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1 **Forest resilience and tipping points at different spatio-temporal scales:**
2 **approaches and challenges**

3

4 **Running head: Forest resilience to environmental change**

5

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39 **Summary**

- 40 1. Anthropogenic global change compromises forest resilience, with profound
41 impacts to ecosystem functions and services. This synthesis paper reflects on the
42 current understanding of forest resilience and potential tipping points under
43 environmental change, and explores challenges to assessing responses using
44 experiments, observations and models.
- 45 2. Forests are changing over a wide range of spatio-temporal scales, but it is often
46 unclear if these changes reduce resilience or represent a tipping point. Tipping
47 points may arise from interactions across scales, as processes such as climate
48 change, land-use change, invasive species, or deforestation gradually erode
49 resilience and increase vulnerability to extreme events. Studies covering
50 interactions across different spatio-temporal scales are needed to further our
51 understanding.
- 52 3. Combinations of experiments, observations, and process-based models could
53 improve our ability to project forest resilience and tipping points under global
54 change. We discuss uncertainties in changing CO₂ concentration and quantifying
55 tree mortality as examples.
- 56 4. *Synthesis:* As forests change at various scales, it is increasingly important to
57 understand whether and how such changes lead to reduced resilience and potential
58 tipping points. Understanding the mechanisms underlying forest resilience and
59 tipping points would help in assessing risks to ecosystems, and presents
60 opportunities for ecosystem restoration and sustainable forest management.

61 Keywords: climate change, CO₂, drought, environmental change, mortality, regime shifts,
62 review, spatio-temporal scales, vegetation–climate interactions, vulnerability

63 **Introduction**

64 Global environmental changes in, for instance, atmospheric CO₂ concentration,
65 climate, nitrogen deposition, and their interactions are affecting forests around the world
66 (Hyvönen *et al.* 2007; Phillips *et al.* 2009; Lindner *et al.* 2010; Dietze & Moorcroft 2011;
67 Brouwers *et al.* 2012; Poulter *et al.* 2013). These changes occur in combination with
68 direct local anthropogenic drivers of forest change such as land conversion and intensive
69 forest management (e.g., Malhi *et al.* 2008; Barona *et al.* 2010; DeFries *et al.* 2010;
70 Gibbs *et al.* 2010; Kurz 2010; Vayreda *et al.* 2012; Bryan *et al.* 2013). The structural
71 (e.g., reduction in biomass or canopy cover) and functional changes (e.g., changes in
72 community structure) in forests in response to these global and local drivers may
73 compromise the capacity of forest ecosystems to recover from natural or human-induced
74 perturbations (Laurance 2004; Lenton *et al.* 2008). Resilience theory suggests that
75 ecosystems exhibit threshold responses to changing environmental drivers, and move
76 towards a new regime when a critical threshold is exceeded (Scheffer *et al.* 2001;
77 Scheffer *et al.* 2003). However, while evidence for the effects of gradual environmental
78 change on forests exists, the theory of regime shifts has rarely been tested in forest
79 ecosystems and evidence for tipping points at which feedbacks cause ecosystems to enter
80 alternative stable states remains sparse (Hirota *et al.* 2011).

81 In the scope of the special feature on “Forest Resilience, Tipping Points and Global
82 Change Processes”, we reflect here on the current understanding of forest resilience and
83 potential tipping points under environmental change at different spatial and temporal
84 scales, and the challenges to **quantify these ecosystem attributes** with experiments,
85 observations and models.

86 **Concepts and definitions**

87 We use the term forest resilience in the sense of Scheffer (2009) as “the ability of a
88 forest to absorb disturbances and re-organize under change to maintain similar
89 functioning and structure”. This definition is wider than what is understood as
90 “ecological resilience” (sensu Holling 1973) to account for the fact that systems rarely
91 recover to exactly the same pre-disturbance conditions (Scheffer 2009). Furthermore this
92 definition allows resilience to be framed as the rate of recovery after a disturbance and as
93 the maximum disturbance a forest can absorb before switching to a different **ecosystem**
94 **type** (Gunderson 2000; Scheffer 2009) – both being important features of resilience in the
95 context of global change. In systems with multiple stable states, reduced resilience can
96 lead to regime shifts (Scheffer *et al.* 2001). Scheffer (2009) defines a regime shift as a
97 “relatively sharp change from one regime to a contrasting one, where a regime is a
98 dynamic ‘state’ of a system with its characteristic stochastic fluctuations and/or cycles”.
99 A tipping point describes a threshold in conditions at which a small change in conditions
100 leads to a strong change in the state of a system (cf. Brook *et al.* 2013).

101 A typical example to illustrate these concepts is the so-called “Amazon forest
102 dieback” (White *et al.* 1999, Cox *et al.* 2004, Malhi *et al.* 2008; Rammig *et al.* 2010).
103 Model simulations including changing precipitation and/or ongoing anthropogenic
104 deforestation in the Amazon show reduced evapotranspiration and hence lower amounts
105 of water recycled for regional precipitation (e.g. Cox *et al.* 2004, Sampaio *et al.* 2007;
106 Costa & Pires 2010). **Such an altered hydrological cycle** may lead to further tree
107 mortality and reduces forest resilience to recover from fire and drought. Repeated
108 occurrences of strong drought/fire years, for example in the context of El-Nino events,

109 could drive the Amazon past a tipping point into a savannah-like state. Sampaio *et al.*
110 (2007) **suggested** that at 40% deforestation, such a regime shift could occur in the
111 Amazon basin. Hirota *et al.* (2011) **predicted** that the south-eastern parts of the Amazon
112 are the least resilient and most likely to turn into savannah or a treeless state.

113 Another example to illustrate resilience and tipping points in forests at a different
114 spatio-temporal scale is the analysis of drought-induced mortality by Camarero *et al.*
115 (2015). They suggest a framework in which already stressed trees with reduced resilience
116 are further affected by drought up to a point where hydraulic failure occurs or carbon
117 reserves are depleted and additional drought stress can lead to **widespread** tree mortality
118 **and a tipping point.**

119 The spatio-temporal scales at which forest resilience and potential tipping points
120 can be assessed are of critical importance in understanding and interpreting ecological
121 processes (Wiens 1989; Levin 1992). While sophisticated concepts and methods for
122 delineating scales have been discussed recently (Angeler *et al.* 2011; Chave 2013; Allen
123 *et al.* 2014; Nash *et al.* 2014; Soranno *et al.* 2014), we here use the following scale
124 classification to group studies that are relevant to address our main objective of
125 understanding forest resilience and tipping points (Table 1). We refer to ‘local’ scale as
126 the spatial extent from hundreds of m² up to 10 km², ‘regional’ scale as larger areas
127 spanning >10 km² to water catchment, ecoregion, country or continental-level, and the
128 ‘global’ scale. For temporal scales, we define ‘short-term’ as periods of up to 10 years
129 capturing processes such as tree mortality, and ‘long-term’ as decadal to millennial time
130 periods capturing longer-term processes such as species replacement (see Chapin *et al.*
131 2004; Hughes *et al.* 2013a).

132 **At which temporal and spatial scales can forest resilience and potential tipping**
133 **points be assessed?**

134 *Local scale responses*

135 At the local scale, short-term and long-term responses to environmental change
136 have been well documented in different types of forests (Table 1). **For example,**
137 Mediterranean ecosystems have been profoundly transformed by long human use and
138 their response is well studied across different continents. The capacity of Mediterranean
139 ecosystems to respond to disturbances strongly interacts with climate condition.
140 Vegetation changes in **the driest** regions tend to be persistent and sometimes very
141 difficult to reverse because of positive feedbacks that maintain alternative vegetation
142 states (Holmgren & Scheffer 2001; Acacio *et al.* 2007, 2009, Kefi *et al.* 2007).
143 Mediterranean climate regions are likely to become drier and warmer over the decades to
144 come (Stocker *et al.* 2013), which will likely impact on their resilience as is already
145 occurring in southwest Western Australia (e.g. Brouwers *et al.* 2012). Here, forest tree
146 species are increasingly showing severe dieback and mortality in response to extreme
147 climatic conditions (Bader *et al.* 2014, Matusick *et al.* 2012, Matusick *et al.* 2013) but
148 whether this constitutes a tipping point is unclear.

149 Allen *et al.* (2010) concluded that in already dry regions, forests are most
150 vulnerable to further drought possibly indicating reduced resilience. It is precisely these
151 dry regions that have become drier during the second half of the last century (Bates *et al.*
152 2008; Steinkamp & Hickler 2015). Relative to the small spatial extent of forests with a
153 dry climate, many of the observed drought-induced forest mortality events in Allen *et al.*
154 (2010) occurred in drought-prone forests.

155

156 *Regional scale responses*

157 At the regional scale, short and long-term responses to environmental change have
158 been documented in different forest types (Table 1). Allen *et al.* (2010) provide examples
159 of reduced resilience due to drought-induced tree mortality over both short and long
160 periods of time. **Their findings are** confirmed by a recent risk analysis of ecosystem
161 vulnerability to drought by Van Oijen *et al.* (2013) indicating that drought vulnerability is
162 expected to increase in Southern Europe.

163 Inferring resilience at regional scales is challenging. Hirota *et al.* (2011) and Staver
164 *et al.* (2011) inferred tropical forest resilience from remotely-sensed tree cover
165 distribution. They studied tree cover classes over different precipitation levels that
166 suggest instabilities of forest cover. The “resilience maps” of Hirota *et al.* (2011) show
167 the probability of finding tropical forests, savannas and treeless conditions in a specific
168 location given the mean annual precipitation. These maps highlight which parts of Africa,
169 Australia and South America are more or less likely to persist in certain vegetation state
170 if disturbed pointing towards possible tipping points. This approach has also been used to
171 infer the resilience of boreal ecosystems (Scheffer *et al.* 2012a). However, Hanan *et al.*
172 (2014) recently pointed out that such tree cover datasets may be unsuitable for the
173 diagnosis of alternative stable states due to their inherent error distribution. Moreover,
174 remotely-sensed data are two-dimensional, time-delayed and often not available as time
175 series.

176 For the Amazon forests, Cox *et al.* (2004) have projected a tipping point based on
177 climate-change induced rainfall reductions leading to vegetation-atmosphere feedbacks

178 and further drying using coupled carbon cycle-climate models. However, in more recent
179 studies, Cox *et al.* (2013) and Huntingford *et al.* (2013) show that the Amazon is
180 probably more resilient than projected in the original Cox *et al.* (2004) study. This change
181 in perspective is due to a better understanding of model uncertainties. Uncertainties with
182 regard to parameterization and structural representation of physiological processes such
183 as CO₂-fertilization or responses to elevated temperatures have been highlighted as being
184 more important than uncertainties related to emission scenarios and climate projections
185 (Huntingford *et al.* 2013). However, another study, using an Earth System Model, found
186 projected changes in dry-season length to be the dominant single factor explaining
187 differences in forest dieback projections (Good *et al.* 2013).

188

189 *Global scale responses*

190 Recently, the potential for an anthropogenically-driven global tipping point of the
191 biosphere has been discussed (Barnosky *et al.* 2012; Brook *et al.* 2013; Hughes *et al.*
192 2013b; Lenton & Williams 2013). Barnosky *et al.* (2012) argue that in the past, state
193 shifts of the totality of the global ecosystem have occurred and that a tipping point of the
194 Earth's biosphere is plausible given the strong and enduring alterations of natural
195 ecosystems by human interventions such as land-use change. Brook *et al.* (2013)
196 highlighted three criteria that need to be fulfilled for such a state shift to occur globally:
197 1) a spatially homogenous response towards changing environmental conditions, 2) an
198 interconnection of responses, and 3) a spatial homogeneity of drivers of environmental
199 change. They conclude that spatial heterogeneity in drivers of, and responses to,
200 environmental change as well as the lack of continental connectivity are smoothing

201 global-scale responses and will therefore unlikely result in a global tipping point (Brook
202 *et al.* 2013). Hughes *et al.* (2013b) argue that the speed of change does not determine the
203 presence or absence of a global tipping point but rather the nonlinear relation between the
204 driving force of ecosystem change and the state of the ecosystem. Lenton & Williams
205 (2013) add that it is the existence of possible feedbacks (and the balance between positive
206 and negative feedbacks) between different components of the Earth system that
207 ultimately determines whether a global tipping of the biosphere exists. They also stress
208 that a clear definition of the “biosphere” is needed to discuss the possibility of a global
209 tipping point. Lenton & Williams (2013) argue that although a strong global ecological
210 response may be perceived as a tipping point of the biosphere, it is not necessarily
211 associated with a tipping point caused by a feedback within the biosphere itself. They
212 agree with Brook *et al.* (2013) in that interactions of smaller-scale tipping points that
213 influence and trigger each other are more likely than a global tipping point (Lenton &
214 Williams 2013). However, Lenton & Williams (2013) also point out that under certain
215 circumstances a cascade of tipping points may lead to a tipping point with a global reach.
216

217 *Interactions across scales*

218 Besides the individual impacts of natural and anthropogenic pressures, it is perhaps
219 primarily the interaction of processes across scales that determine forest resilience and
220 tipping points (cf. Gunderson & Holling 2002). For example, the interaction of changes
221 in longer-term mean climate with changes in short-term climate variability determines
222 plant responses to climate change (Reyer *et al.* 2013). In regions where recent climate
223 change has had a significant impact, tipping points may occur when extreme climatic

224 events take place. Hence, continuous slow changes in climatic conditions alter the
225 resilience of forests until extreme events or disturbances, such as prolonged drought, push
226 a specific forest ecosystem across a tipping point into a new state. We therefore argue
227 that, in regions where gradual and persistent long-term drying and warming trends are
228 evident, forest resilience and tree health has likely decreased (e.g., van Mantgem *et al.*
229 2009; Brouwers *et al.* 2012). This decrease maybe a consequence of idiosyncratic
230 interactions of increasing physiological stress, altered natural disturbance regimes and
231 comparably rapid climatic changes, which makes forests vulnerable to regime shift in the
232 future. Similar gradual erosion of resilience through land-use change, invasive species
233 and deforestation may increase vulnerability to extreme events pushing forests towards a
234 tipping point.

235 Interaction across scales may however also increase resilience at larger scales.
236 Higgins & Scheiter (2012) for example, show that although potentially large areas across
237 Africa are threatened by regime shifts in vegetation cover, asynchrony in their timing
238 may dampen their effect on the Earth system globally. Thus, although abrupt transitions
239 can occur locally with potentially devastating effects, they may smooth out on larger
240 spatial scales and prevent strong regional to global scale tipping points (Higgins &
241 Scheiter 2012). Similarly, it is important to consider that over larger spatial or temporal
242 scales, there is also a larger potential for adaptation of species and communities to
243 changing conditions, which may increase resilience and further dampen the possibility for
244 a tipping point.

245 **What are the challenges for understanding forest resilience and tipping points**
246 **under global environmental change?**

247 This section focuses on the challenges in capturing different environmental
248 changes in experiments, observations and models to assess the effects of changing
249 environmental conditions on forests and how this limits our understanding of resilience
250 and tipping points (Table 2). There are, in theory, a number of early warning signals
251 when approaching a regime shift. For instance, these include indicators related to the
252 ‘critical slowing down’ of a system under stress, a flickering in time-series of relevant
253 indicators (e.g. population abundance, nutrient flows), or simply approaching a state
254 where the system has not been observed under current conditions (see Scheffer *et al.*
255 (2012b) and Camarero *et al.* (2015)). However, the ability to predict a tipping point will
256 remain limited due to the inherent stochasticity of the mechanisms involved (Scheffer *et*
257 *al.* 2012b).

258 Another challenge for understanding forest resilience and tipping points is that
259 background conditions are changing, for example CO₂-concentration and temperature.
260 Changes in human-driven pressures such as alterations of fire regimes, deforestation,
261 management and their interactions, also need to be considered. Consequently, to deepen
262 our understanding of forest resilience and tipping points integrating insights from
263 experiments, observations and modelling is needed. Experiments may be helpful to
264 determine potential thresholds of ecosystem variables that influence tipping point
265 behaviour, particularly when manipulating whole ecosystems (e.g., Nepstad *et al.* 2007,
266 Brando *et al.* 2008). Observations show conditions under which tipping of a forest
267 ecosystem is possible or has already happened (e.g., Leadley *et al.* 2010). Taken together,

268 this understanding of resilience and tipping points may help to improve process-based
269 models.

270 Process-based models can be used as diagnostic tools to understand system
271 components that are complicated or costly to measure or as predictive tools that allow
272 using different scenarios to project forest responses to changing environmental conditions
273 (e.g., Reyer *et al.* 2014). **Improving process-based models is crucial, because they tend to**
274 **be very complex and often include mechanisms that are still poorly understood,**
275 **particularly under changing environmental conditions.** With regard to the application of
276 such models to assess resilience and detect tipping points, there is prospect for
277 implementing observations and experimentally- or theoretically-derived mechanisms in
278 models. For example, integrating species-specific rooting profiles into a forest model has
279 been shown to affect competition in mixed forests (Reyer *et al.* 2010). Similar
280 implementations in dynamic global vegetation models could help to better explain forest-
281 savannah interactions as a response to changes in extreme precipitation (Kulmatiski &
282 Beard 2013).

283 Nonetheless, because models are simplified representations of reality, they should
284 always be considered as generators of hypotheses or projectors of possible pathways, and
285 therefore further checked against **experimental and independent data on system**
286 **responses.** Most current forest and vegetation models were not meant to simulate tipping
287 points and may not be able to do so because of underpinning assumption like the
288 inclusion of equilibrium pools representing an average steady state response, and the lack
289 of feedbacks between vegetation and climate. Moreover, most models still do not contain
290 disturbance processes (e.g. pathogens/insects, wind-throw), which are crucial for

291 simulating mortality of trees and abrupt vegetation shifts (Steinkamp & Hickler 2015). A
292 future challenge is to incorporate these processes in forest models to better simulate
293 resilience and tipping points. In a first attempt ‘tipping point’ behaviour could be
294 implemented into models by introducing them explicitly, depending on threshold values.
295 However, in that case the model would depend totally on the parameter or threshold
296 value imposed. The larger challenge is to build models that do not have these explicit
297 thresholds hard-coded, but have tipping point as an emerging property as a result of the
298 combination of the underlying processes included in the model.

299 Although most forest models are still limited for exploring tipping points and
300 regime shifts, they are usually able to identify indicators of reduced resilience, for
301 example by predicting changes in biogeochemical cycles. A metric developed by Heyder
302 *et al.* (2011) indicates severe ecosystem change highlighting loss of resilience and the
303 potential approach of tipping points (Gerten *et al.* 2013; Warszawski *et al.* 2013).
304 Recently, also more simple ecological models have been developed that are explicitly
305 designed to simulate regime shifts (e.g., Staver & Levin 2012; van Nes *et al.* 2013). In
306 the following sections we take the example of CO₂-effects and mortality as two key
307 challenges for understanding forest resilience and tipping points under changing
308 environmental conditions in process-based forest models.

309

310 *Effects of changing CO₂-concentrations*

311 From a plant’s perspective, it is not the role of CO₂ in atmospheric forcing that is
312 most important, but its direct effect on photosynthesis and gas exchange. Since rising
313 CO₂ tends to increase productivity and reduce water use, it may increase forest resilience

314 or lead to greening of non-forested ecosystems (e.g. Higgins & Scheiter 2012). However,
315 there are counter-examples where rising CO₂ has decreased resilience. In some cases,
316 elevated CO₂ has increased plant leaf area thus increasing the impact of drought when it
317 occurs (Ghannoum & Way 2011). Also, since elevated CO₂ reduces transpiration, leaf
318 temperatures tend to increase, which may increase the impact of extremely high
319 temperatures (Warren *et al.* 2011) and decrease resilience to frost events (Barker *et al.*
320 2005). Increased productivity under elevated CO₂ may also increase litter and reduce
321 litter decomposition rates (Hyvönen *et al.* 2007) leading to increased fuel and higher
322 vulnerability to fire.

323 Although the effects of elevated CO₂ can be observed close to natural sources of
324 CO₂ (Haettenschwiler *et al.* 1997), derived from time-series of measured forest functions
325 under the recent increase in CO₂ (e.g., Keenan *et al.* 2013) or inferred from
326 paleoecological data, experiments and models are most commonly used to study how
327 trees and forests respond to CO₂. The logistics involved in experiments manipulating
328 atmospheric CO₂ levels within existing forests are tremendous and explain why, to date,
329 very few of these experiments exist in natural or semi-natural forests (Norby *et al.* 2010;
330 Leuzinger & Bader 2012; Bader *et al.* 2013). Such experiments remain largely artificial,
331 because the atmospheric CO₂ increase has to occur stepwise instead of gradually as in
332 reality. Furthermore, because transpiration is affected through stomatal closure, forests
333 under elevated atmospheric CO₂ affect local climate (e.g. air humidity). These changes,
334 however, do not feed back on the canopy under study, as the surrounding non-treated
335 trees dominate the climate feedbacks (see Leakey 2009). Tipping points are not to be
336 expected via the direct CO₂ response, but rather via the much more important indirect

337 transpiration response (Holtum & Winter 2010; Hartmann 2011). For example, the
338 rainfall amount and pattern will determine when the CO₂-induced water response starts to
339 become important (Leuzinger & Körner 2010; Hovenden *et al.* 2014). This CO₂-induced
340 water response is likely to be the main process that affects resilience and determines
341 whether a forest tips into an alternate state.

342 In models, CO₂ effects on forest productivity are key uncertainties. Crucial
343 assumptions relate to whether photosynthesis and stomatal conductance are proportional
344 to CO₂ levels and how this translates to carbon sequestration, how leaf-level processes
345 are coupled to the atmosphere, and how drought affects stomatal conductance or how
346 rainfall is intercepted (Medlyn *et al.* 2011). For example, decreasing productivity under
347 climate change may only be observed in those models that are assuming no interaction
348 between changing temperatures and CO₂-concentrations (Medlyn *et al.* 2011; Reyer *et al.*
349 2014). Models that include a nitrogen cycle and interactions with CO₂ provide a better
350 representation of CO₂ effects on forest productivity (Grant 2013; Zaehle *et al.* 2014).

351

352 *Mortality*

353 Mortality of individual trees does not mean that resilience of the forest is impaired
354 or a tipping point may occur. However, improving our understanding of mortality will
355 enhance our capacity to simulate forest resilience and tipping points. The mechanistic
356 controls over tree mortality remain a major uncertainty in modelling forest resilience to
357 drought-induced mortality (McDowell *et al.* 2011; Adams *et al.* 2013). Many tree species
358 across the globe operate with small 'safety margins' for xylem embolism and cavitation
359 (Choat *et al.* 2012) and vulnerability to drought is a key factor of tree mortality (Allen *et*

360 *al.* 2010; Table 1). Mortality is particularly challenging to predict because tree death can
361 occur from a variety of causes, including resource limitation, environmental stress, or
362 large-scale natural disturbance. These causes are also strongly interdependent, as reduced
363 carbon or water stores impair a tree's capacity to defend against pests, or to withstand
364 drought. Predicting the onset of mortality thus requires an integrated framework for
365 quantifying critical thresholds and feedbacks in tree responses to physiological stress
366 (McDowell *et al.* 2011).

367 Regional-scale analyses of tree mortality from forest inventory or forest monitoring
368 plot networks offer outstanding opportunities for quantifying mortality patterns. Long-
369 term, plot-based records have been used to reveal increases in mortality rates over the
370 past 50 years both in the western US and Canada (van Mantgem *et al.* 2009; Peng *et al.*
371 2011). **Such** observations can help inform and calibrate the mechanisms used to predict
372 mortality in process-based models, or can serve as a basis for hybrid approaches that
373 combine mechanistic and phenomenological elements to derive predictions of mortality
374 and its role in defining forest resilience or tipping points.

375

376 *Combination of methods*

377 A combination of experiments, observations and models may help to better
378 understand scale-dependent responses (Fig. 1). Leaf-level CO₂-effects are well-
379 understood in the laboratory but integrating this mechanistic knowledge with experiments
380 and observations of larger-scale CO₂-effects in models in conjunction with other
381 ecophysiological and demographic processes is necessary to paint a more realistic picture
382 of forest responses to elevated CO₂ (Field *et al.* 1995).

383 Advances have also been made in experiments and observations with regard to the
384 mechanisms underpinning forest growth. While there is empirical evidence that net
385 primary production is at least partly sink- rather than source- driven (Körner 2003;
386 Muller *et al.* 2011; Fatichi *et al.* 2014), current modelling approaches still rely on
387 photosynthesis-driven (i.e., source-driven) plant growth (e.g., Sitch *et al.* 2003; Bonan *et*
388 *al.* 2003; Krinner *et al.* 2005; Sitch *et al.* 2008; Bonan *et al.* 2011). This is highly relevant
389 because photosynthesis often correlates with productivity and there is a danger of
390 obtaining the right answer for the wrong reason. Sensitivity analyses of vegetation
391 models have shown an unrealistic importance of mostly photosynthesis-related
392 parameters (Pappas *et al.* 2013). However, if tipping points are to be simulated
393 accurately, it is imperative that the causal mechanisms in modelling plant growth are
394 correct, which may involve the reconsideration of the core architecture of vegetation
395 models (Fatichi *et al.* 2014).

396 Besides combinations of experiments, observation and models, the integration of
397 different model types can help to better understand forest resilience. For example,
398 Schelhaas *et al.* (submitted) combined simulations of a process-based forest growth
399 model by Reyer *et al.* (2014) with species distribution maps from Hanewinkel *et al.*
400 (2013). By doing this, they could assess where tree species would need to be changed by
401 forest managers as a consequence of changing species distributions as well as changing
402 productivity under climate change to increase forest resilience.

403

404 **Concluding remarks**

405 This paper shows that forests are changing over a wide range of spatial and
406 temporal scales. There seems to be more evidence for ongoing changes at smaller spatial
407 and shorter temporal scales and in particular areas such as the Mediterranean. But also
408 larger and longer spatio-temporal scales as well as other forest types face strong changes
409 (Table 1). However, in many cases it is not clear if these changes reduce resilience **or a**
410 **tipping point is about to be reached**. Our synthesis indicates that global-scale disruptions
411 of forest ecosystems are unlikely. We argue that studies covering interactions across a
412 range of spatio-temporal scales are needed to further our understanding of forest
413 resilience and tipping points. Changing CO₂ concentration and tree mortality are
414 processes that require an integration of results from experiments, observations and
415 models to improve the ability of process-based models to simulate forest resilience and
416 potential tipping points.

417 While acknowledging the important role of gradual changes in affecting resilience
418 of forests under global change and the lack of evidence for mechanisms leading to tipping
419 points, we stress that tipping points are important to investigate from a risk assessment
420 perspective. This means that even though a low likelihood is attributed to a specific high-
421 impact event such as a tipping point, it is still important to discuss if we are willing to
422 take the risk of such events to occur. Especially because reduced resilience and potential
423 tipping points may have a profound effect on ecosystem functions and services. Such an
424 approach requires assessments of how society values ecosystem functions and services
425 and would benefit from framing forests as social-ecological systems affected by press and
426 pulse dynamics (cf. Collins *et al.* 2011). At the same time, a better understanding of

427 resilience and tipping points may actually highlight opportunities for ecosystem
428 restoration (e.g. Holmgren *et al.* 2013) or sustainable forest management (Puettmann *et*
429 *al.* 2009; Rist & Moen 2013) which may provide strong co-benefits for improving human
430 livelihoods.

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446 **References**

- 447 Acácio, V. & Holmgren, M. (2014) Pathways for resilience in Mediterranean cork oak
448 land use systems. *Annals of Forest Science*, **71**, 5-13.
- 449 Acácio, V., Holmgren, M., Jansen, P.A., & Schrotter, O. (2007) Multiple Recruitment
450 Limitation Causes Arrested Succession in Mediterranean Cork Oak Systems. *Ecosystems*,
451 **10**, 1220-1230.
- 452 Acácio, V., Holmgren, M., Rego, F., Moreira, F., & Mohren, G.M.J. (2009) Are drought
453 and wildfires turning Mediterranean cork oak forests into persistent shrublands?
454 *Agroforestry Systems*, **76**, 389-400.
- 455 Adams, H.D., Williams, A.P., Xu, C., Rauscher, S.A., Jiang, X., & McDowell, N.G.
456 (2013) Empirical and process-based approaches to climate-induced forest mortality
457 models. *Frontiers in Plant Science*, **4**.
- 458 Allen, C.D., Macalady, A.K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier,
459 M., Kitzberger, T., Rigling, A., Breshears, D.D., Hogg, E.H., Gonzalez, P., Fensham, R.,
460 Zhang, Z., Castro, J., Demidova, N., Lim, J.-H., Allard, G., Running, S.W., Semerci, A.,
461 & Cobb, N. (2010) A global overview of drought and heat-induced tree mortality reveals
462 emerging climate change risks for forests. *Forest Ecology and Management*, **259**, 660-
463 684.
- 464 Bader, M.K.F., Ehrenberger, W., Bitter, R., Stevens, J., Miller, B.P., Chopard, J., Rüger,
465 S., Hardy, G.E.S.J., Poot, P., Dixon, K.W., Zimmermann, U., & Veneklaas, E.J. (2014)
466 Spatio-temporal water dynamics in mature *Banksia menziesii* trees during drought.
467 *Physiologia Plantarum*, online first.
- 468 Bader, M.K.F., Leuzinger, S., Keel, S.G., Siegwolf, R.T.W., Hagedorn, F., Schleppei, P.,
469 & Körner, C. (2013) Central European hardwood trees in a high-CO₂ future: synthesis of
470 an 8-year forest canopy CO₂ enrichment project. *Journal of Ecology*, **101**, 1509-1519.
- 471 Barker, D.H., Loveys, B.R., Egerton, J.J.G., Gorton, H., Williams, W.E., & Ball, M.C.
472 (2005) CO₂ enrichment predisposes foliage of a eucalypt to freezing injury and reduces
473 spring growth. *Plant, Cell & Environment*, **28**, 1506-1515.
- 474 Barnosky, A.D., Hadly, E.A., Bascompte, J., Berlow, E.L., Brown, J.H., Fortelius, M.,
475 Getz, W.M., Harte, J., Hastings, A., Marquet, P.A., Martinez, N.D., Mooers, A.,
476 Roopnarine, P., Vermeij, G., Williams, J.W., Gillespie, R., Kitzes, J., Marshall, C.,
477 Matzke, N., Mindell, D.P., Revilla, E., & Smith, A.B. (2012) Approaching a state shift in
478 Earth's biosphere. *Nature*, **486**, 52-58.
- 479 Barona, E., Ramankutty, N., Hyman, G., & Coomes, O. (2010) The role of pasture and
480 soybean in deforestation of the Brazilian Amazon. *Environmental Research Letters*, **5**,
481 024002.
- 482 Bates, B.C., Hope, P., Ryan, B., Smith, I., & Charles, S. (2008) Key findings from the
483 Indian Ocean Climate Initiative and their impact on policy development in Australia.
484 *Climatic Change*, **89**, 339-354.

485 Benton, M.J. & Twitchett, R.J. (2003) How to kill (almost) all life: the end-Permian
486 extinction event. *Trends in Ecology & Evolution*, **18**, 358-365.

487 Bonan, G.B., Lawrence, P.J., Oleson, K.W., Levis, S., Jung, M., Reichstein, M.,
488 Lawrence, D.M., & Swenson, S.C. (2011) Improving canopy processes in the
489 Community Land Model version 4 (CLM4) using global flux fields empirically inferred
490 from FLUXNET data. *Journal of Geophysical Research: Biogeosciences*, **116**, G02014.

491 Bonan, G.B., Levis, S., Sitch, S., Vertenstein, M., & Oleson, K.W. (2003) A dynamic
492 global vegetation model for use with climate models: concepts and description of
493 simulated vegetation dynamics. *Global Change Biology*, **9**, 1543-1566.

494 Brando, P.M., Nepstad, D.C., Davidson, E.A., Trumbore, S.E., Ray, D., & Camargo, P.n.
495 (2008) Drought effects on litterfall, wood production and belowground carbon cycling in
496 an Amazon forest: results of a throughfall reduction experiment. *Philosophical
497 Transactions of the Royal Society B: Biological Sciences*, **363**, 1839-1848.

498 Brook, B.W., Ellis, E.C., Perring, M.P., Mackay, A.W., & Blomqvist, L. (2013) Does the
499 terrestrial biosphere have planetary tipping points? *Trends in Ecology & Evolution*, **28**,
500 396-401.

501 Brouwers, N.C., Mercer, J., Lyons, T., Poot, P., Veneklaas, E., & Hardy, G. (2012)
502 Climate and landscape drivers of tree decline in a Mediterranean ecoregion. *Ecology and
503 Evolution*, **3**, 67-79.

504 Brouwers, N.C., Matusick, G., Ruthrof, K., Lyons, T., & Hardy, G. (2013) Landscape-
505 scale assessment of tree crown dieback following extreme drought and heat in a
506 Mediterranean eucalypt forest ecosystem. *Landscape Ecology*, **28**, 69-80.

507 Brouwers, N.C., van Dongen, R., Matusick, G., Coops, N.C., Strelein, G., & Hardy, G.
508 (in review) Inferring drought and heat sensitivity across a Mediterranean forest region.
509 *Forestry*, in review.

510 Bryan, J.E., Shearman, P.L., Asner, G.P., Knapp, D.E., Aoro, G., & Lokes, B. (2013)
511 Extreme Differences in Forest Degradation in Borneo: Comparing Practices in Sarawak,
512 Sabah, and Brunei. *PLOS One*, **8**, e69679.

513 Camarero, J.J., Gazol, A., Sangüesa-Barreda, G., Oliva, J., & Vicente-Serrano, S.M.
514 (2015) To die or not to die: early-warning signals of drought-induced tree die-off.
515 *Journal of Ecology*.

516 Chapin, F.S., Callaghan, T.V., Bergeron, Y., Fukuda, M., Johnstone, J.F., Juday, G., &
517 Zimov, S.A. (2004) Global Change and the Boreal Forest: Thresholds, Shifting States or
518 Gradual Change? *AMBIO: A Journal of the Human Environment*, **33**, 361-365.

519 Choat, B., Jansen, S., Brodribb, T.J., Cochard, H., Delzon, S., Bhaskar, R., Bucci, S.J.,
520 Feild, T.S., Gleason, S.M., Hacke, U.G., Jacobsen, A.L., Lens, F., Maherali, H.,
521 Martinez-Vilalta, J., Mayr, S., Mencuccini, M., Mitchell, P.J., Nardini, A., Pittermann, J.,
522 Pratt, R.B., Sperry, J.S., Westoby, M., Wright, I.J., & Zanne, A.E. (2012) Global
523 convergence in the vulnerability of forests to drought. *Nature*, **491**, 752-755.

524 Ciais, P., Reichstein, M., Viovy, N., Granier, A., Ogee, J., Allard, V., Aubinet, M.,
525 Buchmann, N., Bernhofer, C., Carrara, A., Chevallier, F., De Noblet, N., Friend, A.D.,

526 Friedlingstein, P., Grunwald, T., Heinesch, B., Keronen, P., Knohl, A., Krinner, G.,
527 Loustau, D., Manca, G., Matteucci, G., Miglietta, F., Ourcival, J.M., Papale, D.,
528 Pilegaard, K., Rambal, S., Seufert, G., Soussana, J.F., Sanz, M.J., Schulze, E.D., Vesala,
529 T., & Valentini, R. (2005) Europe-wide reduction in primary productivity caused by the
530 heat and drought in 2003. *Nature*, **437**, 529-533.

531 Collins, S.L., Carpenter, S.R., Swinton, S.M., Orenstein, D.E., Childers, D.L., Gragson,
532 T.L., Grimm, N.B., Grove, J.M., Harlan, S.L., Kaye, J.P., Knapp, A.K., Kofinas, G.P.,
533 Magnuson, J.J., McDowell, W.H., Melack, J.M., Ogden, L.A., Robertson, G.P., Smith,
534 M.D., & Whitmer, A.C. (2011) An integrated conceptual framework for long-term social-
535 ecological research. *Frontiers in Ecology and the Environment*, **9**, 351-357.

536 Costa, M.H. & Pires, G.F. (2010) Effects of Amazon and Central Brazil deforestation
537 scenarios on the duration of the dry season in the arc of deforestation. *International*
538 *Journal of Climatology*, **30**, 1970-1979.

539 Cox, P.M., Betts, R.A., Collins, M., Harris, P.P., Huntingford, C., & Jones, C.D. (2004)
540 Amazonian forest dieback under climate-carbon cycle projections for the 21st century.
541 *Theoretical and Applied Climatology*, **78**, 137-156.

542 Cox, P.M., Pearson, D., Booth, B.B., Friedlingstein, P., Huntingford, C., Jones, C.D., &
543 Luke, C.M. (2013) Sensitivity of tropical carbon to climate change constrained by carbon
544 dioxide variability. *Nature*, **494**, 341-344.

545 DeFries, R.S., Rudel, T., Uriarte, M., & Hansen, M. (2010) Deforestation driven by urban
546 population growth and agricultural trade in the twenty-first century. *Nature Geoscience*,
547 **3**, 178-181.

548 Dietze, M.C. & Moorcroft, P.R. (2011) Tree mortality in the eastern and central United
549 States: patterns and drivers. *Global Change Biology*, **17**, 3312-3326.

550 Fatichi, S., Leuzinger, S., & Körner, C. (2014) Moving beyond photosynthesis: from
551 carbon source to sink-driven vegetation modeling. *New Phytologist*, **201**, 1086-1095.

552 Field, C.B., Jackson, R.B., & Mooney, H.A. (1995) Stomatal responses to increased CO₂:
553 implications from the plant to the global scale. *Plant, Cell and Environment*, **18**, 1214-
554 1225.

555 Fisher, R.A., Williams, M., Da Costa, A.L., Malhi, Y., Da Costa, R.F., Almeida, S., &
556 Meir, P. (2007) The response of an Eastern Amazonian rain forest to drought stress:
557 results and modelling analyses from a throughfall exclusion experiment. *Global Change*
558 *Biology*, **13**, 2361-2378.

559 Fisher, R.A., Williams, M., Do Vale, R.L., Da Costa, A.L., & Meir, P. (2006) Evidence
560 from Amazonian forests is consistent with isohydric control of leaf water potential. *Plant,*
561 *Cell & Environment*, **29**, 151-165.

562 Ghannoum, O. & Way, D.A. (2011) On the role of ecological adaptation and geographic
563 distribution in the response of trees to climate change. *Tree Physiology*, **31**, 1273-1276.

564 Gibbs, H.K., Ruesch, A.S., Achard, F., Clayton, M.K., Holmgren, P., Ramankutty, N., &
565 Foley, J.A. (2010) Tropical forests were the primary sources of new agricultural land in

566 the 1980s and 1990s. *Proceedings of the National Academy of Sciences*, **107**, 16732–
567 16737.

568 Good, P., Jones, C., Lowe, J., Betts, R., Gedney, N., (2013) Comparing Tropical Forest
569 Projections from Two Generations of Hadley Centre Earth System Models, HadGEM2-
570 ES and HadCM3LC. *Journal of Climate* **26**, 495-511.

571 Grant, R.F. (2013) Modelling changes in nitrogen cycling to sustain increases in forest
572 productivity under elevated atmospheric CO₂ and contrasting site conditions.
573 *Biogeosciences*, **10**, 7703-7721.

574 Gunderson, L. & Holling, C.S., eds. (2002) Panarchy - Understanding Transformations in
575 Human and Natural Systems, pp 507. Island Press, Washington DC, US.

576 Hanan, N.P., Tredennick, A.T., Prihodko, L., Bucini, G., & Dohn, J. (2014) Analysis of
577 stable states in global savannas: is the CART pulling the horse? *Global Ecology and*
578 *Biogeography*, **23**, 259-263.

579 Hanewinkel, M., Cullmann, D.A., Schelhaas, M.-J., Nabuurs, G.-J., & Zimmermann,
580 N.E. (2013) Climate change may cause severe loss in the economic value of European
581 forest land. *Nature Climate Change*, **3**, 203-207.

582 Hartmann, H. (2011) Will a 385 million year-struggle for light become a struggle for
583 water and for carbon? – How trees may cope with more frequent climate change-type
584 drought events. *Global Change Biology*, **17**, 642-655.

585 Hättenschwiler, S., Miglietta, F., Raschi, A., & Körner, C. (1997) Thirty years of in situ
586 tree growth under elevated CO₂: a model for future forest responses? *Global Change*
587 *Biology*, **3**, 463-471.

588 Higgins, S.I. & Scheiter, S. (2012) Atmospheric CO₂ forces abrupt vegetation shifts
589 locally, but not globally. *Nature*, **488**, 209-212.

590 Hirota, M., Holmgren, M., Van Nes, E.H., & Scheffer, M. (2011) Global Resilience of
591 Tropical Forest and Savanna to Critical Transitions. *Science*, **334**, 232-235.

592 Holling, C.S. (1973) Resilience and Stability of Ecological Systems. *Annual Review of*
593 *Ecology and Systematics*, **4**, 1-23.

594 Holmgren, M., Hirota, M., van Nes, E.H., & Scheffer, M. (2013) Effects of interannual
595 climate variability on tropical tree cover. *Nature Climate Change*, **3**, 755–758.

596 Holmgren, M. & Scheffer, M. (2001) El Nino as a Window of Opportunity for the
597 Restoration of Degraded Arid Ecosystems. *Ecosystems*, **4**, 151-159.

598 Holtum, J.A.M. & Winter, K. (2010) Elevated [CO₂] and forest vegetation: more a water
599 issue than a carbon issue? *Functional Plant Biology*, **37**, 694-702.

600 Hovenden, M.J., Newton, P.C.D., & Wills, K.E. (2014) Seasonal not annual rainfall
601 determines grassland biomass response to carbon dioxide. *Nature*, **511**, 583-586.

602 Hughes, T.P., Linares, C., Dakos, V., van de Leemput, I.A., & van Nes, E.H. (2013a)
603 Living dangerously on borrowed time during slow, unrecognized regime shifts. *Trends in*
604 *Ecology & Evolution*, **28**, 149–155.

605 Hughes, T.P., Carpenter, S., Rockström, J., Scheffer, M., & Walker, B. (2013b)
606 Multiscale regime shifts and planetary boundaries. *Trends in Ecology & Evolution*, **28**,
607 389-395.

608 Huntingford, C., Zelazowski, P., Galbraith, D., Mercado, L.M., Sitch, S., Fisher, R.,
609 Lomas, M., Walker, A.P., Jones, C.D., Booth, B.B.B., Malhi, Y., Hemming, D., Kay, G.,
610 Good, P., Lewis, S.L., Phillips, O.L., Atkin, O.K., Lloyd, J., Gloor, E., Zaragoza-Castells,
611 J., Meir, P., Betts, R., Harris, P.P., Nobre, C., Marengo, J., & Cox, P.M. (2013) Simulated
612 resilience of tropical rainforests to CO₂-induced climate change. *Nature Geoscience*, **6**,
613 268-273.

614 Hyvönen, R., Ågren, G.I., Linder, S., Persson, T., Cotrufo, M.F., Ekblad, A., Freeman,
615 M., Grelle, A., Janssens, I.A., Jarvis, P.G., Kellomäki, S., Lindroth, A., Loustau, D.,
616 Lundmark, T., Norby, R.J., Oren, R., Pilegaard, K., Ryan, M.G., Sigurdsson, B.D.,
617 Strömgren, M., van Oijen, M., & Wallin, G. (2007) The likely impact of elevated [CO₂],
618 nitrogen deposition, increased temperature and management on carbon sequestration in
619 temperate and boreal forest ecosystems: a literature review. *New Phytologist*, **173**, 463-
620 480.

621 Keenan, T.F., Hollinger, D.Y., Bohrer, G., Dragoni, D., Munger, J.W., Schmid, H.P., &
622 Richardson, A.D. (2013) Increase in forest water-use efficiency as atmospheric carbon
623 dioxide concentrations rise. *Nature*, **499**, 324-327.

624 Kefi, S., Rietkerk, M., Alados, C.L., Pueyo, Y., Papanastasis, V.P., ElAich, A., & de
625 Ruiten, P.C. (2007) Spatial vegetation patterns and imminent desertification in
626 Mediterranean arid ecosystems. *Nature*, **449**, 213-217.

627 Körner, C. (2003) Carbon limitation in trees. *Journal of Ecology*, **91**, 4-17.

628 Krinner, G., Viovy, N., de Noblet-Ducoudré, N., Ogée, J., Polcher, J., Friedlingstein, P.,
629 Ciais, P., Sitch, S., & Prentice, I.C. (2005) A dynamic global vegetation model for studies
630 of the coupled atmosphere-biosphere system. *Global Biogeochemical Cycles*, **19**,
631 GB1015.

632 Kulmatiski, A. & Beard, K.H. (2013) Woody plant encroachment facilitated by increased
633 precipitation intensity. *Nature Climate Change*, **3**, 833-837.

634 Kurz, W.A. (2010) An ecosystem context for global gross forest cover loss estimates.
635 *Proceedings of the National Academy of Sciences*, **107**, 9025-9026.

636 Kurz, W.A., Dymond, C.C., Stinson, G., Rampley, G.J., Neilson, E.T., Carroll, A.L.,
637 Ebata, T., & Safranyik, L. (2008) Mountain pine beetle and forest carbon feedback to
638 climate change. *Nature*, **452**, 987-990.

639 Laurance, W.F. (2004) Forest-climate interactions in fragmented tropical landscapes.
640 *Philosophical Transaction of the Royal Society B*, **359**, 345-352.

641 Leadley, P., Pereira, H.M., Alkemade, R., Fernandez-Manjarrés, J.F., Proença, V.,
642 Scharlemann, J.P.W., & Walpole, M.J. (2010). Biodiversity Scenarios: Projections of
643 21st century change in biodiversity and associated ecosystem services, Montreal.

644 Leakey, A.D.B. (2009) Rising atmospheric carbon dioxide concentration and the future
645 of C₄ crops for food and fuel. *Proceedings of the Royal Society B*, **276**, 2333-2343.

- 646 Lenton, T.M., Held, H., Kriegler, E., Hall, J.W., Lucht, W., Rahmstorf, S., &
647 Schellnhuber, H.J. (2008) Tipping elements in the Earth's climate system. *Proceedings of*
648 *the National Academy of Sciences*, **105**, 1786-1793.
- 649 Lenton, T.M. & Williams, H.T.P. (2013) On the origin of planetary-scale tipping points.
650 *Trends in Ecology & Evolution*, **28**, 380-382.
- 651 Leuzinger, S. & Körner, C. (2010) Rainfall distribution is the main driver of runoff under
652 future CO₂-concentration in a temperate deciduous forest. *Global Change Biology*, **16**,
653 246-254.
- 654 Leuzinger, S. & Bader, M.K.F. (2012) Experimental vs. modeled water use in mature
655 Norway spruce (*Picea abies*) exposed to elevated CO₂. *Frontiers in Plant Science*, **3**,
656 229.
- 657 Levin, S.A. (1992) The Problem of Pattern and Scale in Ecology: The Robert H.
658 MacArthur Award Lecture. *Ecology*, **73**, 1943-1967.
- 659 Lindner, M., Maroschek, M., Netherer, S., Kremer, A., Barbati, A., Garcia-Gonzalo, J.,
660 Seidl, R., Delzon, S., Corona, P., Kolström, M., Lexer, M.J., & Marchetti, M. (2010)
661 Climate change impacts, adaptive capacity, and vulnerability of European forest
662 ecosystems. *Forest Ecology and Management*, **259**, 698-709.
- 663 Malhi, Y., Aragão, L.E.O.C., Galbraith, D., Huntingford, C., Fisher, R., Zelazowski, P.,
664 Sitch, S., McSweeney, C., & Meir, P. (2009) Exploring the likelihood and mechanism of
665 a climate-change-induced dieback of the Amazon rainforest. *Proceedings of the National*
666 *Academy of Sciences*, 10.1073/pnas.0804619106
- 667 Malhi, Y., Roberts, J.T., Betts, R.A., Killeen, T.J., Li, W., & Nobre, C.A. (2008) Climate
668 Change, Deforestation, and the Fate of the Amazon. *Science*, **319**, 169-172.
- 669 Matusick, G., Ruthrof, K.X., Brouwers, N.C., Dell, B., & Hardy, G.J. (2013) Sudden
670 forest canopy collapse corresponding with extreme drought and heat in a mediterranean-
671 type eucalypt forest in southwestern Australia. *European Journal of Forest Research*,
672 **132**, 497-510.
- 673 Matusick, G., Ruthrof, K.X., & Hardy, G.E.S.J. (2012) Drought and heat triggers sudden
674 and severe dieback in a dominant Mediterranean-type woodland species. *Open Journal of*
675 *Forestry*, **2**, 183-186.
- 676 May, R.M. (1977) Thresholds and breakpoints in ecosystems with a multiplicity of stable
677 states. *Nature*, **269**, 471-477.
- 678 McDowell, N.G., Beerling, D.J., Breshears, D.D., Fisher, R.A., Raffa, K.F., & Stitt, M.
679 (2011) The interdependence of mechanisms underlying climate-driven vegetation
680 mortality. *Trends in Ecology & Evolution*, **26**, 523-532.
- 681 Medlyn, B.E., Duursma, R.A., & Zeppel, M.J.B. (2011) Forest productivity under climate
682 change: a checklist for evaluating model studies. *Wiley Interdisciplinary Reviews:*
683 *Climate Change*, **2**, 332-355.
- 684 Michaelian, M., Hogg, E.H., Hall, R.J., & Arsenault, E. (2011) Massive mortality of
685 aspen following severe drought along the southern edge of the Canadian boreal forest.
686 *Global Change Biology*, **17**, 2084-2094.

687 Misson, L., Degueldre, D., Collin, C., Rodriguez, R., Rocheteau, A., Ourcival, J.-M., &
688 Rambal, S. (2011) Phenological responses to extreme droughts in a Mediterranean forest.
689 *Global Change Biology*, **17**, 1036-1048.

690 Muller, B., Pantin, F., Génard, M., Turc, O., Freixes, S., Piques, M., & Gibon, Y. (2011)
691 Water deficits uncouple growth from photosynthesis, increase C content, and modify the
692 relationships between C and growth in sink organs. *Journal of Experimental Botany*, **62**,
693 1715-1729.

694 Nascimento, M.T., da Silva Carvalho, L.C., Barbosa, R.I., & Villela, D.M. (2014)
695 Variation in floristic composition, demography and above-ground biomass over a 20-year
696 period in an Amazonian monodominant forest. *Plant Ecology & Diversity*, **7**, 293-303.

697 Nepstad, D.C., Tohver, I.M., Ray, D., Moutinho, P., & Cardinot, G. (2007) Mortality of
698 large trees and lianas following experimental drought in an Amazon forest. *Ecology*, **88**,
699 2259-2269.

700 Norby, R.J., Warren, J.M., Iversen, C.M., Medlyn, B.E., & McMurtrie, R.E. (2010) CO₂
701 enhancement of forest productivity constrained by limited nitrogen availability.
702 *Proceedings of the National Academy of Sciences*, **107**, 19368-19373.

703 Pappas, C., Fatichi, S., Leuzinger, S., Wolf, A., & Burlando, P. (2013) Sensitivity
704 analysis of a process-based ecosystem model: Pinpointing parameterization and structural
705 issues. *Journal of Geophysical Research: Biogeosciences*, **118**, 505-528.

706 Peng, C., Ma, Z., Lei, X., Zhu, Q., Chen, H., Wang, W., Liu, S., Li, W., Fang, X., &
707 Zhou, X. (2011) A drought-induced pervasive increase in tree mortality across Canada's
708 boreal forests. *Nature Climate Change*, **1**, 467-471.

709 Phillips, O.L., Aragão, L.E.O.C., Lewis, S.L., Fisher, J.B., Lloyd, J., López-González, G.,
710 Malhi, Y., Monteagudo, A., Peacock, J., Quesada, C.A., van der Heijden, G., Almeida,
711 S., Amaral, I.d., Arroyo, L., Aymard, G., Baker, T.R., Bánki, O., Blanc, L., Bonal, D.,
712 Brando, P., Chave, J., de Oliveira, A.t.C.A., Cardozo, N.D.v., Czimczik, C.I.,
713 Feldpausch, T.R., Freitas, M.A., Gloor, E., Higuchi, N., Jiménez, E., Lloyd, G., Meir, P.,
714 Mendoza, C., Morel, A., Neill, D.A., Nepstad, D., Patiño, S., Peñuela, M.C., Prieto, A.,
715 Ramírez, F., Schwarz, M., Silva, J., Silveira, M., Thomas, A.S., Steege, H.t., Stropp, J.,
716 Vásquez, R., Zelazowski, P., Dávila, E.A., Andelman, S., Andrade, A., Chao, K.-J.,
717 Erwin, T., Di Fiore, A., C, E.d.H., Keeling, H., Killeen, T.J., Laurance, W.F., Cruz,
718 A.P.a., Pitman, N.C.A., Vargas, P.N., Ramírez-Angulo, H., Rudas, A., Salamão, R.,
719 Silva, N., Terborgh, J., & Torres-Lezama, A. (2009) Drought Sensitivity of the Amazon
720 Rainforest. *Science*, **323**, 1344-1347.

721 Phillips, O.L., van der Heijden, G., Lewis, S.L., López-González, G., Aragão, L.E.O.C.,
722 Lloyd, J., Malhi, Y., Monteagudo, A., Almeida, S., Dávila, E.A., Amaral, I., Andelman,
723 S., Andrade, A., Arroyo, L., Aymard, G., Baker, T.R., Blanc, L., Bonal, D., de Oliveira,
724 A.C.A., Chao, K.-J., Cardozo, N.D., da Costa, L., Feldpausch, T.R., Fisher, J.B., Fyllas,
725 N.M., Freitas, M.A., Galbraith, D., Gloor, E., Higuchi, N., Honorio, E., Jiménez, E.,
726 Keeling, H., Killeen, T.J., Lovett, J.C., Meir, P., Mendoza, C., Morel, A., Vargas, P.N.,
727 Patiño, S., Peh, K.S.H., Cruz, A.P., Prieto, A., Quesada, C.A., Ramírez, F., Ramírez, H.,
728 Rudas, A., Salamão, R., Schwarz, M., Silva, J., Silveira, M., Ferry Slik, J.W., Sonké, B.,

- 729 Thomas, A.S., Stropp, J., Taplin, J.R.D., Vásquez, R., & Vilanova, E. (2010) Drought–
730 mortality relationships for tropical forests. *New Phytologist*, **187**, 631-646.
- 731 Poulter, B., Pederson, N., Liu, H., Zhu, Z., D'Arrigo, R., Ciais, P., Davi, N., Frank, D.,
732 Leland, C., Myneni, R., Piao, S., & Wang, T. (2013) Recent trends in Inner Asian forest
733 dynamics to temperature and precipitation indicate high sensitivity to climate change.
734 *Agricultural and Forest Meteorology*, **178-179**, 31-45.
- 735 Puettmann, K., Coates, K.D., & Messier, C. (2009) A critique of Silviculture - Managing
736 for Complexity Island Press, Washington, D.C.
- 737 Raffa, K.F., Aukema, B.H., Bentz, B.J., Carroll, A.L., Hicke, J.A., Turner, M.G., &
738 Romme, W.H. (2008) Cross-scale Drivers of Natural Disturbances Prone to
739 Anthropogenic Amplification: The Dynamics of Bark Beetle Eruptions. *BioScience*, **58**,
740 501-517.
- 741 Rammig, A., Jupp, T., Thonicke, K., Tietjen, B., Heinke, J., Ostberg, S., Lucht, W.,
742 Cramer, W., & Cox, P. (2010) Estimating the risk of Amazonian forest dieback. *New*
743 *Phytologist*, **187**, 694-706.
- 744 Reyer, C., Lasch, P., Mohren, G.M.J., & Sterck, F.J. (2010) Inter-specific competition in
745 mixed forests of Douglas-fir (*Pseudotsuga menziesii*) and common beech (*Fagus*
746 *sylvatica*) under climate change - a model-based analysis. *Annals of Forest Science*, **67**.
- 747 Reyer, C., Lasch-Born, P., Suckow, F., Gutsch, M., Murawski, A., & Pilz, T. (2014)
748 Projections of regional changes in forest net primary productivity for different tree
749 species in Europe driven by climate change and carbon dioxide. *Annals of Forest*
750 *Science*, **71**, 211-225.
- 751 Reyer, C., Leuzinger, S., Rammig, A., Wolf, A., Bartholomeus, R.P., Bonfante, A., de
752 Lorenzi, F., Dury, M., Gloning, P., Abou Jaoudé, R., Klein, T., Kuster, T.M., Martins,
753 M., Niedrist, G., Riccardi, M., Wohlfahrt, G., de Angelis, P., de Dato, G., François, L.,
754 Menzel, A., & Pereira, M. (2013) A plant's perspective of extremes: Terrestrial plant
755 responses to changing climatic variability. *Global Change Biology*, **19**, 75-89.
- 756 Rist, L. & Moen, J. (2013) Sustainability in forest management and a new role for
757 resilience thinking. *Forest Ecology and Management*, **310**, 416-427.
- 758 Sampaio, G., Nobre, C., Costa, M.H., Satyamurty, P., Soares-Filho, B.S., & Cardoso, M.
759 (2007) Regional climate change over eastern Amazonia caused by pasture and soybean
760 cropland expansion. *Geophysical Research Letters*, **34**, L17709.
- 761 Scheffer, M., Carpenter, S., Foley, J.A., Folke, C., & Walker, B. (2001) Catastrophic
762 shifts in ecosystems. *Nature*, **413**, 591-596.
- 763 Scheffer, M. & Carpenter, S.R. (2003) Catastrophic regime shifts in ecosystems: linking
764 theory to observation. *Trends in Ecology & Evolution*, **18**, 648-656.
- 765 Scheffer, M. (2009) Critical Transitions in Nature and Society. Princeton University
766 Press.
- 767 Scheffer, M., Bascompte, J., Brock, W.A., Brovkin, V., Carpenter, S.R., Dakos, V., Held,
768 H., van Nes, E.H., Rietkerk, M., & Sugihara, G. (2009) Early-warning signals for critical
769 transitions. *Nature*, **461**, 53-59.

770 Scheffer, M., Hirota, M., Holmgren, M., Van Nes, E.H., & Chapin, F.S. (2012a)
771 Thresholds for boreal biome transitions. *Proceedings of the National Academy of*
772 *Sciences*, doi: 10.1073/pnas.1219844110.

773 Scheffer, M., Carpenter, S.R., Lenton, T.M., Bascompte, J., Brock, W., Dakos, V., van de
774 Koppel, J., van de Leemput, I.A., Levin, S.A., van Nes, E.H., Pascual, M., &
775 Vandermeer, J. (2012b) Anticipating Critical Transitions. *Science*, **338**, 344-348.

776 Schelhaas, M., Nabuurs, G., Hengeveld, G., Reyer, C., Hanewinkel, M., Zimmermann,
777 N., & Cullmann, D. (submitted) Adaptive forest management to account for climate
778 change-induced productivity and species suitability changes in Europe. *Regional*
779 *Environmental Change*.

780 Sitch, S., Huntingford, C., Gedney, N., Levy, P.E., Lomas, M., Piao, S.L., Betts, R.,
781 Ciais, P., Cox, P., Friedlingstein, P., Jones, C.D., Prentice, I.C., & Woodward, F.I. (2008)
782 Evaluation of the terrestrial carbon cycle, future plant geography and climate-carbon
783 cycle feedbacks using five Dynamic Global Vegetation Models (DGVMs). *Global*
784 *Change Biology*, **14**, 2015-2039.

785 Sitch, S., Smith, B., Prentice, I.C., Arneth, A., Bondeau, A., Cramer, W., Kaplan, J.O.,
786 Levis, S., Lucht, W., Sykes, M.T., Thonicke, K., & Venevsky, S. (2003) Evaluation of
787 ecosystem dynamics, plant geography and terrestrial carbon cycling in the LPJ dynamic
788 global vegetation model. *Global Change Biology*, **9**, 161-185.

789 Staver, A.C., Archibald, S., & Levin, S.A. (2011) The Global Extent and Determinants of
790 Savanna and Forest as Alternative Biome States. *Science*, **334**, 230-232.

791 Staver, A.C. & Levin, S. (2012) Integrating Theoretical Climate and Fire Effects on
792 Savanna and Forest Systems. *The American Naturalist*, **180**, 211-224.

793 Steinkamp, J. & Hickler, T. (2015) Is drought-induced forest dieback globally
794 increasing? *Journal of Ecology*.

795 Stocker, T.F., Qin, D., Plattner, G.-K., Alexander, L.V., Allen, S.K., Bindoff, N.L.,
796 Bréon, F.-M., Church, J.A., Cubasch, U., Emori, S., Forster, P., Friedlingstein, P., Gillett,
797 N., Gregory, J.M., Hartmann, D.L., Jansen, E., Kirtman, B., Knutti, R., Krishna Kumar,
798 K., Lemke, P., Marotzke, J., Masson-Delmotte, V., Meehl, G.A., Mokhov, I.I., Piao, S.,
799 Ramaswamy, V., Randall, D., Rhein, M., Rojas, M., Sabine, C., Shindell, D., Talley,
800 L.D., Vaughan, D.G., & Xie, S.-P. (2013). Technical Summary. In *Climate Change 2013:*
801 *The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment*
802 *Report of the Intergovernmental Panel on Climate Change* (eds T.F. Stocker, D. Qin, G.-
803 K. Plattner, M. Tignor, S.K. Allen, J. Boschung, A. Nauels, Y. Xia, V. Bex & P.M.
804 Midgley), pp. 33-115. Cambridge University Press, Cambridge, United Kingdom and
805 New York, NY, USA.

806 van Mantgem, P.J., Stephenson, N.L., Byrne, J.C., Daniels, L.D., Franklin, J.F., Fulé,
807 P.Z., Harmon, M.E., Larson, A.J., Smith, J.M., Taylor, A.H., & Veblen, T.T. (2009)
808 Widespread Increase of Tree Mortality Rates in the Western United States. *Science*, **323**,
809 521-524.

810 van Nes, E.H., Hirota, M., Holmgren, M., & Scheffer, M. (2013) Tipping points in
811 tropical tree cover: linking theory to data. *Global Change Biology*, **20**, 1016-1021.

812 van Oijen, M., Beer, C., Cramer, W., Rammig, A., Reichstein, M., Rolinski, S., &
813 Soussana, J.-F. (2013) A novel probabilistic risk analysis to determine the vulnerability
814 of ecosystems to extreme climatic events. *Environmental Research Letters*, **8**, 015032.

815 Vayreda, J., Martinez-Vilalta, J., Gracia, M., & Retana, J. (2012) Recent climate changes
816 interact with stand structure and management to determine changes in tree carbon stocks
817 in Spanish forests. *Global Change Biology*, **18**, 1028-1041.

818 Warren, J.M., Norby, R.J., & Wullschleger, S.D. (2011) Elevated CO₂ enhances leaf
819 senescence during extreme drought in a temperate forest. *Tree Physiology*, **31**, 117-130.

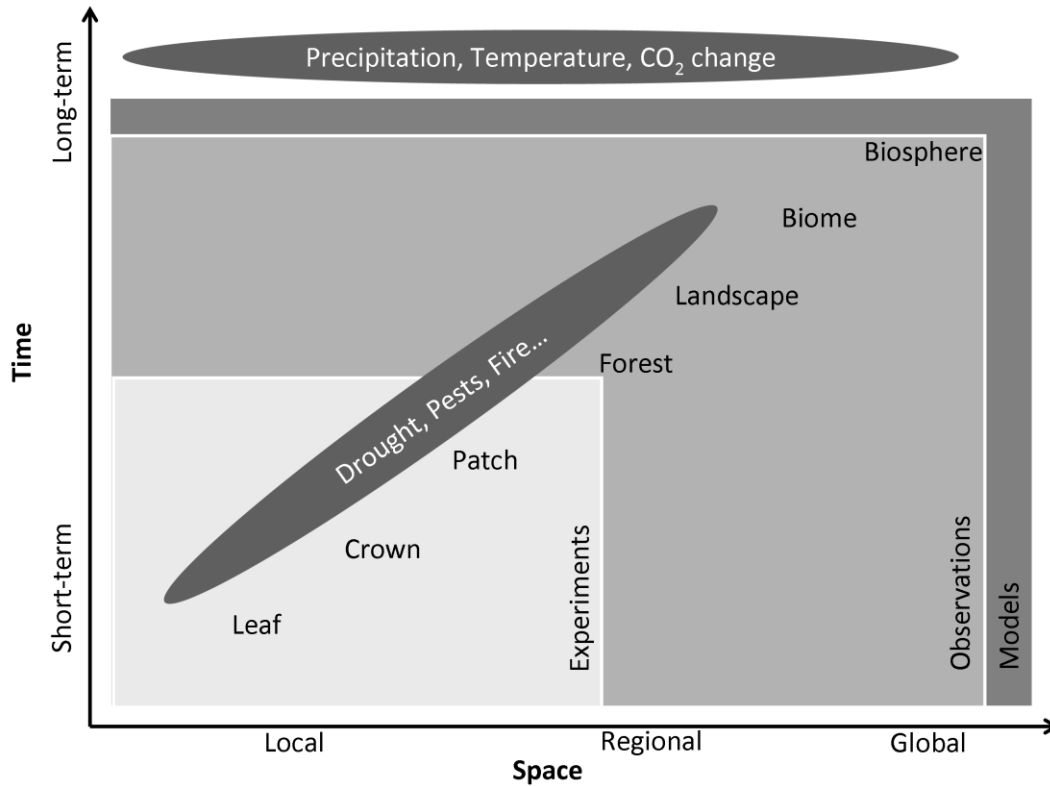
820 White, A., Cannell, M.G.R., & Friend, A.D. (1999) Climate change impacts on
821 ecosystems and the terrestrial carbon sink: a new assessment. *Global Environmental*
822 *Change*, **9**, Supplement 1, S21-S30.

823 Wiens, J.A. (1989) Spatial Scaling in Ecology. *Functional Ecology*, **3**, 385-397.

824 Zaehle, S., Medlyn, B.E., De Kauwe, M.G., Walker, A.P., Dietze, M.C., Hickler, T., Luo,
825 Y., Wang, Y.-P., El-Masri, B., Thornton, P., Jain, A., Wang, S., Warlind, D., Weng, E.,
826 Parton, W., Iversen, C.M., Gallet-Budynek, A., McCarthy, H., Finzi, A., Hanson, P.J.,
827 Prentice, I.C., Oren, R., & Norby, R.J. (2014) Evaluation of 11 terrestrial carbon–
828 nitrogen cycle models against observations from two temperate Free-Air CO₂ Enrichment
829 studies. *New Phytologist*, **202**, 803-822.

830

831 **Figures**



832

833 Figure 1: Temporal and spatial scales at which different research approaches

834 (experiments, observations and models) are available to assess forest resilience and

835 potential tipping points. Drought, pests, fire and other processes that structure the forests

836 such as heatwaves or also deforestation can occur across different spatio-temporal scales.

837 Precipitation, temperature and CO₂ changes cover all spatial scales but only long time

838 scales as we refer to them occurring within the context of climate change and not as part

839 of short-term meteorological variability. The figure is adapted from Gunderson & Holling

840 (2002).

841 **Tables**

842 **Table 1.** Examples of changes in forests that are possibly related to reduced resilience and tipping points in different types of forest
 843 ecosystems across different temporal and spatial scales as defined in the text. Observed examples in **bold**, projected or theoretical
 844 examples in normal font

| | Local (<~10km ²) | Regional (10km ² -continental scale) | Global |
|-------------------------|--|---|--|
| Short-term (<~10 years) | <ul style="list-style-type: none"> • Mediterranean: -Drought and heat-induced tree dieback in southwest Australia (Matusick <i>et al.</i> 2012; Bader <i>et al.</i> 2014) -Drought and fire have induced transition from forest and savannas to shrublands in south Portugal (Acacio <i>et al.</i> 2007, 2009; Acacio and Holmgren 2014) -Drought induced increase in tree mortality in Spain (Camarero <i>et al.</i> 2015) • Different forest types -Drought-induced forest die-back around the world (Allen <i>et al.</i> 2010) -Low safety margin of many species worldwide to drought stress (Choat <i>et al.</i> 2012) | <ul style="list-style-type: none"> • Mediterranean -Drought and heat induced patchy forest die-back and mortality across a Mediterranean-climate ecoregion in southwest Australia (Brouwers <i>et al.</i> 2013; Matusick <i>et al.</i> 2013 Brouwers <i>et al.</i> in review) -Gradual long-term declines in rainfall and increasing temperatures affecting tree health in southwest Australia (Brouwers <i>et al.</i> 2012) • Tropical -Resilience of three alternative stable states of tree covers depends on precipitation in Africa, Australia and South America (Hirota <i>et al.</i> 2011) -Large parts of Amazon and Congo forest could be either forest or savannah, depending on fire regime (Staver <i>et al.</i> 2011) • Boreal -Bark beetle-induced tree mortality in western North America (Kurz <i>et al.</i> 2008; Raffa <i>et al.</i> 2008) -Drought-induced dieback of aspen ecotone in midcontinental North America (Michaelian <i>et al.</i> 2011) • Different forest types -Drought-induced forest die-back around the world (Allen <i>et al.</i> 2010) | <ul style="list-style-type: none"> • Catastrophic geophysical events with wide-spread biological consequences (e.g. asteroid strike, supervolcanoes, cosmic radiation from a nearby supernova (e.g. Benton & Twitchett 2003)) |
| Long-term | <ul style="list-style-type: none"> • Tropical -Drought decreases biomass in a | <ul style="list-style-type: none"> • Mediterranean -Increasing drought stress in Southern Europe (van Oijen <i>et al.</i> | <ul style="list-style-type: none"> • State-shift of the global biosphere (Barnosky <i>et al.</i> |

(10-1,000 years)

Monodominant Amazon forest
(Nascimento *et al.* 2014)

• **Different forest types**

-**Drought-induced forest die-back around the world** (Allen *et al.* 2010)

-Drought-induced mortality
(Steinkamp & Hickler 2015)

2013)

• **Tropical**

-Climate-change induced dieback of the Amazon (Cox *et al.* 2004; Malhi *et al.* 2009 but see also Cox *et al.* 2013; Huntingford *et al.* 2013)

• **Boreal**

-**Boreal biome transitions** (Scheffer *et al.* 2012a)

• **Different forest types**

-**Drought-induced forest die-back around the world** (Allen *et al.* 2010)

2012; Hughes *et al.* 2013b;
Brook *et al.* 2013; Lenton
& Williams 2013)

845 **Table 2.** Examples of changing environmental conditions that are relevant for assessing forest resilience and tipping points and
 846 challenges in understanding them in different research approaches

| Changing conditions | Observations | Experiments | Models |
|---------------------|---|--|---|
| CO ₂ | <ul style="list-style-type: none"> • Long time series available only close to natural CO₂-sources which usually represent very specialized environments (e.g., Haettenschwiler <i>et al.</i> 1997) • Europe fluxtower records are generally not yet long enough to provide long-term average references (Ciais <i>et al.</i> 2005) | <ul style="list-style-type: none"> • Only small spatial and temporal coverage of experiments, costly, few in mature stands (Norby <i>et al.</i> 2010; Bader <i>et al.</i> 2013), no tropical forests but new FACE experiment starting in Amazon • CO₂ increased stepwise vs. gradual change in reality | <ul style="list-style-type: none"> • CO₂ assumptions in models: sink- vs. source-driven models (Cox <i>et al.</i> 2013; Fatichi <i>et al.</i> 2014) • Assessment of CO₂ response requires N availability to be included in model (Grant 2013) |
| Temperature | <ul style="list-style-type: none"> • Time series are easy to observe, but the problem is mostly the disentanglement by concurrent changes such as precipitation, CO₂ and nitrogen | <ul style="list-style-type: none"> • Lack of whole tree warming experiments • Mostly small spatial and temporal coverage, typically greenhouse experiments or open-top chambers | <ul style="list-style-type: none"> • Temperature responses in models are poorly represented • Acclimation of model parameters is poorly represented |
| Drought | <ul style="list-style-type: none"> • Drought and heat often act together, and their interactions need to be considered (Allan <i>et al.</i> 2010; Matusick <i>et al.</i> 2013; Brouwers <i>et al.</i> 2013) • Drought impact responses of forest vegetation are highly variable depending on the positioning within the landscape (Brouwers <i>et al.</i> 2013, Brouwers <i>et al.</i> in review) | <ul style="list-style-type: none"> • Expensive, challenging and laborious rainfall exclusion experiments (REE) (Nepstad <i>et al.</i> 2007; Phillips <i>et al.</i> 2010; Misson <i>et al.</i> 2011) • Lateral flow of water not completely controlled in REEs (Fisher <i>et al.</i> 2006) • REEs limited because they alter only rainfall, and not temperature, VPD or radiation (Fisher <i>et al.</i> 2007) • Few actual tropical drought experiments exist (Phillips <i>et al.</i> 2009; da Costa <i>et al.</i> 2010) | <ul style="list-style-type: none"> • Mechanisms of drought-induced mortality such as embolism and cavitation not well covered in many models (Choat <i>et al.</i> 2012; Steinkamp & Hickler 2015) |

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