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FOREST ECOLOGY: The fate of Amazonia

A fifty year observational record of Central Amazon forest reveals the multifaceted nature of tree death and concerning signs of vulnerability to increasing heat.

Emanuel Gloor

Amazon forests - by far the largest tropical forests of the world - are often referred to as the lungs of the planet because they cycle huge amounts of carbon and oxygen. In parallel they pump even larger quantities of water into the atmosphere. They host an incredible diversity of life and are of global importance for atmospheric carbon levels and climate. These forests are experiencing a rapidly warming and increasingly erratic climate as well as rising atmospheric CO₂ levels¹. Thus, the fate of these forests is of global concern but remains highly uncertain. Writing in *Nature Climate Change* Izabela Aleixo and co-authors² provide important new insights into rainforest resilience based on a truly unique 50-year record of mature tree phenology and mortality in Central Amazonian.

The significance of the Amazon forests for the global carbon cycle, and potentially future climate warming, is evident in the global atmospheric CO₂ record measured at Mauna Loa, Hawaii, which started just seven years earlier than this study. Inter-annual anomalies of the atmospheric CO₂ growth rate are in synchrony with the main global climate oscillation, El Niño. These anomalies are known to be primarily the result of drier than usual conditions across large parts of the Amazon and its effect on forest carbon uptake and release. Thus the Amazon acts effectively as a global atmospheric CO₂ pacemaker. Atmospheric CO₂ records also reveal a growing imbalance in the global atmospheric carbon budget³. The imbalance is caused by steadily increasing carbon uptake on land³, and Amazon forests are an important contributor to this growing carbon sink⁴. In recent decades plants have also become substantially more efficient at fixing carbon per unit of water lost, which is possibly because of beneficial effects of elevated atmospheric CO₂⁵.

The rapidly changing climate and environmental conditions experienced by Amazonia are likely to have both negative and positive effects on the trees. As trees take up CO₂ from the atmosphere they lose large amounts of water, and to stay alive they need to keep their living tissue well-watered. Consequently they continually draw water from the soil to the canopy through narrow conducting vessels. Loss of water from the canopy increases with temperature because water loss is controlled by vapour pressure difference between leaves and the outside air. This in turn leads to increased tension in water filaments and eventually embolism (creation of air bubbles), resulting in failure of the tree hydraulic system and damage to the vessels⁶. Anomalously high temperatures may also have direct negative effects on vital processes in trees. For example at temperature levels above around 28°C carbon assimilation rates tend to decrease and at yet higher temperatures photosystems will be damaged⁷. On the other hand increased CO₂ is expected to stimulate growth which in turn will lead to shifts in tree population demography and has been hypothesized to accelerate the life cycle of trees, increasing the rate of turnover. Increased turnover rates will tend to reduce the amount of carbon stored in living trees though, because at steady state carbon stored in forests equals the product of turnover rate and productivity.

A number of approaches have been pursued to investigate how Amazonia's forests will develop. Famous modelling studies suggested that large swaths of Amazon forests may turn

into savannahs but important forest dynamics processes were incompletely represented in those simulations⁸. Much has been learned about controls of forest productivity from forest-atmosphere carbon and water flux measurements, for example, that there are different controls on forest productivity in different parts of the Amazon⁹. Repeat censuses of hundreds of 1 ha intact forest plots, widely distributed across the Amazon, have revealed that these forests are a large although weakening carbon sink, with tree mortality steadily increasing over most recent decades. Measurements taken, typically every 3 to 5 years, such as diameter of each tree in a plot and whether a tree is dead or alive, are simple but powerful measures of forest health⁴. There has also been substantial progress in mechanistic and physiological understanding of the effects of drought and temperature on trees and identification of threshold response levels^{6,10,11}. Currently the large-scale spatial surveys of tree vulnerability needed to generalize these results are lacking. Two drought experiments in Eastern Amazonia have provided important insights into long-term drought effects, revealing substantial resilience to drought, however, these sites are unlikely to be representative of most of the Amazon forests¹¹.

Aleixo and colleagues add empirical evidence of the factors which control tropical forest tree mortality. The study is based on two time-series which recorded the status of trees and climatic conditions on a monthly basis in Central Amazonia, close to Manaus, over the past 50 years. The record is exceptional because of its length, one of the longest if not the longest existing, and its high time-resolution. This offers unprecedented data with which to understand the controls and causes of tree mortality, including factors such as life history strategies and climate conditions. The authors also apply an innovative approach to attribute mortality to particular causes. Some of the findings are not un-expected. Firstly as originally healthy trees were selected there is no mortality during the first 10 years, then mortality starts to increase as the trees age. Droughts cause most mortality in pioneer species – which tend to be less drought-tolerant, compared to late-successional high wood density species – and thus are particularly vulnerable. This may be significant for predicting future compositional changes. Furthermore variability in drought induced mortality followed the rhythm of El Niño events which was also in line with expectation. There are surprises too however, for example storms were found to particularly affect large trees of late-successional species, which are usually thought to be most resistant to storms. Perhaps most importantly non-linear responses to heat anomalies are found, with mortality increasing rapidly above 29.5 °C. This points to a possible Achilles heel of these forests to climate change.

Aleixo et al.'s study is a beautiful example of the exceptional value of detailed long-term records which are rare in the tropics. Their study is however from just one location and provides incomplete mechanistic insight into the causes of tree death. Further research should focus on improving understanding of the mechanisms of heat and drought induced tree death. Wider spatial coverage will also help to generalise our understanding. The most promising mechanistic indicators of tree vulnerability are likely to be species specific hydraulic and thermal safety margins for given climatic conditions. Further work is still needed to establish the predictive power of these approaches though. Targeted controlled indoors and outdoors heat and drought experiments would be valuable, particularly in Southern Amazonia which is climatically threatened but lacks such studies. Improved mechanistic understanding should also be validated with results from regular widespread forest censuses as well as remote sensing surveys. Taken together gained insights would much improve our capacity to predict the fate of Amazonia's forests under climate change.

Of course deforestation must also be tackled if these Amazonian forests are to survive into the future.

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Tree death after 2015/16 drought in Tapajos, Santarem, Brazil, credit Fernando Espirito-Santo)