

1 **Extreme Weather and Climate Events with Ecological Relevance –** 2 **A review**

3 Caroline C. Ummenhofer¹ and Gerald A. Meehl²

4 ¹Department of Physical Oceanography, Woods Hole Oceanographic Institution, Woods Hole, Massachusetts, USA

5 ²NCAR Climate and Global Dynamics Laboratory, National Center for Atmospheric Research, Boulder, Colorado,
6 USA

7
8 **Review article** for *Philosophical Transactions of the Royal Society of London B* – Special issue
9 on “Behavioural, ecological and evolutionary responses to extreme climatic events”
10

11 **Abstract**

12 Robust evidence exists that certain extreme weather and climate events, especially daily
13 temperature and precipitation extremes, have changed in regard to intensity and frequency over
14 recent decades. These changes have been linked to human-induced climate change, while the
15 degree to which climate change impacts an individual extreme climate event (ECE) is more
16 difficult to quantify. Rapid progress in event attribution has recently been made through
17 improved understanding of observed and simulated climate variability, methods for event
18 attribution and advances in numerical modelling. Attribution for extreme temperature events is
19 stronger compared to other event types, notably those related to the hydrological cycle. Recent
20 advances in the understanding of ECEs, both in observations and their representation in state-of-
21 the-art climate models, open new opportunities for assessing their effect on human and natural
22 systems.

23 Improved spatial resolution in global climate models and advances in statistical and dynamical
24 downscaling now provide climatic information at appropriate spatial and temporal scales.
25 Together with the continued development of Earth System Models that at increasing complexity
26 simulate biogeochemical cycles and interactions with the biosphere, these make it possible to
27 develop a mechanistic understanding how ECEs affect biological processes, ecosystem
28 functioning and adaptation capabilities. Limitations in the observational network, both for
29 physical climate system parameters and even more so for long-term ecological monitoring, have
30 hampered progress in understanding bio-physical interactions across a range of scales. New
31 opportunities for assessing how ECEs modulate ecosystem structure and functioning arise from
32 better scientific understanding of ECEs coupled with technological advances in observing
33 systems and instrumentation.

34
35 **Key words:** extreme events, climate variability, climate change, detection and attribution, event
36 attribution, ecological impacts

37 **1. Introduction and motivation**

38 A recent publication by the National Academy of Sciences (NAS 2016) is the latest addition to a
39 series of focused summary reports (IPCC 2012a; 2013; Grotjahn et al. 2014) that highlight
40 mounting evidence that extreme weather and climate events have been changing in regard to
41 intensity, frequency, and duration in the last few decades. Daily temperature and precipitation
42 extremes in particular have been observed to increase in frequency and intensity, which has been
43 linked to human-induced climate change (Bindoff et al. 2013; Zwiers et al. 2013; Stott 2016).

44 In contrast, the degree to which climate change impacts an individual extreme weather or
45 climatic event is more difficult to determine and quantify. This applies especially when
46 considering that a variety of natural and anthropogenic factors, such as internal modes of climate
47 variability, various man-made emissions, land-use change etc., need to be taken into account
48 when attributing individual weather or climate events to causal factors. Solow (2015) cautioned
49 that the concept of attributable risk for single events in a climate change context is inherently
50 difficult given the rarity of extreme climatic events (ECEs) and the limited reliable climatic
51 record. Extreme events by definition are rare occurrences and in most places few examples of
52 past events are seen in the observational record (NAS 2016).

53 However, recent rapid progress in event attribution has been made through improved
54 understanding of observed and simulated climate variability, increasing observational
55 capabilities, methods for event attribution, and advances in numerical modelling. The American
56 Meteorological Society’s annual report of extreme events that occurred in the previous year was
57 first published in 2012 with 6 extreme event studies for the year 2011 (Peterson et al. 2012). The
58 number of studies rose sharply to 32 extreme events last year (Herring et al. 2015), covering all
59 continents and much broader types of events and impacts during 2014 (Stott 2016). The National
60 Academy of Sciences report thus concluded that “in many cases, it is now often possible to make
61 and defend quantitative statements about the extent to which human-induced climate change (or
62 another causal factor, such as a specific mode of natural variability) has influenced either the
63 magnitude or the probability of occurrence of specific types of events or event classes (NAS
64 2016).”

65 There has also been substantial progress made recently in assessing ECEs according to the latest
66 Intergovernmental Panel on Climate Change (IPCC) assessment report 5 (AR5), compared to the
67 previous AR4 report (IPCC 2013; Alexander 2016). Recent advances in the understanding of
68 ECEs, both in observations and their representation in state-of-the-art climate model simulations,
69 open new opportunities for assessing the effect of ECEs on human and natural systems at
70 relevant scales. In particular, improved spatial resolution in global climate models combined
71 with advances in statistical and dynamical downscaling (e.g., regional model configurations)
72 now provide climatic information at the appropriate spatial and temporal scales: with these, it is
73 possible to develop a mechanistic understanding how ECEs in the physical climate system affect
74 biological processes, ecosystem functioning and adaptation capabilities.

75 It is evident that ECEs, especially large-scale events such as subcontinental-scale drought or
76 heatwaves, can have profound effects on ecosystems (Smith 2011). This was shown for example
77 for arid and semiarid ecosystems in response to hydroclimatic disturbances associated with El
78 Niño-Southern Oscillation (ENSO) events in Australia and the Americas (Holmgren et al. 2006
79 and references therein): more specifically, ECEs can trigger ecosystem-level disturbances
80 through changing species composition and diversity (i.e., organisation) and functional attributes
81 (Parmesan et al. 2000). For marine ecosystems, ECEs are also considered a key driver of
82 biodiversity patterns (e.g., Wernberg et al. 2016). Addressing how such episodic events affect
83 species distribution is regarded as crucial to advance predictive models of species distribution
84 and ecosystem structure in the future, beyond their current basis on gradual warming trends
85 (Wernberg et al. 2013). Though when assessing 238 widespread species in England, Palmer et al.
86 (2016) found extreme biological responses linked individually to climate, but long-term
87 trends of widespread species were not (yet) simultaneously dominated by ECEs.

88 The representation of large-scale to regional-scale ECEs is within the capabilities of current
89 generation climate models, while ECEs on local and subgrid-scale (on the order of metres to
90 dozens of kilometres) still pose challenges. The specifics of the ecosystem response, including
91 initial resistance, evolution of the response, and the system's resilience to return to its original
92 condition, depend on the characteristics of the biological system and the level of the disturbance
93 (Parmesan et al. 2000). When considering ECEs as disturbances, these include frequency,
94 intensity, duration, seasonality, and preconditioning. Recent improvements have been made in
95 the observational networks to evaluate ECE characteristics with regard to data homogeneity
96 (Alexander 2016), as well as spatial and temporal coverage and resolution through advanced
97 technologies. Remotely sensed data sets of the climate system with short return intervals at
98 identical locations and near-global coverage (Frank et al. 2015) provide major advances in
99 understanding changes by quantifying processes and spatiotemporal states of the atmosphere,
100 land and oceans (Yang et al. 2013). This applies to biological systems for example through
101 global satellite monitoring of climate-induced vegetation disturbances (McDowell et al. 2015) or
102 ocean colour remote sensing for phytoplankton blooms since the 1970s (Blondeau-Patissier et al.
103 2014). As such, satellite-based data sets are becoming long enough to be used in detection-
104 attribution studies for ECEs (Easterling et al. 2016).

105 This review provides an overview of the current understanding of changes in ECEs and how they
106 are quantified. For a detailed assessment of ECEs, the reader is referred to recent papers
107 providing an in-depth review of various aspects of changes in ECEs, their detection and
108 attribution (e.g., Westra et al. 2014; Alexander 2016; Easterling et al. 2016; Stott et al. 2016).
109 Here, particular focus is on ECEs with ecological relevance and covering different realms of the
110 climate system and across a range of spatial and temporal scales. It is by no means meant as an
111 exhaustive accounting of changes in ECEs or their ecological impacts, but focuses mostly on
112 ecosystems and community ecology. The remainder of the review is structured as follows:
113 Section 2 defines ECEs and highlights how their definition might affect the assessment of

114 changes, while Section 3 reviews detection and attribution of events. Section 4 details observed
115 and simulated changes in ECEs with ecological relevance, along with examples from the
116 terrestrial/atmosphere and ocean realms. Section 5 discusses current challenges and opportunities
117 in understanding how ECEs affect biological systems, followed by conclusions provided in
118 Section 6.

119

120 **2. Extreme climatic events**

121 Different definitions for ECEs exist, such as those detailed in Table 1 in van de Pol et al. (2016)
122 in this issue. In this review, we follow the climatological definition used by the IPCC Special
123 Report on Extreme events (IPCC 2012a) for a climate extreme (extreme weather or climate
124 event; Figure 1): i.e., the occurrence of a weather or climate variable above (below) a threshold
125 value near the upper (lower) end of the range of observed records of the variable. Definitions of
126 thresholds can vary, but are typically 10%, 5% or 1% relative to a reference period, though
127 absolute thresholds are sometimes considered as well (e.g., for critical threshold temperatures for
128 physiological responses; Seneviratne et al. 2012). However, in absolute terms, what is considered
129 an extreme event will vary in different locations: ECE characteristics are intimately tied to a
130 location's mean climatic condition and its variability. For example, a record daily maximum
131 temperature in the Sahara is higher than for Alaska; for the latter, the absolute value for this
132 record temperature will also exhibit much greater seasonal dependence given the temperature
133 range between winter and summer at higher latitudes.

134 Several characteristics of extreme events are of interest. These include the magnitude of ECEs,
135 the probability or return frequency, the duration of the ECE, the spatial extent, timing, onset date,
136 or seasonality, and preconditioning (Seneviratne et al. 2012). Preconditioning in this context
137 refers to antecedent conditions that facilitate or enable a certain extreme event to occur or modify
138 its characteristics. For example, antecedent soil moisture deficits that accumulate over the course
139 of several months in winter/spring have been shown to exacerbate summer heat wave and
140 drought conditions (e.g., Fischer et al. 2007), as dry soils may amplify extreme maximum
141 temperatures through feedbacks with evapotranspiration (Whan et al. 2015; Meehl et al. 2016).
142 Changes in these ECE characteristics have been investigated in climate change studies, though
143 the majority of research has focused on ECE changes with regard to magnitude and
144 probability/return frequency.

145 To define ECEs, thresholds, percentiles, or return values are defined with respect to a reference
146 period, which is often historical, i.e. 1961-1990. The choice of reference period can affect the
147 assessed changes and whether it is considered to be static or transient (Seneviratne et al. 2012;
148 Sippel et al. 2015): if ECEs are defined based on a percentile of the probability distribution,
149 shifts in the mean (without any change in the shape of the distribution) will not lead to a relative
150 change in the frequency of the extremes. Sippel et al. (2015) cautioned, though, that
151 standardisation to a reference period can introduce an inhomogeneity when calculating

152 temperature variability and extremes, with a risk of arbitrarily inflating extremes, and suggested
153 an analytical correction. A series of studies demonstrate that observed changes in the frequency
154 of extremes are consistent with overall shifts in the distribution (e.g., Ballester et al. 2010;
155 Hartmann et al. 2013; Rhines and Huybers 2013). While counts of threshold exceedance, such as
156 frequency and duration, closely follow mean changes, variations in intensity or severity are
157 considerably more sensitive to changes in the shape of the probability distribution (Fig. 1; e.g.,
158 Fischer and Schär 2010; Hartmann et al. 2013). There is also ongoing debate about the role of
159 changes in the variance and higher order moments, such as skewness, in addition to the mean
160 (Hartmann et al. 2013). Furthermore, the statistics of ECEs are particularly sensitive to data
161 availability, quality, and consistency.

162 Some limitations were previously noted with regard to defining ECEs as probability-based or
163 threshold-based (Seneviratne et al. 2012): events from the extreme tails of the probability
164 distribution do not necessarily have to be extreme in terms of impact. Impact-related thresholds
165 are variable in space and time, such that definitions for ECEs need to be modified for different
166 locations and time periods (e.g., seasons). To account for this, ECEs can be defined
167 quantitatively in two ways: (1) related to a specific threshold (possibly impact-related); or (2)
168 related to their probability of occurrence (Seneviratne et al. 2012). These definitions are not
169 necessarily diametric; impacts on society or ecosystem responses are often extreme, irrespective
170 of whether a probability- or threshold-definition has been used.

171

172 **3. Detection and attribution of ECEs**

173 Reliable detection and attribution of changes in specific climatic events and their impacts are key
174 for understanding the scientific basis of climate change and for successful decision making to
175 enable adaptation and mitigation (Hegerl et al. 2010; Easterling et al. 2016). Similarly, to assess
176 how ECEs impact structure and functioning of populations, individual species, or entire
177 ecosystems, detection and attribution approaches are crucial.

178 Detection refers to the process of demonstrating that an ECE characteristic (or climate variable
179 more broadly) has changed with respect to some previous period in a defined statistical sense;
180 however, no reason for that change is provided (Hegerl et al. 2010; Easterling et al. 2016). In
181 observations, such a change is identified if its likelihood of occurrence by chance due to internal
182 variability alone is considered to be small (Bindoff et al. 2013). In contrast, attribution is the
183 process of assessing the relative contributions from multiple causal factors to an ECE change or
184 event; it also assigns a statistical confidence to this conclusion. Attribution is thus more complex
185 than detection, as it combines statistical analysis with physical understanding (Bindoff et al.
186 2013; Solow 2016). One can attribute an observed ECE change to a specific causal factor
187 through demonstrating that the change is consistent with a process-based model that includes this
188 factor and is inconsistent with an alternate model that is otherwise identical, but excludes the

189 factor. This assessment also needs to take into account internal chaotic variability and
190 uncertainties in observations and responses to external causal factors (Bindoff et al. 2013).

191 Approaches for detection and attribution for a particular event can be classified into two
192 categories (IPCC 2013): (1) studies that use the observational record to assess whether a change
193 in the probability or magnitude of an ECE has occurred; (2) studies based on climate model
194 simulations (coupled or using a subset of components only) to compare characteristics of the
195 event in simulations with and without anthropogenic climate change; a combination of both
196 approaches is often used as well (IPCC 2013). Stott (2016) further divides the latter into two
197 types of methods as follows: (1) exceeding a certain climate index in extended coupled climate
198 model simulations with and without climate change; (2) using a large ensemble of atmosphere-
199 only simulations that use observed boundary conditions, such as sea surface temperatures (SST),
200 to evaluate if the climate index of interest, with or without the factor included, occurs at a
201 changed frequency (Stott 2016; Stott et al. 2016). This approach is not limited to atmosphere-
202 only configurations, where an atmospheric model is forced by observed boundary conditions
203 (e.g., SST), but could also be applied to ocean models forced with atmospheric boundary
204 conditions (e.g., winds, precipitation, heat fluxes).

205 Overall, the evidence for detecting a human influence on temperature extremes has strengthened
206 since the IPCC Special Report on Extreme events (IPCC 2012a). Global-scale daily temperature
207 extremes have increased in frequency and intensity since the 1950s, very likely due to
208 anthropogenic influences, and heat wave probabilities have doubled in some locations (IPCC
209 2013). Stott (2016) also highlights that specific event attribution for extreme temperature events,
210 such as record daily temperatures or heat waves, is stronger compared to other types of events,
211 notably those related to changes in the hydrological cycle.

212 Despite substantial recent improvements in models, reanalyses¹ and satellite records, detection
213 and attribution of human influence on the water cycle and in particular regional precipitation
214 remains challenging (Zwiers et al. 2013; Alexander 2016; Sarojini et al. 2016; Stott et al. 2016).
215 To disentangle the complex regional-scale changes in precipitation, a highly noisy variable,
216 several factors are likely to affect the anthropogenic response: (1) how external forcing affects
217 internal modes of climate variability, which can alter the frequency or amplitude of the mode or
218 in turn modify its precipitation teleconnections; (2) responses to different external drivers (e.g.,
219 aerosols, ozone) vary for precipitation; (3) the spatial expression of the precipitation response to
220 external forcing contains signals that are due to thermodynamic as well as dynamic changes,
221 which arise due to altered atmospheric energetics, moisture content, and large-scale circulation
222 (Sarojini et al. 2016).

¹ Reanalyses combine observations with an unchanging data assimilation scheme and model to provide a dynamically consistent estimate of the climate state over the instrumental period (CDG 2016).

223 **4. Changes in ECEs with ecological relevance**

224 Robust changes in many ECEs have been observed in the second half of the 20th Century. Shifts
225 in the frequency of ECEs can arise due to different changes, as highlighted exemplarily for a
226 temperature distribution in Figure 1: ECEs can occur more frequently due to a shift in the mean,
227 be associated with shifts in the variability of the distribution, as well as changes in its symmetry
228 or skewness (Fig. 1; IPCC 2012b).

229

230 **4.1 Terrestrial/atmosphere**

231 *a) Temperature extremes*

232 For temperature, changes in the distribution are especially pronounced for increases in maximum
233 and minimum temperatures (Donat et al. 2013b). There is robust evidence across multiple
234 datasets that minimum temperatures across the globe are rising faster, which could lead to a
235 decline in the daily temperature range (IPCC 2013). Globally, a decrease in the number of cold
236 days and nights is considered very likely, while the number of warm days and nights increased.
237 Regional variations exist, with Europe and Asia exhibiting especially pronounced decreases in
238 cold nights (Choi et al. 2009; Donat et al. 2013a, b). For North America, it is projected that the
239 total area experiencing freezing days will contract by ~6% by 2070, with the number of freezing
240 days declining by 10-90 days depending on the region (Rawlins et al. 2016). It has been shown
241 for the U.S. (Meehl et al. 2009, Rowe and Derry 2012), Australia (Trewin and Vermont 2010)
242 and Europe (Beniston 2015) that the ratio of daily record high temperatures to daily record low
243 temperatures has been increasing, with the average for the first decade of the 21st Century for
244 these regions being about two to one (i.e., two daily record highs are set for every one daily
245 record low). The shift in the chances for more record highs than record lows relates to the
246 increase in average temperatures over this time period in these locations. This ratio is projected
247 to increase in the future as the climate continues to warm (Meehl et al. 2009; Beniston 2015;
248 Meehl et al. 2016).

249 Confidence in trends in temperature extremes is high for North and Central America (e.g.,
250 Peterson et al. 2008), Europe (e.g., Andrade et al. 2012), Asia (e.g., Choi et al. 2009), Southeast
251 Asia and Oceania (e.g., Caesar et al. 2011). Trends in the climate models with regard to the
252 frequency of extreme warm and cold days and nights since the 1950s are consistent with
253 observations and are projected to continue to change into the 21st Century (IPCC 2013). A
254 decrease of frost days, an increase in growing season length, an increase in the number of warm
255 nights, and an increase in heat wave intensity over the U.S. have been attributed mostly to
256 increases in human-produced greenhouse gases (Meehl et al. 2007). Heat-related extremes and
257 some precipitation extremes have also been attributed to human influences on climate (Coumou
258 and Rahmstorf 2012). Changes in regional temperature extremes have been associated with
259 changing global and regional atmospheric circulation and SST patterns (Scaife et al. 2008;
260 Hartmann et al. 2013). High temperature extremes have been shown to substantially affect

261 individual species, as shown for example for negative effects on clutch size for a particular bird
262 species (Marrot et al. 2016) and on overwintering success of butterfly species in the UK (Long et
263 al. 2016), or for ecosystems through overall contractions or shifts in the distribution range of
264 species habitat, as critical temperature thresholds are exceeded (Fischlin et al. 2007; Handmer et
265 al. 2012).

266 *b) Precipitation extremes*

267 According to theoretical thermodynamic understanding, the water-holding capacity of the
268 atmosphere scales with temperature and an intensification of extreme precipitation is expected in
269 a warming world (e.g., Trenberth et al. 2003; Meehl et al. 2005; Held and Soden 2006; Wentz et
270 al. 2007; Pall et al. 2011; Hartmann et al. 2013; Lehmann et al. 2015). According to the well-
271 known Clausius-Clapeyron relationship, the saturation-specific humidity increases by ~7% per
272 °C of warming, with higher levels of moisture available and intensifying rainfall. This was also
273 found in observed annual maximum daily rainfall rate increases of 5.9-7.7% for globally
274 averaged surface temperatures (Westra et al. 2013). However, in their review of subdaily
275 extreme rainfall changes, Westra et al. (2014) described observed and simulated rates of extreme
276 precipitation increases double of that suggested by Clausius-Clapeyron at temperatures below
277 20°C. Short-duration (<1day) storms were most likely to occur more often, which might increase
278 the frequency and magnitude of flash floods (Westra et al. 2014). Since the 1950s, heavy
279 precipitation events have likely increased in frequency over land globally, especially over North
280 America and Europe, while confidence in heavy precipitation over other land areas was only
281 medium (IPCC 2013). A shift to more extreme precipitation patterns with more heavy rainfall
282 and longer dry intervals (Tebaldi et al. 2006) has been shown to decrease the rain use efficiency
283 across biomes. This is most pronounced for arid grasslands and Mediterranean forests (16-20%),
284 due to higher water stress conditions and reduced vegetation production (Zhang et al. 2013).
285 Feng et al. (2013) also highlighted changes in the rainfall seasonality in the tropics over the 20th
286 Century: they observed increasing interannual variability of seasonality over large parts of the
287 dry tropics (arid and semi-arid regions), with shifts in seasonal magnitude, timing, and duration,
288 all factors that are of importance for local ecological processes.

289 Changes in regional precipitation can arise due to both a thermodynamic as well as a dynamic
290 contribution (i.e., including changes in circulation, modes of variability, and teleconnections;
291 Sarojini et al. 2016). Westra et al. (2014) highlighted the importance of research efforts focusing
292 on improving our understanding of local-scale thermodynamic effects and large-scale
293 atmospheric circulation in modulating subdaily extreme rainfall intensity. A series of studies
294 have recently found that regional SST warming played a role in intensifying extreme
295 precipitation events (Evans and Boyer-Souchet 2012; Meredith et al. 2015; Trenberth et al. 2015;
296 Ummenhofer et al. 2015). For example, Australia experienced extreme rainfall conditions during
297 the 2010/11 La Niña event that led to extensive flooding in the northeast of the country
298 (Ummenhofer et al. 2015 and references therein). As demonstrated in atmospheric circulation
299 model experiments based on 2010/11 ocean conditions with and without long-term warming

300 included, both dynamic and thermodynamic factors led to the intensification of the rain-
301 producing atmospheric circulation conditions (Ummenhofer et al. 2015). The resultant
302 widespread wet conditions in the interior of the Australian continent, which included a rare
303 filling of Lake Eyre (Pook et al. 2014), led to unusually high growth of the semi-arid vegetation,
304 accounting for record global terrestrial carbon uptake in 2010/11 (Poulter et al. 2014).

305 *c) Heat waves and droughts*

306 Heat waves over large areas of Europe, Australia, and Asia have likely become more frequent,
307 while droughts more intense and/or longer in many regions since the 1970s (IPCC 2013). Severe
308 heat waves, such as the one in Europe in 2003 (Beniston et al. 2004; Stott et al. 2004; Fischer et
309 al. 2007; Garcia-Herrera et al. 2010), Australia in 2009, Russia in 2010 (Matsueda 2011;
310 Barriopedro et al. 2011; Trenberth and Fasullo 2012), and the USA in 2010/11 (Hoerling et al.
311 2013), are often associated with persistent blocking high pressure systems (Meehl and Tebaldi
312 2004). These circulation regimes are projected to become more frequent, intense, and persistent
313 in the 21st Century, leading to an intensification of heatwaves in Europe and North America
314 (Meehl and Tebaldi 2004). Summers like 2003 over Europe are likely to occur twice a decade in
315 the late 21st Century (Christidis et al. 2015). Assessing seasonal temperature and circulation
316 regime changes over Europe for 1960-2000, Cassou and Cattiaux (2016) found an earlier onset
317 of summer: they related this to an earlier disappearance of winter snow in Eastern Europe that
318 hastened the typical summertime formation of a blocking high pressure system over Europe. This
319 was associated with more clear-sky days with increased incoming short-wave radiation and
320 anomalous easterly advection of warm air from the continental interior earlier in the year
321 (Cassou and Cattiaux 2016).

322 During the 2003 heatwave, unprecedented reduction in Europe's gross primary productivity
323 occurred that reversed the effect of four years of net ecosystem carbon sequestration, with a 30%
324 reduced primary productivity and lower ecosystem respiration (Ciais et al. 2005). Several recent
325 reviews (Reichstein et al. 2013; Frank et al. 2015) investigated how ECEs affect terrestrial
326 ecosystems and, in particular, the carbon cycle. ECEs, such as droughts and heatwaves, severely
327 affect forests and grasslands through changes in plant physiology, phenology and carbon
328 allocation. They also lead to increased tree mortality, shifts in vegetation composition,
329 degradation and desertification, along with erosion (Reichstein et al. 2013). Advances have been
330 made recently in understanding how droughts affect tropical forests on molecular, cellular,
331 individual, species, community and landscape level (Corlett 2016). In a review on ecological
332 impacts of droughts on the Amazon, Asner and Alencar (2010) found the hydrological function
333 of floodplains significantly affected by droughts and fires and burn scars were more frequent
334 during drought years; they also highlighted the importance of integrating multiple lines of
335 evidence from remote sensing of hydrological, disturbance-fire, and physiological impacts with
336 field measurements, to reduce uncertainty of basin-level responses to drought (Asner and
337 Alencar 2010). Droughts are most likely to have the largest and most long-lasting impacts
338 globally due to large indirect and lagged impacts and long recovery especially for forest

339 ecosystems (Frank et al. 2015). Examples include the rapid subcontinental die-off of woody
340 plants during the 2000-2004 drought in the Southwest United States, when >90% of the
341 dominant pine species died as a consequence of 15 months of soil water content deficits
342 (Breshears et al. 2005, Rich et al. 2008); the intense 2005 drought affecting the Amazon forest
343 ecosystem to a degree that reversed its role as a long-term carbon sink (Phillips et al. 2009); and
344 a global overview of drought and heat-induced tree mortality studies from the Americas,
345 Australia, Europe, and Asia, indicating that no forest type or climate zone is invulnerable to
346 ECEs even in environments not normally considered water-limited (Allen et al. 2010).

347 Focusing on the 2003 European summer, Garcia-Herrera et al. (2010) concluded that a
348 northward displacement of the North Atlantic subtropical high and anomalous Mediterranean
349 SST contributed to the heat wave. Investigating the role of soil moisture-atmosphere interactions,
350 Fischer et al. (2007) found an early spring soil moisture deficit to be instrumental in accounting
351 for the severity of the summer heat wave in Europe. They linked the decrease in springtime soil
352 moisture to a precipitation deficit along with strong positive radiative anomalies and early
353 vegetation green-up (Fischer et al. 2007). Similarly, Wolf et al. (2016) found increased
354 vegetation growth and carbon uptake during the record-breaking warmth and early arrival of
355 spring 2012. Increased carbon uptake in spring could have enhanced depletion of soil water
356 through higher evapotranspiration and exacerbated summer drought conditions, highlighting the
357 importance of land-atmosphere feedbacks during ECEs (Sippel et al. 2016). For the Great Plains
358 in the Midwest US, enhanced local land-atmosphere feedbacks are likely associated with an
359 amplification of future heat waves due to stronger subseasonal summertime temperature
360 variability (Teng et al. 2016).

361 Droughts can also affect freshwater ecosystems, such as streams, rivers, lakes and wetlands,
362 stressing and depleting both fauna and flora as shown for the so-called Big Dry or Millennium
363 Drought for Southeast Australia (Bond et al. 2008 and references therein), floodplains in the
364 Amazon (Asner and Alencar 2010) and in a review based on studies from the US, Europe and
365 Australia, while impacts particularly in Asia, Africa, and South America have not been
366 documented in the published literature (Mosley 2015). Droughts can result in poor water quality,
367 habitat loss and changed biotic interactions, which will impact aquatic biota and ecosystem
368 functioning in both flowing and standing water systems, where the effects of drought on
369 population and community structure are better understood than impacts on ecosystem processes
370 (Bond et al. 2008).

371 *d) Wildfires*

372 The frequency of wildfires is related to temperature, moisture and fuel loads, which in turn are
373 affected by species composition and age structure (Parmesan et al. 2000). Littell et al. (2009)
374 found antecedent climatic conditions, such as winter precipitation for shrub and grassland
375 ecosystems and summer droughts in forests, to be an important factor accounting for trends in
376 the areal extent burned in the western US. Extended periods of drought, especially if they are
377 followed by extreme heat and low humidity, provide ideal conditions for wildfires, often incited

378 by lightning associated with thunderstorms at the end of the drought (Parmesan et al. 2000).
379 Assessing changes in fire severity in the western US, Miller et al. (2009) found substantial
380 increases in mean and maximum fire size and the annual area burned since the 1980s, indicating
381 that forest fuels were no longer a limiting factor for fire occurrence. Sudden changes in wildfire
382 activity in forests in the northern Rocky Mountains in the mid-1980s, with more frequent large-
383 scale fires, longer-lasting wildfires and a longer wildfire season, were associated with earlier
384 spring snowmelt and increased spring and summer temperatures (Westerling et al. 2006). In light
385 of warming regional temperatures and changing precipitation, along with current trends in
386 increasing wildfire severity, it is important to address the implications of ongoing fire
387 suppression. Especially since severe wildfires can have extensive ecological impacts, including
388 forest fragmentation, erosion rates, carbon sequestration, wildlife habitat availability, and post-
389 fire seedling recruitment (Miller et al. 2009). Several studies emphasised the importance of the
390 interaction of the physical climate system and biological processes across temporal and spatial
391 scales to explain climate-wildfire interactions: Marlon et al. (2012) ascertained that improved
392 understanding of the causes and consequences of forest wildfires in the western US is crucially
393 dependent on integrated information of climate change and human activity across a range of
394 temporal scales. Parisien and Moritz (2009) advocated further work for improved understanding
395 of direct causal factors that control wildfires across a range of spatial scales. Alencar et al. (2015)
396 linked increased fire incidence in dense forests in the Amazon basin to severe, ENSO-related
397 droughts, when the end of the dry season was delayed by a month, resulting in larger burn scars
398 and overall extent of the area burned; in contrast, open and transitional forests with higher
399 deforestation rates burned more frequently, suggesting that climate-mediated forest flammability
400 was exacerbated by landscape fragmentation (Alencar et al. 2015). Investigating preconditioning
401 of devastating bushfires in Southeast Australia in February of 1983 and 2009, Cai et al. (2009)
402 associated these with characteristic Indian Ocean conditions with a positive Indian Ocean
403 Dipole, rather than El Niño events, through impacts on soil moisture, as shown for prolonged
404 Southeast Australian droughts (Ummenhofer et al. 2009).

405

406

407 **4.2 Ocean**

408 *a) Marine heat waves and cold spells*

409 In analogy to heat waves in the atmosphere, the marine environment also experiences sustained
410 extreme temperature events, so called ‘marine heat waves’. It is defined as a prolonged discrete
411 event with anomalously warm water and characteristics include its spatial extent, intensity,
412 duration, and rate of evolution (Hobday et al. 2016). Marine heat waves can have extensive
413 ecological implications, including shifts in species range (Smale and Wernberg 2013), local
414 extinctions (Wernberg et al. 2016) and economic impacts when affecting aquaculture or
415 important fishery species (Mills et al. 2013). Some of the recent observed marine heat waves
416 with extensive ecological implications occurred in the northern Mediterranean in 2003 (Garrabou

417 et al. 2009), the 2011 ‘Ningaloo Niño’ in Western Australia (Wernberg et al. 2013), and in the
418 northwest Atlantic in 2012 (Mills et al. 2013). Investigating the frequency of marine heat waves
419 in the North Pacific and Atlantic since the 1950s, Scannell et al. (2016) found the probability of
420 marine heat waves to be a trade-off between size, duration, and intensity, which are modulated
421 by a region’s specific variability, as well as by modes of climate variability and anthropogenic
422 warming. Marine heat waves have been observed more frequently in the last decades and are
423 projected to become more frequent in a warming climate (Hobday et al. 2016), though decadal
424 variability likely plays a role as well (Feng et al. 2015). Wernberg et al. (2013, 2016) linked
425 regime shifts of Western Australian temperate reef ecosystems to continuing ocean warming and
426 extreme marine heat waves. These resulted in a significant range contraction of kelp forests,
427 which were being replaced by communities typical of subtropical and tropical waters (Wernberg
428 et al. 2013, 2016). Di Lorenzo and Ohman (2013) showed that cumulative responses to
429 atmospheric forcing can help explain large-amplitude state transitions in marine ecosystems,
430 allowing better interpretation of both abrupt responses and gradual changes (e.g., to long-term
431 warming) in biological systems.

432 An example of a record-setting ocean heat wave was the one that occurred in the North Pacific
433 from 2013-2015 (Di Lorenzo and Mantua 2016). It was one of the largest marine heat waves
434 ever recorded, with SST anomalies exceeding three standard deviations in consecutive years (Di
435 Lorenzo and Mantua 2016). It is possible that this record-breaking ocean heat wave could have
436 been the most ecologically significant in recorded history (Di Lorenzo and Mantua 2016).
437 Impacts included sea lion, whale, and sea bird mortality events (NOAA 2016a,b, Opar 2015),
438 very low ocean primary productivity (Whitney 2015), and the largest algal bloom on record that
439 negatively impacted shellfish along the western coast of North America (NOAA 2016c). This
440 event was characterised by an overall warming trend in the North Pacific Ocean superimposed
441 with anomalously warm interannual SSTs in the Gulf of Alaska and along the west coast of
442 North America that persisted and grew due to alternating mid-latitude-tropical and tropical-mid-
443 latitude interactions, with the possibility that such events could increase in the future in
444 association with an increase in winter-time variance of climate over the North Pacific (Di
445 Lorenzo and Mantua 2016).

446 Another example of an ocean heat-wave impact was associated with the 2015-2016 El Niño that
447 produced extremely high tropical SSTs in regions where coral reefs experienced the third mass
448 bleaching event in recorded history (NOAA 2015). All these mass bleaching events occurred in
449 conjunction with El Niño events since 1997 (first mass bleaching was 1998, the second was
450 2010; NOAA 2015), and occurred when steadily rising SSTs from human-caused warming had
451 warm El Niño SST anomalies superimposed, thus crossing the tolerance threshold and causing
452 reefs to bleach. In previous mass bleaching events, a certain percentage of bleached reefs died,
453 thus raising the prospect of large-scale coral reef mortality arising from this ECE related to the
454 2015-2016 El Niño event. For example, there was a reported bleaching of over 90% of the Great
455 Barrier Reef in Australia by early 2016 (ARC 2016). The prospects for even greater mass

456 bleaching events increase during future El Niño events as the climate continues to warm, with
457 dire consequences for the overall health and sustainability of coral reef ecosystems (Buddemeier
458 et al. 2004).

459 In contrast, marine cold spells can also severely impact ecosystem structure (e.g., Lirman et al.
460 2011; Firth et al. 2011). Subtropical Florida experienced a severe cold spell in early 2010, with
461 severe impacts for terrestrial and marine species, including coral reef communities (Lirman et al.
462 2011), non-native crabs (Canning-Clode et al. 2011) and important gamefish (Adams et al.
463 2012). According to Lirman et al. (2011), the Florida Reef Tract experienced the most severe
464 coral mortality on record in response to the cold-water anomaly in January 2010, which
465 disproportionately affected shallow reef habitats that had exhibited resilience to prior disturbance
466 events. However, such abnormal cold winters may be a critical ‘reset’ mechanism for marine
467 invasive species, as the cold snap can limit the range expansion of subtropical species (Canning-
468 Clode et al. 2011). For a non-native crab that had extended its range into the southern US and
469 mid-Atlantic coast from the Caribbean, Canning-Clode et al. (2011) suggested that this explained
470 the crab’s sudden disappearance after 2010, as the subtropical species had been unable to tolerate
471 the prolonged extreme cold temperatures in early 2010.

472 *b) Other ECEs affecting marine biological systems*

473 Reviewing how marine organisms in the coastal environment are affected by climate change,
474 Harley et al. (2006) distinguished changes in the physical environment related to sea level rise,
475 changing circulation, pH, CO₂, and UV. Emergent ecological responses could be divided into
476 distributional shifts (e.g., zonation patterns and biogeographical ranges), changes in species
477 composition, diversity and community structure, changing primary and secondary production
478 and population dynamics (Hartley et al. 2006). ECEs are likely a controlling factor how changes
479 in the physical environment exert their influence on biological systems in the marine
480 environment. In addition to the temperature-related marine heat waves and cold snaps, these
481 ECEs include, for example, severe storms (Byrnes et al. 2011; Sanchez-Vidal et al. 2012; De’ath
482 et al. 2012), extreme wave activity (Smale and Vance 2016), extreme sea level (Woodworth et
483 al. 2011; Rhein et al. 2013), and salinity changes and floods (Gillanders and Kingsford 2002;
484 Marques et al. 2007; Lejeune et al. 2009).

485 In a synthesis study, Vose et al. (2014) examined changes in ECEs associated with extratropical
486 storms, winds and waves, and found that storm frequency and intensity had increased in the
487 Northern Hemisphere cold season since the 1950s, along with an increase in extreme winds over
488 the oceans since the 1980s. Extreme waves along the Pacific US coast have increased moderately
489 since the 1950s, while the evidence for other US coastlines is inconclusive (Vose et al. 2014).
490 Extreme wave heights have been observed to increase in many regions around the world, such as
491 for the US Pacific Northwest (Ruggiero et al. 2010; Vose et al. 2014), along the South American
492 Pacific coast since the 1980s (Izaguirre et al. 2013) and for the North Atlantic over the 20th
493 Century (Bertin et al. 2013). Using a multi-model ensemble, Hemer et al. (2013) found the
494 annual mean significant wave height to decrease by 25% globally by 2070-2100, while only 7%

495 of ocean areas, mostly in the Southern Ocean, exhibited an increase over the same timeframe. In
496 contrast, according to Mori et al. (2013), significant wave height is projected to increase globally
497 by 15% by the end of the 21st Century, exceeding the projected changes in surface pressure and
498 wind speed. Similarly, Wang et al. (2014) found significant wave height increases in the eastern
499 Pacific and for the Southern Hemisphere extratropics by the end of the 21st Century. Extreme
500 wave heights are also likely to double and triple in coastal regions, such as for Chile, the Gulf of
501 Bengal, South and East Asian coasts and the Gulf of Mexico due to increased sea level pressure
502 gradients and surface winds (Wang et al. 2014).

503 Physical disturbance through extreme wave action represents a major factor for coastal and near-
504 shore biological communities how changing storm characteristics can affect natural systems. For
505 example, kelp forest structure can be modified by changes in severe storms and the associated
506 wave activity (Smale and Vance 2016). The 2013-2014 storm season in the Northeast Atlantic
507 was unusually severe, resulting in extensive flooding and exhibiting extreme wave activity
508 (Huntingford et al. 2014; Matthews et al. 2014; Masselink et al. 2016). Smale and Vance (2016)
509 found the warm water kelp species to be more affected by the stormy 2013-2014 conditions than
510 the more hardy cold water kelp species. They cautioned that climate-driven shifts towards more
511 mixed canopies in the Northeast Atlantic due to warming temperatures might erode the kelp
512 communities' resistance to such storm disturbances (Smale and Vance 2016). For the California
513 coast, Byrnes et al. (2011) showed that, while moderate levels of severe storms (i.e. one storm
514 every 3-4 years) help maintain complexity in kelp forest food webs, more frequent severe storms
515 (i.e. at annual frequency) lead to a decrease in diversity in giant kelp forests. In the Adriatic,
516 Perkol-Finkel and Airoldi (2010) attributed a loss of subtidal algal forests to several extreme
517 storm events, compounded by long-term human-induced habitat instability.

518 Sanchez-Vidal et al. (2012) highlighted that severe coastal storms do not only affect the
519 shoreline communities, but also have the potential to affect deep-sea ecosystems. This was
520 observed during an exceptionally strong storm along the Spanish coast in December 2008 that
521 initiated shelf sediment movement and redistribution across the adjacent deep basin that caused
522 abrasion and burial of the benthic communities in the Western Mediterranean (Sanchez-Vidal et
523 al. 2012). The storm also affected the biodiversity of a coralligenous outcrop in the Northwest
524 Mediterranean, with exposed and impacted sites experiencing major shifts in species
525 composition immediately following the storm and loss of cover of benthic species in the range of
526 22-58%, with fragile species impacted more (Teixido et al. 2013).

527 Furthermore, extremes in biogeochemical properties in the marine environment can also affect
528 ecosystem structure and functioning. Investigating episodes of high carbon dioxide (CO₂)
529 concentrations in sea water, McNeil and Sasse (2016) found that the amplitude of the annual CO₂
530 cycle is increasing with rising greenhouse gas emissions. By the second half of the 21st Century,
531 major fisheries in the Southern Ocean, Pacific, and Atlantic may be periodically exposed to CO₂
532 concentrations that have detrimental physiological and neurological effects on marine animals
533 (McNeil and Sasse 2016).

534 **5. Challenges and opportunities in assessing how ECEs impact biological** 535 **systems**

536 Despite advances in the field of event attribution in recent decades, challenges remain.
537 Improvements in statistical methodology, observations, climate and weather modelling will
538 likely allow for better understanding of ECEs and event attribution (NAS 2016). Event
539 attribution is most skillful when combining evidence based on theory (sound physical
540 understanding of the processes involved), observations (long-term observational records exist
541 that allow placing the event in a historical context), and numerical model simulations (adequately
542 simulated by models to allow replicating the event and for the right reason). In addition, event
543 types purely meteorological in nature, i.e. not confounded by factors, such as resource
544 management or infrastructure, allow for more reliable event attribution (NAS 2016).

545 Irrespective of the approach, the success of detection and attribution relies on a model's ability to
546 represent the relevant processes and their interactions over the region and season of interest
547 (Sarojini et al. 2016). Confidence in attributing changes in ECEs to anthropogenic forcing is
548 most pronounced when considering event types related to regional and global temperature (Stott
549 2016), such as extreme heat and cold events, hydrological drought and intense precipitation
550 (NAS 2016). Improved process-representation through better model dynamics, improved model
551 parametrisations, and higher horizontal and vertical model resolution have led to improved
552 representation of regional-scale climate variability. However, considerable further advances are
553 required to represent fine temporal and spatial scales, at which ECEs in precipitation are
554 experienced at a local level (Sarojini et al. 2016, and references therein). In addition, low-
555 frequency natural variability, such as that associated with Atlantic or Pacific Decadal Variability,
556 can affect the reliability of event attributions (NAS 2016). Given the shortness of the
557 observational record relative to the multi-decadal nature of these modes of variability, they
558 remain a challenging aspect also for climate model simulations of ECEs (Meehl et al. 2000).
559 Furthermore, this is not just a challenge for model simulations of ECEs, but when considering
560 the length of the instrumental record: as recently shown by Abram et al. (2016), industrial-era
561 warming commenced as early as the mid-19th century and therefore instrumental records in many
562 regions are too short to comprehensively assess anthropogenic climate change. This has to be
563 taken into consideration when addressing detection and attribution to assess anthropogenic
564 contributions to specific events (cf. also recent reviews by Easterling et al. 2016 and Stott et al.
565 2016 on event attribution).

566 On the biological side, data have traditionally been gathered at single sites (e.g., field stations) or
567 more rarely within a region (Parmesan et al. 2000). Extended cross-regional long-term
568 observations are limited, even though sustained monitoring is important for assessing integrated
569 responses of ecosystems to ECEs to account for long-term effects in subsequent years (Sippel et
570 al. 2016). For example, maintaining long time-series has been the key problem in understanding
571 variability and change in marine biodiversity and ecosystems in response to environmental
572 factors (Mieszkowska et al. 2014). In their review, Jentsch et al. (2007) concluded that long-term

573 observations and experimental studies in different ecosystem types and across a range of spatial
574 and temporal scales is crucial for advancing the understanding how ECEs affect biological
575 systems. The largely local and site-specific nature of existing long-term biological records,
576 paired with still comparatively coarse climatic information from current-generation reanalysis
577 products and climate models leads to a mismatch in the spatial and temporal scale of available
578 data for addressing how biological systems respond to climate variability and change. This is
579 even more exacerbated in the case of ECEs, which are rare events by definition. To sufficiently
580 sample a distribution to allow inferences about its tails, extended time-series are required.

581 Improved understanding of bio-physical interactions across a range of spatial and temporal scales
582 (Prairie et al. 2012) is not only important for quantifying how ECEs affect biological systems.
583 Parmesan (2006) considers the current lack of mechanistic understanding of the effect of
584 ecological, behavioural, and evolutionary responses to ECEs a crucial limitation in assessing
585 ecosystem adaptation to climate change more generally. In particular, developing process-based
586 concepts of the biological systems' response to ECEs is crucial for predicting the impacts of
587 changes in the climate system on ecosystem functioning in future (Parmesan et al. 2000).

588 Recent advances and enhanced capabilities in observing systems provide new avenues for
589 developing a mechanistic framework to understand interactions between the physical climate
590 system and biological processes. To advance understanding of how ECEs affect ecosystem
591 functioning, remote sensing in particular allows for concurrent observations of physical and
592 biological parameters at comparable spatial and temporal resolution (Prairie et al. 2012). For
593 example, remote sensing with short return intervals at identical locations and near-global
594 coverage facilitates monitoring of soil properties, concurrent vegetation states (e.g., biomass, leaf
595 area index) and radiative properties like fractions of absorbed radiation (Frank et al. 2015).
596 Concurrent impacts on plant physiology, photosynthesis, respiration, mechanical damage for
597 trees (e.g., snow and ice breakage, wind throw) and effects on topsoil erosion can thus be
598 documented, as well as lagged impacts like changes in plant phenology, reduced plant growth,
599 increased mortality and changes in plant species composition (Frank et al. 2015). Vrieling et al.
600 (2016) for example use a remotely-sensed normalised difference vegetation index to predict
601 seasonal forage availability ahead of time to cover livestock losses by pastoralist households in
602 East Africa during drought periods through early insurance payments to allow purchase of
603 forage, water, or medicines to protect livestock.

604 When investigating how ECEs impact the terrestrial carbon cycle, Frank et al. (2015) found the
605 (sub)tropics to be largely understudied in regard to ground-based case studies as compared with
606 those obtained via remote sensing. To be able to upscale how ECEs affect biological systems
607 and, more specifically, the global carbon-climate feedbacks on a global scale, more extensive
608 regional studies are required (Frank et al. 2015). Zscheischler et al. (2013) presented a
609 methodological framework to assess how ECEs affect state and functionality of terrestrial
610 ecosystems on a global scale by identifying spatiotemporally contiguous signals of extremes in
611 different Earth observation products. Using the fraction of absorbed photosynthetically active

612 radiation to detect extremes in vegetation activity over the past 30 years, they demonstrated that
613 the size distribution of extremes follows a distinct power law (Zscheischler et al. 2013).
614 Furthermore, based on a hierarchy of models ranging from purely data-driven to semi-empirical
615 and dynamic vegetation, land-surface models and remote sensing products, Zscheischler et al.
616 (2014a) found that the total effect of negative extremes in the global primary production is of a
617 similar magnitude as the mean terrestrial carbon sink. Furthermore, carbon cycle extremes
618 exhibit an uneven spatial distribution with ‘hotspot’ regions in many semiarid monsoon-affected
619 regions and are strongly associated with water scarcity (Zscheischler et al. 2014a,b Frank et al.
620 2015). The lack of biological observations is particularly true for marine ecosystems, as changes
621 in the ecosystem structure of many habitats (e.g., kelp forests and seagrass meadows) cannot be
622 remotely sensed. Considering that these habitats play a key role in marine carbon cycling and are
623 affected by ECEs, monitoring of marine ecosystems at appropriate spatial and temporal scales is
624 even more lacking than for terrestrial ecosystems.

625 Meta-analysis is considered a powerful method of quantitative data synthesis in ecological
626 research (Hays et al. 2005). This could be combined with extended observational records, remote
627 sensing capabilities and climate model output at increasingly finer resolution, both from global
628 climate models and regional model configurations, to address interactions of the physical and
629 biological systems across a range of temporal and spatial scales.

630
631

632 **6. Summary**

633 How ECEs affect ecosystems largely depends on the magnitude, spatial and temporal extent, as
634 well as timing of the anomalous climatic event (Sippel et al. 2016). As such, perspectives
635 spanning across spatial and temporal scales on how biological and physical systems interact
636 (Figure 2) are crucial (Prairie et al. 2012) for improved process-understanding of ecosystem
637 responses to ECEs. Limitations in our current observational network (e.g., Alexander 2016), both
638 for physical climate system parameters and even more so for long-term ecological monitoring,
639 have hampered progress in this regard. This is especially pronounced when considering ECEs,
640 which by definition are rare events. The observing systems of the physical climate, and even
641 more so for the biological system, are limited with regard to depth (time dimension) or breadth
642 (spatial scales), or both. The mismatch of the available and required scales in observations had
643 been compounded in (global) climate models, suffering from a discrepancy in the explicitly
644 resolved spatial and temporal scales and those required for ecological impact research.

645 New opportunities for assessing how ECEs modulate structure and functioning of ecosystems
646 arise from recent technological advances in observing systems and instrumentation (e.g., through
647 advanced remote sensing capabilities). These allow for monitoring at increased spatial and
648 temporal resolution for both physical and biological parameters concurrently at appropriate
649 resolution (Prairie et al. 2012). Parmesan et al. (2000) further saw potential for advances in

650 ecological and evolutionary theory (population dynamics, physiological energetics and
651 community structure) leading to greater descriptive and predictive power as a result of better
652 alignment of ECE analyses of biological and physical system parameters. They saw this as a
653 potential outcome of improved coupling of in-depth climatological analyses and biological
654 processes that would allow us to better characterise the complex interactions between climatic
655 conditions and natural systems spanning the spatial and temporal spectrum across which these
656 interactions can occur (cf. Fig. 2). Bailey and van de Pol (2016) also pointed out that multi-event
657 studies that combine long-term field studies and experiments with modelling are crucial for a
658 better understanding of the mechanisms and for improving the predictions of how ECEs affect
659 natural systems. This is especially the case given the rarity of such events and the challenges
660 with collecting ecological time series of sufficient length. Extensions of the historical
661 observational record through climate quality reanalyses or through longer term archives from
662 palaeo proxies (e.g., tree rings, stalagmites, and sediments) are also crucial for ensuring a record
663 of sufficient length to reliably quantify trends and sample the characteristics of the ECEs in the
664 physical climate system across a range of spatial and temporal scales (NAS 2016; Sippel et al.
665 2016). Improvements in statistical methodology and in numerical modelling, including but not
666 limited to model resolution and improved parametrisations, provide the necessary tools to
667 advance our understanding of the physical mechanisms that lead to ECEs (Easterling et al. 2016;
668 NAS 2016) and how their characteristics are changing in a warming world. Stott (2016) stresses
669 the importance of developing new methods to conclusively link the changes in ECEs to their
670 meteorological and climatic drivers. This applies similarly to addressing ECEs and their impacts
671 on species, populations, and ecosystems as a whole. Current-to-next generation global climate
672 models, along with higher-resolution regional models, provide new tools and opportunities for
673 developing a mechanistic, process-based understanding of where, when, and how ECEs impact
674 biological systems.

675
676

677 **Acknowledgments**

678 Portions of this study were supported by the Regional and Global Climate Modeling Program
679 (RGCM) of the U.S. Department of Energy's Office of Biological & Environmental Research
680 (BER) Cooperative Agreement #DE-FC02-97ER62402, and the National Science Foundation.
681 The National Center for Atmospheric Research is sponsored by the National Science Foundation.
682

683 **Author Contributions**

684 The paper was written by C.C.U. with contributions from G.A.M.

685

686 **Competing Interests**

687 We have no competing interests.

688 **References**

- 689 Adams AJ, Hill JE, Kurth BN, Barbour AB (2012) Effects of a severe cold event on the subtropical, estuarine-
690 dependent common snook, *Centropomus undecimalis*. *Gulf and Caribbean Research*, 24, 13-21.
- 691 Alencar AA, Brando PM, Asner GP, Putz FE (2015) Landscape fragmentation, severe drought, and the new Amazon
692 forest fire regime. *Ecological Applications*, 25, 1493-1505.
- 693 Alexander LV (2016) Global observed long-term changes in temperature and precipitation extremes: A review of
694 progress and limitations in IPCC assessments and beyond. *Weather and Climate Extremes*, 11, 4-16.
- 695 Allen CD, Macalady AK, Chenchouni H, Bachelet D, McDowell N, Vennetier M, Kitzberger T, Rigling A,
696 Breshears DD, Hogg EH, Gonzalez P, Fensham R, Zhang Z, Castro J, Demidova N, Lim J-H, Allard G, Running
697 SW, Semerci A, Cobb N (2010) A global overview of drought and heat-induced tree mortality reveals emerging
698 climate change risks for forests. *Forest Ecology and Management*, 259, 660-684.
- 699 Andrade C, Leite S, Santos J (2012) Temperature extremes in Europe: Overview of their driving atmospheric
700 patterns. *Natural Hazards and Earth System Sciences*, 12, 1671-1691.
- 701 ARC (2016) Only 7% of the Great Barrier Reef has avoided coral bleaching. [https://www.coralcoe.org.au/only-7-](https://www.coralcoe.org.au/only-7-of-the-great-barrier-reef-has-avoided-coral-bleaching/)
702 [of-the-great-barrier-reef-has-avoided-coral-bleaching/](https://www.coralcoe.org.au/only-7-of-the-great-barrier-reef-has-avoided-coral-bleaching/).
- 703 Asner GP, Alencar A (2010) Drought impacts on the Amazon forest: the remote sensing perspective. *New*
704 *Phytologist*, 187, 569-578.
- 705 Bailey LD, van de Pol M (2016) Tackling extremes: challenges for ecological and evolutionary research on extreme
706 climatic events. *Journal of Animal Ecology*, 85, 85-96.
- 707 Ballester J, Giorgi F, Rodo X (2010) Changes in European temperature extremes can be predicted from changes in
708 PDF central statistics. *Climatic Change*, 98, 277-284.
- 709 Barriopedro D, Fischer EM, Luterbach J, Trigo R, Garcia-Herrera R (2011) The hot summer of 2010: Redrawing the
710 temperature record map of Europe. *Science*, 332, 220-224.
- 711 Beniston M (2004) The 2003 heat wave in Europe: A shape of the things to come? An analysis based on Swiss
712 climatological data and model simulations. *Geophysical Research Letters*, 31, L02202.
- 713 Beniston M (2015) Ratios of record high to record low temperatures in Europe exhibit sharp increases since 2000
714 despite a slowdown in the rise of mean temperatures. *Climatic Change*, 129, 225-237.
- 715 Bertin X, Prouteau E, Letetrel C (2013) A significant increase in wave height in the North Atlantic Ocean over the
716 20th Century. *Global and Planetary Change*, 106, 77-83.
- 717 Bindoff NL, Stott PA, AchutaRao KM, Allen MR, Gillett N, Gutzler D, Hansingo K, Hegerl G, Hu Y, Jain S,
718 Mokhov II, Overland J, Perlwitz J, Sebbari R, Zhang X (2013) Detection and Attribution of Climate Change: from
719 Global to Regional. In: *Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to*
720 *the Fifth Assessment Report of the Intergovernmental Panel on Climate Change* [Stocker, T.F., D. Qin, G.-K.
721 Plattner, M. Tignor, S.K. Allen, J. Boschung, A. Nauels, Y. Xia, V. Bex, P.M. Midgley (eds.)]. Cambridge
722 University Press, Cambridge, United Kingdom and New York, NY, USA.
- 723 Blondeau-Patissier D, Gower JFR, Dekker AG, Phinn SR, Brando VE (2014) A review of ocean color remote
724 sensing methods and statistical techniques for the detection, mapping and analysis of phytoplankton blooms in
725 coastal and open oceans. *Progress in Oceanography*, 123, 123-144.
- 726 Bond NR, Lake PS, Arthington AH (2008) The impacts of drought on freshwater ecosystems: an Australian
727 perspective. *Hydrobiologia*, 600, 3-16.
- 728 Breshears DD, Cobb NS, Rich PM, Price KP, Allen CD, Balice RG, Romme WH, Kastens JH, Floyd ML, Belnap J,
729 Anderson JJ, Myers OB, Meyer CW (2005) Regional vegetation die-off in response to global-change-type
730 drought. *Proceedings of the National Academy of Sciences*, 102, 15144-15148.
- 731 Buddemeier RW, Kleypas JA, Aronson RB (2004) Coral reefs and global climate change: Potential contributions of
732 climate change to stresses on coral reef ecosystems. *Pew Center on Global Climate Change*,
733 http://www.c2es.org/docUploads/Coral_Reefs.pdf.
- 734 Byrnes JE, Reed DC, Cardinale BJ, Cavanaugh KC, Holbrooks SJ, Schmitt RJ (2011) Climate-driven increases in
735 storm frequency simplify kelp forest food webs. *Global Change Biology*, 17, 2513-2524.
- 736 Caesar J, Alexander LV, Trewin B, Tse-ring K, Sorany L, Vuniyayawa V, Keosavang N, Shimana A, Htay MM,
737 Karmacharya J, Jayasinghearachchi A, Sakkamart J, Soares E, Hung LT, Thuong LT, Hue CT, Dung NTT, Hung
738 PV, Cuong HD, Cuong NM, Sirabaha S (2011) Changes in temperature and precipitation extremes over the Indo-
739 Pacific region from 1971 to 2005. *International Journal of Climatology*, 31, 791-801.
- 740 Cai W, Cowan T, Raupach MR (2009) Positive Indian Ocean Dipole events precondition southeast Australia
741 bushfires. *Geophysical Research Letters*, 36, L19710, doi:10.1029/2009GL039902.

742 Canning-Clode J, Fowler AE, Byers JE, Carlton JT, Ruiz GM (2011) ‘Caribbean Creep’ chills out: Climate change
743 and marine invasive species. PLoS ONE, 6, doi:10.1371/journal.pone.0029657.

744 Cassou C, Cattiaux J (2016) Disruption of the European climate seasonal clock in a warming world. Nature Climate
745 Change, 6, 589-594.

746 CDG (2016) Climate Data Guide on Atmospheric Reanalysis: Overview & Comparison Tables,
747 <https://climatedataguide.ucar.edu/climate-data/atmospheric-reanalysis-overview-comparison-tables>, accessed Oct
748 9, 2016.

749 Choi G, Collins D, Ren G, Trewin B, Baldi M, Fukuda Y, Afzaal M, Pianmana T, Gomboluudev P, Huong PTT,
750 Lias N, Kwon W-T, Boo K-O, Cha Y-M, Zhou Y (2009) Changes in means and extreme events of temperature
751 and precipitation in the Asia-Pacific Network region, 1955-2007. International Journal of Climatology, 29, 1906-
752 1925.

753 Christidis N, Jones GS, Stott PA (2015) Dramatically increasing chance of extremely hot summers since the 2003
754 European heatwave. Nature Climate Change, 5, 46-50.

755 Ciais P, Reichstein M, Viovy N, Granier A, Ogee J, Allard V, Aubinet M, Buchmann N, Bernhofer C, Carrara A,
756 Chevallier F, De Noblet N, Friend AD, Friedlingstein P, Grünwald T, Heinesch B, Keronen P, Knohl A, Krinner
757 G, Loustau D, Manca G, Matteucci G, Miglietta F, Ourcival JM, Papale D, Pilegaard K, Rambal S, Seufert G,
758 Soussana JF, Sanz MJ, Schulze ED, Vesala T, Valentini R (2005) Europe-wide reduction in primary productivity
759 caused by the heat and drought in 2003. Nature, 437, 529-533.

760 Corlett RT (2016) The impacts of droughts on tropical forests. Trends in Plant Science, 21, 584-593.

761 Coumou D, Rahmstorf S (2012) A decade of weather extremes. Nature Climate Change,
762 doi:10.1038/NCLIMATE1452.

763 De’ath G, Fabricius KE, Sweatman H, Puotinen M (2012) The 27-year decline of coral cover on the Great Barrier
764 Reef and its causes. Proceedings of the National Academy of Sciences, 109, 17995-17999.

765 Di Lorenzo E, Ohman MD (2013) A double-integration hypothesis to explain ecosystem response to climate forcing.
766 Proceedings of the National Academy of Sciences, 110, 2496-2499.

767 Di Lorenzo E, Mantua N (2016) Multi-year persistence of the 2014-2015 North Pacific marine heatwave. Nature
768 Climate Change, doi:10.1038/nclimate3082.

769 Donat MG, Alexander LV, Yang H, Durre I, Vose R, Caesar J (2013a) Global land-based datasets for monitoring
770 climatic extremes. Bulletin of the American Meteorological Society, 94, 997-1006.

771 Donat MG, Alexander LV, Yang H, Durre I, Vose R, Dunn RJH, Willett KM, Aguilar E, Brunet M, Caesar J,
772 Hewitson B, Jack C, Klein Tank AMG, Kruger AC, Marengo J, Peterson TC, Renom M, Oria Rojas C, Rusticucci
773 M, Salinger J, Elayah AS, Sekele SS, Srivastava AK, Trewin B, Villarreal C, Vincent LA, Zhai Z, Zhang X,
774 Kitching S (2013b) Updated analyses of temperature and precipitation extreme indices since the beginning of the
775 twentieth century: The HadEX2 dataset. Journal of Geophysical Research: Atmospheres, 118, 2098-2118.

776 Easterling DR, Kunkel KE, Wehner MF, Sun L (2016) Detection and attribution of climate extremes in the observed
777 record. Weather and Climate Extremes, 11, 17-27.

778 Evans JP, Boyer-Souchet I (2012) Local sea surface temperatures add to extreme precipitation in northeast Australia
779 during La Nina. Geophysical Research Letters, 39, L10803.

780 Feng M, Hendon HH, Xie S-P, Marshall AG, Schiller A, Kosaka Y, Caputi N, Pearce A (2015) Decadal increase in
781 Ningaloo Niño since the late 1990s. Geophysical Research Letters, 42, 104-112.

782 Feng X, Porporato A, Rodriguez-Iturbe I (2013) Changes in rainfall seasonality in the tropics. Nature Climate
783 Change, 3, 811-815.

784 Firth LB, Knights AM, Bell SS (2011) Air temperature and winter mortality: implications for the persistence of the
785 invasive mussel, *Perna viridis* in the intertidal zone of the south-eastern United States. Journal of Experimental
786 Marine Biology and Ecology, 400, 250-256.

787 Fischer EM, Seneviratne SI, Vidale PL, Luthi D, Schär C (2007) Soil moisture-atmosphere interactions during the
788 2003 European summer heat wave. Journal of Climate, 20, 5081-5099.

789 Fischer EM, Schär C. (2007) Consistent geographical patterns of changes in high-impact European heatwave.
790 Nature Geoscience, 3, 398-403.

791 Fischlin A, Midgley GF, Price JT, Leemans R, Gopal B, Turley C, Rounsevell MDA, Dube OP, Tarazona J, and
792 Velichko AA (2007) Ecosystems, their properties, goods, and services. In: Climate Change 2007: Impacts,
793 Adaptation and Vulnerability. Contribution of Working Group II to the Fourth Assessment Report of the
794 Intergovernmental Panel on Climate Change [Parry, M.L., O.F. Canziani, J.P. Palutikof, P.J. van der Linden and
795 C.E. Hanson (eds.)]. Cambridge University Press, Cambridge, UK, pp. 211-272.

796 Frank D, Reichstein M, Bahn M, Thonicke K, Frank D, Mahecha MD, Smith P, van der Velde M, Vicca S, Babst F,
797 Beer C, Buchmann N, Canadell JG, Ciais P, Cramer W, Ibrom A, Miglietta F, Poulter B, Rammig A, Seneviratne

798 SI, Walz A, Wattenbach M, Zavala MA, Zscheischler J (2015) Effects of climate extremes on the terrestrial
799 carbon cycle: concepts, processes and potential future impacts. *Global Change Biology*, 21, 2861-2880.

800 Garcia-Herrera R, Diaz J, Trigo RM, Luterbacher J, Fischer EM (2010) A review of the European summer heat
801 wave of 2003. *Critical Reviews in Environmental Science and Technology*, 40, 267-306.

802 Garrabou J, Coma R, Bensoussan N, Bally M, Chevaldonne P, Cigliano M, Diaz D, Harmelin JG, Gambi MC,
803 Kersting DK, Ledoux JB, Lejeune C, Linares C, Marschal C, Perez T, Ribes M, Romano JC, Serrano E, Teixido
804 N, Torrents O, Zabala M, Zuberer F, Cerrano C (2009) Mass mortality in Northwestern Mediterranean rocky
805 benthic communities: effects of the 2003 heat wave. *Global Change Biology*, 15, 1090-1103.

806 Gillanders BM, Kingsford MJ (2002) Impact of changes in flow of freshwater on estuarine and open coastal habitats
807 and the associated organisms. *Oceanography and Marine Biology Annual Review*, 40, 233-309.

808 Grotjahn R, Barlow M, Black R, Cavazos T, Gutowski W, Gyakum J, Katz R, Kumar A, Leung L-Y, Schumacher
809 R, Wehner M (2014) US CLIVAR workshop on analyses, dynamics, and modeling of large-scale meteorological
810 patterns associated with extreme temperature and precipitation events. US CLIVAR Report 2014-2, US CLIVAR
811 Project Office, Washington, DC, 42 pp.

812 Handmer J, Honda Y, Kundzewicz ZW, Arnell N, Benito G, Hatfield J, Mohamed IF, Peduzzi P, Wu S, Sherstyukov
813 B, Takahashi K, Yan Z (2012) Changes in impacts of climate extremes: human systems and ecosystems. In:
814 *Managing the Risks of Extreme Events and Disasters to Advance Climate Change Adaptation* [Field, C.B., V.
815 Barros, T.F. Stocker, D. Qin, D.J. Dokken, K.L. Ebi, M.D. Mastrandrea, K.J. Mach, G.-K. Plattner, S.K. Allen, M.
816 Tignor, P.M. Midgley (eds.)]. A Special Report of Working Groups I and II of the Intergovernmental Panel on
817 Climate Change (IPCC). Cambridge University Press, Cambridge, UK, and New York, NY, USA, pp. 231-290.

818 Harley CDG, Hughes AR, Hultgren KM, Miner BG, Sorte CJB, Thornber CS, Rodriguez LF, Tomanek L, Williams
819 SL (2006) The impacts of climate change on coastal marine systems. *Ecology Letters*, 9, 228-241.

820 Hartmann DL, Klein Tank AMG, Rusticucci M, Alexander LV, Brönnimann S, Charabi Y, Dentener FJ,
821 Dlugokencky EJ, Easterling DR, Kaplan A, Soden BJ, Thorne PW, Wild M, Zhai PM (2013) Observations:
822 Atmosphere and surface. In: *Climate Change 2013: The Physical Science Basis. Contribution of Working Group I
823 to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change* [Stocker, T.F., D. Qin, G.-K.
824 Plattner, M. Tignor, S.K. Allen, J. Boschung, A. Nauels, Y. Xia, V. Bex, P.M. Midgley (eds.)]. Cambridge
825 University Press, Cambridge, United Kingdom and New York, NY, USA.

826 Hays GC, Richardson AJ, Robinson C (2005) Climate change and marine plankton. *Trends in Ecology and
827 Evolution*, 20, 337-344.

828 Hegerl GC, Hoegh-Guldberg O, Casassa G, Hoerling MP, Kovats RS, Parmesan C, Pierce DW, Stott PA (2010)
829 Good practice guidance paper on detection and attribution related to anthropogenic climate change. In: *Meeting
830 Report of the Intergovernmental Panel on Climate Change Expert Meeting on Detection and Attribution of
831 Anthropogenic Climate Change* [Stocker, T.F., C.B. Field, D. Qin, V. Barros, G.-K. Plattner, M. Tignor, P.M.
832 Midgley, K.L. Ebi (eds.)]. IPCC Working Group I Technical Support Unit, University of Bern, Bern, Switzerland.

833 Held IM, Soden BJ (2006) Robust responses of the hydrological cycle to global warming. *Journal of Climate*, 19,
834 5686-5699.

835 Hemer MA, Fan Y, Mori N, Semedo A, Wang XL (2013) Projected changes in wave climate from a multi-model
836 ensemble. *Nature Climate Change*, 3, 471-476.

837 Herring SC, Hoerling MP, Kossin JP, Peterson TC, Stott PA (2015) Explaining extreme events of 2014 from a
838 climate perspective. *Bulletin of the American Meteorological Society*, 96, S1-S172.

839 Hobday AJ, Alexander LV, Perkins SE, Smale DA, Straub SC, Oliver ECJ, Benthuisen JA, Burrows MT, Donat
840 MG, Feng M, Holbrook NJ, Moore PJ, Scannell HA, Sen Gupta A, Wernberg T (2016) A hierarchical approach to
841 defining marine heatwaves. *Progress in Oceanography*, 141, 227-238.

842 Hoerling M, Kumar A, Dole R, Nielsen-Gammon JW, Eischeid J, Perlwitz J, Quan X-W, Zhang T, Pegion P, Chen
843 M (2013) Anatomy of an extreme event. *Journal of Climate*, 26, 2811-2832.

844 Holmgren M, Stapp P, Dickman CR, Gracia C, Graham S, Gutierrez JR, Hice C, Jaksic F, Kelt DA, Letnic M, Lima
845 M, Lopez BC, Meserve PL, Milstead WB, Polis GA, Previtali MA, Richter M, Sabate S, Squeo FA (2006)
846 Extreme climatic event shape arid and semi-arid ecosystems. *Frontiers in Ecology and the Environment*, 4, 87-95.

847 Huntingford C, Marsh T, Scaife AA, Kendon EJ, Hannaford J, Kay AL, Lockwood M, Prudhomme C, Reynard NS,
848 Parry S, Lowe JA, Screen JA, Ward HC, Roberts M, Stott PA, Bell VA, Bailey M, Jenkins A, Legg T, Otto FEL,
849 Massey N, Schaller N, Slingo J, Allen MR (2014) Potential influences on the United Kingdom's floods of winter
850 2013/14. *Nature Climate Change*, 4, 769-777.

851 IPCC (2012a) *Managing the risks of extreme events and disasters to advance climate change adaptation. A Special
852 Report of Working Groups I and II of the Intergovernmental Panel on Climate Change* [Field, C.B., V. Barros,

853 T.F. Stocker, D. Qin, D.J. Dokken, K.L. Ebi, M.D. Mastrandrea, K.J. Mach, G.-K. Plattner, S.K. Allen, M.
854 Tignor, P.M. Midgley (eds.]). Cambridge University Press, Cambridge, UK, and New York, NY, USA, 582 pp.

855 IPCC (2012b) Summary for Policymakers. In: Managing the Risks of Extreme Events and Disasters to Advance
856 Climate Change Adaptation [Field, C.B., V. Barros, T.F. Stocker, D. Qin, D.J. Dokken, K.L. Ebi, M.D.
857 Mastrandrea, K.J. Mach, G.-K. Plattner, S.K. Allen, M. Tignor, P.M. Midgley (eds.)]. A Special Report of
858 Working Groups I and II of the Intergovernmental Panel on Climate Change. Cambridge University Press,
859 Cambridge, UK, and New York, NY, USA, pp. 3-21.

860 IPCC (2013) Summary for Policymakers. In: Climate Change 2013: The Physical Science Basis. Contribution of
861 Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change [Stocker,
862 T.F., D. Qin, G.-K. Plattner, M. Tignor, S.K. Allen, J. Boschung, A. Nauels, Y. Xia, V. Bex, P.M. Midgley
863 (eds.)]. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.

864 Izaguirre C, Mendez FJ, Espejo A, Losada IJ, Reguero BG (2013) Extreme wave climate change in Central-South
865 America. *Climatic Change*, 119, 277-290.

866 Jentsch A, Kreyling J, Beierkuhnlein (2007) A new generation of climate-change experiments: events, not trends.
867 *Frontiers in Ecology and the Environment*, 5, 365-374.

868 Lehmann J, Coumou D, Frieler K (2015) Increased record-breaking precipitation events under global warming.
869 *Climatic Change*, 132, 501-515.

870 Lejeusne C, Chevaldonne P, Pergent-Martini C, Boudouresque CF, Perez T (2009) Climate change effects on a
871 miniature ocean: the highly diverse, highly impacted Mediterranean Sea. *Trends in Ecology and Evolution*, 25,
872 250-260.

873 Leonard M, Westra S, Phatak A, Lambert M, van den Hurk B, McInnes K, Risbey J, Schuster S, Jakob D, Stafford-
874 Smith M (2014) A compound event framework for understanding extreme impacts. *WIREs Climate change*, 5,
875 113-128.

876 Lirman D, Schopmeyer S, Manzello D, Gramer LJ, Precht WF, Muller-Karger F, Banks K, Barnes B, Bartels E,
877 Bourque A, Byrne J, Donahue S, Duquesnel J, Fisher L, Gilliam D, Hendee J, Johnson M, Maxwell K, McDevitt
878 E, Monty J, Rueda D, Ruzicka R, Thanner S (2011) Severe 2010 cold-water event caused unprecedented mortality
879 to corals of the Florida Reef Tract and reversed previous survivorship patterns. *PLoS ONE*, 6,
880 doi:10.1371/journal.pone.0023047.

881 Little JS, McKenzie D, Peterson DL, Westerling AL (2009) Climate and wildfire burned in western U.S.
882 ecoprovinces, 1916-2003. *Ecological Applications*, 19, 1003-1021.

883 Long OMc, Warren R, Price J, Brereton TM, Botham MS, Franco MA (2016) Sensitivity of UK butterflies to local
884 climatic extremes: Which life stages are most at risk? *Journal of Animal Ecology*, doi: 10.1111/1365-2656.12594.

885 Masselink G, Castelle B, Scott T, Dodet G, Suanes S, Jackson D, Flocc'h F (2016) Extreme wave activity during
886 2013/2014 winter and morphological impacts along the Atlantic coast of Europe. *Geophysical Research Letters*,
887 43, 2135-2143.

888 Marlon JR, Bartlein PJ, Gavin DG, Long CJ, Anderson S, Briles CE, Kendrick JB, Colombaroli D, Hallett DJ,
889 Power MJ, Scharf EA, Walsh MK (2012) Long-term perspectives on wildfires in the western USA. *Proceedings*
890 *of the National Academy of Sciences*, 109, E535-E543.

891 Marques SC, Azeiteiro UM, Martinho F, Pardal MA (2007) Climate variability and planktonic communities: The
892 effect of an extreme event (severe drought) in a southern European estuary. *Estuarine, Coastal and Shelf Science*,
893 73, 725-734.

894 Marrot P, Garant D, Charmantier A (2016) Multiple extreme climatic events strengthen selection for earlier breeding
895 in a wild passerine. *Philosophical Transactions B*, submitted.

896 Matthews T, Murphy C, Wilby RL, Harrigan S (2014) Stormiest winter on record for Ireland and UK. *Nature*
897 *Climate Change*, 4, 738-740.

898 Matsueda M (2011) Predictability of Euro-Russian blocking in summer of 2010. *Geophysical Research Letters*, 38,
899 L06801, doi:10.1029/2010GL046557.

900 McDowell NG, Coops NC, Beck PSA, Chambers JQ, Gangodagamage C, Hicke JA, Huang C-y, Kennedy R,
901 Krofcheck DJ, Litvak M, Meddens AJH, Muss J, Negron-Juarez R, Peng C, Schwantes AM, Swenson JJ, Vernon
902 LJ, Williams AP, Xu C, Zhao M, Running SW, Allen CD (2015) Global satellite monitoring of climate-induced
903 vegetation disturbances. *Trends in Plant Science*, 20, 114-123.

904 McNeil BI, Sasse TP (2016) Future ocean hypercapnia driven by anthropogenic amplification of the natural CO₂
905 cycle. *Nature*, 529, 383-386.

906 Meehl GA, Zwiers F, Evans J, Knutson T, Mearns LO, Whetton P. (2000) Trends in extreme weather and climate
907 events: issues related to modeling extremes in projections of future climate change. *Bulletin of the American and*
908 *Meteorological Society*, 81, 427-436.

909 Meehl GA, Tebaldi C (2004) More intense, more frequent, and longer lasting heat waves in the 21st Century.
910 Science, 305, 994-997.

911 Meehl GA, Arblaster JM, Tebaldi C (2005) Understanding future patterns of precipitation in tensity in climate
912 model simulations. Geophysical Research Letters, 32, L18719, doi: 10.1029/2005GL023680.

913 Meehl GA, Arblaster JM, Tebaldi C (2007) Contributions of natural and anthropogenic forcing to changes in
914 temperature extremes over the U.S. Geophysical Research Letters, 34, L19709, doi:10.1029/2007GL030948.

915 Meehl GA, Tebaldi C, Walton G, Easterling D, McDaniel L (2009) The relative increase of record high maximum
916 temperatures compared to record low minimum temperatures in the U.S. Geophysical Research Letters, 36,
917 L23701, doi:10.1029/2009GL040736.

918 Meehl GA, Tebaldi C, Adams-Smith D (2016) U.S. daily temperature records past, present and future. Proceedings
919 of the National Academy of Sciences, in press.

920 Meredith EP, Semenov VA, Maraun D, Park W, and Chernokulsky AV (2015) Crucial role of Black Sea warming in
921 amplifying the 2012 Krymsk precipitation extreme. Nature Geoscience, 8, 615-619.

922 Mieszkowska N, Sugden H, Firth LB, Hawkins SJ (2014) The role of sustained observations in tracking impacts of
923 environmental change on marine biodiversity and ecosystems. Philosophical Transactions of the Royal Society A,
924 372, doi:10.1098/rsta.2013.0339.

925 Miller JD, Safford HD, Crimmins M, Thode AE (2009) Quantative evidence for increasing forest fire severity in the
926 Sierra Nevada and Southern Cascade Mountains, California and Nevada, USA. Ecosystems, 12, 16-32.

927 Mills KE, Pershing AJ, Brown CJ, Yong C, Fu-Sung C, Holland DS, Lehuta S, Nye JA, Sun JC, Thomas AC, Wahle
928 RA (2013) Fisheries management in a changing climate: Lessons from the 2012 ocean heat wave in the Northwest
929 Atlantic. Oceanography, 26, 191-195.

930 Miralles DG, Teuling AJ, Heerwaarden CC, Vila-Guerau de Arellano J (2014) Mega-heatwave temperatures due to
931 combined soil desiccation and atmospheric heat accumulation. Nature Geoscience, 7, 345-349.

932 Mori N, Shimura T, Yasuda T, Mase H (2013) Multi-model climate projections of ocean surface variables under
933 different climate scenarios – Future change of waves, sealevel and wind. Ocean Engineering, 71, 122-129.

934 Mosley LM (2015) Drought impacts on the water quality of freshwater systems; review and integration. Earth-
935 Science Reviews, 140, 203-214.

936 NAS (2016) Attribution of extreme weather events in the context of climate change. National Academies of
937 Sciences, Engineering, and Medicine, Washington, DC, National Academies Press. doi:10.17226/21852.

938 NOAA (2015) NOAA declares third ever coral bleaching event.
939 <http://www.noaanews.noaa.gov/stories2015/100815-noaa-declares-third-ever-global-coral-bleaching-event.html>.

940 NOAA (2016a) 2013-2016 California sea lion unusual mortality event in California.
941 <http://www.nmfs.noaa.gov/pr/health/mmume/californiasealions2013.html>.

942 NOAA (2016b) 2015 Large whale unusual mortality event in the Western Gulf of Alaska.
943 http://www.nmfs.noaa.gov/pr/health/mmume/large_whales_2015.html.

944 NOAA (2016c) NOAA Fisheries mobilizes to gauge unprecedented West Coast toxic algal bloom.
945 http://www.nwfsc.noaa.gov/news/features/west_coast_algal_bloom/index.cfm.

946 Opar, A. (2015) Lost at Sea: starving birds in a warming world. Audubon Magazine.
947 <https://www.audubon.org/magazine/march-april-2015/lost-seastarving-birds-warming-world>.

948 Pall P, Aina T, Stone DA, Stott PA, Nozawa T, Hilberts AGJ, Lohmann D, Allen MR (2011) Anthropogenic
949 greenhouse gas contribution to flood risk in England and Wales in autumn 2000. Nature, 470, 382-385.

950 Palmer G, Platts PJ, Brereton T, Chapman JW, Dytham C, Fox R, Pearce-Higgins JW, Roy DB, Hill JK, Thomas
951 CD (2016) Climate change, climatic variation, and extreme biological responses. Philosophical Transactions B,
952 submitted.

953 Parisien M-A, Moritz MA (2009), Environmental control on the distribution of wildfire at multiple spatial scales.
954 Ecological Monographs, 79, 127-154.

955 Parmesan C, Root TL, Willig MR (2000) Impacts of extreme weather and climate on terrestrial biota. Bulletin of the
956 American Meteorological Society, 81, 443-450.

957 Parmesan C (2006) Ecological and evolutionary responses to recent climate change. Annual Review of Ecology,
958 Evolution, and Systematics, 37, 637-669.

959 Perkol-Finkel S, Airoldi L (2010) Loss and recovery potential of marine habitats: An experimental study of factors
960 maintaining resilience in subtidal algal forests at the Adriatic Sea. PLoS ONE, 5,
961 doi:10.1371/journal.pone.0010791.

962 Peterson TC, Zhang XB, Brunet-India M, Vazquez-Aguirre JL (2008) Changes in North American extremes derived
963 from daily weather data. Journal of Geophysical Research: Atmospheres, 113, D07113.

964 Peterson TC, Stott PA, Herring S (2012) Explaining extreme events of 2011 from a climate perspective. *Bulletin of*
965 *the American Meteorological Society*, 93, 1041-1067.

966 Phillips OL, et al. (2009) Drought sensitivity of the Amazon rainforest. *Science*, 323, 1344-1347.

967 Pook M, Risbey JS, Ummenhofer CC, Briggs PR, Cohen TJ (2014) A synoptic climatology of heavy rain events in
968 the Lake Eyre and Lake Frome catchments. *Frontiers in Environmental Science*, 2, 54.

969 Poulter B, Frank D, Ciais P, Myneni RB, Andela N, Bi J, Broquet G, Canadell JG, Chevallier F, Liu YY, Running
970 SW, Sitch S, van der Werft GR (2014) Contribution of semi-arid ecosystems to interannual variability of the
971 global carbon cycle. *Nature*, 509, 600-603.

972 Prairie JC, Sutherland KR, Nickols KJ, Kaltenberg AM (2012) Biophysical interactions in the plankton: A cross-
973 scale review. *Limnology and Oceanography: Fluids and Environments*, 2, 121-145.

974 Rawlins M, Bradley R, Diaz H, Kimball J, Robinson D (2016) Future decreases in freezing days across North
975 America. *Journal of Climate*, doi:10.1175/JCLI-D-15-0802.1.

976 Reichstein M, Bahn M, Ciais P, Frank D, Mahecha MD, Seneviratne SI, Zscheischler J, Beer C, Buchmann N, Frank
977 DC, Papale D, Rammig A, Smith P, Thonicke K, van der Velde M, Vicca S, Walz A, Wattenbach M (2013)
978 Climate extremes and the carbon cycle. *Nature*, 500, 287-295.

979 Rhein M, Rintoul SR, Aoki S, Campos E, Chambers D, Feely RA, Gulev S, Johnson GC, Josey SA, Kostianoy A,
980 Mauritzen C, Roemmich D, Talley LD, Wang F (2013) Observations: Ocean. In: *Climate Change 2013: The*
981 *Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental*
982 *Panel on Climate Change* [Stocker, T.F., D. Qin, G.-K. Plattner, M. Tignor, S.K. Allen, J. Boschung, A. Nauels,
983 Y. Xia, V. Bex, P.M. Midgley (eds.)]. Cambridge University Press, Cambridge, United Kingdom and New York,
984 NY, USA.

985 Rhines A Huybers P (2013) Frequent summer temperature extremes reflect changes in the mean, not the variance.
986 *Proceedings of the National Academy of Sciences*, 110, E546.

987 Rich PM, Breshears DD, White AB (2008) Phenology of mixed woody herbaceous ecosystems following extreme
988 events: net and differential responses. *Ecology*, 89, 342-352.

989 Rowe CM, Derry LE (2012) Trends in record-breaking temperatures for the conterminous United States.
990 *Geophysical Research Letters*, 39, L16703, doi:10.1029/2012GL052775.

991 Ruggiero P, Komar PD, Allan JC (2010) Increasing wave heights and extreme value projections: The wave climate
992 of the U.S. Pacific Northwest. *Coastal Engineering*, 57, 539-552.

993 Sanchez-Vidal A, Canals M, Calafat AM, Lastras G, Pedrosa-Pamies R, Menendez M, Medina R, Company JB,
994 Hereu B, Romero J, Alcoverro T (2012) Impacts on the deep-sea ecosystem by a severe coastal storm. *PLoS*
995 *ONE*, 7, doi:10.1371/journal.pone.0030395.

996 Sarojini BB, Stott PA, Black E (2016) Detection and attribution of human influence on regional precipitation.
997 *Nature Climate Change*, 6, 669-675.

998 Scaife A, Folland C, Alexander L, Moberg A, Knight J (2008) European climate extremes and the North Atlantic
999 Oscillation. *Journal of Climate*, 21, 72-83.

1000 Scannel HA, Pershing AJ, Alexander MA, Thomas AC, Mills KE (2016) Frequency of marine heatwaves in the
1001 North Atlantic and North Pacific since 1950. *Geophysical Research Letters*, 43, 2069-2076.

1002 Seneviratne SI, Nicholls N, Easterling D, Goodess, Kanae S, Kossin J, Luo Y, Marengo J, McInnes K, Rahimi M,
1003 Reichstein M, Sorteberg A, Vera C, Zhang X (2012) Changes in climate extremes and their impacts on the natural
1004 physical environment. In: *Managing the Risks of Extreme Events and Disasters to Advance Climate Change*
1005 *Adaptation* [Field, C.B., V. Barros, T.F. Stocker, D. Qin, D.J. Dokken, K.L. Ebi, M.D. Mastrandrea, K.J. Mach,
1006 G.-K. Plattner, S.K. Allen, M. Tignor, P.M. Midgley (eds.)]. A Special Report of Working Groups I and II of the
1007 Intergovernmental Panel on Climate Change (IPCC). Cambridge University Press, Cambridge, UK, and New
1008 York, NY, USA, pp. 109-230.

1009 Sheehan P (1995) Assessments of ecological impacts on a regional scale. *SCOPE 53 – Methods to assess the effects*
1010 *of chemicals on ecosystems*, pp. 28, <http://www.scopenvironment.org/downloadpubs/scope53/chapter14.html>.

1011 Sippel S, Zscheischler J, Heimann M, Otto FEL, Peters J, Mahecha MD (2015) Quantifying changes in climate
1012 variability and extremes: Pitfalls and their overcoming. *Geophysical Research Letters*, 42, 9990-9998.

1013 Sippel S, Zscheischler J, Reichstein M (2016) Ecosystem impacts of climate extremes crucially depend on the
1014 timing. *Proceedings of the National Academy of Sciences*, 113, 5768-5770.

1015 Smale DA, Wernberg T (2013) Extreme climatic event drives range contraction of a habitat-forming species.
1016 *Proceedings of the Royal Society B*, 280, doi: 10.1098/rspb.2012.2829.

1017 Smale DA, Vance T (2016) Climate-driven shifts in species' distributions may exacerbate the impacts of storm
1018 disturbances on North-east Atlantic kelp forests. *Marine and Freshwater Research*, 67, 65-74.

1019 Smith MD (2011) The ecological role of climate extremes: current understanding and future prospects. *Journal of*
1020 *Ecology*, 99, 651-655.

1021 Solow AR (2015) Extreme weather, made by us? *Science*, 349, 1444-1445.

1022 Solow AR (2016) On detecting ecological impacts of extreme climate events and it matters. *Philosophical*
1023 *Transactions B*, submitted.

1024 Stott PA, Stone DA, Allen MR (2004) Human contribution to the European heatwave of 2003. *Nature*, 432, 610-
1025 614.

1026 Stott P (2016) How climate change affects extreme weather events. *Science*, 352 (6293), 1517-1518.

1027 Stott PA, Christidis N, Otto FEL, Sun Y, Vanderlinden J-P, van Oldenborgh GJ, Vautard R, von Storch H, Walton
1028 P, Yiou P, Zwiers FW (2016) Attribution of extreme weather and climate-related events. *Wiley Interdisciplinary*
1029 *Reviews: Climate Change*, 7, 23-41.

1030 Tebaldi C, Hayhoe K, Arblaster JM, Meehl GA (2006) Going to the extremes: An intercomparison of model-
1031 simulated historical and future changes in extreme events. *Climatic Change*, 79, 185-211.

1032 Teixido N, Casas E, Cebrian E, Linares C, Garrabou J (2013). Impacts on coralligenous outcrop biodiversity of a
1033 dramatic coastal storm. *PLoS ONE*, 8, doi:10.1371/journal.pone.0053742.

1034 Teng H, Branstator G, Meehl GA, Washington WM (2016) Projected intensification of subseasonal temperature
1035 variability and heat waves in the Great Plains. *Geophysical Research Letters*, 43, 2165-2173.

1036 Trenberth KE, Dai A, Rasmussen RM, Parsons DB (2003) The changing character of precipitation. *Bulletin of the*
1037 *American Meteorological Society*, 84, 1205-1217.

1038 Trenberth KE, Fasullo JT (2012) Climate extremes and climate change: The Russian heat wave and other climate
1039 extremes of 2010. *Journal of Geophysical Research*, 117, D17103.

1040 Trenberth KE, Fasullo JT, Shepherd TG (2015) Attribution of climate extreme events. *Nature Climate Change*, 5,
1041 725-730.

1042 Trewin B, Vermont H (2010) Change in the frequency of record temperatures in Australia, 1957-2009. *Australian*
1043 *Meteorological and Oceanographic Journal*, 60, 113-119.

1044 Ummenhofer CC, England MH, McIntosh PC, Meyers GA, Pook MJ, Risbey JS, Sen Gupta A, Taschetto AS
1045 (2009), What causes southeast Australia's worst droughts? *Geophysical Research Letters*, 36, L04706,
1046 doi:10.1029/2008GL036801.

1047 Ummenhofer CC, Sen Gupta A, England MH, Taschetto, AS, Briggs P, Raupach MR (2015) How did ocean
1048 warming affect Australian rainfall extremes during the 2010/2011 La Nina event? *Geophysical Research Letters*,
1049 42, 9942-9951.

1050 van de Pol M, Jenouvrier S, Visser M (2016) Introduction and synthesis: Ecological and evolutionary response to
1051 extreme climatic events: challenges and research directions. *Philosophical Transactions B*, submitted.

1052 Vose RS, Applequist S, Bourassa MA, Pryor SC, Barthelmie RJ, Blanton B, Bromirski PD, Brooks HE, DeGaetano
1053 AT, Dole RM, Easterling DR, Jensen RE, Karl TR, Katz RW, Klink K, Kruk MC, Kunkel KE, MacCracken MC,
1054 Peterson TC, Shein K, Thomas BR, Walsh JE, Wang XL, Wehner MF, Wuebbels DJ, Young RS (2014)
1055 Monitoring and understanding changes in extremes: Extratropical storms, winds, and waves. *Bulletin of the*
1056 *American Meteorological Society*, 95, 377-386.

1057 Vrieling A, Meroni M, Mude AG, Chantarat S, Ummenhofer CC, and de Bie CAJM (2016) Early assessment of
1058 seasonal forage availability for mitigating the impact of drought on East African pastoralists. *Remote Sensing of*
1059 *Environment*, 174, 44-55. Wentz FJ, Ricciardulli L, Hilburn K, Mears C (2007) How much more rainfall will
1060 global warming bring? *Science*, 317, 233-235.

1061 Wang XL, Feng Y, Swail VR (2014) Changes in global ocean wave heights as projected using multimodel CMIP5
1062 simulations. *Geophysical Research Letters*, 41, 1026-1034.

1063 Wentz FJ, Ricciardulli L, Hilburn K, Mears C (2007) How much more rain will global warming bring? *Science*,
1064 317, 233-235

1065 Wernberg T, Smale DA, Tuya F, Thomsen MS, Langlois TJ, de Bettignies T, Bennett S, Rousseaux CS (2013) An
1066 extreme climatic event alters marine ecosystem structure in a global diversity hotspot. *Nature Climate Change*, 3,
1067 78-82.

1068 Wernberg T, Bennett S, Babcock RC, de Bettignies T, Cure K, Depczynski M, Dufois F, Fromont J, Fulton CJ,
1069 Hovey RK, Harvey ES, Holmes TH, Kendrick GA, Radford B, Santana-Garconn J, Saunders BJ, Smale DA,
1070 Thomsen MS, Tuckett CA, Tuya F, Vanderklift MA, Wilson S (2016) Climate-driven regime shift of a temperate
1071 marine ecosystem. *Science*, 353, 169-172.

1072 Westerling AL, Hidalgo HG, Cayan DR, Swetnam TW (2006) Warming and earlier spring increase western U.S.
1073 forest wildfire activity. *Science*, 313, 940-943.

1074 Westra S, Alexander LV, Zwiers FW (2013) Global increasing trends in annual maximum daily precipitation.
1075 *Journal of Climate*, 26, 3904-3918.

1076 Westra S, Fowler HJ, Evans JP, Alexander LV, Berg P, Johnson F, Kendon EJ, Lenderink G, Roberts NM (2014)
1077 Future changes to the intensity and frequency of short-duration extreme rainfall. *Reviews of Geophysics*, 52, 522-
1078 555.

1079 Whan K, Zscheischler J, Orth R, Shongwe M, Rahimi M, Asare EO, Seneviratne SI (2015) Impact of soil moisture
1080 on extreme maximum temperatures in Europe. *Weather and Climate Extremes*, 9, 57-67.

1081 Whitney FA (2015) Anomalous winter winds decrease 2014 transition zone productivity in the NE Pacific.
1082 *Geophysical Research Letters*, 42, 428-431.

1083 Wolf S, Keenan TF, Fisher JB, Baldocchi DD, Desai AR, Richardson AD, Scott RL, Law BE, Litvak ME, Brunsell,
1084 NA, Peters W, van der Laan-Luijkx IT (2016) Warm spring reduced carbon cycle impact of the 2012 US summer
1085 drought. *Proceedings of the National Academy of Sciences*, 113, 5880-5885.

1086 Woodworth PL, Menendez M, Gehrels WR (2011) Evidence for century-timescale acceleration in mean sea levels
1087 and for recent changes in extreme sea levels. *Surveys Geophysics*, 32, 603-618.

1088 Yang J, Gong P, Fu R, Zhang M, Chen J, Liang S, Xu B, Shi J, Dickinson R (2013) The role of satellite remote
1089 sensing in climate change studies. *Nature Climate Change*, 3, 875-1001.

1090 Zhang Y, Moran MS, Nearing MA, Campos GEP, Huete AR, Buda AR, Bosch DD, Gunter SA, Kitchen SG,
1091 McNab WH, Morgan JA, McClaran MP, Montoya DS, Peters DPC, Starks PJ (2013) Extreme precipitation
1092 patterns and reductions of terrestrial ecosystem production across biomes. *Journal of Geophysical Research -*
1093 *Biogeosciences*, 118, 148-157.

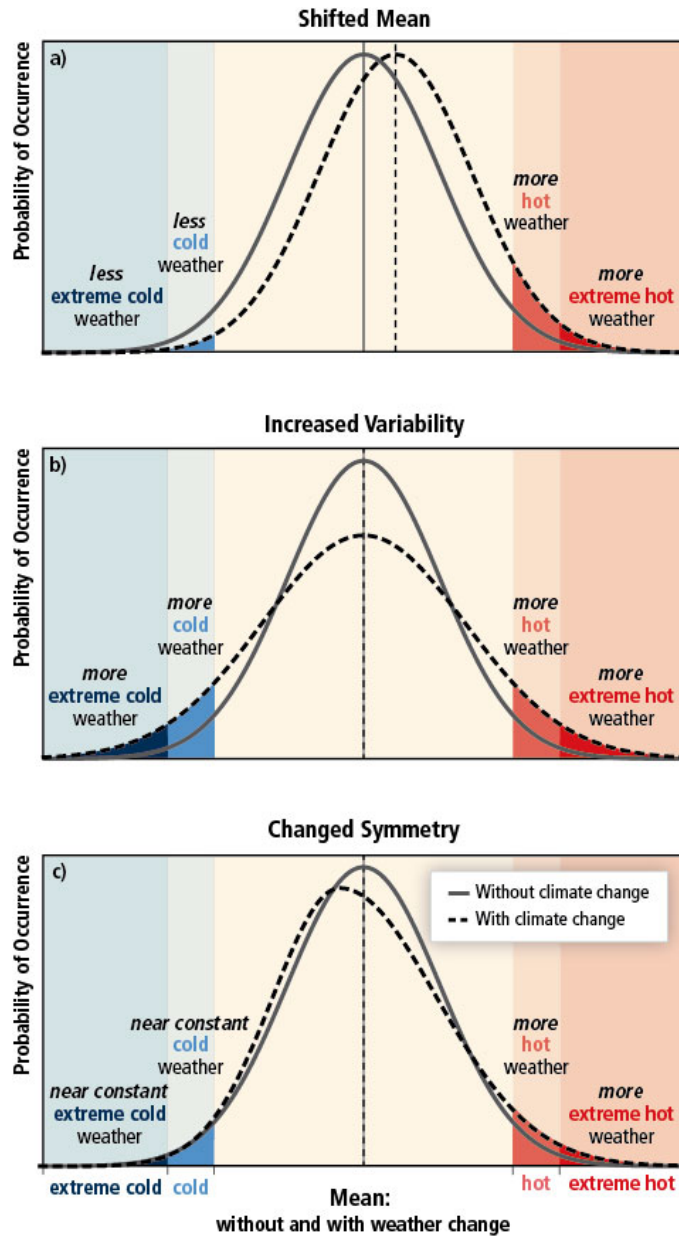
1094 Zscheischler J, Mahecha MD, Harmeling S, Reichstein M (2013) Detection and attribution of large spatiotemporal
1095 extreme events in Earth observation data. *Ecological Informatics*, 15, 66-73.

1096 Zscheischler J, Mahecha MD, von Buttler J, Harmeling S, Jung M, Rammig A, Randerson JT, Schölkopf B,
1097 Seneviratne SI, Tomelleri E, Zaehle S, Reichstein M (2014a) A few extreme events dominate interannual
1098 variability in gross primary production. *Environmental Research Letters*, 9, 035001, doi:10.1088/1748-
1099 9326/9/3/035001.

1100 Zscheischler J, Reichstein M, Harmeling S, Rammig A, Tomelleri E, Mahecha MD (2014b) Extreme events in gross
1101 primary production: a characterization across continents. *Biogeosciences*, 11, 2909-2924.

1102 Zwiers FW, Alexander LV, Hegerl GC, Knutson TR, Kossin JP, Naveau P, Nicholls N, Schär C, Seneviratne SI,
1103 Zhang X (2013) Climate extremes: Challenges in estimating and understanding recent changes in the frequency
1104 and intensity of extreme climate and weather events. In: *Climate Science Serving Society: Research, Modelling*
1105 *and Prediction Priorities*. pp. 339-389.

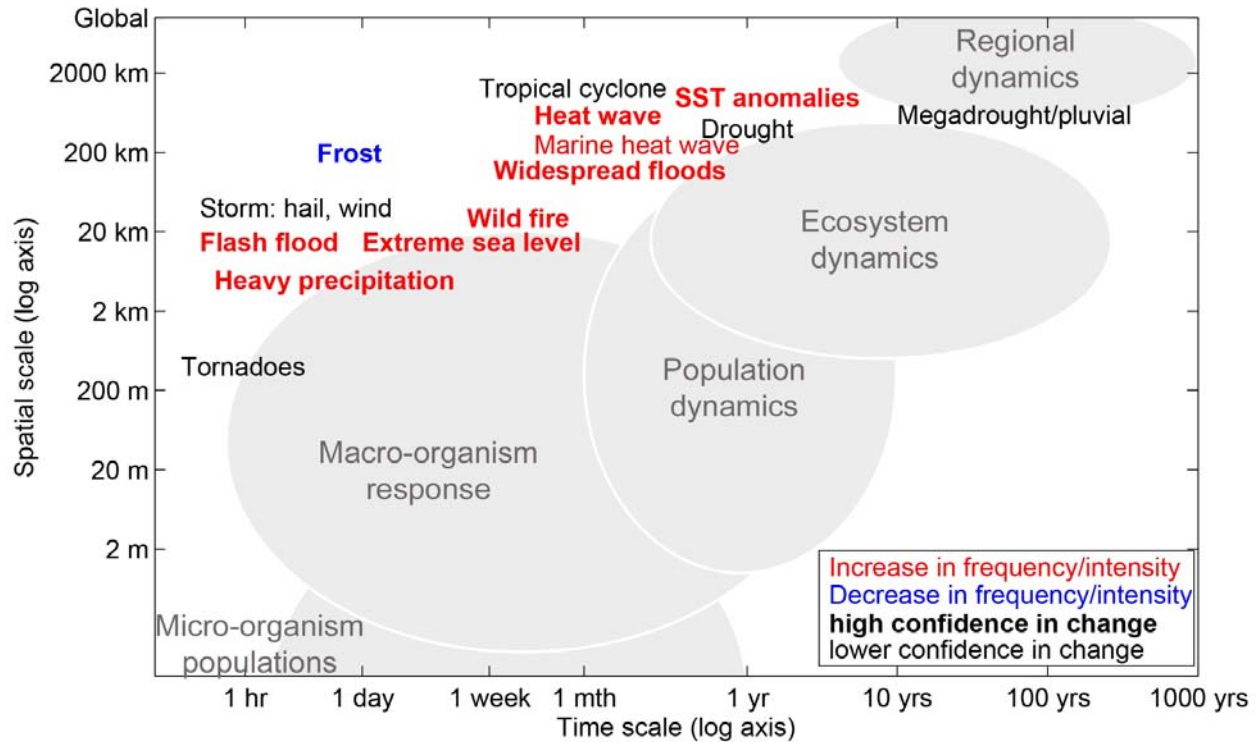
1106



1108

1109 **Figure 1:** Schematic highlighting the effect of changes in the temperature distribution on ECE
 1110 occurrence between present and future climate conditions: (a) effects of a simple shift of the
 1111 entire distribution toward a warmer climate; (b) effects of an increase in temperature variability
 1112 with no shift in the mean; (c) effects of an altered shape of the distribution, in this example a
 1113 change in asymmetry toward the hotter part of the distribution. Reproduced from IPCC (2012b).

1114



1115

1116 **Figure 2:** Spatial and temporal scales of typical ECEs and scales of biological systems (grey).
 1117 Individuals, populations and ecosystems within these respond to environmental stressors. Red
 1118 (blue) labels indicate an increase (decrease) in the frequency or intensity of the event, with bold
 1119 font reflecting confidence in the change. For each ECE type indicated in the figure, ECEs are
 1120 likely to affect biological systems at all temporal and spatial scales located to the left and below
 1121 the specific ECE position in the figure [Modified from Leonard et al. 2014 and Sheehan 1995].

1122