IDEAS AND PERSPECTIVES

Tree growth sensitivity to climate is temporally variable

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Abstract
Despite a long history of discussion of 'non-stationarity' in dendrochronology, researchers and modellers in diverse fields commonly rely on the implicit assumption that tree growth responds to climate drivers in the same way at any given time. Synthesising recent work on drought legacies and other climate-related phenomena, we show tree growth responses to climate are temporally variable, and that abrupt variability is commonly observed in response to diverse events. Thus, we put forth a 'growth-climate sensitivity' framework for understanding temporal variability (including non-stationarity) in the sensitivity of tree growth to climate. We argue that temporal variability is ubiquitous, illustrating limits to the ways in which tree growth is often conceptualised. We present two conceptual hypotheses (homoeostatic sensitivity and dynamic sensitivity) for how tree growth sensitivity to climate varies, and evaluate the evidence for each. In doing so, we hope to motivate increased investigation of the temporal variability in tree growth through innovative disturbance or drought experiments, particularly via the inclusion of recovery treatments. Focusing on growth-climate sensitivity and its temporal variability can improve prediction of the future states and functioning of trees under climate change, and has the potential to be incorporable into predictive dynamic vegetation models.

Keywords
Climate change, divergence, drought, legacies, memory, sensitivity, stationarity, temporal variability, tree rings.

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INTRODUCTION

Dynamics and processes governing the states and variability in tree growth are critical drivers of terrestrial biosphere responses to climate change. Forests are major components of global carbon fluxes and sinks (Bonan 2008; Pan *et al.* 2011), and predicting their behaviour under increasingly novel regional and global climate events (Overpeck 2013; Sobel *et al.* 2016; Richardson et al. 2018) is challenging (Luo *et al.* 2015), but also essential to forecasting impacts of future climate change on the terrestrial biosphere. Unfortunately for modellers, trees are long-lived organisms, and their responses to climate integrate variability across multiple time scales, from sub-daily to centuries. This 'integration' of antecedent climate has been evaluated with tree-ring data sets through a variety of approaches both classically (Fritts *et al.* 1971; LaMarche 1974), and more recently in studies considering multi-year lags (e.g. Sarris *et al.* 2007, Mazza and Manetti 2013, Bond-Lamberty *et al.* 2014, Peltier *et al.* 2018). The explanatory power of these approaches, however, still tends to be relatively poor, particularly considering the huge amount of tree-ring data available across species, elevations and continents (Zhao *et al.* 2018), and the over-representation of trees that are highly sensitive to climate in available data sets (Nehrbass-Ahles *et al.* 2014; Klesse *et al.* 2018; Gut *et al.* 2019). Any aspiring

dendrochronologist may be surprised to find it can be challenging to detect strong correlations among tree-ring widths and any single climatic variable, and a number of methods have been developed for discovering these correlations (e.g. response coefficients; Fritts 1962, Blasing *et al.* 1986). Even so, at the individual-level, tree-ring widths may not clearly relate to climate, and the strongest correlations tend to emerge at larger spatial scales, beyond the plot level (e.g. Swetnam 1993, Stahle *et al.* 2000).

Once a strong relationship between growth (ring widths) and climate is established, tree growth is often conceptualised as a constant function of climate covariates. That is one often assumes that (1) given sufficient knowledge of the strength and direction of the relationships, (2) tree growth can be predicted at any time as a constant function of those climate covariates. Implicit is the assumption that trees *respond in the same way at any given time* to climate drivers, by producing a certain amount of growth given particular values of these drivers. This may be familiar to some as the dendrochronological interpretation of the principle of uniformity (Fritts & Swetnam 1989), more specifically referred to as *stationarity* (Wilmking *et al.* 2017). *Stationarity* is a key assumption of dendrochronological reconstructions – it would be impossible to reconstruct past climates if trees responded differently to climate in the past than they did during the instrumental

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record. At large scales, summarising across many individuals, *stationarity* is often supported, particularly after detrending to remove troublesome 'biological' information.

For example 'age effects' are removed through a variety of approaches (reviewed in Fritts and Swetnam 1989), and more flexible spline-based approaches can remove other biological information (e.g. competition, Cook & Peters 1981). The goal of such detrending is to remove variability unrelated to climate, enhancing the underlying climate signal. In reality though, isolation of climate signals can be extremely challenging, particularly in the presence of low-frequency variability (Cook *et al.* 1995; Melvin & Briffa 2008). However, for the purposes of modelling and predicting carbon fluxes and stocks across the terrestrial biosphere, the absolute magnitude of secondary growth in trees is important, rather than standardised growth indices, given that absolute growth is directly related to carbon fluxes (Rocha *et al.* 2006; Teets *et al.* 2018). As we argue below, while *stationarity* may adequately describe average responses at large scales (e.g. regional tree-ring networks), individual trees may still experience transient perturbations or directional changes in their climate responses.

Such *non-stationarity* of tree growth-climate sensitivities has been frequently discussed in dendrochronology (Fritts *et al.* 1971). While software tools for evaluating the stationarity of growth–climate relationships have existed for some time (Biondi & Waikul 2004), a recent meta-analysis has shown stationarity was ignored or tests were inadequate to detect it in about 2/3 of nearly 2000 published studies (Wilmking *et al.* 2020). Despite evidence for non-stationarity in a majority of these studies, average citation counts show studies assuming stationarity received twice the number of citations as those that did not (Wilmking *et al.* 2020). This suggests that while discussion of non-stationarity in dendrochronology has existed for many years, awareness of non-stationarity is not widespread, or is ignored, perhaps particularly among non-specialists. Non-stationarity as considered in dendrochronology tends to describe or imply smooth changes in growth–climate relationships, and it is often treated as a feature to be removed or minimised by detrending approaches. This has primarily been evaluated via simplistic moving window approaches with a common window size of 30 years (Biondi & Waikul 2004; Wilmking *et al.* 2020). As we will argue, changes in tree growth response to climate variables can in fact be abrupt, occur from one year to the next, can occur following diverse events, and arises from physiological processes that are not well understood.

Expanding upon the concept of non-stationarity, we posit that, in general, trees do not respond to climate drivers in the same way at any given time (Fig. 1). While average responses are a useful statistical framework that can robustly represent overall growth behaviours, if the state of predictive models and knowledge of tree function are to be advanced, we argue it is time for explicit consideration of the temporal variability in tree growth responses to climate. This is particularly relevant as predictions are extended further into the future, and thus into increasingly novel climatic conditions (Seager *et al.* 2007; Mora *et al.* 2013; Williams *et al.* 2013).

Here, we define *temporal variability in tree growth sensitivity* as any change in the quantifiable response of tree growth
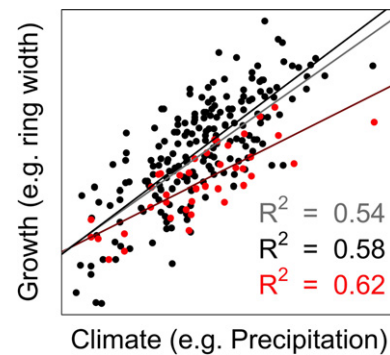
Figure 1 Tree growth in relationship to a climate covariate, such as precipitation, based on simulated data that is representative of typical patterns seen in real data. The black symbols depict trees in a 'normal' state, and red symbols depict trees in a 'perturbed' state, such as would occur immediately following severe drought events (but after the drought has passed). A linear regression was fit to all points (both states combined) to illustrate the 'average' relationship that would be inferred from such data (gray line; associated R2 given in gray). Separate regressions for each tree state were also conducted (normal: black line and text; perturbed: red line and text). While the average fit to all points is adequate, it misses the detail that trees are less sensitive to precipitation following drought events (shallower slope of red versus gray line). That is, the sensitivity of trees to precipitation is temporally variable.

(usually ring width) to climate variables; for ease, we will refer to this as *variable growth-climate sensitivity*. Variable growth-climate sensitivity is distinct from the direct impacts of some event on the amount of growth, wherein perturbations (e.g. low seasonal precipitation) can alter (e.g. reduce) growth without altering the sensitivity of growth to climate. Variable growth-climate sensitivity describes how trees experiencing the same climate forcing at different times (or under different physiological states) may respond differently to that climate forcing, as measured through the increment of growth produced in response to that forcing (Fig. 1). For example if tree A experienced a severe disturbance (e.g. defoliation) in the previous year, it may grow less than expected under average seasonal precipitation, given the historical average growth response to precipitation. In contrast, growth in tree B, which did not experience a recent disturbance, may exhibit a growth response to this same 'average precipitation' that more closely matches the historical average growth response to precipitation. Another way to conceptualise this is that tree A and tree B are in different physiological states, and despite receiving the same amount of water in a particular year, they do not produce the same amount of growth.

While there are many physiological or physical processes that could lead to variable growth-climate sensitivity, from a modelling or forecasting perspective, each would lead to altered correlation among tree-ring widths and climate. We suggest that abstracting numerous and somewhat poorly known potential physiological impacts into changes in the sensitivity of tree growth to climate is a useful strategy. This is particularly true because we are increasingly interested in improving our ability to predict the responses of trees and forests to climatic variability in the context of ongoing and future climate change.

Thus, variable growth-climate sensitivity encompasses earlier dendrochronological concepts of non-stationarity, including those related to the so-called 'divergence problem' (discussed later), but also includes more recently quantified drought legacies and other phenomena. As we will describe, while the mechanisms underlying certain processes (e.g. masting or nutrient pulses) leading to variable growth-climate sensitivity may be apparent (Reimchen & Arbellay 2019), others (e.g. drought legacies, decline or lagged mortality, climate change forcings) are still poorly understood (Peltier & Ogle 2019b). The impacts of these drivers, however, are all potentially quantifiable through their effects on the sensitivity of tree growth to climate, with potentially strong links to key quantities of interest, such as aboveground biomass, carbon fluxes and transpiration. Additionally, the large amount of existing tree-ring data provides myriad opportunities to explore these concepts (Zhao *et al.* 2018), results from which can motivate new manipulative experiments (discussed later).

We first briefly describe the breadth of recent and past research documenting variable tree growth-climate sensitivity in response to numerous processes, demonstrating the ubiquity of variable sensitivity, and pointing towards potential underlying mechanisms. Consequently, we hypothesise (H1) that tree growth-climate sensitivities quantified through typical statistical methods are representative of 'target' growth-climate sensitivities (homeostatic sensitivity). Distinct from the concept of *stationarity* (Fig. 2a), *homeostatic sensitivity* describes trees that respond similarly to climate across time and over a range of conditions according to some baseline growth-climate sensitivity (Fig. 2b, line A). That is trees usually produce a certain amount of growth in response to specific climate conditions (target sensitivity). However, sufficiently extreme temporary conditions or states may perturb tree physiological homeostasis, leading to deviations from that target or baseline sensitivity (Fig. 2b). An implication of this hypothesis is that trees will return to their target growth-climate sensitivity (i.e. homeostasis) given sufficient time and favourable conditions (see *Drought legacies*), or die if conditions do not improve (see *Directional changes*). Thus, trees would still appear to exhibit *stationarity* at large scales and over long time periods (Fig. 2b, line A), and would only show variable sensitivity under extreme physiological perturbations or disturbance during short intervals (Fig. 2b, recovery period). We also propose a competing hypothesis (H2) where a target sensitivity does not exist. Here, tree growth sensitivity to climate is an emergent property of inter-annually dynamic prioritisation of different physiological functions, particularly allocation of carbon resources (dynamic sensitivity, Fig. 2c). Under H2, growth-climate sensitivities vary over time, and sensitivity estimates assuming *stationarity* essentially average these dynamic sensitivities over the period of investigation. Under this hypothesis, the interpretation of *stationarity* would be different, simply reflecting that limiting factors (say low precipitation) at a given site or region tend not to change very often.

We emphasise that the homeostatic and dynamic sensitivity hypotheses are not mutually exclusive, but represent conceptual endpoints for thinking about tree growth-climate sensitivities. For example one might imagine a tree maintains a target
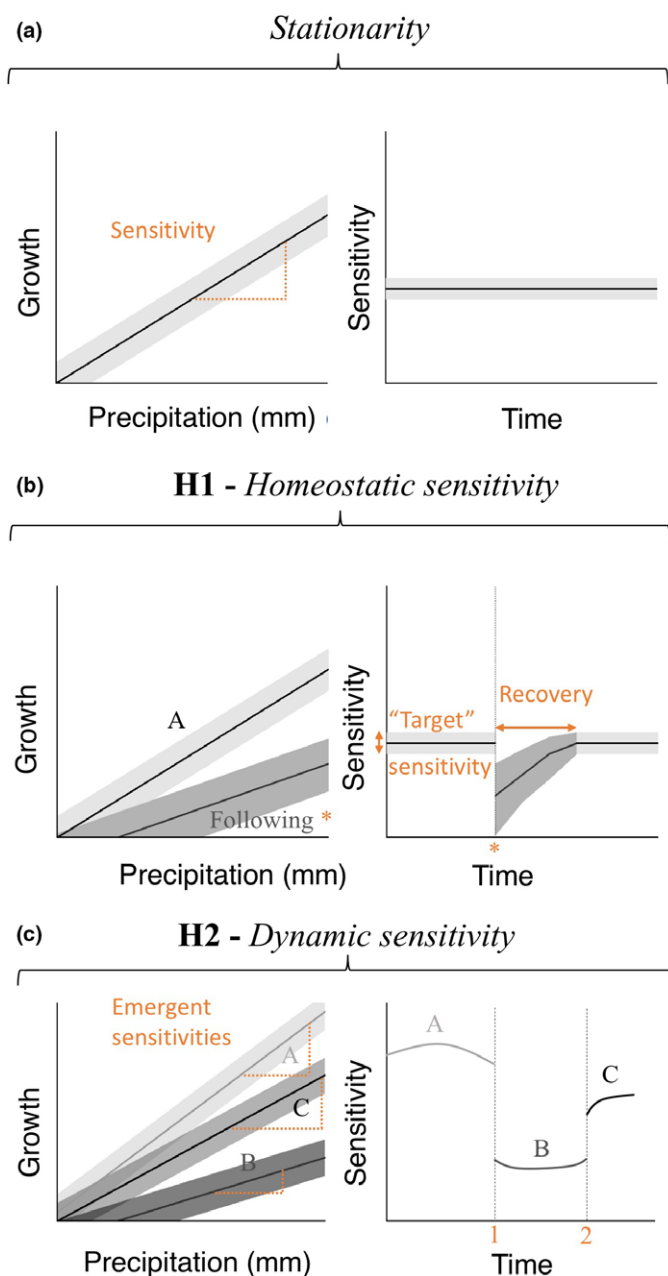
Figure 2 Three hypotheses for tree growth-climate sensitivity, shown as the slope of a given growth-climate relationship. (a) Growth-climate sensitivity is often treated as temporally invariant at large scales or across long time periods, following the principle of stationarity. Thus, growth responds in the same way at all times to precipitation, leading to constant sensitivity across time (black lines with gray shading). However, in individual trees and under certain situations, sensitivity may vary with time. Two new hypotheses for how variable growth-climate sensitivities may emerge are: (b) homeostatic sensitivity (H1), where trees generally maintain a target, baseline sensitivity (A, black lines, light gray shading), where growth-climate sensitivity only changes (gray lines, dark gray shading) following after trees experience a significant perturbation (orange asterisk) to physiologic homeostasis; and (c) dynamic sensitivity (H2), where a target sensitivity does not exist, but rather growth-climate sensitivity is an emergent property of the physiological status of trees at any given time, and thus can vary over time. Physiological states give rise to different 'emergent' growth-climate sensitivities, and thus, these sensitivities vary across time, as illustrated for a tree at times A (light gray lines and light gray shading), B (dark gray lines and dark gray shading), and C (black lines and medium gray shading) across two state changes occurring at time 1 and 2.

sensitivity until a sufficiently extreme perturbation induces a state change (hysteresis), leading to homeostasis around a new (altered) growth-climate sensitivity. Homeostatic growth-climate sensitivity is likely to emerge from homeostasis in other tree traits, such as root-shoot ratio, hydraulic conductance, or labile carbon stores (examples below). However, both hypotheses (homeostatic vs. dynamic) require recognition of the temporal variability in tree growth-climate sensitivity, and provide different lenses for conceptualising this variability in the examples described below.

TEMPORAL VARIABILITY IN GROWTH-CLIMATE SENSITIVITY IS UBIQUITOUS

Perhaps the strongest evidence for variable growth-climate sensitivity comes from recent work documenting widespread legacies of drought in tree growth (Anderegg *et al.* 2015). Using a large tree-ring data set, Anderegg *et al.* (2015) quantified the responses of ring-width chronologies to cumulative water deficit (a drought or moisture index) for the years before drought events. Prediction of ring-width in the 1–4 years following drought using the same pre-drought responses led to systematic prediction error, whereby ring-width was over-predicted by the pre-drought climate sensitivities (Anderegg *et al.* 2015). Thus, this study implies altered (reduced) ring-width sensitivity to moisture availability is a common, global response of trees to many unique drought events. Unlike evidence for non-stationarity from the dendrochronology literature (see below), this study quantifies abrupt, disjunct changes in growth-climate sensitivity, where sensitivity is significantly perturbed from 1 year (drought year) to the next (year after drought).

Other studies have followed, including quantification of legacies occurring at the ecosystem scale from eddy-flux covariance data sets (Schwalm *et al.* 2017), and numerous other tree-ring based studies focused on the southwestern US (Peltier *et al.* 2016; Gao *et al.* 2018; Peltier & Ogle 2019a), the western US (Peltier & Ogle 2019b), the eastern US (Kannenberg *et al.* 2018), the conterminous US (Dannenberg *et al.* 2019), the Northern Hemisphere (Wu *et al.* 2018), and global syntheses (Yin & Bauerle 2017; Huang *et al.* 2018). Drought legacies have also been shown in tree seedlings in the tropics (O'Brien *et al.* 2017). Many of these studies implicitly assume homeostatic sensitivity (H1), as most quantify a recovery period, equivalent to the amount of time it takes for trees to return to a target growth-climate sensitivity.

Given the growing body of work exploring drought legacies, studies explicitly interested in experimentally identifying the mechanisms underlying lagged drought recovery are emerging. However, a key challenge is that legacies are most easily detected at large spatial scales. With few exceptions, detection of drought legacies is accomplished by data syntheses, primarily using tree-ring or flux-tower networks (Anderegg *et al.* 2015; Peltier *et al.* 2016; Schwalm *et al.* 2017; Jiang *et al.* 2019). Drought legacies at large scales are generally associated with at most about a 10% decrease in growth in the year after drought (Anderegg *et al.* 2015). However, changes in growth-climate sensitivity may not be extremely large (Fig. 1), so tree- and site-level variability likely obscures these patterns at

smaller scales. Perhaps for this reason, our mechanistic insight is currently limited to generalisations made from large-scale syntheses. To promote broader exploration of the drivers and causal factors underlying drought legacies, and variable growth-climate sensitivity in general, *we highlight four general classes of mechanisms of variable growth-climate sensitivity*. In doing so, we argue that these mechanisms each impact growth-climate sensitivity and carbon status, quantities that can be readily incorporable into predictive models. The four classes of mechanisms include: physical, hydraulic, carbon source-sink dynamics and structural. We argue that the mechanisms underlying how individual trees differentially respond to climate during different time periods – particularly physiological processes – are not fully understood, but can be explored using tree rings and focused experimental design.

WHAT ARE THE UNDERLYING MECHANISMS?

Physical factors describe changes in growth-climate sensitivity not arising directly from changes in tree physiology. For example access to and recharge of deep soil water may be an important factor underlying precipitation and drought legacies. Some trees rely on deep soil water, and in some cases this can be extremely deep (e.g. >10 m; Nardini *et al.* 2016). Observations of 'rock-moisture' and co-occurring roots at depths > 15 m suggest deep soil water reserves may decouple trees from current climate conditions (Rempe & Dietrich 2018). Access to deep sources is also likely a major factor in the unexpected survival of *Pinus edulis* trees under severe experimental drought and heat in New Mexico (McDowell *et al.* 2019). We suggest that under multi-year or extreme drought events, trees may exhaust more shallow or intermediate water sources, and thus be 'forced' to explore deeper sources, where they have comparatively fewer roots. Intermediate and deep water sources are often recharged infrequently, making soil water scarce in subsequent years, and leading to uncharacteristically reduced growth responses to precipitation inputs. It follows that improved understanding of how mature trees (particularly large ones [Kerhoulas & Kane 2012]) access and utilise different soil water sources is likely necessary to make these observations generalisable towards prediction. These physical impacts are difficult to differentiate from their downstream effects on tree physiology (e.g. cavitation, see below). As we argue later, an intermediate solution is to quantify the impact of severe drought on tree growth-climate sensitivities in diverse environments. But, improved characterisation of the physiological status of impacted trees could distinguish physical versus physiological causes of variable growth-climate sensitivities.

From the perspective of drought legacies, lasting *hydraulic* damage is perhaps the most commonly invoked mechanism, and was the primary cause posited by Anderegg *et al.* (2015), who showed larger legacy effects were more often found in species with lower hydraulic safety margins. Cavitation-induced changes in sapwood conducting area are highly consistent with *homeostatic sensitivity*, where trees must regain lost sapwood conducting area to achieve pre-drought growth-climate sensitivities. For example Trugman *et al.* (2018) showed multiple drought-related phenomena could be reproduced by

a simulation model that incorporated drought-induced loss of sapwood conducting area. In particular, their model could simulate drought legacies in addition to greater mortality of larger or older trees during drought (Stovall *et al.* 2019), and for multiple years after drought (e.g. Bigler *et al.* 2007), consistent with Darcy's law (McDowell & Allen 2015). A key component of this model was the interaction between carbon demands for xylem regrowth in post-drought years (to replace cavitated sapwood) and photosynthetic production of carbon by a water-limited canopy (due to the loss of sapwood conductance; Trugman *et al.* 2018). Lagged tree mortality occurred when trees were unable to close the gap between canopy water demands and stem conductance capacity, resulting in inability to achieve positive carbon balance. Larger trees were more likely to die because they produced narrower rings, and thus required more years of post-drought growth to regain a given sapwood area. Hence, short-term limitations imposed by hydraulic damage can change the way that trees respond to climate, leading to temporal variation in growth-climate sensitivity. These types of dynamics have also been observed in growth-climate sensitivities of dying trees (see *directional changes*), where *homeostatic sensitivity* arises from trees balancing carbon and water demands, and trees die when they fail to return to their target growth-climate sensitivities.

Carbon source-sink dynamics are perhaps the most poorly understood potential mechanisms contributing to variable growth-climate sensitivity. In particular, changes in the size, location, or mobility of transient stores of non-structural carbohydrates (NSCs) during drought events likely play a prominent role in slow recovery. NSCs are drawn upon to support early season wood growth, particularly earlywood (Belmecheri *et al.* 2018; Szejner *et al.* 2018). In the post-drought recovery period, there is some evidence that NSCs are preferentially allocated to either damaged canopies as photosynthesis is upregulated (Kannenberg *et al.* 2019), or to the rhizosphere to prioritise soil resource scavenging (Hagedorn *et al.* 2016). These two studies, in particular, suggest a strategy for returning to and maintaining a target growth-climate sensitivity via preferential allocation of NSCs to different sinks. At shorter time-scales, direct environmental (climatic) limitations on the activity of carbon sinks may promote accumulation of NSCs (Fatichi *et al.* 2014), which could lead to subsequent variation in growth-climate response or lagged growth surpluses (McDowell 2011). Under *dynamic sensitivity*, growth-climate sensitivities, particularly of earlywood formation, could simply emerge from the balance of available NSCs and sink demands for carbon, whereas *homeostatic sensitivity* may result from trees preferentially reallocating NSC reserves following stress. Consequently, variability in recovery times across species, sites, or individuals could be associated with variability in pre-drought NSC pool size, differences in NSC allocation priorities, or differences in the climatic sensitivity of different carbon sinks. Understanding the importance of carbon source-sink dynamics to variable growth-climate sensitivity requires improved understanding of NSC dynamics, especially the role of deep or old NSC reserves (Carbone *et al.* 2013).

Structural changes to trees are most consistent with a *dynamic sensitivity* hypothesis, where stress induced changes in crown or hydraulic architecture, particularly the ratios of biomass partitioned among different organs, may result in different emergent growth-climate sensitivities. For example crown damage may lead to slow recovery of tree growth following drought events. This may be particularly important in conifers with annual needle crops, which rely on previous year's needles for some component of their assimilatory capacity (LaMarche Jr & Stockton 1974; Fritts 1976). Drought stress could reduce photosynthetic capacity of older needles (Naidu *et al.* 1993; Balster & Marshall 2000), or result in the dropping of older needles. This reduction in crown area could influence tree growth for multiple subsequent years if multiple needle cohorts are required to regain pre-drought total leaf area (suggested in Peltier *et al.* 2016). Similar effects could result from coarse-scale crown damage, such as branch shedding or dieback under drought (Rood *et al.* 2000). This dynamic has recently been referred to as 'structural overshoot', where tree crowns may be built up during climatically favourable periods, but become mismatched to climate during subsequent dry periods (Jump *et al.* 2017). Of course, climatic, disturbance or insect-related stress also alters xylem and sapwood features, including ring widths. Narrower rings contain fewer conduits (compared to wider rings), and in individuals or species where a small number of active sapwood rings support hydraulic conductance, successive narrow rings may subsequently limit tree growth, even under favourable conditions, if they limit water supply to the crown.

That growth-climate sensitivities may be emergent from the structure and form of individual trees is particularly obvious in closed-canopy forests where competition is a major driver of both function and survival (Purves *et al.* 2007; Arellano *et al.* 2019). Whether or not growth-climate sensitivities can be considered homeostatic might depend on the degree to which a tree species' allometric relationships are constrained by interactions with other individuals. This may consequently be less important in semi-arid or Mediterranean forests with more open canopies than in temperate or tropical systems. But the drivers of drought legacies then might vary across space, where favourable climatic conditions may result in greater competitive impacts on drought recovery (Schemske *et al.* 2009). In support of this idea, drought recovery time has been shown to be long in tropical forests, but also in boreal forests (Schwalm *et al.* 2017).

OTHER PERTURBATIONS TO GROWTH-CLIMATE SENSITIVITY

Other perturbations distinct from drought can also lead to variable growth-climate sensitivity, and seem most consistent with *dynamic sensitivity*. Because growth is inherently a function of carbon (NSC) availability – although, some component of growth is controlled directly by climate via temperature (Hoch *et al.* 2002) or water availability (McDowell 2011) – we may posit that any event or process that leads to significant changes in the carbon status of a tree may in turn lead to changes in the growth response of that tree to climate. We thus suggest other perturbations to a tree's growth-climate sensitivity are best contextualised as changes in the availability or allocation of NSCs within trees, resulting in

dynamic sensitivity. Evidence for this appears in recent work showing that lagged effects of climate on ring widths in beech (*Fagus sylvatica*) are explained by masting (Hacket-Pain *et al.* 2018); that is a shift in allocation away from secondary growth towards reproduction. Similarly, outbreaks of defoliating insects likely lead to similar legacies as carbon is diverted away from radial growth in favour of foliage regrowth during recovery (e.g. Speer *et al.* 2001). Reimchen and Arbellay (2019) have also documented extensive lags (up to 5 years) in the growth responses of riparian trees to salmon runs. These lags imply that the associated nutrient pulses led to multi-year changes in how trees respond to climate (*dynamic sensitivity*), likely because of altered resource stoichiometry (Sterner & Elser 2002) and associated shifts in tree carbon balance.

At large spatial scales, extremely wet years, not just drought years, can have lasting legacies on tree growth (Jiang *et al.* 2019). Similar to Anderegg *et al.* (2015), Jiang *et al.* (2019) fit a linear model to ring-width data using moisture-related climate covariates between 1948 and 2013, and compared model predictions to actual ring widths after both extreme dry (drought) and wet events. While they confirmed over-prediction of ring widths following droughts, they also found the model under-predicted growth after extremely wet years, and the under-prediction errors were comparable both in magnitude ($93 \pm 8\%$) and duration (1–5 years) to the drought over-prediction errors (Jiang *et al.* 2019, but see Dannenberg *et al.* 2019). Across space, they also showed these 'moisture legacies' were largest and most prevalent in more arid regions, suggesting trees are more sensitive to climate (moisture) if they have recently experienced a very favourable year, but only if they grow in moisture-limited sites. In combination with drought legacies, this work provides the strongest support for the argument that variable growth-climate sensitivity is widespread and common, and it suggests that such sensitivity is likely dynamically determined by available moisture or NSC resources. We argue that NSCs are an important driver of both legacy and non-legacy related growth-climate variability, as NSC reserves represent the link between past conditions and current physiological behaviour (i.e. growth).

DIRECTIONAL CHANGES

There can also be directional changes in tree growth-climate sensitivities. Examples include loss of vigour or tree growth 'decline', where trees that died after a disturbance (e.g. drought) exhibited altered growth sensitivities for many years prior to death (e.g. Ogle *et al.* 2000, Bigler *et al.* 2007). A global synthesis of tree growth patterns preceding mortality has shown this dynamic to be widespread and consistent across different taxonomic groups (particularly for gymnosperms; Cailleret *et al.* 2017). Decline processes offer some support for homeostatic sensitivity (H1), as trees that fail to return to some target growth-climate sensitivity (pre-disturbance sensitivity) eventually die. This suggests that an improved understanding of the drivers and mechanisms of variable growth-climate sensitivities may also lead to improved understanding of factors underlying tree mortality.

The 'divergence problem' is perhaps the most acknowledged directional change in tree responses to climate. Divergence is most consistent with dynamic sensitivity (H2), where the inferred temperature signal in tree-ring time-series changed during the last half-century (Jacoby & D'Arrigo 1995; D'Arrigo *et al.* 2008; Salzer *et al.* 2014). For trees in certain high latitude or high elevation sites, temperatures reconstructed from tree-ring widths have recently diverged from observed temperatures, suggesting non-stationarity in their growth-climate (temperature) sensitivity. This non-stationarity could reflect changes in the drivers of tree growth at these sites, or changes in the carbon balance of these trees (Hoch *et al.* 2002). Other anthropogenic causes of divergence, including increased drought stress or changes in the relative limitations placed on growth by temperature and moisture, are also suggested (D'Arrigo *et al.* 2008). It is unclear if there is a single mechanism underlying divergence, but global change factors, such as rising atmospheric CO_2 concentrations or other anthropogenic influences (Levesque *et al.* 2017; Peñuelas *et al.* 2017; Maxwell *et al.* 2019), may alter tree growth-climate sensitivities at other sites. For example this has been demonstrated in the decoupling of tree growth and summer moisture for *Abies cephalonica* on an island in Greece (Koutavas 2013). Changes in the carbon balance could lead to differences in how trees translate climate variation into growth, and thus *dynamic sensitivity* (Fig. 2c), perhaps through altered carbon allocation priorities or timing. For example warmer temperatures can lead to altered growth phenology (Adams *et al.* 2015), potentially leading to changes in the timing of seasonal carbon uptake and respiration.

Whether or not global increases in moisture limitation of forested ecosystems (Babst *et al.* 2019) are linked to changes in the sensitivity of tree growth remains unknown. We suggest, however, that widespread changes in the sensitivity of tree growth to precipitation are possible under increasing aridity, especially if the relative limitations of different climate variables on growth are altered by changing mean climate conditions (Stine & Huybers 2017; Stine 2019). Changes in growth-climate sensitivity might also reflect changes in tree physiological states, particularly related to changes in carbon source-sink dynamics or reduction in mean sapwood area across time. Unfortunately, we lack a predictive understanding of variable growth-climate sensitivity, in part because we have limited understanding of the dominant mechanisms and how they may interact. The mechanisms described herein are variously noted in other studies, but researchers tend to emphasise their preferred explanation, and no study is comprehensive in its interpretations (with respect to mechanisms). In this way, the dialogue around changes in growth-climate sensitivity, and drought legacies in particular, is reminiscent of discussions on the mechanisms of drought-induced tree mortality (McDowell *et al.* 2008). In reality, just as in those discussions, underlying causes of variable growth-climate sensitivity lie at the intersection of multiple co-occurring and inter-related physiological processes (Sevanto *et al.* 2014). Thus we ask: how do we go about (1) predicting temporal variability in growth-climate sensitivity? And, (2) how do we improve our understanding of its drivers?
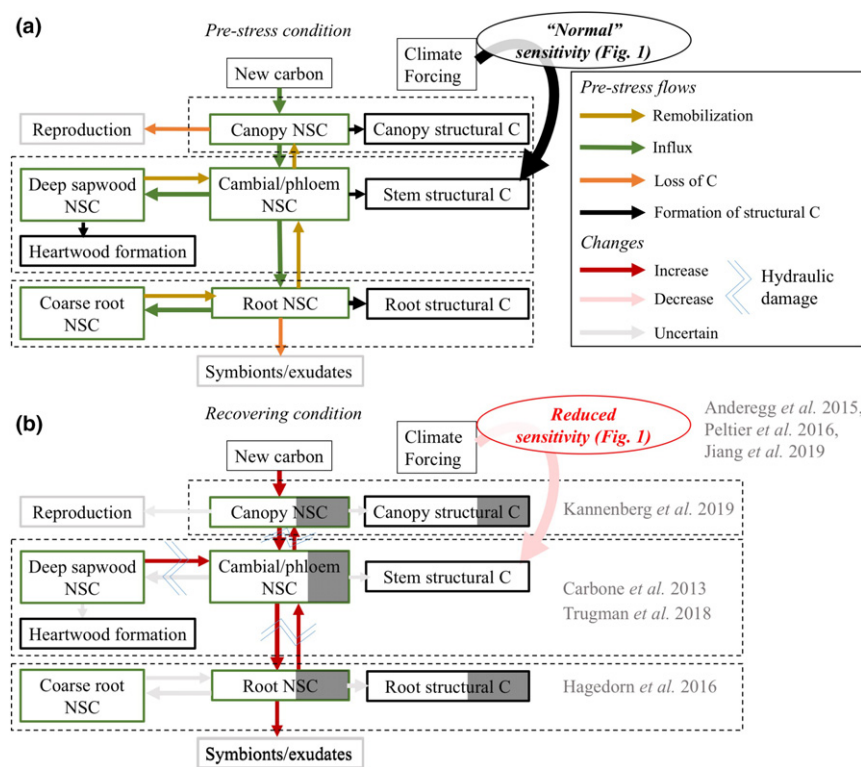
Figure 3 A simplified representation of major pools (boxes) and fluxes (arrows) of non-structural carbohydrates within trees under (a) non-stressed conditions and (b) in a recovering condition following, for example, a drought event. The potential effects of hydraulic damage are indicated by zig-zagged blue lines across certain fluxes. The color of flux arrows in (a) indicates the type of flux (remobilization, yellow; influx, green; loss, orange; or formation of structural C, black). The color of flux arrows in (b) indicates hypothesized changes in the flux rate during the recovering period (where gray indicates uncertain changes), and dark gray shading of pools indicates a reduction in the pool size compared to non-stressed pool sizes (more gray area = greater reduction). Gray text at right in (b) indicates key publications quantifying or exploring post-drought changes in relevant sensitivities, pools, or processes.

REVISITING OUR (CONCEPTUAL) MODELS

Given the evidence across multiple time scales, and in response to diverse types of events and drivers, temporal variability in tree growth-climate sensitivity should be considered in predictive models of individuals and land surfaces. These responses are only partially captured by the current generation of land carbon models, which tend to underestimate the severity and duration of drought impacts on productivity (Kolus *et al.* 2019), and it remains unclear whether a single modelling framework or statistical approach is capable of improved representation (e.g. Bond-Lamberty *et al.* 2014; Ogle *et al.* 2015; Trugman *et al.* 2019). As we have shown, many causes of variable growth-climate sensitivity likely arise from or can be conceptualised as changes in the supply or allocation of NSC reserves within individual trees (perhaps most consistent with *dynamic sensitivity*, H2). Hence, continuing improvement of dynamic carbon allocation schemes within dynamic global vegetation models (DGVMs, De Kauwe *et al.* 2014; Gim *et al.* 2017; Montané *et al.* 2017), and for individual- or cohort-based models (Fisher *et al.* 2018), is an obvious first step to include variable growth-climate sensitivity. But, this can only capture certain elements of variable growth-climate sensitivity, as changes in carbon (NSC) pool sizes and allocation priorities among organs may be a consequence of other factors (e.g. hydraulic damage, crown area reductions), rather than the root causal factor. As we have

argued, many underlying mechanisms are potentially interconnected. For example while drought may induce organism wide changes in allocation and carbon pool sizes, some of these changes are a consequence of induced physiological constraints (e.g. hydraulic damage), which do not change the size of structural carbon stocks (e.g. stem structural carbon) but rather render a portion of those stocks non-functional (e.g. decreased sapwood conductance, Fig. 3).

It is clear that species hydraulic traits are of critical importance to understanding variable growth-climate sensitivity, particularly across species (Anderegg *et al.* 2016; Trugman *et al.* 2019; and Fig. 3). Whether or not cavitation may be repaired, or the degree to which conductance can be regained by the growth of additional rings, is taxon-specific and closely related to wood anatomy. For example some angiosperm species have demonstrated limited capacity to refill embolised vessels (e.g. Love and Sperry 2018), but this is not the case for most conifers. Perhaps because of their ring-porous wood anatomy, oak species have been shown to exhibit positive drought legacies, wherein they support increased radial wood growth following drought events (Anderegg *et al.* 2015; Peltier *et al.* 2016). This could be an adaptive response to drought, wherein post-drought production of a single large ring, with large vessel elements characteristic of oaks, can compensate for loss of conductance in older rings. Similar dynamics in oak species could explain very different growth patterns preceding mortality, where oaks tend not to exhibit the 'decline'

processes more commonly observed in gymnosperms and some angiosperms (Cailleret *et al.* 2017).

Given the complexity of the potential impacts of climate change drivers (e.g. drought) on tree growth, it is difficult to perfectly simulate carbon dynamics across all tree organs through time (Fig. 3). Drought impacts both carbon sources (photosynthesis) and the activity of carbon sinks (growth and reproduction) (Hartmann & Trumbore 2016), as well as allocation among organs within the tree, probably in ways that differ across species, site and individuals. For example evidence for tradeoffs among competing sinks like defence (as resin duct production) and reproduction effort has been shown in *Pinus edulis* (Redmond *et al.* 2019). Though there are promising avenues for furthering our understanding of carbon allocation processes (Box 1), we argue our understanding of these processes is incomplete, particularly in terms of how they may be altered during periods of imbalance between carbon supply (source) and demand (sinks). Studies of changes in the movement of carbon during and following drought stress, for example are still uncommon (Hagedorn *et al.* 2016, Kannenberg *et al.* 2019), and results may not be generalisable across species or sites. Thus, a major focus of future work should be on new measurements of carbon allocation processes among different organs and sinks across timescales of stress and recovery (Fig. 3b). These types of longitudinal, high resolution physiological experiments (Hagedorn *et al.* 2016, Kannenberg *et al.* 2019) are time-consuming and intensive, and we suggest to simultaneously leverage existing data sets that cover large spatial and temporal scales, such as tree rings, but also remotely sensed measures of productivity and physiological function (Asner *et al.* 2016; Brodrick *et al.* 2019).

As a first step, we suggest to conceptualise growth-climate sensitivity as an emergent property of the internal, potentially unobserved physiological processing of past and current environmental and disturbance information by individual trees (and organs) to produce growth (Fig. 4). Individual trees (rather than, e.g. stand-level dendrochronologies) should be the focus of this work, due to the potentially idiosyncratic responses of trees to their own unique climate and disturbance histories. For example within forests (Fig. 4c), suppressed (shaded) and dominant (canopy) individuals may respond completely differently to climate extremes due to differences in their physiological status (e.g. NSCs, Fig. 4d) at the onset of a given perturbation. This also creates a limitation to using tree ring data sets in that certain drivers (e.g. climate vs. competition) of growth-climate variability may be difficult to distinguish from one another. For example trees might show rapid recoveries following drought at some sites due to competitive release from dead neighbours.

Implementing statistical models that consider variable growth-climate sensitivity for individuals can also provide simulation targets for process-based models. Different drivers of variable sensitivity would need to be incorporated in different ways, but using observed growth-climate sensitivities provides an initial and common framework for doing so (Figs 3 and 4). This is particularly true as repeated stress or disturbance events accumulate to affect tree function, resulting in the need to understand and quantify the associated impacts of compounded stress (Peltier & Ogle 2019b). Perfect simulation

Box 1. Radiocarbon bomb-spike dating

Radiocarbon bomb-spike dating presents one promising avenue for improving our understanding of transient dynamics in tree carbon allocation. This method can be used to quantify the mean time passed since photosynthetic fixation of carbon from the atmosphere, when applied to NSCs in plant tissues (e.g. Carbone *et al.* 2013). Key to this method is the atmospheric record of the radiocarbon bomb-spike (Levin & Kromer, 2004), which is sampled by photosynthetic carbon fixation. The technical difficulty and cost of sample preparation and measurement, particularly with respect to extracting uncontaminated NSC (Trumbore *et al.*, 2015), coupled with limited access to Accelerator Mass Spectrometry among ecologists has likely contributed to a lack of widespread implementation of this technique. However, radiocarbon bomb-spike dating presents a unique tracer of different-aged NSC pools in trees. Simultaneous measurement of all tree organs across a time-series of pre-stress, stress (or masting, extreme wetness, etc.), and recovery conditions, coupled with growth and/or water status measurements, would provide key data for improving our understanding of transient carbon allocation dynamics. Such 'physiological snapshots' of tree carbon and water status could greatly further our understanding of the physiological mechanisms underlying temporal plasticity in tree growth-climate sensitivity.

of the carbon dynamics associated with, for example multiple consecutive years of drought and associated pest outbreaks, is likely extremely challenging (Fig. 3). Representation of the impacts of such events on NSC storage and growth-climate sensitivity is perhaps more tractable.

Certain single disturbances such as fire and stochastic treefall are already incorporated into DGVMs (Thonicke *et al.* 2001; Sitch *et al.* 2003; Longo *et al.* 2019), but disturbances that alter the carbon status of individuals (e.g. bark beetles) are infrequently incorporated (Medvigy *et al.* 2012; Huang *et al.* 2019). Extreme climate years could be conceptualised in mechanistic models as disturbances leading to changes in carbon allocation, but could also be modelled as temporary changes in the sensitivity of cambial growth or carbon supply to climate variables, using average responses from empirical drought legacy studies (both in magnitude and duration). Behaviour consistent with *homeostatic sensitivity* would probably be most readily incorporated in this way. A key limitation is that existing dendrochronology data sets are biased towards certain species, sites and individuals (Nehrbass-Ahles *et al.* 2014; Klesse *et al.* 2018; Zhao *et al.* 2018), and often focus on sites characterised by high growth-climate sensitivities (Douglass 1941). Thus, there is a pressing need to better understand the prevalence and magnitude of these legacy effects on growth-climate sensitivities across more diverse species and ecosystems.

Finally it is important to note certain instances of variable growth-climate sensitivities could result from incomplete treatment of lagged growth-climate responses (e.g. 'memory') in models (Liu *et al.* 2019). Trees store NSCs for decades, and are
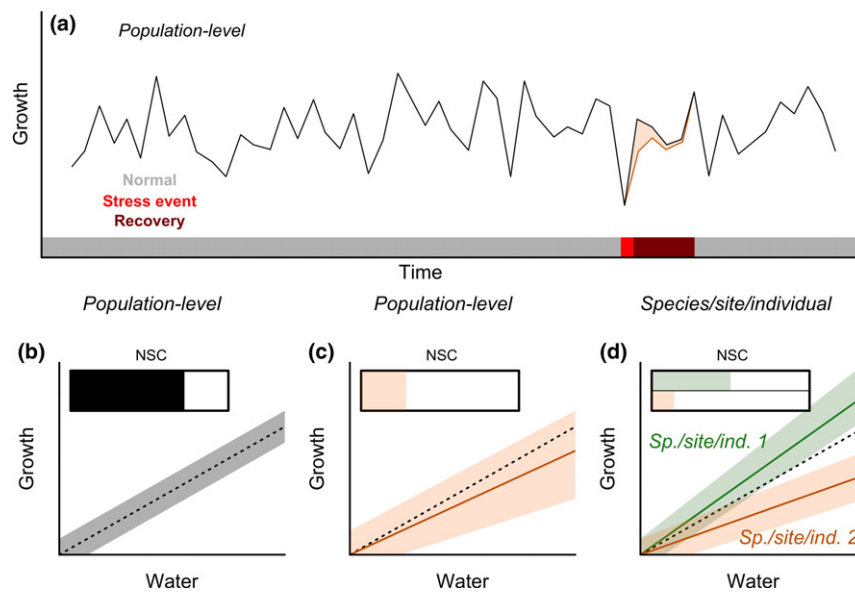
Figure 4 (a) Time-series of tree growth (black line) across normal periods (gray shading) and through one stress event (red shading) and recovery period (dark red shading). Stress events such as droughts may lead to prediction error (orange shading) if pre-event growth-climate sensitivities are used to predict post-event growth (orange line) because carbon status and tree growth responses to climate differ between (b) normal periods (dashed lines with gray shading) and (c) stress and recovery periods (orange line and shading). However, (d) different species ('Sp.'), sites, or even individuals ('ind.') may respond differently to this stress, and express different changes in their growth-climate sensitivities, according to their functional traits, carbon allocation strategies, or pre-stress physiological or hydraulic status. For example, the uncertainty in population-level responses in (c) may be resolved in (d) when independently considering responses of young trees (e.g., green line and shading) and old trees (e.g., orange line and shading), the latter having higher carbon costs of recovery (Trugman et al., 2018). The insets in (b), (c), and (d) denote potential NSC pool sizes; NSC pools may be reduced in stress-recovery periods [inset in (c)] compared to normal periods [inset in (a)], but NSC pool responses may vary, again, among species, sites, or individuals [inset in (d)].

able to draw upon extremely old reserves during periods of stress (Carbone *et al.* 2013). Statistical modelling of lagged tree growth responses or their climatic memory (Ogle *et al.* 2015) has been applied primarily in the southwestern US (Peltier *et al.* 2016, 2018; Peltier & Ogle 2019a, b). Such studies have shown that climate conditions several years prior to the year of ring formation, particularly drought conditions, continue to influence growth in subsequent years, especially during drier periods. It is possible that some observations of drought legacies could simply emerge from incomplete representation of a tree's full responses to antecedent climate, rather than temporally variable growth sensitivities. We have shown that using models that do not consider antecedent climate over multiple years into the past (i.e. assumption of shorter climatic memory) resulted in apparently larger drought legacy effects (Peltier & Ogle 2019b). These legacy effects are reduced when considering longer potential climatic memory of tree growth. This suggests that we should consider the role of climatic memory in tree growth processes, and that statistical models provide another way to continue exploring the prevalence and mechanisms of temporal variability in growth-climate sensitivity.

CONCLUSIONS

Inclusion of variable growth-climate sensitivity in future modelling or simulation efforts would be difficult without improved understanding of the mechanisms driving this variability, interactions among different mechanisms, and the prevalence of homeostatic versus dynamic growth-climate

sensitivities. For example does variable growth-climate sensitivity reflect transient perturbations to homeostatic sensitivities (H1), or is such variability an emergent property of dynamic sensitivities (H2) arising from interactions between the states of internal tree carbon pools, or a combination of both (H1 and H2)? We hope this perspective will motivate experimental studies that simultaneously monitor tree growth and local climate, in combination with manipulations of NSC pools, crown area, deep soil moisture or hydraulic function, among others, to evaluate the strength of H1 and H2 and the underlying mechanisms. Of particular value are experiments that can distinguish the competing roles of multiple mechanisms, for example hydraulic damage and NSC depletion.

Experiments that induce drought legacies will also be highly informative. For example while a large amount of research has investigated the mechanisms of tree mortality (Adams *et al.* 2017), these experiments rarely allow trees to recover from stress, despite that recovery treatments can often reveal unique insights (Hammond *et al.* 2019; Sapes *et al.* 2019). Much of our understanding of drought impacts on tree physiology and growth comes from such experiments, which are often aimed at testing mechanisms of mortality. As such, our understanding of resilience, legacies and recovery is necessarily limited by the relative paucity of data on stress recovery in mature trees.

Ultimately, many of the mechanistic drivers of temporal variability in growth-climate sensitivity are intertwined. We suggest, however, that each impacts the status of tree NSC pools either directly or indirectly (Figs 3 and 4), representing a potential starting place for evaluating the physiological basis

of these responses. Ultimately, an improved, holistic understanding of the mechanisms of variable growth-climate sensitivity is required, and will improve our ability to predict the growth of different species (with different traits) under climate change. Thus, we hope increased recognition and consideration of the temporal variability in tree growth-climate sensitivity can improve our ability to predict the future states and functioning of forests. At the least, we hope readers will reconsider the utility of temporally invariant statistical models of tree growth responses to climate, place more emphasis on understanding the 'noise' in these relationships, and explore the limits of our understanding of tree growth.

AUTHORSHIP

DP conceived of the ideas with significant input from KO. DP wrote the first draft of the manuscript, and KO contributed substantially to revisions.

PEER REVIEW

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DATA ACCESSIBILITY STATEMENT

This manuscript contains no new data.

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