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Abstract

The terrestrial biosphere is a key component of the global carbon cycle and is heavily influenced by climate. Climate variability can be diagnosed through metrics ranging from individual environmental variables, to collections of variables, to the so-called climate modes of variability. Similarly, the impact of a given climate variation on the terrestrial carbon cycle can be described using several metrics, including vegetation indices, measures of ecosystem respiration and productivity and net biosphere-atmosphere fluxes. The wide range of temporal (from sub-daily to paleoclimatic) and spatial (from local to continental and global) scales involved requires a scale-dependent investigation of the interactions between the carbon cycle and climate. However, a comprehensive picture of the physical links and correlations between climate drivers and carbon cycle metrics at different scales remains elusive, framing the scope of this contribution. Here, we specifically explore how climate variability metrics (from single variables to complex indices) relate to the variability of the carbon cycle at sub-daily to interannual scales (i.e. excluding long-term trends). The focus is on the interactions most relevant to the European terrestrial carbon cycle. We underline the broad areas of agreement and disagreement in the literature, and conclude by outlining some existing knowledge gaps and by proposing avenues for improving our holistic understanding of the role of climate drivers in modulating the terrestrial carbon cycle.

1. Background

The carbon cycle (C-cycle) is the result of complex biogeochemical processes affecting the exchange and storage of carbon (C) among the different components of the Earth System. It significantly affects the atmospheric concentrations of CO₂ and other greenhouse gases, as well as key ecosystem services such as forest and crop productivity and, more generally, the exchanges of energy and water between the Earth’s surface and the atmosphere. The terrestrial biosphere is a major component of the global C-cycle (Ciais et al 2013), and is heavily influenced by climate variability on timescales ranging from hours to decades and longer (e.g. Urbanski et al 2007, Pappas et al 2017). In turn, the control exerted by the C-cycle on atmospheric composition and surface-atmosphere fluxes implies that changes in the C-cycle can affect climate on a variety of scales (e.g. Adams and Piovesan 2005). Climate and the C-cycle are therefore tied into complex, multi-scale and multi-process feedback loops. A robust understanding of this host of interactions is necessary both in the short-to-medium term, to elucidate the mechanisms driving natural climate and ecosystem variability, and in the longer term, to make well-informed predictions of future planetary change (Zscheischler et al 2017).

C-cycle-climate links are the subject of a wide body of literature based on observational data, controlled experiments and analytical and numerical models (e.g. Piao et al 2013, Friedlingstein et al 2014, Zhang et al 2016, Zhang et al 2017, Zscheischler et al 2017). Nevertheless, while accounting for a large share of the inter-annual variability in atmospheric CO₂ fluxes, the terrestrial C-cycle remains the least constrained component of the global C budget (Le Quéré et al 2013).
In particular, our understanding of the effect size and sign of climate drivers across different spatial and temporal scales is still incomplete.

Climate variability can be diagnosed through a wide variety of metrics, ranging from individual environmental variables, such as temperature or precipitation, to multi-variate indices, such as drought indices (e.g. Vicente-Serrano et al. 2010), to the so-called climate modes of variability—namely recurrent oscillatory or semi-oscillatory atmospheric and/or oceanic patterns (e.g. Hurrell et al. 2001). Each of these metrics highlights specific processes and spatial and temporal scales in the atmosphere and oceans. In turn, the effects of a given climate variation (as summarized by one or more metrics) on the C-cycle can be described using a large number of diagnostics, including vegetation indices, ecosystem respiration and productivity measures and net biosphere-atmosphere fluxes. Each of these can be further determined from a variety of different in situ and remote measurements—capturing dynamics occurring at different spatial and temporal scales. Understanding to what degree climate variability, by affecting specific processes, can predict C-cycle patterns at a given scale is therefore far from trivial.

Here, we review the current knowledge on the links between climate drivers and the terrestrial C-cycle. We specifically address the extent to which correlations between individual climate and C-cycle metrics have been investigated, and the level of agreement across studies. The focus is on sub-daily to inter-annual timescales and on Europe.

We ultimately aim to present the reader with a critical summary of our current knowledge on the topic and propose avenues for future research. This effort is motivated by the need to: (i) quantify C-cycle–climate interactions across scales to objectively evaluate Earth System Models used for projecting the global future; and (ii) identify areas of broad agreement or disagreement and (iii) existing knowledge gaps in the literature.

In this context, Europe emerges as a region of interest due to the considerable uncertainty in both estimates of the present-day net C uptake by the European terrestrial biosphere (e.g. Reuter et al. 2017) and projections of the European C-cycle under future climates (e.g. Morales et al. 2007). Indeed, raw model estimates of climate change impacts on the European C-cycle deviate significantly from those issued from emerging constraints approaches (Mystakidis et al. 2016). This does not detract from the value of similar reviews focussing on other regions such as the tropics or the third pole that are, however, beyond the scope of this contribution.

After detailing the review’s scope and approach, we summarise the different climate and C-cycle metrics discussed here, to provide a self-contained one-stop reference for readers from both the climate and biogeochemical cycles domains (section 2). Next, we provide a brief quantitative overview of the approaches and spatio-temporal focus of the literature included in this review (section 3), before summarising and discussing it based on the timescale of interest (section 4). We allow some overlap between the different sub-sections to avoid artificially splitting the discussion of processes relevant at multiple timescales. For each timescale, we discuss the explanatory power of different classes of climate metrics (from single variables to complex variability indices) and, where relevant, spatial scales. We conclude with a critical discussion of the state-of-the-art and suggestions for future research (section 5).

2. Materials and methods

2.1. Scope of the review

The review focuses on the climate drivers of the variability of the terrestrial C-cycle in Europe, on sub-daily to interannual timescales. We consider variability in the sense of behaviour of the system in a quasi-equilibrium state, while we do not discuss long-term trends linked to paleo-climatic processes or anthropogenic forcing—i.e. those aspects changing the statistical properties of the system over multi-decadal to longer timescales. Timescales are defined based on the physical link between the climate driver and the metric used to quantify the C-cycle variability, as opposed to the timescale of the variability itself. For example, if changes in summertime soil moisture affect the same-season C fluxes, and thus lead to year-to-year changes in the net C flux of a given region, we consider the link between soil moisture and C fluxes as a seasonal process. However, if the summertime soil moisture in a given year affects the C fluxes of the following year’s growing season, then we consider the link between soil moisture and C fluxes to be an interannual process. This choice is motivated by the fact that the timescales of the physical drivers of C-cycle variability are objective, although they may not always be easy to determine. Results related to single climate and C-cycle extreme events are only briefly discussed. While events in the tails of the distribution may be locally or regionally very important (e.g. Ciais et al. 2005, Zscheischler et al. 2014), they are often dominated by distinct physical processes, and thus merit a detailed discussion beyond the scope of the present review. For an overview of the role of climate extremes on the C-cycle, we refer the reader to Reichstein et al. (2013) and Sippel et al. (2018).

Finally, we discuss and contextualise the results of papers with a primarily observational emphasis, and do not provide a review of modelling studies.

2.2. Literature search

We conducted a systematic search of the peer-reviewed literature discussing the terrestrial C-cycle in Europe and climate—terrestrial C-cycle links. The first step was a search using the Web of Science (Thomson Reuters) engine, performed in May 2018. The following general keywords were used, to ensure including publications from a broad range of relevant sub-disciplines: Terrestrial Carbon Cycle + Europe
Keywords: Terrestrial Carbon Cycle + Europe

Keywords: Terrestrial Carbon Cycle + Climate variability

A total of 88 references included in the quantitative analysis

Figure 1. Flow chart of the literature review process.

(213 results) and Terrestrial Carbon Cycle + Climate Variability (881 results). The first article of the resulting list was published in 1991; 86% of the articles were published in or after 2005. A caveat of choosing general keywords, as opposed to more detailed terms referring to specific geographical domains, metrics or processes, is that our search may have overlooked relevant publications with a specific focus. Starting from our search results, we then removed doubles and excluded articles: (i) discussing primarily model output or focussing on the validation and/or development of numerical models; (ii) analysing aquatic ecosystems or the aquatic C-cycle; (iii) with an explicit focus on geographical regions outside of Europe; (iv) analysing palaeoclimatic variations in the C-cycle or; (v) the impact of anthropogenic climate change on the C-cycle. Articles focussing on the plot or smaller scale or on specific plant species were retained only when they provided additional insights into results of studies focussing on larger spatial scales. Articles focussing on individual extreme events were generally excluded, except for a small number that either provide a comprehensive review of the latter field (see section 2.1) or seminal results which are relevant in a broader C-cycle variability context. These last two selection steps were performed at the authors’ discretion. The above resulted in a total of 63 articles being retained. Additional relevant articles were identified by the authors through the reference lists of the initial group of selected articles, through the ‘cited by’ functions of Google Scholar and Web of Science, and during the peer-review process. This partially obviates the shortcoming discussed above concerning the choice of keywords. A final list of 88 articles is therefore included in the quantitative analyses in sections 3 and 4. A schematic of this process is provided in figure 1. The reference list additionally includes articles providing useful background material on climate variability or the terrestrial C-cycle, review articles as well as some articles that were excluded in steps (i)–(v) above on the basis of their main focus, but presented parts of the analysis which were relevant to specific points of the discussion in section 4. An example are studies conducted outside of Europe investigating climate drivers, biomes or ecosystems relevant for the latter domain.

2.3. Metrics of climate variability

There is no single definition nor any universally accepted measure of climate variability. We outline here the climate variability metrics discussed in section 4.

2.3.1. Single observables

Single observables are measurable variables (more precisely, quantities) of the climate system. Some commonly used observables are temperature, wind, humidity and precipitation. Means or extremes of individual observables can be of direct relevance to biological and ecological processes; for example: annual mean temperature, maximum and minimum temperatures of the warmest and coldest months, etc.

2.3.2. Multivariate metrics

Multivariate metrics combine individual variables. These metrics therefore describe properties of the climate system that are not directly measurable as a single physical quantity. For example, widely used drought indices often combine temperature, precipitation and a number of additional variables depending on their complexity (e.g. McKee et al 1995, Vicente-Serrano et al 2010). Another example of particular relevance to the terrestrial C-cycle is vapour pressure deficit (VPD), namely the difference between the moisture in the air and how much moisture the air could hold if it were saturated.
2.3.3. Climate modes of variability
These climate metrics refer to recurrent climate patterns, typically oscillatory or semi-oscillatory in nature. The modes of variability are often discussed in combination with climate teleconnections, namely systematic links between geographically remote climate anomalies (Glantz et al 1991). The interest in such patterns is that they typically correspond to specific regional climate anomalies, and therefore provide a convenient summary of complex changes in several observables. To express the level of activity and phase of these patterns in a format amenable to analysis, they are often expressed in terms of numerical indices (hereafter referred to as Climate Indices). One of the most widely-studied modes of variability, which also has a large impact on the European C-cycle, is the North Atlantic Oscillation (NAO; Hurrell et al 2001; see also section 4.2). The NAO, which is also an example of teleconnection, describes fluctuations in sea-level pressure between the semi-permanent Icelandic low pressure and the semi-permanent Azores high pressure. Generally, a positive NAO during the winter months is characterized by enhanced westerly winds across the North Atlantic, leading to wetter, stormier and milder climate conditions over the northern part of Europe and drier conditions over the Mediterranean area. We summarise the climate modes of variability discussed in the present review in table 1.

2.4. Carbon cycle metrics
We outline here the C-cycle metrics discussed in section 4, which we group according to whether they are direct or indirect measures of the C-cycle. There are some inconsistencies in their precise definitions in the literature, such that the definitions we provide here do not match exactly some of those found in the cited literature.

2.4.1. Direct metrics
The most commonly used quantities to monitor and describe the C-fluxes and balances in ecosystems are: (i) Gross Primary Productivity (GPP), (ii) Gross Ecosystem Productivity (GEP), (iii) Net Primary Productivity (NPP), (iv) Net Ecosystem Exchange (NEE) or Net Ecosystem Productivity (NEP), (v) Net Biome Productivity (NBP) and (vi) Ecosystem Respiration (Re)—including both autotrophic (Ra) and heterotrophic respiration (Rh).

GPP refers to the total amount of C fixed in the process of photosynthesis by plants in an ecosystem. Although GPP and GEP are often used interchangeably, they do differ to some extent, with GEP containing a photosynthetic component that is not included in GPP (Waring and Running 1998). NPP is GPP minus the amount of C respired by plants themselves (Ra) so that NPP refers to the actual net production of organic C by plants plus C export in organic form such as roots and mycorrhizal transfer. NEP is defined as GPP minus ecosystem respiration (or NPP minus Rh), whereas NEE is the net CO2 flux from the ecosystem to the atmosphere (Chapin et al 2006). NEP and NEE differ in two ways. First, NEP is conventionally positive when the ecosystem is acting as a CO2 sink, while NEE is negative. Second, NEE accounts for CO2 emissions that are not exchanged with the atmosphere as NEE—e.g. CO2 from respiration that dissolves in water and is exchanged via dissolved inorganic C. An estimate of the NBP is provided by the difference between NEE and C losses due to disturbances such as fire, harvest of ecosystem products, and exchanges of compounds other than CO2 (Schulze et al 2000, Chapin et al 2006). Finally, Ra is the respiration by autotrophic organisms—chiefly plants—while Rh refers to the respiration by heterotrophic organisms. Rh is dominated by respiration from organisms living in the soil and the litter layer and decomposing organic matter that has reached the soil as litter fall, root turnover, root exudation, mortality of organisms and faecal matter. Rh also includes C released in the decomposition of standing dead trees and coarse woody debris. The sum of Ra and Rh is also referred to as total CO2 efflux or simply ecosystem respiration. Respiration is also often partitioned between total soil respiration (Rs) and above-ground plant respiration (Barba et al 2018), where Rs includes both autotrophic (root) and heterotrophic (microbial) components.

C fluxes have been extensively measured by gas exchange chambers at leaf-to-plant scales. However,
Re and allocation of fixed C at plot level are still expensive to measure and remain poorly quantified (Anav et al 2015). NPP can also be measured at plot scale, but in practice it is a complex, labour-intensive process in which accumulation and turnover of biomass from different plant components (roots, leaves, shoots, etc) should be accounted for over a given period of time. This in turn compromises the accuracy of NPP assessments at plot scale. At plot-to-landscape scales (0.1–2 km), there exist more than 600 tower stations worldwide for the measurement of CO₂ fluxes between the ecosystem and the atmosphere based on the eddy covariance (EC) technique (Baldocchi et al 2001, Friend et al 2007). These measurements incorporate a wealth of complex soil processes as well as the signal of vegetation structure and the interactions between different ecosystem components. Flux towers measure NEE continuously, and several algorithms have been developed to separate Re and GEP from NEE at ecosystem scale. At landscape-to-regional or global scales, these C fluxes cannot be measured directly, so upscaling and alternative measuring techniques are needed. The steadily increasing number of Earth observations, in particular since the start of the satellite era, has allowed researchers to largely overcome this limitation. Thus, combining CO₂ fluxes form EC towers with remotely-sensed variables (such as the vegetation indices discussed below) provides a basis to robustly upscale surface-atmosphere CO₂ fluxes to larger areas (Jung et al 2011). Many remote sensing-based GPP products are available to conduct regional to global scale analyses (see Anav et al 2015, for a review).

2.4.2. Indirect metrics
Other quantities, while not directly referring to C fluxes and balances, can provide valuable information on the terrestrial C-cycle. The hydrological cycle and its variability significantly influence the C-cycle of terrestrial ecosystems. In this sense, Water Use Efficiency (WUE)—the rate of C uptake per unit of water lost through evapotranspiration—is an important indicator for understanding how the hydrological and C cycles interact. Spatio-temporal variations of this ratio inform on how the coupled C-water cycles of terrestrial ecosystems change in response to climate variability (e.g. Xue et al 2015, Sun et al 2016, Yang et al 2016).

The C balance can be also monitored via observables that serve as proxies for different C fluxes and budgets. For example, the Leaf Area Index (LAI) represents the projected area of leaves over a unit of land. A long-term global LAI dataset is critical to monitoring global vegetation dynamics. Likewise, vegetation indices based on plants’ reflected and emitted radiation are amongst the most widely used C-cycle proxies since they are typically well-correlated with GPP (e.g. Wylie et al 2003). A range of such indices exist, the most widely-used of which is the Normalized Difference Vegetation Index (NDVI) (Cramer et al 1999, Running et al 1999, Parazoo et al 2014). All these indices have the advantage of being measurable from satellite platforms, thus allowing large-scale analyses. CO₂ records at Mauna Loa (Hawaii; Wang et al 2014a, 2014b) have also been used to constrain the global terrestrial C-cycle.

3. Climate drivers and scales of carbon cycle variability in the literature
The literature included in the review spans a broad range of approaches and spatio-temporal scales. Figure 2 shows how frequently a certain category occurs in our dataset. The relative frequencies refer to studies falling into a given category, but the same study may cover more than one category. Most studies retrieved data from EC stations, direct ground measurements and satellite remote sensing (figure 2(a)). These methods are well-suited to regional scale analyses (after spatial averaging of plot-scale EC data) investigating seasonal to annual timescales (figures 2(b) and (c)). Indeed, the regional analyses account for approximately 50% and the seasonal to annual timescales account for approximately 72% of all the approaches reported in the studies considered here, although this fraction varies considerably for different C-cycle proxies. The C-cycle proxies most frequently analysed encompass NEE/NEP, GPP, various respiration fluxes, and proxies of leaf area (figure 2(d)). These are spread relatively evenly across plant functional types (figure 2(e)), although this result is partially affected by the large number of studies (nearly 50%) discussing large-scale (e.g. with remote sensing products) or multi-site analyses including all types of vegetation. In 64% of the cases, univariate correlations were proposed to explain trends in C-cycle proxies. Very few analyses attempted to explain C-cycle variability using only climate variability indices (6%), although a larger number of studies has combined these with correlations based on meteorological variables (36%). The most frequently used indices were ENSO and the NAO, followed by the AO (figure 2(f)).

4. A synthesis of emerging climate drivers of carbon cycle variability
Figure 3 shows the relative number of publications that support a given response of a C-cycle proxy to specific climate variability metrics. The correlations in the figure are pooled from all studies in our database, regardless of their specific spatial and temporal scale. While most C-cycle proxies tend to be positively correlated with temperature and precipitation, responses to soil moisture, radiation, and climate indices are more variable. However, the limited sample size in some cases does not allow reaching solid
conclusions. A detailed discussion of the key mechanisms behind such responses, and in particular those at the basis of the contrasting signs of some correlations across studies, is provided in sections 4.1–4.3.

4.1. Hourly to seasonal drivers

Even on very short timescales, climatic factors strongly govern the C-cycle variability, including C exchanges with the atmosphere. We discuss respiration, gross productivities and net productivities separately.

4.1.1. Respiration

Respiration is mostly positively correlated with precipitation, soil moisture and temperature (figure 3(b)). Soil CO₂ fluxes typically increase within minutes after a precipitation pulse, and decline slowly during the subsequent dry periods (e.g. Jarvis et al 2007, Talmon et al 2011). This rapid change has been ascribed to consumption of dead microbial biomass or microbial by-products released at rewetting (osmolytes), or by utilization of labile C made available by increased pore hydraulic connectivity or aggregate disruption in re-wetted soil (Homyak et al 2018). These respiration pulses have been identified by in situ eddy covariance measurements, rainfall manipulation experiments and laboratory incubators (e.g. Lee et al 2004, Xu and Baldocchi 2004, Huxman et al 2004b, Jassal et al 2005, Ivans et al 2006, Jarvis et al 2007, Jongen et al 2011, Talmon et al 2011). Drier soils typically show a stronger response to wetting (Talmon et al 2011, for a dry Mediterranean climate), including large changes in C mineralisation rates (Birch 1964, Fischer 2009). A consequence of this is that the C outflux due to soil wetting can significantly impact the net C gain in Mediterranean environments (Jarvis et al 2007).

The persistence of the change in C release rate induced by soil wetting is likely directly controlled by the substrate moisture content. For short-lived precipitation pulses and conditions favouring rapid litter drying, the flux enhancement can last less than 1 h (Lee et al 2004), whereas strong precipitation events coupled with low soil evaporation can lead to multi-day respiration peaks (Xu et al 2004). These respiration pulses are also modulated by other environmental...
variables, such as overlying vegetation and microtopography (Huxman et al 2004b). The precipitation pulse size can regulate the C balance, by determining the temporal duration of activity for different components of the biota (Huxman et al 2004b). Weak pulses affect primarily Rh. Larger pulses may affect plant activity, leading to periods of C accumulation after the initial C outflux via respiration, with response times of up to several weeks (Noormets et al 2008). Conversely, respiration is depressed at low soil moisture and when plant activity fuelling rhizosphere microorganisms is low (Zhang et al 2018).

Soil respiration generally increases with (soil) temperature, but temperature, precipitation and soil moisture interact in defining respiration rates (Davidson et al 1998, Moyano et al 2013, Hursh et al 2017). In a range of Northern Hemisphere biomes, soil respiration is well correlated with average temperature on monthly timescales, with the slope of this relation being affected by water availability (Law et al 2002). The relative importance of the two controls varies greatly, with soil moisture dominating in seasonally-dry and temperate regions (Davidson et al 1998, Law et al 2002, Jarvis et al 2007, Noormets et al 2008, Talamon et al 2011).

The consensus on the above correlations is generally high, despite some outlying results in the literature. For example, Re did not correlate with changes in temperature (soil or air) and responded weakly to changes in soil moisture in a mixed deciduous forest, with relatively high and uniform precipitation (Urbanski et al 2007). This unexpected result possibly reflects diverging responses from the different soils present within the footprint of the flux tower used in the study.

4.1.2. Gross productivities

VPD, temperature and soil moisture are significant controls of GPP and GEP over large parts of the globe (figure 3(c)). In general, for a given VPD, high soil moisture promotes gas fluxes and C fixation (unless water logging occurs). For a given soil moisture, high VPD increases transpiration rates while decreasing C uptake by reducing stomatal conductance to water vapour and CO2, resulting in increased GPP/stomatal

![Figure 3. Relative frequencies of occurrence of correlations (see legend) between climatic variables (temperature, precipitation, soil moisture (SM), and solar radiation (Rad)) or indices (NAO and AO are combined), and C-cycle proxies: (a) leaf area or other measures of greenness, (b) soil or ecosystem respiration, (c) GPP, and (d) NEP or -NEE. In the legend, correlations that are positive in Northern regions and negative in Southern regions (Pos. N, neg. S) or vice versa (Pos. S, neg. N) are separated from correlations valid over the whole or the majority of the study area (Negative, No correlation, Positive); ‘Other’ indicates correlations that vary spatially or temporally and cannot be grouped in the above main categories. Numbers refer to the sample size for each pair of variables. For clarity, only the correlations emerging with the two most studied climate indices (ENSO and NAO/AO; see figure 2(f)) are reported.](image-url)
conductance ratios (Q Zhang, personal communication). Temperature acts as an additional factor affecting directly photosynthetic capacity and indirectly gas fluxes by modulating VPD. In Europe, soil moisture controls are dominant in the dry summers of the Mediterranean region, VPD is key over parts of central Europe and minimum daily temperature is most relevant over Scandinavia, parts of Eastern and South-Eastern Europe and higher elevations (Madani et al 2017; see also Seddon et al (2016), using a vegetation productivity metric related to GPP).

On short timescales (hourly to daily) soil moisture and VPD are largely decoupled. Eddy covariance fluxes show that VPD constrains evapotranspiration (ET) and stomatal conductance more than soil moisture during periods of hydrological stress in a range of wet and mesic biomes (Novick et al 2016). On the contrary, in arid and semi-arid ecosystems soil moisture levels constrain gas fluxes more than VPD (Madani et al 2017), albeit in a potentially nonlinear fashion. Noormets et al (2008) found that during dry years in a mixed oak woodland, a maximum of GEP emerged at intermediate soil moisture levels—likely due to the influences of water stress for low moisture and light limitation for high moisture.

In water-stressed conditions, VPD is generally negatively correlated with GEP and WUE (e.g. Law et al 2002, Noormets et al 2008). In the absence of water stress, the opposite correlation can emerge, with a higher VPD promoting GPP (e.g. Madani et al 2017 for northern temperate biomes). This relation at high latitudes is largely due to the strong correlation between VPD and temperature, which is itself positively correlated with photosynthesis and thus GPP there. The strength of the temperature control on GPP in the mid- to high-latitudes can vary with biome; for example, the GPP of deciduous forests increases more strongly with warm temperatures during the early growing season than that of needle leaf forests (Welp et al 2007).

4.1.3. Net productivities

Net C uptake responses combine the effects of temperature and hydrological controls on its two components: respiration and gross productivity. Generally, environmental conditions favouring photosynthesis over respiration promote net C gains—e.g. low VPD and temperature close to the photosynthetic thermal optimum. Nevertheless, even within the same ecosystem and biome, there can be significant differences in the C-cycle responses to a given forcing, as the result of the competing responses of Re and gross productivity (see Law et al 2002, Urbanski et al 2007; see also section 4.2). These different responses make extrapolation of plot or local-scale results to larger domains challenging.

Changes in specific humidity and precipitation are associated with changes in net CO₂ uptake at hourly to monthly scales across a broad range of mid- and high-latitude biomes (Allard et al 2008, Fang and Michalak 2015, Ishizawa et al 2016), including grasslands (e.g. Nagy et al 2007) and forests (e.g. Allard et al 2008). Precipitation and summertime net CO₂ uptake correlate positively over northern Eurasia with a one-month lag (Ishizawa et al 2016). This lag likely captures the enhanced vegetation productivity rather than the Rh response. At shorter timescales (daily to multi-daily), the latter dominates and the opposite correlation emerges, with rainfall events followed by net C release (e.g. Nagy et al (2007) looking at the growing season of a European grassland). Net productivities can also be sensitive to precipitation variability within a season, given an unchanged net precipitation amount. Grasslands display a higher NPP variability than many other biomes, and are thus of particular interest in this context (e.g. Knapp and Smith 2001, Huxman et al 2004a). The response to increasingly intermittent and intense precipitation ranges from decreased NPP in mesic grasslands (Knapp et al 2002) to strong NPP increases in mixed and semi-arid grasslands (Heisler-White et al 2009). These contrasting responses are likely due to the effects of soil moisture variability (even when the mean soil moisture is the same) on plant water stress. Even considering the same grassland plot, NEE responses can vary significantly. A given plot can display monthly-mean NEE responses of opposite sign when irrigated throughout the growing season, and the same holds for grassland plots at different elevations, even when they have very small differences in mean growing season soil moisture (Risch and Frank 2007). Thus, the response of NEE and NPP to precipitation variability is ultimately governed by concurrent soil moisture, especially in semi-arid ecosystems.

Temperature and solar radiation can also significantly affect the net C uptake at hourly to monthly timescales. For example, temperature and photosynthetically active radiation alone can explain the bulk of the hourly to seasonal NEE variability, especially in the early part of the growing season, in mixed deciduous forests (Urbanski et al 2007). However, site-specific factors such as terrain slope can significantly modulate the linkages between daily temperature and ecosystem fluxes (Re, GEP and NEP), as observed in a variety of mid-latitude biomes (Reyes et al 2017).

An intuitive summary of this complex web of interactions is provided by Pappas et al (2017), who constructed an ecosystem variability measure by combining a range of C-cycle metrics. The analysis of the spectral variability in climate drivers and C-cycle metrics showed that ecosystem variability in extratropical forests is confined within a hydro-meteorological envelope, with precipitation defining the lower limit and energy (namely, temperature and radiation) the upper limit of plausible variability regimes.
The occurrence of extreme events, lying beyond the variability experienced within every season, can either replicate the C-cycle responses described above, albeit with larger magnitudes, or lead to more complex responses. For example, individual severe rainstorms were shown to account for a large fraction of net annual C losses in mid-latitude forests (Lee et al 2004), in agreement with the links between precipitation and soil processes discussed above. At the same time, storms and the resulting tree damage can lead to increased amounts of woody debris on the forest floor, in turn increasing Rh and affecting C uptake capacity on monthly to interannual timescales, with changes beyond those expected from the precipitation response alone (Lindroth et al 2009, Liu et al 2011).

4.2. Seasonal to annual drivers
We first consider how climate variability can affect the seasonality of the C-cycle through its impact on plant phenology and the conditions of peak plant productivity. Next, we discuss separately respiration, gross productivities, net productivities and climate indices. The latter provide a unique perspective on the impact of regional multivariate climate anomalies on the C-cycle.

4.2.1. Phenology
The complex interplay between climate conditions and plant phenology has been discussed extensively in the literature (e.g. Chmielewski and Rötzer 2001, Richardson et al 2013, Gill et al 2015 and references therein). Phenology is primarily modulated by temperature, although photoperiod and water availability can also play important roles. Warmer spring temperatures are generally associated with advances in the timing of leaf flushing (e.g. Thompson and Clark 2008, Richardson et al 2013), although the response may be modulated by confounding factors (thus posing a serious problem for warming experiments Wolkovich et al 2012). For example, a larger local spring temperature variance, associated with an increased risk of frost, can lead to decreased phenological sensitivity to warming (Wang et al 2014a, 2014b). Similarly, changes in pre-season characteristics, such as reduced winter chill, may weaken the response to warmer springs due to opposing effects on plant phenology (e.g. Cook et al 2012). Climate-driven changes in autumn phenology are not as common as the springtime changes, because autumn phenology is in many cases chiefly driven by photoperiod (Gill et al 2015). Nonetheless, leaf colouring and senescence are delayed when late summer or early autumn temperatures are high (Estrella and Menzel 2006, Doi and Takahashi 2008, Delpierre et al 2009), albeit with some exceptions in the boreal zone (Jeong et al 2011).

While temperature is generally the strongest climatic control on growing season timing, water availability may further constrain the period of leaf presence and activity. Involuntary changes in soil moisture, induced in warming experiments, have been identified as one of the possible causes of discrepancies between experiments and field observations (Wolkovich et al 2012). Typically, spring and summer precipitation have the largest impacts on concomitant vegetation activity (Zeppel et al 2014). However, this pattern does not hold for seasonally-dry regions such as the Mediterranean, where winter precipitation plays a major role in recharging soil moisture (e.g. Piøvesan and Schirone 2009). Seasonal precipitation controls phenology particularly in arid/semi-arid regions, where it can exert a stronger control than temperature (Yi et al 2010, Liu et al 2016). For example, in Mediterranean grasslands leaves senesce in the dry season and the amount and timing of precipitation then regulate the start of the growing season (Jongen et al 2011). However, precipitation can play an important role also at comparatively mesic locations (Zeppel et al 2014 and references therein). In general, dry conditions can delay the start of the growing season, halt normal plant development and even completely inhibit the regular summertime peak of biological activity (e.g. Xu and Baldocchi 2004, Ciais et al 2005, Noormets et al 2008). In contrast to these positive correlations with water availability, higher precipitation prior to the end of the growing season anticipates leaf senescence over Scandinavia, possibly due to limitations in nutrient availability driven by excessive soil moisture (Liu et al 2016). Moreover, the timings of spring and autumn phenology can be correlated due to both leaf traits (such as leaf life span) and the negative impact of earlier plant growth on summer water availability (Liu et al 2016).

4.2.2. Respiration
Within-season patterns of temperature and soil moisture are direct drivers of the seasonality of respiratory fluxes (e.g. Janssens et al 2001, Hibbard et al 2005, Bahn et al 2008, Lund et al 2010). While higher temperature promotes respiration (at a given soil moisture level), the soil respiration response to soil moisture typically exhibits a maximum at intermediate moisture levels\(^8\). Therefore, changes in respiration due to, e.g. increasing soil moisture, depend on the antecedent conditions (Moyano et al 2013, Zhang et al 2018). As previously highlighted in section 4.1, correlations between respiration rates and temperature and soil moisture are typically positive, although the non-linear character of the respiration-soil moisture relationship leads to comparatively more varied results in the literature (figure 3(b)).

Positive correlations between temperature and Re have been found, for example, in autumn in boreal forests (Vesala et al 2010) and in winter across a variety of mid and high-latitude ecosystems (Wang et al 2011). Wang et al (2011) further found that winter

\(^8\) In contrast, methane production increases with soil moisture level when anaerobic conditions prevail.
temperatures drive spatial Re patterns in forest, grasslands and croplands. On annual timescales, the role of temperature can become harder to detect. Bahn et al (2010) concluded that total annual soil respiration can be estimated solely based on soil respiration at mean annual temperature across biomes, although soil moisture provides an important second-order control that becomes more relevant at lower latitudes (Reichstein et al 2007b, Ballantyne et al 2017). Correlations between soil respiration and annual temperature anomalies have also been found across a range of mid-latitude ecosystems: such correlation were strong and positive in some cases (Bond-Lamberty and Thomson 2010) and weak in others (Law et al 2002, where the focus was on Re). In arctic and boreal ecosystems, both positive (e.g. Dorrepaal et al 2009) and negative (Bond-Lamberty and Thomson 2010, Bond-Lamberty et al 2012) correlations were found. These contrasting results may partly stem from confounding factors, such as water stress in boreal trees under warmer temperatures (e.g. Bond-Lamberty and Thomson 2010), and partly by the fact that annual mean temperature can mask asymmetric seasonal temperature changes that affect Re (Zhu et al 2018). Indeed, even when annual temperatures correlated only weakly with respiration, monthly timescales at individual sites showed significant correlations (Law et al 2002; see also section 4.1).

Precipitation, by affecting soil moisture, also exerts a strong and predominantly positive control on Re rates globally (figure 3(b)), ranking in some studies as the first or second most important factor (Bahn et al 2010, Chen et al 2014). Water limitation effects are particularly relevant in arid or semi-arid ecosystems (Bahn et al 2010). These effects appear both along latitudinal gradients, with dryness becoming the dominant limiting factor at mid-to-low latitudes (Yi et al 2010), and through time at a given site. For example, field measurements in Mediterranean ecosystems have shown that the presumed enhancement of Re due to temperature increases may be offset by the soil moisture effect (Qi et al 2002, Jongen et al 2011). This link is also supported by experimental evidence, which points to increases in growing-season Re with warming temperatures only in the absence of water limitation (Wu et al 2011). The effect of wintertime precipitation anomalies on Re may instead not be significant, as found by Wang et al (2011) across a variety of temperate and boreal ecosystems.

Soil moisture not only controls the Re fluxes, but also modifies the respiration’s sensitivity to temperature, leading to a complex feedback loop (Zhang et al 2018). The temperature sensitivity of Re is itself non-linear, further complicating the picture (Qi et al 2002). As a result of these and other factors, respiration in cold, mesic ecosystems appears more sensitive to the temperature signal than in tropical and sub-tropical areas (Song et al 2014).

Other climate variables can also significantly affect respiration rates. For example, below-freezing temperatures and wintertime snow-cover can both modulate soil temperature and limit the effect of precipitation on soil moisture, thus affecting the observed respiration rate (e.g. Wang et al 2011). Monsen et al (2006) found a strong link between snow cover and Rs, which was explained by the presence of temperature-sensitive microbial flora living under the snow, whose activity is strongly reduced under modified snowpack and temperature conditions. Annual potential radiation can also modulate the sensitivity of Re to temperature, with its effect being most marked over boreal regions (Song et al 2014).

4.2.3. Gross productivities
As for Re, hydro-climatic parameters modulate gross productivity and its seasonality. Again, the effects of temperature, precipitation, soil moisture (and the associated droughts and precipitation extremes), and radiation differ across ecosystems and biomes. These differences are evident in the variety of correlation types found across studies for the different climate drivers (figures 3(a) and (c)).

Mean annual temperature is positively correlated with annual GEP and explains 50% of its variation across Northern Hemisphere biomes, almost twice as much as the annual local water balance (Law et al 2002; see also Gonsamo et al 2016, for NDVI). NDVI shows the strongest sensitivity to temperature in spring (Gong and Shi 2004), although it is positively correlated to growing season temperatures in the high latitudes (Zhao et al 2018).

However, there is a strong latitudinal gradient in the climate controls on gross productivity: while at mid-to-high latitudes GPP is positively affected by mean annual temperature, at lower latitudes, where water stress can be a strong limiting factor, it correlates positively and significantly with water availability (Reichstein et al 2007a; figure 3(c)). GPP and related metrics in these regions can also be sensitive to the timing of precipitation (e.g. Misson et al 2010, Jongen et al 2011).

Latitudinal gradients emerge also within the same ecosystem or climate variable. For example, higher temperatures benefit a larger percentage of the population of a given tree species at more northern rather than southern sites in the Eurasian taiga (Lloyd et al 2011) and across Fennoscandia (Ruiz-Pérez and Vico, personal communication). Higher than normal radiative input benefits the high latitudes but suppresses plant activity in the Mediterranean region (Beer et al 2010), such that in correlation maps radiation can emerge as an important control also in Southern Europe (Gonsamo et al 2016). Temperature and precipitation effects also show opposite-sign correlations with NDVI over Northern and Southern Europe (Zhao et al 2018). Indeed, while positive correlations
between the annually averaged NDVI (in turn related to GPP) and temperature were found in the northern mid-to-high latitudes (Ichii et al. 2002, Gong and Shi 2003, Peñuelas et al. 2007, Gonsamo et al. 2016), negative correlations between temperature and annual GPP emerged over Southern Europe. The latter were ascribed to increasing transpiration rates and decreasing water availability with increasing temperature (e.g. Ciais et al. 2005). The latitudinal gradients only provide a first-order picture: the specific regions over which each climate driver dominates vary across studies, with sometimes contrasting results. For example, Beer et al. (2010) found a strong positive effect of precipitation on median annual GPP across a large part of continental Europe, including Eastern/North-Eastern Europe, while Gonsamo et al. (2016) highlighted these as radiation and temperature-dominated regions.

The influence of precipitation is particularly complex, as it is likely modulated by plant phenology and its effects on water loss via transpiration. The timing of the growing season onset can affect spring and summer WUE, by modulating the relative changes in GPP and evapotranspiration (Jin et al. 2017, studying mid-latitude broadleaf forests), as well as enhance levels of water stress in the later part of the growing season (Buermann et al. 2003). An additional layer of complexity originates from the statistically different GEP power spectra at sub-seasonal and longer timescales exhibited by different plant functional types (Stoy et al. 2009).

To summarize, the spread in gross productivity responses to warming and water availability can to first order be traced along a wet and cold versus warm and dry environmental gradient (Peñuelas et al. 2007), although numerous studies have highlighted more complex spatio-environmental variations.

4.2.4. Net productivities
Net C fluxes on a seasonal to annual basis depend on the length of the growing season, as well as on the impacts of mean weather and its variability on gross productivity and respiration. GPP appears to be a dominant control on NEP annual variability, with Re explaining ~1% of the annual variance of NEP across Europe (Reichstein et al. 2007a). In support of this, Zhang et al. (2014) found that the annual NPP/GPP ratio is constrained to a relatively narrow range, and that its variability is strongly controlled by climatic parameters. Nevertheless, Re can play a non-negligible role in modulating the net C exchange for specific biomes and seasons (e.g. Yu et al. 2016). To complicate the picture, GPP and Re often show same-sign responses to changes in temperature and water availability, albeit with different sensitivities, leading to a compensatory behaviour which makes NEP less responsive to climate drivers than may be otherwise expected (e.g. Reichstein et al. 2007b). The importance of compensation may depend strongly on the spatial scale considered, with large-scale analyses implicitly accounting for potentially large compensating changes at different locations (Jung et al. 2017). These effects in turn result in several different correlations being highlighted in the literature (figure 3(d)). Moreover, there is often a temporal decoupling of GPP and Re (in many mid-latitude sites Re peaks later than GPP (Zhang et al. 2018)) leading to a potentially strong sensitivity of net C fluxes to the timing and duration of the growing season (e.g. Malhi et al. 1999, Richardson et al. 2013).

Longer growing seasons have been associated with higher annual NEP in forest biomes throughout Europe (Allard et al. 2008, Fu et al. 2017). However, others have found that the annual NEP does not necessarily increase with a longer growing season (e.g. Dunn et al. 2007), or that changes may be heavily biome-dependent (Welp et al. 2007). The possibility of a weak correlation between annual NEP and length of growing season may be explained through the effect of enhanced soil organic C decomposition induced by warming, which counterbalances higher annual GPP in warmer years (e.g. Bahn et al. 2010).

The effects of phenology and growing season length are superimposed on strong latitudinal gradients. In agreement with the patterns observed for GPP and Re individually, annual NEE at mid-to-high latitudes decreases with increasing mean annual temperature (i.e. high temperature promotes C accumulation), while at mid-to-low latitudes it increases with increasing dryness (dry conditions promote C emission), as photosynthetic activity is inhibited more than Re (Yi et al. 2010). Broadly consistent conclusions were also drawn from biome-specific analyses (e.g. Dunn et al. 2007, Jongen et al. 2011, Niip et al. 2015) and for NPP, albeit showing a weaker relation and with a strong radiation control (Nemani et al. 2003). The boundary between the temperature and water-controlled zones lies around 45 ° N (Yi et al. 2010, Yue et al. 2017), and can be seen as a transition zone where many sites are co-limited by temperature and dryness.

Latitudinal gradients also emerge for the responses to intense precipitation episodes and droughts. Comparatively mesic ecosystems display negative annual above-ground NPP responses to extreme precipitation while xeric ecosystems generally display an above-ground NPP increase, as precipitation alleviates the recurrent constraints of water stress there (Zeppel et al. 2014). Regarding droughts, Peng et al. (2017) found a positive correlation between NPP and the annual standardised precipitation-evapotranspiration index—one of the many multivariate indices used to diagnose droughts. This correlation was evident across the Mediterranean region and into Eastern Europe, with drought episodes having a negative impact on NPP, especially in the Iberian Peninsula. Interestingly, Eastern Europe emerges as one of the global hotspots for NEP sensitivity to drought (Schwalm et al. 2010). In line with the North–South dichotomy discussed above, no clear relationship between dry spells and net productivity decreases was found over Northern
Europe, which even displayed local NEP enhancement under drier conditions. While the focus here is not on extreme events, it is worth mentioning that prolonged drought conditions can drive large NEE anomalies across biomes, severely reducing C uptake or even turning C sinks into sources (Zeng et al. 2005, Nagy et al. 2007, Pereira et al. 2007). Indeed, past severe European droughts have provoked significant continent-wide increases in net C release at seasonal to annual timescales (e.g. Caissi et al. 2005).

Other studies have reported findings in contrast with the above. While Yi et al. (2010) argued that higher temperatures can promote C sinks, Schneising et al. (2014) concluded that warmer years lead to higher growth rates of atmospheric CO₂ in the Northern Hemisphere, indicating a reduced efficiency of the terrestrial C sink. This apparent discrepancy may be due to Schneising et al.’s choice of a full hemispheric domain, and to the fact that higher temperatures can exacerbate water stress in many regions. Reichstein et al. (2007a), on the other hand, found a weak correlation between NEP and mean annual temperature across Europe regardless of latitude, while water availability played an important role, especially in the Southern part of the continent. Other studies have instead highlighted weak relations between annual above-ground NPP and relative drought years across biomes, possibly due to the presence of buffering mechanisms reducing the impact of drought on productivity (Knapp and Smith 2001). The lack of strong correlations and clear patterns linking net productivity and mean annual indicators may result from different ecosystem sensitivities to environmental factors, which can mask large-scale responses to mean annual forcings (Yuan et al. 2009). It may also derive from the use of temporally smoothed or spatially aggregated meteorological drivers, which do not accurately include both low and high-frequency variability components (Medvigy et al. 2010) and ignore within-year cancellation.

The above motivates assessing climatic controls at the biome and seasonal scales. Indeed, biome-specific differential controls on GPP and Re can strongly affect net C flux sensitivity (e.g. Dunn et al. 2007, Nagy et al. 2007, Urbanski et al. 2007). In many biomes, the overall sensitivity of annual GPP to water stress is larger in magnitude than that of Re (Nagy et al. 2007, Noormets et al. 2008, Schwalm et al. 2010). On the contrary, Re is typically more sensitive than productivity to temperature (Malhi et al. 1999, Ballantyne et al. 2017). However, the balance between the two may be dependent on the actual temperature itself (Wang et al. 2008), with GPP changes dominating in cold climates (Fernández-Martínez et al. 2014). Moreover, some correlations between climate variables and net C fluxes change their sign depending on the season (Ishizawa et al. 2016, Yue et al. 2017). For example, Ishizawa et al. (2016) found that the high-latitude correlation between CO₂ flux anomalies and temperature switched from negative in June to positive in July and August. The proposed mechanism for this pattern was that warmer early-season weather stimulates vegetation growth and CO₂ uptake, while later in the season the effect of temperature-enhanced soil respiration dominates. Accordingly, warmer spring temperatures drive a larger NEP in temperate and boreal deciduous broadleaf forests (Fu et al. 2017). Similarly, winter droughts—associated with a temperature-driven increase in GEP—favour a higher net CO₂ uptake in mid-to-high latitudes (Schwalm et al. 2010), while during summertime above-average soil moisture is key to enhanced net C uptake in boreal forests (Ishizawa et al. 2016). Interestingly, in Mediterranean ecosystems annual NEE is more sensitive to spring, rather than annual, precipitation (Allard et al. 2008, Misson et al. 2010), possibly due to the long-term effects of stresses occurring during leaf expansion and early wood production. Similar considerations also hold for mid-latitude forests, where drought between bud-break and full leaf expansion can lead to a severe reduction in net annual C accumulation (Noormets et al. 2008). Indeed, spring is the season when the link between NEP and precipitation is strongest across a range of biomes (Schwalm et al. 2010).

4.2.5. Climate indices and the carbon cycle

Climate indices (table 1) provide a concise summary of the prevailing weather conditions and regional soil moisture anomalies on seasonal and longer scales (e.g. Sheffield and Wood 2008). At these timescales, and for Europe, the NAO and the closely related Arctic Oscillation (AO) have catalysed the attention in the literature (40% of the publications dealing with climate indices; figure 2(f)). The variability in the timing of spring onset in Europe has been linked to the sign and strength of the preceding winter’s NAO, with a moderate negative correlation (i.e. a higher NAO index (NAOI) leading to earlier spring onset (Stockli and Vidale 2004)). However, continent-wide values mask very different correlations at the regional scale. In general, a strong negative NAO-spring onset correlation emerges in Western-Central and Northern Europe, while a weaker positive correlation values are found in the Mediterranean region and parts of Iberia (Maignan et al. 2008, Nordli et al. 2008). There are notable local exceptions, such as the positive NAO causing heavy snow over mountainous or cold regions of Northern Europe, which may delay the spring onset there (Shutova et al. 2006). The large-scale dipole effect is associated with the opposite impact of the NAO on winter temperature and precipitation over the Northern (wetter and warmer) and Southern (drier and colder) parts of the continent, as well as with the strong dependence of spring and summer productivity on water availability over relatively dry regions such as the Iberian Peninsula (Zeppel et al. 2014). Indeed, in the Mediterranean region—but also elsewhere in Europe—winter precipitation is fundamental in recharging
soil water. Wintertime precipitation anomalies, closely associated with the NAO, may thus significantly affect the following growing season (Piovesan and Schiro
nez 2000, Peters et al 2010). In general agreement with this large-scale picture, the late-winter NAOI is positively correlated with late-winter and spring NDVI over Continental and Northern Europe (Li et al 2016), while it is associated with low vegetation activity in the following spring and summer over the Iberian Peninsula (Gouveia et al 2008). Similar spatial relations were found for LAI (Dahlin and Ault 2018) and growing-season NDVI (Gonsamo et al 2016), while simultaneous correlations between vegetation activity and the spring NAO are generally weak (Gong and Ho 2003, Nordli et al 2008).

Other studies have, however, highlighted that regional NDVI responses may differ significantly between spring and summer (Gouveia et al 2008); and that the choice of the winter months over which the NAOI is defined can alter the spatial correlation pattern with the following spring/summer NDVI (Li et al 2012). This is reflected by the variable correlations found across studies between NAO/AO and measures of greenness (figure 3(a)). For example, Patra et al. (2005) found a negative correlation between the NAOI and 5-month lagged C sink strength over Europe, in agreement with the continent-wide negative late-winter NAO—summer NDVI correlation found by Gouveia et al. (2008), but in contrast with the spring patterns discussed above. Moreover, the NAO’s effects on plant pheno
logy may be heavily species-dependent, with conifer species responding more to the winter NAO and broadleaf species being more sensitive to growing-season indices (Fernandez-Martinez et al 2017).

The seasonal pattern of NDVI has also been linked to the AO index, especially during spring (Buermann et al 2003). Springs preceded by a positive phase of the AO are often warmer over Eurasia, in turn leading to enhanced greenness. In contrast, positive AO phases are often followed by a decline in greenness in central Europe during the summer, possibly because of reduced summertime precipitation. Similarly, cumulative annual vegetation greenness in the Southern Spain and Mediterranean regions may be negatively affected by positive AO phases during the preceding winter (Potter et al 2007).

On a global scale, ENSO has a major impact on the terrestrial C-cycle (e.g. Behrenfeld et al 2001, Anderegg et al 2015b), but its effects are more evident in tropical rather than mid and high-latitude regions (e.g. Chen et al 2004, Hashimoto et al 2004, Bowman et al 2017). Nonetheless, annual as well as seasonal NPP and LAI over Europe display moderate negative correlations with the ENSO index (Bastos et al 2013, Dahlin and Ault 2018), as illustrated by the mainly negative or neutral correlations in figure 3(a). Similarly, Chen et al (2004) noted a positive impact of negative ENSO phases on the growth of temperate evergreen forests. These links are likely mediated by temperature and water availability anomalies, as El-Niño episodes (positive ENSO) were found to increase evaporation and reduce NDVI over a large part of Europe (Miralles et al 2014). In agreement with this, the El-Niño event of 2010 was associated with a higher CO2 source in central Europe than the following La-Niña (negative ENSO) year (Bowman et al 2017), which instead led to very high NPP values across the continent (Bastos et al 2013). As a result, NEE over Europe shows a positive correlation with ENSO, albeit with important differences depending on region, El Niño event and method for calculating NEE (Schwalm et al 2011).

Other climate indices, related to both tropical and extra-tropical variability modes, may also be correlated to C-cycle proxies over Europe. Gonsamo et al (2016) found that the winter SCA is negatively correlated with same-year vegetation productivity in Continental and Eastern Europe. This can be explained by the fact that the positive phase of the winter SCA is associated with cold air accumulation over a vast area extending from Western Europe to Siberia. A similar, albeit weaker, correlation pattern was found between productivity and the PNA, suggesting that the winter NAO and SCA patterns can explain the same-year vegetation productivity variations across a large portion of the continent. Finland is an exception, as the EA/WR may actually be the dominant variability mode there, due to its strong link to the start, end and length of the growing season (Irannezhad and Klove 2015). Dahlin and Ault (2018) found a significant footprint of the IODM on European LAI, with positive correlations over Western Europe and negative correlations further east.

It is also possible to study the interplay of different climate indices, and its effect on the terrestrial C-cycle. In fact, the climatic footprint of the positive or negative phase of a given index can be strongly modulated by the concomitant phase of a separate variability mode. For example, the in and out-of-phase variations of the NAO and EA indices result in different seasonal patterns of NDVI and vegetation activity (Bastos et al 2016). The co-occurrence of NAO and EA positive phases results in an overall enhancement of full-year NDVI over Europe, with the exception of the Iberian Peninsula. During years when both indices are in the negative phase, very cold conditions occur over large parts of Europe, leading to more precipitation in the form of snow. The later snow melting reduces spring NDVI but at the same time ensures soil water availability later in the growing season over central Europe, leading to an overall increase in summer and fall NDVI. Similarly, Buermann et al’s (2003) results point to potential overlaps between the AO and ENSO signals during spring over Central Europe—with both driving warmer, greener conditions over the region in their positive phases. The NAO’s footprint over Europe also interacts with slower variability modes such as...
the AMO. The combination of AMO and NAO variations provides a strong control on water availability and temperature over South-Western Europe. Forest productivity over Iberia peaks for positive AMO and negative NAO phases, and reaches a minimum for negative AMO and negative NAO phases (Madrigal-González et al 2017). The latter combination corresponds to the most positive winter water balance, but also to lower temperatures, suggesting that energy limitations dominate over water availability. More recently, the influence of ENSO in combination with the Interdecadal Pacific Oscillation (IPO) has been analysed. In Europe, the correlation between growing-season NDVI and ENSO/IPO is mostly weak, with limited areas of significant negative correlations over Iberia and significant positive correlations over southern Fennoscandia, where vegetation growth is enhanced during El Niño years and IPO warm phases (Zhao et al 2018)

Finally, Belmecheri et al (2017) proposed an alternative approach to study the link between the large-scale atmospheric variability and the C-cycle, by relating seasonal temperature and precipitation anomalies to the location of the Jet Stream (a climatological narrow, fast-flowing mid-latitude wind which flows from the West to the East). This points to potentially significant correlations with C-cycle indicators over Europe, although the topic is yet to be systematically explored.

4.3. Annual and longer drivers
There are interactions whereby climate conditions in a given year or set of years affect the C-cycle in subsequent years. We discuss these ‘memory’ or ‘legacy’ effects in the following, replicating the structure of section 4.1.

4.3.1. Respiration
Legacy effects on soil respiration at interannual scales may not always be large (e.g. Misson et al 2010), although there is evidence that low Rh in very dry years may lead to higher Rh in following years. This results, once soil water content recovers, from the undecomposed residues from the previous year (Arnone et al 2008). Furthermore, previous-year plant activity (as represented by NDVI) is needed to explain soil respiration patterns in high-latitude sites (Bond-Lamberty et al 2012).

4.3.2. Gross productivities
Productivity is sensitive to legacy effects, since climate variations can have long-term consequences on plant development. Specifically, drought conditions can lower forest NDVI up to four years after their occurrence, while grasslands and shrublands tend to have a memory limited to 1–2 years (Wu et al 2018). However, the timescale of this response may be ecosystem and species-dependent (Pereira et al 2007). Conversely, physiological adjustment to water stress and responses to previous-year climatic conditions may alter responses to drought (Knapp and Smith 2001), thus driving a complex set of interactions between climatic conditions in different years.

Although beyond the scope of this review, we note that slower modes of climate variability, such as the AMO or PDO, have been investigated in association with long-term C-cycle trends (e.g. Gonsamo et al 2016, Zhao et al 2018). However, the available data is typically insufficient to make conclusive statements concerning the low-frequency variability they drive.

4.3.3. Net productivities
Climate-driven changes in respiration and gross productivity, cause potentially large long-term changes in net C fluxes. For example, the strength of the terrestrial CO2 sink in the Northern Hemisphere mid-to-high latitudes shows a significant positive correlation with temperature at 1.5–2 year lags (Adams and Piovesan 2005). This is likely the consequence of the temperature-driven enhancement of the nutrient recycling, favouring increased NPP. However, high temperatures may also lead to more frequent and marked water stress conditions, with multi-year negative effects on net ecosystem C uptake (Arnone et al 2008, for a prairie ecosystem).

Water availability is indeed a key factor in legacy effects, and previous-year precipitation controls a significant fraction of current year above-ground NPP across a range of mid-latitude dry and mesic biomes (Sala et al 2012). Tree-dominated ecosystems are particularly sensitive to these legacy effects (Piovesan and Schirone 2000, Granier et al 2007), with tree growth affected up to 4 years after a drought event (Anderegg et al 2015a). For example, the deleterious effects of drought on plant nutrient content may have limited long-term productivity and WUE in a Mediterranean forest ecosystem (Misson et al 2010). Even in environments that are not typically water stressed, such as boreal forests, the effects of water balance anomalies may cumulate on long timescales and influence the NEE variability of the subsequent year (Dunn et al 2007). At the same time, when drought episodes lead to extensive vegetation mortality, net C uptake may increase in the following years thanks to enhanced availability of light to previously shaded plants and nutrients released from the previous years’ residues (Peters et al 2010). Thus, ecosystem variability displays interannual persistence, underscored by memory effects and slow recovery rates (Pappas et al 2017).

The interannual responses of NEE to the above climate drivers are superimposed on those of other long-term drivers, such as CO2 fertilisation (e.g. Ainsworth et al 2019), increased Nitrogen deposition (e.g. Hyvönen et al 2007) and large-scale reforestation (e.g. Tan and Li 2015). Additionally, interannual NEE variations can be modulated by changes in the underlying ecosystem physiology or structural ecosystem changes (Urbanski et al 2007, Sala et al 2012).
Quantifying flux variability at long timescales thus requires taking into account both the ecosystem response to climatic variability and possible changes and adaptations taking place as a result of such variability (Stoy et al 2009). Disturbances combining climatic and non-climatic factors, such as unfavourable weather conditions combined with parasite or disease outbreaks or fires, can also play an important role (e.g. Potter et al 2007).

5. Discussion and conclusions

The terrestrial carbon cycle (C-cycle) is a crucial component of the global climate system. A robust understanding of the complex web of interactions linking climate drivers to the terrestrial C-cycle is necessary to elucidate the processes driving natural climate and ecosystem variability, and to improve future projections. Yet, our mechanistic understanding of the terrestrial C-cycle–climate interactions is far from complete, as emerges from the often contrasting observations (figure 3). Indeed, the terrestrial C-cycle remains a poorly constrained component in both global Earth System Models (e.g. Piao et al 2013, Friedlingstein et al 2014, Prentice et al 2015) and regional simulations (e.g. Morales et al 2007).

Here, we have reviewed the current knowledge on climate drivers of the terrestrial C-cycle variability at time scales ranging from sub-daily (e.g. the response of respiration to wetting) to interannual (whereby the climate of one season or year can influence the C-cycle of the following years). The focus was primarily on observational studies in Europe.

A wide range of C-cycle metrics have been analysed, with NEE (or NEP), GPP, various respiration fluxes, and proxies of leaf area emerging as the most widely used. The associated climate metrics are predominantly individual observables, such as temperature or precipitation, or multivariate quantities, such as drought indices. Recently, a growing number of studies has also focussed on climate modes of variability, which conveniently summarise a large amount of climate information into a single index. Most studies have focussed on the seasonal to annual scale, here defined as C-cycle changes occurring in the same season or year as the climate signal driving them. The timescale attracting the least attention is the interannual and longer variability (excluding long-term trends).

Our review highlights several areas of strong agreement, but also combinations of climate and C-cycle metrics and timescales where significant disagreements emerge. Examples of areas of strong agreement are: the role of temperature, precipitation and soil moisture on respiration rates, or precipitation on gross productivity. Conversely, the correlations between climate metrics and greenness proxies emerge as very variable across studies. Such disagreements may originate from the choice of temporal or spatial domains. For example, annual averages can mask seasonal changes in C-cycle responses. Similarly, continent-wide or larger averages can mask latitudinal gradients underscoring the different physical processes governing the C-cycle at regional scales. Other discrepancies are more complex to identify and resolve. Studies based on plot to landscape-scale measurements (e.g. flux towers) may be affected by balancing effects between the different types of vegetation and soils within the tower footprint, while studies based on satellite retrievals or inversions may be affected by the data product chosen, especially on regional scales. Finally, a number of studies have highlighted a potentially large intrinsic variability in the response of a given biome, ecosystem, or even plot, to similar climate forcings. The extent to which this may impair our understanding of the terrestrial C-cycle–climate interactions is difficult to quantify from the current literature, and is one of the key areas we have identified as requiring further investigation.

Based on the above, we formulate recommendations for future research. In terms of topic coverage, there is the need for more detailed observational analyses of interannual and longer-term variability. This is crucial from both a predictability and a longer-term global change viewpoint. We further argue that studies should specifically address existing disagreements in the literature, and try to identify whether disagreements are the results of the methods employed or of complex ecosystem-specific mechanisms. Indeed, there is a range of known factors potentially affecting the results of C-cycle–climate analyses that are likely relevant, but yet to be extensively analysed. These include, amongst others, the role of changes in plant phenology; changes in the structure of the climate modes of variability, as a result of both natural low-frequency variability and anthropogenic forcing; influences of topography; intrinsic variability in the response of a given ecosystem, biome, or even plot, to similar forcings. From a modelling point of view, many state-of-art ESMs adopt static plant functional type parametrisations. However, the studies we reviewed showed that different plant functional types can respond differently to similar climate drivers (e.g. Zeppel et al 2014). Thus, assuming static functional types does not allow capturing variations in the sensitivity of vegetation to climatic conditions when vegetation types change. In the context of our rapidly changing climate, this underscores the need to test the validity limits of current parameterizations against observations.

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