From tree to forest: Multiple carbon sink constraints

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Forests are the largest carbon sinks among terrestrial ecosystems. They sequestrate carbon primarily through tree growth but are currently under severe threat from global change. Recently, Tavares et al.[1] identified a crucial trait, the xylem hydraulic safety margin (HSM), for predicting the risk of drought-induced tree mortality and biomass in Amazon forests. They also found that old-growth forests with wide HSMs build more biomass, while fast-growing forests are exposed to greater hydraulic risks and have a higher mortality rate. Therefore, they speculated that climate change could lead to further reductions in plant HSMs in the Amazon, resulting in a potential loss of biomass, which, in turn, would have major impacts on the carbon sink. However, a global perspective is urgently needed to evaluate the effects of global change on tree mortality and carbon sinks that encompass different physiological mechanisms and environmental factors across temporal and spatial scales. Therefore, we created a framework to examine forest response and adaptation in the context of future global change and discussed each issue (Figure 1).

From an ecophysiological perspective, the trade-off between plant growth and mortality explained the results in the Amazon while suggesting more. Numerous studies have shown the trade-off that fast-growing trees are likely to achieve tall statures as large trees and contribute the dominant biomass in forests but at the cost of higher vulnerability to hydraulic embolism.[2] However, the high mortality risk for large trees is not only due to hydraulic limitations but also other disturbances, including warming, wind, fire, and human activities such as logging, all of which disproportionately affect large trees and, thus, exacerbate the cascading decline in forest carbon budgets. For Tavares et al.,[1] drought events are the most important factor affecting Amazon forest dynamics. Therefore, they used six hydraulic traits to predict forest aboveground biomass (AGB) and found that HSMs are associated with stem mortality rate and ⊿AGB (AGB changes between approximately 10-year survey intervals). Although drought can act as a precursor to subsequent disturbances, such as fire and insect infestation, in regions where tree growth and mortality are limited by other factors, like sunlight and temperature, more traits are needed to predict biomass changes. For example, traits

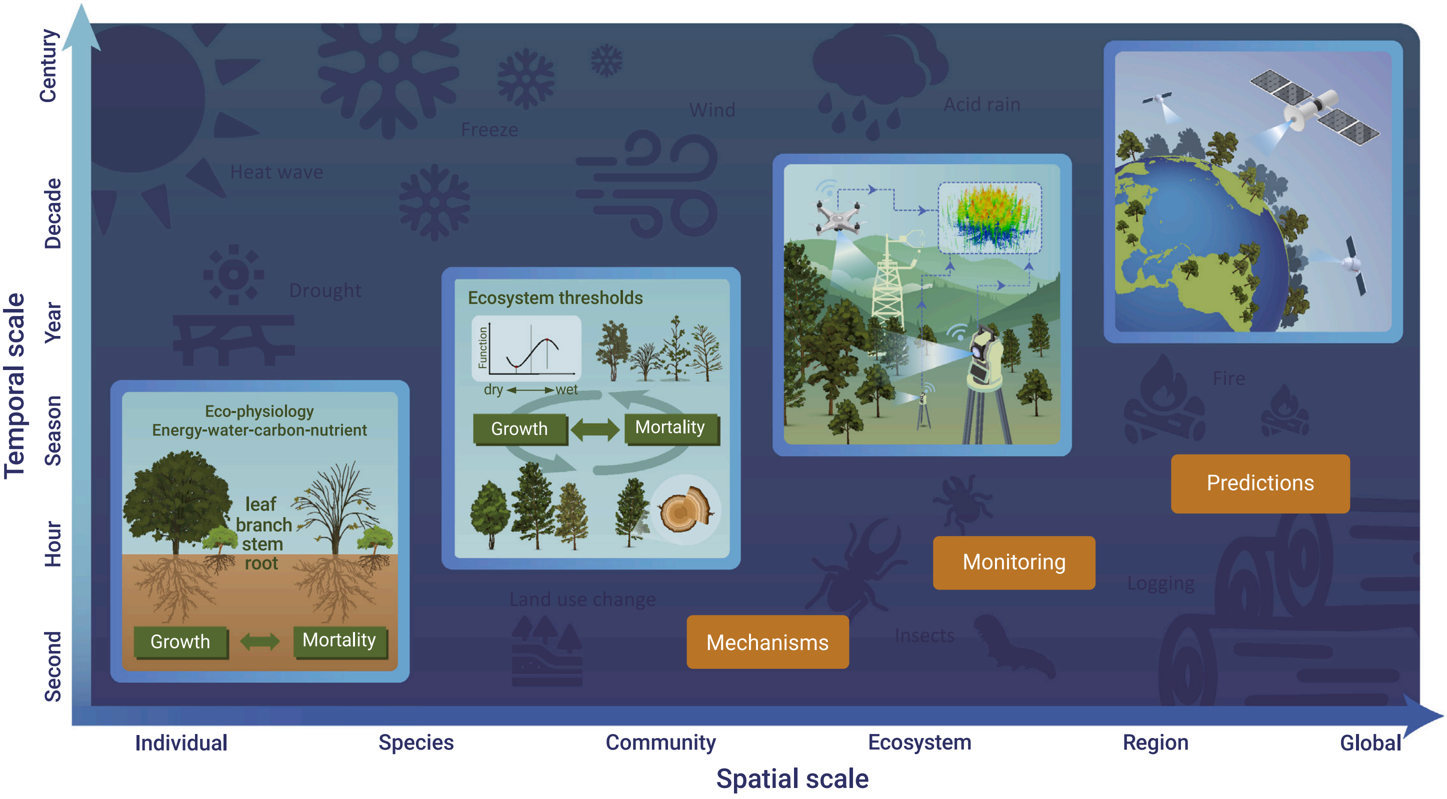

Figure 1. Schematic representation of carbon sink constraints under global change The framework includes different environmental thresholds across temporal-spatial scales, leading to changes in tree demography and shifts in community structures and ecosystem stages. The coupling between carbon and water is the fundamental mechanism underlying the trade-off between growth and mortality across these scales. Multiple processes, such as carbon-water exchange through leaf stomata and maintenance of carbon-water balance at the individual and ecosystem levels, collectively drive the regional and global cycles of carbon and water.

associated with growth (e.g., photosynthetic rate, stomatal conductance, leaf area index, carbohydrate content, or longevity) and mortality take precedence over drought (e.g., plant thermal safety margin, mechanical properties, flammability, or biochemical defenses).[3] These traits may reveal broader physiological mechanisms for accurately predicting forest carbon dynamics, especially when multiple climate stresses occur simultaneously in the future.

Tree mortality can significantly alter species components and community structures in forests, leading to different biomass responses in different regions, depending on vegetation types and environmental drivers. Tavares et al.[1] found that species in the southern and western Amazon are more susceptible to drought (lower HSMs and more deciduousness) and experience higher mortality and biomass decline compared with species in the central eastern Amazon, which may trigger xerophilization of these forests. In contrast, the long-term forest inventory in Tibet (1973–2018) has shown that the biomass of deciduous broadleaved forests has increased significantly since 1999, while the biomass of the evergreen coniferous forests has decreased. Unlike the Amazon drought, such a transition of species components in alpine forests is believed to be caused by climate warming, wildfires, and deforestation. Regarding community structure, long-term plot inventories have shown that large old trees have gradually disappeared worldwide over the past century. For example, *in situ* surveys combined with dendroecological data have shown that the density of small trees in Tibetan forests has increased rapidly since the 1950s, when dramatic warming and rising of CO_2 began. Such phenomena also occurred in the US, Australia, Sweden, and Brazil, leading to significant biomass declines.

At the ecosystem level, the study of vegetation thresholds and their environmental drivers is critical for predicting carbon sinks. Tavares et al.[1] demonstrated the importance of HSMs in predicting long-term carbon sequestration, bridging the knowledge gap between carbon sinks and climate change through plant physiological mechanisms. However, the plant HSM is a flexible trait that can vary temporally and spatially even within the same species. Therefore, frequent measurements of HSMs are required to determine the water threshold in real time. In addition, it is more difficult to estimate environmental thresholds for ecosystems[4] because the trade-off between growth and mortality is closely related to the balance between ecosystem resilience and resistance to disturbance. Thus, a stress that exceeds the threshold for individual trees may not necessarily reach the threshold for the entire ecosystem, and even when the stress exceeds the threshold for the ecosystem, the forest can re-establish a new equilibrium, whereupon the ecosystem functions may be promoted through shifts in species components or resource partitioning. Generally, a forest and its biomass are stable as long as external disturbances do not exceed its ecosystem threshold. However, because ecosystem thresholds vary across biomes and by time periods, precise and timely quantification of the thresholds is critical for biomass monitoring.

From a technical perspective, Tavares et al.[1] used a traditional method to estimate biomass from tree diameter at breast height (DBH), height, wood density, and demographic data, while multi-source remote sensing can determine biomass at larger scales in more precise and efficient ways. For example, researchers found drought-induced tree mortality rate two times higher in taller trees than smaller ones by tracking mortality over approximately two million trees individually, which was only possible using fine-resolution light detection and ranging (LiDAR) data. With sample plots as quadrats, LiDAR and ground-penetrating radar (GPR) can make inferences about the biomass from tree to forest. LiDAR can provide precise quantification of three-dimensional forest structures, allowing precise positioning and identification of individual trees. GPR transmits high-frequency electromagnetic waves into the ground and receives the reflected waves. Variations in waveform, amplitude, and time characterize the location, morphology, and burial depth of subsurface media, making it easy to calculate belowground biomass, which is very important for forest ecology. Using tree structural parameters of each components (leaves, branches, trunks, and roots), the total biomass of individual trees can be accurately determined by allometric growth equations. In addition, large-scale machine learning-based models can improve the efficiency and precision of individual tree segmentation and tree structural estimations, such as measurements of DBH, height, and crown size of trees.

To scale regional monitoring data to a global forecast, the combination of multi-temporal, broad-scale remote sensing imagery, such as Landsat and Moderate Resolution Imaging Spectroradiometer (MODIS) with fine-resolution LiDAR (aboveground) and GPR (belowground) datasets can achieve near-global coverage of land surface changes and carbon dynamics over decades. Additionally, large-scale remote sensing validated by field observations can provide insights into how vegetation has been disturbed by and recovered from natural disasters, which, in turn, can support process-based modeling and prediction of future carbon sinks. With the rapid accumulation and development of remote sensing data, new algorithms, and process-based modeling, forest biomass estimation and prediction can be greatly improved at multiple temporal-spatial scales.

Forest biomass dynamics are influenced not only by the trade-off between growth and mortality in climatically normal years[1] but also by natural extreme disturbances. The latter factor is even more important because of the increasing frequency and severity of extreme events, such as heatwaves, droughts, high winds, floods, freezes, and cascading disasters, such as wildfires, insect attacks, and landslides. There is growing evidence of large-scale tree mortality because of disturbances that have led to abrupt declines in biomass in many biomes worldwide.[3] Examples include trees burned in devastating wildfires in the western US, Australia, and boreal forests; tree mortality caused by extreme droughts in Mediterranean climates; and insect attacks on vulnerable trees suffering from droughts. A mechanistic understanding of how forests are disturbed by and recover from these disasters can improve forest ecosystem modeling and prediction of forest carbon sinks in the context of global change in the future. Human activities are also changing forest biomass dynamics through deforestation, reforestation, and protection of natural forests.[5] These activities have contributed to global greening through plantations in Asia but have also caused enormous carbon emissions in the Amazon through deforestation and farming. Thus, to better understand forest carbon dynamics, comprehensive assessments of natural disturbances and human activities are essential to complement natural forest growth.

Overall, we hope that this framework of multiple constraints on forest carbon sinks can provide a roadmap for plant physiologists, ecologists, hydrologists, geographers, and climatologists to study forest responses and adaptations to future global change and to promote interdisciplinary collaboration.

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DECLARATION OF INTERESTS

The authors declare no competing interests.