



1 **Evaluating state-of-the-art process-based and data-driven**
2 **models in simulating CO₂ fluxes and their relationship with**
3 **climate in western European temperate forests**
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35 **Abstract.**

36

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

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55 **Key words:** Net ecosystem exchange, gross primary production, ecosystem respiration, climate, annual cycle,
56 annual budget, interannual variability, trend

57



58 **1 Introduction**

59

60 Among all their environmental benefits, forest ecosystems are efficient carbon sinks and constitute a potential
61 lever for climate change mitigation. At the global scale, forest ecosystems cover about 30% of landmasses. They
62 represent the largest part of the land carbon sink (Lindeskog et al., 2021), with up to 20-50% of anthropogenic
63 CO₂ emissions (land-use changes excluded) sequestered for the 2000-2010 period (Pan et al., 2011; Le Quéré et
64 al., 2018; Pugh et al., 2019). Despite the fertilization effect of increased atmospheric CO₂ concentrations (Walker
65 et al., 2020; IPCC, 2023) and the warming-induced lengthening of the growing season (Prislan et al., 2019; Menzel
66 et al., 2020; IPCC, 2023), the evolution in the net ecosystem exchange (NEE) suggests a recent decrease of annual
67 CO₂ storage in forest ecosystems of temperate Europe, due to severe heat waves and droughts that affected
68 Northern regions in 2018 and Central-Southeastern regions in 2020 (Smith et al., 2020; Thompson et al., 2020;
69 van der Woude et al., 2023). This trend results from a combination of multiple factors. In France, for instance, the
70 CO₂ storage by forests dropped from ~53 Mt CO₂ year⁻¹ to ~32Mt CO₂ year⁻¹ between 2005-2013 and 2012-2020,
71 mostly due to increased timber-extraction (+20%), climate-related mortality (+54%) and decreased biological
72 production (-10%) (IGN, 2022; Chuine et al., 2023). Such a continental-to-country scale evolution of forest-related
73 CO₂ fluxes needs to be refined at a finer spatial grain to better account for the contributing influence of different
74 forest stands and to clarify the role of forest ecosystems in the CO₂ budget at a territorial level and their leverage
75 in mitigating climate change impacts.

76 A territorial-scale assessment remains, however, challenging. Measuring NEE and its two components, gross
77 primary production (GPP) quantifying CO₂ sequestration through photosynthesis and ecosystem respiration
78 (RECO) releasing CO₂ through autotrophic and heterotrophic processes, is expensive since it requires the
79 installation and maintenance of flux towers measuring eddy covariance above the canopy (Burba, 2021). The
80 FLUXNET initiative provides over 1500 site-years of quality-controlled flux tower data from 212 sites around the
81 globe, using the same ONEFlux processing pipeline to foster inter-site comparisons (Pastorello, 2020). At the
82 European scale, the Integrated Carbon Observation System (ICOS) network provides standardized and open data
83 from 98 ecosystem stations across 16 countries. The flux towers remain limited in number and unevenly distributed
84 spatially, which makes it impossible to study CO₂ fluxes directly in unequipped sites. Process-based and data-
85 driven models allow us to tackle the above limitation. Process-based models, such as dynamical vegetation models,
86 are routinely used to assess CO₂ flux exchanges between the atmosphere and the biosphere (Friedlingstein et al.,
87 2023). These are mechanistic models (Friedlingstein et al., 2006; Sitch et al., 2008), which allow for testing the
88 response of CO₂ fluxes to individual and combined forcing. Data-driven models rely on the identification of
89 statistical relationships between flux tower measures by eddy-covariance and corresponding land use, vegetation
90 properties and climate characteristics. Based on these statistical relationships, empirical models are built and used
91 for upscaling, i.e., for assessing CO₂ fluxes in regions where they are not measured (Jung et al., 2009, 2019, 2020;
92 Tramontana et al., 2016; Zhuravlev et al., 2022). Both approaches have limitations. For instance, estimations of
93 CO₂ flux exchanges are highly sensitive to physical parameterizations (Cai and Prentice, 2020) and atmospheric
94 forcing (Wu et al., 2017; Hardouin et al., 2022) in process-based models. Regional CO₂ flux upscaling methods
95 are also limited by the sparse and uneven distribution of flux tower measurements, and limitations of the underlying
96 statistical methods used in data-driven models (Jung et al., 2020).



97 This study aims at comparing the respective strengths and limitations of process-based and data-driven approaches
98 to capture the recent temporal dynamics of CO₂ flux exchanges observed in western European temperate forest
99 ecosystems, with a focus on evergreen needleleaf forests (ENFs) and deciduous broadleaf forests (DBFs). The first
100 objective is to discuss their capability to simulate the mean state, interannual variability and trend in NEE and,
101 when available, GPP and RECO. Previous observation-based studies have shown that CO₂ flux exchanges depend
102 on multiple factors not necessarily related to climate such as soil properties (Kurbatova et al., 2008; Besnard et al.,
103 2018; Curtis and Gough, 2018; Martinez del Castillo et al., 2022), forest management practices (Carrara et al.,
104 2003; Scott et al., 2004; Saunders et al., 2012), tree age (Kurbatova et al., 2008; Besnard et al., 2018; Chuine et
105 al., 2023) and tree species (Carrara et al., 2003, 2004; Welp et al., 2007; von Buttlar et al., 2018; Zheng et al.,
106 2021; Kong et al., 2022) among many others. On average, the annual cycle of CO₂ flux exchanges significantly
107 differs between ENFs and DBFs since photosynthesis can occur all year long in the former, while is bounded from
108 spring (bud break) to fall (leaf senescence) in the latter. As a result, DBFs tend to be a net CO₂ sink during the
109 warm season, and CO₂ source during the cold season (Granier et al., 2002; Welp et al., 2007); whereas, ENFs can
110 persist as a CO₂ sink year-around under favorable meteorological conditions (Mizoguchi et al., 2012). At the
111 interannual timescale, Welp et al. (2007) found that the NEE variability is greater and mainly driven by GPP in
112 Alaskan DBFs and by RECO in the ENFs. This is at odds with Yuan et al. (2009) who found the opposite pattern
113 in 30 northern-hemisphere sites, suggesting latitudinal (hence climate) dependency in the results.

114 The second study objective is to examine the influence of climate on the temporal variability of CO₂ flux exchanges
115 in temperate DBFs and ENFs in terms of annual cycle (monthly timescale), interannual variability (monthly and
116 annual timescales) and trend (annual timescale). The recent record-breaking temperatures and long drought
117 episodes observed e.g., in Central Europe in 2003, Central and Northern Europe in 2018 and Central and
118 Southeastern Europe in 2022, have been accompanied by sharp reductions in forest CO₂ uptake (Ciais et al., 2005;
119 Thompson et al., 2020; van der Woude et al., 2023). Understanding the role of climate on forest NEE temporal
120 dynamics requires accounting for both monthly and annual budgets since potential compensations of CO₂ fluxes
121 can occur across the annual cycle. This is the case in 2018 in Northern Europe when increased CO₂ uptake in
122 spring (due to anomalously warm conditions) was offset by an anomalous decrease in summer (due to heat and
123 drought), resulting in week NEE anomalies at the annual timescale (Thompson et al., 2020). Understanding the
124 role of climate on NEE also requires assessing how the much larger GPP and RECO component fluxes may
125 respond differently to climate. The annual cycle and, to a lesser extent, the interannual variability of these CO₂
126 fluxes are driven by temperature and the water cycle, including soil moisture (Haszpra et al., 2005; Tang et al.,
127 2013; Kong et al., 2022; Sharma et al., 2022; Li et al., 2023). Welp et al. (2007) showed that DBFs are more
128 sensitive to soil moisture changes in ENFs than in DBFs, and that decreased GPP under water stress was observed
129 in DBFs only. The authors attributed this difference to a possible buffer effect in ENFs' soils that is damping out
130 temperature increases and to a lower stomatal sensitivity of conifers. In addition, the soil respiration increases
131 exponentially with temperature (van't Hoff, 1898; Meyer et al., 2018) until a maximum temperature threshold is
132 reached, which rarely occurs in extratropical soils (von Buttlar et al., 2018). However, when extreme temperatures
133 are combined with soil water stress, clearer GPP and RECO answers come out. For instance, Ciais et al. (2005)
134 estimated a 30% decrease in GPP and moderate RECO tail-off during the 2003 severe heat and drought event in
135 Central Europe, resulting in a lower net carbon uptake. The larger contribution of GPP on NEE interannual
136 variability remains site and stand dependent (Welp et al., 2007; Yuan et al., 2009). Finally, despite strong effects



137 of recent heat waves and droughts, the NEE does not always show clear trends in response to recent and projected
138 climate change (Ahlström et al., 2012; Abdalla et al., 2013; Tang et al., 2013; Kong et al., 2022; Martinez del
139 Castillo et al., 2022; Li et al., 2023). One possible hypothesis, tested in our study, is a potential compensation of
140 trends between GPP and RECO.

141 The novelties of this study rely on (i) the comparison between two data-driven models providing CO₂ flux
142 estimations either globally but at coarse resolution (0.5° x 0.5°) or locally but at the hectometric resolution and (ii)
143 the inclusion of a newly released process-based model constrained by soil moisture satellite data, which provides
144 CO₂ flux estimations for each plant functional type at relatively high space-time resolution (daily; 9 km mesh with
145 1 km sub-grids). Another originality relies on the multi-scale (annual cycle, interannual variability and trend)
146 assessment of the temporal variability in estimated NEE (and its two components) and its climate drivers.

147 The paper is structured as follows. Section 2 presents the materials and methods. Section 3 presents our results at
148 the monthly and annual timescales and Sections 4 and 5 discuss the results and give the main conclusions,
149 respectively.

150 **2 Materials & Methods**

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152 **2.1 Site description**

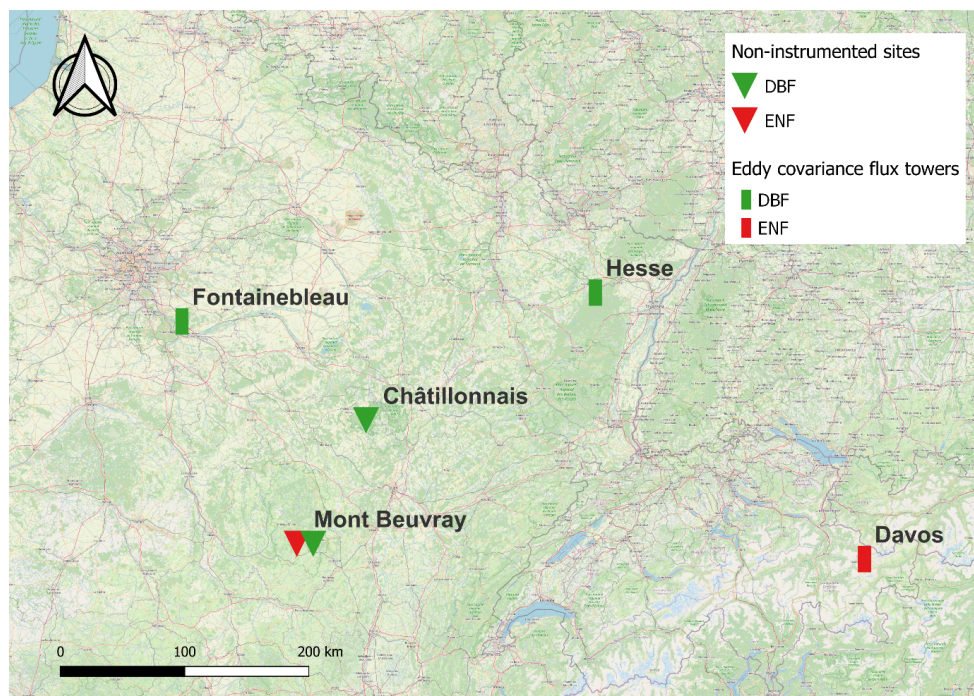
153

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

157

158 The first non-instrumented site is located in the National Park of Forests, a 240,000 ha park mostly covered by
159 DBFs (50%). One DBF plot of 25 ha is selected because soil respiration measures are conducted there by the
160 Biogéosciences laboratory since 2020. This DBF plot, named “Châtillonnais (DBF)” hereafter, is located on a
161 ~380 m plateau and characterized by uneven-aged and mixed DBFs dominated by beech (*Fagus sylvatica*) and
162 oaks (*Quercus robur*, *Quercus petraea*) with no silvicultural interventions for ~30 years and by oolitic limestone
163 soils. The second site is located in the Regional Natural Park of Morvan, on the Mont Beuvray, a semi-mountainous
164 domain of 950 ha peaking at 821 m and sitting on volcanic-sedimentary rocks. The Mont Beuvray location is
165 particularly impacted by climate change (Castel et al., 2019), with a mean warming trend reaching 2°C more than
166 the neighboring lowlands over the 1958-2015 period. Two plots are considered for Mont Beuvray: one even-aged
167 large-sized Douglas fir (*Pseudotsuga menziesii*) plots of 15 ha classified as ENF and one even-aged beech plot
168 with continuous cover of 8 ha classified as DBF. These plots are named “Mont Beuvray (DBF)” and “Mont
169 Beuvray (ENF)” hereafter.

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173 **Figure 1:** Location of the study sites. The rectangles correspond to FLUXNET sites where CO₂ fluxes are
174 measured by eddy covariance flux towers and estimated by process-based and data-driven models. The triangles
175 correspond to non-instrumented sites where CO₂ fluxes are estimated by process-based and data-driven models
176 only. Symbols in green and red correspond to DBF and ENF sites, respectively. © OpenStreetMap contributors
177 2021. Distributed under the Open Data Commons Open Database License (ODbL) v1.0.

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180 To compare the CO₂ flux dynamics of these sites and to evaluate the accuracy of data-driven and process-based
181 models, we selected three forest tower sites from the FLUXNET network for their resemblance to the
182 aforementioned ones in terms of location, climate or stand characteristics:

- 183 - Two lowland DBFs. The “Fontainebleau” site (FR-Fon) is located in the domanial forest of Barbeau
184 (southeast of Paris), dominated by oak (*Qu. petraea*) and characterized by a loamy soil on top of burstones
185 and deeper marls. The “Hesse” site (FR-Hes) is located in the plain east of the Vosges mountains,
186 dominated by beech (*Fagus sylvatica*) and characterized by a deep silty clay soil on sandstone;
- 187 - One midland ENF, “Davos” (CH-Dav), located in the middle range of the subalpine belt in the eastern
188 part of the Swiss Alps at 1639 m, dominated by Norway spruce (*Picea abies*) and characterized by a thin
189 soil on schists and gneiss.

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194 **2.2 Carbon flux data**

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196 Measured CO₂ fluxes are used as a reference to evaluate outputs from two data-driven and two process-based
 197 models (Table 1). They come from the Warm Winter 2020 release (Warm Winter 2020 Team and ICOS Ecosystem
 198 Thematic Centre, 2022), an update of the FLUXNET2015 dataset (Pastorello et al., 2020) available on the ICOS
 199 platform (<https://www.icos-cp.eu/data-products>). For each site, we selected daily time series of NEE
 200 (NEE_VUT_REF) accounting for multiple friction velocity thresholds and associated with a favorable quality
 201 control flag above 80%, GPP (GPP_DT_VUT_REF) and RECO (RECO_DT_VUT_REF). GPP and, to a lesser
 202 extent, RECO are less sensitive to the partitioning method (Fig. A1) and the climate – CO₂ flux relationship is
 203 similar regardless of the partitioning method used. Here, we retained those CO₂ flux data derived from the daytime
 204 flux partitioning method (Lasslop et al., 2010). The temporal coverage of the data is site dependent: 7 years for
 205 Hesse, 18 for Fontainebleau and 24 for Davos (Table 1).
 206

	Observations	Process-based models		Data-driven models	
	FLUXNET	SMAP-L4C	LPJ-GUESS	CarbonSpace	FluxCom
Parameters	NEE, GPP, RECO, weather	NEE, GPP, RECO	NEE, GPP, RECO	NEE	NEE, GPP, RECO
Timescale	Daily	Daily	Hourly	Monthly	Monthly
Spatial resolution	Local	9 km	50 km	Hectometric	50 km
Temporal coverage	Davos: 01/02/1997 – 12/31/2020 Hesse: 01/01/2014 – 12/31/2020 Fontainebleau: 03/11/2005 – 12/31/2022	31/03/2015 – 21/09/2023	01/01/2010 00:00 – 31/12/2022 23:00	01/2000 – 08/2023	01/1979 – 12/2018
Characteristics	Standardized and filtered measurements from flux towers	Carbon model with 1km sub-grids and soil moisture assimilation	Dynamic global vegetation model forced by climate data (ERA5)	Machine learning based estimations, integrating satellite vegetation proxies, climate and flux tower measurements	
References	Pastorello et al. (2020); Warm Winter 2020 Team & ICOS Ecosystem Thematic Centre, 2022)	Jones et al. (2017); Kimball et al. (2022)	Smith et al., (2001, 2014); Wu (2023)	Zhuravlev et al. (2022)	Jung et al. (2019, 2020)

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



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

223

224 The second data-driven model comes from the FLUXCOM products (Tramontana et al., 2016; Jung et al., 2019,
225 2020) retrieved from the data portal of the Max Planck Institute for Biochemistry (<https://www.bgc-jena.mpg.de>).
226 The FLUXCOM products use eddy-covariance data from 224 flux-tower sites from the FLUXNET La Thuile
227 dataset (<http://fluxnet.fluxdata.org/data/la-thuile-dataset/>) and the CarboAfrica network (Valentini et al., 2014),
228 including Hesse data between 1997 and 2006 and Fontainebleau between 2005 and 2006. Cross-validations are
229 thus possible with most of our data from the Warm Winter 2020 release. The FLUXCOM products have been
230 shown to accurately estimate the mean annual and seasonal cycles of CO₂ fluxes (Tramontana et al., 2016; Jung
231 et al., 2020; He et al., 2022). Among the various forcing datasets available, we retained three of them, all forced
232 by hourly meteorological data from the ERA5 reanalysis (Hersbach et al., 2020) and providing global maps of
233 monthly NEE, GPP and RECO derived with a daytime partitioning on a 0.5° x 0.5° horizontal grid for the 1979-
234 2018 period. As for FLUXNET, the partitioning method does not significantly affect the CO₂ fluxes (Fig. A2).
235 The three datasets differ according to the algorithm used to build the statistical model: Random Forest (RF;
236 Breiman, 2001), Multivariate Adaptive Regression Splines (MARS; Friedman, 1991) and Artificial Neural
237 Networks (ANNs; Papale and Valentini, 2003). Unlike the CarbonSpace model, their coarse horizontal resolution
238 precludes the ability to account for individual forest stands. Despite these limitations, the three FLUXCOM
239 datasets allow to assess uncertainties induced by the statistical model used for upscaling CO₂ fluxes and to get
240 access to NEE and its two components.

241

242 The two process-based models are the Lund-Postdam-Jena General Ecosystem Simulator (LPJ-GUESS; Smith et
243 al., 2001, 2014) and the version 7 of the NASA Soil Moisture Active Passive Mission Level 4 Carbon (SMAP-
244 L4C; Jones et al., 2017; Kimball et al., 2022) models. The LPJ-GUESS is a dynamic global vegetation model
245 simulating the effects of environmental change in vegetation represented by plant functional types (PFTs), soil
246 hydrology and biogeochemistry (Smith et al., 2001). The model is widely used to study ecosystems, including CO₂
247 fluxes (Smith et al., 2001, 2014; Bayer et al., 2015; Lindeskog et al., 2021; Sathyanadh et al., 2021; Bergkvist
248 et al., 2023). The simulations used here were derived from Wu (2023) using version 4 of LPJ-GUESS in cohort mode
249 forced with hourly ERA5-land reanalysis (Muñoz-Sabater et al., 2021) and observed atmospheric CO₂



250 concentrations. The cohort mode means that woody plants of the same size and age are represented by a single
251 average individual. Each PFT is represented by multiple average individuals, and one PFT cohort is defined as the
252 average of several individuals. We retrieved hourly NEE, GPP and RECO on a 0.5° x 0.5° horizontal grid for the
253 2010-2022 period from the ICOS website ([https://meta.icos-](https://meta.icos-cp.eu/collections/NZNSUglRn0VeXmGDovuVY0ec)
254 [cp.eu/collections/NZNSUglRn0VeXmGDovuVY0ec](https://meta.icos-cp.eu/collections/NZNSUglRn0VeXmGDovuVY0ec)). Like the FLUXCOM products, the horizontal resolution of
255 LPJ-GUESS outputs is too coarse to distinguish plots over the Mont Beuvray and Châtillonnais.

256
257 The SMAP (Soil Moisture Active Passive) Level 4 Carbon model product (SMAP-L4C) is produced operationally
258 by the NASA SMAP mission and can be considered as a reanalysis product since it uses the Goddard Earth
259 Observing System version 5 (GEOS-5) land model to assimilate SMAP L-band microwave observations and is
260 forced with observed land cover and vegetation from the Moderate Resolution Imaging Spectroradiometer
261 (MODIS) and Visible Infrared Imaging Radiometer Suite (VIIRS). The global processing is conducted on 1 km
262 sub-grids using spatially aggregated MODIS PFTs and VIIRS fPAR inputs, allowing to distinguish up to eight
263 individual PFTs within each 9 km x 9 km product grid cell. However, the model processing uses coarser spatial
264 resolution (9 km and 0.25 degree) daily inputs from the SMAP L4 soil moisture (L4_SM) and GMAO Forward
265 Processor (FP) surface meteorology. Among other variables, the SMAP-L4C outputs provide daily NEE and GPP
266 (RECO deduced from the difference between NEE and GPP), in a consistent global grid from March 2015 to
267 September 2023 for each PFT, including DBFs and ENFs (Jones et al., 2017; Kimball et al., 2022). The 1-km PFT
268 subclass distinction allows to differentiate ENF and DBF behavior over the Mont Beuvray plots. The L4C product
269 is derived using coupled photosynthetic light-use efficiency and soil organic matter decomposition models to
270 estimate daily NEE and its component carbon fluxes; where, GPP is reduced from PFT-specific optimal rates for
271 unfavorable daily climate conditions including cold temperatures, low light levels, excessive atmospheric vapor
272 pressure deficits and low root zone (0-1m depth) soil moisture levels defined from SMAP L4_SM and GMAO FP
273 meteorology. Details of the model algorithms and the calibration, validation, and performance of the L4C version
274 7 product used in this study are given in the associated product quality assessment report (Endsley et al., 2023).

275

276 2.3 Climate data

277

278 Climate parameters are extracted from the version 2 of the operational chain Safran-ISBA-Modcou (SAFRAN-
279 SIM2; Soubeyroux et al., 2008). SAFRAN-SIM2 is a hydrometeorological reanalysis produced by Météo-France
280 at a 8 km spatial resolution from 1958 onwards. For each of the five sites, we extracted the nearest grid point for
281 2 m temperature (T in °C), soil water index of the first two meters (SWI in %), liquid, solid and total precipitation
282 (PRELIQ, PRENEI and PRE_SUM in mm), real and potential evapotranspiration (EVAP and ETP in mm) and 2
283 m relative humidity (HU in %). In addition, we calculated the air Vapor Pressure Deficit (in Pa), an integrative
284 metric accounting for both heat and water stress effects (Carrara et al., 2004; von Buttlar et al., 2018; Kong et al.,
285 2022; van der Woude et al., 2023). The VPD is defined as the difference between the amount of moisture that is
286 actually in the air and the amount of moisture that air could hold at saturation. The VPD is computed using the
287 Tetens formula (Monteith and Unsworth, 2007) following Eq. (1):

$$288 \quad VPD = \left(1 - \frac{HU}{100}\right) * \text{saturation vapor pressure} = \left(1 - \frac{HU}{100}\right) (610.78 * \exp\left(\frac{T}{T+237.3}\right) * 17.2694) \quad (1)$$

289



290 Preliminary analyses show that the SAFRAN-SIM2 reanalysis accurately captures the temporal variability and
291 magnitude of 2 m temperature and precipitation compared to observations provided by the three FLUXNET sites
292 (Fig. A3), despite biased solid precipitation in Davos. For this reason and for conciseness, we consider only
293 SAFRAN-SIM2 regardless of the site and CO₂ flux product.

294

295

296 **2.4 Methodology**

297

298 For the gridded datasets (SAFRAN-SIM2, FLUXCOM, LPJ-GUESS and SMAP-L4C), we extracted the nearest
299 grid point to the flux tower sites and to the center of Mont Beuvray and Châtillonnais plots. Since all datasets have
300 different temporal resolution and units (Table 1), they all have been converted to tCO₂ ha⁻¹ month⁻¹ and aggregated
301 at the monthly timescale. From these monthly values, we computed the mean annual cycle by averaging all years
302 available in each dataset, as well as its interannual variability defined as the standard deviation of monthly values.
303 The annual budget was calculated as the sum of the monthly values, only for complete years (i.e. when no monthly
304 value is missing). Fontainebleau is the only site presenting gaps in the observed time series (in 2005, 2014 and
305 2017) due to too low-quality control values. The mean annual budget is then computed together with its interannual
306 variability following the same procedure described above.

307

308 The model skill in capturing observed CO₂ flux temporal variability at the monthly and annual timescales is
309 assessed over overlapping periods between each model and each observation. Magnitude and co-variability errors
310 are assessed in terms of bias and Bravais-Pearson correlation coefficient (R) or coefficient of determination (R²),
311 respectively. The evaluation is done considering raw monthly values to focus on the annual cycle, as well as
312 monthly anomalies (i.e., removal of the mean annual cycle) and raw annual values to focus on interannual
313 variability at the monthly and annual timescales, respectively.

314

315 The R and R² metrics are also used to assess the relationship between climate variables and CO₂ fluxes at the
316 monthly (raw and anomalous values) and annual (raw values) timescales. In addition, a composite approach is
317 performed to examine monthly climate anomalies associated with large negative and positive monthly anomalies
318 in CO₂ fluxes (NEE, GPP and RECO). Large negative/positive CO₂ flux anomalies are defined as standardized
319 anomalies (mean=0, standard deviation=1) below/above -0.5/+0.5. Tests with stricter threshold values (e.g., -1/+1)
320 lead to similar results but limit the size of the samples. The difference between the two groups is tested for
321 significance based on the non-parametric Mann-Whitney *U* test (McKnight and Najab, 2010).

322

323 **3 Results**

324

325 **3.1 Monthly timescale**

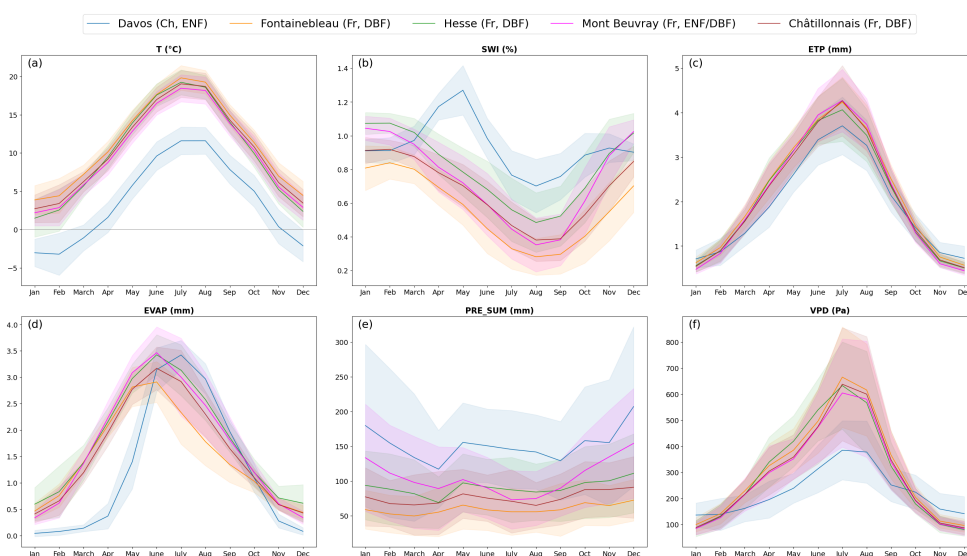
326

327 **3.1.1 Mean annual cycle and interannual variability in climate and CO₂ fluxes**

328



329 Figure 2 shows the mean annual cycle and interannual variability of T and main surface water cycle parameters
 330 associated with each site. All sites follow similar patterns of T, ETP, EVAP and VPD with the greatest values in
 331 summer and the lowest in winter. The annual cycle in SWI is reversed, with drier soils in late summer and wetter
 332 soils in winter. The total precipitation is evenly distributed throughout the year for sites in plain (Fontainebleau
 333 and Hesse and Châtillonnais), in contrast with mountainous sites (Davos and Mont Beuvray) where precipitation
 334 amounts are larger during winter than summer. The interannual variability (shadings on Fig. 2) is particularly
 335 pronounced all year long for PRE_SUM and from spring to fall for VPD, highlighting strong year-to-year
 336 fluctuations of the water cycle.
 337



338
 339

340 **Figure 2:** Mean annual cycle and interannual variability in monthly (a) 2 m air temperature (T), (b) soil moisture
 341 of the first two meters (SWI), (c) potential evapotranspiration (ETP), (d) real evapotranspiration (ETR), (e) total
 342 precipitation (liquid + solid: PRE_SUM) and (f) vapor pressure deficit (VPD) for each study site (colors, see insert)
 343 for the 1990–2023 period. Climate conditions in each site are extracted from the nearest grid point of the 8 km x
 344 8 km SAFRAN-SIM2 reanalysis. Bold lines show the mean annual cycle. Shadings show interannual variability
 345 computed as the standard deviation of each month of the period.
 346

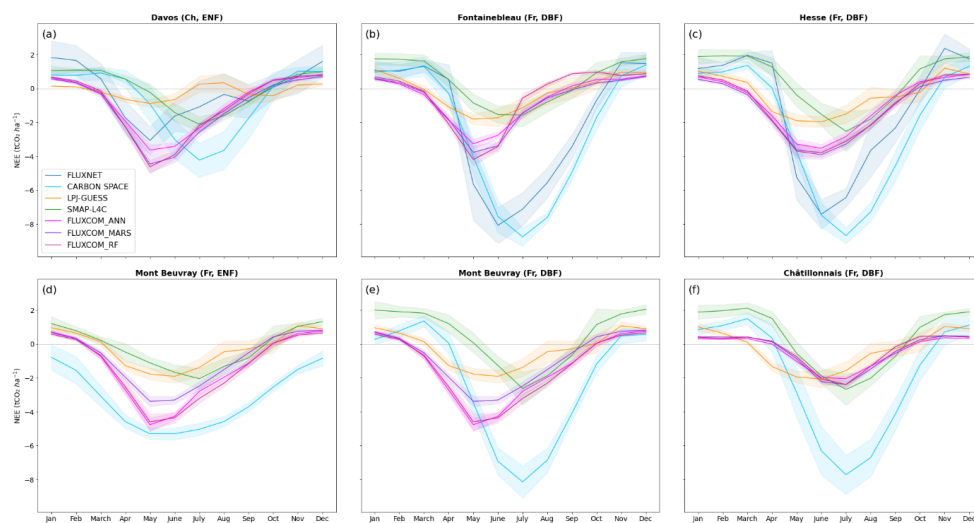
347

348 Due to its much higher elevation, Davos depicts different climate conditions than the other sites with (i) lower T
 349 by up to ~10 °C all year long, (ii) wetter soils, especially in spring due to mild temperature, low evaporation and
 350 snow melting (not shown), (iii) larger precipitation amounts all year long with snowfall from October to April (not
 351 shown) and (iv) delayed EVAP peak in late summer. While this site is not an analogue of the Mont Beuvray ENF
 352 site, it remains the most representative one available in the FLUXNET network.
 353

354 The mean annual cycle of monthly NEE is marked in all study sites (Fig. 3). Temperate forest ecosystems release
 355 CO₂ during winter and sequester CO₂ during summer, with higher values in summer than in winter. While this
 356 overall cycle prevails all years, the sign of the NEE can be reversed from one year to another in spring and fall in

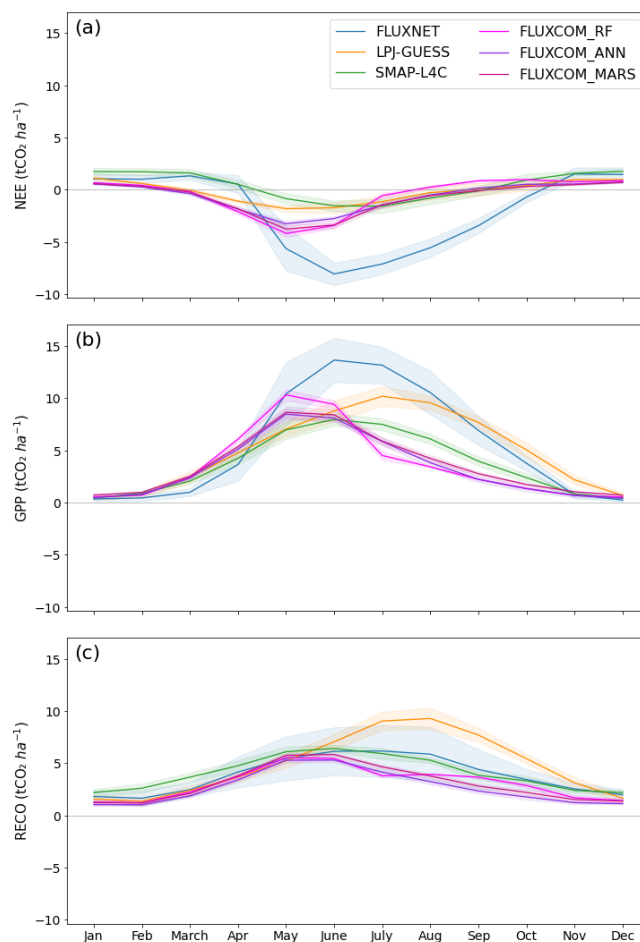


357 almost all products and sites, indicating that during these seasons the forest ecosystems can be either a CO₂ source
 358 or a CO₂ sink. Seasonal contrasts are stronger in DBF than ENF sites, consistent with the DBF leafing seasonality
 359 and with previous studies hypothesizing a buffer effect in ENF soils (e.g., Welp et al., 2007; Zheng et al., 2021).
 360 The magnitude of interannual variability seems also to be influenced by forest stand characteristics (e.g., in Mont
 361 Beuvray in the SMAP-L4C and CarbonSpace models), with e.g. a variability 40% higher for DBFs than ENFs
 362 simulated by the CarbonSpace model in Mont Beuvray in July. Despite high coupling between GPP and RECO,
 363 the NEE mean annual cycle is mostly driven by GPP in summer and by RECO in winter regardless of the sites, as
 364 illustrated for one DBF site in Fig. 4.
 365



366
 367

368 **Figure 3:** Same as Fig. 2 but for monthly NEE in the (a-c) three FLUXNET sites and (d-f) three non-instrumented
 369 sites located in Burgundy as measured by eddy-covariance (FLUXNET) and simulated by data-driven
 370 (CarbonSpace and FLUXCOM) and process-based (LPJ-GUESS and SMAP-L4C) models. The longest available
 371 period for each site and dataset is retained. See Table 1 for details. For LPJ-GUESS, SMAP-L4C and FLUXCOM
 372 models, the nearest grid point from each site is shown. Results from LPJ-GUESS and FLUXCOM are similar in
 373 panels (d-e) due to coarse horizontal resolution (0.5° x 0.5°) and no distinction between forest stands (DBF or
 374 ENF).



375

376

377 **Figure 4:** Same as Fig. 3 but for monthly (a) NEE, (b) GPP and (c) RECO in the Fontainebleau DBF site according
 378 to FLUXNET observations, FLUXCOM data-driven and LPJ-GUESS and SMAP-L4C process-based models. The
 379 CarbonSpace model is not shown since GPP and RECO are not available for this model.

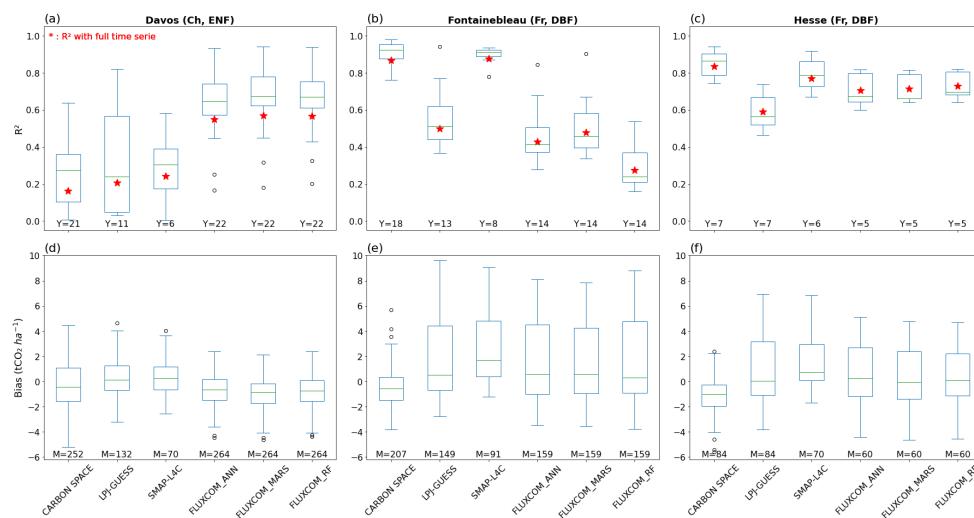
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381

382 The model skill in capturing monthly NEE depends on the metrics, sites and products (Fig. 5). Overall, the annual
 383 cycle in NEE is better represented in the two DBF sites, located in the plain, than the ENF site, Davos, located in
 384 the Alps Mountain area (Fig. 5a-c). The reverse holds in terms of magnitude (Fig. 5d-f). In Davos, all models
 385 reasonably capture the magnitude of monthly NEE, with inter-quartile in the -2 and +2 tCO₂ ha⁻¹ range, while the
 386 FLUXCOMs are the only models to reasonably capture the NEE annual cycle (R² inter-quartile in the 0.6-0.7
 387 range). In the two DBF sites, the CarbonSpace data-driven model clearly provides the best scores for both metrics
 388 (R² in the 0.8-0.9 range and bias in the 0 – -2 tCO₂ ha⁻¹ range), suggesting an added value of very high spatial
 389 resolution upscaling for representing CO₂ flux annual cycle and magnitude. The remaining models strongly
 390 underestimate the CO₂ uptake during summer and CO₂ release during winter, with 25% of the NEE values



391 associated with biases exceeding 3-4 tCO₂ ha⁻¹ in both DBF sites. Interestingly, the model deficiencies in capturing
 392 (i) the annual cycle in NEE is mainly linked to poorly resolved temporal variability of RECO (Fig. A4) and (ii)
 393 the biased NEE magnitude is mainly linked to underestimated CO₂ uptake by photosynthesis (Fig. A5).
 394



395
 396

397 **Figure 5:** Skill of data-driven and process-based models in capturing the (a-c) annual cycle and (d-f) magnitude
 398 in monthly NEE for each FLUXNET site. (a-c) The quality of the annual cycle is assessed through the coefficient
 399 of determination (R^2) between simulated and observed monthly NEE (12 values) computed for each overlapping
 400 year (labeled on panels a-c). (d-f) The magnitude errors are computed as the difference (i.e., bias) between
 401 simulated and observed NEE for each month of the overlapping period (labeled on panels d-f). The boxes have
 402 lines at the lower quartile, median, and upper quartile values. The whiskers are lines extending from each end of
 403 the boxes to show the extent of the range of the data within 1.5 by inter-quartile range from the upper and lower
 404 quartiles. Circles are outliers and red crosses in panels (a-c) are R^2 computed considering the full monthly
 405 timeseries at once (e.g., 252 months for the first from left boxplot in panel a).
 406

407

408 The annual cycle and magnitude of NEE simulated in the ENF and the two DBF non-instrumented plots (Fig. 3d-
 409 f) closely resemble those simulated in the instrumented sites (Fig. 3a-c). The two main exceptions concern all-
 410 year-long CO₂ sequestration simulated by the CarbonSpace model in the Mont Beuvray ENF site, and much
 411 weaker CO₂ sequestration peak simulated by the FLUXCOM models in the Châtillonnais DBF site. Based on these
 412 results, the CarbonSpace data-driven model appears to be the best compromise to capture the annual cycle and
 413 magnitude of NEE associated with both ENFs and DBFs. The results also demonstrate that process-based and
 414 data-driven models have their own strengths and weaknesses and are thus complementary.

415

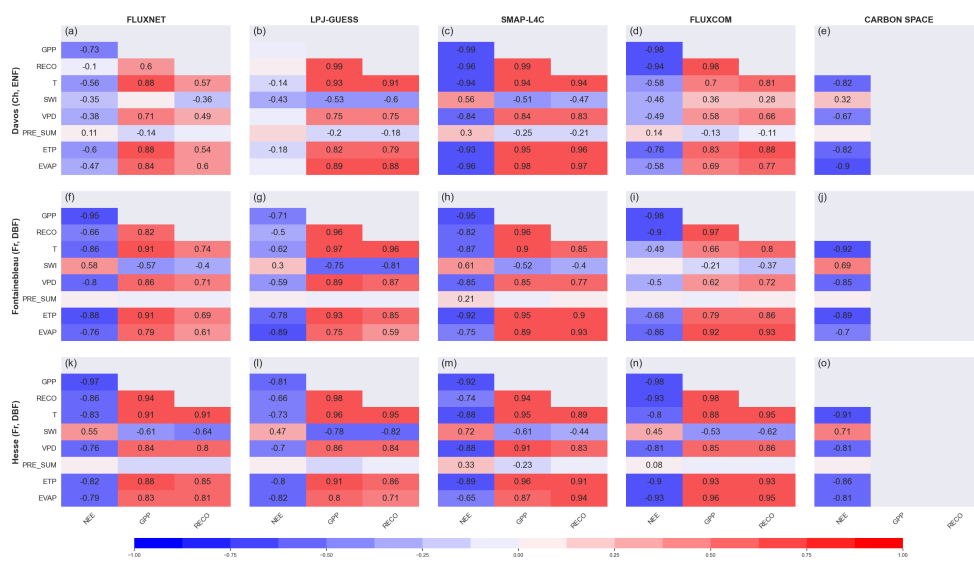
416 3.1.2 Climate – CO₂ flux relationship

417

418 The CO₂ flux – climate relationship is assessed considering both raw monthly values to account for the annual
 419 cycle and monthly anomalies (i.e., mean annual cycle removed) to focus on interannual variability.



420 The synchronous relationship between the annual cycle of CO₂ fluxes and that of various climate parameters is
 421 assessed through a correlation analysis of raw monthly time series (Fig. 6). Regardless of the sites and models, T,
 422 VPD, ETP and EVAP correlate the most with NEE. For these parameters, the correlation coefficients are negative
 423 meaning that CO₂ uptake increases with higher T, VPD and evapotranspiration. The weakest correlations are found
 424 for PRE_SUM and, to a lesser extent, SWI. Although we can hypothesize that climate variables are interdependent,
 425 a variance inflation factor (VIF) calculation highlighted the existence of multicollinearity only between ETP and
 426 VPD (VIF>5 in almost all sites and models).



428

429

430 **Figure 6:** Bravais Pearson correlation coefficient values (shadings) between the three CO₂ flux variables from
 431 each model and site, and the associated SAFRAN-SIM2 climate parameters associated with each site location.
 432 Climate parameters include 2 m air temperature (T in °C), soil water index (SWI in %), vapor pressure deficit
 433 (VPD in Pa), total precipitation (PRE_SUM in mm), potential and real evapotranspiration (ETP and EVAP in
 434 mm). (a-e) Davos, (f-j) Fontainebleau and (k-o) Hesse FLUXNET sites. Correlations are computed considering all
 435 months and all years for overlapping periods between climate and CO₂ flux datasets. See Table 1 for details. The
 436 FLUXCOM multi-model mean is shown in panels d,i,n for conciseness since the three FLUXCOM models provide
 437 similar results. GPP and RECO are not shown in panels e,j,o because they are not provided by the CarbonSpace
 438 data-driven model. Only correlation values significant at the 90% confidence level are written.

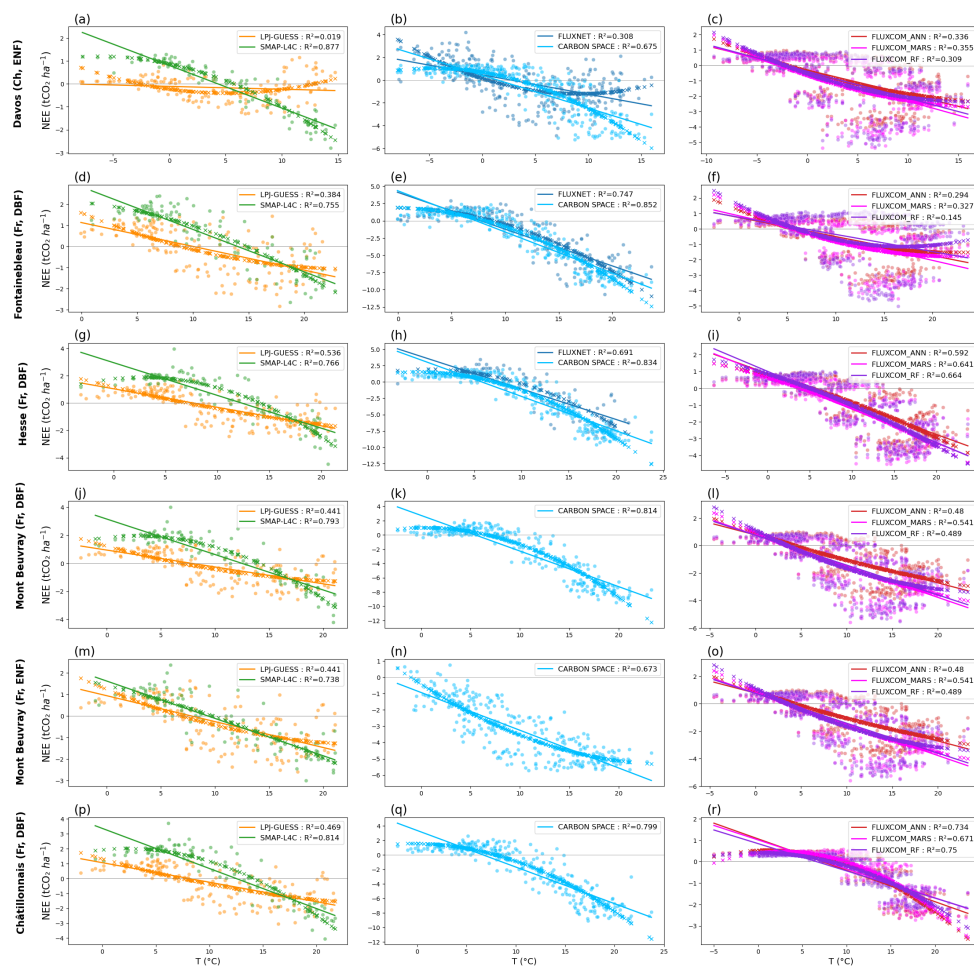
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440

441 Three main results emerge when comparing the influence of climate on the annual cycle in NEE, GPP and RECO.
 442 First, the climate influence is most of the time greater on GPP than RECO, particularly in the FLUXNET
 443 observations, meaning that photosynthesis is more affected by climate conditions than are respiration processes.
 444 Second, the climate influence can be strong on both GPP and RECO but weak on NEE (Fig. 6). This is for instance
 445 the case in Davos where the correlation coefficient between T and LPJ-GUESS-simulated CO₂ fluxes exceeds 0.9
 446 for both GPP and RECO while remains weak and barely significant for NEE. Last, the climate influence on the



447 annual cycle in simulated CO₂ fluxes highly depends on the model capability to capture the CO₂ flux annual cycle.
 448 From this point of view, the CarbonSpace data-driven and SMAP-L4C process-based models often depict stronger
 449 CO₂ fluxes – climate relationships than the remaining models, consistent with more accurate simulation of the CO₂
 450 flux annual cycle (Fig. 3).
 451



452
 453

454 **Figure 7:** Simple linear and 2nd order polynomial regressions between monthly 2 m temperature from SAFRAN-
 455 SIM2 (x-axis) and NEE (y-axis) from all datasets and sites. (a,d,g,j,m,p) LPJ-GUESS and SMAP-L4C process-
 456 based models. (b,e,h,k,n,q) FLUXNET observations and CarbonSpace data-driven model. (c,f,i,l,o,r) FLUXCOM
 457 data-driven models. The coefficient of determination (R²) in the insert is derived from the linear regression.
 458

459

460 A particular attention is given on the relationship between T and NEE (Fig. 7) to further discuss uncertainties
 461 induced by the products and dependencies to forest stand conditions. The relationship is systematically weaker (i)
 462 in Davos than in other sites regardless of the product and (ii) in the two coarse resolution models (LPJ-GUESS
 463 and FLUXCOM) regardless of the site. The relationship is linear-like in ENF sites regardless of the dataset and



464 the CO₂ flux. This contrasts with DBF sites where the observed T – NEE relationship is polynomial with an evident
 465 threshold effect. Below 10°C, the NEE turns positive, indicating a net ecosystem carbon loss, and stabilizes in the
 466 0–2 tCO₂ ha⁻¹ range. This threshold effect corresponds to the low biological activity of DBFs under cold conditions,
 467 hence weak to no CO₂ uptake by photosynthesis. This threshold effect results thus from GPP only, as reflected by
 468 the flattening of the GPP curve at low T (Fig. A6) unlike the linear RECO – T relationship (Fig. A7). Among the
 469 models, the SMAP-L4C and CarbonSpace are the only models to capture the observed threshold, highlighting the
 470 usefulness of distinguishing the PFT in the model outputs.

471

472 The above analyses (Figs. 6-7) depict significant relationships between climate and CO₂ fluxes when accounting
 473 for the annual cycle. Once the latter is removed (see section 1.4 for details), most of the correlation values are
 474 higher for process-based than data-driven models, remain of the same sign but are of weaker magnitude for GPP
 475 and RECO and are almost negligible for NEE (Fig. 8). Positive anomalies in GPP and RECO are associated with
 476 positive anomalies in T, VPD and ETP and negative anomalies in soil moisture (SWI) and, to a lesser extent,
 477 precipitation in most sites and products. The reverse holds true for negative GPP and RECO anomalies. The similar
 478 response of GPP and RECO to the climate anomalies induces a compensation effect on the residual NEE carbon
 479 flux, resulting in weak NEE anomalies. The sign of NEE anomalies is uncertain among the sites and the products
 480 and depends on which of the two components is associated with the largest anomalies. While the models tend to
 481 exaggerate the observed relationship between CO₂ flux and climate anomalies, especially the process-based
 482 models, the overall picture is satisfactorily captured.

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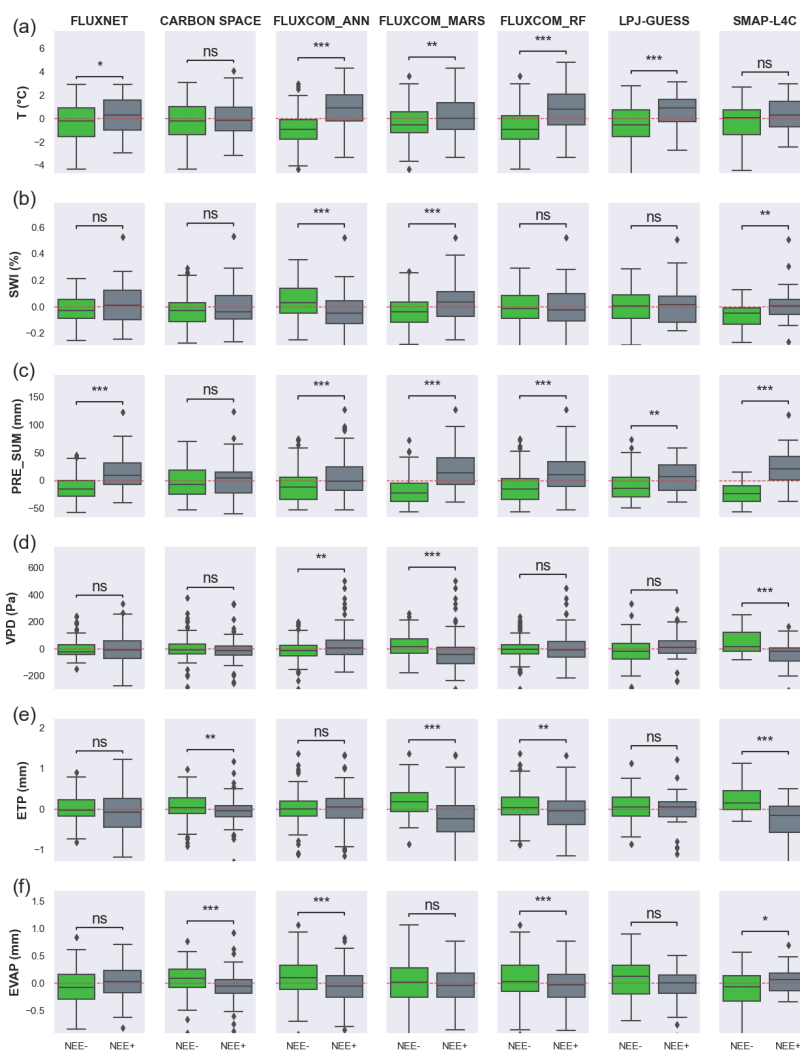
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Figure 8: Same as Fig. 6 but after removing the mean annual cycle.

In addition to the correlation analysis, for which few disagreements can lead to poor correlation values, we now investigate climate anomalies associated with the largest anomalies in monthly CO₂ fluxes (see Section 2.4 for

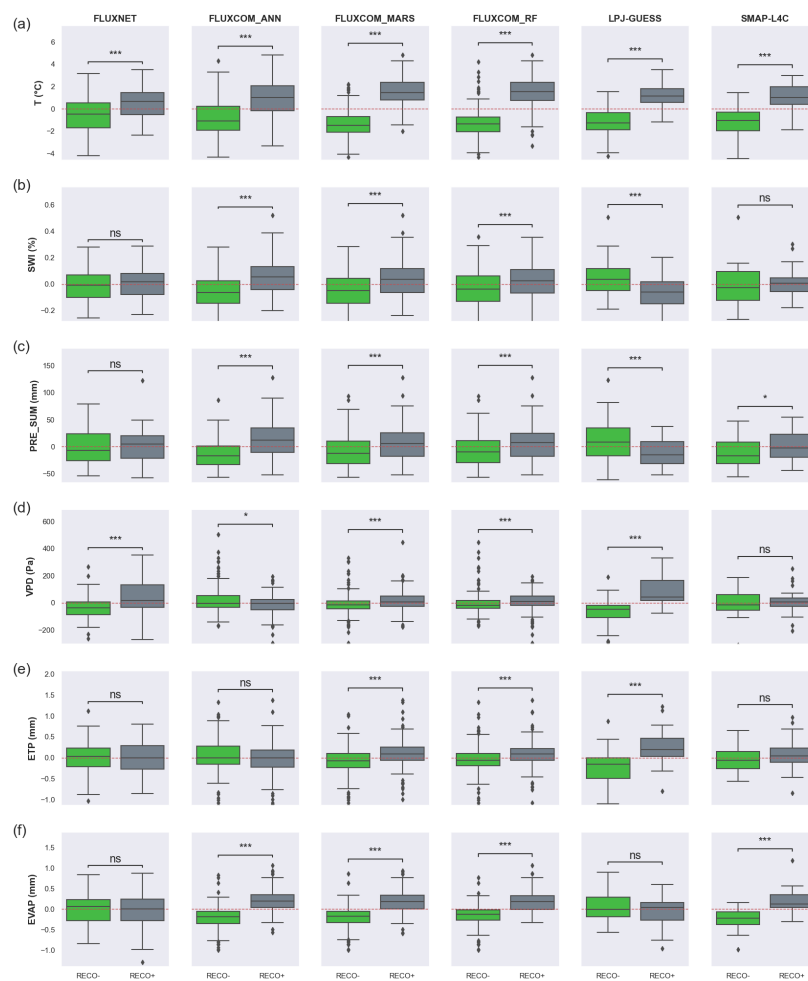


491 details). Results are shown for the Fontainebleau DBF site only for conciseness in Figs. 9-11. The main results can
492 be summarized as follows. Two main climate parameters, PRE_SUM and T, appear to significantly influence the
493 largest CO₂ flux monthly anomalies in almost all datasets. Wet anomalies significantly favor anomalies that are
494 positive for RECO and negative for GPP, hence less CO₂ uptake (Figs. 9c, 10c and 11c), and vice versa for dry
495 anomalies. Warm anomalies are associated with large positive NEE anomalies (i.e., strong CO₂ emissions or weak
496 CO₂ uptake) and vice versa for cold anomalies (Fig. 9a). In turn, the DBF ecosystem sequesters less (more) CO₂
497 during anomalously warm (cold) conditions. This result is more clearly driven by RECO (Fig. 10a) than GPP (Fig.
498 11a), consistent with an exponential response of respiration to T (van't Hoff, 1898). Some relationships are
499 opposite in sign between the process-based models and the data-driven models, highlighting strong uncertainties
500 induced by the approach. For instance, anomalously dry soil is associated with RECO and GPP anomalies that are
501 positive in the process-based models, especially LPJ-GUESS, while negative in the FLUXCOM data-driven
502 models (Figs. 10b and 11b).
503



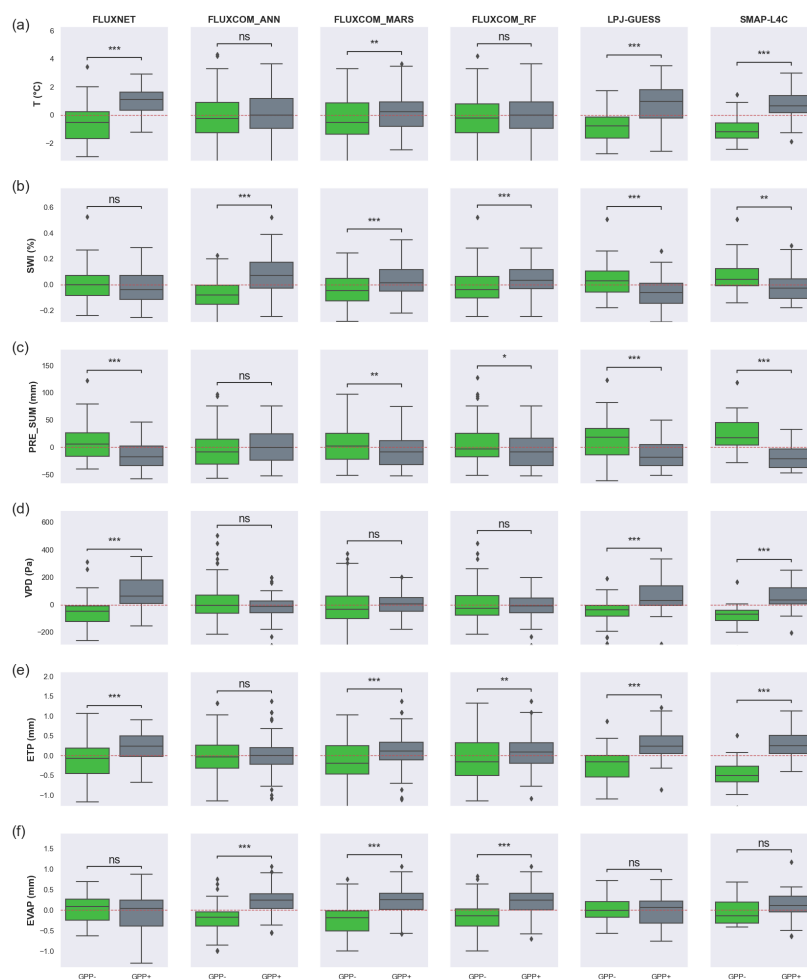
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506 **Figure 9:** Monthly climate anomalies associated with large negative and positive anomalies in monthly NEE
 507 (NEE- and NEE+, respectively) for each dataset in the Fontainebleau DBF site. (a) 2m temperature (°C). (b) Soil
 508 water index (%). (c) Total precipitation (mm/month). (d) Vapor pressure deficit (Pa). (e) Potential
 509 evapotranspiration (mm/month). (f) Real evapotranspiration (mm/month). NEE- (NEE+) anomalies are defined as
 510 standardized anomalies (mean=0; standard deviation=1) below -0.5 (above 0.5). The boxes have lines at the lower
 511 quartile, median, and upper quartile values. The whiskers are lines extending from each end of the boxes to show
 512 the extent of the range of the data within 1.5 by inter-quartile range from the upper and lower quartiles. Circles are
 513 outliers. The symbol ns indicates no statistically significant difference in climate anomalies between NEE- and
 514 NEE+ according to a Mann-Whitney *U* test. The symbols *, ** and *** correspond to significant differences at
 515 the 90, 95 and 99% confidence level according to the same test.
 516



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Figure 10: Same as Fig. 9 but for RECO.



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Figure 11: Same as Fig. 9 but for GPP.

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This section demonstrates that the annual cycle of monthly CO₂ fluxes is sharply driven by climate, while its interannual variability is not a simple response to climate anomalies. Most of the models accurately capture the observed annual cycle and its relationship with climate. However, the interannual variability of monthly CO₂ flux anomalies are not necessarily phased between observations and models (i.e., weak co-variability), especially for NEE, and the models tend to exaggerate the impact of climate on CO₂ flux interannual variability.



536 **3.2 Annual timescale**

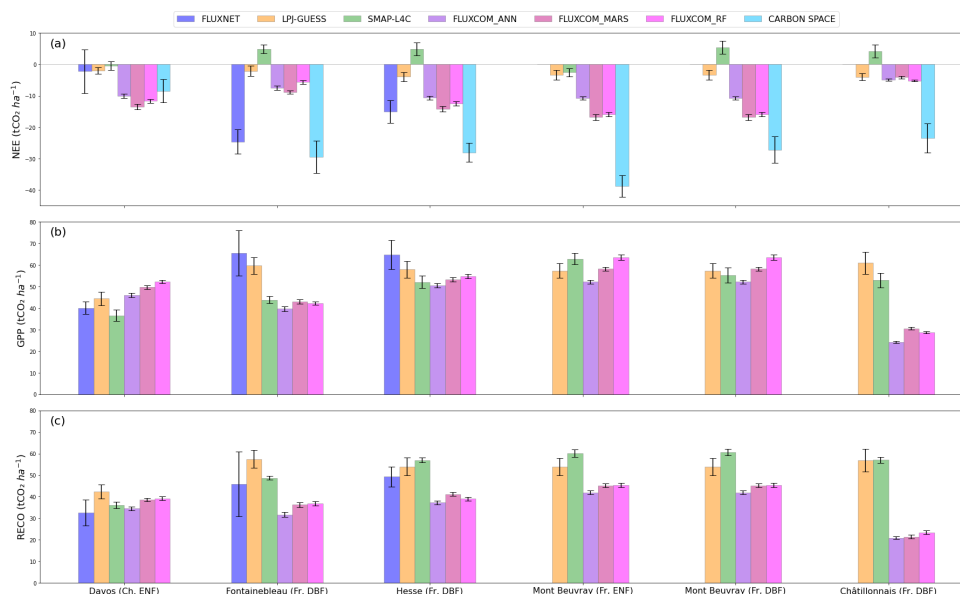
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538 **3.2.1 Mean annual budget and interannual variability**

539

540 In the observations, the mean annual CO₂ sequestration of the ecosystems is, on average, far weaker in the ENF
 541 site (-2.24 tCO₂ ha⁻¹ year⁻¹) than the DBF sites (-24.63 tCO₂ ha⁻¹ year⁻¹ in Fontainebleau and -15.14 tCO₂ ha⁻¹ year⁻¹
 542 in Hesse), while the reverse holds in terms of interannual variability (±6.92 against 3.92 and 3.60 tCO₂ ha⁻¹ year⁻¹
 543 respectively) (Fig. 12a). The large contrast between DBF and ENF sites may not be transposable since climate
 544 in Davos is atypical, with much colder and wetter mean conditions and larger year-to-year variability compared to
 545 the remaining sites (Fig. 2). Only the two process-based models (LPJ-GUESS and SMAP-L4C) provide mean
 546 annual CO₂ uptake values comparable to observations in Davos. However, this might be a coincidence since these
 547 models strongly underestimate the NEE annual budget in the other sites due to underestimated GPP (Fig. 12b) and
 548 overestimated RECO (Fig. 12c). In particular, the NEE annual budget is positive in all DBF sites in the SMAP-
 549 L4C owing to a too short duration of the uptake season simulated by this model (Fig. 3), resulting in annual GPP
 550 bias of e.g. -21.77 tCO₂ ha⁻¹ year⁻¹ in Fontainebleau (Fig. 12b).

551



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553

554 **Figure 12:** Mean annual budget (bars) and interannual variability (whiskers) in (a) NEE, (b) GPP and (c) RECO
 555 for each site and dataset. Note that the results are similar in the Mont Beuvray ENF and DBF sites for the LPJ-
 556 GUESS and FLUXCOM models due to their coarse resolution and no distinction of the forest stand in the outputs.
 557

558 Except in Davos, the two data-driven models perform reasonably well to capture the observed magnitude of NEE
 559 annual budget, despite CO₂ uptake in DBF sites is underestimated by 15 to 20 tCO₂ ha⁻¹ year⁻¹ in Fontainebleau
 560 by the FLUXCOM models and overestimated by 19.99 tCO₂ ha⁻¹ year⁻¹ in Hesse by the CarbonSpace model. Over
 561 Mont Beuvray, the annual CO₂ uptake is greater in the ENF than the DBF site for the models distinguishing the

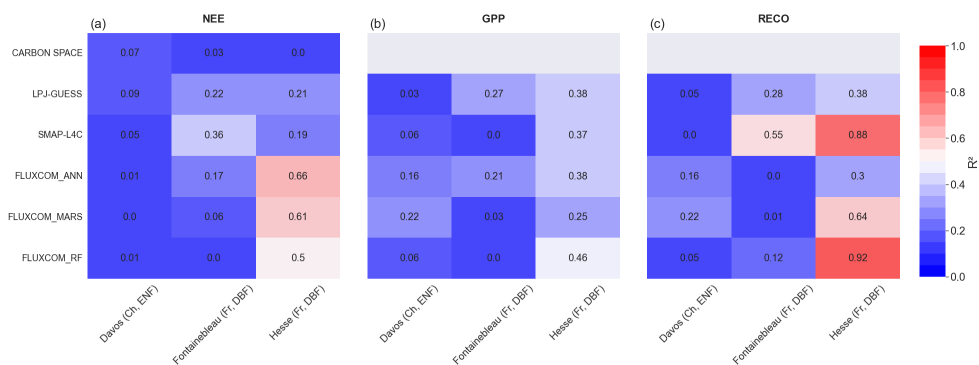


562 PFTs in their outputs (i.e., CarbonSpace and SMAP-L4C). This might be explained by a basal area reaching 49 m²
 563 ha⁻¹ in average in the ENF plot against 32 m² ha⁻¹ in the DBF one (for a volume of 656 m³ ha⁻¹ and 404 m³ ha⁻¹;
 564 data based on forest inventory), inducing a weaker photosynthetic activity in the DBF (Fig. 12b). This hierarchy
 565 cannot be captured by the FLUXCOM and LPJ-GUESS models by construction since the two Mont Beuvray plots
 566 are part of the same grid point and ENF and DBF are not distinguished.

567

568 At the interannual timescale, the forest ecosystem systematically acts as a CO₂ sink (Fig. 12), except (i) in Davos
 569 for the observations and the SMAP-L4C model and (ii) in all DBF sites for the SMAP-L4C model where NEE is
 570 always positive (i.e., CO₂ release), as already discussed. The magnitude of interannual variability in annual NEE
 571 is the largest and the closest to the observed one for the CarbonSpace model (± 3.92 and 5.16 tCO₂ ha⁻¹ year⁻¹ in
 572 Fontainebleau), and the lowest and farthest from the observed one for the FLUXCOM models (± 0.55 tCO₂ ha⁻¹
 573 year⁻¹ in Fontainebleau with FLUXCOM_MARS), a statement also prevailing for GPP and RECO.

574



575
576

577 **Figure 13:** Coefficient of determination (numbers and shadings) between modelled and measured fluxes in the
 578 FLUXNET sites at the annual timescale.

579

580

581 Beyond the magnitude of interannual variability, a critical question concerns the model capability to capture the
 582 observed year-to-year fluctuations of annual CO₂ fluxes (Fig. 13). No model succeeds at capturing the observed
 583 NEE, GPP and RECO interannual variability in Davos, suggesting deficiencies of state-of-the-art models in
 584 simulating CO₂ flux interannual variability in mountainous regions. At least for SMAP-L4C, this may be due to
 585 the inability of the coarse (0.25 degree resolution) GEOS FP daily meteorology and (9-km grid) SMAP L4 soil
 586 moisture to capture the larger spatial heterogeneity in local climate conditions imposed from the complex mountain
 587 terrain at this site. For the remaining sites, the models tend to better perform with GPP and RECO than NEE. The
 588 CarbonSpace model fails at capturing the observed interannual variability in annual NEE ($R^2 \leq 0.08$). Despite biased
 589 annual mean conditions (Fig. 12), the SMAP-L4C performs reasonably well, with R^2 of 0.36 and 0.55 for NEE
 590 and RECO in Fontainebleau and 0.88 for RECO in Hesse (Fig. 13). This model is the only one to be forced by
 591 satellite observation informed soil moisture, suggesting this parameter is valuable for simulating realistic year-to-
 592 year fluctuations of annual CO₂ fluxes. The FLUXCOM models also capture correctly the interannual variability
 593 in Hesse for all CO₂ fluxes and perform better (with still low R^2) in Davos for GPP and RECO than the other



594 models. Importantly, this skill is not “forced” by construction since the Davos site is not used to train the
 595 FLUXCOM models, and there is no or few (2) overlapping years between the period used to train the models and
 596 that analyzed in our study for Hesse and Fontainebleau. The LPJ-GUESS provides intermediate scores, with R^2 in
 597 the 0.3 – 0.4 range. These results indicate that (i) models accounting for climate variability better capture
 598 interannual variability in CO₂ fluxes and (ii) the simulated interannual variability is closer to observations at the
 599 annual than monthly timescale.

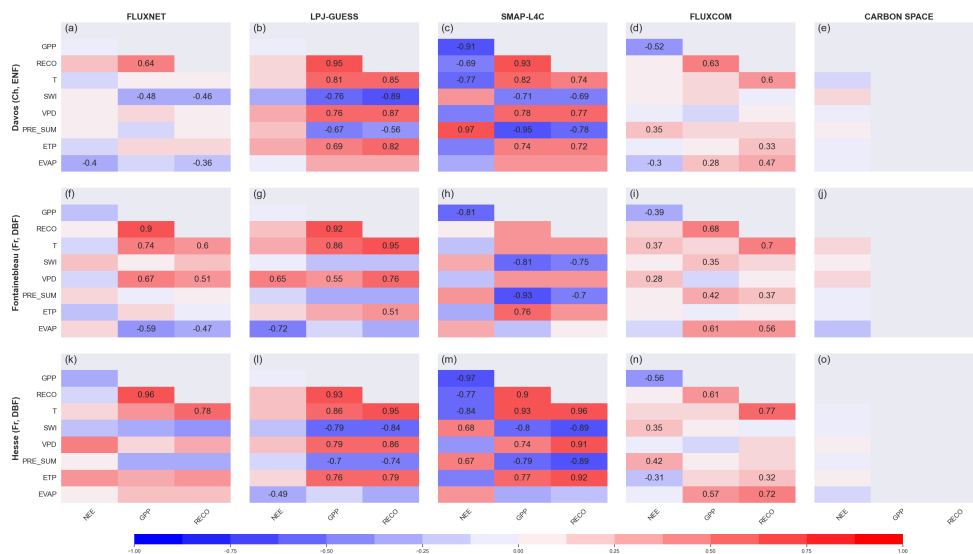
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601 3.2.2 Relationship with climate

602

603 Overall, the interannual co-variability between CO₂ flux and climate is qualitatively similar at the annual (Fig. 14)
 604 than the monthly (Fig. 8) timescale, with correlation values of the same sign. The main difference concerns less
 605 significant correlation values at the annual than monthly timescale for most variables, probably due to a sample
 606 size effect since the number of years under study is limited. The only exception concerns a stronger precipitation
 607 – CO₂ flux relationship at the annual than monthly timescale for the two process-based models, especially for GPP
 608 and RECO with decreased CO₂ fluxes during wet years.

609



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612 **Figure 14:** Same as Fig. 6 but for raw annual values.

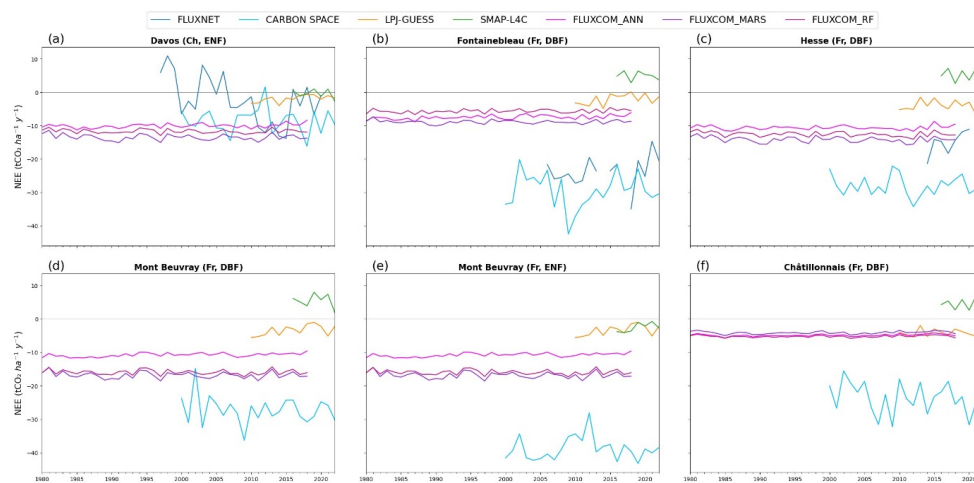
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614

615 The “long-term” evolution in the NEE annual budget does not depict any trend but is characterized by strong year-
 616 to-year fluctuations, except for the FLUXCOM models depicting surprisingly flat variability (Fig. 15). A modest
 617 increase is looming in the very last years of FLUXNET data, especially in DBF plots (Fig. 15b-c) but, as for all
 618 other models, the temporal coverage seems too short and the interannual variability too strong to settle any
 619 conclusion. Our result contrasts with recent literature pointing towards reduced CO₂ uptake in Europe (Smith et
 620 al., 2020; Thompson et al., 2020; Chuine et al., 2023; van der Woude et al., 2023). Possible reasons involve the



621 limited number of sites under study, the fact that eddy-covariance flux tower measurements may be located in
622 healthy forest ecosystems and potential compensation effects between GPP trends and RECO trends. The latter
623 point is critical, at least in the FLUXNET observations and LPJ-GUESS simulations (Figs. A8-A9). To further test
624 this hypothesis, Figure 16 shows the temporal evolution of annual anomalies in observed CO₂ fluxes and climate
625 parameters in the Fontainebleau DBF site. While annual NEE anomalies do not depict any trend (Fig. 16a), GPP
626 and RECO anomalies are most frequently negative before 2014 and positive afterwards (Fig. 16b). The time series
627 is too short to conclude whether such an evolution is reminiscent of a trend or a decadal-like variability. However,
628 this pattern is consistent with the evolution of annual climate anomalies depicting drier conditions, larger potential
629 evapotranspiration and colder temperature before 2014 than afterwards (Fig. 16c-e).
630

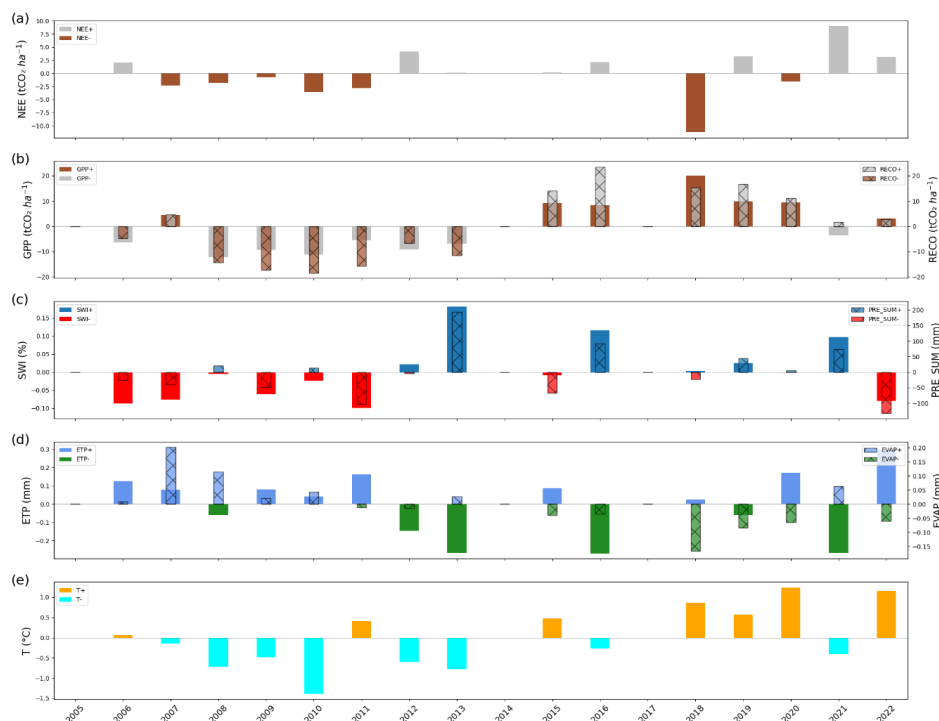


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633 **Figure 15:** Annual NEE for the longest available period for each site and dataset. Gaps are due to not complete
634 years (e.g. FLUXNET data in Fontainebleau in panel b).

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637

638 **Figure 16:** Evolution of annual anomalies in observed CO₂ budget and SAFRAN-SIM2 climate in Fontainebleau
 639 between 2005 and 2022. (a) NEE. (b) GPP and RECO. (c) Soil moisture and total precipitation. (d) Real and
 640 potential evapotranspiration. (e) 2 m temperature. Anomalies are computed as the difference between each year
 641 and the 2005-2022 averaged conditions. The years 2005, 2014 and 2017 have not been accounted for because of
 642 missing CO₂ flux data.

643

644

645 **4 Discussion**

646

647 This study aims at evaluating process-based and data-driven models in capturing CO₂ flux temporal dynamics of
 648 temperate forest ecosystems and their relationships with climate. Such an evaluation is required to question the
 649 extent to which these models may provide relevant information for monitoring CO₂ temporal dynamics and
 650 understanding their drivers in temperate forests where no CO₂ measure is available.

651

652 First, we show that the model skill depends on the target. On the one hand, the magnitude and pattern of the annual
 653 cycle, annual budget and the range of interannual variability (i.e., standard deviation of monthly or annual values)
 654 are better captured by the CarbonSpace data-driven model than the remaining models. This added value was
 655 expected in e.g. Fontainebleau, since this site is included in the pool of flux tower measurements used for the
 656 model calibration, but not in Hesse since this site is not included. Furthermore, the CarbonSpace clearly
 657 outperforms the other data-driven models tested (FLUXCOM models set with different AI algorithms), which are



658 also calibrated with flux tower measurements. This suggests that the accurate skill of the CarbonSpace model relies
659 also on the inclusion of high resolution multi-spectral satellite data allowing to assess CO₂ dynamics at the
660 hectometric scale and to distinguish different PFTs. On the other hand, the co-variability between observations
661 and models, and between CO₂ fluxes and climate depends on whether the focus is on the annual cycle or on the
662 interannual variability. When focusing on the annual cycle (Figs. 4-7), the co-variability is the largest for models
663 capturing the observed annual cycle in CO₂ fluxes, with CarbonSpace providing the best scores. When focusing
664 on the interannual variability of monthly anomalies and annual budgets (Figs. 8 and 14), models forced by dynamic
665 climate data (LPJ-GUESS, SMAP-L4C and FLUXCOM) clearly outperform the CarbonSpace model, which is
666 forced by static climate data. In particular, the SMAP-L4C provides satisfactory results, suggesting that soil
667 moisture is a key parameter for monitoring the interannual variability of CO₂ fluxes.

668

669 Second, we show that the CO₂ flux – climate relationship is stronger for GPP and RECO than NEE and that the
670 sign of the relationship between GPP/RECO and climate is relatively similar among the sites and products both
671 along the annual cycle and from year-to-year (monthly anomalies and raw annual budgets). Both RECO and GPP
672 increase when 2 m temperature, vapor pressure deficit and evapotranspiration increase and when precipitation and
673 soil moisture decrease, in line with the literature (Haszpra et al., 2005; Tang et al., 2013; Kong et al., 2022; Li et
674 al., 2023; Sharma et al., 2022). The NEE – climate relationship is more complex. Along the annual cycle, NEE is
675 mainly driven by RECO during winter and GPP during summer in all datasets. From year-to-year, the magnitude
676 of NEE anomalies is weak in most cases and their sign depends on the magnitude of the response of GPP and
677 RECO. The latter point induces site dependencies and disagreements between observations and models and
678 between models. From this point of view, models providing the three CO₂ fluxes (i.e., NEE, GPP and RECO)
679 allow for a better understanding on CO₂ exchanges between the atmosphere and forest ecosystems. In addition,
680 our study focuses on the synchronous relationship between CO₂ fluxes and individual climate parameters.
681 Considering lead-lag relationships as well as the influence of combined climate parameters would be the next step
682 to account for the long term effect of droughts and heatwaves on forest ecosystems (Ciais et al., 2005; von Buttlar
683 et al., 2018). Similarly, the number of study sites was too limited to account for the influence of variable soil
684 properties (Kurbatova et al., 2008; Besnard et al., 2018; Curtis and Gough, 2018; Martinez del Castillo et al.,
685 2022), forest management practices (Carrara et al., 2003; Scott et al., 2004; Saunders et al., 2012) and stand age
686 (Kurbatova et al., 2008; Besnard et al., 2018; Chuine et al., 2023).

687

688 Third, distinguishing forest stands is critical for a fine scale assessment of CO₂ temporal variability (Carrara et al.,
689 2003, 2004; Welp et al., 2007; von Buttlar et al., 2018; Zheng et al., 2021; Kong et al., 2022). Among the models
690 tested, the two high spatial resolution models (SMAP-L4C and CarbonSpace) distinguish forest stands, which is
691 not the case in the 50-km resolution models (LPJ-GUESS and FLUXCOM). Our results suggest an added value
692 of models accounting for forest stands since they are the only models to capture a clear decrease of CO₂ uptake
693 during winter in DBF plots (Fig. 3), which is consistent with the literature (Granier et al., 2002; Welp et al., 2007).
694 They are also the only models to capture the observed polynomial relationship between monthly 2 m temperature
695 and NEE over the DBF plots (Fig. 7). We have, however, to acknowledge that the temporal variability of CO₂
696 fluxes is poorly captured in the Davos ENF site, even in the SMAP-L4C and CarbonSpace models. The main
697 reason involves the atypical behavior of CO₂ fluxes in mountainous regions. Additional sites would be needed to



698 further understand the different responses of CO₂ fluxes to climate under DBF and ENF plots, which is out of the
699 scope of this study.

700

701 Last, there is a hiatus in the literature regarding the emergence of trends in NEE. Some studies suggest a recent
702 decline of CO₂ uptake by forest ecosystems in Europe (Smith et al., 2020; Thompson et al., 2020; Chuine et al.,
703 2023; van der Woude et al., 2023), while some others suggest no trend in either the recent decade or in climate
704 projections (Ahlström et al., 2012; Abdalla et al., 2013; Tang et al., 2013; Kong et al., 2022; Martinez del Castillo
705 et al., 2022; Li et al., 2023). The hiatus may be explained by the location of the sites or regions under study, (ii)
706 the limited temporal depth of observations (and models), (iii) whether or not these sites/regions have been affected
707 by wildfires and diseases (e.g., bark beetles) and (iv) whether or not wildfires and diseases are accounted for by
708 the models. Our results are more nuanced. We found that the evolution of the NEE annual budget does not depict
709 any trend but that GPP and RECO may have increased recently in the observations and some models.

710

711 **5 Conclusion**

712

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

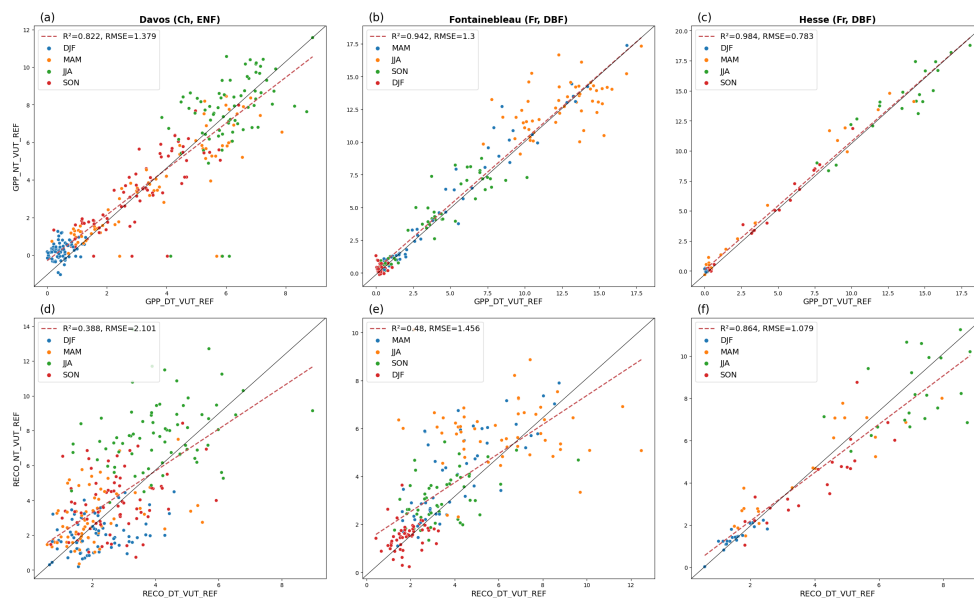
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734 **Appendices**

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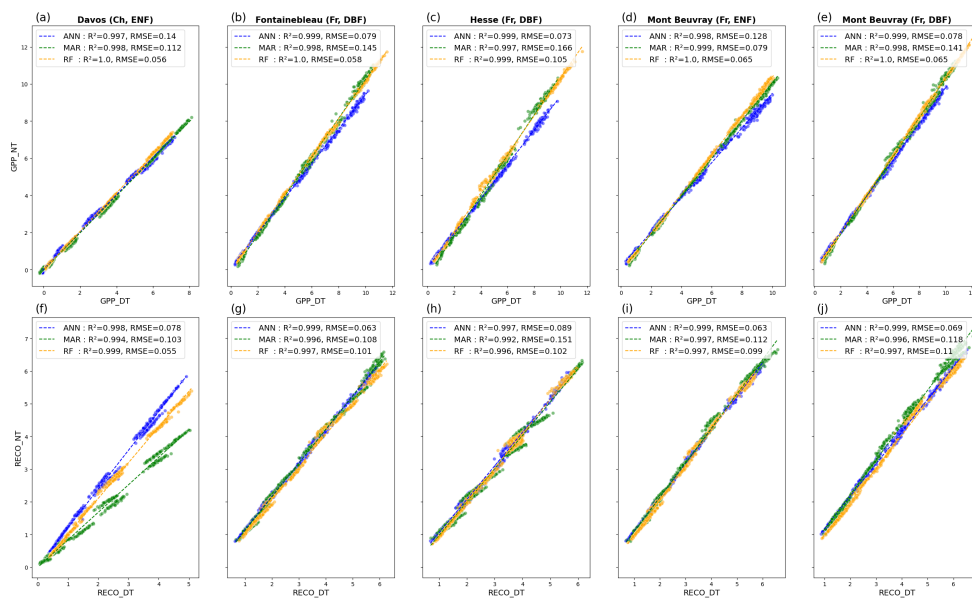


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739 **Figure A1:** Comparison between (a-c) GPP and (d-f) RECO using the daytime partitioning (x-axis) and the
740 nighttime partitioning (y-axis) for the three FLUXNET sites at the monthly timescale. The four colors correspond
741 to the four seasons. The red line shows the linear regression between the two approaches, together with the
742 coefficient of determination (R^2) and root mean squared error (RMSE) labeled in the insert. The black line shows
743 the 1-by-1 correspondence.
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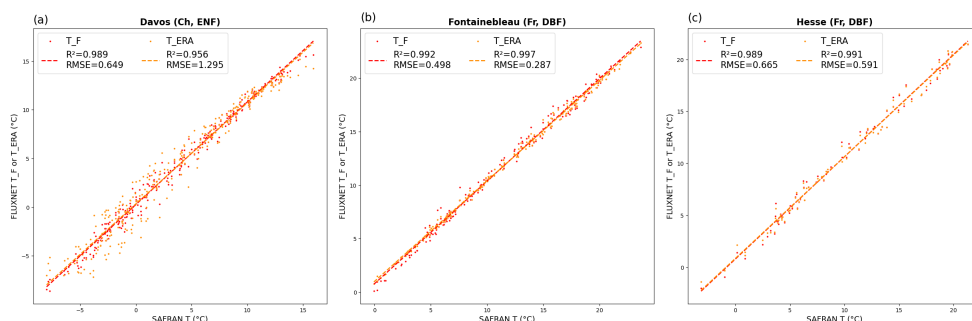
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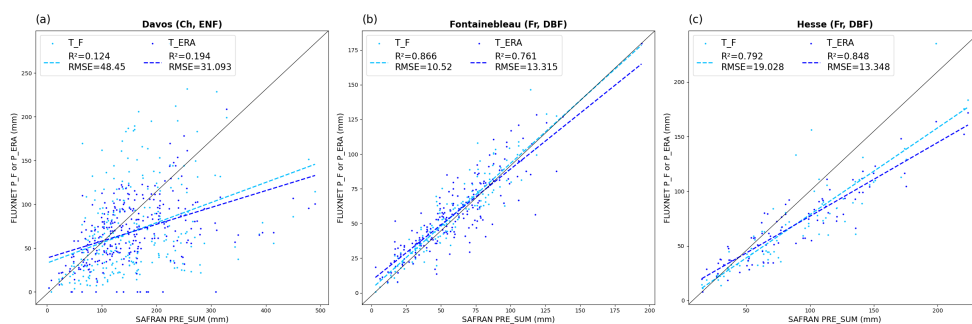
Figure A2: Comparison between FLUXCOM-simulated (a-e) GPP and (f-j) RECO using the daytime partitioning (x-axis) and the nighttime partitioning (y-axis) for the three FLUXNET sites at the monthly timescale. The three colors correspond to the three artificial intelligence algorithms. The colored lines show the linear regression between the two approaches, together with the R² and RMSE metrics labeled in the insert.



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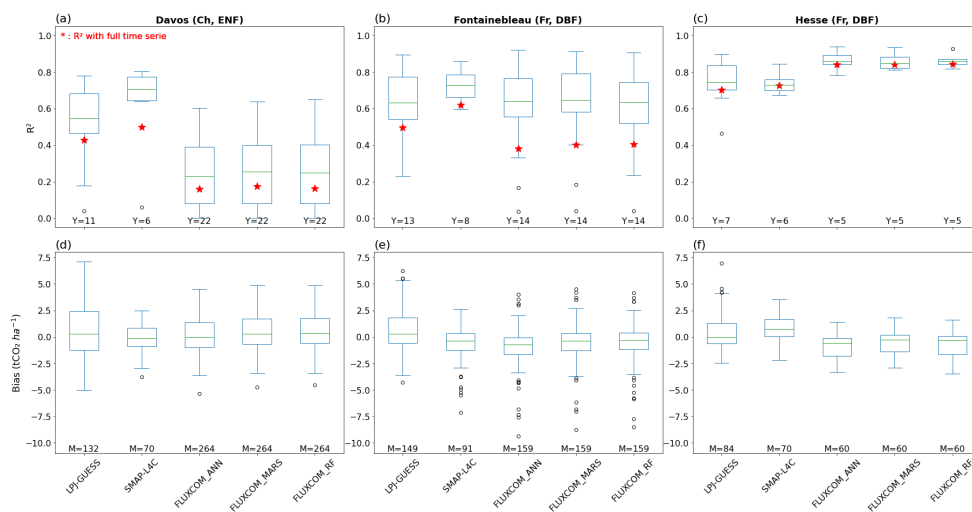


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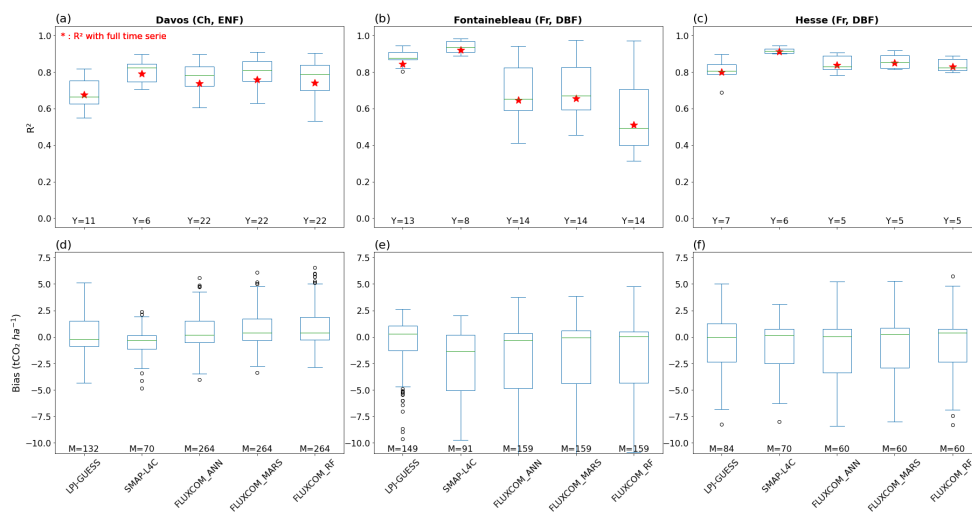
757 **Figure A3:** Comparison between the SAFRAN-SIM2 reanalysis (x-axis) and the FLUXNET observations (y-axis)
 758 for (a-c) 2 m temperature and (d-f) total precipitation for the three FLUXNET sites at the monthly timescale. The
 759 SAFRAN-SIM2 data correspond to the nearest grid point to each FLUXNET site. The SAFRAN-SIM2 –
 760 FLUXNET comparison is done using the raw and ERA-INTERIM-corrected observations, labeled T_F/P_T and
 761 T_ERA/P_ERA, respectively. The colored lines show the linear regression between the two datasets, together with
 762 the coefficient of determination (R^2) and the root mean square error (RMSE) labeled in the insert.

763



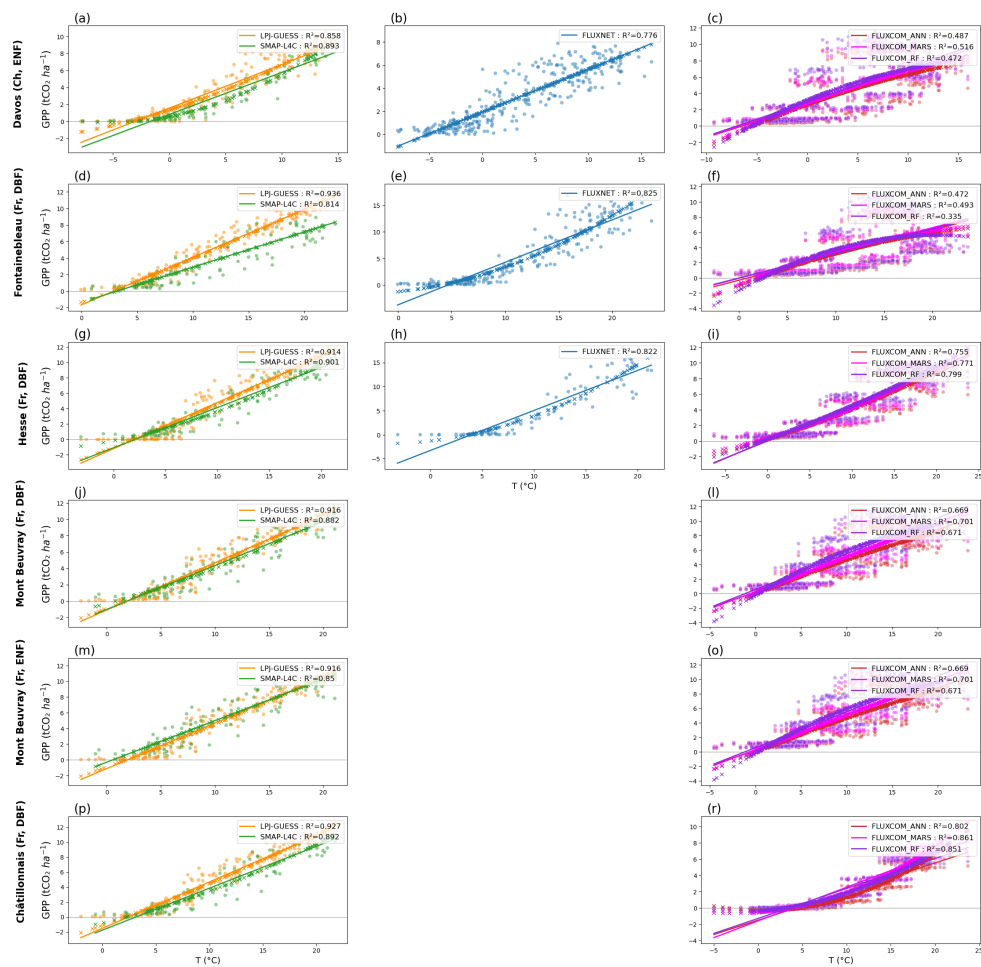
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Figure A4: Same as Fig. 5 but for RECO.



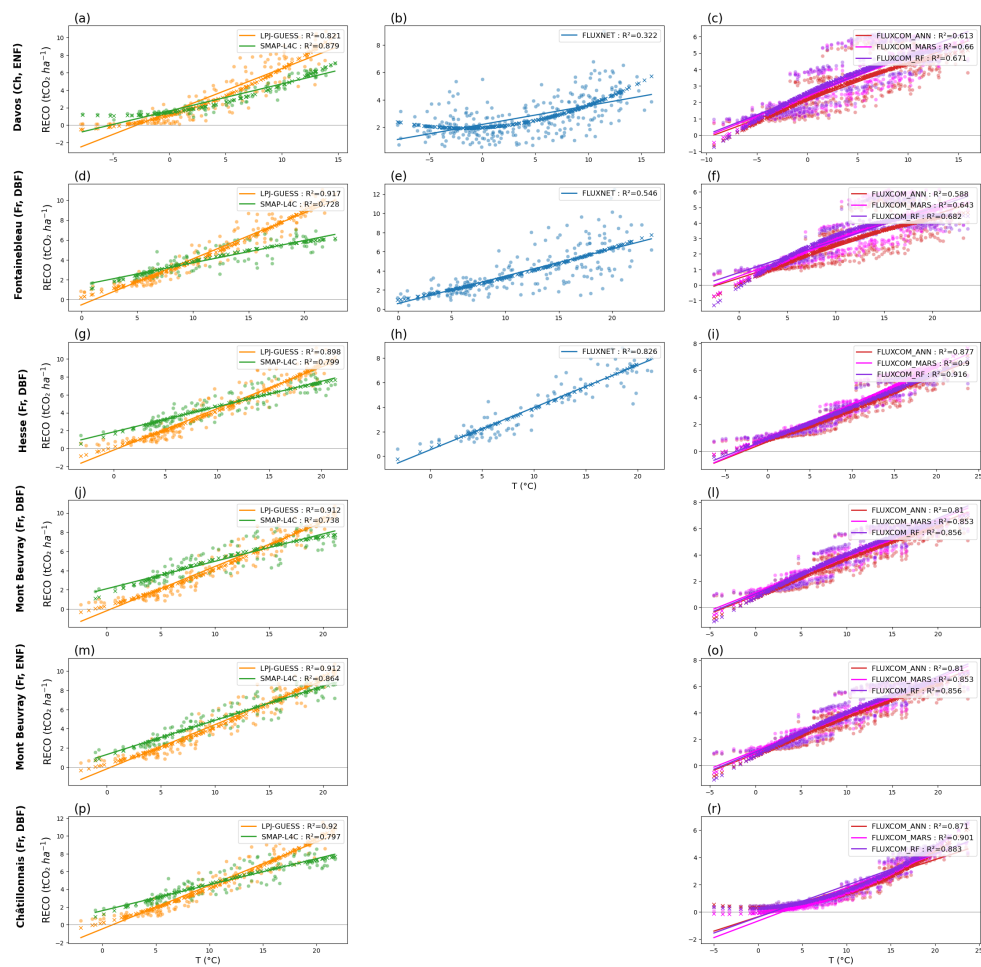
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Figure A5: Same as Fig. 5 but for GPP.



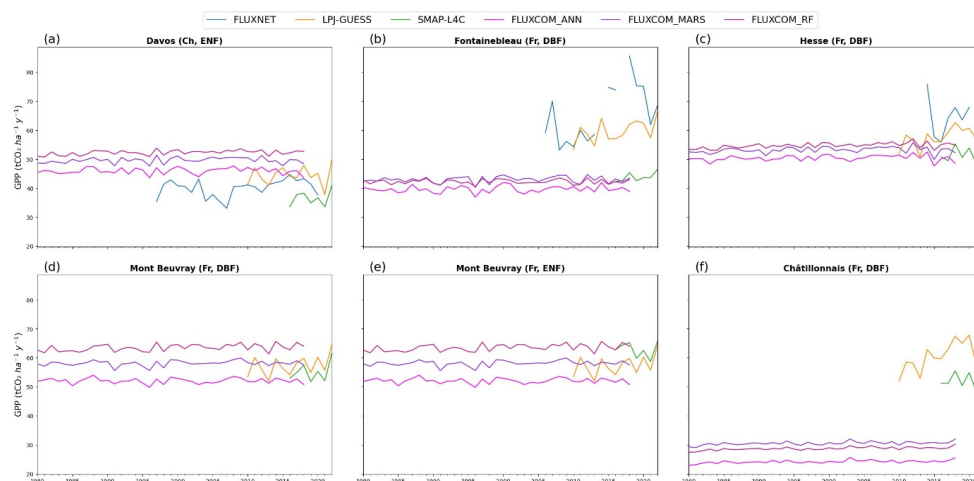
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Figure A6: Same as Fig. 5 but for GPP.



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Figure A7: Same as Fig. 5 but for RECO.



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



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Figure A9: Same as Fig. 15 but for RECO.



785 **Acknowledgement**

786

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788 Berveiller for useful discussions on eddy covariance measurements.

789

790

791 **Conflict of Interest**

792

793 The authors declare no competing interests.

794

795

796 **Data Availability**

797

798 Climate parameters from the SAFRAN-SIM2 are available at <https://meteo.data.gouv.fr>. CO₂ fluxes from the
799 FLUXOM data-driven model are available at <https://www.bgc-jena.mpg.de>. Those from LPJ-GUESS and SMAP-
800 L4C process-based models are available at <https://meta.icos-cp.eu/collections/NZNSUglRn0VeXmGDovuVY0ec>
801 and <https://nsidc.org/data/spl4cmdl/versions/7>, respectively.

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