

Enhanced vegetation drought resistance associated with elephant disturbance in Africa

Wei Li

wli2019@tsinghua.edu.cn

Tsinghua University <https://orcid.org/0000-0003-2543-2558>

Minxuan Sun

Tsinghua University

Fabio Berzaghi

World Maritime University

Lei Zhu

Department of Earth System Science, Tsinghua University <https://orcid.org/0000-0002-2146-6438>

Philippe Ciais

CEA CNRS UVSQ, Centre d'Etudes Orme des Merisiers <https://orcid.org/0000-0001-8560-4943>

Martin Brandt

Københavns Universitet <https://orcid.org/0000-0001-9531-1239>

David Makowski

INRAE - University of Paris-Saclay <https://orcid.org/0000-0001-6385-3703>

Truman Young

UC Davis <https://orcid.org/0000-0002-7326-3894>

Duncan Kimuyu

Karatina University <https://orcid.org/0000-0001-6077-4970>

Jacob Goheen

Iowa State University

Yi Leng

Tsinghua University

Zhe Zhao

School of Life Science, Taizhou University

Mengjie Han

Tsinghua University

Jiaying He

State Key Laboratory of Resources and Environmental Information System, Institute of Geographic Sciences and Natural Resources Research, Chinese Academy of Sciences

Nan Meng

Tsinghua University

Jiaxin Zhou

Tsinghua University

Jinfeng Chang

Zhejiang University <https://orcid.org/0000-0003-4463-7778>

Yao Zhang

Peking University <https://orcid.org/0000-0002-7468-2409>

Dan Zhu

Peking University <https://orcid.org/0000-0002-5857-1899>

Yitong Yao

California Institute of Technology

Bo Pan

Yunnan Key Laboratory of Soil Carbon Sequestration and Pollution Control, Faculty of Environmental Science and Engineering, Kunming University of Science and Technology

Qing Zhao

Institute of Eco-environmental and Soil Sciences, Guangdong Academy of Sciences

Article

Keywords:

Posted Date: October 13th, 2026

DOI: <https://doi.org/10.21203/rs.3.rs-10699055/v1>

License: © ⓘ This work is licensed under a Creative Commons Attribution 4.0 International License.

[Read Full License](#)

Additional Declarations: There is **NO** Competing Interest.

Enhanced vegetation drought resistance associated with elephant disturbance in Africa

Minxuan Sun^{1,2}, Fabio Berzaghi³, Lei Zhu¹, Philippe Ciais⁴, Martin Brandt⁵, David Makowski⁶, Truman Young⁷, Duncan Kimuyu⁸, Jacob R. Goheen⁹, Yi Leng¹, Zhe Zhao¹⁰, Mengjie Han¹, Jiaying He¹¹, Nan Meng¹, Jiaxin Zhou¹, Jinfeng Chang¹², Yao Zhang¹³, Dan Zhu¹³, Yitong Yao¹⁴, Bo Pan¹⁵, Qing Zhao¹⁶, Wei Li^{1,2,*}

¹Department of Earth System Science, Ministry of Education Key Laboratory for Earth System Modeling, Institute for Global Change Studies, Tsinghua University, Beijing, China

²Ministry of Education Ecological Field Station for East Asian Migratory Birds, Beijing, China

³Ocean Sustainability, Governance and Management, World Maritime University, Malmö, Sweden

⁴Laboratoire des Sciences du Climat et de l'Environnement, LSCE/IPSL, CEA-CNRS-UVSQ, Université Paris-Saclay, Gif-sur-Yvette, France

⁵Department of Geosciences and Natural Resource Management, University of Copenhagen, Copenhagen, Denmark

⁶Unit MIA-PS, INRAE AgroParisTech University, Paris-Saclay, Palaiseau 91120, France

⁷Department of Plant Sciences, University of California, Davis, CA, USA

⁸Department of Natural Resources, Karatina University, Karatina, Kenya

⁹Department of Natural Resource Ecology and Management, Iowa State University, USA

¹⁰School of Life Science, Taizhou University, Taizhou 318000, China

¹¹State Key Laboratory of Resources and Environmental Information System, Institute of Geographic Sciences and Natural Resources Research, Chinese Academy of Sciences, Beijing, China

¹²College of Environmental and Resource Sciences, Zhejiang University, Hangzhou, China

¹³College of Urban and Environmental Sciences, Peking University, Beijing, China

¹⁴Division of Geological and Planetary Sciences, California Institute of Technology, Pasadena, California, USA

¹⁵Faculty of Environmental Science & Engineering, Kunming University of Science & Technology, Kunming 650500, China

¹⁶Guangdong Key Laboratory of Integrated Agro-environmental Pollution Control and Management, Institute of Eco-environmental and Soil Sciences, Guangdong Academy of Sciences, Guangzhou 510650, China

*Correspondence to Wei Li: wli2019@tsinghua.edu.cn

Elephants can alter vegetation structure and dynamics by reducing resource competition among trees through thinning out shrubs and small trees. Yet, the impact of elephant disturbance on vegetation functioning in extreme climates remains poorly understood. Here, we estimate the effects of African elephant disturbance on sub-Saharan vegetation structure and vegetation drought resistance using multiple satellite-based observation datasets. We find that tree height and tree cover in areas of Africa with elephants are higher than in neighboring areas without elephants. Changes in vegetation structure in areas with elephants create a cooler microclimate, which enhances vegetation drought resistance through alleviated local drought conditions. During drought, this enhanced resistance helps avoid $21.8 \pm 3.9\%$ and $8.1 \pm 3.7\%$ losses in vegetation greenness and productivity, respectively. These changes in vegetation structure and drought resistance occur with both forest and savanna elephants. Our study implies the important role of elephants in shaping local vegetation structures and functions and its potential repercussions on carbon and water cycling, and calls for greater efforts on the conservation of wild megaherbivores in Africa.

Intense and frequent droughts can significantly reduce vegetation growth and increase mortality¹, leading to a reduced carbon sink and exacerbated climate change². Previous work has indicated that vegetation drought resistance varies substantially depending on species type, species abundance and vegetation structure^{3, 4, 5, 6}. For example, increased mortality of small trees can potentially alter the course of future forest succession, while the loss of large trees leads to significant reductions in carbon storage and ecosystem function⁷. Vegetation structure (e.g., tree canopy cover, tree height) is shaped by numerous factors such as climate, soil and disturbances. Nevertheless, even under comparable climatic and soil conditions, central African forests manifest reduced tree densities, larger tree diameters, and higher biomass than their Amazonian counterparts^{8, 9}. These distinctive features could partly result from the disturbance due to megaherbivores, particularly elephants (forest elephants, *Loxodonta cyclotis* and savanna elephants, *Loxodonta africana*)^{10, 11, 12, 13, 14}. Elephants are regarded as ecosystem engineers due to their huge body, destructive feeding mode and extensive daily movement range required to meet energy demands¹⁵. During herd migrations they break and uproot shrubs and smaller trees (usually <30 cm in diameter)^{12, 16}. In addition, megaherbivores play a significant role in nutrient storage and cycling¹⁷ since they transfer carbon and nutrients from small trees and shrubs to soil through dung and urine, with the nutrients being subsequently reintroduced to large trees¹⁸. Consequently, elephants drive a long-term shift in resource competition dynamics, fostering the growth of surviving trees and gradually leading to greater canopy density and elevated tree height over approximately 50-150 years¹². However, despite evidence from local field observations, whether elephants can change the vegetation structure on a large scale remains unclear.

The altered vegetation structure due to elephant disturbance may further affect vegetation drought resistance. There is an ongoing debate regarding the size-dependent responses of individual trees to drought^{3, 6, 7, 9, 19, 20, 21, 22, 23}. Extensive observations have shown a higher mortality rate of taller trees during drought due to the higher risk of hydraulic failure and carbon starvation^{6, 19, 24}. In contrast, some studies argue that taller trees may have a greater capacity to withstand episodic water stress due to their enhanced water storage and efficient water use^{23, 25}.

Differences in vegetation demography (e.g., composition of shrubs, and small and large trees) may also affect the microclimate since closed canopies exhibit higher transpiration and more shading than open canopies²⁶. This microclimate buffering effect will further increase the vegetation resistance to drought. Therefore, we hypothesize that changes in vegetation structure induced by elephants will also change the vegetation's resistance to drought.

Here, we combine satellite observations and the International Union for Conservation of Nature (IUCN) African Elephant Database to evaluate the drought resistance of vegetation in areas with elephants in Africa, compared to nearby paired areas without elephants (Methods and Fig. S1). We analyze the differences in vegetation structure (i.e., tree height²⁷ and tree canopy cover²⁸) between areas with and without elephants and their impacts on local microclimate. Drought events are defined by the three-month integrated Standardized Precipitation Evapotranspiration Index (SPEI), with an SPEI below -1 indicating drought conditions^{29, 30}, and we pinpoint the regions that exclusively encountered drought events in the El Niño event of 2015-2016 (Methods and Fig. S1a). Drought resistance, defined as the capacity to resist and keep functioning under drought conditions, is estimated by the relative changes of vegetation greenness (i.e., normalized difference vegetation index, NDVI) and productivity (i.e., contiguous solar-induced fluorescence, SIF)³¹ from the period before drought to the drought period^{3, 32} (Eq. (2) and (3) in Methods). Regions with intense human activity, identified from human footprint³³ datasets (Methods), are excluded. To avoid confounding by protection status, paired areas with and without elephants are also controlled to be either both inside or both outside protected areas, based on boundaries from the world database on protected areas (WDPA). We also ensure that paired sites differ minimally in topography (Methods).

Vegetation structure differences between areas with and without elephants

We analyze the vegetation structure differences between areas with and without elephants in drought affected regions in Africa (Fig. S1c). Within these regions, tree height and tree cover in areas with elephants are significantly (Wilcoxon test, $p < 0.001$) higher than those in nearby areas without elephants. Areas with elephants exhibit an increased tree height of 1.15 ± 0.07 meters (mean $\pm$ standard error (s.e.)) and an increased tree cover of $2.82 \pm 0.25\%$ (Fig. 1a, b). Even after separating out the areas with forest and savanna elephants, tree height and tree cover are still significantly higher than in the nearby areas without elephants (Fig. S2; Fig. S3a, b; Fig. S4 and Supplementary Text 1). Elephants appear to have a greater impact on vegetation structure in forests influenced by forest elephants than in savannas influenced by savanna elephants (Fig. S3a, b). Additional analyses show that the observation of higher tree height and tree cover in areas with elephants remains robust irrespective of whether or not the areas are affected by drought (Fig. S5). This evidence is also consistent with the finding that elephants increase tree height and tree cover, both when analyzing paired sites within protected areas alone, and when analyzing those outside protected areas alone (Fig. S6a, b and Supplementary Text 2). This finding is further corroborated by observations of higher tree height and tree cover obtained from different satellite-based tree height³⁴ and tree cover products³⁵ (Fig. S7), and supported by the higher aboveground biomass and leaf area index observed in elephant areas compared to nearby areas without elephants (Fig. S8a, b). In addition, we independently validate these patterns using georeferenced photographic records from iNaturalist (Methods, Supplementary Text 3 and Fig. S9). We further incorporate data from the Kenya Long-term

Exclosure Experiment (KLEE), based on 17,277 tree height measurements across megaherbivore exclusion treatments, which consistently confirmed significant positive effects of elephants on tree height, aligning with our landscape-level findings (Supplementary Text 4 and Fig. S10).

To assess whether these differences reflect causal effects rather than environmental covariation, we further applied four machine learning based causal inference methods. The estimated average treatment effects (ATE) of elephants on vegetation structure range from 0.29 m (standardization) to 1.69 m (inverse probability weighting, IPW) for tree height, and 0.64 % (standardization) to 3.58 % (IPW) for tree cover (Fig. 1c, d). Except for the matching method applied to tree cover (Fig. 1d), all 95% confidence intervals of ATE excluded zero, indicating robust and statistically significant positive effects of elephants on vegetation structure.

The differences in tree height and tree cover between areas with and without elephants (Δ Tree height and Δ Tree cover) are significantly correlated with elephant population density (Fig. 2). While these results indicate a generally positive effect of elephant presence on vegetation structure at the continental scale, the relationship between elephant population density and differences in vegetation structure suggests a potential upper threshold beyond which impacts may shift from positive to negative (Fig. 2). As elephant density increases, Δ Tree height and Δ Tree cover generally decline in both the country-level elephant density analysis (Fig. 2a, b and Fig. S11a, b) and the patch-level analysis with elephant densities derived from surveyed sites (Fig. 2c, d). Both analyses exhibit a transition from positive to negative values, with the threshold appearing to fall within approximately 0.6-1.5 elephants km^{-2} . This reversal indicates a negative impact on vegetation structure in areas with high elephant densities. In fact, in countries with the highest elephant density (over 0.6 per km^2) including Zimbabwe, Botswana, Swaziland, and South Africa (Table S1), tree height and tree cover are significantly lower in areas with elephants than nearby areas without elephants (Fig. S11c-f, Supplementary Discussion 1).

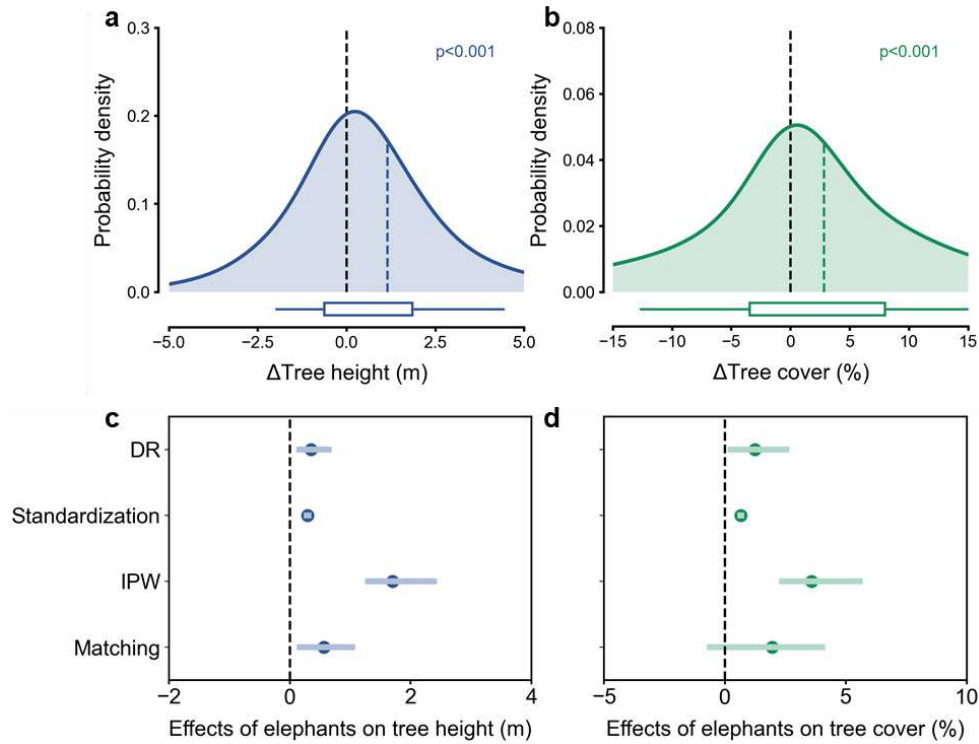


Fig. 1 | Differences in tree height (Δ Tree height) and tree cover (Δ Tree cover) between nearby areas with elephants and without elephants, and average treatment effect (ATE) of elephants on vegetation structure. a and b, Kernel density distributions of Δ Tree height and Δ Tree cover between the paired neighbor areas with and without elephants. Colored dashed lines show the mean values (N=2945 and 3038 for Δ Tree height and Δ Tree cover). The boxes and whiskers represent the 10th, 25th, 75th and 90th percentiles. c and d, ATEs of elephants on tree height and tree cover derived from four causal inference methods (double robust, DR; standardization; inverse probability weighting, IPW; Matching; see Methods) adjusting for confounding factors using gradient boosting. Colored points indicate estimated ATE values, while horizontal bars represent 95% confidence intervals (CIs, computed by the bootstrapping method).

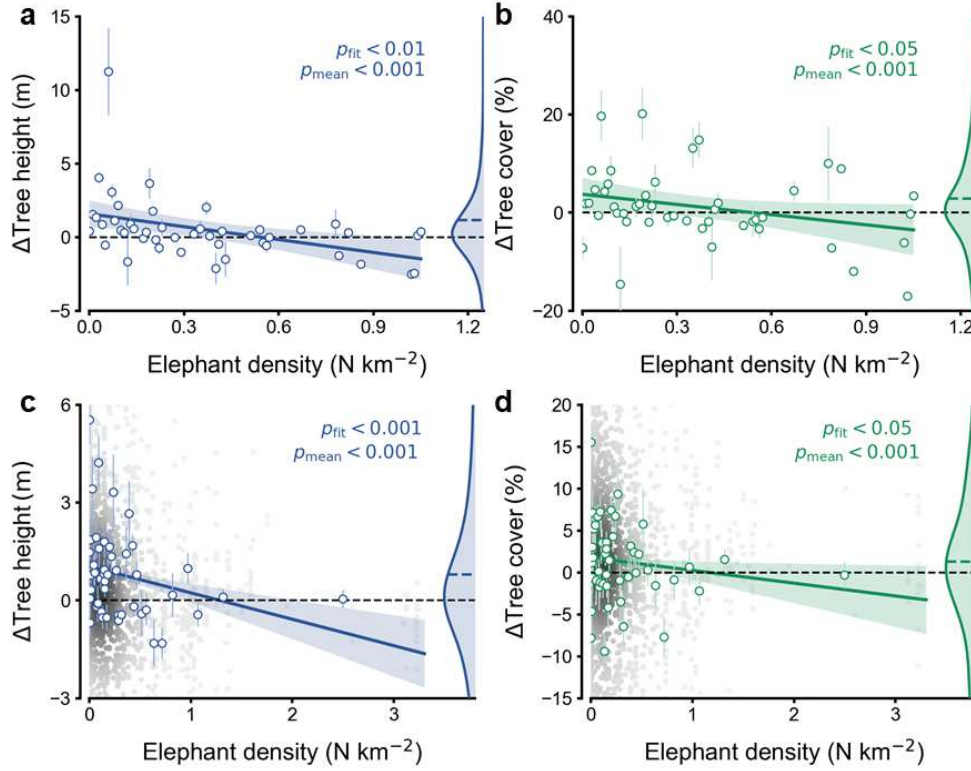


Fig. 2 | Relationship of differences in tree height (Δ Tree height) and tree cover (Δ Tree cover) between nearby areas with elephants and without elephants with elephant density. **a, b,** Relationship between Δ Tree height and Δ Tree cover with elephant density using the country-level elephant density. Circles represent country-level elephant densities (i.e., each circle corresponds to one country), and error bars denote the standard error of Δ Tree height or Δ Tree cover. Country-level elephant density was calculated from the total elephant number and their activity range in each African country (Methods, Fig. S12a and Table S1), and assigned to all areas with elephants within each country. **c, d, Relationships of Δ Tree height and Δ Tree cover with elephant density using patch-level elephant density derived from site-level records. Patch-level elephant density was calculated by linking surveyed elephant observations to the protected-area patches in which they occurred, based on boundaries from the World Database on Protected Areas (WDPA; Methods and Fig. S12b, c).** Correlations were fitted to Δ Tree height or Δ Tree cover across all $0.25^\circ \times 0.25^\circ$ grid cells ($N=2302$), with background colors indicating data density (darker colors for more data). Circles representing the mean within each density bin with standard errors are shown to enhance visualization of the relationship. Kernel density distribution of Δ Tree height and Δ Tree cover between nearby areas with and without elephants are shown on the right. p_{fit} denotes the significance of the fitted relationship, and p_{mean} denotes the significance that the mean value of Δ Tree height and Δ Tree cover differ from zero.

Impacts of differences in vegetation structure on microclimate

Our second hypothesis is that changes in vegetation structure would alter the microclimate through biophysical effects³⁶. Indeed, we find that areas with elephants have a significantly lower land surface temperature (LST) than the nearby areas without elephants in these drought-affected regions (Fig. 3). The LST difference (Δ LST) is -0.16 ± 0.02 during the El Niño years of

2015-2016 and -0.17 ± 0.02 °C during the years before the El Niño event (2012-2014) (Fig. 3a, b). The results of lower LST in areas with elephants than in areas without elephants are robust, regardless of the drought or non-drought status of the regions and periods (Fig. S13). This cooling effect is consistent across both forests and savannas, and the only exception of savannas influenced by savanna elephants during the year before the El Niño event (2012-2014), where it is not statistically significant (Supplementary Text 1 and Fig. S3c, d). Overall, differences in the cooling effect between forests and savannas are less pronounced. As expected, Δ LST is significantly ($p < 0.001$) correlated with Δ Tree height and Δ Tree cover (Fig. 3c, d), implying a stronger extra cooling effect with increasing differences in tree height and tree cover. The extra cooling effect is mainly the result of a greater release of latent heat, through higher evapotranspiration, in areas with larger trees (Fig. S8c, S14, Supplementary Text 5).

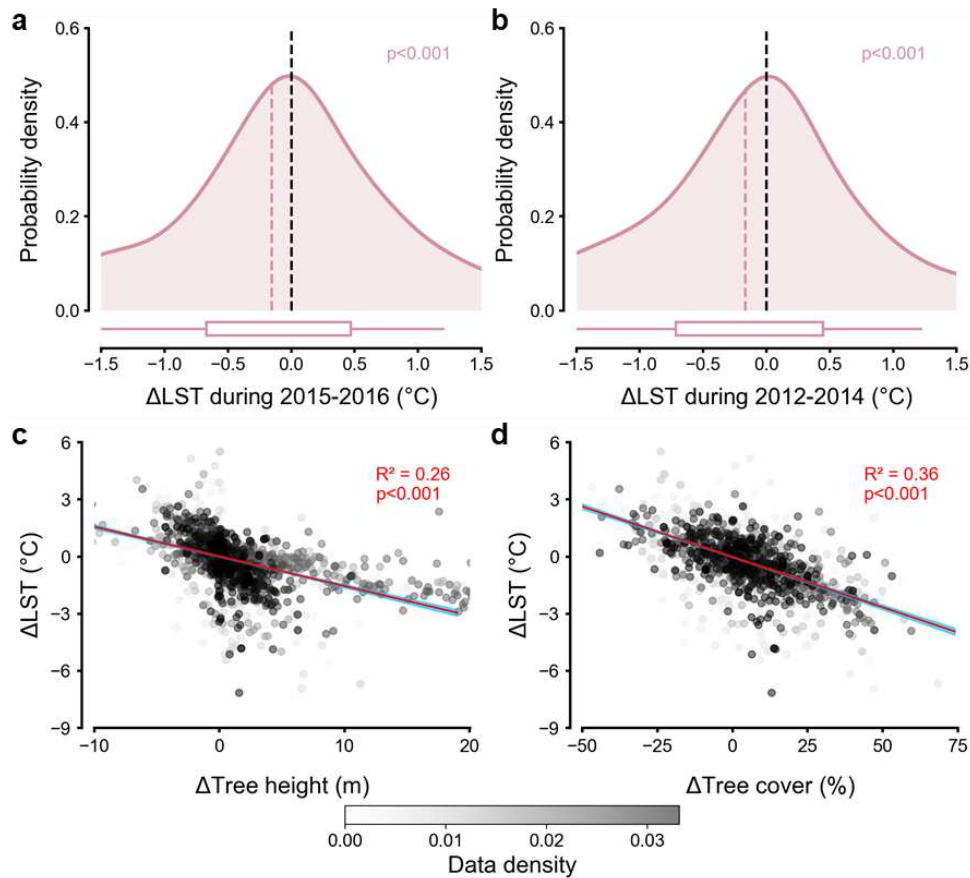


Fig. 3 | Kernel density distributions of land surface temperature difference between nearby areas with and without elephants (Δ LST) and the relationship between Δ LST and differences in tree height (Δ Tree height) and tree cover (Δ Tree cover). Δ LST in the El Niño years (2015-2016) and the years before the El Niño event (2012-2014) is shown in **a** and **b**. Colored dashed lines indicate the mean values ($N=3194$ and 5732 for Δ LST in 2015-2016 and 2012-2014, respectively). The boxes and whiskers represent the 10th, 25th, 75th and 90th percentiles. Relationships between Δ LST and (**c**) Δ Tree height and (**d**) Δ Tree cover ($N=2861$). Red lines indicate fitted regression lines, and blue shaded areas represent the associated 95% confidence intervals (fitted value $\pm 1.96 \times$ SE of prediction). The regression slopes were -0.16 °C per meter (95% CI: -0.17 to -0.15) for Δ Tree height and -0.053 °C per percentage point (95% CI: -0.056 to -0.05) for Δ Tree cover.

Enhanced drought resistance in areas with elephants

We further analyze the drought resistance in areas with elephants and the nearby areas without elephant during the El Niño years of 2015-2016. Drought resistance is significantly ($p<0.001$) higher in the areas with elephants than in the nearby paired areas (Fig. 4b). The enhanced drought resistance in areas with elephants than nearby areas without elephants helps avoid a $21.8\pm3.9\%$ loss in vegetation greenness (NDVI) and an $8.1\pm3.7\%$ loss in productivity (SIF) during drought (Fig. 4d). This higher drought resistance is still found when the habitats occupied by forest elephants and savanna elephants are separated (Fig. S3e, f). The NDVI and SIF-defined drought resistance patterns are generally consistent, and enhanced drought resistance is found in most grid cells (Fig. 4a, c). The magnitude of the SIF-defined drought resistance is larger than the NDVI-defined resistance (Fig. 4b), and drought resistance changes defined by SIF in areas with savanna elephants are greater than those in areas with forest elephants (Fig. S3f). This may be caused by the asynchronous responses of leaf trait (NDVI) and photosynthesis (SIF) to drought.

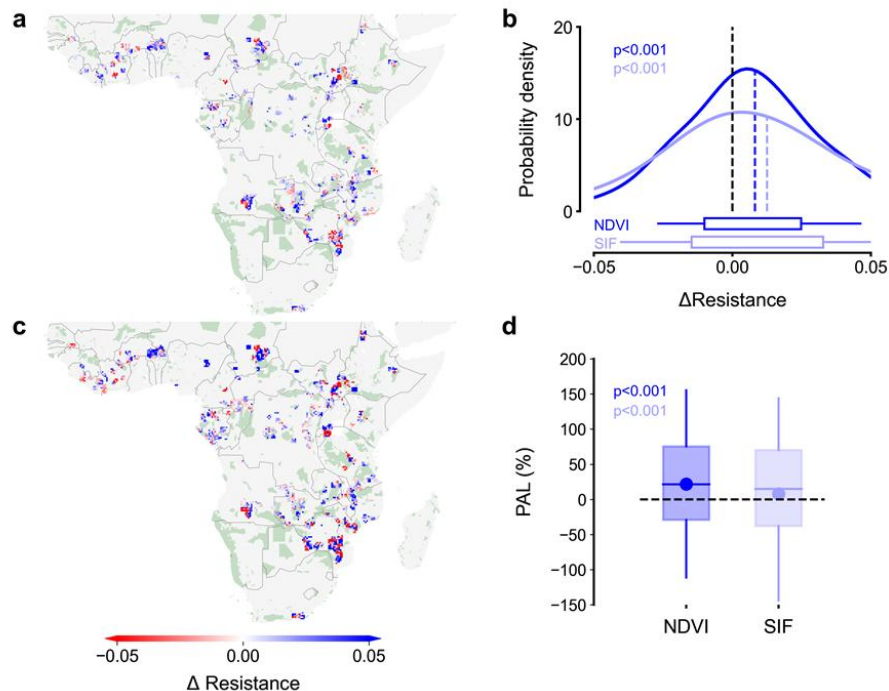


Fig. 4 | Difference in drought resistance between nearby areas with and without elephants ($\Delta\text{Resistance}$) in Africa during the El Niño years of 2015-2016. Drought resistance is calculated as the relative changes in NDVI (a) and SIF (c) before and during the drought period, and $\Delta\text{Resistance}$ is the difference between paired neighbor areas with and without elephants ($N=1883$ and 2354 for $\Delta\text{Resistance}_{\text{NDVI}}$ and $\Delta\text{Resistance}_{\text{SIF}}$). Green patches represent the protected areas. Paired sites with and without elephants are controlled as either both inside or both outside protected areas (Methods). The kernel density distributions of $\Delta\text{Resistance}$ are shown in b, with the colored dashed lines indicating the mean values. The percentage of avoided greenness or productivity loss (PAL) due to enhanced drought resistance associated with elephants in d is calculated as the changes in drought resistance associated with elephants ($\Delta\text{Resistance}$) relative to the vegetation greenness or productivity reduction affected by drought (Methods). The boxes and whiskers represent the 10th, 25th, 75th and 90th percentiles, and the blue dots and horizontal lines show the mean and median values of the data, respectively.

We explore the possible mechanisms of the enhanced drought resistance in areas with elephants where trees are taller and denser. The drought resistance difference ($\Delta\text{Resistance}$) is significantly ($p < 0.001$ and $p < 0.001$ for NDVI- and SIF-defined resistance) correlated with both differences in tree height ($\Delta\text{Tree height}$) and tree cover ($\Delta\text{Tree cover}$) (Fig. 5a, c and Table S2). Although there is some debate over the drought responses of small and large trees²², larger trees could be more resistant to drought because they have deeper roots and the physiological capacity to minimize water potential decline during droughts^{9, 37}. However, we find that, after controlling for the difference in LST, the correlations of $\Delta\text{Resistance}$ with $\Delta\text{Tree height}$ and $\Delta\text{Tree cover}$ become insignificant or shift from positive to negative (Fig. 5b, d and Table S2 and Supplementary Text 6). These findings imply that the enhanced drought resistance is more likely due to the mediated microclimate during droughts than the physiological properties of larger trees.

The path analysis from the structural equation modeling (SEM) analysis shows that changes in vegetation structure (termed $\Delta\text{Vegetation_structure}$, and including $\Delta\text{Tree height}$ and $\Delta\text{Tree cover}$) influence the drought resistance differences ($\Delta\text{Resistance}$) mainly via ΔLST (Fig. 5e). $\Delta\text{Vegetation_structure}$ has a significantly ($p < 0.001$) negative relationship with ΔLST (-0.6) and SPEI (-0.11), while ΔLST has a significantly negative correlation with $\Delta\text{Resistance}$ (correlation coefficients are -0.35 and -0.6 for the NDVI- and SIF-defined resistances, respectively). The impact of vegetation structure on local temperature is mediated by differences in evapotranspiration (ΔET) and albedo (ΔAlbedo), with $\Delta\text{Vegetation_structure}$ having a positive relationship with ΔET (0.40), and ΔET a negative relationship with ΔLST (-0.26). In contrast, $\Delta\text{Vegetation_structure}$ shows a negative relationship with ΔAlbedo (-0.42), but ΔAlbedo shows an insignificant correlation with ΔLST . This finding is consistent with the significantly higher ΔET and lower ΔAlbedo in areas with elephants than in the nearby areas without elephants (Supplementary Text 5, Fig. S8c, d and Fig. S14). The direct pathways from $\Delta\text{Vegetation_structure}$ to $\Delta\text{Resistance}$ (physiological responses) indicate a significant correlation coefficient of -0.24 between $\Delta\text{Vegetation_structure}$ and SIF-defined resistance and an insignificant correlation with NDVI-defined resistance. Again, these results confirm our hypothesis that the higher drought resistance in areas with large trees is primarily due to the mediated microclimate rather than physiological responses. Additionally, we also find a significant pathway from elephant density to $\Delta\text{Vegetation_structure}$, consistent with the relationship between $\Delta\text{Vegetation_structure}$ and elephant density shown in Fig. 2.

These mechanisms are also verified by a machine-learning attribution (Supplementary Text 7, Fig. S15), which also shows that ΔLST and ΔET are the most important factors explaining the spatial variations of $\Delta\text{Resistance}$ (Fig. S15a), and that $\Delta\text{Resistance}$ is negatively related to ΔLST after controlling for other factors (Fig. S15b). These findings are consistent with the significant negative correlations between ΔLST and differences in vegetation structure (Fig. 3c, d), and with the significant negative correlation between ΔLST and $\Delta\text{Resistance}$ (both defined by NDVI or SIF) (Fig. S16).

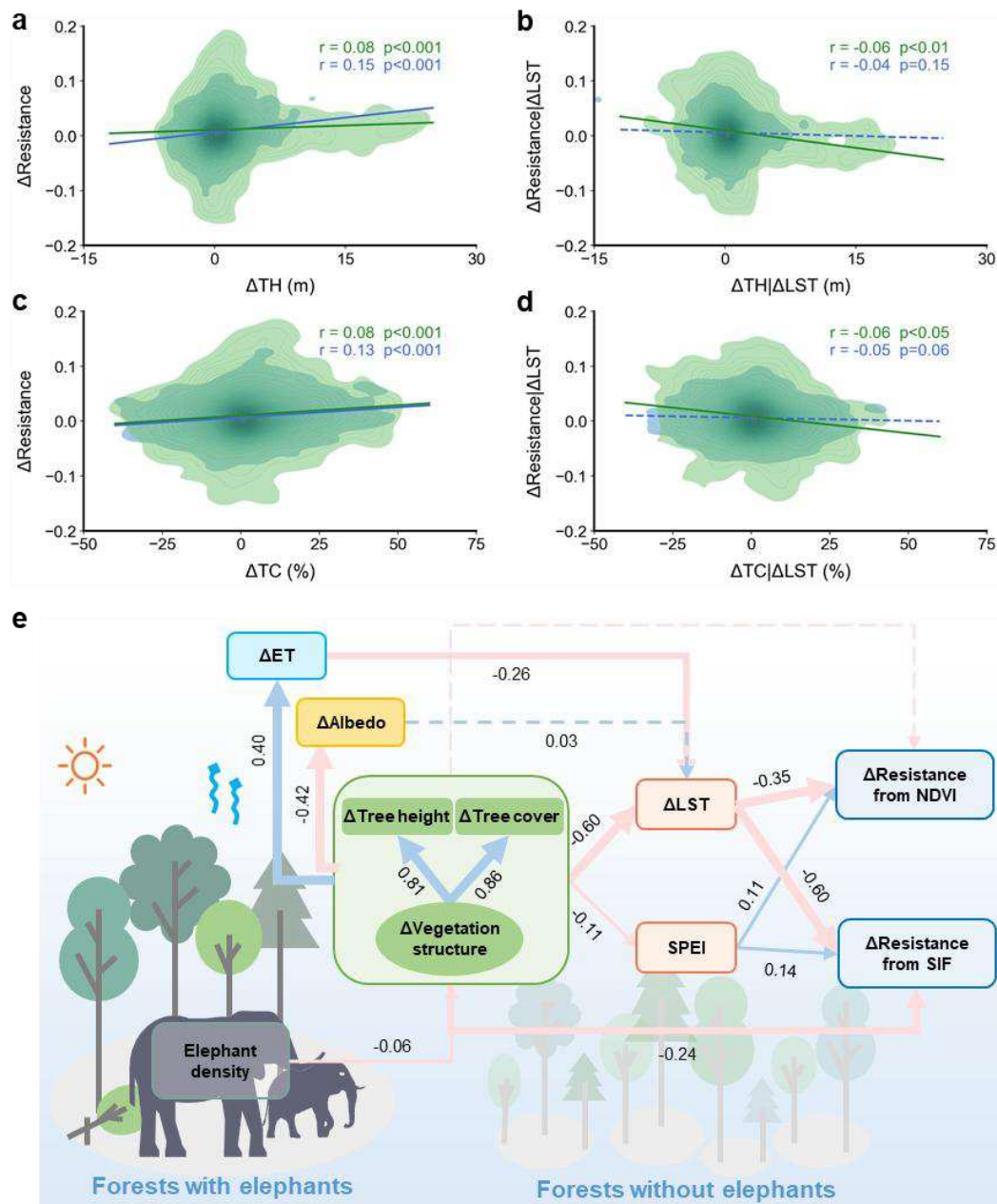


Fig. 5 | Correlations of differences in drought resistance ($\Delta\text{Resistance}$) with differences in tree height ($\Delta\text{Tree height}$) and tree cover ($\Delta\text{Tree cover}$) before and after controlling for differences in land surface temperature (ΔLST). a and c show the correlations without considering the influence of ΔLST , while b and d show the partial correlations after controlling for ΔLST ($N=1642$ and 2094 for correlations of $\Delta\text{Resistance}$, defined by NDVI (blue) and SIF (green) respectively, with $\Delta\text{Tree height}$ and $\Delta\text{Tree cover}$). Color scales of shaded areas indicate data density with darker colors for more data. e, Pathways depicting the association among changes in forest structure ($\Delta\text{Vegetation_structure}$) influenced by elephants and alterations in drought resistance ($\Delta\text{Resistance}$) observed between nearby areas with and without elephants. Factor loadings between variables and different widths of arrows represent the effect magnitude. Dashed, blue and pink arrow lines represent insignificant effects, positive effects, and negative effects, respectively ($N=1381$).

Discussion

Our study, based on remote sensing data, confirms that the field-observed vegetation structure changes induced by elephants may exist on a large scale^{11, 12}. Elephants typically refrain from browsing late-successional trees, which are unappetizing due to their high concentrations of defensive compounds^{11, 38}. The selective removal of small trees may reinforce the self-thinning process as larger trees suppress the growth of smaller ones through their advantages in the competition for water, light and nutrients^{7, 26, 39, 40}. The subsequent interaction with soil and excreta will also form a positive feedback loop on carbon and nutrients for the remaining trees¹⁸, intensifying the elephant effects on vegetation structure for between 50 and 150 years¹².

Differences in vegetation structure in areas with elephants further impact the local microclimate, because larger trees usually have greater evapotranspiration which uses more latent heat and cools the surface⁴¹ (Fig. S8c and Fig. S14a, b). Denser tree canopies can also cool the ground-layer by buffering heat and providing more shade in the understory^{42, 43}. During extreme heat and drought such enhanced cooling effects in the microclimate would thus help to mitigate water stress^{36, 44}. The lower LST in areas with elephants compared to that in areas without elephants is observed in both drought and non-drought affected regions and in both the El Niño years and the years before the El Niño event (Fig. 3a, b and Fig. S13). This may indirectly support the causality between Δ Resistance and Δ LST that Δ Resistance is mainly caused by Δ LST. However, the opposite – a higher drought resistance causing a lower LST – may also reinforce the correlation between Δ Resistance and Δ LST. In fact, regardless of the presence of elephants, tall and dense forests show a stronger drought resistance than short and open forests in Africa (Supplementary Text 8 and Fig. S17).

There is an extensive debate on the size-dependent responses of trees to drought. Some studies have reported a higher mortality rate in taller trees during droughts, due to hydraulic failure and carbon starvation^{6, 19, 24}, while others have argued that the increase in xylem tension with tree height can regulate crown conductance and sapwood hydraulic conductivity²², potentially minimizing water potential decline during droughts. Taller trees also have greater capacitance, more water storage, higher water use efficiency, and improved water transport to counteract the hydraulic resistance of pathlength, enabling them to endure episodic water stress^{23, 25}. However, our study finds that the higher drought resistance in areas with large trees is mainly due to the mediated microclimate, and the physiological responses are less obvious on the large scale (Fig. 5), providing an alternative mechanism possibly explaining the different drought responses of small and large trees.

Due to the lack of spatially explicit data for elephant density, we assume that elephant density is homogeneous in the elephant area within each country (Methods): an assumption which may induce uncertainties. To further confirm the actual presence of elephants, we assimilated data on the field-observed presence of elephants from iNaturalist (<https://www.inaturalist.org/observations>), a widely used biodiversity monitoring platform that aggregates georeferenced observations and photographs contributed by researchers and citizen scientists. The results of increased tree height and tree cover, decreased LST and enhanced drought resistance remain consistent at these field observation sites (Supplementary Text 3 and Fig. S9b-e). In addition, limitations in the resolution of SPEI data (most at 0.05°-0.5°) can hinder the differentiation of heterogeneity between areas with and without elephants, and also

restrict the number of paired site samples, leading to potential uncertainties. However, we test different SPEI data with different moving window sizes, and the results from these sensitivity tests provide robust evidence of the altered vegetation structure and functions, suggesting a possible ecological role of elephants (Supplementary Text 9.1 and Fig. S18).

We have conducted further sensitivity tests involving using different methods to select paired sites and different methods to define drought. All these tests show robust evidence of enhanced drought resistance in areas with elephants than the nearby areas without elephants (Fig. S19–S30, Supplementary Text 9.2–9.8). Together with the machine-learning-based estimates of the average treatment effects of elephant presence on vegetation structure (Fig. 1c, d; Methods), these sensitivity analyses reduce the likelihood that the observed patterns are driven solely by the measured environmental and anthropogenic covariates. Nevertheless, unmeasured confounding factors may still exist (Supplementary Discussion 2). Although the SEM analysis could suggest plausible causal pathways, its results remain based on correlations and depend on data quality and model assumptions, and ultimately reflect structured correlations rather than definitive causation. Long-term data would provide more insight into tracking changes in elephant disturbances compared to the space-for-time method adopted here (Supplementary Discussion 3). The ecological functions of megaherbivores such as elephants might not be apparent in the short term since responses of vegetation structure and nutrient cycling to disturbance can take decades⁴⁵, making it challenging to predict the long-term impacts of megaherbivores on the ecosystem^{46, 47} (Supplementary Text 10 and Fig. S31, S32). The detected vegetation structure changes in the present day could be a legacy effect of the previous presence of elephants, as elephant numbers have declined by 62% from 2002 to 2011⁴⁸. Additionally, elephant paths can act as firebreaks protecting fire-sensitive vegetation, and exactly how interactions between elephants and fires govern vegetation dynamics requires further investigation^{49, 50, 51}. Integrating elephant-plant interactions into vegetation models would provide a useful tool to improve our understanding of the impacts of elephants on vegetation dynamics and atmosphere-biosphere feedbacks^{47, 52}.

Our findings highlight the important role of African elephants on improving vegetation resistance to drought, especially given the expected increase in drought events due to future climate change^{53, 54}. However, the elephant population is rapidly declining^{48, 55}, due to threats from poaching and human-wildlife conflicts, which could decrease the metabolism and functioning of ecosystem⁵⁶. For example, elephants often adjust their behavior due to human activity, resulting in, for instance, decreased travel distances, smaller home range sizes, and fewer exploratory movements^{57, 58, 59, 60}. Elephants may also raid plantations close to human settlements⁶¹. Approximately 1.52 million km² of potential elephant habitats remain unprotected. This accounts for 47.7% of the total elephant area and includes 1.11 million km² of savanna elephant habitat and 0.40 million km² of forest elephant habitat (Fig. S33). These unprotected areas are also inhabited by nearly half a billion people⁶², exacerbating human-wildlife conflicts. Thus, it is crucial to reconcile elephant protection with the livelihoods of local people. Simple isolated enclosures with fences may not work, considering the complexity of the environment, and isolated conservation projects may also fail by resulting in overcrowding, impeded movement, and diminished genetic variability^{63, 64, 65, 66}. When elephant density becomes excessively high within limited areas, their impacts on vegetation structure may turn negative (Supplementary Discussion 1 and Fig. 2). This pattern is supported by both modelling and

observational evidence^{12, 67, 68} (Supplementary Discussion 1 and Fig. 2), and resembles the degradation caused by excessive grazing pressure in grassland ecosystems^{69, 70, 71}. While all analyses consistently supported this pattern, the potential transition threshold (approximately at an elephant density of 0.6-1.5 km⁻²) should be regarded as indicative rather than definitive, given the difficulty of precisely determining such a turning point. Instead, elephant conservation must fully consider both space and connectivity – by, for example, establishing connectivity channels⁶² – to ensure the sustainable stability of the elephant population.

Methods

African elephant database

The African Elephant Database (AED) produced by the African Elephant Specialist Group (AfESG) of the IUCN Species Survival Commission, stands as the most comprehensive database on the status of any wild mammal species⁷². It holds data from surveys and questionnaires conducted in 37 African elephant range states from 2006 to 2015 and documents the current elephant populations in African countries (Table S1). Elephant numbers were determined using a combination of observations from fixed-wing aircraft, helicopters and vehicles and dung density estimates. African elephants inhabit a diverse range of habitats, making the definition and mapping of elephant activity ranges challenging. The AfESG first drew range maps based on questionnaires and boundaries such as protected areas, rivers or mountains⁷³, and then categorized elephant ranges as known, possible, doubtful, or non-range to assign credit ratings. We used the “known” and “possible” distribution range in our analysis (Fig. S1b). The AED also outlines the movement boundaries of African savanna elephants (*Loxodonta africana*) and forest elephants (*Loxodonta cyclotis*). The distinction between forest and savanna elephants is identified by a genetic distribution map of forest and savanna elephants^{74, 75, 76}. Based on the IUCN habitat classification, forest elephants predominantly inhabit tropical and subtropical moist forests, while savanna elephants inhabit tropical and subtropical dry forests, savannahs and shrublands. Thus, we also calculated the structure and functions of the separate impacts of forest elephants and savanna elephants by further controlling forest and savanna habitat types between the paired sites (Supplementary Text 1 and Fig. S2, S3, S4).

To calculate elephant density, we first extracted the population data for each country from the 2016 IUCN African Elephant Status Report⁴⁸ (Table S1). We calculated the elephant density by dividing the national total elephant number by the elephant activity area, and assumed that the elephant density was homogeneous in the elephant area within each country (Fig. S12a). This estimate may have uncertainties due to the absence of elephants in some regions or incomplete surveys (to 103,355 forest elephants in Central Africa potentially unaccounted⁴⁸). To verify the actual presence of elephants, we used data from iNaturalist (<https://www.inaturalist.org/observations>), a widely used biodiversity monitoring platform that aggregates georeferenced observations and photographs contributed by researchers and citizen scientists. We focused on regions with these field-observed elephant presences to analyze the changes in vegetation structure and function induced by elephants as a sensitivity test (Supplementary Text 3 and Fig. S9).

Paired sites selection

Vegetation structure was calculated from 30 m resolution tree height data for 2019 from Potapov *et al.*²⁷ and tree canopy cover data for 2019 from Reiner *et al.*²⁸. The biophysical effects were estimated using 1 km MODIS 8-day daytime land surface temperature (LST) data averaged over 2015-2016. We used the paired sites method^{77, 41, 78} to calculate the differences in tree height (Δ Tree height), tree canopy cover (Δ Tree cover) and LST (Δ LST) between nearby areas with and without elephants. All datasets with various resolutions were first resampled to 0.01° . Each 0.01° pixel was labeled as “with elephants” or “without elephants” using the AED elephant range data. Within each $0.25^\circ \times 0.25^\circ$ moving window^{41, 78}, we then paired pixels by taking the average value of all “with-elephant” pixels and subtracting the average of all “without-elephant” pixels during drought periods (Fig. S34).

$$\Delta Variable = V_{elephants} - V_{non_elephants} \quad (1)$$

Where $\Delta Variable$ is the difference in variables between the nearby areas with and without elephants, calculated by the paired sites method. $V_{elephants}$ is the variable value in the areas with elephants, $V_{non_elephants}$ is the value in the nearby areas without elephants. We selected only those grid cells where both areas with and without elephants cover more than 5% of the grid cell area. Paired sites are calculated at a $0.01^\circ \times 0.01^\circ$ resolution within these $0.25^\circ \times 0.25^\circ$ moving grid cells, with each $0.25^\circ \times 0.25^\circ$ grid cell containing 625 (25×25) $0.01^\circ \times 0.01^\circ$ pixels. Specifically, if both areas with and without elephants have more than 31 0.01° pixels (i.e., >5% of the total 0.25° grid cell area), the 0.25° grid cell is selected for comparison. We applied additional sensitivity tests using thresholds of 0% to 20% at an interval of 5% during paired sites selection (Supplementary Text 9.2 and Fig. S19). If there is insufficient matching area with or without elephants in the grid cell, we searched the surrounding eight grid cells to match the paired area.

We controlled for covariates in the paired sites selection methods to exclude confounding factors other than elephant existence, including the 100 m resolution Human Footprint Index (HFI)³³, elevation and slope from the ~ 1 km Global 30 Arc-Second Elevation (GTOPO30) dataset. These variables were all resampled to 0.01° (~ 1 km). We filtered out 0.01° pixels with $HFI > 15$ in each $0.25^\circ \times 0.25^\circ$ moving grid cell. We also excluded $0.25^\circ \times 0.25^\circ$ grid cells with differences in elevation between areas with and without elephants greater than 200 m, and differences in slope greater than 10° (Fig. S35a and Supplementary Methods 1).

Additionally, approximately half of the elephant range overlaps with protected areas (Fig. S33). It thus raises the possibility that observed differences in vegetation structure and function between areas with and without elephants could be influenced by protection status rather than elephant presence. To address this, we strictly controlled for protection status when selecting paired sites by ensuring that each paired site was either both inside or both outside protected areas (Supplementary Text 2, and Fig. S6). Protected ranges were obtained from the world database on protected areas (WDPA)⁷⁹. These bias control measures were consistently applied across all comparative analyses in our study.

The data, which have various resolutions, were first resampled to 0.01° , and then selected by the paired sites method in each moving $0.25^\circ \times 0.25^\circ$ grid cell. Paired sample sizes may differ due to missing values of each dataset. For example, sample sizes for Δ Tree height, Δ Tree cover and Δ LST are 2945, 3038 and 3194, respectively. Detailed information on the sample size can be found in the captions of the figures.

Linear regression analyses were then used to examine the relationships between the

difference in tree height and tree canopy cover with elephant density, and with Δ LST (Fig. 2 and Fig. 3c, d).

As sensitivity tests, we also calculated the changes between paired sites using the satellite-based 10 m resolution tree height data for 2020 from *Lang et al.*³⁴, 30 m resolution tree canopy cover data for 2010 from *Hansen et al.*³⁵ (Fig. S7), 100 m CCI above ground biomass for 2018 from *Santoro and Cartus*⁸⁰, and 500 m MODIS 8-day leaf area index (LAI) data averaged over 2015-2016 (Fig. S8a, b). The results from these sensitivity tests using alternative datasets validated the key finding of altered vegetation structure by elephants.

As a sensitivity test, we also selected paired sites in moving windows of $0.5^\circ \times 0.5^\circ$ and $2^\circ \times 2^\circ$, and obtained consistent results (Supplementary Text 9.1 and Fig. S18), we also controlled for precipitation, road density and fire frequency (Supplementary Text 9.3, Fig. S20 and Fig. S21). We also constrained the paired sites selection within the same ecological regions, as defined by the “Ecoregions 2017” map⁸¹ (Supplementary Text 9.4 and Fig. S22). To account for uncertainties in elephant habitat ranges, we applied both inward and outward buffers of 1-5 km for elephant habitat boundaries, and then calculated the differences between paired sites in areas with and without elephants (Supplementary Text 9.5 and Fig. S23). We also calculated differences between areas without elephants after excluding all possible elephant ranges and areas with elephants (Supplementary Text 9.5 and Fig. S24). Because differences in the areas between paired sites may introduce uncertainties, we also tested comparisons with similar areas for the paired sites to ensure the even sample sizes (Supplementary Text 9.6 and Fig. S25).

We also calculate the differences in tree height and tree cover between areas with and without elephants adopted the “matching method” from *Andam et al.*⁸² (Supplementary Text 9.7 and Fig. S26). This method employs random selections of plots and controlled confounding factors through the Mahalanobis distances, which may help partly overcome the spatial dependences of neighboring grid cells (Supplementary Discussion 4).

Causal inference methods

We further conducted a causal inference analysis to quantify the effect of elephants on vegetation structure while accounting for potential confounding factors using machine learning-based methods. Specifically, we assessed the average treatment effect (ATE) of elephant presence on tree height and tree cover using four methods of causal inference already applied in different research fields: matching, inverse probability weighting (IPW), standardization, and double robust (DR)^{83, 84, 85} (Fig. S36). Matching is a widely used approach in causal inference to estimate ATE by pairing treated and control observations with similar environmental and topographic characteristics, thereby minimizing confounding bias^{85, 86, 87}. In our main text, we paired sites within each moving $0.25^\circ \times 0.25^\circ$ grid cell, a well-established approach in large-scale ecological analyses^{77, 41, 78}. Matching was also implemented using Mahalanobis distances⁸² (Supplementary Text 9.7) or propensity scores⁸⁸. IPW adjusts for confounding factors by assigning a weight to each sample site based on the estimated propensity scores of elephant presence, such that sites with lower propensity scores receive higher weights and those with higher propensity scores receive lower weights^{85, 89, 90}. This weighting creates a pseudo-population where confounding factors are balanced, allowing for causal inference of elephants’ effects on vegetation structure and providing an estimated value of ATE.

Standardization estimates the causal effect of elephants by explicitly modeling vegetation outcomes as functions of both treatment and confounding variables^{83, 84, 85}. Here, standardization was implemented using machine learning regressions. Specifically, a machine learning model was trained to predict tree height or tree cover for each paired sample both with and without elephants. The difference between these two predictions represents the local treatment effect, and averaging across all sample sites provides an estimated value of ATE. DR combines IPW and standardization by integrating both the treatment model (propensity scores) and the outcome model^{85, 89} to estimate ATE. It remains consistent if either model is correctly specified, offering the most stable and efficient estimate of the causal effect of elephants on forest structure.

In this analysis, we randomly selected fifty 3×3 0.01° pixel patches in each moving $0.25^\circ \times 0.25^\circ$ grid cell. The mean value of each patch was used as a sample for machine learning. To ensure representativeness, only samples composed entirely of valid drought pixels were retained (see Methods for the drought definition). To minimize potential spatial spillover between areas with and without elephants, we applied a 2-pixel buffer along the boundaries of elephant range, and excluded all samples overlapping with these buffer zones. To further reduce sample imbalance between elephant and non-elephant areas, we excluded grid cells where the ratio of patch counts between the two categories exceeded 1:5 or 5:1.

We then used the selected patch samples to train a gradient boosting model with confounding factors (listed in Table S3) to (1) classify elephant presence and estimate the propensity scores, and (2) predict vegetation structure, including tree height and tree cover. The resulting propensity scores and predicted tree height and tree cover were then used in subsequent matching, IPW, standardization, and DR analyses. The full analytical workflow is illustrated in Fig. S36.

The gradient boosting models performed well (Fig. S37), with an area under the receiver operating characteristic curve (AUC) of 0.75 for the classification model. The regression models predicting tree height and tree cover achieved R^2 values of 0.92 and 0.75, and root mean square errors (RMSE) of 2.94 m and 14.94%, respectively. All reported model performance is based on out-of-fold (OOF) predictions^{91, 92} generated through five-fold group cross-validation, in which each model is evaluated on data completely unseen during training (4:1 train–test split in each fold), providing an unbiased estimate of generalization performance.

Site-level data of elephant density and presence

To validate our results using the site-level evidence, we compiled a new dataset of site-level elephant density records from multiple sources: (1) 414 survey-based density estimates reported in the African Elephant Status Report⁴⁸, (2) 1298 records from the global tetrapod population density database TetraDENSITY 2.0⁹³, and (3) 237 elephant density sites synthesized for Central and West Africa in *Berzaghi et al. (2022)*⁹⁴. All datasets include spatial coordinates of surveyed or literature-derived elephant populations. We removed duplicate records, records without coordinates, and sites outside the IUCN elephant range boundaries. This resulted in 782 unique survey sites (Fig. S12c), covering a broad gradient of elephant densities (0–7.2 individuals km^{-2}) across most major elephant habitats in Africa.

Elephants are highly mobile and site survey locations capture only instantaneous, localized observations, whereas tree height and tree cover reflect long-term vegetation structure. We thus

linked each site to the protected-area patch containing it to approximate the actively used elephant habitat range, using boundaries from the world database on protected areas (WDPA) (Fig. S12b). We then overlaid these protected areas with the African Elephant Database (AED) habitat ranges to identify protected areas without elephants, and calculated differences in tree height and tree cover between protected areas containing surveyed sites and nearby protected areas without elephants within each $0.25^\circ \times 0.25^\circ$ moving grid cell. Relationships between these differences and elephant density were examined using linear regression.

In addition to the site level elephant density data, we also used elephant presence observation data from iNaturalist (<https://www.inaturalist.org/observations>), a widely used biodiversity monitoring platform that aggregates georeferenced observations and photographs contributed by researchers and citizen scientists. As of August 2024, there were 16,700 observations available. We focused on regions with these field-observed elephant presences to analyze the changes in vegetation structure and function induced by elephants as a sensitivity test (Supplementary Text 3 and Fig. S9). Furthermore, we integrated data from the Kenya Long-term Exclosure Experiment (KLEE), which includes 17,277 tree height measurements across megaherbivore exclusion treatments, providing additional independent experimental validation (Supplementary Text 4 and Fig. S10).

Vegetation drought resistance

To identify drought events, we employed the Standardized Precipitation Evapotranspiration Index (SPEI), which measures the standardized difference between water supply (precipitation) and water demand (potential evapotranspiration)⁹⁵. SPEI is an ecologically relevant metric for assessing vegetation responses to drought, with negative values indicating drier-than-usual conditions and positive values indicating wetter-than-usual conditions^{5, 96, 97}. We used a high-resolution African SPEI dataset derived from the Climate Hazards group InfraRed Precipitation with Station data (CHIRPS) precipitation estimates and the Global Land Evaporation Amsterdam Model (GLEAM) potential evaporation estimates⁹⁸. This dataset has a spatial resolution of 0.05° and covers the period from 2012 to 2016. Additionally, we utilized the 0.5° SPEI dataset sourced from the global SPEI database to assess the robustness of our results^{95, 99}.

Drought events are defined as periods for which the three-month integrated SPEI remains below -1 for at least three consecutive months^{29, 30}. We focused on drought events in 2015-2016 due to their prevalence – primarily as a result of the influence of El Niño – during this period. We excluded regions with multiple drought events and analyzed regions where, within the period of 2012~2016, droughts only occurred in 2015 or 2016 (Fig. S1c).

Drought resistance is the capacity of vegetation to prevent a decrease in ecological performance during drought events, and can be estimated as the ratio between a given indicator during and before the drought period^{3, 32}. Here, we use the 500-m MODIS Normalized Difference Vegetation Index (NDVI) and the 0.05° global spatially continuous solar-induced fluorescence (SIF) as indicators of tree growth states³¹. We calculated the average NDVI and SIF values for the three years before a drought event (2012-2014, a gap window of the El Niño/Southern Oscillation (ENSO) annual cycle¹⁰⁰) to establish a baseline for the non-drought affected state of vegetation. We then examined the changes in NDVI and SIF during the drought periods in 2015-2016 (years with strong El Niño events¹⁰⁰) to evaluate how vegetation

responded to drought. The drought resistance is then given by the ratio of vegetation condition during ($NDVI_d, SIF_d$) and before droughts ($NDVI_{pre}, SIF_{pre}$):

$$Resistance_{NDVI} = \frac{NDVI_d}{NDVI_{pre}} \quad (2)$$

$$Resistance_{SIF} = \frac{SIF_d}{SIF_{pre}} \quad (3)$$

A resistance value < 1 indicates that vegetation experiences a reduction in productivity during droughts. We used the paired sites method (Eq. (1)) to calculate the difference in drought resistance ($\Delta Resistance$) between areas with elephants and without elephants. We tested $\Delta Resistance$ in all drought-affected areas (Fig. S27c, d) and in areas with drought-induced productivity reduction (Fig. 4a-c) with consistent results (Supplementary Text 9.8). Sample sizes are 3194 and 3191 for $\Delta Resistance_{NDVI}$ and $\Delta Resistance_{SIF}$ in all drought-affected areas, and 1883 and 2354 for $\Delta Resistance_{NDVI}$ and $\Delta Resistance_{SIF}$ in areas with drought-induced productivity reduction.

Additionally, we calculated the percentage of avoided greenness, or the productivity loss (PAL), due to enhanced drought resistance induced by elephants. To do so we used the changes in drought resistance induced by elephants ($\Delta Resistance$) relative to the greenness or productivity reduction affected by drought ($1 - Resistance_{non_elephants}$):

$$PAL = \frac{\Delta Resistance}{1 - Resistance_{non_elephants}} \times 100\% \quad (4)$$

PAL quantifies the impact of elephants on mitigating the drought effects on vegetation greenness and productivity. A PAL-value of 10%, for instance, indicates that the reduction of greenness or productivity during droughts in areas with elephants is 10% smaller than the reduction in the nearby areas without elephants.

Partial correlation and path relationship analysis

We used partial correlation analysis to analyze the relationship between the drought resistance difference ($\Delta Resistance$ from NDVI and SIF) and the vegetation structure difference ($\Delta Tree$ height and $\Delta Tree$ cover) after controlling for other factors. Partial correlations measure the strength of association between two variables, with the effects of a set of controlling random variables removed¹⁰¹. It thus helps find out whether the correlation between $\Delta Resistance$ and difference in vegetation structure is produced by other confounding environment factors. Here, we controlled for the difference in land surface temperature (ΔLST), SPEI. The partial correlation coefficient was estimated as:

$$r = \frac{r_{t-r} - r_{t-r} \times r_{t-c}}{\sqrt{(1 - r_{r-c}^2) \times (1 - r_{t-c}^2)}} \quad (5)$$

Where r_{t-r} is the Spearman's rank correlation coefficient between forest structure difference and $\Delta Resistance$, r_{t-c} is the correlation between forest structure difference and the controlling variables, and r_{r-c} is the correlation between $\Delta Resistance$ and the controlling variables. Statistical significance was determined using the cumulative density function of Student's t-distribution with the corresponding degrees of freedom.

We used structural equation modeling (SEM) to analyze the path relationships between $\Delta Resistance$ and the vegetation structure difference. This analysis was conducted using the *lavaan* package¹⁰² in R, which employs a covariance-based approach to model multivariate

relationships by reproducing the single variance-covariance matrix of the data. We designed a model based on the possible interrelationships by which vegetation structure change shaped by elephants may impact the drought resistance through changing the microclimate conditions, especially the land surface temperature (Fig. 5e). We set a latent variable as change in vegetation structure (termed $\Delta\text{Vegetation_structure}$), comprising $\Delta\text{Tree height}$ and $\Delta\text{Tree cover}$. $\Delta\text{Vegetation_structure}$ was placed as the endogenous variable that impacts the difference in vegetation drought resistance ($\Delta\text{Resistance}$ from NDVI and SIF), through changes in climate conditions (including ΔLST and SPEI). We assumed that $\Delta\text{Vegetation_structure}$ is influenced by elephant density, and that $\Delta\text{Vegetation_structure}$ shapes the local LST through adjustments in evapotranspiration (ΔET) and albedo (ΔAlbedo). The evapotranspiration and albedo data are from the 250-m FAO water productivity open access portal (WaPOR) evapotranspiration dataset, and the 500-m MCD43A3 albedo dataset, respectively.

We assessed the goodness-of-fit for SEM by using measurements of comparative fit index¹⁰³ and the Tucker-Lewis index¹⁰⁴ (CFI and TLI, normalized to the 0-1 range, where a larger value indicates a better fit), the root mean squared error of approximation¹⁰⁵ and the standardized root mean squared residual¹⁰⁶ (RMSEA and SRMR, normalized to the 0-1 range, a smaller value indicating a closer-fitting model). The model shows a good performance with CFI, TLI, RMSEA and SRMR values of 0.95, 0.90, 0.09 and 0.05, respectively. Details on the validity of goodness of fit and loading factors in the model are shown in Table S4. The sample sizes are 1642 and 2094 of $\Delta\text{Resistance_NDVI}$ and $\Delta\text{Resistance_SIF}$ for the partial correlation analysis, and 1381 for the structural equation modeling (SEM).

In addition, machine-learning attribution was used to analyze the contributions of different factors to the resistance difference (Supplementary Methods 2 and Supplementary Text 7).

Data availability

Information on the main datasets used in this study is listed in Table S5. The elephant distribution data can be obtained from the IUCN Red List of Threatened Species (<https://www.iucnredlist.org/>) and elephant population data from IUCN: African elephant status report 2016 (<https://portals.iucn.org/library/node/46878>). The 30-m resolution tree cover map for 2019 from PlanetScope can be downloaded from <https://doi.org/10.21203/rs.3.rs-1816495/v2>. The 30-m resolution tree height map for 2019 can be downloaded from <https://doi.org/10.1016/j.rse.2020.112165>. The 100-m biomass data from CCI-Biomass in 2018 are accessible on <https://dx.doi.org/10.5285/5f331c418e9f4935b8eb1b836f8a91b8>. The 500 m NDVI and 1 km LST products are obtained from <https://ladsweb.modaps.eosdis.nasa.gov/>. The 0.05°SIF data can be downloaded from <https://doi.org/10.5194/bg-15-5779-2018>. The 0.5° SPEI data is accessible at <https://spei.csic.es/database.html>. The 0.05° SPEI data is accessible at https://data.ceda.ac.uk/neodc/spei_africa/data_. The world database on protected areas (WDPA) data can be downloaded from www.protectedplanet.net.

Code availability

All the python analysis scripts are available in a public repository <https://github.com/SunMX-2024/elephant-disturb> with the source data provided.

Acknowledgements

This study was supported by Yunnan Provincial Science and Technology Project at Southwest United Graduate School (grant number: 202302AO370001), the National Natural Science Foundation of China (grant number: 42175169, 42401311), the Hainan Institute of National Park Research Program KY-23ZK01, and the CALIPSO (Carbon Loss In Plants, Soils and Oceans) project, funded through the generosity of Eric and Wendy Schmidt on the recommendation of the Schmidt Science Program, the U.S. National Science Foundation (grant number: 19-31224), and U.S. Environmental Protection Agency STAR Fellowship, a Smithsonian Predoctoral Fellowship, and the American Society of Mammalogists' Fellowship.

Author contributions

W.L. designed the research. M.S. performed the analysis. M.S. and W.L wrote the draft; and F.B., L.Z., P.C., M.B., D.M., T.Y., D.K., R.G., Y.L., Z.Z., M.H., J.H., N.M., J.Z., J.C., Y.Z., D.Z., Y.Y., B.P., and Q.Z. contributed to the interpretation of the results and the writing of the paper.

Competing interests

The authors declare no competing interests.

References

1. Chen L, Huang JG, Alam SA, Zhai L, Dawson A, Stadt KJ, *et al.* Drought causes reduced growth of trembling aspen in western Canada. *Glob Chang Biol* 2017, **23**(7): 2887-2902.
2. Anderegg WRL, Kane JM, Anderegg LDL. Consequences of widespread tree mortality triggered by drought and temperature stress. *Nature Climate Change* 2012, **3**(1): 30-36.
3. Au TF, Maxwell JT, Robeson SM, Li J, Siani SMO, Novick KA, *et al.* Younger trees in the upper canopy are more sensitive but also more resilient to drought. *Nature Climate Change* 2022, **12**(12): 1168-1174.
4. Liu D, Wang T, Peñuelas J, Piao S. Drought resistance enhanced by tree species diversity in global forests. *Nature Geoscience* 2022, **15**(10): 800-804.
5. Anderegg WRL, Trugman AT, Badgley G, Konings AG, Shaw J. Divergent forest sensitivity to repeated extreme droughts. *Nature Climate Change* 2020, **10**(12): 1091-1095.
6. Bennett AC, McDowell NG, Allen CD, Anderson-Teixeira KJ. Larger trees suffer most during drought in forests worldwide. *Nat Plants* 2015, **1**: 15139.
7. Gora EM, Esquivel-Muelbert A. Implications of size-dependent tree mortality for tropical forest carbon dynamics. *Nat Plants* 2021, **7**(4): 384-391.
8. Lewis SL, Sonke B, Sunderland T, Begne SK, Lopez-Gonzalez G, van der Heijden GM, *et al.* Above-ground biomass and structure of 260 African tropical forests. *Philos Trans R Soc Lond B Biol Sci* 2013, **368**(1625): 20120295.
9. Bennett AC, Dargie GC, Cuni-Sanchez A, Tshibamba Mukendi J, Hubau W, Mukinzi JM, *et al.* Resistance of African tropical forests to an extreme climate anomaly. *Proc Natl Acad Sci U S A* 2021, **118**(21).
10. Greve M, Lykke AM, Fagg CW, Bogaert J, Friis I, Marchant R, *et al.* Continental-scale variability in browser diversity is a major driver of diversity patterns in acacias across Africa. *J Ecol* 2012, **100**(5): 1093-1104.

- 732 11. Berzaghi F, Bretagnolle F, Durand-Bessart C, Blake S. Megaherbivores modify forest structure
733 and increase carbon stocks through multiple pathways. *Proc Natl Acad Sci U S A* 2023, **120**(5):
734 e2201832120.
- 735 12. Berzaghi F, Longo M, Ciais P, Blake S, Bretagnolle F, Vieira S, *et al.* Carbon stocks in central
736 African forests enhanced by elephant disturbance. *Nature Geoscience* 2019, **12**(9): 725-729.
- 737 13. Douglas S, Agus S. Forest Tree Persistence, Elephants, and Stem Scars. *BIOTROPICA* 2004,
738 **36**(4): 505-521.
- 739 14. Harrison RD, Tan S, Plotkin JB, Slik FJW, Detto M, Brenes T, *et al.* Consequences of
740 defaunation for a tropical tree community. *Ecology letters* 2013, **16** 5: 687-694.
- 741 15. Poulsen JR, Rosin C, Meier A, Mills E, Nunez CL, Koerner SE, *et al.* Ecological consequences
742 of forest elephant declines for Afrotropical forests. *Conserv Biol* 2018, **32**(3): 559-567.
- 743 16. Bakker ES, Gill JL, Johnson CN, Vera FW, Sandom CJ, Asner GP, *et al.* Combining paleo-data
744 and modern exclosure experiments to assess the impact of megafauna extinctions on woody
745 vegetation. *Proc Natl Acad Sci U S A* 2016, **113**(4): 847-855.
- 746 17. Doughty CE, Roman J, Faurby S, Wolf A, Haque A, Bakker ES, *et al.* Global nutrient transport
747 in a world of giants. *Proc Natl Acad Sci U S A* 2016, **113**(4): 868-873.
- 748 18. Sitters J, Kimuyu DM, Young TP, Claeys P, Olde Venterink H. Negative effects of cattle on soil
749 carbon and nutrient pools reversed by megaherbivores. *Nature Sustainability* 2020, **3**(5): 360-
750 366.
- 751 19. Stovall AEL, Shugart H, Yang X. Tree height explains mortality risk during an intense drought.
752 *Nat Commun* 2019, **10**(1): 4385.
- 753 20. McDowell NG, Allen CD. Darcy's law predicts widespread forest mortality under climate
754 warming. *Nature Climate Change* 2015, **5**(7): 669-672.
- 755 21. Rowland L, da Costa AC, Galbraith DR, Oliveira RS, Binks OJ, Oliveira AA, *et al.* Death from
756 drought in tropical forests is triggered by hydraulics not carbon starvation. *Nature* 2015,
757 **528**(7580): 119-122.
- 758 22. Fernández-de-Uña L MVJ, Poyatos R, Mencuccini M, McDowell NG. The role of height-driven
759 constraints and compensations on tree vulnerability to drought. *New Phytologist* 2023, **239**(6):
760 2083-2098.
- 761 23. Domec JC, Gartner BL. Relationship between growth rates and xylem hydraulic characteristics
762 in young, mature and old-growth ponderosa pine trees. *Plant, Cell & Environment* 2003, **26**(3):
763 471-483.
- 764 24. Anderegg WRL, Klein T, Bartlett M, Sack L, Pellegrini AFA, Choat B, *et al.* Meta-analysis
765 reveals that hydraulic traits explain cross-species patterns of drought-induced tree mortality
766 across the globe. *Proceedings of the National Academy of Sciences* 2016, **113**(18): 5024-5029.
- 767 25. Daley MJ, Phillips NG, Pettijohn JC, Hadley J. Hydraulic responses to environmental
768 perturbations in *Tsuga canadensis* and *Betula lenta*. *Tree Physiol* 2008, **28**(9): 1341-1348.
- 769 26. Ma Q, Su Y, Niu C, Ma Q, Hu T, Luo X, *et al.* Tree mortality during long-term droughts is lower
770 in structurally complex forest stands. *Nat Commun* 2023, **14**(1): 7467.
- 771 27. Potapov P, Li X, Hernandez-Serna A, Tyukavina A, Hansen MC, Kommareddy A, *et al.*
772 Mapping global forest canopy height through integration of GEDI and Landsat data. *Remote*
773 *Sensing of Environment* 2021, **253**.
- 774 28. Reiner F, Brandt M, Tong X, Skole D, Kariryaa A, Ciais P, *et al.* More than one quarter of
775 Africa's tree cover is found outside areas previously classified as forest. *Nature Communications*

2023, **14**(1): 2258.

29. Xu L, Chen N, Zhang X. Global drought trends under 1.5 and 2 °C warming. *International Journal of Climatology* 2018, **39**(4): 2375-2385.

30. Schwalm CR, Anderegg WRL, Michalak AM, Fisher JB, Biondi F, Koch G, *et al.* Global patterns of drought recovery. *Nature* 2017, **548**(7666): 202-205.

31. Zhang Y, Joiner J, Alemohammad SH, Zhou S, Gentine P. A global spatially contiguous solar-induced fluorescence (CSIF) dataset using neural networks. *Biogeosciences* 2018, **15**(19): 5779-5800.

32. Lloret F, Keeling EG, Sala A. Components of tree resilience: effects of successive low-growth episodes in old ponderosa pine forests. *Oikos* 2011, **120**(12): 1909-1920.

33. Mu H, Xuecao L, Yanan W, Huang J, Du P, Su W, *et al.* A global record of annual terrestrial Human Footprint dataset from 2000 to 2018. *Scientific Data* 2022, **9**: 176.

34. Lang N, Jetz W, Schindler K, Wegner JD. A high-resolution canopy height model of the Earth. *Nature Ecology & Evolution* 2023, **7**(11): 1778-1789.

35. Hansen MC, Potapov PV, Moore R, Hancher M, Turubanova SA, Tyukavina A, *et al.* High-Resolution Global Maps of 21st-Century Forest Cover Change. *Science* 2013, **342**(6160): 850-853.

36. Zellweger F, De Frenne P, Lenoir J, Vangansbeke P, Verheyen K, Bernhardt-Römermann M, *et al.* Forest microclimate dynamics drive plant responses to warming. *Science* 2020, **368**(6492): 772-775.

37. McDowell N, Pockman WT, Allen CD, Breshears DD, Cobb N, Kolb T, *et al.* Mechanisms of plant survival and mortality during drought: why do some plants survive while others succumb to drought? *New Phytol* 2008, **178**(4): 719-739.

38. Poorter L, Bongers F. Leaf traits are good predictors of plant performance across 53 rain forest species. *Ecology* 2006, **87**: 1733-1743.

39. Forrester DI. Linking forest growth with stand structure: Tree size inequality, tree growth or resource partitioning and the asymmetry of competition. *Forest Ecology and Management* 2019, **447**: 139-157.

40. Pillet M, Joetzer E, Belmin C, Chave J, Ciais P, Dourdain A, *et al.* Disentangling competitive versus climatic drivers of tropical forest mortality. *J Ecol* 2018, **106**: 1165-1179.

41. Li Y, Zhao M, Motesharrei S, Mu Q, Kalnay E, Li S. Local cooling and warming effects of forests based on satellite observations. *Nat Commun* 2015, **6**: 6603.

42. De Frenne P, Zellweger F, Rodríguez-Sánchez F, Scheffers BR, Hylander K, Luoto M, *et al.* Global buffering of temperatures under forest canopies. *Nat Ecol Evol* 2019, **3**(5): 744-749.

43. Sanczuk P, De Pauw K, De Lombaerde E, Luoto M, Meeussen C, Govaert S, *et al.* Microclimate and forest density drive plant population dynamics under climate change. *Nature Climate Change* 2023, **13**(8): 840-847.

44. De Frenne P, Rodríguez-Sánchez F, Coomes DA, Baeten L, Verstraeten G, Vellend M, *et al.* Microclimate moderates plant responses to macroclimate warming. *Proceedings of the National Academy of Sciences* 2013, **110**(46): 18561-18565.

45. Harrison RD, Tan S, Plotkin JB, Slik F, Detto M, Brenes T, *et al.* Consequences of defaunation for a tropical tree community. *Ecology Letters* 2013, **16**(5): 687-694.

46. Dirzo R, Young HS, Galetti M, Ceballos G, Isaac NJB, Collen B. Defaunation in the Anthropocene. *Science* 2014, **345**(6195): 401-406.

820 47. Berzaghi F, Verbeeck H, Nielsen MR, Doughty CE, Bretagnolle F, Marchetti M, *et al.* Assessing
821 the role of megafauna in tropical forest ecosystems and biogeochemical cycles – the potential
822 of vegetation models. *Ecography* 2018, **41**(12): 1934-1954.

823 48. Thoules; CR, Dublin; HT, Blanc; JJ, Skinner; DP, Daniel; TE, Taylor; RD, *et al.* African
824 Elephant Status Report 2016: an update from the African Elephant Database; 2016.

825 49. Pellegrini AFA, Pringle RM, Govender N, Hedin LO. Woody plant biomass and carbon
826 exchange depend on elephant-fire interactions across a productivity gradient in African savanna.
827 *J Ecol* 2017, **105**(1): 111-121.

828 50. Shannon G, Thaker M, Vanak AT, Page BR, Grant R, Slotow R. Relative Impacts of Elephant
829 and Fire on Large Trees in a Savanna Ecosystem. *Ecosystems* 2011, **14**(8): 1372-1381.

830 51. Cardoso A, Malhi Y, Oliveras I, Lehmann D, Ndong J, Dimoto E, *et al.* The Role of Forest
831 Elephants in Shaping Tropical Forest–Savanna Coexistence. *Ecosystems* 2020, **23**.

832 52. Berzaghi F, Zhu D, Alroy J, Ciais P. Trait-based mechanistic approach highlights global patterns
833 and losses of herbivore biomass functional diversity. *Functional Ecology* 2024, **38**(4): 808-819.

834 53. Dai A. Increasing drought under global warming in observations and models. *Nature Climate*
835 *Change* 2013, **3**(1): 52-58.

836 54. Naumann G, Alfieri L, Wyser K, Mentaschi L, Betts RA, Carrão H, *et al.* Global Changes in
837 Drought Conditions Under Different Levels of Warming. *Geophysical Research Letters* 2018,
838 **45**: 3285 - 3296.

839 55. Maisels F, Strindberg S, Blake S, Wittemyer G, Hart J, Williamson L, *et al.* Devastating decline
840 of forest elephants in Central Africa. *PLoS ONE* 2013, **8**: e59469.

841 56. Enquist BJ, Abraham AJ, Harfoot MJB, Malhi Y, Doughty CE. The megabiota are
842 disproportionately important for biosphere functioning. *Nat Commun* 2020, **11**(1): 699.

843 57. Taylor L, Vollrath F, Lambert B, Lunn D, Douglas-Hamilton I, Wittemyer G. Movement reveals
844 reproductive tactics in male elephants. *Journal of Animal Ecology* 2019, **89**.

845 58. Beirne C, Houslay TM, Morkel P, Clark CJ, Fay M, Okouyi J, *et al.* African forest elephant
846 movements depend on time scale and individual behavior. *Sci Rep* 2021, **11**(1): 12634.

847 59. Blake S, Deem SL, Strindberg S, Maisels F, Momont L, Isia I-B, *et al.* Roadless Wilderness
848 Area Determines Forest Elephant Movements in the Congo Basin. *PLOS ONE* 2008, **3**(10):
849 e3546.

850 60. Wall J, Wittemyer G, Klinkenberg B, LeMay V, Blake S, Strindberg S, *et al.* Human footprint
851 and protected areas shape elephant range across Africa. *Current Biology* 2021: 1-9.

852 61. Tucker MA, Böhning-Gaese K, Fagan WF, Fryxell JM, Van Moorter B, Alberts SC, *et al.*
853 Moving in the Anthropocene: Global reductions in terrestrial mammalian movements. *Science*
854 2018, **359**(6374): 466-469.

855 62. Huang RM, Mare C, Guldemon RAR, Pimm SL, van Aarde RJ. Protecting and connecting
856 landscapes stabilizes populations of the Endangered savannah elephant. *Sci Adv* 2024, **10**(1):
857 eadk2896.

858 63. van Aarde R, Pimm S, Guldemon R, Huang R, Maré C. The 2020 elephant die-off in Botswana.
859 *PeerJ* 2021, **9**: e10686.

860 64. van Aarde R, Jackson T, Ferreira S. Conservation science and elephant management in Southern
861 Africa. *South African Journal of Science* 2006, **102**: 385-388.

862 65. Woodroffe R, Hedges S, Durant S. To Fence or Not to Fence. *Science (New York, NY)* 2014,
863 **344**: 46-48.

- 864 66. Epps C, Palsbøll P, Wehausen J, Roderick G, Ramey R, McCullough D. Highways block gene
865 flow and cause a rapid decline in genetic diversity of desert bighorn sheep. *Ecology Letters* 2005,
866 **8**: 1029-1038.
- 867 67. Khosa A, Ndagurwa HGT, Witkowski ETF, Mutematemi SA, Mrewa AT, Zisadza J, *et al.* The
868 impact of elephants (*Loxodonta africana*) on the Baobab (*Adansonia digitata*) in a semi-arid
869 savanna. *Global Ecology and Conservation* 2023, **46**.
- 870 68. Abraham JO, Goldberg ER, Botha J, Staver AC. Heterogeneity in African savanna elephant
871 distributions and their impacts on trees in Kruger National Park, South Africa. *Ecology and*
872 *Evolution* 2021, **11**(10): 5624-5634.
- 873 69. Filazzola A, Brown C, Dettlaff M, Amgaa B, Grenke J, Bao T, *et al.* The effects of livestock
874 grazing on biodiversity are multi-trophic: a meta-analysis. *Ecology Letters* 2020, **23**: 1298-1309.
- 875 70. Zalai T, Borza S, Lukács BA, Végvári Z. The influence of grazing intensity and wetland
876 availability on breeding shorebird populations in a Eurasian steppe. *Global Ecology and*
877 *Conservation* 2025, **59**: e03557.
- 878 71. Zhou G, Zhou X, He Y, Shao J, Hu Z, Liu R, *et al.* Grazing intensity significantly affects
879 belowground carbon and nitrogen cycling in grassland ecosystems: a meta-analysis. *Global*
880 *Change Biology* 2017, **23**(3): 1167-1179.
- 881 72. The IUCN Red List Threatened Species (IUCN, 2022). [cited]Available from:
882 <http://www.iucnredlist.org/>
- 883 73. African Elephant Status Report 2007: an update from the African Elephant Database.
- 884 74. Mondol S, Moltke I, Hart J, Keigwin M, Brown L, Stephens M, *et al.* New evidence for hybrid
885 zones of forest and savanna elephants in Central and West Africa. *Molecular ecology* 2015, **24**.
- 886 75. Gobush KS, Edwards, C.T.T, Maisels, F., Wittemyer, G., Balfour, D. & Taylor, R.D. African
887 Forest Elephant(*Loxodonta cyclotis*). 2021 [cited]Available from:
888 <https://www.iucnredlist.org/species/181007989/204404464>
- 889 76. Gobush KS, Edwards, C.T.T, Balfour, D., Wittemyer, G., Maisels, F. & Taylor, R.D. African
890 Savanna Elephant(*Loxodonta africana*). 2022 [cited]Available from:
891 <https://www.iucnredlist.org/species/181008073/223031019>
- 892 77. Zhu L, Li W, Ciais P, He J, Cescatti A, Santoro M, *et al.* Comparable biophysical and
893 biogeochemical feedbacks on warming from tropical moist forest degradation. *Nature*
894 *Geoscience* 2023, **16**(3): 244-249.
- 895 78. Duveiller G, Hooker J, Cescatti A. The mark of vegetation change on Earth's surface energy
896 balance. *Nature Communications* 2018, **9**(1): 679.
- 897 79. IUCN U-Wa. Protected Planet: The World Database on Protected Areas (WDPA) and World
898 Database on Other Effective Area-based Conservation Measures (WD-OECM). 2024
899 [cited]Available from: www.protectedplanet.net
- 900 80. Santoro MC, O. . ESA Biomass Climate Change Initiative (Biomass_cci): Global datasets of
901 forest above-ground biomass for the years 2010, 2017 and 2018, v3. In: Analysis NECfED,
902 editor.: Santoro, M.; Cartus, O. ; 2021.
- 903 81. Dinerstein E, Olson D, Joshi A, Vynne C, Burgess N, Wikramanayake E, *et al.* An Ecoregion-
904 Based Approach to Protecting Half the Terrestrial Realm. *BioScience* 2017, **1**: 1-12.
- 905 82. Andam KS, Ferraro PJ, Pfaff A, Sanchez-Azofeifa GA, Robalino JA. Measuring the
906 effectiveness of protected area networks in reducing deforestation. *Proceedings of the National*
907 *Academy of Sciences* 2008, **105**(42): 16089-16094.

- 908 83. Nogueira AR, Pugnana A, Ruggieri S, Pedreschi D, Gama J. Methods and tools for causal
909 discovery and causal inference. *WIREs Data Mining and Knowledge Discovery* 2022, **12**(2):
910 e1449.
- 911 84. Chatton A, Rohrer JM. The Causal Cookbook: Recipes for Propensity Scores, G-Computation,
912 and Doubly Robust Standardization. *Advances in Methods and Practices in Psychological*
913 *Science* 2024, **7**(1): 25152459241236149.
- 914 85. Mendes C, Aldebert K, Brun F, Makowski D. Causal analysis methods for estimating the impact
915 of drought and cold events on crop yields in France. *European Journal of Agronomy* 2025, **170**:
916 127743.
- 917 86. Rosenbaum PR. Overt Bias in Observational Studies. In: Rosenbaum PR (ed). *Observational*
918 *Studies*. Springer New York: New York, NY, 2002, pp 71-104.
- 919 87. Rubin DB. *Matched Sampling for Causal Effects*. Cambridge University Press: Cambridge,
920 2006.
- 921 88. Teo HC, Lamba A, Ng SJW, Nguyen AT, Dwiputra A, Lim AJY, *et al*. Reduction of deforestation
922 by agroforestry in high carbon stock forests of Southeast Asia. *Nature Sustainability* 2025, **8**(4):
923 358-362.
- 924 89. Funk MJ, Westreich D, Wiesen C, Stürmer T, Brookhart MA, Davidian M. Doubly Robust
925 Estimation of Causal Effects. *American Journal of Epidemiology* 2011, **173**(7): 761-767.
- 926 90. Lee BK, Lessler J, Stuart EA. Improving propensity score weighting using machine learning.
927 *Statistics in Medicine* 2010, **29**(3): 337-346.
- 928 91. Rosa GJM. The Elements of Statistical Learning: Data Mining, Inference, and Prediction by
929 HASTIE, T., TIBSHIRANI, R., and FRIEDMAN, J. *Biometrics* 2010, **66**(4): 1315-1315.
- 930 92. Wolpert DH. Stacked generalization. *Neural Networks* 1992, **5**(2): 241-259.
- 931 93. Santini L, Mendez Angarita VY, Karoulis C, Fundarò D, Pranzini N, Vivaldi C, *et al*.
932 TetraDENSITY 2.0—A Database of Population Density Estimates in Tetrapods. *Global Ecology*
933 *and Biogeography* 2024, **33**(12): e13929.
- 934 94. Berzaghi F, Chami R, Cosimano T, Fullenkamp C. Financing conservation by valuing carbon
935 services produced by wild animals. *Proceedings of the National Academy of Sciences* 2022,
936 **119**(22): e2120426119.
- 937 95. Vicente-Serrano SM, Beguería S, López-Moreno JI. A Multiscalar Drought Index Sensitive to
938 Global Warming: The Standardized Precipitation Evapotranspiration Index. *Journal of Climate*
939 2009, **23**: 1696-1718.
- 940 96. Li X, Piao S, Wang K, Wang X, Wang T, Ciais P, *et al*. Temporal trade-off between gymnosperm
941 resistance and resilience increases forest sensitivity to extreme drought. *Nature Ecology &*
942 *Evolution* 2020, **4**(8): 1075-1083.
- 943 97. Au TF, Maxwell JT, Novick KA, Robeson SM, Warner SM, Lockwood BR, *et al*. Demographic
944 shifts in eastern US forests increase the impact of late-season drought on forest growth.
945 *Ecography* 2020, **43**(10): 1475-1486.
- 946 98. Peng J, Dadson S, Hirpa F, Dyer E, Lees T, Miralles DG, *et al*. A pan-African high-resolution
947 drought index dataset. *Earth System Science Data* 2020, **12**(1): 753-769.
- 948 99. Beguería S, Vicente-Serrano S, Reig F, Latorre B. Standardized precipitation evapotranspiration
949 index (SPEI) revisited: Parameter fitting, evapotranspiration models, tools, datasets and drought
950 monitoring. *International Journal of Climatology* 2014, **34**.
- 951 100. Chen Y, Morton DC, Andela N, van der Werf GR, Giglio L, Randerson JT. A pan-tropical

952 cascade of fire driven by El Niño/Southern Oscillation. *Nature Climate Change* 2017, **7**(12):
953 906-911.

954 101. Baba K, Shibata R, Sibuya M. Partial correlation and conditional correlation as measure of
955 conditional independence. *Australian & New Zealand Journal of Statistics* 2004, **46**: 657-664.

956 102. Rosseel Y. lavaan: An R Package for Structural Equation Modeling. *J Stat Softw* 2011, **48**.

957 103. Hu L-t, Bentler PM. Fit indices in covariance structure modeling : Sensitivity to
958 underparameterized model misspecification. *Psychological Methods* 1998, **3**: 424-453.

959 104. Bentler P, Bonett D. Significance Tests and Goodness-of-Fit in Analysis of Covariance
960 Structures. *Psychological Bulletin* 1980, **88**: 588-606.

961 105. Browne MW, Cudeck R. Alternative Ways of Assessing Model Fit. *Sociological Methods &*
962 *Research* 1992, **21**(2): 230-258.

963 106. Hu Lt, Bentler PM. Cutoff criteria for fit indexes in covariance structure analysis: Conventional
964 criteria versus new alternatives. *Structural Equation Modeling: A Multidisciplinary Journal*
965 1999, **6**(1): 1-55.

966

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- [Slelephants260814.docx](#)