with increasing forest productivity and dynamism [9]. Second, known atmospheric CO_2 concentrations and atmospheric-transport models suggest that the tropics are either neutral or a small net source of carbon (0–2 Pg C yr^{-1}). Thus, as deforestation, fires, logging, fragmentation, rivers and wetlands collectively are a major source of carbon to the atmosphere (2–4 Pg C yr^{-1}), an intact-forest carbon sink is likely to be required to balance the tropical and global carbon budgets from the late 20th century [10].

Wright considers the future of tropical forests, but excludes predictions from modelling. One state-of- the-art model predicts that half the Amazon rainforest could die off during this century under 'business-as-usual' CO_2 emission predictions ([11], although other scenarios are possible [12]). Wright's focus on single study sites and community-ecology studies at the expense of other evidence is likely to have downplayed the importance of global changes to tropical forests (and vice versa). This sends a worryingly ambivalent message about the future of tropical forests to students, scientists, policy makers and civil society as a whole.

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Letter Response

Response to Lewis *et al.*: The uncertain response of tropical forests to global change

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I thank Lewis *et al.* for their letter [1] in response to my recent review article in *TREE* [2], but argue here that the response of tropical forests to global and regional anthropogenic change, hereafter anthropogenic change, is highly uncertain despite evidence marshaled elsewhere [1,3,4]. Here, I pose six questions to pinpoint sources of this uncertainty.

First, are old-growth tropical forests carbon sinks? Repeated censuses of small tropical forest plots detect increasing aboveground biomass (AGB), which suggests that they are [3]. By contrast, models of latitudinal atmospheric CO_2 concentration gradients that incorporate ocean processes identify a large CO_2 source in tropical and southern lands and a larger CO_2 sink in tropical oceans (https://www.icdc7.com/proceedings/abstracts/jacobson1FF224Oral.pdf). One of these assessments is thus incorrect.

Second, are apparent AGB increases real? Many sources of artifact have been debated [1–4], whereas others have not. Specifically, many plots were first censused by one investigator and re-censused by others using 'progressively refined' protocols [3]; thus it is difficult to compare such results accurately. I would like to see an analysis that is limited to censuses conducted by the same lead personnel using the same protocols within each plot. Such an analysis has yet to be presented.

Third, if AGB increases are real, would they necessarily imply a response to anthropogenic change? Assuming that tropical forests were in equilibrium before anthropogenic change, AGB increases become evidence for increases in some limiting resource (e.g. CO_2, nitrogen or light), which is attributed to anthropogenic change [3,4]. However, the assumption is certainly false for forests that are recovering from disturbances, where AGB will increase because the forest is regenerating.

Fourth, is disturbance widespread? Hurricanes, downbursts associated with convectional storms, drought and/or fire disturb most tropical forests repeatedly during each tree generation [2,5,6]. Anthropogenic disturbance is also likely to have been a common occurrence for some

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time; for example, up to 100 000 000 people inhabited the Americas in 1491, when neotropical forests were widely managed for useful trees or converted to agriculture [7]. Thus, diverse disturbances disrupt forests repeatedly, even on continental scales.

Fifth, do tree-plot censuses distinguish between responses to anthropogenic change and recovery after disturbance, as attempted elsewhere [1,3,4]? These attempts compare changes in AGB, growth and mortality observed in tropical forests with those expected as even-aged stands regenerate. Minimum size thresholds that exclude smaller trees from censuses can compromise such comparisons [2]. There is a more fundamental problem, however. Windthrow, drought and fire leave a patchwork of dead trees intermixed with survivors [5,6] and small stands accumulate the imprint of several disturbances within one tree lifetime. The expected pattern of change in AGB, growth and mortality is unclear for mixed-age stands recovering from multiple disturbances.

Sixth, does evidence suggest that recent increases in AGB represent prolonged recovery after infrequent disturbances? Exactly this occurred in the Atlantic forest of Brazil, where decadal increases in AGB followed rapid declines during El Niño events [8]. This is also likely to have occurred in Panama, where drought increased tree mortality during the 1982–1983 El Niño event and AGB was monitored from 1985 to 2000 [9]. Nonetheless, the confidence interval for AGB change spanned zero (from -0.68 to $0.63\,\mathrm{Mg\,ha^{-1}\,y^{-1}}$) and thus provided no evidence for an AGB increase.

Large AGB increases are suggested when the Panama data are presented by microhabitat (Table 1 in [1]) because area and biology are neglected. Large AGB increases characterize microhabitats that accounted for 2% (swamp), 3% (streamsides) and 4% (young forest) of the 50-ha sample [9]. AGB should increase as young forest regenerates. The drought-sensitive trees found in swamp and streamside areas suffered elevated mortality during the 1982–1983 El Niño event and compensatory increases in AGB followed, just as in the Atlantic forest of Brazil. By contrast, AGB declined in microhabitats that accounted for 50% (low plateau) and 23% (slope) of the area [9]. Thus, AGB change cannot be distinguished from zero for the largest tropical forests sample yet assembled [9].

Does other evidence suggest AGB responses to anthropogenic change? A widespread change in canopy texture is consistent with increased productivity and also with recovery from disturbance [10]. Unfortunately, radiometric problems beset this analysis, which compared Landsat 1/2 and Landsat 4/5 imagery (A. Sanchez-Azofeifa, personal communication). Changes have also been documented in tropical forest plant species composition, with lianas increasing in old-growth tropical forests. Recovery from disturbance can be discounted because lianas become less important along tropical forest chronosequences, thus lianas should decrease rather than increase through time. Independent methods have confirmed the increase in lianas, and anthropogenic change might be responsible [11,12].

My disagreement with Lewis *et al.* [1,3,4] concerns their conclusion that AGB is increasing in old-growth tropical forests. Their interpretations can be debated (Questions 2–6 above) and independent evidence contradicts their conclusion (Question 1). Plants will respond as anthropogenic change increases tropical temperatures, atmospheric CO_2 concentrations, nitrogen and pollutant deposition and possibly alters light levels, rainfall regimes and storm severity. Recent models predict wildly different responses (references in [1,2]) and I agree with Lewis *et al.* that this is indeed an alarming message.

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