SPECIAL FEATURE – ESSAY REVIEW
FOREST RESILIENCE, TIPPING POINTS AND GLOBAL CHANGE PROCESSES

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

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Summary

1. Anthropogenic global change compromises forest resilience, with profound impacts to ecosystem functions and services. This synthesis paper reflects on the current understanding of forest resilience and potential tipping points under environmental change and explores challenges to assessing responses using experiments, observations and models.

2. Forests are changing over a wide range of spatio-temporal scales, but it is often unclear whether these changes reduce resilience or represent a tipping point. Tipping points may arise from interactions across scales, as processes such as climate change, land-use change, invasive species or deforestation gradually erode resilience and increase vulnerability to extreme events. Studies covering interactions across different spatio-temporal scales are needed to further our understanding.

3. Combinations of experiments, observations and process-based models could improve our ability to project forest resilience and tipping points under global change. We discuss uncertainties in changing CO_2 concentration and quantifying tree mortality as examples.

4. *Synthesis*. As forests change at various scales, it is increasingly important to understand whether and how such changes lead to reduced resilience and potential tipping points. Understanding the mechanisms underlying forest resilience and tipping points would help in assessing risks to ecosystems and presents opportunities for ecosystem restoration and sustainable forest management.

Key-words: climate change, CO_2, drought, environmental change, mortality, plant–climate interactions, regime shifts, review, spatio-temporal scales, vulnerability

Introduction

Global environmental changes in, for instance, atmospheric CO$_2$ concentration, climate, nitrogen deposition and their interactions are affecting forests around the world (Hyvönen *et al.* 2007; Phillips *et al.* 2009; Lindner *et al.* 2010; Dietze & Moorcroft 2011; Brouwers *et al.* 2012; Poulter *et al.* 2013). These changes occur in combination with direct local anthropogenic drivers of forest change such as land conversion and intensive forest management (e.g. Malhi *et al.* 2008; Barona *et al.* 2010; DeFries *et al.* 2010; Gibbs *et al.* 2010; Kurz 2010; Vayreda *et al.* 2012; Bryan *et al.* 2013). The structural (e.g. reduction in biomass or canopy cover) and functional changes (e.g. changes in community structure) in forests in response to these global and local drivers may compromise the capacity of forest ecosystems to recover from natural or human-induced perturbations (Laurance 2004; Lenton *et al.* 2008). Resilience theory suggests that ecosystems exhibit threshold responses to changing environmental drivers and move towards a new regime when a critical threshold is exceeded (Scheffer *et al.* 2001; Scheffer & Carpenter 2003). However, while evidence for the effects of gradual environmental change on forests exists, the theory of regime shifts has rarely been tested in forest ecosystems and evidence for tipping points at which feedbacks cause ecosystems to enter alternative stable states remains sparse (Hirota *et al.* 2011).

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

Concepts and definitions

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

A typical example to illustrate these concepts is the so-called Amazon forest dieback (White, Cannell & Friend 1999; Cox *et al.* 2004; Malhi *et al.* 2008; Rammig *et al.* 2010). Model simulations including changing precipitation and/or ongoing anthropogenic deforestation in the Amazon show reduced evapotranspiration and hence lower amounts of water recycled for regional precipitation (e.g. Cox *et al.* 2004; Sampaio *et al.* 2007; Costa & Pires 2010). Such an altered hydrological cycle may lead to further tree mortality and reduces forest resilience to recover from fire and drought. Repeated occurrences of strong drought/fire years, for example in the context of El-Nino events, could drive the Amazon past a tipping point into a savanna-like state. Sampaio *et al.* (2007) suggested that at 40% deforestation, such a regime shift could occur in the Amazon basin. Hirota *et al.* (2011) predicted that the south-eastern parts of the Amazon are the least resilient and most likely to turn into savanna or a treeless state.

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

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

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

LOCAL SCALE RESPONSES

At the local scale, short-term and long-term responses to environmental change have been well documented in different types of forests (Table 1). For example, Mediterranean ecosystems have been profoundly transformed by long human use and their response is well studied across different continents. The capacity of Mediterranean ecosystems to respond

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

	Local (<~10 km²)	Regional (10 km² continental scale)	Global
Short-term (<~10 years)	**Mediterranean:** • **Drought and heat-induced tree dieback in south-west Australia (Matusick, Ruthrof & Hardy 2012; Bader *et al.* 2014)** • **Drought and fire have induced transition from forest and savannas to shrublands in south Portugal (Acácio *et al.* 2007, 2009; Acácio & Holmgren 2014)** • **Drought-induced increase in tree mortality in Spain (Camarero *et al.* 2015)** **Different forest types** • **Drought-induced forest die-back around the world (Allen *et al.* 2010)** • **Low safety margin of many species world-wide to drought stress (Choat *et al.* 2012)**	**Mediterranean** • **Drought and heat-induced patchy forest dieback and mortality across a Mediterranean climate ecoregion in south-west Australia (Brouwers *et al.* 2013; Matusick *et al.* 2013)** • **Gradual long-term declines in rainfall and increasing temperatures affecting tree health in south-west Australia (Brouwers *et al.* 2012)** **Tropical** • **Resilience of three alternative stable states of tree covers depends on precipitation in Africa, Australia and South America (Hirota *et al.* 2011)** • **Large parts of Amazon and Congo forest could be either forest or savanna, depending on fire regime (Staver, Archibald & Levin 2011)** **Boreal** • **Bark beetle-induced tree mortality in western North America (Kurz *et al.* 2008; Raffa *et al.* 2008)** • **Drought-induced dieback of aspen ecotone in mid-continental North America (Michaelian *et al.* 2011)** **Different forest types** • **Drought-induced forest dieback around the world (Allen *et al.* 2010)**	• 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 (10–1000 years)	**Tropical** • **Drought decreases biomass in a Monodominant Amazon forest (Nascimento *et al.* 2014)** **Different forest types** • **Drought-induced forest dieback around the world (Allen *et al.* 2010)** • Drought-induced mortality (Steinkamp & Hickler 2015)	**Mediterranean** • Increasing drought stress in southern Europe (van Oijen *et al.* 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)**	• State shift of the global biosphere (Barnosky *et al.* 2012; Brook *et al.* 2013; Hughes *et al.* 2013b; Lenton & Williams 2013)

to disturbances strongly interacts with climate condition. Vegetation changes in the driest regions tend to be persistent and sometimes very difficult to reverse because of positive feedbacks that maintain alternative vegetation states (Holmgren & Scheffer 2001; Acácio *et al.* 2007, 2009; Kefi *et al.* 2007). Mediterranean climate regions are likely to become drier and warmer over the decades to come (Stocker *et al.* 2013), which will likely impact on their resilience as is already occurring in south-west Western Australia (e.g. Brouwers *et al.* 2012). Here, forest tree species are increasingly showing severe dieback and mortality in response to extreme climatic conditions (Matusick, Ruthrof & Hardy 2012; Matusick *et al.* 2013; Bader *et al.* 2014), but whether this constitutes a tipping point is unclear.

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

REGIONAL-SCALE RESPONSES

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

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

For the Amazon forests, Cox *et al.* (2004) have projected a tipping point based on climate-change-induced rainfall reductions leading to vegetation–atmosphere feedbacks and further drying using coupled carbon cycle-climate models. However, in more recent studies, Cox *et al.* (2013) and Huntingford *et al.* (2013) show that the Amazon is probably more resilient than projected in the original Cox *et al.* (2004) study. This change in perspective is due to a better understanding of model uncertainties. Uncertainties with regard to parameterization and structural representation of physiological processes such as CO_2 fertilization or responses to elevated temperatures have been highlighted as being more important than uncertainties related to emission scenarios and climate projections (Huntingford *et al.* 2013). However, another study, using an Earth System Model, found projected changes in dry-season length to be the dominant single factor explaining differences in forest dieback projections (Good *et al.* 2013).

GLOBAL-SCALE RESPONSES

Recently, the potential for an anthropogenically driven global tipping point of the biosphere has been discussed (Barnosky *et al.* 2012; Brook *et al.* 2013; Hughes *et al.* 2013b; Lenton & Williams 2013). Barnosky *et al.* (2012) argue that in the past, state shifts of the totality of the global ecosystem have occurred and that a tipping point of the Earth's biosphere is plausible given the strong and enduring alterations of natural ecosystems by human interventions such as land-use change. Brook *et al.* (2013) highlighted three criteria that need to be fulfilled for such a state shift to occur globally: (i) a spatially homogenous response towards changing environmental conditions, (ii) an interconnection of responses and (iii) a spatial homogeneity of drivers of environmental change. They conclude that spatial heterogeneity in drivers of, and responses to, environmental change as well as the lack of continental connectivity is smoothing global-scale responses and will therefore unlikely result in a global tipping point (Brook *et al.* 2013). Hughes *et al.* (2013b) argue that the speed of change does not determine the presence or the absence of a global tipping point but rather the nonlinear relation between the driving force of ecosystem change and the state of the ecosystem. Lenton & Williams (2013) add that it is the existence of possible feedbacks (and the balance between positive and negative feedbacks) between different components of the Earth system that ultimately determines whether a global tipping of the biosphere exists. They also stress that a clear definition of the 'biosphere' is needed to discuss the possibility of a global tipping point. Lenton & Williams (2013) argue that although a strong global ecological response may be perceived as a tipping point of the biosphere, it is not necessarily associated with a tipping point caused by a feedback within the biosphere itself. They agree with Brook *et al.* (2013) in that interactions of smaller-scale tipping points that influence and trigger each other are more likely than a global tipping point (Lenton & Williams 2013). However, Lenton & Williams (2013) also point out that under certain circumstances, a cascade of tipping points may lead to a tipping point with a global reach.

INTERACTIONS ACROSS SCALES

Besides the individual impacts of natural and anthropogenic pressures, it is perhaps primarily the interaction of processes

across scales that determine forest resilience and tipping points (cf. Gunderson & Holling 2002). For example, the interaction of changes in longer-term mean climate with changes in short-term climate variability determines plant responses to climate change (Reyer *et al.* 2013). In regions where recent climate change has had a significant impact, tipping points may occur when extreme climatic events take place. Hence, continuous slow changes in climatic conditions alter the resilience of forests until extreme events or disturbances, such as prolonged drought, push a specific forest ecosystem across a tipping point into a new state. We therefore argue that, in regions where gradual and persistent long-term drying and warming trends are evident, forest resilience and tree health have likely decreased (e.g. van Mantgem *et al.* 2009; Brouwers *et al.* 2012). This decrease may be a consequence of idiosyncratic interactions of increasing physiological stress, altered natural disturbance regimes and comparably rapid climatic changes, which makes forests vulnerable to regime shift in the future. Similar gradual erosion of resilience through land-use change, invasive species and deforestation may increase vulnerability to extreme events pushing forests towards a tipping point.

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

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

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

Another challenge for understanding forest resilience and tipping points is that background conditions are changing, for example CO_2 concentration and temperature. Changes in human-driven pressures, such as alterations of fire regimes, deforestation, management and their interactions, also need to be considered. Consequently, to deepen our understanding of forest resilience and tipping points integrating insights from experiments, observations and modelling is needed. Experiments may be helpful to determine potential thresholds of ecosystem variables that influence tipping point behaviour, particularly when manipulating whole ecosystems (e.g. Nepstad *et al.* 2007; Brando *et al.* 2008). Observations show conditions under which tipping of a forest ecosystem is possible or has already happened (e.g. Leadley *et al.* 2010). Taken together, this understanding of resilience and tipping points may help to improve process-based models.

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

Nonetheless, because models are simplified representations of reality, they should always be considered as generators of hypotheses or projectors of possible pathways and therefore further checked against experimental and independent data on system responses. Most current forest and vegetation models were not meant to simulate tipping points and may not be able to do so because of underpinning assumption like the inclusion of equilibrium pools representing an average steady state response and the lack of feedbacks between vegetation and climate. Moreover, most models still do not contain disturbance processes (e.g. pathogens/insects, wind-throw), which are crucial for simulating mortality of trees and abrupt vegetation shifts (Steinkamp & Hickler 2015). A future challenge is to incorporate these processes in forest models to better simulate resilience and tipping points. In a first attempt, 'tipping point' behaviour could be implemented into models by introducing them explicitly, depending on threshold values. However, in that case, the model would depend totally on the parameter or threshold value imposed. The larger challenge is to build models that do not have these explicit thresholds hard-coded, but have tipping point as an emerging property as a result of the combination of the underlying processes included in the model.

Although most forest models are still limited for exploring tipping points and regime shifts, they are usually able to

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

Changing conditions	Observations	Experiments	Models
CO_2	• Long time series available only close to natural CO_2-sources, which usually represent very specialized environments (e.g. Hättenschwiler et al. 1997) • Europe flux tower records are generally not yet long enough to provide long-term average references (Ciais et al. 2005)	• Only small spatial and temporal coverage of experiments, costly, few in mature stands (Norby et al. 2010; Bader et al. 2013), no tropical forests but new FACE experiment starting in Amazon • CO_2 increased stepwise vs. gradual change in reality	• CO_2 assumptions in models: sink- vs. source-driven models (Cox et al. 2013; Fatichi, Leuzinger & Körner 2014) • Assessment of CO_2 response requires N availability to be included in model (Grant 2013)
Temperature	• Time series are easy to observe, but the problem is mostly the disentanglement by concurrent changes such as precipitation, CO_2 and nitrogen	• Lack of whole tree warming experiments • Mostly small spatial and temporal coverage, typically glasshouse experiments or open-top chambers	• Temperature responses in models are poorly represented • Acclimation of model parameters is poorly represented
Drought	• Drought and heat often act together, and their interactions need to be considered (Allen et al. 2010; Brouwers et al. 2013; Matusick et al. 2013) • Drought impact responses of forest vegetation are highly variable depending on the positioning within the landscape (Brouwers et al. 2013)	• Expensive, challenging and laborious rainfall exclusion experiments (REE) (Nepstad et al. 2007; Phillips et al. 2010; Misson et al. 2011) • Lateral flow of water not completely controlled in REEs (Fisher et al. 2006) • REEs limited because they alter only rainfall, and not temperature, VPD or radiation (Fisher et al. 2007) • Few actual tropical drought experiments exist (Phillips et al. 2009; da Costa et al. 2010)	• Mechanisms of drought-induced mortality such as embolism and cavitation not well covered in many models (Choat et al. 2012; Steinkamp & Hickler 2015)

identify indicators of reduced resilience, for example by predicting changes in biogeochemical cycles. A metric developed by Heyder *et al.* (2011) indicates severe ecosystem change highlighting loss of resilience and the potential approach of tipping points (Gerten *et al.* 2013; Warszawski *et al.* 2013). Recently, simpler ecological models have been developed that are explicitly designed to simulate regime shifts (e.g. Staver & Levin 2012; van Nes *et al.* 2013). In the following sections, we take the example of CO_2 effects and mortality as two key challenges for understanding forest resilience and tipping points under changing environmental conditions in process-based forest models.

EFFECTS OF CHANGING CO_2 CONCENTRATIONS

From a plant's perspective, it is not the role of CO_2 in atmospheric forcing that is most important, but its direct effect on photosynthesis and gas exchange. Since rising CO_2 tends to increase productivity and reduce water use, it may increase forest resilience or lead to the greening of non-forested ecosystems (e.g. Higgins & Scheiter 2012). However, there are counter-examples where rising CO_2 has decreased resilience. In some cases, elevated CO_2 has increased plant leaf area, thus increasing the impact of drought when it occurs (Ghannoum & Way 2011). Also, since elevated CO_2 reduces transpiration, leaf temperatures tend to increase, which may increase the impact of extremely high temperatures (Warren, Norby & Wullschleger 2011) and decrease resilience to frost events (Barker *et al.* 2005). Increased productivity under elevated CO_2 may also increase litter and reduce litter decomposition rates (Hyvönen *et al.* 2007), leading to increased fuel and higher vulnerability to fire.

Although the effects of elevated CO_2 can be observed close to natural sources of CO_2 (Hättenschwiler *et al.* 1997), derived from time series of measured forest functions under the recent increase in CO_2 (e.g. Keenan *et al.* 2013) or inferred from paleoecological data, experiments and models are most commonly used to study how trees and forests respond to CO_2. The logistics involved in experiments manipulating atmospheric CO_2 levels within existing forests are tremendous and explain why, to date, very few of these experiments exist in natural or semi-natural forests (Norby *et al.* 2010; Leuzinger & Bader 2012; Bader *et al.* 2013). Such experiments remain largely artificial, because the atmospheric CO_2 increase has to occur stepwise instead of gradually as in reality. Furthermore, because transpiration is affected through stomatal closure, forests under elevated atmospheric CO_2 affect local climate (e.g. air humidity). These changes, however, do not feed back on the canopy under study, as the surrounding non-treated trees dominate the climate feedbacks (see Leakey 2009). Tipping points are not to be expected via the direct CO_2 response, but rather via the much more important indirect transpiration response (Holtum & Winter 2010; Hartmann 2011). For example, the rainfall amount and pattern will determine when the CO_2-induced water response starts to become important (Leuzinger & Körner 2010; Hovenden, Newton & Wills 2014). This CO_2-induced water response is likely to be the main process that affects resilience and determines whether a forest tips into an alternate state.

In models, CO_2 effects on forest productivity are key uncertainties. Crucial assumptions relate to whether photosynthesis and stomatal conductance are proportional to CO_2 levels and how this translates to carbon sequestration, how leaf-level processes are coupled to the atmosphere, and how drought affects stomatal conductance or how rainfall is intercepted (Medlyn, Duursma & Zeppel 2011). For example, decreasing productivity under climate change may only be observed in those models that are assuming no interaction between changing temperatures and CO_2-concentrations (Medlyn, Duursma & Zeppel 2011; Reyer *et al.* 2014). Models that include a nitrogen cycle and interactions with CO_2 provide a better representation of CO_2 effects on forest productivity (Grant 2013; Zaehle *et al.* 2014).

MORTALITY

Mortality of individual trees does not mean that resilience of the forest is impaired or a tipping point may occur. However, improving our understanding of mortality will enhance our capacity to simulate forest resilience and tipping points. The mechanistic controls over tree mortality remain a major uncertainty in modelling forest resilience to drought-induced mortality (McDowell *et al.* 2011; Adams *et al.* 2013). Many tree species across the globe operate with small 'safety margins' for xylem embolism and cavitation (Choat *et al.* 2012) and vulnerability to drought is a key factor of tree mortality (Allen *et al.* 2010; Table 1). Mortality is particularly challenging to predict because tree death can occur from a variety of causes, including resource limitation, environmental stress or large-scale natural disturbance. These causes are also strongly interdependent, as reduced carbon or water stores impair a tree's capacity to defend against pests, or to withstand drought. Predicting the onset of mortality thus requires an integrated framework for quantifying critical thresholds and feedbacks in tree responses to physiological stress (McDowell *et al.* 2011).

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

COMBINATION OF METHODS

A combination of experiments, observations and models may help to better understand scale-dependent responses (Fig. 1). Leaf-level CO_2-effects are well understood in the laboratory,
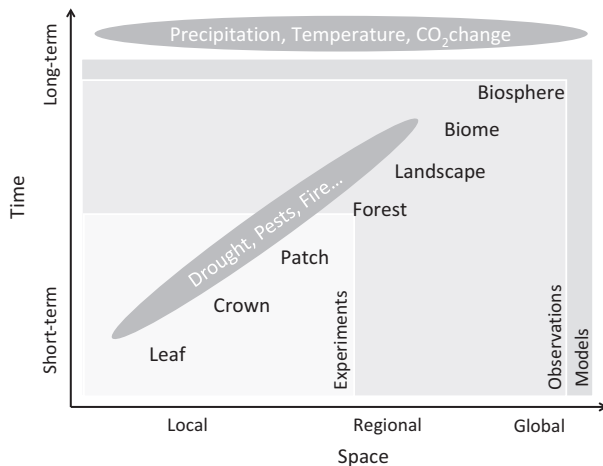
Fig. 1. Temporal and spatial scales at which different research approaches (experiments, observations and models) are available to assess forest resilience and potential tipping points. Drought, pests, fire and other processes that structure the forests such as heatwaves or also deforestation can occur across different spatio-temporal scales. Precipitation, temperature and CO_2 changes cover all spatial scales but only long time scales as we refer to them occurring within the context of climate change and not as part of short-term meteorological variability. The figure is adapted from Gunderson & Holling (2002).

but integrating this mechanistic knowledge with experiments and observations of larger-scale CO_2-effects in models in conjunction with other ecophysiological and demographic processes is necessary to paint a more realistic picture of forest responses to elevated CO_2 (Field, Jackson & Mooney 1995).

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

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

Concluding remarks

This paper shows that forests are changing over a wide range of spatial and temporal scales. There seems to be more evidence for ongoing changes at smaller spatial and shorter temporal scales and in particular areas such as the Mediterranean. But also larger and longer spatio-temporal scales as well as other forest types face strong changes (Table 1). However, in many cases, it is not clear whether these changes reduce resilience or whether a tipping point is about to be reached. Our synthesis indicates that global-scale disruptions of forest ecosystems are unlikely. We argue that studies covering interactions across a range of spatio-temporal scales are needed to further our understanding of forest resilience and tipping points. Changing CO_2 concentration and tree mortality are processes that require an integration of results from experiments, observations and models to improve the ability of process-based models to simulate forest resilience and potential tipping points.

While acknowledging the important role of gradual changes in affecting resilience of forests under global change and the lack of evidence for mechanisms leading to tipping points, we stress that tipping points are important to investigate from a risk assessment perspective. This means that even though a low likelihood is attributed to a specific high-impact event such as a tipping point, it is still important to discuss whether we are willing to risk such events occurring, especially, because reduced resilience and potential tipping points may have a profound effect on ecosystem functions and services. Such an approach requires an assessment of how society values ecosystem functions and services and would benefit from framing forests as social–ecological systems affected by press and pulse dynamics (cf. Collins *et al.* 2011). At the same time, a better understanding of resilience and tipping points may actually highlight opportunities for ecosystem restoration (e.g. Holmgren *et al.* 2013) or sustainable forest management (Puettmann, Coates & Messier 2009; Rist & Moen 2013), which may provide strong co-benefits for improving human livelihoods.

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Data accessibility

This synthesis paper does not use original data.

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