LETTERS
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Remotely sensed resilience of tropical forests

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Recent work suggests that episodes of drought and heat can bring forests across climate zones to a threshold for massive tree mortality[1]. As complex systems approach a threshold for collapse they tend to exhibit a loss of resilience, as reflected in declining recovery rates from perturbations[2]. Trees may be no exception, as at the verge of drought-induced death, trees are found to be weakened in multiple ways, affecting their ability to recover from stress[3,4]. Here we use worldwide time series of satellite images to show that temporal autocorrelation, an indicator of slow recovery rates[5], rises steeply as mean annual precipitation declines to levels known to be critical for tropical forests. This implies independent support for the idea that such forests may have a tipping point for collapse at drying conditions. Moreover, the demonstration that reduced rates of recovery (slowing down) may be detected from satellite data suggests a novel way to monitor resilience of tropical forests, as well as other ecosystems known to be vulnerable to collapse.

An overview of tree mortality events across continents and climate zones suggests that drought and elevated temperatures can bring forests to a threshold for massive die-off[1]. For tropical forests, there is an extra dimension to such mortality events, as they could tip forests into a fire-dominated savannah state from which recovery is difficult. Different lines of evidence point to such a scenario. First, evidence for bistability of savannah versus forest comes from a series of recent remote sensing and modelling studies[6,7]. Second, field experiments (through throughfall displacement) have confirmed that drought can invoke mortality among large canopy trees in Amazonian[8,9] and Indonesian forests[10]. Third, a long-term fire experiment in the southeastern Amazon recently showed that in dry years, tree mortality rises sharply, driving the system towards an alternative self-stabilizing fire-dominated savannah state[11].

What precisely causes trees to succumb so massively across the globe during droughts and heat waves remains a topic of debate[12], but the emerging view is that, rather than studying isolated elements such as hydraulic failure or carbon starvation, we need a focus on systemic resilience of trees[3]. A detailed ground study[13] recently revealed how tree death involves a loss in canopy evaporative area, sapwood area, carbon uptake and hydraulic capacity, embolism and hydraulically limited canopy conductance, altogether making it increasingly difficult to bounce back from the effects of a drought, as reflected in a loss of recovery rates of foliage after a drought. This is in line with the finding that in Amazon trees, drought leads to reduced maintenance and defence investment undermining resilience[4].

This raises the question if we could somehow detect low resilience as an indicator of the risk of forest mortality. Resilience can be characterized by the rate at which a system recovers from perturbations. Experimental perturbations are a good way to detect such slowness, but are necessarily limited in scale. On the other hand, natural systems are continuously subject to stochastic perturbations resulting from fluctuations in the weather and other factors. The resulting fluctuations in the state of a system can reflect slowing down through an increase in temporal autocorrelation, in the sense that the states of the system, on subsequent moments in time, become more correlated[2,5]. Such slowing down does not result in less change (and thus in less variance), but rather in slower change over time, triggering the increase in temporal autocorrelation[2,5].

Slowing down in the vicinity of a critical threshold has been observed across a wide range of complex systems[2,14–17]. To see if there is evidence of slowing down in forests as conditions become critical, we analysed patterns of temporal autocorrelation in satellite data from intact evergreen tropical forests in South America, Africa and Southeast Asia. We do not aim to detect change in slowness over time, as this requires very long time series covering a period of gradual environmental change[18]. Instead, we analyse spatial patterns of inferred slowness. As an indicator of the state of the forest we used Normalized Difference Vegetation Index (NDVI). The NDVI is commonly used as a proxy of plant activity, biomass and cover to assess vegetation dynamics from space[19]. We used viewing-angle-corrected measurements and selected data to minimize cloud- and haze-induced errors. Also, as an independent indicator of the condition of forests we analysed patterns in the Vegetation Optical Depth (VOD), a measure of water content in aboveground biomass derived from remotely sensed RADAR data[20]. As an indicator of slowing down we measured temporal autocorrelation from monthly NDVI and VOD time series after removing the seasonal cycle and trends. We used additive regression models to simultaneously assess the relationship of temporal autocorrelation to mean annual precipitation, mean annual temperature and soil quality, as well as potential confounding factors (tree cover, seasonality of vegetation, temporal autocorrelation of precipitation, percentage of missing data due to cloudiness) and spatial coordinates (to account for potential unobserved spatially correlated drivers). A detailed description of the methods and the data is given in the Supplementary Information.

We find that temporal autocorrelation in NDVI and VOD on all three continents increases markedly when mean annual precipitation falls below around 1,500 mm (Fig. 1). Interpreting temporal autocorrelation as an indicator of critical slowing down[2], this is consistent with the idea that under such conditions the tall canopy trees of intact forests approach a tipping point for mortality. The relationship between mean annual precipitation and apparent slowness we find is closely in line with the relationship between resilience and rainfall inferred indirectly from the global probability

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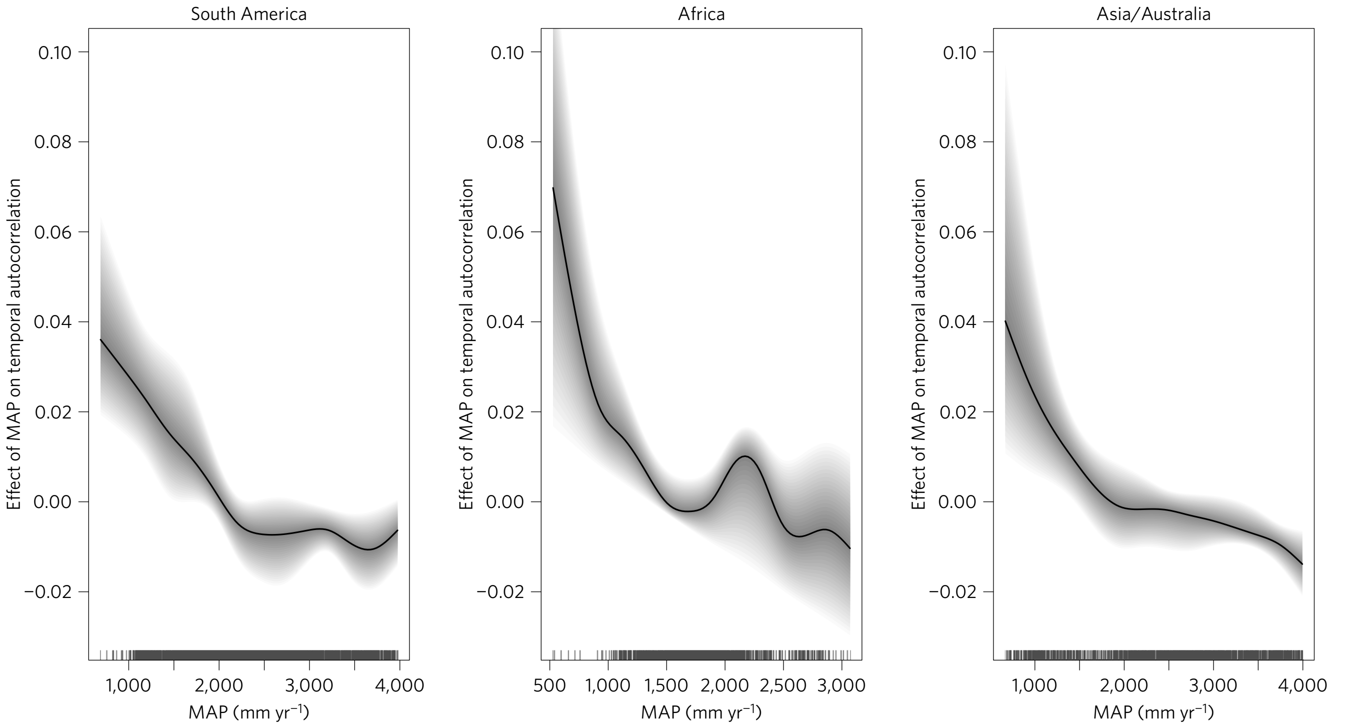

Figure 1 | Slowness of dynamics of intact tropical forest as a function of mean annual precipitation on different continents. Slowness is reflected by temporal autocorrelation of NDVI (MODIS 2000–2011) and mean annual precipitation (MAP) from TRMM data of 2000–2011. The black solid lines represent the mean curve from an ensemble of six curves (that is, three detrending methods and two indicators of temporal autocorrelation, see supplements). The grey shaded area highlights the range of the six individual ensemble members. The distribution of the available MAP observations is indicated by the density of the vertical lines above the *x*-axis.

density of forests[6]. The probability of finding tropical forest drops steeply around a mean annual precipitation of 1,500 mm (refs 6,21), and regrowth rates of secondary neotropical forests fall around the same threshold[22].

Temporal autocorrelation of NDVI and VOD also tends to increase with mean annual temperature (the only exception being the NDVI pattern for Africa, Supplementary Figs 4 and 5). These patterns suggest that resilience of tropical forest may be reduced at higher temperatures, consistent with the finding that higher daily minimum temperatures are associated to decelerating growth rates in tropical forest trees[23]. Indeed, worldwide cases of massive tree mortality are associated systematically not only to drought but also to elevated temperatures[1].

In contrast to these striking patterns of temporal autocorrelation across continents, we find no consistent relationships between precipitation levels or temperature and the standard deviation of NDVI and VOD fluctuations (instead standard deviation is mainly linked to seasonality, see Supplementary Figs 6 and 7). This may seem at odds with the idea that slowing down can cause variance to increase[2], but is consistent with the observation that, unlike temporal autocorrelation, variance is highly sensitive to other mechanisms that cause variance to either rise or decrease towards a tipping point[24].

There are a few obvious candidates for potential confounding factors that could provide alternative explanations for the increase of temporal autocorrelation of NDVI under dry conditions. First, temporal autocorrelation in precipitation could cause temporal autocorrelation in NDVI; second, cloudiness or haze could cause observation error with a time signature; and third, although we selected only evergreen forests, imperfect seasonal detrending of foliage variation in drier areas could affect temporal autocorrelation in NDVI and VOD. Temporal autocorrelation of precipitation as a driver can be excluded, as it was not correlated to temporal autocorrelation in NDVI (Supplementary Fig. 3). For filtering out cloudiness, and detrending and removing seasonality effects, we explored a range of methods (see Supplementary Information). The uncertainty ranges produced by this ensemble approach indicate that the results are robust (grey bands in Fig. 1 and Supplementary Figs 4–7). More importantly, our analysis is based on additive regression models, and the sharp rise of temporal autocorrelation below 1,500 mm mean annual precipitation (Fig. 1) arises despite the fact that we included tree cover, the seasonal amplitude of NDVI, the percentage of missing data due to cloudiness, and the temporal autocorrelation of precipitation in the models (Supplementary Fig. 3). This makes it unlikely that the rise of temporal autocorrelation at low rainfall (or at higher temperatures) is an artefact of these factors.

The robustness of our results suggests that the elevated temporal autocorrelation of NDVI we detect may indeed reflect slowness. Such slowness could be due to intrinsic differences in forest composition, such as dominance by species that react more slowly to variations in rainfall. Although we limited our analysis to evergreen tropical forests it is possible that vegetation composition plays a role in patterns of slowness. On the other hand, the field evidence for slowing down of foliage recovery in trees at elevated risk of dying[13] supports the view that critical slowing down related to the proximity of a tipping point is a plausible contributing factor. This suggests that we may interpret temporal autocorrelation as an independent indicator of fragility of tropical forest (Fig. 2). Obviously, the true distance to a tipping point for these forests remains in fact unknown, as there is no 'gold standard' indicator. The prediction of resilience based on the empirical relationship between the distribution of forest and mean annual precipitation[6] seems reasonable as a first approximation, but forest resilience will be mediated by other environmental factors and species traits that affect plant growth rates and capacity

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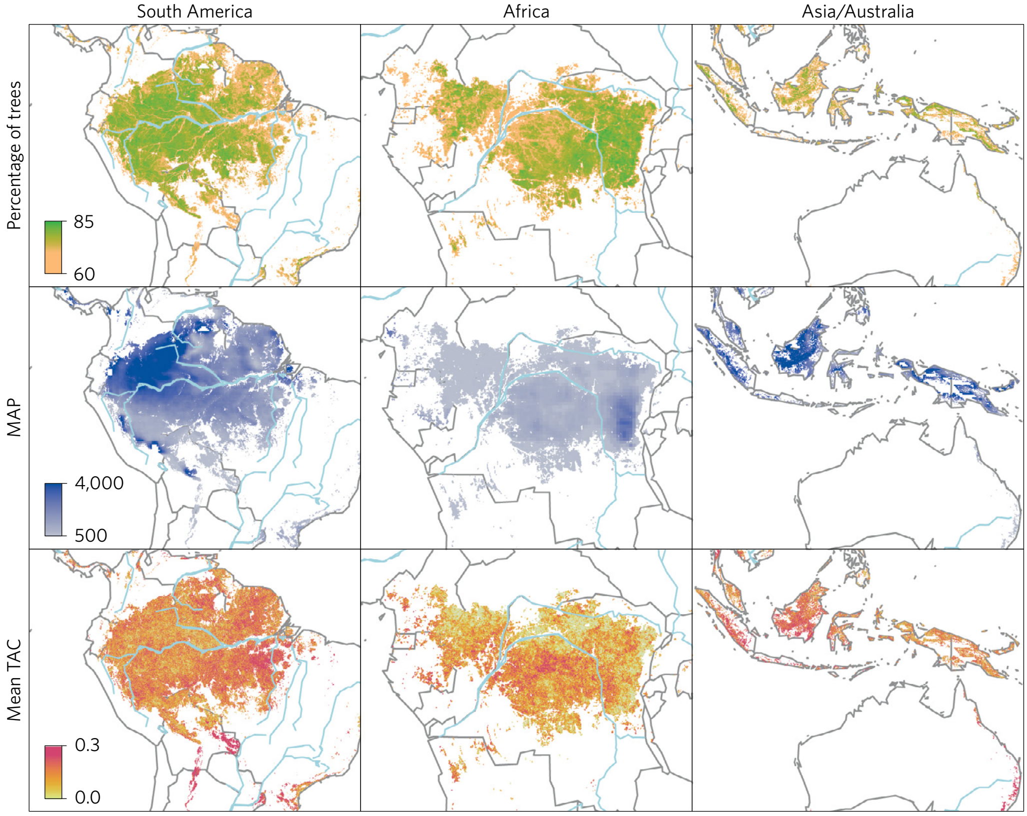

Figure 2 | Distribution of tropical forest cover (top), mean annual precipitation (middle) and remotely sensed slowness (bottom) across continents. Distribution of tropical forests is represented by the 2010 MODIS tree cover, mean annual precipitation (MAP (mm yr^{-1})) is based on TRMM 2000–2011, and slowness is indicated by the temporal autocorrelation (TAC, mean estimation derived from an ensemble of different methods) derived from MODIS NDVI time series.

to recover from perturbations. By contrast, our remotely sensed slowness (temporal autocorrelation) is potentially a direct indicator of resilience, since it actually measures properties of the forest, rather than predicting them from environmental conditions. Therefore, temporal autocorrelation might help detecting areas where forests could have a low resilience even if annual precipitation is high.

Indeed, elevated temporal autocorrelation is sometimes found in places where one would not necessarily expect low resilience based on mean annual precipitation alone (Fig. 2). For example, in Asia, temporal autocorrelation is particularly high on Sumatra and East Kalimantan, suggesting that these (intact) forests might be close to the fire-related tipping point to savannah despite the relatively high rainfall. This is in line with the fact that these are precisely the areas hit by massive spreading fires during droughts related to El Niño over the past years[25]. There are also differences between the continents. For instance, temporal autocorrelation of NDVI and VOD is lower in Africa than in the Amazon at comparable rainfall levels (Fig. 2 and Supplementary Table 4). This could be due to various factors, but one interpretation could be that, compared to the Amazon, African forests might be relatively more resilient, which resonates with the finding that the forests of central Africa have a lower sensitivity to drought events, as inferred from canopy responses measured by microwave scatterometer data[26], and also with palaeoecological evidence that tropical forests in Africa recovered faster from past disturbance events than forests in Asia and South America[27]. One possibility is that long-term historical drought events and other frequent disturbances promoted the adaptive capacity of African forests by selecting for stress-tolerant tree species[27,28].

Obviously, systems may also become slower for other reasons than critical slowing down at a tipping point. Despite all efforts to exclude competing explanations, our results remain correlational. To obtain a more detailed insight into the causes of the remotely sensed slowness, it would be good to have long-term field study sites along a gradient of rainfall conditions, where the physiological response of key species to natural climate variation is carefully monitored. Ideally, replicated perturbation experiments would be added to tell whether remotely inferred slowing down is indeed a reasonable indicator of the proximity of a tipping point in intact tropical forest. Such information would be invaluable, although clearly this kind of long-term field research is challenging. Meanwhile, results from two relevant field experiments that we are aware of are consistent with our hypothesis. First, a recent comparison of two comparable long-term drought experiments in the Amazon revealed a marked difference in tree mortality[9], consistent with what would be expected on the basis of differences in resilience between the sites as inferred from temporal correlation. Specifically, the higher rate of tree mortality at the Tapajós long-term throughfall exclusion experiment when compared to the Caxiuanã experiment[9] corresponds to a higher measured temporal autocorrelation (mean ACF 0.17 for Tapajós versus 0.12 for Caxiuanã). Second, a long-term experiment in southeastern Amazon, where we find the highest temporal autocorrelation (Fig. 2), suggests proximity to a tipping point where tree mortality rises sharply, driving the system towards an alternative self-stabilizing fire-dominated savannah state[11].

While such experimental evidence remains rare, the fact that on all three continents we see the rise of temporal autocorrelation at the 1,500 mm precipitation level known to be critical for tropical forest suggests that such remotely sensed autocorrelation may capture the signal of slowing down at the tipping point for forest collapse. This is further supported by the fact that some eye-catching deviations from the patterns expected from precipitation levels are consistent with independent indicators of resilience, such as the tolerance of African forests to droughts. Also, our results are in line with the emerging insight that drought combined with heat[23] may bring forests worldwide to tipping points for massive tree mortality[1]. Perhaps most importantly, the idea that slowing down may indicate the proximity of a tipping point for forest die-off is well in line with detailed on-the-ground studies suggesting that a compromised systemic potential to recover from stress, as reflected for instance in slower foliage recovery during drought, may be key to predicting tree death[3,13].

The future resilience of tropical forests will depend on simultaneous changes in climate, atmospheric carbon concentration, and land use[29]. Models predict an increase in tropical forest biomass worldwide during the twenty-first century[30], consistent with field observations suggesting that mature tropical forests are currently gaining biomass[31]. On the other hand, these positive effects could in some regions be off-set by the combination of increases in temperature[23], rainfall variability[32], and fire frequency and intensity[11]. At the same time, reduction of tree cover by logging poses a formidable threat to tropical forests. Apart from the direct loss of forest from logging, removal of trees increases the risk of triggering an irreversible shift to a fire-dominated savannah-like system[33]. Our findings suggest that despite the challenging complexity of the mechanisms that regulate resilience, the proximity of a tipping point for collapse may be monitored through remotely sensed slowing down.

Our results also hint at the possibility that time series of satellite data might be used to map resilience in a broader range of systems that are suspected to have tipping points for catastrophic change, such as boreal ecosystems, tundra, lakes and dry lands[34]. As climatic change and other drivers are likely to affect ecosystems worldwide, it is an exciting prospect that increasingly available high-resolution satellite data might offer possibilities to monitor resilience of such systems globally using generic indicators such as critical slowing down.

Methods

Methods and any associated references are available in the online version of the paper.

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Author contributions

M.S., M.Hirota, M.Holmgren, E.H.V.N. and J.V. conceived the idea of the study; J.V., N.U. and A.Z. analysed the data; M.S., J.V., M.Herold, M.Hirota, M.Holmgren and E.H.V.N. interpreted the results; M.S. wrote the paper; all authors discussed the results and revised the manuscript.

Additional information

Supplementary information is available in the online version of the paper. Reprints and permissions information is available online at www.nature.com/reprints. Correspondence and requests for materials should be addressed to J.V. or M.S.

Competing financial interests

The authors declare no competing financial interests.

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Methods

Here we provide a summary of the methods used for this study. The technical details are explained together with additional results (figures, and tables) in the Supplementary Methods.

We processed MODIS Normalized Difference Vegetation Index (NDVI, 2000–2011) and Vegetation Optic Depth (VOD, 2002–2011) data for the global tropical forests (35° S and 15° N) (Supplementary Information 1). We limited our analysis to intact forest by combining the World Intact Forest Landscape map and the Global Land Cover 2000 map and by eliminating areas with a tree cover lower than 60% based on the MODIS percentage tree cover product. Mean Annual Precipitation was derived from the latest global rainfall data available at the Climatic Research Unit (CRU) and Tropical Rainfall Measuring Mission (TRMM) data sets (see Supplementary Fig. 1). Soil fertility was derived from the Harmonized World Soil Database. We used generalized additive regression models (GAM) to assess the relationship between temporal autocorrelation and mean annual precipitation, tree canopy cover, seasonality, mean annual temperature, soil fertility, temporal autocorrelation in precipitation, cloud cover and geographical location (Supplementary Information 3 and 4). Before analysis, NDVI time series were detrended and deseasonalized using a range of methods (Supplementary Information 2), and multiple methods were applied to characterize temporal autocorrelation (Supplementary Information 2). Models are fitted for all combinations of detrending and temporal autocorrelation (TAC) methods, and the uncertainty arising from these different methodologies is reflected by the grey bands in ensemble result figures.