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Environmental and anthropogenic drivers of soil methane fluxes in forests: global patterns and among-biomes differences

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Abstract

Forest soils are the most important terrestrial sink of atmospheric methane (CH_4). Climatic, soil and anthropogenic drivers affect CH_4 fluxes, but it is poorly known the relative weight of each driver and whether all drivers have similar effects across forest biomes. We compiled a database of 478 *in situ* estimations of CH_4 fluxes in forest soils from 191 peer reviewed studies. All forest biome (boreal, temperate, tropical and subtropical) but savannas act on average as CH_4 sinks, which presented positive fluxes in 65% of the sites. Mixed effects models showed that combined climatic and edaphic variables had the best support, but anthropogenic factors did not have a significant effect on CH_4 fluxes at global scale. This model explained only 19% of the variance in soil CH_4 flux which decreased with declines in precipitation and increases in temperature, and with increases in soil organic carbon, bulk density and soil acidification. The effects of these drivers were inconsistent across biomes, increasing the model explanation of observed variance to 34% when the drivers have a different slope for each biome. Despite this limited explanatory value, which could be related to the use of soil variables calculated at coarse scale (~1km); our study shows that soil CH_4 fluxes in forests are determined by different environmental variables in different biomes. The most sensitive system to all studied drivers were the temperate forests, while boreal forests were insensitive to climatic variables, but highly sensitive to edaphic factors. Subtropical forests and savannas responded similarly to climatic variables, but differed in their response to soil factors. Our results suggest that the increase in temperature predicted in the framework of climate change would promote CH_4 emission (or reduce CH_4 sink) in subtropical and savannas forests, have no influence in boreal and temperate forests and promote uptake in tropical forests.

Keywords

CH_4 uptake; CH_4 emission; static chamber; global change; greenhouse gases (GHG); native forest; planted forest

1. Introduction

Methane (CH_4) is a greenhouse gas (GHG) with a radiative forcing 28 times stronger than carbon dioxide (CO_2) and, therefore, with a high impact on global warming (IPCC, 2014). It is produced naturally in wetlands and lakes, but 75% of CH_4 emissions are from anthropogenic sources such as fossil fuel combustion, irrigated rice cultivation, enteric fermentation of domestic ruminants, biomass burning and landfills (Kirschke et al., 2013). This GHG is mostly consumed in the troposphere through oxidation by hydroxyl ($^{\bullet}OH$) radicals (90%), whereas only 6% is oxidized by methanotrophs in aerated soils (Kirschke et al., 2013; Le Mer & Roger, 2001). Despite its small proportion, it is a sink that can be directly affected by human interventions through land use conservation, change or intensification. Soils of forest ecosystems are the most important terrestrial component acting as a sink of atmospheric CH_4 (Dutaur & Verchot, 2007). Of the total CH_4 consumed in soils at global scale, 60% corresponds to forest ecosystems which uptake 9.16 Tg CH_4 yr^{-1}, followed by grasslands with 3.73 Tg CH_4 yr^{-1} (Dutaur & Verchot, 2007; Yu, Huang, Zhang, Li, & Sun, 2017). However, declines in soil CH_4 uptake has been identified in several forests across the globe, as a consequence of the join effect of climate change and land use changes (Han & Zhu, 2020; Ni & Groffman, 2018). Therefore, unravelling the combination of the environmental drivers that determines the CH_4 flux in forest soils, both in natural and planted forests, and whether them have similar behaviour in response to they across biomes, is a crucial step to improve our ability to manage -to some extent- CH_4 mitigation and to predict the potential changes of this process under global warming.

At soil level, CH_4 is produced by methanogenic microorganism (methanogens) as an end result of the anaerobic digestion of organic matter, but also it is consumed by biological oxidation carried out by methane-oxidizing bacteria (methanotrophs) (Le Mer & Roger, 2001). Each of these processes has different environmental requirements, being methanogenesis dominant under anaerobic conditions and methanotrophy active under aerobic conditions (Le Mer & Roger, 2001). Therefore, the net CH_4 flux in soils depend on the interplay between aerobic and anaerobic conditions mainly driven by temporal and spatial dynamics of soil water balance (Le Mer & Roger, 2001; Liu, Estiarte, & Peñuelas, 2019; Ni & Groffman, 2018). Furthermore, net negative soil CH_4 flux (hereafter soil CH_4 uptake) occur when oxidation process overcomes the methanogenesis (Le Mer & Roger, 2001). Because soil water balance at ecosystem level is controlled by precipitation (water input) and temperature (evaporative output), as well as the vegetation cover, large-scale variations in soil CH_4 uptake could be closely linked to climatic variation. However, global scale empirical models considering sole climatic variables have shown to have a limited explicative power (with an explained variance lower than 10%) (Dutaur & Verchot, 2007; Liu et al., 2019). In contrast, higher predictive power was reached when soil variables influencing methanotrophy had been added to climatic predictors by Yu et al. (2017). In that study, however, the increase in goodness-of-fit was achieved by adding complex CH_4 flux - soil predictors relationships (i.e. considering non-lineal parameters and transformations of the original variables), which reduce their explicative power for strategies of forest management and conservation practices. Nevertheless, that study remarks that adding soil variables could enable a better explanation of large-scale variations in soil CH_4 flux in forests worldwide.

Several soil variables are known to affect CH_4 fluxes in forests (see Table 1). Soil texture and bulk density directly regulate soil water availability and, then, CH_4 diffusion (Del Grosso et al., 2000; Ridgwell, Marshall, & Gregson, 1999). For instance, well drained soils (*i.e.* those with higher sand content and lower bulk density) may favour methanogenesis at high water content and promote methanotrophy at drier conditions due to increased gas diffusion into the soil and from the atmosphere (Del Grosso et al., 2000; Hiltbrunner, Zimmermann, Karbin, Hagedorn, & Niklaus, 2012). On the other hand, although soil organic carbon may also regulate water retention and indirectly affect net CH_4 flux, its impact is directly related to control the total mineralizable carbon stimulating methanogenesis (von Fischer & Hedin, 2007). Finally, additional variables such as soil pH and nitrogen availability also affect net CH_4 flux in soils as a result of changes in bacteria community composition, mostly impacting methanotrophic community (Aronson & Helliker, 2010; Hiltbrunner et al., 2012; Tate, 2015). Despite of these widely reported evidences of the effects of soil variables on net CH_4 flux, their relative importance in forests at global scale is virtually unknown (but see Yu et al. 2017 for the magnitude of effects of soil variables).

Previous studies integrating data from forest ecosystems across the globe have found that variability in soil CH_4 flux was greater within than among biomes (Dutaur & Verchot, 2007; Liu et al., 2019; Yu et al., 2017). Although these results suggest that in average soil CH_4 flux does not differ substantially among biomes, they do not allow us to understand which are the environmental drivers behind the observed patterns, and therefore if they could respond differentially to changes in those drivers. In this regard, a regional study carried out in China showed that soil CH_4 flux in boreal and temperate forests responded to climate differentially than forests located in tropical and subtropical biomes (Fang et al., 2010). Furthermore, these authors also reported biome-specific responses of soil CH_4 flux to nitrogen-related variables. In addition, meta-analyses have also found different responses among biomes to soil nutrients addition, soil texture and warming (Aronson & Helliker, 2010; Dijkstra et al., 2012). Biome-specific soil CH_4 flux - environmental relationships would be due to multiple causes (Fang et al., 2010), being possibly related to the most limiting factor for CH_4 oxidation within each biome.

In the present study, we evaluated the effects of multiple climate and soil properties on the spatial variation of soil methane (CH_4) fluxes in forests from different biomes at global scale. Because recent evidence suggests that anthropogenic disturbances such as forest conversion to secondary or to the commercial plantation as well as increases in urbanization are potential determinants of soil CH_4 flux (Han & Zhu, 2020; Zhang et al., 2014), we also included variables related to these factors. We used *in situ* soil measures of CH_4 fluxes from 191 peer reviewed studies spanning a wide range of climates, soil attributes and anthropogenic conditions, belonging to the five principal forest biomes (boreal, temperate, tropical, subtropical and savanna). With this dataset, we attempted to answer the following questions: (1) Which combination of climatic, soil and human footprint factors better explains the spatial variation in forest soil CH_4 fluxes at global scale?, and (2) To what extent do the magnitude and direction of these variables differ among biomes? At the global scale, the soil net CH_4 flux in forests could be mainly determined by climatic drivers because they are the main controlling factors on both microbial activity/abundance (including methanotrophs and methanogens which consume and produce CH_4; respectively) and soil water balance (Serna-Chavez, Fierer, & Van Bodegom, 2013; Tang et al., 2020). Nevertheless, soil chemical and physical properties may modulate the effects of precipitation and temperature on water balance and ultimately affect soil net CH_4 flux (Del Grosso et al., 2000). Additionally, human impact through forest conversion or urbanization also may affect soil net CH_4 flux by altering soil attributes or indirectly modifying biogeochemical and water cycles (Han & Zhu, 2020; Ni & Groffman, 2018; Zhang et al., 2014). Therefore, we hypothesized (H1) that soil net CH_4 flux is determined by a combination of these drivers and not by isolated factors. However, we additionally hypothesized (H2) that the direction and magnitude of drivers´ effects on soil CH_4 flux change across biomes because different environmental factors limit biological activity and alter soil water balance and O_2 availability among them. For example, in boreal forests the limiting factor for CH_4 oxidation is the low temperature, so increases in temperature may favour CH_4

oxidation (Fang et al., 2010). In contrast, in tropical forests, where the temperature is not the main biological limiting factor, increases in temperature may promote net CH_4 emission over oxidation because methanotrophs fail to compete when soil O_2 is limited (Fang et al., 2010). These relationships may be modulated by co-variations in precipitation, soil parameters and human impact (Aronson, Allison, & Helliker, 2013).

2. Materials and methods

2.1. Data collection

We compiled a database of *in situ* measures of soil CH_4 fluxes in forests using two sources of peer-reviewed papers: (1) existing datasets previously compiled and published (Castaldi, Ermice, & Strumia, 2006; Dutaur & Verchot, 2007; Feng et al., 2020; Ni & Groffman, 2018) and (2) from Scopus ® (Elsevier B.V.). We searched peer-reviewed papers in Scopus using the following terms: "methane" OR "CH4" AND "soil*" AND "forest*". Then, considering both sources, we identified potential studies (around 600) published up to December 2019 (Figure S1). From the potential studies, we selected those studies that meet the following criteria: (a) studies with measurements of soil CH_4 fluxes using the static chamber method and gas chromatography technique, (b) reporting soil CH_4 fluxes values as averages at annual temporal resolution estimated from, at least, two measurements obtained at dry and wet season, and (c) that represent field conditions without additional experimental treatments (i.e. control or unmanaged plots). Two articles of the 1980 decade were discarded because they did not explicitly include geographic location. Although there are different methods for estimation of CH_4 fluxes under field conditions, we selected static chamber-gas chromatography method because it was particularly developed to measure gas emissions in the soil-atmosphere interface (Feng et al., 2020; Hutchinson & Livingston, 2001). Also, we discarded studies with closed chamber where CH_4 fluxes were determined using laser detection due to that it represent <1% of studies found in Scopus. Therefore, we homogenised our database using studies whose determination of CH_4 concentration was done with gas chromatography following to previous global studies (Liu et al., 2019; Ni & Groffman, 2018; Yu et al., 2017). Thus, after the selection process, we retained 191 studies that yielded 478 observational units from different forests around the world (Figure 1). Within each study, we considered as an observational unit each forest plot identified by different geographic coordinates or local site names (i.e. spatially independent plots) detailed by the authors.

Due to studies varied in temporal frequency of the field measurements and presented different units (µg m^{-2} h^{-1},g m^{-2} d^{-1}, and kg ha^{-1} yr^{-1}), we included the average values obtained from the data measured within the same year (annual average of CH_4 flux) and reported in tables or in the main text of the original studies, which were all standardized to kg ha^{-1} yr^{-1}. When it was not available, data were extracted from figures using Data Thief III (https://datathief.org/) and, then, annual average was calculated as the mean value of all measurements performed into one year and also standardized to kg ha^{-1} yr^{-1}. When soil CH_4 flux was available for more than one year at the same observational unit we used the mean value of reported measurements. Thus, our measurements represent the average rate of soil CH_4 flux at annual scale, which is appropriate to our objective since that illustrates in average terms whether a site tends to be soil CH_4 sink or source as well as the magnitude of these net fluxes (Liu et al., 2019; Yu et al., 2017). We checked if the temporal resolution would have influence the soil CH_4 flux adding the number of measurements used to estimate annual average as a fixed predictor in our statistical models (see Data analysis below).

Additionally, for each observation we extracted from the original article ancillary data such as latitude, longitude, time-interval of experimental period (and standardized to months), age of plantation, time of recent wildfire, biome classification (boreal, temperate, tropical, subtropical and savanna -sparse-woodland forests), forest type (natural or plantation) and landscape position (upland or floodplain). Of particular interest for our study was biome classification, and therefore we assigned each site to one of five general biomes or forest type using three sources of information: (i) from authors' description in each original article, and (ii) from shapefile contained in a global database of vegetation species composition (sPlot, Bruelheide et al., 2019). We considered biome classifications (boreal, temperate, tropical and subtropical) for each observational sample, which is based on climatic determinants related to changes in latitude. Unlike to this classification, savanna ecosystems are not determined by latitudinal location but by edaphic and disturbance agents (high fire frequency and herbivore pressure) that modify the vegetation structure generating systems with discontinuous tree canopy cover on a continuous grass layer (Ratnam et al., 2011; Scholes & Archer, 1997). Because of these systems are widely distributed across middle and higher latitudes (de la Cruz, Quintana-Ascencio, Cayuela, Espinosa, & Escudero, 2017) and have recently been classified as "tropical savanna biome" due to their different structure and functioning than tropical and subtropical forests (Ratnam et al., 2011), we considered sites on savannas as a different category of biome.

2.2. Soil and climate factors

Soil data for each observational unit were extracted from the Global Soil Dataset in Earth System Models (GSDE) at 1 km^2 of gridded resolution (Shangguan, Dai, Duan, Liu, & Yuan, 2014). The soil data included soil organic carbon (SOC, %), soil total nitrogen (STN, %), soil pH (measured in water), sand, clay and silt content (all in %), and bulk density (BD, $g \cdot cm^{-3}$ in volume). We used soil variables of superficial soil layer (0 – 10 cm) due to their characteristics have relatively more influence on the exchange of CH_4 between soil and atmosphere than attributes at deeper soil layers (Le Mer & Roger, 2001; Von Fischer, Butters, Duchateau, Thelwell, & Siller, 2009; von Fischer & Hedin, 2007).

Climate data were obtained from WorldClim 2, a climatic global database at 1 km x 1 km of spatial resolution (Fick & Hijmans, 2017). We extracted mean annual temperature (MAT, in ºC) and mean annual precipitation (MAP, in mm). Additionally, we extracted 17 bioclimatic variables related with the seasonal pattern of MAP and MAT. Elevation data (m a.s.l.) were obtained from SRTM (Shuttle Radar Topographic Mission) (Farr et al., 2007).

All data were integrated in R software (R Core Team, 2016) and data processing and extraction were performed with “raster” R package (Hijmans et al., 2020). In the cases of GSDE and SRTM, the spatial resolution was converted to 1 km x 1 km to match the resolution of the other gridded database.

2.3. Anthropogenic factors

We characterized land-use intensity using ancillary information provided by authors in each paper and, then, we classified each observational unit as “primary forest” (without reported human disturbances), “secondary forest” (whose structure is derived from regrowing after human disturbances), “reforestation” (restocking with monospecific or mixed forest stand), “afforestation” (forest crops on previous grassland ecosystems, i.e. ecosystems where trees never have grown before) and agroforestry systems (forest production is combined with natural or cultivated pastures or croplands). We defined these categories using the Glossary of Forest Engineering Terms from U.S. Forest Service. Additionally, because previous meta-analyses have shown that the impact of conversion from primary to secondary forest, reforestation or agroforestry on soil CH_4 efflux varied with the time interval since land-use change occurred (Han & Zhu, 2020), and similar temporal variations have been observed in afforestation systems (Benanti, Saunders, Tobin, & Osborne, 2014; Hiltbrunner et al., 2012), then, we subdivided these categories into recent (<15 years old), past (16 - 50 years) and ancient impact (>50 years old) subcategories.

Finally, we characterized each observational unit with the Human Footprint Index (HFI) extracted from The Global Human Footprint Dataset of the Last of the Wild Project, Version 2, 2005 (LWP-2) (WCS & CIESIN, 2005). This index integrates nine global data layers covering human population pressure (population density), human land use and infrastructure (built-up areas, night-time lights, land use/land cover), and human access (coastlines, roads, railroads, navigable rivers). The HFI is available at 1 km spatial resolution, higher HFI values indicating higher human pressure by urbanization. We used this index due to previous studies have shown that soil CH_4 uptake was significantly lower in urban than in rural forest soils (Ni & Groffman, 2018; Zhang et al., 2014). These reductions are associated with the direct environmental changes driven by urbanization, such as atmospheric N deposition, increases in toxic compounds affecting the methanotrophic community; and indirect effects on soil water balance and regulation (Goldman, Groffman, Pouyat, McDonnell, & Pickett, 1995; Ni & Groffman, 2018; Zhang et al., 2014).

2.4. Data analysis

We used linear mixed models (LMM) to evaluate the influence of the climate, soil and disturbance predictors on soil CH_4 flux (Zuur, Ieno, Walker, Saveliev, & Smith, 2009). LMM approach allowed us to answer our questions through the sequential determination of optimal fixed and random effect structures using Akaike's information criterion (AIC) values (Zuur et al., 2009). Thus, we proposed the following steps:

Firstly, we evaluated which is the best combination of factors (i.e. predictor or independent variables) to explain the spatial variation in soil CH_4 flux. We compared AIC values of models with different factors (fixed effects) defined *a priori* (see Introduction) and identified the "best model" that minimizes the AIC value. The *soil model* included SOC, STN, BD, sand content and pH as fixed factors (predictors). The *climate model* included MAP, MAT and their quadratic terms, and the interaction between MAP and MAT because their relevant role affecting soil CH_4

flux in forests (Liu et al., 2019). The *Anthropogenic model* included land use type, time since last fire (years), and human footprint index. We also fitted additive models: *soil + climate model*, *soil + anthropogenic model*, *climate + anthropogenic model*; and finally, a *full model* (soil + climate + anthropogenic model) and a *null model* (without predictors). In all models, biome was included as a random factor to take into account differences among biomes by estimating different intercepts for each biome (Zuur et al., 2009). Soil CH_4 flux was modelled considering a Gaussian error distribution. All models fitted showed Gaussian and homoscedasticity of their standardized residuals ($p > 0.05$ of Kolmogorov-Smirnov test), and did not present collinearity among predictors (Variance Inflation Factors < 2.8). Because models differed in fixed factors but shared the same random effects, the AIC values were obtained using maximum-likelihood (ML) as the algorithm for the estimation of regression coefficients (Zuur et al., 2009). When AIC values of two or more models differed by less than two units ($\Delta AIC < 2$), we retained the model with highest AIC weight (w_i), which estimates the likelihood of a model given the data, ranging from 0 (null support) to 1 (higher support) (Burnham & Anderson, 2002). Fixed effects (*i.e.* independent variables) were previously transformed to standardized version (z-score), which allows evaluating effects of the predictors in relative terms. Soil clay and silt content, as well as coefficient of variation of MAP and standard deviation of MAT, were not included in the models due to they were strongly correlated with other variables (Pearson $r > 0.80$).

Secondly, we estimated the relative importance and the effects of the factors included in the best model determined in the first step following multi-model selection approach (Burnham & Anderson, 2002). We fitted multiple models containing different combinations of all predictors included in the best model identified in the first step. These models were ordered based on their AIC (from lower to higher values), and we estimated their AIC weight (w_i). Then, the relative importance of the individual predictors (p_j) was estimated as the sum of the w_i of the models where each predictor (p_j) occurs. The direction and magnitude of the effects of the factors were estimated from the regression coefficient (and standard error) values and the statistical significance of the best model using restricted maximum likelihood (REML) (Zuur et al., 2009).

Thirdly, we explored whether the effects of each factor (direction and magnitude of the regression coefficients) do vary among biomes. We have taken advantage of mixed-effects models which allow cross-scale integration for evaluation of predictor effects at different spatial or temporal scales (Qian, Cuffney, Alameddine, McMahon, & Reckhow, 2010), particularly when samples size is unbalanced among levels of a categorical variable restricting ANCOVA type analysis (Zuur et al., 2009), as our case. Then, we fitted a mixed model that allowed the intercept and the partial regression coefficients of the significant predictors to vary among biomes (random intercept and slope models, Zuur et al., 2009). For this model, we maintained the same fixed effects structure as in the "best model". We compared AIC values among random intercept and slope model, the "best model" (random intercept model) and the null model to evaluate the plausibility of varying predictor explaining spatial variations in soil CH_4 flux.

Finally, we checked if soil CH_4 flux responses are influenced by additional factors by adding to the best model several co-variables such as time-interval of experimental period, multiple interactions among soil and climate variables and quadratic terms of soil predictors. Also, models with latitude and longitude as lineal predictors were fitted to overcome issues related to spatial autocorrelation. In addition, we evaluated whether landscape position (upland or floodplain) may explain spatial variation in soil CH_4 flux including them as random factors and comparing with the best model retained in the first step. In no case these models improved the explanation by reducing the AIC (Table S2 and S3). Therefore, we considered that the best model identified in the first step is a robust approach to understand the main environmental drivers of the observed spatial variation in soil CH_4 flux.

3. Results

Soil CH_4 flux average was negative in forests worldwide (Figure 2a), with 90 % of the sites showing flux values below 0 kg· ha^{-1}·yr^{-1}. A similar proportion is consistent across biomes (> 90% of sites showing soil CH_4 flux values below 0), except for the savanna biome, where 62% of the sites showed positive flux values. In agreement with this, the savanna was the only biome that showed a positive mean value of soil CH_4 flux (Figure 2b and Table S1); and where the highest positive value of soil CH_4 was registered (39.55 kg· ha^{-1}·yr^{-1}, Figure 2b and Table S1). On the other hand, the subtropical forests showed the lowest mean value of soil CH_4 flux (Figure 2b) and had the absolute minimum value (-39 kg· ha^{-1}·yr^{-1}) (Figure 2b; Table S1). We found that both at global and biome scale, the soil CH_4 fluxes showed positive values of kurtosis (Table S1) indicating that the most frequent flux values are close to the mean value. This pattern highlights that both negative and positive extreme values of soil CH_4 flux are rarely observed (Table S1 and Figure S2).

3.1. Soil, climate and anthropogenic disturbances on soil CH_4 flux

The model with the lowest AIC explaining spatial variation in soil CH_4 flux included both soil and climatic variables (Table 2). In addition, this model had the highest support (greatest w_i) but explained only 19% of the variance in soil CH_4 flux (Table 2); therefore, further interpretations were based on the *soil + climate model*. Among the predictors included in this best model, the most important were MAP, MAT, and their interaction term, soil pH, soil organic carbon (SOC) and soil bulk density (BD) (Figure 3a). Soil CH_4 flux decreased linearly with MAP, but this effect changed to positive either at sites with higher MAT and at sites with low MAP as indicated by significant and positive MAP x MAT interaction coefficient (Figure 3b and Figure S3). On the other hand, soil CH_4 flux decreased with increases in soil pH, while that the effects of SOC and BD showed a positive relationship with soil CH_4 flux (Figure 3b). Soil predictors were independent of the climate variables (interaction model discarded by AIC, Table S2). Additionally, we found that soil CH_4 flux responded positively to MAT, but only at warmer sites (with MAT > 18.2 ºC, Figure S3) as denoted by statistical significance of their quadratic term (Figure 3b). Finally, we found that including predictors related to human footprint or pressure (land-use categories and HFI) did not improve the model fitting (their AIC were higher than AIC of the best model, $\Delta AIC > 2$; Table 2).

3.2. Evaluating the effect of the drivers across biomes

The model whose partial regression coefficients varied among biomes had higher support to the "best model" (which does not have slope variations) since their AIC values differed by more than 2 units ($\Delta AIC > 2$; Table 3), increasing the explained variance to 34%. Variations in soil CH_4 flux in Boreal biome were insensitive to variations in climate predictors, but negative soil CH_4 flux (an indicator of uptake) was associated to increases in SOC and BD and decreases in pH (Fig. 3c). In savanna, negative soil CH_4 flux was associated with increases in BD, while positive soil CH_4 flux was related to increases in MAT and pH (Fig. 3c). In subtropical forests, a negative trend in soil CH_4 flux was associated with increases in pH, but a positive relationship was associated with MAT and SOC (Fig. 3c). In tropical forests, soil CH_4 flux was negatively correlated to MAT and SOC (Fig. 3c). In the opposite extreme, soil CH_4 flux in temperate forests was insensitive to variations in MAT but was positively correlated with SOC and BD, and negatively associated with increases in MAP and pH (Fig. 3c).

4. Discussion

Our global synthesis showed that soil CH_4 flux is influenced by a combination of soil and climatic factors in forests worldwide. By adding soil variables, we reached better explicative power than previous global studies (Feng et al., 2020; Liu et al., 2019), suggesting that soil CH_4 fluxes in forest ecosystems are driven not only by precipitation and temperature variations, but also by the influence of soil biotic and physical properties. Although this joint effect on soil CH_4 flux has been previously identified by process-based (Ridgwell et al., 1999) and empirical models (Dutaur & Verchot, 2007; Feng et al., 2020; Yu et al., 2017), here we advanced on two aspects: (1) we quantified the relative importance of these factors and (2) we determined that the magnitude and direction of these drivers vary among biomes. The latter is very important because despite most of the forests have similar average CH_4 fluxes; these are the result of a different response to environmental drivers, suggesting a differential soil CH_4 response to climate change in the different systems. Thus, our study allows us a better understanding of the cross-scaling controls on soil CH_4 fluxes, and also represents a starting point for future development of more accurate predictive models.

4.1. Global soil CH_4 fluxes patterns and their environmental drivers:

As expected, our best-fitting model identified that soil CH_4 flux responded strongly to climate variables, with a primary effect of the MAP and MAT. Precipitation effect on CH_4 flux is driven by the soil water balance, ultimately affecting biological CH_4 oxidation rate and, indirectly, gas diffusivity (Del Grosso et al., 2000; Ridgwell et al., 1999). We found that soil CH_4 fluxes decreased with increased MAP, which means that at global scale a higher uptake (negative flux value) is observed in sites with more precipitation, possibly because of reductions in the biological activity of methanotrophic organisms in water-limited environments rather than restricted gas diffusion (Serrano-Silva, Sarria-Guzmán, Dendooven, & Luna-Guido, 2014). Manipulative and process-based studies conserving soil structure constant (and, therefore, gas diffusivity constant) have found that reduced soil water was correlated with steepest declines in CH_4 uptake (Del Grosso et al., 2000; Ridgwell et al., 1999; Von Fischer et al., 2009). Thus, our study reinforces the idea of the prevalent role of the precipitation promoting biological oxidation of CH_4 in forest soils (Fang et al., 2010; Liu et al., 2019; Yu et al., 2017).

We found a positive and significant relationship between soil CH_4 flux and MAT indicating increases in CH_4 emissions with increases in temperature. Increases in temperature would induce an increase in evapotranspiration and soil desiccation which, in turn, may enhance CH_4 oxidation (Castro, Steudler, Melillo, Aber, & Bowden, 1995); however, this increase in MAT would also reduce methanotrophs abundance (Nazaries, Karunaratne, Delgado-Baquerizo, Campbell, & Singh, 2018) and/or inhibit the action of the enzymes involved in the CH_4 oxidation (Aronson et al., 2013), which may result in a reduced CH_4 uptake. Moreover, MAT and MAP act in an additive form to control CH_4 flux (positive and significant MAP x MAT effect, Figures 2a and S3), indicating that concomitant increases in temperature and precipitation would favour CH_4 emission or reduce CH_4 uptake. This additive effect is expected because the join action of several non-exclusive mechanisms, including reduced CH_4 oxidation by declines in enzyme activity, fail in competing for O_2 of methanotrophs and reduced CH_4 diffusion under soil water saturation, and favoured methanogenesis in a warmer and anoxic environment (Aronson et al., 2013; Del Grosso et al., 2000; Serrano-Silva et al., 2014). Overall, our results indicate that the probability of soil CH_4 uptake in forests increases at middle range precipitation (1500 – 2500 mm/yr) and middle temperature (0 – 18 ºC), but decreases towards either low precipitation (< 680 mm/yr) or high-temperature conditions (above MAT of 18.3ºC) (Figure S3 and S4).

We also found a negative influence of soil pH and positive effects of soil organic carbon and bulk density on soil CH_4 flux, indicating that reduced CH_4 uptake occurs in forests with soil acidification and higher soil carbon stock and compaction. Reduced CH_4 oxidation with decreasing in soil pH (soil acidification) may be associated to that methanotrophs are sensitive to acid conditions, possibly related to increases in concentrations of heavy metals (such as Al^{3+}) whose toxicity inhibit the methanotrophs activity (Le Mer & Roger, 2001; Weslien, Kasimir Klemedtsson, Börjesson, & Klemedtsson, 2009; Zhang et al., 2014). On the other hand, increases in soil organic carbon promote increments in microbial carbon decomposition and respiration which, in turn, may favour CH_4 production over CH_4 oxidation (Tate, 2015; Verchot, Davidson, Cattânio, & Ackerman, 2000; Wanyama et al., 2019). In contrast, the effects of bulk density on soil CH_4 flux have a physical origin, altering the capacity of gases diffusion in soils which lead to an environment limited by O_2 (*i.e.* anaerobic) (Del Grosso et al., 2000; Wanyama et al., 2019). Importantly, our best-fitting model showed that standardized coefficients of both soil organic carbon and bulk density were above 0.20, representing changes in net CH_4 flux of at least 20 %

along soil fertility and aeration gradients. Consistent with Yu et al. (2017), these results provide evidence that soil variables could explain orthogonal variations of soil CH_4 flux unexplained by climate drivers. Regarding limitations of our approach, it is important to note that in this study we used soil variables at 1 km of spatial resolution, which may not reflect accurate soil attributes at the local scale where *in situ* measurements were collected. Although this approach allows us to avoid biases associated with having multiple methodological soil determinations, units of measurements and missing data, it probably limited the explanatory power of our model.

Our study suggests that the indicators of human footprint or pressure have less support than soil and climate variables explaining the spatial variation in soil CH_4 flux in forests worldwide. This result contrasts with a recent global meta-analysis which showed that soil CH_4 uptake decreases by conversion from primary to secondary forest (*i.e.* degraded condition) or reforestation (*i.e.* mono-specific plantation) (Han & Zhu, 2020). Our results also contrast with empirical studies showing that soil CH_4 uptake is favoured in aging afforestation compared with recent afforestation and pasture or cropland (Fest, Wardlaw, Livesley, Duff, & Arndt, 2015; Hiltbrunner et al., 2012; Priano et al., 2014; Verchot et al., 2000; Wanyama et al., 2019) . These differences may be explained by two reasons; on the one hand, our study compares forests under different land-use categories among geographically distant sites, while the above-cited articles made comparisons within the same site. Therefore, among-site environmental differences are relatively more important than within-site differences in land-use in our study. On the other hand, the effects of land-use on soil CH_4 flux are partially explained by changes in soil variables related to bulk density and soil organic carbon (Han & Zhu, 2020; Hiltbrunner et al., 2012). Possibly, at a global scale, human pressure impact on soil CH_4 flux may be overridden by large scale environmental gradients, while land-use impact may be important at a local scale, as shown by Han & Zhu (2020).

4.2. Differences in soil CH_4 fluxes among biomes

We found that both the direction and magnitude of the effects of climatic and soil drivers on soil CH_4 flux varied among biomes. This result concurs with our second hypothesis and possibly is related to among-biomes difference in factors that act limiting the biological activity of methanotrophs and methanogens (Aronson et al., 2013).

In Boreal forests, and in contrast to our expectation of a positive temperature influence on CH_4 uptake, spatial variations in soil CH_4 flux were associated with soil drivers but not with climatic drivers. When the temperature is predominantly low, both CH_4 and O_2 diffusion into soils are not limited, but biological oxidation is limited due to low microbial activity (Fang et al., 2010; Tang et al., 2020). Thus, in Boreal forests, CH_4 oxidation would be enhanced when soil variables may promote microbial activity such as an increase of carbon substrate (high SOC) in addition to alkaline soil conditions (high pH) (Fang et al., 2010; Ullah, Frasier, Pelletier, & Moore, 2009; Ullah & Moore, 2011).

Temperate forests showed high sensitivity to all studied drivers but MAT. However, temperature and precipitation act synergistically promoting soil CH_4 emission when both variables are high (see MAP x MAT interaction in Fig. 3c). This pattern has been described previously for temperate forests and could be a result of limited methanotrophy activity due to the combined effect of high temperature and reduced O_2 by soil water saturation (Aronson et al., 2013). In tropical forests, the soil CH_4 emission was also promoted by the joint effect of high MAP and MAT. However, in contrast to the temperate forests, precipitation has no effect on CH_4 fluxes whereas temperature did present a negative influence. The low sensitive of tropical forests to MAP could be due to they are systems not limited by soil water, being other factors more limiting. In these systems, high temperature could increase soil evaporation, thus favouring CH_4 diffusion and uptake (Fang et al., 2010). Subtropical forests showed intermediate responses among temperate and tropical forests, with strong and positive effect of MAT promoting soil CH_4 emission.

Soil CH_4 flux in savannas was insensitive to variations in mean annual precipitation, even when these systems are highly limited by soil water. This suggests that the mean annual input of water is not a relevant indicator of ecosystem functioning, being the magnitude and temporal distribution of rain pulses a better predictor of biological activity (Williams, Hanan, Scholes, & Kutsch, 2009). Moreover, although drought conditions could favour CH_4 uptake by enhancing gas diffusion into the soils (Aronson et al., 2013; Liu et al., 2019), where soil conditions are predominantly dry such as in savannas, methanotrophs sustain a reduced metabolic activity and, consequently, a low CH_4 consumption (Galbally, Kirstine, Meyer, & Wang, 2008). As in other subtropical systems, CH_4 fluxes in the savanna were positively related with MAT, and presented a negative interaction between MAP and MAT. These similar responses to climatic variables may be due that both savannas and subtropical forests are mostly located in similar geographic regions (Fig 1a).

However, their responses to edaphic drivers were different between subtropical forests and savannas, highlighting the role of soil conditions on the structure of these last ecosystems (Ratnam et al., 2011). The net CH_4 emission in the savannas could be the result of a sustained methanogenic activity in deep anaerobic soil depths, but this hypothesis needs to be tested with measurements focused on these particular systems.

The most intriguing results were two general different patterns observed: a) the boreal forests have similar average CH_4 fluxes than most of the studied biomes (Figure 2b), but their responses to environmental drivers differed from them (Figure 3c), while savannas have a different average CH_4 flux (Figure 2b) than the other systems, with net positive values (emission), but their general responses to the drivers were similar than those observed in some of the biomes (Figure 3c). The most inconsistent response of CH_4 fluxes to the studied drivers among the biomes was observed in relation to MAT, which could be due to, at least in part, the different optimal temperature for soil CH_4 oxidation of methanothrophs in the different biomes (Kalyuzhnaya, Gomez, & Murrell, 2019), which increases from low to middle latitude regions (Cai & Yan, 1999; Castro et al., 1995; Fang et al., 2010), and as well as by changes in methanotropic community composition (and consequently, their ability of CH_4 oxidation) (Zeng et al., 2019).

4.3. Conclusions and final remarks

Our study showed that net CH_4 fluxes in forests soils result from the simultaneous influence of multiple environmental drivers related to climate and soil variables, with a low direct impact of anthropogenic disturbance. The effects of different factors such as mean annual precipitation and temperature, soil organic carbon, pH and texture on net CH_4 flux had previously been identified in quantitative and qualitative reviews (Dutaur & Verchot, 2007; Feng et al., 2020; Han & Zhu, 2020; Le Mer & Roger, 2001; Tate, 2015); nevertheless, evaluations integrating simultaneous determinants has received less attention (but see Fang et al., 2010 for a regional analysis; and Yu et al., 2017 for a global example). Additionally, we quantified for the first time that, to different biomes, the main climatic and soil variables that determine the magnitude and direction of soil CH_4 fluxes are not the same.

The biome-specific relationship between soil CH_4 flux and environmental drivers identified in this study has important implications for global change impact on forests worldwide. We found that temperature was a significant driver of CH_4 fluxes both at global and biome scales. However, its influence was different on the different biomes, suggesting that the increase in temperature predicted in the framework of climate change would promote CH_4 emission (or at least, reduce the soils CH_4 sink potential) in subtropical and savannas forests, have no influence in boreal and temperate forests and promote uptake in tropical forests.

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Data Sharing and Data Accessibility

The data that support the findings of this study are openly available in figshare at https://doi.org/10.6084/m9.figshare.12860750.v1.

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Table 1. Summary of the different environmental drivers that have been identified to affects soil CH_4 flux in forest ecosystems at regional and at global scale. Response in our study is based on net CH_4 flux and, therefore, negative flux is considered CH_4 uptake.

Type	Predictor	Response	Mechanism	Ref.
Climatic	Mean annual precipitation (MAP)	Unimodal negative	Oxidation is limited by gas diffusion at higher water availability and by biological activity at water stress conditions	1; 3; 4
	Mean annual temperature (MAT)	Linear positive	Higher temperature reduces the biological activity of methanotropic bacteria, which are more sensitive to temperature than methanogenics	5; 6; 7
	MAP x MAT	Positive	Effects of MAP depend on levels of MAT, with stronger and positive MAP effect under warm conditions	5
Soil	Bulk density	Linear positive	Limit the gas diffusion and oxygenation when soils are more compacted due to increases in water retention.	3; 4; 8
	Sand content	Linear negative	Increases water drainage favouring soil oxygenation and CH_4 oxidation	4
	Organic content	Linear negative	Directly, promote the availability of mineralised carbon and, consequently, stimulate the methanogenic activity. Indirectly, increase water retention	4; 8
	Nitrogen content	Linear positive	Higher N content inhibit methanotrophy, because they compete for N soil with ammonia oxiders organisms	5
	pH	Linear positive	Increases in acidification reduce methanotrophy activity and CH_4 uptake, as well as, modifying the structure of methanotrophic community	9; 10
Human footprint	Land Use		CH_4 fluxes vary among land use forest, being higher in primary forest than secondary forest or reforestation and afforestation; and increase with	11; 12; 13

			time since land-use change occurred.	
	Urbanization	Linear negative	Reductions in CH_4 uptake are associated with the direct environmental changes driven by urbanization (atmospheric N deposition and toxic compounds affecting the methanotrophy; and indirect effects on soil water balance and regulation).	10; 14; 15

References (Ref.): 1 - Curry, 2007; 2 - Liu et al., 2019; 3 - Ridgwell et al., 1999; 4 - Yu et al., 2017; 5 - Aronson et al., 2013; 6 - Dijkstra et al., 2012; 7 - Dutaur & Verchot, 2007; 8 - Del Grosso et al., 2000; 9 – Weslien et al., 2009; 10 - Zhang et al., 2014; 11 - Han & Zhu, 2020; 12 - Hiltbrunner et al., 2012; 13 – Benanti et al. 2014; 14 - Ni & Groffman, 2018; 15 - Goldman et al., 1995

Table 2. Summary of model comparison and selection based on Akaike information criterion (AIC) for evaluate the influences of multiple climate, soil and human pressure drivers on soil CH4 flux in forest worldwide. Each model includes different combinations of climate (mean annual precipitation and temperature, and their interaction), soils (soil organic carbon, soil total nitrogen, bulk density and pH) and human pressure indicators (age of plantation, time of fire and human influence index). The last two columns shows variance explained by considering fixed predictor (marginal, mR^2) and by considering fixed plus random factors (conditional, cR^2). Random factor included in all models correspond to biome (see Figure 1).

Models	df	AIC	ΔAIC	w_i	mR^2	cR^2
Soil + Climate	13	1301.6	0	0.97	0.15	0.17
Soil + Climate + Human footprint	25	1308.9	7.2	0.03	0.18	0.21
Climate	7	1315	13.4	0.001	0.09	0.11
Climate + Human footprint	20	1318.9	17.3	<0.001	0.14	0.15
Soil	8	1330.2	28.6	<0.001	0.05	0.10
Soil + Human footprint	20	1335.3	33.7	<0.001	0.08	0.14
Null	3	1343.2	41.6	<0.001		0.05
Human footprint	15	1345.7	44	<0.001	0.04	0.10

Table 3. Summary of the comparison and selection of models based on Akaike information criterion (AIC) to evaluate whether the effects of the significant climate and soil predictors on soil CH4 flux varied among biomes. The random intercept and slope model included the same combinations of fixed factors of the best model (random intercept model see Table 2 and S1), but their random structure allows to partial regression coefficients of significant predictors vary among biomes. The last two columns show variance explained by considering fixed predictor (marginal, mR^2) and by considering fixed plus random factors (conditional, cR^2).

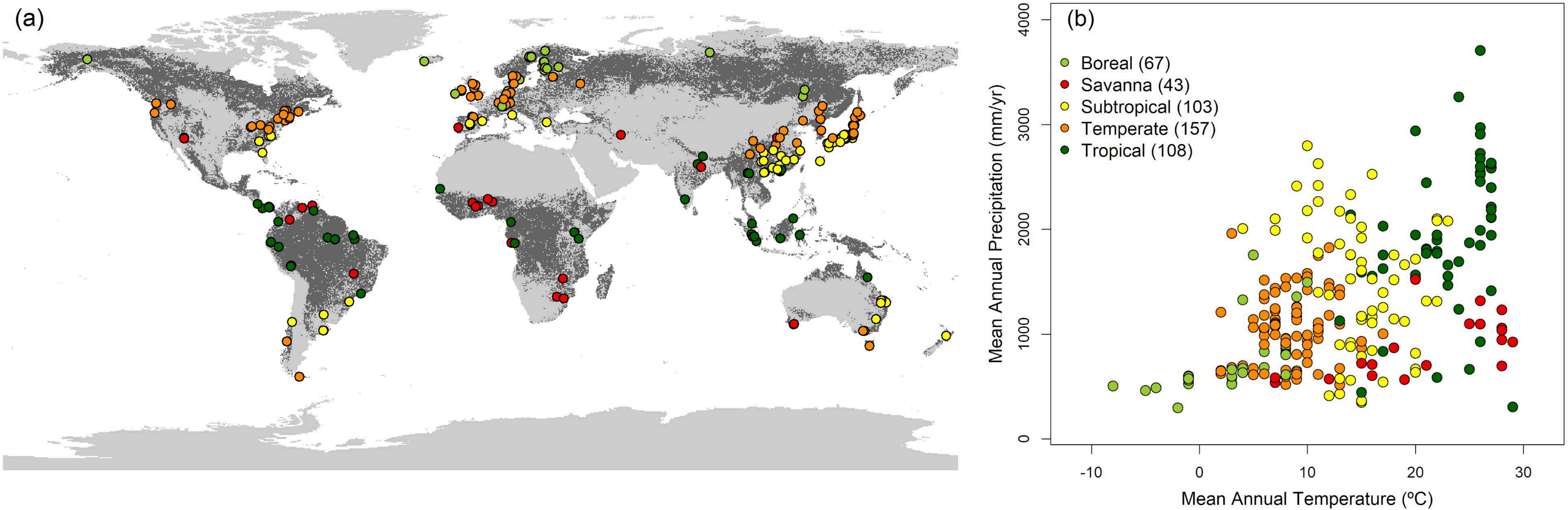
Models	df	AIC	ΔAIC	w_i	mR^2	cR^2
Random intercept and slope model	40	1342.2	0	0.66	0.08	0.34
Random intercept model	13	1344.5	2.3	0.21	0.15	0.19
Null model	3	1345.5	3.3	0.13	0.07	

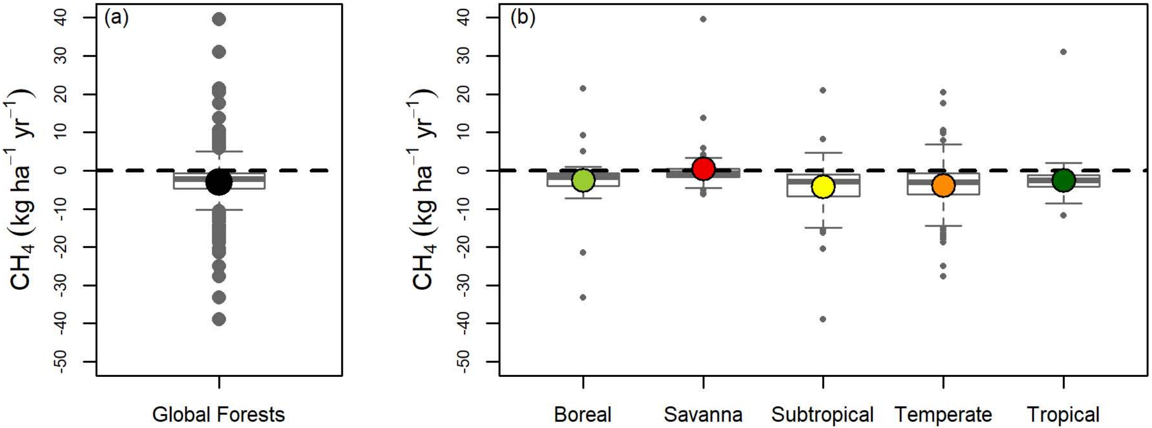
Figure captions

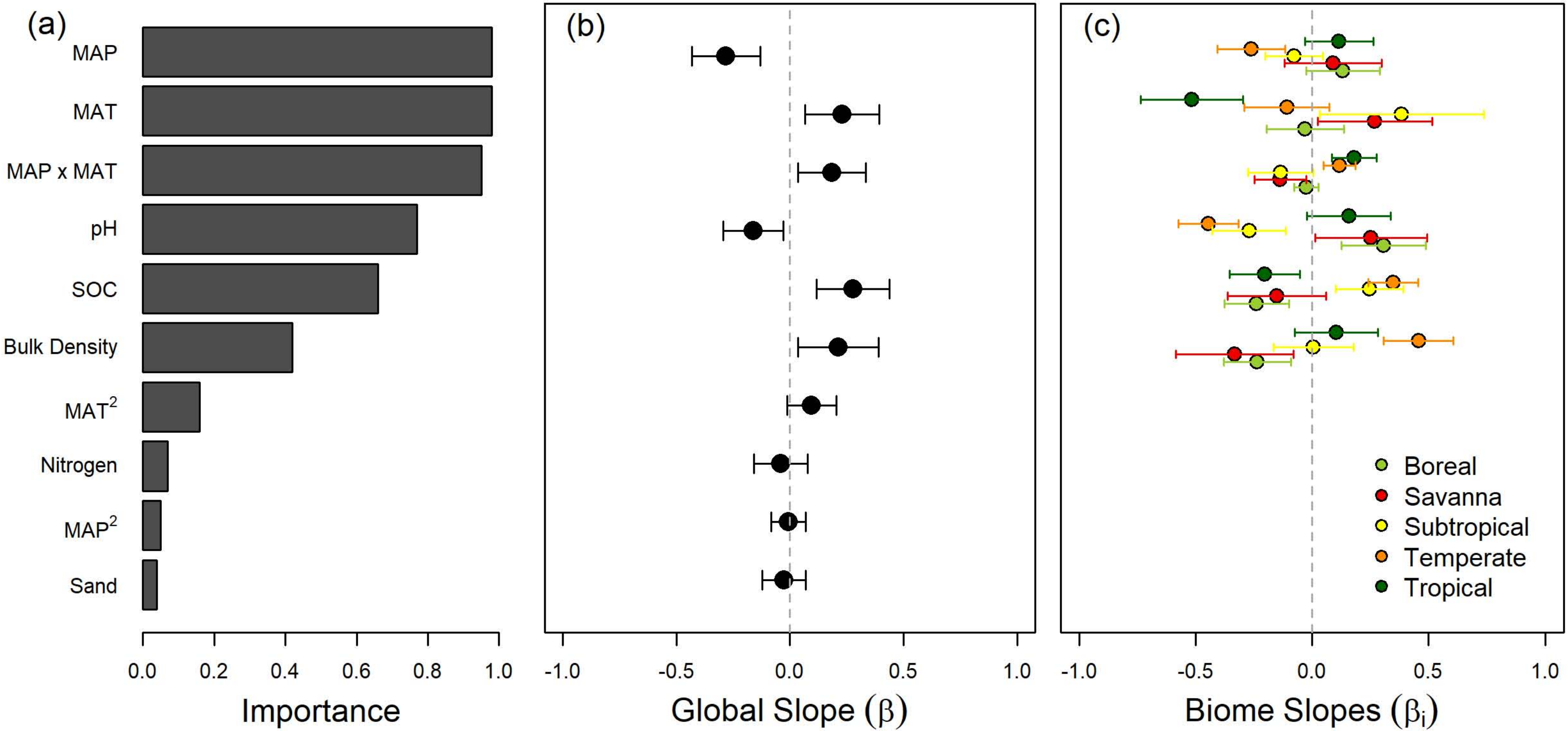
Figure 1. (a) Geographic location of the measurement sites included in this survey, and (b) their climatological distribution considering mean annual temperature and mean annual precipitation. Dark grey shades in (a) show the spatial distribution of the world forests according to FAO. Colour dots in both panels indicate the correspondence between each observational site and biome categories according to Whittaker classification.

Figure 2. Measured annual *in situ* soil CH_4 flux in forests at global and biome scales. Boxplots show 25th and 75th percentiles and the median is showed as horizontal lines within the boxes. The whiskers indicate the 10th and 90th percentiles. Mean values are showed by coloured dots.

Figure 3. Summary of the importance and effects of the climatic and soil drivers on soil CH_4 flux at global and biome scales. (a) The relative importance of each predictor explaining spatial variations in soil CH_4 flux at global scale. (b) Regression coefficients of each predictor included in the best model (see Table 2) at global scale and (c) at biome scale. Whiskers in (b) and (c) represent the 95% of confidence intervals.


(a)
(b)
Boreal (67)
Savanna (43)
Subtropical (103)
Temperate (157)
Tropical (108)
Mean Annual Precipitation (mm/yr)
0
1000
2000
3000
4000
Mean Annual Temperature (ºC)
-10
0
10
20
30


(a)
(b)
CH$_4$ (kg ha^{-1} yr^{-1})
40
30
20
10
0
-10
-20
-30
-40
-50
Global Forests
Boreal
Savanna
Subtropical
Temperate
Tropical


(a)
MAP
MAT
MAP x MAT
pH
SOC
Bulk Density
MAT^2
Nitrogen
MAP^2
Sand
0.0
0.2
0.4
0.6
0.8
1.0
Importance
(b)
-1.0
-0.5
0.0
0.5
1.0
Global Slope (β)
(c)
Boreal
Savanna
Subtropical
Temperate
Tropical
-1.0
-0.5
0.0
0.5
1.0
Biome Slopes (β_i)