Greenhouse gas fluxes over managed grasslands in Central Europe

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Abstract

Central European grasslands are characterized by a wide range of different management practices in close geographical proximity. Site-specific management strategies strongly affect the biosphere-atmosphere exchange of the three greenhouse gases (GHG) carbon dioxide (CO_2), nitrous oxide (N_2O) and methane (CH_4). The evaluation of environmental impacts at site level is challenging, because most *in-situ* measurements focus on the quantification of CO_2 exchange, while long-term N_2O and CH_4 flux measurements at ecosystem scale remain scarce.

Here, we synthesized ecosystem CO_2, N_2O and CH_4 fluxes from 14 managed grassland sites, quantified by eddy covariance or chamber techniques. We found that grasslands were on average a CO_2 sink (-1783 to -91 g CO_2 m^{-2} yr^{-1}), but a N_2O source (18 – 638 g CO_2-eq. m^{-2} yr^{-1}), and either a CH_4 sink or source (-9 to 488 g CO_2-eq. m^{-2} yr^{-1}). The net GHG balance (NGB) of nine sites where measurements of all three GHGs were available was found between -2761 and -58 g CO_2-eq. m^{-2} yr^{-1}, with N_2O and CH_4 emissions offsetting concurrent CO_2 uptake by on average 21 ± 6% across sites. The only positive NGB was found for one site during a restoration year with ploughing. The predictive power of soil parameters for N_2O and CH_4 fluxes was generally low and varied considerably within years. However, after site-specific data normalization we

identified environmental conditions that indicated enhanced GHG source/sink activity ('sweet spots') and gave a good prediction of normalized overall fluxes across sites. The application of animal slurry to grasslands increased N_2O and CH_4 emissions. The N_2O-N emission factor across sites was 1.8 ± 0.5%, but varied considerably at site level among the years (0.1 – 8.6%). Although grassland management lead to increased N_2O and CH_4 emissions, the CO_2 sink strength was generally the most dominant component of the annual GHG budget.

Introduction

Central European grasslands are characterized by a wide range of different management practices, ranging from intensively managed lowland pastures and meadows to rather extensively managed high alpine grasslands (Gilmanov *et al.*, 2007; Bahn *et al.*, 2008; Wohlfahrt *et al.*, 2008a). Farming systems operate within their socio-economic and environmental boundaries, leading to management decisions that define type, frequency, timing and intensity of management events (Huber *et al*., 2013, Huber *et al*., 2014).

Grassland management-such as the amount and type of fertilizer applied, the frequency of cutting or the duration of grazing-strongly impacts the exchange of greenhouse gases (GHG), water and energy between the grassland ecosystem and the atmosphere and subsequently affects the biogeochemical cycling of carbon (C) and nitrogen (N) (Schulze *et al.*, 2009). Annual GHG budgets of grasslands, consisting of the three GHGs carbon dioxide (CO_2), nitrous oxide (N_2O) and methane (CH_4), are thus influenced directly by management (Lal, 2010; Gelfand *et al.*, 2011). The atmospheric concentrations of all three trace gases are still increasing at present, with anthropogenic activities being the major driver (IPCC, 2013). Both N_2O and CH_4 have high warming potentials, 298 (N_2O) and 34 (CH_4) times that of a corresponding mass of CO_2 emitted on a 100-year time horizon (IPCC, 2013). Agricultural grassland management activities are

closely connected to emissions of both non-CO_2 gases and to the uptake or emission of CO_2 (Tubiello *et al.*, 2015). Emissions of N_2O and CH_4 can contribute to an increase of the net GHG balance (NGB) of a grassland, offsetting concurrent CO_2 sequestration in terms of CO_2-equivalents (Liu & Greaver, 2009; Schulze *et al.*, 2009). This offset can be large and can even result in shifting a grassland from being a net GHG sink to a net source. The CO_2 sink strength as well as the N_2O and CH_4 source strengths of grasslands have been found to vary significantly across years and sites (Soussana *et al.*, 2007; Gilmanov *et al.*, 2010).

N_2O is produced by microbial activities in soils, mainly via nitrification and denitrification processes. N_2O can also be consumed by microbial processes such as denitrification, so that the net flux of N_2O observed at the soil surface is the result of simultaneously occurring production and consumption processes (Butterbach-Bahl *et al.*, 2013). The production of soil N_2O is controlled by various factors, such as soil water content, temperature, pH and the amount of available labile C and N (Holtan-Hartwig et al., 2002; Barnard et al., 2005; Prentice & Ri, 2008). N_2O production in soils is fueled by high N availability, which is mainly caused by the application of organic (solid manures or liquid slurries) and synthetic fertilizers to soils, but also due to the cultivation of legumes (Davidson, 2009; Fowler *et al.*, 2009; Lüscher *et al.*, 2014). For grasslands and meadows, additional N input might originate from livestock excreta (urine and faeces) (Galloway *et al.*, 2003; Saggar *et al.*, 2013; Paustian *et al.*, 2016). Application of organic and inorganic fertilizers have been shown to result in soil N_2O emission peaks, the magnitude of which depends on form, amount and timing of applied N as well as presence or absence of organic matter (Laville *et al.*, 2011). Due to the high spatial and temporal variability of N_2O production, estimating national and sub-national emissions remains difficult and is associated with major uncertainties (Reay *et al.*, 2012). The importance of soils as sinks for atmospheric

N_2O seems to be small and not to exceed 2% of current estimated sources (Schlesinger, 2013), and it is rather unlikely that fertilized agricultural soils act as N_2O sinks (Syakila & Kroeze, 2011).

CH_4 is mainly produced by single-celled archaea (methanogens) that are found in anaerobic microsites in the soil, water-saturated zones with high C content and the rumen of ruminants (Baldocchi *et al.*, 2012; Hiller *et al.*, 2014). Methanogenesis is the end point of the anaerobic breakdown of organic matter (Whalen, 2005). In Europe, the vast majority of agricultural CH_4 emissions originates from enteric fermentation (77%), but a considerable amount is also released as a consequence of manure decomposition processes (9%) during manure management (FAOSTAT, 2017). High CH_4 emissions were correspondingly reported from regions with intensive agriculture and animal husbandry (Barnosky, 2008; Schulze *et al.*, 2009; Frankenberg *et al.*, 2011). The major global sinks for CH_4 are biological oxidation by aerobic and anaerobic methanotrophs at CH_4 production sites, and photochemical oxidation by hydroxyl radicals in the atmosphere (Tate, 2015). Aerobic soils constitute an additional CH_4 sink, with atmospheric CH_4 diffusing into the soil and being oxidized by methanotrophic bacteria (Dunfield, 2007; Dutaur & Verchot, 2007; Unteregelsbacher *et al.*, 2013). In these well-aerated soils, observed net CH_4 uptake is also the consequence of CH_4 consumption (methanotrophy) being larger than the CH_4 production (methanogenesis) in the soil (Conrad, 2009). Oxidation rates are influenced by abiotic factors such as soil moisture and soil temperature, with changes in soil moisture accounting for most of the observed variability (Price *et al.*, 2004; Tate, 2015).

In Europe, 21% of the terrestrial surface is currently dedicated to agriculture (FAOSTAT, 2017). Most agricultural land is used for arable crops (59%), followed by permanent meadows and pastures (38%) and permanent crops, e.g. vines and olive trees (3%). In 2014, European

agriculture contributed 11% to global total GHG emissions from agriculture (FAOSTAT, 2017). Total European N_2O emissions in terms of CO_2-equivalents have exceeded CH_4 emissions since 2011, with N_2O contributing 52% (CH_4: 48%) to total European GHG emissions in 2014 (FAOSTAT, 2017). Although CH_4 emissions from enteric fermentation constitute the largest single source of GHGs from agriculture in Europe (2014: 38%), aggregated N_2O emissions from agricultural soils comprise an even larger share (46%), mainly as a consequence of nitrification and denitrification processes driven by synthetic and organic fertilizer application to the agricultural land (Soussana *et al.*, 2007; FAOSTAT, 2017). Manure related N_2O and CH_4 emissions in Europe, comprising CH_4 and N_2O emissions from manure management along with N_2O emissions from organic fertilizer and manure from grazing animals that is left on pastures, account for 30% of the total agricultural GHG emissions (FAOSTAT, 2017).

The net ecosystem exchange of CO_2 is the most important constituent of the grassland C cycle. The role of the CO_2 flux for the GHG budget can become even more pronounced in grasslands, as such ecosystems are often limited by soil N availability, and N addition during fertilization increases the CO_2 sink more than the N_2O and CH_4 sources (Gomez-Casanovas *et al.*, 2016). Although the CO_2 flux in response to abiotic, biotic and management drivers was studied previously (e.g., Wohlfahrt *et al.*, 2008a; Peichl *et al.*, 2013), direct measurements (of one year or longer) of N_2O and CH_4 grassland fluxes in combination with CO_2 fluxes are still rare (Kroon *et al.*, 2010; Hörtnagl & Wohlfahrt, 2014; Merbold *et al.*, 2014).

The accurate quantification of the three GHGs CO_2, N_2O and CH_4 is relevant for climate policy. Following the Paris Climate Agreement (UNFCCC, 2015), each signing partner country is requested to accurately report GHG emissions from different sectors, e.g. from agriculture, forestry and other land use (AFOLU). In addition, countries are required to identify potential

GHG mitigation options. However, long-term measurements of GHG emissions from grasslands, which are part of the AFOLU sector, remain scarce. *In-situ* data have the potential to adequately reflect the small-scale variability of GHG emissions at farm scale, needed to give specific mitigation recommendations to stakeholders. In addition, they provide the data basis for biogeochemical process model development and validation. Availability and continuity of such direct ecosystem GHG flux measurements is crucial for assessing the GHG reduction potential of different management strategies (Luyssaert *et al.*, 2014).

In this study, we examined the GHG emission intensity of meadows and pastures. To this end, we analyzed available GHG measurements of 14 differently managed grassland sites in Central Europe across different environmental settings. Our specific objectives were (1) to provide an overview of currently available *in-situ* GHG measurements over managed grasslands, (2) to test the applicability of soil temperature and water-filled pore space, two key parameters for soil biogeochemistry and widely available in combination with flux measurements, for the prediction of N_2O and CH_4 fluxes across grassland sites, (3) to quantify the impact of fertilizer application on observed N_2O and CH_4 emissions, and (4) to provide net GHG balances and N_2O-N emission factors for all sites by gap-filling direct measurements at ecosystem scale.

Materials and Methods

This synthesis paper investigated CO_2, CH_4 and N_2O fluxes from ten Central European grasslands along an elevation gradient (Table 1). Four out of the ten grasslands (FR-LAQ, CH-FRU, DE-FEN, CH-CHA) were divided into two separate areas with different management, leading to 14 grassland sites in total.

Research sites and management

The research sites span an altitudinal gradient from 400 – 1978 m a.s.l in Central Europe, with mean annual temperatures (MAT) ranging between -1.4 and 9.1°C and mean annual precipitation (MAP) ranging between 852 and 1682 mm (Table 1). Sites included in this study, listed in altitudinal order from highest to lowest, were the extensively managed site CH-AWS (1978 m a.s.l.), the extensive pasture AT-STU-P (1870 m a.s.l.), the extensive meadow AT-STU-M (1820 m a.s.l.), the semi-natural grassland site Laqueuille that was divided into two adjacent paddocks with intensive (FR-LAQ-I) and extensive (FR-LAQ-E) management (1040 m a.s.l.), the subdivided mountain rangeland at Früebüel, which consisted of the intensively managed site CH-FRU-I and the extensive site CH-FRU-E (982 m a.s.l.), the intensively managed AT-NEU (970 m a.s.l.), the extensive meadow DE-GAP (734 m a.s.l.), Fendt with an intensively and extensively managed paddock (DE-FEN-I, DE-FEN-E, 600 m a.s.l.), and the intensive site Chamau, which was subdivided into two areas during a chamber measurement campaign in 2010 / 2011 (CH-CHA-I1, CH-CHA-I2), while in 2012, CH_4 and N_2O fluxes were measured using the eddy covariance technique covering both areas (CH-CHA, 393 m a.s.l.) (Table 1).

Management practices carried out at the studied grassland sites included the application of inorganic and organic fertilizer, mowing and grazing. The amount and type of fertilizer, the frequency of cutting and the intensity and duration of grazing at the different sites were highly variable (Table 1). Thirteen of the 14 sites were fertilized between one and six times per year. Organic fertilizer was applied at 12 of the 14 sites, ranging from 33 to 365 kg N ha^{-1} yr^{-1}. The amount of organic fertilizer spread at CH-AWS when cattle were grazing was unknown. Synthetic fertilizer was applied only at FR-LAQ-I (214 kg N ha^{-1} yr^{-1}) and CH-CHA (2012: 17 kg N ha^{-1} yr^{-1}), but only at CH-CHA in combination with slurry. Of the 14 sites, only one was not

fertilized during the investigated time period (FR-LAQ-E). However, for all grazed sites additional N input came from excretion of grazing animals onto the pasture.

Ten sites were cut at least once per year, whereas some intensively managed sites were cut up to five times per year. Ten sites were grazed by cattle and / or sheep between 1 – 170 days yr^{-1}. CH-CHA was ploughed for grassland restoration and resown in early 2012. Further details including key references for each site are given in Table 1.

Flux measurements

The net ecosystem exchange of the three major GHGs (CO_2, N_2O, and CH_4) was calculated using the eddy covariance (EC, Baldocchi *et al.*, 1988) or chamber techniques, whereby for the latter either automatic (AC) or manual chambers (MC) were used (Table 1). Data availability and temporal resolution of measurements of the three targeted GHGs varied considerably across all sites. N_2O fluxes were available from all 14 sites, while CO_2 fluxes were available from ten and CH_4 fluxes from 13 sites (Figure 1). Measurement campaigns at the sites lasted between six months (AT-STU-P) and more than five years (FR-LAQ-I, FR-LAQ-E) (Table S2).

Measurements covering all three GHGs over at least one full year were available from eight sites, with results from two sites based on continuous EC measurements (AT-NEU, CH-CHA) and from six sites based on EC in combination with MC measurements (CH-AWS, CH-FRU-I, CH-FRU-E, DE-FEN-I, CH-CHA-I1, CH-CHA-I2,). CO_2 measurements for CH-AWS were only available during the growing season. Two sites had CO_2 and N_2O data available for multiple years, but no (FR-LAQ-E) or limited (FR-LAQ-I during two grazing seasons) CH_4 measurements. Measurements of N_2O and CH_4 without simultaneous CO_2 measurements were carried out at four sites, either over multiple years (DE-GAP, DE-FEN-E) or over one growing

season only (AT-STU-P, AT-STU-M). Generally, data coverage was lowest for sites sampled with MCs (20 – 93 measurement days) and highest for AC and EC sites (318 – 1373 measurement days). Additional details on flux calculation methods as well as site and instrument setup are given in Table 1 and in the Supplement.

Daily average (DA) flux values were used for analyses in this study. Due to the different temporal resolutions of the measurement methods, the calculation of DA fluxes for each site and day followed different approaches: for chamber measurements, mean values across all replicates were calculated. When at least one replicate average was available for a given day (MC, AC), the flux was assumed to be representative for the whole day (24 hours). For EC data, daily average fluxes were calculated from a minimum of 21 half-hourly flux values. Applying these minimum thresholds resulted in a tradeoff between overall data availability and representativity of a given calculated daily average flux.

Flux rates in this study are given as mg CO_2 m^{-2} h^{-1} for CO_2, and µg m^{-2} h^{-1} for N_2O and CH_4. Fluxes are reported following the convention used in micrometeorology, where positive fluxes mean a transport from the ecosystem to the atmosphere, negative fluxes mean the opposite.

Gap-filling

Fluxes were gap-filled for the calculation of site-specific GHG budgets, N_2O-N emission factors (EFs) and NGBs. While CO_2 fluxes were gap-filled following Reichstein *et al.* (2005), the gap-filling (GF) for N_2O and CH_4 was based on a running median (RM) approach, which comprised several steps. First, the continuous RM DA flux was calculated for each site and GHG using pre-defined time windows of varying lengths, selected as to best describe the measured DA flux pattern over the course of a full year. For sites where multiple years of measured N_2O data were

available, the calculation of the RM was based on the average of all available fluxes for a specific day of the year, except for CH-CHA, where the ploughing year 2012 and the following year 2013 were treated separately. Typical sizes of the RM time window were 15 – 120, 60, 60 days for MC, AC, EC data, respectively (Table 1). Potential remaining data gaps at the beginning and end of specific years were then filled by repeating the median flux value closest to the gap. This yielded a continuous estimate for the RM flux of a site for each day and year. The main reason for choosing the RM approach was that it is less sensitive to outliers, i.e. to sharp emission peaks in the data, in contrast to filling data gaps with the arithmetic mean or by linear interpolation. Second, the RM daily average flux time series was then used to substitute data gaps in the measured daily average time series with the corresponding RM value of the given day of the year, resulting in complete, gap-filled N_2O and CH_4 flux time series for the year. The RM method consequently leads to cumulative fluxes representative for a given site, but it is not suitable for predicting or simulating GHG emission pulses, e.g. as a consequence of management or freeze/thaw periods. Thus, budgets calculated from the RM method are likely to underestimate the "true" budget at a specific site. From the grazed meadow FR-LAQ-I, CH_4 measurements were only available during the growing season with cattle present in the measurement footprint. To achieve year-round CH_4 budgets, time periods without cattle were gap-filled with a constant, low CH_4 emission value (160 µg m^{-2} h^{-1}), similar to flux rates observed during ungrazed time periods at another site in an earlier study (Dumortier *et al.*, 2017).

Ancillary data

Measurements of ancillary data included ambient air temperature (TA in °C), soil temperature (TS in °C), soil water content (SWC in vol. %), and precipitation (mm) (Table 1). Measured soil

parameters were bulk density (BD) and pH. SWC was converted to water-filled pore space (WFPS) by first calculating the total porosity (TP) of the soil in percent for each site as

$$TP = \left(1 - \frac{BD}{PD}\right) \quad , \qquad (2)$$

where BD is the bulk density for each site and PD is the particle density assumed as 2.65 g cm^{-3}. In a second step, TP (%) was used to calculate WFPS (%) following

$$WFPS = \left(\frac{SWC}{TP}\right), \qquad (3)$$

where SWC is the soil water content (volumetric %) as measured at each site.

Normalization

In order to identify environmental conditions conducive to enhanced GHG source/sink activity, measured non-gapfilled daily average N_2O and CH_4 fluxes were investigated in relation to different combined classes of the two potential drivers soil temperature (TS) and soil moisture (given in water-filled pore space, WFPS). One approach to account for diverse environmental conditions and soil physical properties while also improving comparability across sites is the normalization of all involved variables to their respective percentile values at site level. Daily average flux values of N_2O and CH_4 fluxes, as well as TS and WFPS measurements at each site were converted to an index in the range 0 to 100% based on the cumulative empirical probability density function (cePDF) of each variable at each site. That is, the index value corresponds with the percentile value of the original measurements in relation to the site-specific cePDF. These index values were further aggregated in graphical displays by showing the median of the index values from all sites within each aggregation unit. Following this approach facilitated the identification of common emission/deposition sweet spots, i.e. environmental conditions that

contribute to an increase or decrease of GHG fluxes. The use of strictly linear, site-specific percentile values for sweet spot analyses had the advantage of investigating fluxes in relation to site-specific ranges of potential drivers (Luo *et al.*, 2013).

For the quantification of the fertilization effect, daily average fluxes in the period starting 7 days before and ending 7 days after the event were normalized by the 7-day flux average before the event, not including the day of the event (day 0) (see Figure 8 and 9).

Data analysis

Site-specific of N_2O-N emission factors (EFs) are expressed as the ratio between annual N_2O-N budgets after gap-filling and the amount of applied fertilizer. Results from multiple linear regression analyses (MLR) were checked for multicollinearity by inspecting the eigenvalues of soil temperature and water-filled pore space in a correlation matrix. Eigenvalues across all sites were found between 0.37 and 1.63, indicating no multicollinearity problems. The adjusted coefficient of determination (r^2_{adj}) corresponds to r^2 after adjustment based on the degrees of freedom of the respective model, i.e. r^2 is adjusted to the number of regressors and the sample size. As such, r^2_{adj} is an indicator for the utility of a regression model, especially for MLR models, by describing the explained variation in the dependent variable above what would be expected by chance. Data analyses were based on daily average values. Plots and statistical analyses were done using the free and open source programming language *Python* (version 3.6.0, Python Software Foundation), including the packages *pandas* (version 0.20.3; McKinney, 2010), *numpy* (version 1.13.1; Van Der Walt *et al.*, 2011), *matplotlib* (version 2.0.2; Hunter, 2007) and *statsmodels* (version 0.8.0; Seabold & Perktold, 2010). Significance levels given in regression analyses correspond to the two-tailed *P*-values using Wald Test with t-distribution of the test

statistic. Sites included in figures and tables of this manuscript are listed in descending order of elevation from top to bottom and left to right. Average values are given ± standard error of the mean (SEM) where possible.

Results

Greenhouse gas measurements

The CO_2 flux was available from nine sites and showed highest net CO_2 uptake during spring and summer, reflecting time periods of high plant productivity (Figure 2a). During these warmer seasons, measured median fluxes ranged between -1.02 (AT-NEU in spring) and -0.09 mg CO_2 m^{-2} h^{-1} (CH-FRU-E in spring), except for spring at CH-CHA, which was characterized by net CO_2 losses (0.12 mg CO_2 m^{-2} h^{-1}). Measured CO_2 uptake generally decreased during colder months, with measurements indicating small uptake or emission of CO_2 (-0.28 to 0.28 mg CO_2 m^{-2} h^{-1}). The average annual CO_2 flux across all sites, calculated from gap-filled data, was -1426 ± 248 g CO_2 m^{-2} yr^{-1}, with strongest CO_2 uptake in spring (-855 ± 80 g CO_2 m^{-2}), followed by summer (-577 ± 100 g CO_2 m^{-2}) and autumn (-131 ± 83 g CO_2 m^{-2}). Winter was on average a CO_2 source (137 ± 52 g CO_2 m^{-2}).

N_2O was emitted from all grasslands and during all seasons, except for AT-NEU, where small uptake rates of -2 µg N_2O m^{-2} h^{-1} were recorded during spring (Figure 2b). The median of directly measured seasonal fluxes at the emitting sites ranged between 0.1 (FR-LAQ-I in winter) and 240 µg N_2O m^{-2} h^{-1} (CH-CHA-I2 in summer). The average annual N_2O flux across all sites, calculated from gap-filled data was 2664 ± 1024 mg N_2O m^{-2} yr^{-1}, with strongest emissions in summer (1063 ± 381 mg N_2O m^{-2}) and weakest emissions during winter (422 ± 204 mg N_2O m^{-2}).

Median seasonal CH_4 fluxes calculated from chamber measurements were generally negative, ranging between -46 (AT-STU-M) and -6 µg CH_4 m^{-2} h^{-1} (DE-FEN-I), indicating uptake of atmospheric CH_4 by grassland soils (Figure 2c). Methane chamber emissions were found only during winter at four sites (CH-FRU-I, DE-GAP, CH-CHA-I1, CH-CHA-I2; ranging between 0.3 and 8 µg CH_4 m^{-2} h^{-1}). In contrast to chamber measurements, median CH_4 fluxes from EC measurements were all positive during all seasons, with highest emissions observed at FR-LAQ-I during spring when cattle were present within the flux footprint (4565 µg CH_4 m^{-2} h^{-1}). After gap-filling, the average CH_4 flux across all sites, not including FR-LAQ-I, amounted to 36 ± 85 mg CH_4 m^{-2} yr^{-1}, with strongest CH_4 emissions in autumn (18 ± 22 mg CH_4 m^{-2}).

Effect of two drivers on N_2O and CH_4 exchange

The identification of GHG source/sink sweet spots in relation to specific soil moisture and temperature conditions at the site level worked best with sites where flux measurements were taken at high temporal resolution, i.e. based on EC and AC measurements (Figure 3, Figure 4). For example, N_2O emissions at FR-LAQ-I were highest when WFPS was above 75% and lowest with TS below 5°C, conditions during which low emissions could also translate into small uptake of N_2O (Figure 3a, Table 2). However, other sites deviated from this observation. N_2O emissions at AT-NEU were highest with TS above 15°C or below 5°C and WFPS around or below 50%. Similar emission patterns were also found at DE-FEN-E, with highest emissions occurring at TS > 15°C or < 5°C, and lowest N_2O emissions with WFPS < 50%. CH-CHA was the only site where WFPS frequently exceeded 90% (interquartile range: 85 – 94%). During these overall wet conditions, when the soil was almost fully water-saturated, observed N_2O emissions at CH-CHA were low. Chamber measurements at the same site in previous years, prior to grassland restoration, revealed a somewhat contrasting flux pattern, but were performed during generally

warmer time periods (data not shown). Merging all site-level observations showed that the highest N_2O percentile flux generally occurred during warm and wet periods, with considerably lower percentile fluxes during colder time periods (Figure 3b).

In comparison to N_2O, the investigation of CH_4 at site level revealed flux patterns that in many cases were dominated by uptake of atmospheric CH_4 by soils (Figure 4a). Therefore, interpreting flux patterns was more challenging because most sites could act both as a clear sink or a source for CH_4 during different time periods. Thus, upper flux percentiles did not necessarily reflect CH_4 emission, but equated to low CH_4 uptake at some sites. Across 13 investigated sites for which CH_4 measurements were available, ten sites were dominated by CH_4 uptake, with only two sites (AT-NEU, CH-CHA) showing clear emission patterns, not including FR-LAQ-I (Table 2, Figure 4a). Both DE-FEN-I and DE-FEN-E showed highest CH_4 uptake with TS > 15°C and WFPS < 50%, weakest CH_4 uptake was observed with WFPS above or around 50% (DE-FEN-I, DE-FEN-E) and TS < 10°C (DE-FEN-E). For AT-NEU, uptake was mainly observed at intermediate WFPS and TS around 10°C, while highest CH_4 emissions occurred with TS > 10°C (Figure 4a). Across all sites, the CH_4 percentile flux increased with increasing WFPS and decreasing TS (Figure 4b).

Normalized N_2O and CH_4 flux patterns across all sites, based on the same classes of TS and WFPS as shown in Figure 3b and Figure 4b could well be explained by either TS or WFPS in a simple linear regression (Figure 5). Soil temperature was a significant driver for N_2O ($r^2 = 0.88$, $P < 0.001$) and CH_4 fluxes ($r^2=0.35$, $P < 0.05$). WFPS had high predictive power for CH_4 exchange ($r^2 = 0.84$, $P < 0.001$) and was a significant driver for N_2O fluxes ($r^2 = 0.54$, $P < 0.05$).

In order to test if the predictive power of TS and WFPS for flux percentiles across all sites also succeeds at the site level, multiple linear regression (MLR) and simple linear regression (SLR)

analyses were performed on measured, log-transformed daily average N_2O and CH_4 fluxes for each site. Data included in these analyses were not gap-filled, measured during snow-free conditions and not directly disturbed by cutting and fertilization management events, i.e. data from the three days directly after a management event were excluded from these analyses (Table 3). The explained variance of N_2O fluxes in a MLR was low for most sites, with a coefficient of determination (r^2) of 0.19 on average, ranging between 0.02 (DE-FEN-E) and 0.47 (CH-FRU-E). TS as predictor variable in a SLR at site level generally explained only a small fraction of observed flux patterns (significant r^2 between 0.01 and 0.27), similarly low values were found for WFPS (significant r^2 between 0.01 and 0.29).

Similar to N_2O fluxes, the combined explanatory power of the potential driver variables TS and WFPS for observed CH_4 flux patterns was limited (r^2 = 0.23, on average), but yielded good results for the extensive high altitude site CH-AWS (r^2 = 0.77). For the remaining sites, significant r^2 ranged between 0.04 (AT-NEU) and 0.40 (CH-FRU-E, DE-GAP). The explained variance for subdivided sites was higher for the less intensively managed part of the grassland. For example, r^2 was higher for CH-FRU-E than for CH-FRU-I (r^2 = 0.40 vs. 0.19), and higher for DE-FEN-E than for DE-FEN-I (r^2 = 0.32 vs. 0.22). The SLR identified WFPS as a relatively good predictor variable for the high altitude site CH-AWS (r^2 = 0.72). However, the high predictive power of TS and WFPS for percentile-normalized N_2O and CH_4 fluxes, respectively, across all sites (Figure 5) was not supported by MLR and SLR analyses of log-transformed data at site level.

Regression analyses indicated that the role of the two potential driver variables TS and WFPS in driving N_2O and CH_4 fluxes can be vastly different across sites, i.e. the spatial domain (Table 3). Therefore, in a next step, we analyzed their predictive power for measured, non-gapfilled data in

the temporal domain. To this end, we investigated the explained variance of observed N_2O and CH_4 fluxes by the combined use of TS and WFPS as predictors in a moving 35-day time window (Figure 6, Figure 7). In order to perform this analysis, long-term data recorded at high temporal resolution were required. This requirement was met by six sites in this study, namely those that used either EC or AC measurements for the quantification of N_2O or CH_4 fluxes (FR-LAQ-I, FR-LAQ-E, AT-NEU, DE-FEN-I, DE-FEN-E, CH-CHA). The analysis revealed that the role of WFPS and TS as driving variables of observed fluxes varied considerably over the course of the measurement periods. During the growing season, both variables often predicted observed N_2O fluxes with high precision and significance ($P < 0.05$), with maximum r^2 ranging between 0.71 (AT-NEU in summer 2010) and 0.90 (DE-FEN-E in summer 2012) for individual sites (Figure 6). In contrast, their explanatory value was low and often close to zero during cold time periods and snow cover when N_2O fluxes were low. Especially for N_2O fluxes, results during certain time windows were often in strong contrast to results from the MLR analyses in Table 3. For example, at DE-FEN-E, WFPS and TS were poorly correlated with N_2O fluxes with all measurements considered ($r^2 = 0.02$, Table 3), but both predictors explained up to 90% of observed fluxes between 25 June and 30 July 2012 at the same site (Figure 6). Similar results were also found for CH_4, with maximum r^2 between 0.41 (AT-NEU autumn/winter 2010) and 0.92 (DE-FEN-I and DE-FEN-E in summer/autumn 2013) in certain time windows (Figure 7). Generally, using TS and WFPS as predictors for measured fluxes in pre-defined time windows yielded better and more significant results for N_2O than for CH_4 (Figure 6, Figure 7).

Fertilization effect on N_2O and CH_4 fluxes

The availability of flux measurements for the time period before, during and after fertilization events allowed for an evaluation of the management impact on observed N_2O and CH_4 exchange.

Flux data around multiple fertilization dates were available from three grasslands, all of which used slurry as fertilizer (DE-FEN-I, DE-FEN-E, CH-CHA). Slurry application resulted in clear N_2O emission peaks at all three sites either on the day of application or during the following 7 days (Figure 8). In comparison to the seven days preceding the application, N_2O emissions across all sites were on average 10 times higher on the day of fertilization, 5 times higher one day after fertilization, and 2 times higher over the following six days. N_2O fluxes stayed elevated for a few days after the event, reaching pre-fertilization flux rates again on day 3 – 7 after fertilizer application. Average N_2O emission rates during the seven days before management for CH-CHA (125 ± 45 μg N_2O m^{-2} h^{-1} on average) were high in comparison to DE-FEN-I (23 ± 7 μg N_2O m^{-2} h^{-1}) and DE-FEN-E (13 ± 5 μg N_2O m^{-2} h^{-1}).

The high N_2O emissions after fertilization of the grassland had a strong impact on the total amount of N_2O-N that was emitted from the respective grassland to the atmosphere over the course of the year. For example, cumulative N_2O-N emissions from the grassland at CH-CHA amounted to 2.6 kg N ha^{-1} over the course of 2013 (Table 6). During the same year, 0.7 kg N ha^{-1} were emitted immediately after four fertilization events, i.e. N_2O-N emissions over the course of the fertilization day and the following week after subtraction of pre-fertilization flux rates, which is equal to 28% of the annual cumulative N_2O-N emissions. Hence, each fertilizer application resulted in immediate N_2O-N emissions of 7 ± 1% of the annual cumulative loss. Similar results were also found at DE-FEN-I between 2012 and 2014 (7 ± 2% per fertilization), demonstrating the impact of fertilizer application on the annual N_2O budget.

Similar to N_2O emissions, CH_4 fluxes were elevated on the day of slurry application (Figure 9). However, methane emissions decreased earlier in comparison to N_2O emissions and reached pre-fertilization values one or two days after fertilization. Unlike N_2O, the grasslands at DE-FEN-I

and DE-FEN-E were a CH_4 sink before fertilizer application, albeit flux averages were characterized by high standard errors. For DE-FEN-I and DE-FEN-E, average CH_4 uptake rates of -11 ± 3 and -26 ± 19 μg m^{-2} h^{-1}, respectively, were found over the course of the seven days preceding management. Manure application turned the two grasslands from a sink to a source of CH_4, with high emissions on the day of fertilization (1271 ± 440 and 212 ± 250 μg m^{-2} h^{-1}, respectively) and a rapid decrease of CH_4 emissions in the following week (-4 ± 8 and -25 ± 16 μg m^{-2} h^{-1}, respectively). In contrast, the grassland at CH-CHA was mostly a CH_4 source before fertilization (17 ± 78 μg m^{-2} h^{-1}), with elevated emission peaks on the day of slurry application (637 ± 239 μg m^{-2} h^{-1}) and CH_4 emission rates that stayed elevated during the week after fertilization (228 ± 72 μg m^{-2} h^{-1}).

GHG budgets

In-situ measurements over multiple years in combination with subsequent gap-filling allowed for the calculation of site-specific annual GHG budgets (Table 4). During the investigated time periods in this study, all ten sites for which the CO_2 flux was quantified for at least one year were a CO_2 sink, ranging between -2806 g CO_2 m^{-2} yr^{-1} (CH-FRU-I) and -91 ± 20 g CO_2 m^{-2} yr^{-1} (AT-NEU, 2010-2011). All 14 sites with N_2O measurements were a N_2O source, emitting between 18 g CO_2 m^{-2} yr^{-1} (AT-STU-P) and 638 ± 519 g CO_2 m^{-2} yr^{-1} (CH-CHA, 2012-2013). Findings for the 13 sites with CH_4 measurements were more diverse, with nine sites acting as a methane sink, ranging between -9 g CO_2-eq. m^{-2} yr^{-1} (CH-AWS, AT-STU-M) and -1 ± 2 g CO_2-eq. m^{-2} yr^{-1} (DE-GAP, 2012-2013; DE-FEN-I, 2012-2014). Three sites (AT-NEU, DE-FEN-I, CH-CHA) were a CH_4 source (3 to 41 CO_2-eq. m^{-2} yr^{-1}). Strongest CH_4 emissions were found for the heavily grazed FR-LAQ-I, where cattle were present in the EC footprint, amounting to 488 ± 100 CO_2-eq. m^{-2} yr^{-1} on average between 2010 and 2011 (Table 4).

The full NGB was calculated for nine sites where concurrent measurements of all three GHGs (CO_2, N_2O, CH_4) were available. Despite the offset of CO_2 uptake by mainly N_2O and to some extent CH_4 emissions, the NGB of the grasslands was strongly negative, with minimum and maximum CO_2-eq. uptake of -58 ± 32 g CO_2-eq. m^{-2} yr^{-1} (AT-NEU, 2010-2011) and -2761 g CO_2-eq. m^{-2} yr^{-1} (CH-FRU-I), respectively (Table 4). The annual CO_2 sink strength of the grasslands was offset by concurrent N_2O and CH_4 fluxes by between 2% (CH-FRU-I) and 48% (FR-LAQ-I, 2008-2013). On average across all sites, the CO_2 flux offset amounted to 21 ± 6% (Table 4).

The fluxes of all three GHGs (CO_2, N_2O and CH_4) were generally characterized by strong inter-annual variability (Table 4). For example, CO_2 uptake at FR-LAQ-I between 2008 and 2011 was found between -1537 and -814 g CO_2 m^{-2} yr^{-1}. During the same time period, N_2O emissions (between 48 and 247 g CO_2-eq. m^{-2} yr^{-1}) offset the CO_2 uptake by 6 – 17%. The biggest difference between years was found for CH-CHA, where grassland restoration in 2012 included ploughing, sowing, fertilizer and pesticide application as well as regular harvests. In the same year, the first resowing after ploughing failed and vegetation was almost absent until summer. The NGB of CH-CHA during the restoration year 2012 amounted to 2446 g CO_2-eq. m^{-2}-the highest across all sites-as a consequence of high CO_2 (1246 g CO_2 m^{-2}) and N_2O emissions (1157 g CO_2-eq. m^{-2}), along with relatively low CH_4 emissions (43 g CO_2-eq. m^{-2}; Table 4). However, in 2013, CH-CHA changed from being a GHG source to a strong GHG sink (-4514 g CO_2-eq. m^{-2}), with high CO_2 uptake (-4671 g CO_2 m^{-2}) and considerably lower N_2O emissions (119 g CO_2-eq. m^{-2}), while CH_4 emissions remained similar (38 g CO_2-eq. m^{-2}). The inter-annual variability of CH_4 fluxes was generally lower than that of CO_2 and N_2O fluxes (Table 4).

Historically, considerably more measurements are available for grassland CO_2 fluxes, while data for N_2O and CH_4 remain still relatively sparse. Therefore, we set site-specific budgets presented in this study in relation to previous studies that investigated N_2O and CH_4 exchange over grasslands (Table 5). Out of 46 sites with N_2O measurements (including sites in this study), 43 sites were on average N_2O sources, albeit over sometimes vastly different measurement campaign lengths (Table 5). In the literature, we found N_2O fluxes from 13 European grasslands where measurements covered at least one full year and management was similar to sites investigated in this study (grasslands with ID 23, 24, 32, 34, 38-40, 44, 45, 49-52 in Table 5). At these sites, the overall yearly flux average amounted to 43 ± 21 µg N_2O m^{-2} h^{-1}, similar to average fluxes of 55 ± 21 µg N_2O m^{-2} h^{-1} from the twelve sites with year-round measurements in this study (Table 5). The comparison of CH_4 fluxes across sites is more challenging, as some sites reported CH_4 flux rates with or without considering grazing animals in the investigated area (Table 5). We found that CH_4 flux rates from EC measurements for the grazed site FR-LAQ-I (yearly average: 1639 ± 336 µg CH_4 m^{-2} h^{-1}) were comparable to sites that used the SF_6 tracer technique (ID 52: 1021 µg CH_4 m^{-2} h^{-1}, ID 44: 1288 µg CH_4 m^{-2} h^{-1}; Soussana *et al.*, 2007b) and to a recent EC study at a Belgian pasture with cattle in the flux footprint (ID 30: 1107 µg CH_4 m^{-2} h^{-1}; Dumortier *et al.*, 2017b). Methane emissions found for FR-LAQ-I were also in the same order of magnitude as emissions from a fen meadow (ID 40, Kroon *et al.*, 2010) and a peatland pasture (ID 29, Baldocchi *et al.*, 2012), but much lower than emissions from a flooded grassland (ID 20, Hernandez *et al.*, 2014). Excluding peatlands, CH_4 fluxes were generally low and found between -59 and 136 µg CH_4 m^{-2} h^{-1}, when cattle were not considered in flux calculations. In total, 17 of 41 sites with CH_4 measurements, including sites in this study, reported uptake over yearly or shorter time horizons (Table 5).

The availability of gap-filled N_2O measurements for all ten fertilized sites in combination with detailed information about the amount of fertilizer applied to the grassland enabled the calculation of yearly N_2O-N emission factors (EFs; Table 6). After gap-filling, N_2O budgets for a total of 21 years were available. Minimum cumulative N_2O-N emissions as well as the lowest EF were found for AT-NEU in 2010 (0.19 kg N ha^{-1}; EF: 0.1%), while maximum emissions and the highest EF were found for CH-CHA during the restauration year in 2012 (24.70 kg N ha^{-1}; EF: 8.6%). For the sites where several years of data were available, cumulative N_2O-N emissions and EFs were found to vary between years. For example, emissions ranged from 0.57 to 5.28 kg N ha^{-1} yr^{-1} at FR-LAQ-I between 2008 and 2013, corresponding to EFs of 0.3 – 2.5%. Our findings indicate that the ten fertilized sites in this study emitted on average 1.8 ± 0.5% of the applied fertilizer N back to the atmosphere (Table 6).

Discussion

Soil environmental conditions can influence N_2O and CH_4 fluxes by providing ideal conditions for GHG producing or consuming microbial communities (Li *et al.*, 1992; Holtan-Hartwig *et al.*, 2002; Barnard *et al.*, 2005; Dijkstra *et al.*, 2013). Therefore, we expected clear relationships between soil conditions and magnitude of fluxes across timescales. However, regression analyses for site-level flux observations revealed low or inconsistent explanatory power of TS and WFPS (Table 3, Figure 6, Figure 7). The role of the two variables as flux drivers became more apparent after identification of site-specific GHG sweet spots (Figure 3, Figure 4). Low N_2O emissions at CH-CHA during wet conditions could be the consequence of increased N_2O reduction to N_2 during denitrification compared to production (Figure 3a). When the soil water content is high, the available time for the reduction of N_2O to N_2 during the last step of denitrification is increased, reducing N_2O release to the atmosphere (Clough *et al.*, 2005; Wu *et al.*, 2013). The

clear N_2O uptake in intermediate TS classes at AT-NEU indicated time periods when N_2O reduction in the soil exceeded concurrent N_2O production (Figure 3a; Chapuis-Lardy *et al.*, 2007; Hörtnagl & Wohlfahrt, 2014). However, based on available data it was not possible to conclude whether the observed net uptake was the consequence of increased reduction of N_2O, e.g. due to increased respiration of heterotrophic bacteria, or reduced N_2O production rates, e.g. due to cool temperatures (Chapuis-Lardy *et al.*, 2007). Still, at AT-NEU, the observation of clear N_2O uptake with TS < 10°C and WFPS < 50% but clear N_2O emission at TS > 10°C during similar soil moisture conditions suggests that reduced N_2O production rates were the main driver behind measured net N_2O uptake in this soil moisture range. At the same time, N_2O uptake at relatively high WFPS > 50% could be mainly the consequence of increased reduction rates (Figure 3a; Wu *et al.*, 2013).

Generally, the warming effect on N_2O fluxes was inconsistent at site level, similar to findings from other studies (e.g., Bijoor *et al.*, 2008; Hu *et al.*, 2010). Across all sites, the clear relationship between N_2O fluxes and TS indicated that increasing temperature fuels denitrification turnover processes in the soil, leading to enhanced N_2O emissions (Figure 3b, Figure 5a). Elevated N_2O fluxes at low TS were probably the consequence of emission bursts during freeze/thaw cycles (Risk *et al.*, 2013). For CH_4, reduced percentile fluxes at high TS in combination with relatively low WFPS both across all grassland sites (Figure 5b) and at the site-level (e.g. DE-FEN-E, Figure 4) are in contrast to findings for wetlands, rice paddies and aquatic ecosystems (Yvon-Durocher *et al.*, 2014), but similar to findings for montane grasslands (Unteregelsbacher *et al.*, 2013). The strong correlation between CH_4 fluxes and WFPS is supported by previous studies (Le Mer & Roger, 2001; Wang *et al.*, 2015; Hofmann *et al.*, 2016).

Site-specific properties of managed grasslands have the potential to change over relatively short timescales, depending on the frequency and intensity of management events along with environmental conditions. For example, trampling by grazing animals or use of heavy machinery can increase soil compaction and negatively impact soil structure (Ball, 2013). This in turn can affect soil conditions crucial to the production or consumption of GHGs in the soil, such as WFPS. Furthermore, the input of external fertilizer affects nutrient availability in the soil to varying extends and can also impact soil pH, depending on fertilizer type and amount as well as the timing of its application (Saggar *et al.*, 2013). Thus, GHG emissions/deposition sweet spots are not only different among sites (Figure 3, Figure 4), but are also most likely not persistent, depending on applied management strategies, environmental conditions and shifting microbial communities in response thereof (Jones *et al.*, 2014). The detection of sweet spots is therefore of high interest for developing site-specific GHG mitigation strategies, which need to be adapted over the course of a year. For example, the knowledge about sweet spots could assist in scheduling site-specific fertilization dates in such a way that fertilizer is only applied during time periods with low GHG emission impact, i.e. when the normalized flux in specific combined classes of the two potential drivers TS and WFPS is known to be low (Figure 3, Figure 4). In addition, significant relationships between normalized fluxes and potential drivers across sites indicated that site-specific data normalization prior to analyses could facilitate the detection of correlations (Figure 5) and thus improve methods for calculating GHG budgets on a continental scale.

The application of slurry coincided with elevated N_2O emissions (Figure 8), which is in accordance with findings in earlier studies (Neftel *et al.*, 2010; Jones *et al.*, 2011). Increased N_2O emissions were expected, as N input via fertilization constitutes the most concentrated input of

anthropogenic N, with high soil N availability fueling N_2O production by nitrifying/denitrifying bacterial communities (Firestone & Davidson, 1989; Davidson, 2009). The high impact of fertilization on N_2O emissions at CH-CHA were probably the consequence of generally warm temperatures around 20°C in combination with considerably wetter soil conditions in comparison to DE-FEN-I and DE-FEN-E. After some fertilization applications, N_2O emissions stayed elevated the longest with warm or increasing TS in combination with WFPS quickly decreasing from high to intermediate values, for example on 16 August 2012 at CH-CHA (Figure 8). This observation at CH-CHA could indicate that N_2O emissions after fertilizer application were additionally fueled due to decreasing reduction rates of N_2O to N_2 as a consequence of declining WFPS (Wu *et al.*, 2013). However, the exact causes why N_2O emissions stayed elevated over a given period of time are difficult to determine without additional measurements, such as soil oxygen and substrate availability. For CH-CHA during the restoration year 2012, soil water content, soil and air temperature, N input via fertilization and the net CO_2 exchange as a proxy for plant activity were identified as potential drivers for measured N_2O fluxes (Merbold *et al.*, 2014). The same study found reduced N_2O-N EFs during time periods of high productivity or vice versa, suggesting a fast turnover of mineral N as possible explanation for this observation. However, in this study we were not able to replicate this finding at the annual timescale, as the relationship between net CO_2 flux and N_2O-N EFs across sites was generally low (data not shown). With the average N_2O-N EF across sites in this study being clearly higher than the IPCC Tier 1 EF of 1% and given the high variability of N_2O-N EFs across site-years, more direct long-term measurements are needed to improve and develop sophisticated Tier 2 and Tier 3 EFs for their application at the national scale (IPCC, 2006; Table 6).

Emission peaks after slurry application were also observed for CH_4 and supported earlier findings (e.g. Mori & Hojito, 2015). However, at DE-FEN-I and DE-FEN-E, CH_4 emissions decreased more rapidly to pre-fertilization levels than N_2O fluxes, suggesting that large amounts of CH_4 were released from the slurry itself as opposed to being produced in the soil (Chadwick *et al.*, 2000). In contrast, elevated CH_4 emissions at CH-CHA after fertilization suggested that small amounts of CH_4 were produced in the soil, possibly from organic matter supplied in the slurry, i.e. through the microbial degradation of volatile fatty acids (Sherlock *et al.*, 2002). Furthermore, CH_4 oxidation by soil microorganisms was possibly reduced due to elevated NH_4^+ soil concentrations following N fertilizer applications inhibiting the CH_4 oxidation capacity, effectively increasing emissions from the soil (Bodelier & Laanbroek, 2004). The different emission patterns at CH-CHA and DE-FEN-I/DE-FEN-E after fertilizer application are probably due to the respective measurement methods at the sites (Figure 8). Eddy covariance fluxes at CH-CHA are based on an integral signal calculated from high-frequency samples from the whole footprint, comprising both hot spots of high CH_4 emissions but also smaller areas of CH_4 uptake (Baldocchi *et al.*, 2012). In comparison, chamber measurements at DE-FEN-I and DE-FEN-E represent the exchange over a much smaller area of the grassland, resulting in a more immediate response of the measured signal to fertilizer application in the chambers. Due to this small-scale variability being an integral component of the EC method, fluxes are probably dampened and lower than what would be expected from laboratory or chamber experiments.

At all sites presented in this manuscript, the CO_2 flux was the predominant component of the annual GHG budget (Table 4). Our observation that N_2O and CH_4 emissions in terms of CO_2-equivalents offset 21 ± 6% of concurrent CO_2 uptake is similar to the 18% reported for European grasslands (Schulze et al., 2009). Even at the heavily grazed site FR-LAQ-I, which was

characterized by high ruminant CH_4 emissions by grazing animals in the EC flux footprint, the grassland was a clear GHG sink (Table 4), supporting earlier observations (Chang et al., 2015). Still, high CH_4 emissions at FR-LAQ-I highlighted the need to consider grazing cattle during the evaluation of grassland GHG budgets (e.g., Martin *et al.*, 2010).

We found that year-round GHG measurements are necessary for unbiased GHG budget calculations, mainly due to relevant N_2O and CH_4 flux contributions during spring and winter (Figure 2). Spring N_2O emissions were most likely dominated either by freeze-thaw emission bursts or high soil moisture conditions after snowmelt (Risk *et al.*, 2013), winter N_2O production can still occur at low temperatures in frozen soil (Teepe *et al.*, 2001; Zhu *et al.*, 2005; Wertz *et al.*, 2013). For CH_4, we assume that seasonal fluxes were mainly driven by the presence or absence of anaerobic CH_4-producing microsites in the soil, the application of slurry as fertilizer, as well as temperature (Chadwick *et al.*, 2000; Treat *et al.*, 2014). The role of snow accumulation during winter on observed CH_4 emissions needs further investigation (Blanc-Betes *et al.*, 2016).

Direct long-term measurements at site level are of highest importance to quantify the annual GHG exchange. With N_2O and CH_4 flux gap-filling being a source of uncertainty, continuous GHG measurements at high temporal resolution are crucial for reliable GHG budget estimates (Mishurov & Kiely, 2011; Barton *et al.*, 2015). In this study, the availability of high-resolution data from AC and EC measurements facilitated the application of advanced statistical methods, e.g. the quantification of fertilization impacts on GHG fluxes (Figure 8, Figure 9). For future studies, we recommend simultaneous chamber and EC measurements in the same flux footprint to investigate potential biases of the different methods (Eugster & Merbold, 2015). Reducing the uncertainty in quantifying N_2O and CH_4 budgets at the site level is ideally done using a multi-step approach and comprises (1) spatial snapshot measurements of small areas for the identification of

emission hot spots in order to understand footprint source/sink heterogeneity, (2) capturing temporal high fluxes, and (3) identifying environmental conditions that indicate enhanced GHG source/sink activity, i.e. sweet spots. While (1) is best achieved via chamber measurements using multiple plots (Skiba *et al.*, 2009; Cowan *et al.*, 2015), (2) and (3) are best investigated via long-term automatic chamber or eddy covariance measurements at high temporal resolution, thus covering a wide range of environmental conditions while considering spatial information from (1) during data interpretation. For grazed sites, knowledge of animal movements and distribution of manure pats in the flux footprint have to be considered for in depth analyses of GHG source/sink behavior (Felber *et al.*, 2015). This is of special importance for the EC method, by which small-scale emission and deposition hot spots are integrated spatially (Baldocchi *et al.*, 2012). In addition, future research should also focus on the development and improvement of meaningful land use indices that consider specific management strategies at the site-level and aggregate available site information into objective categories. While we are aware of existing indices for land use intensity (e.g., Blüthgen *et al.*, 2012), we refrained from applying them due to various simplifications that lead to indices lacking representativity for sites included in this study. The availability of representative, objective land use indices would allow accurate classifications of managed grasslands into meaningful categories, and thus improved statistical analyses of *in-situ* data across sites. Generally, it is challenging to attribute annual budgets to specific management strategies. The main reason for this is the finding that site-specific GHG fluxes vary considerably between years despite similar management (Table 4). This observation mandates the inclusion of extended datasets in GHG analyses that comprise comprehensive soil and management information, but also the application of advanced statistical methods (e.g., Dengel *et al.*, 2013).

Central European grassland sites in this study were characterized by site-specific management strategies that reflected the wide range of site characteristics and exemplified the complexity of managed grassland ecosystems in geographical proximity. The CO_2 sink strength as the predominant component of the annual GHG budget highlighted the need to conduct CO_2 flux measurements at the site-level. However, the impact of N_2O and CH_4 on the annual NGB of the grassland is substantial at many sites. Therefore, due to the absence of robust relationships between N_2O and CH_4 fluxes and environmental drivers, long-term *in-situ* measurements are crucial in reliably assessing the full annual NGB of specific grasslands. This is especially important during extreme management events such as grassland restoration that includes ploughing, which have the potential to change an otherwise strong annual GHG sink to a source.

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Tables

Table 1 Basic information for each research site included in this study.

Site	CH-AWS	AT-STU-P	AT-STU-M	FR-LAQ-I	FR-LAQ-E
Location	Alp Weissenstein, Switzerland	Stubai Valley, Austria	Stubai Valley, Austria	Laqueuille, France	Laqueuille, France
Latitude	46° 34′ 59″ N	47° 12′ 87″ N	47° 12′ 88″ N	45° 38′ 00″ N	45° 38′ 00″ N
Longitude	9° 47′ 25″ E	11° 30′ 33″ E	11° 30′ 58″ E	2° 44′ 00″ E	2° 44′ 00″ E
Elevation (m)	1978	1870	1820	1040	1040
Management	extensive	extensive	extensive	intensive	extensive
MAT (°C)	-1.4	3.0	3.0	7.0	7.0
MAP (mm)	1214	1097	1097	1200	1200
Snow cover days	166	124	128	25-91	25-91
Grass (%)	95	n.a.	54	69	77
Clover (%)	< 5	n.a.	5	11	4
Grazing days yr^{-1}	< 20	120	70	142 - 170	142 - 170
Grazing animals d^{-1}	20 cows	~7 cows, 15 sheep	~7 cows, 15 sheep	9 - 14 cows	7 - 9 cows
Cutting events	0	0	1	0	0
Harvest C / N (kg ha^{-1} DW)	0	0	unknown	0	0
Fertilization events	1	1	1	3	0
Organic fertilizer C / N (kg ha^{-1} yr^{-1})	unknown	1390 / 70 (solid manure)	1390 / 70 (solid manure)	0	0
Mineral fertilizer N (kg ha^{-1} yr^{-1})	0	0	0	214	0
CO_2 / N_2O / CH_4 flux method	EC / MC / MC	None / MC / MC	MC / MC / MC	EC / AC / EC	EC / AC / none
CO_2 / N_2O / CH_4 measurement days	339 / 20 / 20	0 / 27 / 26	0 / 51 / 50	1373 / 1123 / 318	863 / 878 / 0
Chamber plots	16	5	5	4	4
GF_{RM} window size (days)	60	60	60	60	60
Reference	Imer *et al.* (2013)	Schmitt *et al.* (2010)	Schmitt *et al.* (2010)	Klumpp *et al.* (2011a) Allard *et al.*(2007)	Klumpp *et al.* (2011a) Allard *et al.*(2007)

Table 1 Continued.

Site	CH-FRU-I	CH-FRU-E	AT-NEU	DE-GAP
Location	Früebüel, Switzerland	Früebüel, Switzerland	Neustift, Austria	Garmisch-Partenkirchen, Germany
Latitude	47° 6′ 57″ N	47° 6′ 57″ N	47° 07′ 00″ N	47° 28' 32.12" N
Longitude	8° 32′ 16″ E	8° 32′ 16″ E	11° 19′ 07″ E	11° 3' 44.47" E
Elevation (m)	982	982	970	734
Management	intensive	extensive	intensive	extensive
MAT (°C)	6.1	6.1	6.5	6.8
MAP (mm)	1682	1682	852	1371
Snow cover days	111	111	93 / 92	72 – 91
Grass (%)	n.a.	n.a.	20-40	52
Clover (%)	5 - 25	5 - 25	5	8
Grazing days yr^{-1}	29	10	0	0
Grazing animals d^{-1}	54-57 cows	40-56 cows	0	0
Cutting events	1	2	2010: 3 2011: 3	2012: 3 2013: 3
Harvest C / N (kg ha^{-1} DW)	1482 / 95	4389 / 280	2010: 3470 / 169 2011: 3676 / 180	2012: 2940 / 150 2013: 4507 / 245
Fertilization events	3	1	2010: 1 2011: 1	2012: 1 2013: 2
Organic fertilizer C / N (kg ha^{-1} yr^{-1})	939 / 159 (slurry)	495 / 33 (slurry)	2730 / 341 (solid manure & slurry)	2012: 390 / 61 (slurry) 2013: 1071 / 122 (slurry)
Mineral fertilizer N (kg ha^{-1} yr^{-1})	0	0	0	0
CO_2 / N_2O / CH_4 flux method	EC / MC / MC	EC / MC / MC	EC / EC / EC	all: MC
CO_2 / N_2O / CH_4 measurement days	570 / 35 / 34	571 / 35 / 35	769 / 598 / 596	0 / 92 / 93
Chamber plots	6	10	0	3
GF_{RM} window size (days)	15	60	15	120
Reference	Imer *et al.* (2013)	Imer *et al.* (2013)	Hörtnagl & Wohlfahrt (2014) Wohlfahrt *et al.* (2008)	Lu, (2016)

Table 1 Continued.

Site	DE-FEN-I¶	DE-FEN-E¶	CH-CHA-I1	CH-CHA-I2†	CH-CHA§
Location	Fendt, Germany	Fendt, Germany	Chamau, Switzerland	Chamau, Switzerland	Chamau, Switzerland
Latitude	47° 82′ N	47° 82′ N	47° 12′ 37″ N	47° 12′ 37″ N	47° 12′ 37″ N
Longitude	11° 06′ E	11° 06′ E	8° 24′ 38″ E	8° 24′ 38″ E	8° 24′ 38″ E
Elevation (m)	600	600	393	393	393
Management	intensive	extensive	intensive	intensive	intensive
MAT (°C)	8.6	8.6	9.1	9.1	9.1
MAP (mm)	933	933	1151	1151	1151
Snow cover days	43 – 54	43 – 54	< 7	< 7	< 7
Grass (%)	42	42	80	80	60
Clover (%)	18 – 26	18 – 26	20	20	40
Grazing days yr^{-1}	0	0	2010: 0 2011: 18	2010: 50 2011: 18	2012: 7 2013: 1
Grazing animals d^{-1}	0	0	2010: 0 2011: 50 - 60 sheep	2010: 40 – 160 sheep 2011: 50 – 60 sheep	2012: 50 sheep 2013: 70 sheep
Cutting events	2012: 5 2013: 4 2014: 5	2012: 3 2013: 3 2014: 3	2010: 5 2011: 5	2010: 4 2011: 5	2012: 5 2013: 5
Harvest C / N (kg ha^{-1} DW)	2012: 4790 / 389 2013: 6374 / 420 2014: 5841 / 289	2012: 4664 / 273 2013: 4437 / 247 2014: 3989 / 169	2010: 3449 / 222 2011: 2468 / 159	2010: 1262 / 81 2011: 1850 / 119	2012: 1500 / 96 2013: 4233 / 272
Fertilization events	2012: 5 2013: 6 2014: 4	2012: 1 2013: 2 2014: 1	2010: 5 2011: 6	2010: 5 2011: 6	2012: 6 2013: 4
Organic fertilizer C / N (kg ha^{-1} yr^{-1})	2012: 2204 / 312 (slurry) 2013: 3310 / 365 (slurry) 2014: 2503 / 243 (slurry)	2012: 389 / 61 (slurry) 2013: 1071 / 122 (slurry) 2014: 288 / 61 (slurry)	2010: 1426 / 253 (slurry) 2011: 1222 / 254 (slurry)	2010: 1487 / 194 (slurry) 2011: 1510 / 258 (slurry)	2012: 2233 / 269 & 2013: 978 / 232 (slurry)
Mineral fertilizer N (kg ha^{-1} yr^{-1})	0	0	0	0	2012: 17 2013: 0
CO_2 / N_2O / CH_4 flux method	all: MC & AC	all: MC & AC	EC / MC / MC	EC / MC / MC	EC / EC / EC
CO_2 / N_2O / CH_4 measurement days	1096 / 626 / 629	0 / 659 / 659	676 / 38 / 36	698 / 38 / 37	715 / 694 / 694
Chamber plots	6	6	8	8	0
GF_{RM} window size (days)	60	60	30	30	60
Reference	Lu, (2016) Zeeman *et al.* (2017)	Lu, (2016)	Imer *et al.* (2013)	Imer *et al.* (2013)	Merbold *et al.* (2014)

¶ Grass and clover percentages are given as fraction of total dry weight and is not related to spatial coverage;
† CH-CHA-I2 2010: rolling and resowing in March/April, herbicide in July;
§ CH-CHA 2012: ploughing on 2 February, resowing, rolling, harrowing in March and April, herbicide/pesticide in July and September;
& During 2012, solid manure was applied in January, otherwise slurry.

Abbreviations: MAP, mean annual precipitation; MAT, mean annual temperature; DW, dry weight; GF_{RM}, gap-filling with running median;
Flux measurement method: AC, automatic chambers; EC, eddy covariance method; MC, manual chambers;

Table 2 Percentile distribution of measured, non-gapfilled N_2O (F_{N2O}) and CH_4 (F_{CH4}) fluxes, soil temperature (TS) and water-filled pore space (WFPS) for data shown in Figure 3-Figure 5 for each site. P_{zf} corresponds to the zero-flux percentile, i.e. the percentile rank where the flux was found to be zero; P_{25} and P_{75} refer to the 25th and 75th percentile, i.e. values in-between give the interquartile range; P_{50} corresponds to the 50th percentile (median).

		Flux (µg m^{-2} h^{-1})			TS (°C)			WFPS (%)		
Site	**P_{zf}**	**P_{25}**	**P_{50}**	**P_{75}**	**P_{25}**	**P_{50}**	**P_{75}**	**P_{25}**	**P_{50}**	**P_{75}**
F_{N2O}										
CH-AWS	0	5	17	73	10	12	12	38	55	64
STU-P	4	5	6	10	11	12	13	44	51	54
STU-M	15	4	8	13	9	11	12	59	62	68
FR-LAQ-I	10	3	12	29	7	12	15	59	63	69
FR-LAQ-E	9	2	6	13	6	10	14	61	66	70
CH-FRU-I	2	7	21	33	10	12	14	57	77	82
CH-FRU-E	0	9	17	23	10	12	14	57	77	82
AT-NEU	35	-4	4	20	2	11	15	50	61	68
DE-GAP	15	2	11	22	10	15	20	59	68	71
DE-FEN-I	5	10	17	41	6	12	18	55	67	71
DE-FEN-E	4	6	11	21	7	13	18	54	61	65
CH-CHA-I1	0	18	39	133	12	16	19	64	82	89
CH-CHA-I2	1	27	56	238	12	16	19	64	82	89
CH-CHA	12	16	56	264	5	13	18	85	91	94
Range (min, max)	0, 35	-4, 27	4, 56	10, 264	2, 12	10, 16	12, 20	38, 85	51, 91	54, 94
F_{CH4}										
CH-AWS	n.a.	-41	-28	-18	10	12	12	38	55	64
STU-P	85	-40	-29	-18	11	12	14	41	50	54
STU-M	95	-56	-40	-24	10	11	13	59	62	68
CH-FRU-I	81	-22	-17	-8	10	12	14	54	77	81
CH-FRU-E	86	-20	-12	-9	10	12	14	57	77	82
AT-NEU	27	-6	36	76	2	11	15	50	61	68
DE-GAP	77	-26	-12	-1	10	15	20	59	68	71

DE-FEN-I	87	-18	-10	-5	6	12	18	55	67	71
DE-FEN-E	87	-18	-11	-6	7	13	18	54	61	65
CH-CHA-I1	80	-15	-14	-2	13	16	19	63	82	89
CH-CHA-I2	81	-16	-12	-4	12	16	19	64	82	89
CH-CHA	36	-115	111	364	5	13	18	85	91	94
Range (min, max)	27, 95	-115, -6	-40, 111	-24, 364	2, 13	11, 16	12, 20	38, 85	50, 91	54, 94

Table 3 Regression analysis using daily averages with log-transformed CH_4 (F_{CH4}) and N_2O (F_{N2O}) flux rates as dependent variables. Soil temperature (TS) and water-filled pore space (WFPS) were used as driver variables. Before log-transformation, the site-specific minimum flux + 1 was added to observed fluxes. Only background fluxes were included in the regression analysis, time periods in temporal proximity to management events (cutting, fertilization) and periods of snow cover were excluded from the analysis. Linear models: $y = ax + by + c$ for multiple linear regression, $y = dx + e$ for simple linear regression. n, number of available measurement days used in the regression analyses; r^2_{adj}, coefficient of determination after adjustment based on the degrees of freedom of the respective model; stars indicate significance levels: *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$;

		Multiple linear regression (TS + WFPS)					**Simple linear regression**							
				Regression coefficients					**Regression coefficients**				**Regression coefficients**	
Site	**Measurement technique**	**n**	**r^2 (r^2_{adj})**	**c (intercept)**	**a (TS)**	**b (WFPS)**	**n**	**r^2 (r^2_{adj})**	**e (intercept)**	**d (TS)**	**n**	**r^2 (r^2_{adj})**	**e (intercept)**	**d (WFPS)**
log(F_{N2O})														
CH-AWS	MC	19	0.31 (0.22)	-0.269	0.011	0.007*	19	0.07 (0.01)	-0.056	0.021	19	0.29 (0.25)*	-0.164	0.007*
AT-STU-P	MC	21	0.13 (0.04)	0.024	0.003	0.000	21	0.13 (0.09)	0.032	0.003	21	0.00 (-0.05)	0.072	0.000
AT-STU-M	MC	18	0.46 (0.38)*	-0.235*	0.010**	0.003*	18	0.24 (0.19)*	0.009	0.008*	18	0.08 (0.02)	-0.035	0.002
FR-LAQ-I	EC	570	0.10 (0.10)***	-0.213	0.022***	0.003	684	0.05 (0.05)***	0.027	0.013***	570	0.01 (0.01)*	0.422***	-0.004*
FR-LAQ-E	AC	591	0.10 (0.09)***	-0.198	0.021***	0.002	711	0.05 (0.04)***	0.033	0.012***	591	0.01 (0.01)*	0.404***	-0.003*
CH-FRU-I	MC	33	0.24 (0.19)*	-0.085	0.010**	0.002*	33	0.11 (0.08)	0.099*	0.006	33	0.01 (-0.02)	0.130*	0.001
CH-FRU-E	MC	27	0.47 (0.43)***	-0.097	0.012***	0.001**	27	0.27 (0.24)**	0.029	0.008**	27	0.05 (0.01)	0.095*	0.001
AT-NEU	EC	400	0.14 (0.10)***	0.460***	0.003**	-0.002***	400	0.06 (0.06)***	0.321***	0.005***	400	0.12 (0.11)***	0.513***	-0.002***
DE-GAP	MC	59	0.21 (0.18)**	-0.204*	0.005*	0.004***	59	0.01 (-0.01)	0.108**	0.002	67	0.08 (0.06)*	-0.028	0.002*
DE-FEN-I	AC	244	0.03 (0.03)*	0.151	0.004	0.000	506	0.08 (0.08)***	0.078***	0.006***	244	0.02 (0.02)*	0.306***	-0.002*
DE-FEN-E	AC	299	0.02 (0.02)*	-0.013	0.002	0.002*	547	0.01 (0.01)**	0.107***	0.002**	303	0.02 (0.01)*	0.062	0.002*
CH-CHA-I1	MC	31	0.19 (0.13)	-1.135	0.028	0.014*	33	0.02 (-0.02)	0.228	0.009	31	0.08 (0.05)	-0.278	0.008
CH-CHA-I2	MC	54	0.14 (0.10)*	-1.067	0.038**	0.012*	56	0.05 (0.04)	0.121	0.020	54	0.01 (-0.01)	0.168	0.003
CH-CHA	EC	610	0.15 (0.15)***	3.407***	-0.008*	-0.025***	610	0.02 (0.02)***	1.003***	0.010***	610	0.14 (0.14)***	2.981***	-0.021***
log(F_{CH4})														
CH-AWS	MC	19	0.77 (0.74)***	0.047	-0.015	0.009***	19	0.00 (-0.06)	0.304	0.004	19	0.72 (0.71)***	-0.085	0.009***
AT-STU-P	MC	26	0.03 (-0.05)	1.809***	-0.006	0.000	26	0.03 (-0.01)	1.792***	-0.006	26	0.00 (-0.04)	1.717***	0.000
AT-STU-M	MC	20	0.05 (-0.06)	0.285	0.021	0.004	20	0.05 (-0.01)	0.548*	0.019	20	0.00 (-0.05)	0.687	0.001

FR-LAQ-I	AC	148	0.24 (0.23)***	0.552	0.182***	0.011	178	0.24 (0.24)***	1.388***	0.171***	148	0.00 (-0.00)	4.393***	-0.011
FR-LAQ-E	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.
CH-FRU-I	MC	32	0.19 (0.13)	-0.038	0.006	0.004*	32	0.00 (-0.03)	0.363***	-0.003	32	0.16 (0.14)*	0.082	0.004*
CH-FRU-E	MC	27	0.40 (0.35)**	0.014	-0.003	0.004**	27	0.11 (0.07)	0.430***	-0.014	27	0.40 (0.37)***	-0.043	0.005***
AT-NEU	EC	398	0.04 (0.03)***	1.716***	0.008***	0.002*	398	0.02 (0.02)**	1.855***	0.006**	398	0.01 (0.00)	1.865***	0.001
DE-GAP	MC	58	0.40 (0.37)***	0.280	-0.004	0.010***	58	0.13 (0.12)**	0.988***	-0.011**	68	0.18 (0.16)***	0.282	0.008***
DE-FEN-I	AC	244	0.22 (0.21)***	0.185*	0.000	0.005***	509	0.14 (0.14)***	0.599***	-0.007***	244	0.22 (0.22)***	0.196***	0.005***
DE-FEN-E	AC	299	0.32 (0.32)***	0.226***	-0.002	0.006***	549	0.16 (0.16)***	0.628***	-0.008***	303	0.30 (0.29)***	0.149***	0.007***
CH-CHA-I1	MC	29	0.10 (0.03)	0.191	-0.006	0.002	31	0.07 (0.04)	0.329***	-0.008	29	0.07 (0.03)	0.002	0.003
CH-CHA-I2	MC	54	0.20 (0.17)**	-0.099	0.000	0.004**	55	0.06 (0.04)	0.300***	-0.006	54	0.20 (0.19)***	-0.111	0.004***
CH-CHA	EC	609	0.00 (-0.00)	3.154***	0.003	0.000	609	0.00 (0.00)	3.187***	0.002	609	0.00 (-0.00)	3.305***	-0.001

Table 4 Annual cumulative CO_2, N_2O and CH_4 site budgets, calculated from gap-filled data. For sites where more than one year of measurements were available, multi-year averages ± the standard error of the mean are given. Net greenhouse gas balance (NGB) is given as the sum of CO_2 flux + N_2O flux + CH_4 flux. CO_2 flux offset represents the percentage of CO_2 uptake that is offset by N_2O and CH_4 fluxes, i.e. corresponds to the ratio between the sum of N_2O flux + CH_4 flux and the CO_2 flux. For NGB and the CO_2 flux offset, numbers are shown in brackets if not all three compounds were measured.

Site	**Year**	**Cumulative budgets (g CO_2-eq. m^{-2} yr^{-1})**				**CO_2 flux offset**
		CO_2 flux	**N_2O flux**	**CH_4 flux**	**NGB**	
CH-AWS	2010/11	-1783	107	-9	-1685	5%
AT-STU-P	2011	n.a.	18	-7	(11)	n.a.
AT-STU-M	2011	n.a.	20	-9	(11)	n.a.
FR-LAQ-I	2008	-1537	93	n.a.	(-1444)	(6%)
	2009	-1444	247	n.a.	(-1197)	(17%)
	2010	-814	48	388	-378	54%
	2011	-1019	68	588	-363	64%
	2012	n.a.	56	n.a.	(56)	n.a.
	2013	n.a.	25	n.a.	(25)	n.a.
	2008-2013	-1204 ± 172	90 ± 33	488 ± 100	-626	48%
FR-LAQ-E	2008	-1276	17	n.a.	(-1259)	(1%)
	2009	-657	30	n.a.	(-627)	(5%)
	2010	-916	20	n.a.	(-897)	(2%)
	2011	n.a.	23	n.a.	(23)	n.a.
	2012	n.a.	16	n.a.	(16)	n.a.
	2013	n.a.	10	n.a.	(10)	n.a.
	2008-2013	-950 ± 179	19 ± 3	n.a.	(-931)	(2%)
CH-FRU-I	2010/11	-2806	47	-2	-2761	2%

CH-FRU-E	2010/11	-1371	40	-4	-1335	3%
AT-NEU	2010	-111	10	14	-87	22%
	2011	-70	30	11	-29	59%
	2010-2011	-91 ± 20	20 ± 10	13 ± 2	-58	36%
DE-GAP	2012	n.a.	25	1	(26)	n.a.
	2013	n.a.	27	-3	(24)	n.a.
	2012-2013	n.a.	26 ± 1	-1 ± 2	(25)	n.a.
DE-FEN-I	2012	-737	101	9	-627	15%
	2013	-954	57	1	-896	6%
	2014	-1238	37	-1	-1202	3%
	2012-2014	-976 ± 145	65 ± 19	3 ± 3	-909	7%
DE-FEN-E	2012	n.a.	38	4	(42)	n.a.
	2013	n.a.	52	-3	(49)	n.a.
	2014	n.a.	36	-3	(33)	n.a.
	2012-2014	n.a.	42 ± 5	-1 ± 2	(41)	n.a.
CH-CHA-I1	2010/11	-2403	245	-2	-2160	10%
CH-CHA-I2	2010/11	-912	370	-2	-544	40%
CH-CHA	2012§	1246	1157	43	2446	-96%
	2013	-4671	119	38	-4514	3%
	2012-2013	-1713 ± 2959	638 ± 519	41 ± 3	-1034	40%
Mean across sites						21 ± 6%

§ CH-CHA 2012: year of grassland restoration (including ploughing)

Table 5 Literature overview of N_2O and CH_4 measurements over grassland sites in comparison to gap-filled findings in this study, flux rates are given in µg m^{-2} h^{-1}.

ID	Site	Reference	Years	Time	Method	Sampling freq.	Management	N_2O Min	N_2O Max	N_2O Mean ± SEM	CH_4 Min	CH_4 Max	CH_4 Mean ± SEM	Notes
1	CH-AWS	this study	2010/11	YR	MC	~WK	G, (F)	0 DY	181 DY	41 YR	-57 DY	-15 DY	-30 YR	¶
2	AT-STU-P	this study	2011	GWS	MC	WK	G, F	-5 DY	22 DY	7 DY	-86 DY	75 DY	-23 DY	¶
3	AT-STU-M	this study	2011	GWS	MC	WK	G, C, F	-8 DY	26 DY	8	-114 DY	49 DY	-32	¶
4	FR-LAQ-I	this study	CH_4: 2010-2011, N_2O: 2008-2013	CH_4: GWS, N_2O: YR	CH_4: EC, N_2O: AC	DY	G, F	-94 DY	1298 DY	34 ± 13 YR	-206 DY	12459 DY	1639 ± 336 DY	cows in footprint
5	FR-LAQ-E	this study	2008-2013	YR	AC	DY	G	-32 DY	199 DY	7 ± 1 YR				
6	CH-FRU-I	this study	2010/11	YR	MC	~WK	G, C, F	-7 DY	126 DY	18	-37 DY	63 DY	-6	¶
7	CH-FRU-E	this study	2010/11	YR	MC	~WK	G, C, F	0 DY	282 DY	15	-57 DY	24 DY	-12	¶
8	AT-NEU	this study	2011	YR	EC	20 Hz	C, F	-277 DY	121 DY	8 ± 4 YR	-1911 DY	602 DY	41 ± 5 YR	
9	DE-GAP	this study	2012-2013	YR	MC	WK	C, F	-11 DY	127 DY	10 ± 0 YR	-70 DY	404 DY	-4 ± 7 YR	
10	DE-FEN-I	this study	2012-2014	YR	AC	DY	C, F	-8 DY	2055 DY	25 ± 7 YR	-57 DY	6377 DY	11 ± 10 YR	
11	DE-FEN-E	this study	2012-2014	YR	AC	DY	C, F	-8 DY	366 DY	16 ± 2 YR	-54 DY	8907 DY	-2 ± 8 YR	
12	CH-CHA-I1	this study	2010/11	YR	MC	~WK	G, C, F	-1 DY	849 DY	94	-23 DY	111 DY	-5	¶
13	CH-CHA-I2	this study	2010/11	YR	MC	~WK	G, C, F	-4 DY	1529 DY	142	-28 DY	20 DY	-6	¶
14	CH-CHA	this study	2012-2013	YR	EC	20 Hz	G, C, F	-803 DY	4868 DY	244 ± 199	-1327 DY	4234 DY	136 ± 8	2012: grassland restoration
15	Inner Mongolia	Wolf *et al.* (2010)	2007/2008	YR	AC	>DY	none	-8 SM	75 SM	4				steppe grassland
16	LCRC, USA	Chiavegato *et al.* (2015)	2012-2013	GZS	MC	DY	none	0 WW	5 WW	2 ± 2 YR	-45 WW	0 WW	-23 ± 23 YR	*, ¶
17	Inner Mongolia	Wolf *et al.* (2010)	2007/2008	YR	AC	>DY	G	-9 SM	31 SM	0				steppe grassland
18	LCRC, USA	Chiavegato *et al.* (2015)	2011-2013	GZS	MC	DY	G	7 WW	64 WW	41 ± 17 YR	-35 WW	145 WW	48 ± 52 YR	¶, *, irrigated
19	LCRC, USA	Chiavegato *et al.* (2015)	2011-2013	GZS	MC	DY	G	6 WW	83 WW	39 ± 23 YR	-55 WW	125 WW	43 ± 53 YR	¶, *
20	Estero Dulce, MX Boquilla de Oro, MX	Hernandez *et al.* (2014) Hernandez *et al.* (2014)	2010-2012	YR	MC	bi-MN	G				6070 DS	181210 RS	116760 YR	¶, flooded grassland
21	Nam Co, CN	Wei *et al.* (2014)	2009-2013	GWS	MC	WK	G				-96 YR	-49 YR	-72 ± 3 YR	¶, steppe
22	Nam Co, CN	Wei *et al.* (2014)	2012-2013	GWS	MC	WK	G				-74 YR	-37 YR	-59 ± 4 YR	¶, meadow
23	Bugac, HU	Soussana *et al.* (2007)	2002-2004	YR	CH4: EST, N2O: MC, TDL		G	15 YR	18 YR	17 ± 1 YR	117 YR	218 YR	167 ± 50 YR	†
24	Laqueuille, FR (E)	Soussana *et al.* (2007)	2002-2004	YR	CH4: SF6, N2O: MC, TDL		G	3 YR	3 YR	3 ± 0 YR	636 YR	719 YR	678 ± 42 YR	†
25	Haibei, CN	Li *et al.* (2015)	2013	GWS	MC	DY	G	-2 MN	9 MN	4 ± 3 MN	-17 MN	13 MN	2 ± 9 MN	¶, #, alpine meadow
26	Haibei, CN	Li *et al.* (2015)	2013	GWS	MC	DY	G	-1 MN	11 MN	5 ± 3 MN	-2 MN	25 MN	12 ± 8 MN	¶, #, alpine steppe
27	MUDF4, NZ	Bhandral *et al.* (2010)	2003/04	GWS, WIN	MC	DY	G	98 DY	1074 DY	301 ± 40				$
28	Easter Bush, GB	Dengel *et al.* (2011)	2010	GWS	EC	20 Hz	G				0 DY	4167 DY	1043 DY	sheep pasture
29	Sherman Island, US	Baldocchi *et al.* (2012)	2007-2010	GWS	EC	10 Hz	G						1320 ± 1014 YR	peatland pasture, cows
30	Dorinne, BE	Dumortier *et al.* (2017)	2013	YR	EC	10 Hz	G				63	14554	1107 YR	&, cattle pasture
31	Mooloolah Valley, NZ	Rowlings *et al.* (2015)	2007-2008	YR	AC	DY	G	1 DY	761 DY	31 ± 8 YR				subtropical pasture
32	Oensingen, CH (E)	Soussana *et al.* (2007)	2002-2004	YR	MC, TDL		C	-4 YR	-4 YR	-4 ± 0 YR				
33	Sapporo, JP	Kim & Tanaka (2015)	1996/97	GWS, WIN	MC	>=MN	C	4 DY	14 DY	8 SUM / 13 WIN	-24 DY	0 DY	-10 SUM / 0 WIN	
34	Dümmer peatland, DE	Beyer *et al.* (2015)	2007-2011	YR	MC	bi-WK	C	0 YR	2 YR	10 ± 7 YR	-47 YR	48 YR	-14 ± 8 SEM YR	fen grassland
35	Nasu, JP	Mori & Hojito (2014)	2008-2010	YR	MC	~WK	C, F	-26 DY	111 DY	10 ± 4 YR	-173 DY	167 DY	-18 ± 0 YR	F: PK
36	Nasu, JP	Mori & Hojito (2014)	2008-2010	YR	MC	~WK	C, F	-33 DY	1493 DY	84 ± 37 YR	-173 DY	3028 DY	16 ± 9 YR	F: SL, PK
37	Nasu, JP	Mori & Hojito (2014)	2008-2010	YR	MC	~WK	C, F	-13 DY	1754 DY	88 ± 34 YR	-156 DY	334 DY	-15 ± 8 YR	F: MA, PK
38	Oensingen, CH (I)	Soussana *et al.* (2007)	2002-2004	YR	MC, TDL		C, F	19 YR	35 YR	27 ± 8 YR				
39	Lille Valby, DK	Soussana *et al.* (2007)	2002-2004	YR	MC, TDL		C, F	5 YR	14 YR	10 ± 4 YR				
40	Oukoop, NL	Kroon *et al.* (2010b)	2006-2008	YR	EC, QCL		C, F	274 YR	285 YR	274 YR	1701 YR	2009 YR	1884 YR	fen meadow
41	Edinburgh, GB	Cowan *et al.* (2015)	2013	SUM	MC	>DY	G, F	11	7022	47 DY				§, sheep
42	Sherman Island, US	Teh *et al.* (2011)	2007/08	YR	EC	10 Hz	G, F						312 YR	peatland pasture, daytime
43	Sherman Island, US	Teh *et al.* (2011)	2007/08	YR	MC	WK	G, F	196 DY	7397 DY	419 YR			1436 YR	¶, peatland pasture
44	Laqueuille, FR (I)	Soussana *et al.* (2007)	2002-2004	YR	CH4: SF6, N2O: MC, TDL		G, F	12 YR	14 YR	13 ± 1 YR	1255 YR	1322 YR	1288 ± 33 YR	†
45	Malga Arpaco, IT	Soussana *et al.* (2007)	2002-2004	YR	CH4: EST, N2O: MC, TDL		G, F	0 YR	0 YR	0 YR	301 YR	301 YR	301 ± 0 YR	†
46	Easter Bush, GB	Jones *et al.* (2011)	2003/07/08	GWS	MC		G, F	128 CP	876 CP	415 ± 120 CP				**
47	Easter Bush, GB	Jones *et al.* (2011)	2003/07/08	GWS	EC		G, F	69 CP	1472 CP	411 ± 196 CP				**
48	MUDF4, NZ	Bhandral *et al.* (2010)	2003/04	GWS, WIN	MC	DY	G, F	164 DY	2645	631 ± 109				$, irrigated

49	Donoughmore, IE	Mishurov & Kiely (2010)	2004-2008	YR	EC	10 Hz	G, C, F	-28 MN	503 DY MN	86 ± 9 YR				F: SL, MF
50	Easter Bush, GB	Soussana *et al.* (2007)	2002-2004	YR	CH4: SF6, N2O: MC, TDL		G, C, F	10 YR	41 YR	26 ± 15 YR	686 YR	820 YR	753 ± 67 YR	†
51	Carlow, IE	Soussana *et al.* (2007)	2002-2004	YR	CH4: SF6, N2O: MC, TDL		G, C, F	1 YR	20 YR	11 ± 10 YR	5357 YR	703 YR	619 ± 84 YR	†
52	Lelystad, NL	Soussana *et al.* (2007)	2002-2004	YR	CH4: SF6, N2O: MC, TDL		G, C, F	50 YR	122 YR	86 ± 36 YR	586 YR	1456 YR	1021 ± 435 YR	†
53	Dischma Valley, CH	Merbold *et al.* (2013)	2010, 2011 (Nov – Apr)	WIN	SP	WK	G, C, F	3 MN	70 MN	36 WIN	-13 MN	-5 MN	-8 WIN	¶

¶ Methane emissions from enteric fermentation not included.

* Measurements were only carried out during a 14d time span after grazing.

† CH_4 fluxes include only enteric fermentation measured either using the SF_6 tracer technique or estimated using a CH_4 emission rate (see equation 1 in Soussana *et al.* (2007)).

Measurements in May, August and October.

$ Measurements were only carried during a 14-17d time span after two fertilization events in January and September. Mean: per fertilizer application.

& Minimum value: cattle-free pasture; maximum value: cattle confined to flux footprint area.

§ Dataset: 3d. Measurements were carried out between 10a.m. and 4p.m. GMT. Maximum: manure perimeter.

** The study investigated fluxes during six comparison periods, covering the months of March – July. Each comparison period lasted between 2 and 28d.

Abbreviations: ID, identification number for text references; Sites: E, extensive management; I, intensive management; LCRC, Michigan State Univ. Lake City AgBioResearch Center; MUDF4, Massey Univ. Nº 4 Dairy Farm; Method: AC, automatic chambers; EC, eddy covariance method; EST, estimated (see †); MC, manual chambers; SF6, SF6 tracer technique; SP, snow profile method; TDL, tunable diode laser method; Sampling frequency or averaging time: CP, mean over comparison period, see notes; DS, dry season mean; DY, daily; GWS, growing season; GZS, grazing season; MN, monthly; MS, multi-site mean; SEM, standard error of monthly or yearly mean; SM, single measurement mean from three chambers; SUM, summer; WIN, winter; WK, weekly; WW, mean over two weeks; YR, year-round or yearly mean; Management: C, cutting; F, fertilization; (F), amount of fertilizer unknown; G, grazing; Notes: MA, manure; MF, mineral fertilizer; PK, synthetic P and K fertilizers; SL, slurry;

Table 6 N_2O emission factors for fertilized sites with known amount of applied fertilizer in this study. Cumulative N_2O emissions for each site were calculated from complete time series after gap-filling via the running median method. For sites with measurements spanning over multiple years, the site mean was calculated as the mean of the respective annual values ± the standard error of the mean. The site CH-AWS was not included in this table because the amount of applied fertilizer was unknown.

Site	Year	Available data (days)	Cumulative N_2O emissions (kg N ha^{-1})	Organic fertilizer input (kg N ha^{-1})	Mineral fertilizer input (kg N ha^{-1})	Emission factor (%)
CH-FRU-I	2010/11	35	1.02	159	0	0.6
CH-FRU-E	2010/11	35	0.83	33	0	2.5
AT-NEU	2010	215	0.19	341	0	0.1
	2011	296	0.64	341	0	0.2
	site mean	256 ± 41	0.41 ± 0.22	341	0	0.1 ± 0.1
FR-LAQ-I	2008	185	1.97	0	214	0.9
	2009	103	5.28	0	214	2.5
	2010	258	1.02	0	214	0.5
	2011	195	1.46	0	214	0.7
	2012	198	1.21	0	214	0.6
	2013	184	0.57	0	214	0.3
	site mean	187 ± 20	1.92 ± 0.70	0	214	0.9 ± 0.8
DE-GAP	2012	37	0.51	61	0	0.8
	2013	55	0.57	122	0	0.5
	site mean	46 ± 9	0.54 ± 0.03	92 ± 31	0	0.7 ± 0.2
DE-FEN-I	2012	128	2.16	312	0	0.7
	2013	202	1.21	365	0	0.3
	2014	296	0.76	243	0	0.3
	site mean	209 ± 49	1.38 ± 0.41	307 ± 35	0	0.4 ± 0.1
DE-FEN-E	2012	127	0.83	61	0	1.4
	2013	236	1.08	122	0	0.9
	2014	296	0.76	61	0	1.2
	site mean	220 ± 49	0.89 ± 0.10	81 ± 20	0	1.2 ± 0.1
CH-CHA-I1	2010/11	38	5.22	190	0	2.7
CH-CHA-I2	2010/11	38	7.89	219	0	3.6
CH-CHA	2012	328	24.70	269	17	8.6
	2013	360	2.55	232	0	1.1
	site mean	344 ± 16	13.62 ± 11.07	251 ± 19	9 ± 9	4.9 ± 2.2
Mean across sites ± SEM						**1.8 ± 0.5**

Figure captions

Figure 1 Time periods, measurement techniques and number of available days with measurements of CO_2, N_2O and CH_4 fluxes. The order of sites from top to bottom follows the elevational gradient, with the highest site listed first. Numbers in brackets refer to the number of chamber replicates. See Table 1 for site name abbreviations. AC, automatic chambers; EC, eddy covariance; MC, manual chambers.

Figure 2 Boxplots of measured, non-gapfilled CO_2, N_2O, and CH_4 fluxes. Note the axis break in the N_2O and CH_4 panels. The order of the sites from left to right follows the elevational gradient, starting with the highest elevation site on the left. Colored boxes show the interquartile range (IQR = Q3 – Q1) of measured data at the respective site, black solid lines inside the colored boxes correspond to the median value. Whiskers extending from the boxes show the range of non-outlier data, defined as Q3 + 1.5 IQR for the upper limit, and as Q1 – 1.5 IQR for the lower limit. Data points beyond the whiskers are considered outliers and plotted as individual points. Colors show the season of the year: spring (March – May, green), summer (June – August, red), autumn (September – November, orange) and winter (December – February, blue). See Table 1 for site name abbreviations.

Figure 3 Hexbin plots of measured, non-gapfilled N_2O fluxes in twelve combined classes of soil temperature and water-filled pore space. Prior to analysis, daily average values of all three variables at each site were converted to an index in the range 0 to 100%, based on the cumulative empirical probability density function (cePDF) of each variable at each site, i.e. the index corresponds with the percentile value of the original measurements in relation to the site-specific cePDF. Colored (red-to-blue gradient) hexbins show the percentile N_2O flux in the respective combined class, while white hexbins show the lack of measurements. (a) Aggregated N_2O flux

percentile values for each site, showing the median of each percentile flux within each aggregation unit. Black dots in hexbins indicate that the respective median percentile flux corresponds to N_2O uptake, while the absence of black dots indicates N_2O emission. The order of sites from left to right and from top to bottom follows the elevational gradient, with results for the highest site shown at the top left. (b) Aggregated N_2O flux percentile values across all sites, calculated as the median of site-level hexbin values in (a), when data from at least two sites were available for a specific combined class. Additional information on percentile distributions at each site is given in Table 2. See Table 1 for site name abbreviations.

Figure 4 Hexbin plots of measured, non-gapfilled CH_4 fluxes in twelve combined classes of soil temperature and water-filled pore space. Prior to analysis, daily average values of all three variables at each site were converted to an index in the range 0 to 100%, based on the cumulative empirical probability density function (cePDF) of each variable at each site, i.e. the index corresponds with the percentile value of the original measurements in relation to the site-specific cePDF. Colored (red-to-blue gradient) hexbins show the percentile CH_4 flux in the respective combined class, while white hexbins show the lack of measurements. The site FR-LAQ-I was not included for this analysis due to the presence of cattle in the flux footprint. (a) Aggregated CH_4 flux percentile values for each site, showing the median of each percentile flux within each aggregation unit. Black dots in hexbins indicate that the respective median percentile flux corresponds to CH_4 uptake, while the absence of black dots indicates CH_4 emission. The order of sites from left to right and from top to bottom follows the elevational gradient, with results for the highest site shown at the top left. (b) Aggregated CH_4 flux percentile values across all sites, calculated as the median of site-level hexbin values in (a), when data from at least two sites were

available for a specific combined class. Additional information on percentile distributions at each site is given in Table 2. See Table 1 for site name abbreviations.

Figure 5 Linear regression analysis of average percentile fluxes across sites in classes of (a) soil temperature and (b) water-filled pore space, based on the respective hexbin classes shown in Figure 3b for N_2O fluxes and Figure 4b for CH_4 fluxes. The shaded area refers to the standard deviation of average percentile fluxes in the respective soil temperature or water-filled pore space class. Percentile distributions for each site along with percentile ranges across all sites in this analysis are given in Table 2.

Figure 6 Explained variance (r^2) from a multiple linear regression analysis of measured, non-gapfilled, log-transformed N_2O daily average fluxes in dependence of soil temperature (TS) and water-filled pore space (WFPS), performed in a moving time window of 35 days. Results were calculated if a minimum of 13 days of data were available within a specific time window. Blue markers denote days with snow cover, vertical lines show management events (dotted: cutting, dashed: fertilization), grey horizontal bars show the regression time window for the respective r^2. Red dots mark time periods where the regression was significant at $P < 0.05$. See Table 1 for site name abbreviations.

Figure 7 Explained variance (r^2) from a multiple linear regression analysis of measured, non-gapfilled, log-transformed CH_4 daily average fluxes in dependence of soil temperature (TS) and water-filled pore space (WFPS), performed in a moving time window of 35 days. Results were calculated if a minimum of 13 days of data were available within a specific time window. Blue markers denote days with snow cover, vertical lines show management events (dotted: cutting, dashed: fertilization), grey horizontal bars show the regression time window for the respective r^2. Red dots mark time periods where the regression was significant at $P < 0.05$. Note that no CH_4

measurements were available for FR-LAQ-E and that cattle were present in the flux footprint for CH_4 measurements at FR-LAQ-I. See Table 1 for site name abbreviations.

Figure 8 Measured, non-gapfilled N_2O fluxes at three sites during each fertilizer application of liquid slurry. Left panel: daily average fluxes for seven pre-fertilization days (-7 to -1), the day of application (0) and seven post-fertilization days (1 to 7), expressed in μg m^{-2} h^{-1}. Right panel: absolute ratio of measured fluxes to the 7-day pre-fertilization average for each management event. See Table 1 for site name abbreviations.

Figure 9 Measured, non-gapfilled CH_4 fluxes at three sites during each fertilizer application of liquid slurry. Left panel: daily average fluxes for seven pre-fertilization days (-7 to -1), the day of application (0) and seven post-fertilization days (1 to 7), expressed in μg m^{-2} h^{-1}. Right panel: absolute ratio of measured fluxes to the 7-day pre-fertilization average for each management event. See Table 1 for site name abbreviations.