

Climate impact on mean annual cycle and interannual variability of CO₂ fluxes in European DBF and ENF forests: insights from observations and state-of-the-art data-driven and process-based models

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Abstract.

The impact of climate on the annual cycle and interannual variability of CO₂ fluxes is assessed in European evergreen needleleaf (ENF) and deciduous broadleaf (DBF) forests using observations from 19 sites alongside process-based and data-driven model outputs. We first evaluate the models' ability to reproduce observed patterns before using them as complementary tools to investigate climate influences. All models capture the temporal phasing of CO₂ fluxes, including the shorter CO₂ sequestration period in northern than southern Europe, the more pronounced annual cycle for DBFs than ENFs in central Europe, and strong interannual variability across all sites. However, they struggle to accurately reproduce the magnitude of observed fluxes, generally underestimating both sequestration strength and interannual variability. Across all datasets, CO₂ sequestration is favored under relatively hot and dry conditions from late spring to early fall. The coupling between climate and CO₂ fluxes is, however, stronger in northern and central Europe than in southern Europe, where climate seasonality is less pronounced. At the interannual timescale, the climate impact on observed CO₂ fluxes appears spatially noisy due to limited temporal coverage and differences in data availability across sites. Despite uncertainties, the models provide a clearer picture of climate influences, revealing spatial and seasonal variations. Atmospheric factors (i.e., 2 m temperature and vapor pressure deficit) primarily drive interannual CO₂ flux variability in northern and central Europe, whereas soil moisture plays a dominant role in southern Europe. Winter and fall CO₂ release increases with elevated temperature and VPD in northern and central Europe but under low VPD in southern Europe. In northern and central Europe, CO₂ sequestration is enhanced by anomalously hot and dry conditions in spring, while by anomalously cold and wet conditions in summer. In southern Europe, CO₂ sequestration is also favored by anomalously cold and wet conditions from May to September.

Key words: Net ecosystem exchange, gross primary production, ecosystem respiration, climate, annual cycle, interannual variability, DBF, ENF

a supprimé: This study evaluates two process-based (LPJ-GUESS and SMAP-L4C) and two data-driven (CarbonSpace and FLUXCOM) models to capture the temporal variability of CO₂ flux exchanges (GPP, RECO and NEE) of evergreen needleleaf and deciduous broadleaf forests (ENFs and DBFs) in temperate western Europe and its relationship with climate. Three sites from the FLUXNET network are considered together with two non-instrumented sites located in Burgundy (North-East France). The focus is put on the representation of the annual cycle, annual budget, interannual variability and “long-term” trend. The data-driven models are the best models for representing the mean annual cycle and mean annual budget in CO₂ fluxes despite magnitude uncertainties. In particular, the models accounting for plant functional types in their outputs tend to simulate more marked annual cycle and lower annual CO₂ sequestration for DBFs than ENFs in Burgundy. At the interannual timescale, the CO₂ flux – climate relationship is stronger for GPP and RECO than NEE, with increased CO₂ fluxes when 2 m temperature, vapor pressure deficit and evapotranspiration increase and when precipitation and soil moisture decrease. The models forced by dynamic climate conditions clearly outperform those driven by static climate conditions. The “long-term” trend is not obvious for NEE neither in the observations nor in the simulations, partly because both GPP and RECO tend to increase in western Europe. Our results suggest that the spatial resolution of the climate drivers is likely very important for capturing spatial and temporal patterns in CO₂ exchanges and point towards the need to choose the appropriate model and spatial resolution according to the scientific question to deal with.

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1 Introduction

Forest ecosystems are the largest part of the land CO₂ sink (Lindeskog et al., 2021), with up to 20-50% of anthropogenic CO₂ emissions (land-use changes excluded) sequestered for the 2000-2010 period (Le Quéré et al., 2018; Pugh et al., 2019; Pan et al., 2024). In Europe, recent estimations suggest a slight increase in CO₂ sequestration by forest ecosystems over the 2000-2021 period mainly due to the fertilization effect of increased atmospheric CO₂ concentration (Prentice et al., 2001; Piao et al., 2009; Schimel et al., 2015; Walker et al., 2020; Sitch et al., 2024). This trend remains, however, weak, because the fertilization effect has almost been compensated by a decrease in CO₂ sequestration induced by climate change (Sitch et al., 2024). The extent to which climate controls CO₂ flux exchanges between the atmosphere and European forest ecosystems is thus a burning question in the context of climate change.

Numerous studies have demonstrated the strong influence of climate on CO₂ exchanges between the atmosphere and forest ecosystems. The annual cycle, and to a lesser extent, interannual variability of these fluxes, are driven by factors such as incident shortwave radiation, temperature, atmospheric evaporative demand, and the water cycle, including soil moisture dynamics (Haszpra et al., 2005; Tang et al., 2014; von Buttlar et al., 2018; Kong et al., 2022; Sharma et al., 2022; Li et al., 2023; Xu et al., 2023). The dominant climate factor influencing CO₂ fluxes depends on the specific component considered. The variability in net ecosystem exchanges (NEE) is a mixed response of its two components: gross primary production (GPP), which sequesters CO₂ into the ecosystem through photosynthesis, and ecosystem respiration (RECO), which releases CO₂ into the atmosphere from forest metabolism (autotroph respiration) and the decomposition of organic matter by fungi and bacteria (heterotrophic respiration). GPP is primarily driven by vapour pressure deficit (VPD), shortwave radiation, temperature, and soil moisture, while RECO is mainly influenced by precipitation, soil moisture, and temperature (Messori et al., 2019).

The influence of climate on CO₂ fluxes also depends on several additional factors, with seasonality playing a crucial role. Severe heat waves and droughts acted to reduce CO₂ sequestration in summer at the Europe-wide scale in 2003 (Ciais et al., 2005), in northern Europe in 2018 (Smith et al., 2020; Thompson et al., 2020) and in central and southeastern Europe in 2022 (van der Woude et al., 2023). On the other hand, anomalously high temperature under normal soil moisture conditions in spring set favourable growth conditions, hence increased CO₂ sequestration, such as in northern Europe in 2018 (Smith et al., 2020). The climatic zone under consideration is also a key factor. For instance, GPP is mostly influenced by soil moisture in the Mediterranean region, VPD over parts of central Europe and temperature over Scandinavia, parts of eastern and south-eastern Europe and higher elevations (Seddon et al., 2016; Madani et al., 2017). The influence of climate on CO₂ flux exchanges is further shaped by various factors, including soil properties (Kurbatova et al., 2008; Besnard et al., 2018; Curtis and Gough, 2018; Martinez del Castillo et al., 2022), forest management practices (Carrara et al., 2003; Saunders et al., 2012), tree age (Kurbatova et al., 2008; Besnard et al., 2018) and tree species (Carrara et al., 2003; Carrara et al., 2004; Welp et al., 2007; Kong et al., 2022).

Assessing the impact of climate on CO₂ flux exchanges remains challenging. The main reason involves the scarcity of multi-year CO₂ fluxes measured by eddy covariance above the canopy (Burba, 2021). At the European scale,

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a supprimé: Among all their environmental benefits, forest

a supprimé: efficient carbon sinks and constitute a potential lever for climate change mitigation. At the global scale, forest ecosystems cover about 30% of landmasses. They represent

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a supprimé: . Despite the fertilization effect of increased atmospheric CO₂ concentrations (Walker et al., 2020; IPCC, 2023) and the warming-induced lengthening of the growing season (Prislan et al., 2019; Menzel et al., 2020; IPCC, 2023), the evolution in the net ecosystem exchange (NEE) suggests a recent decrease of annual CO₂ storage in forest ecosystems of temperate Europe, due to severe heat waves and droughts that affected Northern regions in 2018 and Central-Southeastern regions in 2020 (Smith et al., 2020; Thompson et al., 2020; van der Woude et al., 2023). This trend results from a combination of multiple factors. In France, for instance, the CO₂ storage by forests dropped from ~53 Mt CO₂ year⁻¹ to ~32Mt CO₂ year⁻¹ between 2005-2013 and 2012-2020, mostly due to increased timber-extraction (+20%), climate-related mortality (+54%) and decreased biological production (-10%) (IGN, 2022; Chuine et al., 2023). Such a continental-to-country scale evolution of forest-related CO₂ fluxes needs to be refined at a finer spatial grain to better account for the contributing influence of different forest stands and to clarify the role of forest ecosystems in the CO₂ budget at a territorial level and their leverage in mitigating climate change impacts. A territorial-scale assessment remains, however, challenging. Measuring NEE and its two components, gross primary production (GPP) quantifying CO₂ sequestration through photosynthesis and ecosystem respiration (RECO) releasing CO₂ through autotrophic and heterotrophic processes, is expensive since it requires the installation and maintenance of flux towers measuring eddy covariance above the canopy (Burba, 2021). The FLUXNET initiative provides over 1500 site-years of quality-controlled flux tower data from 212 sites around the globe, using the same ONEflux processing pipeline to foster inter-site comparisons (Pastorello, 2020).

the Integrated Carbon Observation System (ICOS) network provides standardized and open data from 98 ecosystem stations across 16 countries. The flux lower measurements remain limited in number and temporal depth and unevenly distributed spatially, making it difficult to assess the impact of climate on the interannual variability (and trend)s in CO₂ flux exchanges and to map them. Process-based and data-driven models allow us to tackle the above limitations. Process-based models, such as dynamical vegetation models, are routinely used to assess CO₂ flux exchanges between the atmosphere and the biosphere (Friedlingstein et al., 2023). These are mechanistic models (Friedlingstein et al., 2006; Sitch et al., 2008) allowing for testing the response of CO₂ fluxes to individual and combined forcing (Sitch et al., 2024). Data-driven models rely on the identification of statistical relationships between flux tower measures by eddy-covariance and corresponding land use, vegetation properties and climate characteristics. Based on these statistical relationships, empirical models are built and used for upscaling, i.e., for assessing CO₂ fluxes in regions where they are not measured (Tramontana et al., 2016; Jung et al., 2019; Jung et al., 2020; Zhuravlev et al., 2022). Both approaches have limitations. Estimations of CO₂ flux exchanges are highly sensitive to physical parameterizations (Cai and Prentice, 2020) and atmospheric forcing (Wu et al., 2017; Hardouin et al., 2022) in process-based models. The reliability of data-driven models is limited by the sparse and uneven distribution of flux tower measurements, and by the underlying statistical methods used to build them (Jung et al., 2020). While not perfect, process-based and data-driven models provide satisfactory results for capturing large-scale patterns compared to e.g. satellite estimations (Wang et al., 2023). This makes them valuable complementary tools to observational data.

Most recent studies examining the influence of climate on the temporal dynamics of European forest CO₂ fluxes rely on case studies and primarily focus on spring and summer conditions (Smith et al., 2020; Thompson et al., 2020; van der Woude et al., 2023). However, a more comprehensive assessment is needed across the entire annual cycle, as CO₂ release during fall and winter is expected to increase under climate change. Additionally, climate conditions vary significantly between northern and southern Europe, necessitating a broader spatial perspective. These objectives are addressed at the monthly timescale, which is considered sufficiently fine to capture both the CO₂ flux annual cycle and its interannual variability.

This study addresses these gaps by investigating the impact of climate on both the annual cycle and interannual variability of CO₂ fluxes in European evergreen needleleaf (ENF) and deciduous broadleaf forests (DBF). Using ICOS network observations alongside state-of-the-art data-driven and process-based model estimates, we first characterize the observed annual cycle and interannual variability of CO₂ fluxes across Europe. We then evaluate model performance in capturing the temporal phasing and magnitude of these fluxes at the site scale. Finally, we assess the influence of climate on both seasonal and interannual CO₂ flux variations, leveraging the extended temporal coverage provided by models.

2 Materials & Methods

2.1 Site description

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a supprimé: This study aims at comparing the respective strengths and limitations of process-based and data-driven approaches to capture the recent temporal dynamics of CO₂ flux exchanges observed in western European temperate forest ecosystems, with a focus on evergreen needleleaf forests (ENFs) and deciduous broadleaf forests (DBFs). The first objective is to discuss their capability to simulate the mean state, interannual variability and trend in NEE and, when available, GPP and RECO. Previous observation-based studies have shown that CO₂ flux exchanges depend on multiple factors not necessarily related to climate such as soil properties (Kurbatova et al., 2008; Besnard et al., 2018; Curtis and Gough, 2018; Martinez del Castillo et al., 2022), forest management practices (Carrara et al., 2003; Scott et al., 2004; Saunders et al., 2012), tree age (Kurbatova et al., 2008; Besnard et al., 2018; Chuine et al., 2023) and tree species (Carrara et al., 2003, 2004; Welp et al., 2007; von Buttlar et al., 2018; Zheng et al., 2021; Kong et al., 2022) among many others. On average, the annual cycle of CO₂ flux exchanges significantly differs between ENFs and DBFs since photosynthesis can occur all year long in the former, while is bounded from spring (bud break) to fall (leaf senescence) in the latter. As a result, DBFs tend to be a net CO₂ sink during (... [1]

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Out of the 24 ENF and DBF sites from the ICOS network, we selected the 19 sites (Fig. 1), 13 classified as ENF and 6 as DBF, for which observed CO₂ fluxes are available for at least 5 years (Table 1). These sites allow to sample the different climatic zones of Europe. Three ENF sites (FR-Bil, FR-FBn and IT-SR2) are located in the northern region of southern Europe, close to 45°N, and ranging from sea level to 400 m in elevation. They are characterized by mild, wet winters and hot dry summers, with annual mean temperature and precipitation of 12.9–13.90 °C and 700–960 mm, respectively. Four ENF sites (FI-Hyy, FI-Let, SE-Nor and SE-Svb) are located in northern Europe (60–65°N) at an elevation below 270 m. They are characterized by subarctic climate with annual mean temperature and precipitation of 1.8–6.5 °C and 586–711 mm, respectively. The remaining twelve sites (6 DBFs and 6 ENFs) are situated in central Europe within the 45–60°N, 2.5–20°E domain, encompassing a wide range of elevations (40–1730 m) and spanning temperate to continental climates. As a result, they exhibit substantial variability in annual mean temperature (4.3–11.4 °C) and precipitation (563–1338 mm).

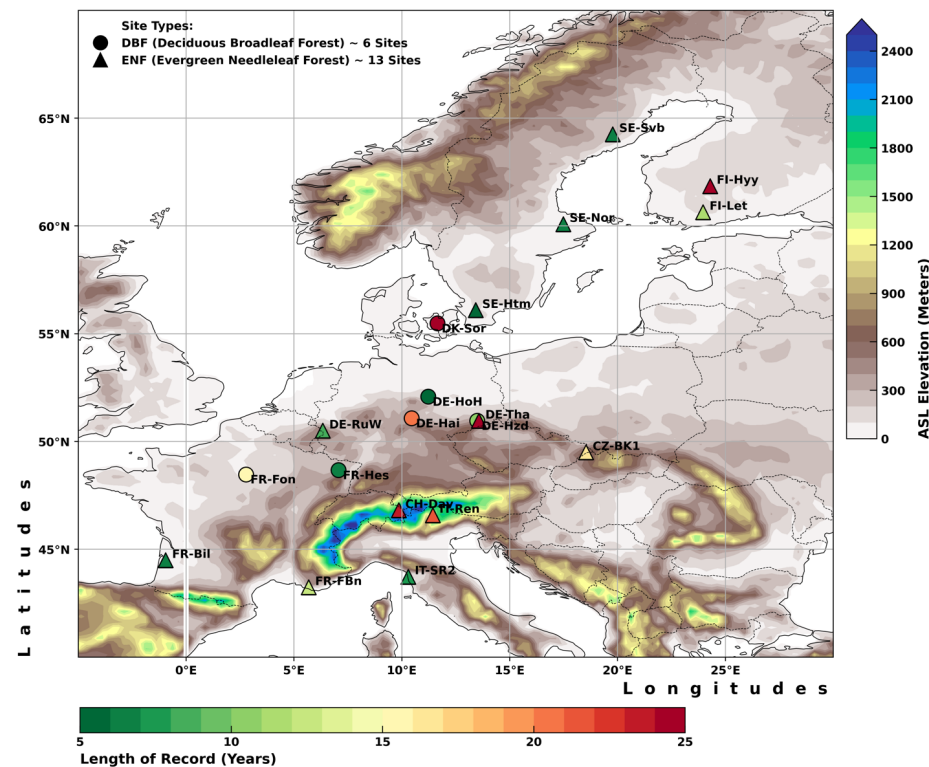


Figure 1. Location of the CO₂ flux measurement sites from the FLUXNET network across Europe selected for this study. The symbol “●” corresponds to the 6 sites located in Deciduous Broadleaf Forest (DBF) while the symbol “▲” indicates the 13 sites located in the Evergreen Needleleaf Forests (ENF). The vertical colour scale represents the terrain height (ASL) in meters. The horizontal colour scale indicates the length of the CO₂ flux record for each site. The elevation layer comes from National Geophysical Data Center/NESDIS/NOAA/U.S. Department of Commerce (1995): TerrainBase, Global 5 Arc-minute Ocean Depth and Land Elevation from the US National Geophysical Data Center (NGDC), <https://doi.org/10.5063/E08M-4482>. Distributed under CC by 4.0.

a supprimé: This study focuses on five forest sites: two non-instrumented sites in northeastern France where NEE, GPP and RECO are simulated by process-based and data-driven models, and three sites from the FLUXNET network where NEE is measured and GPP and RECO are calculated (Fig. 1).

The first non-instrumented site is located in the National Park of Forests, a 240,000 ha park mostly covered by DBFs (50%). One DBF plot of 25 ha is selected because soil respiration measures are conducted there by the Biogéosciences laboratory since 2020. This DBF plot, named “Châtillonnais (DBF)” hereafter, is located on a ~380 m plateau and characterized by uneven-aged and mixed DBFs dominated by beech (*Fagus sylvatica*) and oaks (*Quercus robur*, *Quercus petraea*) with no silvicultural interventions for ~30 years and by oolitic limestone soils. The second site is located in the Regional Natural Park of Morvan, on the Mont Beuvray, a semi-mountainous domain of 950 ha peaking at 821 m and sitting on volcanic-sedimentary rocks. The Mont Beuvray location is particularly impacted by climate change (Castel et al., 2019), with a mean warming trend reaching 2°C more than the neighboring lowlands over the 1958–2015 period. Two plots are considered for Mont Beuvray: one even-aged large-sized Douglas fir (*Pseudotsuga menziesii*) plots of 15 ha classified as ENF and one even-aged beech plot with continuous cover of 8 ha classified as DBF. These plots are named “Mont Beuvray (DBF)” and “Mont Beuvray (ENF)” hereafter.

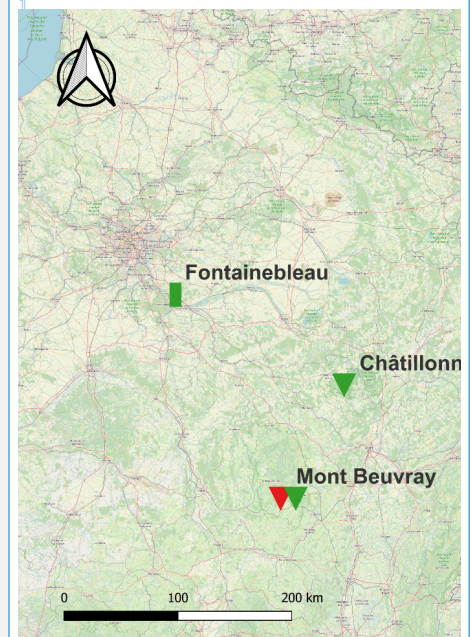


Figure 1: Location of the study sites. The rectangles correspond to FLUXNET sites where CO₂ fluxes are measured by eddy covariance flux towers and estimated ... [5]

Table 1. European FLUXNET sites examined in this study.

Site Name	Site ID	Latitude (°North)	Longitude (°East)	Elevation (Meters)	Land cover	Period of record	Length of record (Years)	MAT (°C)	MAP (mm)
<i>Northern Europe (Above 60°N)</i>									
Svartberget	SE-Svb	64.25611	19.7745	267	ENF	2014/01 – 2020/12	7	1.8	614.0
Hyytiälä	FI-Hyy	61.8474	24.2948	181	ENF	1996/01 – 2020/12	25	3.5	711.0
Lettosuo	FI-Let	60.6418	23.9595	111	ENF	2009/01 – 2020/12	12	4.6	627.0
Norunda	SE-Nor	60.0865	17.4795	45	ENF	2014/01 – 2020/12	7	6.5	586.0
<i>Central Europe (45°N – 60°N)</i>									
Hyltemossa	SE-Htm	56.09763	13.41897	115	ENF	2015/01 – 2020/12	6	7.4	707.0
Soroe	DK-Sor	55.4859	11.6446	40	DBF	1996/01 – 2020/12	25	9.0	640.0
Hohes Holz	DE-HoH	52.08656	11.22235	193	DBF	2015/01 – 2020/12	6	9.1	563.0
Hainich	DE-Hai	51.0792	10.4522	430	DBF	2000/01 – 2020/12	21	8.3	744.0
Hetzdorf	DE-Hzd	50.96381	13.48978	395	DBF	2010/01 – 2020/12	11	7.6	877.0
Tharandt	DE-Tha	50.9626	13.5651	385	ENF	1996/01 – 2020/12	25	8.1	829.0
Wustebach	DE-RuW	50.50493	6.330962	610	ENF	2012/01 – 2020/12	9	7.5	1250.0
Bily Kriz	CZ-BK1	49.5021	18.5369	875	ENF	2004/01 – 2020/12	17	6.2	1338.1
Hesse	FR-Hes	48.6741	7.06465	310	DBF	2014/01 – 2020/12	7	10.0	889.0
Fontainebleau- Barbeau	FR-Fon	48.4764	2.7801	103	DBF	2005/01 – 2020/12	16	11.4	678.9
Davos	CH-Dav	46.8153	9.8559	1639	ENF	1997/01 – 2020/12	24	4.3	876.0
Renon	IT-Ren	46.5869	11.4337	1730	ENF	1991/01 – 2020/12	22	4.9	970.8
<i>Southern Europe (Below 45°N)</i>									
Bilos	FR-Bil	44.49365	–0.95609	39	ENF	2014/01 – 2020/12	7	12.9	960.1
San Rossore 2	IT-SR2	43.732	10.2909	4	ENF	2013/01 – 2020/12	8	15.3	950.0
Font-Blanche	FR-FBn	43.24079	5.67865	436	ENF	2008/01 – 2020/12	13	13.9	700.0

Columns 1–5 provide information on the site, including its name, ID, latitude, longitude, and elevation. Columns 6–8 describe the land cover classification, the period of available records, and the record length for each FLUXNET site. Columns 9–10 present the site's mean annual climatic characteristics, including temperature (MAT) and precipitation (MAP).

2.2 Carbon flux data

2.2.1 Observations

Measured CO₂ fluxes come from the Warm Winter 2020 (Team and Centre, 2022), an update of the FLUXNET2015 dataset (Pastorello et al., 2020) available on the ICOS platform (<https://www.icos-cp.eu/data-products>). For each site, we selected daily time series of NEE (NEE_VUT_REF), GPP (GPP_DT_VUT_REF) and RECO (RECO_DT_VUT_REF), the latter two fluxes being derived from the daytime flux partitioning method (Lasslop et al., 2010). Preliminary analyses show weak impact of the partitioning method (not shown).

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a supprimé: are used as a reference to evaluate outputs from two data-driven and two process-based models (Table 1). They ...

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a supprimé:) accounting for multiple friction velocity thresholds and associated with a favorable quality control flag above 80%, GPP (GPP_DT_VUT_REF) and RECO (RECO_DT_VUT_REF). GPP and, to a lesser extent, RECO are less sensitive to the partitioning method (Fig. A1) and the climate – CO₂ flux relationship is similar regardless of the partitioning method used. Here, we retained those CO₂ flux data...

a supprimé: The temporal coverage of the data is site dependent: 7 years for Hesse, 18 for Fontainebleau and 24 for Davos (Table 1)

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The temporal coverage of the data varies by site (Table 1): less than 10 years for eight sites (SE-Svb, SE-Nor, SE-Htm, DE-HoH, DE-RuW, FR-Hes, FR-Bil, and IT-SR2), between 10 and 20 years for five sites (FI-Let, DE-Hzd, CZ-BK1, FR-Fon, and FR-FBn), and more than 20 years for six sites (FI-Hyy, DK-Sor, DE-Hai, DE-Tha, CH-Dav, and IT-Ren). Given these limitations, the observational dataset likely lacks sufficient temporal depth to robustly assess the impact of climate on tower CO₂ flux interannual variability, highlighting the usefulness of models as complementary tools.

2.2.2 Data-driven models

Four data-driven models are used in this study (Table 2). The first data-driven model has been developed by the CarbonSpace company. The CarbonSpace model is designed to quantify carbon exchange at the site-scale by integrating remote sensing data, meteorological variables, and eddy-covariance flux measurements. A lagrangian particle dispersion model is used for footprint gas attribution. A machine learning model is used to solve the non-linear regression problem of estimating fluxes from remote sensing and meteorological variables (Zhuravlev et al., 2022). For this study, the learning method was updated from the kernel method used in Zhuravlev et al. (2022) to an ensemble tree method (Chen and Guestrin, 2016). The key advantages of the Carbon Space model include its scalability, high spatial resolution, and improved prediction accuracy through robust data quality control and advanced machine learning techniques. Carbon Space provides monthly NEE only but at a very high spatial resolution (few hectares) from 01-2000 to 08-2023. This allows to get as close as possible to the 19 sites (around 1.8 ha centered on each tower) and their associated CO₂ flux measurement footprints.

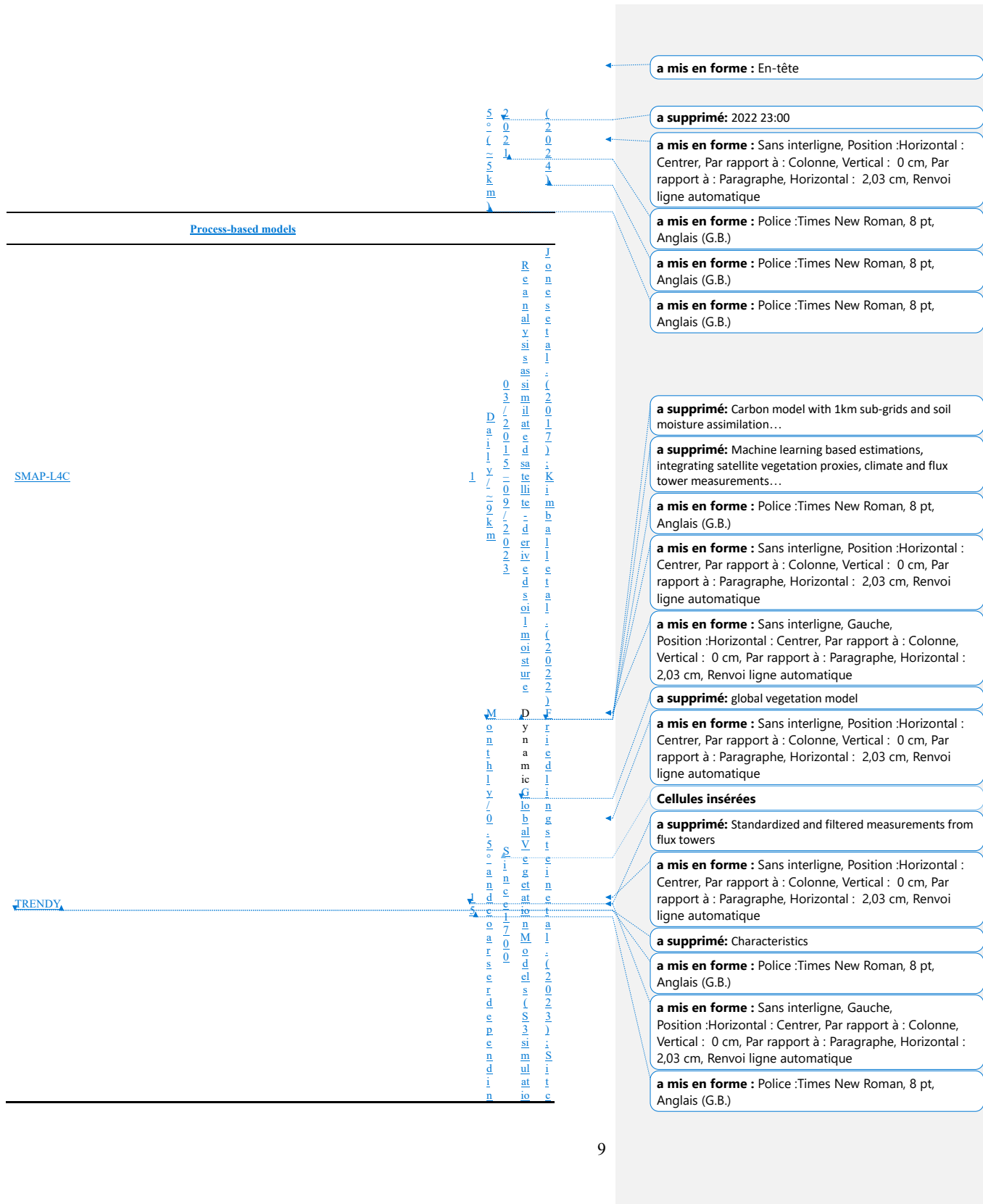
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The second and third data-driven models come from the FLUXCOM initiative (Tramontana et al., 2016; Jung et al., 2019; Jung et al., 2020) and have been retrieved from the data portal of the Max Planck Institute for Biochemistry (<https://www.bgc-jena.mpg.de>). The FLUXCOM models use eddy-covariance data from 224 flux-tower sites from the FLUXNET La Thuile dataset (<http://fluxnet.fluxdata.org/data/la-thuille-dataset/>) and the CarboAfrica network (Valentini et al., 2014). Among the various models available, we retained two models: a 3-member ensemble forced by both ERA5 reanalysis (Hersbach et al., 2020) and satellite data from the Moderate Resolution Imaging Spectroradiometer (MODIS) and a 9-member ensemble forced by MODIS only. The members differ by the machine learning method used to build each of the two models detailed in Jung et al. (2019). These models, named FLUXCOM-ERA5 and FLUXCOM-MODIS hereafter, provide global maps of monthly NEE, GPP and RECO derived with a daytime partitioning. The FLUXCOM-ERA5 model has a coarser resolution (0.5° x 0.5°) than the FLUXCOM-MODIS (0.08° x 0.08°) but covers a longer period (1979-2018 versus 2001-2015).

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572 Table 2. Data-driven and process-based models used in this study.
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Type and Name of the Dataset	Ensemble Members	Temporal and Spatial Resolution	Temporal Coverage Available	Description
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a supprimé: data (ERA5)

a supprimé: Pastorello et al. (2020); Warm Winter 2020 Team & ICOS Ecosystem Thematic Centre, 2022)

a supprimé: Smith et al., (2001, 2014); Wu (2023)

a supprimé: Zhuravlev et al. (2022)

a supprimé: Jung et al. (2019, 2020)

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a supprimé: Table 1: Summary of the datasets used in this study.

10

687 **2.2.3 Process-based models**
688
689 Two process-based models are considered (Table 2): the SMAP (Soil Moisture Active Passive) Level 4 Carbon
690 model (SMAP-L4C hereafter) and an ensemble of Dynamic Global Vegetation Models (DGVM) from the
691 TRENDY project (<https://sites.exeter.ac.uk/trendy>). The SMAP-L4C product is produced operationally by the
692 NASA SMAP mission. It can be considered as a reanalysis product since it uses the Goddard Earth Observing
693 System version 5 (GEOS-5) land model to assimilate SMAP L-band microwave observations and is forced with
694 observed land cover and vegetation from the Moderate Resolution Imaging Spectroradiometer (MODIS) and
695 Visible Infrared Imaging Radiometer Suite (VIIRS). The global processing is conducted on 1 km sub-grids using
696 spatially aggregated MODIS PFTs and VIIRS fPAR inputs, allowing to distinguish up to eight individual plant
697 functional types (PFTs) within each 9 km x 9 km product grid cell. However, the model processing uses coarser
698 spatial resolution (9 km and 0.25 degree) daily inputs from the SMAP L4 soil moisture (L4_SM) and GMAO
699 Forward Processor (FP) surface meteorology. Among other variables, the SMAP-L4C outputs provide daily NEE
700 and GPP (RECO deduced from the difference between NEE and GPP) in a consistent global grid from March 2015
701 to September 2023 for each PFT, including DBFs and ENFs (Jones et al., 2017; Kimball et al., 2022). The 1-km
702 PFT subclass distinction allows the differentiation of ENF and DBF. The L4C product is derived using coupled
703 photosynthetic light-use efficiency and soil organic matter decomposition models to estimate daily NEE and its
704 component carbon fluxes, where GPP is reduced from PFT-specific optimal rates for unfavourable daily climate
705 conditions, including cold temperatures, low light levels, excessive atmospheric vapour pressure deficits and low
706 root zone (0-1m depth) soil moisture levels defined from SMAP L4_SM and GMAO FP meteorology. The
707 associated product quality assessment report gives details of the model algorithms and the calibration, validation,
708 and performance of the L4C version 7 product used in this study (Endsley et al., 2023).
709
710 In addition to SMAP-L4C, this study also uses outputs from 15 Dynamic Global Vegetation Models (DGVMs) of
711 the Trends and Drivers of Regional-Scale Terrestrial Sources and Sinks of Carbon Dioxide (TRENDY version 12)
712 project. These models are routinely mobilised to assess global carbon budget trends and for attributing changes to
713 CO₂, climate and land use (Friedlingstein et al., 2023; Sitch et al., 2024). Appendix Table 1 provides the list of the
714 15 DGVMs used in this study. Here, we used outputs from the S3 scenario, with simulations starting in 1700 and
715 forced by time-varying observed CO₂, climate and land use change. All simulations have horizontal resolution of
716 0.5° x 0.5° and monthly outputs.

719 2.2.4 Climate data

720
721 To investigate the impact of climate on CO₂ fluxes, we use the ERA5-Land dataset (Muñoz-Sabater et al., 2019)
722 produced by the European Centre for Medium-Range Weather Forecasts (ECMWF). This dataset results from the
723 ECMWF land surface model (HTESSSEL) operating at 0.1° spatial resolution and forced by the ERA5 reanalysis
724 (Hersbach et al., 2020). This product provides hourly outputs for land surface, hydrological and meteorological
725 variables from 1950 onwards. In this study, we use incident shortwave radiation, temperature at 2 m (T_{2m}) and
726 averaged soil moisture (SM_{AVG}). We use the average of the four ERA5-Land soil moisture layers (0–7 cm, 7–28
727 cm, 28–100 cm, and 100–289 cm), representing the volumetric soil water content at different depths. Results

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a déplacé vers le haut [5]: The first data-driven model has been developed by the CarbonSpace company.

a supprimé: It makes use of (i) a Lagrangian particle dispersion model to account for the footprint of each tower flux site and (ii) a gradient-boosted decision tree based non-linear regression (Chen, 2016) to derive one statistical model per land-cover class. This approach follows that described in Zhuravlev et al. (2022), but with a revised regression methodology and without use of meteorological variables. The Hesse flux tower site is not part of the 84 stations in the FLUXNET2015 dataset used in the model input. A cross-validation is thus possible with Hesse and with measures made after 2015 for the other sites (i.e. 7 years in Davos, 9 years in Fontainebleau). The current model takes the aggregated Köppen–Geiger climate map at 1-km resolution (Beck et al., 2018) as a static predictive variable, but does not yet include temporal climate variability. It provides monthly NEE only but at a very high spatial resolution (few hectares) from 01-2000 to 08-2023. This allows to get as close as possible to the 3 flux tower sites (around 1.8 ha centered on each tower) and their associated CO₂ flux measurement footprints, while also distinguishing each non-instrumented plot (see section 2.1 for details on the area considered).

The second data-driven model comes from the FLUXCOM products (Tramontana et al., 2016; Jung et al., 2019, 2020) retrieved from the data portal of the Max Planck Institute for Biochemistry (<https://www.bgc-jena.mpg.de>). The FLUXCOM products use eddy-covariance data from 224 flux-tower sites from the FLUXNET La Thuile dataset (<http://fluxnet.fluxdata.org/data/la-thuille-dataset/>) and the CarboAfrica network (Valentini et al., 2014), including Hesse data between 1997 and 2006 and Fontainebleau between 2005 and 2006. Cross-validations are thus possible with most of our data from the Warm Winter 2020 release. The ... [64]

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a supprimé: (Jones et al., 2017; Kimball et al., 2022). The 1-km PFT subclass distinction allows to differentiate ENF and DBF behavior over the Mont Beuvray plots.

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a supprimé: Climate parameters are extracted from the version 2 of the operational chain Safran-ISBA-Modcou (SAFRAN-SIM2; Soubeyroux et al., 2008). SAFRAN ... [66]

obtained with incident shortwave radiation and T_{2m} lead to similar results. We therefore show the results for T_{2m} only. We also use relative humidity together with T_{2m} to compute the air vapour pressure deficit (VPD), an integrative metric accounting for both heat and water stress effects (Carrara et al., 2004; von Buttlar et al., 2018; Kong et al., 2022; van der Woude et al., 2023). The VPD is defined as the difference between the amount of moisture that is actually in the air and the amount of moisture that air could hold at saturation. The VPD is computed using the Tetens formula (Monteith and Unsworth, 2007) following Eq. (1):

$$VPD = \left(1 - \frac{RH}{100}\right) * \text{saturation vapor pressure} = \left(1 - \frac{RH}{100}\right) (610.78 * \exp\left(\frac{T}{T+237.3} * 17.2694\right)) \quad (1)$$

In the end, three ERA5-Land climate variables (T_{2m} , SM_{AVG} and VPD) are used to assess the impact of climate on the annual cycle and interannual variability of CO_2 fluxes. These variables capture the influence of thermal, hydrological, and atmospheric moisture demand conditions on CO_2 flux dynamics.

2.3 Methodology

For the gridded datasets (ERA5-Land, FLUXCOM, TRENDY, and SMAP-L4C), we extracted the nearest grid point to each flux tower site. Note that SMAP-L4C simulates spurious CO_2 fluxes at the DE-Hzd site. Therefore, this site is not included in the analysis for this model. Since these datasets have varying temporal resolutions (Tables 1 and 2), all were aggregated to a monthly timescale. From these monthly values, we computed the mean annual cycle by averaging all available years in each dataset, along with interannual variability, defined by the standard deviation and coefficient of variation.

Model skill in capturing observed CO_2 flux variability is evaluated over overlapping periods between each model and observation. The number of overlapping years varies significantly across model-observation pairs (Fig. 2a). Magnitude and co-variability errors are assessed using bias and the Bravais-Pearson correlation coefficient (R), respectively. For the annual cycle, we computed monthly biases for each overlapping year and present the mean bias averaged across all months and years. Model skill in reproducing the seasonal timing of CO_2 fluxes is assessed by correlating the 12 monthly modelled and observed values within each overlapping year, with the multi-year mean R reported. Correlations are considered significant at the 95% confidence level if the mean p-value is below 0.05. For interannual variability, biases are calculated as the difference between modelled and observed standard deviations for each month. Co-variability between observed and modelled CO_2 fluxes is assessed only for model-observation pairs with at least 10 overlapping years, ensuring robust signal detection. Correlations were deemed significant when $p < 0.05$.

The impact of climate on CO_2 fluxes is assessed for overlapping years between each CO_2 flux dataset and ERA5-Land. The number of overlapping years varies widely across datasets (Fig. 2b), ranging from low coverage in observations and SMAP-L4C to over 70 years in TRENDY. The correlation coefficient (R) was used to assess climate impacts, with the mean R reported for the annual cycle and individual R values for interannual variability. To ensure results were not driven by long-term trends, analyses have been conducted using both raw and detrended

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climate time series (not shown), yielding similar outcomes. Additionally, for observed CO₂ fluxes, we verified ERA5-Land climate data reliability by comparing results with observed climate measurements from the FLUXNET database (not shown).

For conciseness, we primarily present results using the ensemble mean of FLUXCOM (ERA5 and MODIS) and TRENDY models. However, uncertainties arising from machine learning methods and DVGM physical parameterizations are discussed in the model evaluation section.

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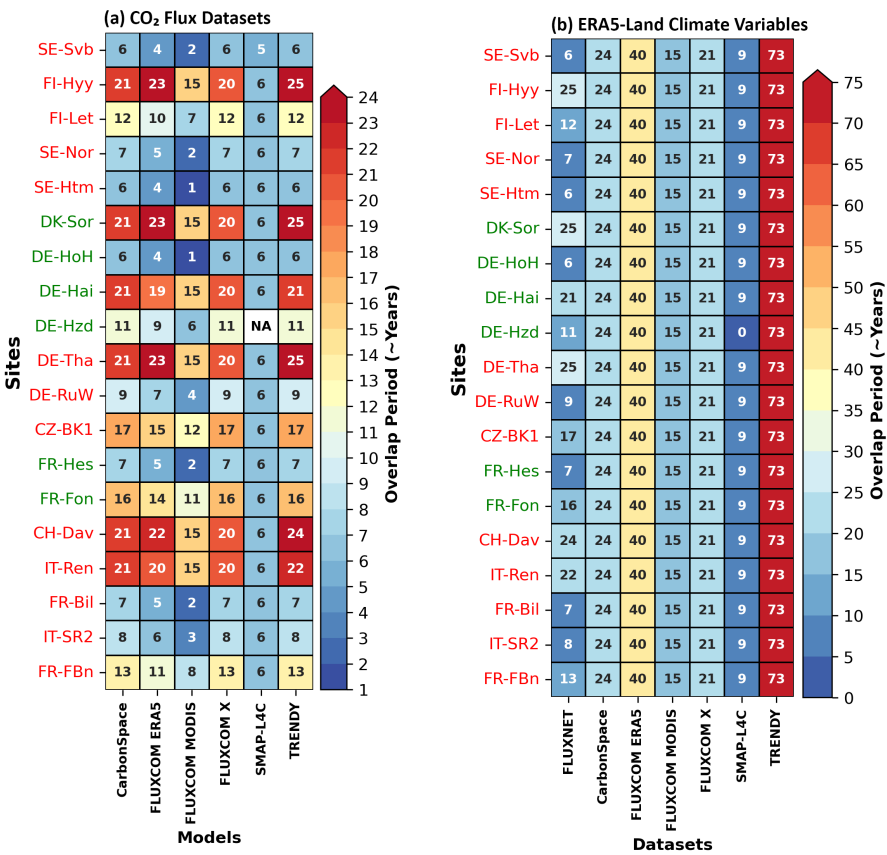


Figure 2. Number of overlapping years between (a) observed and modelled CO₂ fluxes, and (b) ERA5-Land climate and observed and modelled CO₂ fluxes. The overlapping periods in panel (a) are used to assess the model's ability to capture the annual cycle and interannual variability of CO₂ fluxes. In panel (b), the overlapping periods are used to evaluate the co-variability between CO₂ fluxes and the annual cycle and interannual variability of ERA5-Land climate.

3 Results

3.1 Observed climate and CO₂ fluxes mean annual cycle and interannual variability

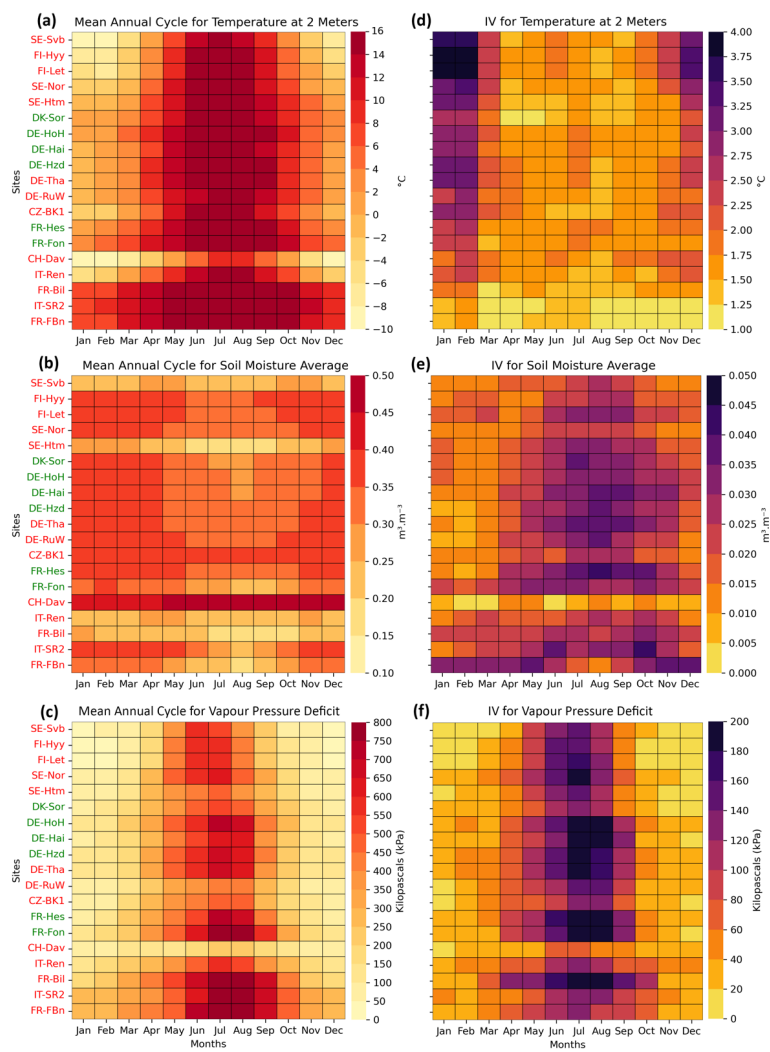


Figure 3. (a-c) Mean annual cycle and (d-f) interannual variability in monthly 2 m air temperature (T_{2m}), soil moisture (SM_{avg}), and vapour pressure deficit (VPD), respectively, for each study site for the 1979–2023 period. Climate conditions at each site are extracted from the nearest grid point of the $9\text{ km} \times 9\text{ km}$ ERA5-Land product.

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1025 ENF sites are displayed in red text, while DBF sites are highlighted in green. Sites are ordered from north to south
1026 based on their latitude.

1027
1028 Figure 3 shows the mean annual cycle and interannual variability of T_{2m} , SM_{AVG} and VPD associated with each
1029 site. Overall, all sites depict higher T_{2m} and VPD and lower SM in summer than in winter (Figs. 3a-c). A south-
1030 north gradient is evident, with more marked annual amplitude and shorter summer in northern than southern
1031 Europe. Few sites deviate from this pattern, including e.g., the Alpine site (CH-Dav), which depicts relatively cold
1032 and wet conditions, as well as low VPD, all year long. While the interannual variability of T_{2m} is the largest in
1033 winter regardless of the site, it significantly increases from south to north (Fig. 3d). The reverse is found for VPD,
1034 with higher interannual variability in summer than winter, especially south of 60°N (Fig. 3f). The interannual
1035 variability in SM_{AVG} (Fig. 3e) is low all year long in the Alpine site, relatively low in northern Europe, high from
1036 spring to summer in the mid-latitudes and in fall and winter in the Mediterranean region (FR-FBn). Interestingly,
1037 the pattern of SM_{AVG} interannual variability significantly differs from that of VPD, suggesting soil moisture
1038 variability to be much more driven by precipitation than evapotranspiration variability.

1039
1040 Figure 4a displays the mean annual cycle of monthly NEE, GPP and RECO as provided by FLUXNET
1041 observations. The mean annual cycle in NEE is not necessarily phased on that of GPP and RECO, the two latter
1042 reaching their highest values from May to August in most sites. Significant differences are found between northern
1043 (SE-Nor, FI-Let, FI-Hyy and SE-Svd) and southern (FR-FBn, IT-SR2 and FR-Bil) Europe, where ENF sites only
1044 are available. The annual cycle is more marked and the sequestration period (i.e., month associated with negative
1045 NEE values) is shorter in the former than the latter region. Temperature conditions (and light availability) are the
1046 main drivers explaining these differences. In central Europe, where both ENF and DBF sites are available, there
1047 is a clear impact of land cover class. The DBF sites show pronounced annual cycle with strong CO_2 uptake (below
1048 $-3 \text{ tCO}_2\text{ha}^{-1}$) from May to August, and up to some extent in September, and strong CO_2 release the remaining
1049 months (above $2 \text{ tCO}_2\text{ha}^{-1}$). Conversely, the ENF sites show smoothed annual cycle: the summer peak of CO_2
1050 sequestration barely exceeds $-3 \text{ tCO}_2\text{ha}^{-1}$ and the winter peak of CO_2 release rarely exceeds $1 \text{ tCO}_2\text{ha}^{-1}$. Two sites
1051 deviate from the general pattern: the DE-Hzd DBF site, which acts as a CO_2 source nearly year-round, and the DE-
1052 RuW ENF site, which remains a consistent CO_2 sink on average.

1053
1054 The interannual variability of NEE, GPP, and RECO, as defined by the standard deviation metric, tends to be
1055 stronger during the growing season (spring to fall) than in winter at almost all sites (Fig. 4b). The exact pattern
1056 depends on the CO_2 flux, site and land cover class considered. GPP is always close to zero during winter in DBF
1057 sites since trees are not photosynthetically active. This is not the case for ENF sites, particularly those located in
1058 central Europe (DE-RuW and CZ-BK1). The interannual variability of RECO is substantial in summer only in
1059 northern Europe. However, it can be non-negligible in other seasons in central and southern Europe. There,
1060 significant differences between geographically close sites (e.g., FR-Bil and IT-SR2) suggest additional drivers
1061 such as soil properties. The interannual variability of NEE is (i) weaker than that of GPP and RECO, likely due to
1062 the strong coupling between GPP and RECO, (ii) primarily driven by RECO in winter and (iii) a complex response
1063 of GPP and RECO in the remaining seasons. Note that the pattern of CO_2 flux interannual variability depends on
1064 the metric used to assess it. When defined using the coefficient of variation, interannual variability is low in

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a supprimé: The R and R^2 metrics are also used to assess the relationship between climate variables and CO_2 fluxes at the monthly (raw and anomalous values) and annual (raw values) timescales. In addition, a composite approach is performed to examine monthly climate anomalies associated with large negative and positive monthly anomalies in CO_2 fluxes (NEE, GPP and RECO). Large negative/positive CO_2 flux anomalies are defined as standardized anomalies (mean=0, standard deviation=1) below/above $-0.5/+0.5$. Tests with stricter threshold values (e.g., $-1/+1$) lead to similar results but limit the size of the samples. The difference between the two groups is tested for significance based on the non-parametric Mann-Whitney U test (McKnight and Najab, 2010).[¶]

Results[¶]

Monthly timescale[¶]

Mean annual cycle and interannual variability in climate and CO_2 fluxes[¶]

Figure 2 shows the mean annual cycle and interannual variability of T and main surface water cycle parameters associated with each site. All sites follow similar patterns of T, ETP, EVAP and VPD with the greatest values in summer and the lowest in winter. The annual cycle in SWI is reversed, with drier soils in late summer and wetter soils in winter. The total precipitation is evenly distributed throughout the year for sites in plain (Fontainebleau and Hesse and Châtillonnais), in contrast with mountainous sites (Davos and Mont Beuvray) where precipitation amounts are larger during winter than summer. The interannual variability (shadings on Fig. 2) is particularly pronounced all year long for PRE_SUM and from spring to fall for VPD, highlighting strong year-to-year fluctuations of the water cycle.[¶]

... [98]

summer and high in winter for GPP and RECO, with increasing variability toward the north. For NEE, variability remains significant throughout the year, particularly from fall to winter (Fig. A1).

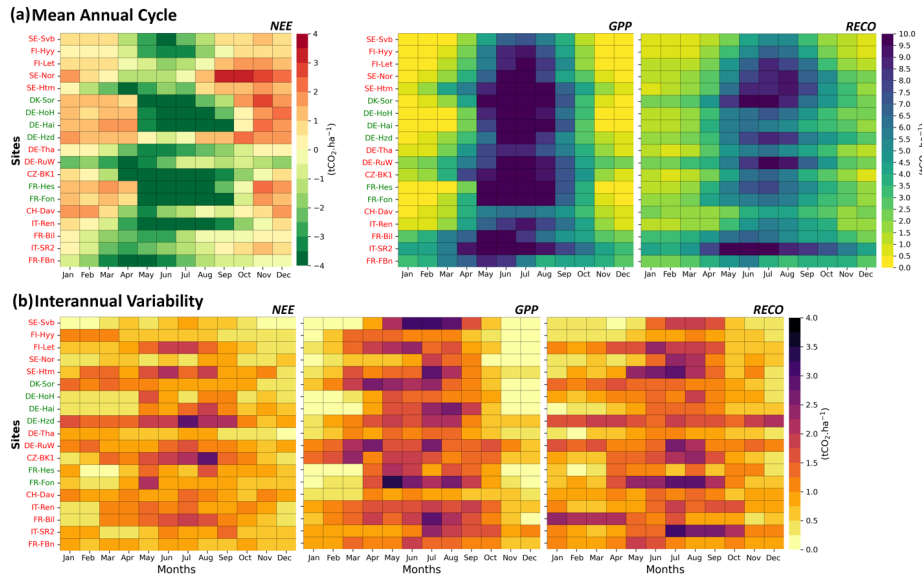


Figure 4. (a) Mean annual cycle and (b) interannual variability in monthly NEE, GPP and RECO (from left to right, respectively) as measured by eddy-covariance over the most extended available period for each site (see Table 1 for details). ENF sites are displayed in red text, while DBF sites are highlighted in green. Sites are ordered from north to south based on their latitude.

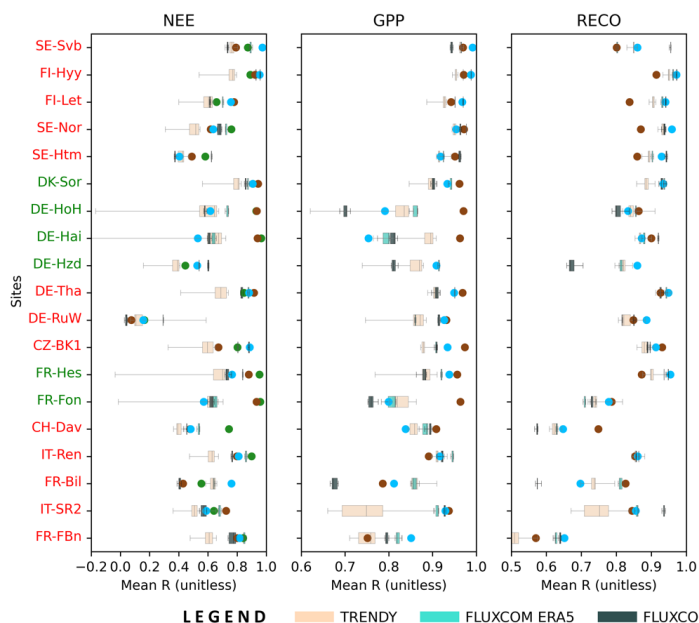
Overall, the mean annual cycle of observed CO₂ fluxes in European forests follows a clear spatial pattern driven by climate conditions and land cover class. In contrast, the interannual variability of observed CO₂ fluxes exhibits greater spatial noise across Europe and depends on the metric used. Nevertheless, it remains significant, highlighting the importance of assessing the impact of climate on it throughout the annual cycle.

3.2 Model evaluation in capturing the mean annual cycle and interannual variability of CO₂ fluxes

3.2.1 Mean annual cycle

The model skill in capturing the observed annual cycle and the magnitude in CO₂ fluxes is assessed in terms of correlation and mean bias, respectively (see section 2.3 for details). All models accurately capture the observed annual cycle of GPP and RECO, with correlation values often above 0.8 (Fig. 5a). The model skill is poorer but still correct for NEE, with correlation values remaining above 0.6 for most sites and models. The weaker correlation found for NEE compared to GPP and RECO is not surprising, as accurately estimating the NEE annual cycle requires precise estimation of both the temporal phasing and magnitude of GPP and RECO.

(a) FLUXNET vs Models (Mean Correlation)



(b) FLUXNET vs Models (Mean Biases)

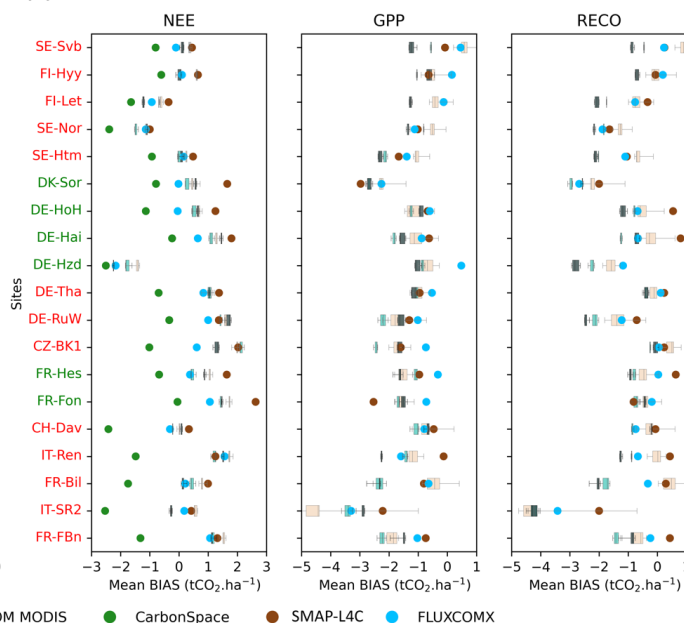


Figure 5. Model skill in capturing (a) the annual cycle and (b) magnitude of observed NEE, GPP and RECO. The model skill in capturing the annual cycle is assessed through the Bravais-Pearson correlation coefficient (R) calculated between the simulated and observed annual cycle of monthly CO₂ fluxes (12 values) for each year of the overlapping period. The multi-year mean R values are shown. The mean magnitude error is shown. Results are displayed using colored dots for single member models (CarbonSpace, FLUXCOM-X and SMAP-L4C) and boxplots for multi-member FLUXCOM models and the multi-model TRENDY ensemble. The boxes have lines at the lower quartile, median, and upper quartile values. The whiskers are lines extending from each end of the boxes to show the extent of the full range of the data, including outliers. The colour attributed to each model is detailed in the legend. ENF sites are displayed in red text, while DBF sites are highlighted in green. Sites are ordered from north to south based on their latitude.

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a déplacé vers le bas [12]: Same as Fig.

a supprimé: 2 but for monthly NEE in the (a-c) three FLUXNET sites and (d-f) three non-instrumented sites located in Burgundy as measured by eddy-covariance (FLUXNET) and simulated by data-driven (CarbonSpace and FLUXCOM) and process-based (LPJ-GUESS and SMAP-L4C) models. The longest available period for each site and dataset is retained. See Table 1 for details. For LPJ-GUESS, SMAP-L4C and FLUXCOM models, the nearest grid point from each site is

a supprimé: from LPJ-GUESS and FLUXCOM are similar in panels (d-e) due to coarse horizontal resolution (0. ... [101]

a supprimé: 4:

a supprimé: 3 but for monthly (a) NEE, (b) GPP an ... [102]

a supprimé: CarbonSpace model is not shown since ... [103]

a supprimé: . The remaining models strongly under ... [104]

a supprimé: (i.e., bias)

a supprimé: NEE

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a mis en forme : Couleur de police : Automatique

a mis en forme ... [100]

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a supprimé: (labeled on panels d-f).

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a supprimé: range of the data within 1.5 by inter-qt ... [105]

1263 Despite reasonable annual cycles, the models struggle in capturing the observed magnitude of RECO and GPP
1264 (Fig. 5b). Three groups emerge. The first group includes the FLUXCOM (ERA5, MODIS and X) and TRENDY
1265 models, which underestimate both GPP and RECO by about similar amounts, resulting in relatively “weak”
1266 positive biases in NEE. The second group corresponds to the SMAP-L4C model, which overestimates RECO by
1267 $1 \text{ tCO}_2 \text{ ha}^{-1} \text{ month}^{-1}$ while underestimating GPP by the same amount, leading to a systematic underestimation of
1268 CO_2 sequestration by approximately $2 \text{ tCO}_2 \text{ ha}^{-1} \text{ month}^{-1}$. The last group is the Carbon Space data-driven model,
1269 which is the only model that systematically overestimates CO_2 sequestration, by up to $2.5 \text{ tCO}_2 \text{ ha}^{-1} \text{ month}^{-1}$.
1270 However, the cause of this overestimation is unclear, as this model does not provide separate GPP and RECO
1271 estimates.

1272 ▲
1273 Figure 5 highlights key insights into model behaviour. First, the data-driven and SMAP-L4C models generally
1274 outperform the TRENDY models in capturing the annual cycle of CO_2 fluxes but do not necessarily provide better
1275 estimates of flux magnitude. Second, models that accurately represent the annual cycle can still struggle with
1276 magnitude. This is exemplified by the Carbon Space data-driven model, which ranks among the best for annual
1277 cycle representation but severely overestimates CO_2 sequestration in many sites. Third, the machine learning
1278 methods used in the FLUXCOM-ERA and FLUXCOM-MODIS ensembles have little impact on both the annual
1279 cycle and magnitude of CO_2 fluxes. The input data itself appears to be more important, with the FLUXCOM
1280 models accounting for both vegetation and climate (i.e., ERA5 and X) yielding more reliable results than those
1281 accounting for vegetation alone (MODIS). Additionally, FLUXCOM-X improves upon the previous model
1282 generation for most sites. Finally, the inter-model spread within the TRENDY ensemble is much smaller for CO_2
1283 flux magnitude than for temporal variability, suggesting that the primary source of uncertainty in DGVMs lies in
1284 the temporal phasing of the fluxes rather than their magnitude.

1285 1286 1287 3.2.2 Interannual variability

1288
1289 We qualitatively evaluate how well the models capture the observed interannual variability of CO_2 fluxes in terms
1290 of magnitude (monthly bias analysis) and temporal phasing (correlation analysis) over the overlapping period of
1291 each model-observation pair.

1292
1293 All models strongly underestimate the magnitude in NEE interannual variability all year long (Fig. 6), particularly
1294 during summer where biases often exceed $2.5 \text{ tCO}_2 \text{ ha}^{-1} \text{ month}^{-1}$. This is a well-known bias of current data-driven
1295 and process-based models (e.g., Lin et al., 2023; Nelson et al., 2024). The only exception is the CarbonSpace
1296 model that produce weak positive or negative biases at most sites.

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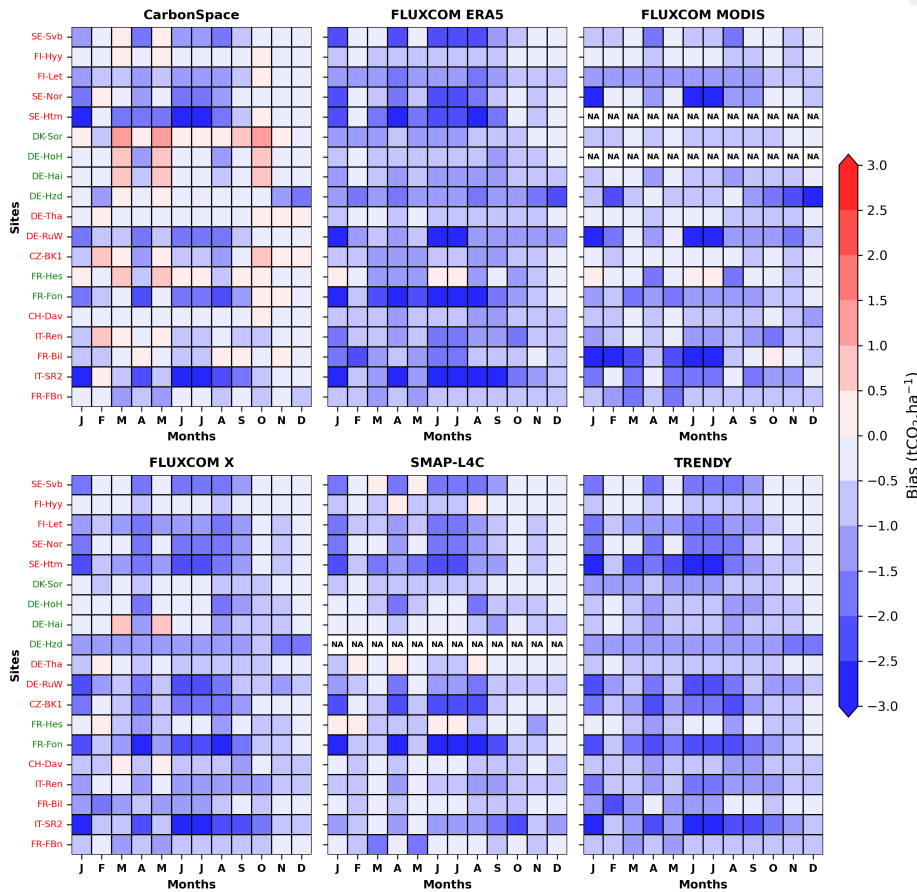


Figure 6. Model skill in capturing the observed magnitude in monthly NEE interannual variability. Model skill is assessed by computing biases between modelled and observed NEE interannual variability, as defined by the standard deviation of monthly fluxes. The number of years included varies depending on the model–observation pair, as shown in Fig. 2a. Cells labelled “NA” indicate cases where the overlap criterion is not met. For conciseness, biases are computed using the ensemble mean for FLUXCOM-ERA5, FLUXCOM-MODIS, and TRENDY models. ENF sites are displayed in red text, while DBF sites are highlighted in green. Sites are ordered from north to south based on their latitude.

Figure 7 shows the correlations between the modelled and observed interannual variability in monthly NEE. Correlation values are predominantly positive across Europe, though they are often low and not statistically significant ($p > 0.05$). The correlation values tend to be higher in fall for northern Europe sites and all year long in central Europe regardless of the model. The frequent lack of statistical significance in correlations can largely be attributed to the limited number of overlapping years. This is further supported by the fact that, except for Davos, correlation values tend to be higher and more likely to reach the 95% confidence level in model–observation pairs with a greater number of overlapping years (e.g., DK-Sor, DE-Hai and DE-Tha). Another challenge in capturing the observed temporal phasing of NEE interannual variability is that it requires accurately simulating the

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interannual variability of both GPP and RECO. The latter is generally better represented by models than NEE variability itself (compare Fig. 7 with Figs. A2–A3). Scale inconsistencies may also contribute to the discrepancies. While flux tower observations reflect local variability, most models represent regional-scale fluxes (and drivers). This is supported by the Carbon Space model, the only site-scale model used in this study, which produces more satisfactory results, with positive correlation values for almost all sites and all months.

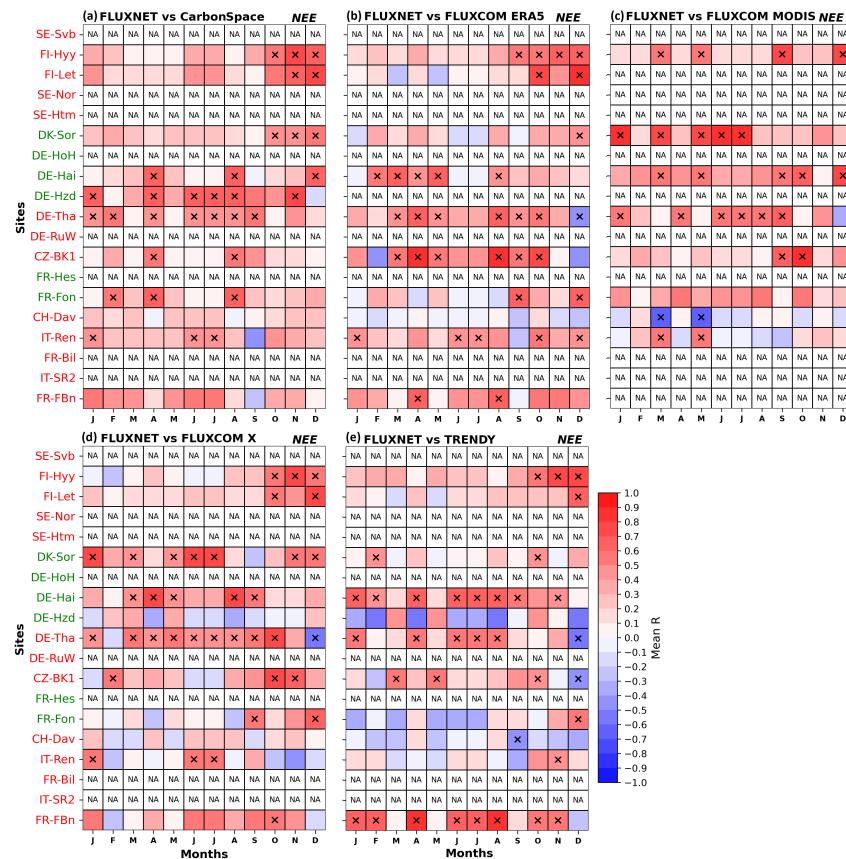


Figure 7. Model skill in capturing the observed temporal phasing in monthly NEE interannual variability. Model skill is assessed using the Bravais-Pearson correlation coefficient (R), calculated for each month where at least 10 years of overlap exists between each model–observation pair. The number of years included varies depending on the model–observation pair, as shown in Fig. 2a. Correlation values marked with “x” are significant at the 95% confidence level according to the Bravais-Pearson test. Cells labelled “NA” indicate cases where the overlap criterion is not met. For conciseness, the correlation analysis is performed using the ensemble mean for FLUXCOM-ERA5, FLUXCOM-MODIS, and TRENDY models. ENF sites are displayed in red text, while DBF sites are highlighted in green. Sites are ordered from north to south based on their latitude.

The spread among members of the FLUXCOM ensembles is low (not shown), regardless of whether they account for climate alone or both climate and vegetation. However, Figure 7 reveals significant differences between the

1337 [FLUXCOM](#) products (ERA5, MODIS, and X; Fig. 7b–d). These differences are not necessarily due to the type of
1338 data used in these data-driven models, as the analysis periods differ between them. In contrast, the correlations
1339 between observations and the TRENDY ensemble mean (Fig. 7e) mask substantial variability among individual
1340 TRENDY models, with no single model consistently outperforming the others (Fig. A4).

1341
1342 These qualitative results suggest that the interannual variability of simulated NEE is at least partially aligned with
1343 that of observed CO₂ fluxes, supporting the use of models to assess the impact of climate on CO₂ flux interannual
1344 variability.

1347 3.3 Climate – CO₂ flux relationship

1348 3.3.1 Annual cycle

1350 [Figure 8](#) assesses the co-variability between the annual cycle of CO₂ fluxes and climate variables (T_{2m} , SM_{AVG} ,
1351 and VPD) through correlation analysis. For conciseness, correlations are computed using the ensemble mean of
1352 CO₂ fluxes for FLUXCOM (ERA5 and MODIS) and TRENDY models. The inter-member dispersion in
1353 FLUXCOM and inter-model dispersion in TRENDY, shown in Fig. A5, are similar to those in Fig. 5 and are
1354 therefore not discussed here.

1356 [The annual cycle](#) of CO₂ fluxes is closely linked to climate in both observations and models, as evidenced by
1357 statistically significant correlations at the 95% confidence level. The influence of climate on the annual cycle of
1358 CO₂ fluxes is generally stronger for GPP and RECO than for NEE, particularly for T_{2m} (Fig. 8a). Over Europe,
1359 GPP, RECO and CO₂ sequestration (i.e., negative NEE) tend to be higher when T_{2m} and VPD are high and SM_{AVG}
1360 is low. In turn, CO₂ fluxes are amplified in summer and damped in winter. Among the climate variables, T_{2m} and
1361 VPD exhibit stronger correlations with the CO₂ flux annual cycle than SM_{AVG} , reflecting their more pronounced
1362 seasonality (Fig. 3).

1364
1365 This climate – CO₂ flux relationship is particularly evident in northern and central Europe, where there is strong
1366 agreement between observations and models, as well as across different models. The only exception in central
1367 Europe is the Alpine site (CH-Dav), where SM_{AVG} is positively correlated with GPP and RECO and negatively
1368 correlated with NEE. This discrepancy arises because CH-Dav is the only site in the study where SM_{AVG} is higher
1369 in summer than in winter (Fig. 3b). In contrast, in southern Europe, the relationship between climate and NEE
1370 does not reach the 95% confidence level in observations. However, the models show a similar relationship to that
1371 found in northern and central Europe, albeit with weaker correlations. Whether this disagreement stems from the
1372 limited number of observational years available for these sites (7 to 13 years, see Table 1) or from an
1373 overestimation of climate impact on the CO₂ flux annual cycle remains an open question.

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a déplacé (et inséré) [17]

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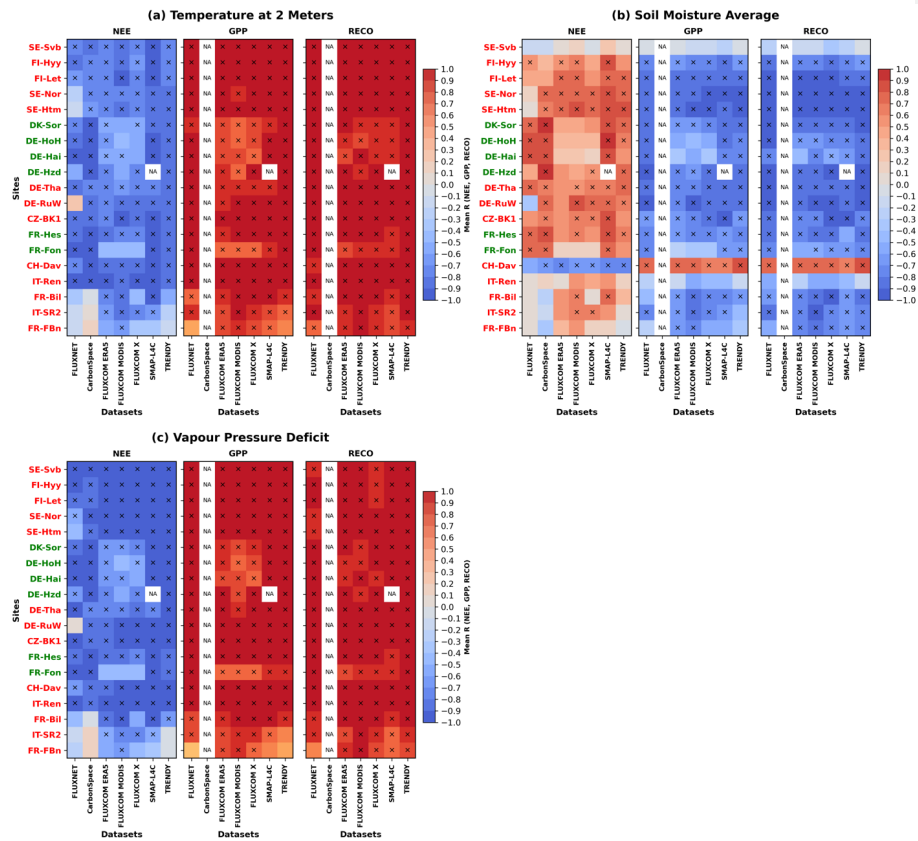


Figure 8. Co-variability in the annual cycle of CO₂ fluxes and (a) 2 m temperature, (b) soil moisture, and (c) vapour pressure deficit across all sites and datasets. Co-variability is assessed through Bravais-Pearson correlation, computed annually between CO₂ fluxes and ERA5-Land climate data, then averaged across years. The number of years included varies depending on the data, as shown in Fig. 2d. Correlation values marked with 'x' are significant at the 95% confidence level according to the Bravais-Pearson test. Cells labelled 'NA' indicate cases where GPP and RECO are unavailable (CarbonSpace) or where CO₂ flux data are corrupted (SMAP-L4C). For conciseness, correlations are computed using the ensemble mean of CO₂ fluxes for FLUXCOM (ERA5 and MODIS) and TRENDY models. ENF sites are displayed in red text, while DBF sites are highlighted in green. Sites are ordered from north to south based on their latitude.

Figure 8 also reveals differences in model behaviour. First, the climate – CO₂ flux relationship appears sensitive to land cover class only in data-driven models. In the FLUXCOM models (ERA5, MODIS, X), this relationship is weaker for DBFs than ENFs in central Europe, whereas the Carbon Space model shows the opposite pattern. This sensitivity to land cover class may reflect model discrepancies, as the observed climate – CO₂ flux relationship does not depict such an ENF–DBF distinction. The reason for this discrepancy remains, however, unclear, given that these data-driven models are based on the same FLUXNET sites. Second, process-based models tend to overestimate the impact of climate on the annual cycle of CO₂ fluxes across all sites. For example, the SMAP-L4C model amplifies the influence of T_{2m} and S_{MAVG} on NEE, particularly in northern Europe (Fig. 8a-b). Meanwhile, in the TRENDY models, VPD emerges as the dominant driver of the NEE annual cycle (Fig. 8c). These results

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suggest that process-based models may underestimate the role of additional factors, such as soil properties, in shaping the CO₂ flux annual cycle.

3.3.2 Interannual variability

We now investigate the interannual co-variability between CO₂ fluxes and climate, with a particular focus on how this relationship evolves throughout the annual cycle. Figure 9 illustrates the interannual relationship between climate and NEE for each month through correlation analysis. The relationship is notably noisier in the observations compared to the models, due to the limited observational record and site-specific variations in measurement periods, and highlights model sensitivity. Nonetheless, the general pattern remains consistent, showing distinct differences between northern/central Europe and southern Europe.

In northern and central Europe, the correlation patterns of NEE with T_{2m} and VPD are similar (Fig. 9a and c), highlighting the strong coupling between these two climate variables. The NEE interannual variability is correlated positively with T_{2m}, VPD and, to a lesser extent, SM_{AVG} in winter and fall. This means that anomalously high T_{2m}, VPD and SM_{AVG} favor CO₂ release during the cold seasons. This pattern is similar for GPP and RECO (Figs. A6-A7), but correlations are stronger for RECO, highlighting its significant contribution to NEE interannual variability during the cold seasons. In spring (March–May), the relationship between NEE and T_{2m}/VPD reverses compared to the cold season pattern, meaning that anomalously low T_{2m} and VPD promote CO₂ sequestration. The NEE–SM_{AVG} relationship, however, varies between northern and central Europe. In northern Europe, depending on the dataset, SM_{AVG} and NEE interannual variability are not consistently linked, with correlations either weak and insignificant or strong but inconsistent throughout the spring season (Fig. 9b). In contrast, a clear relationship emerges in central Europe, where correlations are significantly positive across most sites and datasets, though their strength remains uncertain (with SMAP-L4C showing much larger correlation values). The increase in spring CO₂ sequestration under anomalously dry soil conditions is likely driven by elevated T_{2m} and VPD, leading to enhanced evapotranspiration and drier soils. During the peak of the summer season (July–August), NEE is positively correlated with T_{2m} and VPD and negatively correlated with soil moisture across most sites in northern and central Europe.

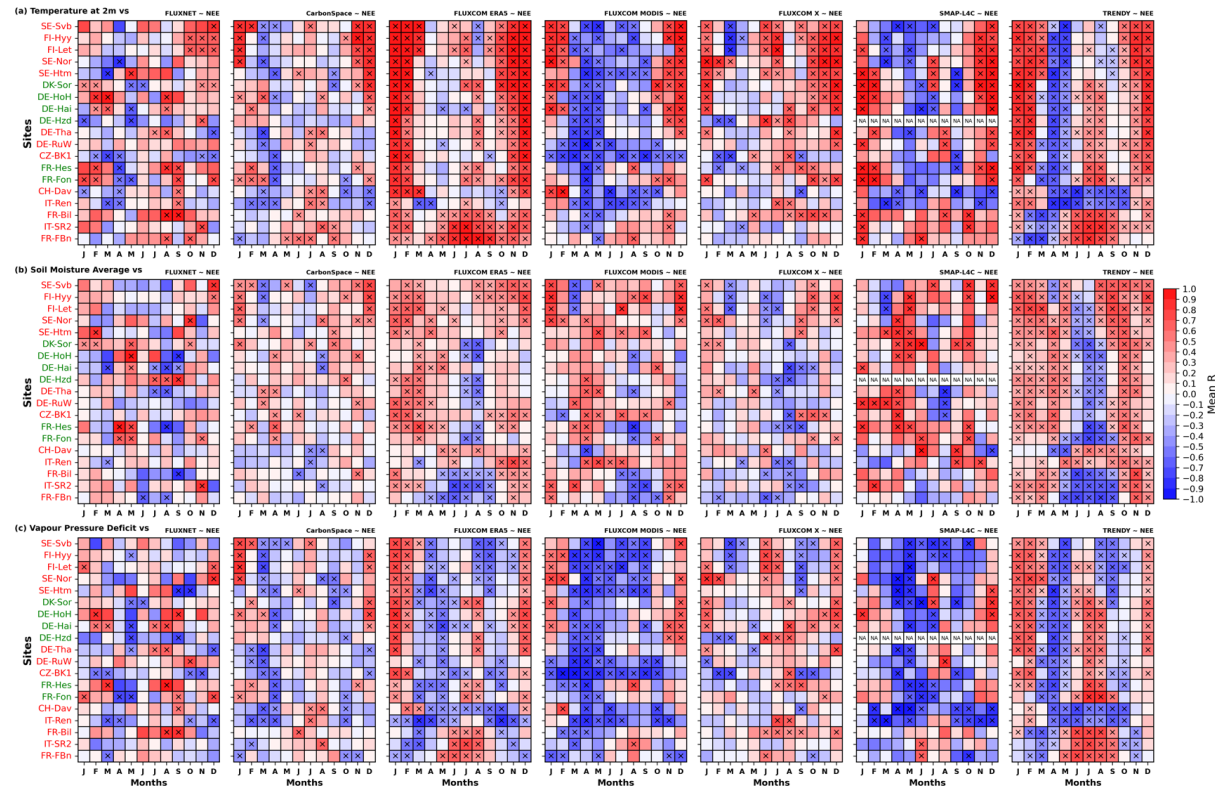


Figure 9. Interannual co-variability between NEE and (a) 2 m temperature, (b) soil moisture and (c) vapour pressure deficit for each month, all sites and all datasets. The co-variability is assessed through Bravais Pearson correlation computed for each month between CO₂ fluxes and ERA5-Land climate data. The number of years included varies depending on the data, as shown in Fig. 2d. Correlation values marked with 'x' are significant at the 95% confidence level according to the Bravais-Pearson test. Cells labelled 'NA' indicate cases where CO₂ flux data are corrupted (SMAP-L4C). For conciseness, correlations are computed using the ensemble mean of CO₂ fluxes for FLUXCOM (ERA5 and MODIS) and TRENDY models. ENF sites are displayed in red text, while DBF sites are highlighted in green. Sites are ordered from north to south based on their latitude.

In southern Europe (FR-Bil, IT-SR2, and FR-FBn), the influence of climate on NEE interannual variability is more uncertain, particularly for T_{2m} and VPD, as both the sign and strength of their correlations with NEE vary across datasets. Correlations are generally weak and/or barely significant in the observations, the CarbonSpace model, FLUXCOM-MODIS, and SMAP-L4C models. In FLUXCOM-ERA5, the correlation signs for T_{2m} and VPD are inconsistent (except in summer), whereas in TRENDY, they remain consistent except in fall. This inconsistency is not observed for GPP and RECO (Figs. A6–7). In summer, most datasets indicate that anomalously low T_{2m} and VPD, along with anomalously high SM_{AVG} , enhance both GPP and RECO. This suggests that NEE interannual variability in southern Europe results from a complex interplay between GPP and RECO contributions. Moreover, the opposing correlation signs between $NEE-T_{2m}$ and $NEE-VPD$ in southern Europe suggest that VPD in drier, hotter environments is more strongly influenced by atmosphere-surface feedbacks than by large-scale atmospheric conditions. In contrast, the impact of SM_{AVG} on NEE interannual variability shows greater inter-dataset agreement (Fig. 9b), with positive correlations in winter and fall and negative correlations in summer. This indicates that excess winter precipitation, leading to wetter soils, enhances CO_2 release, whereas increased summer precipitation or reduced evapotranspiration promotes CO_2 sequestration.

4 Discussion

This study aims at assessing the impact of climate on annual cycle and interannual variability of monthly CO_2 fluxes in European DBFs and ENFs through conjointly analysing observations from the FLUXNET network and state-of-the-art data-driven and process-based models.

As a first step, we assess the model abilities to reproduce the observed mean annual cycle and interannual variability of CO_2 fluxes. This evaluation presents two key challenges. First, the temporal coverage of observations in the FLUXNET database is often limited, making it difficult to extract robust signals, particularly for interannual variability. Second, there is a spatial scale mismatch between site-level observations, representing fluxes from the tower footprint to several square kilometers (Göckede et al., 2008), and most models used in this study, which simulate fluxes at regional to large scales, except for the hectometric-scale CarbonSpace model. Given these constraints, our evaluation should be considered qualitative rather than strictly quantitative.

The models reasonably capture both the annual cycle and interannual variability of observed CO_2 fluxes, though with some magnitude discrepancies. In particular, the models accurately capture the north-to-south gradient, with increased length in the CO_2 sequestration period from northern to southern Europe, as well as the more pronounced annual cycle in DBFs than ENFs. With the exception of the CarbonSpace model, which overestimates CO_2 sequestration across all European sites, most models tend to underestimate GPP and overestimate RECO, resulting in a near systematic underestimation of CO_2 sequestration.

The interannual variability in the models is weaker than in the observations, consistent with previous studies (e.g., Nelson et al., 2024). Yet, the co-variability between observed and simulated CO_2 fluxes remains correct despite the aforementioned constraints. This agreement was expected for data-driven models, as they incorporate

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The annual cycle

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a supprimé: and magnitude of NEE simulated in the ENF and the two DBF non-instrumented plots (Fig. 3d-f) closely resemble those simulated in the instrumented sites (Fig.

a supprimé: The two main exceptions concern all-year-long CO_2 sequestration simulated by the CarbonSpace model in the Mont Beuvray ENF site, and much weaker CO_2 sequestration peak simulated by the FLUXCOM models in the Châtillonnais DBF site. Based on these results, the CarbonSpace data-driven model appears to be the best compromise to capture the annual cycle and magnitude of NEE associated with both ENFs and DBFs. The results also demonstrate that process-based and data-driven models have their own strengths and weaknesses and are thus complementary.¶

Climate – CO_2 flux relationship¶

... [106]

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FLUXNET observations in their development. However, it was less anticipated for process-based models, which do not assimilate direct CO₂ flux measurements. Their ability to capture observed interannual variability likely stems from the fact that TRENDY models are driven by observed CO₂ concentrations, land-use changes, and climate data, while the SMAP-L4C model benefits from the assimilation of satellite-derived soil moisture observations.

Despite uncertainties, our results highlight that state-of-the-art models are valuable tools for complementing observations, particularly in assessing the impact of climate on the interannual variability of CO₂ fluxes by significantly expanding the number of studied years and the spatial domain. The relationship between CO₂ fluxes and climate is analysed for both the annual cycle and interannual variability using synchronous correlation analyses between each CO₂ flux and individual climate variables, including 2 m temperature (T_{2m}), vapour pressure deficit (VPD), and soil moisture (SM_{AVG}).

Regarding the annual cycle, the influence of climate on CO₂ fluxes is stronger in northern and central Europe than in southern Europe, where seasonal climate variations are less pronounced. In southern Europe, both the agreement between observations and models and the consistency among different data-driven and process-based models are weaker. The spread within members (FLUXCOM-ERA5 and FLUXCOM-MODIS), and DVGMs (TRENDY), is also larger. We hypothesize that part of this model uncertainty stems from the limited number of ENF sites in southern Europe, leading to weak constraints for data-driven models and fewer reference points for calibrating DVGMs. However, it is worth noting that the uncertainty associated with the machine learning methods used to develop data-driven models remains low, whereas inter-DGVM spread can be substantial.

Regarding interannual variability, the climate impact on CO₂ fluxes can be summarized in three points. First, climate impacts more strongly GPP and RECO than NEE, regardless of the site and dataset. Since NEE is the difference between GPP and RECO, its interannual variability arises from various combinations of these two components. For instance, reduced CO₂ sequestration can result from a greater increase in RECO compared to GPP, a larger decrease in GPP than in RECO, a decrease in GPP with no change in RECO, or an increase in RECO without any change in GPP. Such complexity implies that the influence of climate on NEE is less direct and likely more intricate than its effects on GPP and RECO. Second, the climate impact significantly changes along the annual cycle with noticeable differences between northern/central and southern Europe, regardless of land cover class. For conciseness, we discuss only results for NEE. In northern and central Europe, CO₂ sequestration is closely linked to T_{2m} and VPD, whereas in southern Europe, soil moisture emerges as the dominant driver. These findings reinforce the role of soil moisture as the primary control on NEE in southern Europe, though not necessarily on its components (i.e., GPP and RECO), refining previous studies (Seddon et al., 2016; Madani et al., 2017). In northern and central Europe, most models indicate that CO₂ sequestration is enhanced by anomalously low T_{2m} and VPD and anomalously high SM_{AVG} in summer, whereas the opposite pattern prevails in spring. This finding aligns with previous case studies showing that heatwaves and droughts reduce summer CO₂ sequestration (Ciais et al., 2005; Smith et al., 2020; Thompson et al., 2020; van der Woude et al., 2023). It also highlights that anomalously warm and dry springs may, in some cases, enhance CO₂ sequestration, likely because soil moisture levels remain sufficient during this period, in line with e.g. Delpierre et al. (2009) and Smith et al. (2020). Such a

1913 [transition from spring to summer is less evident in southern Europe, which instead exhibits contrasting patterns](#)
1914 [between late fall–winter and early spring–early fall.](#)

1915
1916 [Finally, we acknowledge that the general patterns discussed above do not always hold at specific sites. This](#)
1917 [suggests the influence of additional factors, such as soil properties, forest management practices, tree age and tree](#)
1918 [species \(see references in the Introduction\). Assessing the impact of these factors on CO₂ flux variability falls](#)
1919 [beyond the scope of this study, as it would require detailed site-specific information not available in the FLUXNET](#)
1920 [database and not fully represented in the models used.](#)

1923 5 Conclusion

1925 [This study makes use of state-of-the-art data-driven and process-based models to complement observations for](#)
1926 [assessing the impact of climate on the annual cycle and interannual variability of monthly CO₂ fluxes in European](#)
1927 [DBFs and ENFs. Output from different data-driven models \(CarbonSpace and FLUXCOM-ERA5, -MODIS and](#)
1928 [-X\) and process-based models forced by realistic conditions \(assimilation of satellite derived soil moisture in](#)
1929 [SMAP-L4C and time-varying CO₂ concentration, land-use and climate in TRENDY DVGMS\) are analysed](#)
1930 [conjointly with CO₂ measurements from 19 sites \(6 DBFs and 13 ENFs\) of the FLUXNET network. Across](#)
1931 [Europe, a clear north-south gradient emerges in the annual cycle of CO₂ fluxes. The length of the CO₂ sequestration](#)
1932 [season increases southwards in link with more favourable climate conditions for photosynthesis in southern than](#)
1933 [northern Europe. This large-scale pattern is perturbed locally by site elevation and other site factors not included](#)
1934 [in the study \(e.g., soil properties and forest age\). It is also perturbed by land cover class, with more pronounced](#)
1935 [annual cycle of DBFs than ENFs in central Europe. The interannual variability of CO₂ fluxes does not exhibit such](#)
1936 [a north-south gradient, regardless of the metric used \(standard deviation or coefficient of variation\). However, it](#)
1937 [remains strong across all seasons, with spring and summer showing high variability based on standard deviation,](#)
1938 [and autumn and winter based on the coefficient of variation.](#)

1940 [The models accurately capture the observed features despite magnitude differences. Compared to observations,](#)
1941 [the CO₂ sequestration is weaker in regional-scale models and stronger in the hectometric-scale CarbonSpace data-](#)
1942 [driven model. All models underestimate the interannual variability of CO₂ fluxes, as already reported \(Lin et al.](#)
1943 [2023; Nelson et al., 2024\). However, the interannual variability of modelled fluxes correlates well with the](#)
1944 [observations. This supports the use of models to complement observations, whose limited temporal coverage](#)
1945 [hinders the assessment of climate impacts on CO₂ interannual variability. The influence of climate on CO₂ flux](#)
1946 [interannual variability changes along the annual cycle and a clear distinction emerges between northern/central](#)
1947 [Europe and southern Europe despite model dependencies. Atmospheric factors \(i.e., 2 m temperature and vapour](#)
1948 [pressure deficit\) dominate CO₂ fluxes interannual variability in northern and central Europe, while soil moisture](#)
1949 [dominates in southern Europe. Winter and fall CO₂ release increases under elevated temperature and VPD in](#)
1950 [northern and central Europe and under low VPD in southern Europe. The CO₂ sequestration increases under](#)
1951 [anomalously hot and dry conditions in spring and cold and wet conditions in summer in northern/central Europe.](#)
1952 [Anomalously cold and wet conditions also favor CO₂ sequestration in southern Europe from May to September.](#)

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a supprimé : This study questions the strengths and limitations of state-of-the-art data-driven and process-based models to monitor and understand the temporal variability CO₂ exchanges between the atmosphere and western European temperate forest ecosystems where no flux tower measurements are available. Output from two data-driven models (CarbonSpace and FLUXCOM using different AI algorithms) and two process-based models (LPJ-GUESS and SMAP-L4C) are inter-compared over two non-instrumented sites (Châtillonnais and Mont Beuvray, France) and compared to CO₂ flux measurements from three flux tower sites (Davos, Fontainebleau and Hesse) from the FLUXNET network retained due to their proximity with the non-instrumented sites in terms of location, climate and forest stand. The focus is put on the representation of the annual cycle, annual budget, interannual variability and long-term trend in CO₂ fluxes (NEE, GPP and RECO), as well as their relationship with various climate parameters. Our results indicate that no model systematically outperforms the others. The best model in terms of representing the mean annual cycle and annual budget is not necessarily the best in capturing interannual variability. Overall, the data-driven models perform best in representing the CO₂ flux mean annual cycle and annual budget, despite considerable uncertainties from one approach to another (CarbonSpace versus FLUXCOM). As far as interannual co-variability with climate is concerned, the best performing models are those forced by dynamic instead of static climate conditions. Our results suggest that the spatial resolution of the climate drivers is likely very important in capturing spatial and temporal patterns in CO₂ exchange (e.g., in complex mountain areas). The ability to distinguish PFT spatial heterogeneity is only partially effective in representing this. Our results finally point towards the need to choose the appropriate model and spatial resolution according to the scientific question to deal with and to develop high spatial resolution models forced by dynamic climate conditions to allow for a fine scale representation of CO₂ flux temporal dynamics at the territorial level.

1991
1992
1993
1994
1995
1996

[These results highlight the significant space-time variability in the impact of climate on forest CO₂ fluxes across Europe. This variability underscores the importance of considering regional and seasonal differences when assessing the effects of climate change on CO₂ fluxes. Neglecting these variations could lead to oversimplified conclusions and hinder the development of accurate predictions and effective mitigation strategies.](#)

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Table A1. List of TRENDY DVGMs used in this study.

Columns 1 and 2 provide the name of the DGVM and its corresponding reference, respectively.

2001
2002

a mis en forme : Interligne : simple

2003
2004

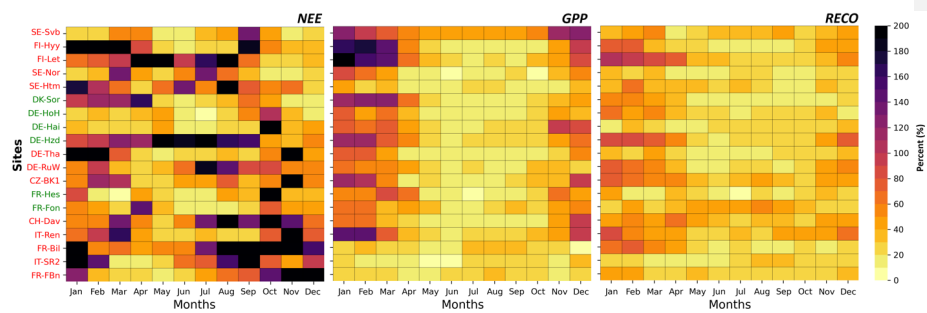


Figure A1. Same as Fig. 4b but using the coefficient of variation as a metric for interannual variability.

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Automatique

a mis en forme : Couleur de police : Automatique

2005
2006

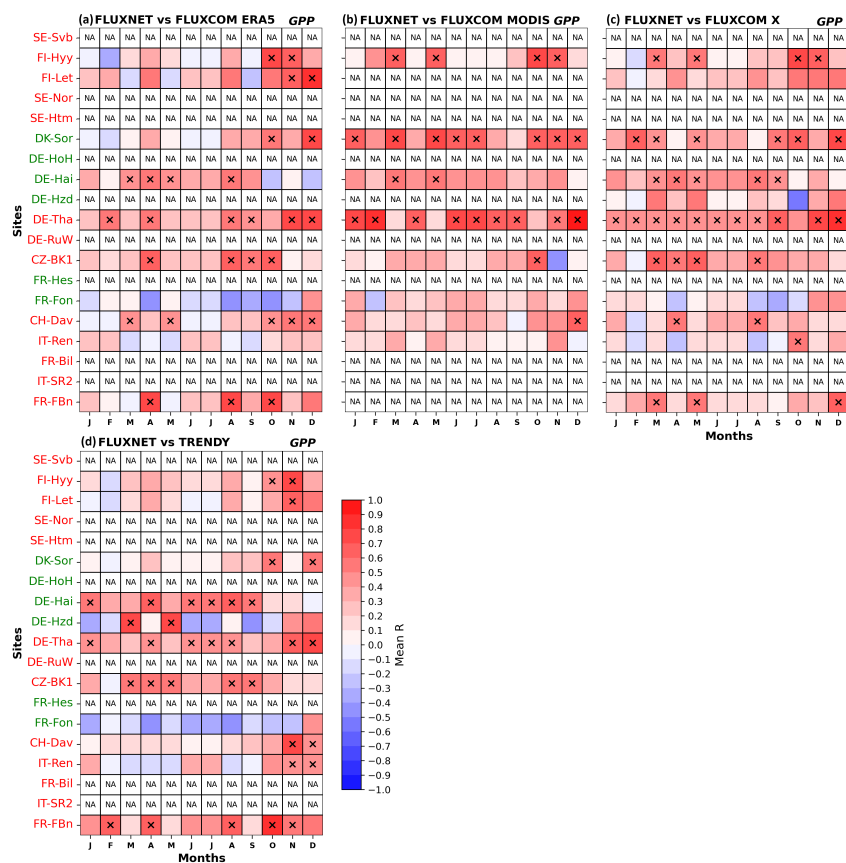
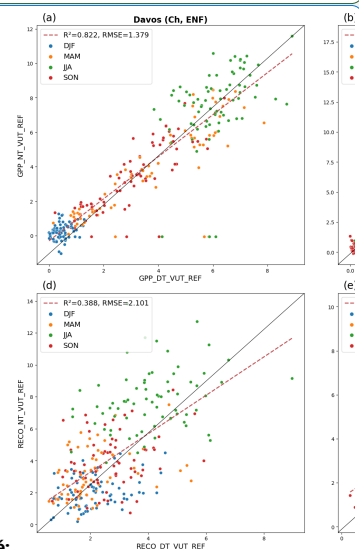


Figure A2. Same as Fig. 7 but for GPP.

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a supprimé:

Figure A1: Comparison between (a-c) GPP and (d-f) RECO using the daytime partitioning (x-axis) and the nighttime partitioning (y-axis) for the three FLUXNET sites at the monthly timescale. The four colors correspond to the four seasons. The red line shows the linear regression between the two approaches, together with the coefficient of determination (R^2) and root mean squared error (RMSE) labeled in the insert. The black line shows the 1-by-1 correspondence.

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... [121]

2047
2048

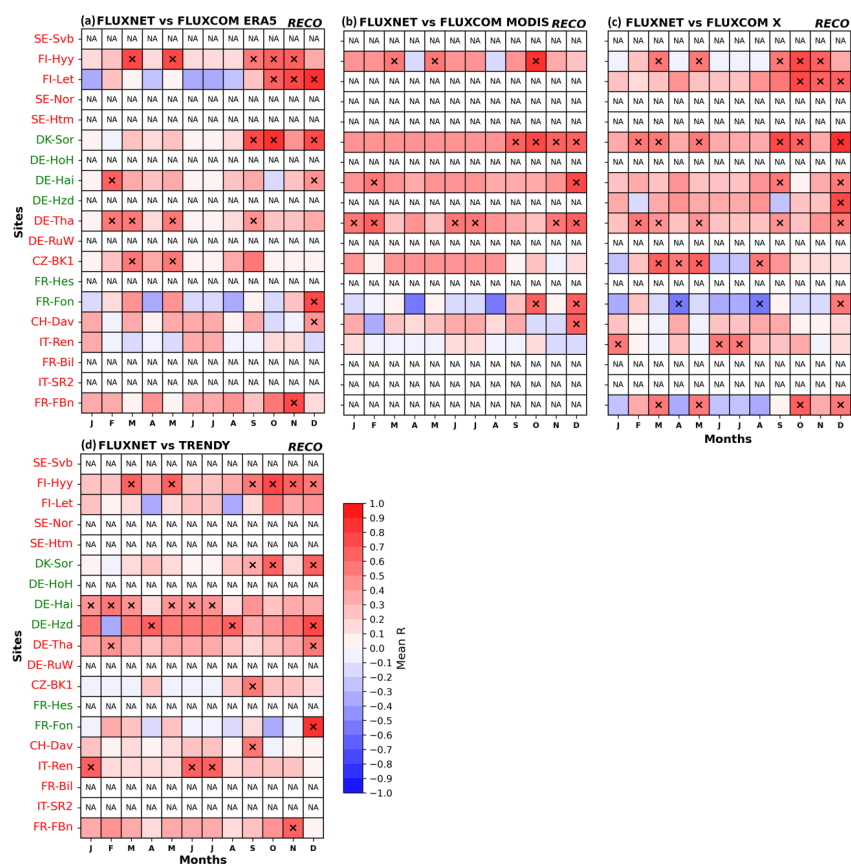


Figure A3. Same as Fig. 7 but for RECO.

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a supprimé: GPP.

a mis en forme : Police :Gras

a mis en forme : Interligne : simple

2051
2052

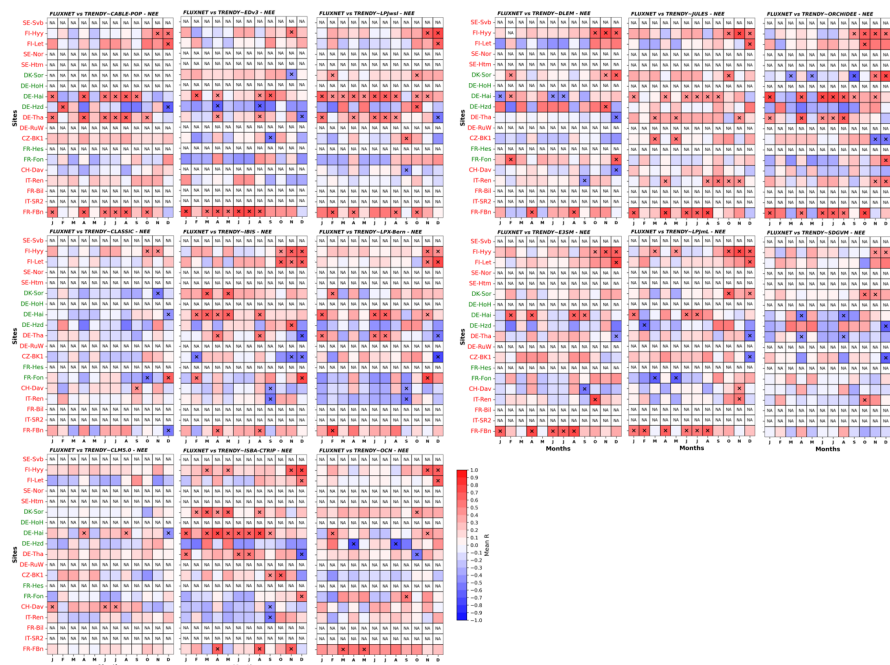
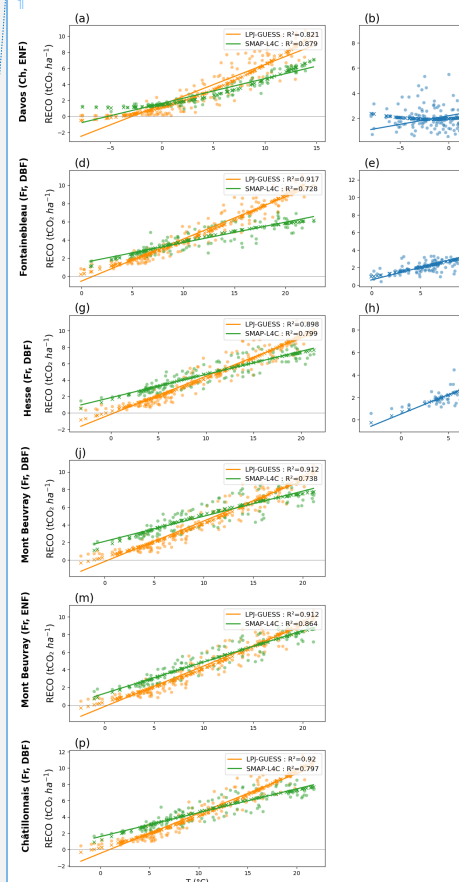


Figure A4. Same as Fig. 7c but for each TRENDY model considered in this study.

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a supprimé: A7:

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a supprimé: RECO.

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a mis en forme : En-tête

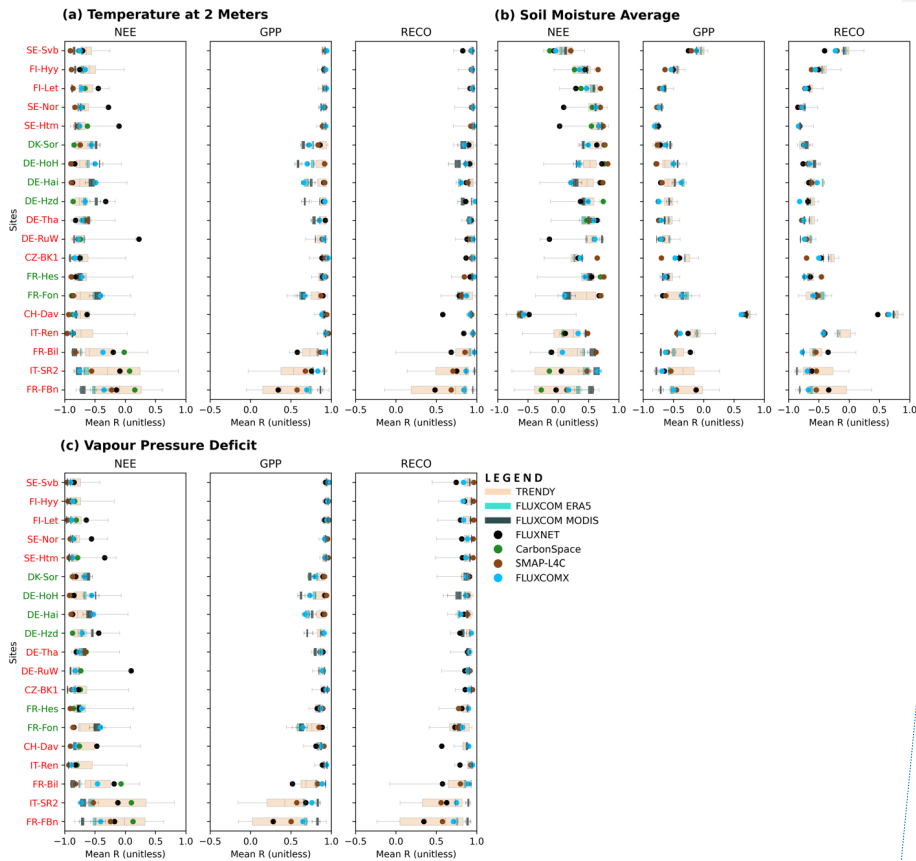


Figure A5. Same as Fig. 5 but for the relationship between the annual cycle of CO₂ fluxes and (a) 2 m temperature, (b) soil moisture, and (c) vapour pressure deficit. This relationship is evaluated using Bravais-Pearson correlation. For details, refer to the legend caption of Fig. 8.

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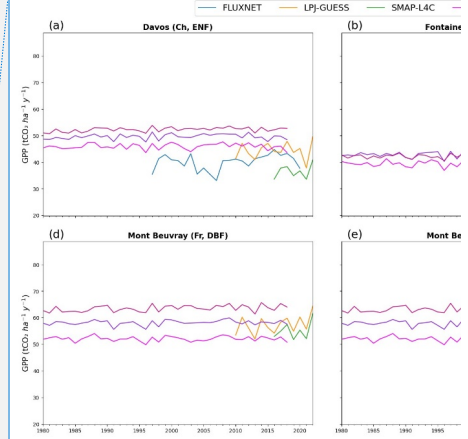
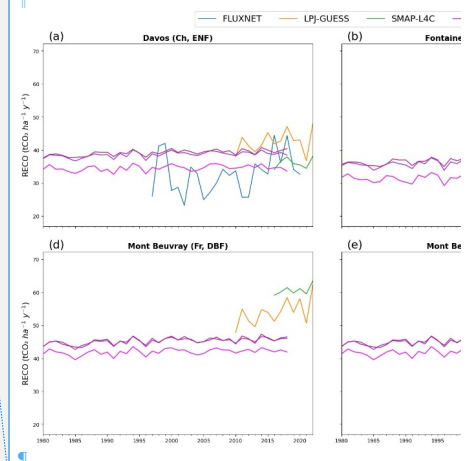


Figure A8: Same as Fig. 15 but for GPP.

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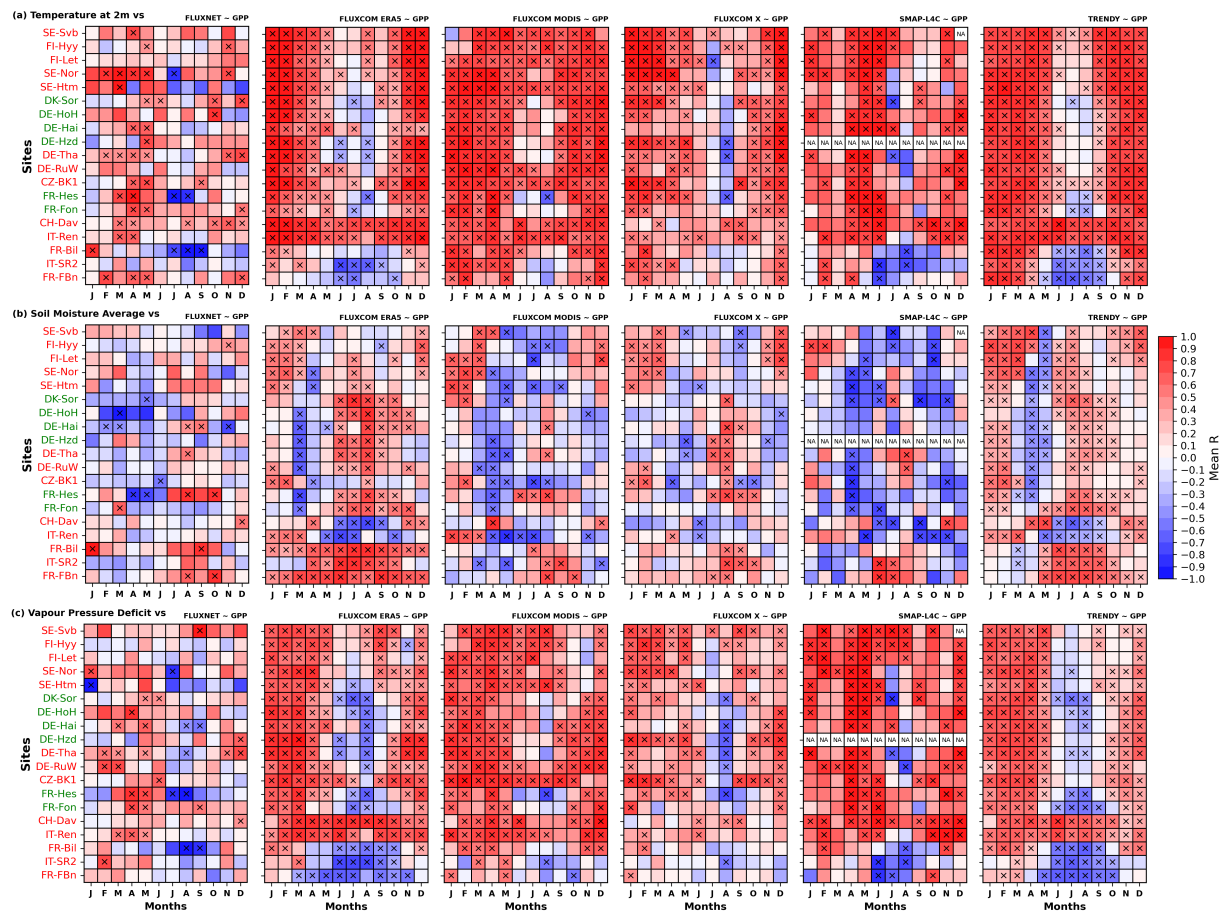


Figure A6. Same as Fig. 9 but for GPP.

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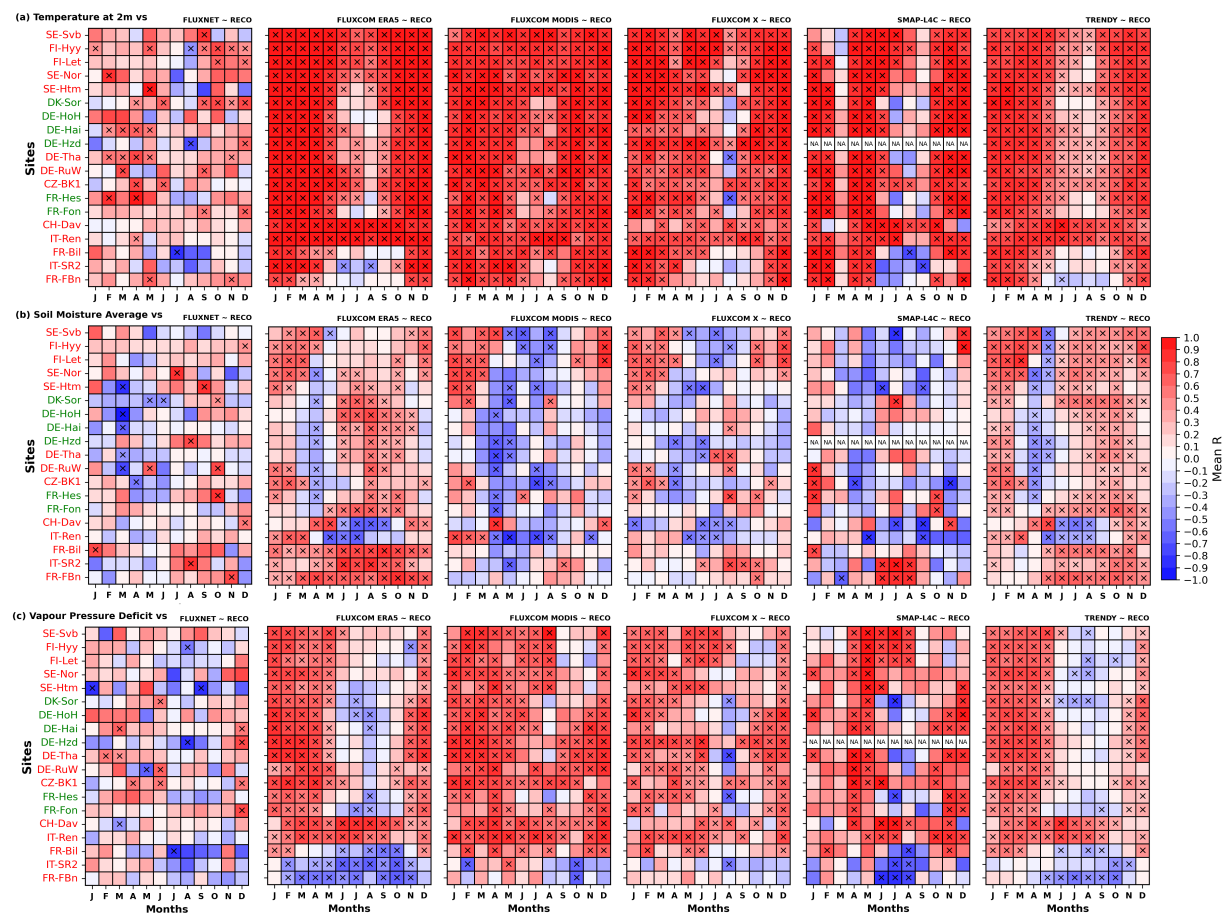


Figure A7. Same as Fig. 9 but for GPP.

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Author contribution

JC conceived the study. JC, AU, and GM collected the data and developed the analysis scripts. GM and JC drafted the first version of the manuscript. AU and JC drafted the second version. All co-authors contributed to its review.

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Data Availability

Climate parameters from the ERA5-Land are available at <https://cds.climate.copernicus.eu/datasets/reanalysis-era5-land>. CO₂ fluxes from the FLUXOM data-driven model are available at <https://www.bgc-jena.mpg.de> and https://meta.icos-cp.eu/collections/zfwf1Ak2I7OlziGDTX8XI6_T. Those from TRENDY and SMAP-L4C process-based models are available on request to Professor Stephan Sitch (s.a.sitch@exeter.ac.uk) and at <https://nsidc.org/data/spl4cmdl/versions/7>, respectively.

Conflict of Interest

The authors declare no competing interests.

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Conflict of Interest¶

The authors declare no competing interests.¶

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a mis en forme : Couleur de police : Automatique

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