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Frank, Dorothea[1]; Reichstein, Markus[1]; Bahn, Michael[2]; Frank, David[3,17]; Mahecha, Miguel D.[1], Smith, Pete[4], Thonicke, Kirsten[5,22]; van der Velde, Marijn[6,21]; Vicca, Sara[7]; Babst, Flurin[3,18], Beer, Christian[1,19]; Buchmann, Nina[8]; Canadell, Josep G.[9], Ciais, Philippe[10], Cramer, Wolfgang[11]; Ibrom, Andreas[12], Miglietta, Franco[13,20], Poulter, Ben[10], Rammig, Anja[5,22]; Seneviratne, Sonia I.[8]; Walz, Ariane[14]; Wattenbach; Martin[15]; Zavala, Miguel A.[16]; Zscheischler, Jakob[1]

[1] Max Planck Institute for Biogeochemistry, 07745 Jena, Germany

[2] Institute of Ecology, University of Innsbruck, 6020 Innsbruck, Austria

[3] Swiss Federal Research Institute WSL, 8903 Birmensdorf, Switzerland

[4] University of Aberdeen, Institute of Biological and Environmental Sciences, 23 St Machar Drive, Aberdeen, AB24 3UU, UK

[5] Potsdam Institute for Climate Impact Research (PIK) e.V., 14773 Potsdam, Germany

[6] International Institute of Applied Systems Analysis (IIASA), Ecosystems Services and Management Program, A-2361 Laxenburg, Austria

[7] Research Group of Plant and Vegetation Ecology, Biology Department, University of Antwerp, Wilrijk, Belgium

[8] ETH Zurich, 8092 Zurich, Switzerland

[9] Global Carbon Project, CSIRO Oceans and Atmosphere Flagship, GPO Box 3023, Canberra, ACT 2601, Australia

[10] IPSL – Laboratoire des Sciences du Climat et de l'Environnement CEA-CNRS-UVSQ, 91191 Gif sur Yvette, France

[11] Institut Méditerranéen de Biodiversité et d'Ecologie marine et continentale (IMBE), Aix Marseille Université, CNRS, IRD, Avignon Université, Aix-en-Provence, France

[12] Department of chemical and biochemical Engineering, Technical University of Denmark, (DTU), Frederiksborgvej 399, 4000 Roskilde, Denmark

[13] IBIMET-CNR, Via Caproni, 8 50145 Firenze – Italy

[14] University of Potsdam, Institute of Earth and Environmental Science, 14476 Potsdam, Germany

[15] Helmholtz Centre Potsdam, GFZ German Research Centre For Geosciences, 14473 Potsdam, Germany

[16] Forest Ecology and Restoration Group, Universidad de Alcalá, Alcalá de Henares, Madrid, Spain

[17] Oeschger Centre for Climate Change Research, University of Bern, CH-3012 Bern, Switzerland

[18] Laboratory of Tree-Ring Research, The University of Arizona, 1215 E Lowell St, Tucson, AZ 85721, USA

[19] Stockholm University, Department of Environmental Science and Analytical Chemistry (ACES), and the Bolin Centre for Climate Research, 10691 Stockholm, Sweden.

[20] FoxLab, Fondazione E.Mach, Via Mach 1 30158 San Michele a/Adige (Trento) - Italy

[21] currently at MARS Unit, Institute for Environment and Sustainability, Joint Research Centre, European Commission, Via E. Fermi 2749, I-21027 Ispra (VA), Italy

[22] Berlin-Brandenburg Institute of Advanced Biodiversity Research (BBIB), 14195 Berlin, Germany

Corresponding author: Dorothea Frank, Max Planck Institute for Biogeochemistry, Hans-Knöll-Strasse 10, 07745 Jena, Germany, e-mail: dfrank@bgc-jena.mpg.de, phone: +49 3641 576284, fax: +49 3641 577200

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Abstract

Extreme droughts, heat waves, frosts, precipitation, wind storms and other climate extremes may impact the structure, composition, and functioning of terrestrial ecosystems, and thus carbon cycling and its feedbacks to the climate system. Yet, the interconnected avenues through which climate extremes drive ecological and physiological processes and alter the carbon balance are poorly understood. Here we review literature on carbon-cycle relevant responses of ecosystems to extreme climatic events. Given that impacts of climate extremes are considered disturbances, we assume the respective general disturbance-induced mechanisms and processes to also operate in an extreme context. The paucity of well-defined studies currently renders a quantitative meta-analysis impossible, but permits us to develop a deductive framework for identifying the main mechanisms (and coupling thereof) through which climate extremes may act on the carbon cycle. We find that ecosystem responses can exceed the duration of the climate impacts *via* lagged effects on the carbon cycle. The expected regional impacts of future climate extremes will depend on changes in the probability and severity of their occurrence, on the compound effects and timing of different climate extremes, and on the vulnerability of each land-cover type modulated by management. Though processes and sensitivities differ among biomes, based on expert opinion we expect forests to exhibit the largest net effect of extremes due to their large carbon pools and fluxes, potentially large indirect and lagged impacts, and long recovery time to re-gain previous stocks. At the global scale, we presume that droughts have the strongest and most widespread effects on terrestrial carbon cycling. Comparing impacts of climate extremes identified *via* remote sensing *vs.* ground-based observational case studies reveals that many regions in the (sub-)tropics are understudied. Hence, regional investigations are needed to allow a global upscaling of the impacts of climate extremes on global carbon-climate feedbacks.

Introduction

There is widespread recognition that climate change is having, and will continue to have, fundamental impacts on the natural environment and on human wellbeing (Parry *et al.,* 2007). Current projections, based upon contrasted emission scenarios, suggest somewhere between 0.3 and 4.8°C warming by the end of this century (IPCC, 2013). The associated modification of the climate system strongly influences the carbon cycling of the terrestrial biosphere and thus land-atmosphere CO_2 fluxes (Fischlin *et al.,* 2007). An important observation is that climate change, and increasing concentrations of atmospheric greenhouse gases, not only lead to gradual mean global warming but may also change the frequency, the severity and even the nature of extreme events (IPCC, 2013). A relatively small change in the mean or variance of a climate variable, inherently leads to disproportionally large changes in the frequency of extremes, i.e. the infrequent events at the high and low end of the range of values of a particular variable (Nicholls & Alexander, 2007). Furthermore, climate change can fundamentally alter the inherent variability of temperature, precipitation and other weather phenomena (Seneviratne *et al.,* 2012). State-of-the-art climate models project global intensification of heavy precipitation events and heat extremes, and regions with stronger or longer-lasting droughts (Fischer & Knutti, 2014, IPCC, 2013).

Concerns about increasing variability of temperature and precipitation patterns and climate extremes were first articulated over two decades ago by Katz & Brown (1992), and became widely acknowledged after the second IPCC assessment of climate change in 1995 (Nicholls & Alexander, 2007). These concerns were raised because many biological systems (including human societies) are more sensitive to climate extremes than to gradual climate change, due to typically greater response strengths and shorter response times (Hanson *et al.,* 2006).

Key characteristics of the climate such as heat waves, seem to have already been modified beyond the natural variability within which society and its economic, social and political systems have developed (Schär *et al.,* 2004; Soussana *et al.,* 2010). Both the public media and the scientific community have recognized the widespread consequences of climate extremes such as e.g. the European heat wave in 2003 (Ciais *et al.,* 2005; Reichstein *et al.,* 2007; Bastos *et al.,* 2013a), the heat wave and associated forest fires in Greece in 2007 (Founda & Giannakopoulos, 2009), the dry spells in the Amazon basin in 2005 (Phillips *et al.,* 2009) and 2010 (Lewis *et al.,* 2011), in the U.S.A. 2000-2004 (Breshears *et al.,* 2005; Schwalm *et al.,* 2012), the forest fires in Russia in 2010 (Barriopedo *et al.,* 2011; Konovalov *et al.,* 2011; Coumou & Rahmstorf, 2012; Bastos *et al.,* 2013a), the Pakistan Floods in 2010 (Hong *et al*., 2011; Houze *et al*., 2011; Trenberth & Fasullo, 2012), the storm Lothar in Europe in 1999 (Lindroth *et al*., 2009), hurricane Katrina in the U.S. in 2005 (Chambers *et al*., 2007), or the ice-storm in southern and central China in 2008 (Stone 2008, Sun *et al*., 2012), and the 2010-2011 La Nina rains over Australia (Boening *et al*., 2012; Poulter *et al*., 2014). These documented recent events demonstrate the massive impacts climate extremes can have on harvests, economies and human health, as well as on the carbon balance of terrestrial ecosystems (IPCC, 2012; Reichstein *et al.,* 2013).

Alterations of the biosphere´s carbon balance through changes in the strength of carbon uptake or losses in turn affect the climate system (Friedlingstein *et al.,* 2006; Frank *et al.,* 2010). In addition, extreme drought will often reduce evapotranspiration and its cooling effect and thereby causes a positive local feedback on warming (e.g. Seneviratne *et al.,* 2010; Teuling *et al.,* 2010; Mueller & Seneviratne, 2012; Peng *et al.,* 2014). Regional assessments clearly indicate the relevance of climate extremes on the carbon cycle and potential climate feedbacks (e.g. for drought extreme in Europe, Ciais *et al.,* 2005; Reichstein *et al.,* 2007; and for western North America, Schwalm *et al*., 2012). Yet a synthesis of the direct and indirect impacts of climate extremes on the carbon cycle and the underlying mechanisms, is still lacking. In a recent broad perspective, Reichstein *et al.* (2013) highlighted the possibility that climate extremes and their impacts on the global carbon cycle may lead to an amplification of positive climate-carbon cycle feedbacks. However, the underlying mechanisms, and how they likely apply to current and future response patterns observed in different biomes and ecosystem types, have not yet been synthesized in detail, especially with respect to possible differences in response time (concurrent / lagged) and direction of impacts (direct / indirect). Such detailed information is needed, given the complexity of carbon-cycle responses to climate extremes, and their dependence on background climate and ecosystem conditions (Knapp *et al.,* 2008).

In this review we aim to, 1) develop a coherent conceptual framework based on logically deductive reasoning for integrating direct and indirect effects climate extremes could have on the carbon cycle and to identify the main mechanisms underlying these effects, 2) synthesize how different types of ecosystems are affected by climate extremes based on available well documented case studies, and 3) provide an overview of likely responses of the terrestrial carbon cycle in relation to likely future climate extremes, and the specific role of lagged impacts.

At the outset, we acknowledge that the lack of systematically collected data and the highly non-linear responses of ecosystems to extreme events makes a quantitative meta-analysis of effects of climate extremes on the carbon cycle across the range of observational and experimental studies virtually impossible (cf. also Vicca *et al*., 2014). While there is ample information in the literature on specific effects of extreme climatic conditions (experimentally induced or naturally occurring) on specific ecosystems, the severity of these extreme conditions and their consequences has often not been systematically evaluated. This is not only due to a lack of common metrics reported across the various studies (e.g. Vicca *et al*., 2012), but also complicated by the fact that climate extremes are by definition rare and their effects are highly context-dependent, typically threshold-based and highly non-linear (e.g. Knapp *et al*., 2008, Smith *et al*., 2011, Bahn *et al*., 2014). Thus, in our review, we rely on a qualitative, logically deductive reasoning, supported by multiple case studies, combined with remote sensing based global analysis to derive hypotheses on potential effects of climate extremes on the terrestrial carbon cycle.

Definitions

Climate extremes and impacts

Terms, such as 'climate extremes', 'weather extremes' or 'extreme weather events', are used in various ways in the scientific literature. Thus, for clarity we provide and briefly justify the definitions we use in this review:

An '*extreme*', as stated in Seneviratne *et al.* (2012) is "the occurrence of a value of a weather or climate variable above (or below) a threshold value near the upper (or lower) ends of the range of observed values of the variable" within a defined climate reference period (e.g. 1981-2010). Thus, '*climate extreme*' is an aggregate term encompassing both 'extreme weather' and 'extreme climate' events. The distinction of weather events and climate events is related to the time scale. An extreme climate event occurs on longer time-scales than an extreme weather event, and can be the accumulation of extreme weather events. This definition follows the IPCC Special Report on Managing the Risks of Extreme Events and Disasters to Advance Climate Change Adaptation (Seneviratne *et al.,* 2012).

However, the above definitions reflecting climatological considerations do not consider potential consequences for the biosphere and the carbon cycle. Smith (2011) suggested that one has to specifically address events where both climate is anomalous and the biosphere experiences a pronounced impact outside the bounds of what is considered normal variability. Along these lines we use the term '*extreme impact*' to describe, from a functional perspective, when a resilience threshold ('extreme response threshold', *sensu* Smith 2011) is passed, placing the ecosystem and associated carbon cycling into an unusual or rare state. Thresholds are typically exceeded when stressor dose (i.e., cumulative amount defined by stress intensity multiplied by stress duration) reaches a critical level (e.g., during flooding, drought and / or extended periods of exceptionally high or low temperatures), or when the intensity of an extreme climatic event is critically high (e.g., during a storm). Thresholds can be passed at organ, plant or community level, and lead to emergent carbon cycle impacts at ecosystem level. We note that the definition of "extreme impact" may partly overlap with the concept of "disturbance" as it is commonly used in ecology (White & Jentsch 2001). Here, we consider every climate extreme which has an impact on the ecosystem carbon cycle a "disturbance", but note that not every disturbance is caused by climate extremes. A typical example is fire, which can be part of a system intrinsic disturbance cycle. But in this study, we consider those fires which are of rare magnitude or even are unprecedented, and likely facilitated by extreme climate conditions. Given that impacts caused by "climate extremes" can be considered "disturbances", we assume that respective general mechanisms and processes induced by "disturbances" also operate in this specific "extreme" context.

In order to specifically address extreme impacts with repercussions to the carbon cycle, denoted as "carbon cycle extreme", and to entail anomalies in biosphere-atmosphere carbon fluxes or extreme changes in ecosystem carbon pools, it is useful to distinguish '*concurrent*' versus '*lagged*' and '*direct*' versus '*indirect*' impacts (Fig. 1). These four categories of impacts indicate how they are related to the stressor. Concurrent impacts begin to occur during the climate extreme, while lagged impacts occur sometime thereafter. Direct impacts are only caused by the climate extreme (either concurrently or lagged) if, and only if, a threshold of the climatic stress dose (dashed line in Fig. 1A) is passed. Indirect impacts are facilitated by the climate extreme by increasing the susceptibility of the ecosystem, but directly initiated by another (not necessarily extreme *per se*) external trigger. Hence, here the likelihood (P) of an extreme system response is a function of both the susceptibility and the characteristics of the external trigger (cf. Fig 1B and D).

Examples for these four categories of impacts are:

1. Direct, concurrent impact: wind-throw caused by storm; ice breakage; reduced productivity or increased mortality during drought, thermal stress or flooding (cf. Figure 1A)
2. Indirect, concurrent impact: loss of biomass or soil organic matter due to fire caused by lightning or human ignition, facilitated by an ongoing extreme dry and/or warm event (cf. Figure 1B)
3. Direct, lagged impact: reduced productivity / growth in the year(s) following the year of an extreme drought, caused e.g. by carbohydrate depletion / reduced bud development / partial mortality during a drought in the previous year (cf. Figure 1C)
4. Indirect, lagged impact: increased pest- or pathogen-caused mortality following a climate extreme; loss of biomass or soil organic matter due to fire facilitated through deadwood accumulation after a wind-throw; loss of soil carbon due to erosion during heavy precipitation or permafrost thawing and carbon losses as indirectly facilitated by reduced vegetation cover and / or changes in soil hydrophobicity following overgrazing, drought or fire (cf. Figure 1D)

Any effect, which can be attributed to a previous climate extreme, is termed here a “legacy effect” and hence per definition time-lagged compared to the “climate extreme” (please note that we prefer this terminology compared to the sometimes synonymously used anthropomorphic term “memory effect” (Walter *et al*., 2013)). Legacy effects can include both changes in ecosystem states or process rates after the termination of a climate extreme, as well as altered ecosystem responses to environmental conditions, including subsequent extremes, and are often related to changes in species composition and their functional attributes (e.g. Smith 2011, Sala *et al*., 2012).

It should be noted that is essential to define the time-scale under scrutiny when quantifying the overall effect of a `climate extreme´ on the carbon cycle (Fig. 2). It is the time-scale determining the degree to which concurrent and lagged effects alter the carbon balance of an ecosystem. Negative concurrent effects, often related to the resistance of an ecosystem to an extreme event, may in the long run be balanced by enhanced regrowth during recovery (Fig. 2), depending on the resilience of the system. Lagged effects may impair the ability of an ecosystem to recover from an extreme event and may thereby alter the ecosystem carbon balance over a given period (Fig. 2).

Impacts of climate extremes on the terrestrial carbon cycle: Mechanisms and processes

Climate extremes can impact the structure, composition, and functioning of terrestrial ecosystems and can thereby severely affect the regional carbon cycle, with the potential of causing a shift from a carbon sink towards a carbon source. During the "European 2003 heat wave", which was an extreme drought event, Western European ecosystems were estimated to have lost an amount of CO_2 comparable to that which had been absorbed from the atmosphere during the previous three to five years under normal weather conditions (Ciais *et al.,* 2005; Reichstein *et al.,* 2007; Vetter *et al.,* 2008). Likewise, during the 2000-2004 drought, the strength of the western North American carbon sink declined substantially, with reductions ranging between 30 and 298 Tg C yr^{-1} (Schwalm *et al.,* 2012). In 2004, heavy precipitation associated with Typhoon Mindulle led to a particulate organic carbon flux of 0.5 Mt over a 96 hour period, with subsequent rapid burial of the terrestrial carbon in the ocean (Goldsmith *et al*., 2008). Also, extreme wind storms and cyclones can severely impact the regional carbon balance: In 1999 storm Lothar reduced the European C sink by 16 Mt C, which corresponds to 30% of Europe's net biome production (Lindroth *et al*., 2009) and, hurricane Katrina in 2005 destroyed an amount equivalent to 50 - 140% of the net annual U.S. C sink in forest trees (Chambers *et al*., 2007). Fires, pest and pathogen outbreaks are obviously not climate extremes, but can be facilitated by climate extremes. Extreme fire events release large quantities of carbon to the atmosphere. For example, in Indonesia, people had drained and deforested tropical wetlands which they then ignited to burn the debris awaiting the rain season to extinguish the fires, which failed due to the onset of the strong El-Niño Southern Oscillation in 1997/98, which instead burnt the duff layers and vegetation releasing between 0.81 and 2.57 Gt C (Page *et al.,* 2002). This amount was equivalent to the estimated annual release (van der Werf *et al*., 2010) and, together with the extreme fire events occurring in

Siberia, produced a signal detected by atmospheric CO_2 and CH_4 monitoring stations (Simpson *et al.,* 2006). Pest and pathogen outbreaks can have large impacts on forest carbon stocks and fluxes, and may impact the regional carbon cycle (Hicke *et al.*, 2012), as was the case in a mountain pine beetle outbreak in British Columbia of unprecedented extent and severity, which converted the forest from a small net carbon sink to a large net carbon source (during and immediately after the outbreak) with an estimated cumulative regional impact of 270 Mt C for 2000–2020 (Kurz *et al.*, 2008b).

To be able to generalize and project presumable impacts of climate extremes on the carbon cycle, an understanding of the likely mechanisms and processes involved in extreme impacts is crucial. In this section, we review the primary environmental-biological processes according to their hypothesized relevance to different ecosystems, and the cascade of associated consequences. The complex pathways of how climate extremes may act on the major processes and components of the terrestrial CO_2 balance are illustrated in Figure 3. We then provide a schematic overview of possible concurrent, lagged, direct and indirect impacts of climate extremes on processes underlying ecosystem carbon dynamics highlighting the importance of lagged impacts (Fig. 4).

Direct impacts

Temperature extremes can directly and concurrently impact photosynthesis and respiration (cf. Fig.3a, b). Effects differ between species, ecosystem types and biomes, and may change seasonally and even diurnally through hardening responses (Larcher 2003). Concurrent direct impacts of extremely high temperatures range from disruptions in enzyme activity affecting photosynthesis and respiration, to changes in growth and development (Larcher, 2003; Schulze *et al.,* 2005; Lobell *et al.,* 2012; Niu *et al.,* 2014). Likewise, extremely low temperatures impact physiological functions and developmental processes. Frost damage is perhaps the most important direct concurrent impact of cold climate extremes. In this context, timing is a crucial factor: in temperate ecosystems risk of plant damage is particularly high in spring when temperatures drop below freezing after an early warming event (Bokhorst *et al.,* 2009; Migliavacca *et al*., 2009), or during cold outbreaks when autumn hardening is insufficient, or when a protective snow cover is absent during extreme frost. In addition to frost damage of needles, xylem embolism in response to freeze-thaw cycles frequently adds to the factors decreasing plant vitality (Fig. 3a) (Sperry & Sullivan, 1992; Mayr *et al.,* 2003, 2007).

Unusual warming events at the end of the winter season in temperate and boreal climates can induce plant activity too early, a phenomenon that has been called “false spring” (e.g. Marino *et al.,* 2011). Extreme warm late winters together with the general trend of average warming may lead to earlier onset of the seasonal plant development, unfulfilled chilling requirements, i.e. the exposure to cool temperatures that is required before dormancy can be broken. A general trend of earlier onset of greening has been observed at local scales, from phenological gardens across Europe and globally from remote sensing NDVI data (Myneni *et al.,* 1997; Menzel *et al.,* 2006; Pilegaard *et al.,* 2011). If plants switch from dormancy to physiological activity earlier, they may become more susceptible to frost events with strong negative consequences, such as tissue mortality (Polle *et al.,* 1996), increased tree crown transparency (Dittmar & Elling, 2007), and reduced tree growth (Dittmar *et al.,* 2006) and plant performance (Kreyling, 2010).

Drought extremes may have manifold impacts on the carbon cycle *via* direct concurrent impacts (e.g. on plant physiology and soil microbial activity), direct lagged impacts (e.g. on the phenology of plants, reduced growth in the following year due to lower carbohydrate storage in the year of the drought, altered composition of plant species, soil microbial community structure and activity), as well as indirect lagged impacts, e.g. by drought-facilitated pest and pathogen outbreaks or fire ignition and spread (see Figures 3 and 4). Effects of drought on gross ecosystem productivity are typically larger than for ecosystem respiration (Schwalm *et al*., 2010; cf. Fig. 3b).

Drought stress occurs if the water potential of an organism / tissue drops below a critical threshold. For example, in temperate and Mediterranean forest ecosystems, decreased transpiration, gross photosynthesis and respiration were observed when relative root extractable soil water dropped below 40% (Granier *et al.,* 2007). High temperatures and low relative humidity (often expressed at the vapour pressure deficit) serve to increase evaporative demand, and drought stress of plants occurs when soil water supply can no longer meet the plant evaporative demand (e.g., Sperry, 2000). Plant available water is influenced by soil type and local surface and subsurface characteristics, such as the depth to the groundwater level or bedrock. The amount of water actually available to a plant depends strongly on the distribution of soil water across the profile in relation to root depth and type (Schachtschabel *et al.,* 1992; Tolk, 2003; White, 2006; Vicca *et al*., 2012).

Droughts and extreme high temperatures (heat waves), both to be considered climate extremes in their own right, cannot be seen as independent phenomena since in many (transitional climate) regions droughts additionally are connected with high temperature extremes (Mueller & Seneviratne, 2012) (Fig. 3b). The combination of high temperatures and droughts initiate a positive regional feedback mechanism (e.g. Durre *et al.,* 2000; Seneviratne *et al.,* 2006; Fischer *et al.,* 2007; Vautard *et al.,* 2007; Zampieri *et al.,* 2009; Diffenbaugh & Ashfaq, 2010; Hirschi *et al.,* 2011): the precipitation deficits and enhanced evaporative demand generally associated with warm spells (e.g. atmospheric blockings) triggers soil moisture deficit, thus suppressing evaporative cooling (Teuling *et al.,* 2010) and leading to hotter and drier conditions if soil moisture becomes limiting for evapotranspiration (Seneviratne *et al.,* 2010). Warmer temperatures additionally increase vapour pressure deficit, even without a concurrent reduction in rainfall, and this process alone causes extra drought stress (Williams *et al.,* 2012). In addition, there are likely also non-local feedbacks between drought conditions and heat waves, for instance through the advection of dry air or the modification of regional-scale circulation patterns (e.g. Vautard *et al.,* 2007; Haarsma *et al.,* 2009).

Plants may respond to drought stress by structural or physiological adjustments such as decreased leaf area index, changes in the root-shoot ratio, or changes in osmolyte concentration (Larcher, 2003; Breda *et al.,* 2006). The ability of plants to extract water from deeper layers under soil moisture stress, up to some limit, has been reported (e.g., Nepstad *et al.,* 1994; Canadell *et al.,* 1996; Wan *et al.,* 2002; Teuling *et al.,* 2006). Drought decreases CO_2 assimilation rates (according to our definitions, a direct concurrent impact) by reducing stomatal and mesophyll conductance, the activity and concentrations of photosynthetic enzymes (Lawlor, 1995; Chaves *et al.,* 2009; Keenan *et al.,* 2010) and reducing sink strength (Palacio *et al*., 2014). Generally, direct concurrent drought impacts are larger for plant photosynthesis than for respiration of plants (Atkin & Macherel, 2009) and ecosystems (Schwalm *et al.,* 2010; Shi *et al.,* 2014) (Fig. 3b).

In addition to direct concurrent drought impacts like decreased carbon (and nutrient) assimilation (Fig. 3b), drought may have lagged impacts on the carbon cycle *via* the re-allocation of existing stored reserves for repair, maintenance (including that of hydraulic integrity), growth and defence, as well as indirect lagged impacts (Fig. 4) by increasing the ecosystems' vulnerability to additional stressors such as pests and pathogens, or subsequent drought events (Breda *et al.,* 2006; Desprez-Lousteau *et al.,* 2006; McDowell *et al.,* 2011; Sala *et al.,* 2012; Keith *et al.,* 2012).

Water stress has a direct, concurrent impact on microbial activity, which depends on the presence of water films for substrate diffusion and exo-enzyme activity (Davidson & Janssens, 2006), whereas indirect and lagged drought impacts on microbial activity may be initiated by various mechanisms such as a decreased input of labile carbon into the soil due to reduced plant productivity (Araus *et al*., 2002; Reddy *et al*., 2004), and altered soil nutrient retention and availability (Muhr *et al*., 2010; Bloor & Bardgett, 2012). Drought may also alter microbial community structure (Sheik et al., 2011) with consequences for carbon cycling (Fig.4; direct concurrent and (in-)direct lagged impact via changes in species composition) (Fuchslueger *et al*., 2014). In Mediterranean ecosystems, for example, fungi were less affected by drought than bacteria and controlled soil organic matter decomposition (Curiel-Yuste *et al.,* 2011). While soil and ecosystem respiration are reduced by drought, rewetting by rainfall following drought can strongly stimulate soil CO_2 emissions to levels substantially exceeding pre-drought (or control) rates, with immediate consequences for the carbon cycle (Fig. 2, Jarvis *et al.,* 2007; see also reviews by Borken & Matzner 2009; Kim *et al.,* 2012, Vicca *et al*., 2014). Different mechanisms act when drying-rewetting cycles become more pronounced. Among others, physical disruption of aggregates (Borken & Matzner, 2009), increased soil water repellency (Goebel *et al.,* 2011) and altered nutrient retention (Borken & Matzner, 2009; Bloor & Bardgett, 2012) can be responsible for legacy effects on microbial activity and respiration, by modifying substrate and nutrient availability (indirect and lagged impact).

The magnitude of the impact on key ecosystem processes from an altered quantity, frequency or intensity of precipitation critically depends on the ecosystems' (seasonally varying) baseline water limitation (Gerten *et al.,* 2008). In addition to intensity and duration, the timing of droughts is a crucial factor due to the pronounced seasonal cycle of many ecosystems and land uses (Allard *et al.,* 2008; Unger *et al.,* 2009; Misson *et al.,* 2010, 2011; De Boeck *et al.,* 2011).

Extreme precipitation events may alter soil CO_2 fluxes and CO_2 uptake by plants during water logging phases (direct concurrent impacts on the carbon cycle), may lead to flooding-related tree mortality (Kramer *et al*., 2007) and may cause topsoil erosion (Fig. 3c; see also below and Figure 4) with losses of particulate and dissolved organic carbon from terrestrial to riverine ecosystems (Hilton *et al.,* 2008; Dinsmore *et al.,* 2013). In more water-limited systems, longer intervals between rainfall events may increase the duration and severity of soil drought stress. In contrast, longer intervals between heavy rainfall events may reduce periods of anoxia and be favourable to plant growth in more hydric ecosystems (see also Knapp *et al.,* 2008). The impacts of extreme precipitation events are often exacerbated by their association, in most climatic regions, with extreme wind storms/ cyclones.

Ice-storms are a form of extreme precipitation that occurs when liquid precipitation (often in a supercooled state) freezes shortly after contact with the terrestrial surface. The growing layer of ice can add substantial weight to vegetation and therefore result in the loss of branches, limbs, or uproot entire trees (Bragg *et al*., 2003; McCarthy *et al*., 2006; Sun *et al*., 2012).

Extreme wind storms and tropical cyclones are often associated with extreme precipitation events (see above), but have the additional potential to cause, depending upon their intensity severe damage and direct concurrent impacts on the carbon cycle (Fig. 3d) *via* defoliation, damage to branches, and wind throw or flooding by (e.g., saltwater) storm surges related tree mortality (Conner & Inabinette, 2003; MCPFE, 2007; Chambers *et al.*, 2007; Imbert and

Portecop, 2008; Zeng *et al.,* 2009; Negrón-Juárez *et al.,* 2010a) and lodging in agroecosystems (when crop stems are broken and crops are flattened). In addition, in forests, wind throw can cause long-term indirect lagged impacts on the carbon balance *via* tree mortality and dry dead wood accumulation that may facilitate lagged insect outbreaks or massive fires (Fig. 3d; see also below). Individual extreme storms and cyclones can severely impact the regional carbon balance (e.g. Lindroth *et al*., (2009) for Europe or Chambers *et al.* (2007) for the U.S.). For example, in October 2005, Hurricane Wilma made landfall over the Yucatán peninsula with particularly intense winds. Immediate reductions in leaf area and productivity were observed, while in the year following the hurricane, increased carbon emissions from soils were observed that were attributable to the addition of nitrogen-rich organic matter (Vargas 2012). Depending on the spatial and temporal scale considered, the frequency and intensity of the storm/cyclone, the characteristics of the impact and the recovery processes involved, the overall carbon balance can vary between a source and a sink (Fig. 2; see e.g., Fisk *et al*., 2012).

Soil erosion can be caused by the extreme precipitation events and extreme wind storms (or a combination of both) and is co-determined by topography, soil characteristics, vegetation cover and human activities (e.g. Lal *et al*., 2013) with significant on- and off-site impacts. Extreme weather events can result in direct, rapid and substantial local soil carbon losses (Hilton *et al*., 2008; Jung *et al*., 2012), and subsequent transport/redistribution and deposition (Goldsmith *et al*., 2008). Soils are especially susceptible to erosion if vegetation cover is low, e.g. crop ecosystems at fallow stages or grasslands after drought periods. Soil carbon loss due to erosion can therefore be a direct concurrent as well as an indirect lagged climate extreme impact (see Figure 4). In addition, soil erosion leads to losses of soil nutrient and water retention capacity, and to a generally lower productivity on eroded soils (Lal & Pimentel, 2008), inducing further (indirect) lagged impacts on the ecosystems carbon cycle. Eroded soil and mobilized soil organic matter is often redeposited within the same ecosystem at short-time scales, but soil organic carbon can also be laterally exported from a particular ecosystem (VandenBygaart *et al*., 2012; Behre & Kleber, 2013). The deposition and subsequent residence time of carbon removed with eroded soil determines the contribution of soil organic carbon erosion to CO_2 fluxes (van Oost *et al.,* 2007; Lal & Pimentel, 2008). Soil erosion processes can also increase the terrestrial carbon sink if eroded carbon is not transformed to CO_2, but trapped in deposits with longer residence times than the original soil (van Oost *et al.,* 2007; Hilton *et al.,* 2008). Hence erosion and subsequent sedimentation affects the overall land carbon budget, but the net effect of erosion on the carbon cycle remains controversial (Lal, 2009) and improved, scientifically-rigorous terminology may be needed to describe landscape soil carbon turnover (Behre & Kleber, 2013).

Indirect Impacts

While extreme droughts, heat waves, frosts, precipitation and wind storms are climate extremes, soil erosion can be a direct concurrent impact of extreme precipitation and/ or wind storms and, additionally, may be amplified by indirect lagged climate extreme impacts (cf. Fig.4); fires and pest and pathogen outbreaks are impacts facilitated by climate extremes (cf. Fig.4), but initiated by another trigger (not necessarily an extreme event *per se*) (cf. Fig. 1B, 1D).

Fire related losses of biomass or soil organic matter generally occur as an indirect, and often lagged, impact of climate extremes (cf. Fig. 3b, 3d; Fig.4) and are caused by the interaction between biotic (e.g., fuel load) and abiotic factors (e.g. dry weather, wind velocity, fuel continuity, slope of terrain and landscape fragmentation,) and human ignition (Moriondo *et al.,* 2006; Bowman et al., 2009; Aldersley *et al*., 2001; Pausas & Paula 2012). Fire frequency and intensity is highly sensitive to climate extremes because fire behaviour responds immediately to fuel moisture, which is affected by the combination of precipitation, relative humidity, air temperature and wind speed (Moriondo *et al.,* 2006). Fires release carbon stored in biomass and organic soils to the atmosphere in form of CO_2, CO, CH_4 and other climate relevant trace gases and aerosols, but can also serve to prevent land-atmosphere CO_2 fluxes when burned organic matter (i.e., charcoal) is formed during the combustion process. Charcoal is typically more resistant to decomposition and is thought to contribute to long term carbon sequestration in soils (Preston & Schmidt, 2006; Schmidt *et al.,* 2011), although recent advances point to a much faster decomposition rate which depends on thermal conditions during formation and soil conditions afterwards, than previously thought (Major *et al.,* 2010; Singh *et al.,* 2012; Kasin *et al.,* 2013).

Extreme fire events release large quantities of carbon to the atmosphere (Page *et al.*, 2002) and may have long-lasting consequences on vegetation composition (Bond *et al.,* 2005), soil structure, hydrophobicity and nutrient availability (Certini, 2005) with presumable multiple indirect and lagged impacts on the terrestrial carbon cycle (cf. Figs. 3b, 4). Carbon stored in litter, and organic soils such as peat, is burned during high-intensity but slow-spreading fires, and can be irreversibly destroyed, particularly during peat fires where carbon accumulated over very long time-scales is immediately released, but can be additionally accelerated by another trigger (Page *et al.,* 2002; Turetsky *et al.,* 2011a). Note, however, that not all climate-induced fires are carbon cycle extremes, but are within the range of the particular disturbance regime. For instance, frequent and low intensity savannah fires (Archibald *et al.,* 2012) may release over a year as much CO_2 as would have been decomposed otherwise by microbes (Li *et al.,* 2013).

The occurrence, frequency and magnitude of **insect and pathogen outbreaks** are often related to natural cycles in population size, driven by predictor-prey type dynamics (Jepsen *et* *al.,* 2009; Kausrud *et al.,* 2012). But there is consensus - despite many uncertainties – that climate conditions influence strength and timing of insect/pathogen outbreaks *via* changes in dispersal, reproduction, development of host plants, and mortality and distributional range changes of insect herbivores (Netherer & Schopf 2010; Cornelissen 2011). Different types of climate extremes may therefore catalyse insect and pathogen outbreaks leading as we hypothesize towards indirect lagged impacts on the carbon cycle (see Figures 3 and 4). Warm temperatures appear to favour radical increases in insect populations as a result of reduced mortality during the cold season, accelerated insect development rates, and earlier flight periods (Virtanen *et al.,* 1998; Stahl *et al.,* 2006; Robinet and Roques 2010; Johnson *et al.,* 2010). We regard these patterns as an indirect lagged impact of fewer cold temperature extremes (cf. Figs. 3a, 4). Mechanisms, associated with indirect lagged impacts of extreme heat and drought (cf. Figures 3b, 4), were observed during the European 2003 heat wave. Soil water deficits appeared to lower tree resistance to pest attacks, i.e. a positive drought - disease association, and defoliators additionally benefitted from increased nitrogen in plant tissues linked to moderate or intermittent drought stress (Desprez-Lousteau *et al.,* 2006; Rouault *et al.,* 2006). Multiple examples of how primary productivity and carbon stocks are reduced by insects and pathogens, and changes in carbon sink strength, are given in Hicke *et al.* (2012).

Impacts of extreme events on different ecosystem types

Ecosystems react differently to climate extremes: therefore we deduce that a climate extreme of a given magnitude will not have the same impact in a forest, grassland, peatland or cropland. With both large aboveground carbon stocks (standing biomass) and carbon uptake being affected by climate extremes, we expect the largest net effects on the terrestrial carbon balance in forests compared to other ecosystems. Forest carbon stocks may be lost or reduced as CO_2 rapidly by fire (as an indirect concurrent or lagged effect due to drought and heat extremes; Fig.4), or more slowly during the decomposition of dead wood after extreme wind and ice-storms or forest dieback after an extreme drought, which lead to lagged carbon emissions for a presumable long period after the climate extreme has occurred.

There are notable differences in how individual tree species respond to intra-annual climatic extremes including the timing of maximum sensitivity (Babst *et al.,* 2012), and the complexity of forest ecosystem dynamics makes prediction of the impacts of extreme events on carbon cycling challenging (Rammig *et al.,* 2014). At the same time, we hypothesize the complexity of forest ecosystems contributes to their resilience to climate extreme related impacts as e.g., heterogeneous forests are known to be less susceptible to wind-throw (Lindroth *et al.,* 2009), insect outbreaks (Drever *et al.,* 2006), and mass movements (Bebi *et al.,* 2009) (see S1, section A. for biome-specific extremes and related impacts). Forests generally have better access to deeper ground water than grasslands, and are reported to be likely less strongly affected by drought and heat waves (Teuling *et al.,* 2010). However, once their mortality thresholds are passed, we suppose forests to be less resilient to extreme events than grasslands, which have evolved to recover rapidly from disturbances. Natural grasslands prevail in regions where climatic constraints limit the occurrence of woody life forms (Suttie *et al.,* 2005). Grasslands are typically characterized by comparatively higher turnover rates compared to woody vegetation and we therefore assume grasslands to be more resilient to climate extremes than forests (see S1, section B. for more details). In this context, amongst the climate extremes, drought is expected to have the largest effect on the carbon cycle of grasslands (Zavalloni *et al.,* 2008; Gilgen and Buchmann, 2009; van der Molen *et al.,* 2011), while other extremes (e.g. wind storms) play a smaller if not negligible role (Reichstein *et al.,* 2013). However, degradation feedbacks, as triggered by e.g. grazing pressure (Albertson *et al.,* 1957), erosion (Breshears *et al.,* 2003) or fire combined with extreme precipitation events, may amplify effects of extreme drought and lead to substantial soil carbon losses. In comparison to forests, when normalizing for the per cent of bare soil, potential post-fire erosion tends to be lower in grassland (Johansen *et al.,* 2001).

Peatlands have characteristics in common with both forests and grasslands, namely large organic carbon stocks and a clear dominance of belowground carbon stocks, respectively. The large carbon stocks stored in peatlands are mainly protected by decomposition-limiting low temperatures and/or high water levels (Freeman *et al.,* 2001). Peatland carbon stocks are highly susceptible to immediate oxidation by fire (van der Werf *et al.,* 2008, 2010; Turetsky *et al.,* 2011a, b) and drought- or drainage- induced processes of microbial decomposition of organic carbon (Jungkunst & Fiedler, 2007; Couwenberg *et al.,* 2010; Frolking *et al.,* 2011). Therefore we hypothesize peatlands to be highly susceptibility to drought extremes and fire events caused by climate extremes (see S1, section C for more details).

Croplands are distinct from forests, grasslands, and peatlands, in that most crops are planted and harvested on an annual basis. The response of croplands is strongly coupled to the timing of the climate extreme, i.e. the sensitivity of the growth stage of the impacted crop (e.g. van der Velde *et al.,* 2012) and the management actions taken (e.g., Porter & Semenov, 2005; Ramankutty *et al.,* 2008; van der Velde *et al.,* 2010; Lobell *et al.,* 2012). In croplands, many climate extreme impacts can (theoretically) be mitigated through management, either within the same year (e.g. irrigation, replanting of a failed crop), or through longer term adaptation (e.g. changed rotations, drought and/or heat resistant cultivars). Lagged impacts of more than one year are of minor importance in croplands compared with the other ecosystem types.

A quantitative and systematic assessment of the impacts from different types of extreme events is currently limited by the number of observed case studies, a general lack of systematic data, and a lack of common metrics across experimental and impact studies (see introduction). It is therefore currently only possible to provide a detailed literature survey about how drought, wind storms, temperature and precipitation extremes, may possibly act on carbon cycle processes in forests, grasslands, peatlands and croplands (see S1).

Future climate extremes and their impact on the carbon cycle

There are inherently few data available to make robust assessments regarding changes in the frequency or intensity of carbon cycle extremes. First of all, climate extremes are hard to predict, as many predictions of climate extremes are either not sufficiently well resolved (e.g. heavy precipitation) or associated with high uncertainties (e.g. drought) in current climate models (Seneviratne *et al.,* 2012). Even in leading sectorial (e.g. agriculture) models, the effects of high temperatures, increased climate variability and several other growth-limiting factors such as soil nutrients, pests and weeds are not yet fully understood, and thus not implemented (Soussana *et al.,* 2010). Hence, it is very difficult to anticipate future impacts of climate extremes on the global carbon cycle. Thus, we here only hypothesize the most important current and future risks of the terrestrial carbon cycle in the face of climate extremes given the available literature.

In those parts of the boreal zone where litter and soil moisture will likely decrease e.g. *via* rising temperatures and decreasing precipitation (Seneviratne *et al.,* 2012) and earlier snowmelt (Grippa *et al.,* 2005), we hypothesize an increased risk that extreme dryness and tree mortality will increase the susceptibility to triggers such as lightning and human ignition, causing fires as an indirect concurrent or lagged effect (c.f. Fig. 1D, Figure 4; Michaelian *et al.,* 2011).

On the other hand, according to current climate projections, large areas in the boreal zone will likely become wetter (IPCC, 2013). More extreme snow fall has the potential to lead to stronger insulation of the soil in the winter. The higher soil temperatures may favour the thawing of permafrost (Zhang *et al.,* 2001; Gouttevin *et al.,* 2012), but also increase mineralization and growing season productivity (Monson *et al.,* 2006). Assessment of the magnitude and timing of these two opposing effects will require further research. As host-pathogen interactions are strongly influenced by weather and climate, we further hypothesize that decreased frost occurrence and fewer cold extremes will facilitate pest and pathogen outbreaks (e.g., Virtanen *et al.*, 1998, Hicke *et al.*, 2011; Samaraju *et al.*, 2012; Price *et al.*, 2013) with supposed important indirect and lagged impacts on the carbon cycle.

Temperate regions, being situated between cold boreal and warm, summer-dry Mediterranean regions are susceptible to temperature and precipitation extremes, droughts and storms, and impacts facilitated by them. Storms are considered to be the most important natural disturbance agent in temperate European forests, and even a small increase in storm frequency could potentially lead to a long-term reduction of the carbon stock (Fuhrer *et al.,* 2006; Lindroth *et al.,* 2009). Yet, current predictions of changes in storm intensity and frequency are not very robust (IPCC, 2013), such that no speculation on future impacts of storms on ecosystem is possible.

In contrast, we conjecture that in dry temperate regions there will be a sizeable negative effect on the carbon cycle through drought extremes, because towards the drier border of temperate regions there is consensus among climate models that, for example, the number of consecutive dry days will increase (Seneviratne *et al.,* 2012). Droughts, often occurring in concert with heat waves, can extend spatially across sub-continental domains and have a pronounced effect on forests, grasslands and croplands (Reichstein *et al.,* 2007; Schwalm *et al.,* 2010). Yet, the potentially mitigating effect of increased plant water use efficiency through increased CO_2 concentrations needs to be scrutinized in future research (e.g. Morgan *et al*., 2011, Zscheischler *et al*., 2014c).

Mediterranean and sub-tropical ecosystems are already shaped by strong seasonality of water availability. Changes in precipitation patterns with longer dry spells and more intense precipitation events are very likely (Seneviratne *et al.,* 2012). We suggest that in forests these changing patterns will contribute to higher tree mortality rates, increased fire activity in forests, and thus more sparse vegetation, and therefore as an indirect lagged effect (cf. Fig. 1D, Fig. 4) enhanced soil erosion, with expected negative consequences for ecosystem productivity (e.g. Allen *et al.,* 2010; Williams *et al.,* 2012). We further hypothesize that such positive feedback loops within the ecosystem triggered and enforced by alternating dry spells and subsequent heavy precipitation are even more likely and rapidly to occur in grasslands and cropland (e.g. with lower thresholds) because the non-woody vegetation with shorter turnover is likely to respond faster.

In the tropics, susceptibility of the carbon cycle to climate extremes will strongly depend on the interaction with human drivers. For example, fire risk is low in undisturbed Amazonian rainforests, and almost all fires are a consequence of land-use related burning activities (Aragão & Shimabukuro, 2010). Once burnt, forests are more susceptible to repeated burning, creating a positive feedback, which has the potential to transform large parts of rainforests into degraded forests or even savannah (Barlow *et al.,* 2008; Brando *et al.,* 2012; Brando *et al.,* 2014; Morton *et al.,* 2013). Changes in precipitation patterns with longer dry spells might additionally increase fire risk with decreasing canopy closure. While tropical forests and cropping systems are susceptible to long-term droughts, heavy precipitation and wind storms, future projections of these climatic extremes are particularly uncertain. The effect of high temperatures on photosynthesis is the second crucial mechanism that can directly impact tropical forests, where the most intensive CO_2-emission scenarios yield temperatures sufficient to damage photosynthesis and growth (Doughty & Goulden, 2008). But the long-term acclimation, and adaptation potential of tropical forest ecosystems (e.g. shift to heat-tolerant species) is not well known (Corlett, 2011; Smith & Dukes, 2013). We expect also the susceptibility of tropical peatlands to climate extremes to be strongly dependent on the interaction with human drivers, as peatland carbon stocks are highly susceptible to fires and drought- or drainage- induced microbial decomposition processes of their organic carbon stocks (see section above). Thus, we hypothesize that climate extremes will affect the tropical rainforest and peatland carbon cycle substantially, but the magnitude will strongly depend on the local human influence on these carbon stocks.

Outlook: On improving detection and prediction of global carbon cycle extremes

From a mechanistic and process perspective it is clear that climate extremes can have a profound impact on the carbon cycle, and case studies have reported such impacts (Figure 5). However, great challenges remain for both a rigorous global quantification of carbon cycle extremes and estimation of the future impacts on terrestrial-atmosphere CO_2 fluxes, and hence carbon-cycle climate feedbacks.

Remote sensing of the biosphere from space with a short return interval to identical locations and nearly global coverage offers promising perspectives to detect extreme anomalies in the biosphere in a consistent way (but see below). Land-surface states can be estimated by analysing the interaction of electromagnetic radiation (from visible to microwave) with the vegetation or upper centimetres of the soil *via* relatively well-evaluated radiation transfer models and their inversion. Thus, vegetation states (e.g. leaf area index, biomass) and radiative properties (e.g. fractions of absorbed radiation) can be monitored, albeit they require improvements to correct retrieved signals affected by noise and biases related to atmospheric conditions. Direct methods exist for use on the ground (Pan *et al.,* 2011; Baldocchi *et al.,* 2012; Babst *et al.,* 2014) and can be combined with remote sensing and modelling approaches to infer carbon cycling at the global scale (Jung *et al.,* 2011).

Zscheischler *et al.* (2013) have taken a first approach to detect extreme changes in fAPAR (fraction of absorbed photosynthetically active radiation) and GPP (Zscheischler *et al.* 2014a) associated with climate anomalies that occurred during the last three decades and their association with climate anomalies. They presented four major findings: 1) The total effect of negative carbon cycle GPP extremes is of a similar magnitude as the mean terrestrial carbon sink, 2) The spatial distribution of extremes is highly uneven with ‘hotspot’ regions in many semiarid monsoon-affected regions, 3) The distribution of extreme carbon impacts follows a power law, and 4) The detected carbon cycle extremes are statistically mostly strongly associated with droughts. The background map in Figure 5 shows the spatial distribution of carbon cycle extremes detected in the Zscheischler *et al.* studies. Many regions, where case studies have reported carbon cycle extremes, are also detected by the global remote sensing-based approach, but not all. In particular, Amazonian extreme anomalies in the carbon cycle suggested by Phillips *et al.* (2009) or Negrón-Juárez *et al.* (2010b) are not evident in the remote sensing-supported analysis of Zscheischler *et al.* (2013), and are only seen in one model in the analysis of negative extremes in four different data-driven and modelled GPP estimates (Zscheischler *et al.* 2014a). One reason for this might be the lack of sensitivity of fAPAR in dense evergreen vegetation (data-driven estimates of GPP often rely strongly on fAPAR). Evergreen vegetation often changes its physiology without strong alterations in the leaf or canopy reflective properties. This effect has also been observed outside tropical regions, for instance, during the extreme heat and drought in Europe 2003 (Reichstein *et al.,* 2007). Currently, more direct observations of photosynthetic processes *via* fluorescence offer the potential to overcome this problem (Frankenberg *et al.,* 2011; Guanter *et al.,* 2014), as well as combined observations of greenness indices and land surface temperature (Mildrexler *et al*., 2009). However, one striking feature of Figure 5 is the lack of presumably reported extreme impacts on the carbon cycle in some hotspot areas seen by the satellite data analysis. These include North East Brazil, the Indian subcontinent, East Asia, and particularly sub-Saharan Africa. To our understanding, without observations and experiments in those tropical hotspot areas, it will be hard to fully understand carbon climate cycle feedbacks and the role of carbon cycle extremes therein at a global scale.

According to our understanding, not all climate extremes cause extreme impacts in ecosystems, but they can have in-/direct and/or immediate/lagged effects. Lagged effects can either slow down the carbon cycle, when reduced vegetation productivity and/or wide-spread mortality after an extreme drought are not compensated by regeneration, but they can also accelerate the carbon cycle, when, e.g., productive tree and shrub seedlings cause rapid regrowth after windthrow or fire. Likewise, not all terrestrial carbon cycle extremes are propagated immediately into the atmosphere. For example, an extreme mortality event increases coarse woody debris, which is then slowly decomposed during the following years. Terrestrial carbon cycle extremes leading to structural changes without immediate fluxes to the atmosphere are currently globally undetectable due to lack of observation capabilities. LiDAR or Radar satellite missions with sufficient spatial and temporal resolution should be encouraged to increase such capabilities in the future. Detection systems need to resolve processes that cause immediate or lagged effects at different spatial and temporal scales, as the resilience of the respective ecosystem differ by ecosystem type.

This review also showed the lack of quantitative and consistent experimental data on the impact of climate extremes on the terrestrial carbon cycle, such that our conclusions are largely based on expert knowledge, scattered case studies and logical reasoning. Future experimental and observational designs should have a clear definition of the extreme conditions at the onset (e.g. by return interval), a consistent classification of resulting (extreme) impacts and should consider testing hypotheses around the conceptual framework presented in Fig. 1. In particular, indirect effects (Fig. 1B, D) need to receive increased attention in our opinion, given the complexity of the mechanisms involved and the paucity of current studies.

Future experiments should not only strive towards increasing comparability of treatments across case-studies, as suggested above; they should also account for increasing severity of future climate extremes and test more explicitly for threshold effects and mortality and recovery responses after extreme events, including those related to changing shifts of ecosystem states (Smith *et al*., 2011, Beier *et al*., 2012, Bahn *et al.,* 2014). Gradient studies that contain at least one very extreme (and possibly unrealistic) treatment would be particularly useful for this (Kreyling *et al*., 2014). Future experiments should address lagged and legacy effects more consistently, as well as ecosystem responses to multiple subsequent climate extremes, with the aim of elaborating mechanisms, as e.g. related to stress physiology, mortality and community assembly, as well as plant-soil interactions and soil processes at large (Backhaus *et al*., 2014; Kopittke et al. 2014; Vicca *et al*., 2014). Only through holistic approaches will we be able to fully understand the impacts of climate extremes on ecosystem carbon cycling; information needed to obtain realistic predictions of future carbon cycling and climate feedbacks. For more details and best-practice guidance in climate change experiments that aim to improve our understanding of the impacts of climate extremes, we refer to Beier *et al*., 2012; Vicca *et al*., 2012, 2014; Kreyling *et al*., 2014.

For ecosystems dominated by long-lived species such as forests, a better integration of experimental and modelling studies is needed, with experiments targeting critical hypotheses underlying model assumptions or specific mechanisms (e.g. processes linked to ecosystem transitions). State-of-the-art coupled climate-carbon cycle models (CMIP5) indicate a stronger negative effect of carbon cycle extremes than the above-mentioned observation driven estimates (Reichstein *et al.,* 2013), and an increasing absolute effect in the future. However, a reliable projection of the future impact of climate extremes on the terrestrial carbon cycle must rely on improved earth-system modelling, as well as improved description of the biospheric responses. Higher spatial (both horizontal and vertical) resolution and better representation of convective processes and clouds are pre-requisites for the simulation of climate extremes, and particularly hydro-meteorological extremes. On the biosphere modelling side, all processes leading to direct/indirect, as well as concurrent/lagged impacts

(Figure 4), need to receive attention. In particular, vegetation mortality in response to climate extremes (e.g. drought) and its mechanisms are increasingly well documented. Effort needs to be taken now to include this knowledge into global biosphere models. Including pest and pathogens, their reaction to climate extremes such as cold extremes and their effect on the carbon-cycle within an integrated modelling system at global scale is likely still too ambitious and needs landscape-modelling approaches, where lateral interactions are considered. Promising local- to regional-scale approaches do exist here and need to be further developed (Seidl *et al.,* 2011). Representation of these impacts into carbon cycle models will likely increase projected effects of climate extremes on the carbon cycle. On the other hand, we have to note that fundamental adaptive processes, such as acclimation, plasticity, migration, selection and evolution have the potential to mitigate effects of climate extremes. Modelling approaches accounting for these adaptations urgently need to be underpinned with more observational data and further developed (Scheiter *et al.,* 2013).

This study underlines the demand for better structured impacts studies of climate extremes on terrestrial ecosystems and the carbon cycle which follow a standardized protocol and definitions and allow for intercomparison studies. It has also shown the varying depth of analysis for different types of climate extremes, as well as identifying critically understudied regions. The findings underline the importance of biospheric processes in modulating impacts of climate extremes to assess the feedback to the global carbon cycle. In other words, biospheric processes are likely to determine the reaction of the global carbon cycle to climate extremes under global change.

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Supporting Information legend

S1

Supporting information S1 provides a detailed literature survey about how climate extremes act on forests, grasslands, peatlands and croplands.

Figure legends

Figure 1: Schematic diagram illustrating direct concurrent and lagged (A, B) and indirect concurrent and lagged (C, D) impacts of climate extremes and corresponding extreme ecosystem responses. In the direct case the extreme impact occurs if (and only if) a threshold is reached, i.e. a critical dose (blue line) is passed. In the indirect case, the climate extreme increases the susceptibility (red line) to an external trigger (climatic or non-climatic, extreme or not extreme). The likelihood as a function of the trigger and the susceptibility is indicated with the symbol “P” in the circle. Concurrent responses start during the climate extreme, but may last longer for indefinite time (dashed extensions of green boxes). Lagged responses only happen after the climate extreme. The responses can be of different non-linear shapes as indicated in Fig. 2.

Figure 2: Hypothesized temporal dynamics of direct and indirect concurrent and lagged effects of climate extremes (examples: drought / heat wave; storm) and of ecosystem recovery on the ecosystem carbon balance. (Note that for simplicity regrowth after fire and pest outbreak are not shown in this figure). Line colours correspond to the colour of the climate extreme in the figure.

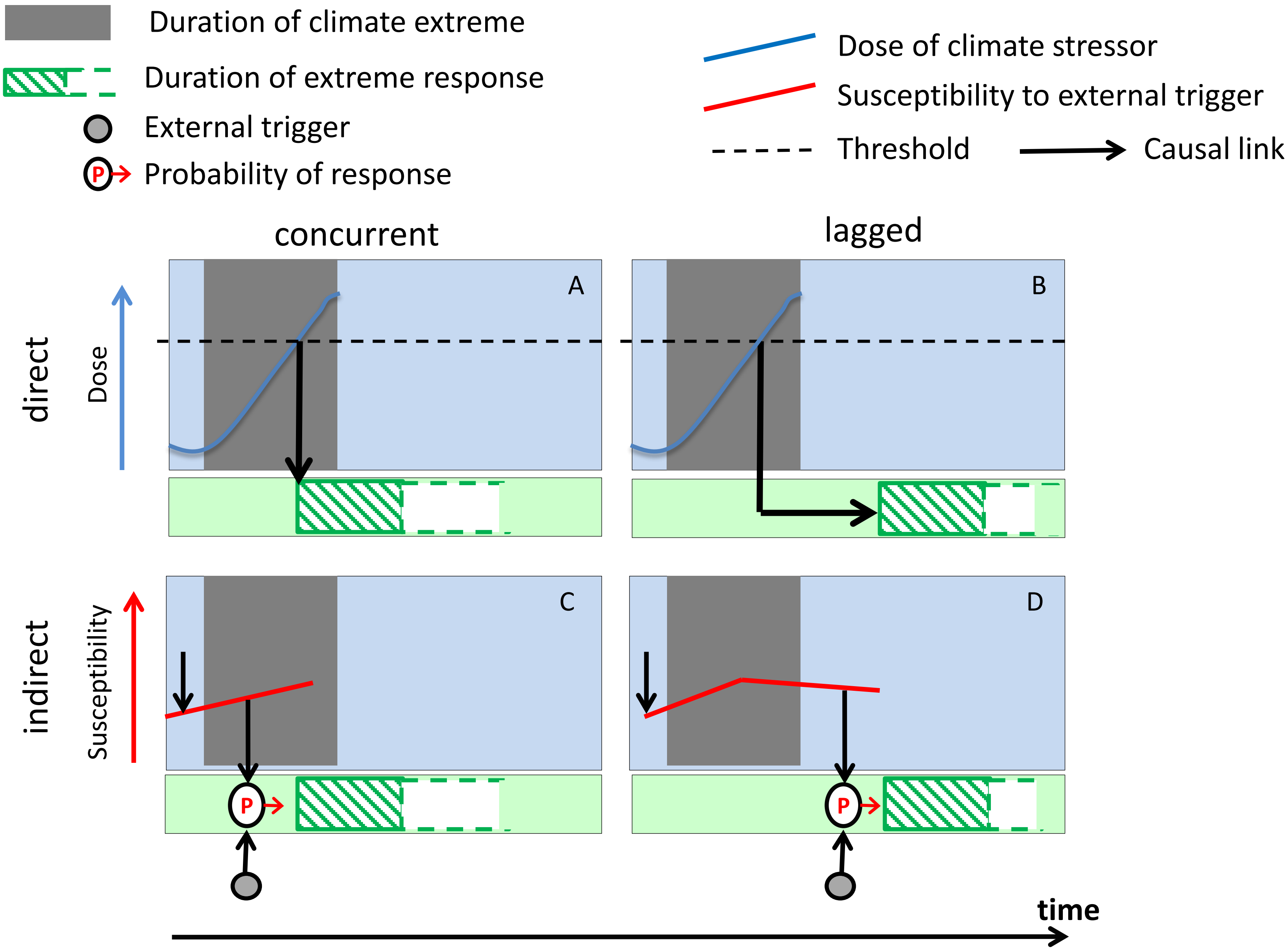
Figure 3: Processes and mechanisms underlying impacts of climate extremes on the carbon cycle. Positive/ enhancing impacts with a “+” and negative/reducing impacts with a “-“ sign; predominant (in-)direct impacts (dashed) arrows (for further details please see text); importance of impact/relationship is shown by arrow width (high=thick, low=thin) (modified after Reichstein *et al*., 2013).

Figure 4: Schematic overview of concurrent, lagged, direct and indirect impacts of climate extremes on processes underlying ecosystem carbon dynamics. Respective references (selection of examples) are indicated as followed: **1** [Larcher, 2003; Mayr *et al.,* 2007]; **2** [Larcher, 2003; Schulze *et al.,* 2005; Lobell *et al.,* 2012; Porter & Semenov, 2005; Niu *et al.,* 2014]; **3** [Larcher, 2003; Breda *et al.,* 2006; Keenan *et al.,* 2010; Reichstein *et al.,* 2007; Mission *et al.,* 2010; Schwalm *et al.,* 2010; Eamus *et al.,* 2013]; **4** [Rosenzweig *et al.,* 2002; Vervuren *et al.,* 2003; Kreuzwieser *et al.,* 2004; van der Velde *et al.,* 2012]; **5** [Nykänen *et al.,* 1997; Irland 2000; Chagnon 2000; Hao *et al.,* 2011; Sun *et al.,* 2012]; **6** [Berry *et al.,* 2003; Fuhrer *et al.,* 2006; MCPFE, 2007; Lindroth *et al.,* 2009; Zeng *et al.,* 2009; Negrón-Juárez *et al.,* 2010b]; **7** [Larcher 2003; Schulze *et al.,* 2005; Dittmar *et al.,* 2007; Bokhorst *et al.,* 2009]; **8** [Larcher, 2003; Porter & Semenov, 2005; Breda *et al.,* 2006; Lobell *et al.,* 2012]; **9** [Barber *et al.,* 2000; Eilmann *et al.,* 2011; Fuhrer *et al.,* 2006; Phillips *et al.,* 2009; Michaelian *et al.,* 2010; McDowell *et al.,* 2013; Peñuelas *et al.,* 2013)]; **10** [Vervuren *et al.,* 2003; Posthumus *et al.,* 2009]; **11** [MCPFE, 2007; Chambers *et al.,* 2007; Zeng *et al.,* 2009; Negrón-Juárez *et al.,* 2010a, b]; **12** [Fuhrer *et al.,* 2006; Hilton *et al.,* 2008; Garciía-Ruiz *et al.,* 2013]; **13** [Wang *et al.,* 2006; Shinoda *et al.,* 2011]; **14** [Jentsch *et al.,* 2011; Fuchslueger *et al.,* 2014]; **15** [Moriondo *et al.,* 2006; Ganteaume *et al.,* 2013]; **16** [Porter & Semenov, 2005; Jentsch *et al.,* 2009; Mission *et al.,* 2011; Nagy *et al.,* 2013), Peñuelas *et al.,* 2013]; **17** [Breda *et al.,* 2006; McDowell *et al.,* 2008, 2011, 2013; Walter *et al.,* 2012]; **18** [Breda *et al.,* 2006; Adams *et al.,* 2009; Allen *et al.,* 2010; Michaelian *et al.,* 2010; McDowell *et al.,* 2008, 2011; Granda *et al.,* 2013]; **19** [Kreyling *et al.,* 2011; Suarez & Kitzberger, 2008; Diez *et al.,* 2012]; **20** [Larcher, 2003; Walter *et al.,* 2013]; **21** [Virtanen *et al.,* 1998; Stahl *et al.,* 2006; Robinet and Roques 2010; Kausrud *et al.,* 2012]; **22** [Breda *et al.,* 2006; Desprez-Lousteau *et al.,* 2006; Rouault *et al.,* 2006; MCPFE, 2007; McDowell *et al.,* 2008, 2011; Jactel *et al.,* 2012; Keith *et al.,* 2012; Kausrud *et al.,* 2012; Walter *et al.,* 2012]; **23** [Schlyter *et al.,* 2006,

MCPFE, 2007; Komonen *et al.,* 2010]; **24** [Trigo *et al.,* 2006; Wendler *et al.,* 2011]; **25** [Kurz *et al.,* 2008a]; **26** [Øygarden, 2003; Valentin *et al.,* 2008; Thothong *et al.,* 2011]; **27** [Sheik *et al.,* 2011; Yuste *et al.,* 2011; Fuchslueger *et al.,* 2014]; **28** [Sowerby *et al.,* 2008].

Figure 5: Global distribution of extreme events in the terrestrial carbon cycle, and approximate geographical locations of published climate extremes with impacts on the carbon cycle. Extreme events in the carbon cycle are defined as contiguous regions of extreme anomalies of GPP during the period 1982-2011 (modified after Zscheischler *et al.,* 2014b). Colour scale indicates the average reduction in gross carbon uptake compared to a normal year due to negative extremes in GPP. Units are gram carbon per square meter per year. The map highlights the IPCC regions with the following references to the published climate extremes.

References ad Fig. 5: **1** *pest outbreaks Canada/North America* [Soja *et al.,* 2007; Kurz *et al.*, 2008b], **2** *ice storm North America* [Irland, 2000], **3** *drought US* [Breshears *et al.,* 2005; Schwalm *et al.,* 2012], **4** *heavy storm Southern US* [Chambers *et al.,* 2007; Zeng *et al.,* 2009; Negrón-Juárez *et al.,* 2010a], **5** *heavy storm Amazon* [Negrón-Juárez *et al.,* 2010b], **6** *drought Amazon* [Tian *et al.,* 1998; Phillips *et al.,* 2009; Lewis *et al.,* 2011], **7** *heavy storm Europe* [Fuhrer *et al.,* 2006; Lindroth *et al.,* 2009], **8** *drought and heat extreme Europe* [Ciais *et al.,* 2005; Reichstein *et al.,* 2007], **9** *extreme drought, heat and fire in Russia* [Barriopedo *et al.,* 2011; Konovalov *et al.,* 2011; Coumou & Rahmstorf, 2012; Bastos *et al.,* 2013a], **10** *ice storm China* [Stone, 2008; Sun *et al.,* 2012)], **11** *fire, drought SE Asia* [Page *et al.,* 2002; Schimel & Baker, 2002], **12** *drought Australia* [Haverd *et al.,* 2013], **13** *heavy precipitation Australia* [Bastos *et al.,* 2013b; Haverd *et al.,* 2013], **14** *heavy precipitation Southern Africa* [Bastos *et al.,* 2013b].


Duration of climate extreme
Duration of extreme response
External trigger
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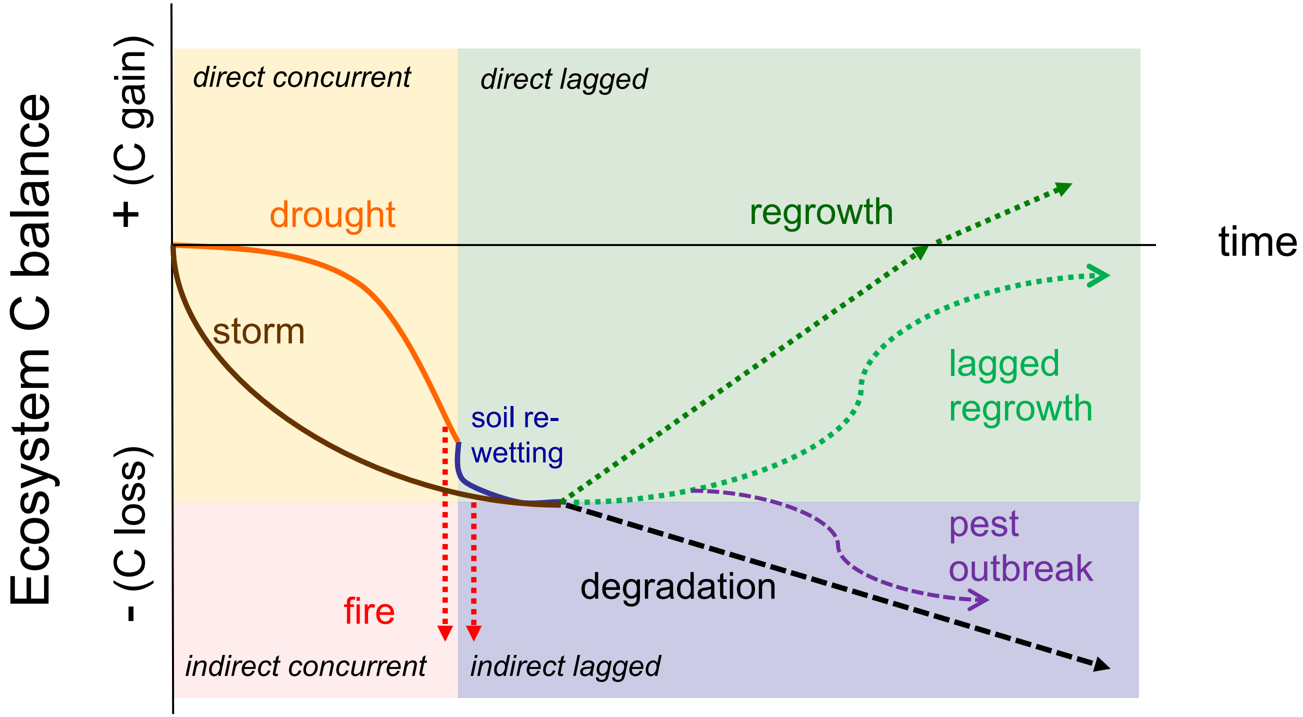
Ecosystem C balance
+ (C gain)
- (C loss)
time
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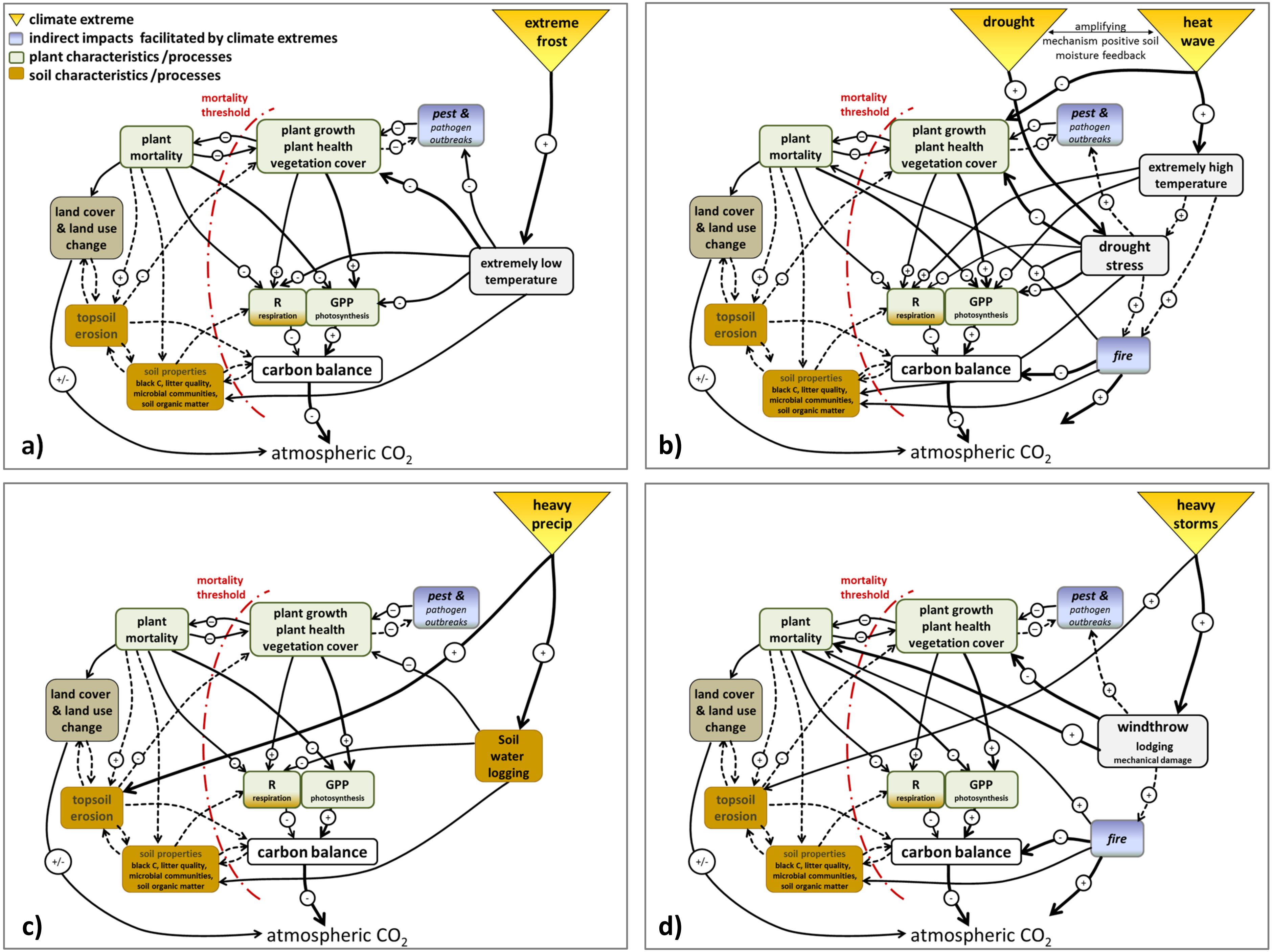
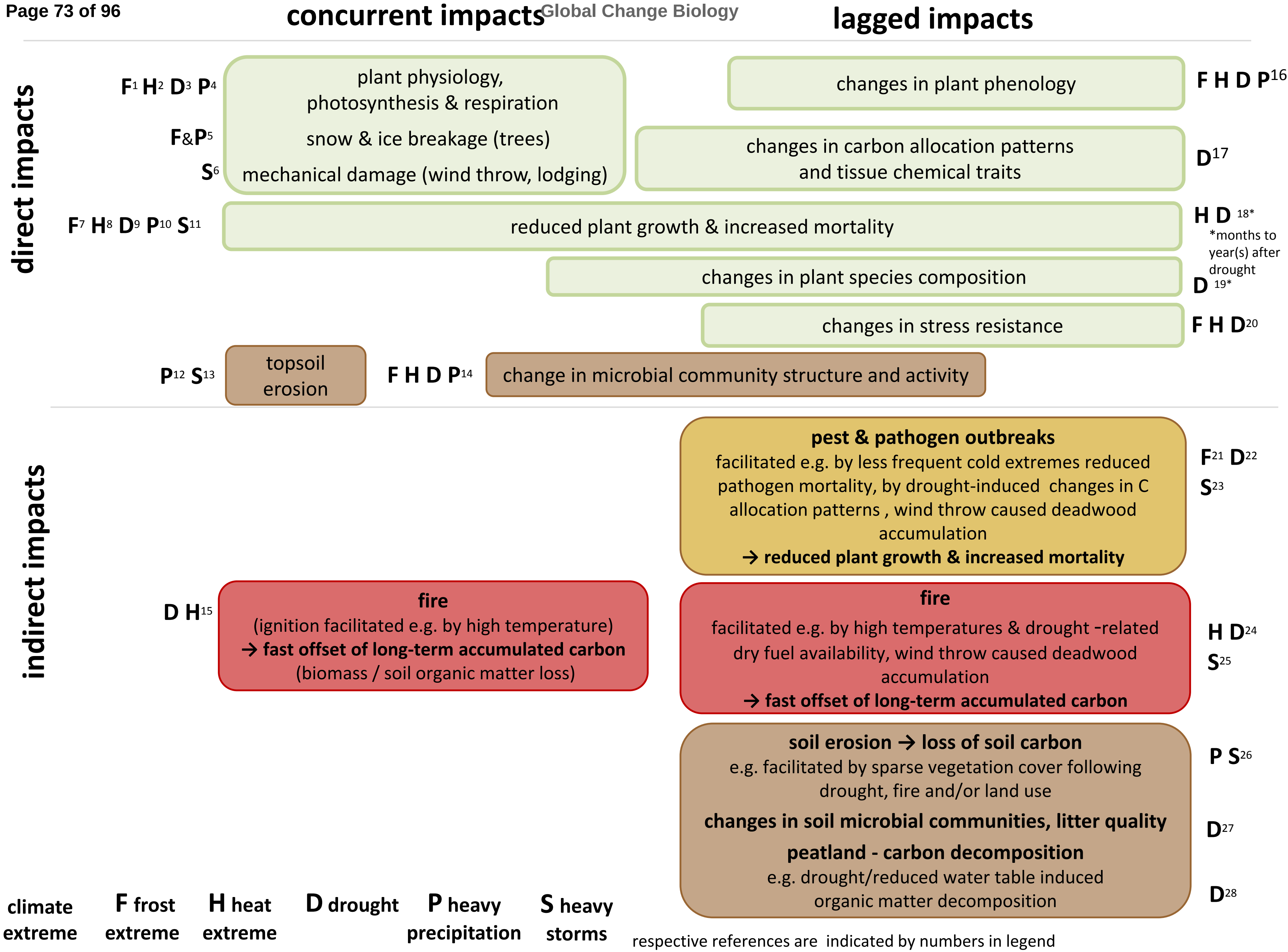
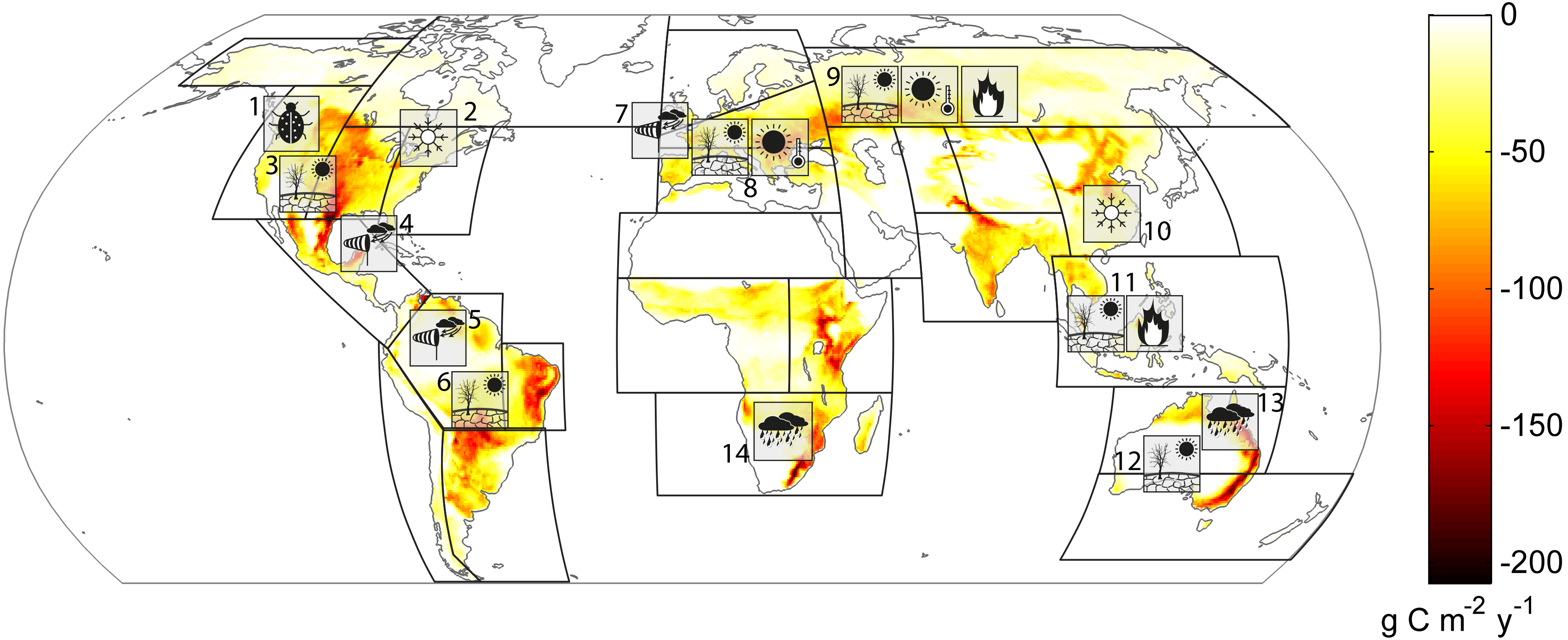

▽ climate extreme
▨ indirect impacts facilitated by climate extremes
🟩 plant characteristics / processes
▨ soil characteristics / processes
extreme frost
mortality threshold
plant mortality
plant growth plant health vegetation cover
pest & pathogen outbreaks
land cover & land use change
extremely low temperature
R respiration
GPP photosynthesis
topsoil erosion
soil properties black C, litter quality, microbial communities, soil organic matter
carbon balance
+/-
atmospheric CO_2
a)
drought
amplifying mechanism positive soil moisture feedback
heat wave
extremely high temperature
drought stress
fire
b)
heavy precip
Soil water logging
c)
heavy storms
windthrow lodging mechanical damage
d)


concurrent impacts
lagged impacts
direct impacts
F1 H2 D3 P4
plant physiology, photosynthesis & respiration
F&P5
snow & ice breakage (trees)
S6
mechanical damage (wind throw, lodging)
changes in plant phenology
F H D P16
changes in carbon allocation patterns and tissue chemical traits
D17
F7 H8 D9 P10 S11
reduced plant growth & increased mortality
H D 18*
*months to year(s) after drought
changes in plant species composition
D 19*
changes in stress resistance
F H D20
P12 S13
topsoil erosion
F H D P14
change in microbial community structure and activity
indirect impacts
pest & pathogen outbreaks
facilitated e.g. by less frequent cold extremes reduced pathogen mortality, by drought-induced changes in C allocation patterns , wind throw caused deadwood accumulation
→ reduced plant growth & increased mortality
F21 D22
S23
D H15
fire
(ignition facilitated e.g. by high temperature)
→ fast offset of long-term accumulated carbon
(biomass / soil organic matter loss)
fire
facilitated e.g. by high temperatures & drought -related dry fuel availability, wind throw caused deadwood accumulation
→ fast offset of long-term accumulated carbon
H D24
S25
soil erosion → loss of soil carbon
e.g. facilitated by sparse vegetation cover following drought, fire and/or land use
P S26
changes in soil microbial communities, litter quality
D27
peatland - carbon decomposition
e.g. drought/reduced water table induced organic matter decomposition
D28
climate extreme
F frost extreme
H heat extreme
D drought
P heavy precipitation
S heavy storms
respective references are indicated by numbers in legend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Supporting Information S1

Supporting information S1 provides a literature survey about how climate extremes may possibly act on forests (A), grasslands (B), peatlands (C) and croplands (D).

A. Forests

Forests cover about 30% of the global land area and play an important role in the global carbon cycle (Canadell & Raupach, 2008; FAO, 2010; Pan *et al.,* 2011). In addition to their large carbon pools and fluxes, characteristics of forests that likely make them susceptible to climate extremes, in terms of the terrestrial carbon cycle, include:

- the long lifespan of individual organisms that store carbon in living tissues, structural and hydraulic infrastructures
- location of meristems where (re)growth can happen after an extreme event,
- a high sensitivity to diverse climatic extremes at multiple spatiotemporal scales
- lagged physiological and cascading ecological processes leading to long-term changes in growth and/or mortality
- high vulnerability of carbon stocks and long recovery time to re-gain previous stocks following extreme event impacts
- low migration rates in response to environmental changes compared to short-living species

We hypothesize drought to be the primary control on both inter-annual variability of forest productivity and long-term tree survival. In trees, vulnerability to drought-induced hydraulic failure (Choat *et al.,* 2012, but see Klein *et al.,* 2014) may have both concurrent and lagged (often carbohydrate and mortality related) consequences for the carbon cycle. Besides hydraulic failure, tree mortality following drought and heat waves has been suggested to be caused by carbon starvation and / or cellular metabolism limitation (Adams *et al.,* 2009; Sala *et al.,* 2010; McDowell *et al.,* 2011, 2013). Repeated stress from one or multiple extreme climate events in combination with non-climatic disturbances can lead to a long-term recovery-response of a forest or to a downward spiral into decline and mortality thereby enhancing negative impacts of drought on the carbon sequestration potential (Rouault *et al.,* 2006; Sánchez-Salguero *et al.,* 2012).

Similar to temperate regions, drought is a significant driver of the physiology and carbon cycling of Mediterranean (Granier *et al.,* 2007; Schwalm *et al.,* 2012) and tropical forests (Tian *et al.,* 1998; Phillips *et al.,* 2009; Clark *et al.,* 2010). Tropical wet forest tree growth was found to be highly sensitive to the current range of dry season conditions and to moderate (1–2°C) variations in mean annual night-time temperature (Clark *et al.,* 2010). The severe droughts in the Amazon during 2005 and 2010 caused a significant large-scale increase in tree mortality with an estimated committed biomass carbon loss of up to 1.6 Pg C and 2.2 Pg C (Phillips *et al.,* 2009; Lewis *et al.,* 2011). However, a recent analysis (Cox *et al.,* 2013) suggests stronger resilience to warming than previously (Cox *et al.,* 2004) reported and radiocarbon evidence for living trees older than 1000 years demonstrates that trees have survived though several mega-El-Niño type droughts during the past millennium (Chambers *et al.,* 1998). Thus to our understanding it remains unclear how vulnerable and how close the Amazon or other tropical forests, which may be even more sensitive to drought (Meir & Woodward, 2010), are to climate driven biome shifts.

The 2003 European heat wave strongly affected the hydraulic balance in many tree species with symptoms ranging from partial crown necrosis to death (Martinez-Meier *et al.,* 2008, Eilmann *et al.,* 2009, 2011), whereas a positive growth response was observed at higher elevations across the Alps (Jolly *et al.,* 2005). Also, in boreal ecosystems, a positive temperature extreme during the growing season tends to result in enhanced productivity (Esper *et al.,* 2002; Babst *et al.,* 2013), but a positive temperature extreme occurring during the winter will most likely tend to increase respiration, and therefore result in a loss of carbon from the ecosystem (Piao *et al.,* 2008).

Heavy snow fall may result in crown, stem breakage, and even fully uproot trees. Nykänen *et al.* (1997) estimated an average annual timber loss of 4x106 m³ across Europe due to snow damage. Spring and autumn snowfall (when deciduous trees still hold foliage) and snow temperatures around 0°C (high water content and enhanced abilities to accumulate) increase the likelihood of damage (Nykänen *et al.,* 1997) as do higher wind speeds (Valinger & Fridman, 1999).

Storms are considered to be the most important natural disturbance agent in temperate European forests and even a small increase in storm frequency could potentially lead to a long-term reduction of the carbon stock (Fuhrer *et al.,* 2006). The large storm “Lothar” in central Europe killed the equivalent of 16 Tg C tree biomass (Lindroth *et al.,* 2009), and hurricanes Katrina and Rita destroyed 43.9 ± 8.4 Tg C and 37.9 ± 6.4 Tg C of living biomass, respectively (Negrón-Juárez *et al.,* 2010a). Katrina alone caused a total biomass loss estimated around 50–140% of the net annual U.S. carbon sink of forest trees (Chambers *et al.,* 2007).

Forest fires released around half of the average annual 2.0 Pg C globally emitted by fires between 1997 and 2009 (van der Werf *et al.,* 2010). Fire regimes are regarded as highly non-linear, where under extreme climate conditions the burnt area can increase by an order of magnitude (Sukhinin *et al.,* 2004; Vivchar, 2011). Lagged effects due to precipitation deficits overlaid with spring droughts caused extreme fire events in Siberian permafrost regions (Forkel *et al.,* 2012).

Outbreaks of forest insects damage around $35x10^6$ ha of forest annually primary in the temperate and boreal zones (FAO, 2010). Climate extremes may impact the outbreak strength, timing and frequency as well as the host plant resistance. The European 2003 heat wave showed the importance of soil water status in tree resistance against pest attacks (c.f. Desprez-Lousteau *et al.,* 2006; Rouault *et al.,* 2006). In north-western North America favourable climate conditions, such as e.g. reduced minimum winter temperature (i.e. less cold extremes, cf. Fig. 3a, Fig.4), have resulted in the most extensive and severe bark beetle damages ever reported (Kurz *et al.,* 2008). Vast expanses of forest have become a net carbon source and this is predicted to persist at least until 2020.

B. Grasslands

Grasslands are characterized by high turnover rates and a rapid recovery from disturbance. Amongst the climate extremes, drought has the presumably largest effect on the carbon cycle of grasslands, with substantial implications also for society. For example, during the 2003 summer drought in Central Europe, grassland production ceased completely in certain areas, resulting in an annual decrease of fodder production across Europe between 30% and 60% (EEA, 2005). Typically, drought effects are higher for above-ground productivity (e.g. Kahmen *et al.,* 2005; De Boeck *et al.,* 2011; Fay *et al.,* 2011) than for below-ground productivity, resulting in changes in carbon allocation belowground and an increased root-to-shoot ratio (e.g., Dukes *et al.,* 2005; Gilgen & Buchmann, 2009; Burri *et al.,* 2014). As for forests, soil respiration of grasslands decreases when soil moisture drops below critical thresholds (Knapp *et al.,* 2002; Bahn *et al.,* 2008; Joos *et al.,* 2010; Burri *et al.,* 2014), with consequences for annual soil respiration (Ma *et al.,* 2007; Bahn *et al.,* 2010). However, rainfall following drought may rapidly and strongly stimulate soil CO_2 emissions (Borken & Matzner, 2009), and in semi-arid grasslands may cause higher respiratory CO_2 losses than from the rest of dry season (Xu *et al.,* 2004).

The magnitude and direction of carbon cycle responses to reduced precipitation and drought depend strongly on the climatic context and background soil moisture conditions. While in semiarid and arid climates water availability severely limits ecosystem carbon acquisition (Hunt *et al.,* 2004) and soil respiratory carbon losses, the response in temperate conditions is less clear (Bloor *et al.,* 2010). In humid climates and under very wet conditions, reduced precipitation has even been shown to increase aboveground plant growth and ecosystem carbon uptake (Jaksic *et al.,* 2006; Gilgen & Buchmann, 2009; Peichl *et al.,* 2011).

In addition to the amount, seasonal variability and timing of precipitation and associated drought may strongly alter key carbon cycling processes and plant community composition (Knapp *et al.,* 2002; Harper *et al.,* 2005; De Boeck *et al.,* 2011). In fact, the timing of precipitation may affect carbon cycling even more strongly than changes in rainfall quantity (Chou *et al.,* 2008; Hovenden *et al*., 2013). In dry grasslands, the effects from the combined timing and size of rainfall events are crucial (Thomey *et al.,* 20011) as these factors co-determine critical soil moisture thresholds (Vargas *et al.,* 2012).

Experiments on simplified sown experimental grasslands revealed a high recovery potential of plant growth (Zavalloni *et al.,* 2008; De Boeck *et al.,* 2011). High resilience of key plant ecophysiological processes as well as soil carbon fluxes after prolonged droughts was observed also in managed temperate grasslands (Gilgen & Buchmann, 2009; Joos *et al.,* 2010; Signarbieux & Feller, 2011). Furthermore, changes in vegetation structure and composition in response to drought can contribute to the resilience of grasslands, and may alter above- and belowground productivity and CO_2 fluxes (including their response functions to climate) beyond the direct physiological response (Kreyling *et al.,* 2008; Talmon *et al.,* 2011; van der Molen *et al.,* 2011), but might also result in increased weed pressure (Gilgen *et al.,* 2010).

Drought may have strong interactive effects with high temperatures, which increase water vapour pressure deficits and the soil water stress, and can amplify detrimental effects of drought on the physiology of organisms, e.g. during heat waves (Chaves & Oliveira, 2004; De Boeck *et al.,* 2011). An anomalously warm year was shown to exert both immediate and lagged effects on the net ecosystem exchange of CO_2 of a tallgrass prairie (Arnone *et al.,* 2008). This extreme decreased NEE immediately via drought effects on net primary productivity and in the following year by stimulating the respiration of soil heterotrophs. In a future climate, elevated CO_2 may buffer effects of drought on grassland productivity by increasing water use efficiency (Owensby *et al.,* 1997). The combination of warming, elevated CO_2 and limiting soil moisture may favour C_4 over C_3 grasses and may thereby result in higher productivity in semi-arid grasslands than expected (Morgan *et al.,* 2011).

Heavy rainfall, particularly after prolonged drought periods, can lead to degradation via soil erosion in already degraded grasslands that lack grass cover. While intense rainfall has less pronounced effects on erosion in grasslands and rangelands than in arable lands (van Oost *et al.,* 2007), once degradation feedbacks come into play, more frequent extreme events may contribute to a desertification of semi-arid to arid grassland particularly when (over-)grazing or fire act as an additional pressure. Heavy or prolonged rainfall can also cause water-logging in grasslands, affecting root mortality, forage quality and quantity, and ultimately vegetation composition.

Fires are an important factor of ecosystem dynamics in (sub-)tropical grasslands or savannahs, where the vegetation has adapted and co-evolved re-sprouting traits coinciding to a certain fire frequency (Pausas *et al*., 2004, 2009). Fires in grasslands and savannahs contributed 44% to the total global fire carbon emissions during 2001–2009 due to frequent burning of large areas (van der Werf *et al.,* 2010). Due to vast regeneration of grasslands, fluxes and species composition can return to pre-fire conditions within a few months. Castaldi *et al.* (2010) observed that one month after burning a tropical grassland, CO_2 emissions were significantly lower in burned plots than in the control plots, but after eight months they no longer differed.

C. Peatlands

Peatlands contain in about 400 Mha between 400 to 600 Pg C (Frolking *et al.,* 2011); the carbon stored in peatlands is protected primarily by the prevailing environmental conditions that limit decomposition: low temperatures and/or high water levels (Freeman *et al.,* 2001), which makes peatlands hotspots in terms of potentially large feedbacks to global change. Peatlands are particularly susceptible to oxidation of the carbon stocks by fire and biological decomposition processes, which may be induced by drought. Fires cause immediate oxidation of large amounts of carbon stored in peat soils (van der Werf *et al.,* 2008; Hooijer *et al.,* 2010), whereas droughts can substantially increase soil carbon efflux following soil aeration (Freeman *et al.,* 2001). Moreover, Sowerby *et al.* (2008) found a persistent stimulation of decomposition rates in a peatland experiment that was exposed to repeated summer droughts, which was confirmed by Couwenberg *et al.* (2010) for South-east Asia and Turetsky *et al.* (2011a) in northern peatlands. This persistent stimulation of soil decomposition was related to incomplete recovery of the soil moisture content upon rewetting, which was most likely due to increased soil hydrophobicity. Hence, legacy effects of drought and also of fire, which can increase soil hydrophobicity (Howell *et al.,* 2006), can substantially increase the impact of a particular extreme event on the large carbon stocks stored in peatlands.

Because of the vast quantities of carbon stored in organic soils (Tarnocai *et al.,* 2009; Page *et al.,* 2011), changes in depth of the water-table from drainage or from drought can expose large areas of carbon to rapid decomposition and decay.

We assume the vulnerability of peatland ecosystems to climate extremes to increase because of human land use change in tropical regions (Hooijer *et al.,* 2010), and because of chronic climate change in high-latitude regions (Turetsky et al 2002; Turetsky *et al.,* 2011b).

D. Croplands

Climate variability and climate extremes strongly affect crop production and thus the long-term carbon balance. Lagged ecosystem impacts of more than one year are of minor importance in croplands; however, lagged impacts do occur due to adaptive changes in the management of arable systems linked to climate extremes and climate change. Indeed, human response to climate extremes, in terms of adaptive management, is one of the greatest uncertainties when attempting to predict the impact of climate extremes on the carbon balance of croplands (Klein Goldewijk & Ramankutty, 2004; Porter & Semenov, 2005; Ramankutty *et al.,* 2008).

Efficient and effective agricultural practice requires that farmers adapt to climate variability. Climate extremes can impact crops via both negative impacts on plant physiological processes and direct physical damage, as well as by affecting the timing and conditions of field operations. The impact of a climate extreme on a certain crop is a function of the timing and type of climate extreme in relation to the sensitivity of the growth stage of the impacted crop (e.g. van der Velde *et al.,* 2012). Even during climate extremes, farmers will pursue strategies to minimize impacts on final crop harvests. Irrigation, for example, can be used during a heat wave to lower ambient field temperature (by ~3-4 °C at an ambient temperature >35 °C), thus minimizing crop heat stress and leading to lower crop losses than would otherwise occur (van der Velde *et al.,* 2010). The use of light-reflecting particle films sprayed over field crops and orchards is another adaptive measure (Glenn & Puterka, 2005). The use of kaolin powder, for instance, can effectively induce radiation loads and excessive heat during extreme events by increasing surface albedo, thus reducing physiological plant damage (Rosati *et al.,* 2006). Adaptive management actions can be immediate, but can also be longer term, such as the use of more heat resistant varieties, or changes in the rotation such as shifting to winter crops (Porter & Semenov, 2005; Lobell *et al.,* 2012; Ramankutty *et al.,* 2008). Adaptive management may lead to co-benefits or trade-offs; Increased irrigation e.g. may lead to increased root biomass growth, higher microbial activity, or increased erosion rates, variously leading to either increased or decreased soil organic carbon levels. Expected crop failure – for instance a crop affected by drought – can also cause a farmer to decide not to harvest the crop, potentially leading to a larger incorporation of biomass into the soil.

Drought stress is one of the most damaging climate extremes affecting crop growth and productivity, especially if it occurs in connection with high temperatures. The 2003 heat wave in parts of Europe reduced crop yields by 20% compared to the mean for 1991-1999 (Fuhrer *et al.,* 2006). Farmers adapt to or mitigate against drought by irrigation. Globally, the area of irrigated land is increasing due to agricultural intensification with consequences for water resources (Nellemann *et al.,* 2009). Introduction of drought resistant crops as well as the use of perennial grain crops with deeper rooting systems (Glover *et al.,* 2010) is another important longer term adaptation strategy.

Long term effects of extreme high temperatures on crop growth and the associated carbon cycle are uncertain due to the complex interaction of different factors (although threshold temperatures for damage of enzymatic reactions and shifts in phenology are well defined; Porter & Semenov; 2005, Lobell *et al.,* 2012). An early effect of heat stress is a change in the photosynthetic pathways following protein damage, reducing the efficiency of photosynthesis. If exposure is long, protein damage and enzyme dysfunction become permanent and lead to irreversible plant damage or death. Effects of extreme high temperatures depend on crop type, variety and genotype, the development stage of the crop at the time of the event, the duration of the event, and its combination with other environmental stressors such as ozone (Fuhrer, 2003). High temperatures shift and/or shorten the phenological development stages, which can also affect yield and biomass production (Larcher, 2003; Porter & Semenov, 2005; Lobell *et al.,* 2011, 2012). Heat stress can also decrease pollination efficiency and grain production by seed abortion, thereby decreasing yields. In addition to day-time temperature effects, crops are also affected by high night-time temperatures, which increases the loss of carbon due to higher respiration rates, and thereby reduces yields in rice and cotton - but uncertainties concerning net carbon storage remain high (Peng *et al.,* 2004; Loka & Oosterhuis, 2010).

Although most of the above-ground biomass in croplands is removed during harvest, biomass production determines the amount of carbon entering the soil with above- and below-ground litter ultimately impacting soil organic carbon levels. However, high temperature can also affect the harvest index, increasing the uncertainty about the net effect of high temperature events (Porter and Semenov 2005). This is important as soil organic carbon represents the only long term carbon storage in croplands (Freibauer *et al.,* 2004; Smith 2004; Smith *et al.,* 2010; Ciais *et al.,* 2010; Smith 2012). Importantly, soil organic carbon is in itself temperature sensitive, which makes the net storage in croplands an uncertain entity (Ciais *et al.,* 2010; Davidson & Janssens, 2006; Schulze *et al.,* 2009).

There are clear indications of the importance of frost damage in affecting changes in the carbon cycle, especially in winter crops (from plant damage to crop failure), but uncertainty remains high and evidence is too sparse to estimate the overall net effect (Bélanger *et al.,* 2002; Gu *et al.,* 2008).

Heavy rain and storm events can destroy above-ground biomass by damage or destruction of the crop, and they can lead to erosion and dislocation of soil, and consequently soil organic carbon loss. Heavy rain can also lead to water logging of soils affecting plant roots, subsequently leading to suboptimal growth and carbon cycling in soils (Fuhrer *et al.,* 2006). Nevertheless, contrasting crop responses to excess precipitation can also occur, for instance in 2007 high summer precipitation rates in France led to low wheat yields but very high maize yields (van der Velde *et al.,* 2012). The excessive rain directly impacted the wheat crop, with excessive soil moisture favouring pest and disease development, increasing lodging, and reducing grain quality (Mars Bulletin, 2007), followed by poor field accessibility hindering wheat harvest. By contrast, maize productivity was not affected and the dry conditions that followed the wet spell at the beginning of September 2007, coupled with high residual soil moisture levels, led to favourable conditions for maize –which in France is not harvested until mid-October (Mars Bulletin, 2007). Adaptive responses to extreme wind experienced during storms can include windbreaks, which can contribute to producer profitability and environmental quality (e.g. Brandle *et al.,* 2004), by protecting cropland fields against extreme wind impacts on crops and soil. During the 20th Century, shorter cereal varieties with a lower risk of lodging, have replaced taller varieties. Longer term adaptive management to high winds and heavy rainfall could involve shorter and sturdier varieties.

Mid-latitude regions (between about 30° and 50°) can experience hail events that may reach extreme intensities with the kinetic energy of hailstones proportional to the 4th power of their diameter (Eccel & Ferrari, 1997). Hail fall may cause severe defoliation in the majority of broad leaf crop species and in corn. Defoliations greater than 90% have been reported for corn and soybeans. Recent observations in the Eastern Alps show that hail intensities have significantly increased by 1.22–1.69% per year from 1975 to 2009 (Eccel *et al.,* 2012). The possibility to predict hail events is low as they may occur under diverse meteorological conditions (Garcıa-Ortega *et al.,* 2011).

Tolerable natural soil erosion rates are generally lower than rates experienced in cropland. Current estimates of soil erosion rates in cropping systems are highly variable and amongst others dependent on slope and tillage practices. Best estimates suggest that soil erosion rates are about two to three magnitudes higher than the rate of soil formation through weathering and dust deposition (Pimentel & Kounang, 1998; Brantley *et al.,* 2007). Single events can have a substantial impact on sediment load over a given time period (e.g. Thothong *et al.,* 2011). Indeed, single exceptional rainfall events can trigger extreme runoff and widespread erosion in areas normally not exposed to a high risk of erosion. In Norway, erosion events

(>100 tons ha^{-1}) resulted from a combination of extreme rainfall, agricultural management practices, low vegetation cover and a saturated soil overlying a frozen subsoil (Øygarden, 2003). In areas with an increased likelihood of extreme precipitation, erosion and loss of soil and soil organic carbon away from the impacted cropland is a risk. Also in this case, the use of perennial grain crops can be seen as possible adaptive measure, as those crops could potentially reduce the impact of extremes on erosion and soil degradation, NO_3 leaching, and soil carbon loss (Culman *et al.,* 2013). Their use requires, however, proper assessment of the net balance between the advantage of increased extreme event adaptation and the disadvantage of limited yield levels that can be achieved in the good years (Glover *et al.,* 2010).

Fire is of minor importance with regard to the carbon balance of croplands globally. Agricultural waste burning contributed approx. 3% to the total global fire carbon emissions during 2001–2009 (van der Werf *et al.,* 2010). Reduction in litter input to the soil by burning can reduce soil organic carbon content (Lal, 2007), but the production and incorporation of charcoal in soil may have beneficial impacts (Skjemstad *et al.,* 2002); the net effect remains uncertain.

Climate change – specifically increased temperatures and wetness – is generally thought to spread pests and pathogens beyond their current range, and to introduce alien species into new croplands, as well as increasing their multiplication rates (Gregory *et al.,* 2009). For instance, the survival of *O. poecilus* (rice stink bug) is dependent on the off-season rainfall affected by ENSO (Sutherland & Baharally, 2003). The interactions between crops, pests and pathogens are complex and poorly understood in the context of climate change, but it is clear that crops will be more susceptible to pests and diseases if previously weakened by extreme temperature, drought or other adverse impacts (Gregory *et al.,* 2009). Weed-crop interactions will change, with positive or negative consequences for the crop, while weeds (like crops) can benefit from a positive CO_2 fertilization effect (Patterson, 1995). In the context of food security, rodent outbreaks associated with an extreme event, cyclone Nargis, impacted agricultural production in Asia (Singleton *et al.,* 2010). The overall impact of pests and pathogens on crops, and the carbon balance of croplands remain uncertain.

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