



Recent changes in the dominant environmental controls of net biome productivity

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Abstract. In the last decades terrestrial ecosystems have reabsorbed on average more than one quarter of anthropogenic emissions (Le Quéré et al., 2018). However, this large carbon sink is modulated by climate and is therefore highly variable in time and space. The magnitude and temporal changes of the sensitivity of terrestrial CO₂ fluxes to climate drivers are key factors to determine future atmospheric CO₂ concentration and climate trajectories. In the literature there is so far a strong focus on the climatic controls of inter-annual variability, while less is known about the key drivers of the sub-annual variability of the fluxes. This latter temporal scale is relevant to assess which climatic drivers dominate the seasonality of the fluxes and to understand which factors limit the net ecosystem CO₂ exchange. Here, we investigated the global sensitivity of terrestrial CO₂ fluxes to three key climate drivers (i.e. global radiation, temperature and soil water content) from weekly to seasonal temporal scales, in order to explore the short-term interdependence between climate and the terrestrial carbon budget. We observed that the CO₂ exchange over most of the land surface is controlled by temperature during the carbon uptake period, while radiation is the most widespread dominant climate driver during the carbon release period. As expected, soil water content plays a key role in arid regions of the southern hemisphere. Looking at the decadal trend of these sensitivities we observed that the importance of radiation as a driver is increasing over time, while we observed a decrease in sensitivity to temperature in Eurasia. Overall, we show that the temporal variation of the fluxes due to a specific driver is dominated by the temporal changes in ecosystem sensitivity rather than to the temporal variability of the driver itself. Ultimately this analysis shows that the response of the ecosystem to climate drivers is significantly changing both in space and in time, with potential repercussion on the future terrestrial CO₂ sink and therefore on the role that land may play in climate mitigation.

1 Introduction

Just over one quarter of the anthropogenic emissions of carbon dioxide (CO₂) on average are reabsorbed by terrestrial ecosystems (Le Quéré et al., 2018). This large sink is influenced by climate and therefore by its short- and long-term



variability (Beer et al., 2010; Ciais et al., 2005; Rödenbeck et al., 2018; Sitch et al., 2015). In fact, key climate drivers like radiation, temperature, precipitation regime and soil moisture control the fundamental processes of photosynthesis and respiration that are modulating the net ecosystem CO₂ exchange (Reich et al., 2018). Moreover, climate change is affecting the phenological cycle of plants and, therefore, the functioning of ecosystems which in turn affect climate (Richardson et al., 2013). Due to this interrelation, model studies show that the response of land CO₂ fluxes to climate drivers may strongly determine the future climate trajectories (Friedlingstein et al., 2001). Ultimately, the large uncertainty of climate projections could be significantly improved with a better understanding of vegetation response to the climate variability observed in the past (Papagiannopoulou et al., 2017).

In the last decades the climate sensitivity of terrestrial ecosystem CO₂ exchange has been investigated at different temporal and spatial scales and with a variety of measurement techniques ranging from eddy covariance, which continuously monitor fluxes at local scale (Baldocchi, 2003; Baldocchi et al., 2001), to indirect measurements based on remote sensing retrievals. A range of sensors on different satellite platforms are continuously monitoring in different wavebands (i.e. optical, thermal, microwave, etc.) the structural and functional properties of global vegetation. Earth observations proved to be an invaluable source of information to assess land climate interactions at large scale and to constrain model representation (Alkama and Cescatti, 2016; Duveiller et al., 2018).

Evidence-driven model products based on data assimilation are another valuable source to analyze the vegetation-climate inter-play and can be used to assess the generalizability of ground-based observations (Fernández-Martínez et al., 2019). Among these, atmospheric inversions (such as the Jena CarboScope Inversion used here) combine modeled atmospheric transport with high precision measurements of atmospheric CO₂ concentrations to derive surface fluxes (Rödenbeck et al., 2003). Atmospheric inversions are particularly suitable for the assessment of vegetation-climate interactions because these data-products are not assuming a-priori any inter-play between climate and fluxes. Besides, inversions provide global data over several decades and are therefore useful to assess temporal changes at large spatial scale.

The sensitivity of ecosystems to climate variability has been so far mostly investigated at annual scale, while it is still poorly investigated across multiple sub-annual temporal scales. However, it is at the weekly or monthly scales where climate variability is directly acting on ecosystems (e.g., though heat waves, droughts, or cold spells), while annual anomalies are just the sum over such sub-annual responses. Besides, climate variability can have different impacts on the CO₂ flux (enhancing or dampening its variability) depending on the time period of the year when it occurs (Marcolla et al., 2011; Sippel et al., 2016). Thus, it is important to assess the limiting climate factors that control weekly or monthly evolution of carbon fluxes in order to assess the vulnerability and forecast the future evolution of the ecosystem carbon budgets (De Keersmaecker et al., 2015; le Maire et al., 2010).

With our analysis we aim at i) analyzing the limiting factors of global net biome productivity (NBP) fluctuations from weekly to seasonal time scales ii) assess how the NBP sensitivity to the main climate drivers is changing in time and iii) factoring out the importance of the temporal changes of the drivers and of the sensitivity-to-drivers in determining the total temporal variability of CO₂ fluxes.



65 Global radiation, temperature and soil water content were chosen among the meteorological drivers of the fluxes (Jung et al.,
2017) in order to identify the dominant driving variable at weekly, monthly and seasonal time scale in two key periods of the
ecosystem carbon budget, namely the Carbon Uptake Period when the land acts as a sink (CUP) and the Carbon Release
Period when it acts as a source (CRP). Finally, the temporal trends of the sensitivities to the three drivers were analyzed
separately in order to assess how long-term changes in the background climate may have affected the climate sensitivity of
70 terrestrial biomes.

2 Materials and Methods

2.1 Datasets

Gridded global flux estimates were obtained from the top-down product Jena CarboScope CO₂ Inversion (version s85_v4.1)
(Rödenbeck et al., 2003). Atmospheric inversions yield surface flux fields that achieve the best match to high-precision
75 measurements of atmospheric CO₂ concentrations, where the fluxes are linked to atmospheric mole fractions by modeled
atmospheric transport. Atmospheric transport is simulated here by the global three-dimensional transport model TM3
(Heimann and Körner, 2003) driven by meteorological data from the NCEP reanalysis (Kalnay et al., 1996). The product
version used in this analysis covers the period 1985-2016 at daily time scale; however, since the inversion uses temporal a-
priori correlations that smooth away any flux variations faster than about a week, the minimum time resolution we analyzed
80 is 7 days. The Jena Inversion is particularly suited for the analysis of temporal trends and variability since it is based on a
temporally constant observation network, in order to minimize spurious influences from the beginning or ending of data
records on the spatio-temporal variation of the fluxes.

Concerning climate variables, global radiation (RG), air temperature (TA) and soil water content (SWC) were identified as
drivers for NBP (Jung et al., 2017; Ma et al., 2007; Papagiannopoulou et al., 2017). These environmental variables are
85 generally recognized as the major factors driving the variation of CO₂ fluxes from hourly to multi-day time scale (Chu et al.,
2016; Richardson et al., 2007), while the response at longer time scales becomes more complex and often involves indirect
effects through functional changes (Teklemariam et al., 2010). Global radiation and air temperature data were retrieved from
the WFDEI database (Weedon et al., 2014). The dataset covers the period 1985-2016 with a spatial resolution of 0.5°x0.5°
and a temporal resolution of 1 day. The WFDEI meteorological forcing data set has been generated using the same
90 methodology as the WATCH Forcing Data (WFD) by making use of the ERA-Interim reanalysis data. The ERA-Interim
dataset, provided by the European Centre for Medium-Range Weather Forecasts (ECMWF), was used for soil water content
(level 2, from 0.07 to 0.28 m depth). ERA-Interim is a global atmospheric reanalysis from 1979, continuously updated in real
time (Berrisford et al., 2011).



2.2 Statistical data analysis

95 All datasets were aggregated at the spatial resolution of the inversion product ($5^\circ \times 3.75^\circ$) with the R package “raster” using the mean of the variables (Hijmans, 2017). A moving window of 7, 30, 90 days was then applied to the data to have data at weekly, monthly and seasonal time scale respectively.

Multi-linear regression models have been extensively used to assess the inter-linkages between global vegetation and climate (Barichivich et al., 2014; Nemani et al., 2003). In this study regressions were estimated at pixel level using the R package “glmnet” (Friedman et al., 2010), which is suitable to calculate linear regression coefficients in case of collinearity, as it is often the case with multiple climate drivers. The presence of collinearity was assessed computing the variance inflation factor, which measures how much the variance of a regression coefficient is inflated due to multi-collinearity in the model (Gareth et al., 2014). When multi-collinearity occurs, least squares estimates are unbiased, but their variances are so large that they may be completely inaccurate. Hence, to account for collinearity the loss function is modified in a way that not only the sum of squared residuals is minimized, but also the size of parameter estimates is penalized, in order to shrink them towards zero. The penalization equals the square of the magnitude of coefficients. All coefficients are shrunk by the same factor (so none are eliminated). A tuning parameter (λ) controls the strength of the penalty term. When $\lambda = 0$, the regression equals an ordinary least squares regression. If $\lambda = \infty$, all coefficients are shrunk to zero. The ideal penalty is therefore somewhere in between 0 and ∞ and gives the minimum mean cross-validated error. Regression coefficients were estimated first using the entire time series, and then separately for the Carbon Uptake Period (CUP, GPP dominated) and the Carbon Release Period (CRP, TER dominated). Since gross primary productivity (GPP) and terrestrial ecosystem respiration (TER) cannot be derived from inversion products, we performed regression analysis using NBP of CUP and of CRP as proxies of GPP and TER, respectively (Migliavacca et al., 2011, 2015). Climatological CUP and CRP were identified using the seasonality of NBP (sign convention: $\text{NBP} > 0$ corresponds to uptake) for each pixel, with periods with $\text{NBP} > 0$ being classified as CUP and periods with $\text{NBP} < 0$ as CRP. The absolute value of standardized coefficients was used as a measure of the relative importance of the drivers.

The temporal variability in land fluxes due to temporal variation in the drivers and in the ecosystem sensitivity-to-drivers were estimated and their effect on the total temporal change of NBP was disentangled according to the following equation:

$$\left. \frac{d\text{NBP}}{dt} \right|_{\text{driver}} = \frac{dm_{\text{driver}}}{dt} \text{driver}(t) + m_{\text{driver}}(t) \frac{d(\text{driver})}{dt}$$

where m_{driver} is the slope of a driver in the multi-linear regression.

120 In order to assess the temporal variation of the sensitivity, the observation period was split into 8 sub-periods of 4 years each. For each sub-period a multi-linear regression was estimated at pixel level, obtaining 8 angular coefficients (i.e. sensitivities) for each driver (m_{driver}). Average values of the drivers were also calculated for each sub-period. The contribution of the sensitivity-to-driver temporal change was obtained estimating a linear regression for the 8 angular coefficients against time,



and the temporal sensitivity obtained from the regression ($\frac{dm_{driver}}{dt}$) was multiplied by the average value of the driver in the sub-periods. The contribution of the driver temporal change was obtained estimating a linear regression of the sub-periods' average driver values against time, and the temporal sensitivity of the driver was multiplied by the sensitivity-to-driver coefficients. Finally the values obtained for the 8 sub-periods were averaged.

3 Results and Discussion

The climate driver that controls the sub-annual fluctuation of the net ecosystem CO₂ exchange in most of the northern hemisphere is radiation, with an increasing relevance from the weekly to seasonal temporal scale (Figure 1). In the southern hemisphere soil water content controls NBP in the driest regions of Africa and South America while radiation and temperature dominate elsewhere.

Positive correlation between drivers and NBP dominate the global picture, meaning that on average C uptake is larger during periods with higher temperature, radiation and soil water content. Surprisingly, negative correlation with radiation occurs in the northernmost latitudes, suggesting a strong increase of respiration at the peak of the growing season. These results are in line with the recent findings about the effect of the anticipation of CUP in the boreal zone on the reduction of NBP due to the summer drought (Buermann et al., 2018). Negative correlation with radiation occurs also in tropical regions where most probably high radiation load is related to stressful conditions (e.g. water limitation, heat stress, or a combination of the two). Overall, the frequency of pixels having radiation as dominant variable, increases at decreasing time resolution (from 49% to 59%), while the relative frequency of positive coefficients slightly decreases.

Temperature is the second most frequent dominant variable and controls the tropics in the northern hemisphere, the southernmost latitudes and East Asia. As for radiation, the effect of temperature on the weekly to seasonal variation in NBP is mostly positive (Wu et al., 2015) except in the Middle East. Soil water content controls the boreal latitudes and has a negative effect on the carbon fluxes (drier periods show higher uptake); while in arid regions of the southern hemisphere it has a positive effect (humid periods show higher CO₂ flux). A similar pattern of sensitivity to water availability at monthly time scale is reported in Seddon et al., (2016) and agrees with what was observed by Green et al., (2019) analyzing outputs from four Earth system models. They report a reduction in CO₂ uptake due to soil moisture variability justified by the non-linear response of carbon uptake to water stress. According to this study the most affected regions are those characterized by seasonally dry climate, like tropical savannahs and semi-arid monsoonal regions. A faster atmospheric CO₂ growth in drier periods is also reported in Humphrey et al., (2018), who conclude that drier years are associated with a weakening of the land carbon sink. However, a study on the potential climatic constraint (Nemani et al., 2003) based on monthly climate statistics over two decades at the end of the twentieth century (1982-1999) ascribes different roles to the drivers, with water availability limiting vegetation growth over 40% of the land surface followed by temperature (33%) and radiation (27%).

Since the processes involved in the CO₂ exchange are different between the Carbon Uptake Period (CUP) and the Carbon Release Period (CRP), the regression analysis performed for the entire time series (Figure 1) was repeated separately for



CUP and CRP (Figure 2). In the continental regions, the variability in the period dominated by photosynthesis (CUP) is mostly driven by temperature followed by global radiation, and generally both drivers have a positive impact on NBP, while the temperate zone is mostly radiation-driven. In Canada, Siberia, and Russia warmer periods are the most productive during the growing season. These results are in accordance with a study performed on 23 FLUXNET sites (Baldocchi, 2008) that shows how variations in GPP at northern sites can be explained to a large extent by mean annual temperature (Reichstein et al., 2007). Rödenbeck et al., (2018), working at inter-annual time scale, observed the same correlation sign of NBP and temperature during spring and autumn in all northern extra-tropical land areas, a signal which is consistent with photosynthesis being temperature limited in this time of the year. During CUP in the southern hemisphere an important role is played by the soil water content which is positively correlated with NBP fluxes across the Tropical region.

The carbon release period of the Northern hemisphere is mostly driven by global radiation, which positively impacts on the NBP fluxes, with the exception of the most northern latitudes. Interestingly, where temperature is the dominant driver in the northern hemisphere it has a negative impact on CRP fluxes, likely related to the off-season stimulation of ecosystem respiration. The impact of radiation on CRP fluxes clearly depends on the climate zone. In the northern hemisphere, the most productive weeks of CRP are those with higher radiation (which means those at the beginning and at the end of the CRP). On the contrary, radiation has a negative impact on the CRP fluxes in the southern hemisphere, while the effect of the soil water content is generally positive. Temperature controls the most southern latitudes with a positive coefficient, and the intermediate latitudes with a negative one.

The global frequency and sign of the dominant drivers is summarized in Figure 3 for CUP and CRP at different temporal resolutions. The most frequent dominant variable during CUP is air temperature with a high dominance of positive coefficients, followed by radiation. Where soil water content is the dominant variable it has a positive impact on carbon uptake almost everywhere. During CRP the most frequent variable is global radiation, and the frequency of negative coefficients is much higher if compared to CUP. Temperature is the second most frequent dominant variable and has mostly a negative impact on NBP. This plot shows an important asymmetry in the sign of the controlling drivers between the CUP and CRP. While the former is stimulated by the increase in the drivers on a large fraction of the Earth surface (more than 80% on average for all drivers), the latter shows a mixed pattern where the CO₂ sink is stimulated in about half of the planet and depressed in the other half concerning radiation. Concerning temperature, the key parameter in a global change perspective, the asymmetry is even stronger, with a control overwhelmingly positive in the CUP (in ~85% of the temperature-dominated surface at all the investigated temporal resolutions) and mostly negative (in 76%, 68% and 45% of the temperature-dominated surface at 7, 30 and 90 days respectively) in the CRP. This pattern is likely due to the positive response of both photosynthesis and ecosystem respiration to increasing temperatures. This asymmetry in the response of photosynthesis and respiration to temperature is at the base of the large uncertainty of the terrestrial C budget under climate change (Friedlingstein et al., 2014).

In a scenario of rapidly changing climate it is particularly important to assess how the sensitivity of NBP to the different drivers is changing over time and in which geographic regions. To this end, Figure 4 summarizes global maps of the



averages (left) and temporal trends (right) of the regression coefficients (with respect to all-year time series and at 7 days temporal resolution). The average regression coefficient of global radiation is positive in most of the northern hemisphere, which means that NBP increases at increasing radiation. This effect has increased in the last decades, likely due to the increasing leaf area index (LAI) and primary productivity of the northern regions, leading to increased light use efficiency. On the contrary, in the southern hemisphere the average sensitivity is mostly negative and the trends are heterogeneous.

Concerning temperature, NBP in North America and northern Europe shows a positive sensitivity, while southern Europe, large fractions of Asia and the Tropical belt show negative sensitivity. In Eurasia, the sensitivity of NBP to temperature is decreasing with time, in agreement with Piao et al., (2017), who report a declining temperature response of spring NPP ascribed to reduced chilling during dormancy and emerging light limitation. Interestingly an opposite positive trend of temperature sensitivity occurs in North America.

A mostly positive sensitivity of NBP to soil water content occurs in regions where evapotranspiration is supply limited and water stress may limit productivity. On the contrary, in northern regions, where evaporation is limited by atmospheric demand, the sensitivity is negative. The trend in the sensitivity to water availability does not show a clear spatial pattern, likely due to the complex interplay between changes in precipitation and evapotranspiration in the different regions. Ultimately the sensitivity is likely to decrease where water availability is increasing, and vice versa it may increase in areas that are experiencing a decline in soil water content. In order to explore the relationships between sensitivities and background climate, results shown in the maps of Figure 4 are summarized in the scatter plots of Figure 5, where sensitivities and their temporal trend for all the pixels are plotted according to climate coordinates (i.e. annual cumulative rainfall and mean temperature). A clear pattern is emerging for radiation, with negative sensitivities in regions with high and very low temperature independently from precipitation values, while at intermediate temperatures it has a positive effect on fluxes. In addition, the climate dependence of the trend in sensitivity to radiation generally follows the pattern of the mean sensitivity, with positive trends in climate regions characterized by positive sensitivity and vice-versa. This bimodal distribution of sensitivity and trends is clearly leading to an increase of the spatial (and climatic) variance in the response of ecosystem to radiation. The on-going acceleration of the terrestrial carbon cycle due to the increase of GPP and TER is likely leading to this bipolar pattern. Similarly to radiation, temperatures also show positive sensitivities at intermediate mean temperatures. In addition, the different patterns of temperature and radiation trends suggest that the underlying processes triggered by the two drivers are likely different. The climate dependence of the trend in sensitivity to temperature doesn't follow the pattern of the mean sensitivity, being opposite in sign at intermediate temperatures leading in this way to a homogenization of its spatial variability. The sign and magnitude of the sensitivity of NBP to soil water content is clearly controlled by the background mean temperature, with a sharp threshold at about 7 °C between regions with positive and negative sensitivity. On average the sensitivity to soil water content is increasing in regions warmer than 0 °C, but with considerable local variation, suggesting in general an increasing impact of water limitations on the fluctuations of the terrestrial carbon cycle, as also reported by (Jung et al., 2017).



Maps of the trends in the sensitivity of NBP to climatic drivers are shown in Figure 6, separately for CUP and CRP. The sensitivity of NBP to radiation is increasing in most of the northern hemisphere both during CUP and CRP, suggesting that NBP seasonality is increasingly controlled by light-limited photosynthesis, likely due to a combination of warming, a consequent extended growing season length and greening. The increase of light-limitation goes hand in hand with the decline of temperature limitation, in particular during the CRP in Eurasia. Opposite trends of sensitivity to radiation and temperature occur also in the Amazon, where during the CUP we observe an increasing control of radiation and decreasing control of temperature, and the opposite during CRP. The sensitivity to soil water content is mostly increasing, in particular during CRP in most regions except Europe in line with the recent findings by Buermann et al., (2018) about the increasing role of water limitation in the boreal zone. In general soil water content shows an increasing control on the seasonality of NBP also in the US and in tropical regions, confirming the increasing relevance of water stress on primary productivity (Jung et al., 2010).

The strongest signal that is emerging from the analysis is the broad increase in the sensitivity to radiation during CUP in the northern hemisphere, while it is decreasing in most of the southern hemisphere. On the contrary, the sensitivity to temperature is generally decreasing everywhere, with the exception of the most northern and southern latitudes which host temperature-limited ecosystems. The pattern of the soil water content is less clear. Arid zones exhibit a weak increase in soil water content control, which confirms recent published results that documents how the inter-annual variability of the planet is controlled by arid zones (Ahlstrom et al., 2015). For the interpretation of these results it is important to consider that the ecosystem carbon exchange is controlled by light only in ideal growing condition, when neither temperatures nor water are limiting photosynthesis. From the positive trends in light sensitivity observed here one could infer that global changes in climate have eased the growing conditions of plants (Nemani et al., 2003). In particular, the positive trend in sensitivity to solar radiation during CPU in the boreal zone can be interpreted as a tendency toward improved growing conditions due to a decline of low temperature limitations.

Finally, we factored out the two contributions to the temporal trend in NBP (Figure 7), namely the temporal trend of the climatic drivers (right column) and the temporal trend of the ecosystem sensitivity to the driver (left column). Results show that the temporal trend in sensitivity is generally bigger than the corresponding contribution due to temporal change in the driver. This finding suggests that the ongoing structural and physiological changes in vegetation functional characteristics are affecting the temporal variability of NBP more than the climate variability per se (Marcolla et al., 2011; Richardson et al., 2007). In particular, the large increase in the sensitivity to radiation (likely related to the greening of the planet) dominates the radiation-related changes of NBP in almost the entire northern hemisphere. In contrast, trends in temperature sensitivity cause a decline in NBP in Eurasia and part of North America, while the temperature increase itself causes increasing NBP just like radiation.



4 Conclusions

- 255 - We focused this analysis on climate drivers of the sub-annual variability of land CO₂ fluxes as derived from an atmospheric inversion in order to characterize the key driver in the different world regions and climates. The short-term drivers of NBP can be interpreted as the limiting factors of the ecosystem carbon budget at weekly to seasonal scale. Advancing the knowledge on the limiting factors and their variation in the recent decades is important to understand and predict the impact of climate change on the terrestrial carbon budget.
- 260 - Given that the atmospheric inversion does not allow a direct separation of NBP in gross primary productivity and ecosystem respiration, we analyzed two contrasting periods: the carbon uptake periods (CUP) when NBP is dominated by photosynthesis and the carbon release period (CRP) when NBP is dominated by respiration.
- On average, during the year we show that solar radiation is driving the variations in the seasonality of the fluxes in the northern hemisphere, and soil water content in the southern hemisphere. More specifically, during the CUP we can detect three clear driving factors, temperature in the northernmost regions, radiation in the temperate regions and soil water content in the tropical region, with temperature being the most common driver. During the CRP a large fraction of the planet is radiation-controlled, with positive correlation in the northern hemisphere and negative in the southern.
- 265 - Looking at the temporal dynamic of the climatic control, air temperature shows a positive correlation with NBP in Eurasia, but with a decline in sensitivity over time; on the contrary, sensitivity to radiation is increasing almost in the entire boreal hemisphere both during CUP and CRP, suggesting that CO₂ fluxes are becoming increasingly light-limited.
- 270 - This analysis reveals the strength of the climatic controls on the terrestrial carbon budget and their clear dependence on the background climate. It also shows how the recent trend in climate combined with CO₂ fertilization and photosynthetic potentials is substantially changing the climate response of the terrestrial biosphere.
- 275 - Factoring out the sources of temporal variability of NBP we showed that CO₂ fluxes are more intensively controlled by the variation in the ecosystem sensitivities to climate drivers than by the temporal changes of the drivers. This means that the indirect impact of climate change on the ecosystem sensitivity may actually be more relevant than the direct impact of the climate on the terrestrial CO₂ fluxes.
- 280 - Overall this analysis shows how important climate is in determining the sensitivities of NBP to environmental controls and how rapidly these sensitivities are changing in time, likely leading to new and still un-experienced relationships between climate and the terrestrial carbon budget.



Author contribution. AC and BM conceived the study and designed the methods. CR provided the Jena CarboScope data. BM performed the data analysis. AC and BM interpreted the results. MM and CR contributed to the improvement of the methods and to the interpretation of results. AC and BM wrote the manuscript with contributions from the other co-authors.

Competing interests. The authors declare that they have no conflict of interest

Data availability.

The Jena CarboScope database can be found at <http://www.bgc-jena.mpg.de/CarboScope/>

WFDEI database at http://www.eu-watch.org/data_availability

ERA-Interim database at <https://www.ecmwf.int/en/forecasts/datasets/reanalysis-datasets/era-interim>

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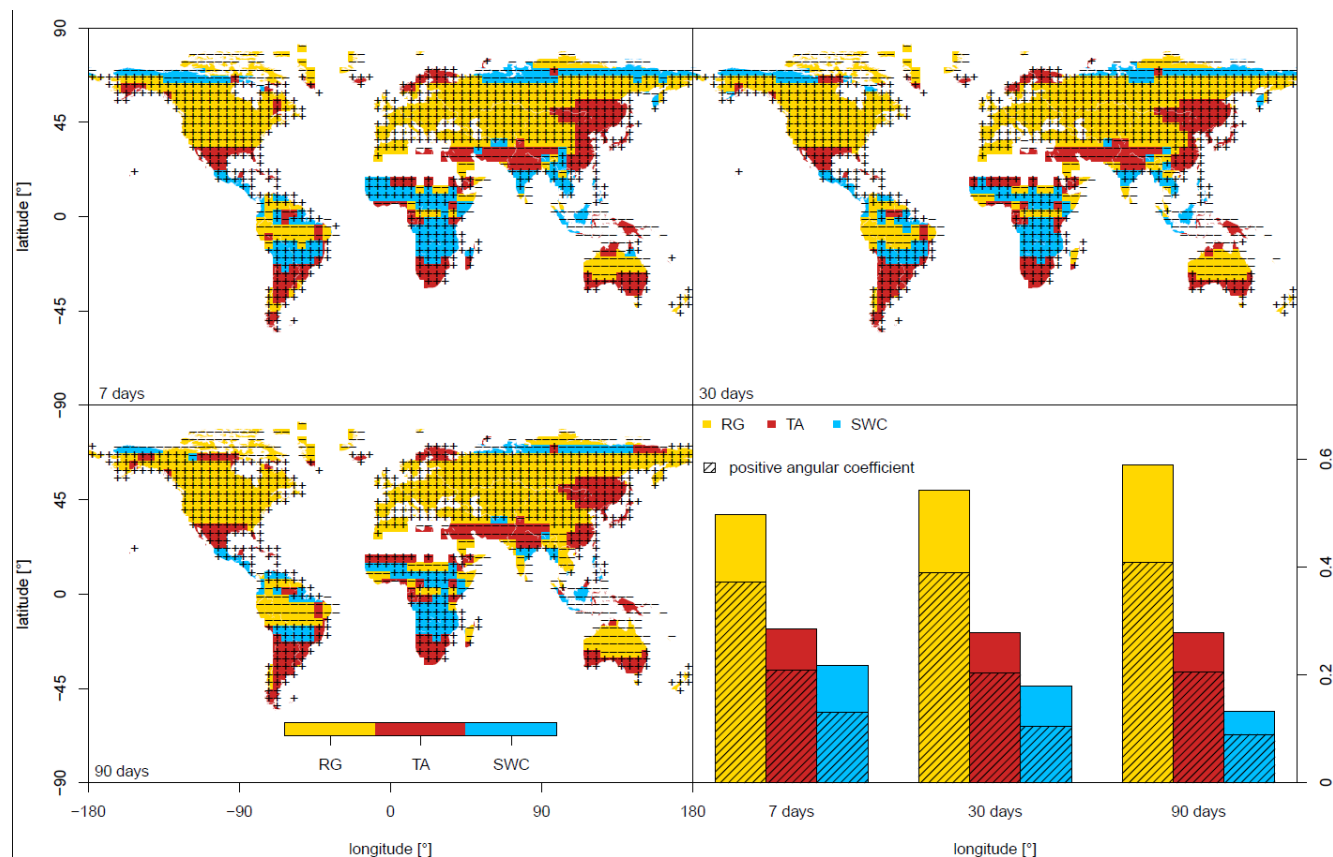
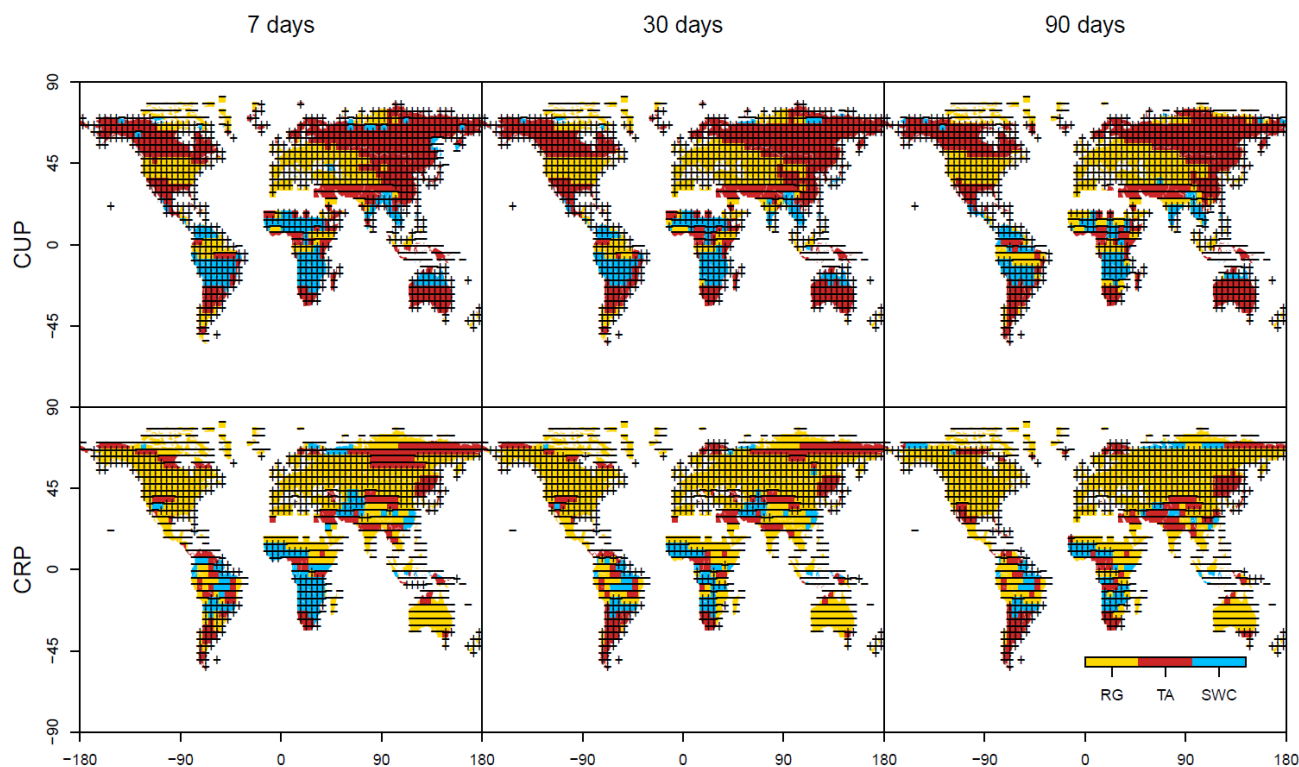
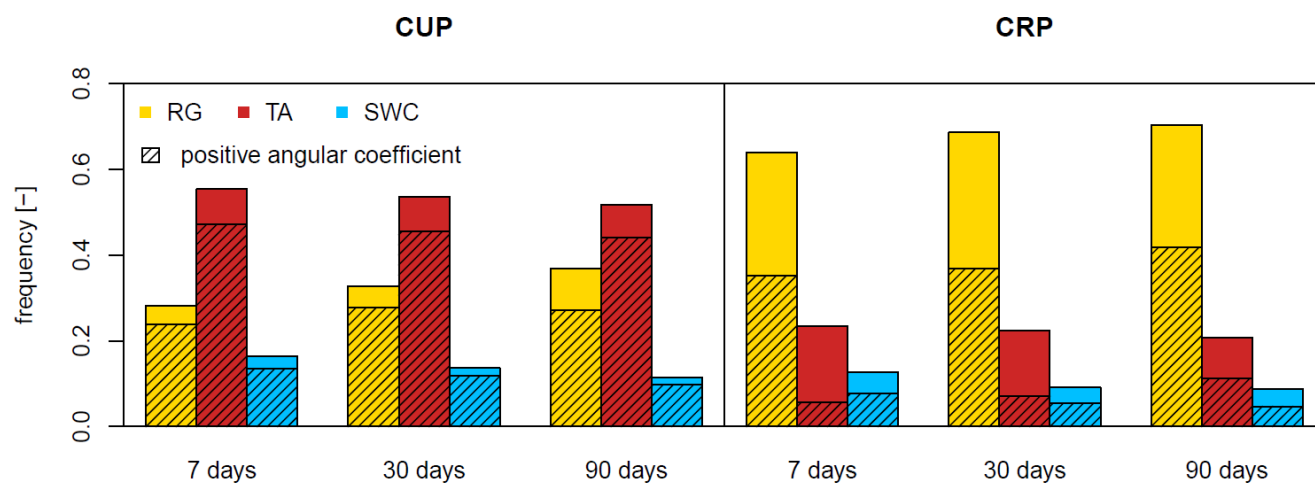


Figure 1 - Maps of the dominant drivers calculated over the entire time series and sign of their angular coefficients in a multi-linear regression. Results are shown for three temporal resolutions, namely 7, 30 and 90 days. Bottom right panel: frequency of each dominant variable for the three analyzed temporal resolutions, dashed areas represent the frequency of positive angular coefficients.

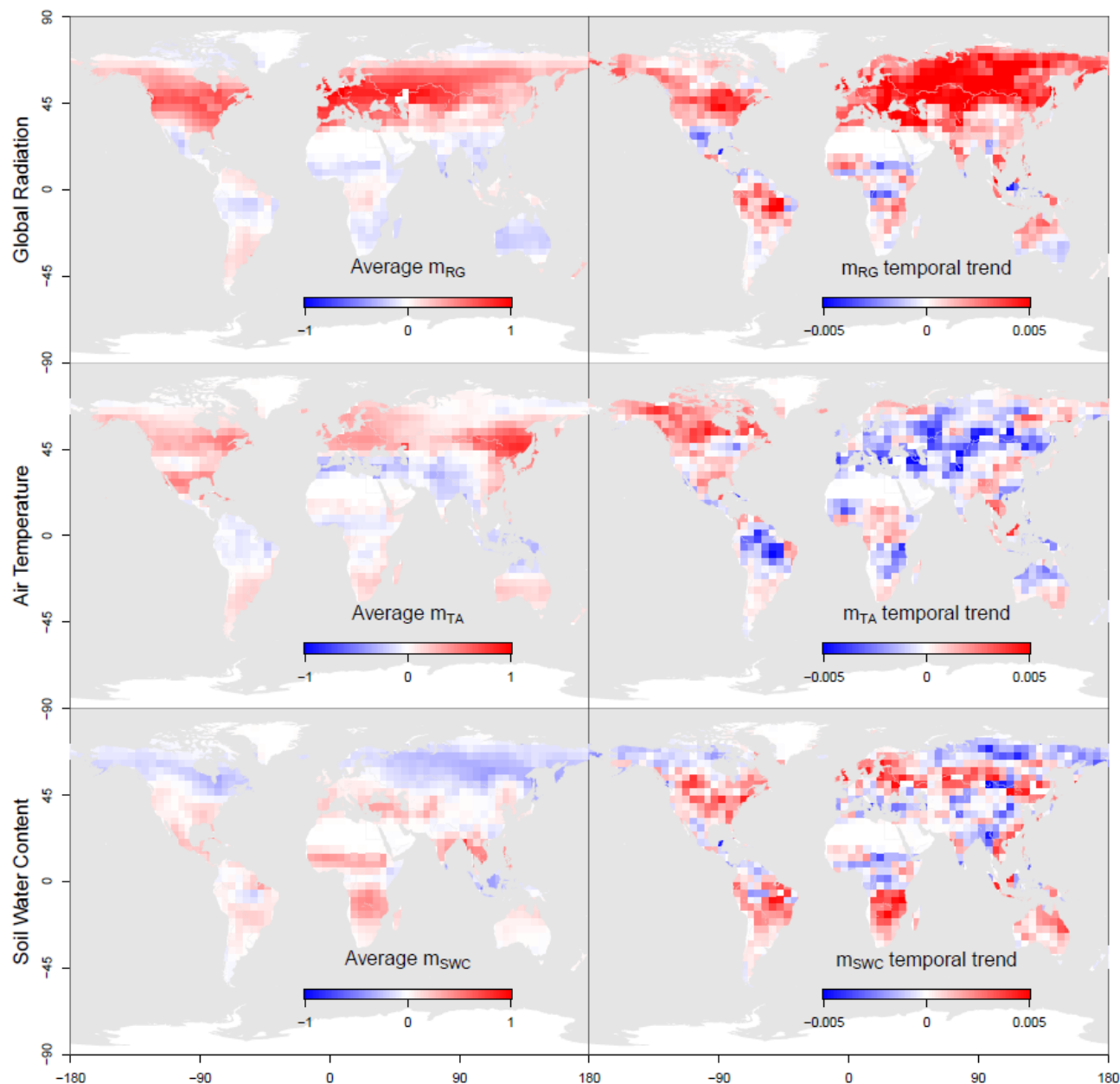


450 **Figure 2 - Maps of the dominant drivers and sign of their angular coefficients in a multi-linear regression calculated separately for Carbon Uptake Period (CUP, top row) and Carbon Release Period (CRP, bottom row). Results are shown for three temporal resolutions, namely 7, 30 and 90 days.**



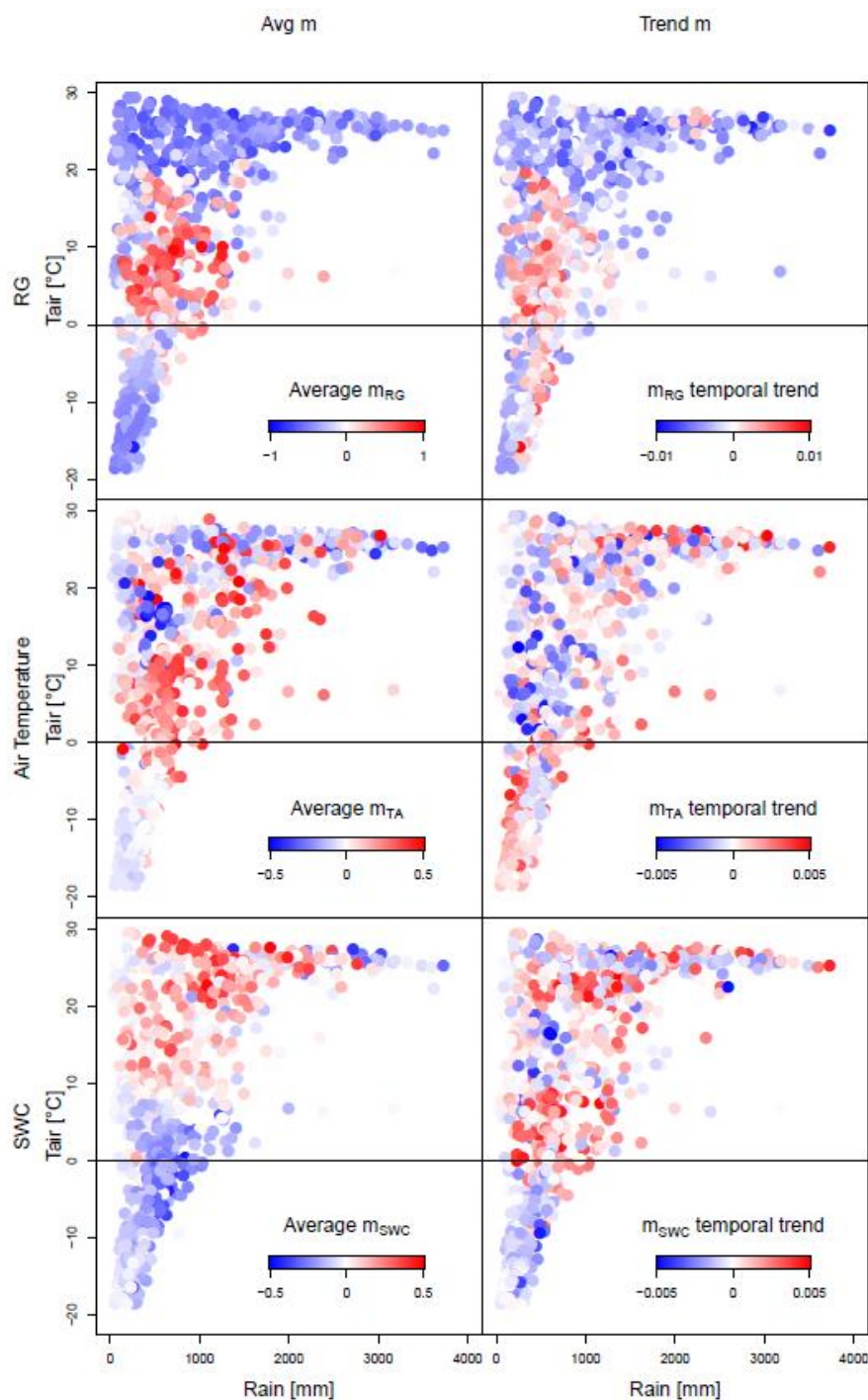
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Figure 3 - Frequency of the dominant variables plotted for Carbon Uptake Period (CUP) and Carbon Release Period (CRP) at different temporal resolutions (7, 30 and 90 days), and frequency of dominant variables with positive coefficients (dashed bars).



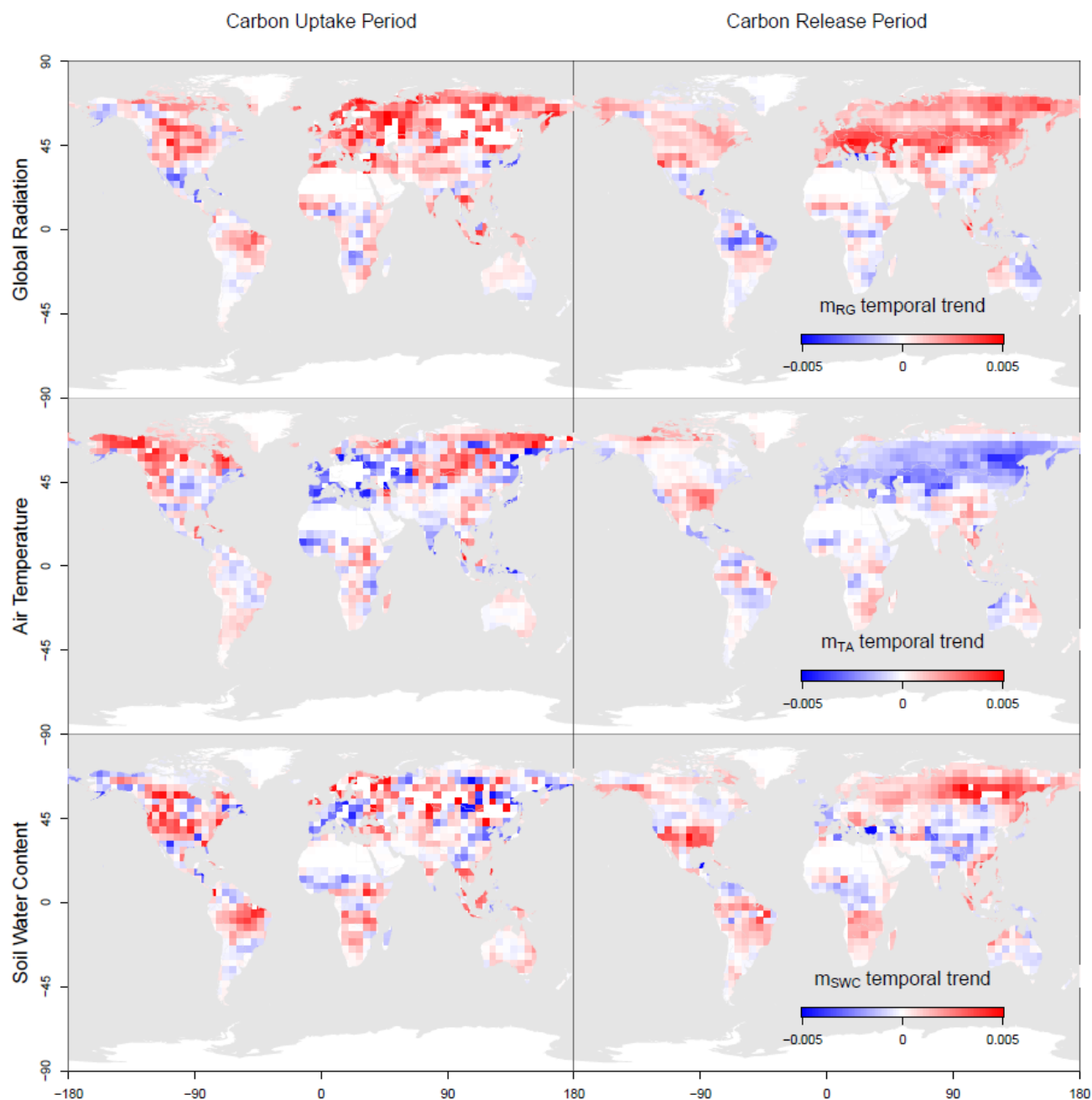
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Figure 4 – Maps of magnitude (left column) and trends (right column) of the sensitivity of Net Biome Productivity (NBP) to global radiation (first row), air temperature (second row) and soil water content (third row) at weekly time scale.

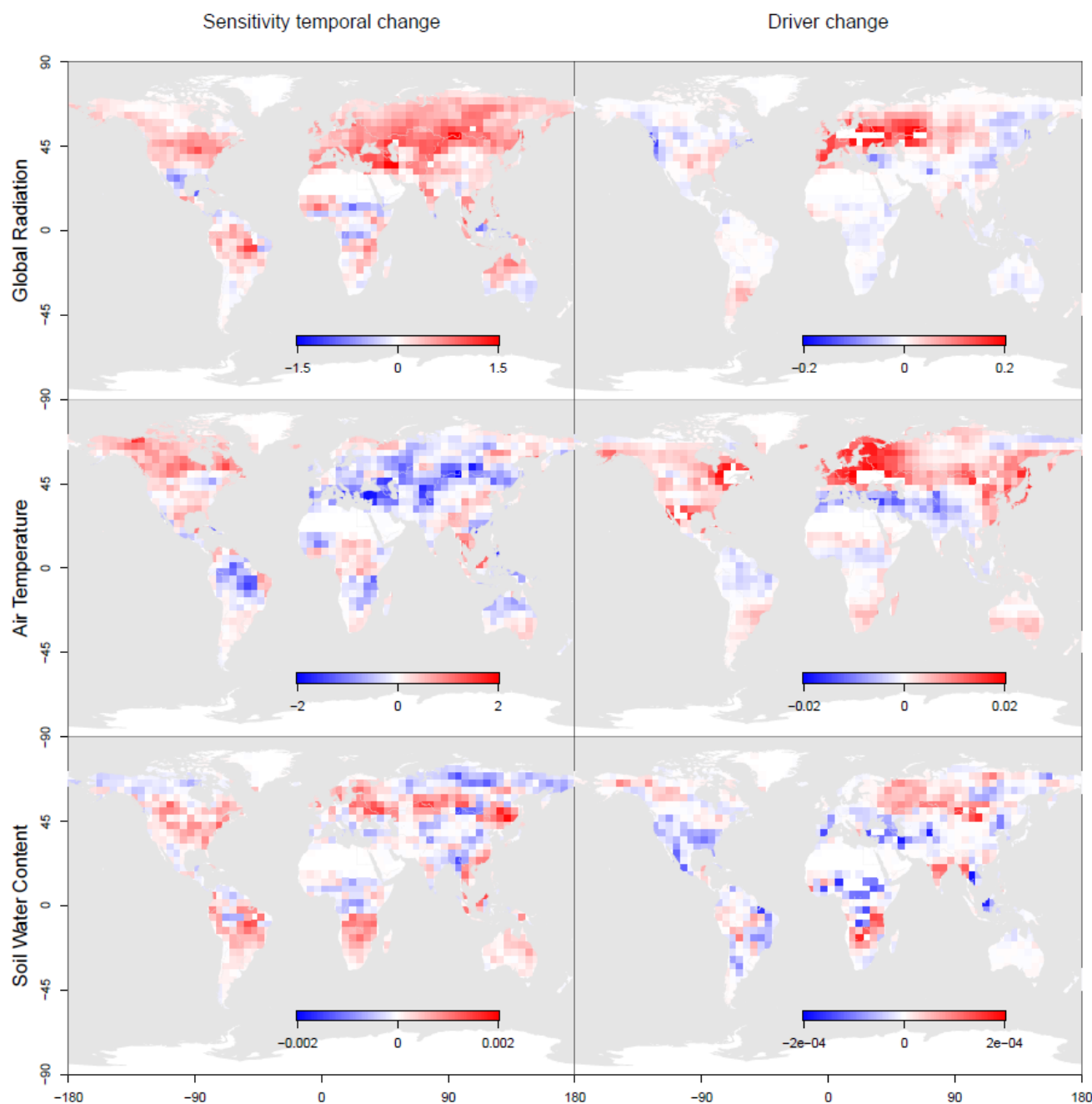


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Figure 5 – Scatter plots of sensitivity to climate drivers (left column) and of trends of the sensitivities (right column) plotted in a precipitation- temperature space at weekly time scale.



470 Figure 6 – Maps of sensitivity temporal trends separately shown for Carbon Uptake Period (CUP, left column) and Carbon Release Period (CRP, right column) at weekly time scale. Maps are plotted for global radiation (first row), air temperature (second row) and soil water content (third row).



475 **Figure 7 – Maps of the average contribution of sensitivity temporal change (left column) and of the temporal change of the driver (right column) to the total temporal variability of Net Biome Productivity (NBP) in the investigated period. Maps are plotted for global radiation (first row), air temperature (second row) and soil water content (third row).**