INTRODUCTION

Climate change and deforestation reduces the resilience of rainforest ecosystems (Hirota et al., 2011; van Nes et al., 2016), and thus compromise their capacity to remain forests despite various perturbations (Davidson et al., 2012; Malhi et al., 2008). Resilience is quantified and analysed by constructing a ‘stability landscape’, in which valleys (‘basins of attraction’) represent ‘stable states’ and hilltops represent ‘unstable states’ under transition (Figure 1). Resilience is then measured as the width of the basin of attraction around a

Hydroclimatic adaptation critical to the resilience of tropical forests

Chandrakant Singh1,2 | Ruud van der Ent3,4 | Lan Wang-Erlandsson1,2 | Ingo Fetzer1,2

1Stockholm Resilience Centre, Stockholm University, Stockholm, Sweden
2Bolin Centre for Climate Research, Stockholm University, Stockholm, Sweden
3Department of Water Management, Faculty of Civil Engineering and Geosciences, Delft University of Technology, Delft, The Netherlands
4Department of Physical Geography, Faculty of Geosciences, Utrecht University, Utrecht, The Netherlands

Correspondence
Chandrakant Singh, Stockholm Resilience Centre, Stockholm University, Stockholm, Sweden.
Email: chandrakant.singh@su.se

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Abstract
Forest and savanna ecosystems naturally exist as alternative stable states. The maximum capacity of these ecosystems to absorb perturbations without transitioning to the other alternative stable state is referred to as ‘resilience’. Previous studies have determined the resilience of terrestrial ecosystems to hydroclimatic changes predominantly based on space-for-time substitution. This substitution assumes that the contemporary spatial frequency distribution of ecosystems’ tree cover structure holds across time. However, this assumption is problematic since ecosystem adaptation over time is ignored. Here we empirically study tropical forests’ stability and hydroclimatic adaptation dynamics by examining remotely sensed tree cover change (ΔTC; aboveground ecosystem structural change) and root zone storage capacity (Sr; buffer capacity towards water-stress) over the last two decades. We find that ecosystems at high (>75%) and low (<10%) tree cover adapt by instigating considerable subsoil investment, and therefore experience limited ΔTC—signifying stability. In contrast, unstable ecosystems at intermediate (30%–60%) tree cover are unable to exploit the same level of adaptation as stable ecosystems, thus showing considerable ΔTC. Ignoring this adaptive mechanism can underestimate the resilience of the forest ecosystems, which we find is largely underestimated in the case of the Congo rainforests. The results from this study emphasise the importance of the ecosystem’s temporal dynamics and adaptation in inferring and assessing the risk of forest-savannah transitions under rapid hydroclimatic change.

KEYWORDS
alternative stable states, ecosystem change, forest-savanna transition, remote sensing, spatio-temporal approach, subsoil adaptation, transient state
稳定状态，其侵蚀向分岔点（即稳定状态和不稳定状态接触的点）（Hirota et al., 2011; van Nes et al., 2016）（图1a）。在一个吸引域内，稳定的反馈帮助生态系统保持其结构和功能特性，对抗干扰（Holling, 1973）。该生态系统最终会回到其固有的稳定状态（‘最低点’）时，扰动会在系统上释放（图1b,c）。在吸引域之外，即超过阈值（‘最高点’）时，自我强化的反馈将使生态系统转变为另一种稳定状态（Hirota et al., 2011; Holling, 1973）。因此，更好地理解稳定性和恢复力对评估生态系统对未来（气候或非气候）条件变化的适应性和系统风险是有帮助的（Anderegg et al., 2020）。

由于缺乏动态分析的时间序列（Cole et al., 2014; Damgaard, 2019），我们目前对热带陆地生态系统稳定性的理解是基于树冠频率分布的空间-时间假设（Dantas et al., 2016; Hirota et al., 2011; Staver et al., 2011a, 2011b），即一个空间-时间假设（Figure 1a）。根据这个假设，频率分布决定了吸引域的大小（即，宽度和深度）在概念上的稳定性景观，这被解释为生态系统的稳定性（深的盆地，更稳定，反之亦然）和恢复力（宽的盆地，更恢复力和反之亦然）随时间变化（Scheffer et al., 2009）（Figure 1a）。然而，对这些生态系统的动态支持尚未进行过调查。可用的更长的时间序列遥感数据现在允许更好地代表这些生态系统的状态和恢复力随时间的变化（Damgaard, 2019; Reyer et al., 2015; Singh et al., 2022）。

在这里，据我们所知，第一次分析了遥感监测的树冠变化（ΔTC）跨越两个世纪，以探究雨林的稳定性和恢复力。已经广泛认识到，生态系统对任何干扰的反应被捕捉在生态系统的暂态状态（Heimann & Reichstein, 2008; Turner et al., 2003; Wieczynski et al., 2019）。基于这一点，我们假设生态系统的暂态状态应与空间-时间假设的景观相似（Figure 1a）。因此，一个高度恢复力的生态系统不显示出显著的ΔTC随时间变化，而是一个低恢复力的生态系统。

我们的假设表明了ΔTC与生态系统的恢复力之间的相关性。然而，以前的研究忽略了这种相关性，只考虑了气候—特别是平均降水量（P）—当量化森林恢复力时（Hirota et al., 2011; van Nes et al., 2016）。

图1 稳定性的生态系统景观随不同平均降水量（mm年⁻¹）变化。 (a) 该景观，最初是基于树冠频率分布的空间-时间假设（Dantas et al., 2016; Hirota et al., 2011; Staver et al., 2011a, 2011b）。这一研究将‘树冠频率’与‘树冠变化随时间’（空间-时间）的定量替代（spatio-temporal）用于南美洲和非洲的不同降水类群，我们假设这应该与原始景观相似。稳定和不稳定状态（例如，局部最小值和局部最大值）分别对应于山谷（i.e. local minima）和山丘（i.e. local maxima）在稳定性景观中。 (b, c) 一个生态系统的恢复力在稳定性景观中表示为吸引域宽度的生态系统稳定状态，这会向分岔点倾斜（i.e. a point where stable and unstable states collide; depicted in (a)）。扰动推动生态系统向山丘顶峰，而当扰动释放时，生态系统返回到其稳定状态。
et al., 2011; Staal et al., 2018). Recent insights, however, hint towards the necessity to also incorporate the buffering capacity of the forest ecosystems, an aspect that is often lacking when representing the ecohydrology of tropical terrestrial ecosystems (van Oorschot et al., 2021; Reyer et al., 2015; Singh et al., 2020). By including root zone storage capacity ($S_r$), we account for the buffering capacity of the ecosystem in quantifying resilience. $S_r$ represents the maximum amount of subsoil moisture available to the ecosystems to buffer water deficit during dry periods (Wang-Erlandsson et al., 2016). This aspect acknowledges that ecosystems respond to water stress (defined here as a deficit in soil water availability inhibiting plant growth) by actively investing in their above- and belowground structures to maximise their hydrological benefits (Migilavacca et al., 2021; Singh et al., 2020). Thus, the resulting resilience metric, by also explicitly considering the ecosystems’ adaptive and buffering strategies, should be consistent with actual $\Delta TC$.

2 | METHODS

2.1 | Study area

This paper focuses on the tropical terrestrial ecosystems of South America and Africa, but the whole study area is slightly larger: 12°N–50°S for South America and 20°N–35°S for Africa. We have used a global administrative database from the Food and Agriculture Organisation (FAO; http://www.fao.org/geonetwork/) to define geographical boundaries for each country and do not have any political intentions behind our research.

2.2 | Data

We used remotely sensed gauge-corrected precipitation and evaporation data for our analysis. The daily estimates of precipitation were obtained from the Climate Hazards Group InfraRed Precipitation with Station data (CHIRPS) (Funk et al., 2015) at 0.05° spatial resolution for the years 2000–2019. Furthermore, evaporation in this paper is defined as the sum of all evaporative moisture from the soil and terrestrial vegetation, including those from interception (Miralles et al., 2020). The evaporation datasets chosen for this study were free from any prior assumptions related to biome-dependent parameterisation (such as plant function types, stomatal conductance, maximum root allocation depth) and soil layer depth (represents maximum depth of moisture uptake) to avoid any artificially introduced transitions between different biomes. Furthermore, these datasets were either derived or validated from actual evaporation estimates (e.g. FLUXNET sites). These conditions narrowed our prospect of using the widely available evaporation datasets. Nevertheless, we created an equally-weighted ensemble of evaporation using three datasets: (i) Breathing Earth System Simulator (BESt) (Jiang & Ryu, 2016) (ii) Penman-Monteith-Leuning (PML) (Zhang et al., 2016) and (iii) FLUXCOM-RS (Jung et al., 2019). Whilst i and ii were obtained at 0.5°, iii was obtained at 0.083° spatial resolution. All three evaporation datasets were obtained at a monthly timescale for the years 2001–2012. We downscaled these datasets from monthly to daily timescale using the daily estimate of the ERA5 (Hersbach et al., 2020) evaporation at 0.25° spatial resolution.

The aboveground structure of the ecosystem was analysed using the remotely-sensed MOD44B (version 6) annual tree cover (TC) dataset (Dimiceli et al., 2017) at a fine resolution of 250 m × 250 m for the years 2000–2019. Here, a TC value of 50% would represent a ground coverage of 50% by the canopy in the whole pixel. Furthermore, to minimise the human influence on this analysis, we removed the pixels with human-influenced land use and non-terrestrial land cover using the European Space Agency’s (ESA) Globcover land-use classification at 300 m resolution. Ultimately, all the mentioned above datasets were spatially interpolated to 250 m using bilinear interpolation, except for the land-use dataset which was interpolated using nearest-neighbour interpolation.

2.3 | Spatio-temporal approach for determining ecosystem states

For evaluating these stable and unstable states, a sample size (n) of 1,000,000 pixels each—from both continents—from all the 250 m × 250 m pixels was chosen and analysed separately for South America and Africa. This sample was used to determine the tree cover change ($\Delta TC$) in the ecosystem structure in the last two decades as follows:

$$\Delta TC = TC_{2017-2019} - TC_{2000-2002}$$

where $TC_{2017-2019}$ and $TC_{2000-2002}$ represent the mean of the tree cover for the years 2017–2019 and 2000–2002, respectively. Then, we classified the sample (n) into four classes based on mean precipitation ($P$; Figure 2a,c), with each $P$ class representing 25% of the total land area. We further separated each of these $P$ classes into tree cover gain (i.e., $\Delta TC > 0$) and tree cover loss ($\Delta TC < 0$) (Figure 2a,c).

After classifying, we grouped the samples into separate bins sorted by mean tree cover (i.e., $\overline{TC}_{2017-2019}$; Figure 2a,c), such that each bin represented an equal area (i.e. 2500 sampled pixels = 156.25 km²). Lastly, to relate stable and unstable states with the ecosystem’s structural change, the 13.4% of the bins with the highest change (i.e. highest $\Delta TC_{\text{median}}$) from all the classes combined were categorised as unstable. Moreover, 38.2% of the bins with the lowest change (i.e. lowest $\Delta TC_{\text{median}}$) were classified as stable. The justification behind selecting the % of stable and unstable bins was based on the area under the distribution curve (Figure S1).

These stable and unstable bins, which were analysed separately for tree cover gain and loss pixels at each $P$ class, were plotted spatially at 250 m resolution (Figure 2). For example, our sample analysis suggests that the unstable bins for tree cover loss in South America at $P$ class of 0–985 mm year⁻¹ falls approximately between 40% and 60% $\overline{TC}_{2017-2019}$ (Figure 2a). This will be spatially plotted in...
reality (population) for all the pixels falling between 40% and 60% TC2017−2019 at P of 0–985 mm year−1 for the pixels where ΔTC < 0.

2.4 | Root zone storage capacity

For our analysis, we have considered root zone storage capacity (Sr; derived from daily precipitation and evaporation data) to represent the adaptive buffer capacity of the ecosystem to absorb and adapt to water-stress conditions. Sr is the maximum amount of available subsurface moisture that vegetation can store and utilise through their roots for transpiration during dry periods (i.e. periods in which evaporation is greater than precipitation, irrespective of the seasons) (Gao et al., 2014; Wang-Erlandsson et al., 2016). Plants can increase their Sr by expanding their roots in the soil laterally as well as vertically. We adopted the mass-balance approach by Singh et al. (2020) to derive Sr from precipitation and evaporation estimates (Supplementary Method 1 in Supplementary Information). The underlying assumption of this approach is that ecosystems would not invest in expanding their storage capacity more than necessary to bridge the water-deficits it experiences (Wang-Erlandsson et al., 2016).

2.5 | Forest resilience and validation

We adapted Hirota et al. (2011) methodology for determining resilience using logistic regressions (Supplementary Method 3 in Supplementary Information). The logistic regression predicts the probability of forest (tree cover >50%) as a function of the independent variable. Hirota et al. (2011) had only considered P as the independent variable. However, the new resilience metric
proposed in this study also considered $S$, as an independent variable representing the drought buffer capacity of the forest ecosystems. Here, we experimented with $\bar{P}$ and $S$, independently and its combination, and chose the best performing model to represent the ecosystem state (Table S1). We modified the $S$ values for all the regions with tree cover <30% to 99th percentile of each continent’s $S$. This is because we assume that forest ecosystems will maximise their storage capacity (i.e. maximise $S$) before transitioning to a savannah (Singh et al., 2020). Lastly, we validate the resilience estimates of $\bar{P}$ and $\bar{P} + S$, combination for both tree cover loss and gain samples separately against observed $\Delta TC$, and assess their performance using spearman rank correlation. A high positive or negative spearman correlation would indicate a high strength and consistency between the resilience estimates and $\Delta TC$.

3 | RESULTS AND DISCUSSION

3.1 | Tree cover change in relation to stability equilibria

Our spatio-temporal analysis consistently shows low $\Delta TC$ for ecosystems at both high (>75%) and low (<10%) tree cover, whereas high $\Delta TC$ is observed for ecosystems at intermediate (30%–60%) tree cover (Figure 2a,c). A low $\Delta TC$ for both high and low tree cover ecosystems can be the result of either a minimal perturbation on the ecosystem over the last two decades (2000–2019), or a robust adaptive mechanism that is able to offset the experienced perturbations without considerable change in the ecosystem structure (Singh et al., 2020), which we, therefore, perceive as ‘stable’. Conversely, a high $\Delta TC$ at intermediate tree cover (Figure 2a,c) implies that the ecosystems in these ranges have been potentially influenced by either strong perturbations (Sutherland et al., 2018) (e.g. deforestation) causing significant changes to their ecosystem structure, or the adaptive mechanism under hydroclimatic changes has modified the ecosystem structure to utilise available resources efficiently. Since we exclude human influences, these high $\Delta TC$ can solely be explained by tree mortality under climate-induced water and fire stress (van Nes et al., 2018; Staver et al., 2011a) or tree growth under the influence of wetter climate (Holmgren et al., 2006), thus resulting in these ecosystems undergoing the observed regime shift (Hirota et al., 2011; Scheffer et al., 2009). The self-amplifying feedback between forest and climate also leads to considerable changes to ecosystem structure, such that forest loss facilitates dry conditions, and dry conditions further influence forest mortality (Staal et al., 2020; Zemp et al., 2017). Overall, structural changes to these ecosystems are much steeper than what we observed for ecosystems in their stable states (Figure 2a,c). Thus, we consider such ecosystems as ‘unstable’. These spatio-temporal patterns against different $\bar{P}$ levels (Figure 2a,c) further strengthen the presence of stability and instability in terrestrial ecosystems, which previous studies observed using a space-for-time assumption (Dantas et al., 2016; Hirota et al., 2011; Staver et al., 2011a, 2011b), can also manifest as actual $\Delta TC$ over time across the broader tree cover structures.

A closer look at these stable states (i.e. stable-low and -high tree cover bins representing a series of numerical ranges highlighted in dark brown and green, respectively, in Figure 2a,c and spatially highlighted in Figure 2b,d) reveals certain dissimilarities across the $\bar{P}$ classes. Stable-high tree cover bins decrease gradually with decreasing $\bar{P}$ (Figure 2a,c), thereby implying the inability of the forest ecosystems to maintain their dense structural characteristics under drier conditions (Singh et al., 2020). Here, an increase in $\Delta TC$ with decreasing $\bar{P}$ suggests that these ecosystems are undergoing a shift to a savannah-like open-canopy structure due to intensifying water and fire stress (Hirota et al., 2011; Moser et al., 2010; Zemp et al., 2017). Reversely, stable-low tree cover bins decrease with increasing $\bar{P}$ (Figure 2a,c). Here, an increase in wetter conditions in the ecosystem helps suppress a fire, thereby preventing fire-driven seedling mortality (Moser et al., 2010), and drives more soil water storage under a wetter climate (Guan et al., 2015). All these factors thus help promote forest growth and colonisation (Hirota et al., 2011; Uriarte et al., 2018). Nevertheless, the shifting potential, in both these cases, generally manifests itself as a relatively high $\Delta TC$ within the stable extent (e.g. relatively high $\Delta TC$ for $\bar{P} < 985$ mm year$^{-1}$ for South America and $\bar{P} < 1468$ mm year$^{-1}$ for Africa at a tree cover >70% in Figure 2), with some exceptions (Figure S3).

Interestingly, we also observe that for most of the $\bar{P}$ classes, the extent of the unstable bins (i.e. ranges highlighted in red and blue in Figure 2a,c) is almost similar for both tree cover loss and gain segments. In contrast to stable states, higher potential—suggesting amplified feedback—for both tree cover loss and gain at intermediate tree cover was already hypothesised in a space-for-time based approach (Hirota et al., 2011) (Figure 1a) and is confirmed by observable evidence at field scale. For example, open forest structure is promoted under increasingly drier conditions (McAlpine et al., 2018), the influence of fire (Pivello et al., 2021) and fragmentation (Nikonovas et al., 2020). Whereas, forest growth is promoted under El Niño-southern oscillation influenced wet conditions (Gutiérrez et al., 2008; Holmgren et al., 2006), sustainable management (Chazdon et al., 2020; Lewis et al., 2019; Wilson et al., 2019) and conservation efforts undertaken by local authorities to reduce deforestation, extensive grazing and wildfires (Cheung et al., 2010; Guedes Pinto & Voivodic, 2021; Sánchez-Cuervo et al., 2012).

Our spatio-temporal approach provides empirical evidence to this $\Delta TC$ potential at continental scales, as well as proves that the ecosystem change leading to a regime shift—in the context of both tree cover loss and gain—is indeed intensified at intermediate tree cover (Hirota et al., 2011) (Figure 2). This change in tree cover structure ($\Delta TC$) across different $\bar{P}$ levels, thus, agrees with our spatio-temporal hypothesis (Figures 1a and 2). Furthermore, spatially mapping these stable and unstable states provides us with key regions where forest conservation and management efforts need to be strengthened.
3.2 | Forest stability and adaptation dynamics

But why can forest ecosystems maintain stability at different $P$ levels and how does that relate to $\Delta TC$ (Figure 2)? The results from our $S_r$ analysis suggest that forest ecosystems maintain their tree cover structure at decreasing $P$ by increasing investment in their subsoil structure (Figure 3). Here, we observe a steep increase in $S_r$ with both decreasing $P$ and tree cover (Figure 3). In South America, within the stability extent of tree cover from 85% to 75%, the $S_r$ increases up to 600 mm with decreasing $P$ (Figure 3a). For Africa, although only a small portion of the forest is in this comparatively low $S_r$ high- tree cover stable state, we still observe a steep increase in $S_r$ near the stable-high tree cover state with decreasing $P$ (Figure 3b). The least $\Delta TC$ within this stability extent reveals that stabilising feedbacks within the stable-high tree cover (forest) ecosystems' respond to the change in $P$ by instigating $S_r$ investment (Figures 2 and 3). This $S_r$ investment, in reality, is the vertical and lateral growth of roots, allowing for more subsoil moisture storage. This subsoil storage thereby assists the forest ecosystems in maintaining their (stable) dense tree cover structure even under hydroclimatic stresses (Schenk & Jackson, 2002; Singh et al., 2020). However, this stabilising feedback of $S_r$ investment to keep the ecosystems in a stable-high tree cover state starts to change as we move to the intermediate tree cover.

At (unstable) intermediate tree cover, we find $\Delta TC$ to gradually increase and maximise around 40%–50% tree cover (Figure 2). We also find that the steep increase in $S_r$ gradually maximises around the 70%–60% tree cover and remains unchanged between 60% and 30% tree cover (Figure 3), thus suggesting causation between maximum $S_r$ investment and changes to ecosystem structure. When analysing the changes to the forest ecosystems' structure against varying levels of drought and fire stress at the local scale (Figures S4 and S5), we observe that unstable forest ecosystems—in comparison to stable-high tree cover ecosystems—have often maximised their $S_r$ investment and show deterioration to a savannah-like state.

These deteriorations are not sudden but gradual over time. This suggests that there exists a certain maximum investment potential beyond which the shift from forest to a savannah state becomes eminent (Singh et al., 2020), which manifests itself as a relatively high rate of $\Delta TC$ over time for the unstable forest ecosystems (Figure 2; Figures S4 and S5). Considering $S_r$ along with $P$, therefore, has allowed us to evaluate the invisible buffering responses of forest ecosystems which otherwise are not apparent but are critical to the stability of the forest ecosystems. Overall, these responses are specifically catered towards efficiently optimising the available water resources and modifying the ecosystem's aboveground tree cover structure (Migliavacca et al., 2021), and thus is able to manifest the shifts between the transient (stable and unstable) states as different magnitudes of $\Delta TC$.

3.3 | Resilience of the rainforest

This study quantifies resilience using logistic regression that predicts the probability of the occurrence of a forest ecosystem (tree cover >50%) as a function of both $P$ and $S_r$ for respective continents (Tables S1 and S2). It predicts resilience between a scale of 0 to 1, where 1 represents the highest probability of finding forest—interpreted as a highly resilient forest ecosystem against

![Figure 3](https://example.com/figure3.png)

**Figure 3** Relationship between mean precipitation ($P$) and root zone storage capacity ($S_r$) for (a) South America and (b) Africa. The solid lines correspond to median $S_r$ for the bins of tree cover loss (left) and gain (right) in Figure 2. The points on the solid lines represent the centre of the individual bins. The (horizontal) dashed lines correspond to the minimum and maximum extent of the stable-high and -low tree cover ecosystems, respectively, as defined in Figure 2a,c.
perturbations—given the \( P \) and \( S_r \) estimates in the recent decades. Figure 4 shows that the most resilient forests are located in the central and central-western parts of Amazon rainforests in South America, and a major portion of the central Congo rainforests in Africa. At the same time, the least resilient forests are in the central-eastern and southern corridor of the Amazon rainforest (along the ‘Amazonian arc of deforestation’) and northern and southern parts of the Congo rainforest (Figure 4).

The \( P + S_r \)-based resilience metric shows that the resilience of a large portion of the Congo rainforest is higher than previously presumed (based on \( P \) only) (Hirota et al., 2011), whereas the resilience of Amazon rainforests shows minor differences (Figure 4; Figure S6) (Staal et al., 2018). Due to the unique evolutionary history of their respective ecology and climatology (Morley, 2000), high wet-season precipitation has allowed for Amazonian rainforest species to have larger subsoil storage (i.e. \( S_r \)) to buffer the water deficit than the Congo rainforests (Guan et al., 2015; Zhou et al., 2014). The grass species in Congo rainforests, on the contrary, have evolved to be highly water-efficient (Still et al., 2003). This reduces the competitiveness between trees and grasses for

**Figure 4** Resilience of the rainforest ecosystem. These resilience estimates are derived using the logistic regression based on \( P \) and \( S_r \) for both (a) South America and (b) Africa. Here, a value of ‘1’ implies a forest ecosystem with the highest resilience, and ‘0’ implies a forest ecosystem with the lowest resilience. Comparing the two resilience metrics, we observed that by considering only \( P \) (in resilience calculation), the resilience estimates show considerable differences for the Amazon and Congo rainforests (exact difference in Figure S6). Regions with tree cover \( \leq 50\% \) and human-influenced land use (see Section 2) are masked.

**Figure 5** Validating the resilience estimates of the rainforest ecosystem with actual tree cover change (\( \Delta TC \)) for (a) South America and (b) Africa. The samples are divided into 20 equally weighted intervals (similar to Figure 2). The dots in blue (i.e., \( \Delta TC \geq 0 \)) and red (i.e., \( \Delta TC < 0 \)) correspond to our \( P \) and \( S_r \) resilience metric, whereas dots in black correspond to \( P \)-derived resilience estimates. The shaded regions represent the first and third quantile. The statistical test calculates the Spearman rank correlation (Sp. corr.) coefficient with an associated \( p \)-value.
moisture uptake (Singh et al., 2020), thereby increasing the resilience of the overall Congo rainforest ecosystem, even with low $S_r$ against water deficit. Therefore, including $S_r$ in our resilience metric has allowed us to capture this grass species-induced drought coping strategy in Congo rainforests, which otherwise is hard to detect with just $P$. Nevertheless, the resilience of both these rainforest ecosystems are declining due to increasing regional climatic risks (Phillips et al., 2009) and combined feedbacks from local deforestation and human-induced fires (Davidson et al., 2012; Malhi et al., 2008).

Validation with actual $\Delta TC$ shows that the $P + S_r$-based resilience estimates perform better than only the $P$-based resilience (Figure 5). The performance of these resilience metrics based on $\Delta TC$ further strengthens our original hypothesis that more resilient ecosystems will tend to have lower $\Delta TC$ and vice versa (Figures 1a and 5). Although $P$ is an important variable defining the broad influence of moisture on the ecohydrology of the ecosystem, considering $S_r$ accounts for the local-scale ecosystem adaptation of forests to buffer and withstand hydroclimatic changes (Singh et al., 2020), and is thus able to better represent the resilience of the rainforest ecosystems (Table S1). This better representation of ecosystem resilience can play a crucial role in management and conservation efforts (Newton, 2016).

4 | CONCLUSIONS

We demonstrate that our observation-based spatio-temporal approach, which analyses $\Delta TC$ and $S_r$ over the last two decades, provides empirical evidence of alternative stable states in the tropical terrestrial ecosystem of South America and Africa. We observe that the stable ecosystems at $>75\%$ and $<10\%$ tree cover show low $\Delta TC$ by instigating higher $S_r$ investment. For stable ecosystems, $S_r$ investment does not come at the expense of changes in aboveground forest structure. Compared to stable ecosystems, unstable ecosystems show much high $\Delta TC$ manifesting at intermediate tree cover of 30%–60% due to the inability of the ecosystems to utilise a similar level of investment. These tree cover ranges of stability and instability resemble the stability landscape of the previous space-for-time substitution-based approach.

By only considering $P$, the resilience of the ecosystems can be underestimated, which we observe for a considerable portion in the Congo rainforests. Only by modifying the existing, commonly used $P$-based resilience metric with an extended $P + S_r$ metric, we account for both the influence of hydroclimate (i.e. $P$) and the hydroclimatic adaptive capacity of the ecosystem (i.e. $S_r$). Furthermore, the $P + S_r$ resilience metric shows better performance and consistency with actual $\Delta TC$, thus strengthening its performance over the $P$-based metric. Overall, this study accounts for the ecosystems temporal and adaptation dynamics which are becoming increasingly important to assess the transient state of the ecosystems under rapidly changing hydroclimatic conditions.

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CONFLICT OF INTEREST

The authors declare no competing interests.

DATA AVAILABILITY STATEMENT

The python and google earth engine code used for the analyses presented in this study is available from GitHub: https://github.com/chandrankant6492/Ecosystems-stability-and-resilience. The python code for calculating root zone storage capacity is also available from GitHub: https://github.com/chandrankant6492/Drought-coping-strategy. The resilience maps generated for this study are available at Zenodo: https://doi.org/10.5281/zenodo.5878792. Other publicly available datasets that support the findings of this study are available at: (P-CHIRPS) https://data.chc.ucsb.edu/products/CHIRPS-2.0/, (E-BESS) ftp://147.46.64.183/, (E-FLUXCOM) ftp.bgc-jena.mp.de, (E-PML) https://data.csiro.au/collections/#collection/CIsiro:17375v2, (MOD44B_v6) https://lpdac.usgs.gov/products/mod44bv006/, (Globcover) http://due.esrin.esa.int/page_globcovcover.php, (SPEI) https://spei.csic.es/databases.html, (FireCCI51) https://geogra.uah.es/fire_cci/firecci51.php

ORCID

Chandrakant Singh https://orcid.org/0000-0001-9092-1855
Ruud van der Ent https://orcid.org/0000-0001-5450-4333
Lan Wang-Erlandsson https://orcid.org/0000-0002-7739-5069
Ingo Fetzer https://orcid.org/0000-0001-7335-5679

REFERENCES

Anderegg, W. R. L., Trugman, A. T., Badgley, G., Konings, A. G., & Shaw, J. (2020). Divergent forest sensitivity to repeated extreme droughts. Nature Climate Change, 10(12), 1091–1095. https://doi.org/10.1038/s41558-020-00919-1
Chazdon, R. L., Lindenmayer, D., Guariqueta, M. R., Crouzeilles, R., Benayas, J. M. R., & Chavez, E. L. (2020). Fostering natural forest regeneration on former agricultural land through economic and policy interventions. Environmental Research Letters, 15(4), 043002. https://doi.org/10.1088/1748-9326/ab79e6
Cheung, K. C., Liebisch, D., & Marques, M. C. M. (2010). Forest recovery in newly abandoned pastures in southern Brazil: Implications for the Atlantic rain forest resilience. Natureza & Conservação, 08(01), 66–70. https://doi.org/10.4322/natcon.00801010
Cole, L. E. S., Bhagwat, S. A., & Willis, K. J. (2014). Recovery and resilience of tropical forests after disturbance. Nature Communications, 5(1), 3906. https://doi.org/10.1038/ncomms4906
Damgaard, C. (2019). A critique of the space-for-time substitution practice in community ecology. Trends in Ecology & Evolution, 34(5), 416–421. https://doi.org/10.1016/j.tree.2019.01.013
Dantas, V. D. L., Hirota, M., Oliveira, R. S., & Pausas, J. G. (2016). Disturbance maintains alternative biome states. Ecology Letters, 19(1), 12–19. https://doi.org/10.1111/ele.12537

Davidson, E. A., de Araújo, A. C., Artaxo, P., Balch, J. K., Brown, I. F., C. Bustamante, M. M., Coe, M. T., DeFries, R. S., Keller, M., Longo, M., Munger, J. W., Schroeder, W., Soares-Filho, B. S., Souza, C. M., & Wofsy, S. C. (2012). The Amazon basin in transition. Nature, 481(7381), 321–328. https://doi.org/10.1038/nature10717

Dimiceli, C., Carroll, M., Sohlberg, R., Kim, D. H., & Kelly, M. (2017). MOD44B MODIS/terrestrial vegetation continuous fields yearly L3 global 250m SIN grid V006 [Data set]. NASA EOSDIS Land Processes DAAC. https://doi.org/10.5067/MODIS/MOD44B.006

Funk, C., Peterson, P., Landsfeld, M., Pedreros, D., Verdin, J., Shukla, S., Husak, G., Rowland, J., Harrison, L., Hoell, A., & Michaelson, J. (2015). The climate hazards infrared precipitation with stations—A new environmental record for monitoring extremes. Scientific Data, 2(1), 150066. https://doi.org/10.1038/sdata.2015.66

Gao, H., Hrachowitz, M., Schymanski, S. J., Fenicia, F., Sriwongsitanon, S., herman, L., Stricker, L., Estrella, P., Van Der Velde, G., & Figliuolo, N. (2016). Climate change, deforestation, and the fate of the Amazon. Science, 319(5860), 169–172. https://doi.org/10.1126/science.1146961

Guan, K., Pan, M., Li, H., Wolf, A., Wu, J., Medvigy, D., Caylor, K. K., Gutiérrez, A. G., Barbosa, O., Christie, D. A., Del-Val, E., Ewing, H., Heimann, M., & Reichstein, M. (2008). Terrestrial ecosystem carbon dynamics and climate feedbacks. Nature Climate Change, 1(5), 250–254. https://doi.org/10.1038/nclimate4515

Gutiérrez, A. G., Barbosa, O., Christie, D. A., Del-Val, E., Ewing, H. A., Jones, C. G., Marquet, P. A., Weathers, K. C., & Armesto, J. (2012). Disturbance maintains alternative biome states. Perspectives in Ecology and Conservation, 4, 1–23. https://doi.org/10.1111/1365-2745.12337

Holmgren, M., López, B. C., Gutiérrez, J. R., & Squeo, F. A. (2006). Herbivory and plant growth rate determine the success of El Niño Southern Oscillation-driven tree establishment in semiarid South America. Global Change Biology, 12(12), 2263–2271. https://doi.org/10.1111/j.1365-2486.2006.01261.x

Jiang, C., & Ryu, Y. (2016). Multi-scale evaluation of global gross primary productivity and evapotranspiration products derived from Breathing Earth System Simulator (BESS). Remote Sensing of Environment, 186, 528–547. https://doi.org/10.1016/j.rse.2016.08.030

Jung, M., Koirala, S., Weber, U., Ichii, K., Gans, F., Camps-Valls, G., Papale, D., Schwalm, C., Tramontana, G., & Reichstein, M. (2019). The FLUXCOM ensemble of global land-atmosphere energy fluxes. Scientific Data, 6(1), 74. https://doi.org/10.1038/s41597-019-0076-8

Lewis, S. L., Wheeler, C. E., Mitchard, E. T. A., & Koch, A. (2019). Restoring natural forests is the best way to remove atmospheric carbon. Nature, 568(7750), 25–28. https://doi.org/10.1038/d41586-019-01026-8

Malhi, Y., Roberts, J. T., Betts, R. A., Killeen, T. J., Li, W., & Nobre, C. A. (2008). Climate change, deforestation, and the fate of the Amazon. Science, 319(5860), 169–172. https://doi.org/10.1126/science.1146961

McAlpine, C. A., Johnson, A., Salazar, A., Sytkus, J., Wilson, K., Meijaard, E., Seabrock, L., Dargusch, P., Nordin, H., & Sheil, D. (2018). Forest loss and Borneo’s climate. Environmental Research Letters, 13(4), 044009. https://doi.org/10.1088/1748-9326/aaa4ff

Migliavacca, M., Musavi, T., Mahecha, M. D., Nelson, J. A., Kruj, J., Baldocchi, D. D., Perez-Priego, O., Christiansen, R., Peters, J., Anderson, K., Bahn, M., Black, T. A., Blanken, P. D., Bonal, D., Buchmann, N., Caldararu, S., Carrara, A., Carvalhais, N., Cescatti, A., … Reichstein, M. (2021). The three major axes of terrestrial ecosystem function. Nature, 598(7881), 468–472. https://doi.org/10.1038/s41586-021-03939-9

Miralles, D. G., Brutsaert, W., Dolman, A. J., & Gash, J. H. (2020). On the use of the term “Evapotranspiration”. Water Resources Research, 56(11). https://doi.org/10.1029/2020WR028055

Morley, R. J. (2000). Origin and evolution of tropical rain forests. John Wiley & Sons. https://www.cabdirect.org/cabdirect/abstract/20000612672

Moser, B., Templer, C., Schneider, G., & Wohlgemuth, T. (2010). Potential shift in tree species composition after interaction of fire and drought in the Central Alps. European Journal of Forest Research, 129(4), 625–633. https://doi.org/10.1007/s10342-010-0363-6

Newton, A. C. (2016). Biodiversity risks of adopting resilience as a policy goal. Conservation Letters, 9(5), 369–376. https://doi.org/10.1111/conl.12227

Nikonorovs, T., Spessa, A., Doerr, S. H., Clay, G. D., & Mezbahuddin, S. H. (2020). Near-complete loss of fire-resistant primary tropical forest cover in Sumatra and Kalimantan. Communications Earth & Environment, 1(1), 1–8. https://doi.org/10.1038/s43247-020-00069-4

Phillips, O. L., Aragão, L. E. O. C., Lewis, S. L., Fisher, J. B., Lloyd, J., Lugo-González, G., Malhi, Y., Monteagudo, A., Peacock, J., Quesada, C. A., van der Heijden, G., Almeida, S., Amaral, I., Arroyo, L., Aymard, G., Baker, M., Bannik, O., Blanc, L., Bonal, D., … Torres-Lezama, A. (2009). Drought sensitivity of the Amazon rainforest. Science, 322(5919), 1344–1347. https://doi.org/10.1126/science.1164033

Pivello, V. R., Vieira, I., Christianini, A. V., Ribeiro, D. B., da Silva Menezes, L., Berlinck, C. N., Melo, F. P. L., Marengo, J. A., Tonskundt, C. G., Tomas, W. M., & Overbeck, G. E. (2021). Understanding Brazil’s catastrophic fires: Causes, consequences and policy needed to prevent future tragedies. Perspectives in Ecology and Conservation, 19(3), 233–255. https://doi.org/10.1016/j.pecon.2021.06.005

Reyer, C. P.O., Brouwers, N., Ramig, A., Brook, B. W., Epila, J., Grant, R. F., Holmgren, M., Langerwisch, F., Leuzinger, S., Lucht, W., Medlyn, B., Pfieker, M., Steinkamp, J., Vanderwel, M. C., Verbeeck, H., & Villela, D. M. (2015). Forest resilience and tipping points at different spatio-temporal scales: Approaches and challenges. Journal of Ecology, 103(1), 5–15. https://doi.org/10.1111/1365-2745.12337

Sánchez-Cuervo, A. M., Aide, T. M., Clark, M. L., & Etter, A. (2012). Land cover change in colombia: surprising forest recovery trends between 2001 and 2010. PLoS One, 7(8), e43943. https://doi.org/10.1371/journal.pone.0043943

Scheffer, M., Bascompte, J., Brock, W. A., Brown, V., Carpenter, S. R., Dakos, V., Held, H., van Nes, E. H., Rietkerk, M., & Sugihara, G. (2009). Early-warning signals for critical transitions. Nature, 461(7260), 53–59. https://doi.org/10.1038/nature08227
