

# Tropical forests and global change: filling knowledge gaps

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**Tropical forests will experience major changes in environmental conditions this century. Understanding their responses to such changes is crucial to predicting global carbon cycling. Important knowledge gaps exist: the causes of recent changes in tropical forest dynamics remain unclear and the responses of entire tropical trees to environmental changes are poorly understood. In this Opinion article, we argue that filling these knowledge gaps requires a new research strategy, one that focuses on trees instead of leaves or communities, on long-term instead of short-term changes, and on understanding mechanisms instead of documenting changes. We propose the use of tree-ring analyses, stable-isotope analyses, manipulative field experiments, and well-validated simulation models to improve predictions of forest responses to global change.**

## Changing biomass in tropical forests

Tropical forests cover just 7% of the Earth's land surface but store 25% of global terrestrial carbon and account for one-third of net primary productivity [1]. Because tropical forests are so rich in carbon, their net loss or uptake of carbon has important implications for atmospheric CO<sub>2</sub> levels [2]. Past increases in atmospheric CO<sub>2</sub> levels, increased nutrient deposition and climatic changes are likely to have affected tree growth and forest dynamics. Understanding the accumulated impacts of these changes – which we term ‘global-change factors’ – is crucial for predicting future dynamics of tropical forests and for informing adaptation policies [3]. Here we focus on the effects of changing climate and nutrient availability on relatively undisturbed tropical forests, leaving out the direct effects of other anthropogenic disturbances (exploitation) [4].

There is a growing body of empirical evidence for changing biomass (and carbon) in relatively undisturbed tropical forests over the past few decades. A range of studies in permanent sample plots (see Glossary) located in intact tropical forests have reported increasing biomass [2,5] and tree growth rates [6] over the past decades. Other studies have found that tree growth rates decreased [7] or fluctuated over time [8,9]. Although these studies have

established the foundation for reporting changes in tropical forest dynamics, permanent plot data are not well suited – and have so far failed – to identify the causes of the observed biomass changes [10] (see [11] for an exception). Permanent-plot studies do not allow separation of the effects of different global change factors [11] and offer limited possibilities to relate biomass (or tree growth) changes to climatic variation because they are usually remeasured after approximately 5 years. As a result, suggested causes for the changing dynamics in undisturbed tropical forests still range from shifts in climatic and atmospheric conditions (CO<sub>2</sub>, rainfall, temperature) to increased nutrient deposition and recovery after major disturbances [2,5]. This poor understanding of the effects of global change on tropical forests is worrying because it hampers our ability to forecast forest responses, estimate the probability of tropical forest dieback, and develop effective adaptation strategies to future global changes [3].

In this Opinion article, we posit that major advances in the field can be achieved with new research approaches. We first briefly discuss knowledge gaps in the field, drawing on recently published reviews [2–4,10–13] to show that knowledge gaps primarily relate to poor understanding of tree- and population-level responses to global changes. We then suggest that filling these knowledge gaps requires a different research strategy, one that focuses on trees instead of leaves or entire forest stands, considers long-term

## Glossary

**Individual-based models:** a specific type of population model in which the growth, survival, and reproduction of each individual are simulated over time in response to its environment.

**Intrinsic water-use efficiency (iWUE):** the ratio of net CO<sub>2</sub> assimilation to stomatal conductance.

**Isotopomer:** a molecule carrying a heavy isotope in a particular group.

**Mechanistic tree-growth models:** software tools that use knowledge on physiological processes in trees and tree responses to environmental conditions to simulate tree growth over time.

**Permanent sample plots:** areas of forest – usually 1–50 ha in size – where all trees above a certain minimum size are tagged and mapped and their diameter and status (alive, dead, newly recruited) is recorded repeatedly (every 1–5 years).

**Population models:** software tools that predict the development of natural populations of trees (or other species) in time, based on information on growth, survival, and reproduction.

**Species-range modeling:** the simulation of (changes in) the geographic distribution of species in response to (changes in) climate.

**Stable-isotope analyses:** chemical analyses to determine the fraction of stable isotopes in plant materials. Stable isotopes are variations of an element that differ in the number of neutrons in the nucleus and as a result have different physical and chemical properties (Box 2).

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instead of short-term changes, and focuses on understanding mechanisms instead of describing patterns and documenting changes. We argue that four research approaches that are rarely used in tropical forests have the potential to help fill these knowledge gaps: (i) tree-ring analyses; (ii) stable-isotope analyses; (iii) well-validated mechanistic simulation models; and (iv) large-scale manipulative experiments. We introduce and discuss these approaches and make a plea to integrate existing and proposed research approaches to accelerate developments in this field.

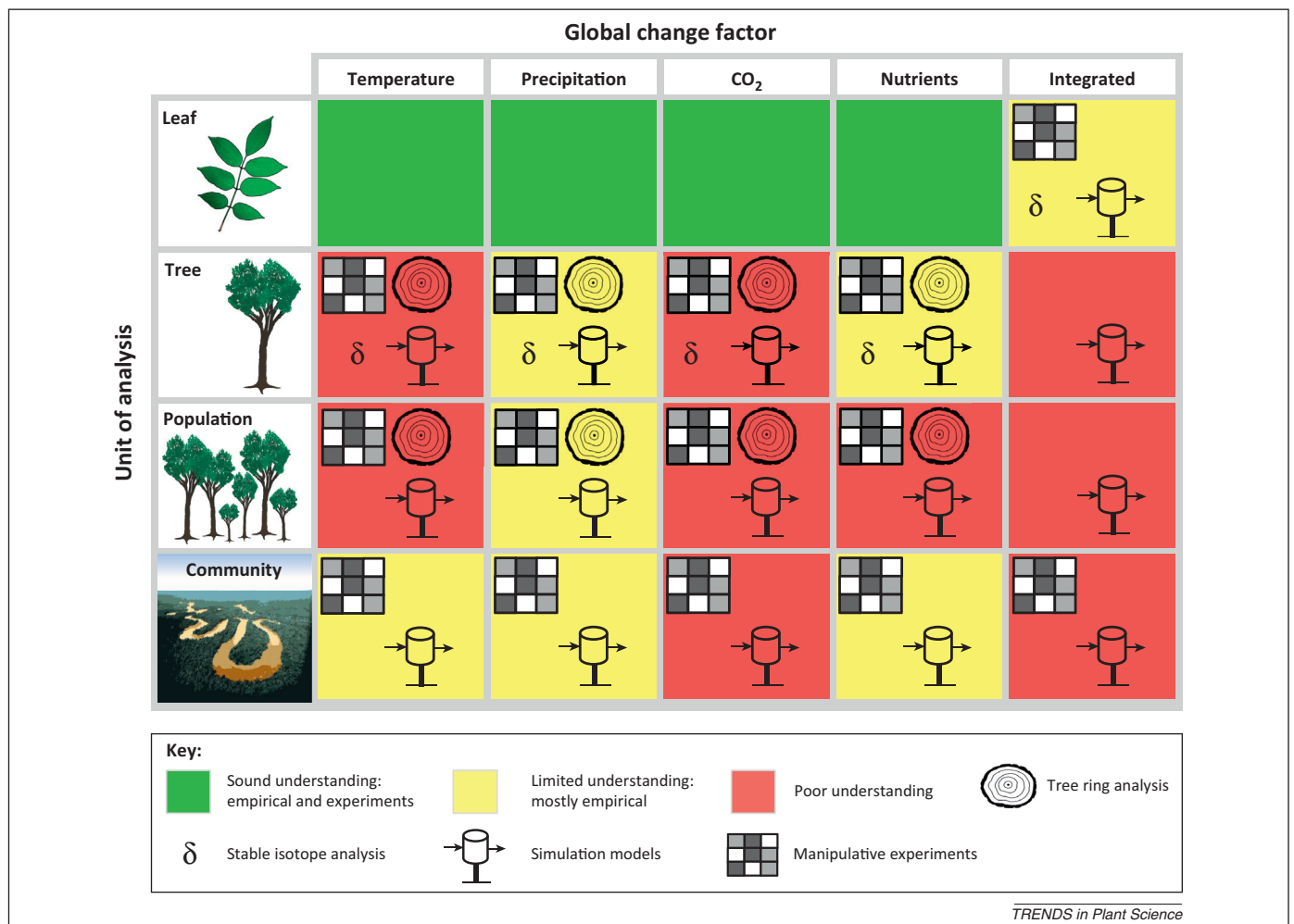
### Gaps in knowledge

#### Leaf and tree level

Major advances in the field of the climate sensitivity of forest trees have been achieved in experimental studies of leaf-level physiological responses (photosynthesis, respiration) to changing environmental conditions (reviewed in [14,15]). Overall, there is good theoretical and empirical understanding of how rates of leaf photosynthesis respond to changes in CO<sub>2</sub> level, temperature, and availability of nutrients and water (Figure 1). It is, however, desirable to study responses to integrated effects of warming and CO<sub>2</sub>

enrichment in the field, on leaves attached to trees, and for a larger set of species.

By contrast, understanding of environmental changes at the level of mature trees is limited (Figure 1). The fate of carbon in trees is poorly understood and this greatly limits our ability to predict how climate-induced changes in leaf photosynthesis and respiration influence growth in woody biomass [16]. Plot and tree-ring studies have reported reduced diameter growth during low-rainfall and high-temperature years [8,9,17], but hardly anything is known about the effects of gradual climatic changes. Manipulative experiments in which global change factors have been altered are rare. Nutrient addition studies (N + K) have reported stimulation of diameter growth for small trees [18] and experimental drought studies have reported strong reductions in tree growth and survival [19]. So far, the effects of either CO<sub>2</sub> increase or warming have been experimentally tested only for tropical seedlings (and tree leaves [20] or branches [21]). Seedling studies showed declining biomass growth with increasing temperature [22] and growth stimulation after CO<sub>2</sub> enrichment [12]. Although these studies provide insights into climate-change effects on a crucial stage in a



**Figure 1.** Knowledge gaps and new research approaches in the field of global-change impacts on tropical forests. Colors indicate our level of understanding of the responses of leaves, individual trees, tree populations, and forest communities to four global-change factors and their integrated effect. Symbols in colored cells indicate proposed research approaches to fill knowledge gaps. Tree-ring analysis: climate-growth relations and detecting long-term growth changes. Stable-isotope analysis: <sup>13</sup>C, <sup>18</sup>O, and <sup>15</sup>N from tree rings. Simulation models: mechanistic tree-growth models, population models, and community-level models. Manipulative experiments: free-air CO<sub>2</sub> enrichment (FACE), warming, and changing water availability. Population and community level are typically at the 10–500 ha scale. Note that changes in light levels (i.e., global dimming/brightening or changes in cloud cover) were not included in this scheme.

## Opinion

tree's life, the responses of mature trees are likely to be different and are more relevant for understanding carbon dynamics.

*Population and community level*

Any change in the biomass of a forest community is the integrated effect of species-specific demographic responses of all tree species in that community. Differential responses of species to global-change factors may change competition and the relative abundance of species in the community [12]. These compositional shifts may also change forest dynamics and influence carbon fluxes. The shifts in tree species composition that have been documented in Amazonian forests [23] are consistent with such climate-induced community change but it is unclear whether they can be attributed to climatic changes. Understanding the causes of recent changes in the biomass (and composition) of tropical forests would greatly benefit from knowledge of the demographic responses of all (or the most dominant) tree species in the community. In temperate forests, recent analyses have yielded important insights regarding the climate sensitivity of tree populations [24]. Such understanding is lacking for tropical tree species; it is unknown how populations respond to precipitation changes, heat, and enrichment of CO<sub>2</sub> or nutrients (Figure 1). This knowledge gap also limits possibilities to make inferences about the potential migration of species under climate change, a potentially important way for tree species to cope with climate change in the long run [3].

The responses of tree communities to drought have been studied in 'natural' [25] and controlled experiments [19], revealing a marked but transient reduction in forest biomass with drying [19]. Interestingly, so far no experiments have been done to study the effect of increasing rainfall, although such changes may occur in some tropical forest areas. The absence of free-air CO<sub>2</sub> enrichment (FACE) experiments, which evaluate the effect of CO<sub>2</sub> enrichment on tropical forest biomass and dynamics, is particularly notable [26]. CO<sub>2</sub> fertilization is one of the routinely proposed [2] – but also hotly debated [12] – causes of recent biomass increase in tropical forests. However, this hypothesis can be tested only in manipulative experiments. Understanding the magnitude of CO<sub>2</sub> fertilization is also crucial to quantifying its contribution to mitigating the risk of tropical forest dieback and realistically simulating the magnitude of a CO<sub>2</sub>-fertilization effect in dynamic global vegetation models (DGVMs). Finally, there is a poor understanding of the interactive effects of CO<sub>2</sub> enrichment, increased temperature, and changing rainfall on tree populations and forest communities.

**New focus***Individual trees*

There are major knowledge gaps in our understanding of individual tree responses to global change and these greatly limit the interpretation of observed changes in tropical forest dynamics. It is at the level of individual trees that climate-induced shifts in leaf-level photosynthesis or respiration translate into changes in tree growth or mortality risk [27] and that acclimation to global-change factors will occur [3]. Thus, analyses of global-change effects should be

conducted at this level before aggregating to population or community level [24]. The many millions of repeated tree measurements in permanent sample plots [2,5] offer possibilities for such individual-level analyses [24,28] and for validating tree-growth models. Mechanistic simulation models of canopy trees offer the possibility to test tree-level acclimation and responses to environmental changes. These large trees probably constitute the next frontier of climate-change studies in tropical forests. This is challenging, because modeling, manipulating, and measuring them is notoriously difficult.

*Relevant temporal scales*

There are good reasons for studying the effects of global change on tropical forests at the scale of multiple decades to centuries. This corresponds to the typical lifespan of tropical trees [17], the scale at which trees acclimate to atmospheric changes [3], the return time of large-scale disturbance events that drive tropical forest dynamics [29,30], and the temporal scale of interest regarding climate change. Yet, virtually all studies have been restricted to timescales of days to a few decades. As a consequence, there is a substantial disjunction between the relevant temporal scale and the realized scale of most studies performed so far. This scale gap limits our ability to predict the effects of global change on tropical forest dynamics [12] and to disentangle global-change effects from the likely gradual fluctuations in tree growth that occur as forests recover from past disturbances [11]. Long-term plot studies and tree-ring studies increase the timescale of study and help to overcome this scale-gap problem [11].

**New methods**

We propose four methods that will help to fill the knowledge gaps identified in Figure 1. Although these methods have great potential, they have rarely been used. To realize their full potential, they need to be integrated and combined with existing methods. Box 1 includes a non-exhaustive list of ideas for such integrated analyses.

*Tree-ring analyses*

Although research on tree rings in the tropics has been ongoing for decades, the number of studies has increased dramatically in the past decade [17,31,32]. The potential to further expand studies that use tree rings in tropical tree species is considerable. For instance, recent reviews and species lists include over 100 ring-forming tree species from seasonally dry to wet tropical forests [17,33] and many more species are being evaluated for their dendrochronological potential. In addition, intensive sampling of stable isotopes from wood or cellulose to derive annualized diameter growth for non-ring-forming tree species has shown considerable promise (see below) [34,35]. Benefits of conducting tree-ring studies rather than plot studies include: growth data are at centennial rather than decadal scales [17,31,32,36,37]; growth rates are at annual rather than 5-year resolution [8]; and wood samples of tree rings contain an archive with valuable information (see below).

Yet, like any other method used in forest research, there are limitations to tropical tree-ring studies. Tree-ring studies primarily yield information on growth rates and

**Box 1. Ideas for integrated analyses**

There is a pressing need to integrate existing and new methodological approaches to fill the knowledge gaps identified in Figure 1 in the main text. Fortunately, there are ample opportunities to do so. Some ideas for integrated approaches include the following:

- The combined analysis of growth changes (from permanent sample plots or tree rings) and carbon-isotope ( $\delta^{13}\text{C}$ ) fractions (from tree rings) assists in identifying the causes of observed growth changes.
- Potential shifts in population dynamics due to long-term changes in tree growth can be evaluated using population models parameterized with demographic data from permanent sample plots.
- Carbon isotope ( $\delta^{13}\text{C}$ ) fractions in leaves or wood produced during (natural) heating, rainfall-change or  $\text{CO}_2$ -enrichment experiments can be used to interpret  $\delta^{13}\text{C}$  patterns in tree rings.
- Long-term series of oxygen isotopic ( $\delta^{18}\text{O}$ ) fractions obtained from tree rings may be used as inputs in tree- or forest-growth models to simulate effects of variation in rainfall.
- Annual variation in net ecosystem carbon exchange rates from flux towers can be correlated with ring width from trees in the proximity of the towers to evaluate whether tree-ring width is a good proxy for ecosystem-level  $\text{CO}_2$  exchange.
- Tree-simulation models can be validated using (annual variation in) diameter growth rates from permanent plots, tree rings, or manipulative experiments or by (annual variation in) stable carbon-isotope fractions ( $\delta^{13}\text{C}$ ) observed in tree rings or leaves.
- A detailed reconstruction of the disturbance history of forest stands based on tree-ring analyses can assist in interpreting observed growth trends in permanent sample plots.
- Observed annual variation in diameter growth or forest biomass can be compared with vegetation indices from satellite images to quantify large-scale variation in carbon stocks.

not on mortality or recruitment, although recruitment rates can be inferred from age distributions [29]. In addition, tree-ring studies evaluating growth trends may yield apparent historical growth increases that are generated by sampling biases [33,38]. We expect that rapid methodological developments in chemical and physical wood analyses, sampling design, statistical analyses, and tree-growth modeling will reduce these limitations in the coming decade.

Tree-ring studies have been used to detect gradual changes in tree growth at decadal to centennial scales, reporting increased growth for several species [39–41]. A larger set of studies has considered relationships between ring widths and climatic variation, revealing moderate-to-strong sensitivity of radial growth to anomalies in rainfall, temperature, and/or sea surface temperature [17,37].

**Stable-isotope analyses**

Tree-ring series are valuable archives of past environmental conditions, physiology, and physiological responses to environmental variation of a tree during its entire lifetime. This information is stored in the signature of stable isotopes and anatomical characteristics in the wood of tree rings. Below we discuss the contributions of three stable isotopes; Box 2 provides background information.

First, stable carbon isotope ( $\delta^{13}\text{C}$ ) values in wood cellulose are a proxy for the internal  $\text{CO}_2$  concentration in the leaves and can be used to estimate intrinsic water-use efficiency (iWUE). Stable carbon-isotope studies in tropical tree rings have suggested an increase of iWUE over the past decades [34,40,42]. Combining  $\delta^{13}\text{C}$  trends with trends in tree growth [40] is a promising tool for detecting

**Box 2. Using stable isotopes to identify causes of changing tree growth**

Stable isotopes are variations of the same element that differ in mass (i.e., number of neutrons), causing them to have different physical, chemical, and biological properties. These differences cause stable isotopes to be present in plant material, such as wood and cellulose, in different fractions [62].

**Carbon-13**

Most of the world's carbon has six protons and six neutrons ( $^{12}\text{C}$ ); however, a small fraction has seven neutrons ( $^{13}\text{C}$ ). Plants have a higher affinity for  $^{12}\text{CO}_2$  than for  $^{13}\text{CO}_2$  and 'discriminate' against  $^{13}\text{CO}_2$ . The amount of discrimination depends on the ratio of leaf intercellular  $\text{CO}_2$  concentration ( $C_i$ ) to atmospheric  $\text{CO}_2$  concentration ( $C_a$ ) and is recorded in cellulose as the ratio between  $^{12}\text{C}$  and  $^{13}\text{C}$  ( $\delta^{13}\text{C}$ ) [63].  $C_i$  (inferred from  $\delta^{13}\text{C}$ ) can be used to estimate iWUE, the efficiency of  $\text{CO}_2$  assimilation compared with water loss by transpiration [64], assuming a constant leaf-to-air humidity gradient ( $A_w$ ). Care should be taken that, with rising temperature,  $A_w$  will probably increase and real water use efficiency (WUE) might be much lower than expected from the calculation of iWUE.

**Oxygen-18**

Tree rings contain fractions of the heavy oxygen isotope  $^{18}\text{O}$  in addition to the much more abundant lighter oxygen isotope  $^{16}\text{O}$ . The fraction of heavy oxygen ( $\delta^{18}\text{O}$ ) in cellulose of tree rings can be used as a proxy for the regional  $\delta^{18}\text{O}$  signal in rainwater in tropical climates [65]. As clouds move inland, the heavy  $^{18}\text{O}$  condenses more easily, making the isotopic content of the remaining vapor increasingly lighter, a process that is more dominant in years with intense rainfall [66,67]. Relatively high  $\delta^{18}\text{O}$  fractions in wood cellulose may thus reflect relatively dry periods (years).

 **$^{15}\text{N}$  Nitrogen**

A recent development in tropical forest trees is the study of stable isotopes of nitrogen.  $\delta^{15}\text{N}$  is the ratio of  $^{15}\text{N}$  to  $^{14}\text{N}$ . Direct discrimination against  $^{15}\text{N}$  during N uptake by plants only occurs if N demand is low compared with N supply [68]. Thus, plant  $\delta^{15}\text{N}$  is a proxy for the  $\delta^{15}\text{N}$  of the N sources under most field conditions [68]. The  $\delta^{15}\text{N}$  of these N sources (such as  $\text{NO}_3^-$  and  $\text{NH}_4^+$ ) can vary considerably depending on the rates of mineralization, nitrification, and denitrification. Hence, changes in the (local) nitrogen cycle have been inferred from  $\delta^{15}\text{N}$  trends in tree rings [50]. However, some caution is needed when interpreting  $\delta^{15}\text{N}$  trends, because nitrogen can be translocated across the stem before it is fixed in the heartwood [48].

In addition to stable isotope fractions, the anatomical properties of wood also provide valuable information about tree growth responses to climatic variability [69,70] and multiproxy analyses combining these approaches are particularly promising strategies for identifying how climatic changes affect tree growth.

changes in tree physiology [43] and for identifying the main driver of growth changes because – all else being equal – the isotopic signature of the effects of  $\text{CO}_2$  fertilization differs from that of nutrient enrichment.

Second, the stable oxygen-isotope fractions ( $\delta^{18}\text{O}$ ) in tree rings can be used as a proxy for rainfall because rainwater in dry years is enriched in  $^{18}\text{O}$ . Stable oxygen isotopes from tree rings have been used to reconstruct historical precipitation at regional [44] and even continental scales [45,46]. Given that trees occupy almost every corner of the terrestrial tropics and instrumental climatic data in the tropics are available only for recent decades,  $\delta^{18}\text{O}$  series are excellent tools for reconstructing historical precipitation.

Third, the  $^{15}\text{N}$  fraction in tree-ring wood potentially contains information about the nitrogen cycle [47–49].



## Opinion

Increasing  $\delta^{15}\text{N}$  values during the past decades were found in trees from Thailand and Panama [50]. This suggests a more open nitrogen cycle, possibly because of increased nitrogen deposition. Other stable isotopes and isotopomers [51] that have not yet been used in tropical tree rings may yield additional climatic or physiological proxies.

### Manipulative experiments

Although opportunistic natural experiments, such as occasional dry and hot years, have been valuable for assessing direct and transient effects of drought and/or heat at a large scale [25], they have several obvious limitations: unpredictable timing, no formal controls, and no separation of global-change factors (heat and drought often go hand in hand). Manipulative experiments are therefore needed to disentangle the effects of separate and interacting global-change factors. The need for large-scale and long-term experiments that manipulate  $\text{CO}_2$ , temperature, water availability and nutrients, has been expressed repeatedly [26,52]. We argue that such experiments should in particular include  $\text{CO}_2$ , temperature, and water availability because: (i) the role of  $\text{CO}_2$  fertilization as an important driver of increased tropical forest biomass is under debate [2,12]; (ii) the strength of  $\text{CO}_2$  fertilization is a major source of uncertainty in climate-carbon-cycle models and in quantifying the risk of tropical forest die-back [53]; (iii) the degree to which  $\text{CO}_2$  fertilization can mitigate the negative effects of warming on tree growth is poorly understood [12]; and (iv)  $\text{CO}_2$  fertilization is thought to operate mainly through increased water-use efficiency [10]. Such experiments need to focus on the effects on canopy trees because these dominate carbon dynamics. Canopy cranes and other techniques that allow forest canopy access greatly facilitate experimental manipulation and measurement of the forest canopy. We are glad that plans for  $\text{CO}_2$ -addition experiments in the Brazilian Amazon are being made [54] and an experimental drought experiment is planned in Queensland, Australia (S.G. Laurance, *personal communication*).

### Well-validated simulation models

Simulation models are required at the level of individuals, populations, and tree communities. At the individual level, simulation models are needed to understand the combined effects of precipitation changes, ambient  $\text{CO}_2$ , temperature, and nutrients on tree growth and survival. They can also be used to quantify the acclimation potential of tropical trees to global-change factors. Such models need to start from underlying physiological processes and functional plant traits (Box 3) [55]. Mechanistic plant models have been developed and tested for a few species in tropical [56,57] and temperate [58] forests. It is crucial that these models are realistically parameterized and well validated (Box 1) to generate reliable insights for models at population and community levels.

At the population level, the challenge will be to estimate the demographic consequences of expected changes in the growth and survival of individual trees. This will be particularly challenging if interactions with other species are included – a potentially important pathway of climate-induced shifts in tree populations. Such analyses require

### Box 3. Modeling approaches

Models for understanding climate impact on carbon cycles in tropical forests face important challenges at the tree, population, and community levels.

#### Mechanistic and trait-based models

Tree-growth models should mechanistically link climate conditions, resource acquisition, allocation, and functional plant traits to tree growth and survival [55]. Models should be built for canopy trees – rather than for seedlings – and include functional traits and plastic trait responses [71] that drive differential responses to climate across species [72]. Ideally, these models integrate the traits that influence photosynthetic responses to climate (e.g., total leaf area, leaf assimilation capacity, minimum leaf water potentials, cavitation vulnerability), respiration costs (e.g., leaf nitrogen contents), and turnover rate of tree parts (e.g., leaf lifespan, sapwood lifespan) [72] and, whenever possible, information on roots (e.g., root turnover, root nitrogen content). Models can then be fed with observed or reconstructed past climate data or projected future climate data to quantify the effects of various climatic changes on tree growth. Mechanistic and trait-based models are not necessarily limited to the tree level but can also be constructed at population and stand level [73].

#### Plant functional types

The high taxonomic diversity of tropical tree species has complicated the study of tropical tree responses to global change. As a result, such studies have been performed for only a very few species so far. To overcome this hurdle, we need to search for responses to global-change factors that are similar for groups of tree species. Next, such groups of species – plant functional types (PFTs) – need to be characterized by their functional traits [74]. This flexible approach to establishing PFTs may result in PFTs that differ from those commonly used in studies on tree diversity. The above-mentioned approach of mechanistic tree-growth models should help to define PFTs with respect to global-change responses. These PFTs can then be used to simulate population dynamics and changes in tree species composition at the local community level using population models and individual-based models for PFTs. Finally, and importantly, such new sets of PFTs with similar responses to global change need to be included in dynamic global vegetation models – which typically include just a couple of very broad PFTs for tropical forest trees [75] – to increase the reliability of their predictions.

flexible population models or individual-based models [28] that generate information about changes in population size, recruitment, and expected lifespans. Parameterization of these models can be achieved using the output of tree-level models and they can be validated using observed fluctuations in population sizes and size distributions. The results obtained from models are an important input for species-range modeling and community-level models.

At the community level, there is a need to more realistically parameterize and validate DGVMs, the main tool for predicting large-scale responses of tropical forests to climate change [59]. Despite their dominant role in the literature, the contribution of these models to a fundamental understanding of tropical forest responses to climate change has been limited. Major uncertainties remain regarding the physiological responses to climate changes of plants and trees in DGVMs [60]. Consequently, the results of these models need to be interpreted cautiously. The output of tree- and population-level models can be used to provide more realistic parameterization of DGVMs. An alternative and potentially powerful approach is the use of optimization models (OMs), which start from the theory of

optimal plant function and are driven by evolutionary and physiological principles [61]. So far, DGVMs and OMs have not accounted for the high taxonomic and functional diversity of tropical tree species, which is likely to have limited the degree of realism of model output (Box 3).

### Concluding remarks

Research on the responses of tropical forests to global change has been primarily focused at the leaf and community levels. The paucity of studies at individual tree and population levels has left important gaps in knowledge. These knowledge gaps preclude the interpretation of the observed community-level changes in tropical forest biomass and dynamics because insights into short-term and small-scale leaf-level responses to global-change factors cannot be easily scaled up to interpret community-level trends over longer periods of time. We have argued that the focus in this field of research needs to shift to the study of individual trees and populations and to consider the relevant timescale for tree-growth and forest dynamics. We have discussed four methods that have substantial, but underexploited, potential to contribute to the field and can be combined with existing approaches. Improved insights into global-change effects on tropical forests are needed to predict the fate of these globally important ecosystems, inform international policy makers, and guide conservation and management efforts. We are confident that the new methodological approaches proposed here will contribute to such improved insights.

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