilizer/manure application	Reduces CH ₄ uptake by changing soil microbial population in the long term and blocking the enzyme system of methanotrophs in the short term	Mosier et al. (1991) and Hütsch. (2001),
		Increased N ₂ O emissions	Mosier et al. (1991) and Schelde et al. (2012)
	Cropping/vegetation growth	Enhances microbial processes by supplying them with carbon substrates	Raich and Tufekcioglu (2000) and Kuzyakov and Cheng (2001)
		Influences microbial processes by regulating the soil micro-climate	Raich and Tufekcioglu (2000)
		Higher ecosystem respiration rates during plant growth stage	Lohila et al. (2003) and Raich and Potter (1995)
Slope positions	Slope	Higher N ₂ O emissions at the footslope compared to steep and shoulder positions	Vilain et al. (2010)

Note. Only a few examples from the literature are included.

production and consumption at micro-site scales by regulating water and nutrient retention capacities and soil aeration (Ball, 2013; Ball et al., 1997). At a landscape-scale, slope positions also need to be considered, as they regulate hydrological flow patterns, which control soil moisture content and the distribution of organic matter and nutrients due to lateral transport processes (Vilain et al., 2010, Table 1). Additionally, seasonal weather variations affect plant growth, nutrients, and water availability in soils and generally the soil temperature (Contosta et al., 2011; Schelde et al., 2012), that is, factors that subsequently regulate microbial activities.

Heterogeneities of landscape features and soil conditions, such as those mentioned above, result in large spatial-temporal variabilities of soil GHG fluxes but are still largely unexplored, especially at landscape-scales. The scarcity of exploration is due to the high human and time resource requirements for conducting small-scale measurements of GHG fluxes at landscape-scales in order to investigate their potential controlling factors. As a result, so far, most studies on the spatial-variability of soil GHG fluxes have been conducted at a laboratory scale through incubation measurements under standardized conditions (e.g., Arias-Navarro et al., 2017; Mathieu et al., 2006). However, few studies have evaluated this through direct field measurements, though these studies

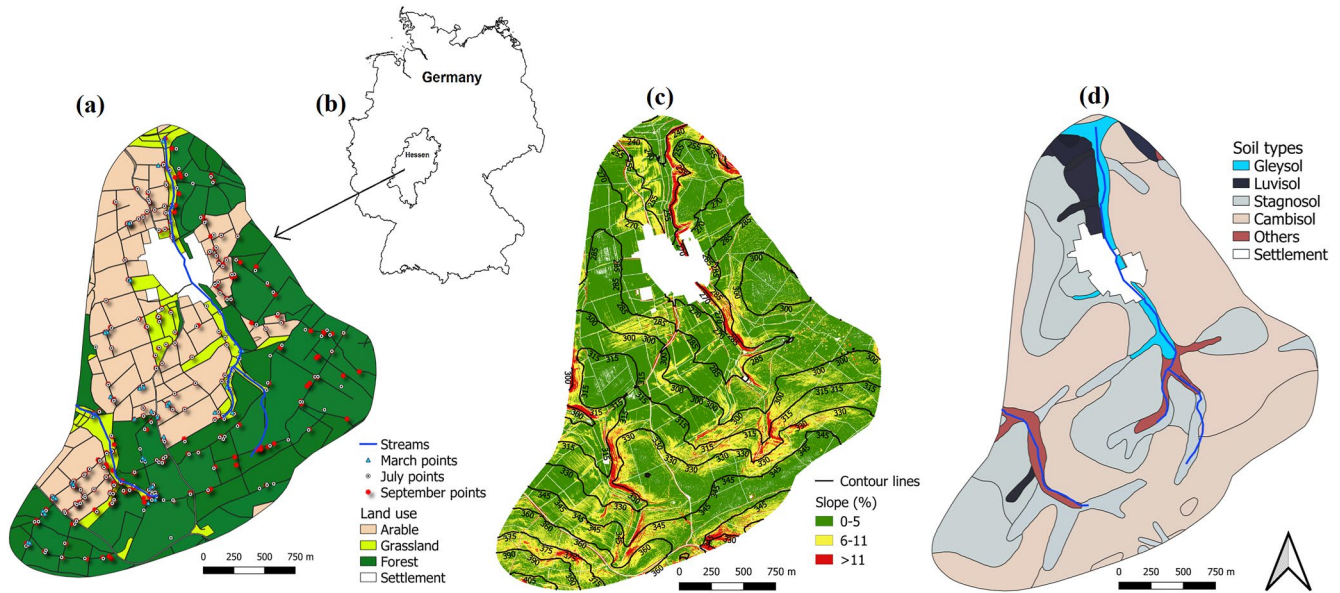


Figure 1. Maps showing (a) the land uses/land cover (CORINE land cover, 2018) and location of the sampling points during the spring, summer, and autumn field campaigns, (b) the location of the landscape in Germany, (c) landscape slope with contour lines and (d) the soil types in the study landscape (geoportal Hesse).

usually focus on well-defined field plots of sizes <1 ha (e.g., Flessa et al., 1995; Hereş et al., 2020; Nkongolo et al., 2010). These obvious short-comes call for a more comprehensive field-based sampling approach that explores the importance of heterogeneities of landscape features and soil conditions on the small-scale variability of GHG fluxes within landscapes in order to better constrain the controlling environmental factors. Based on such an assessment, it would also be possible to calculate the number of chamber measurement locations required to estimate surface GHG fluxes from large landscapes of about 10 km^2 within a specific range of uncertainty.

This study was thus designed to assess the number of measurement locations required to estimate surface GHG fluxes at a landscape-scale using chamber measurements. Furthermore, we aimed to understand better the underlying controls of small-scale spatial variations in GHG fluxes and assess how they may be considered for accurately estimating fluxes at a landscape-scale. The Schwingbach landscape in central Germany was chosen for this study as it contains a mix of land use/land cover (forest, grassland, and arable lands) representative of the region and has varying slope and soil type conditions. The specific objectives of this study were: (a) to determine the influence of land use, soil type, slope, and seasonality on soil and ecosystem respiration (SR/ER-CO_2), CH_4 and N_2O fluxes, (b) to investigate the effects of soil physico-chemical properties and vegetation on the fluxes, and (c) to determine the minimum number of measurement locations required to estimate landscape fluxes with a pre-defined uncertainty. We hypothesized that marked seasonal differences in soil GHG fluxes occur, closely linked to plant growth and soil environmental conditions. We also hypothesized that slope and soil type might play an insignificant role compared to land use since land use already reflects the landscape's slope and soil property differences. Moreover, we hypothesized that the spatial-temporal variation of N_2O fluxes is higher than CO_2 and CH_4 fluxes, and thus more chamber measurement locations will be required to estimate landscape N_2O fluxes.

2. Materials and Methods

2.1. Site Description

The Schwingbach landscape is located at Hüttenberg municipality ($50^\circ30'4.23 \text{ N}$, $8^\circ33'2.82 \text{ E}$) in Hesse, Germany (Figure 1). It covers an area of approximately 6 km^2 (exclusive of the human settlement area and road networks). The landscape has gentle slopes (mean 8%) and spans an altitudinal gradient of 233–415 m above sea level. Two streams (Schwingbach and Vollnkirchener Bach) drain the landscape (Orlowski et al., 2014, 2016). The predominant land uses in the landscape are forests (57%) and arable lands (34%). Grasslands (8%) are mainly found in riparian areas along the streams (CORINE landcover, 2018; Figure 1a). The most common grass species are meadow foxtail (*Alopecurus pratensis*), Bulbous oat grass (*Arrhenatherum elatius*), meadow fescue (*Festuca*

pratensis), and red clover (*Trifolium pratense*). The forest land cover is comprised of mixed (44%), deciduous (32%), and coniferous (23%) trees. The main tree species observed at forest sites included European beech (*Fagus sylvatica*), spruce (*Picea abies*), European oak (*Quercus robur*), and Scots Pine (*Pinus sylvestris*). The main soil type is cambisol (69%), and forests and croplands mainly cover these soils. Stagnosol (23%) and luvisol (2%) are dominant in the croplands, while gleysol (5%) are located in the riparian areas, which are predominantly grasslands (geoportale Hessen; Figure 1d). The topsoil layers (0–5 cm depth) of arable and grassland soils are of a silt loam texture, while the forest soils (0–5 cm depth) are primarily of sandy loam texture with significant gravel content (Sahraei et al., 2020). Bedrock geology consists mainly of argillaceous shale, greywacke, and loess (Orlowski et al., 2016). The climate is temperate oceanic (Cfb, Köppen climate classification) with mean annual precipitation and temperature of 623 mm and 9.6°C, respectively, for the period 1969–2019 (Sahraei et al., 2021). Crops are mainly barley, wheat, and rapeseed (Houska et al., 2017). The farmers mainly apply nitrogen-based fertilizers (approximate mean 170 kg N ha⁻¹). Basal fertilizers are applied around the end of March before sowing and top dressing around May. Plowing is usually conducted before sowing (early March) and after harvesting (early August).

2.2. Identifying Representative Sampling Points for GHG Flux Measurements

We used a stratified sampling plan to identify sampling points for GHG flux measurements that well represent the spatial variability of landscape characteristics, that is, land use, soil type, and slope. In the plan, polygon-based maps for land use/land cover (forest, grassland, arable) and soil type (cambisol, stagnosol/gleysol, and luvisol) were rasterized to a target resolution of 5 × 5 m (Figure 1). Landscape slope was computed from a 5 × 5 m resolution Digital Elevation Model (DEM) obtained from the Shuttle Radar Topography Mission (SRTM) (Retrieved 1 March 2020) and classified into 3 classes (0–5, 6–11, and >11%; Figure 1c). The raster layers were merged, and a 50 m buffer zone along the roads was created for practical reasons of easier accessibility of sites during field measurements. A total of 270 random sampling points (the maximum number of study points that could be measured within a 10-day seasonal field campaign) were identified, considering a buffer zone of a minimum distance of 20 m around each point. The distribution of the random points was weighted based on the percentage distribution of land uses within the landscape (Text S1 in Supporting Information S1).

2.3. Sampling Strategy

Landscape-scale GHG flux measurements were carried out in three campaigns of 2–10 days to capture different climatic seasons and land management practices. Campaign I: early spring, 14–15 March 2020, was chosen to capture GHG fluxes at the start of the vegetation period. During this period, most arable fields were plowed and bare (Figure S1a in Supporting Information S1), and only a few had winter cover crops. In total, GHG fluxes at 42 sampling points were measured as COVID restrictions did not allow for more sampling days. Campaign II: summer, 30 June till 9 July 2020, represented GHG fluxes at the peak of the growing season. Crops such as wheat, barley, and rapeseed dominated the arable fields (Figure S1b in Supporting Information S1). During this campaign, soil GHG fluxes at 246 points were monitored. Campaign III: early autumn, 8–17 September 2020, captured fluxes after crop harvesting and tillage of the arable lands (Figure S1c in Supporting Information S1). In this last campaign, we sampled 268 points out of the targeted 270 points. It is noteworthy that the respiratory fluxes measured at the forest sites in this study were only soil respiration (SR-CO₂) since the measurements were conducted on the forest floor, which had little or no undergrowth. However, the fluxes measured at arable and grassland sites were ecosystem respiration (ER-CO₂) as all of the above-ground biomass was included in the chambers during the measurements (Figure S1b in Supporting Information S1).

2.4. Flux Measurements

Field measurements of soil GHG fluxes at the pre-selected sites were carried out using the fast-box chamber technique (Hensen et al., 2013). This technique allows the measurement of changes in chamber headspace GHG concentrations in the field with highly sensitive laser spectroscopy instrumentation. Therefore, chamber closure times can be limited to a few minutes, and several measurements at various sites can be run within a day. We used opaque polypropylene chambers (37 × 26.5 × 12.5 cm; length, width and height, respectively), which were mounted on metal chamber collars installed at each study site. The collars were installed in every measurement campaign immediately before flux measurements. Immediate measurement of fluxes after installation of

chamber collars has been previously shown to affect the accuracy of GHG fluxes through root and soil disturbance (Heinemeyer et al., 2011; Keller et al., 2000; Wang et al., 2005). However, Keller et al. (2000) showed no immediate effects on soil N₂O fluxes on the same day, but the effects on soil N₂O fluxes only became significant a few days after installation. Moreover, Wang et al. (2005) showed that the effect of chamber collar installation on forest soil respiration depends on the insertion depth. For 3 cm insertion depth, that is, 1 cm more than in our study, they found a reduction in soil respiration by about 20%. Investigating forest, heathland, and pasture ecosystems, Heinemeyer et al. (2011), reported an overall decrease in soil respiration of about 15% following the insertion of chamber collars, with the least impact in the deep-rooted grasslands. Therefore, based on these studies and the collar insertion depth of 2 cm in our study, we assume that soil respiration rates are under-estimated by at most 20%. Moreover, we believe there was no significant effect on our estimates of CH₄ and N₂O fluxes as the physical disturbance of inserting collars to 2 cm soil depth on the soil structure is rather small given the size of our chambers. To counter the effect of lateral gas diffusion that may occur due to the minimal collar soil insertion depth, we limited chamber closure (measuring) time to 3–7 min per site. The linearity of the fluxes was checked for each measurement. Chamber measurements have also been shown to overestimate soil respiration during low atmospheric turbulence (Brændholt et al., 2017), which may account for additional positive biases in our measured SR fluxes.

A pump system was used to circulate chamber air at a rate of about 200 ml min⁻¹ through 1/8 Teflon tubing to the gas analyzers and back to the chamber, allowing proper air mixing during GHG concentration measurements. We used a roundly folded Teflon tube (1 m in length and 3 mm diameter) on one side of the chamber, exposing the chamber headspace to the atmospheric pressure to minimize pressure-induced gas fluxes within the chamber due to the venturi effect. The chambers at the forest sites were deployed under the forest canopy on the leaf litter. For taller vegetation, for example, field crops during the cropping season, we used chamber extensions (70 cm height; Figure S1b in Supporting Information S1). A small fan (4 cm in diameter) was operated to guarantee air mixing within these tall chamber extensions. The fan was run at a gentle speed to maintain an air circulation speed of less than 0.5 m s⁻¹ inside the chambers, thus avoiding turbulence-induced fluxes (Pavelka et al., 2018).

Gas concentrations of N₂O and CH₄ were analyzed using an Off-Axis Integrated Cavity Output Spectroscopy (OA-ICOS) analyzer (Los Gatos Research, Inc, CA, USA) with a precision of 1.0 (N₂O) and 2.0 (CH₄) ppbv per second for the respective gases. Concurrently, CO₂ concentrations were analyzed using an infrared gas analyzer (LI-840A & LI-850, LI-COR Biosciences, Lincoln, NE, USA) with a precision of 1.0 ppmv per second. The detection limits for CO₂, CH₄, and N₂O fluxes were 0.73 mg CO₂-C m⁻² h⁻¹, 0.48 μg CH₄-C m⁻² h⁻¹, and 0.56 μg N₂O-N m⁻² h⁻¹ respectively. Both analyzers were synchronized and measurements were recorded at a rate of every 5 s. The high accuracy and sensitivity of the analyzers allowed the restriction of measurements to a short chamber deployment period of around 5–10 min at each site depending on the given concentration increase or decrease over time.

The GHG concentration measurements were done during daylight between 7.00 a.m. and 5.00 p.m., with a daily average of 21–27 sites. On each sampling day, the measurements were carried out at random sites spread across different land uses and random sections of the landscape to minimize mistaking site-specific differences with intra-daily variations of GHG fluxes related to soil temperature and moisture. The measurements during each campaign were restricted to 10 days to minimize inter-daily variations of weather conditions (Figure S2 in Supporting Information S1) and their potential effect on the soil parameters and GHG fluxes. To statistically test this assumption, we used a one-way ANOVA analysis to compare changes in weather patterns with variations in soil moisture and GHG fluxes. The results of the analysis showed that significantly ($p < 0.05$) different days in terms of GHG fluxes and soil moisture were not consistent with the days having different weather conditions (Table S2 in Supporting Information S1). Based on these results, all the variability in soil moisture content and GHG fluxes within the same season were linked to spatial differences related to land use.

The area-related C and N gas mass flux F (mass m⁻² h⁻¹) was calculated from the linear change of measured gas mixing ratios (ppmv) over time in the chamber headspace (Equation 1).

$$F = \frac{dq}{dt} * \frac{P * V * M}{R * T * A} \quad (1)$$

Where dq/dt is the change in gas mixing ratios over time (h⁻¹), P is atmospheric pressure (atm), V is chamber volume (m³), M is the molar mass of the gas (mass mol⁻¹), R is the universal gas constant (m³ atm K⁻¹ mol⁻¹), T is air temperature (K), and A is the area of the chamber (m²). The changes in GHG concentrations with time were

always linear during the short chamber closure times. All regression slopes from the linear relationships with a p -value of <0.001 were accepted. Flux calculations were done in R using the “gasfluxes” package.

2.5. Determination of Vegetation Cover and Soil Properties

Quantifying the vegetation cover within the landscape during the three campaigns was done using the normalized difference vegetation index (NDVI). The NDVI quantifies vegetation intensity as a ratio from -1 to 1 by measuring the difference between reflectance in the near-infrared (NIR) region where green chlorophyll-rich vegetation reflects and the red region where the vegetation absorbs. The NDVI was computed from Sentinel-2 images (with $<5\%$ cloud cover) derived from Google Earth Engine with a 30 m resolution for the specific period of field measurements.

Concurrent with the flux measurements, soil and air temperatures were measured in the field using temperature probes and sensors (Ebro EBI 20-T1). For each GHG flux measurement, additional soil samples from the mineral layer at 0–20 cm depth in the grassland and arable soils and around 7–20 cm depth at forest sites. The samples were taken in duplicates using standard cylindrical soil corers (volume 100 cm³). The samples were analyzed for bulk density, gravimetric soil moisture, pH, texture, and soil carbon and nitrogen contents. Soil pH was measured in a suspension (1:2.5 soil and 0.01M CaCl₂) using a calibrated electrode pH meter (WTW pH 526 MultiCal). Intact soil core samples were pre-weighed and oven-dried at 105°C for 24 hr for gravimetric moisture content and bulk density analysis.

Mineral nitrogen was analyzed on soil extracts (1:5 soil and 1M KCL) using the colorimetric method, where vanadium chloride (VCL₃) and griess reagents were used for NO₃-N analysis (Hood-Nowotny et al., 2010). The reaction of sodium salicylate and sodium dichloroisocyanurate was used for NH₄-N analysis (Bolleter et al., 1961). The absorbance of NO₃-N and NH₄-N were then measured in triplicates at 540 and 660 nm wavelengths, respectively, using an EPOCH microplate spectrophotometer (BioTek Inc. USA).

Soil dissolved organic carbon (DOC) and total dissolved nitrogen (TDN) concentrations were analyzed on soil extracts (1:5 soil and 1M KCL) using a multi-N/C—TOC analyzer (model 3100, Analytik Jena GmbH, Germany). Soil total organic carbon (TOC) and nitrogen (TN) were analyzed on pre-dried (60°C for 24 hr) and sieved soil samples using an elemental analyzer (EA) and loss-on-ignition (LOI) method (soil TOC cube, Elementar Analysensysteme GmbH). Soil texture analysis was conducted on pre-processed soil samples (oven-dried at 40°C for 48 hr, sieved with 2 mm mesh, and organic matter $>1.5\%$ destroyed with hydrogen peroxide). Clay and silt were measured with a PARIO device (METER Group, Inc, USA) using the integral suspension pressure method, while sand content was determined through sieving (Durner et al., 2017). Soil texture was then computed automatically using the PARIO software.

2.6. Chamber Measurement Locations Required for Landscape GHG Flux Estimates

The number of measurement locations required to effectively estimate SR/ER-CO₂, CH₄, and N₂O fluxes in each land use were estimated via bootstrapping, where we compared the mean fluxes of samples of different sizes “ n ” with the mean flux of the entire population of size “ N ” (true-mean). For this analysis, the GHG fluxes were converted to similar units (CO₂ equivalents mg m⁻² h⁻¹), and we only used the flux data for summer and autumn campaigns, which had the largest number of GHG observations (37–98 sites) per land use. We calculated the GHG flux uncertainties (within a 90% confidence interval) as the differences between the assumed true mean ($n = N$) and the means of the resampled (10,000 times) reduced population sizes of n ($n = 5, 15, 25, 35, \dots, N$).

To calculate the minimum number of chamber measurement locations that may potentially lead to significant GHG flux uncertainties, we used fixed uncertainty thresholds referenced from global annual mean/median GHG flux estimates. The fixed uncertainties were GHG-specific and set at three thresholds, that is, half, actual, and twice the global mean/median estimates of each respective GHG flux. For CO₂, we used the global median soil respiration of around 7,500 kg ha⁻¹ yr⁻¹ CO₂-C; 313.9 CO₂ equivalents mg m⁻² h⁻¹ (Jian et al., 2021). Global forest soil CH₄ uptake rates of about 2.81 kg ha⁻¹ yr⁻¹ CH₄-C; 1.2 CO₂ equivalents mg m⁻² h⁻¹ and the global soil N₂O flux average of around 0.67 kg ha⁻¹ yr⁻¹ N₂O-N; 3.2 CO₂ equivalents mg m⁻² h⁻¹ were assumed (Ni & Groffman, 2018; Tian et al., 2020). The required number of chamber measurement locations to achieve the respective flux estimates within the three fixed uncertainty thresholds were then calculated. We further expressed the required number of chamber measurement locations for these fixed uncertainties per area coverage (km⁻²) of each land use.

2.7. Statistical Analyses

Analyses of variances (Type II) from linear mixed-effects models were used to assess the influence of land use/land cover, season, soil type, and slope on GHG fluxes and soil properties such as mineral nitrogen, soil moisture, and temperature (R package “lme4”). Random effects of sites and repeated measures were included in the models. Performances of the significant models ($p < 0.05$) were then assessed using conditional r^2 values, that is, variance explained by both fixed effects and random effects in the mixed models (R package “MuMIn”). A Tukey post hoc analysis of least-square means was used to determine significant differences (p -value < 0.05) amongst individual levels within each grouping factor.

To identify significant (p -value < 0.05) relationships between the fluxes and site properties such as soil temperature, gravimetric moisture, pH, bulk density, $\text{NO}_3\text{-N}$, $\text{NH}_4\text{-N}$, TDN, DOC, TN, TOC, and NDVI, multiple linear regression models based on the stepwise selection of independent variables were used (R function “step”). The analysis was performed on data separated by land use to determine GHG controlling factors in the different land uses. Covariations in the independent variables were tested and considered during model construction. The direction and strengths of the resulting relationships were interpreted as suggestions of possible underlying biogeochemical production or consumption processes of the GHGs, as shown in previous soil studies (e.g., Castro et al., 1995; Hütsch, 2001; Stehfest & Bouwman, 2006; Yao et al., 2020). Most soil properties, CO_2 and N_2O fluxes were skewed and thus transformed using the natural logarithm before statistical analysis. The spatial variance of fluxes was computed based on the coefficient of variance (CV%). The CV% was calculated as the ratio of the standard deviation to the mean expressed as a percentage. For CH_4 and N_2O fluxes, only CH_4 uptake rates and N_2O emissions were considered in the calculation of CV% since they formed the bulk of our measures (88% CH_4 uptake rates and 86% N_2O emissions). This omission of CH_4 emission and N_2O uptake in the CV calculation was done to create datasets with uniform values (i.e., only negative CH_4 and only positive N_2O fluxes) to enable a relative comparison of the variability of the fluxes. All statistical analyses were performed in R software version 3.2.6.

3. Results

3.1. Site Properties

Arable and grassland sites were mainly composed of mineral soils within the 0–20 cm sampled depths. The forest sites mostly had three soil layers (litter layer, humus layer, and mineral soil) within the 0–20 cm depths. The thickness of litter and humus layers varied from site to site but were located within 0–7 cm depths. The mineral soil layer was mostly from 7 cm downwards. Across the three sampling campaigns and land uses, soil temperature, gravimetric soil moisture (%), pH, and bulk density ranged from 7–36°C, 0.3%–41%, 3–7 g cm^{-3} , and 0.2–1.5 g cm^{-3} , respectively. The highest soil temperatures were observed in summer and autumn. Gravimetric soil moisture content was significantly higher ($p < 0.05$; Table 2) in the spring and summer seasons than in autumn. Soil TOC and TN did not change across seasons, while in contrast, the dissolved forms of carbon and nitrogen showed significant seasonal variations. Soil DOC, $\text{NO}_3\text{-N}$, and $\text{NH}_4\text{-N}$ were higher during the summer growing season than in autumn. Vegetation cover (NDVI) was also highest in summer as compared to spring and autumn (Table 2; Figure 2).

Regarding land use, forest sites had the lowest topsoil pH (Table 2; Figure 2), higher soil TOC and DOC concentrations, and C:N ratios than grassland and arable sites at all seasons. Soil $\text{NO}_3\text{-N}$ concentrations were higher in arable soils across all seasons. In contrast, the effect of land use on soil $\text{NH}_4\text{-N}$ concentrations differed amongst seasons. During summer, the highest soil $\text{NH}_4\text{-N}$ concentrations were found in forest and grassland sites, while in autumn, the highest $\text{NH}_4\text{-N}$ were found in soils of arable sites. Vegetation cover (NDVI) was higher at forest sites than at grassland and arable sites (Table 2; Figure 2). However, it is noteworthy that the NDVI in the forest ecosystems represented the canopy cover, not the forest undergrowth that our chamber measurements captured.

3.2. Soil and Ecosystem Respiration (SR/ER- CO_2)

Across all measuring periods, soil and ecosystem respiration rates ranged from 9–877 $\text{mg CO}_2\text{-C m}^{-2} \text{h}^{-1}$. The CO_2 effluxes did not show any significant daytime variations across all sites, despite the measurements being done at different times of the day with significant temperature changes in summer and autumn (Figure S3, S4, and S5 in Supporting Information S1). The analysis of spring daytime variations in fluxes was omitted due to

Table 2

The Analysis of Variance (Type II) Results From Linear Mixed-Effects Models on the Effect of Seasonality, Land Use, Soil Type, and Slope on the Fluxes, Soil Variables, and the Vegetation Index

Dependent variables	Type 2 ANOVA table									
	Marginal r^2	Conditional r^2	Season		Land use		Soil type		Slope	
			F-value	Sig	F-value	Sig	F-value	Sig	F-value	Sig
GHG fluxes										
SR/ER CO ₂ -C (mg m ⁻² h ⁻¹) ^a	0.58	0.64	73.2	***	31.1	***	6.5	*		ns
CH ₄ -C flux (μg m ⁻² h ⁻¹)	0.27	0.36	8.1	**	60.8	***		ns		ns
N ₂ O-N (μg m ⁻² h ⁻¹) ^{a,b}	0.28	0.35	16.7	***	29.6	***		ns		ns
Soil properties										
Soil temperature (°C)	0.12	0.66	6.7	**		ns		ns	4.5	*
PH	0.52	0.68	3.4	ns	173.7	***	7.9	**	4.9	**
Gravimetric soil moisture (%) ^a	0.49	0.81	17.8	***	31.8	***	38.0	***		ns
Bulk density (g cm ⁻³)	0.35	0.45	5.3	*	111.2	***		ns		ns
NO ₃ -N (mg kg ⁻¹ dry soil) ^a	0.24	0.37	15.4	**	48.6	***		ns		ns
NH ₄ -N (mg kg ⁻¹ dry soil) ^a	0.36	0.38	145.1	***	3.5	*		ns		ns
DOC (mg kg ⁻¹ dry soil) ^a	0.49	0.60	25.1	***	150.4	***		ns		ns
TDN (mg kg ⁻¹ dry soil) ^a	0.19	0.21	71.3	***	2.8	ns		ns		ns
Soil TN (%) ^a	0.28	0.57	3.2	ns	74.3	***		ns		ns
Soil TOC (%) ^a	0.52	0.67		ns	203	***		ns		ns
C:N ratio ^a	0.58	0.76	17.0	***	204.3	***	5.6	*		ns
Vegetation index (NDVI)	0.64	0.75	39.5	***	258.6	***		ns		ns
Sand content (%)	0.06	0.94			4.9	**	6.9	**	3.7	*
Silt content (%)	0.04	0.97			6.9	*		ns	2.7	ns
Clay content (%)	0.01	0.97			3.8	*	2.9	ns		ns

Note. Random effects of sites and repeated measures were also included in the models (see detailed description in statistics). The level of significance (sig) indicates whether the fixed effects were significant ($p < 0.05$) or not significant (ns).

^aNatural logarithm (base 10) transformation. ^b19 μg N m⁻² h⁻¹ were added before log transformation of N₂O fluxes Marginal r^2 = Variance explained by fixed effects only, Conditional r^2 = Variance explained by fixed and random effects of site and sampling date. * p -value < 0.05. ** p -value < 0.01. *** p -value < 0.001. ns p -value > 0.05.

few data point distributions across the two measurement days. The flux rates were 2–3 folds higher during the growing season in summer than in spring and autumn (Table 2; Figure 3; Table S3 in Supporting Information S1). The comparison of the respiratory fluxes across all land uses showed 1.8 folds lower fluxes at forest sites than at arable and grassland sites. This result reflected the differences in the quantified fluxes, that is, SR (little or no above-ground biomass) at forest sites and ER (with above-ground biomass) at arable and grassland sites. The ER fluxes were significantly higher at grassland compared to arable sites. Regarding soil types, we found that the measured CO₂ fluxes were higher in the gleysol and stagnosol category than in the other soil types, but this effect may be an artifact since gleysols are only used as grasslands in the catchment (Figure 1). Slope did not significantly influence the SR/ER fluxes (Table 2; Table S3 in Supporting Information S1).

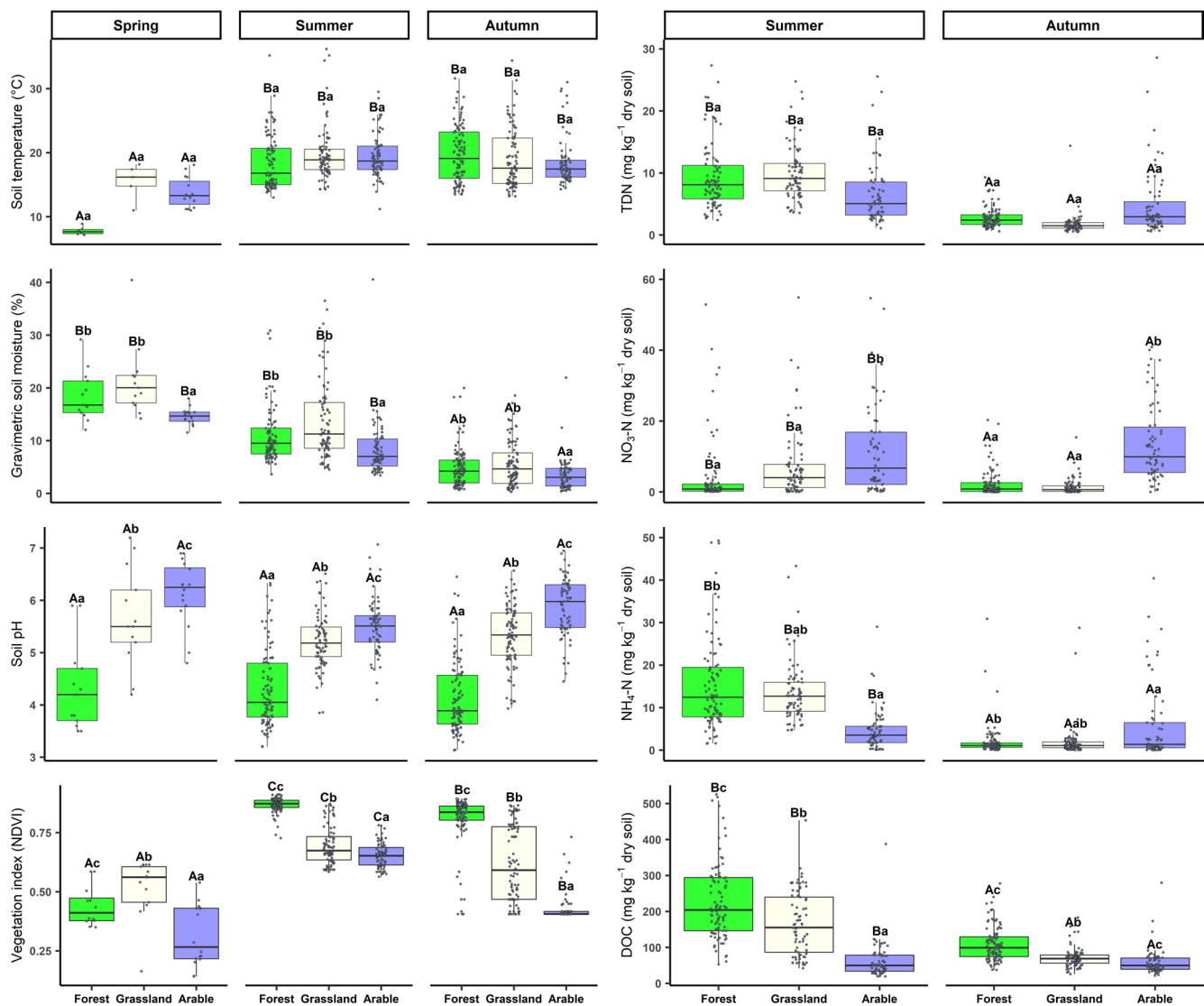


Figure 2. Box plots showing the distribution of soil and vegetation properties across the different seasons for the different land uses. The upper-case and lower-case letters indicate significant differences ($p < 0.05$) between seasons and land uses, respectively, based on Tukey post hoc analyses of least-square means from the linear mixed-effects models (Table 2).

3.3. Methane (CH_4) Fluxes

The study landscape was mostly a net sink for atmospheric CH_4 (mean \pm SE of $-34.1 \pm 2.3 \mu\text{g CH}_4\text{-C m}^{-2} \text{h}^{-1}$), with overall fluxes ranging from -214 to $221 \mu\text{g CH}_4\text{-C m}^{-2} \text{h}^{-1}$. CH_4 uptake rates were up to fourfold higher after the crop growing season in autumn compared to the spring and summer seasons. Soils of forest sites showed the highest rates of atmospheric CH_4 uptake, while arable sites were often weak net sources, particularly during the growing season in summer (Table 2; Figure 3; Table S3 in Supporting Information S1). However, neither soil types nor slope significantly influenced the soil CH_4 fluxes (Table 2).

3.4. Nitrous Oxide (N_2O) Fluxes

Soils in the study landscape were notable net sources of N_2O (mean \pm SE of $24.7 \pm 2.3 \mu\text{g N}_2\text{O-N m}^{-2} \text{h}^{-1}$), with fluxes ranging from -18 to $281 \mu\text{g N}_2\text{O-N m}^{-2} \text{h}^{-1}$. Similar to SR-CO_2 , N_2O fluxes were 3 and 4 folds higher during the growing season in summer than in autumn and spring (Table 2; Figure 3; Table S3 in Supporting Information S1). We observed the highest N_2O fluxes at arable sites during the growing season, with magnitudes of

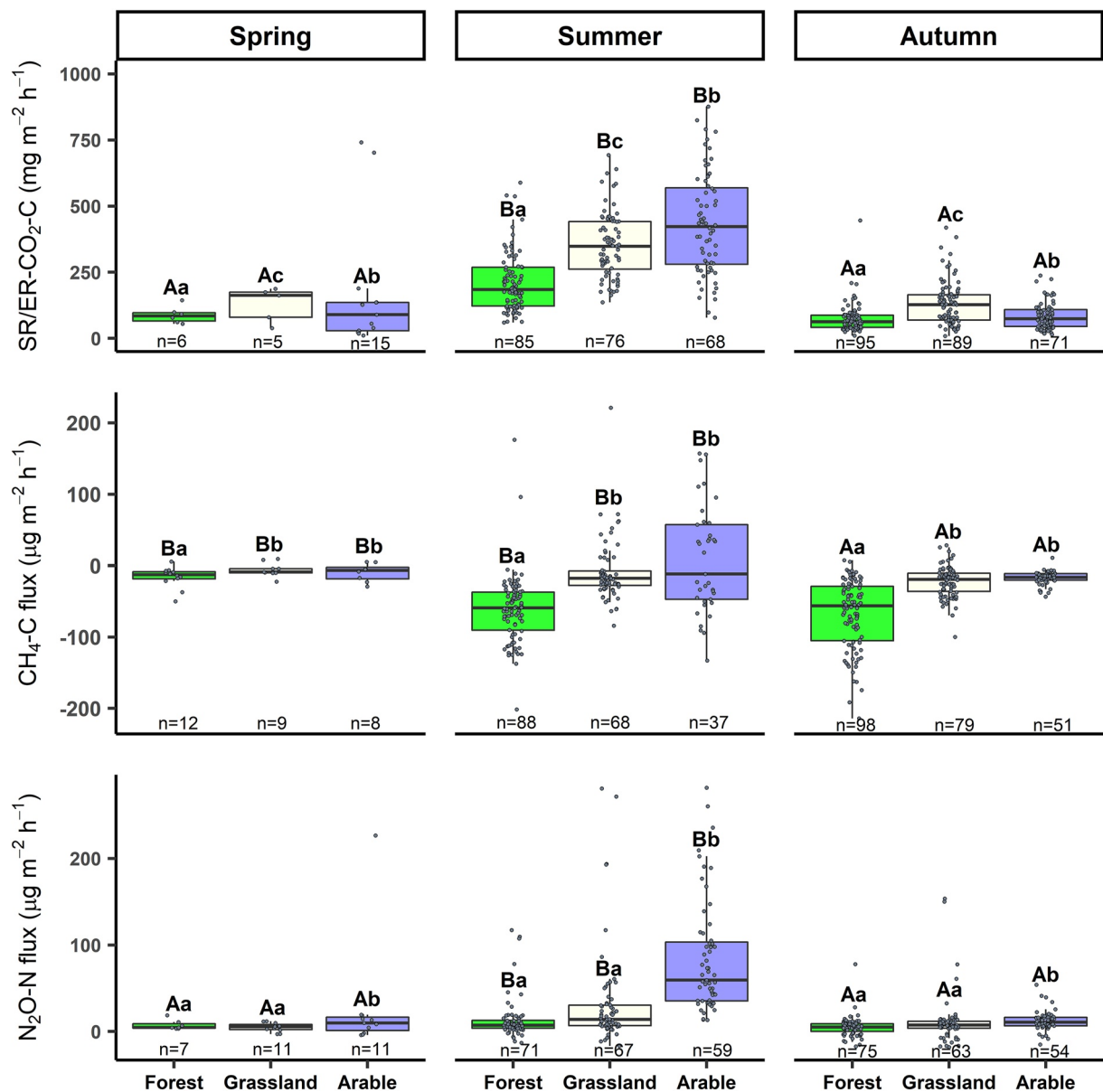


Figure 3. Box plots showing the distribution of fluxes (SR/ER-CO₂, CH₄ and N₂O) in each land use category across the different seasons. The upper-case and lower-case letters indicate significant differences ($p < 0.05$) between seasons and land uses, respectively, based on Tukey post hoc analyses of least-square means from the linear mixed-effects models (Table 2).

up to 2.6 and 6 times higher than those from grassland and forest sites. However, such a vast difference between land uses regarding the N₂O flux magnitudes were not found in the spring and autumn seasons (Figure 3). N₂O fluxes did not differ significantly with soil type and slope categories (Table 2).

3.5. Regression Between Site Properties and Soil GHG Fluxes

The stepwise multiple linear regression analysis indicated that combinations of different soil physico-chemical properties best explained the fluxes measured in the different land uses/land cover (Table 3, panel a–c). Soil respiration at the forest sites was positively related to gravimetric soil moisture, DOC, and NH₄-N concentrations and negatively related to soil TOC, sand content, and NO₃-N concentration ($r^2 = 0.58$). At grassland sites, ecosystem respiration was also positively related to gravimetric soil moisture and NH₄-N concentration ($r^2 = 0.48$).

Ecosystem respiration at arable sites was also positively related to NDVI, gravimetric soil moisture, and TDN and negatively related to soil TOC ($r^2 = 0.68$) (Table 3, panel a).

Prediction of CH₄ fluxes by soil physico-chemical properties was generally weak across all land uses. All positive relationships with CH₄ fluxes were interpreted as negative relationships with CH₄ uptake rates as they formed the bulk (88%) of our measures. We found a negative relationship between CH₄ uptake rates and a combination of soil NO₃-N concentration, gravimetric soil moisture, and soil temperature in forest soils. CH₄ uptake rates were also negatively related to gravimetric soil moisture and soil pH at grassland sites. At arable sites, CH₄ uptake rates were negatively related to vegetation cover (NDVI) only (Table 3, panel b).

The relationships of N₂O fluxes with measured environmental parameters were stronger for sites located on arable land ($r^2 = 0.47$) as compared to grassland ($r^2 = 0.15$) and forest ($r^2 = 0.11$) sites. Forest soil N₂O fluxes were positively related to gravimetric soil moisture content only. At grassland sites, the N₂O fluxes were positively related to soil TDN and gravimetric soil moisture content and negatively related to clay and sand content. The N₂O fluxes at arable sites were positively related to a combination of NDVI and soil NO₃-N concentrations (Table 3, panel c).

3.6. Spatial-Temporal Variation of Landscape GHG Fluxes

The spatial variability of our measured fluxes differed amongst seasons and land uses. For SR/ER-CO₂, the coefficient of variation (CV) ranged from 35% to 143% across the different seasons and land uses (Table S4 in Supporting Information S1). The CV values at forest sites showed an increasing trend across the seasons, with a lower value (37%) in spring and a higher value (72%) in autumn. Grassland and arable ecosystems had lower CV values during summer, which coincidentally had higher CO₂ effluxes (Figure 3). CH₄ uptake rates had a narrower range of spatial variability than the other GHG fluxes, with CVs spanning from 50% to 76%. Comparing across the seasons, the CVs were generally lower during summer than in spring and autumn in all the land uses. A declining trend was observed in the CH₄ CV values at arable sites across seasons from spring (71%) to autumn (50%).

N₂O emissions had the highest spatial variances compared to CO₂ and CH₄, with a broader range of CVs (56%–192%). The CV values for N₂O emissions at grassland sites had an uptrend from spring (56%) to autumn (173%), while arable sites depicted a downtrend from 192% in spring to 70% in autumn. However, at forest sites, the highest CV values were observed during summer, when N₂O emissions were highest. In comparison across the land uses, arable sites showed a wider range of variances (70%–192%), followed by grasslands (56%–173%) and forest sites (75%–150%) across all seasons.

3.7. Chamber Measurement Locations Required for Landscape GHG Flux Estimates

Based on the results from the bootstrap analysis, the relationships between the uncertainties of the mean landscape GHG fluxes and the number of measured sites followed a logarithmic decline (Figure 4; Table S9 in Supporting Information S1). The summer campaign had up to 7.7 folds higher uncertainty values than the autumn campaign for a similar number of measurement locations. This finding was also evident across the land uses, where arable land exhibited higher uncertainties for all three GHG fluxes compared to grasslands and forests during the summer campaign. Overall, comparing the uncertainties across the three GHG fluxes (CO₂ equivalents mg m⁻² h⁻¹), a similar number of measurement locations resulted in up to two orders of magnitude higher uncertainty values for SR/ER-CO₂ compared to N₂O fluxes and CH₄ uptake rates across the landscape.

Based on the logarithmic relationships, we calculated the number chamber of measurement locations required to achieve fixed uncertainties of roughly 0.5, 1, and 2 folds of each GHG flux's global annual mean/median. When the required number of measurement locations in each land use were expressed per unit area (km⁻²) of each land use, a range of 1–39, 1–42, and 1–154 measurement locations were required for estimation of SR/ER-CO₂, CH₄, and N₂O respectively, within the different fixed uncertainty thresholds (Table 4). Forest and arable lands required a lower range (1–29) of measurement locations for all the GHG fluxes compared to grasslands (1–154). However, the total number of sites sampled per km² was also higher in grasslands than in arable land and forest due to their relatively low area of coverage (0.5 km²) within the landscape (Figure 1a; Table S10 in Supporting Information S1). Comparing across the seasons, up to 1.5–6 folds more measurement locations were required for

Table 3
Results of Multiple Linear Regression Analyses Between Site Properties and Soil Greenhouse Gas Fluxes

Forest	Grassland					Arable				
	Predictor variables	B	Standard error	p-value	Degrees of freedom	Predictor variables	B	Standard error	p-value	Degrees of freedom
<i>(a) SR/ER-CO₂-C flux (mg m⁻² h⁻¹)</i>										
(Intercept)	3.50	0.48	***	***	155	(Intercept)	4.30	0.09	***	113
Gravimetric soil moisture (%) ^a	0.21	0.07	*	***	155	Gravimetric soil moisture (%) ^a	0.41	0.05	***	113
DOC (mg kg ⁻¹ dry soil) ^a	0.29	0.11	**	***	155	NH ₄ -N (mg kg ⁻¹ dry soil) ^a	0.12	0.03	***	113
Soil TOC (%) ^a	-0.43	0.13	**	***	155	Soil TOC (%) ^a	-0.38	0.15	*	113
Sand content (%)	-1.72	0.47	***	***	155	TDN (mg kg ⁻¹ dry soil) ^a	0.16	0.07	*	113
NO ₃ -N (mg kg ⁻¹ dry soil) ^a	-0.06	0.03	*	***	155					
NH ₄ -N (mg kg ⁻¹ dry soil) ^a	0.27	0.04	***	***	155					
Adjusted <i>r</i> ²	0.58				155	Adjusted <i>r</i> ²	0.48			113
Model <i>p</i> -value	<2.2e-16				155	Model <i>p</i> -value	<2.2e-16			113
^a =Log transformed										
<i>B = model coefficients of intercept and slope</i>										
<i>Degrees of freedom</i>										
<i>(b) CH₄-C flux (μg m⁻² h⁻¹)</i>										
(Intercept)	-135.26	17.02	***	***	155	(Intercept)	-115.35	23.61	***	113
NO ₃ -N (mg kg ⁻¹ dry soil) ^a	1.79	1.79	***	***	155	PH	16.02	4.41	***	113
Gravimetric soil moisture (%) ^a	13.05	4.11	**	***	155	Gravimetric soil moisture (%) ^a	8.01	2.72	**	113
Soil temperature (°C)	2.70	0.75	***	***	155	Vegetation index (NDVI)	73.06	35.95	*	113
Adjusted <i>r</i> ²	0.20				155	Adjusted <i>r</i> ²	0.12			113
Model <i>p</i> -value	3.82E-09				155	Model <i>p</i> -value	2.34E-05			113
<i>B = model coefficients of intercept and slope</i>										
<i>Degrees of freedom</i>										

Table 3
Continued

Forest			Grassland			Arable					
Predictor variables	B	Standard error	p-value	Predictor variables	B	Standard error	p-value	Predictor variables	B	Standard error	p-value
<i>B = model coefficients of intercept and slope</i>											
Degrees of freedom			173	Degrees of freedom			153	Degrees of freedom			94
(c) N_2O-N flux ($\mu g\ m^{-2}\ h^{-1}$) ^a											
(Intercept)	2.82	0.10	***	(Intercept)	3.25	0.39	***	(Intercept)	1.65	0.24	***
Gravimetric soil moisture (%) ^a	0.21	0.05	***	TDN (mg kg ⁻¹ dry soil) ^a	0.25	0.09	***	Vegetation index (NDVI)	3.87	0.40	***
				Clay content (%)	-2.68	1.02	**	NO ₃ -N (mg kg ⁻¹ dry soil) ^a	0.07	0.03	*
Adjusted r^2			0.11	Gravimetric soil moisture (%) ^a	0.20	2.14	*				
Model p-value			2.58E-05	Sand content (%)	-1.37	0.63	*	Adjusted r^2			0.47
^a =Log transformed				Adjusted r^2			0.15	Model p-value			5.08E-15
<i>B = model coefficients of intercept and slope</i>				Model p-value			4.54E-04	^a =Log transformed			
				<i>B = model coefficients of intercept and slope</i>				<i>B = model coefficients of intercept and slope</i>			
Degrees of freedom			151	Degrees of freedom			97	Degrees of freedom			100

Note. The Considered Parameters were: soil Temperature, Gravimetric Soil Moisture, pH, Bulk Density, NO₃-N, NH₄-N, TDN, DOC, TN, TOC, C:N, Soil Type (Clay/Sand/Silt Content), and NDVI. ^aLog transformed. *p-value < 0.05. **p-value < 0.01. ***p-value < 0.001.

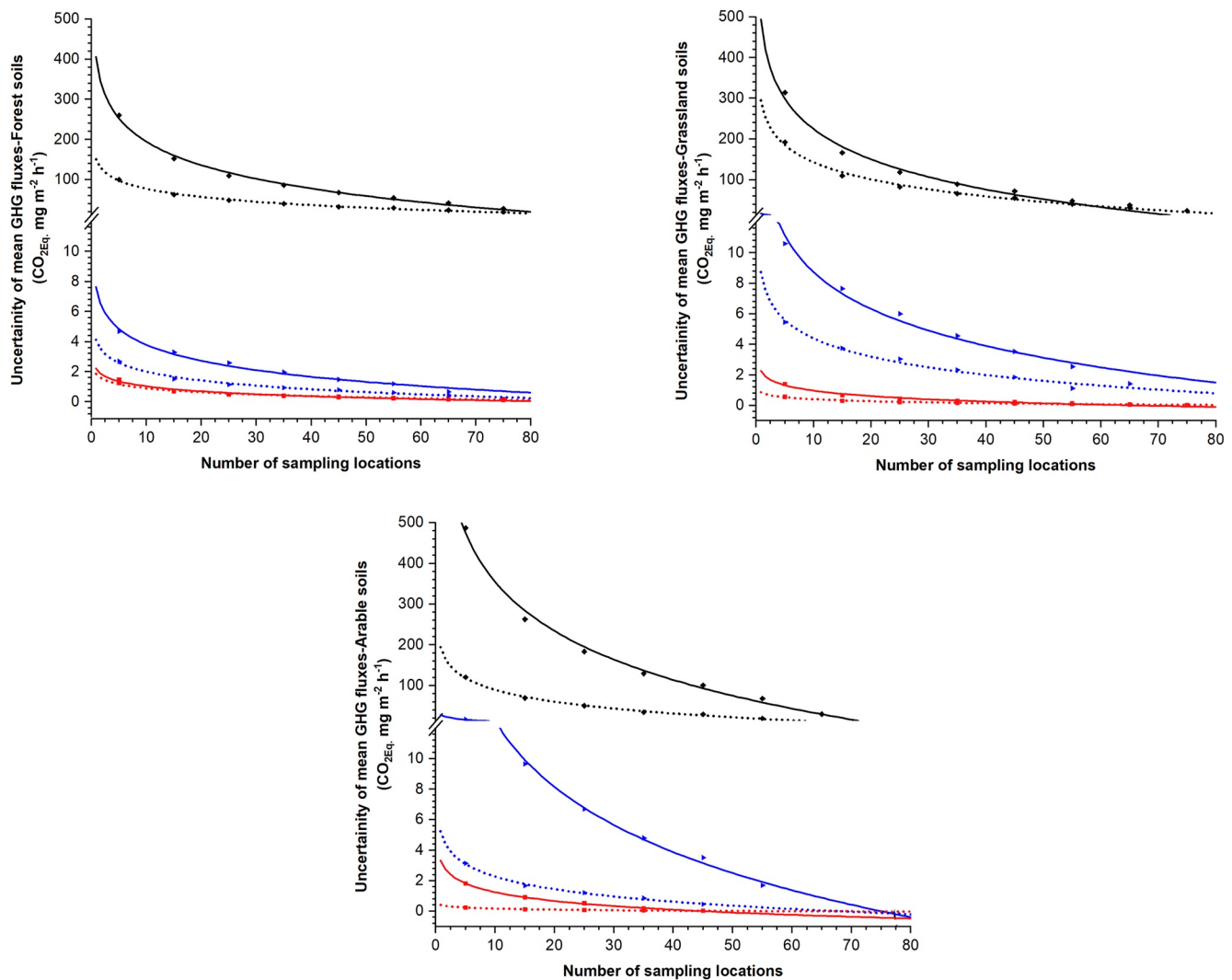


Figure 4. Logarithmic regressions of the number of stratified sampling locations for different uncertainties ($\pm\text{CO}_2$ equivalents $\text{mg m}^{-2} \text{h}^{-1}$) in the mean greenhouse gas fluxes across the forest, grassland, and arable ecosystems. The solid lines represent summer fluxes, and dotted lines show the autumn fluxes. The black, blue, and red colors represent SR/ER- CO_2 , N_2O , and CH_4 fluxes.

all the GHG fluxes in summer compared to autumn, corresponding to the period with higher SR/ER- CO_2 and N_2O emissions and lower CH_4 uptake rates.

4. Discussion

Investigating the spatial-temporal patterns of soil GHG fluxes and the underlying controls is crucial for a better understanding of landscape fluxes. This information can also contribute to the development of effective sampling strategies for larger-scale field measurements targeted to improve GHG estimates and narrow the uncertainties in upscaling measured fluxes to landscape-scales. In this study, we investigated the potential link of spatial-temporal variability of soil GHG fluxes with predictors of land use/land cover, slope, and soil properties. We also assessed the number of chamber measurement locations required to reliably estimate landscape fluxes within pre-defined uncertainties.

4.1. Soil and Ecosystem Respiration (SR/ER- CO_2)

Soil respiration (SR) includes autotrophic respiration from below-ground plant biomass (i.e., primarily roots) and heterotrophic respiration from soil microbial decomposition of organic matter. Ecosystem respiration (ER)

Table 4

The Number of Chamber Measurement Locations Per km² in Each Land Use Resulting in Greenhouse Gas Flux Uncertainty (\pm) Thresholds Roughly Equivalent to 0.5, 1, and 2 Times the Global Annual Mean/Median Flux Estimates in the Case of Carbon Dioxide and Nitrous Oxide Emissions and Methane Uptake Rates

Uncertainty (threshold)	Uncertainty (CO ₂ eq. mg m ⁻² h ⁻¹)	SR/ER CO ₂ -C emissions					
		Summer			Autumn		
		Forest	Grassland	Arable	Forest	Grassland	Arable
0.5	± 157.0	5	39	15	1	16	1
1	± 313.9	1	9	6	1	1	1
2	± 627.9	1	2	1	1	2	1
CH ₄ -C uptake rates							
0.5	± 0.6	7	42	11	7	7	1
1	± 1.2	2	13	5	1	2	1
2	± 2.4	1	1	1	1	2	1
N ₂ O-N emissions							
0.5	± 1.6	13	154	29	5	103	9
1	± 3.2	4	98	22	1	41	2
2	± 6.4	1	39	13	1	6	1

Note. The analysis was done for the summer and autumn measuring campaigns only.

additionally includes autotrophic respiration from above-ground vegetation (Oertel et al., 2016). In this study, we quantified ER at grassland and arable sites and SR at forest sites (due to the lack of above-ground vegetation). As a result, the magnitude of respiratory CO₂ effluxes and the spatial-temporal trends and controls are discussed separately.

4.1.1. Forest (Soil Respiration)

Mean SR fluxes at our forest sites are within the same order of magnitude as those measured at a 15-year-old spruce forest in Ireland, a temperate mixed forest in Germany, and a beech forest in Romania (Saiz et al., 2006; Oertel et al., 2015; Hereş et al., 2021; Table S5 in Supporting Information S1). Our forest fluxes are also comparable with those reported from a pine forest in Canada (Peichl et al., 2010). Similar to mean SR fluxes, the spatial variances (CV%) of SR fluxes at our forest sites are of the same order of magnitude as the CVs from plot-scale SR measurements in temperate spruce and beech forests (Saiz et al., 2006; Hereş et al., 2021; Table S6 in Supporting Information S1).

The temporal variations of SR at our forest sites were mainly attributed to seasonal changes in weather conditions that influenced soil environmental conditions. We observed the highest SR fluxes during the summer field campaign, while lower fluxes were observed at the start of the growing season and during the autumn campaign. This finding can be explained by warmer temperatures, higher soil moisture, and higher soil DOC observed in that period, which may have enhanced root and microbial respiration. Stimulated soil respiration rates at higher soil temperatures and moisture during summer have also been reported in other studies in forest ecosystems (Raich & Potter, 1995; Saiz et al., 2006). The positive relationships of soil respiration with soil moisture content and DOC, which we found in our forest soils, further support this argument.

Additionally, the negative relationship of CO₂ effluxes in forest soils with soil NO₃-N concentrations in this study may suggest suppression of soil respiration under increasing nitrate availability. In their meta-analysis, Janssens et al. (2010) also found an approximate 17% decline in microbial respiration due to nitrogen fertilization in temperate forest soils. The average NO₃-N concentration in our forest sites was two folds higher than those reported in other temperate forest studies (Merino et al., 2004; Peichl et al., 2010), supporting the possibility that elevated soil NO₃-N conditions may have led to a decline in soil respiration rates.

4.1.2. Grassland and Arable Land (Ecosystem Respiration)

Compared to other temperate studies, our mean ecosystem respiration fluxes for grassland sites are in the same order of magnitude as the mean fluxes measured at grassland sites in Missouri and central Italy (Nkongolo et al., 2010; Francioni et al., 2019; Table S5 in Supporting Information S1). The spatial variance (CV%) of the ER fluxes at our grassland sites is also similar to the variability observed at temperate grassland sites in Missouri (Nkongolo et al., 2010; Table S8 in Supporting Information S1). On the contrary, our arable sites had up to three folds higher mean ER rates than those reported for other temperate agricultural systems during the growing season (Buczko et al., 2015; Francioni et al., 2019). This finding can be attributed to differences in measurements since we measured ER fluxes at our arable sites, that is, including above-ground biomass, whereas in the other studies, above-ground biomass was clipped within the chamber frames before the flux measurements. The spatial variances at our arable sites were also higher and had a wider range than the variability observed for SR values of other arable soils in Germany (Buczko et al., 2015). These differences are also an artifact of measuring methodology as we measured ER and not SR at arable sites.

Similar to forest sites, the temporal variations of ER fluxes at our grassland and arable sites were also attributed to seasonal changes in weather conditions, which influenced soil environmental conditions and vegetation properties such as biomass and coverage. The warmer soil temperatures and higher vegetation cover (biomass) enhanced the ER rates during the growing season. The increase in ER fluxes may be explained by higher autotrophic respiration from below and above-ground biomass and enhanced rhizosphere respiration due to the supply of labile root exudates to soil microbes (Kuzyakov & Cheng, 2001). The positive relationship between ER fluxes and vegetation cover (NDVI) at our arable sites further supports the argument that higher plant biomass was the primary reason for enhanced ecosystem respiration during the summer. In a study at agricultural fields in Finland, Lohila et al. (2003) found higher ER rates during the crop growing season, which they also attributed to an increase in root and above-ground biomass, leading to increased plant and soil respiration.

Land use influenced the ER fluxes in our study as we observed higher rates at grassland sites compared to arable sites. This observation agrees well with the findings of other studies (Frank et al., 2006; Raich & Tufekcioglu., 2000). In their study conducted in the USA, Frank et al. (2006) found two-fold higher ER flux rates in grasslands compared to wheat sites which they attributed to the presence of higher root biomass in grasslands. Denser root networks in grasslands relative to plant size can contribute to the increased root and microbial respiration by providing a large surface area to volume ratio for organic carbon respiration.

Additionally, soil moisture content influenced the ER fluxes. Based on multiple linear regression analyses, our results showed a positive relationship between gravimetric moisture content and ER at both grassland and arable sites. Such a positive relationship has been reported in other grassland and arable studies in temperate ecosystems (e.g., Buczko et al., 2015; Schauffer et al., 2010) when other factors are not limiting.

4.2. Methane (CH₄) Fluxes

In our study, forest soils dominantly acted as net sinks of atmospheric CH₄. Our mean CH₄ uptake rate is within the same order of magnitude as uptake rates reported for other temperate forest soils (e.g., Butterbach-Bahl et al., 2002; Butterbach-Bahl & Papen, 2002; Merino et al., 2004; Peichl et al., 2010; Table S6 in Supporting Information S1). The spatial variability of our CH₄ uptake rates is comparable to those observed in Germany's spruce and beech forest sites (Table S8 in Supporting Information S1). The grassland sites in this study were also net sinks of CH₄, with comparable average uptake rates as observed for temperate grassland sites elsewhere (e.g., Hortnagl et al., 2017; Nkongolo et al., 2010). The spatial heterogeneity of the grassland sites was lower but within the range of the variance reported for other grassland systems (Table S8 in Supporting Information S1). Similar to forest and grassland sites, arable soils in this study were also net sinks of CH₄ with comparable average uptake rates as observed elsewhere (Table S6 in Supporting Information S1). However, the spatial variance of the CH₄ fluxes at the arable sites was similar to the variance found at cropland sites in Germany (Flessa et al., 1995).

Temporally, lower CH₄ uptake rates were observed during the spring and summer measuring periods, coinciding with generally higher gravimetric soil moisture contents. Similar to respiratory CO₂ fluxes, soil moisture is an important parameter regulating CH₄ dynamics in soils. It controls soil-gas diffusion, exerting physiological stress on methanotrophs, thus promoting methane production while hampering CH₄ oxidation under wetter and more anaerobic soil conditions (Le Mer & Roger, 2001). The decline in atmospheric CH₄ uptake with increasing

gravimetric soil moisture in grassland and forest soils in this study further supports this argument and thus also confirms the findings by other studies on the importance of soil moisture as a regulator of soil CH₄ fluxes (e.g., Ambus & Christensen, 1995; Merino et al., 2004).

Compared across the three land uses (forests, grasslands, and croplands), soils of forest sites were the strongest methane sinks. This finding is similar to a meta-analysis that found forest soils to be stronger CH₄ sinks compared to soils of grasslands and arable lands (Boeckx & Cleemput, 2001). The lower CH₄ uptake rates in grasslands and arable lands have been attributed to anthropogenic disturbances of the soil structure, the addition of NH₄-based fertilizers, as well as changes in soil pH due to liming activities, which collectively can inhibit CH₄ oxidation (Boeckx & Cleemput, 2001; Hütsch, 2001; Täumer et al., 2020). Soil structure changes due to tillage and mowing often lead to increased soil compaction. Soil compaction hampers gas transfers in soils, hindering the diffusion of atmospheric CH₄ to its oxidation sites that are usually located at 5–20 cm soil depths (Butterbach-Bahl & Pape, 2002), hence decreasing CH₄ uptake rates (Ambus & Christensen, 1995; Hütsch et al., 1993).

Elevated soil mineral nitrogen concentrations, usually found in agricultural soils due to the application of fertilizers, result in shifts of microbial communities from those dominated by methanotrophs in unfertilized soils to those dominated by ammonium oxidizers in fertilized soils (Castro et al., 1995; Hütsch, 2001). In a study comparing fertilized and unfertilized soils, Castro et al. (1995) found 15%–64% lower annual CH₄ uptake rates in soils that had received NH₄-NO₃ fertilizers. Their results agree well with our findings that rates of CH₄ uptake declined with increasing soil NO₃-N concentrations in forest soils, which may indicate the dominance of ammonium oxidizers over methanotrophs. It points out that increased nitrogen deposition in forest soils, which originates not only from the surrounding agricultural landscapes through NH₃ volatilization but also from long-range atmospheric N deposition, may significantly reduce the atmospheric methane uptake capabilities of forest soils (Steinkamp et al., 2000).

Soil pH also seemed to play an essential role in controlling CH₄ fluxes at the landscape-scale and across land uses. Our results showed higher CH₄ uptake rates in the more acidic forest soils (average pH 4) compared to grassland and arable sites, which had an average soil pH of 5 and 6, respectively. This observation is in line with Hütsch (2001), who found that methanotrophic activity decreased markedly with increasing soil pH in their review of CH₄ fluxes in arable landscapes. The influence of soil pH is further supported by the negative relationship between soil pH and CH₄ uptake rates in grassland soils in this study. However, a similar relationship was missing in arable soils.

4.3. Nitrous Oxide (N₂O) Fluxes

Compared to other temperate studies, the mean N₂O fluxes from the forest, grassland, and arable sites in our study are well within the magnitudes reported in other studies (Table S7 in Supporting Information S1). The spatial variances (CV%) of N₂O fluxes observed at the forest, grassland, and arable sites are within the ranges of the CV values found elsewhere (Table S8 in Supporting Information S1). However, the spatial heterogeneity of N₂O fluxes in arable soils spans a lower range than those reported in plot-scale studies of other arable sites in Germany (Flessa et al., 1995; Röver et al., 1999).

Temporal patterns of higher N₂O emissions during the growing seasons, particularly at arable sites, coincided with the period after both basal fertilizer application and top dressing. This finding is further supported by the higher availability of inorganic nitrogen observed during our summer field campaign. Schelde et al. (2012) also found high N₂O fluxes from cropland soils in a mixed land use catchment in Denmark during the growing season, which they attributed to enhanced availability of inorganic N due to mineral fertilizer applied during the planting period. The presence of crops during this season may have favored higher N₂O production in two ways. One is by increasing root respiration, which creates anaerobic microsites that promote denitrification. The second is by increasing root exudation that supplies labile carbon substrates to the denitrifying microbes (Malique et al., 2019). This finding is also supported by the positive relationship of soil N₂O fluxes with vegetation cover (NDVI) at arable sites in this study.

The magnitude of landscape N₂O emissions was in the order of arable > grasslands > forests soils and was closely related to soil NO₃-N concentrations, which also followed a similar trend. We also found a significant positive relationship between N₂O emissions and soil NO₃-N at arable soils, similar to earlier studies (e.g., Ambus et al., 2006; Vilain et al., 2010; Yao et al., 2020). In a recent meta-analysis of global N₂O and soil data,

Yao et al. (2020) pointed out that the soil $\text{NO}_3\text{-N}$ intensity, that is, the average concentration of $\text{NO}_3\text{-N}$ in soil, can explain up to 57% of variations in annual N_2O emissions. However, our study found a much lower explanatory power of soil $\text{NO}_3\text{-N}$ (Table 3, panel c), which may be explained by our study design as we focused on snapshot measurements and not on establishing annual flux estimates.

4.4. Chamber Measurement Locations Required for Landscape GHG Flux Estimates

In this study, we found that with an increasing number of measurement locations, the uncertainties of the landscape GHG flux estimates may be significantly reduced. While this finding is similar to those previously found in temperate (e.g., Saiz et al., 2006; Savage & Davidson, 2003) and tropical studies (e.g., Arias-Navarro et al., 2017), our study, for the first time, indicates the minimum number of measurement locations needed for reducing uncertainties in flux estimates based on direct field measurements across a relatively vast landscape. SR/ER- CO_2 and N_2O fluxes were the most sensitive to changes in the measurement locations, with larger uncertainties resulting from a similar number of sites compared to CH_4 fluxes. This finding suggests that the uncertainty of mean landscape fluxes increases with the magnitude of the fluxes, as was evident in our study where landscape fluxes, expressed as CO_2 equivalents, decreased by up to 10 folds in the order of SR/ER- CO_2 fluxes > N_2O fluxes > CH_4 fluxes. However, when the uncertainties of fluxes are referenced to GHG-specific thresholds based on global mean/median annual flux estimates, significant uncertainties of more than the global annual mean (uncertainty threshold 1; Table 4) at landscape-scale are made if N_2O flux measurements are carried out at <4 and <22 locations (per km^2) in forest and arable ecosystems, respectively, during the peak summer period. Contrary to N_2O , much lower chamber measurement locations of <2 and <6 at arable and forest ecosystems were required to estimate landscape CH_4 and SR/ER- CO_2 fluxes within a similar uncertainty (uncertainty threshold one in Table 4). Such a finding suggests that using a relatively low number of chamber measurement sites results in more significant uncertainty when estimating landscape-scale N_2O fluxes than when estimating gaseous carbon fluxes. Furthermore, it emphasizes the importance of getting the N_2O fluxes right in terms of the number of chamber measurement locations (this study) and the intensity of measurements (Barton et al., 2015) so as to achieve more accurate landscape flux estimates. Our findings call for revisiting the current chamber measurement strategy as, for example, outlined in the Global Research Alliance N_2O chamber methodology guidelines (de Klein et al., 2020).

For similar fixed thresholds of uncertainties, grasslands required up to an order of magnitude higher number of measurement locations than forest and arable lands. Three possible explanations may account for the high number of sites required at grasslands. First, our grassland sites were mainly located close to the streams and may have had higher finer scale variabilities in GHG fluxes due to variable soil moisture conditions affecting production or consumption processes at micro-scales. Second, the management of grasslands in the landscape also differed, with some under extensive management and others under intensive management. Both reasons are supported by the up to 2 folds higher spatial variabilities in GHG fluxes measured at grassland sites than in forest and arable lands, which indicate fine-scale heterogeneities. In addition, we may have captured more of these fine-scale heterogeneities in the fluxes at grassland soils since we also measured the fluxes at a higher number of sites per km^2 to enable land-use comparisons. We contend that due to the heterogeneous nature of our grasslands and their low area of coverage (<1 km^2), our recommended number of sites may not apply to more homogeneous grasslands with similar management practices, stable field conditions, and larger areas of coverage. For that reason, we chose to limit our recommendations of the suitable number of chamber measurement locations to the forest and arable ecosystems in our study, which had relatively large areas of coverage (>1 km^{-2}) and thus may better represent other similar ecosystems within the temperate region.

Hot “moments” and hot “spots” of landscape GHG fluxes also influenced the preferred number of chamber measurement locations for the forest and arable ecosystems. This finding is supported by the up to 10 times higher number of sites required per km^2 for SR/ER- CO_2 and N_2O flux estimates in summer when the fluxes were higher than in the autumn season. Contrary to SR/ER- CO_2 and N_2O fluxes, more sites were needed for CH_4 in autumn during the peak CH_4 uptake period than in summer. While fixed uncertainties equal to the global mean/median flux estimates represent critical thresholds that may determine whether a landscape is a net sink or source of a given GHG, we recommend using the number of chamber measurement locations that lead to half this uncertainty (uncertainty threshold 0.5; Table 4). Such numbers will potentially aid in significantly constricting GHG flux uncertainties from local to global scales, particularly in arable ecosystems that are hot “spots” for all three GHG

fluxes. However, we acknowledge the limitation of this study's seasonal/temporal scope as measurements were carried out in only one campaign (about 10 days) in each of the three (spring, summer, and autumn) seasons. Future studies should therefore explore more continuous time series of well spatially distributed and stratified flux chamber measurements to fully understand the effects of seasonality on the number of chamber measurements required to accurately quantify landscape-scale GHG fluxes.

5. Conclusions

Our study provides insights into soil and vegetation properties controlling the spatial-temporal patterns of soil GHG fluxes and implications on the precision of GHG flux estimates within a mixed land use landscape. Land use and seasonality rather than soil type and slope strongly influenced soil physical-chemical properties and fluxes. Soil properties such as soil moisture, TDN, DOC, and vegetation (NDVI), largely explained the spatial-temporal variations in our quantified GHG fluxes. These soil properties usually vary over short distances due to different water and nutrient retention capacities of soils, explaining the fine-scale spatial variabilities in GHG effluxes found in this study. This finding emphasizes the importance of stratified sampling approaches that consider multiple landscape characteristics for site selection during flux measurements to reduce possible uncertainties in the estimates.

The number of chamber measurement locations required for accurate surface flux estimates increased with the magnitude of flux and differed depending on the type of flux, land use, and seasonality related to both climatic and land management practices. To the best of our knowledge, our study is the first to provide the number of chamber measurement locations required for accurate landscape GHG flux estimates based on an extensive spatial data set of direct field measurements using a stratified sampling approach. In comparison to eddy covariance towers with limited ability to capture fine-scale heterogeneity of landscape GHG fluxes, our results can be combined with remote sensing data to create detailed landscape surface maps, enabling the identification of GHG hot “spots” for targeted future mitigation strategies.

Data Availability Statement

All data used within this study is free available on a Zenodo repository <https://doi.org/10.5281/zenodo.6821111>.

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