

1 **A plant's perspective of extremes: Terrestrial plant responses to changing climatic**  
2 **variability**

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4 This is the pre-peer reviewed version of the following article: **Reyer C, S Leuzinger, A**  
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6 **Abou Jaoudé, T Klein, TM Kuster, M Martins, G Niedrist, M Riccardi, G Wohlfahrt, P**  
7 **De Angelis, G de Dato, L François, A Menzel, M Pereira (2013) *A plant's perspective of***  
8 ***extremes: Terrestrial plant responses to changing climatic variability*. *Global Change***  
9 ***Biology* 19:75-89,** which has been published in final form at  
10 <http://onlinelibrary.wiley.com/doi/10.1111/gcb.12023/abstract>.

11  
12 Running title: Plant and changing climatic variability

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20 Keywords: climate change, plant phenology, plant physiology, observations, experiments,  
21 models, combined approaches

22 Type of paper: Review

1 **Abstract**

2 We review here observational, experimental and model results dedicated to how plants  
3 respond to extreme climatic conditions induced by changing climatic variability.  
4 Distinguishing between impacts of changing mean climatic conditions and changing climatic  
5 variability on terrestrial ecosystems is generally underrated in current studies. The goals of  
6 our review are thus (1) to identify plant processes that are vulnerable to changes in the  
7 variability of climatic variables rather than to changes in their mean, and (2) to  
8 depict/evaluate available tools to quantify responses of plants to changing climatic variability.  
9 We find that phenology is largely affected by changing mean climate but also that impacts of  
10 climatic variability are much less studied but potentially damaging. We note that plant water  
11 relations seem to be very vulnerable to extremes driven by changes in temperature and  
12 precipitation and that changing heatwaves and flooding have stronger impacts on  
13 physiological processes than changing mean climate. Moreover, interacting phenological and  
14 physiological processes are likely to add further complexity to plant responses to changing  
15 climatic variability. Phenological and physiological processes and their interactions culminate  
16 in even more sophisticated responses to changing mean climate and climatic variability at the  
17 species and community level. Generally, observational studies are well suited to study plant  
18 responses to changing mean climate, but less suitable to gain a mechanistic understanding of  
19 plant responses to climatic variability. Experiments seem best suited to simulate extreme  
20 events and temporal resolution and model structure are crucial in models to capture plant  
21 responses to changing climatic variability. We highlight that a combination of experimental,  
22 observational and /or modeling studies have the potential to overcome important caveats of  
23 the respective individual approaches.

24

## 1 **1. Introduction**

2 Although the spatial and temporal extent of future climatic changes is still partly uncertain  
3 (IPCC 2007a), it is likely that the adaptive capacity of terrestrial plants and ecosystems will  
4 be exceeded in many regions (IPCC 2007b). Already today, changes in ecological responses  
5 to climate change can be observed for individual species and ecosystems (e.g. Allen &  
6 Breshears 1998; Gitlin *et al.* 2006) but also across species and organizational scales (e.g.  
7 Walther *et al.* 2002; Allen *et al.* 2010; Lindner *et al.* 2010). Climate change may manifest  
8 itself in two fundamentally different ways: in a change in the mean of for example  
9 temperature or precipitation, or a change in their variability (i.e. variance or distribution (Fig.  
10 1); Rummukainen 2012; Seneviratne *et al.* 2012). We define extreme events from this strictly  
11 climatological perspective as increase in climatic variability (increasing variance or  
12 distribution) in opposition to change in mean climate. Our aim is to emphasize the generally  
13 unrecognized distinction between impacts of changing mean climate and changing climatic  
14 variability on terrestrial ecosystems.

15 We center but do not limit our synthesis on a plant's perspective of temperature and  
16 precipitation extremes, since these are the most important climatic determinants of plant  
17 growth and survival globally (e.g. Boisvenue & Running 2006). Observations since 1950  
18 show that the length of warm spells and heat waves increased (e.g. Barriopedro *et al.* 2011;  
19 Rahmstorf & Coumou 2011; Seneviratne *et al.* 2012). More intense and longer droughts are  
20 observed but at the same time the number of heavy precipitation events increased  
21 (Seneviratne *et al.* 2012 and references therein). Future projections on changes in climatic  
22 variability show strong spatial and temporal heterogeneity (Giorgi *et al.* 2004; Orlowsky &  
23 Seneviratne 2012) and are highly uncertain (Seneviratne *et al.* 2012). Using multi-model  
24 experiments, Barriopedro *et al.* (2011) for instance found that the probability of summer  
25 heatwaves may increase by a factor of 5-10 in the future while Schär *et al.* (2004) predict that

1 temperature variability will increase by a factor of 2 in Europe. Projected changes in extreme  
2 precipitation events (droughts or flooding) are even more uncertain. Orlowsky & Seneviratne  
3 2011 derived from their simulations with an ensemble of Global Circulation Models (GCMs)  
4 robust projections on increasing droughts over the Mediterranean and increasing heavy  
5 precipitation over the Northern high latitudes.

6 While changes in the mean values are important, there is evidence that plants respond to  
7 extreme rather than to average conditions (Chapin *et al.* 1993; Knapp *et al.* 2002; van Peer *et*  
8 *al.* 2004; Weltzin *et al.* 2003; Bokhorst *et al.* 2007; Jentsch & Beierkuhnlein 2008).  
9 Additionally to that, different physiological processes at the species, community or ecosystem  
10 level affect the response of plants to climatic variability (Fig. 2). To account, e.g., for  
11 changing precipitation distributions, Knapp *et al.* (2002) decreased precipitation frequency  
12 but not its total amount in a mesic grassland leading to more intense precipitation events.  
13 They found reduced carbon turnover but increased species diversity. Thus, impacts on  
14 physiological processes influence carbon and water cycles at local and regional scales. The  
15 carbon cycle is sensitive to drought (e.g. Ciais *et al.* 2005; van der Molen 2011; Wu *et al.*  
16 2012). The water cycle may also be strongly impacted by drier conditions because under  
17 drought evapotranspiration tends to decrease, which leads to lower evaporative cooling  
18 (Teuling *et al.* 2010). In combination, warming and drought can therefore lead to additional  
19 warming of an ecosystem (Seneviratne *et al.* 2006; Fischer *et al.* 2007; Kuster *et al.* 2012).

20 In addition to the impacts of changing climatic variability, the physiological and ecological  
21 response of terrestrial plants depends also on interactions between species (Thorpe *et al.*  
22 2011) and natural adaptation and acclimation. The water available for plants depends on the  
23 water holding capacity of the soil (Kramer & Boyer 1995; Porporato *et al.* 2004; Leuzinger &  
24 Körner 2010; Raz-Yaseef *et al.* 2010), competition with other plants (Casper & Jackson 1997)  
25 and precipitation patterns (Knapp *et al.* 2008). The latter has different effects on soils with

1 high or low water holding capacity (i.e. a stronger or weaker buffer against drought; Knapp *et*  
2 *al.* 2008) or on flood occurrence, which is an important driver of plant distribution (Crawford  
3 1992; Colmer & Flowers 2008; Parolin & Wittmann 2010). Furthermore, interactions  
4 between changing climatic variables as well as thereby induced community shifts may affect  
5 the response of plants to new conditions (Langley & Megonigal 2010; de Boeck *et al.* 2011).  
6 For example, a drier and warmer climate will exert stronger constraints on plant growth than a  
7 warmer but also wetter climate; or rising CO<sub>2</sub> may alleviate the impact of drought (Morgan *et*  
8 *al.* 2004; Holtum & Winter 2010). Moreover, more prolonged dry periods will alternate with  
9 more intensive rainfall events, both within and between years, which will change soil  
10 moisture dynamics (Weltzin *et al.* 2003; Porporato *et al.* 2004; Fay *et al.* 2008; Knapp *et al.*  
11 2008; Bartholomeus *et al.* 2011a). Eventually, it is also crucial how quickly plant  
12 communities adapt genetically to the imposed changes. The IPCC (2007b) concluded that the  
13 rate of natural adaptation will be slower than the rate of climate change. Natural adaptation  
14 differs in between species: while species with short generation times may adapt within years,  
15 e.g. Rehfeldt *et al.* (2001) estimate that it will take 2-12 generations (an equivalent of 200-  
16 1200 years) for a coniferous trees species to show genetic adaptation in response to climatic  
17 change. All these factors determine whether plants at a specific site will experience changing  
18 climatic variability as extreme or not.

19 Thus, the vulnerability of terrestrial plants to climate change will, besides changes in the  
20 mean, largely depend on the changes in the climatic variability and the occurrence of extreme  
21 events. The understanding of this difference in experiments and model simulations requires  
22 very good knowledge of the baseline or control climate (especially the background variability  
23 to which plants are adapted to). This complies with the fact that extreme conditions per se  
24 have shaped ecosystems for a long time (Körner 1998, 2003) and may also foster adaptation  
25 and thus decrease sensitivity (Hegerl *et al.* 2011). The plant's response to specific

1 environmental conditions produces their specialized set of traits which allows them to prevail  
2 over competitors and occupy a specific habitat (Körner 1998, 2003). We use the term ‘stress’  
3 throughout this review according to Lortie *et al.* (2004) to refer to situations in which plants  
4 experience critical environmental conditions beyond what they experience normally (Chapin  
5 1991) such that damage to vital function occurs (see Gaspar *et al.* 2002).

6 In this paper we strive to answer the following questions:

- 7 • Which plant processes are vulnerable to changes in the variability of climatic drivers  
8 rather than to changes in their mean?
- 9 • How can we quantify responses of plants to changing climatic variability?

10 We present evidence from experiments, observations and modeling studies that help to  
11 understand the current and future responses of individuals and communities to changing  
12 variability, with a particular focus on temporal and spatial patterns. These examples also help  
13 to identify important research gaps. We do not aim to cover the literature on these topics  
14 systematically.

1 **2. Which plant processes are vulnerable to changes in the variability of climatic drivers**  
2 **rather than to changes in their mean?**

3 The vulnerability of plants refers to their susceptibility to adverse effects of environmental  
4 change (IPCC 2007b). Estimates of vulnerability depend on the definitions (e.g. the definition  
5 of death (Zeppel *et al.* 2011)) and the spatiotemporal scale considered. The ultimate limit to  
6 withstanding environmental stress from an individual plant's perspective is mortality due to  
7 physiological failure ("You can only die once") but at the community level, already  
8 reductions in growth and subsequently competitiveness may constitute a limit to species  
9 fitness. For commercial crops it may even be a critical reduction in productivity so that  
10 cultivation is discontinued.

11 In the following sections, we discuss the vulnerability of phenological and (individual and  
12 interacting) physiological processes to changes in the climatic variability rather than the mean  
13 of climatic drivers and we highlight how these play out at the species and the community  
14 level (see schematic overview in Fig. 2). Our list of examples is not exhaustive but meant to  
15 illustrate this important difference between changes in climatic variability rather than the  
16 mean.

17 **2.1. Phenological processes**

18 One of the well-studied responses of plant species or communities to environmental change is  
19 phenology, which tracks seasonal events in generative and vegetative plant growth. Given the  
20 predominant influence of climate (with the important exception of photoperiodism, see  
21 Körner & Basler 2010), phenology has emerged as a key tool in identifying fingerprints of  
22 anthropogenic climate change in nature (Menzel *et al.* 2006). Observed large-scale  
23 phenological changes such as an earlier onset of leaf unfolding/ flowering (Menzel & Fabian  
24 1999; Walther *et al.* 2002; Parmesan & Yohe 2003; Root *et al.* 2003; Menzel *et al.* 2006) are



1 mainly driven by changes in mean climatic conditions especially temperature (Vitasse *et al.*  
2 2009; Polgar & Primack 2011; see also Table 1).

3 Phenological changes in response to changing climatic variability are much less studied  
4 although they clearly interact with phenological changes induced by changing mean climate.  
5 For example, in the temperate and boreal zones which are often temperature limited, a central  
6 trade-off revolves around maximizing the vegetation period while avoiding frost damage  
7 (Kramer *et al.* 2010). An untimely response to early warm spells may be fatal but can bring  
8 enormous advantages for early successional or opportunistic species (r-strategists, Leuzinger  
9 *et al.* 2011a). In contrast, long-lived, late successional species often have chilling  
10 requirements and photoperiodic safety mechanisms (Heide 1993) and thus may be in a  
11 position to avoid increasing risks of late frost due to changing climatic variability but would  
12 also benefit less from early warm spells. This is supported by the fact that the risk of damage  
13 due to late frost events has not increased so far for several coniferous and broad-leaved  
14 species in Central Europe (Scheifinger *et al.* 2003; Menzel *et al.* 2003). Besides this example,  
15 there is further evidence, that extreme events may alter phenological responses depending on  
16 their timing and strength (e.g. Jentsch *et al.* 2009; Menzel *et al.* 2011). This can lead to  
17 unexpected effects such as second flowering in autumn or extended flowering until the  
18 beginning of winter for some species (Luterbacher *et al.* 2007). Moreover, extreme warm  
19 spells decreased the differences in spring phenology between urban and rural sites (Jochner *et*  
20 *al.* 2011). Furthermore, only half of the trees reached leaf maturity in an extreme drought  
21 experiment in the Mediterranean (Misson *et al.* 2011). Overall, the response of phenology to  
22 climatic variability seems to be less well understood than to changing mean climate although  
23 increasing climatic variability may have a strong damaging potential.

## 1 2.2. Physiological processes

2 We here focus on the response of plant water relations such as transpiration to climatic  
3 variability (drought/heat waves and excess water). Increasing temperatures and/or heat waves  
4 combined with less or more variable precipitation events lead to prolonged dry periods and  
5 high atmospheric demand for plant transpiration, which determine drought stress of plants  
6 beyond changes in mean climate (Schimper 1903; Porporato *et al.* 2004). Barriopedro *et al.*  
7 (2011) predict such an increase in drought events for the 21st century and the consequences  
8 for plant physiology are well documented (e.g. Leuzinger *et al.* 2005; Bréda *et al.* 2006;  
9 Granier *et al.* 2007) although not all mechanism are fully understood. There is an ongoing  
10 debate about two competing response strategies to drought: Isohydric plants may respond by  
11 closing their stomates thus reducing their water loss but eventually facing carbon starvation,  
12 whereas anisohydric plants keep their stomates open thus running the risk of hydraulic failure  
13 (Mc Dowell *et al.* 2008; Sala *et al.* 2010; Zeppel *et al.* 2011). Furthermore, Craine *et al.*  
14 (2012) highlighted the importance of the timing of an extreme event for grassland  
15 productivity. The response of plants to drought is of such an importance that Hartmann (2011)  
16 refers to it as a "change of evolutionary forces" from competition for light to competition for  
17 water and carbon. The responses of plants to climatic variability and particularly drought have  
18 important consequences for net primary productivity (NPP) and hence carbon cycling even at  
19 large spatial scales such as Europe (Ciais *et al.* 2005; Dury *et al.* 2011). Thus, plant responses  
20 to increasing drought events and heat waves influence plant functioning across spatial and  
21 temporal scales.

22 Also climatic variability resulting in excess water (i.e. flooding or waterlogging), can induce  
23 important physiological responses by terrestrial plants. Due to waterlogging O<sub>2</sub> diffusion and  
24 supply to the roots is reduced, and the oxygen demand of plant roots, (i.e. root respiration –  
25 oxygen consumption in the roots), a process that increases with rising temperatures, cannot be

1 fulfilled (Lloyd & Taylor 1994; Blom & Voesenek 1996; Kozłowski 1997; Amthor 2000).  
2 This results in waterlogging/ oxygen stress, i.e. lack of oxygen due to high soil moisture  
3 contents (Bartholomeus *et al.* 2008). Both the oxygen supply and demand may be affected by  
4 a more extreme climate, due to more intense precipitation and higher temperatures,  
5 respectively. Therefore, to analyze the effects of low soil oxygen availability on species  
6 performance, it is necessary to integrate the soil physical and plant physiological processes,  
7 thus accounting for both the oxygen supply to and oxygen demand of plant roots  
8 (Bartholomeus *et al.* 2011b). Besides reduced root respiration rates, the decrease of water  
9 absorption due to waterlogging stress causes sensitive plants to wilt in a similar way to  
10 drought (Jackson & Drew 1984). Many species already growing in flood-prone habitats have  
11 developed different strategies to survive hypoxia, by producing aerenchyma and/or  
12 adventitious roots in response to an increase in the concentration of ethylene and auxin (Blom  
13 & Voesenek 1996). Flooding can also give rise to detrimental effects at leaf level, by inducing  
14 stomatal closure and, consequently, limiting gas exchange and plant growth (Kramer 1951;  
15 Chen *et al.* 2005; Rengifo *et al.* 2005; Fernandez 2006). Thus, similarly to drought, extremes  
16 of excess water, in combination with higher temperatures, strongly alter plant physiological  
17 processes.

18 In conclusion, we note that plant water relations seem to be very vulnerable to increasing  
19 variability in temperature and precipitation and that changing heatwaves and flooding have  
20 stronger impacts on physiological processes than changing mean climate (see also Table 1).

### 21 **2.3. Interacting physiological processes**

22 The interaction of physiological processes may strongly affect the response of plants to  
23 changing climatic variability. Interactions among several global change drivers or between  
24 global change drivers and other environmental variables, may result in other growth-limiting

1 factors (e.g. soil type) becoming less important. Drought periods for example may have the  
2 potential to not only determine growth or mortality in an ecosystem but also to cause shifts in  
3 growth-limiting factors, e.g. nutrient limitations. For example, in an experiment of Kuster *et*  
4 *al.* (2012) oaks were grown on two different soil types with different nutrient availabilities.  
5 Under well-watered conditions, growth on one soil was lower due to nutrient-limiting  
6 conditions, whereas under repeated drought periods these differences disappeared. This shows  
7 that growth-limiting factors such as nutrient availability can become less important under  
8 changing climatic variability, while they may persist if only changes in mean climate are  
9 considered. There are many other examples of interacting processes under changing climatic  
10 variability such as ozone stress during periods of high temperature (Matyssek *et al.* 2010;  
11 Pretzsch & Dieler 2011).

12 The interactions of physiological processes can however be even more intriguing: In coastal  
13 habitats (i.e. the interface of terrestrial and aquatic habitats) which are not only saline, but are  
14 also prone to flooding (e.g. mangroves and salt marshes) (Colmer & Flowers 2008) *Tamarix*  
15 *africana* Poir., for example, showed a reduction of CO<sub>2</sub> assimilation rates only in young  
16 *Tamarix africana* Poir. leaves after 45 days under continuous flooding with saline water (200  
17 mM), while old leaves and the aboveground relative growth rate were not affected by the  
18 treatment (Abou Jaoudé *et al.* 2012). Thus while parts of the plants actually responded to  
19 flooding, this was not the case for the entire plant. This example is rather related to changes in  
20 mean climatic conditions (i.e. temperature-induced rising sea levels) but it highlights that  
21 changing climatic variability is likely to add even another level of complexity to already  
22 complex interactions of physiological processes.

## 1    **2.4.    Species-level processes**

2    At the species level, responses of different genotypes to climate provide information how a  
3    species may react to changing climatic variability. Since genotypic variation results in  
4    different sensitivity thresholds of distinct ecotypes to changing climatic variability it can  
5    partly substitute lacking data of changing climatic variability for a specific genotype. In an  
6    ecotype study (Klein *et al.* submitted) that included all three climate types (meso-  
7    Mediterranean (MM), thermo-Mediterranean (TM), and semi-arid (SA) within the natural  
8    distribution of the forest tree *Pinus halepensis* Mill. (and hence three very different  
9    combinations of mean climate and climate variability), two major physiological adjustments  
10    were identified: (1) shortening of the growing season length (from 165 to 100 days) to match  
11    a shorter rainy season and (2) increasing water use efficiency (from 80, to 95, to 110  $\mu\text{mol}$   
12     $\text{CO}_2 \text{ mol}^{-1} \text{ H}_2\text{O}$  under MM, TM, and SA climates respectively). However the sensitivity  
13    threshold differed in between ecotypes: Northern ecotypes mainly responded to the change  
14    MM to TM, whereas Southern ecotypes responded to the change TM to SA. At the species  
15    level, the study showed that higher xylem sensitivity to embolism in specific ecotypes  
16    matched previous reports (Atzmon *et al.* 2004; Schiller *et al.* 2009) of significantly higher  
17    mortality rates in these ecotypes under yet harsher conditions. These observations suggest that  
18    while hydraulic constraints in response to climatic variability limited the distribution of a tree  
19    species, plasticity in water use efficiency and growth phenology enabled its success under a  
20    wide range of climatic conditions.

## 21    **2.5.    Community-level processes**

22    At the community level, phenological, physiological and species-level processes as well as  
23    their interaction culminate in complex responses to changing mean climate and climatic  
24    variability (Fig. 2). Species range shifts have been associated with changes in mean climate

1 (Lenoir *et al.* 2008; Harsch *et al.* 2009) but also with changing climatic variability (Kelly &  
2 Goulden 2008; Doak & Morris 2010). They lead to a disruption of ecological communities  
3 and species interactions due to different dispersal speed and success. These processes differ  
4 between the trailing and the leading edge of a population (Kramer *et al.* 2010; Doak & Morris  
5 2010). From a community's perspective such range shifts may entail positive (e.g. release  
6 from competition) and negative (e.g. loss of important pollinator) consequences. Despite  
7 these importance consequences of range shifts, it is yet unclear whether changing mean  
8 climate or changing climatic variability will be the more important driver of range shifts.

9 At community level, for annual plants, the variability of rainfall is important for the success  
10 of germination. Increasing climate variability can have both negative and positive effects on  
11 species persistence and thus plant population dynamics (Levine *et al.* 2008). Climatic  
12 fluctuations, for example, may enable species to avoid interspecific competition if species  
13 differ in the years in which they perform (e.g. reproduce or grow) best (Levine & Rees 2004).  
14 Dormancy and germination biology determine whether temporal variability favors or inhibits  
15 species persistence (Levine & Rees 2004) and can thus be limiting for a species (Godefroid *et*  
16 *al.* 2011). Temporal variation in resource availability as induced by climatic variability may  
17 reduce the effects of competitive exclusion, allowing more species to coexist (Knapp *et al.*  
18 2002).

19 A combination of extremes/multiple stresses may not only hamper performance but may also  
20 drive extinctions (Smith & Huston 1989; Niinemets & Valladares 2006). Although functional  
21 trade-offs exist in adjusting to multiple environmental limitations (Holmgren *et al.* 1997;  
22 Silvertown *et al.* 1999), adapting to one stressor may go at the cost of adapting to another  
23 (Holmgren *et al.* 1997; Niinemets & Valladares 2006). This trade-off among the tolerances to  
24 multiple environmental limitations hampers niche differentiation (Niinemets & Valladares  
25 2006). Bartholomeus *et al.* (2011a) demonstrated that the interaction between both the wet

1 and dry extremes of plant water stress (oxygen/waterlogging and drought stress) is  
2 particularly detrimental to the survival of specialists and of endangered plant species. Both  
3 wet and dry weather extremes may increase due to changing climatic variability, thus  
4 increasing the risk of a combination of these stressors to occur at a site (Knapp *et al.* 2008;  
5 Bartholomeus *et al.* 2011a). This may favor generalists over specialists and rare species and  
6 thus change vegetation dynamics and associated ecosystem services in response to changing  
7 climatic variability at the community level.

### 1    **3. How can we quantify responses of plants to changing climatic variability?**

2    Just as responses to global change in general (Rustad 2008), the responses of plants to  
3    changing climatic variability can be assessed in observational, experimental and modeling  
4    studies and combinations of these approaches (Fig. 2). All these approaches have their  
5    limitations in assessing a plant's perspectives of extremes: on the one hand, observational  
6    studies are by definition 'opportunistic' in the sense that extreme conditions such as a long-  
7    lasting drought can not be planned (Smith 2011). On the other hand, scaling and higher-order  
8    interactions are an important issue in experimental and modeling studies (Leuzinger *et al.*  
9    2011b; Wolkovich *et al.* 2012). Furthermore, it is crucial for any type of study that claims to  
10    assess climate variability to report whether changing mean climate and/or changing climatic  
11    variability have truly been measured and what the background variability of the system is. We  
12    qualitatively show this in Table 2 for a number of studies cited above as a first attempt to  
13    foster consistent reporting of studies dealing with climatic variability.

#### 14    **3.1. Observational studies**

15    Observational studies elucidate plant's perspectives of extremes, if by chance they cover  
16    extremes. This makes them inherently opportunistic (Smith 2011). Similarly to experimental  
17    studies, space can be substituted with time in observations. Thus, observations from 'extreme'  
18    (from a plant's perspective) sites (e.g. from the leading and trailing edge of population (Doak  
19    & Morris 2010)) can help us learning about the limits and coping range of plants. To this end,  
20    GIS mapping of 'extreme' sites within a species' distribution requires careful interpolation of  
21    weather/climate data collected at appropriately distributed climate stations (see also Sect. 3.3).  
22    However, 'extreme' sites are sometimes only poorly studied since they represent marginal  
23    ecosystems, whose services are not fully valued by society and have thus been outside the  
24    main focus of researchers. The psamphilic plants and vegetation of the beaches and dunes of



1 the Portuguese coast, for example, are highly adapted to very specific environmental  
2 conditions and directly exposed to sea level rise, storms and severe erosion processes. Unless  
3 their ecological requirements, functioning as communities and most influential physical  
4 drivers are understood, it will be difficult to study their responses to future climate change  
5 (Martins *et al.* 2011).

6 Generally, observational studies are well suited to study plant responses to changing mean  
7 climate, since long-term ecological data can be matched with increasingly available climatic  
8 observations. They are less suitable to gain a mechanistic understanding of plant responses to  
9 climatic variability since usually too many factors are involved and not all are measured.

### 10 **3.2. Experimental studies**

11 Experiments allow for controlled conditions and factorial experiments in the field and  
12 laboratory, have a long history in ecological research and are of crucial importance for global  
13 change studies (Luo *et al.* 2011)). When quantifying climate change impacts however, field  
14 experiments can usually only test a limited number of factors and their combinations due to  
15 financial and logistic constraints (Templer & Reinmann 2011). Therefore, interactions can  
16 often not be fully assessed (e.g. Wolkovich *et al.* 2012). Furthermore, to provide answers to  
17 the question of how extreme climatic events impact on ecosystems, experimenters should  
18 make sure the applied treatment is indeed 'extreme' beyond the current background  
19 variability of the system, running the risk of killing plants (Leuzinger & Thomas 2011; Beier  
20 *et al.* 2012).

21 Also, the temporal scale influences the outcome of an experiment. A comparable set of factors  
22 and a minimal experimental duration, for example, for all drought experiments would  
23 therefore be desirable. However, even then, most experiments would have to stop after few  
24 years. This raises the question whether the experiment actually simulates extreme situations

1 or long-term change and whether the system recovers after the experiment ends. The high  
2 diversity in the response of growth parameters of oaks to drought as discussed in Kuster *et al.*  
3 (2012), shows that in experimental conditions, e.g. treatment duration and intensity, tree age  
4 or experimental set up, have to be considered in the evaluation of drought effects on trees.  
5 Thus it is crucial to assess what degree of change and what temporal scale experiments cover  
6 if we want to evaluate whether they actually simulate responses to changing climatic  
7 variability, or rather to changing mean climate.

8 In a transplantation study, for example, the effect of a drying and warming trend was obtained  
9 by comparing tree performance in Rome (Italy), Tel Aviv (Israel) and Yatir (Israel) along a  
10 precipitation gradient (Klein *et al.* submitted). The sites differed significantly in their mean  
11 annual precipitation, each representing a different climate type, but the responses were  
12 interpreted as drought acclimation. Results from this study captured many plant adjustments  
13 that were induced by both phenotypic plasticity and locally adapted ecotypes. Such  
14 transplantation experiments along altitudinal or latitudinal gradients do not require  
15 manipulation of the environment and may be an alternative to laboratory/greenhouse  
16 experiments. So far, transplantation experiments have not been considered in comparative  
17 studies of different artificial warming methods (e.g. Aronson & McNulty 2009). However,  
18 such experiments seem to be well adapted especially for long term experiments, as they  
19 project a realistic simulation of future climate conditions considering also the length of the  
20 growing period, one of the most important limiting factors in alpine plant growth (Jonas *et al.*  
21 2008). Similar to laboratory/greenhouse experiments it is crucial that the results are  
22 interpreted in terms of changing mean climate and changing variability.

### 1 3.3. Modeling

2 Models can be used as diagnostic and predictive tools that integrate results from experiments  
3 and observation to gain mechanistic understanding and allow testing hypothesis generated  
4 from field data, experiments and theory (Leuzinger & Thomas 2011; Luo *et al.* 2011). Models  
5 have to be designed for a specific purpose and here we discuss which are suitable to simulate  
6 plant responses to changing climate variability. This is a highly relevant question, since  
7 models that account for extremes may require a different structure, e.g. an appropriate time  
8 resolution to capture an extreme precipitation event. Many forest models for example use  
9 monthly input data and are thus unable to account for short-term extreme events (e.g.  
10 Bugmann 2001). Forcing such a model with daily weather instead with monthly climate data  
11 improved its performance (Stratton *et al.* 2012). Zimmermann *et al.* (2009) argue that for  
12 capturing some ecosystem responses even daily climate data may be insufficient since they  
13 smooth meteorological extremes.

14 Generally, effects of climate change on ecosystems are analyzed by driving simulation  
15 models with output from global and regional circulation models (GCMs and RCMs). To  
16 account for the uncertainty of climate change projections, besides different scenarios, also  
17 several GCM/RCMs (e.g. Buisson *et al.* 2010) and different realizations of a scenario may be  
18 used. Many models do not use the original GCM/RCM data at hourly resolution (which may  
19 also not always be available) but only daily or monthly aggregations and thus strictly  
20 speaking miss some of the meteorological variability. The CARAIB dynamic vegetation  
21 model (Otto *et al.* 2002; Laurent *et al.* 2008; Dury *et al.* 2011), for example, derives daily  
22 values of meteorological variables, as usual in large-scale simulations, from monthly mean  
23 outputs from GCM/RCMs using a stochastic weather generator (Hubert *et al.* 1998). The  
24 sequences of daily temperature or precipitation produced by the stochastic generator are  
25 renormalized to the monthly values generated by the RCMs. Thus the precise day-to-day

1 sequence of an extreme event in the model, such as a drought period or a succession of heat  
2 wave days (Beniston *et al.* 2007; Déqué 2007), depends on the distribution functions used in  
3 the stochastic generator, although the monthly values of the climate model are not altered.  
4 While evidently it is challenging for such large scale modeling efforts to integrate high-  
5 frequency climate variability, these studies are necessary to assess different feedbacks of  
6 vegetation types (e.g. feedbacks of ecosystem response to drying on near-surface temperature  
7 differ between forest and grassland ecosystems (Teuling *et al.* 2010) at the global scale.

8 Also, species distribution models face the challenge of including changing climate variability.  
9 Usually, they use information on species distribution (both potential from expert knowledge  
10 or forest communities, and actual from inventories and landcover-data) together with climate  
11 data to construct bioclimatic ranges (also called climate envelopes). They show a two  
12 dimensional frequency distribution of e.g. temperature and precipitation, indicating the mean  
13 climatic range, in which the analyzed species (potentially) exist. Extrapolation of this  
14 information allows identifying regions with comparable climate to e.g. estimate a (extended)  
15 potentially occupied habitat (Guisan & Zimmermann 2000) or new growing areas outside the  
16 recent (actual or potential) distribution (Miller *et al.* 2004; Peters *et al.* 2004). Also the match  
17 of actual and future suitable ranges can be identified, classifying species into tolerant or  
18 intolerant to expected climatic conditions (Dunk *et al.* 2004; Gibson *et al.* 2004). This  
19 provides further understanding about expanding or shrinking habitats under changing climate  
20 (Erasmus *et al.* 2002; Midgley *et al.* 2006). Usually, climate envelopes are derived from mean  
21 values (e.g. mean temperature) and are thus designed to assess impacts of changes in mean  
22 climate. Consequently especially regions at the edge of the distribution range may appear  
23 suitable, but in reality maximum or minimum precipitation or temperature may determine the  
24 distribution range (or other, non-climatic factors such as soil type or herbivory). This can  
25 partly be circumvented by including standard deviations as variables (Zimmermann *et al.*

1 2009), and species distribution models could also be built with extremes (e.g. maximum  
2 temperature or minimum precipitation) to enhance the predictive power. Zimmermann *et al.*  
3 (2009) for example found that incorporating climatic extremes slightly improved models of  
4 species range limits, since it corrected local over- and underprediction, but they also argue  
5 that climate variability rather complements the response to mean climate. Thus including  
6 climate variability is one uncertainty of species distribution models that has to be considered  
7 to assess compliance of climate envelopes (Gloning *et al.* in prep.).

8 While generally process-based modeling is required to derive climate-robust relationships to  
9 predict vegetation characteristics (Franklin 1995; Guisan & Zimmermann 2000; Schwalm &  
10 Ek 2001; Botkin *et al.* 2007; Suding *et al.* 2008; Hajar *et al.* 2010), this is even more evident  
11 when considering changing climate variability in particular. Bartholomeus *et al.* (2011b)  
12 demonstrated that, in contrast to process-based relationships between site factors and  
13 vegetation characteristics, relations based on indirect site factors produce systematic  
14 prediction errors when applied outside their calibration range, and so cannot be used for climate  
15 projections. Mean groundwater level, for example, is only an indirect site factor related to  
16 plant performance, as it is the interaction between soil-water-plant-atmosphere that essentially  
17 determines if plants suffer from drought stress or oxygen/waterlogging stress. When, for  
18 example, soil moisture availability is too low to meet the water demand for transpiration, a  
19 plant suffers from drought stress (Reddy *et al.* 2004; Schimper 1903). This so-called  
20 physiological drought (Schimper 1903), implies that not only water availability but also  
21 vegetation's demand for water has to be considered. Instead, more process-based explanatory  
22 variables are needed to predict the effects of changing climate variability on the species  
23 composition of the vegetation. These explanatory variables should consider the interacting  
24 meteorological, soil physical, microbial, and plant physiological processes in the soil-plant-  
25 atmosphere system. Bartholomeus *et al.* (2011a) did so for water related stressors, by

1 simulating respiration reduction (reflecting the combined effect of high temperature and low  
2 oxygen availability), and transpiration reduction (reflecting the combined effect of high  
3 atmospheric water demand and low water availability) for a reference vegetation. The  
4 simulated stress for reference vegetation acts as a habitat characteristic, i.e. a measure for the  
5 moisture regime of the soil to which the actual vegetation will adapt. The use of reference  
6 vegetation improves the applicability of models in which stress measures are implemented,  
7 especially in predicting climate change effects (Dyer 2009).

### 8 **3.4. Combined approaches**

9 Combined approaches unite experimental, observational and/or modeling studies. A recent  
10 meta-analysis shows that the temperature sensitivity of phenology in warming experiments is  
11 underestimated in comparison to observations (Wolkovich *et al.* 2012). It highlights that  
12 observational studies are crucial to test whether experimental results match observations in  
13 natural systems. A combination of laboratory and field studies is necessary to determine  
14 whether thresholds detected in the laboratory, are also likely to occur in the field. This is  
15 especially relevant when calculating the effects of changing climatic variability. We take leaf  
16 gas exchange and ecosystem flux measurement data from Brill *et al.* (2011) as an example of  
17 how to link experiments and observation at different scales and how an experiment can  
18 complement observations to study plant responses to climate variability. Fig. 3 shows that  
19 evapotranspiration measured in the field with the eddy covariance method, was insensitive to  
20 soil drying over the range of soil water contents occurring in the field. The leaf gas exchange  
21 measurements during the laboratory drought experiment when extended to much drier  
22 conditions showed that the plant species occurring at this site start to down-regulate stomatal  
23 conductance at soil water contents close to the wilting point – conditions that have never been  
24 reached in the field during the observational period of 2001-2009. Back-of-the-envelope  
25 calculations suggest that ca. 10 additional rain-free days would have been required even

1 during the 2003 and 2006 droughts in order for plants at this site to experience gas exchange  
2 limitations. Such information is crucial to assess whether responses to changing mean climate  
3 or to changing climate variability are measured.

4 Moreover results can be extended to a larger spatial scale, by combining simulation models  
5 with research tools like raster GIS (Minacapilli *et al.* 2009; Bonfante *et al.* 2011) and Digital  
6 Elevation Model (DEM) derived analysis (MacMillan *et al.* 2000). Furthermore, studies that  
7 combine observational or experimental results - at field scale - with simulation models of  
8 hydro-thermal regime - at landscape scale - allow to quantify the effects of changing climate  
9 variability (Bonfante *et al.* 2010). Riccardi *et al.* (2011) assessed the adaptive capacity of  
10 olive cultivars to future climate by means of a data base of cultivars' climatic requirements,  
11 combined with a spatially distributed model of the soil–plant–atmosphere system. They set up  
12 a database on climatic requirements and defined critical environmental conditions using two  
13 quantitative indicators of soil water availability (the relative evapotranspiration deficit, i.e. the  
14 ratio of actual to maximum evapotranspiration of the crop, and the relative soil water deficit,  
15 i.e. the ratio between the actual and the maximum volume of soil water available to plants  
16 taking into account the water retention characteristics, to get a comparable indicator across  
17 soil types). The response in terms of yield of several olive cultivars to these indicators was  
18 determined through the re-analysis of experimental data derived from scientific literature  
19 (Moriani *et al.* 2003; Tognetti *et al.* 2006). This database on cultivars' requirements was used  
20 in combination with a plant-soil-atmosphere model (SWAP, van Dam *et al.* 2008). The model  
21 was used to describe the soil water regime at landscape scale under future climate scenarios  
22 from statistically down-scaled GCMs, resulting in several realizations (Tomozeiu *et al.* 2007).  
23 The indicators of soil water availability were thus determined in different soil units, and were  
24 compared with the limits set for each cultivar. A cultivar was considered tolerant to expected  
25 climatic conditions when the indicator values resulted above critical values in at least 90% of

1 realizations. While Riccardi *et al.* (2011) did not further specify the climate scenarios and  
2 realizations in terms of changing mean or climate variability, such analysis could be easily  
3 linked to the soil water availability indicators and the related limits for cultivars under climate  
4 change.



#### 1 **4. Conclusions**

2 In this review, we have emphasized that changing climatic variability and the resulting  
3 extreme (climatic) conditions are highly relevant for different plant processes at different  
4 scales in comparison to changes in mean climate. We have also shown how to quantify  
5 responses of plants to changing climate variability: While experiments seem to be well-suited  
6 to study the effects of changing climatic variability it is important to remember that they only  
7 control a limited number of factors. For modeling studies we stress that the model structure  
8 should allow integrating extreme events (e.g. by having the appropriate temporal resolution).  
9 These points highlight the importance of linking experiments, observations, and modeling  
10 studies. We also identified the several research gaps. While knowledge of plant responses to  
11 changing climatic variability for individual processes has to be consolidated, we still lack  
12 knowledge on how interactions of these processes and other environmental variables play out  
13 at different hierarchical levels and in combination with changing mean climatic conditions.  
14 Similarly, while there is room to improve individual methods to study changing climatic  
15 variability, there is a particular need to integrate observations, experiments and models results  
16 across scales.

17 Ultimately, the information on extremes and corresponding vulnerability of plants are crucial  
18 to identify which species and regions (and thus which ecosystem services and functions) are  
19 most at risk from future climate change. Moreover, designing ecosystem-based adaptation  
20 strategies to climate change relies on understanding the interactions between species natural  
21 adaptive capacity and climate change. Analyzing plant responses to climate variability is  
22 important to determine drivers of ecosystem dynamics over time (slow vs. fast processes) and  
23 highlights the importance of extremes to assess the impacts of environmental change on  
24 socio-ecological systems.

25

1 **Acknowledgement**

2 This review synthesizes the results from a session which was held during the 2011 European  
3 Geoscience Union (EGU) general assembly (BG2.7). CR acknowledges funding from the EC  
4 FP7 MOTIVE project (grant agreement no. 226544). SL was funded by EC FP7 ACQWA.  
5 AR acknowledges funding from the EU FP-7 project CARBO-Extreme (grant agreement no.  
6 226701). The work of FdL carried out within the Italian national project AGROSCENARI  
7 (MIPAAF, D.M. 8608/7303/2008).

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34

1 Table 1. Examples of observed plant vulnerabilities to changes in the mean climate and climate variability.

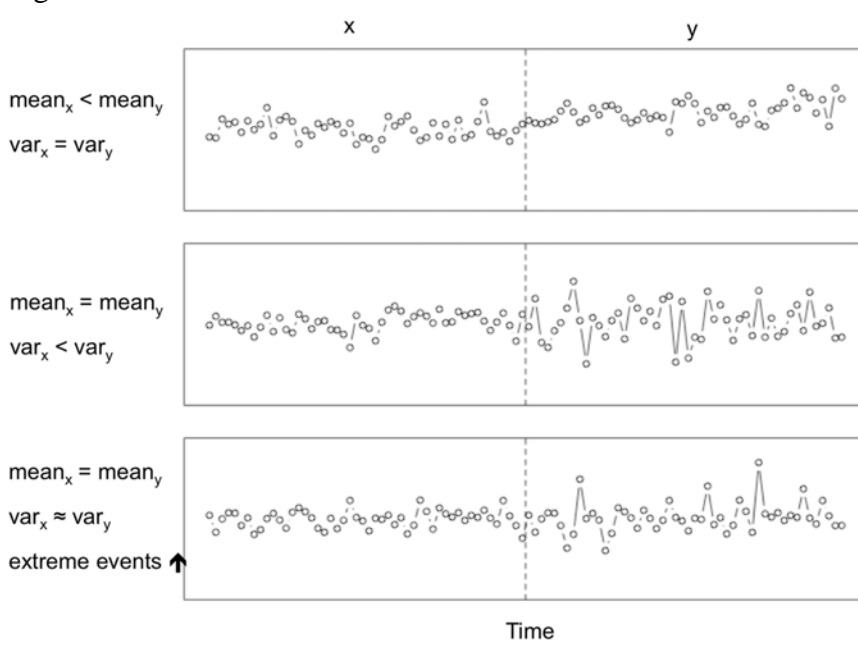
| Process                           | Changing mean   | Effect / Response   | Reference   | Changing variability                                    | Effect / Response  | Reference   |
|-----------------------------------|---|---|---|---|--|---|
| Phenology                         | Increase in mean temperature                          | Prolongation of growing season, earlier onset of leaf unfolding and first flowering, delay of leaf senescence | Menzel & Fabian 1999; Walther <i>et al.</i> 2002; Parmesan & Yohe 2003; Root <i>et al.</i> 2003; Menzel <i>et al.</i> 2006; Polgar & Primack 2011; Vitis <i>et al.</i> 2009 | Early and late frosts, warm spells, drought, heavy rain | Frost damage, possibly fatal damage to opportunistic species, second or extended flowering, advanced mid-flowering, decreased flowering length | Leuzinger <i>et al.</i> 2011a; Luterbacher <i>et al.</i> 2007; Jentsch <i>et al.</i> 2009 |
| Soil organic matter decomposition | Increase in mean temperature                          | Potentially increase in soil organic matter decomposition   | Saxe <i>et al.</i> 2001   | Droughts/heatwaves                                      | Increase in soil water repellency lead to reduced decomposition of soil organic matter   | Goebel <i>et al.</i> 2011   |
| Water relations                   | Increase in night-time warming (and mean temperature) | Slight increases in stomatal conductance  | Albert <i>et al.</i> 2011   | Drought   | Stomatal closure and carbon starvation (isohydric plants) hydraulic failure (anisohydric plants)   | Breda <i>et al.</i> 2006; McDowell <i>et al.</i> 2008                                     |

- 1 Table 2. Are we measuring the impact of mean climate or climate variability? Non-exhaustive list of the studies cited in the text and their  
 2 testing amplitude in comparison to the background variability in the respective study system. The last column indicates in a qualitative way  
 3 how well the testing amplitude accounts for climatic variability in terms of the background variability.

| Study system  | Testing amplitude   | Background variability   | Study type      | Reference                      | Testing climate variability?  |
|---|---|--|-----------------|--------------------------------|---|
| European grassland & heath species  | Drought: 32 days  | Local 100-year extreme drought (number of days with precipitation < 1mm), 33 days of drought in 1976   | Experiment      | Jentsch <i>et al.</i> 2009     | Yes, 100-year-event   |
| European grassland & heath species  | Precipitation: 170mm over 14 days   | Local 100-year rainfall extreme, 152mm of precipitation over 14 days in 1977   | Experiment      | Jentsch <i>et al.</i> 2009     | Yes, 100-year-event   |
| European plant phenology  | +1.5 (warm), +3 (very warm), -1.5 (cold) and -3 (very cold) standard deviations from the long-term mean at the respective grid point to classify warm and cold spells   | Long-term mean   | Observation     | Menzel <i>et al.</i> 2011      | Yes, +/- 3 standard deviations from mean                              |
| Grasslands  | 6-8 large precipitation events per growing season (mean per event = 42 mm)  | The large size and low frequency of precipitation events in the altered precipitation treatment are well within the range of documented precipitation regimes of the past 100 years in this region | Experiment      | Knapp <i>et al.</i> 2002       | Yes, but less than 100-year-event                                     |
| Young oak stands (3 species ( <i>Quercus robur</i> , <i>Quercus petraea</i> , <i>Quercus pubescens</i> ), 4 provenances each) | Amount of irrigation water in drought-treated stands was 60% lower than the long-term mean precipitation (728 mm during the growing season from April to October) in 2007 and 43% lower in 2008 and 2009. Experimental droughts were imposed by stopping irrigation for several consecutive weeks during selected periods in the growing season | Compared to the long-term mean of the site, the amount of irrigation in the control was 16% lower in 2007, 26% higher in 2008 and 30% higher in 2009   | Experiment      | Kuster <i>et al.</i> 2012      | Unclear but testing amplitude much larger than variability in control |
| Mixed broadleaved forest in Central Europe  | Seasonal precipitation: 50% of the 10-year mean from 1989 to 1999, Spring precipitation: below the mean, Mean monthly temperatures: exceeded the long-term mean (1989–1999) (e.g., + 6.8 °C for June).  | Long-term mean   | Observation     | Leuzinger <i>et al.</i> 2005   | Unclear (background variability not further specified) but likely     |
| <i>Pinus halepensis</i> stands (3 contrasting sites, 5 provenances)   | Precipitation in Rome, 766+-156mm; Tel Aviv, 557+-184mm, and Yatir (semi-arid), 279+-88mm   | Long-term mean (differences in mean climate are very large hence testing amplitude equals high background variability but no explicit testing of climate variability)                              | Transplantation | Klein <i>et al.</i> 2012       | Locally unclear but over the species distribution range probably yes  |
| <i>Tamarix africana</i> Poiret  | Continuous soil flooding with fresh and saline water during 45 days   | Not explicitly mentioned, plant survived 45 days of flooding   | Experiment      | Abou-Jaoudé <i>et al.</i> 2012 | Unclear   |

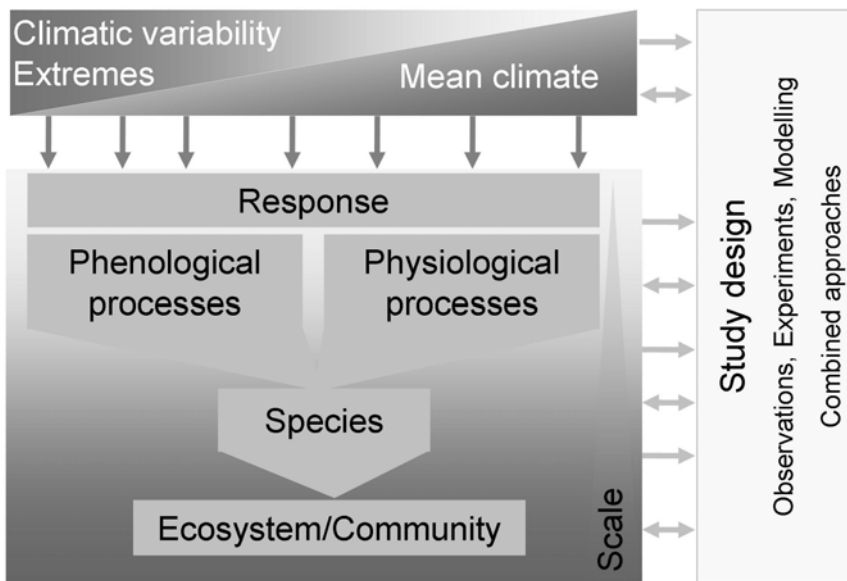


1 Figures:



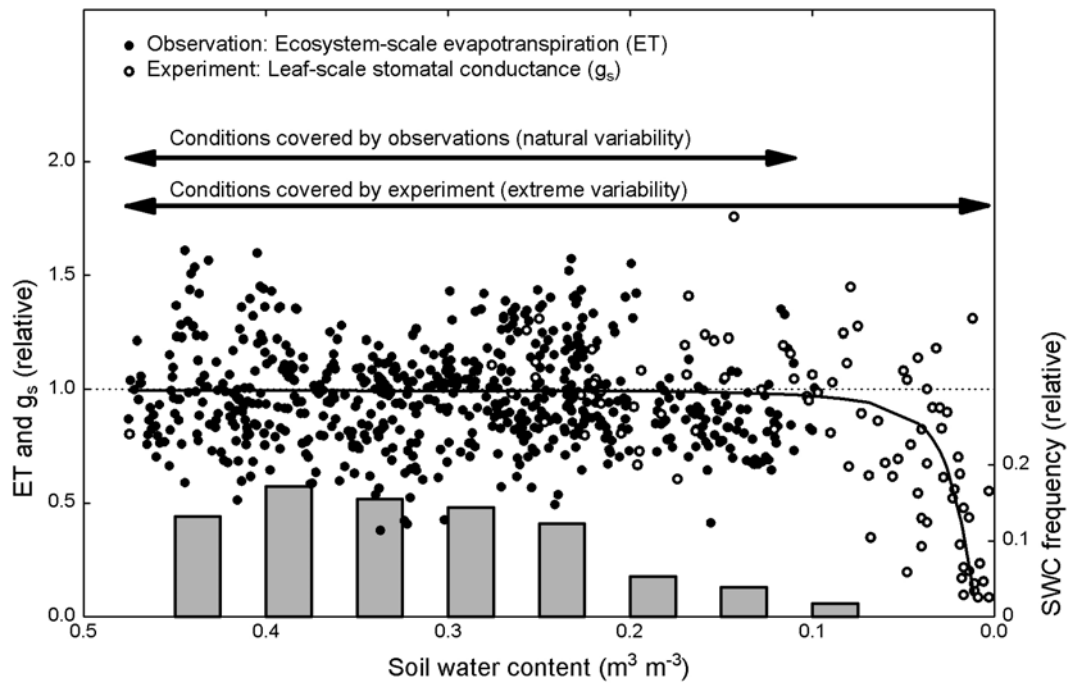
2

3 Figure 1. The three theoretical cases of changing climatic drivers (from top to bottom): (1)  
4 changes in the mean but not the variance, (2) changes in the variance but not the mean of a  
5 variable and (3) both the mean and the background variability remain comparable, but  
6 individual extreme events become more frequent.



7

8 Figure 2. Conceptual overview of the different processes and scales affected by extremes and  
9 the methods to study them.



1

2 Figure 3. Evapotranspiration measured in the field with the eddy covariance method (black  
 3 filled dots) over the range of soil water contents (grey bars) occurring in the field and stomatal  
 4 conductance measured in a laboratory experiment (black open dots). Data from and further  
 5 descriptions available in Brill *et al.* (2011). SWC = Soil Water Content.