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Effects of interannual climate variability on tropical tree cover

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Climatic warming is substantially intensifying the global water cycle[1] and is projected to increase rainfall variability[2]. Using satellite data, we show that higher climatic variability is associated with reduced tree cover in the wet tropics globally. In contrast, interannual variability in rainfall can have neutral or even positive effects on tree cover in the dry tropics. In South America, tree cover in dry lands is higher in areas with high year-to-year variability in rainfall. This is consistent with evidence from case studies suggesting that in these areas rare wet episodes are essential for opening windows of opportunity where massive tree recruitment can overwhelm disturbance effects, allowing the establishment of extensive woodlands. In Australia, wet extremes have similar effects, but the net effect of rainfall variability is overwhelmed by negative effects of extreme dry years. In Africa, effects of rainfall variability are neutral for dry lands. It is most likely that differences in herbivore communities and fire regimes contribute to regulating tree expansion during wet extremes. Our results illustrate that increasing climatic variability may affect ecosystem services in contrasting, and sometimes surprising, ways. Expansion of dry tropical tree cover during extreme wet events may decrease grassland productivity but enhance carbon sequestration, soil nutrient retention and biodiversity[3].

Tropical ecosystems have distinctive patterns of tree cover distribution along precipitation gradients suggesting that treeless areas, savannas and tropical forests may represent alternative stable states separated by critical transitions[4,5]. The apparent existence of alternative attractors in tree cover abundance suggests that regime shifts from one persistent state to an alternative one may be triggered by brief episodes of exceptional environmental conditions[6,7].

Interannual climate variability in the tropics is strongly driven by the El Niño/Southern Oscillation (ENSO) inducing anomalies in rainfall patterns that have profound impacts on the structure and functioning of these ecosystems[8–10]. The overall effect of interannual variation in precipitation across the tropics probably depends on the frequency and intensity of extreme rainfall events. Increased tree mortality coupled to severe drought has been well documented[8,11], but there is also evidence of a positive role of extreme rainy years for episodic tree recruitment in dry woodlands of Australia[12] and South America[13,14]. These observations suggest that whereas seasonal variation of rainfall tends to have a negative effect on tree cover[5,15,16], interannual variation might have different effects depending on the relative role of extreme dry or wet events.

To explore how such opposing effects of climatic variability might affect large-scale patterns of tree cover, we analysed the MODIS (Moderate-Resolution Imaging Spectroradiometer) set of remotely sensed estimates of tree cover resampled in 1-km^2 blocks for tropical and subtropical Africa, Australia and South America (between 35° S and 15° N). We related the percentage of tree cover to mean annual precipitation (MAP) and its seasonal (Markham seasonality index, MSI) and interannual variability described by three indicators, the coefficient of variation (CV), and the frequencies of severely wet (SPIW) and dry (SPID) years, based on the standardized precipitation index (SPI; see Methods). The SPI category has the benefit that, unlike other measures of variability, it is not correlated to the mean annual precipitation (Supplementary Table S1).

Generalized linear models reveal that tree cover is negatively related to interannual variation in rainfall in the wet tropics (MAP > 600 mm yr^{-1}, Supplementary Tables S5 and S6). However, this apparent negative impact of interannual variability decreases with mean annual precipitation (Fig. 1). This is reflected for instance by a significant negative interaction effect of precipitation and its coefficient of variation on tree cover along the whole (dry–wet) climatic gradient (Supplementary Tables S3 and S4). To seek an explanation for this difference between wet and dry tropics we zoom in to the patterns observed in dry regions (MAP ≤ 600 mm yr^{-1}).

The effect of interannual variability on tree cover in the dry tropics varies depending on the continent (Fig. 1). Higher overall interannual variation in rainfall (denoted by CV) may have positive (South America), negative (Australia) or neutral effects (Africa) on tree cover in dry lands (Supplementary Tables S8 and S9). These distinct continental responses may in part be related to the balance of extreme wet and dry events. Tree cover in the dry regions of South America shows a distinct increase with the proportion of extremely wet years (SPIW; Fig. 2). A potential explanation is the role of rainy extremes. Fast and massive tree recruitment in response to a pulse of rainfall can allow juvenile trees to escape from the control by herbivores[17,18] and fire[19]. Given that beyond a critical size, trees become less vulnerable to herbivores and fires, and are also better able to reach deep groundwater with their roots[18,19], a brief rainy window of opportunity can be enough to trigger accession of trees into the canopy layer and facilitate the establishment of a woodland (Fig. 3). The idea that extreme rainy events, such as those associated with ENSO, can open natural windows of opportunity for the regeneration of original dry woodlands and forests is supported by results from experiments at small scales in South America[13,14]. Furthermore, episodic recruitment during extreme rainy ENSO events has been reported frequently in Australia[12] and South America[13,14]. This field-based evidence suggests that the patterns we find, indeed reflect an important mechanism regulating tree cover in these dry regions. However, in other parts of the world the positive effect of

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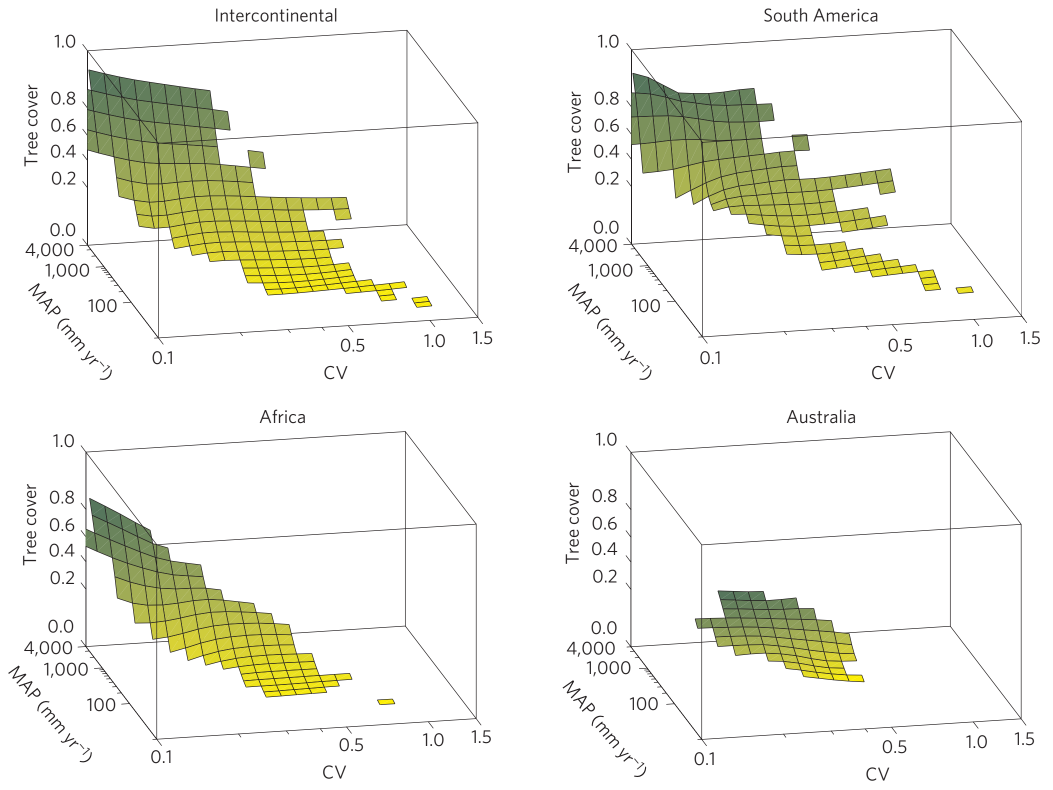

Figure 1 | Interactive effects of MAP and the coefficient of interannual variation in rainfall (CV) on tropical tree cover. Overall (top left) tree cover decreases with interannual variation (CV) in the wet tropics (green), but not in dry regions (yellow) where tree cover may even increase with CV (Supplementary Tables S3 and S4). The response to interannual variability in the dry tropics differs between continents (Supplementary Tables S8 and S9). Whereas an increase with variability is found in South America, tree cover in dry Australia shows an overall decrease towards higher variability. The surfaces are constructed with locally weighted regression[32] as implemented in the curve fitting toolbox of Matlab. The proportion of data points to be used in local regressions (span) was set to 0.6. Before analysis the data were normalized. We show only cells that have at least 5 data points.

rainfall on woodland expansion is less clear. One possibility is that the positive effects of wet events are offset by the effects of extreme droughts as demonstrated for northeastern Australia[20]. Indeed, we found that although tree cover on this continent is positively related to the frequency of extreme wet events (as in South America; Supplementary Table S10), it is negatively related to the frequency of extreme dry events (Supplementary Table S11). In contrast, no such negative effect of dry events could be detected in South America. This difference could be the result of an asymmetry in the frequency and severity of dry versus wet events on these two continents. El Niño, the most extreme ENSO phase, is related to wet events in South American dry lands, but to dry events in Australia, whereas the usually milder La Niña phase has opposite effects on rainfall[9,10].

The relationship between rainfall events and forest establishment is less prominent in African dry lands (Supplementary Tables S8–S11). Interannual variability of rainfall is large in Africa[21], although coupling to ENSO is less clear than on other continents[8]. It may be that the abundant and diverse herbivore fauna in Africa, compared with Australia[16] and South America[22], controls tree recruitment effectively during rainy pulses, maintaining an open landscape that facilitates grass growth and fire occurrence and limits tree recruitment. Furthermore, several studies indicate that the positive response of tree recruitment to rainfall in Africa may be prevented by fire[5,19], herbivore pressure[23], seed limitation[24] or a combination of those[19,25]. Indeed, release from herbivore pressure and seed limitation can boost tree recruitment during rainy events[12–14,17]. Overall, the probability of woodland expansion during large rainy pulses, and its persistence afterwards, will critically depend on the interplay of tree growth rates and disturbance regimes. Factors that increase tree seedling growth rates such as species intrinsic morphological and physiological traits (for example, deep root architectures, nitrogen-fixing capacity), resource availability (for example, soil fertility) and environmental factors that promote growth (for example, topography) will favour tree cover expansion. On the other hand, factors that promote herbivore abundance (for example, intrinsic herbivore growth rate, predator release) or fire occurrence (for example, grass abundance) will limit the effect of rainfall events on tree recruitment. Interestingly, the idea that extreme rainfall events largely drive tree cover dynamics in the dry tropics by allowing juvenile trees to reach a safe size where they are less vulnerable to drought and herbivores[17,18] (Fig. 3) resonates with the emerging view from the wet tropics where savanna–forest transitions are thought to be governed by the interplay between tree growth rate and fire regimes[16,19,26].

All of the variables that we studied are spatially correlated across large scales (Supplementary Fig. S1). Indeed, if we explicitly account for spatial relationships in the models (see Methods), relationships between tree cover and indicators of interannual variability in rainfall and seasonality become largely insignificant (Supplementary Tables S12–S14). The positive effect of extreme wet events is maintained in South America (Supplementary Table S13), but also this relationship can disappear if one offers spatial coordinates linearly as co-variables (tree cover increases northward and westward; results not shown), suggesting that effects of interannual rainfall variability are nearly confounded with global linear change across South America. Indeed, ENSO-driven interannual variability in rainfall is particularly high in the coastal regions of Peru. However, detailed studies along these gradients also show that indicators such as the percentage of extremely wet years or the coefficient of variation are likely to miss important

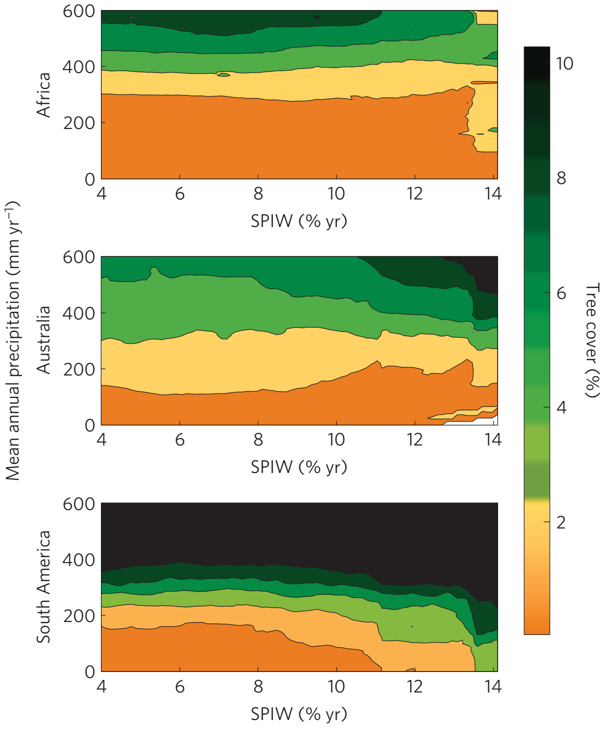

Figure 2 | Dry-land tree cover response to extreme wet events. Tree cover (%) in tropical and subtropical dry lands (MAP ≤ 600 mm) of Africa, Australia and South America as a function of MAP and the percentage of severely wet years (SPIW; years with annual precipitation ≥ +1.5σ the long term average; see Methods).

aspects of climate variability. For instance, controlled experiments across the large latitudinal gradient along the west coast of South America revealed that growth and survival of small trees is governed by an interaction between temperature and rainfall events[13]. Wet events are not only systematically more extreme in the north (Peru), but they also come in summer when plants can respond through high growth rates, whereas in the south (Chile) they come in winter[13]. This illustrates, that the effects of extreme events cannot be captured solely by the indicators we have studied, and that there can be other spatially correlated drivers. How to interpret differences between spatial and non-spatial models in such situations remains controversial[27]. The fact that outcomes depend on analysis techniques implies that we should be careful with our conclusions on the basis of the indicators of climate variability we studied. On the other hand, the extensive field evidence for the role of wet events as windows of opportunity for tree establishment[10,12–14,17–19] and the contrasting effects of Australian dry events[12,20], do suggest that the large-scale relationships between tree cover and climatic variability we find reflect major driving forces.

Our results are particularly relevant in view of the expectation that global climate change may increase the frequency of extreme climate events[2]. Whereas results for tree cover may be neutral in Africa and depend on the balance between wet and dry events in Australia, our results suggest that tree cover could expand with climatic variability in parts of South America. Depending on the perspective, this may imply risks or opportunities for ecosystem services to humanity. Woodland expansion may compromise the productive capacity of semiarid grasslands to sustain wild herbivores and livestock populations[3]. On the other hand, in regions where the loss of original woodlands has resulted in unproductive eroded lands, extreme rainfall events may be used as opportunities to restore forest with associated carbon sequestration, soil nutrient retention and biodiversity gains[3].

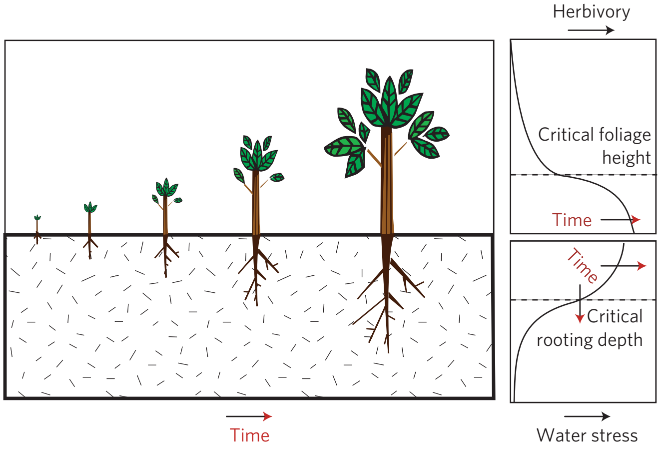

Figure 3 | Schematic diagram of the windows of opportunity theory depicting how a climatic pulse may trigger tree cover expansion. When seedlings grow they become less vulnerable to water stress as the root system extends to deeper soil layers. Simultaneously they become less vulnerable to herbivores as their leaves get high enough to be out of reach of the most important grazers and browsers. A climatic pulse allows plants to succeed running two simultaneous races: one towards drought escape and another one towards herbivore escape[18] (after ref. 33).

Methods

We analysed tree cover distributions on tropical and subtropical Africa, Australia and South America, defined between 35° S and 15° N. Tree cover percentage was based on the MOD44B Collection 3 product[28] at 500-m resolution, computed on the basis of data collected from 31 October 2000 to 9 December 2001. It comprises the canopy cover percentage derived from MODIS satellite measurement of canopy reflectance. On the basis of previous studies[4], we excluded the northern Sahara Desert, which would dominate the patterns by overwhelming large numbers of treeless data points. For the same reason, the Australian Desert was also excluded by extracting a rectangle defined between 110° E and 140° E, 30° S and 20° S.

Climate data were extracted from the Climate Research Unit's (CRU) high-resolution monthly data[29]. This data set is based on climatic observations from meteorological stations interpolated at the resolution of 0.5° (∼55 × 55 km). We computed MAP, the MSI and the interannual indicators of rainfall variability—CV, standard deviation and SPI—based on data for the period 1961–2002.

We used the SPI (ref. 30) to estimate the percentage of severely wet years (SPIW) and dry years (SPID) for each pixel. The SPI is defined as the number of standard deviations above or below the climatological mean precipitation for a certain period and commonly used to estimate extreme climatic events. As we were interested in evaluating interannual variability, SPI values were calculated for each year as the deviations of the yearly mean precipitation from the long-term MAP for the period from 1961 to 2002 (42 years). We calculated for each pixel the proportion of severely wet years with a SPI $\geq +1.5\sigma$ (SPIW) and the proportion of severely dry years with a SPI $\leq -1.5\sigma$ (SPID).

MSI (ref. 31) was used as an estimator of rainfall seasonality to determine the months with more rainfall concentration within a year.

All collected data sets were resampled to approximately 1 km. Geo-processing steps were carried on in ArcGis 10.0 and data extracted using Matlab. Statistical analyses were conducted in R (packages nlme, MuMIn, MASS and gstats), using a random sample of 2,000 pixels per continent for each of the general linear models applied to the data.

We used two types of generalized linear model[27]. We used non-spatial generalized linear models to relate tree cover proportion (arcsin-squared-root transformed) as a function of the climate variables. Before fitting the models, all explanatory climatic variables were scaled as $s(Xi) = (Xi - \min(X))/(\max(X) - \min(X))$. We also fitted spatial generalized least-squares models that account for spatial autocorrelation using an exponential correlation structure[27]. We used the Akaike information criterion to compare between the performance of non-spatial and spatial models, and the L-ratio test to assess the significance of the explanatory variables.

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Author contributions

M. Holmgren and M.S. conceived and wrote the paper. M. Hirota collected the data. All authors analysed and interpreted the data, 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 M. Holmgren

Competing financial interests

The authors declare no competing financial interests.