



Vegetation modulates the impact of climate extremes on gross primary production

Milan Flach^{1,2}, Alexander Brenning², Fabian Gans¹, Markus Reichstein^{1,3}, Sebastian Sippel^{4,5}, and Miguel D. Mahecha^{1,3,6}

¹Max Planck Institute for Biogeochemistry, Department Biogeochemical Integration, P. O. Box 10 01 64, D-07701 Jena, Germany

²Friedrich Schiller University Jena, Department of Geography, Jena, Germany

³German Centre for Integrative Biodiversity Research (iDiv), Leipzig, Germany

⁴Norwegian Institute of Bioeconomy Research, Ås, Norway

⁵ETH Zürich, Institute for Atmospheric and Climate Science, Switzerland

⁶University of Leipzig, Remote Sensing Center for Earth System Research, Germany

Correspondence: Milan Flach (milan.flach@bgc-jena.mpg.de)

Abstract. Drought and heat events affect the uptake and sequestration of carbon in terrestrial ecosystems. Factors such as the duration, timing and intensity of extreme events influence the magnitude of impacts on ecosystem processes such as gross primary production (GPP), i.e. the ecosystem uptake of CO₂. Preceding soil moisture depletion may exacerbate these impacts. However, some vegetation types may be more resilient to climate extremes than others. This effect is insufficiently understood at the global scale and is the focus of this study. Using a global upscaled product of GPP that scales up in-situ land CO₂ flux observations with global satellite remote sensing, we study the impact of climate extremes at the global scale. We find that GPP in grasslands and agricultural areas is generally reduced during heat and drought events. However, we also find that forests, if considered globally, appear not in general to be particularly sensitive to droughts and heat events that occurred during the analyzed period or even show increased GPP values during these events. On the one hand, this is in many cases plausible, e.g. when no negative preconditioning has occurred. On the other hand, however, this may also reflect a lack of sensitivity in current remote sensing derived GPP products to the effects of droughts and heatwaves. The overall picture calls for a differentiated consideration of different land cover types in the assessments of risks of climate extremes for ecosystem functioning.

1 Introduction

We expect that climate change leads to increases in frequencies, durations, intensities, and spatial extents of droughts and heatwaves in the next decades (Meehl et al., 2000; Olesen and Bindi, 2002; Seneviratne et al., 2012; Coumou and Robinson, 2013; Cook et al., 2015; Zscheischler and Seneviratne, 2017). Ecosystems will respond to the events ahead in multiple ways. In particular the processes controlling the terrestrial carbon balance, i.e. photosynthesis and respiratory processes as well as fires and e.g. pest-induced mortality are expected to be affected (Peuelas et al., 2004; Ciais et al., 2005; Vetter et al., 2008; Reichstein et al., 2013; Bastos et al., 2014; Yoshida et al., 2015; Wolf et al., 2016; Brando et al., 2019) (for a recent review see Sippel et al. (2018)). Given that these responses represent feedbacks to the coupled climate–ecosystem dynamics, it is important to



understand which factors generally influence the magnitudes of such impacts at the global scale (Frank et al., 2015). Previous studies have shown that event duration can be as important as intensity in controlling the reduction of gross primary production (GPP), which represents the total ecosystem carbon uptake (Granier et al., 2008; von Buttlar et al., 2018; Orth and Destouni, 2018). In particular, compound extreme events, e.g., the combination of drought and heat stress can increase the impact on
25 GPP as compared to singular stressors (Ciais et al., 2005; AghaKouchak et al., 2014; Zscheischler et al., 2018; von Buttlar et al., 2018). Several case studies point to the crucial role of timing in influencing the magnitude of impacts on ecosystem functioning. Warm and early springs may partly compensate for severe carbon impacts of summer droughts (Wolf et al., 2016). In contrast, soil moisture depletion in spring can even enhance carbon losses during summer (Buermann et al., 2013; Sippel et al., 2017a; Buermann et al., 2018).

30 Probably the least understood aspect is the question how strongly land cover types modulate drought and heat impacts on the fundamental processes controlling ecosystems carbon dynamics, such as gross primary production, ecosystem respiration, and net ecosystem exchange. Evidence from eddy covariance stations (von Buttlar et al., 2018) and case studies using spatiotemporal remote sensing derived data (Wolf et al., 2016; Flach et al., 2018) suggest that certain ecosystems are less vulnerable to heat and drought events than others. However, the question to what degree land cover types shape the impacts of droughts and
35 heatwaves globally remains unclear. Here we aim to specifically investigate the importance of land cover type in controlling the impacts of climate extremes relative to other factors.

When discussing impacts of climate extremes, the crucial question is their definition. If values over some global thresholds are used to detect extremes e.g. in some meteorological variable and investigate anomalies in ecological processes, one might find very different impact patterns as compared to events that are extreme relative to their expected value. Another approach
40 is to consider the joint probability of multiple variables contributing to an event. Here we rely on a multivariate extreme event detection algorithm that can detect extremes in multi-dimensional data sources (Flach et al., 2017, 2018) and restrict our analysis to those events that can be also considered a relative drought and heat event. We estimate anomalies regionally i.e. defining extreme events relative to the typical conditions of the regional growing season. We apply this method jointly to air temperature, surface moisture, and incoming shortwave radiation as fundamental variables to detect relative extreme events.
45 Each event describes a spatiotemporal context that can be described by its spatial extent and duration (Zscheischler et al., 2013; Mahecha et al., 2017). The impacts are then assessed in these areas as anomalies in gross primary production (GPP). Our study addresses the impacts in the time range between 2003 and 2018 globally in different land cover classes and builds on nonlinear predictive models to understand the importance of the driving factors (for details see Methods, Section 2).

2 Methods

50 For detecting hydrometeorological extreme events across ecosystems we need (i) a set of variables describing hydrometeorological extreme events and their impacts on productivity (Section 2.1), (ii) a detection algorithm (Section 2.2), and (iii) an approach to evaluate the hydrometeorological extremes with regard to responses in different ecosystems (Section 2.3).



2.1 Data

To detect hydrometeorological extreme events we use 2-m air temperature, incoming shortwave radiation (both from ERA5, original resolution 0.25° , Copernicus Climate Change Service (C3S) (2017)), and surface moisture (v3.2b, original resolution 0.25° from the GLEAM model-data integration framework, (Miralles et al., 2011; Martens et al., 2017)). We consider surface moisture as a hydrometeorological variable due to its importance for drought detection although it is influenced by vegetation. The impacts of the identified extremes are quantified as anomalies in gross primary productivity (GPP, original resolution $\frac{1}{12}^\circ$ from FLUXCOM-RS, Tramontana et al. (2016)). Anomalies in GPP are computed as deviations from the mean seasonal cycle excluding the extreme year itself. The selected hydrometeorological variables have global coverage and a common spatial resolution of 0.25° , and are used at an eight-daily temporal resolution covering the 2003–2018 period. Land cover classes at $\frac{1}{12}^\circ$ resolution were obtained from MODIS (collection 5, Friedl et al. (2010)) We group the available land cover classes in forest ecosystems (land cover classes containing "forest"), agricultural ecosystems (containing "crop"), and, all remaining other land cover types.

2.2 Preprocessing and anomaly detection

We compute deviations from a smoothed median seasonal cycle in the hydrometeorological variables, which we denote as anomalies. For detecting extreme events, we apply a multivariate anomaly detection procedure described in detail in (Flach et al., 2018). It (i) accounts for seasonal changes in the variance of the anomalies using a moving window technique, and (ii) uses climatic similarities to obtain more robust thresholds for extreme event detection via spatial replicates as proposed by Mahecha et al. (2017) (for more details see the B).

The extreme event detection algorithm itself is applied to the set of hydrometeorological anomaly time series and returns anomaly scores computed by kernel density estimation. Kernel density estimation showed good performance among other possible methods and accounts for nonlinearities in the data (Flach et al., 2017). The resulting anomaly scores can be interpreted as a univariate index of deviation from the general multivariate pattern. We consider the highest 5% of the anomaly scores to be extreme events (95th percentile), which is within the typical range of percentiles defining extreme events (McPhillips et al., 2018).

2.3 Framework for extracting event-based statistics

We use the extracted binary information (extreme / non-extreme) to compute statistics based on the spatio-temporal structure of the extreme events similar to (Lloyd-Hughes, 2011; Zscheischler et al., 2013; Mahecha et al., 2017; Chen et al., 2019). Extreme voxels are considered to belong to the same extreme event if they are connected within a $3 \times 3 \times 3$ (long x lat x time) cube. Note that this definition includes connections over edges. We compute event-based statistics from the 1000 largest extreme events globally as introduced also for the Russian heatwave (Flach et al., 2018). Specifically, we calculate affected volume, centroids, mean and integral of GPP separately for positive and negative anomalies, as well as the distance between the centroids of the positive and the negative anomalies of GPP during the event. We consider an event to be predominantly a

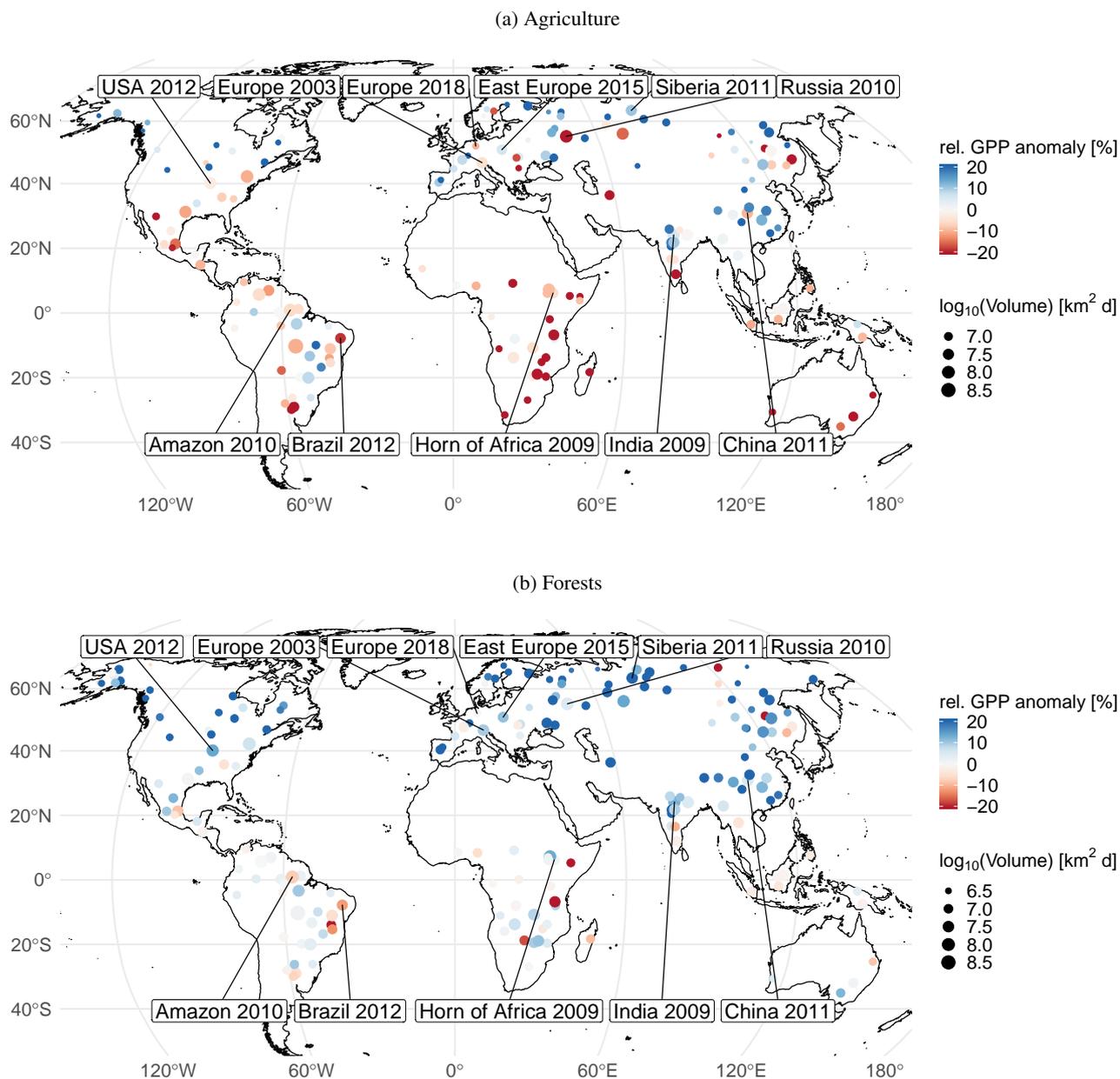


Figure 1. Relative drought and heat events coloured with the relative anomaly in gross primary production for (a) agricultural and (b) forest ecosystems. Point sizes are proportional to the affected volume of the space-time event. The largest and some well known events are labelled.

85 relative drought (relative heatwave) if more than 50% of the surface moisture (temperature) values during the extreme event are beneath (exceed) the 5th (95th) percentile of the variable. We select drought ($n = 98$) and heat ($n = 44$) events and combined drought–heat events ($n = 71$), which are taking place during the growing season (total $n = 213$), i.e. the centroid of the event is



within the half year encompassing the seasonal GPP maximum. Our statistics account for the spherical geometry of the Earth by weighting with the cosine of latitude.

90 Furthermore, we evaluate if the positive and negative anomalies in GPP during the event predominantly have a spatial or temporal component. Therefore, we split the event in parts with enhanced and parts with reduced productivity. Between those two parts, we compute the spatio-temporal distance between the centroids of each part. We consider positive and negative GPP anomalies to occur predominantly spatially if the temporal distance of the centroids is almost simultaneous, i.e. less than one time step in the data (eight days). GPP anomalies are considered to be predominantly temporally changing if the spatial distance of the centroids is less than 110 km (approximately one degree at the equator). Both, spatial and temporal components can be found for centroids which are more than 110 km and more than eight days away.

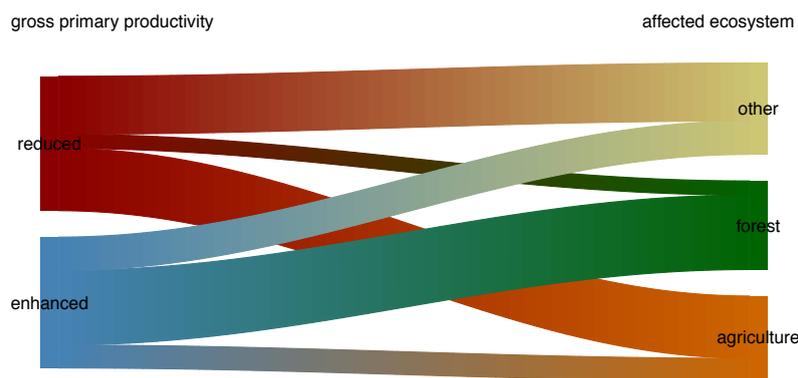


Figure 2. Proportion of GPP anomalies with reduced or enhanced productivity and their distribution in the different ecosystems (growing season events from 2003-2018). Bar sizes are proportional to the affected volume of the identified events. Forests tend to be associated with enhanced productivity rates, while agricultural ecosystems tend to be associated with reduced productivity.

2.4 Statistical model of GPP during extreme events

As we detect heatwaves and droughts relative to the mean seasonal patterns, positive or negative GPP anomalies during the droughts and heatwaves may additionally be influenced by differences in the conditions in the hydrometeorological variables during the extreme event, differences in background climate in which the vegetation is growing, or duration and affected area of the event. We use gradient boosting machines (Friedman, 2001) to predict average GPP anomalies during the event as a function of mean surface moisture, mean temperature, mean radiation during the event, duration, affected area, land cover class, and mean climate during the growing season, i.e. mean temperature and surface moisture during all growing seasons between 2003 and 2018. We tune model parameters (shrinkage parameter, depth of the trees, bag fraction, minimal number of observations per node) by following a workflow described in Elith et al. (2008) using a hyper grid search from 100 different random initialisations of splitting the data into training (75%) and testing (remaining 25%). We compute uncertainty of the variable importance measure described in (Friedman, 2001) from each of the 100 best models of the hyper grid search. Additionally



we use an approach based on Local Interpretable Model-agnostic Explanations (LIME), which tries to predict each single observation in a black box model based on locally weighted regression (Ribeiro et al., 2016). Here, this approach helps to understand (1) the effect of specific land cover classes, and (2) the direction of the effect.

3 Results

Our analysis based on a 5% threshold in the multivariate anomaly scores leads to a detection of 213 events (98 relative droughts, 44 relative heatwaves, 71 compound drought–heatwaves) between 2003 and 2018.

If we only discriminate forest and agricultural ecosystems, we find substantial differences in the direction of the GPP anomalies during extreme droughts and heatwaves in the growing season. In agricultural and other non-forest land-cover types, GPP was reduced during the identified events (agricultural land-cover types: 64% (56–72%) reduction, Figure 1 (a); other ecosystems 60% (53–67%), Appendix Figure A1). In forested areas, instead, a majority of 71% (63–78%, 95% confidence interval) of events shows enhanced productivity (Figure 1 (b)). The dichotomy described in the instantaneous response patterns confirms the overall statistics. Events with their centroid in France 2003, Russia 2010, and Germany 2018 all show bidirectional GPP anomalies that coincide with land-cover type transitions between predominantly forested land cover and others (a detailed illustration of the different events is provided in the supplementary materials) Figure 2 summarizes these findings across all events by relating the global integral areas of positive and negative anomalies in GPP during extreme events to the dominant land cover type.

The events analyzed here are based on relative radiation, heat and water availability anomalies (see Methods). To better understand the role of absolute climate conditions we show the reported GPP anomalies in the terms of absolute temperatures and surface moisture levels in Figure 3(a). The figure shows that reduced rates of GPP tend to coincide with very low surface moisture and high temperature (eight-daily averages). Delineating different ecosystems within this space shows that they are arranged along decreasing surface moisture values. Most extreme events in forests tend to occur under slightly higher surface moisture conditions compared to agricultural and other ecosystems (Figure 3(b)). Forests are hit less frequently critical dry conditions for which we predominantly observe reduced productivity. In contrast, we observe reduced productivity during the events for agricultural ecosystems, which experience frequently critical hot and dry conditions (Figure 3(b)).

While Figure 3(a) shows that temperature and soil moisture have some effect on the direction of the impacts, they are insufficient to explain the observed patterns in detail. To unravel the importance of land cover type and other factors we predict average GPP anomalies using gradient boosting machines ($R^2 = 0.43$, Friedman (2001) Section 2.4) and explore their relative variable importance. Growing season temperature, event duration, and land cover type are, in decreasing order, are the most important variables in the statistical model (Figure 4(a)).

Apart from identifying important variables that explain the GPP anomalies during drought and heat anomalies, we disentangle the direction of each factor's effect in the model, and, in particular for specific land cover classes. Whereas growing season temperature and duration show a negative model coefficient, i.e. a longer duration and a warmer climate are associated with a stronger impact, as expected, productivity in different land cover types is influenced in contrasting ways: Land cover

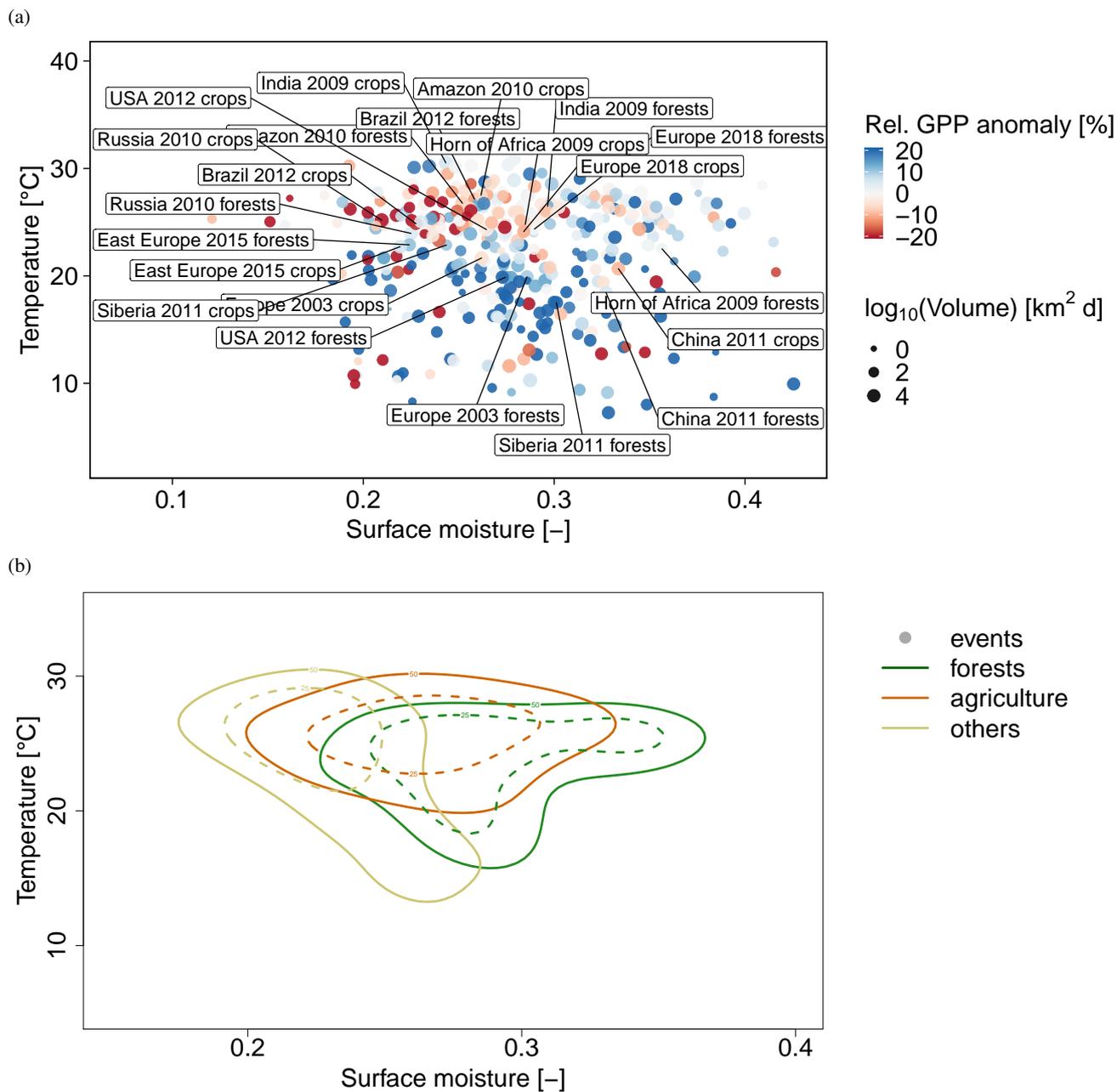


Figure 3. (a) Mean temperature and surface moisture during the relative drought and heat events for forests and agricultural ecosystems. Size and color of the points denote the affected space–time volume and the direction of the impact on productivity. (b) Average conditions in temperature and surface moisture for all ecosystems. Colored lines enclose 25% and 50% of the events within forest, agricultural and other ecosystems.

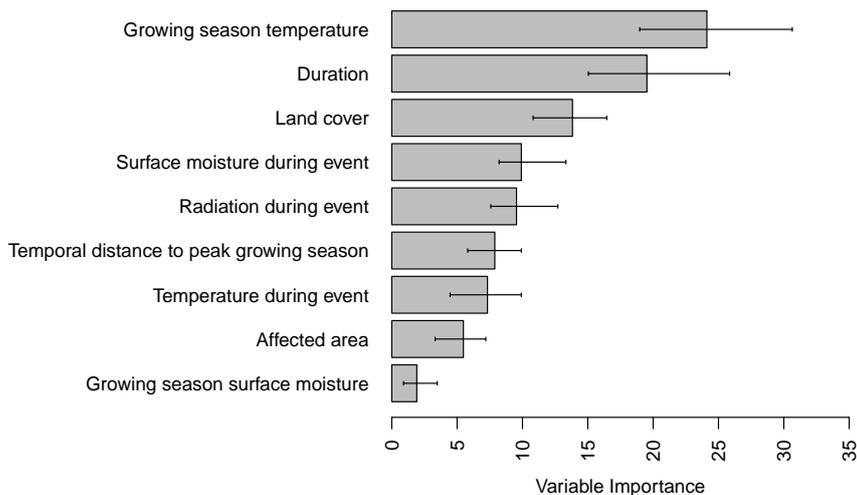


types including forests and woody savannas show increased average GPP during the extreme events. In contrast, agricultural ecosystems (land cover types including crops), grasslands, savannas, and other land cover types reduce average GPP anomalies (Figure 4(b)). Warmer growing season climates and higher temperatures during the event are associated with negative GPP anomalies. In contrast, greater availability radiation and higher surface moisture have a positive influence on the impact.

145 We showed that land cover type is one of the major factors influencing the GPP anomaly during the event. A single hydrometeorological extreme event can affect two or more adjacent land cover types simultaneously with potentially contrasting impacts (spatial contrasting anomalies), but enhanced productivity can also be observed earlier than reduced productivity (or vice versa, temporally contrasting anomalies). To explicitly quantify the role of spatial vs. temporal effects on the GPP anomalies during extreme events we split each event in parts with enhanced and reduced GPP anomalies and compute the centroidal
150 distance in space and time. In fact, positive and negative GPP anomalies mostly co-occur simultaneously in adjacent spatial regions (116 events of 213 events in total within ± 8 days, Figure 5). Especially for large scale events (large volume), a considerable distance of the anomalies can be observed in space and time. However, taking only the temporal distance into account, we have more events with enhanced productivity before the reduced productivity (temporal distance < -8 days, $n = 44$) than after (> 8 days, $n = 33$).



(a)



(b)

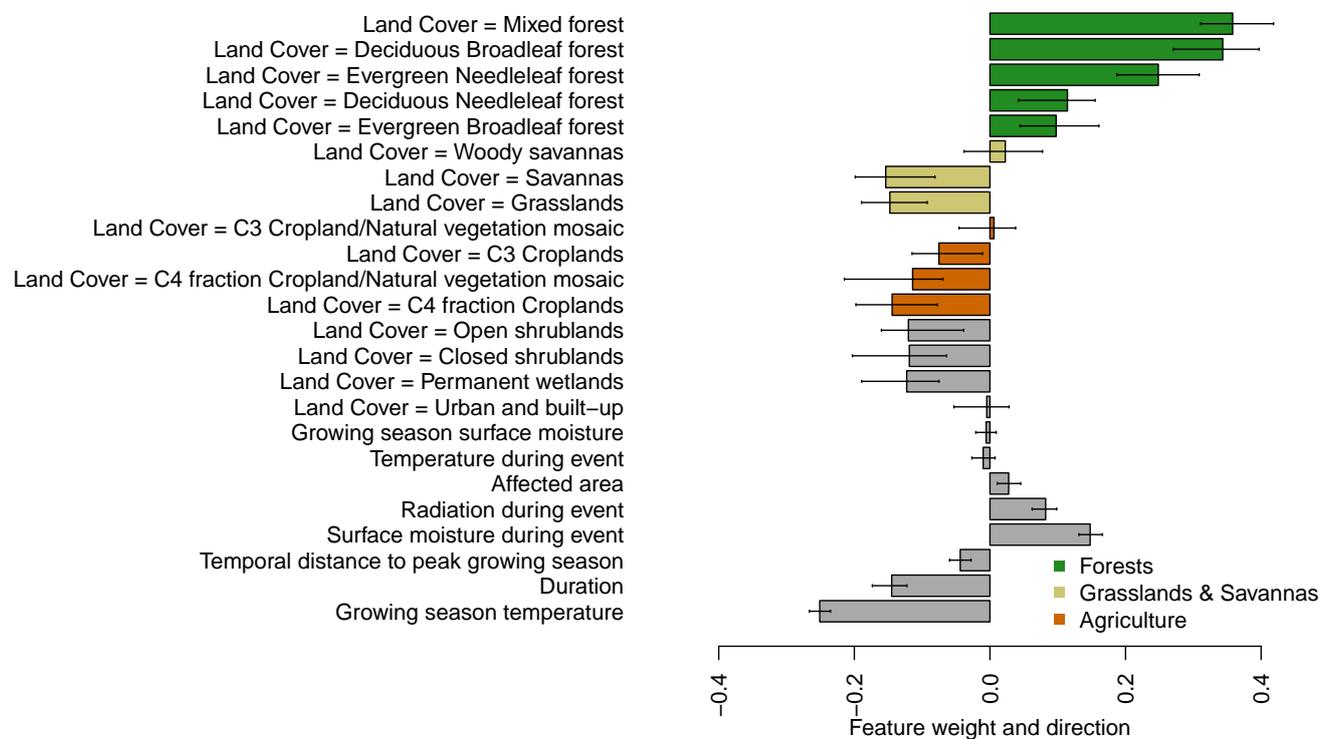


Figure 4. (a) Variable importance of the ten best gradient boosting machines predicting average GPP anomalies during the events, and (b) direction and feature weight of the variables explaining GPP anomalies of the individual events based on linear regression via local interpretable model-agnostic explanations (LIME).

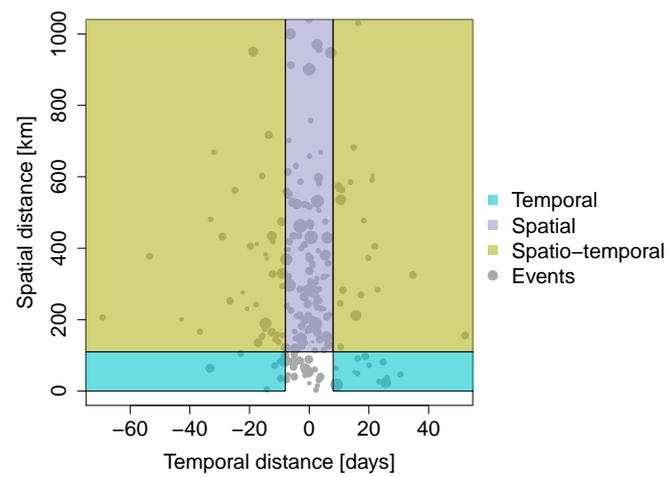


Figure 5. Each extreme event is split into parts with enhanced and reduced GPP anomalies. The centroidal distance between both parts in space and time shows whether contrasting GPP anomalies are predominantly taking place temporally, spatially or spatio-temporally. Point sizes are proportional to the event's affected volume.



155 4 Discussion

Contrasting responses of ecosystems to climate extremes, e.g. in the US in 2012 (Wolf et al., 2016) or in Russia in 2010 (Flach et al., 2018), are not singular cases but are shown to be frequent phenomena in response to hydrometeorological extreme events at the global scale. Within the same extreme event, reduced and enhanced productivity can be observed simultaneously in adjacent spatial regions. This finding complements previous studies on temporal (Wolf et al., 2016; Sippel et al., 2017a; 160 Buermann et al., 2018) or spatial contrasting responses (Jolly et al., 2005; Zaitchik et al., 2006; Lewińska et al., 2016).

This study provides evidence that the impacts of extreme drought or heat anomalies on GPP during growing seasons is, firstly a function of event duration and long-term climate, but secondly, also depends on the affected land cover type. In particular the tendency towards positive vs. negative responses seems to be controlled by tree cover (similar to the results of Ivits et al. (2014); Walther et al. (2019)), i.e. forests seem to show higher resilience to drought and heat anomalies on the 165 short term, which is reflected in a tendency towards positive GPP anomalies during the events. However, our results are based on events that are extreme relative to the regional normal conditions. In the supplementary materials we illustrate a range of events in more detail. For instance, a relative drought or heatwave in a typically wet ecosystem can boost productivity as well as a heatwave in ecosystems that are typically cold (see cases reported e.g. for China 20011, India 2009, and the Siberian heatwave 2011). Both water stress and temperature affect ecophysiological processes in a nonlinear manner. Heat events below 170 optimal temperatures enhance photosynthesis (Wang et al., 2017), or photosynthesis may be enhanced by the radiation surplus during dry periods (Walther et al., 2019) especially at higher latitudes (Bachmair et al., 2018) and as long as ecophysiological limits are not violated. Yet, the prevalence of certain land cover types is partly controlled by climatic gradients, and therefore land cover cannot really be considered independently of the mean climatological conditions that likewise play a role (Figure 3(a)). Climate conditions also lead to adaptation of physiological processes. For instance, forests in dry ecosystems may be 175 characterized by a more conservative water use strategy (Teuling et al., 2010; van Heerwaarden and Teuling, 2014; Ramos et al., 2015) and adapted to drought compared to analogous land cover types whose biogeographic history experienced colder and more moderate conditions (Doughty et al., 2015). Moreover, forests have access to deeper soil water compared to other ecosystems (Yang et al., 2016; Fan et al., 2017). The degree of isohydricity may further differentiate the response of forests, as it differs between tree species (Roman et al., 2015; Ruehr et al., 2015; Yi et al., 2017).

180 Our study only reports on GPP responses during the climatic anomaly without considering the legacy of the events. Responses may emerge with some time lag between weeks to months (Schwalm et al., 2012; Ruehr et al., 2015), or even at longer time scales (years) (Saatchi et al., 2013; Anderegg et al., 2015). Hence, finding enhanced productivity of forests during some heat event does not exclude increased mortality in the long-term. Forest ecosystems are known to potentially respond much delayed to environmental stress, which can trigger strong secondary impacts like insect outbreaks (Hicke et al., 2006; Rouault et al., 2006; Allen et al., 2010), or fires (Brando et al., 2014). In contrast, agricultural systems are known to be very directly 185 vulnerable to droughts (De Keersmaecker et al., 2016; Bachmair et al., 2018). We choose the growing season as time period of interest, which is notably different than summer for some regions, e.g. in the Mediterranean where more positive responses to warm anomalies in the cold season may be expected (Sippel et al., 2017b), and also impacts of droughts may be less than



190 during the dry season (Huang et al., 2018). Note that due to complex interactions between GPP and ecosystem respiration no direct translation of the results into net ecosystem exchange is expected (Richardson et al., 2007).

195 Another aspect to discuss is data quality. Gross primary productivity from FLUXCOM-RS may inherit errors from the underlying remote sensing products; these have, in particular, been discussed for tropical forests (Asner et al., 2004; Asner and Alencar, 2010; Wu et al., 2018). Recently, Stocker et al. (2019) showed at the global scale that remote sensing retrieved GPP underestimates drought impacts due to soil moisture effects on light use efficiency. Comparing our estimates of GPP impacts to published data from eddy covariance stations for two case studies (US 2012, (Wolf et al., 2016), and Europe 2003 (Ciais et al., 2005; Reichstein et al., 2007)) indicates that we do indeed underestimate GPP impact. Thus, we suspect that in addition to the GPP estimates used by Stocker et al. (2019), also FLUXCOM-RS GPP underestimates the impacts of climate extreme events specifically for forest ecosystems. As FLUXCOM-RS exhibits a good agreement for forests globally with GPP estimates based on solar-induced fluorescence (Walther et al., 2019), the lack of sensitivity to drought and heat impacts in forest ecosystems
200 may be a more general issue in remote sensing data.

5 Conclusions

We conclude that a more differentiated consideration of the role of land cover reveals firstly major differences between forest and agricultural ecosystems. These differences may originate from a different (micro-)climate or different water management strategies including the access to deeper soil water or point to more strongly lagged impacts in forest ecosystems. However,
205 the lack of sensitivity of forest ecosystems to droughts and heatwaves is stronger than we would expect it to be. Thus, we think that our results also point towards deficiencies in FLUXCOM-RS derived GPP which are potentially a more general issue in remote sensing derived indices of vegetation activity. These deficiencies call for the development of new global GPP products with a higher sensitivity to droughts and heatwaves, which can unravel the role of forest ecosystems in a more frequently hot and dry future climate.

210 *Data availability.* We use data originating from the FLUXCOM initiative (<http://www.fluxcom.org>), the GLEAM model data integration framework (<https://www.gleam.eu/>), and ERA5 (<https://cds.climate.copernicus.eu/cdsapp#!/home>). The harmonized data set is available within the project Earth System Data Lab (ESDL) and can be accessed here: <https://www.earthsystemdatalab.net/index.php/interact/datalab/>.



Appendix A: Other ecosystems

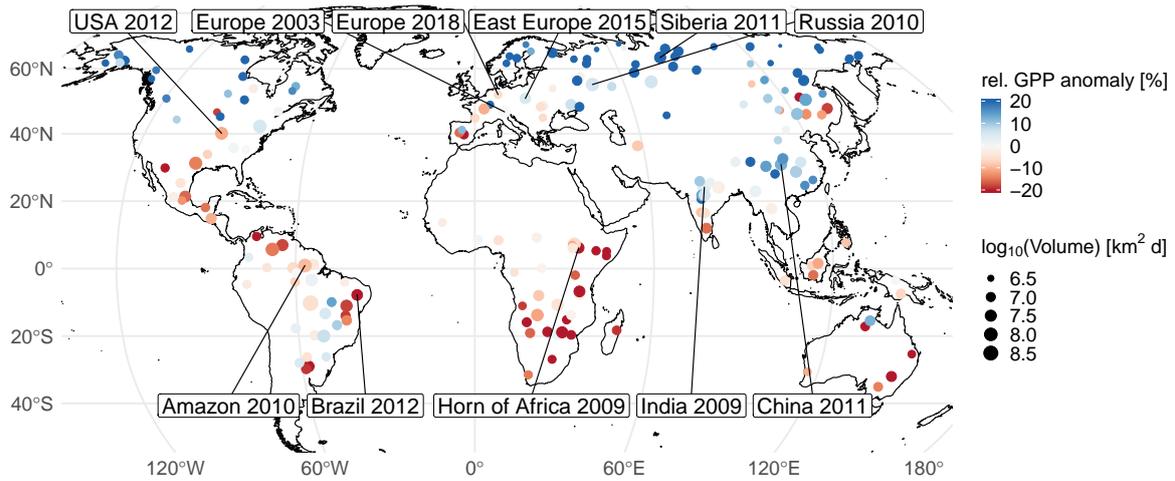


Figure A1. Relative GPP anomalies of other ecosystems (except forests and agriculture) during droughts and heatwaves. Point sizes are proportional to the (space–time) volume of the extreme event.



215 Appendix B: Technical details on the spatial segmentation

We follow the procedure described and developed by Mahecha et al. (2017), which was extended to the multivariate case by Flach et al. (2018). In summary, the used approach defines climatically and phenologically similar regions by using the leading principal components (here: three) of the seasonal cycles of the hydrometeorological variables (temperature, surface moisture, radiation) in addition to the vegetation proxy (gross primary productivity). Similar cycles appear in the same region
220 of the obtained principal component space (Figure B1). Thus, a simple classification can be obtained by dividing the principal component space into equally sized cubes. Here we use 25 breaks for each of the first three principal components, which leads to 814 classes globally of similar climate and phenology. For each pixel, we sample four random spatial replicates from each region to efficiently run the following anomaly detection workflow globally (previously the procedure was used for Europe only).

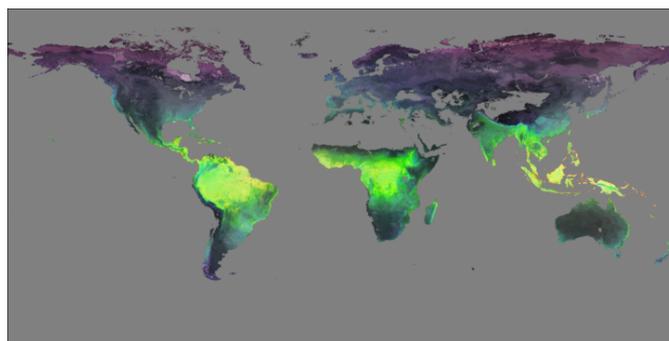


Figure B1. Map of the first three leading principal components (PCs) colored according to the colorspace hue (PC1), saturation (PC2), and, lightness (PC3).



225 *Author contributions.* MF and MDM designed the study in collaboration with AB, FG, SS, MR. MF conducted the analysis and wrote the manuscript with contributions from all co-authors.

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

Acknowledgements. This research was supported by the European Space Agency (project "Earth System Data Lab") and the European Union's Horizon 2020 research and innovation programme (project "BACI", grant agreement no 64176). The authors are grateful to the
230 FLUXCOM initiative (<http://www.fluxcom.org>) for providing the data. MF acknowledges support by the International Max Planck Research School for Global Biogeochemical Cycles (IMPRS).



References

- AghaKouchak, A., Cheng, L., Mazdoyasni, O., and Farahmand, A.: Global warming and changes in risk of concurrent climate extremes: Insights from the 2014 California drought, *Geophys. Res. Lett.*, 41, 8847–8852, 2014.
- 235 Allen, C. D., Macalady, A. K., Chenchouni, H., Bachelet, D., McDowell, N., Venetier, M., Kitzberger, T., Rigling, A., Breshears, D. D., Hogg, E. H. T., Gonzalez, P., Fensham, R., Zhang, Z., Castro, J., Demidova, N., Lim, J.-H., Allard, G., Running, S. W., Semerci, A., and Cobb, N.: A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests, *Forest Ecology and Management*, 259, 660–684, 2010.
- Anderegg, W. R. L., Schwalm, C. R., Biondi, F., Camarero, J. J., Koch, G., Litvak, M., Ogle, K., Shaw, J. D., Shevliakova, E., Williams, A. P., Wolf, A., Ziaco, E., and Pacala, S.: Pervasive drought legacies in forest ecosystems and their implications for carbon cycle models, *Science*, 349, 524–528, 2015.
- 240 Asner, G. P. and Alencar, A.: Drought impacts on the Amazon forest: the remote sensing perspective, *New Phytologist*, 187, 569–578, 2010.
- Asner, G. P., Nepstad, D., Cardinot, G., and Ray, D.: Drought stress and carbon uptake in an Amazon forest measured with spaceborne imaging spectroscopy, *PNAS*, 101, 6039–6044, 2004.
- 245 Bachmair, S., Tanguy, M., Hannaford, J., and Stahl, K.: How well do meteorological indicators represent agricultural and forest drought across Europe?, *Environmental Research Letters*, 13, 034 042, 2018.
- Bastos, A., Gouveia, C. M., Trigo, R. M., and Running, S. W.: Analysing the spatio-temporal impacts of the 2003 and 2010 extreme heatwaves on plant productivity in Europe, *Biogeosciences*, 11, 3421–3435, 2014.
- Brando, P. M., Balch, J. K., Nepstad, D. C., Morton, D. C., Putz, F. E., Coe, M. T., Silverio, D., Macedo, M. N., Davidson, E. A., Nobrega, C. C., Alencar, A., and Soares-Filho, B. S.: Abrupt increases in Amazonian tree mortality due to drought-fire interactions, *Proceedings of the National Academy of Sciences*, 111, 6347–6352, 2014.
- 250 Brando, P. M., Paolucci, L., Ummenhofer, C. C., Ordway, E. M., Hartmann, H., Cattau, M. E., Rattis, L., Medjibe, V., Coe, M. T., and Balch, J.: Droughts, Wildfires, and Forest Carbon Cycling: A Pantropical Synthesis, *Annual Review of Earth and Planetary Sciences*, 47, 555–581, 2019.
- 255 Buermann, W., Bikash, P. R., Jung, M., Burn, D. H., and Reichstein, M.: Earlier springs decrease peak summer productivity in North American boreal forests, *Environ. Res. Lett.*, 8, 024 027, 2013.
- Buermann, W., Forkel, M., O’Sullivan, M., Sitch, S., Friedlingstein, P., Haverd, V., Jain, A. K., Kato, E., Kautz, M., Lienert, S., Lombardozzi, D., Nabel, J. E. M. S., Tian, H., Wiltshire, A. J., Zhu, D., Smith, W. K., and Richardson, A. D.: Widespread seasonal compensation effects of spring warming on northern plant productivity, *Nature*, 562, 110–111, 2018.
- 260 Chen, W., Zhu, D., Huang, C., Ciais, P., Yao, Y., Friedlingstein, P., Sitch, S., Haverd, V., Jain, A. K., Kato, E., Kautz, M., Lienert, S., Lombardozzi, D., Poulter, B., Tian, H., Vuichard, N., Walker, A. P., and Zeng, N.: Negative extreme events in gross primary productivity and their drivers in China during the past three decades, *Agricultural and Forest Meteorology*, 275, 47–58, 2019.
- Ciais, P., Reichstein, M., Viovy, N., Granier, A., Ogée, J., Allard, V., Aubinet, M., Buchmann, N., Bernhofer, C., Carrara, A., Chevallier, F., De Noblet, N., Friend, A. D., Friedlingstein, P., Grünwald, T., Heinesch, B., Keronen, P., Knohl, A., Krinner, G., Loustau, D., Manca, G., Matteucci, G., Miglietta, F., Ourcival, J. M., Papale, D., Pilegaard, K., Rambal, S., Seufert, G., Soussana, J. F., Sanz, M. J., Schulze, E. D., Vesala, T., and Valentini, R.: Europe-wide reduction in primary productivity caused by the heat and drought in 2003, *Nature*, 437, 529–533, 2005.



- Cook, B. I., Ault, T. R., and Smerdon, J. E.: Unprecedented 21st century drought risk in the American Southwest and Central Plains, *Science Advances*, 1, e1400082, 2015.
- 270 Copernicus Climate Change Service (C3S): ERA5: Fifth generation of ECMWF atmospheric reanalyses of the global climate, Copernicus Climate Change Service Climate Data Store (CDS), pp. accessed in April 2019, <https://cds.climate.copernicus.eu/cdsapp#!/home>, 2017.
- Coumou, D. and Robinson, A.: Historic and future increase in the global land area affected by monthly heat extremes, *Environ. Res. Lett.*, 8, 034018, 2013.
- De Keersmaecker, W., van Rooijen, N., Lhermitte, S., Tits, L., Schaminée, J., Coppin, P., Honnay, O., and Somers, B.: Species-rich semi-
275 natural grasslands have a higher resistance but a lower resilience than intensively managed agricultural grasslands in response to climate anomalies, *Journal of Applied Ecology*, 53, 430–439, 2016.
- Doughty, C. E., Metcalfe, D. B., Girardin, C. A. J., Amézquita, F. F., Cabrera, D. G., Huasco, W. H., Silva-Espejo, J. E., Araujo-Murakami, A., da Costa, M. C., Rocha, W., Feldpausch, T. R., Mendoza, A. L. M., da Costa, A. C. L., Meir, P., Phillips, O. L., and Malhi, Y.: Drought impact on forest carbon dynamics and fluxes in Amazonia, *Nature*, 519, 78–82, 2015.
- 280 Elith, J., Leathwick, J. R., and Hastie, T.: A working guide to boosted regression trees, *Journal of Animal Ecology*, 77, 802–813, 2008.
- Fan, Y., Miguez-Macho, G., Jobbágy, E. G., Jackson, R. B., and Otero-Casal, C.: Hydrologic regulation of plant rooting depth, *Proceedings of the National Academy of Sciences*, 82, 201712381, 2017.
- Flach, M., Gans, F., Brenning, A., Denzler, J., Reichstein, M., Rodner, E., Bathiany, S., Bodesheim, P., Guaniche, Y., Sippel, S., and Mahecha, M. D.: Multivariate anomaly detection for Earth observations: a comparison of algorithms and feature extraction techniques, *Earth System
285 Dynamics*, 8, 677–696, 2017.
- Flach, M., Sippel, S., Gans, F., Bastos, A., Brenning, A., Reichstein, M., and Mahecha, M. D.: Contrasting biosphere responses to hydrometeorological extremes: revisiting the 2010 western Russian heatwave, *Biogeosciences*, 15, 6067–6085, 2018.
- Frank, D., Reichstein, M., Bahn, M., Thonicke, K., Frank, D., Mahecha, M. D., Smith, P., van der Velde, M., Vicca, S., Babst, F., Beer, C., Buchmann, N., Canadell, J. G., Ciais, P., Cramer, W., Ibrom, A., Miglietta, F., Poulter, B., Rammig, A., Seneviratne, S. I., Walz, A.,
290 Wattenbach, M., Zavala, M. A., and Zscheischler, J.: Effects of climate extremes on the terrestrial carbon cycle: concepts, processes and potential future impacts, *Global Change Biology*, 21, 2861–2880, 2015.
- Friedl, M. A., Sulla-Menashe, D., Tan, B., Schneider, A., Ramankutty, N., Sibley, A., and Huang, X.: Remote Sensing of Environment, *Remote Sensing of Environment*, 114, 168–182, 2010.
- Friedman, J. H.: Greedy Function Approximation: A Gradient Boosting Machine, *The Annals of Statistics*, 29, 1189–1232, 2001.
- 295 Granier, A., Bréda, N., Longdoz, B., Gross, P., and Ngao, J.: Ten years of fluxes and stand growth in a young beech forest at Hesse, North-eastern France, *Annals of Forest Science*, 65, doi:10.1051/forest:2008052, 2008.
- Hicke, J. A., Logan, J. A., Powell, J., and Ojima, D. S.: Changing temperatures influence suitability for modeled mountain pine beetle (*Dendroctonus ponderosae*) outbreaks in the western United States, *Journal of Geophysical Research: Biogeosciences*, 111, doi:10.1029/2005JG000101, 2006.
- 300 Huang, M., Wang, X., Keenan, T. F., and Piao, S.: Drought timing influences the legacy of tree growth recovery, *Global Change Biology*, 24, 3546–3559, 2018.
- Ivits, E., Horion, S., Fensholt, R., and Cherlet, M.: Drought footprint on European ecosystems between 1999 and 2010 assessed by remotely sensed vegetation phenology and productivity, *Global Change Biology*, 20, 581–593, 2014.
- Jolly, W. M., Dobbertin, M., Zimmermann, N. E., and Reichstein, M.: Divergent vegetation growth responses to the 2003 heat wave in the
305 Swiss Alps, *Geophysical Research Letters*, 32, doi: 10.1029/2005GL023252, 2005.



- Lewińska, K., Ivits, E., Schardt, M., and Zebisch, M.: Alpine Forest Drought Monitoring in South Tyrol: PCA Based Synergy between scPDSI Data and MODIS Derived NDVI and NDII7 Time Series, *Remote Sensing*, 8, doi:10.3390/rs808063, 2016.
- Lloyd-Hughes, B.: A spatio-temporal structure-based approach to drought characterisation, *International Journal of Climatology*, 32, 406–418, 2011.
- 310 Mahecha, M. D., Gans, F., Sippel, S., Donges, J. F., Kaminski, T., Metzger, S., Migliavacca, M., Papale, D., Rammig, A., and Zscheischler, J.: Detecting impacts of extreme events with ecological in situ monitoring networks, *Biogeosciences*, 14, 4255–4277, 2017.
- Martens, B., Miralles, D. G., Lievens, H., van der Schalie, R., de Jeu, R. A. M., Fernández-Prieto, D., Beck, H. E., Dorigo, W. A., and Verhoest, N. E. C.: GLEAM v3: satellite-based land evaporation and root-zone soil moisture, *Geoscientific Model Development*, 10, 1903–1925, 2017.
- 315 McPhillips, L. E., Chang, H., Chester, M. V., Depietri, Y., Friedman, E., Grimm, N. B., Kominoski, J. S., McPhearson, T., Méndez-Lázaro, P., Rosi, E. J., and Shafiei Shiva, J.: Defining Extreme Events: A Cross-Disciplinary Review, *Earth's Future*, 6, 441–455, 2018.
- Meehl, G. A., Zwiers, F. W., Evans, J. L., Knutson, T., Mearns, L. O., and Whetton, P.: Trends in Extreme Weather and Climate Events: Issues Related to Modeling Extremes in Projections of Future Climate Change, *BAMS*, 81, 427–436, 2000.
- Miralles, D. G., Holmes, T. R. H., De Jeu, R. A. M., Gash, J. H., Meesters, A. G. C. A., and Dolman, A. J.: Global land-surface evaporation
320 estimated from satellite-based observations, *Hydrology and Earth System Sciences*, 15, 453–469, 2011.
- Olesen, J. E. and Bindi, M.: Consequences of climate change for European agricultural productivity, land use and policy, *European Journal of Agronomy*, 16, 239–262, 2002.
- Orth, R. and Destouni, G.: Drought reduces blue-water fluxes more strongly than green-water fluxes in Europe, *Nature Communications*, 9, doi:10.1038/s41467-018-06013-7, 2018.
- 325 Peuelas, J., Gordon, C., Llorens, L., Nielsen, T., Tietema, A., Beier, C., Bruna, P., Emmett, B., Estiarte, M., and Gorissen, A.: Noninvasive Field Experiments Show Different Plant Responses to Warming and Drought Among Sites, Seasons, and Species in a North-South European Gradient, *Ecosystems*, 7, 598–612, 2004.
- Ramos, A., Pereira, M. J., Soares, A., do Rosário, L., Matos, P., Nunes, A., Branquinho, C., and Pinho, P.: Agricultural and Forest Meteorology, *Agricultural and Forest Meteorology*, 202, 44–50, 2015.
- 330 Reichstein, M., Ciais, P., Papale, D., Valentini, R., Running, S., Viovy, N., Cramer, W., Granier, A., Ogée, J., Allard, V., Aubinet, M., Bernhofer, C., Buchmann, N., Carrara, A., Grünwald, T., Heimann, M., Heinesch, B., Knohl, A., Kutsch, W., Loustau, D., Manca, G., Matteucci, G., Miglietta, F., Ourcival, J.-M., Pilegaard, K., Pumpanen, J., Rambal, S., Schaphoff, S., Seufert, G., Soussana, J. F., Sanz, M. J., Vesala, T., and Zhao, M.: Reduction of ecosystem productivity and respiration during the European summer 2003 climate anomaly: a joint flux tower, remote sensing and modelling analysis, *Global Change Biology*, 13, 634–651, 2007.
- 335 Reichstein, M., Bahn, M., Ciais, P., Frank, D., Mahecha, M. D., Seneviratne, S. I., Zscheischler, J., Beer, C., Buchmann, N., Frank, D. C., Papale, D., Rammig, A., Smith, P., Thonicke, K., van der Velde, M., Vicca, S., Walz, A., and Wattenbach, M.: Climate extremes and the carbon cycle, *Nature*, 500, 287–295, 2013.
- Ribeiro, M. T., Singh, S., and Guestrin, C.: "Why Should I Trust You?", in: *KDD '16. Proceedings of the 22nd ACM SIGKDD International Conference on Knowledge Discovery and Data Mining.*, pp. 1135–1144, ACM Press, San Francisco, CA, USA, 2016.
- 340 Richardson, A. D., Hollinger, D. Y., Aber, J. D., Ollinger, S. V., and Braswell, B. H.: Environmental variation is directly responsible for short- but not long-term variation in forest-atmosphere carbon exchange, *Global Change Biology*, 13, 788–803, 2007.
- Roman, D. T., Novick, K. A., Brzostek, E. R., Dragoni, D., Rahman, F., and Phillips, R. P.: The role of isohydric and anisohydric species in determining ecosystem-scale response to severe drought, *Oecologia*, 179, 641–654, 2015.



- Rouault, G., Candau, J.-N., Lieutier, F., Nageleisen, L.-M., Martin, J.-C., and Warzée, N.: Effects of drought and heat on forest insect
345 populations in relation to the 2003 drought in Western Europe, *Annals of Forest Science*, 63, 613–624, 2006.
- Ruehr, N. K., Gast, A., Weber, C., Daub, B., and Arneith, A.: Water availability as dominant control of heat stress responses in two contrasting
tree species, *Tree Physiology*, 36, 164–178, 2015.
- Saatchi, S., Asefi-Najafabady, S., Malhi, Y., Aragao, L. E. O. C., Anderson, L. O., Myneni, R. B., and Nemani, R.: Persistent effects of a
severe drought on Amazonian forest canopy, *PNAS*, 110, 565–570, 2013.
- 350 Schwalm, C. R., Williams, C. A., Schaefer, K., Baldocchi, D., Black, T. A., Goldstein, A. H., Law, B. E., Oechel, W. C., U, K. T. P., and
Scott, R. L.: Reduction in carbon uptake during turn of the century drought in western North America, *Nature Geoscience*, 5, 551–556,
2012.
- Seneviratne, S. I., Nicholls, N., Easterling, D., Goodess, C., Kanae, S., Kossin, J., Luo, Y., Marengo, J., McInnes, K., Rahimi, M., Reichstein,
M., Sorteberg, A., Vera, C., and Zhang, X.: Changes in climate extremes and their impacts on the natural physical environment, in:
355 *Managing the Risks of Extreme Events and Disasters to Advance Climate Change Adaptation (IPCC SREX Report)*, edited by Field, C.,
Barros, V., Stocker, T., Qin, D., Dokken, D., Ebi, K., Mastrandrea, M., Mach, K., Plattner, G.-K., Allen, S., Tignor, M., and Midgley, pp.
109–230, Cambridge University Press, 2012.
- Sippel, S., Forkel, M., Rammig, A., Thonicke, K., Flach, M., Heimann, M., Otto, F. E. L., Reichstein, M., and Mahecha, M. D.: Contrasting
and interacting changes in simulated spring and summer carbon cycle extremes in European ecosystems, *Environ. Res. Lett.*, 12, 075 006,
360 2017a.
- Sippel, S., El-Madany, T. S., Mahecha, M. D., Migliavacca, M., Carrara, A., Flach, M., Kaminski, T., Otto, F. E. L., Thonicke, K., Vossbeck,
M., and Reichstein, M.: Warm winter, wet spring, and extreme response in ecosystem functioning on the Iberian Peninsula, *BAMS*,
98, S80–S85, 2017b.
- Sippel, S., Reichstein, M., Ma, X., Mahecha, M. D., Lange, H., Flach, M., and Frank, D.: Drought, Heat, and the Carbon Cycle: a Review,
365 *Current Climate Change Reports*, 4, 266–286, 2018.
- Stocker, B. D., Zscheischler, J., Keenan, T. F., Prentice, I. C., Seneviratne, S. I., and Peñuelas, J.: Drought impacts on terrestrial primary
production underestimated by satellite monitoring, *Nature Geoscience*, 12, 264–270, 2019.
- Teuling, A. J., Seneviratne, S. I., Stöckli, R., Reichstein, M., Moors, E. J., Ciais, P., Luysaert, S., van den Hurk, B., Ammann, C., Bernhofer,
C., Dellwik, E., Gianelle, D., Gielen, B., Grünwald, T., Klumpp, K., Montagnani, L., Moureaux, C., Sottocornola, M., and Wohlfahrt, G.:
370 Contrasting response of European forest and grassland energy exchange to heatwaves, *Nature Geoscience*, 3, 722–727, 2010.
- Tramontana, G., Jung, M., Schwalm, C. R., Ichii, K., Camps-Valls, G., Ráduly, B., Reichstein, M., Arain, M. A., Cescatti, A., Kiely, G.,
Merbold, L., Serrano-Ortiz, P., Sickert, S., Wolf, S., and Papale, D.: Predicting carbon dioxide and energy fluxes across global FLUXNET
sites with regression algorithms, *Biogeosciences*, 13, 4291–4313, 2016.
- van Heerwaarden, C. C. and Teuling, A. J.: Disentangling the response of forest and grassland energy exchange to heatwaves under idealized
375 land–atmosphere coupling, *Biogeosciences*, 11, 6159–6171, 2014.
- Vetter, M., Churkina, M., Jung, M., Reichstein, M., Zaehle, S., Bondeau, A., Chen, Y., Ciais, P., Feser, F., Freibauer, A., Geyer, R., Jones,
C., Papale, D., Tenhunen, J., Tomelleri, E., Trusilova, K., Viovy, N., and Heimann, M.: Analyzing the causes and spatial pattern of the
European 2003 carbon flux anomaly using seven models, *Biogeosciences*, 5, 561–583, 2008.
- von Buttler, J., Zscheischler, J., Rammig, A., Sippel, S., Reichstein, M., Knohl, A., Jung, M., Menzer, O., Arain, M. A., Buchmann, N.,
380 Cescatti, A., Gianelle, D., Kiely, G., Law, B. E., Magliulo, V., Margolis, H., McCaughey, H., Merbold, L., Migliavacca, M., Montagnani,
L., Oechel, W., Pavelka, M., Peichl, M., Rambal, S., Raschi, A., Scott, R. L., Vaccari, F. P., van Gorsel, E., Varlagin, A., Wohlfahrt, G.,



- and Mahecha, M. D.: Impacts of droughts and extreme-temperature events on gross primary production and ecosystem respiration: a systematic assessment across ecosystems and climate zones, *Biogeosciences*, 15, 1293–1318, 2018.
- Walther, S., Duveiller, G., Jung, M., Guanter, L., Cescatti, A., and Camps-Valls, G.: Satellite Observations of the Contrasting Response of
385 Trees and Grasses to Variations in Water Availability, *Geophys. Res. Lett.*, 46, 1429–1440, 2019.
- Wang, E., Martre, P., Zhao, Z., Ewert, F., Maiorano, A., Rötter, R. P., Kimball, B. A., Ottman, M. J., Wall, G. W., White, J. W., Reynolds, M. P., Alderman, P. D., Aggarwal, P. K., Anothai, J., Basso, B., Biernath, C., Cammarano, D., Challinor, A. J., De Sanctis, G., Doltra, J., Dumont, B., Fereres, E., Garcia-Vila, M., Gayler, S., Hoogenboom, G., Hunt, L. A., Izaurralde, R. C., Jabloun, M., Jones, C. D., Kersebaum, K. C., Koehler, A.-K., Liu, L., Müller, C., Kumar, S. N., Nendel, C., O’Leary, G., Olesen, J. E., Palosuo, T., Priesack, E.,
390 Rezaei, E. E., Ripoche, D., Ruane, A. C., Semenov, M. A., Shcherbak, I., Stöckle, C., Stratonovitch, P., Streck, T., Supit, I., Tao, F., Thorburn, P., Waha, K., Wallach, D., Wang, Z., Wolf, J., Zhu, Y., and Asseng, S.: The uncertainty of crop yield projections is reduced by improved temperature response functions, *Nature Plants*, 3, doi:10.1038/nplants.2017.102, 2017.
- Wolf, S., Keenan, T. F., Fisher, J. B., Baldocchi, D. D., Desai, A. R., Richardson, A. D., Scott, R. L., Law, B. E., Litvak, M. E., Brunsell, N. A., Peters, W., and van der Laan-Luijkx, I. T.: Warm spring reduced carbon cycle impact of the 2012 US summer drought, *Proceedings of the National Academy of Sciences*, 113, 5880–5885, 2016.
395
- Wu, J., Kobayashi, H., Stark, S. C., Meng, R., Guan, K., Tran, N. N., Gao, S., Yang, W., Restrepo-Coupe, N., Miura, T., Oliviera, R. C., Rogers, A., Dye, D. G., Nelson, B. W., Serbin, S. P., Huete, A. R., and Saleska, S. R.: Biological processes dominate seasonality of remotely sensed canopy greenness in an Amazon evergreen forest, *New Phytologist*, 217, 1507–1520, 2018.
- Yang, Y., Donohue, R. J., and McVicar, T. R.: Global estimation of effective plant rooting depth: Implications for hydrological modeling,
400 *Water Resources Research*, 52, 8260–8276, 2016.
- Yi, K., Dragoni, D., Phillips, R. P., Roman, D. T., and Novick, K. A.: Dynamics of stem water uptake among isohydric and anisohydric species experiencing a severe drought, *Tree Physiology*, 506, 153, 2017.
- Yoshida, Y., Joiner, J., Tucker, C., Berry, J., Lee, J. E., Walker, G., Reichle, R., Koster, R., Lyapustin, A., and Wang, Y.: The 2010 Russian drought impact on satellite measurements of solar-induced chlorophyll fluorescence: Insights from modeling and comparisons with
405 parameters derived from satellite reflectances, *Remote Sensing of Environment*, 166, 163–177, 2015.
- Zaitchik, B. F., Macalady, A. K., Bonneau, L. R., and Smith, R. B.: Europe’s 2003 heat wave: a satellite view of impacts and land–atmosphere feedbacks, *International Journal of Climatology*, 26, 743–769, 2006.
- Zscheischler, J. and Seneviratne, S. I.: Dependence of drivers affects risks associated with compound events, *Science Advances*, 3, doi:10.1126/sciadv.1700263, 2017.
- 410 Zscheischler, J., Mahecha, M. D., Harmeling, S., and Reichstein, M.: Detection and attribution of large spatiotemporal extreme events in Earth observation data, *Ecological Informatics*, 15, 66–73, 2013.
- Zscheischler, J., Westra, S., Hurk, B. J. J. M., Seneviratne, S. I., Ward, P. J., Pitman, A., AghaKouchak, A., Bresch, D. N., Leonard, M., Wahl, T., and Zhang, X.: Future climate risk from compound events, *Nature Climate Change*, 8, 469–477, 2018.