

Contrasting drought legacy effects on gross primary productivity in a mixed versus pure beech forest

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Abstract. Droughts affect terrestrial ecosystems directly and concurrently, and can additionally induce lagged effects in subsequent seasons and years. Such legacy effects of drought on vegetation growth and state have been widely studied in tree-ring records and satellite-based vegetation greenness, while legacies on ecosystem carbon fluxes are still poorly quantified and understood. Here, we focus on two ecosystem monitoring sites in central Germany with similar climate but characterized by different species and age structures. Using eddy-covariance measurements, we detect legacies on gross primary productivity (GPP) by calculating the difference between random-forest model estimates of potential GPP and observed GPP. Our results showed that at both sites, droughts caused significant legacy effects on GPP at seasonal and annual time scales which were partly explained by reduced leaf development. The GPP reduction due to drought legacy effects is of comparable magnitude to the concurrent drought effects, but differed between two neighbouring forests with divergent species and age structures. The methodology proposed here allows quantifying the temporal dynamics of legacy effects at the sub-seasonal scale and separating legacy effects from model uncertainties. Application of the methodology at a larger range of sites will help quantify whether the identified lag effects are general and on which factors they may depend.

1 Introduction

The frequency, intensity, duration, and spatial extent of drought are expected to increase in the next decades due to anthropogenic global warming in many regions (IPCC, 2022). A great number of studies, considering both long-term observations (Schwalm et al., 2010; Zscheischler et al., 2014) and model simulations (Reichstein et al., 2007; Sun et al., 2015)

across various spatial scales, have shown that droughts concurrently impact the structure and function of terrestrial ecosystems (Assal et al., 2016; Frank et al., 2015; Lewis et al., 2011; Ma et al., 2015; Orth et al., 2020), potentially turning ecosystems from sinks to temporary sources of carbon (Ciais et al., 2005; Reichstein et al., 2013). Therefore, understanding the impact of droughts on terrestrial ecosystems is a key research question in Earth sciences (Piao et al., 2019).

Drought impacts on terrestrial ecosystems are not limited to concurrent effects, but also include legacy effects during the following seasons and years (Anderegg et al., 2015; Frank et al., 2015; Kannenberg et al., 2020). Legacy effects at tree and/or stand scale can be caused by the higher vulnerability to drought due to previous water depletion of the soil (Krishnan et al., 2006; Galvagno et al., 2013), reduced or delayed leaf development (Migliavacca et al., 2009; Rocha and Goulden, 2010; Kannenberg et al., 2019), drought-induced hydraulic damage of the xylem (Anderegg et al., 2013), adjustments in carbon allocation within the trees (Huang et al., 2021), depletion of non-structural carbohydrates (Peltier et al., 2021) due to reduced carbon availability and adjustments in carbon allocation (Hartman and Trumbore, 2016), tree mortality (Allen et al., 2015), as well as reduced resistance to disturbances (e.g. insects outbreaks) due to depleted non-structural carbohydrates (Erbilgin et al., 2021). However, at the ecosystem level the impact of species and age structures on legacy effects are still less understood (Haberstroh and Werner, 2022; Wang et al., 2022).

Tree-ring records cover periods of decades to centuries and can cover multiple drought events, being therefore widely used to analyze inter-annual legacy effects of drought on tree growth (Anderegg et al., 2015; Huang et al., 2018; Kannenberg et al., 2019). Beyond the level of individual trees, satellite-based observations and model outputs, as expressed through vegetation greenness (Wolf et al., 2016; Wu et al., 2018), canopy backscatter (Saatchi et al., 2013), aboveground carbon stocks (Wigneron et al., 2020), and gross primary productivity (Schwalm et al., 2017; Bastos et al., 2020) have also been used to study seasonal and inter-annual legacy effects of drought. However, studies focusing on carbon fluxes, especially based on eddy-covariance measurements, are still rare (Kannenberg et al., 2020). Eddy-covariance data with hydrometeorological variables measured in parallel have the potential to quantify the timing and magnitude of legacy effects at the sub-seasonal and annual scales, and might provide insights into the mechanisms of legacy effects that might not be fully reflected in vegetation indices and tree rings.

Assessments of drought impacts on the ecosystem carbon fluxes usually focus on direct and concurrent effects (Ciais et al., 2005; Reichstein et al., 2007) without considering legacy effects. This is probably due to the challenge to attribute signals in the observations to a previous drought and hence identify them as legacy effects on ecosystem carbon fluxes (Kannenberg et al., 2020), and the inability of models to reproduce these legacy effects (Bastos et al., 2021). A number of studies consider ecosystems to have ‘recovered’ when the target variable such as gross primary productivity (GPP) and tree-ring width returns to the baseline, which is usually based on pre-drought values of the target variable (Bose et al., 2020; González de Andrés et al., 2021; Zhang et al., 2021). However, this might complicate the detection of legacies since GPP recovery dynamics is affected by hydrometeorological conditions in legacy years, which can either stimulate or slow-down recovery. Here, by estimating potential GPP given hydrometeorological conditions in legacy years, we consider that ‘recovery’ happens when the actual GPP reaches the potential GPP under the given hydrometeorological conditions, rather than the absolute flux.

Therefore, we aimed to develop a novel approach to quantify drought legacy effects on GPP at the sub-seasonal and annual scales. To do this, we followed a residual approach (Beringer et al., 2007) to identify legacy effects as the residuals between actual and potential GPP which is estimated by a machine-learning algorithm (specifically Random Forest regression). Furthermore, it is crucial to understand if the residuals are caused by model uncertainties or can be interpreted as legacy effects. By overlooking model uncertainties, one could misinterpret small residuals as ‘legacy effects’. Here we quantified model uncertainties to provide more robust estimates of drought legacies and avoid misinterpretation of results. To test our approach, we used eddy-covariance measurements at two neighbouring sites that experienced similar climate but are characterized by different species and age structures in central Germany. We asked 1) can we detect drought legacy effects on GPP? 2) is the GPP reduction due to drought legacy effects significant compared to the magnitude of drought concurrent effects? 3) how do drought legacy effects on GPP differ at two neighbouring forests with different species and age structures?

2 Data

2.1 Study sites

The two neighboring temperate forest sites studied here, Hainich (DE-Hai, 51°04'46"N, 10°27'07"E) and Leinefelde (DE-Lnf, 51°19'42"N, 10°22'04"E), are located in central Germany, approximately 30 km from each other. These two sites share similar climate conditions, with long-term annual mean of 8 °C for 2-m air temperature and 750 mm of total annual precipitation (Tamrakar et al., 2018). Both sites were affected by the two extreme central European droughts in 2003 and 2018 which reduced gross primary productivity (Fu et al., 2020; Herbst et al., 2015).

The forest at Hainich is an old-growth, uneven aged (1-250 years) mixed forest, dominated by beech (*Fagus sylvatica*, representing approximately 64% of the tree carbon stocks). Ash (*Fraxinus excelsior*, 28%) and sycamore (*Acer pseudoplatanus*, 7%) are co-dominant tree species, and additionally there are few trees of European hornbeam (*Carpinus betulus*), Norway maple (*Acer platanoides*), and other deciduous species (Knobl et al., 2003). The forest at Leinefelde can be characterized as a managed even-aged (ca. 130 years) pure beech forest (Anthoni et al., 2004).

2.2 Eddy-covariance and meteorological measurements

Identical eddy-covariance instrumental setups and data acquisition techniques were carried out at the two sites. The methodology of data collection and quality control followed those of Aubinet et al. (2000). The standard processing methods (Pastorello et al., 2020) adopted by the Integrated Carbon Observation System (ICOS) were used to carry out the gap-filling and the partitioning of net CO₂ exchange (NEE) into gross primary production (GPP) and ecosystem respiration (R_{eco}) using the nighttime partitioning algorithm (Reichstein et al., 2005; Warm Winter 2020 Team and ICOS Ecosystem Thematic Centre 2022). The GPP estimated from the nighttime partitioning algorithm (Reichstein et al., 2005) was used for the analysis (GPP_{NT_VUT_REF}). A detailed description of meteorological data and instrumentation can be found in previous studies (Anthoni et al., 2004; Knobl et al., 2003). We used daily meteorological data alongside carbon and water fluxes, namely GPP,

latent heat flux after the energy balance correction (LE_CORR), which was converted to evapotranspiration (ET) using the heat of vaporization, incoming shortwave radiation (SW_IN), air temperature (TA), vapor pressure deficit (VPD), soil water content at the first layer (SWC_1, 8cm), the second layer (SWC_2, 16cm), the third layer (SWC_3, 32cm), and potential incoming shortwave radiation (SW_IN_POT) for the years 2000-2020 at DE-Hai and 2002-2012, with a gap in 2007-2009, at DE-Lnf.

Additionally, we used daily enhanced vegetation index (EVI) data from the FluxnetEO v1.0 dataset (Walther et al., 2021) for the same years as the eddy-covariance data. EVI was derived from the MCD43A4 product of MODIS with a 500m spatial resolution and we used an average over 2x2 pixels surrounding the tower. We further estimated daily transpiration based on the Transpiration Estimation Algorithm (Nelson et al., 2018).

2.3 ~~Free-ring width~~Radial increment and net primary productivity of fruits and leaves

~~Annual mean tree-ring width (TRW)~~Annual radial increment (RI) –was calculated from ~~measured via~~ permanent band dendrometers ~~which measures change in stem girth (or circumference) over bark. The effect due to the inclusion of shrinkage and swelling of the bark is a negligible uncertainty for four reasons: 1) we used only the annual increment, 2) the dominant species is beech that has only a thin bark, 3) we recorded the final stem diameter of each year in winter, when the water status of the xylem and the bark is relatively constant, and when stem wood or the bark are not affected by frost or late/early growth or water uptake, and 4) in this study we were interested only in the interannual variability of stem growth, which is less affected by shrinkage and swelling at the described temporal scale than absolute growth rates.~~ The dendrometer trees represented the main species and their respective size classes of the main footprint at DE-Hai for the years 2003 to 2020. Because of technical constraints, damages and a natural dieback of single trees, the number of measurement trees per year varied between 54 and 95. Net primary productivity (NPP) of fruits for the years 2003 to 2020, and NPP of leaves for the years 2003 to 2016 resulted from litter samplings (25-29 traps) within the main footprint area of the flux tower. The high fluctuation of annual fruit NPP is caused by the periodically high fruit production (masting) of beech (*Fagus sylvatica*). In most years the proportion of beech fruits (nuts and shells) amounted to almost 92% of total fruit mass. At DE-Lnf these data are not available. A detailed description of measurement and processing methods can be found in a previous study (Mund et al., 2020).

3 Methodology

3.1 Data processing

As the first step, we filtered and processed the eddy covariance and meteorological data in the following way:

- 1) To ensure reliable data for our analysis we used gap-filled daily data for days for which more than 70% of measured and good quality gap-fill data (Reichstein et al., 2005) were available.
- 2) We only used data during the growing season which was defined as the period when GPP was greater than 10% of maximum of GPP as inferred from a smoothed (centered 7-days moving averages) daily average GPP across all years.

127 3) We calculated anomalies of all variables by subtracting the mean seasonal cycle and any significant long-term linear trend,
128 detected by the Mann-Kendall test (Kendall, 1948), as these can obscure drought-related signals. We took the mean of each
129 day across all considered years and then used centered 7-days moving averages to calculate the mean seasonal cycle.
130 4) Furthermore, a 7-days moving average smoothing was applied to the anomaly time series to filter out noise at daily time
131 scales. We expect this to increase the accuracy of our model while preserving drought legacy patterns which rather/better
132 emerge at longer time scales.
133 As for RITRW data, we removed for each individual tree any significant long-term linear trend detected using the Mann-
134 Kendall test (Kendall, 1948).
135

136 3.2 Water availability index estimation

137 Soil moisture at the two study sites was measured only at the upper 30 cm and thus does not account for water availability in
138 deeper layers (see Section 5.4). Therefore, we used a bucket model approach based on observed evapotranspiration and
139 precipitation to estimate a vegetation water availability index, WAI (Tramontana et al., 2016), calculated as:

$$WAI_t = \min(WAI_{max}, WAI_{t-1} + P_t - ET_t) \quad (1)$$

$$WAI_t = \min(WAI_{max}, WAI_{t-1} + P_t - ET_t) \quad (2)$$

140 Where WAI₀ was the initial value of the water availability index (WAI). WAI_{warm-up} was the end value of WAI from the warm-
141 up of the bucket model (Eq. 1). To initialize warm up the bucket model, we ran it 5 times through the first year before starting
142 the actual computation across all considered years.

143 WAI_{t-1} (mm) and WAI_t (mm) were WAI at time step t-1 and t, respectively, P_t (mm), and ET_t (mm) were water availability
144 index, precipitation, and evapotranspiration at time step *t* (Eq. 2). We set the bucket size (i.e. WAI_{max}) as the maximum
145 cumulative water deficit (CWD) at each site. The estimated bucket sizes were 205mm and 191mm at DE-Hai and DE-Lnf,
146 respectively.

147 Additionally, we calculated the CWD, which was estimated from cumulative differences between observed evapotranspiration
148 and precipitation over periods where cumulative net water loss from the soil ($\Sigma (ET-P)$) is positive.

149 To initialize the bucket model, we ran it 5 times through the first year before starting the actual computation across all
150 considered years.

151 3.3 Drought and legacy years selection

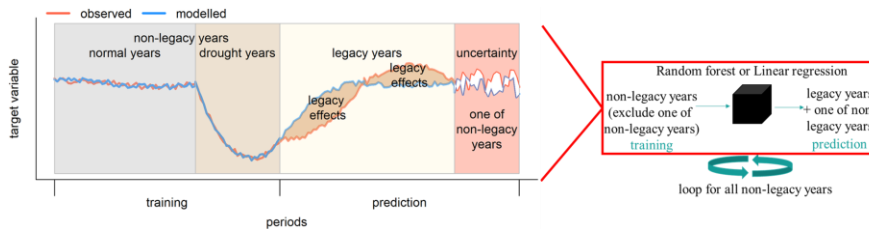
152 Since legacy effects should result from significant impacts of droughts on ecosystems, we adopted a combined driver and
153 impact-based approach to define droughts. Drought years were defined as those years when both low water availability and a
154 concurrent biospheric response were found, and were evaluated as follows:

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155 1) First, we selected the minimum of negative GPP anomalies relative to the mean seasonal cycle during the growing season
 156 (minimum GPP_{anom}) as a proxy to reflect the severity of drought impact on GPP in each year.
 157 2) Then, we calculated the mean WAI anomalies relative to the mean seasonal cycle for days when minimum GPP_{anom} occurred
 158 and the previous 14 days (mean WAI_{anom_15}) to reflect the water availability during the development of the GPP anomaly. To
 159 identify drought-related GPP reductions, we considered only years where negative GPP anomalies were associated with dry
 160 conditions.
 161 3) Finally, we selected the years with both the lowest minimum GPP_{anom} and mean WAI_{anom_15} (Fig. S1). These were -2003
 162 and 2018 at DE-Hai and 2003 at DE-Lnf (2018 data not available here).
 163 In our data, we define non-legacy years as normal and drought years, while legacy years correspond to the two calendar years
 164 following a drought year. Including too few legacy years could lead to an underestimation of legacy effects, and too many
 165 legacy years would result in the lack of training data (see Section 3.4). As a trade-off, we selected a legacy period of two years
 166 and this choice was justified by the fact that GPP anomalies residuals returned to the range of model uncertainties (i.e. 25th-
 167 75th percentiles of model residuals), which is considered as the point when GPP recovers, in 2005 (see Section 4.3) following
 168 the 2003 drought at both sites and, for 2018 at DE-Hai, data was only available up to 2020. This happened in 2005 (see Section
 169 4.3) following the 2003 drought at both sites. For the 2018 drought at DE-Hai, data was only available up to 2020.

171 3.4 Quantification of legacy effects on GPP and transpiration

172 Here, we followed a residual approach (Beringer et al., 2007) to detect drought legacy effects on GPP. To do this, we fitted a
 173 random forest regression model (RF, Breiman 2001) for daily GPP anomalies using the anomalies of hydro-meteorological
 174 variables in non-legacy years as predictors. We chose RF because it has the ability to effectively learn 1) the relationship
 175 between independent and dependent variables regardless of linear or non-linear relationships; 2) the interactions between
 176 independent variables (Ryo and Rillig, 2017). The model was then used to predict GPP anomalies in the legacy years, thereby
 177 reflecting the potential GPP anomalies given the climate conditions in that year. Specifically, the approach included the
 178 following steps (Fig. 1):



179 **Figure 1. Conceptual diagram of quantification of legacy effects.** A random forest (RF) model (or linear regression, represented by the
 180 black cube on the right) was used to determine the relationship between the target variable (GPP_{anom} or R_{ETRW}) and hydro-meteorological
 181 conditions using a training dataset excluding data in legacy years and one of non-legacy years for each loop. The legacy effects could be
 182

quantified as the residuals between observed (red line) and modelled (blue line) target variable (i.e. GPP_{anom} , R_{TRW} , ...) in legacy years. And the residuals between observed and modelled target variable (i.e. GPP_{anom} , R_{TRW} , ...) in all non-legacy years from all loops indicated RF model uncertainties using a leave-one-out approach (see below).

First, all daily data in non-legacy years were used as input for the RF model to determine the relationships between anomalies of GPP (GPP_{anom}) and anomalies of hydro-meteorological variables (SW_IN_{anom} , TA_{anom} , VPD_{anom} , and WAI_{anom}) along with absolute values of SW_IN_POT to capture seasonal variations in the response of ecosystems to hydro-meteorological conditions. These relationships represented long-term controls of climate on GPP, including drought events and near-average or wet conditions. The Out of bag (OOB) scores indicating the prediction ability of RF models were ~0.7 and ~0.8 (where zero indicates no skill and 1 denotes perfect performance) at DE-Hai and DE-Lnf, respectively (Fig. S2). WAI_{anom} is the most important explanatory factor at both sites, followed by SW_IN_{anom} at DE-Hai and the phenological stage (given by SW_IN_POT) at DE-Lnf (Fig. S3). The 'randomForest' package in R 4.0.3 was used, and the number of trees, the number of variables randomly sampled as candidates at each split, and the node size of RF were set to 400, 5, and 5, respectively. Tuning those hyperparameters did not significantly change our results.

Based on these relationships and the meteorological anomalies in legacy years, we used the trained RF model to predict the potential GPP_{anom} in the absence of legacy effects and calculated the model's residuals (GPP_{anom} residuals, i.e. observed minus predicted values), which should reflect legacies from the past drought: negative residuals corresponded to more negative or less positive GPP_{anom} than would be expected given the meteorological conditions in that year, indicating negative legacies of drought, while positive residuals corresponded to less negative or more positive GPP_{anom} , indicating beneficial legacies of drought. In order to reduce the noise at the daily scale, daily results were aggregated to the weekly scale.

To account for model uncertainties and evaluate the significance of legacy effects, we used a leave-one-out approach to quantify model uncertainties. In the training phase, one of the non-legacy years was excluded from the training dataset and the trained RF model was then used to predict the GPP_{anom} in that year. This was done for all non-legacy years, and the GPP_{anom} residuals in non-legacy years for each leave-one-out iteration were then considered as model uncertainties. In order to reduce the noise at the daily scale, all the daily results were aggregated to the weekly scale.

In order to infer possible legacy effects due to plant hydraulic damage, the same method was used to quantify legacy effects on transpiration (Tr) estimated by TEA (Transpiration estimation algorithm) approach (Nelson et al., 2018). The TEA approach first isolates the periods when evapotranspiration is most likely dominated by transpiration. Then, a quantile random forest model (Breiman, 2001; Meinshausen and Ridgeway 2006) is trained during the separated periods and transpiration can be estimated at every time step. More detail can be found in Nelson et al., 2018. ~~Not using~~ We did not use evapotranspiration (ET) ~~is~~ because given a certain amount of energy even though Tr decreases due to plant hydraulic damage but it could be compensated by increased soil evaporation, and the amount of ET might remain ~~be~~ still unchanged.

3.5 Quantification of legacy effects on tree growth

To detect legacy effects on tree growth, we used a multivariate-linear regression instead of RF to develop the relationship between tree growth (detrended ~~radial increment~~~~tree-ring-width~~, ~~RI-TRW~~) due to the fewer data points available. We used the following explanatory variables: detrended ~~growing-season~~~~annual~~ mean WAI, detrended ~~growing-season~~~~annual~~ mean VPD, detrended ~~growing-season~~~~annual~~ mean SW_IN, and detrended ~~growing-season~~~~annual~~ mean TA for each species. We detrended the time series of all variables by removing any significant long-term linear trend detected using the Mann-Kendall test (Kendall, 1948). Annual net primary productivity of fruits (fruits-NPP) particularly was added as an additional predictor to only the model for beech since the high fluctuation of annual fruit NPP could be caused by the periodically high fruit production (masting) of beech. We considered fruits-NPP as a predictor to account for the trade-off between tree growth and reproduction in mast years, which could also cause the change in tree growth in addition to legacy effects from previous droughts (Hacket-Pain et al., 2015).

The strategy to quantify legacy effects and model uncertainties was the same as in the case of GPP. We trained the model in non-legacy years except for each one of them iteratively and predicted potential ~~RI-TRW~~ in legacy years and the year additionally excluded. The residuals between observed and potential ~~RI-TRW~~ in non-legacy years and legacy years were then considered as model uncertainties and legacy effects, respectively.

3.6 Separation of legacy effects on GPP due to structural and physiological effects

Drought legacy effects on GPP might result from changes in canopy structure (structural effects) and photosynthesis capacity (physiological effects) (Kannenberget al., 2019). Combining GPP and satellite-based EVI allows separating these structural and physiological effects. To do this separation, we used two model settings: 1) RF, which was the original setting described in section 3.4, included both structural and physiological effects; 2) RF_{EVI}, which added EVI anomalies as an additional predictor to the original model, only included physiological effects because ~~taking~~-structural effects were already included in reflected by the predictor EVI anomalies ~~into account~~ and GPP_{anom} residuals from this model were expected to be caused by physiological effects. Therefore, physiological legacy effects on GPP were quantified as GPP_{anom} residuals from RF_{EVI} while structural legacies were quantified as the difference between GPP_{anom} residuals from RF and RF_{EVI} (i.e. RF-RF_{EVI}). The same method was used to separate structural and physiological effects of legacy effects on Tr.

3.7 Quantifying concurrent and lagged reduction in GPP from drought

Additionally, we compared the estimated legacy effects on GPP to the concurrent drought-induced GPP anomalies. To compute the concurrent reduction in GPP, we summed up all GPP anomalies over each identified drought period. Here, drought periods were defined as the periods where WAI_{anom} was lower than -1 of standard deviation (WAI_{SD}). WAI_{SD} was calculated for each day of year by using a centered 7-day moving window instead of a single value over the whole time series because WAI_{SD} showed a seasonality. This definition only relied on the water availability without considering biospheric responses because

WAI directly indicated the water supply for vegetation while GPP could include other factors in addition to drought in short periods. We quantified the lagged reduction in GPP at the annual scale as the difference between GPP_{anom} residuals in legacy years and the median of the model uncertainties. To compare the reduction in GPP across sites, both concurrent and lagged values were normalized relative to averaged total GPP over the growing season.

4. Results

4.1 GPP time series in drought and legacy years

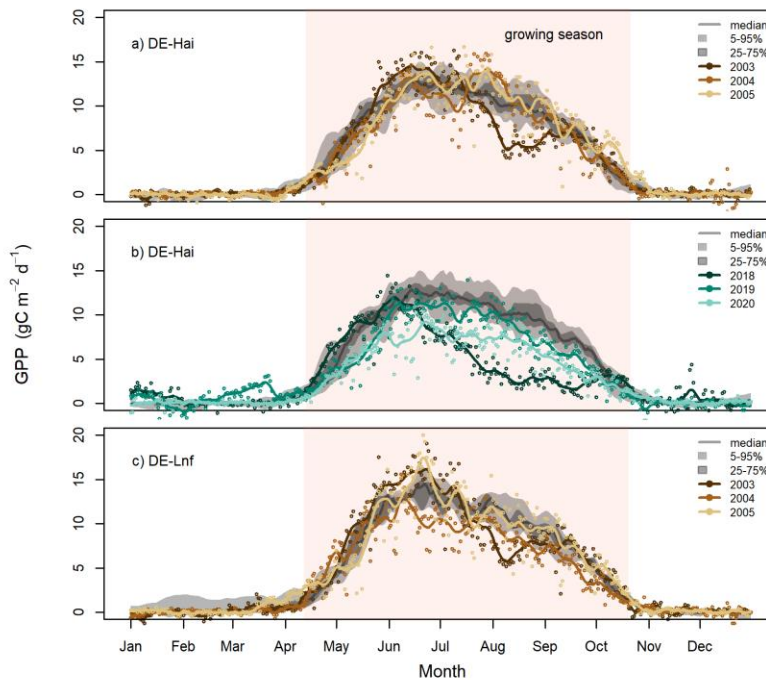
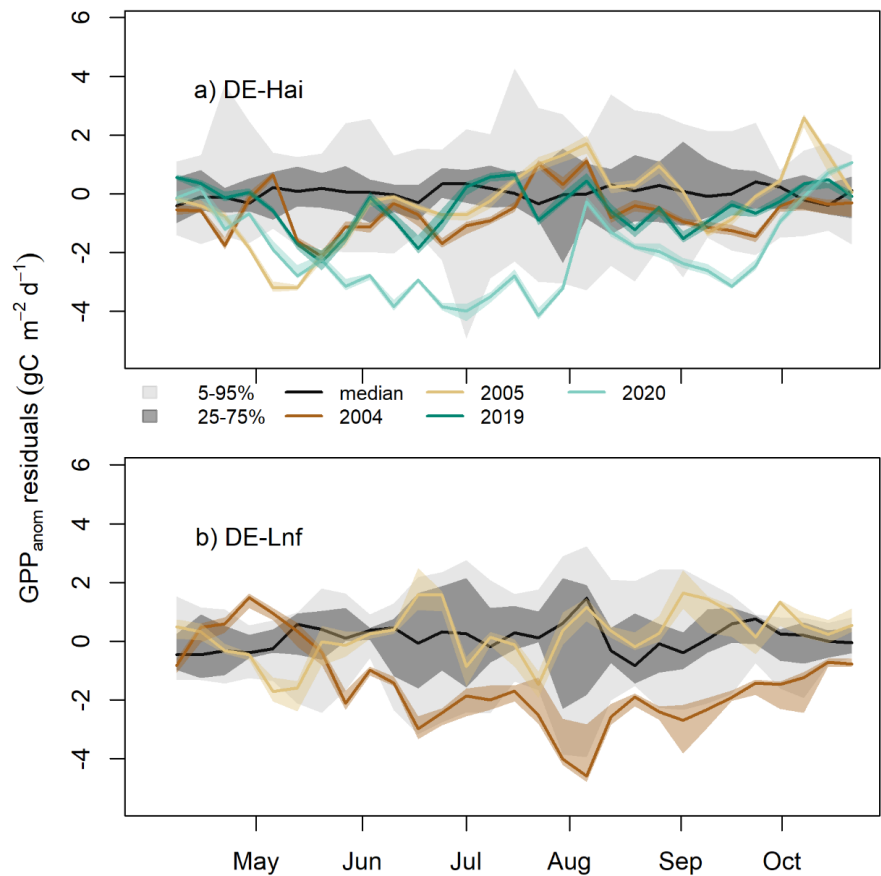


Figure 2. Daily GPP in the selected drought and legacy years at a), b) DE-Hai (showing the 2003 and 2018 droughts, respectively) and c) DE-Lnf (showing the 2003 drought). Daily GPP in the selected drought and legacy years at a) DE-Hai 2003, b) DE-Hai 2018 and c) DE-Lnf 2003 showing the droughts and following legacy years, respectively. Colored points and lines showed original and smoothed (7-days average) GPP, respectively, in drought and legacy years. The grey lines and shaded areas showed the median, 25th-75th

257 (dark grey), and 5th-95th (light grey) percentiles of GPP, respectively, over non-drought and non-legacy years. The shaded coral areas indicate
258 the average growing seasons of DE-Hai and DE-Lnf.

259 In Fig. 2, we show the measured absolute GPP time series in the selected drought (2003 and 2018) and legacy years (2004,
260 2005, 2019, and 2020) together with the long-term median, 25th-75th, and 5th-95th percentiles GPP at DE-Hai and DE-Lnf. In
261 the drought year 2003, GPP was significantly lower than the baseline, defined as the 25th percentile GPP, during July-
262 September at DE-Hai and July-August at DE-Lnf, respectively. In the post-drought years 2004 and 2005, there was no
263 systematic decrease in GPP at DE-Hai, while GPP at DE-Lnf was slightly lower than the baseline during June-August of 2004.
264 During the 2018 drought, GPP significantly differed from the baseline during June-September at DE-Hai. After the 2018
265 drought, we could not find any systematic decrease in GPP in 2019, while GPP was consistently lower than the baseline from
266 mid-May to September of 2020 at DE-Hai.

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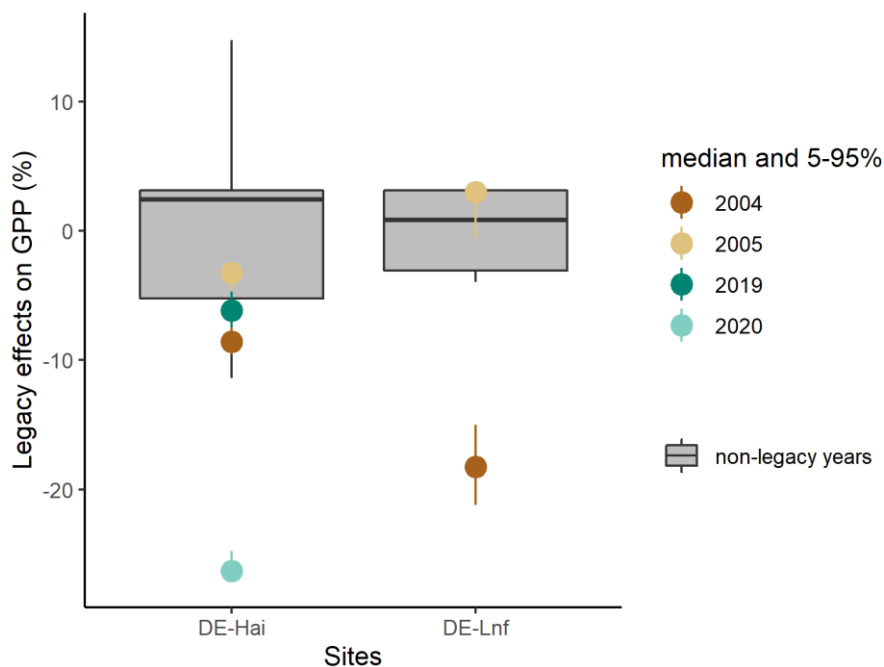


269 **Figure 3. Residuals of GPP anomalies at the seasonal scale in legacy years at a) DE-Hai and b) DE-Lnf.** Residuals of GPP anomalies
270 were characterized by observed minus predicted GPP anomalies (GPP_{anom} residuals). The color lines and bands show the median and 5th-
271 95th percentile GPP_{anom} residuals of ensemble model runs (see Section 3.4), respectively. Negative residuals corresponded to more negative
272 or less positive GPP_{anom} than would be expected given the climate in that year, indicating negative legacies of drought, while positive
273 residuals corresponded to less negative or more positive GPP_{anom}, indicating beneficial legacies of drought. The model uncertainties (dark
274 and light grey shaded area, respectively) are characterized by the 25th-75th and 5th-95th quantile ranges of GPP_{anom} residuals in non-legacy
275 years. The black line represents the median of GPP_{anom} residuals in non-legacy years. The ticks denote the start of each month.
276

At the seasonal scale, residuals of GPP anomalies (GPP_{anom} residuals) showed significant departures from model uncertainties at both sites (Fig. 3). After the 2003 drought at DE-Hai, we found negative residuals below the 25th percentile of model residuals in non-legacy years (model uncertainties) during the early and late growing season of 2004 (April-July, September) and May-June of 2005, and below the 5th percentile for short periods, in April and May of 2004 and May of 2005. After June 2005, residuals were mostly within 5-95% of the model residuals. After the 2018 drought at DE-Hai, we found negative residuals (below 25th percentile of model residuals) during May, June, August, and September of 2019. In 2020, residuals showed a persistent decrease from May to July, and generally stayed well below the 5th and 25th percentile of model residuals from mid-May until July and September, respectively.

After the 2003 drought at DE-Lnf, we found persistent negative residuals were below the 25th percentile of model residuals over almost the complete growing season (from May to October) in 2004 and below the 5th percentile of model residuals for periods in June-September. In 2005, residuals remained mostly within 25th-75th percentiles of model residuals.

4.3 Drought legacy effects on GPP: annual patterns

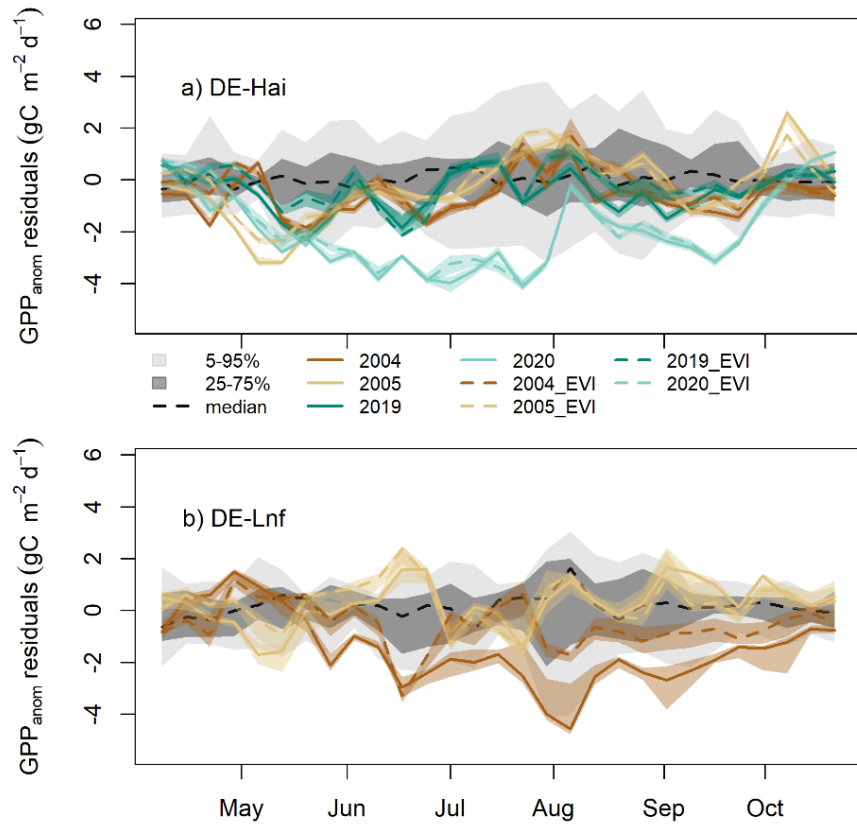


291 **Figure 4. Integrated residuals of GPP anomalies at the annual scale in legacy years at DE-Hai and DE-Lnf.** The color points and line
292 ranges show the median and 5-95% percentile integrated GPP_{anom} residuals of ensemble model runs (see Section 3.4), respectively. The
293 model uncertainties (the boxplot) are characterized as the 25th-75th quantile range of integrated GPP_{anom} residuals in non-legacy years.

294 There were systematic departures of integrated residuals of GPP anomalies in legacy years from model uncertainties at the
295 annual scale (Fig. 4) although the seasonal patterns varied (Fig. 3). After the 2003 drought at DE-Hai, integrated residuals in
296 2004 were significantly below the 25th percentile of model residuals, while integrated residuals were within the 25th-75th
297 percentiles of model residuals in 2005. After the 2018 drought, integrated residuals in 2019 were near the 25th percentiles of
298 model residuals, while in 2020 integrated residuals were far below the 25th percentile of model residuals.

299 At DE-Lnf, after the 2003 drought, integrated residuals in 2004 were below the 25th percentile of residuals in non-legacy
300 years, while integrated residuals almost remained within 25th-75th percentiles of model residuals in 2005.

301 **4.4 Drought legacy effects on GPP due to structural and physiological effects**

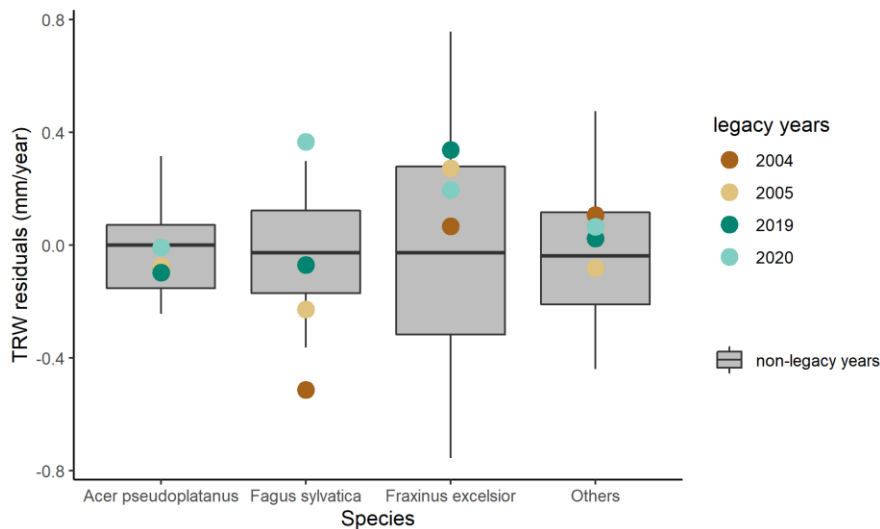


302
303 **Figure 5. Residuals of GPP anomalies from RF and RF_{EVI} (see Section 3.6) in legacy years at a) DE-Hai and b) DE-Lnf.** Residuals of
304 GPP anomalies are characterized by observed minus predicted GPP anomalies (GPP_{anom} residuals). The color lines and bands show the
305 median and 5th-95th percentile GPP_{anom} residuals of ensemble model runs (see Section 3.4), respectively. The solid and dashed lines show
306 the residuals based on RF and RF_{EVI}, respectively. The model uncertainties from RF_{EVI} (dark and light grey shaded area, respectively) are
307 characterized by the 25th-75th and 5th-95th quantile ranges of GPP_{anom} residuals in non-legacy years. The black dashed line was the median
308 of GPP_{anom} residuals from RF_{EVI} in non-legacy years. The ticks denoted the start of each month. [Figure S4 shows the results for April-June](#)
309 [and August-October at DE-Hai in more detail.](#)

310 At the seasonal scale, residuals of GPP anomalies from RF_{EVI} (Res_{EVI}) showed significant departures from GPP_{anom} residuals
311 from RF (Res) over some periods at both sites (Fig. 5). At DE-Hai, we found Res_{EVI} was above Res in the early growing season

312 (April-May) of 2004, 2005, 2019, and 2020, and also in the late growing season of 2004 (August-October) and 2019 (August-
 313 September). After the 2003 drought, we found negative Res_{EVI} below the 25th percentile of model residuals from RF_{EVI} in
 314 non-legacy years (model uncertainties) during the early and late growing season of 2004 (May-July, September) and May of
 315 2005, and below the 5th percentile for short periods, in May of 2005. After the 2018 drought, we found negative Res_{EVI} (below
 316 25th percentile of model residuals) during June of 2019. In 2020, Res_{EVI} showed a persistent decrease from May to July, and
 317 generally stayed well below the 5th and 25th percentile of model residuals from mid-May until July and September, respectively.
 318 At DE-Lnf, Res_{EVI} was below Res from April to mid-May and significantly above Res almost over the growing season of 2004
 319 (from mid-May to September). We found negative Res_{EVI} below the 25th percentile of model residuals from RF_{EVI} in non-
 320 legacy years (model uncertainties) during June, August, and September of 2004, and below the 5th percentile for short periods,
 321 in June and September of 2004.
 322

323 4.5 Drought legacy effects on radial incrementtree-ring-width



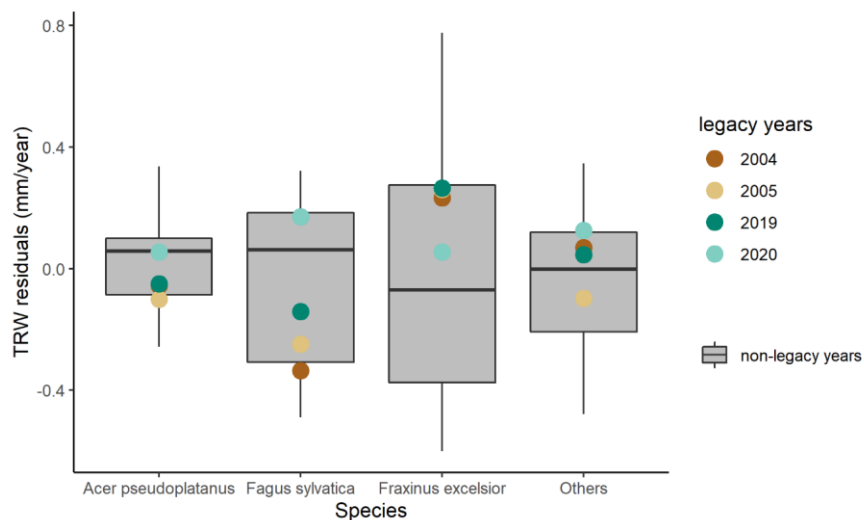
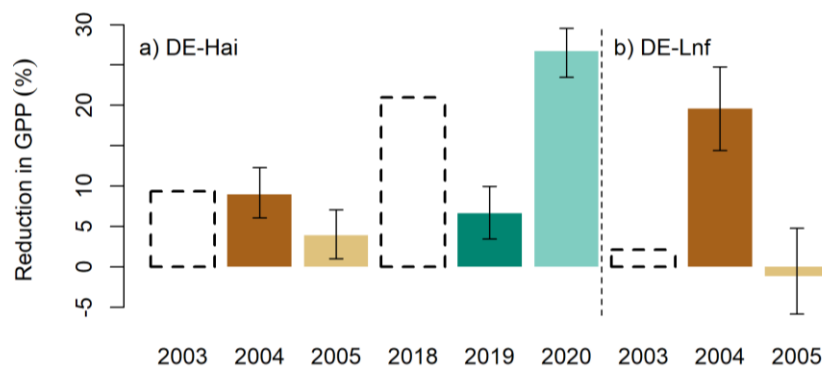


Figure 6. Residuals of R_{ITRW} in legacy years at DE-Hai across species. Residuals of R_{ITRW} are characterized as observed minus predicted R_{ITRW} anomalies (R_{ITRW} residuals). The model uncertainties (the grey area) are characterized as the 25th-75th quantile range of R_{ITRW} residuals in non-legacy years.

To complement the analysis of the legacy effects on GPP at the seasonal and annual scales, we also evaluated legacy effects on tree growth at the annual scale. In the post-drought years 2004 and 2005, R_{ITRW} of *Fagus sylvatica* was below the 25th percentile of model residuals in the post-drought year 2004 and returned to the 25th-75th percentiles of model residuals in 2005. For species of *Acer pseudoplatanus*, *Fraxinus excelsior*, and others, residuals of R_{ITRW} were almost within 25th-75th percentiles of model residuals in 2004 and 2005. After the 2018 drought, R_{ITRW} of *Fagus sylvatica* was within model uncertainties in 2019 while higher than 75th percentile of model residuals in 2020. The residuals of TRW of *Acer pseudoplatanus*, *Fraxinus excelsior*, and others all species for 2019 and 2020 were almost within or close to 25th-75th percentiles of model residuals.

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338 **4.6 Concurrent and lagged reduction in GPP**



339 **Figure 7. Concurrent (dashed black bars) and lagged (colored bars) reduction in GPP from the 2003 and 2018 droughts at a) DE-**
340 **Hai and b) DE-Lnf.** Concurrent impacts in GPP were quantified as the sum of GPP anomalies over drought periods in drought years relative
341 to averaged total GPP over the growing season (see Method). Lagged impacts in GPP are characterized as the difference between GPP_{anom}
342 residuals in legacy years and median of the model uncertainties relative to averaged total GPP over the growing season. Colored bars and
343 error bars show the median and 5-95%, respectively, of lagged reduction in GPP from ensemble model runs.

345 Finally, we compared the concurrent impacts on GPP with the lagged impacts due to drought. We found that, at DE-Hai, the
346 concurrent reduction in GPP was 9.4% relative to averaged total GPP over the growing season (hereinafter) in 2003, while
347 6.1-12.3% indirectly reduced in 2004. And in 2018 concurrent reduction in GPP was 21.0%, while 3.5%-10.0% and 23.5-
348 29.6% indirectly reduced in 2019 and 2020, respectively. At DE-Lnf, the concurrent reduction in GPP was negligible in 2003
349 (2.2%), while we estimated 14.4-24.8% GPP reduction in 2004, which was higher than the corresponding values at DE-Hai in
350 the same year.

352 **5. Discussion**

353 **5.1 A novel methodology to detect drought legacy effects on GPP**

354 There is limited research on discovering legacy effects of drought on the ecosystem carbon cycle using eddy-covariance
355 observations (Kannenberg et al., 2019). Here, we propose a residual-based methodology using a random-forest regression
356 model to detect legacy effects on GPP, and found significant legacy effects on GPP using eddy-covariance data at two forests
357 in central Germany [in the similar climate but with different age and species composition](#). There are three advantages to our
358 methodology: 1) capturing the temporal dynamics of legacy effects at the seasonal scales; 2) separating the influence of

359 meteorological conditions during the post-drought period on recovery rates; 3) estimating model uncertainties to avoid
360 misinterpreting small residuals as ‘legacy effects’.

361 First, because we used measurements with a high temporal resolution (daily), legacy effects could be determined across
362 different time scales. Previous studies based on tree-ring or satellite-greenness data have mainly focused on legacy effects at
363 the annual scale (Anderegg et al., 2015; Wu et al., 2018) or monthly scale (Bastos et al., 2021), but the legacies can be more
364 ephemeral, for example, if they ~~are expressed~~appear only in critical periods of the growing season, as we have found here.
365 Such temporally confined effects may not necessarily manifest themselves at the annual scale. For example, after the 2003
366 drought, the annual GPP at DE-Hai in 2005 was close to normal, which was the 25th percentile of model residuals here, but we
367 found short legacies at the seasonal scale (Fig. 3).

368 Second, recovery is usually considered when the target variable (i.e. GPP, tree-ring width...) returns to the baseline, usually
369 based on pre-drought values of the target variable (Bose et al., 2020; González de Andrés et al., 2021; Zhang et al., 2021).
370 However, meteorological conditions during the recovery period will modulate recovery rates, so that recovery can be delayed
371 e.g. if a drought is followed by other unfavourable climatic conditions. Hence, the evaluation of possible legacy effects should
372 be based on the functional relations between the target variable and meteorological conditions. Our model takes this into
373 account by considering that ecosystems recovered when observed GPP reaches the potential GPP given the meteorological
374 conditions, rather than the absolute flux.

375 Finally, our approach allows ~~determining~~estimating the uncertainties in estimated legacy effects. Previous studies (Anderegg
376 et al., 2015; Huang et al., 2018) quantified legacy effects as the residuals between observed and predicted target variables (i.e.
377 tree-ring width, vegetation indices, ...) in legacy years, but were not able to consider uncertainties of their trained models. Yet,
378 it is crucial to understand if the residuals are caused by model uncertainties or can be interpreted as legacy effects. In this
379 study, legacy effects are identified only when the model residuals are outside the range of the model uncertainties, so that we
380 are confident that the legacies reported here are significant and avoid interpreting residuals caused by model error as legacy
381 effects. A limitation of our approach is that we have to assume that there are no legacy effects in the climate system because
382 this would potentially bias the interpretation of the residuals.

383 The methodology we proposed is able to detect the legacy effects of drought on GPP and can be easily applied to other eddy-
384 covariance sites and variables (i.e. evapotranspiration, transpiration, ...), in order to improve our understanding of drought
385 legacy effects on the ecosystem carbon cycle at different time-scales.

387 5.2 Seasonal and annual legacy drought impacts on GPP

388 We found that residuals of GPP anomalies (GPP_{anom} residuals) in legacy years were significantly larger than model
389 uncertainties at both seasonal and annual scales at both sites, which indicated strong legacy effects of drought on GPP at least
390 in the two years following the drought events.

391 We found negative legacies on GPP (reduced uptake) in the early growing season of all legacy years (2004, 2005, 2019, and
 392 2020) at DE-Hai. Reduced and delayed leaf development due to physiological effects of the 2003 and 2018 droughts (e.g.
 393 metabolic damage, non-structural carbohydrates depletion) could result in reduced ecosystem-level photosynthesis
 394 (Migliavacca et al., 2009; Rocha and Goulden, 2010; Kannenberg et al., 2019), and could potentially explain negative legacies
 395 on GPP at the start of the growing season. In line with this hypothesis, we found the enhanced vegetation index (EVI, a proxy
 396 of leaf area index, Fig. S52 and Fig. S36) at the sites showed lower values than other years in the early growing seasons of
 397 2004, 2005, and 2019 and this delayed spring phenology propagated over the year of 2004 and 2019 with a shift of seasonality.
 398 We found consistently lower values of NPP allocated to foliage growth in 2004 than other years (Fig. S74). Furthermore, the
 399 detected negative legacies in the early growing season became smaller when adding EVI anomalies as an additional predictor
 400 in the random forest model (Fig. 5), indicating that the reduced and delayed leaf development partly explained the estimated
 401 legacy effects by the RF model trained with climate predictors only.

402 Another possible mechanism explaining legacy effects could be hydraulic damage induced by drought (Anderegg et al., 2013),
 403 and therefore insufficient ability of water transport limiting sink strength (Körner, 2015) and photosynthetic capacity (Chen et
 404 al., 2010), at least until damage is repaired. If this was the case, transpiration fluxes should be reduced. However, we did not
 405 find similar negative legacy patterns on transpiration in the early growing season (Fig. S58a). Therefore, hydraulic damage
 406 did not seem a likely cause of drought legacies on GPP for these events. Overall, we cannot pinpoint the physiological causes
 407 of the detected legacy effects due to limited availability of measurements. This calls for establishing more plant-physiological
 408 measurements complementing eddy-covariance and R_{TRW} measurements to capture sufficient information about plant water
 409 relations such as sap flow (Poyatos et al., 2021) and tree water deficit (Nehemy et al., 2021) as well as carbon allocation
 410 (Hartmann et al, 2020) to provide a more detailed process understanding of the mechanisms underlying drought legacy effects.

411 Negative legacies on GPP in terms of lagged reduction in GPP in 2004 at DE-Lnf (14.4-24.8%) were stronger than those at
 412 DE-Hai (6.1-12.3%) in the seasonal and annual scales. The persistence of negative legacies throughout the full growing season
 413 in 2004 indicates that the 2003 drought likely caused stronger damage, especially reduced leaf development which was
 414 supported by largely reduced negative legacies of RF_{EVI} with EVI comparing to RF without EVI (Fig. 5), on the ecosystem at
 415 DE-Lnf than that at DE-Hai. From the community-level perspective, the stronger legacy effects found at DE-Lnf compared to
 416 DE-Hai may have been partly related to differences in forest composition between the two sites (Tamrakar et al. 2018, Pardos
 417 et al., 2021). Measurements of GPP at tree species level were not available, therefore we relied on the legacies found for
 418 R_{TRW} (reflecting growth), available for individual trees at DE-Hai. It should be noted, though, that the relationship between
 419 GPP and growth is complex (Fatichi et al., 2014). Negative legacy effects on R_{TRW} of *Fagus sylvatica*, dominating at DE-
 420 Hai, in 2004 ~~and 2005~~, were found, whereas other co-dominating species (*Acer pseudoplatanus* and *Fraxinus excelsior*) did
 421 not show negative legacies. Therefore, the lower resilience of *Fagus sylvatica* compared to other species may have partly
 422 resulted in stronger negative legacies at the pure European beech forest at DE-Lnf than at DE-Hai. In addition, contrasting
 423 legacy effects of these two sites could also be associated with different age classes and the absolute stand age since the effects
 424 of stand age on determining modulating the heat and drought impact on carbon exchange (Arain et al., 2022) and ecosystem-

level photosynthetic capacity (Musavi et al., 2017) have been recognized. However, the evidence of species diversity and age structure effects on legacy effects needs to be further explored using more sites in the future.

Stronger negative legacy effects on GPP in 2020 than those in other legacy years were found at DE-Hai in the seasonal and annual scales. This might be associated with significant tree mortality in the whole forest covering including the main footprint in the period 2018–2020 (about 6% year⁻¹ between 2017 and 2020 compared to less than 1% year⁻¹ between 2005 and 2017) mainly caused by the storm *Friedrike* in January 2018 and the heat and/or drought in summer 2018 and 2019 (unpublished data). RITRW of *Fagus sylvatica* in 2020, on the contrary, showed slightly positive legacy effects in growth, since only living trees were sampled. This might be explained by the favorable weather conditions in winter/spring 2019/2020 associated with high mineralization rates and reduced competition for nutrients, light and water of the surviving trees (Grossiord, 2020). The RITRW data reflected mean growth signals from individual surviving trees, while the GPP data reflected mean carbon assimilation at stand level, including positive, negative or absent legacy effects at individual tree level as well as the reduction of assimilating individuals due to higher tree mortality.

Overall, we found that the lagged impacts of drought on GPP are significant compared with concurrent drought impacts at the two sites studied here. The lagged reduction in GPP resulting from drought is usually not quantified (Ciais et al., 2005; Reichstein et al., 2007), perhaps because separating legacy effects on ecosystem carbon fluxes from observations is challenging (Kannenberget al., 2019) and process-based models have been shown to miss such legacy effects (Bastos et al., 2021). This implies that the impact of droughts on ecosystem carbon cycling in most studies might be underestimated.

5.3 Importance of deep root-zone soil moisture data

Deep root-zone soil moisture has been recognized as an important water source for vegetation, especially during droughts (Míguez-Macho and Fan, 2021; Werner et al., 2021). Although soil moisture measurements across three soil layers are available at both sites, the deepest depth (ca. 30cm) cannot capture the entire soil water reservoir available for European beech which has been observed to have non-negligible amounts of fine roots below 30cm across different sites (Leuschner et al., 2004; Gessler et al., 2021).

We tested an initial model using anomalies of soil moisture at three layers as predictors (RF_{SM}), and found strong positive legacy effects in the late growing season in 2019 at DE-Hai (Fig. S96), which however could not be reproduced by any of the models using soil moisture information from deeper layers (Fig. S69) including the local water balance (WAI, CWD) and the reanalysis data (ERA5). Comparing the predicted time series of GPP_{anom} of the RF_{SM} model with observations, we found the predicted GPP_{anom} became much more negative in the late growing season while observed GPP_{anom} were close to zero (Fig. S107). Therefore, although soil moisture anomalies in the third layer (30cm) were largely negative when the positive residuals appeared (Fig. S118), soil moisture from layers deeper than 30 cm may maintain the water supply for photosynthesis. Also, we found the evapotranspiration from the shallow layers (0–30cm) estimated by soil moisture decrease was less than the observed evapotranspiration during dry-down periods (Fig. S119), which indicated plant water uptake from layers deeper than

30 cm during dry-down periods, in line with our hypothesis. In summary, these positive patterns are likely due to model errors from incomplete information on the soil-moisture profile rather than actual positive legacy effects. These results highlight the importance of soil moisture measurements that capture the entire root zone for more reliable understanding of ecosystem functioning, particularly in the case of drought legacy effects.

6. Conclusions

The frequency, intensity, duration, and spatial extent of droughts are expected to increase in the next decades due to anthropogenically caused global warming in many regions (IPCC, 2022). Drought not only impacts ecosystems concurrently, but also can have legacy effects on ecosystem carbon fluxes. We developed a residual-based approach using a random forest regression model to detect drought legacies on gross primary productivity (GPP) using eddy-covariance data. The methodology proposed here allows quantifying significant drought legacy effects on GPP at the sub-seasonal and annual scales. ~~To the best of our knowledge, this is the first time that drought legacies on ecosystem carbon fluxes in observation are quantified using are detected in eddy-covariance data.~~ The GPP reduction due to drought legacy effects is of comparable magnitude to the concurrent drought effects at the studied sites, which confirms the importance of legacy effects. We found contrasting legacy effects at two neighbouring forests with different species and age structures, yet the importance of these factors could not be evaluated. Future studies across a larger range of sites will be needed to understand whether the crucial role of legacy effects is general and on which mediating factors they depend.

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491

492 **Author contributions**

493 The study was conceived by X. Yu, A. Bastos, R. Orth, M. Reichstein, and M. Bahn. X. Yu implemented the method and
494 performed the data analyses. A. Knohl, A. Klosterhalfen, and F. Koebsch provided the eddy-covariance data. M. Mund
495 provided the data of radial increment tree ring width and net primary productivity of fruits and leaves. J. A. Nelson helped X.
496 Yu to process the transpiration estimation. S. Walther provided and processed the Enhanced Vegetation Index data. B. D.
497 Stocker suggested quantitatively separating structural and physiological effects. M. Migliavacca helped to interpret the results.
498 X. Yu, A. Bastos, R. Orth, M. Reichstein, and M. Bahn prepared the first draft and all authors contributed to discussion of
499 results and the revisions of the manuscript.
500

501 **Competing interests**

502 At least one of the (co-)authors is a member of the editorial board of Biogeosciences. The peer-review process should be
503 guided by an independent editor, and the authors also have no other competing interests to declare.

504 **Code and data availability**

505 Eddy-covariance and enhanced vegetation index data used are freely accessible. Tree ring width and net primary productivity
506 of fruits and leaves data are available on request to Martina Mund. Our code is available on request.

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Supplement

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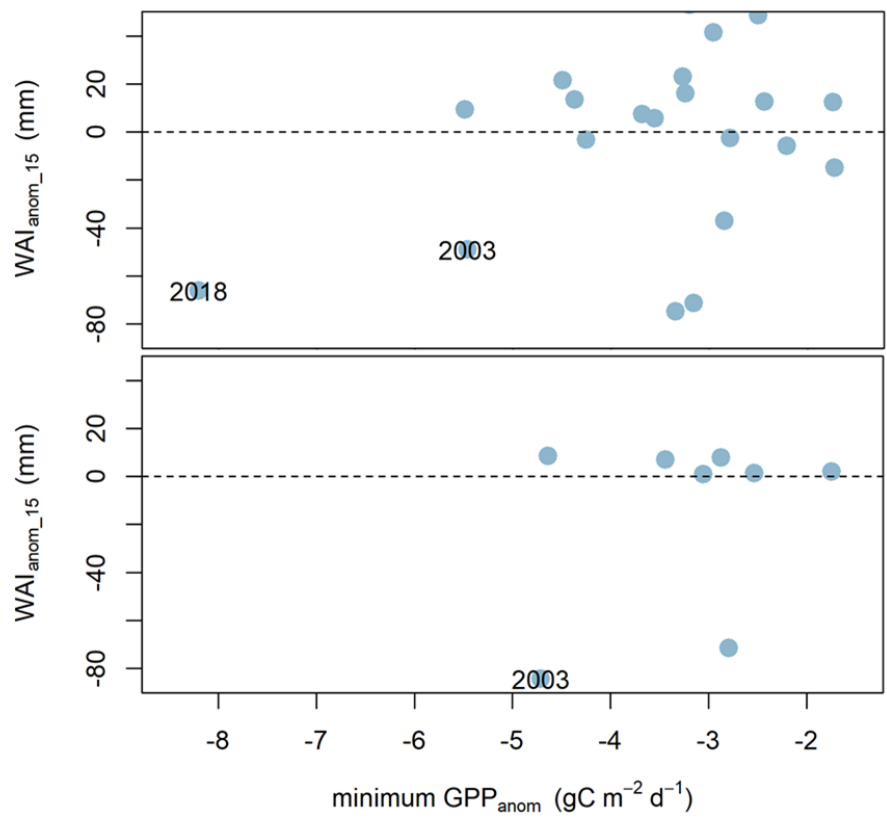
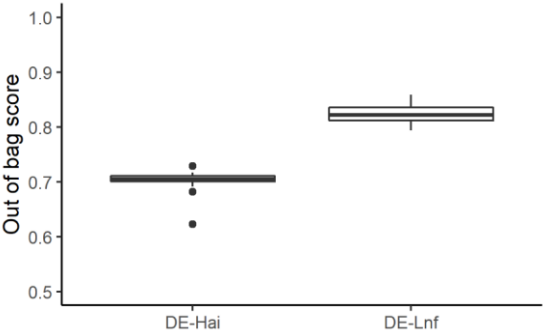


Figure S1. The minimum of GPP anomalies (minimum GPP_{anom}) and WAI anomalies during the day when minimum GPP_{anom} occurs and previous 14 days (mean WAI_{anom_15}) at a) DE-Hai and b) DE-Lnf.



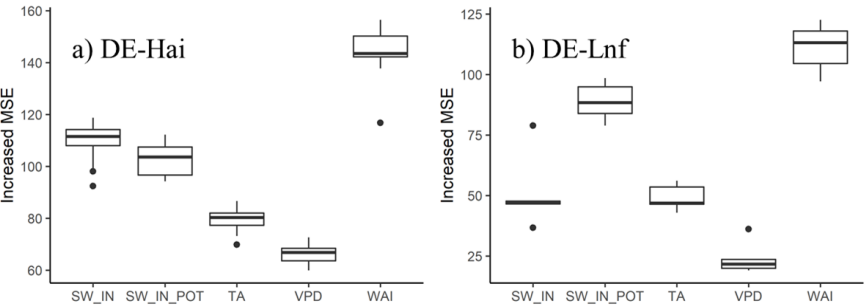
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Figure S2. Out of bag scores of RF models at DE-Hai and DE-Lnf. Since using leave-one-year-out strategy (see Section 3.4), each RF model for a resulting time series has its own OOB score.

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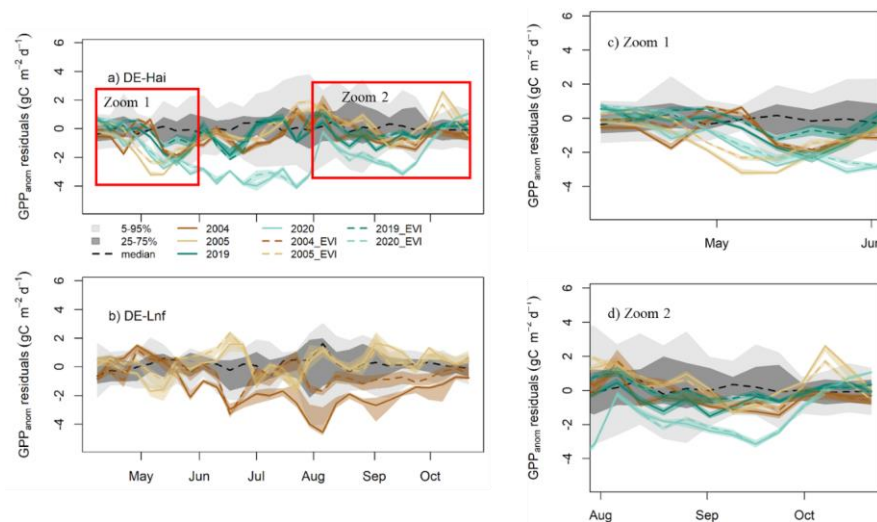


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Figure S3. Variable importance, indicated by increased MSE, of RF models at DE-Hai and DE-Lnf. Since using leave-one-year-out strategy (see Section 3.4), each RF model for a resulting time series has its own variable importance.

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15 **Figure S4. Residuals of GPP anomalies from RF and RF_{EVI} (see Section 3.6) in legacy years at a) DE-Hai and b) DE-Lnf.** Residuals
of GPP anomalies are characterized by observed minus predicted GPP anomalies (GPP_{anom} residuals). The color lines and bands show the
median and 5th-95th percentile GPP_{anom} residuals of ensemble model runs (see Section 3.4), respectively. The solid and dashed lines show
the residuals based on RF and RF_{EVI}, respectively. The model uncertainties from RF_{EVI} (dark and light grey shaded area, respectively) are
characterized by the 25th-75th and 5th-95th quantile ranges of GPP_{anom} residuals in non-legacy years. The black dashed line was the median
20 of GPP_{anom} residuals from RF_{EVI} in non-legacy years. The ticks denoted the start of each month. Panel c and d show in more detail results
in April-June and August-October at DE-Hai, respectively.

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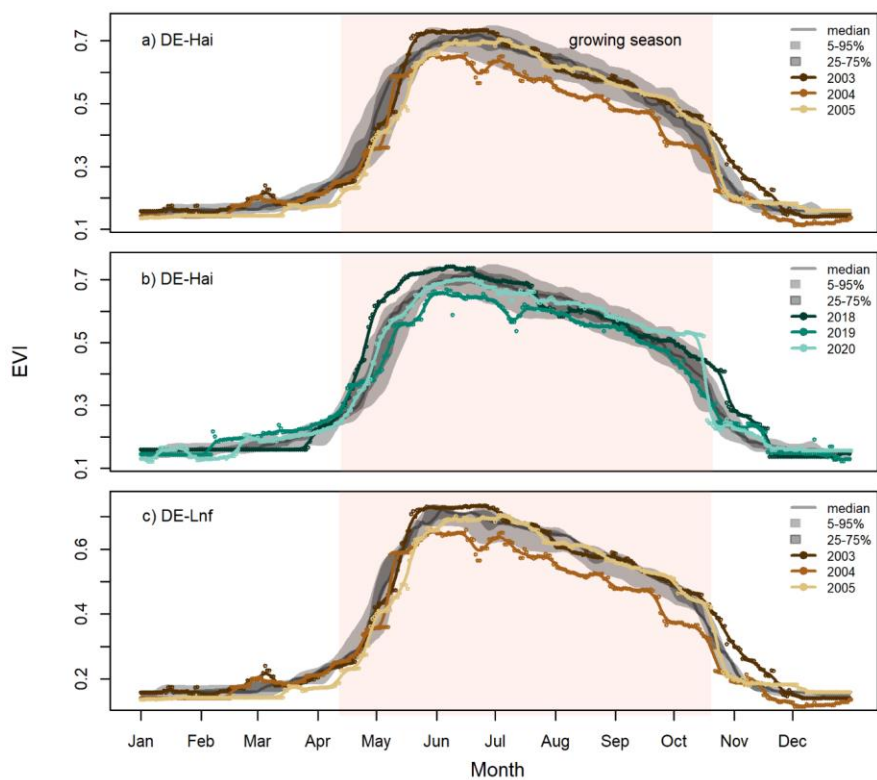


Figure S52. Daily-enhanced vegetation index (EVI) in the selected drought and legacy years at a) DE-Hai (showing the 2003 and 2018 droughts, respectively) and b) DE-Hai (showing the 2003 drought) Daily EVI in the selected drought and legacy years at a) DE-Hai 2003, b) DE-Hai 2018 and c) DE-Lnf 2003 showing the droughts and following legacy years, respectively. Colored points and lines showed original and smoothed (7-days average) EVI, respectively, in drought and legacy years. The grey lines and shaded areas showed the median, 25th-75th (dark grey), and 5th-95th (light grey) percentiles of EVI, respectively, over non-drought and non-legacy years. The shaded coral areas indicated the average growing seasons of DE-Hai and DE-Lnf.

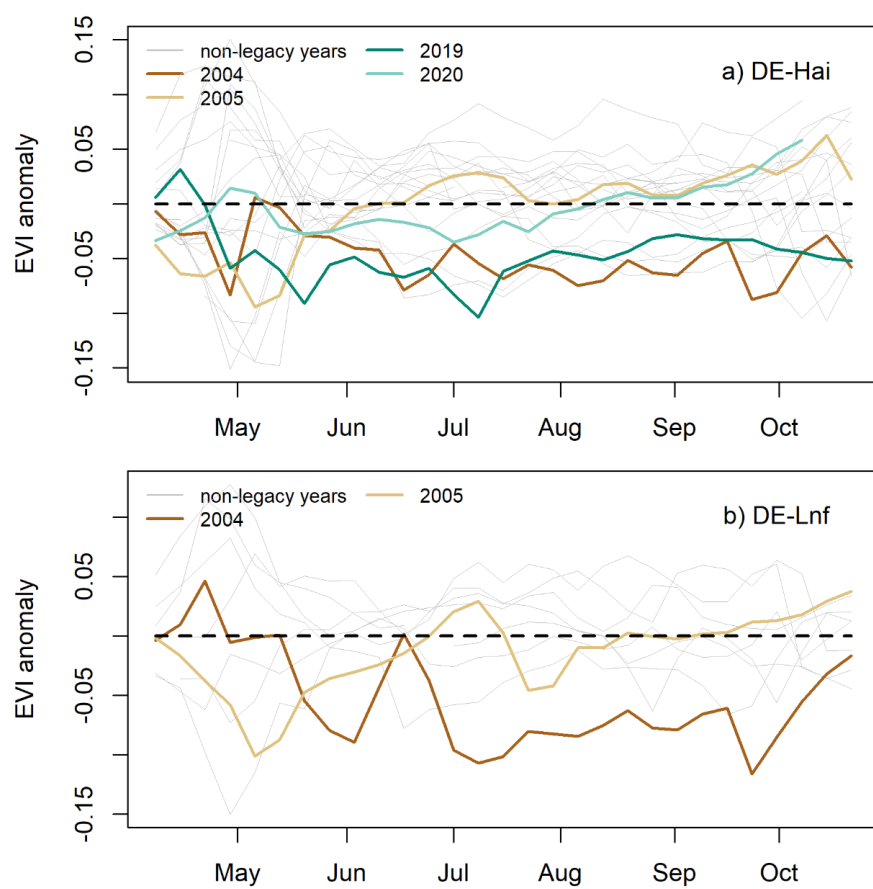


Figure S63. Enhanced vegetation index (EVI) time series at a) DE-Hai and b) DE-Lnf. Colored lines were EVI anomalies in legacy years (2004, 2005, 2019, and 2020), while grey lines were EVI anomalies in non-legacy years (normal and drought years).

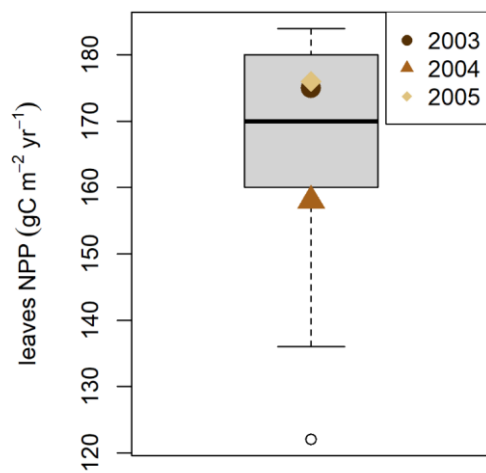


Figure S74. NPP of leaves in the footprint of eddy-covariance tower at DE-Hai. Colored points were leaves NPP in the drought year (2003) and legacy years (2004 and 2005). The boxplot showed NPP of leaves in other years.

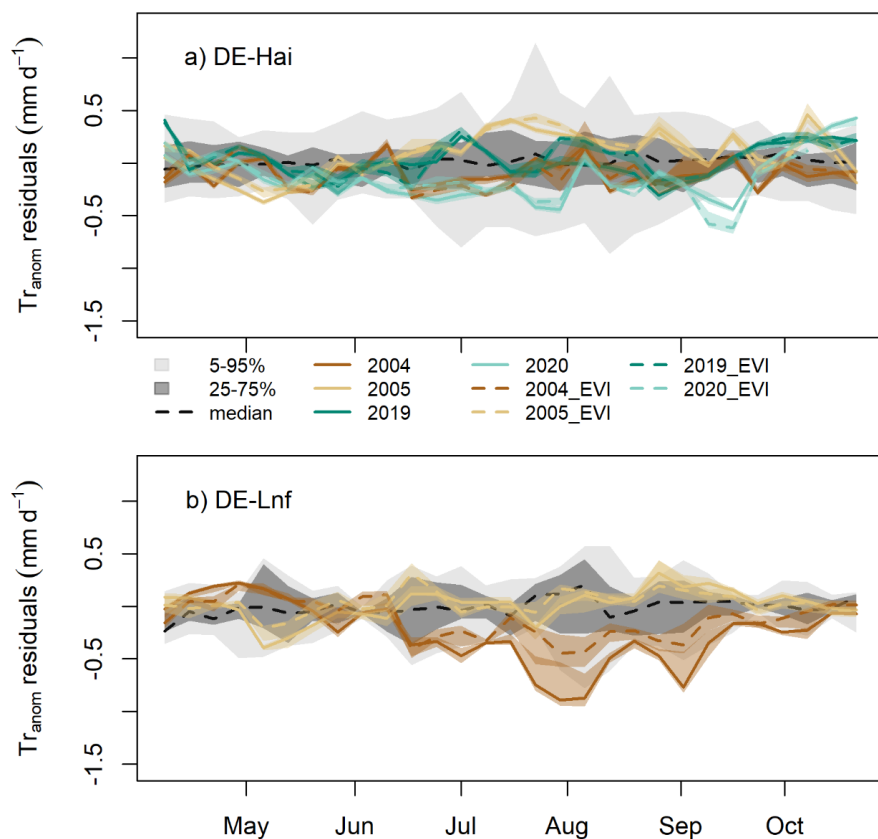


Figure S85. Residuals of transpiration (Tr) anomalies from RF and RF_{EVI} (see Section 3.6) in legacy years at a) DE-Hai and b) DE-Lnf. Residuals of GPP anomalies were characterized by observed minus predicted GPP anomalies (GPP_{anom} residuals). The color lines and bands showed the median and 5th-95th percentile GPP_{anom} residuals of ensemble model runs (see Section 3.4), respectively. The solid and dashed lines showed the residuals based on RF and RF_{EVI}, respectively. The model uncertainties from RF_{EVI} (dark and light grey shaded area, respectively) were characterized by the 25th-75th and 5th-95th quantile ranges of Tr_{anom} residuals in non-legacy years. The black dashed line was the median of Tr_{anom} residuals from RF_{EVI} in non-legacy years. The ticks denoted the start of each month.

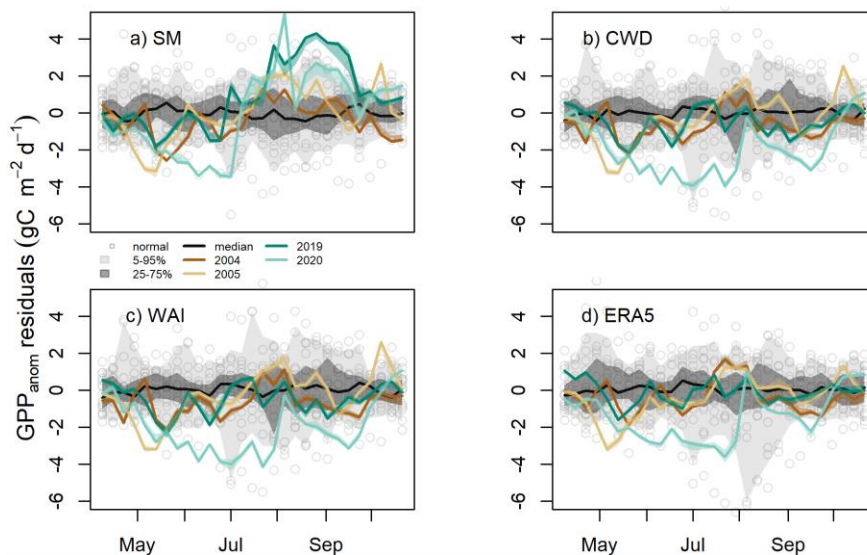
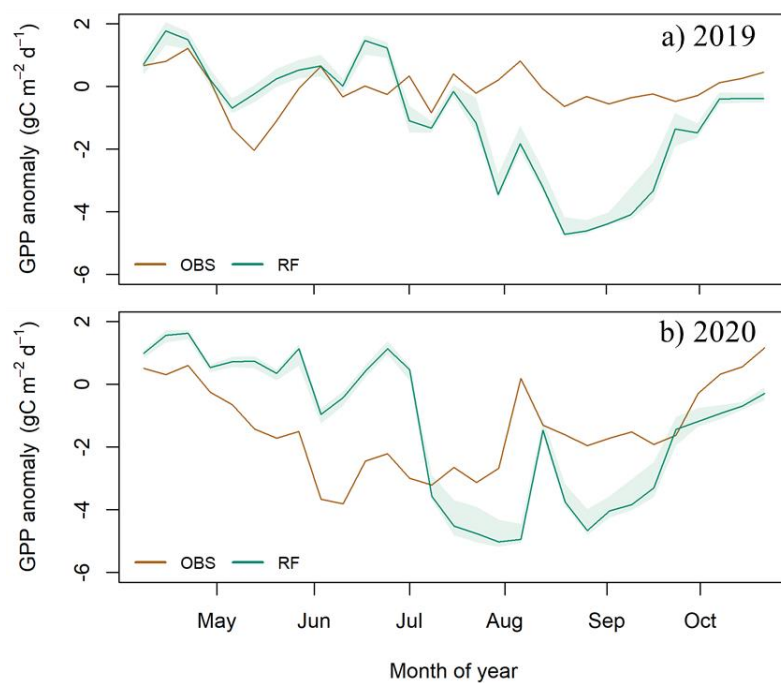
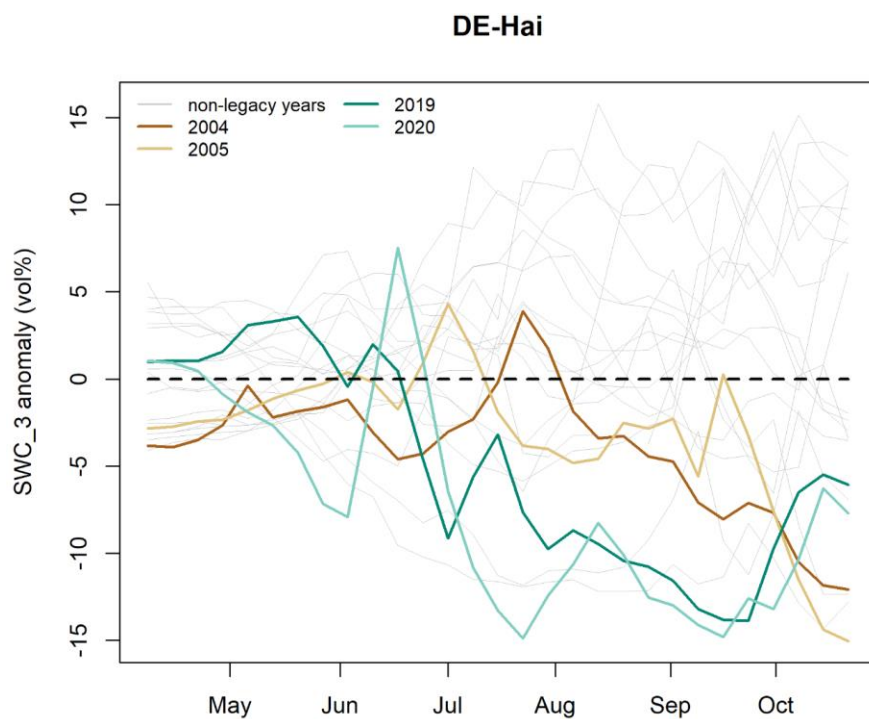


Figure S96. Residuals of GPP anomalies at seasonal scale in legacy years at DE-Hai from a) the model using observed soil moisture (SM), b) the model using cumulative water deficit (CWD), c) the model using estimated water availability index from a bucket model (WAI), and d) the model using soil moisture from ERA5 (ERA5). Legacy effects on GPP was characterized by observed minus predicted GPP anomalies (GPP_{anom} residuals). The model uncertainty (dark and light grey area, respectively) was characterized by the 25%-75% and 5%-95% quantile ranges of GPP_{anom} residuals in non-legacy years. The black line was the median of GPP_{anom} residuals in non-legacy years. CWD was estimated from cumulative differences between observed precipitation and evapotranspiration over dry periods at daily scale.



60 **Figure S107.** Observed (OBS) and predicted (RF) GPP anomalies in a) 2019 and b) 2020 at DE-Hai. The green area was 5-95% of predicted GPP anomalies from all loops (see Method).



65 **Figure S118.** Soil water content at the third layer (30cm) anomalies (SWC_3 anomaly) at DE-Hai. Colored lines were SWC_3 anomalies in legacy years (2004, 2005, 2019, and 2020), while grey lines were SWC_3 anomalies in non-legacy years (normal and drought years).

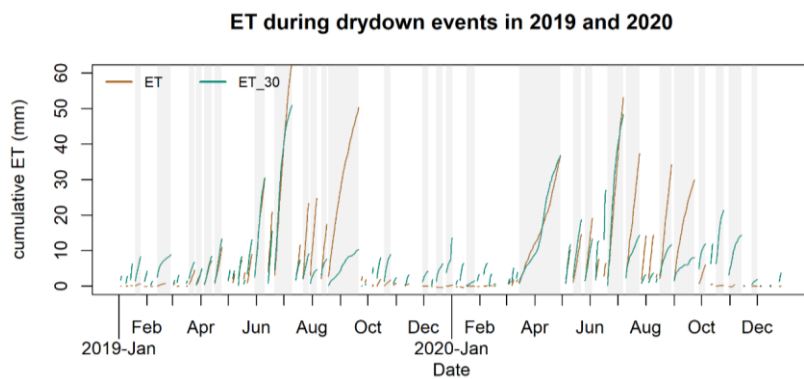


Figure S129. Cumulative evapotranspiration at 0~30cm (ET₃₀) and at the whole soil (ET) during dry-down periods (grey areas) in 2019 and 2020 at DE-Hai. Dry-down periods were identified as the periods when soil moisture at 0~30cm is continuously decreasing. ET₃₀ was estimated by summed soil moisture decreases at 0~30cm during dry-down periods. ET was the summed observation from eddy-covariance measurements during dry-down periods.