



Upscaling of soil methane fluxes from topographic attributes derived from a digital elevation model in a cold temperate mountain forest

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Abstract. Forest soils are generally considered a sink for atmospheric methane (CH₄), but their uptake rate can vary considerably in space and time. This study aimed to investigate the temporal patterns of spatially distributed soil CH₄ fluxes in a topographically complex cold-temperate mountain forest in central Japan. Soil CH₄ fluxes were measured nine times during the snow-free season at multiple locations within a 40-ha area in a forested watershed. A machine-learning approach was developed to upscale measured upland fluxes to the landscape scale, using topographic attributes derived from a digital elevation model and vegetation types. Upland soils were a sink of CH₄, while small wetland patches emitted CH₄ consistently throughout the study period. The accuracy of predicted upland fluxes varied seasonally, with the highest model performance observed in early autumn ($R^2 = 0.67$) and the lowest in mid-summer ($R^2 = 0.28$). Within the study landscape, predicted upland CH₄ fluxes varied significantly across topographic positions, with greater uptake on ridges and slopes than on the plain and foot slopes. Predicted upland CH₄ fluxes ranged from -0.35 to -0.60 g CH₄ ha⁻¹ h⁻¹ in spring, -0.41 to -1.25 g CH₄ ha⁻¹ h⁻¹ in summer, and -0.50 to -0.89 g CH₄ ha⁻¹ h⁻¹ in autumn. Seasonal upland fluxes were highly correlated with the 20-day antecedent precipitation index ($R^2 = 0.71$), revealing the importance of seasonal moisture conditions in regulating CH₄ flux dynamics. This study highlighted the importance of topography in controlling the soil CH₄ fluxes and the efficiency of remote sensing and machine learning approaches in scaling field measurements to the landscape level, enabling visualization of spatial patterns of fluxes across the landscape over time.

1 Introduction

30 Methane (CH₄), the second most important anthropogenic greenhouse gas, contributes substantially to the anthropogenic radiative forcing and is responsible for approximately 0.5°C of current global warming compared to 1850 - 1900 (IPCC, 2023). Natural wetlands (149 Tg CH₄ yr⁻¹) and rice cultivation (30 Tg CH₄ yr⁻¹) are important sources of CH₄; in contrast, upland soils are considered a biological sink of atmospheric CH₄, with an estimated uptake of 25-45 Tg yr⁻¹, contributing 5-7% to the global CH₄ sink (Saunois et al., 2020). Among the upland ecosystems, forest soils account for approximately 60% of global soil CH₄ uptake (Dutaur and Verchot, 2007), and soil uptake rates are particularly high in Japanese mountainous forests due to their high porosity (Ishizuka et al., 2000). CH₄ uptake by forest soils is driven by methane-oxidizing bacteria in oxic soil layers,



whereas anaerobic environments such as wetland soils are usually dominated by methanogenic archaea producing CH₄ (Christiansen et al., 2016). CH₄ production can also occur in upland soils, either in deeper soil layers or in
40 microsites located in otherwise well-aerated soil layers, if anaerobic conditions prevail (Angel et al., 2012). Hence, CH₄ oxidation and production can occur simultaneously at the same location, determining the net flux.

Net soil CH₄ fluxes depend mainly on the soil air-filled porosity (AFP), which in turn depends on total porosity and soil water content. A high AFP enhances gas diffusion in soil and, consequently, microbial CH₄ oxidation (Kruse et al., 1996). Soil organic matter at the soil surface can act as a physical barrier to atmospheric CH₄
45 diffusion and reduce the CH₄ uptake rate (Yu et al., 2017). Conversely, carbon substrates released by the decomposition of soil organic matter can increase CH₄ oxidation activity either by directly stimulating the growth of methanotrophs or by promoting CH₄ production in anaerobic microsites and indirectly supporting the growth of methanotrophs (West and Schmidt, 1999). Additionally, soil nutrients can influence soil CH₄ fluxes by regulating the soil microbial community. The activity of methanotrophic microorganisms is affected by the
50 availability of inorganic nitrogen (Bodelier and Laanbroek, 2004). Although methanotrophic activity can be nitrogen-limited in forest soils (Veldkamp et al., 2013), increasing ammonium (NH₄⁺) concentration often reduces CH₄ uptake due to competitive inhibition by NH₄⁺ of the enzyme methane mono-oxygenase, which can oxidize both CH₄ and NH₄⁺. Nitrate (NO₃⁻) can also be a potent inhibitor of CH₄ oxidation in some soils (Mochizuki et al., 2012). Although temperature affects microbial activities, including methanogenesis and methanotrophy (Luo
55 et al., 2013; Praeg et al., 2017), CH₄ uptake is generally less sensitive to changes in soil temperature than in soil moisture (Epron et al., 2016).

Topography and vegetation cover can create a predictable distribution of soil moisture and nutrients across topographically complex landscapes (Jeong et al., 2017; Murphy et al., 2011). In Japan, forests cover 68% of the land, mostly in mountainous areas. Conifers account for 44% of the total forest area (Lundbäck et al., 2021;
60 Nakamura and Krestov, 2005). Topography is a critical determinant of soil hydrological conditions, from well-drained slopes to waterlogged riparian areas (Kaiser et al., 2018). Topography can also impact soil nutrient availability by altering leaf litter accumulation and the movement of soil nutrients (Osborne et al., 2017; Tateno and Takeda, 2003). The spatial distribution of trees, differences in species abundance across the landscape, and variation in litter chemistry often create heterogeneity in soil nitrogen cycling (Osborne et al., 2017). Furthermore,
65 differences in stem flow and throughfall related to differences in canopy structure between tree species can indirectly influence spatial patterns of soil moisture (Holwerda et al., 2006).

In situ chamber measurements have long been the dominant method for studying CH₄ fluxes in forests, providing insight into the processes that drive them (Brumme and Borken, 1999; Guckland et al., 2009; Itoh et al., 2009). Until recently, most studies reported spatially average flux values measured at several locations (Gomez et al.,
70 2016; Itoh et al., 2009). This method is acceptable for small patches of homogeneous landscapes, such as crops or single-species tree plantations in flat terrain. However, it is inappropriate for more complex landscapes, as the number of sampling points required to obtain an accurate spatially-averaged flux would increase considerably.

In complex terrains, measurement locations can be grouped into several distinct categories according to landforms (Courtois et al., 2018; Gomez et al., 2016; Itoh et al., 2009; Kagotani et al., 2001; Kaiser et al., 2018; Warner et al.,
75 et al., 2018), soil microtopographic features (Epron et al., 2016), vegetation characteristics (Guckland et al., 2009), or land uses (Jacinthé et al., 2015). However, as Vainio et al. (2021) pointed out, aggregation assumes spatial



homogeneity of fluxes within each category or requires a large number of sampling points to capture the spatial heterogeneity, and this approach ignores the spatially continuous nature of soil processes and their drivers.

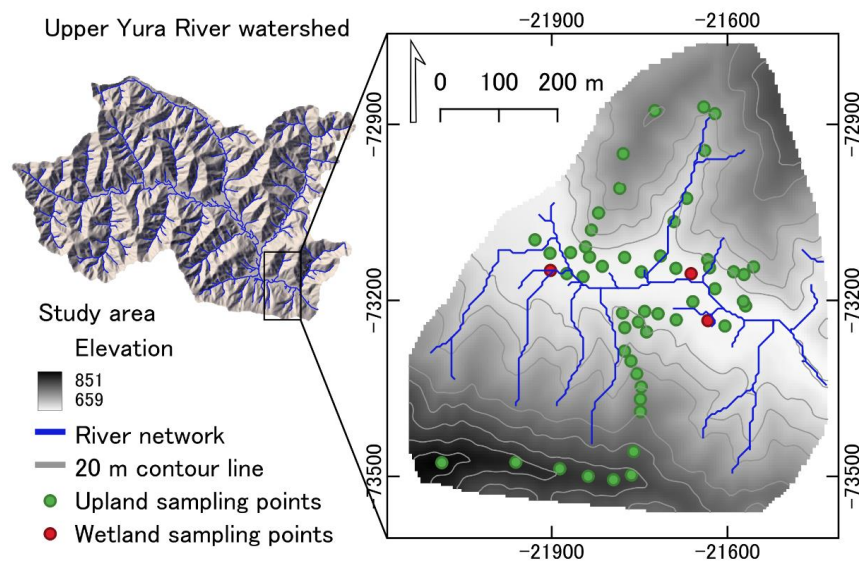
80 More recently, regressions with multiple landscape attributes derived from remote sensing-based maps were successfully applied to upscale CH₄ to a catchment scale (Kaiser et al., 2018). Recent studies conducted on a 12-ha forested watershed (Warner et al., 2019), a 10-ha boreal forest plot (Vainio et al., 2021), two northern peatland-forest-mosaic catchments of 4.5 km² and 7.9 km² respectively (Räsänen et al., 2021), and a 450-ha subarctic tundra (Virkkala et al., 2024) have demonstrated the effectiveness of machine-learning modeling approaches for upscaling CH₄ fluxes from remote sensing data.

85 This study aimed to assess temporal variations of soil CH₄ fluxes across a topographically complex landscape in a cold-temperate mountain forest in central Japan and to estimate soil CH₄ fluxes at the landscape scale. We measured soil CH₄ fluxes several times during the snow-free season at multiple locations within a 40-ha area in a forested watershed. We applied a random forest machine-learning approach in combination with terrain attributes from remotely sensed data, i.e., a digital elevation model (DEM), to upscale measured soil CH₄ fluxes to the
90 landscape level. We hypothesized that (1) terrain attributes related to water accumulation are reliable predictors of soil CH₄ fluxes, (2) predicted soil CH₄ fluxes vary within the landscape depending on topography (3) spatial patterns of uncertainties in predicted soil CH₄ fluxes vary seasonally due to a wet early summer influenced by the East Asian monsoon, and (4) seasonal variations of CH₄ flux at the landscape scale are explained by recent past precipitations.

95 **2 Materials and methods**

2.1 Description of the study site and experimental design

This study was conducted in the forested upper Yura River watershed (35.34 N; 135.76 E) located at the Ashiu Experimental Forest of Kyoto University in northeastern Kyoto Prefecture, Japan (Fig. 1). The mean annual temperature and precipitation were 10.3°C and 2,732 mm, respectively, between 2011 and 2020 and the ground
100 was covered by snow (2-3 m depth) from mid-December to mid-April (Epron et al., 2023). The study area is characterized by a cool-temperate monsoon climate, with a very humid early summer (520 mm in June and July on average between 2011 and 2020) and occasionally heavy precipitation caused by typhoons in late summer. The soils in the study area are classified as brown forest soils according to the Classification of Forest Soils in Japan, with a relatively thick brownish-black A horizon with a crumb structure and a brown B horizon with a blocky
105 structure (Hirai et al., 1988; Ueda et al., 1993). The forest is primarily dominated by *Cryptomeria japonica* D. Don (Japanese cedar, 73% of the basal area in four 1-ha census plots), mixed with more than 50 broadleaved species (Ishihara et al., 2011).



110 **Figure 1: Map of the upper Yura River watershed with an enlargement of the 40.2 ha study area. The green dots represent the 52 flux measurement locations on unsaturated soils (upland) and the red dots the 3 measurement locations on waterlogged wetlands.**

The study site covered an area of 40.2 hectares (Fig. 1) and included a variety of landscapes, ranging from ridges to waterlogged wetlands. It has a mountainous topography with an elevation between 650 and 850 m and slopes that vary from gentle to steep. The site was classified into uplands (including ridges, slopes, foot slopes and plains as topographic positions where the soil is almost always unsaturated), wetlands (small patches with water-saturated soil in the valley), and rivers, accounting for approximately 94%, 1%, and 5% of the total study area, respectively. Soil CH₄ fluxes were measured on 52 sampling points in upland areas, distributed across the four topographic positions, to optimize the representation of topographic and vegetation variations that can influence soil properties and, consequently, soil CH₄ fluxes. We also measured soil CH₄ fluxes in three small wetland patches (one sampling point in each). Unfortunately, the machine learning model we developed (see below) was unable to accurately predict fluxes across the landscape when wetland measurements were included in the training dataset. We recorded the positions of all sampling locations using a portable GPS tracker (Garmin, eTrex® Touch 35) with an accuracy of less than 5 m.

125 **2.2 Flux measurements**

Soil CH₄ fluxes were measured using a static, non-steady-state, non-flow-through system composed of a dark acrylic chamber (20 cm diameter and 12.5 cm height) connected to a cavity-enhanced absorption spectroscopy gas analyzer (Li 7810, Licor; Lincoln, USA) with two PTFE tubes, each 1.8 m long and 4 mm in inner diameter. One week before the first measurements, a 20 cm diameter, 9 cm tall PVC collar was inserted approximately 5 cm into the soil at each of the sampling point. Flux from each collar was measured on nine occasions in 2023: in



early spring after snowmelt (4/27), mid-spring (5/12), late spring (5/31), early summer (7/06), mid-summer (7/26), late summer (9/04), early autumn (10/07), mid-autumn (11/07), and late autumn (11/30).

To measure soil CH₄ flux, the chamber was placed on the collar, and changes in CH₄ and CO₂ concentrations inside were recorded for 4 minutes at a frequency of 1 Hz. The slope of the linear regression of CH₄ concentration over time was used to calculate the soil CH₄ flux:

$$F_{CH_4} = \frac{\Delta[CH_4]}{\Delta t} \times \frac{V \times P}{A \times R \times T}$$

where F_{CH_4} is the soil CH₄ flux, $\frac{\Delta[CH_4]}{\Delta t}$ is the slope of the linear change in CH₄ concentrations over time, V is the system volume (chamber, collar above the ground, tubes, and analyzer), A is the soil area covered by the collar, and R is the ideal gas constant (8.314 J K⁻¹ mol⁻¹). A constant value of 93,525 Pa for an elevation of 650 m was used for the atmospheric pressure (P). The slope was calculated over 90 seconds following Epron et al. (2023). The R^2 of the linear variation of CH₄ concentration was less than 0.9 for a single measurement, and for this measurement, the R^2 of the linear variation of CO₂ concentration was 0.99, indicating that the low R^2 for CH₄ was due to the near-zero CH₄ flux and not to an erroneous measurement.

2.3 Topographic characterization

To characterize and process the terrain attributes related to soil CH₄ fluxes, we used a 0.5 m mesh digital elevation model (DEM) based on airborne laser surveys conducted throughout the upper Yura River watershed in 2012 by the Ashiu Experimental Forest staff. The DEM was further processed and conditioned into a 5 m mesh DEM image according to the GPS tracker's accuracy (less than ≤ 5 m) that was used to locate each collar position, enabling us to identify the corresponding pixels on the terrain attribute grids. We derived several topographic attributes from the DEM using SAGA Next Generation in QGIS (v3.34.5-Prizren). The calculated attributes included aspect, slope, profile curvature (PrC), topographic position index (TPI), topographic wetness index (TWI), and vertical distance to channel network (VDCN). Slope and TPI were used to partition the landscape into ridges, slopes, foot slopes and the plain.

Aspect, slope, and profile curvature were calculated following the 9-parameter 2nd order polynom method (Zevenbergen and Thorne, 1987). Aspect, a circular variable, was transformed into a linear variable by calculating the cosine of the aspect values, resulting in a range from -1 (south) to 1 (north). Negative values of profile curvature indicate a convex surface where the flow of water accelerates as it moves downslope; in contrast, positive values suggest a concave surface where the flow slows down (Pachepsky et al., 2001).

TWI was calculated using the equation $TWI = \ln(CA/slope)$, where CA refers to the catchment area. We derived CA from a filled DEM using the multiple flow direction algorithm (Freeman, 1991; Wang and Liu, 2006). A filled DEM is a hydrologically corrected elevation model in which erroneous surface depressions have been removed to avoid biases in water accumulation and flow direction.

TPI describes the relative position of a location within a landscape, indicating whether it is on a ridge, slope, or valley based on the elevation compared to the surrounding terrain at a specified radius (Ågren et al., 2014).

Positive values indicate ridges; negative values indicate depressions, and zero or near-zero values indicate slopes or flat areas. TPI was calculated at the center of circular areas of 30 m radius using the unfilled DEM.

VDCN was calculated as the elevation difference between each grid cell and the baseline of the nearest stream channel. This parameter serves as a proxy for groundwater depth, with lower VDCN values typically



170 corresponding to areas with shallower groundwater and higher water tables, and higher values indicating deeper groundwater levels often found in upland positions (Bock and Köthe, 2008).

2.4 Vegetation classification

175 Tree inventory was conducted during the flux measurement period to classify the vegetation surrounding the flux measurement points. A circular plot with a 10-meter radius was established, centered at each flux measurement point. Within the plot, all trees were identified at the species level, and their diameter at breast height (DBH) was measured. Vegetation types were classified based on the proportional contribution of coniferous and broadleaved trees to the plot basal area, the sum of cross-sectional areas at breast height of all tree trunks in each plot. Three types were defined: coniferous when the proportional contribution of coniferous trees was higher than 0.75, broadleaf when it was lower than 0.25, or mixed (comprising both coniferous and broadleaf).

2.5 Soil sampling and analysis

180 After completing the flux measurements, soil cores were collected using a sampling cylinder at 0-10 cm depth near the flux measurement points. Samples were sieved at 2 mm and separated into stones and fine earth. The fresh weight of the fine earth fraction was measured before being air-dried. Bulk density of this fraction was determined as the ratio of oven-dried soil (subsample dried at 105°C) to the soil volume. Soil texture was analyzed using the micro-pipette method, following Burt et al. (1993). Total soil carbon (C) and nitrogen (N) contents were measured using a Macro Corder JM 1000CN (J-SCIENCE LAB Co., Ltd., Japan). The soil pH was measured in 185 a suspension (10 g of soil in 25 ml distilled H₂O) after shaking for 1 hour.

2.6 Climatic data

190 Air temperature and rainfall were measured every 10 minutes at a nearby weather station operated by the Field Science Education and Research Centre of Kyoto University. The antecedent precipitation index (API), an indicator of soil moisture conditions, was calculated using the following equation:

$$API_n = \sum_{t=1}^n P_t \times k^t$$

where, P_t is the precipitation during day t , k is the recession coefficient, and n is the number of antecedent days. The parameter k accounts for the water removed from the soil by evapotranspiration and drainage.

2.7 Modeling

195 In this study, modeling was conducted independently for each of the nine measurement dates. We applied quantile regression forests (QRF) introduced by Meinshausen (2006), an extension of the random forests (RF) algorithm. RF is an ensemble learning method that builds a set of regression trees, and the final prediction is the average of all the regression trees, which are evaluated using out-of-bag cross-validation (Breiman, 2001). The QRF algorithm estimates the full conditional distribution of the response variable as a function of its predictors, not just 200 the mean as with the original RF algorithm. Therefore, it is possible to extract the prediction interval for each pixel across the landscape for each measurement period. We followed three steps to develop models for predicting soil CH₄ fluxes at each measurement period. We used the six topographic features (aspect, slope, PrC, TPI, TWI, and VDCN) and the three vegetation types listed above as predictors. Before applying QRFs, we eliminated the less important variables and identified the most relevant predictors for each measurement date, using a variable



205 selection algorithm for random forest models proposed by Genuer et al. (2010) and implemented in the “VSURF”
package for R (Genuer et al., 2015). This approach systematically uses a repeated cross-validation procedure to
rank variables by their importance index and iteratively eliminates the least informative ones to minimize model
error. The result is a refined subset of predictors that enhances model interpretation and predictive performance.
This predictor reduction approach has been previously used for mapping CH₄ fluxes (Räsänen et al., 2021; Warner
210 et al., 2019) and soil properties (Jeong et al., 2017; Miller et al., 2015).
After selecting the relevant predictor variables, the QRF models were trained to predict CH₄ fluxes for each of the
nine measurement dates using the R-packages “caret” (Kuhn and Johnson, 2013) and “quantregForest”
(Meinshausen, 2017). The mtry parameter, which determines the number of randomly selected predictor variables
at each node, was tested from 2 to n-1 (n being the total number of predictors) using leave-one-out cross-validation
215 to minimize prediction error and maximize the variance explained by the model. The ntree parameter was set to
500, ensuring the model constructed an ensemble of 500 decision trees. Furthermore, we calculated the variable's
importance scores using the “vip” R-package (Greenwell and Boehmke, 2020). For each of the nine measurement
dates, model accuracy was evaluated based on the root mean square error (RMSE) and coefficient of determination
(R²). The output of the QRF was a set of conditional prediction distributions of CH₄ fluxes for each landscape
220 pixel and measurement dates. Because these prediction distributions were often not normally distributed, the
medians of the conditional prediction distributions at each pixel were used as the final predictions, and the
interquartile ranges of these distributions were used to quantify the uncertainty in the predictions (Warner et al.,
2019). Prediction uncertainties were expressed as a percentage (i.e., interquartile range of the conditional
prediction distribution divided by the median).

225 2.8 Statistical analysis

We used analysis of variance (ANOVA) to test the differences in soil properties across the topographic positions
and vegetation types. A linear mixed-effect model (LMM) was used to test the effects of topographic positions,
vegetation types, and measurement dates (fixed effects) on measured CH₄ fluxes, where sampling points (collar
ID) were included as a random effect. Similarly, LMM was used to test the relationship between the predicted and
230 measured fluxes (fixed effect), with flux measurement dates as a random effect. The root mean square error
(RMSE) was used to evaluate model performance at each date, and the marginal and conditional coefficients of
the determinant (R_m^2 and R_c^2) were used to determine the strength of the relationship between the predicted and
measured fluxes. LMM was carried out using the ‘lmerTest’ package (Bates et al., 2015; Kuznetsova et al., 2017),
and R_m^2 and R_c^2 were calculated using the ‘MUMIn’ package (Bartoń, 2010). To test the effects of topographic
235 positions and measurement dates on predicted CH₄ fluxes while accounting for spatial autocorrelation, we also
used a linear mixed-effect model. Topographic positions and measurement dates were included in the model as
fixed effects, and pixel ID as a random effect. To eliminate spatial autocorrelation among residuals, we
incorporated an exponential spatial correlation structure based on each pixel coordinate nested within each
measurement date. This was performed using the ‘nlme’ package (Pinheiro et al., 1999). The semi-variogram of
240 the residuals confirmed that the residuals were not spatially correlated. A pairwise comparison across the
topographic positions within each measurement date was performed using the ‘emmeans’ package (Lenth, 2017).
Linear regression models were used to examine the relationship between scaled soil CH₄ fluxes and API. The
recession coefficient (k) and the number of antecedent days (n) were not fixed a priori but optimized to maximize
R² while ensuring the best distribution of the residuals, allowing parameters k and n to vary iteratively from 0.6



245 to 0.9 with an increment of 0.01 and from 0 to 30 with an increment of 0.01, respectively. Using a more complex bivariate model with an exponential function of air temperature did not improve the quality of the fit and returned Q_{10} values that were not significantly different from 1, as previously reported (Epron et al., 2016). Calculations, modelling, and statistical analyses were performed using the R statistical programming environment (R Core Team, 2024).

250 **3 Results**

3.1 Variations in soil properties, vegetation, and methane fluxes across the landscape

Topographic positions influenced several soil properties, whereas vegetation type and its interaction with positions had no significant effects (Table 1). Overall, the bulk density of the fine earth fraction was relatively low due to the presence of stones, highest in the plain ($0.48 \pm 0.05 \text{ g cm}^{-3}$, mean \pm SE and significantly lowest in the ridge
255 ($0.26 \pm 0.04 \text{ g cm}^{-3}$). Soil pH differed significantly across topographic positions ($p < 0.001$), with more acidic conditions observed at higher elevations (ridge: 4.0 ± 0.14) compared to the plain (5.0 ± 0.12). Similarly, total carbon (C) and total nitrogen contents (N) were significantly higher on the ridges ($16.7 \pm 2.2\%$ C and $0.8 \pm 0.10\%$ N) and lower in the plain ($3.9 \pm 0.60\%$ C and $0.3 \pm 0.04\%$ N).

In contrast, the soil texture of the fine earth fraction (clay, silt, and sand) did not vary significantly with topographic
260 positions. Vegetation types varied depending on topographic positions, where broadleaved species dominated in the lower positions (77.8% in the plain and 56.3% in foot slopes), while conifers and their mixtures with broadleaved species dominated the ridges and slopes (Table A1).

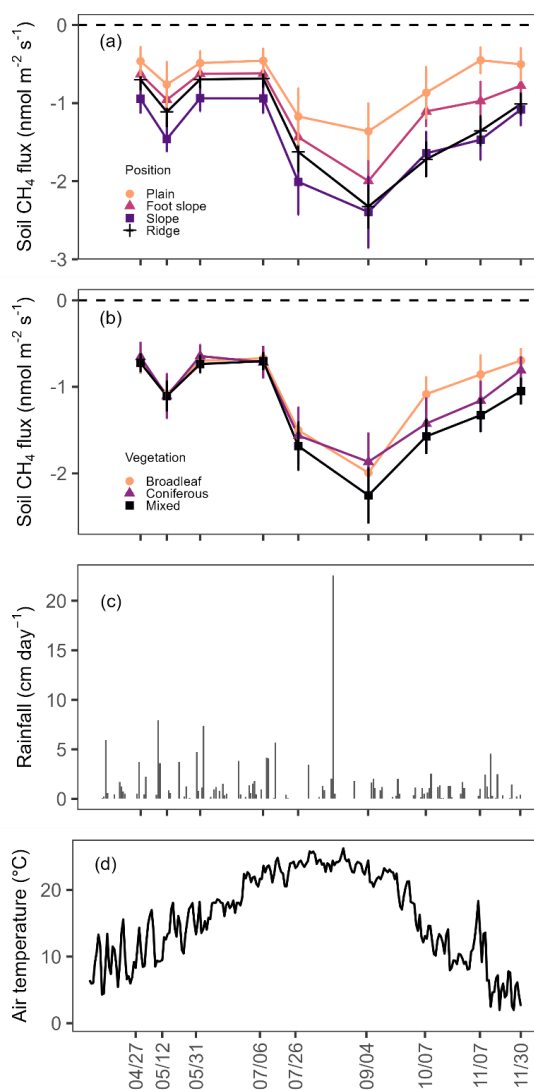
We observed that upland soils consistently uptake CH_4 (negative fluxes, Fig. 2a, b), while soils in the three small wetland patches emitted CH_4 (positive flux, Fig. A1). In the upland areas, the linear mixed-effect model (LMM)
265 indicated that topographic positions ($p = 0.17$) and vegetation types ($p = 0.83$) individually had no significant effects on soil CH_4 fluxes (Fig. 2a, b; Table A2). However, all upland topographic positions and vegetation types showed the same distinct significant variation in CH_4 fluxes across the measurement dates ($p < 0.001$), which was consistent with the seasonal patterns of rainfall and air temperature (Fig. 2; Table A2). Although two-way interactions among positions, vegetation types, and measurement dates were not significant, their three-way interaction was (Table A2). We also found that mean CH_4 fluxes from upland areas were significantly correlated
270 with soil pH ($r = 0.32$; $p < 0.05$, Table A3), while they were not significantly correlated with soil C, N, or bulk density.



275 **Table 1. Soil physical and chemical properties (mean ± standard error) according to topographic positions and vegetation types. Different lowercase letters indicate significant differences between topographic positions and vegetation types ($p < 0.05$). The p-values from two-way ANOVA are shown in the last rows. The number of independent replicates in each factor level is indicated in the first column. Significant differences between fertilization levels are indicated by different lowercase letters.**

Factors	Bulk density (g cm ⁻³)	Clay %	Silt %	Sand %	pH	Total carbon (%)	Total nitrogen (%)
Position:							
Plain (n = 9)	0.48 ± 0.05 a	10 ± 2	28 ± 3	63 ± 5	5.0 ± 0.12 a	3.9 ± 0.60 a	0.3 ± 0.04 a
Foot slope (n = 16)	0.34 ± 0.04 ab	9 ± 2	31 ± 3	60 ± 5	4.5 ± 0.08 b	7.9 ± 0.98 ab	0.5 ± 0.05 a
Slope (n = 14)	0.28 ± 0.03 b	9 ± 1	28 ± 2	63 ± 3	4.3 ± 0.06 bc	10.4 ± 1.50 b	0.6 ± 0.08 ab
Ridge (n = 13)	0.26 ± 0.04 b	9 ± 2	23 ± 4	68 ± 4	4.0 ± 0.14 c	16.7 ± 2.2 c	0.8 ± 0.10 b
Vegetation:							
Broadleaved (n = 19)	0.38 ± 0.04	10 ± 2	29 ± 3	61 ± 4	4.7 ± 0.10	6.8 ± 0.98	0.4 ± 0.05
Coniferous (n = 11)	0.32 ± 0.04	7 ± 1	27 ± 4	66 ± 5	4.3 ± 0.13	11.1 ± 2.37	0.6 ± 0.11
Mixed (n = 22)	0.28 ± 0.03	9 ± 1	26 ± 2	64 ± 3	4.2 ± 0.09	12.4 ± 1.59	0.6 ± 0.07
ANOVA results:							
Position	p < 0.01	p = 0.97	p = 0.43	p = 0.6	p < 0.001	p < 0.001	p < 0.01
Vegetation	p = 0.93	p = 0.37	p = 0.99	p = 0.89	p = 0.89	p = 0.97	p = 0.95
Position × Vegetation	p = 0.45	p = 0.51	p = 0.29	p = 0.21	p = 0.72	p = 0.68	p = 0.59

280



285 **Figure 2: Seasonal variations in soil CH₄ fluxes (mean ± standard error) according to (a) topographic positions (n = 9 for the plain, 16 for foot slopes, 14 for slopes, and 13 for ridges), (b) vegetation types for upland measurement locations (n = 19 for broadleaved, 11 for coniferous, and 22 for mixed), (c) daily precipitation, and (d) daily mean air temperature from April to November in 2023.**

3.2 Selected variables and performance of the upland CH₄ flux models

290 The topographic position index (TPI) was consistently selected in all seasons, with high importance scores, ranging from 0.51 to 0.90, depending on the measurement dates (Table 2). The topographic wetness index (TWI) was selected for most measurement dates, except two, where the vertical distance to the channel network (VDCN) was selected instead. TWI importance scores were high in early spring (0.64), late spring (0.61), and mid-summer



(0.63). VDCN and profile curvature (PrC) were occasionally selected along with TPI and TWI. VDCN showed moderate importance scores, contributing mostly in mid-spring (0.67) and early autumn (0.57). PrC, although less consistently selected, played a role in specific seasons, particularly early spring (0.55) and mid-autumn (0.51).
 295 Vegetation type was never selected in any season.

Table 2. Selected variables for each measurement date, along with the R^2 and root mean square error (RMSE) values to evaluate the accuracy of the quantile regression forests (QRFs) model. Importance scores of the selected variables are shown in parentheses, indicating their contribution to predicting soil CH_4 fluxes.

Measurement dates	Selected variables	R^2	RMSE ($\text{nmol m}^{-2} \text{s}^{-1}$)
2023/04/27	TWI (0.64), TPI (0.63), PrC (0.55)	0.48	0.53
2023/05/12	TPI (0.80), VDCN (0.67)	0.31	0.82
2023/05/31	TWI (0.61), TPI (0.54), VDCN (0.53)	0.46	0.47
2023/07/06	TWI (0.52), TPI (0.58)	0.28	0.51
2023/07/26	TWI (0.63), TPI (0.57), VDCN (0.47)	0.30	1.07
2023/09/04	TWI (0.51), TPI (0.71), VDCN (0.35)	0.43	1.15
2023/10/07	TPI (0.87), VDCN (0.57)	0.67	0.81
2023/11/07	TWI (0.24), TPI (0.90), PrC (0.51)	0.61	0.68
2023/11/30	TWI (0.49), TPI (0.52), VDCN (0.41)	0.44	0.57

300

Model accuracy showed seasonal variation, with the highest obtained in early autumn ($R^2 = 0.67$; $\text{RMSE} = 0.81 \text{ nmol m}^{-2} \text{ s}^{-1}$) and the lowest in early wet summer ($R^2 = 0.28$; $\text{RMSE} = 0.51 \text{ nmol m}^{-2} \text{ s}^{-1}$; Table 2). The relationship between measured and predicted fluxes for each measurement date showed that estimated fluxes were close to the observed fluxes (Fig. 3a-i).

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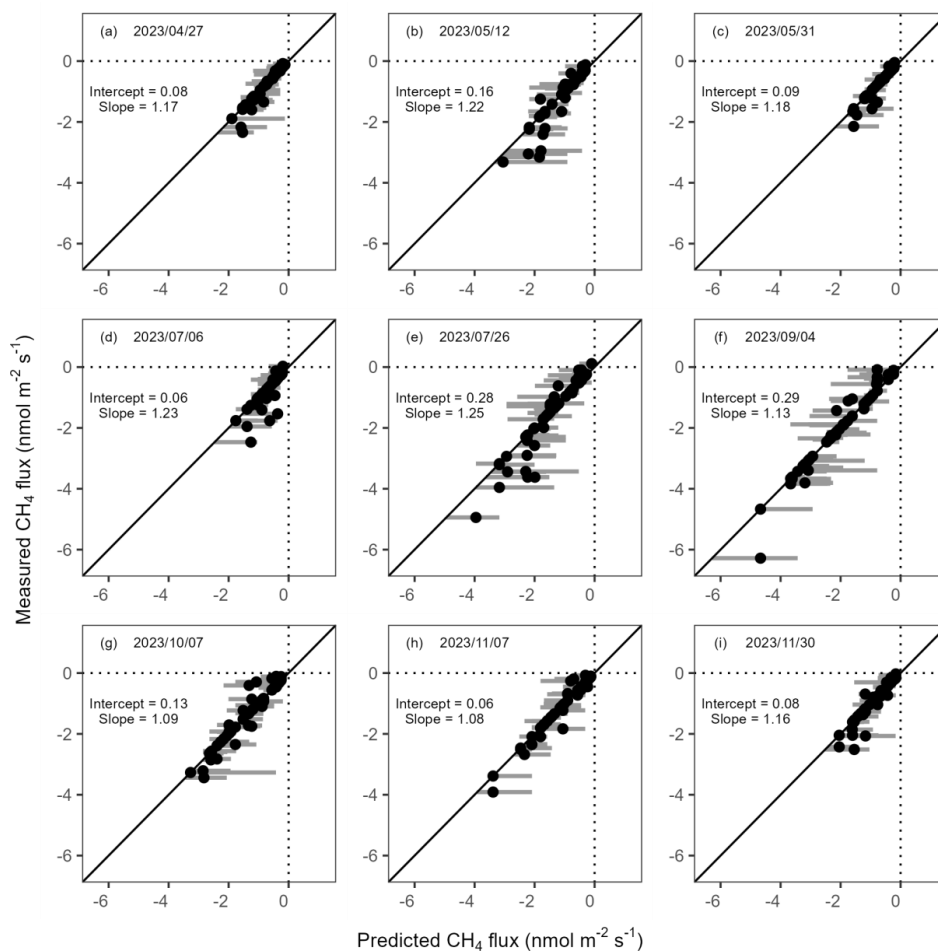


Figure 3: Comparison of predicted (median of the quartile predictions from QRFs) and measured CH₄ fluxes for each measurement date. Vertical bars indicate the interquartile ranges of the prediction distribution. Intercepts and slopes are estimated using a linear mixed-effect model with measurement dates as a random effect (full statistics are shown in Table A4).

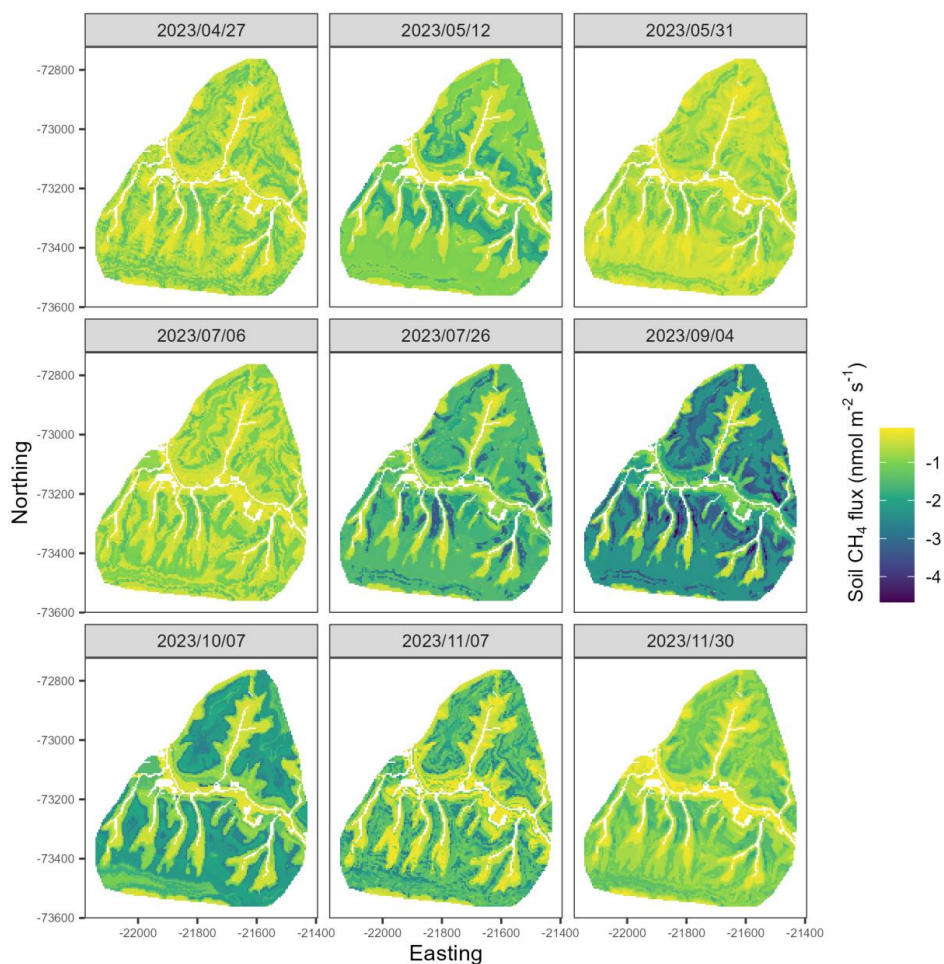
310

Overall, the slope of the relationship between measured and predicted fluxes (fixed effects) was not significantly different from 1 and was similar at all dates. The marginal (R^2_m) and conditional (R^2_c) coefficients of determination were 0.93 and 0.94, respectively, highlighting the consistency of the prediction for all measurement dates (linear mixed model, Table A4).

315

3.3 Predicted upland soil CH₄ fluxes

Predicted median CH₄ fluxes showed significant spatial heterogeneity and temporal variability across the landscape (Fig. 4; Table A6).



320

Figure 4: Maps of predicted soil CH₄ fluxes at each pixel of the study area for each measurement date. Values represent the median of the conditional prediction distribution for each pixel.

325 Spatial trends were consistent across seasons, with the highest net CH₄ uptake observed on ridges and steepest parts of the slopes and decreasing toward the foot slopes near streams and the flat plain (Fig. 5; Table A6).

In early (April 27) and late spring (May 31), CH₄ uptake was low across the landscape. Higher uptake was predicted in mid-spring (May 12), consistent with measurements when there was less rain and warmer temperatures. CH₄ uptake was still low in the early wet summer (July 6) and increased toward the mid to late dry summer (July 26 and Sep 4). Net CH₄ uptake then decreased from early autumn (Oct 7) and reached its lowest rate in late autumn (Nov 30).

330

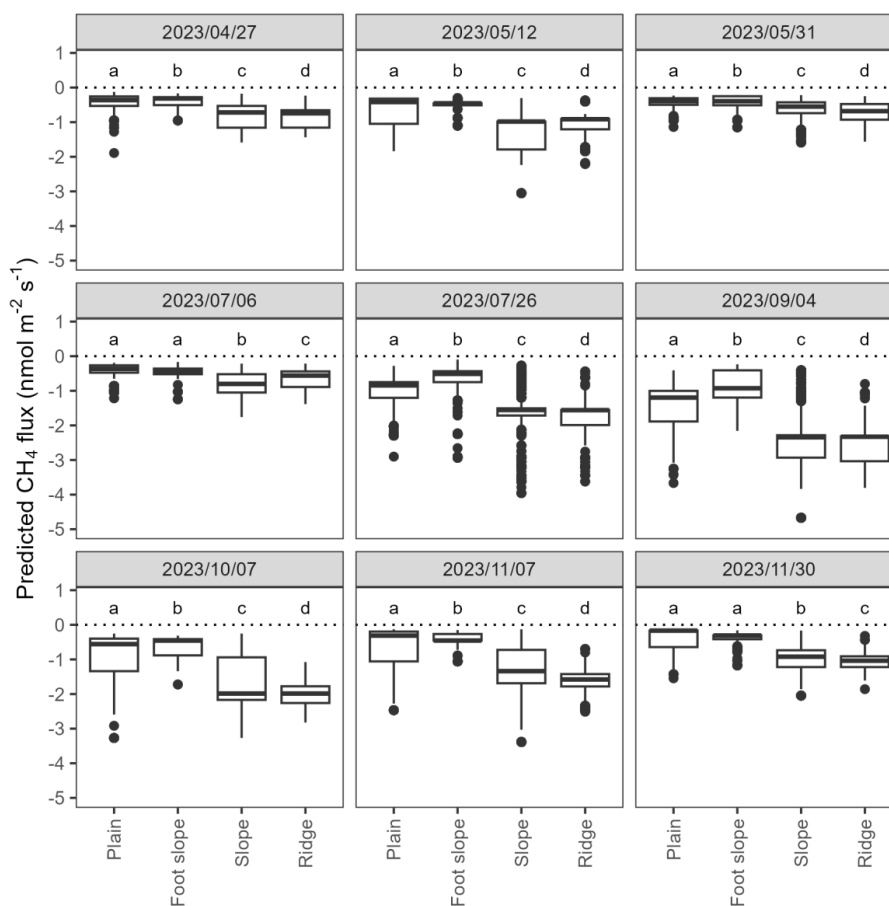


Figure 5: Predicted landscape-scale soil CH₄ fluxes for each measurement date at the pixel level, aggregated by upland topographic positions. Different letters indicate significant differences between topographic positions for each measurement date.

335

3.4 Uncertainty of predicted upland soil CH₄ fluxes

The spatial distribution of the percentage of predicted uncertainty varied across seasons (Fig. 6). The percentage was consistently low to moderate (less than 100%) for pixels on ridges and steep slopes, but extremely high uncertainties (more than 500%) was observed at some dates for low-elevation pixels when predicted fluxes were close to zero. However, low predicted fluxes were often associated with equally low predicted uncertainty (Fig. 6, A2). The proportion of pixels with low uncertainty (<50%) was highest in early autumn (39.7% of the total upland pixels) and lowest in early spring (4.5% of the total upland pixels). In contrast, moderate uncertainty (50-100%) was predominant in most seasons, particularly in spring and autumn, accounting for approximately 50% of the landscape. Moderate to high uncertainty (101-500%) was also predominant at some measurement dates, reaching its highest contribution of the landscape in late spring (47.6%). Extreme uncertainty (>500%) was very rare in all seasons, generally below 0.2%, except for a small peak in late autumn (0.5%) (Table A7).

345

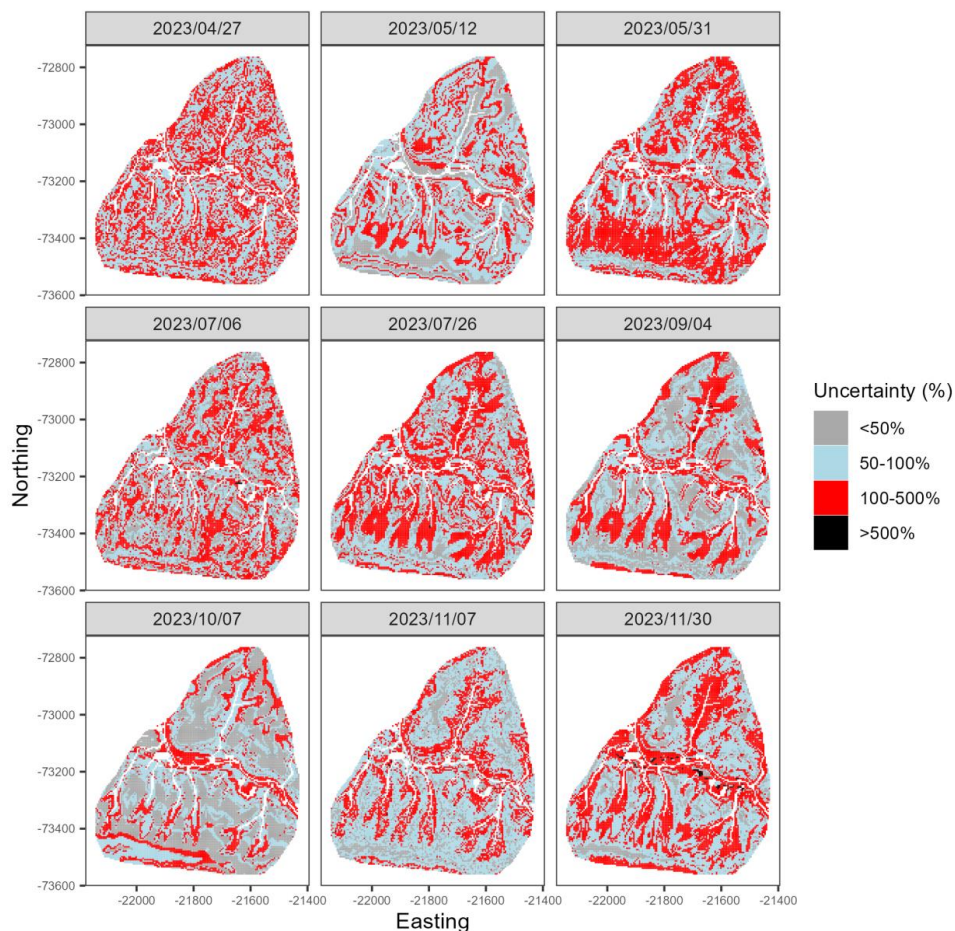


Figure 6. Uncertainty map of predicted soil CH₄ fluxes at each pixel of the study area for each measurement date. Values represent the ratio of the interquartile range to the median of the prediction distribution for each pixel.

350

3.5 Predicted seasonal upland fluxes at the landscape level

The predicted upland CH₄ flux per hectare was calculated as the sum of the predicted fluxes at each pixel multiplied by pixel area (25 m²), and the sum divided by the upland area. Across the landscape, predicted median seasonal fluxes ranged from -0.35 to -0.60 g CH₄ ha⁻¹ hr⁻¹ in spring, from -0.41 to -1.25 g CH₄ ha⁻¹ hr⁻¹ in summer, and from -0.50 to -0.89 g CH₄ ha⁻¹ hr⁻¹ in autumn (Fig. 7a).

355

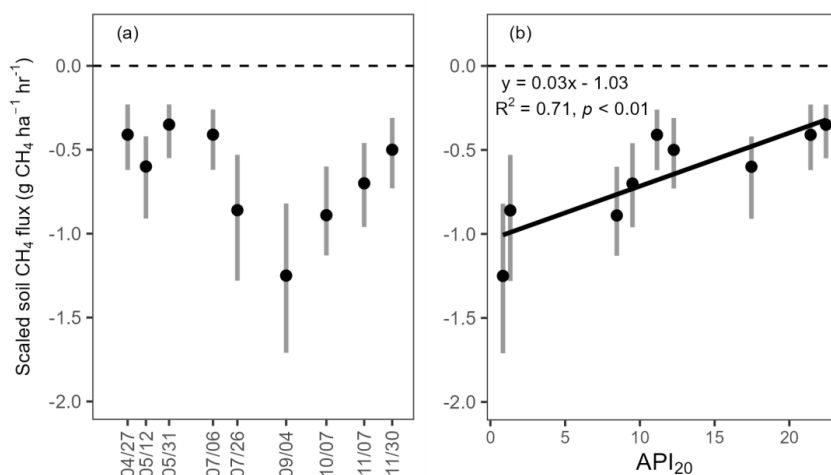


Figure 7: Predicted soil CH₄ fluxes, calculated as the mean of all pixels in the study area, and antecedent precipitation index (API). (a) Seasonal variations in landscape-scaled soil CH₄ fluxes and (b) relationship between landscape-scaled soil CH₄ fluxes and the 20-day API. Vertical bars indicate the uncertainty of the predicted fluxes.

360

This seasonal variation in predicted upland median fluxes was well explained by the 20-day antecedent precipitation index ($R^2 = 0.71, p < 0.01$) with a recession coefficient of 0.71 (Fig. 7b), followed closely by the 30-day ($R^2 = 0.70$) and 7-day ($R^2 = 0.69$) API (Table A8). The average CH₄ uptake by upland soils during the snow-free season was -0.67 (interquartile range: -0.94 to -0.43) g CH₄ ha⁻¹ hr⁻¹.

365 4. Discussion

4.1 Selected variables

We employed quantile regression forest (QRF) models, driven by topographic and vegetation attributes, to upscale *in-situ* soil CH₄ flux measurements from sampling points to the landscape level for each measurement date in all upland topographic positions, but excluding wetlands (1% of our study area). This non-parametric machine learning approach is particularly suited for handling non-linear relationships and complex interactions among predictors (Meinshausen, 2006).

Unexpectedly, vegetation type was never selected despite previous evidence of greater soil CH₄ uptake in plots containing only deciduous broadleaved tree species than in plots containing evergreen coniferous trees, either alone or in mixture (Jevon et al., 2023). The discrepancy between this previous study and our results may be related to the fact that their study area was ten times smaller and more topographically homogeneous than ours (4 *versus* 40 ha). Moreover, soil properties that could explain the lower rate of CH₄ oxidation in coniferous than in broadleaved stands, such as higher acidity (Borken et al., 2003; Hütsch, 1998; Ishizuka et al., 2000) did not differ significantly among the three types of vegetation cover at our site, whereas they differed according to topographic position. Furthermore, vegetation types were not randomly distributed among topographic positions (Table A1), meaning that the confounding effects of vegetation and DEM-derived variables on the prediction soil CH₄ uptake could make it difficult to separate the influence of vegetation and topography in our complex mountain landscape. Among all tested topographic variables derived from the DEM, TWI, TPI, PrC, and VDCN were consistently



385 selected in different models across all measurement periods, emphasizing their importance in upscaling CH₄ fluxes. Overall, the results validated our first hypothesis, as the selected topographic attributes were related to water circulation and accumulation.

Among these variables, TWI represents water accumulation potential and is a common surrogate for soil moisture in mountainous regions. This key factor controls CH₄ fluxes by affecting gas diffusion and microbial activity (Kaiser et al., 2018; Vainio et al., 2021; Warner et al., 2019), as TWI integrates potential inflows and discharges through runoff and drainage (Ågren et al., 2014; Beven and Kirkby, 1979). TWI was selected in seven out of nine 390 measurement periods but not on May 12 and October 7. These two periods correspond to transitional seasons, i.e., mid-spring and early autumn, when the landscape is generally drier, and water does not accumulate.

TPI describes the elevation of a location relative to those of the surrounding terrain within a given radius, allowing the identification of landform positions such as ridges, slopes, and valleys (Ågren et al., 2014). TPI is generally calculated using a non-filled DEM, which is also more representative of local-scale moist depression than TWI 395 doesn't capture, as TWI is calculated using the filled DEM (Kempainen et al., 2018). In our study, TPI was consistently selected in all measurement periods, highlighting that localized moisture, and potentially soil chemistry, are more influential parameters in controlling the CH₄ fluxes at the landscape level. Areas with negative TPI values (e.g., valleys or depressions) typically function as convergence zones, where water and nutrients accumulate due to gravitational flow and reduced drainage. In contrast, positive TPI values (e.g., ridges and 400 convex upper slopes) are more divergent, often characterized by increased drainage and runoff, and limited water and nutrient retention.

Although PrC was significantly correlated to TPI (Table A5), it was selected twice (April 27 and Nov 7). PrC refers to the curvature of the land surface in the direction of the slope (along a flow line). It influences the acceleration or deceleration of surface and subsurface water flow (Ågren et al., 2014). Negative values (concave 405 slopes) tend to slow water movement, promoting water and nutrient accumulation in soils. Conversely, positive values (convex slopes) accelerate flow, often reducing water retention time and lowering nutrient accumulation due to leaching or erosion. Excluding PrC from the list of available variables for selection decreased the model performance for these two dates, probably because PrC helps discriminate between plains and slopes, both of which have near-zero TPI values.

410 VDCN is another important variable reflecting groundwater level conditions. Lower values typically observed near stream channels with higher groundwater level (Bock and Köthe, 2008). When the landscape was drier (May 12 and October 7), and TWI was not selected, TPI and VDCN had more substantial explanatory power. VDCN was also selected several times with TWI. Interestingly, VDCN has been shown to be useful in distinguishing well-drained from poorly drained soils (Bell et al., 1992; Kravchenko et al., 2002). It may explain why, despite 415 significant correlations between VDCN and both TPI and TWI (Table A5), excluding VDCN from the list of variables available for selection decreased model performance. This highlights that TWI and TPI alone were not sufficient to reflect local soil moisture conditions, as drainage conditions can potentially vary across the landscape, which controls soil microhabitat conditions and thus influences CH₄ fluxes.

4.2 Spatial patterns of predicted soil CH₄ fluxes

420 The models revealed clear spatial patterns in soil CH₄ fluxes that were consistent across measurement dates, even though the models selected different variables at each date. Predicted soil CH₄ fluxes closely matched topographic gradients, consistent with our second hypothesis. Ridges and upper slopes exhibited the highest net CH₄ uptake,



functioning as strong sinks for CH₄ across all seasons, whereas CH₄ uptakes were lowest in plain and foot slope positions. These topographic patterns of CH₄ uptake are consistent with previous studies. In a temperate forest in central Ontario, Canada, the highest CH₄ uptake was observed on slopes and ridges (Wang et al., 2013). Similarly, in a temperate forest in Maryland, USA, transition zones were identified as hotspots for CH₄ uptake (Warner et al., 2018). In a tropical forest in China, hillslopes exhibited the highest CH₄ uptake, while lower uptake was observed at the foot slopes and in groundwater discharge areas (Yu et al., 2021). Similarly, CH₄ uptake was greater on ridges than at valley bottoms in a subtropical forest in Puerto Rico (Quebbeman et al., 2022).

In our studied landscape, we observed lower soil bulk density on ridges and slopes than on the plain area, indicating that ridge and slope soils have higher porosity, which is consistent with higher soil CH₄ oxidation rates due to higher diffusion rates of O₂ and CH₄ from the atmosphere through soil pores (Ishizuka et al., 2009). Although we did not assess the methanotroph community structure, the greater atmospheric CH₄ uptake on slopes and ridges is consistent with the community structure observed in a subalpine forest, with type I methanotrophs dominating in riparian soils, whereas type II methanotrophs were more prevalent in upland soils (Du et al., 2015). The higher soil carbon (C) and nitrogen (N) contents observed on ridges and slopes at our site may contribute to higher soil CH₄ uptake, as soil CH₄ uptake has been found to be positively correlated with soil organic matter content in subtropical and temperate forests (Lee et al., 2023). Possible explanations are that higher soil carbon may increase the availability of labile substrates that stimulate methanotrophic activity by increasing CH₄ supply through enhanced methanogenesis in anoxic microsites or by directly providing substrate for facultative methane-oxidizing bacteria, thereby increasing their abundance (Jensen et al., 1998; Semrau et al., 2011; West and Schmidt, 1999). Soil nitrogen was probably predominantly in organic form, and therefore the soil concentration of nitrate and ammonium, known to inhibit CH₄ oxidation by methanotrophs at high concentration (King and Schnell, 1994; Mochizuki et al., 2012), likely remained low (Aronson and Helliker, 2010; Bodelier and Laanbroek, 2004). Nitrogen is an essential nutrient for the growth of methanotrophs, whose activity has been shown to be nitrogen-limited in forest soils (Börjesson and Nohrstedt, 2000; Martinson et al., 2021; Veldkamp et al., 2013). Therefore, mineralization of these low levels of organic nitrogen could alleviate the nitrogen limitation of CH₄ oxidation and partly explain the higher soil CH₄ uptake observed on ridges and slopes, where total nitrogen concentration was higher than at the foot slopes and in the plain.

4.3 Model performance and uncertainty

Soil CH₄ fluxes predicted by QRF models were close to the measured fluxes for all measurement periods (Fig. 3; Table A4), indicating that topographic attributes could be used for upscaling CH₄ fluxes in mountainous landscapes. The performance of the models developed for scaling CH₄ fluxes was comparable to previous studies using topographic data for similar purposes (Kaiser et al., 2018; Vainio et al., 2021; Virkkala et al., 2024; Warner et al., 2019). However, it is important to note that direct comparisons between studies are difficult due to variations in cross-validation approaches, as the choice of cross-validation technique can significantly influence model performance (Roberts et al., 2017).

Unfortunately, it was not possible to accurately predict CH₄ fluxes when measurements collected in wetland patches were included in the training data, probably because neither the topographic features nor the vegetation differed sufficiently between the large areas functioning as CH₄ sinks and the small wetland patches functioning as CH₄ sources in the plain area. Räsänen et al. (2021) noticed that spatial patterns of CH₄ fluxes could be accurately predicted in a northern peatland-forest-mosaic landscape when they were modeled for sinks and sources



separately. This separation was not possible in our study due to the low number of measurement locations in wetlands, related to their small extent (1%) in our upland-dominated landscape.

465 One advantage of the QRF approach is its ability to estimate prediction intervals (Meinshausen, 2006), thus offering insights into the uncertainty associated with the predicted flux value at each pixel. The spatial distribution of the uncertainty associated with the predicted soil CH₄ fluxes varied seasonally (Fig. 6; Table A7) in agreement with our third hypothesis, reflecting both spatial heterogeneity and temporal changes in model confidence. In our study, the spatial patterns of QRF-derived uncertainties were consistently related to topographic position and flux

470 magnitude. Predictions in ridge and steep slope pixels generally exhibited low percentage uncertainties (often below 100%), likely because these well-drained upland areas were well represented in the training data and exhibited relatively stable and high CH₄ uptake across seasons. In contrast, extremely high percentage uncertainties (exceeding 500%) were observed in some low-lying pixels during specific seasons, especially where predicted CH₄ fluxes were close to zero. A crucial methodological point is that percentage uncertainty is a relative

475 measure; even a small absolute uncertainty around a near-zero prediction can yield a very large percentage (Warner et al., 2019). Large absolute uncertainties can result from large differences in fluxes measured at locations with similar topographic characteristics. Since lower fluxes were measured in the flat plain area compared to the ridges and slopes, yet with similar variability (Fig. 2a), high relative uncertainties were often associated with this area characterized by complex hydrological conditions, which are difficult to model accurately.

480 Consistent with our third hypothesis, seasonal differences in the uncertainty distribution were also evident, with the lowest uncertainty in late summer and early autumn, i.e., under warm and dry conditions, indicating better model performance when hydrological conditions were less variable. In contrast, larger uncertainties were produced by the models in early spring and late autumn, as well as in late spring and early summer, when measured and predicted soil CH₄ fluxes were lowest. The East Asian monsoon flow bringing warm and humid air mass and

485 resulting in the rainy season in late spring and early summer, as well as low evapotranspiration in early spring and late autumn, may have introduced greater variability in soil hydrology, contributing to higher uncertainties. Nevertheless, low to moderate uncertainty (<100%) was the most prevalent class across all seasons, consistently accounting for more than half the landscape—up to 80% in late summer and early autumn—while extreme uncertainties (>500%) were rare across all seasons. This suggests that the models performed well overall.

490 Although some areas remain challenging to model, the QRF approach provides generally reliable spatial predictions of soil CH₄ fluxes with quantifiable and interpretable uncertainties.

4.4 Scaled soil CH₄ fluxes and seasonal variation

The upland CH₄ fluxes per hectare were calculated by aggregating pixel-level predictions and normalizing them to the total upland area, allowing for standardized comparison across sites, although there are still very few

495 comparable data available, making it difficult to analyze the causes of differences across sites. Our highest CH₄ uptake in late summer was -1.25 g CH₄ ha⁻¹ hr⁻¹ (interquartile range -1.71 to -0.82), 2.6 times higher in absolute value than in a forested watershed in Maryland, USA (-0.47 g CH₄ ha⁻¹ hr⁻¹, Warner et al. 2019), but slightly lower than in a boreal pine forest in Finland (-1.59 g CH₄ ha⁻¹ hr⁻¹, Vainio et al. 2021).

500 Consistent with our fourth hypothesis, the seasonal variation in predicted upland CH₄ fluxes reflects strong sensitivity to soil moisture dynamics, which were effectively captured using the Antecedent Precipitation Index (API). The API, serving as a proxy for dynamic soil moisture, integrates precipitation over a defined period and includes a recession factor to account for evapotranspiration and drainage. Short durations (e.g., 7 days) reflect



505 surface moisture, while longer durations (e.g., 30 days) capture deeper soil moisture conditions (Schoener and Stone, 2020; Sidle et al., 2000; Yamao et al., 2016). Among the API durations tested, the 20-day API with a recession coefficient of 0.70 showed the highest explanatory power ($R^2 = 0.71$), although using either a 30-day or a 7-day API would provide similar goodness of fit with similar recession coefficients, indicating that soil moisture conditions across different depths had similar influence on CH₄ flux variability. The consistently low recession coefficient (Kohler and Linsley, 1951) suggested that rainwater does not accumulate in our watershed. Higher API values indicate wetter antecedent conditions, which can suppress CH₄ uptake by reducing oxygen availability and thus limiting methanotrophic activity, and by temporarily turning the subsoil condition to anoxic, promoting methane production and reducing net CH₄ uptake (Angel et al., 2012; Hu et al., 2023; Kruse et al., 1996). Conversely, drier periods with lower API values were observed in mid and late summer and earlier autumn, when soils were better aerated, creating favorable conditions for atmospheric CH₄ oxidation and leading to greater CH₄ uptake.

515 **5 Conclusion**

In conclusion, our study showed the dominant role of topography on the spatial variation of soil CH₄ fluxes in upland forest landscapes. The quantile regression forest (QRF) model successfully captured these ridge-to-plain spatial gradients in the upland area where the soil is almost always unsaturated, with strong performance. CH₄ uptake was consistently highest on ridges and slopes, where well-drained soils with lower bulk density and higher porosity supported enhanced methanotrophic activity. Furthermore, the seasonal dynamics of CH₄ uptake were well-captured by the 20-day Antecedent Precipitation Index (API), with a significant positive relationship between API and CH₄ uptake, emphasizing the sensitivity of CH₄ uptake by upland soils to seasonal fluctuations in soil moisture conditions. Our modeling approach was unable to accurately predict CH₄ fluxes when including measurements collected in three wetland patches functioning as CH₄ sources in the plain area (1% of the total landscape). The integration of terrain-based predictors and moisture history provides a reliable framework for scaling soil CH₄ fluxes across complex landscapes, highlighting the importance of considering both static (topographic) and dynamic (climatic) controls in future assessments of CH₄ flux.



530 **Appendix A**

Table A1. Proportion of vegetation types associated with the different topographic positions

Position	Vegetation	Proportion of vegetation type (%)
Plain	Broadleaf	77.8
	Coniferous	11.1
	Mixed	11.1
Foot slope	Broadleaf	56.3
	Coniferous	18.8
	Mixed	25.0
Slope	Broadleaf	21.4
	Coniferous	21.4
	Mixed	57.1
Ridge	Coniferous	30.8
	Mixed	69.2

Table A2. Summary of linear mixed model (LMMs) analyzing the effects of topographic position, vegetation types, date of measurement, and their interactions on measured soil CH₄ fluxes. Collar ID was included as the random effect.

Response variable	Explanatory factors (fixed effects)	p-value
Measured soil CH ₄ fluxes	Position [df = 3]	0.17
	Vegetation [df = 2]	0.83
	Measurement date (DM) [df = 8]	$< 2 \times 10^{-16}$
	Position × Vegetation [df = 5]	0.93
	Position × DM [df = 24]	0.74
	Vegetation × DM [df = 16]	0.51
	Position × Vegetation × DM [df = 40]	0.04

535



Table A3. Spearman’s correlation coefficients and p-values (*p > 0.05, **p > 0.01, *p > 0.001) between soil properties and mean soil CH₄ fluxes. Non-significant coefficients are shown in gray.**

	BD	Clay	Silt	Sand	pH	C%	N%
BD							
Clay	-0.23						
Silt	-0.06	0.40**					
Sand	0.14	-0.73***	-0.93***				
pH	0.47***	0.11	0.03	-0.064			
C%	-0.72***	-0.00	-0.10	0.078	-0.69***		
N%	-0.74***	0.01	-0.11	0.077	-0.65***	0.97***	
Mean CH ₄ flux	0.26	-0.04	-0.11	0.105	0.32*	-0.20	-0.22

540

Table A4. Summary of the linear mixed model (LMMs) analyzing the relationship between the predicted soil CH₄ fluxes and measured soil CH₄ fluxes, where measurement periods were included as the random factor on both slope and intercept. The p-values of the fixed effect were for testing if the intercept was different from zero and the slope different from 1. The marginal (R²_m) and conditional (R²_c) coefficients of determination, and the root mean square error of the model are shown.

545

Fixed effect: predicted CH ₄ flux		Random effects: measurement dates			
Estimate ± SE	p-values		Intercept	Slope	
Intercept	0.12 ± 0.03	from 0: 0.004	2023/04/27	-0.03	0.02
Slope	1.15 ± 0.02	from 0: 2 × 10 ⁻¹¹	2023/05/12	0.00	0.03
		from 1: 0.91	2023/05/31	-0.03	0.02
			2023/07/06	-0.07	0.04
Statistics			2023/07/26	0.05	0.03
n	467		2023/09/04	0.09	-0.05
R ² _m	0.93		2023/10/07	0.03	-0.05
R ² _c	0.94		2023/11/07	-0.01	-0.04
RMSE	0.28		2023/11/30	-0.02	0.01



550 **Table A5. Spearman’s correlation coefficients and p-values (*p > 0.05, **p > 0.01, ***p > 0.001) between topographic attributes: cosine-transformed aspect, slope, profile curvature (PrC), topographic position index (TPI), topographic wetness index (TWI), and vertical distance to channel network (VDCN).**

	Aspect	Slope	PrC	TPI	TWI
Aspect					
Slope	-0.04				
PrC	0.17	-0.01			
TPI	0.16	0.02	0.63***		
TWI	-0.25	-0.58	-0.20	-0.57***	
VDCN	-0.03	0.26	0.46***	0.73***	-0.53***

Table A6. Summary of the LMM analyzing the effects of topographic position and measurement dates (MD) on predicted soil CH₄ fluxes. Pixel ID was included as a random effect, and spatial autocorrelation among residuals eliminated.

Response variables	Explanatory variables	p-values
Predicted median CH ₄ fluxes	Position [df = 3]	< 0.001
	MD [df = 8]	< 0.001
	Position × MD [df = 24]	< 0.001

555

Table A7. Percentage of upland pixels in the study area distributed among four levels of predicted relative uncertainty for soil CH₄ fluxes.

Seasons	Uncertainty			
	< 50%	50 - 99 %	100 - 500%	>5 00%
2023/04/27	4.54%	53.06%	42.35%	0.04%
2023/05/12	19.93%	54.01%	26.06%	-
2023/05/31	8.28%	44.19%	47.54%	-
2023/07/06	21.68%	39.73%	38.50%	0.08%
2023/07/26	13.18%	43.75%	43.05%	0.02%
2023/09/04	30.85%	39.64%	29.35%	0.16%
2023/10/07	39.68%	38.13%	22.19%	-
2023/11/07	16.98%	54.58%	28.37%	0.07%
2023/11/30	11.29%	46.85%	41.34%	0.52%



560 **Table A8. Statistics of the linear relationship between landscape-scaled soil CH₄ fluxes and antecedent precipitation indexes (API). 20 antecedent days provided the best fit. 30 and 7 antecedent days are shown as common metrics in hydrology. Adjusted recession coefficients (k) and determination coefficients (R²) are shown.**

Antecedent days	k	R ²
20	0.70	0.71
30	0.70	0.70
7	0.68	0.69

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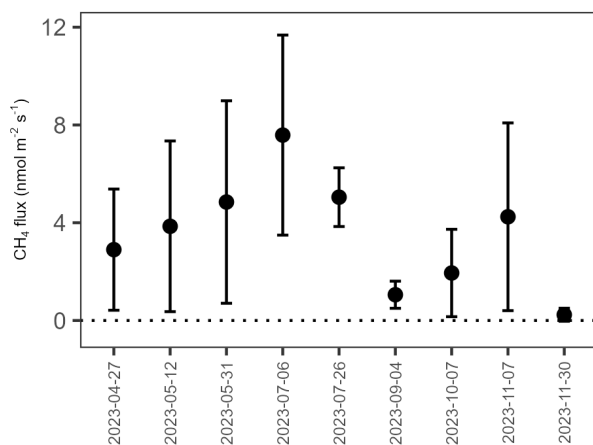
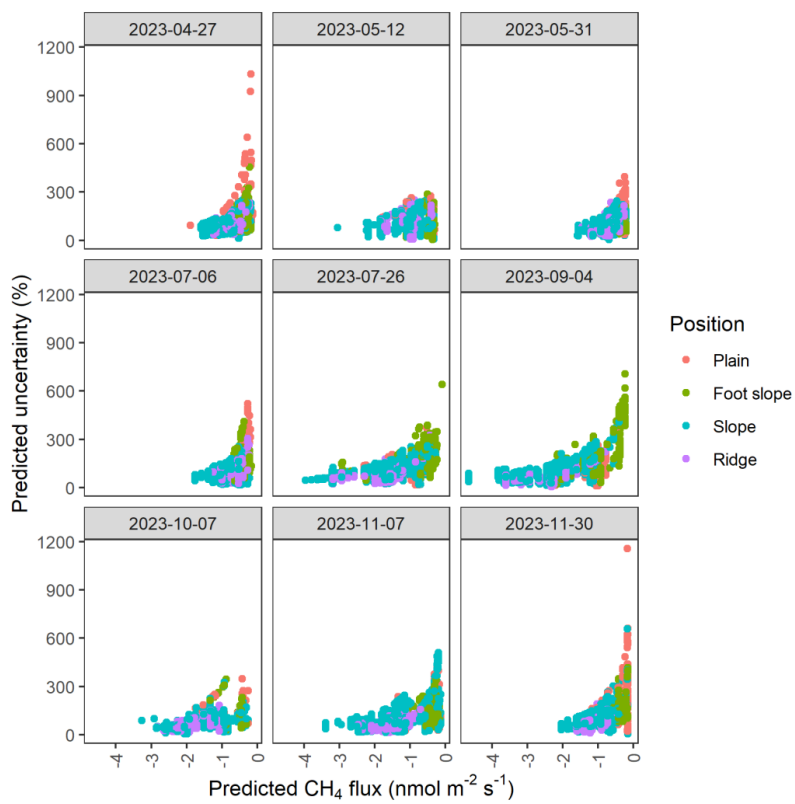


Fig A1. Seasonal variation of soil CH₄ fluxes from wetlands (means and standard error, n = 3).



570 **Fig A2. Relationship between predicted uncertainty and predicted CH₄ fluxes. The highest uncertainty is observed for a near-zero prediction.**



Data availability

The data used in this study are available at The Kyoto University Research Information Repository (KURANAI,

575 DOI: to be added)

Author contribution

DE had the original idea of this research. DE and SKP designed the research framework with suggestions from MD. SKP, DE, and KY conducted the vegetation survey and flux measurements. SKP analyzed and performed the modeling under the supervision of DE. SKP wrote the manuscript that was critically reviewed and edited by all
580 co-authors.

Competing interest

The authors declare that they have no conflict of interest.

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