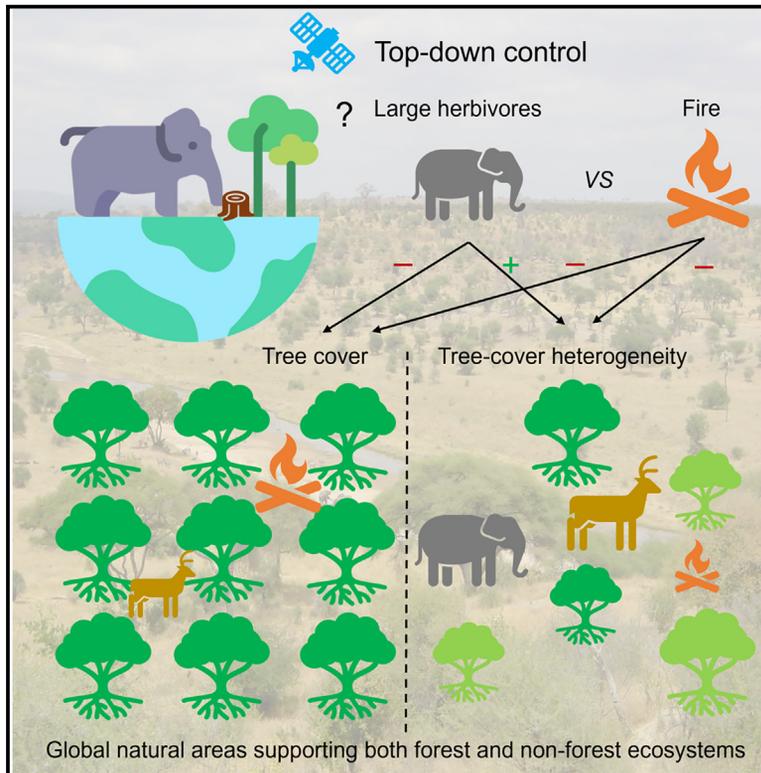


Tree cover and its heterogeneity in natural ecosystems is linked to large herbivore biomass globally

Graphical abstract



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In brief

Understanding what shapes tree distributions across natural landscapes worldwide is crucial for biodiversity and climate action. This study uses global satellite data to reveal that natural ecosystems with more large herbivores like elephants have less dense, but more diverse, tree cover. This finding highlights the need to consider these animals in conservation strategies, not just for their own sake but also for the vital and nuanced role they play in shaping landscapes, affecting biodiversity and nature-based climate change policies.

Highlights

- Top-down trophic control of vegetation openness and heterogeneity manifests globally
- Large herbivores reduce tree cover but boost variability in strictly protected areas
- Fire reduces both landscape-scale tree cover and its spatial heterogeneity
- Megafauna effects are more evident in ecosystems with potentially alternative states



Article

Tree cover and its heterogeneity in natural ecosystems is linked to large herbivore biomass globally

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SCIENCE FOR SOCIETY Maintaining diverse and resilient ecosystems worldwide is vital for biodiversity conservation and climate change mitigation. However, current conservation strategies often overlook the potential role of megafauna (large animals) in shaping ecosystems. Our global study based on satellite data suggests that large herbivores like elephants and deer significantly impact the density and heterogeneity of tree cover in strictly protected areas, particularly in ecosystems with potentially alternative states. This aspect has not been adequately considered in sustainable land management and ecosystem restoration frameworks, and this necessitates a rethinking of global conservation policies and restoration efforts to include large-scale trophic rewilding. In the long term, our findings pave the way for more holistic and effective strategies to conserve and restore more resilient and sustainable ecosystems and landscapes by illuminating the multifaceted ecological-social interactions that shape them.

SUMMARY

Addressing intertwined crises of climate change and biodiversity loss is a pressing global challenge, with trees playing pivotal roles in promoting carbon sequestration and habitat diversity. However, there is a distinct knowledge gap concerning the global drivers shaping tree cover and its heterogeneity, particularly the roles and relative importance of large herbivores and fire compared to climatic and topo-edaphic conditions. Here, we deploy satellite observations of strictly protected areas worldwide to reveal that in regions where vegetation may be in disequilibrium with climate, high biomass of large herbivores, especially browsers, is inversely related to tree cover but positively associated with its spatial heterogeneity. Conversely, fire reduces both tree cover and heterogeneity. These results suggest that top-down megafauna effects on landscape-scale vegetation openness and heterogeneity manifest worldwide. Our finding supports the need to consider megafauna, particularly large herbivores, in ecosystem effects on climate change mitigation and conservation and restoration efforts through trophic rewilding.

INTRODUCTION

Tree cover strongly determines the above-ground carbon sequestration capacity of terrestrial ecosystems,^{1,2} while hetero-

geneity in tree cover is a key control of landscape-scale biodiversity.³ However, a global unified understanding of their driving mechanisms is still lacking. The global distribution of vegetation types and biomes has long been thought to be bottom-up



controlled by the abiotic environment, notably climate and soil. However, the ecological puzzle of open vegetation growing in climates that can support forests,⁴ now understood as alternative biome states,^{5–7} has been recognized for over a century, e.g., by Darwin.⁸ In the tropics and subtropics, many regions suitable for forests are covered by open ecosystems such as woodlands, savannas, shrublands, and grasslands.⁹ Linked to this, the idea that forests cannot grow on grassland soils is increasingly challenged.¹⁰ Although open ecosystems are often assumed to result from anthropogenic deforestation, particularly in Europe and eastern North America¹¹ (but see Svenning¹² and Feurdean et al.¹³), much evidence shows that many open ecosystems are ancient and were widespread before human influence.¹⁴

The realization that the natural vegetation state and tree cover cannot be solely predicted by bottom-up drivers of climate and topo-edaphic conditions has resulted in a substantial body of work showing the importance of top-down control by plant consumers, particularly fire and, to a lesser degree, herbivores.^{4,9,15–18} This work has focused mainly on savannas in Africa and South America.^{15,16,18,19} However, little is known about the global importance of top-down consumers relative to bottom-up drivers⁶ and whether bottom-up drivers modify consumer impacts.¹⁸ Including large herbivores and fire as plant consumers, Bond expanded the “green world” hypothesis to a “multi-colored” world⁴: “brown,” where large herbivores control woody vegetation; “black,” where woody vegetation is primarily regulated by fire; and “green,” where climates control woody vegetation. He hypothesized that areas where vegetation may be in disequilibrium with climate (Whittaker’s “ecosystems uncertain” climate zone) are naturally consumer controlled, in contrast to other areas where tree cover is deterministically determined by climate (Whittaker’s “ecosystems deterministic” climate zone).⁴

Although Bond’s hypothesis has received considerable support,^{5,6,14} the relative importance of fire and large herbivore assemblages, as well as browsers vs. grazers, as controls of natural vegetation structure worldwide remains incompletely understood. Importantly, fire’s effects on vegetation are similar but non-identical to those of its animal counterparts.^{9,15} Fire thrives on plants with properties that can make them less palatable to herbivores, notably high cellulose and lignin resulting in low nitrogen content. Thus, herbivores and fire are competing but distinct consumers of plants.⁴ Their differential effects on, and relative importance in, shaping tree cover and heterogeneity are likely context dependent¹⁶ and poorly understood globally. Compared to small- to medium-sized herbivores, which are top-down controlled by predation and mostly have relatively specialized dietary requirements, large herbivores (≥ 45 kg body mass) are more generalistic, can consume large amounts of low-quality food, and often exhibit little or no top-down regulation^{4,20} but are instead limited by food availability.²¹ Notably, large carnivores do not reduce the total biomass of medium and large herbivores but promote greater dominance by the larger herbivore species.²²

Specifically, large herbivores are hypothesized to promote the openness and heterogeneity of vegetation on a local and landscape scale, primarily through herbivory and physical disturbance or bioturbation (e.g., trampling and wallowing).^{18,23,24} Indeed, palaeoecological evidence indicates that high herbivore densities were associated with high vegetation diversity in Euro-

pean interglacial ecosystems.²⁵ In contrast, evidence from different continents suggests that end-Pleistocene megafauna extinctions promoted tree cover expansion and increased fire frequency and severity,^{26,27} albeit with varying effects.²⁸ Meanwhile, there is strong evidence for top-down control of individual herbivore species on vegetation structure, composition, and functional traits in contemporary ecosystems at local to regional scales.^{23,29,30} However, the global generality of top-down regulation of tree cover by large herbivore assemblages remains to be tested.^{6,23} The central question is the relative importance of climate, plant consumers (large herbivores vs. fire), and topo-edaphic conditions in controlling natural tree cover and its heterogeneity globally and in hypothetically uncertain vs. deterministic ecosystems.

Here, we employ a global-scale macroecological analysis of satellite-derived tree cover estimates using machine-learning-based boosted regression trees (BRTs)³¹ to examine the influence of large herbivores, fire, climate, and topo-edaphic conditions on tree cover and its spatial heterogeneity. Our study focuses on large strictly protected areas inhabited by extant large herbivore species (human footprint ≤ 4 ; [Figure S1](#)), which represent potentially intact landscapes with minimal human influence^{32,33} and offer an ideal focal system for this global assessment. Our primary findings reveal that in areas with potentially alternative ecosystem states, the biomass of large herbivores, especially browsers, is negatively correlated with overall tree cover but positively associated with its spatial heterogeneity. These results suggest that large herbivores are critical agents in shaping and maintaining the structural characteristics of terrestrial ecosystems, which has consequences for carbon sequestration and species diversity. These findings have profound implications for global conservation and ecosystem management strategies. They underline the necessity of incorporating the role of large herbivores in policy frameworks, particularly in the context of the UN Decade on Ecosystem Restoration and the 30 by 30 target,^{34,35} to achieve both biodiversity conservation and climate change mitigation objectives effectively.

RESULTS

Determinants of global tree cover and heterogeneity and their relative importance

First, we assessed to what extent five key environmental (climatic and topo-edaphic) drivers explain spatial patterns of average levels and spatial heterogeneity in tree cover of strictly protected areas worldwide at the landscape scale (148,409 5-km grid cells; [Figures S1](#) and [S2](#)). We calculated the average tree cover and spatial heterogeneity (standard deviation) for each 5-km grid from the tree cover fraction layer of the 100-m-resolution Copernicus global land cover dataset in 2019³⁶ (see [experimental procedures](#)). Environmental variables consist of mean annual temperature, mean annual precipitation, precipitation seasonality, elevation, and soil sand content. Environmental drivers alone explain more of the 10-fold cross-validated variance (see [experimental procedures](#)) in our datasets of tree cover (78.7%) than its heterogeneity (71.2%) globally ([Figures 1A](#) and [1B](#)).

To test whether the role of top-down control on vegetation is stronger in ecosystems with potentially alternative states, global

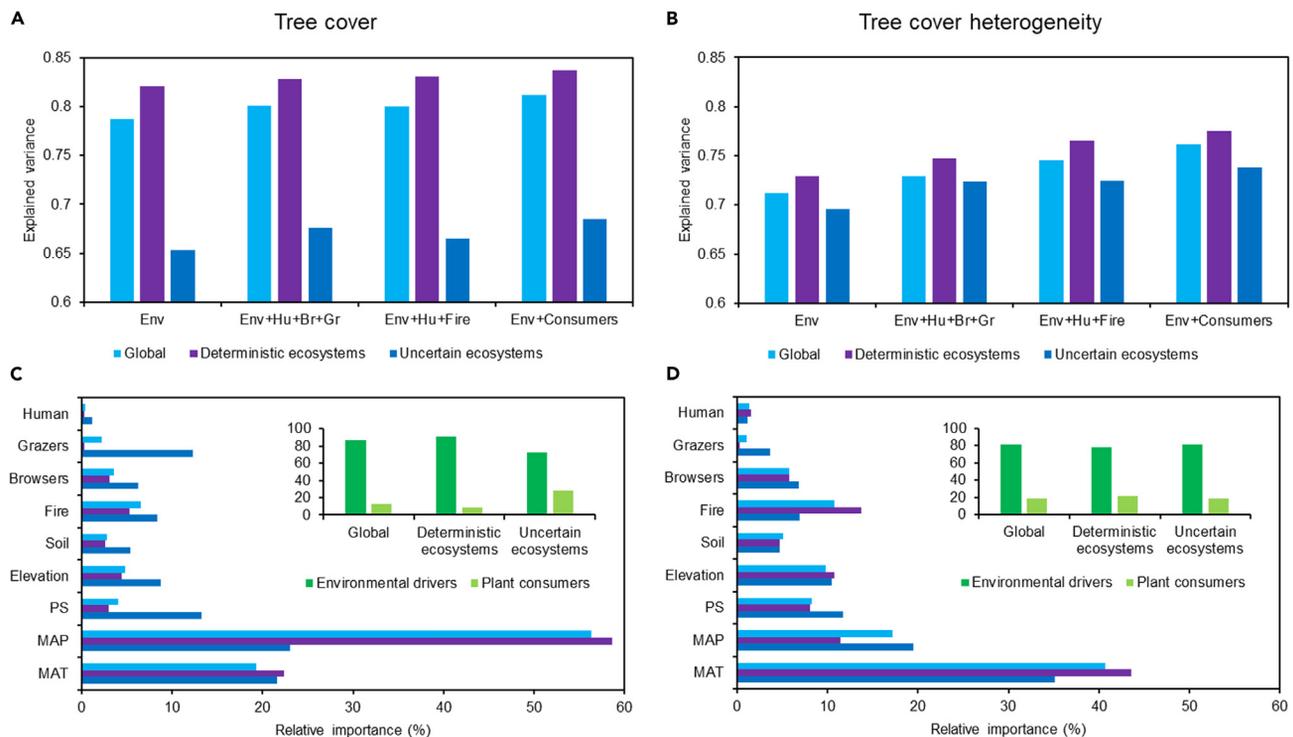


Figure 1. Plant consumers are important in explaining global tree cover and heterogeneity

(A and B) The percentage of explained variance (R^2) by 10-fold cross-validated BRT models for global tree cover (A) and its heterogeneity (B) in large strictly protected areas and their subcategories of hypothetically deterministic and uncertain ecosystems driven by key environmental and plant consumer variables. Env is short for five key environmental variables, including mean annual temperature (MAT), mean annual precipitation (MAP), precipitation seasonality (PS), elevation, and soil sand content (Soil). Hu, human footprint; Br, biomass sum of large browsers ≥ 45 kg; Gr, biomass sum of large grazers ≥ 45 kg; Fire, mean annual cumulative burned area. Plant consumers include Hu, Br, Gr, and Fire.

(C and D) The relative importance of all predictors in BRT models explaining global tree cover (C) and its heterogeneity (D) in large strictly protected areas and their subcategories of deterministic and uncertain ecosystems. The insets in (C) and (D) compare the sums of the relative importance of environmental drivers and plant consumers.

studied areas were further divided into hypothetically uncertain ecosystems (Whittaker's "ecosystems uncertain" climate zone; $n = 45,607$) and deterministic ecosystems ($n = 102,802$) based on an empirical relationship provided by Bond⁴ (see [experimental procedures](#); [Figure S1](#)). The environmental forcing is weaker in uncertain (65.3% and 69.6%) than in deterministic (82.1% and 72.9%) ecosystems, especially for tree cover, indicating that tree cover in uncertain ecosystems is less regulated by environmental factors. Adding plant consumers to environmental drivers, including large herbivores (browsers and grazers; [Table S1](#)), fire (mean annual cumulative burned area), and human footprint, contributed considerably to explaining the variability in tree cover and heterogeneity globally. The best-fitting global models include all predictors, and the explained variance in tree cover (81.2%) is slightly larger than tree cover heterogeneity (76.2%), suggesting relatively more complex mechanisms shaping tree cover heterogeneity than average tree cover. Furthermore, the addition of consumers increased the absolute and relative explained variance in global tree cover heterogeneity (5.0% and 7.0%) more than for average tree cover (2.5% and 3.2%), indicating that plant consumers play a relatively more important role in explaining tree cover heterogeneity than average tree cover.

We then quantified the relative importance of different environmental drivers and plant consumers in explaining global tree

cover and heterogeneity (see [experimental procedures](#)). Mean annual precipitation is the dominant factor (56.4%) controlling tree cover globally ([Figure 1C](#)), consistent with previous African continental- and global-scale studies focusing on tropical savannas.^{15,37} On the contrary, for the first time, we find that mean annual temperature is the leading factor (40.7%) regulating global tree cover heterogeneity ([Figure 1D](#)). As the third most important factor, fire is more important in explaining tree cover heterogeneity (10.7%) than average tree cover (6.5%). The importance of large browsers (3.6%) is slightly greater than large grazers (2.3%) in explaining tree cover compared to the much greater importance of large browsers (5.8%) and the minor contribution of large grazers (1.1%) to tree cover heterogeneity. The human footprint index is the least important and negligible in explaining tree cover (0.4%) and its heterogeneity (1.4%), supporting our assumption of limited human impact in protected areas (PAs) with index values ≤ 4 with potentially intact population densities and biomass of large herbivore assemblages. By dividing the studied PAs into uncertain and deterministic ecosystems, we find that the importance of precipitation in explaining tree cover is substantially lower in uncertain ecosystems (23% vs. 58.6%), while the contributions of fire and large herbivores (browsers and grazers) are considerably higher in uncertain ecosystems ([Figure 1C](#)). Furthermore, the importance of large

grazers (12.3%) for tree cover is substantially higher in uncertain ecosystems compared to a negligible contribution (0.3%) in deterministic ecosystems. In contrast, fire's importance in explaining tree cover heterogeneity is substantially larger in deterministic ecosystems (13.8% vs. 7.0%), while large browsers and grazers are more important in uncertain ecosystems (6.8% vs. 5.8% and 3.6% vs. 0.3%). Overall, unlike the comparable total importance of plant consumers in explaining tree cover heterogeneity in uncertain and deterministic ecosystems, their importance in explaining tree cover is substantially higher in uncertain (28.0%) than in deterministic (9.0%) ecosystems (Figures 1C and 1D), consistent with our finding above and supporting the “ecosystems uncertain” hypothesis.⁴

Potential mechanisms of consumers in explaining tree cover and heterogeneity

Large herbivores: Browsers and grazers

We find an unimodal relationship between tree cover and large browsers in uncertain ecosystems and for two climate zones combined (Figures 2A and S3A), but not in deterministic ecosystems (Figure S4A), excluding the end of the partial dependence plots with sparse data distribution of the biomass sum of large browsers (above 4,000 kg/km²) to avoid uncertainty and potential misinterpretation (Figures S5–S7). This unimodal relation may be explained as an emerging property of two relations at the landscape level: an initial preference relation that browsers are more abundant in more wooded systems than grassy ones before the impact of high browser biomass on the woody cover is strong enough to manifest.¹⁸ Thus, this result suggests that the hypothesized inhibition of tree cover by large browsers is more likely to occur at high biomass levels in uncertain ecosystems. Similarly, a U-shaped relationship between tree cover heterogeneity and large browsers is found in uncertain ecosystems (Figure 2B), which is also observable but not so evident in deterministic ecosystems or when two climate zones are combined (Figures S3B and S10B). In contrast, we find a negative relationship between tree cover and large grazers, especially at high biomass levels in uncertain ecosystems (Figure 2C) but not in deterministic ecosystems (Figure S4C). This result is consistent with the previously hypothesized inhibitory role of large grazers on tree cover in uncertain ecosystems, although it could equally well reflect their selection for more open habitats. Like large browsers, we also find that large grazers are positively associated with tree cover heterogeneity at high biomass levels in uncertain ecosystems (Figure 2D). However, given the minor importance of large grazers in deterministic ecosystems, their relationships with tree cover and heterogeneity found here may not be robust enough compared to those in uncertain ecosystems and should be interpreted with caution. Overall, our results suggest that large herbivores, especially browsers, are likely to inhibit landscape-scale tree cover and promote or maintain its heterogeneity at high biomass levels in uncertain ecosystems globally.

Fire

A near-linear negative relationship is found between global tree cover and fire (Figures 2E, S3E, and S4E), especially in uncertain ecosystems, confirming and extending the finding that fire plays a vital role in maintaining open vegetation, which has previously been shown for tropical and subtropical savannas,¹⁵ in ecosys-

tems worldwide. Moreover, we find a quasi-linear negative relationship between tree cover heterogeneity and fire globally and in both uncertain and deterministic ecosystems (Figure 2F), except for regions with low fire-burned areas (0%–15%) (Figures 2F and S4F), suggesting that fire reduces not only landscape-scale tree cover but also heterogeneity in tree cover.

Relative importance of climate, consumers, and topo-edaphic conditions

As expected, our result shows that climate exerts the dominant control over global tree cover (79.7%), especially in deterministic ecosystems (84.0%) (Figure 3A). However, both plant consumers and topo-edaphic conditions are more important in uncertain ecosystems, with more contributions from plant consumers than topo-edaphic conditions. Thus, our result suggests that in combination with topo-edaphic conditions, plant consumers are likely to interact with climate in shaping tree cover in natural areas under uncertain ecosystems (42% vs. 58%). In contrast, the climate contribution in explaining global tree cover heterogeneity (66.1%) is considerably smaller than in explaining tree cover and of equal size under deterministic and uncertain ecosystems (63.1% vs. 66.3%) (Figure 3B). Plant consumers and topo-edaphic conditions also contribute similarly to tree cover heterogeneity between two climate zones, with uncertain ecosystems showing more close contributions of the two (18.6% vs. 15.1%).

Although large herbivores (browsers and grazers) and fire compete for the same plant biomass,¹⁷ their relative importance in shaping landscape-scale tree cover and heterogeneity globally is still an open question. Globally, our results suggest that large herbivores (5.8%) are equally important as fire (6.5%) in explaining tree cover compared to a slightly larger contribution of large herbivores (6.8%) and a considerably larger contribution of fire (10.7%) to tree cover heterogeneity (Figures 3C and 3D). Moreover, fire is more important than large herbivores in explaining both tree cover and its heterogeneity in deterministic ecosystems, with tree cover heterogeneity showing a substantially larger fire contribution. In contrast, large herbivores are more important than fire in explaining both tree cover and its heterogeneity under uncertain ecosystems, with tree cover having a considerably larger contribution of large herbivores. Finally, quite similar results of potential mechanisms and relative importance of large herbivores and fire in explaining spatial patterns of global tree cover and heterogeneity are observed from BRT analyses only using the empirical density-weighted biomass sum of 58 large herbivore species that have empirical density observations (Figures S8 and S9), suggesting the robustness of our main results based on modeled density estimates of the 102 studied species.

Africa as a mirror of the global patterns

The global-scale relationships between consumers (large herbivores vs. fire) and tree cover (Figure 2) also hold for uncertain ecosystems of the African continent ($n = 31,879$; 69.9% grid cells of uncertain ecosystems studied worldwide), currently hosting the most intact large herbivore assemblages and widespread grass-fueled wildfires³⁸ (Figure S10). Nevertheless, the positive relationship between tree cover heterogeneity and fire in

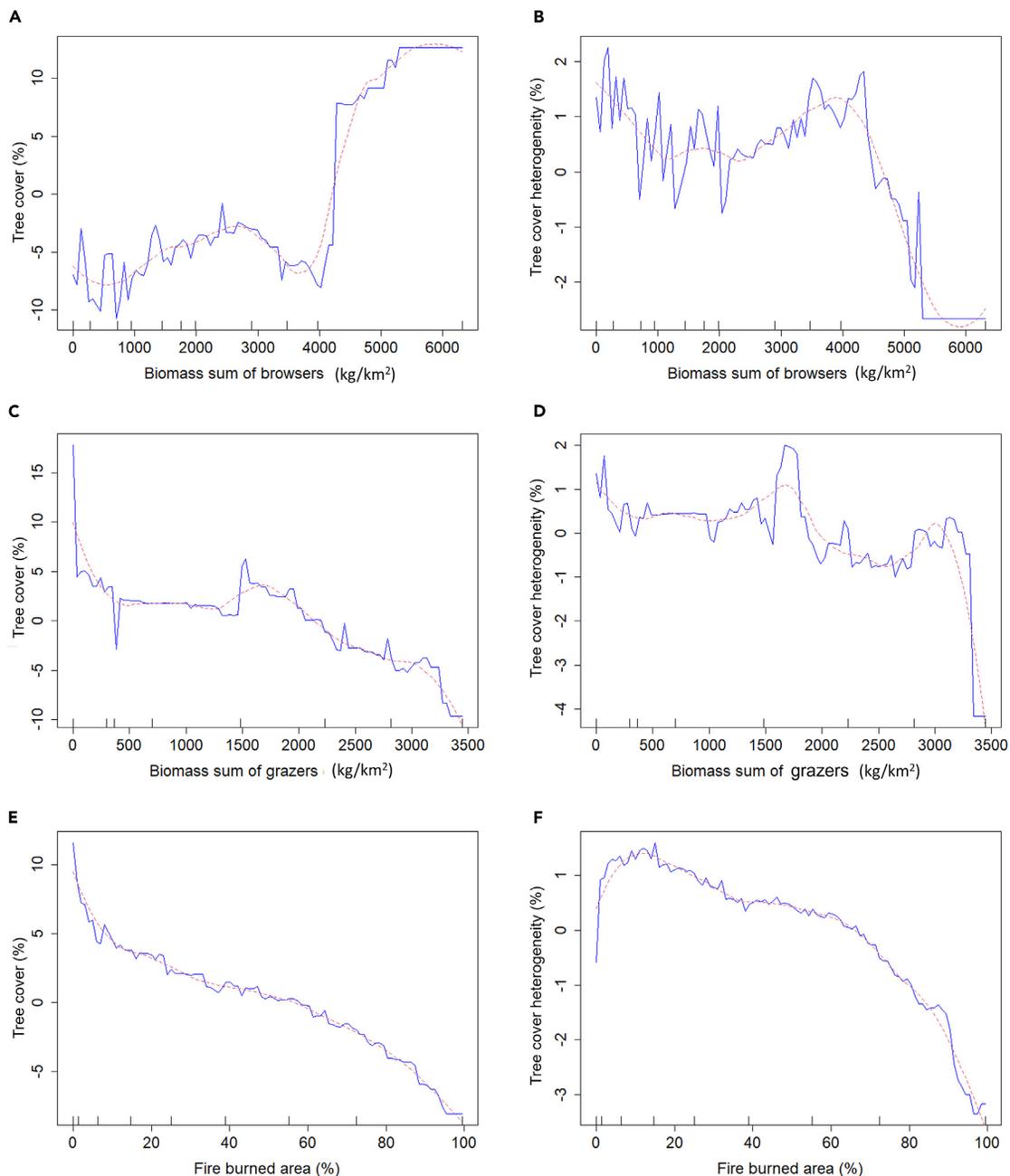


Figure 2. Potential mechanisms of large herbivores (browsers and grazers) and fire in explaining tree cover and heterogeneity in uncertain ecosystems globally

Partial dependence of tree cover (A, C, and E) and its heterogeneity (B, D, and F) in global large strictly protected areas of uncertain ecosystems on biomass sum of large browsers ≥ 45 kg (A and B), biomass sum of large grazers ≥ 45 kg (C and D), and fire burned area (E and F). Partial dependence plots show the dependence of the response variable on a specific predictor after accounting for the average effects of all the other predictors. The y axes are centered on having zero mean, and the trends, rather than the actual values, describe the nature of the dependence of the response variable on the predictors. A smoothed version of the fitted function, shown in a dashed red line, is added for each variable to ease visual interpretation. The small bars on the x axis show the deciles of the data distributions of the predictors.

low-burned areas of both uncertain and deterministic ecosystems indicates that fire could be important in maintaining vegetation heterogeneity in certain areas. Moreover, the global patterns of the relative importance of climate, consumers (large herbivores vs. fire), and topo-edaphic conditions in explaining

tree cover and heterogeneity (Figure 3) also hold for the African continent (Figures S11 and S12). However, for the African continent, large herbivores are marginally less important than fire in explaining tree cover but slightly more important in explaining tree cover heterogeneity in uncertain ecosystems, suggesting

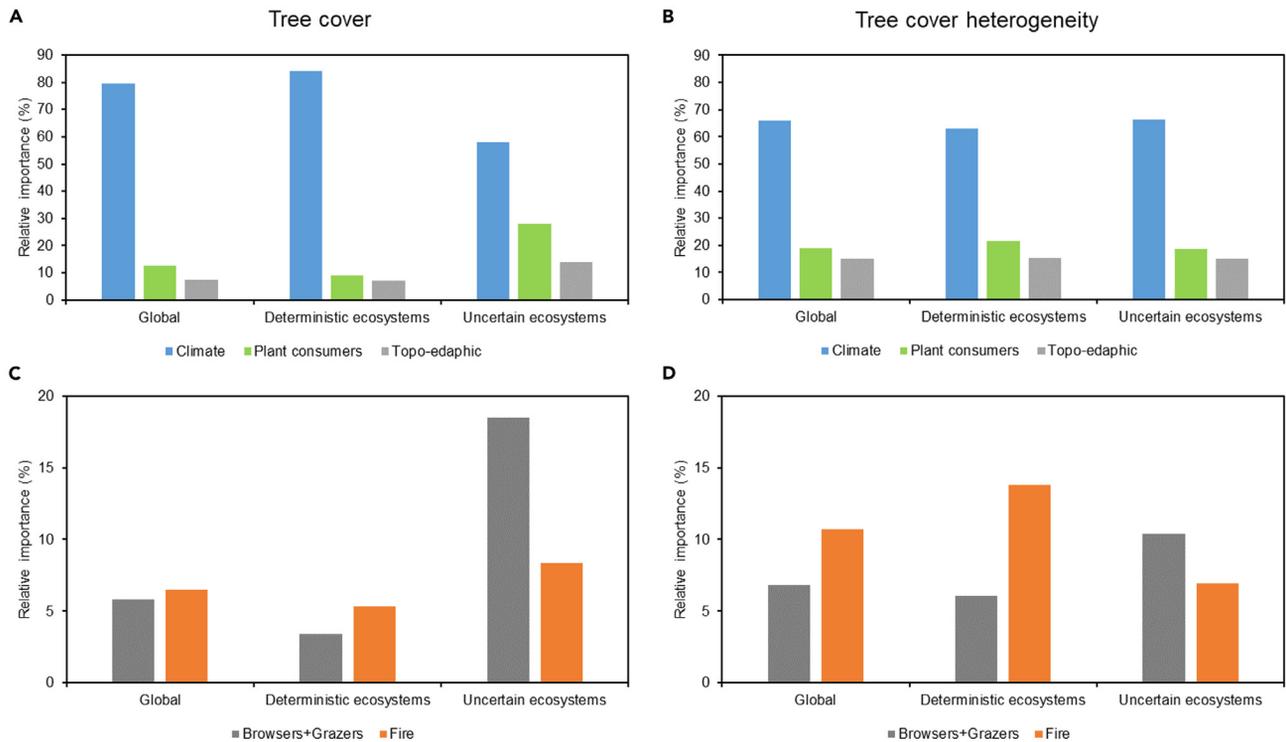


Figure 3. Relative importance of climate, consumers (large herbivores vs. fire), and topo-edaphic conditions in explaining global tree cover and heterogeneity

(A and B) The relative importance sum of climate, plant consumers, and topo-edaphic conditions in BRT models explaining tree cover (A) and heterogeneity (B) in large strictly protected areas globally and their subcategories of deterministic and uncertain ecosystems. Climate variables include mean annual temperature, mean annual precipitation, and precipitation seasonality. Plant consumers: large browsers, large grazers, fire, and human footprint. Topo-edaphic conditions: elevation and soil sand content.

(C and D) The relative importance of large herbivores (sum of browsers and grazers) and fire in BRT models explaining tree cover (C) and heterogeneity (D) in large strictly protected areas globally and their subcategories of deterministic and uncertain ecosystems.

a stronger and more comparable consumer competition of large herbivores and fire in continental Africa than globally (Figures 3 and S11).

DISCUSSION

Our global assessment shows that tree cover and heterogeneity are differentially linked to large herbivores and fire in large strictly PAs. Our result shows that tree cover tends to be lower when there is a high biomass of large herbivores. In contrast, tree cover heterogeneity, key to promoting species diversity,³ is positively linked to high biomass levels of large herbivores. Furthermore, these patterns are more evident in uncertain ecosystems, i.e., Whittaker's "ecosystems uncertain" climate envelope.⁴ In comparison, fire has a negative association with both tree cover and heterogeneity. These global results also hold for the African continent, where large herbivore assemblages are most intact.^{39,40} These relationships are thus general and strong enough to manifest at the landscape scale globally and are consistent with large herbivores (especially browsers) promoting or maintaining landscape-scale vegetation openness and heterogeneity,¹⁸ supporting the "ecosystems uncertain"⁴ hypothesis.

We also find that tree cover is more strongly related to plant consumers (the sum of large herbivores, fire, and human pres-

ures) in uncertain than in deterministic ecosystems compared to a more comparable contribution to tree cover heterogeneity in two climate zones. Although our findings confirm previous work⁴¹ that, on a global scale, climate plays a deterministic role in controlling tree cover, we show that plant consumers along with topo-edaphic conditions likely interact with climate in creating and/or maintaining vegetation openness in uncertain ecosystems. Specifically, our findings suggest that, globally, large herbivores may be more important than fire in explaining variation in tree cover and heterogeneity in uncertain ecosystems, compared to fire with a more important role in deterministic ecosystems.⁶ However, it is unknown to what extent these fires in deterministic ecosystems are natural, given that human fire management is practiced in many PAs worldwide.⁴² These findings strengthen the theoretical foundation for maintaining the landscape biodiversity capacity of global PAs and other natural areas^{43,44} through the sustainable management of extant or introduced large herbivores. Furthermore, they suggest that the structure and functioning of future terrestrial ecosystems will be shaped by the functional integrity of current large herbivore assemblages and their interactions with fires under a changing climate.^{15,18} By providing a called-for but rare external validation of consumer control of tree cover and heterogeneity at the relevant landscape scale in a global context,⁴⁵ our results have

important implications for the fundamental understanding of top-down trophic control and biodiversity effects on terrestrial ecosystems.^{46,47} Finally, our findings provide direct insights into the relevance and importance of large herbivores for the success of global conservation and restoration efforts.^{48,49}

Our result of consumer importance in explaining tree cover and heterogeneity in global strictly PAs is based on the assumption that these well-established natural ecosystems are likely under a long-term (quasi-)equilibrium state with climate and/or consumers and disturbances.⁵⁰ This assumption implies that long-term feedback between vegetation and consumers is also assumed to be at (quasi-)equilibrium,⁵ i.e., the impacts of large herbivores and fire on tree cover and heterogeneity equal their responses to vegetation structure. As this is a global-scale macroecological study that is essentially correlative, we cannot rule out the possibility that large herbivores select for open and heterogeneous habitats created by other disturbances such as fires¹⁵ at first or that browsers select for high tree cover and grazers for low tree cover. However, even if this is the case, large herbivores would still likely act as agents to maintain the openness and heterogeneity of their selected habitats, without which they would ultimately be replaced by closed forests,^{6,7} especially in uncertain ecosystems.^{51–53} The result of lower tree cover at high browser biomass fits only with top-down herbivore effects on vegetation, demonstrated by many local- to regional-scale studies.^{18,25} Complex interactions of selection and influence could create a feedback loop, making it difficult to determine clear cause-and-effect relationships between large herbivores and vegetation structures. Indeed, the feedback between habitat selection and impact probably always occurs simultaneously, which is more of a rule than an exception in ecology.⁵⁴ The worldwide syndrome of woody encroachment⁵⁵ driven by climatic^{56,57} and atmospheric (CO₂ concentrations)^{58,59} changes and human land-use changes (e.g., fire suppression⁶⁰ and land abandonment⁶¹) threatens biodiversity and ecosystem functioning of global open habitats.^{14,62} To what extent large herbivore assemblages limit woody encroachment remains to be empirically tested globally, although there is local to regional evidence that species such as elephants⁶³ and reindeer^{64,65} can limit woody cover increases. A more focused local-to-global evaluation of the temporal manifestation of collective effects of large herbivore assemblages on landscape-scale tree cover and heterogeneity will likely provide more applicable and context-dependent scientific guidance on ongoing or planned ecosystem conservation and restoration efforts, especially for trophic rewilding projects.^{48,49,66}

We found little influence of the human footprint in explaining global tree cover and heterogeneity, which supports the possibility of relatively high potential biomass of large herbivore assemblages and their ecological functioning in our strictly selected PAs (human footprints ≤ 4 ³²). Therefore, it strengthens the reliability of our main findings. Nevertheless, human-induced tree cover losses and increases in heterogeneity often reflect vegetation degradation⁶⁷ (but see Malhi et al.⁶⁸) and are more likely to be associated with adverse effects such as habitat fragmentation⁶⁹ and invasions of non-native species.⁷⁰ Furthermore, human pressures in PAs are likely to reduce the role of large herbivores in regulating tree cover through the depression of their diversity and abundance through hunting, habitat loss, or

a human-induced landscape of fear.^{71,72} Notably, large herbivore biomass in many PAs was estimated to be much lower than is natural due to past extinctions and ongoing human pressures, e.g., poaching.^{73,74} This might also challenge the actual global representativeness of our findings based on estimating collective effects of large herbivore assemblages on tree cover and heterogeneity with a modeled density-weighted total biomass of extant large herbivores⁷⁵ in strictly selected large PAs rather than all natural areas inhabited by large herbivores. Nevertheless, given that spatially explicit mammalian population density data are currently unavailable on a global scale,³⁸ our analysis here should still represent a reasonable global attempt. Finally, although complex in the real world, it is more likely that the long-term average biomass sum of large herbivore assemblages over a specific area, rather than the sum of certain species at a specific time, potentially shapes landscape-scale vegetation structures.

Given the overall importance of top-down control by large herbivores and fire on tree cover and its heterogeneity globally, including in Africa, our results contrast with recent findings by Higgins et al., who, based on environmental niche modeling, propose that climate alone is enough to predict vegetation states, including in “ecosystems uncertain” areas.⁷⁶ By not explicitly exploring the well-established roles of fire and herbivores, it is possible that they inflated the explanatory power of climate, as fire and herbivore densities and functional composition are also affected directly by climate (see also eLetters at <https://www.science.org/doi/10.1126/science.add5190>). This could have profound implications for macroscale ecosystem conservation and restoration, emphasizing the necessity of incorporating both climate factors and top-down controls into management strategies, especially under uncertain climate change scenarios.^{77,78} Furthermore, recognizing the differential responses between deterministic and uncertain ecosystems to various contributing factors like large herbivores and fire calls for more nuanced context-specific ecosystem management and restoration approaches compared to carbon-focused tree planting.⁶⁶ To foster resilient ecosystems and landscapes amid global change, a multiscale, multifactorial strategy, including the understanding and management of large herbivore assemblages and their collective effects on vegetation structure and biodiversity, is vital.^{79,80}

Our result of the global importance of the positive relationship between large herbivores and tree cover heterogeneity is based on satellite-derived tree cover estimates. Although this horizontal characterization of vegetation structure is well suited for widespread open ecosystems (including open woodlands, savannas, shrublands, and grasslands) inhabited by most extant large mammal species, it is less applicable to dense forests. In closed-canopy forests, tree height and spatial heterogeneity are related to landscape-scale biodiversity (especially for avian and arboreal species)^{81–83} and carbon sequestration capacity.⁴⁴ Therefore, a comprehensive investigation of the vertical dimension of global forests, based on recently available high-spatial-resolution vegetation height and canopy vertical structure data from GEDI,⁸⁴ will allow for a more complete understanding of the driving mechanisms of global vegetation structural heterogeneity and their biodiversity.

Considering the potentially different global influences of large herbivores and fire in driving tree cover and heterogeneity found

here, a more comprehensive mechanistic understanding of their separate and interactive roles in shaping global terrestrial biodiversity and ecosystem functioning under a changing climate is needed. This global understanding is crucial for more accurately predicting the Earth's carrying capacity of trees and their restoration potential for carbon sequestration and biodiversity maintenance,² especially in uncertain ecosystems supporting alternative biome states,^{4,6,7} which is vital for jointly solving the dual crises of climate change and biodiversity loss and balancing their potential trade-offs locally and globally in an era of global change.^{43,85} Thus, one of the urgent tasks for improving dynamic global vegetation models and Earth system models is a realistic representation of the spatiotemporal dynamics of large herbivore assemblages and their top-down controls on vegetation through, e.g., herbivory, physical disturbances, and nutrient redistribution.^{80,86,87} Compared to well-established global long-term satellite monitoring of vegetation dynamics, long-term observation of large herbivores on a global scale is challenging and has rarely been done.³⁸ However, technical advances in simultaneous high-spatial-resolution mapping of vegetation and herbivore distribution and densities from space-borne and drone-based sensors,⁸⁸ supported by deep learning algorithms and cloud computing platforms,⁸⁹ will likely provide new insights into how large herbivores' top-down control of global vegetation spatiotemporal dynamics may be realistically represented in the next-generation global ecosystem and Earth system models.

EXPERIMENTAL PROCEDURES

Resource availability

Lead contact

Further information and requests for resources should be directed to and will be fulfilled by the lead contact, Lanhui Wang (lwang@bio.au.dk).

Materials availability

This study did not generate new unique materials.

Data and code availability

The datasets used for this study can be accessed as described below:

The WDPA database is available from Protected Planet (<https://www.protectedplanet.net/en>).

The 2019 Moderate Resolution Imaging Spectroradiometer (MODIS) land cover map is available from <https://lpdaac.usgs.gov/data/>.

The Copernicus 100-m global land cover dataset for 2019 is available at <https://land.copernicus.eu/global/products/lc>.

WorldClim v.2 temperature and precipitation data are available at <https://www.worldclim.org/data/worldclim21.html>.

The global elevation map is available at <http://www.earthenv.org/topography>.

The regridded Harmonized World Soil Database (HWSD) v.1.2 is available at https://daac.ornl.gov/cgi-bin/dsvviewer.pl?ds_id=1247.

IUCN spatial data for terrestrial mammals are available from <https://www.iucnredlist.org/resources/spatial-data-download/>. The PHYLACINE v.1.2.1 database is available at <https://zenodo.org/record/3690867>. The HerbiTraits database is available from <https://doi.org/10.6084/m9.figshare.c.5001971>. Mammal population densities are available from <https://onlinelibrary.wiley.com/doi/full/10.1111/geb.13476>.

The Global Fire Atlas with Characteristics of Individual Fires (2003–2016) is available at https://daac.ornl.gov/cgi-bin/dsvviewer.pl?ds_id=1642.

The global human footprint map for 2009 is available at <https://sedac.ciesin.columbia.edu/data/set/wildareas-v3-2009-human-footprint>.

No custom codes were used. The codes used for BRT modeling are available from the “dismo” R package (<https://cran.r-project.org/web/packages/dismo/index.html>).

Overview

The global dependence (relative importance and potential driving mechanisms) of landscape-scale tree cover and heterogeneity (characterized by satellite-based tree cover estimates) on climate (mean annual temperature, mean annual precipitation, and precipitation seasonality), plant consumers (large herbivores, fire, and human footprint), and topo-edaphic properties (elevation and soil sand content) was determined for global strictly PAs inhabited by extant large herbivore species using a machine learning regression model—BRTs.⁹⁰

Large strictly PAs

Global terrestrial PAs were derived from the January 2022 version of the World Database on Protected Areas (WDPA), co-developed by IUCN and UNEP-WCMC.⁹¹ Since our analysis focuses on terrestrial ecosystems, only terrestrial PAs with polygons were included. Moreover, overlapped or connected PAs were merged into individual PAs. Since complete large herbivore assemblages and functioning are more likely to be preserved in large PAs, we only included all merged PAs with a minimum area of 100 km². This size also ensures enough available areas and representativeness for an unbiased global analysis. All merged PAs were converted to 500-m grid cells and aggregated to 5 km by the number of PA-covered grid cells. To reduce potential human influences, we only included all 5-km grid cells fully covered by PAs. Furthermore, we focus only on strictly protected PAs with human footprints ≤ 4 (less than 10% of the potential maximum value of 50⁹²), representing intact landscapes with little or very limited human pressures.^{32,33} To further minimize human footprint and water inundation effects on our analyses, areas dominated by croplands, cropland/natural vegetation mosaics, urban and built-up lands, permanent wetlands, permanent snow and ice, and water bodies were masked out by the 2019 MODIS land cover map (MCD12Q1 IGBP classification). As a result, 148,409 5-km grid cells of our mapped large strictly PAs globally are covered by valid satellite-based tree cover estimates and environmental and consumer predictors (see below), constituting areas of our global analysis (Figure S1).

To test the “ecosystems uncertain” hypothesis, these areas were further divided into hypothetically uncertain ecosystems (Whittaker’s “ecosystems uncertain” climate zone; $n = 45,607$) and deterministic ecosystems (Whittaker’s “ecosystems deterministic” climate zone; $n = 102,802$) based on an empirical relationship provided by Bond.⁴ The uncertain ecosystems are typically in global warm areas (mean annual temperature: 10°C–30°C of low to mid-latitudes) and are neither too humid nor too arid (mean annual precipitation around 500–1,600 mm). Whittaker’s climate envelope for uncertain ecosystems was the first attempt to identify where forests can co-occur with open grasslands, savannas, and shrublands as a mosaic in the same landscape. However, in addition to the simplifications necessary for binary classification, it should be noted that local climates in certain areas can be highly heterogeneous due to environmental heterogeneity in topography, altitude, proximity to water bodies, soil type, and vegetation cover.

Satellite-based global tree cover data

We used satellite (PROBA-V)-derived fractional tree cover data from the Copernicus Global Land Service 100-m-resolution global land cover dataset³⁶ in 2019 to represent global tree cover estimates. Grids of cropland, built-up, snow and ice, permanent water bodies, and ocean classes in the discrete land cover map were first masked out. The tree cover fraction layer was then used to calculate the average tree cover and spatial heterogeneity (standard deviation) at the landscape scale (region covered by a 5-km grid cell). Only 5-km grids covered by all unmasked 100-m tree cover pixels were kept for further analyses.

Data of environmental and consumer predictors

Climate

Three fundamental climate variables were selected as climatic drivers: mean annual temperature, annual precipitation, and precipitation seasonality. These global data for 1970–2000 at 2.5-min (about 5-km) spatial resolution were from the WorldClim v.2 dataset.

Large herbivores

Here, we define large mammal herbivores as all extant large-bodied wild terrestrial mammal herbivores (≥ 45 kg body mass), excluding critically

endangered (CR) species assessed by IUCN. The species presence ranges were derived from the IUCN Red List v.2021-3. Mammal biomass and diet traits were obtained from the PHYLACINE v.1.2.1 database.⁹³ Mammal population densities (median values) imputed from an additive mixed-effect model of density as a function of body mass, diet, locomotor habits, and environmental conditions with spatial and phylogenetic autocorrelation being accounted for were obtained from Santini et al.⁷⁵ The modeling was based on 5,412 empirical density estimates for 737 (14.5%) terrestrial mammal species from the most recent version of the TetraDENSITY database,⁹⁴ the most comprehensive and state-of-the-art collection of population density data in terrestrial vertebrates. Species with >50% plant diet were selected as herbivores, thus including several omnivorous species (e.g., bears). We used the newly published HerbiTraits database to divide herbivores into browsers (50%–100% browse and 0%–19% graminoid consumption) and grazers (50%–100% graminoid and 0%–19% browse consumption).⁹⁵ Mixed feeders (20%–50% browse and 20%–50% graminoid consumption) were included in browsers due to their potentially similar influences on woody vegetation. For 102 selected species (Table S1), we converted their range polygons into 5-km-spatial-resolution presence/absence grid cells. We then calculated the density-weighted biomass sum of all browsers and grazers for each grid cell (Figure S13).

We further validated the modeled density-weighted biomass sum of large herbivores for 58 (having empirical density estimates) out of 102 studied species with those from empirical density-based estimates (Figures S14 and S15). Since this validation included a majority (57%) of our studied species, the quite reasonable validation results (especially for large browsers: $R^2 = 0.84$; slope = 1.12) should increase the confidence in our analysis and, thereby, the scientific soundness of our main conclusion.

Burned area

The Global Fire Atlas with Characteristics of Individual Fires (2003–2016)⁹⁶ derived from the 500-m-resolution MODIS Collection 6 MCD64A1 burned-area product was used to calculate the mean annual cumulative burned area at 5-km spatial resolution.

Human footprint

The 2009 Human Footprint (2018 release) provides a global map of cumulative human pressures on the environment in 2009 at 1-km spatial resolution.⁹² The human footprint map was developed through cumulative pressure mapping by first standardizing each dataset of built environments, population density, electric infrastructure, croplands, pasturelands, roads, railways, and navigable waterways on a scale of 0 to 10 to obtain individual pressure scores for all datasets, which were then summarized into a single dataset of the human footprint index. Low scores (0–4; less than 10% of the possible maximum score) correspond to regions with little or no human pressure, while highly pressured areas (e.g., large cities) have higher scores with a maximum of 50. Finally, this dataset was aggregated to a 5-km spatial resolution with a majority algorithm.

Topo-edaphic properties

Elevation data were derived from a notably enhanced 250-m-resolution global digital elevation model (DEM) called the Global Multi-resolution Terrain Elevation Data (GMTED2010) due to its global coverage compared to the 90-m-resolution SRTM data. The soil sand fractions were extracted from the regridded HWSO (v.1.2) at 0.05° spatial resolution.

Modeling potential driving mechanisms of tree cover and heterogeneity with BRTs

A machine learning approach of BRTs implemented in the “dismo” package in R (based on the “gbm” package) was applied to model the potential mechanistic relationships of major environmental and plant consumer factors in explaining tree cover and heterogeneity in large strictly PAs globally. We chose BRT because of its advantages of accommodating missing data, being free from prior data transformation or elimination of outliers, fitting complex nonlinear relationships, and automatically handling interaction effects between predictors.

Tree cover and heterogeneity were used as response variables for a global model of all studied PAs and two separate models of PAs categorized into deterministic ecosystems and uncertain ecosystems. The explanatory variables included (1) mean annual temperature; (2) mean annual precipitation; (3) precipitation seasonality; (4) elevation; (5) soil sand content; (6) biomass

sum of large browsers; (7) biomass sum of large grazers; (8) fire burned area; and (9) human footprint.

Collinearity between the predictors will not affect the explanatory power of constructed models because of the decision tree structure of BRT modeling. However, no strong correlation between all predictors is preferred for an unbiased interpretation of the constructed BRT models via the relative importance measure and the partial dependence function described below. Therefore, we calculated the collinearity among the nine predictors globally and for two climatic zones (Tables S2–S4). No strong correlation was detected based on the recommended Pearson correlation coefficients of $|r| > 0.7$, ensuring the robustness of our modeling and the interpretation of the results.

Following Elith et al.,⁹⁰ we used the cross-validation function in the “dismo” package to identify the optimal tree complexity and the number of trees for each model and guard against overfitting.⁹⁷ Based on the number of observations and the modeling performance of our dataset, the bag fraction, learning rate (shrinkage parameter), and tree complexity (number of nodes in a tree) were optimized to be 0.5 and 0.25 for global models (0.15 and 0.2 for uncertain/deterministic ecosystems) and 6, respectively, while the number of trees for each model was then automatically determined by the 10-fold cross-validation procedure by randomly dividing the data into ten subsets and training on each set in turn. The explanatory power (R^2) of each model was calculated as the explained percentage of the mean total deviation in the 10-fold cross-validation, which is more robust by explicitly accounting for the potential sampling variability through the repeated cross-validation procedure.⁹⁸

Estimating the relative importance of all predictors

The relative importance measures of predictor variables were estimated using the Friedman method⁹⁹ implemented in the “gbm” R library. The relative importance of each predictor is scaled as a share of 100%, with higher numbers indicating a greater contribution to the response.

Uncovering potential mechanistic relationships

Partial dependence functions provide graphical representations of the fitted relationships between the response variables and any given predictor, showing the dependence of the response variable on a given predictor after accounting for the average effects of all other predictors in the model.⁹⁷ Although they may not provide a comprehensive description of the potential interactions between predictors, they are valuable in identifying general trends. Therefore, it is important to recognize that the trends, rather than the actual values, describe the nature of the dependence of the response on the predictor variables.

SUPPLEMENTAL INFORMATION

Supplemental information can be found online at <https://doi.org/10.1016/j.oneear.2023.10.007>.

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AUTHOR CONTRIBUTIONS

L.W. and J.-C.S. designed the study. L.W. gathered data and conducted the analyses. The paper was drafted by L.W. with contributions from all authors.

DECLARATION OF INTERESTS

J.-C.S. is an advisory board member of *One Earth*.

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