LETTER

Hot moments in ecosystem fluxes: High GPP anomalies exert outsized influence on the carbon cycle and are differentially driven by moisture availability across biomes

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Abstract

The ‘hot spot-hot moment’ concept is a long-standing and popular framework often invoked to explain spatially or temporally variable rates of biogeochemical cycling. However, this concept has been rarely extended to ecosystem fluxes such as gross primary productivity (GPP), in part due to the lack of a quantitative definition of hot moments that can be applied to large flux datasets. Here, we develop a general statistical framework for quantifying hot moments in GPP and identify their spatial patterns and climatic drivers. Using 308 site-years of eddy covariance data from the FLUXNET2015 dataset spanning 32 U.S. sites, we found hot moments in GPP to comprise a disproportionate percentage of annual carbon (C) uptake relative to the frequency of their occurrence. For example, at five sites over 12% of annual C uptake occurred during the ~2% most extreme half-hourly or hourly observations of GPP. Hot moments were most quantitatively important for the C cycle in short-stature, arid ecosystem such as grasslands, woody savannas, and open shrublands, where these positive anomalies in GPP were caused by increases in moisture availability. In contrast, hot moments were less important for annual C uptake in more mesic ecosystems, where their occurrence was largely determined by high temperature and light availability. Our results point to a need to consider how short-term spikes in environmental conditions exert an outsized influence on annual GPP, and how future shifts in these conditions could impact the terrestrial C cycle.

1. Introduction

Ecosystem processes are inherently heterogeneous. In particular, biogeochemical processes exhibit heterogeneity both spatially and temporally due to the highly variable nature of resource supply and variation in the environmental conditions necessary for high rates of metabolic activity. For example, nutrient and energy cycling in many ecosystems is reliant on the hydrologic transport of limiting substrates to areas that can support rapid rates of metabolic activity (Davidson et al 1993, Boyer et al 2000, Vidon et al 2010). Additionally, spatial and temporal climate variability can result in ‘patchy’ (in space) and ‘flashy’ (in time) biogeochemical processes since the conditions required for active biogeochemical cycling (e.g. warm temperature, sufficient water supply) only occur during a limited subset of the year (Gebauer and Ehleringer 2000, Biederman et al 2017). Thus, spatial and temporal variability in process rates is an important aspect of ecosystem functioning that is contingent on both climate variability and biotic responses.

The ‘hot spot-hot moment’ concept aims to capture the importance of spatial and temporal heterogeneity in ecosystem processes (McClain et al 2003). This framework posits that small areas in space (‘hot spots’) and rare events in time (‘hot moments’) can exert a disproportionate impact on biogeochemical cycling relative to their frequency of occurrence. For example, this concept has been invoked to explain the high rates of biological activity in the rhizosphere (Kuzyakov and Blagodatskaya 2015), the complex interactions between geomorphology and resource supply that cause high variability in riparian nutrient cycling (Harms and Grimm 2008), and the ecological
role of vernal pools in mesic forests (Capps et al 2014). However, recent reviews have shown that this concept has been largely applied to interpret the patchy nature of nitrogen transformations in riparian and aquatic ecosystems (Vidon et al 2010, Bernhardt et al 2017) and has rarely been expanded to whole ecosystem carbon (C) fluxes such as gross primary productivity (GPP) (though see Leon et al 2014, Vargas et al 2018).

One central impediment towards extending this concept to GPP is the lack of a broad quantitative method for classifying hot spots or hot moments. Indeed, this paradigm has been most commonly invoked post-hoc to explain heterogeneous biogeochemical processes and thus there has been a notable lack of progress towards defining a hot spot or hot moment and quantifying its importance for overall ecosystem C balance (Bernhardt et al 2017). Additionally, spatial hot spots cannot yet be quantified in eddy covariance data due to the large—and ever changing—flux footprint, but the high temporal frequency (half-hourly or hourly) at which flux data are analyzed make the eddy covariance approach ideal for investigating hot moments. Due to these limitations, progress towards quantifying the heterogeneous nature of ecosystem C fluxes has been largely operationalized within the context of specific climatic events, most notably precipitation pulses in arid and semiarid ecosystems (e.g. Huxman et al 2004a, 2004b, Jenerette et al 2008, Potts et al 2006, Reynolds et al 2004). While this wealth of research has been invaluable for understanding how the intensity and timing of precipitation influences C cycling in grasslands and shrublands, these studies do not allow for an understanding of the specific meteorological conditions that give rise to hot moments in C fluxes, nor are they necessarily generalizable to other ecosystems or vegetation types that typically experience a more continuous distribution of precipitation.

Several studies have sought to characterize the distribution of ecosystem fluxes across a wide range of sites and quantify the importance of this variability for ecosystem functioning (Zscheischler et al 2014, 2016, Potts et al 2019). These studies have shown that fluxes are highly variable on short timescales in response to changing meteorological conditions and that this temporal variability is an important ecosystem property that partially controls interannual variability in GPP. However, a full mechanistic understanding of when, where, and why hot moments in GPP occur is still lacking, as is a standardized metric for quantifying hot moments in flux data. Considering that current projections indicate widespread increases in the variability of precipitation and temperature (IPCC 2012), understanding which meteorological conditions give rise to anomalies in ecosystem fluxes, and the impact of these anomalies on the broader C cycle, will improve our ability to forecast ongoing changes to the terrestrial C sink.

In this study, we expand the biogeochemical paradigm of ‘hot spots and hot moments’ by developing a statistical framework for identifying hot moments in eddy covariance data. Then, we quantify the role that these short-term, anomalously high periods of GPP play in the C cycle across the U.S. and assess their meteorological drivers. We ask:

(a) What is the quantitative importance of hot moments for the terrestrial C cycle?
(b) In which regions and ecosystems are hot moments most prevalent?
(c) What environmental conditions give rise to hot moments in GPP, and how does the importance of these drivers vary across biomes?

2. Methods

2.1. Data selection and processing

We compiled half-hourly or hourly flux and meteorological data from all U.S. FLUXNET sites in the FLUXNET2015 dataset (fluxnet.fluxdata.org). FLUXNET2015 is a global dataset of eddy covariance data, and associated meteorological measurements that are aggregated to various time scales and subject to standardized quality control, u* filtering, and gap-filling procedures (Papale et al 2006, Vuichard and Papale 2015). This dataset thus serves as a powerful tool for multi-site flux syntheses. All sites selected met the following criteria: each site had at least three years of Tier 1 data available and had not experienced any active human disturbance within the flux record (though irrigated agricultural sites were included). Our final dataset spanned 32 sites, 308 site-years, and 9 biomes (table 1). For this analysis, we focused on flux data that were u* filtered via a variable threshold (i.e. the _VUT_ data product) and partitioned using the daytime approach (Lasslop et al 2010). Some sites in FLUXNET2015 report temperature and vapor pressure deficit (VPD) measurements at different heights or soil water content measurements at different depths. In order to maximize comparability across sites, for all analyses we used meteorological data collected at the height of the primary gas analyzer when possible and the shallowest soil water content data available. We further converted each (half-)hourly rate of GPP (µmol CO₂ m⁻² s⁻¹) to a total amount of C uptake during that period (µmol CO₂ m² per 30 or 60 min). Growing season (defined below) mean, standard deviation (SD), and Pearson’s skewness of the distribution of GPP for all site-years are available in Table S1 (stacks.iop.org/ERL/15/054004/mmedia).

With these data, we sought to quantify the impact of anomalously high observations of GPP (i.e. hot moments) on the C cycle. To do so, we needed to strictly define what data to include in our analysis, since the definition of an anomaly in GPP is highly dependent on the distribution of fluxes in a given site-year. For example, including winter or nighttime...
data (where little or no GPP would occur) would severely right skew the distribution of fluxes in a given year and thus our definition of an ‘anomaly’ would be much less stringent. If we were to include nighttime and winter data, our highest ~20% of GPP values would largely represent observations from the nighttime during the growing season, precluding attribution of specific GPP anomalies to anything other than diurnal cycles in light and seasonal phenology. In order to constrain the flux record to times most conducive to GPP (and thus improve our ability to statistically discern the meteorological drivers of hot moments), we applied standard daytime and growing season cutoffs to the FLUXNET2015 data. First, at each site winter was defined conservatively (DOY before 70 or after 330) and all winter values were replaced with the wintertime mean GPP in order to reduce noise (Keenan et al 2014). Next, for each site-year we constructed smoothed curves of seasonal GPP and daily curves of incoming shortwave radiation using the loess function in R with a span of 0.5. The start of the growing season was considered the first time point at which this curve crossed a threshold of mean winter GPP +30% of mean smoothed GPP amplitude, and the end of the growing season was considered to be the last time point when it fell below this threshold (Keenan et al 2014). Daytime was quantified similarly, where the start of the day was considered the first time point at which a smoothed curve of growing season incoming shortwave radiation was greater than 30% of the mean amplitude and the end of the day was the last time this curve crossed below 30%.

2.2. Quantifying the importance of hot moments in GPP

We sought to quantify the degree to which (half-)hourly anomalies in GPP exerted an impact on annual GPP that was disproportionate to the frequency of their occurrence. Here, we draw on the concept developed by Darrouzet-Nardi and Bowman (2011) and extend their framework to ecosystem fluxes. For each value of GPP, we quantified its ‘rarity’ as a z-score (the number of standard deviations away from the mean). The importance of hot moments was then quantified using a loess function in R with a span of 0.5 to smoothen the seasonal GPP curve and then calculate the mean and standard deviation of GPP over each season. The z-score was calculated for each value of GPP

| Site | Biome | Site Years | MAT (°C) | MAP (mm) | Latitude | Longitude | Data DOI |
|------|-------|------------|----------|----------|----------|-----------|----------|
| US-AR1 | GRA | 4 | 14.4 | 657 | 36.43 | −99.42 | doi.org/10.18140/FLX/1440001 |
| US-AR2 | GRA | 4 | 14.3 | 620 | 36.64 | −99.60 | doi.org/10.18140/FLX/1440002 |
| US-ARM | CRO | 10 | 14.8 | 843 | 36.61 | −99.49 | doi.org/10.18140/FLX/1440003 |
| US-Blo | ENF | 11 | 11.1 | 1226 | 38.90 | −120.63 | doi.org/10.18140/FLX/1440004 |
| US-Cop | GRA | 7 | 9.7 | 323 | 38.09 | −109.39 | doi.org/10.18140/FLX/1440005 |
| US-GBT | ENF | 8 | 0.8 | 1200 | 41.37 | −106.24 | doi.org/10.18140/FLX/1440006 |
| US-GLE | ENF | 11 | 0.8 | 1200 | 41.27 | −106.24 | doi.org/10.18140/FLX/1440007 |
| US-Ha1 | DBF | 22 | 6.6 | 1071 | 42.52 | −72.17 | doi.org/10.18140/FLX/1440008 |
| US-KS2 | CSH | 4 | 21.7 | 1294 | 28.61 | −80.67 | doi.org/10.18140/FLX/1440009 |
| US-Los | WET | 15 | 4.1 | 828 | 46.08 | −89.98 | doi.org/10.18140/FLX/1440010 |
| US-Me6 | ENF | 5 | 7.6 | 494 | 44.32 | −39.32 | doi.org/10.18140/FLX/1440011 |
| US-Me2 | ENF | 13 | 6.3 | 523 | 44.45 | −121.56 | doi.org/10.18140/FLX/1440012 |
| US-Md6 | ENF | 5 | 7.6 | 494 | 44.32 | −121.61 | doi.org/10.18140/FLX/1440013 |
| US-Mb | WET | 5 | 15.9 | 432 | 38.05 | −121.76 | doi.org/10.18140/FLX/1440014 |
| US-Nc1 | CRO | 13 | 10.1 | 790 | 41.17 | −96.48 | doi.org/10.18140/FLX/1440015 |
| US-Nc2 | CRO | 13 | 10.1 | 789 | 41.16 | −96.47 | doi.org/10.18140/FLX/1440016 |
| US-Nc3 | CRO | 13 | 10.1 | 784 | 41.18 | −96.44 | doi.org/10.18140/FLX/1440017 |
| US-Nr1 | ENF | 16 | 1.5 | 800 | 40.03 | −105.55 | doi.org/10.18140/FLX/1440018 |
| US-Pfa | MF | 20 | 4.3 | 823 | 45.95 | −90.27 | doi.org/10.18140/FLX/1440019 |
| US-Prr | ENF | 5 | −2 | 275 | 65.12 | −147.49 | doi.org/10.18140/FLX/1440020 |
| US-Srg | GRA | 7 | 17 | 420 | 31.79 | −110.83 | doi.org/10.18140/FLX/1440021 |
| US-Srm | WSA | 11 | 17.9 | 380 | 31.82 | −110.87 | doi.org/10.18140/FLX/1440022 |
| US-Srv | MF | 14 | 3.8 | 826 | 46.24 | −89.35 | doi.org/10.18140/FLX/1440023 |
| US-Ton | WSA | 14 | 15.8 | 559 | 38.43 | −120.97 | doi.org/10.18140/FLX/1440024 |
| US-Tw1 | WET | 3 | 15.5 | 421 | 38.11 | −121.65 | doi.org/10.18140/FLX/1440025 |
| US-Umb | DBF | 15 | 5.8 | 803 | 45.56 | −84.71 | doi.org/10.18140/FLX/1440026 |
| US-Var | GRA | 15 | 15.8 | 559 | 38.41 | −120.95 | doi.org/10.18140/FLX/1440027 |
| US-Wc | DBF | 16 | 4 | 787 | 45.81 | −90.08 | doi.org/10.18140/FLX/1440028 |
| US-Ws | OSH | 8 | 17.6 | 320 | 31.74 | −110.05 | doi.org/10.18140/FLX/1440029 |
| US-Wc | DBF | 15 | 5.8 | 803 | 45.56 | −84.71 | doi.org/10.18140/FLX/1440030 |
| US-Wc | DBF | 15 | 5.8 | 803 | 45.56 | −84.71 | doi.org/10.18140/FLX/1440031 |
| US-Ws | OSH | 8 | 17.6 | 320 | 31.74 | −110.05 | doi.org/10.18140/FLX/1440032 |
| US-Ws | OSH | 8 | 17.6 | 320 | 31.74 | −110.05 | doi.org/10.18140/FLX/1440033 |
| US-Ws | OSH | 8 | 17.6 | 320 | 31.74 | −110.05 | doi.org/10.18140/FLX/1440034 |
| US-Ws | OSH | 8 | 17.6 | 320 | 31.74 | −110.05 | doi.org/10.18140/FLX/1440035 |
| US-Ws | OSH | 8 | 17.6 | 320 | 31.74 | −110.05 | doi.org/10.18140/FLX/1440036 |
from the growing season daytime mean each data point was), and quantified its influence on the C cycle as the percentage of total growing season GPP that individual (half-)hourly GPP value represented (hereafter, ‘impact’). In order to create a metric that illustrates the importance of hot moments in GPP for the broader C cycle, in each site-year we summed the impact of all points that crossed a 2-SD threshold of rarity. We hereafter refer to this percentage as ‘annual impact’. Thus, our metric of annual impact represents the percentage of growing season GPP due to hot moments (defined as values >2-SD away from the mean). We chose a 2-SD threshold in order to strike a balance between (1) having a sufficiently stringent cutoff so that hot moments are undoubtedly extreme events, and (2) not limiting our sample size if this threshold was too high. Moreover, 2-SD is a threshold that is well established in the literature to be indicative of severe climate anomalies across broad spatial scales (Anderegg et al. 2015, Huang et al. 2018, Wu et al. 2018, Kannenberg et al. 2019, Kolus et al. 2019).

2.3. Meteorological drivers causing hot moments in GPP
In order to assess the short-term meteorological drivers that cause hot moments in GPP, we conducted linear regressions within each site-year between impact and various meteorological data collected during that (half-)hourly period, assessing the strength of this relationship using Pearson’s correlation coefficient. We also quantified the longer-term climatic drivers behind annual impact by conducting linear regressions between climatic conditions in a given growing season (using the site-specific growing seasons as described above), mean annual temperature, mean annual precipitation, and annual impact. For some site-years soil water content data were unavailable (most commonly in wetland sites) and were thus excluded from the analysis.

3. Results and discussion

3.1. The importance of hot moments across biomes
Across all sites, we found that hot moments in GPP exerted an outsized influence on the C cycle relative to the frequency of their occurrence, as (on average) only 2.1% of observations accounted for 5.2% of total GPP during the growing season. The importance of hot moments partially arose due to right skewness in the distributions of GPP during the growing season (mean Pearson’s skewness = 0.22, Table S1), and thus annual impact (i.e. the sum of GPP values >2-SD away from the growing season mean) was highly correlated with the degree to which these distributions were right skewed (r² = 0.74, p < 0.0001). Mean annual impact was also quite variable across sites, ranging from 1.3% (at US-WI3) to 14.2% (at US-SRG). The importance of hot moments varied significantly across biomes, whereby arid, short stature ecosystems had the highest annual impact and wetlands and mesic forests had the lowest (figures 1 and 2). This confirms existing knowledge that fluxes in water-limited systems are highly variable (Reynolds et al. 2004, Leon et al. 2014, Potts et al. 2019) and further suggests that mesic ecosystems can exhibit high variability as well. Finally, the observation that these rare periods of GPP comprise a considerable percentage of growing season GPP across all biomes indicates that hot moments are quantitatively important for the C cycle.

The importance of hot moments (i.e. the size of annual impact) was loosely related to the mean annual temperature (r² = 0.15, p < 0.0001) and mean annual precipitation (r² = 0.11, p < 0.0001) across sites, indicating that hotter and drier ecosystems tended to have more variable distributions of GPP. However, annual impact was much more strongly controlled by climatic conditions within a given growing season (figure 3), and the strength of this relationship changed drastically depending on aridity. In arid sites (35% of sites, defined here as <600 mm mean annual precipitation), annual impact was positively related to growing season temperature (r² = 0.36, p < 0.0001) and vapor pressure deficit (r² = 0.40, p < 0.0001), and negatively related to growing season mean soil water content (r² = 0.24, p < 0.0001). In contrast, annual impact in mesic sites (>600 mm mean annual precipitation) was only significantly correlated with mean growing season vapor pressure deficit, but this relationship was weak (r² = 0.05, p = 0.001). Thus, hot moments were quantitatively most important for C fluxes at dry sites and comprised a larger percentage of growing season GPP during dry years at those sites. This highlights that anomalies in fluxes are likely influenced not only by mean site climate, but also by interannual weather variability (Potts et al. 2019, Xu et al. 2019). The extent to which this dynamic is due to climatic conditions (i.e. hot and dry conditions in already hot and dry sites are prone to suppress GPP) versus vegetation responses (i.e. the plants in arid grasslands, shrublands, and savannas are ecologically suited for high variable photosynthetic rates) could not be resolved with the available data. However, hot moments are often conceptualized as arising due to both the appearance of a limiting resource and the ability of the existing biota to take advantage of that resource, indicating that hot moments in GPP may be driven by both climate conditions and vegetation physiology.

3.2. Meteorological drivers of hot moments
We observed substantial correlations between the importance of hot moments and broad climatic factors—both in terms of mean site climate and variability in weather within a given season. To examine the drivers of these anomalously high periods of GPP in more depth, we conducted linear regressions between our impact metric (the proportion of
total growing season GPP contributed by an individual (half-)hourly flux and various meteorological variables within each site-year. We found that hot moments in GPP were associated with anomalies in temperature, vapor pressure deficit, soil water content, and light availability (i.e. incoming shortwave radiation), though the nature of this relationship differed across biomes (figure 4). In the arid, short stature ecosystems where hot moments contributed most to annual GPP, these periods of high GPP co-occurred with low temperature, low vapor pressure deficit, and high soil water content, indicating that a rapid increase in a particularly limiting resource (i.e. moisture) can drive high rates of photosynthetic activity. Fluctuations in light availability were poorly correlated with hot moments at these
Figure 3. Relationships between growing season mean temperature (Temp), vapor pressure deficit (VPD), and soil water content (SWC) and annual impact across all site-years. Arid ecosystems are considered as mean annual precipitation <600 mm while mesic ecosystems are defined as mean annual precipitation >600 mm. Trendlines represent a significant linear regression.

sites, likely due to the infrequent cloud cover and muted light-use efficiency response that is characteristic of many dry regions (Sun et al. 2000, Stocker et al. 2018). Further, we found that these relationships were weaker when using daily flux data to quantify hot moments, indicating that GPP hot moments in arid ecosystems may be partially driven by sub-daily fluctuations in air temperature and vapor pressure deficit (figure S6). Atmospheric evaporative demand and soil water availability are known to limit GPP (Sippel et al. 2018, Yuan et al. 2019). The observation that hot moments are controlled both by atmospheric demand and soil water availability likely reflects both the dual nature of moisture limitation in terrestrial vegetation (Novick et al. 2016, Sulman et al. 2017), and the fact that anomalies in vapor pressure deficit and soil moisture tend to co-occur (Anderegg et al. 2019, Zhou et al. 2019a, 2019b).

In contrast, hot moments in more mesic ecosystems were not linked to pulses of moisture availability, but instead were associated with high temperature and light availability. Considering that only daytime data were used in our analysis, these correlations could reflect the increased variability of cloud cover during the day in mesic ecosystems and the coupling of cloud cover and air temperature (Sun et al. 2000). Hot moments could also arise due to the influence of temperature and light availability separately. GPP is known to fluctuate due to anomalies in temperature (Desai 2014), chiefly during days with low temperature and light availability. Considering that only daytime data were used in our analysis, these correlations could reflect the increased variability of cloud cover during the day in mesic ecosystems and the coupling of cloud cover and air temperature (Sun et al. 2000). Hot moments could also arise due to the influence of temperature and light availability separately. GPP is known to fluctuate due to anomalies in temperature (Desai 2014), chiefly during days with low temperature and light availability. Thus, while high temperature was associated with hot moments in GPP, this trend could be driven by anomalous cold days inhibiting photosynthesis (thus shifting the GPP distribution to the left), rather than high temperature increasing GPP. Indeed, when quantifying hot moments using daily flux data, we still observed a strong positive relationship between temperature and our impact metric at more mesic sites (figure S6), indicating that hot moments in these biomes are associated with fluctuations in weather that occur on longer time scales than hot moments in arid ecosystems. The direct influence of short-term reductions in radiation on GPP is less well established, and is likely dependent on a suite of complex factors such as existing light limitation and competition (Craine and Dybzinski 2013), the capacity of vegetation to change light-use efficiency (Alton et al. 2007, Jenkins et al. 2007), and how cloud cover alters diffuse versus direct light (Min and Wang 2008, Still et al. 2009, Cheng et al. 2016). However, the ecosystems where hot moments co-occurred with high light availability tended to be dense and wet, which are ecosystems where C uptake is known to be somewhat limited by light (Graham et al. 2003, Oliphant et al. 2011). Ultimately, understanding the interactions between short-term fluctuations in temperature, light, and GPP may be important in mesic ecosystems, but the relatively low annual impact at these sites suggests that temperature and light anomalies—while quantitatively important for causing hot moments—are not a primary factor influencing interannual variation in GPP at these sites.

3.3. Sensitivity analysis: robustness of results to post-processing algorithms

The possibility exists that our results may be partially due to artifacts inherent in the post-processing procedures that FLUXNET2015 uses (i.e. gap-filling and flux partitioning algorithms), rather than actual anomalous GPP events. To quantify potential biases due to post-processing, we conducted our analysis using GPP partitioned with both the nighttime method (Reichstein et al. 2005) and the daytime method (Lasslop et al. 2010). Our results using both partitioning approaches were quantitatively similar, and we observed a strong relationship between annual
Figure 4. Correlation plot representing mean Pearson’s correlation coefficient across site-years of the regression between impact and mean growing season temperature (Temp), vapor pressure deficit (VPD), soil water content (SWC), and incoming shortwave radiation (SW_IN), binned by IGBP land cover type. Biomes are ordered according to mean growing season VPD (low to high). Color represents the Pearson’s correlation coefficient (red is a negative relationship, blue is a positive), while size represents the strength of the relationship (larger dots are a stronger correlation). IGBP codes are described in table 1. The missing value arose since no wetland sites reported SWC values.

impact calculated with either daytime-partitioned or nighttime-partitioned data (figure S1, p < 0.0001, \( r^2 = 0.61 \)). Thus, we focused on daytime-partitioned data since (1) nighttime-partitioned data can have negative values for GPP which slightly skew our calculations of impact, and (2) the daytime approach has recently been shown to be less prone to biases in flux partitioning related to light inhibition of respiration during the day (Keenan et al 2019), which becomes especially important since our analysis was only conducted on daytime data. Additionally, our results were the same after omitting any medium or poor quality gap-filled data (a quality flag of >1 in the FLUXNET2015 dataset, figure S2, p < 0.0001, \( r^2 = 0.87 \)), indicating that FLUXNET gap-filling algorithms were unlikely to have caused hot moments in GPP. We also acknowledge the possibility that hot moments in GPP could be driven by noise in (half-)hourly fluxes or short-term atmospheric transport processes. To circumvent these issues, we replicated our analyses using the daily FLUXNET2015 product and found nearly identical results (figures S3–S6). Since the meteorological drivers of hot moments vary significantly at sub-daily scales (most notably vapor pressure deficit), we focused on half-hourly or hourly data except where noted. Additionally, we explored how altering the thresholds for defining daytime and the growing season influenced our results. We found that altering our definition of a day or growing season did not alter our results, as annual impact calculated with the 30% thresholds described in the methods was strongly correlated with annual impact calculated using thresholds of 20% and 40% (figures S7–S8, all \( r^2 \) between 0.91 and 0.98). Finally, we acknowledge that our choice of a 2-SD cutoff for defining a hot moment is indeed arbitrary. Thus, we also used a more stringent rarity cutoff of 3-SD, which increased mean annual impact by 23% and did not qualitatively alter our results (figure S9). These sensitively analyses indicate that our results were highly robust to methodological choices pertaining to data processing and selection.
4. Conclusions

Here, we have developed a statistical framework for identifying hot moments in eddy covariance data and quantified their importance for ecosystem C uptake. Hot moments comprised a significant percentage of growing season GPP across the U.S. and were particularly impactful for the C cycle in the arid, short stature ecosystems of the U.S. southwest. In these ecosystems, hot moments were associated with short-term increases in moisture (both in the soil and atmosphere), while in more mesic ecosystems, periods of high GPP were linked with high temperature and light availability. In general, our results point to the need to consider how the interactions between various limiting resources influence anomalously high periods of GPP across a range of terrestrial biomes. Further, these results indicate that widespread increases in temperature (Williams et al 2013) and atmospheric demand (Yuan et al 2019), coupled with decreases in soil moisture (Dai 2013), could have the consequence of altering the prevalence and importance of hot moments, as could the shifts in species composition underway across much of the U.S. (Jiang et al 2013, Fei et al 2017). Broad changes in climate and vegetation composition may significantly alter the response of terrestrial ecosystems to climate variability in ways that fundamentally change the temporally heterogeneous nature of GPP.

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Data availability statement

No new data were created or analyzed in this study.

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