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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 CO<sub>2</sub> 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, CO<sub>2</sub>, 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 CO<sub>2</sub> 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 m<sup>2</sup> up to 10 km<sup>2</sup>, ‘regional’ scale as larger areas  
127 spanning >10 km<sup>2</sup> 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 CO<sub>2</sub>-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 CO<sub>2</sub>-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 CO<sub>2</sub>-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 CO<sub>2</sub>-concentrations*

311         From a plant’s perspective, it is not the role of CO<sub>2</sub> in atmospheric forcing that is  
312 most important, but its direct effect on photosynthesis and gas exchange. Since rising  
313 CO<sub>2</sub> 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 CO<sub>2</sub> has decreased resilience. In some cases,  
316 elevated CO<sub>2</sub> has increased plant leaf area thus increasing the impact of drought when it  
317 occurs (Ghannoum & Way 2011). Also, since elevated CO<sub>2</sub> 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 CO<sub>2</sub> 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 CO<sub>2</sub> can be observed close to natural sources of  
324 CO<sub>2</sub> (Haettenschwiler *et al.* 1997), derived from time-series of measured forest functions  
325 under the recent increase in CO<sub>2</sub> (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 CO<sub>2</sub>. The logistics involved in experiments manipulating  
328 atmospheric CO<sub>2</sub> 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 CO<sub>2</sub> 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 CO<sub>2</sub> 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 CO<sub>2</sub> 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 CO<sub>2</sub>-induced water response starts to  
339 become important (Leuzinger & Körner 2010; Hovenden *et al.* 2014). This CO<sub>2</sub>-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, CO<sub>2</sub> effects on forest productivity are key uncertainties. Crucial  
343 assumptions relate to whether photosynthesis and stomatal conductance are proportional  
344 to CO<sub>2</sub> 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 CO<sub>2</sub>-concentrations (Medlyn *et al.* 2011; Reyer *et al.*  
349 2014). Models that include a nitrogen cycle and interactions with CO<sub>2</sub> provide a better  
350 representation of CO<sub>2</sub> 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 CO<sub>2</sub>-effects are well-  
379 understood in the laboratory but integrating this mechanistic knowledge with experiments  
380 and observations of larger-scale CO<sub>2</sub>-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 CO<sub>2</sub> (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 CO<sub>2</sub> 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  
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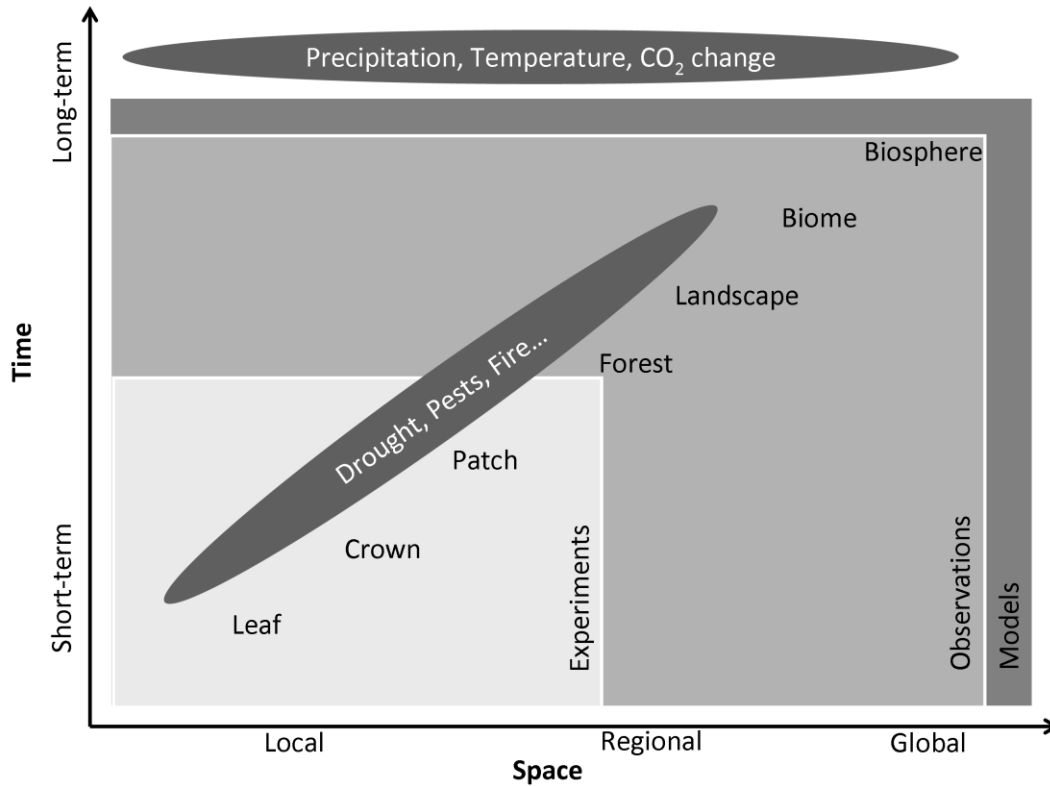
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830

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

(10-1,000 years)	<p><b>Monodominant Amazon forest</b> (Nascimento <i>et al.</i> 2014)</p> <ul style="list-style-type: none"> <li>• <b><u>Different forest types</u></b></li> <li>-<b>Drought-induced forest die-back around the world</b> (Allen <i>et al.</i> 2010)</li> <li>-Drought-induced mortality (Steinkamp &amp; Hickler 2015)</li> </ul>	<p>2013)</p> <ul style="list-style-type: none"> <li>• <b><u>Tropical</u></b></li> <li>-Climate-change induced dieback of the Amazon (Cox <i>et al.</i> 2004; Malhi <i>et al.</i> 2009 but see also Cox <i>et al.</i> 2013; Huntingford <i>et al.</i> 2013)</li> <li>• <b><u>Boreal</u></b></li> <li>-<b>Boreal biome transitions</b> (Scheffer <i>et al.</i> 2012a)</li> <li>• <b><u>Different forest types</u></b></li> <li>-<b>Drought-induced forest die-back around the world</b> (Allen <i>et al.</i> 2010)</li> </ul>	<p>2012; Hughes <i>et al.</i> 2013b; Brook <i>et al.</i> 2013; Lenton &amp; Williams 2013)</p>
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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 <sub>2</sub>	<ul style="list-style-type: none"> <li>• Long time series available only close to natural CO<sub>2</sub>-sources which usually represent very specialized environments (e.g., Haettenschwiler <i>et al.</i> 1997)</li> <li>• Europe fluxtower records are generally not yet long enough to provide long-term average references (Ciais <i>et al.</i> 2005)</li> </ul>	<ul style="list-style-type: none"> <li>• 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</li> <li>• CO<sub>2</sub> increased stepwise <b>vs.</b> gradual change in reality</li> </ul>	<ul style="list-style-type: none"> <li>• CO<sub>2</sub> assumptions in models: sink- vs. source-driven models (Cox <i>et al.</i> 2013; Fatichi <i>et al.</i> 2014)</li> <li>• Assessment of CO<sub>2</sub> response requires N availability to be included in model (Grant 2013)</li> </ul>
Temperature	<ul style="list-style-type: none"> <li>• Time series are easy to observe, but the problem is mostly the disentanglement by concurrent changes such as precipitation, CO<sub>2</sub> and nitrogen</li> </ul>	<ul style="list-style-type: none"> <li>• Lack of whole tree warming experiments</li> <li>• Mostly small spatial and temporal coverage, typically greenhouse experiments or open-top chambers</li> </ul>	<ul style="list-style-type: none"> <li>• Temperature responses in models are poorly represented</li> <li>• Acclimation of model parameters is poorly represented</li> </ul>
Drought	<ul style="list-style-type: none"> <li>• 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)</li> <li>• 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)</li> </ul>	<ul style="list-style-type: none"> <li>• Expensive, challenging and <b>laborious</b> rainfall exclusion experiments (REE) (Nepstad <i>et al.</i> 2007; Phillips <i>et al.</i> 2010; Misson <i>et al.</i> 2011)</li> <li>• Lateral flow of water not completely controlled in REEs (Fisher <i>et al.</i> 2006)</li> <li>• REEs limited because they alter only rainfall, and not temperature, VPD or radiation (Fisher <i>et al.</i> 2007)</li> <li>• Few actual tropical drought experiments exist (Phillips <i>et al.</i> 2009; da Costa <i>et al.</i> 2010)</li> </ul>	<ul style="list-style-type: none"> <li>• Mechanisms of drought-induced mortality such as embolism and cavitation not well covered in many models (Choat <i>et al.</i> 2012; Steinkamp &amp; Hickler 2015)</li> </ul>

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