Detecting vulnerability of humid tropical forests to multiple stressors

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In brief
Rainforests take hundreds of years to be formed into a diverse and complex structure that is lush but fragile. The reason for their fragility is the difficulty to recover from disturbance. Using satellite observations, we show how increasing threats from large-scale deforestation and severe climate conditions over the past four decades have substantially impacted the ecological functions of these forests regionally, pushing them toward a critical point of no recovery and a dryer and less diverse state.

Highlights
- An index to track vulnerability of global rainforests to climate and land use
- Four decades of satellite data show widespread vulnerability across the tropics
- Response of rainforests to heat and drying varies across the continents
- Early warning from the index can identify regions for conservation and restoration
Detecting vulnerability of humid tropical forests to multiple stressors


SUMMARY

Humid tropical forests play a dominant role in the functioning of Earth but are under increasing threat from changes in land use and climate. How forest vulnerability varies across space and time and what level of stress forests can tolerate before facing a tipping point are poorly understood. Here, we develop a tropical forest vulnerability index (TFVI) to detect and evaluate the vulnerability of global tropical forests to threats across space and time. We show that climate change together with land-use change have slowed the recovery rate of forest carbon cycling. Temporal autocorrelation, as an indicator of this slow recovery, increases substantially for above-ground biomass, gross primary production, and evapotranspiration when climate stress reaches a critical level. Forests in the Americas exhibit extensive vulnerability to these stressors, while forests in Africa show relative resilience to climate, and forests in Asia reveal more vulnerability to land use and fragmentation. TFVI can systematically track the response of tropical forests to multiple stressors and provide early-warning signals for regions undergoing critical transitions.
INTRODUCTION

Humid tropical forests (HTFs) (Figure S1) are hyper-diverse and play a dominant role in the functioning of Earth and regulating its climate by accounting for more than half of its life forms, one-third of its metabolic activity, and storing more than half of its vegetation carbon. These forests benefit from relatively warm temperature and high rainfall in equatorial regions that support the storage and processing of larger amounts of carbon via plant productivity and ecosystem respiration than any other biome. During the dry season, tropical trees are the primary source of water released to the atmosphere through evapotranspiration (ET), creating rainfall locally and thousand miles away to maintain their moist environment. These processes have been maintained regularly for millennia with intact forest structure and diversity and stable ecological functions.

However, HTFs are under increasing threats from human-induced and environmental stressors. Between 15% and 20% of HTFs have been cleared since the early 1990s and at least an additional 10% have been degraded.
decline of carbon storage and productivity has been reported regionally due to elevated temperature and droughts. \(^9\)–\(^11\) Water and energy exchanges are suppressed significantly from forest degradation or drying atmosphere.\(^{12}\) Remaining forests are changing into increasingly smaller fragments with substantial biodiversity loss.\(^{13}\) With the projected rate of climate change and escalating land-use activities, these forests will lose their current capacity for global carbon sink and may even become a source of carbon to the atmosphere via changing photosynthesis and respiration rates, losing biodiversity, increasing tree mortality from droughts, and widespread forest collapse via fire.\(^{14}\)

Over recent decades, HTFs have grown increasingly vulnerable to these pressures with high probability of undergoing regime shifts.\(^{15}\) Climate models predict either a tipping point of tropical forests in the form of large-scale tree mortality\(^{16}\) or a more gradual continuous transition to a drier and fire-dominated savanna-like ecosystem,\(^{17}\) both with large uncertainties in future trajectories.\(^{18}\) There is ample evidence from local studies and ecosystem modeling that the HTF vulnerability is eminent,\(^{18}\)–\(^20\) but how forest vulnerability varies across space and time and regionally due to elevated temperature and droughts.\(^{9}\)–\(^11\) Water decline of carbon storage and productivity has been reported via fire.\(^{14}\)

We define a stressor as a condition, event, or a trend related to climate variability and change or forest disturbance, such as the stress from climate change, including climate variability and extremes.\(^{24}\) Vulnerability can be considered as an estimate of the inability of the ecosystem to tolerate stressors.\(^{25}\) This occurs when the ecosystem starts modulating its responses to stressors over time and space and starts losing its resilience or the ability to recover from disturbance.\(^{26}\) To quantify resilience, we evaluated the temporal autocorrelation between each response and stress variables on the monthly time scales after removing the seasonal cycles and trends. Higher temporal autocorrelation points to the slow recovery of the ecosystem if it is exposed to severe stress, which can be considered an important early-warning indicator of critical transitions.\(^{27}\)–\(^29\) We then used additive regression AR1 models to simultaneously assess the relationship of temporal autocorrelation to multiple stressors.\(^{29}\)–\(^30\) The coefficients of the 1-month-lagged response variables can be used to identify regions sensitive to stress and/or with the memory effects and to develop a spatially explicit tropical forest vulnerability index (TFVI) that shows changes of the response variables to long-term trends of multiple stressors. The magnitude and spatial variations of TFVI can identify areas across the tropics that exhibit high vulnerability and risks of a critical transition.

**RESULTS**

**Patterns of forest stressors**

We quantify land-cover and land-use change (LCLUC) stress across the tropics using the spatial variations of TC change and burned area from fire from 1982 to 2018 (Figures 1A and 1B). The percent of TC change at the grid cells includes loss of forest from deforestation and degradation and gain from secondary forest recovery, and afforestation relative to the benchmark forest cover of 1982 (experimental procedures). Changes of TC show that, in the 1980s, more than 340 Mha (10\(^6\) hectares) of tropical forests experienced a net loss (gain-loss) of tree cover, which became more widespread in the 1990s (~390 Mha) and 2000s (~420 Mha), but dropped significantly in 2010s to about 300 Mha (Figure S2). TC loss exhibited uneven patterns globally and across time, with large-scale deforestation and agricultural expansion in the Americas, to small-scale shifting cultivation in Central Africa, and a combination of agroforestry and commodity-driven agriculture in Asia.\(^{31}\) The net loss of TC was consistently higher in the Americas, with an average rate of 2.5 Mha year\(^{-1}\) in the 1980s, 1.2 Mha year\(^{-1}\) in the 1990s, 2.0 Mha year\(^{-1}\) in the 2000s, and 1.6 Mha year\(^{-1}\) in the 2010s. In Africa, the highest rate of TC loss was about 0.6 Mha year\(^{-1}\) from 1982 to 1999 but it dropped significantly to about 0.15 Mha year\(^{-1}\) from 2000 to 2018. More recently (2000–2018), the gross TC loss was about 7.3 Mha year\(^{-1}\), which is comparable with 7.65 Mha year\(^{-1}\) of average rate of forest clearing extracted from the Landsat-based (30-m resolution) forest cover change products (Figure S3).\(^{32}\)

Wildfire impacts on forest cover remained confined to areas where deforestation and human activities are concentrated or across forest-savanna boundaries (Figure 1B). We found the annual rate of burned area (BA) in forest pixels across all HTFs is about 21 Mha year\(^{-1}\) averaged from 1982 to 2018. This estimate may be larger than real area of fire burns due to the coarse resolution of satellite data (500 m) and partial burns within each pixel. Time series of percent of BA show that fire disturbances in the African tropical forests are twice more prevalent and have
larger interannual variability than fires in other continents (Figure S4). Our results suggest that forest fire and other land-use change activities impact approximately 10–15 Mha year\(^{-1}\) (not accounting the overlapped areas) (experimental procedures), causing the reduced intact forests area (>50% TC) from 1,300 Mha in 1982 to less than 1,000 Mha at the end of 2018.

Increasing climate variability and change further exacerbates the land-use stress on tropical forests. Trends of air temperature (Figure 1C) show that regions in the southeast and northwest of the Amazon, Central and West Africa, and tropical Asia have experienced an increase of more than 0.4°C per decade. While tropical forests may show strong resilience to increased temperature,\(^{33}\) the warming trend is also accompanied by atmospheric drying represented by VPD. We find an extensive increase of VPD (>0.01 hPa year\(^{-1}\)) in South America and Central Africa (Figure 1D), including severe anomalies across regions in the southeastern Amazon and Congo Basins during drought years (Figure S5). The VPD trend shows a potential turning point from the early 2000s with approximately 1.5 times larger increase than the first two decades (1982–1999), suggesting a substantially more stress from atmospheric drying across the tropical forests in the last two decades.\(^{34}\)

Impacts of droughts and water stress on tropical forests are detected by the spatial variations of the WB as the difference

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**Figure 1. Spatial patterns of stressors across humid tropical forests**

Patterns of LCLUC indicators are shown as: the trend of annual TC change (1982–2018) capturing deforestation and degradation, and average of maximum fraction of fire burned area (BA) at the pixel over the entire time series (1982–2018). Patterns of climate stressors are shown using trends of air temperature (AT), VPD, and WB from 1982 to 2018 (see experimental procedures).
between monthly water supply from precipitation and the water loss from potential ET (experimental procedures). Trends of WB from 1982 to 2018 (Figure 1E) show heterogeneous and divergent patterns with negative trends developing across the Congo Basin and areas in the south and southwestern Amazon. In contrast, we found increasing water availability in Asia and the northwestern Amazon. However, trends alone may not capture the water stress across the tropics. Stress from WB increases from seasonal anomalies of rainfall and during episodic droughts.7,35,36 The negative trend of rainfall during the driest quarter shows that the western Amazon and its headwaters are emerging as the largest region of seasonal rainfall decline in recent decades (Figure S6). Rainfall trends are more heterogeneous across African and Asian forests, showing patterns of increasing rainfall (Figure S6).

**Patterns of forest responses**

Among ecological responses, we focus on processes associated with the forest carbon cycling by including changes in live AGB from 2000 to 2018, the GPP from 1982 to 2018, ET from 1982 to 2018, and day-time LST from 2000 to 2018, which links forest carbon fluxes with energy cycles and is closely related to forest canopy temperature. Trend analysis shows the spatial patterns of these responses across the tropics (experimental procedures) (Figure 2). We found significant biomass loss in the southern and eastern Amazon and along the Andean...
foothills, Central America, West Africa, and Insular Asia (Figure 2A), where deforestation and degradation have been persistent and widespread (Figure S3). Trends of live biomass across tropics also show extensive areas of forest biomass gain, most importantly in the central and northern Congo Basin and mainland Asia and southern China. Increasing biomass in the Congo Basin may be attributed to the decline of the LCLUC stress and stable productivity due to climate conditions and atmospheric CO₂ fertilization. Increases in biomass in southern China are associated with recent intensive forestry, which significantly expanded across the region over the last 20 years.

Forest productivity shows widespread and strong negative trends in the Amazon Basin over the entire time series (Figure 2B) influenced by frequent droughts, increasing temperature, and VPD since the early 2000s (see supplemental information) (Figure S5). In contrast, forests of the Congo Basin show stable and even increasing carbon productivity in northern and eastern regions (Figure 2B). Forest productivity shows positive trends in large areas of mainland Asia, southern China, and Central America, mostly due to widespread forest recovery from past disturbance, afforestation in recent years, and climate conditions favorable to GPP increase, such as increasing radiation and rainfall.

ET shows a declining trend (Figure 2C), mostly in areas impacted by the LCLUC across the tropics. Southern Amazon, with large-scale forest conversions since the early 1980s, areas in Central America, West Africa and Madagascar, and Insular Asia, with significant loss of intact forests appear as hotspots of long-term loss of ET. In contrast, large areas across the tropics show increasing trends of ET due to increasing rainfall from the intensification of the hydrological cycle (Figure S5) or forest cover gain (e.g., mainland Asia and southern China) from afforestation and plantation systems.

We used the current state of HTF biodiversity intactness (BI) varying between 0 and 1 and representing the present state of biological and structural integrity of tropical forests (Figure 2E) (experimental procedures). This index is used in our analysis to examine the link between forest resilience and its BI. We found high values of intactness (>0.7) ubiquitous across the central Amazon, Congo Basin, and Asia. However, there are also large areas with lower scores of (<0.4) in the southern and western Amazon, along the foothills of the Andes, and the coastlines where most forest clearing and degradation are concentrated. Wetlands of the Congo Basin exhibit fragmentation from dense hydrographic networks and extensive small-scale agriculture and settlements along rivers (Figure 1A), but remain relatively intact in biodiversity (>0.7). A clear contrast between TC change and BI exists in the mainland and Insular Asia where the landscape is highly fragmented due to forest cover change but the biodiversity remains relatively high (>0.7).

Continental comparison of stress and response variables
To facilitate a direct comparison of the ecosystem stressors and responses across space and time, we normalized the distribution of each variable to their long-term mean across HTFs using quantile transform and preserved both negative and positive trends (experimental procedures) (Figures 3A and 3B). We represented the cumulative distributions of normalized stress and response variables for each tropical region separately in cart wheel plots (Figures 3C and 3D). Climate and forest disturbance stressors emerge with similar scores but show larger variability across the tropics (Figure C), while ecosystem responses show relatively higher impacts on functions than states and remain less variable across the tropical regions (Figure 3B). HTFs in the Americas experience relatively similar cumulative climate and LCLUC stress with the exception of fire, whereas forests in Africa and Asia are exposed to relatively higher and lower climate and LCLUC stress, respectively. Overall, we find climate stress in each tropical region rivals LCLUC stress to near 0.4–0.6 of the HTF extent in Americas, about 0.6 in Asia and Oceania, and 0.5 in Africa. Their spatial patterns, however, suggest that the responses of ecosystem functions represented by RF (GPP, ET, LST) are mostly (Rₚ > 0.6) influenced by the patterns of climate stress (Figures S7A and S7C), whereas the ecosystem states (AGB, BI) are mostly (Rₚ > 0.6) impacted by the patterns of forest cover change from LCLUC (Figures S7B and S7D).

Forest vulnerability and resilience
The temporal autocorrelation of ecosystem responses (AR1 model) shows diverse variations along climate and LCLUC gradients across the three continental regions (Figure 4). The increase in temporal autocorrelation means that the state of the ecosystem on subsequent moments in time become more correlated indicating slower recovery rates (slow down) of the system. Temporal autocorrelation of AGB does not show any significant variation along gradients of WB (or precipitation) (Figures S8A–S8C), while GPP exhibits bimodal patterns in the Americas and Asia (Figures 4A and 4C) and increases markedly in regions with lower annual WB in Africa (Figure 4B). In contrast, ET and LST autocorrelation exhibit higher variability along WB gradients across the three continents (Figures 4B and 4C), indicating the potential slowness and even closeness to critical transitions in regions with typically lower WB, more distinctly in Africa (Figures S8H and S8K). The difference between forests of Africa and other continents disappears in patterns of ET and LST autocorrelation with VPD (Figure S9), showing a gradual but significant slow down when VPD increases. Similarly, temporal autocorrelation of ET and LST also tends to increase with TC, suggesting slow down with the loss of TC (Figure S10).

Using the additive AR1 model with multiple stress variables, we map variations of TFVI for each ecosystem response variable across the tropics (Figure 5). The absolute magnitude of TFVI represents the risk of critical transitions that would result in abrupt decreases (negative values) or increases (positive values) of the response variable given long-term trends in the stressors. The larger the absolute value of TFVI, the greater the risk of a critical transition to either higher or lower value of the ecosystem response. All TFVI values for response variables include uncertainties evaluated from the error propagation of AR1 model coefficients and the data layers used for stress and response variables (experimental procedures).

The TFVI for AGB trend shows extensive areas of south and central Amazon Basin (>91 Mha) with significant vulnerability (TFVI < -2) and transition of ecosystem to a low AGB state (Figure 5A). The TFVI captures the spatial patterns of TC loss and shows strong sensitivity to atmospheric drying conditions represented by increasing VPD in the past two decades (Figure S11).
In contrast, forests in mainland Asia, particularly in the greater Mekong region, show a persistent transition to low AGB state from declining trend of tree cover (sensitivity to TC). African forests, particularly in the Congo Basin, show widespread low sensitivity of AGB to climate. Forest productivity (GPP) on the other hand, exhibits widespread vulnerability in the Amazon Basin (>100 Mha), albeit that most areas show only more moderate risk of sustained reduction (TFVI < 0.5). The notable exceptions are areas under substantial LCLUC stress across the arc of deforestation (Figure 5B) (TFVI < 1). In contrast to these striking patterns across the Amazon, most forests across Africa and Asia show low vulnerability to critical transitions in GPP (Figure 5B) due to the low sensitivity of GPP to climate stress (Figure S12); we even found regions across Africa and Asia that show sustained increase of GPP in the east and west of Central Africa due to increasing VPD (potentially more radiation) and mainland Asia and southern China due to increasing forest cover (Figure S12).

The vulnerability of the tropical carbon cycle is also detected in the coupled processes of ET and surface energy balance. TFVI of ET exhibits two distinct patterns across tropical regions (Figure 5C). Areas with extensive trend in forest cover change in the southern and eastern Amazon (>75 Mha), Central America (>12 Mha), eastern Africa and Madagascar (>40 Mha), and Insular Asia (>9 Mha) show strong risk (TFVI < -1.0) toward a critical reduction of ET. At the same time, extensive regions of tropical forests on all continents exhibit a transition to critically higher ET due to sensitivity to increasing VPD and incoming radiation (Figures S6 and S13). Similarly, LST shows almost ubiquitously high vulnerability of persistent warming across the Americas (>400 Mha) with TFVI > 0.5 (Figure 5D). These areas show increasing LST due to a combination of warming climate, increasing VPD, and large-scale loss of tree cover (>100 Mha) from TC trend. Vulnerability of LST is also due to sensitivity to extreme climate anomalies and water stress during droughts, which impacts heat flux and surface energy balance.7,41 Contrary to the Americas, LST of forests in Africa shows low sensitivity to climate trends and anomalies except in areas already impacted by widespread LCLUC (eastern Africa and Madagascar). In Asia LST vulnerability is largely due to LCLUC,
with substantial sensitivity to VPD, particularly in mainland Asia and southern China. The uncertainty ranges of TFVI predicted from the error propagation model (Figure S15) have been taken into account to present only regional patterns of vulnerability that are robust.

**DISCUSSION**

There are some consistent results emerging from our study: (1) among tropical forests, the Amazon shows significantly more vulnerability to climate and land-use stressors than forests in Africa and Asia, (2) forests in continental Africa, although impacted by similar levels of climate stress as the Amazon, show more resilience, and, in Asia, land-use change drives the forest vulnerability, (3) HTF carbon cycling responses (AGB and GPP) are impacted by climate, but so far show more vulnerability to LCLUC pressures, while ET and LST already show significant transitions attributable to both climate and LCLUC, and (4) the autocorrelation results suggest that, except for areas of largescale LCLUC, transitions of forests to a critical state appear to be more gradual than abrupt (Figures 4 and S8–S10). These observations and empirically determined patterns agree with results of multiple studies in recent years focused on HTF resilience in local field experiments, ecosystem modeling, and remote-sensing observations. Our novel approach, however, adds to the increasing evidence by providing patterns of HTF vulnerability based on longer time series of observations (37 years) compared with most observation-based studies. In addition, it allows assessing and quantifying the forest vulnerability based on ecologically important response variables that represent ecosystem states and functions (e.g., AGB, GPP, ET), instead of remote-sensing signals (e.g., optical normalized difference vegetation index) that are indirectly related to the forest function. Finally, our approach produces a spatially explicit index that allows tracking the vulnerability of ecosystem functions to multiple stressors in future.

Differences in patterns of vulnerability at the continental scales are influenced by interactions of recent climate and land-use changes and may also depend on historical human and environmental disturbances, and regional biogeographical and climate variations. We examine these interactions in two regions in the Amazon and Congo Basins (boxes in Figure 5). In the Amazon Basin, the regions with highest vulnerability index in GPP and AGB overlap with areas of large-scale forest degradation and fragmentation and significant VPD trend (Figures 1A and 1D). Both AGB and GPP show high sensitivity to these stressors (Figures S11 and S12). In the Congo Basin, on the other hand, the observed vulnerability pattern is the result of complex processes where carbon loss from small-scale degradation caused by shifting cultivation and logging (Figure 1A) interact with the gain from positive trend of AGB from forest recovery (Figure 2A), and moderate rise of VPD (Figure 1D), accompanied by substantial increase in incoming radiation (Figure S6). Such interactions result in overall low sensitivity of AGB and GPP to both climate and TC change, despite some areas showing relatively low resilience in the case of GPP (Figures S11 and S12). The interactions among multiple stressors may also be modulated with a long history of water stress in Africa, making the forests more adapted to droughts. Alternatively, other differences, such as stable available nutrients, continental scale biogeography, and contemporary drought tolerant species pools, may contribute to continental differences. However, these processes may temporarily reduce the vulnerability of the forest carbon cycling to climate stressors, but these patterns can change drastically as climate forcing increases and larger-scale land-use activities expand across the regions.

Although there is a strong negative trend of WB (increasing water stress) in the Congo Basin compared with the Amazon (Figure 1E), ET and LST show moderate or no trends across the forests. In addition, the patterns of TFVI over the Congo Basin suggest that the LST remains stable and ET shows a potential transition to persistent higher values (Figure 5), mostly driven by a positive sensitivity of ET to increasing VPD (Figure S13) that overcompensates the negative sensitivity to water stress (Figure 1E). We see the increase of temporal autocorrelation with increasing VPD, water stress, and forest cover change in ET and LST in both continents, suggesting a more direct influence of droughts and land-use change on ET and LST. In Asia, there is a moderate increase of LST and ET (Figure 2) but, combined with other climatic and land-use trends in the region, the TFVI shows a relatively high vulnerability with persistent increase in LST in Indonesia, and increased risk of high ET in southern China (Figure 5). These changes can be attributed to the strong sensitivity of LST to atmospheric drying in Java and Borneo (Figure S14), and the tendency of ET to increase as forest cover increases in southern China (Figure S13). Severe precipitation anomaly on forest hydraulic mechanisms can in turn cause increasing tree mortality and declined forest productivity, together resulting in the loss of biomass and GPP, which has been observed in local studies focused on long-term effects of climate. Our results illustrate the conditions under which the ecological functions of tropical forests may slow down or gradually transition to a new state. However, predicting transitions before they
are reached is extremely challenging. The autoregressive model allows us to detect whether the ecosystem is already experiencing vulnerability to climate and LCLUC stressors. This novel approach provides three intrinsic early-warning signals that may indicate if a transition or a tipping point is approaching: (1) sharp rise of autocorrelation indicating how the ecosystem may experience a critical transition if the stress from environmental conditions increases (Figure 4), (2) vulnerability patterns indicating to what extent the sensitivity to climate or LCLUC stress has already pushed the system toward transition (Figure 5), and (3) increased variance of ecosystem response variables (Figures S11–S14). Note that, unlike the striking patterns of the TFVI from the autocorrelation, the increasing variance of the ecosystem response represented by the coefficient of the AR1 model (\(\rho^{<1}\)) may be less consistent. For AGB, the variance is increasing in areas dominated by the land-use change but has no consistent relationship with respect to climate. In contrast, all other ecosystem responses, GPP, ET, and LST, show relatively consistent increase in variance (using values of \(\rho^{>1}\)) with respect to climate and land-use changes. The lack of consistency in patterns of variance and TFVI may suggest that the ecosystem vulnerability (e.g., in the case of AGB) may not be robust; however, there are indications that variance is sensitive to other factors that would cause an increase or decline. Examples of this are shown when environmental factors used as stress variables fluctuate stochastically and the ecosystem becomes less sensitive to these factors near the threshold, or when vulnerability or slowing down reduces the ecosystem’s capacity to follow high-frequency fluctuations in the stress factors. In our analysis, this inconsistency is more obvious in the case of AGB than other ecosystem responses (GPP, ET, and LST) either because of the effect of shorter time series (2000–2018) or longer
time steps (annual versus monthly) in the analyses. Nonetheless, TFVI is a relatively simple and practical index that contains information about the intensity and direction of vulnerable ecosystem responses, and provides reliable geographical extent and shorter lead times to ecosystem transitions. Whether the early-warning signal can be detected sufficiently early remains unclear.28

The consistent vulnerability patterns and the detected temporal autocorrelation for different responses suggest that the slowness of the ecosystem carbon cycling processes is widespread, but with variations in severity across the tropics. Although our results are purely correlational and could conceal competing explanations, the spatial patterns of TFVI appear robust and in agreement with other ground observations. More importantly, our analysis is based on an additive autoregressive model with multiple stressors and it is unlikely that the patterns derived from temporal autocorrelation and TFVI analysis may be artifacts of potential confounding factors.

Satellite observations, even though validated systematically against reference data may have uncertainties in detecting the ecosystem stress and response variables. These uncertainties influence the AR1 model by reducing the autocorrelation and cause either no sensitivity or false resilience to environmental stressors. However, the patterns of vulnerability detected by TFVI remain valid as they depend on higher autocorrelation between stress and response variables that are from independent observations. We performed a detailed uncertainty quantification by propagating errors associated with the remote-sensing observations and the AR1 models for multiple stressors (experimental procedures) and show that the spatial distribution of uncertainty in TFVI for all response variables remain significantly lower than the observed signal in the most vulnerable areas (Figure S15).

The TFVI accounts for multiple factors previously recognized as critical for assessing the vulnerability and sustainability of tropical forests,26 including the increased exposure to risks (through the long-term trends of stressors, the sensitivity of the ecosystems to stressors), fitted sensitivity parameters, and the resilience of the ecosystem (through the autoregressive coefficient). However, this approach has two important limitations. First, our index does not account for the consequences of vulnerability on societies and socio-ecological systems, including the loss of ecosystem function and states on livelihood dependent on the HTFs—HTF risks, following the IPCC AR5 definition.60 Second, by using an AR1 model, our approach implicitly assumes stationarity of both the sensitivity and the resilience of the response variables to climate and LCLUC. We opted for a simplified approach with a smaller number of parameters because the time span of the input data available is still relatively short, and with substantial uncertainty (Figure S15). However, the current approach does not account for the changes of the sensitivity and resilience that the system may experience over time. Changes in autoregressive coefficients have been previously proposed as an important metric for the development of early warning for systems approaching tipping points31 and could be incorporated in the future by expanding the TFVI formulation to be based on autoregressive integrated moving average models with exogenous predictors. Such hybrid models have been used to develop short-term predictions of droughts and fire activity62,63 and could provide the basis for implementing non-stationary models as longer time series of the main stressors and responses for HTFs become available.

The spatial nature of our approach is based on harnessing a wide range of observations sensitive to ecosystem structure traits and functions. We expect that, with longer records and more advanced satellite observations in the near future, TFVI’s ability to provide early-warning signals will significantly improve. Spatial patterns of TFVI can also be used to develop hypotheses and science questions that can be further explored by field experiments and long-term studies. For example, the detection of regions experiencing similar stress but different responses is an ideal case of using TFVI to perform perturbation experiments and examine if the slowness of the ecosystem responses is indeed a reasonable indicator of the ecosystems undergoing critical transitions, such as changes in composition, biodiversity, or carbon cycling.

EXPERIMENTAL PROCEDURES
Resource availability
Lead contact
Further information and requests for resources should be directed to and will be fulfilled by the lead contact, Sassan Saatchi (saatchi@jpl.nasa.gov).

Material availability
This study did not generate new unique materials.

Data and code availability
All original satellite and climate data used in the study can be downloaded freely from the following sites: All Moderate Resolution Imaging Spectroradiometer (MODIS) data are available to download from https://lpdaac.usgs.gov/. QSCAT radar data from BYU (Brigham Young University) Data Center: https://www.scp.byu.edu/, ALOS PALSAR data from the ALOS Research and Application Project of EORC, JAXA: https://www.eorc.jaxa.jp/ALOS/en/palsar_fnt/fnf_index.htm., All ERA-5 climate data from the ECMWF, the European Center for Medium-Range Weather Forecasts: https://www.ecmwf.int/en/research/climate-reanalysis. The GPP data are available from NASA DAAC: https://daac.ornl.gov/cgi-bin/dsviewer.pl?ds_id=1789, the global biomass data are available from https://doi.org/10.5281/zenodo.4161694, the forest cover change data are available from: http://earthenginepartners.appspot.com/science-2013-global-forest, time series of TC data are available from: https://glad.umd.edu/dataset/long-term-global-land-change. All data and codes used to evaluate the conclusions of the paper and generate the figures and tables are available at https://doi.org/10.5281/zenodo.5115158.

Datasets used
We selected the tropical and subtropical moist forests (HTFs) as the domain of our study using the WWF ecoregion map34 (Figure S1). We included tropical and subtropical moist regions in our study area because the exact delineation of the vegetation from wet and evergreen broadleaf forests to moist semi-deciduous broadleaf forests may be difficult across regions. The study domain for the tropical moist forests is more than 2,000 Mha covering all three continents. Unless otherwise noted, all data were reprojected to a 0.1° × 0.1° latitude-longitude grid (about 120 km² near the equator). Datasets used in this study span from 1982 to 2018. Unless otherwise noted, we selected this period because it has the most overlap on datasets that are readily available and provide us with a long time series to quantify impacts of climate change and variability on the ecosystem functions.

Forest stress variables
We selected available datasets to represent LCLUC and climate variables across the tropics. These include TC resulting from deforestation and degradation and forest recovery, and burned areas from forest fire. Climate datasets...
include air temperature, VPD, and precipitation. The variables were produced at either monthly or annual time intervals, depending on data availability.

For forest cover change, we used the Advanced Very High-Resolution Radiometer (AVHRR) vegetation continuous fields (VCF) product to represent the forest TC annually. The original dataset provides cover estimates for trees, short vegetation, and bare ground. Because our focus is on tropical forests, we considered only the TC data.

The original dataset spans from 1982 to 2016 and has missing observations in 1984 and 2000. To harmonize and gap-fill the dataset for the entire study period (1982–2018), we leveraged from the overlapped period of AVHRR and MODIS (2001–2016) to build a linear model of TC between MODIS AVHRR and AVHRR for each pixel. From the linear model, we predicted records for the missing years in 2000, 2017, and 2018 using existing MODIS observations. The missing data in 1994 were gap-filled using the Savitzky-Golay filtering based on neighboring observations in the temporal domain. We also used the Landsat-derived Global Forest Change (GFC) product to identify regions with forest clearing at 30 m spatial resolution.62 We aggregated the data to obtain the percentage of cleared area at 0.1° × 0.1° resolution for each year with the domain of the HTFs. The total areas in GFC forest clearing (2000–2018) have been calculated to demonstrate the spatial patterns (Figure S3A).

We assumed forest degradation to occur in forest areas that were disturbed by logging, fire, and fragmentation and edge effects,65 but where forest cover was not completely lost (forest cover >30%). To classify areas as degraded, we developed annual estimates of degradation using data from the pan-tropical degradation project detecting intact forest loss between 2000 and 2013.57 We set the degradation fraction for each 0.1° × 0.1° pixel calculated from the training data, and applied a machine learning model using boosted trees66 to produce annual series of degradation (2000–2018). This provides us with the percent of degradation at each grid cell that represents mostly the edge effects from deforestation and roads (including some logging roads) and long-term defoliation that may be the impact of mortality and canopy loss from droughts and understory fires.67 The final prediction outputs the percentage of degraded area annually from 2000 to 2018 (Figure S3B). We do not expect that the degradation product can accurately capture the effects of selective logging and small-scale shifting cultivations at the large grid cells.

The final forest cover change maps in the HTF domain were based on AVHRR TC time series from 1982 to 2018, with corrections of forest clearing and deforestation for the period with observations (2000–2018). Assuming that the forest clearing and degradation observations capture the land-use events correctly, the corrected TC can be

$$\text{TC}_i = \text{TC}_i^{0-1} + \left(\text{TC}_i^{0} - \text{TC}_i^{0-1}\right) + D_i$$

where $\text{TC}_i^{0}$ is the corrected TC for year $i$, and $D_i$ is the sum of original TC from the previous year $\text{TC}_i^{0-1}$, plus the observed VCF change ($\text{TC}_i^{0} - \text{TC}_i^{0-1}$), and the correction term $D_i$ due to disturbance events, such as forest clearing and degradation. Although TC observations of earlier years were not corrected, we found the impact of corrections was generally small (1%-3% of the original TC) and disturbances in earlier years were less significant than those in the more recent decades.58

For forest fire, we used the time series of the global BA product-based AVHRR LTRD dataset,78 which covers the period of 1982–2017. It is a monthly dataset with the BA (unit: m²) estimated for each grid cell. We converted the data to areal fraction of BA for the monthly records. The annual sum of BA fraction, in this product, can be higher than 100% for some regions, due to repeated fire events or extensive fires that last longer than a month. However, in our study region of HTF, the BA fraction rarely exceeds 50% in a single year. We added observations in 2018 directly using BA estimates from the MODIS Collection-6 BA data (product name: MCD64A1 v006)79 to complete the record of BA from 1982 to 2018.

For climate data, we used the monthly air temperature ($T$) at 2 m above surface data from the ERA5 reanalysis land dataset72 available from 1981 to 2019 and already at 0.1° × 0.1° resolution. We calculated the long-term trend using the Mann–Kendall test for the annual mean of each pixel, and normalized the trends (see approach below) only when the trends were statistically significant. Because the amount of water needed by the ecosystem is strongly modulated by temperature and radiation, we used the WB to represent the water stress instead of precipitation anomaly. For any given month $j$, $WB_j$ is defined as

$$WB_j = P_j - PET_j$$

We used the Climate Hazards InfraRed Precipitation with Stations (CHIRPS)19 monthly rainfall dataset, which combines precipitation estimates from rain gauges and the Tropical Rainfall Measuring Mission Multi-satellite Precipitation Analysis version 7 (TMPA 3B42) to calibrate high-resolution estimates of precipitation from frequent cold cloud duration events from thermal infrared imagery.19 CHIRPS datasets come at 0.05° resolution, and cover the period from 1981 to present. Similar to the temperature, we normalized the precipitation trends during the driest quarter, and ignored the trends when they were not statistically significant. For the purpose of comparison, we also calculated the rainfall trends for annual mean and driest quarter (Figure S6). Potential evapotranspiration (PET) was obtained from Global Land Evaporation Amsterdam (GLEAM)16,75 which assimilates a suite of remotely sensed data with a water cycle model. In GLEAM, the evaporation of intercepted water is treated independently of the potential transpiration, but here we considered that PET is the sum of their definition of potential evaporation and the evaporation of intercepted rainfall (i.e., PET = $E_p + E_i$ following the Miralles et al. [2011] notation).

For VPD at 2 m, we used data from the ERA5 reanalysis,76 developed by the Center for Medium-Range Weather Forecasts (ECMWF) under the Copernicus Climate Change Service (C3S). ERA5 does not provide VPD directly, but temperature ($T$) and dewpoint temperature ($T_d$) at 2 m. To account for the highly non-linear relationship between temperature and vapor pressure at saturation without relying on hourly data, we estimated VPD for each month ($VPD_m$) from the mean diurnal cycle of each month:

$$VPD = \frac{1}{24} \sum_{h=0}^{23} \frac{1}{24} \left(e^{\frac{T_d}{T}} - e^{\frac{T}{T_d}}\right)$$

where the index $h$ corresponds to the hour-dependent monthly mean values. The saturation vapor pressure at the given the temperature $e(T)$ is calculated following available empirical equation.19

Forest response variables

We selected four ecosystem response variables related to processes associated with forest carbon cycling. For AGB carbon, we used the recent global live biomass carbon products available for download from (https://doi.org/10.5281/zenodo.4161694) and described in detail in Xu et al.52 Annual AGB values at 0.1° × 0.1° grid cells from 2000 to 2018 were estimated globally using a large dataset of ground forest inventory plots of multiple censuses (>200,000 plots), systematic airborne lidar scanning data across global tropical forests (>1 Mha) and satellite lidar from Geoscience Laser Altimeter System lidar sampling measurements of vegetation height structure (>8 million samples). To map AGB, we used time series of global wall-to-wall satellite imagery from microwave and optical sensors at 0.1° spatial resolution to improve the sensitivity and uncertainty of AGB estimation globally and across tropics where cloud cover and sensitivity of satellite data at the native satellite resolution makes it difficult to estimate live biomass carbon. The samples from ground and lidar estimates of AGB included variations of forest types (montane, coastal, mangroves, seasonal), environmental conditions (rainfall seasonality and temperature), and regional variations of average wood density. A spatially balanced sampling inventory of AGB is built to train a spatiotemporal machine learning model based on the Random Forest model that predicts AGB and its uncertainty annually from time series of satellite data from a combination microwave (SeaWinds Scatterometer on QuikSCAT, ALOS PALSAR, Shuttle Radar Topography Mission, SRTM) and optical sensors (MODIS visible and thermal bands), and environmental variables, such as the precipitation from Tropical Rainfall Measuring Mission and Global Precipitation Measurement satellites.

For forest GPP, we used recently developed enhanced global GPP from a combination of remote-sensing, climate, and eddy covariance tower observations globally.13 The enhanced GPP data product is developed from Global Inventory Modeling and Mapping Studies (GIMMS3g) fraction of photosynthetically active radiation record for the period 1982–2016 extended by the MODIS data to 2018, and solar-induced chlorophyll fluorescence from the

We used the Climate Hazards InfraRed Precipitation with Stations (CHIRPS)19 monthly rainfall dataset, which combines precipitation estimates from rain gauges and the Tropical Rainfall Measuring Mission Multi-satellite Precipitation Analysis version 7 (TMPA 3B42) to calibrate high-resolution estimates of precipitation from frequent cold cloud duration events from thermal infrared imagery.19 CHIRPS datasets come at 0.05° resolution, and cover the period from 1981 to present. Similar to the temperature, we normalized the precipitation trends during the driest quarter, and ignored the trends when they were not statistically significant. For the purpose of comparison, we also calculated the rainfall trends for annual mean and driest quarter (Figure S6). Potential evapotranspiration (PET) was obtained from Global Land Evaporation Amsterdam (GLEAM)16,75 which assimilates a suite of remotely sensed data with a water cycle model. In GLEAM, the evaporation of intercepted water is treated independently of the potential transpiration, but here we considered that PET is the sum of their definition of potential evaporation and the evaporation of intercepted rainfall (i.e., PET = $E_p + E_i$ following the Miralles et al. [2011] notation).
Global Ozone Monitoring Experiment-2. An optimal light use efficiency (LUE) model previously derived from the global FLUXNET networks\(^{10,11}\) was used as the primary model to integrate remote-sensing and climate data (VPD, radiation, soil moisture) to estimate long-term (1982–2018) GPP globally at 8-km spatial and biweekly temporal resolutions.

Evapotranspiration (ET) directly quantifies the response of forest water cycling to a combination of forest cover change and climate effects (e.g., droughts).\(^{2,3}\) We used the actual evaporation developed from the GLEAM based on its version 3.3a dataset.\(^{4,5,7}\) The GLEAM v.3.3a dataset provides global ET estimates derived from a combination of reanalysis, in-situ and satellite data for the period of 1980–2018. The original monthly ET data at 0.25° resolution were spatially interpolated to 0.1° resolution using the cubic spline resampling method to match the resolution of other datasets.

We used MODIS Collection-6 day-time LST data (product name: MOD11A2 v008)\(^{8}\) to represent radiative heat exchange of the surface. We performed data pre-processing and internal data quality layers were enabled for screening of atmospheric contamination, including cloud cover and aerosol. For each month, we used the median of all available observations after discarding data considered unreliable based on the quality flags. After screening the data for cloud and aerosol effects, we aggregated all clean 1-km pixels to 0.1° grid using spatial average. In cases of missing pixels, we used the multiple imputation by chained equation method\(^{9}\) for data imputation using nearest observations.

We included the original BI,\(^{10}\) which estimates how the average abundance of native terrestrial species in a region compares with their abundances before extensive human impacts. Most values of BI range from 0 to 1 (it can exceed 1 in a few regions); higher values indicate regions with higher abundance of species richness. The original index (BI) was for the year 2005 and was updated by including annual forest disturbances.\(^{11}\) We aggregated the BI data from the original 1-km spatial resolution to 0.1° x 0.1° grid cells and adjusted for changes of forest cover using the most recent data on land-use change and forest structure. First, we weighted each intactness index with the fraction of deforestation from forest cover change data\(^{12,13}\) and MODIS BA\(^{8}\) from 2005 to 2018. Next, we combined the most recent BI index with the Forest Structural Integrity Index (FSII),\(^{14}\) which includes impacts of human pressure on the forest structural condition. FSII ranges from 0.1 to 18, and the highest values are associated with tall, old-growth forests that experience little human pressure. We scaled FSII by the maximum value to impose a range between 0 and 1 and multiplied the normalized FSII and BI to correct BI for forest structural integrity. The final product provided us with the most recent BI.

Regional aggregates of stress and response variables

To facilitate a direct comparison of aggregate stress and response variables among continents (Figure 3), we applied a consistent and systematic normalization of the variables.\(^{15,16}\) The original distribution of each variable across continents (Figure 3), we applied a consistent and systematic normal-
Because the fitted AR1 model is unbiased, $\Delta C_t(Y)/\Delta C_t = 0$. In addition, if $\Delta C_t \gg 1$ year, we can assume that $\Delta C_t(Y)/\Delta C_t = (\Delta C_t(Y)_{1-\Delta C_t})/\Delta C_t$, and simplify the equation above to be:

$$\text{TFVI}_Y = \Delta C_t(Y) = \frac{1}{1-r_y}(\Delta C_t(Y_{T0}) + \Delta C_t(Y_{T0}) + \Delta C_t(Y_{T0} + \Delta C_t(Y_{T0})_T)).$$

(Equation 10)

where $T_0$, $T_1$, and $T_2$ are the dimensionless long-term trends of (WB), (VPD), and TC, respectively. To estimate the long-term trend of stress variables, we fitted linear models of the normalized time series, assuming time $t$ to span between $t_1$ (first month of the time series) and $t_2$ (last month of the time series). The long-term trend was assumed to be the fitted slope of the linear model:

$$WB = w_2 + w_1 - \frac{t - t_1}{t_2 - t_1}$$

(Equation 11)

$$VPD = v_2 + v_1 - \frac{t - t_1}{t_2 - t_1}$$

(Equation 12)

$$TC = c_2 + c_1 - \frac{t - t_1}{t_2 - t_1}$$

(Equation 13)

The index TFVI$_Y$ represents the risk of long-term transitions due to increase in stress. For example, if the response variable $Y$ is AGB, negative values of TFVI$_Y$ represent risk of long-term biomass loss. The sensitivity coefficients to climate and disturbance can be either positive or negative; using again the example of biomass, negative values of $\Delta W$, $\Delta V$, or $\Delta C$ mean that increasing stress is associated with biomass loss, and thus more likely to contribute to vulnerability. Spatial variations of sensitivity coefficients demonstrate the links of response variables to different stresses across the tropics (Figures S11–S14). The term $r_y$ is associated with the resilience of the system, and it is typically between zero and one. As described in and shown in Equation 10, values near zero indicate high resilience and the ability of the system to quickly return to equilibrium as long as the product between sensitivity and the long-term trend of any of the stressors is not large (i.e., the numerator of Equation 10 is greater than $-1$), as the term $1/(1 - r_y)$ is approximately $1$. In contrast, when $r_y$ values approach 1, anomalies caused even by relatively small anomalies may persist for long periods of time (high vulnerability), as the term $1/(1 - r_y)$ approaches 1, TFVI$_Y$ approaches 1, and TFVI$_Y$ values approach 1, anomalies caused even by relatively small anomalies may persist for long periods of time (high vulnerability), as the term $1/(1 - r_y)$ approaches 1, TFVI$_Y$ approaches 1, anomalies caused even by relatively small anomalies may persist for long periods of time (high vulnerability), as the term $1/(1 - r_y)$ approaches 1, TFVI$_Y$ approaches 1, anomalies caused even by relatively small anomalies may persist for long periods of time (high vulnerability), as the term $1/(1 - r_y)$ approaches 1, TFVI$_Y$ approaches 1, anomalies caused even by relatively small anomalies may persist for long periods of time (high vulnerability), as the term $1/(1 - r_y)$ approaches 1, TFVI$_Y$ approaches 1, anomalies caused even by relatively small anomalies may persist for long periods of time (high vulnerability), as the term $1/(1 - 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AUTHOR CONTRIBUTIONS
S.S. conceived the idea. S.S., M.L., L.X., and Y.Y. designed the research and performed the analysis. S.S. wrote the main manuscript. M.L., L.X., and Y.Y. wrote the methods and the supplementary information. A.E. directed the study, and reviewed and commented on paper. All authors reviewed and edited the paper.

DECLARATION OF INTERESTS
The authors declare no competing interests.

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