LETTER

How many elephants can you fit into a conservation area

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Abstract

The African elephant is the largest extant terrestrial mammal and a reminder of the Pleistocene megafauna. Their survival is, however, dependent on conservation areas. In some conservation areas, rapidly growing elephant populations have led conservation biologists to ask, how many elephants can these areas support? The debate is polarized by arguments for large populations for economic, social, or ethical reasons and arguments for smaller populations that avoid biodiversity loss. We use a novel dynamic modeling approach to assess how climate change-induced vegetation change may influence the capacity of a conservation area to support large herbivores. The model projects that elephant densities and fire have substantial impacts on vegetation under current climatic conditions. Under future conditions, the capacity to support elephants increases due to CO_2-induced increases in woody plant productivity. We conclude that sustainable management in conservation areas needs to be conditioned on the effects of climate change on vegetation.

Introduction

How many individuals a finite resource or area can support is a fundamental question in ecology (Murdoch 1994). In theory, this question is easy to answer (Malthus 1798; Verhulst 1838) and every introductory ecology textbook explains this theory. In practice, the question is difficult to answer (Andrewartha & Birch 1954) because the abiotic and biotic factors that determine population dynamics are not constant in space and time. Additionally, these factors are expected to vary systematically with anticipated climatic and atmospheric changes (IPCC 2007). In this study, we examine the question, how many elephants can a finite conservation area support under current and future climate conditions?

The African elephant (*Loxodonta africana*) is the largest of the extant megaherbivores and Africa is home to an estimated 400,000 individuals (Blanc *et al.* 2007), both inside and outside of formal conservation areas (Blanc *et al.* 2007). The IUCN Red Lists published between 1979 and 2007 categorized elephants as "vulnerable" but successful conservation has improved their status to "near threatened" (Blanc 2008). Conservation areas have played a central role in this improvement and will remain essential for the long-term survival of elephants (Blanc *et al.* 2007). Elephants, however, have the potential to engineer vegetation (Laws 1970; Jones *et al.* 1994; Shannon *et al.* 2008) which can have negative consequences for various plant and animal species (Cumming *et al.* 1997; Goheen *et al.* 2004; Ogada *et al.* 2008; Pringle 2008). Hence, conservation managers are forced to find a balance between managing for flagship species and for biodiversity.

An illustrative example of the problem is the Kruger National Park (KNP), a 19,633-km^2 fenced conservation area in South Africa. Elephant numbers increased from a handful of animals in the early 1900s to 6,500 animals in 1967 (du Toit *et al.* 2003). These dramatic increases led to a management decision that elephant numbers should be held between 7,000 and 8,500 individuals to avoid undesirable impacts on vegetation (Whyte *et al.* 1999). Between 1967 and 1999, the culling of 14,629 elephants kept the elephant population close to this target number (Freeman *et al.* 2009). A policy review in 1995 concluded that this target elephant number was not adequately supported by scientific evidence and imposed a moratorium on culling, which allowed elephant numbers to increase to 12,400 animals in 2006 (Shannon *et al.* 2008). The limited capacity of the KNP and adjacent conservation areas to accommodate elephants means that such rates of increase are not sustainable. Surprisingly, it remains unclear what elephant densities the KNP can sustain without inducing undesirable changes in biodiversity or a catastrophic collapse in the elephant population (Scholes & Mennell 2008).

The assessment of how many elephants a conservation area can support requires the ability to forecast the response of vegetation to elephant herbivory against the backdrop of the physiological and demographic processes that drive vegetation dynamics. We coupled the adaptive Dynamic Global Vegetation Model (aDGVM, Scheiter & Higgins 2009), a state-of-the-art model of savanna vegetation dynamics, with a new model that describes elephant impacts on vegetation. The elephant impact model calculates the amount of grass and tree biomass an elephant population removes from a stand of savanna vegetation, given the number and the spatial distribution of elephants in the conservation area. The aDGVM uses an individual-based structure, allowing the model to condition elephant damage on individual plants. This approach allows us for the first time to explore how megaherbivores, fire, and climate change interact to influence vegetation.

The aims of this study are (1) to explore the sensitivity of vegetation to parameters describing the elephant population and how elephants damage vegetation, (2) to compare the effects of elephants, fire and climate change on vegetation, and (3) to explore how elephant numbers and the spatial distribution of elephants influence vegetation structure under current and future climate conditions. We further discuss the implications for elephant management in conservation areas.

Methods

Model description

We coupled the aDGVM (Scheiter & Higgins 2009), a state-of-the-art savanna vegetation model, with a novel model that simulates elephant impacts on vegetation. The aDGVM integrates routines commonly used in dynamic global vegetation models (DGVMs, Prentice *et al.* 2007) to simulate leaf-level physiology, canopy scaling and plant competition and integrates them with novel submodels that allow plants to dynamically adjust carbon allocation and leaf phenology to environmental conditions. The aDGVM is individual-based which means that it simulates growth, reproduction, and mortality of single trees. This is a prerequisite to adequately describe fire and herbivore impacts on the tree population structure (Higgins *et al.* 2000). The aDGVM estimates fire intensity as a function of fuel loads, fuel moisture, and wind speed (Higgins *et al.* 2008). Hence, fire regimes are driven by vegetation and environmental conditions rather than being an external forcing parameter and respond to climate change. Fire removes aboveground grass biomass and, depending on the fire intensity, fractions of aboveground tree biomass. After fire, vegetation can regrow from root reserves (Bond & Midgley 2001). Running the aDGVM for a site requires only climate and soil data.

The aDGVM was evaluated in Scheiter & Higgins (2009) where we showed that the aDGVM can simulate the distribution of African savannas better than alternative vegetation models and that the aDGVM can simulate biomass observed in a long-term fire manipulation experiment in the KNP (Experimental Burn Plots, Higgins *et al.* 2007).

The elephant impact model (see Table 1 and Supporting Information) is designed to calculate the amount of grass and tree biomass an elephant population removes from a stand (typically one hectare) of savanna vegetation. The amount of biomass removed by elephants is influenced by the elephant density and by the elephant visit frequency at the stand. Grass consumption by elephants is simulated by removing the required amount of aboveground grass biomass. The utilization of trees by elephants is simulated as a function of tree height. The model assumes that elephants prefer trees smaller than 3 m for browsing (Shannon *et al.* 2008) and simulates that bulls uproot larger (5–12.5 m large) trees to make forage available, or for social reasons (Shannon *et al.* 2008). Elephants can strip the bark of trees or uproot trees.

Indices of ecosystem state

To analyze elephant impacts on vegetation, we use four state variables of the model, large (>5 m height) and small (<1 m height) tree density, tree biomass, and visibility. We consider large and small tree densities because they are often monitored as indicators of vegetation heterogeneity (Whyte *et al.* 1999) and of vegetation damage by elephants (Shannon *et al.* 2008). Visibility has a fundamental impact on both trophic interactions and on management decisions, since it defines how likely it is that prey species can detect predators (Riginos & Grace

Table 1 Parameters describing elephant impacts on vegetation; the column "Def" gives default parameter values (used for Figures 1b and 2), the columns "Low" and "High" give the parameter values for low and high elephant impacts used in the factorial design (Figure 1a); low and high parameter values were selected so that plausible ranges of elephant impacts are covered; all details of the elephant model are provided in the Supporting Information

Description	Parameter value			Units
	Def	Low	High	
Elephant visitation frequency at site	6	1	12	$year^{-1}$
Habitat selectivity factor[a]	2	1	10	unitless
Diet mixture parameter	0.5	0.1	0.9	unitless
Wastage of tree biomass	0.1	0.1	1	proportion
Probability for tree uprooting[b]	40	10	90	%
Probability for bark stripping[c]	15	10	50	%
Maximum leaf removal per tree (relative)	0.15	0.05	0.75	proportion
Maximum leaf removal per tree (absolute)[d]	4.3			kg
Grazing by other herbivores	1			kg day^{-1} ha^{-1}
Elephant number in the KNP in 2009[e]	14,350			animals
Biomass consumption per elephant[f]	150			kg day^{-1}
Area of the KNP	19,633			km^2

[a]Habitat selectivity factor 2 corresponds to a density of 1.2 animals/ha, we use this value as a density of 1.13 animals/ha has been reported in a vegetation damage study in the KNP (Shannon *et al.* 2008);
[b]Shannon *et al.* (2008) reports uprooting probabilities of up to 24% of the utilized trees; [c]Shannon *et al.* (2008) reports bark stripping probabilities of up to 21% of the utilized trees; [d]Assumes a mean biomass consumption of 150 kg per elephant per day and a mean tree utilization of 35 trees per elephant per day (Shannon *et al.* 2008); [e]Assumes 12,400 animals in 2006 and 5% growth per year (Shannon *et al.* 2008); [f]Assumes mean elephant weight of 3,000 kg and a biomass requirement of 5% of the body weight per day.

2008; Valeix *et al.* 2009) and it also defines the ease with which tourists can spot game. To calculate visibility, we projected the canopy areas of subsets of the simulated vegetation stand on an edge of the simulated stand. Only trees <2 m were considered. The relation between the subset size and projected canopy area is used as a measure of visibility.

Although these state variables are related to tree density and do not cover all aspects of ecosystem performance, we denote these variables as "ecosystem indicators" in the following.

Defining absolute thresholds for critical changes in the ecosystem indicators is, given the complexity of natural ecosystems, impossible. Within the paradigm of adaptive management (du Toit *et al.* 2003; van Wilgen & Biggs 2011), park managers have sidestepped this problem by defining desirable ecosystem states and critical deviations as warranting management intervention (e.g., Thresholds of Potential Concern in the KNP; du Toit *et al.* 2003; Scholes & Mennell 2008). We therefore explore relative changes of the ecosystem indicators.

Study site and climate conditions

Our modeling approach is general, that is, it only requires site-specific climate and soil conditions to simulate vegetation dynamics. It can thus be applied to any conservation area in Africa. For the purposes of this analysis, we consider a hypothetical park, with conditions similar to those found near Skukuza in the KNP, South Africa (25°1.2′S and 31°28.8′W). We used a site-specific reference climatology for the period between 1961 and 1990 (New *et al.* 2002) and site-specific anomalies in atmospheric CO_2 concentrations, precipitation, and temperature as provided by the Max Planck Institute for Meteorology's (Hamburg) ECHAM5 IPCC projections (Roeckner 2005; IPCC 2007). Climate change projections vary across savanna regions and the scenario for Skukuza is not necessarily representative for African savannas. In general, projections of future climates are uncertain, we therefore use three IPCC scenarios (Special Report on Emissions Scenarios (SRES) B2, A1B, and A2).

We used a CO_2 concentration of 387 ppm, a mean annual temperature of 25.3°C, and mean annual precipitation of 607 mm to represent ambient conditions. The IPCC scenarios B1, A1B, and A2 project CO_2 concentrations of 540, 700, and 830 ppm, mean annual temperatures of 29.1, 29.5, and 30.1°C, and mean annual precipitation of 498, 518, and 534 mm for 2100.

Simulation studies

Data for estimating all parameters of the elephant impact model were not available. For several parameters, data were inadequate or nonexistent. We therefore used a 2^7 full factorial design to test the sensitivity of the four ecosystem indicators to seven parameters of the elephant impact model. The parameters were set to low or high values and vegetation was simulated for all 2^7 possible parameter combinations. Low and high parameter values cover plausible parameter values (Table 1). The results were analyzed by using an analysis of variance (ANOVA).

In a second analysis, we used a 2^3 full factorial design to explore how climate change (ambient or 2100 conditions), fire (suppressed or not suppressed), and elephants (absent or present) influence ecosystem indicators. Vegetation was simulated for all 2^3 possible factor combinations and the results were analyzed by using ANOVA. Simulations were conducted for the IPCC scenarios SRES B1, A1B, and A2 with an elephant density of

0.76 animals km^{-2}. For the scenario A1B, we conducted additional simulations with 0.43 and 1.52 elephants km^{-2}.

To address the question of how many elephants the park can support, one needs to take cognizance of the fact that elephant densities are not homogeneous in space or time (Scholes & Mennell 2008). That is, the often devastating local impacts need to be placed in a landscape context. We assumed that the park consists of different habitat types (for this analysis, four habitat types), where each habitat is characterized by a specific local elephant density. This allows us to simulate heterogeneous elephant densities without explicitly simulating movements of elephant populations. We explored how the ecosystem indicators respond to changes in elephant numbers and to different distributions of elephants across the four habitat types under current and future climate conditions (SRES B1, A1B, and A2).

We use a two-phase model spin-up process. In the first spin-up phase (simulation years 1–150), vegetation was simulated without elephants and fire. This first spin-up phase ensures that the modeled vegetation is in equilibrium with climate and that initial conditions are similar in all simulation runs. In the second spin-up phase (years 151–350), elephants and fire were introduced. The simulated vegetation dynamics are transient, that is, vegetation changes in response to fire and elephants. For the analyses, we averaged simulation results of years 351–500. The model is again in equilibrium and we obtain reliable estimates of the ecosystem indicators.

Results

The sensitivity analysis of the elephant impact model (Figure 1a) revealed that factors that influence the amount of biomass removed from a site (habitat selectivity and wastage), the frequency (visitation frequency), and nature of herbivore damage (bark stripping) decreased the ecosystem indicators. Factors that shifted the biomass removal to a few individuals, rather than spreading it among the population (amount of biomass removed from a tree and probability of uprooting), increased the ecosystem indicators. Elephant's preference for grass had a minor effect on the tree population structure.

The model projects that elephants have generally weaker effects on the ecosystem indicators than climate change and fire, even in simulations with 30,000 elephants in the KNP (Figures 1b and S3). Elephants decrease the tree numbers and the total tree biomass. Fire acts differentially on large and small trees and creates a demographic bottleneck that prevents small trees from making the transition to large trees (Higgins *et al.* 2000). Climate change induces increases in the tree numbers and the total tree biomass. The relative impact of climate change on the ecosystem indicators increases with the CO_2 concentration of the climate scenarios (B1, A1B, and A2).

The biomass simulated under ambient conditions lies in the range of empirically observed biomass. Simulated biomass in presence and absence of fire and elephants is between 3 and 11.3 t/ha, the 10 and 90% quantiles of biomass observed in a fire manipulation experiment at Skukuza are 3.3 and 11.5 t/ha (Higgins *et al.* 2007).

We now turn to the question of how many elephants can be supported by the park without inducing undesired changes in ecosystem indicators. The simulation results indicate that under current climatic conditions and current elephant densities, 50% of the park is weakly and 10% heavily impacted by elephants (Figure 2a), assuming that elephant densities are normally distributed across the four habitats. At higher elephant densities, there is a steady decrease in tree biomass and an increase in visibility. Shifting elephant densities from 0 to 3 elephants km^{-2} reduces tree densities by more than 70% in 90% of the park (Figure 2a). When elephant densities are exponentially distributed across the four habitats, the impacts are restricted to the high elephant density areas, leaving larger proportions of the park uninfluenced by elephants (Figure 2c).

The capacity of the vegetation to tolerate elephants increases dramatically under future climate conditions (Figures 2b and d). For instance, under the scenario A1B, the impact of 4 elephants km^{-2} is comparable to the impact of 0.3 elephants km^{-2} under current climate conditions. The exact capacity to support elephants strongly depends on the climate change scenario and increases with atmospheric CO_2 (Figure S4).

Discussion

The simulation results suggest that the current elephant density of 0.76 animals km^{-2} is, at the park level, well supported by vegetation. Nonetheless, elephant impacts can be severe at the local scale. The model projects that the KNP could currently support elephant densities of 1.5 animals km^{-2}. This is 3.5-fold the elephant density maintained in the KNP during the culling era (0.43 elephants km^{-2}) and twofold the current elephant density (0.76 elephants km^{-2}). This finding agrees with calculations suggesting that the KNP can at least support 20,000 elephants (Pienaar *et al.* 1966) and with the "Elephant Science Roundtable" conclusion (2006) that there is currently "no compelling evidence for the need for immediate, large-scale reduction of elephant numbers in the

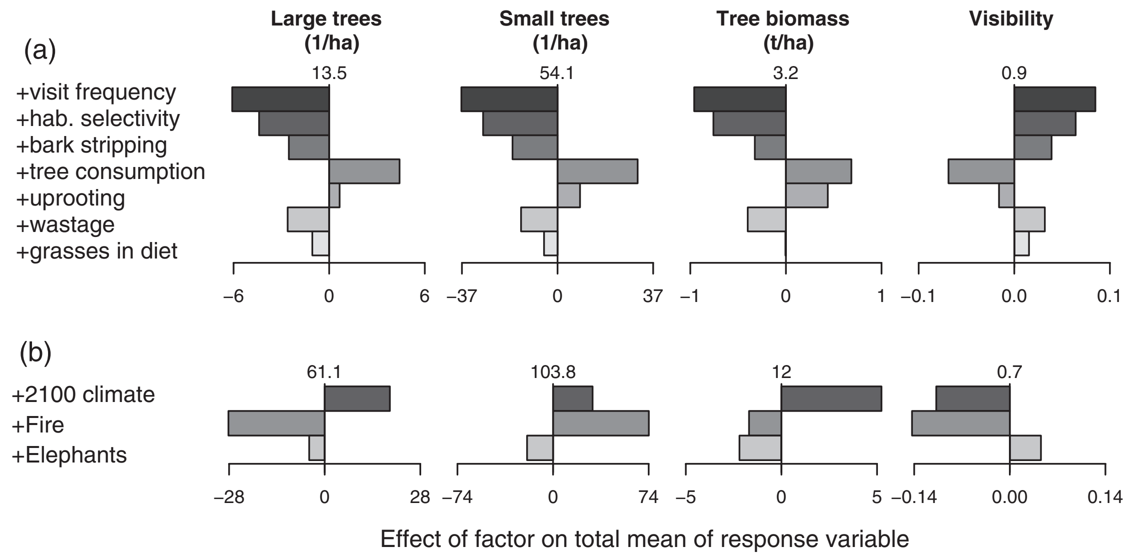

Figure 1 Elephant, fire, and climate change impacts on the tree population. (a) Sensitivity of ecosystem indicators to the elephant model parameters. The bars show how a change from low impact to high impact of different elephant model parameters influences the ecosystem indicators, relative to the mean over all factor combinations (given by the number above the bars for each ecosystem indicator). Parameter values used for the factorial design are given in Table 1. (b) Comparison of elephants, fire suppression, and climate change on the ecosystem indicators. Here, default levels of elephant impact were used (Table 1). Note the different scaling of the axes in panels (a) and (b). Analogous figures for alternative climate scenarios are in the Supporting Information.

KNP" (Owen-Smith *et al.* 2006). Conservation areas other than the KNP (Tsavo East National Park in Kenya, Chobe National Park in Botswana, and Hwange National Park in Zimbabwe) support elephant densities of 1–2 elephants km^{-2}, despite locally severe elephant impacts (Owen-Smith *et al.* 2006).

Our findings have direct implications for park managers, as they suggest that management actions such as water provisioning, fencing, hunting, and human settlements that encourage elephants to visit some sites more regularly and to avoid other sites could significantly impact on ecosystem indicators. This result is consistent with previous studies that showed that water holes and fencing can be used to manipulate local elephant densities (Loarie *et al.* 2009). The elephant management problem appears, at least in theory, to be resolvable: define your preferences for the spatial distribution of different structural vegetation states and then use your management tools to manipulate the spatial distribution of elephants.

The elephant management problem is, however, complicated by climate change. Our simulation results suggest that the capacity of the vegetation to tolerate elephants is set to increase dramatically, irrespective of the IPCC climate change projection. The increased resilience of vegetation to elephant damage is primarily due to CO_2 fertilization which, in the aDGVM, shifts vegetation toward more tree-dominated biomes (Scheiter & Higgins 2009). Although projections of future savanna vegetation dynamics are still uncertain (IPCC 2007; Scheiter & Higgins 2009), several lines of evidence support a strong CO_2-fertilization effect in savannas. Remote sensing studies illustrate that tree cover has increased dramatically between 1937 and 2004 in southern African savannas irrespective of land use, local soil, rainfall regimes, and land tenure (Wigley *et al.* 2010). Bowman *et al.* (2010) also attribute increases in tree cover in Australian savannas to CO_2 fertilization. Open top chamber experiments have shown that trees increase their growth rates and their capacity to resprout after disturbances under elevated CO_2 conditions (Hoffmann *et al.* 2000; Polley *et al.* 2002; Kgope *et al.* 2010). Taken together, these results suggest that vegetation–herbivore interactions in savannas will fundamentally change as climate changes.

We are, however, cautious to suggest that the higher elephant densities suggested by our simulations are tolerable because other co-limiting factors, not included in our analysis may come into play. For instance, at high elephant densities behavioral and demographic factors may limit elephant population size (Chamaillé-Jammes *et al.* 2008) and cause cyclic dynamics of the elephant and vegetation abundance (Caughley 1976). Further, high tree densities induced by CO_2-fertilization may reduce the size

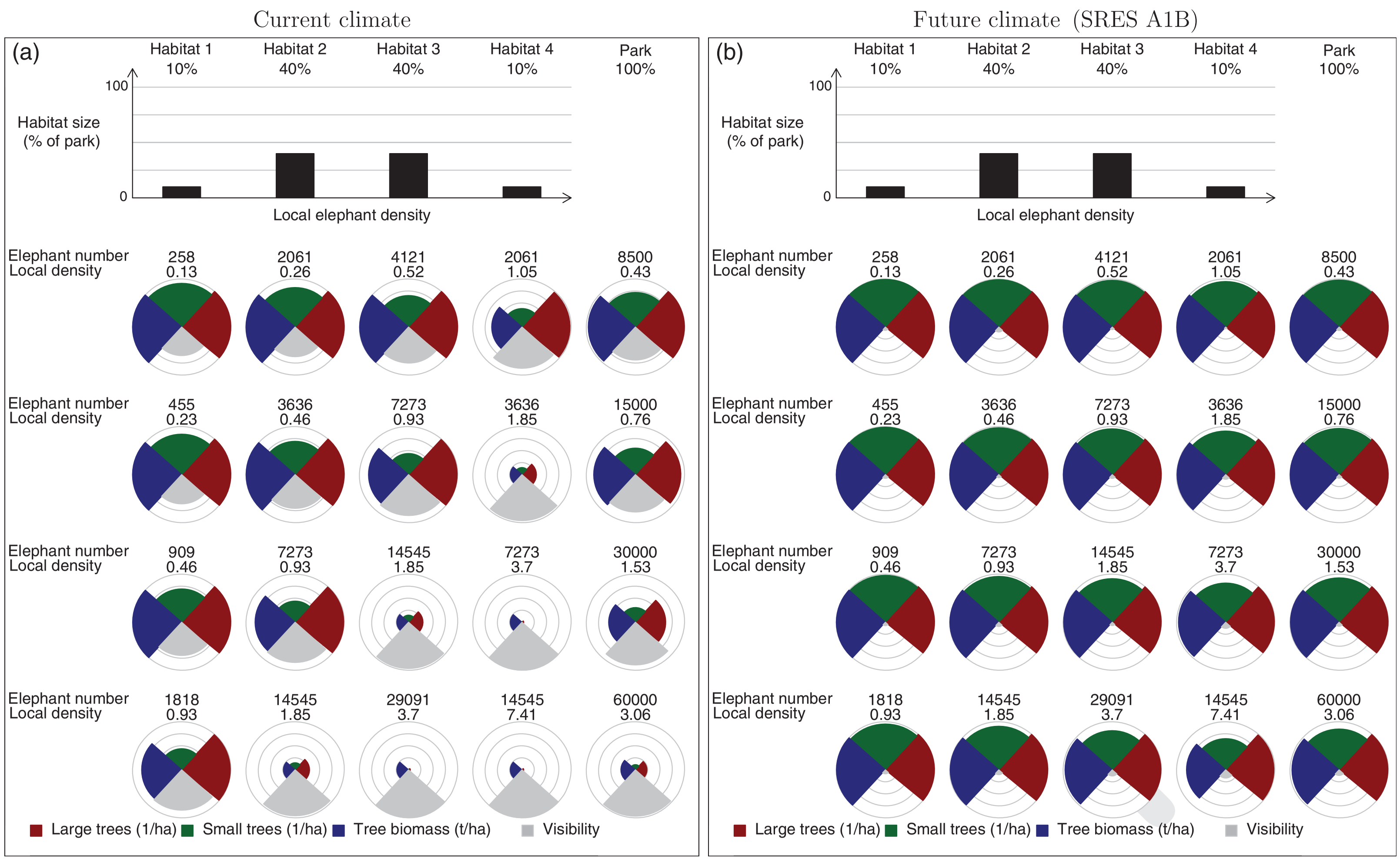

Figure 2 Elephant impacts at the habitat level and the park level (conservation area). The panels show how the spatial elephant distribution in the park and associated local elephant densities in four different habitats influence four ecosystem indicators, relative to the situation without elephants. The gray circles indicate, outward from the center, 25, 50, 75, and 100% levels of the ecosystem indicators relative to the situation without elephants. The bar plot shows the size of different habitat types. The local elephant densities (elephant numbers) of each habitat are provided in the rows "Local density" ("Elephant number") for four park level elephant numbers (8,500, 15,000, 30,000, and 60,000 animals). Analyses were conducted for current (a, c) and 2100 climate conditions (b, d). The elephant distribution across the four habitats in the park is assumed to be normal (a, b) or exponential (c, d). Analogous figures for alternative climate scenarios are in the Supporting Information.

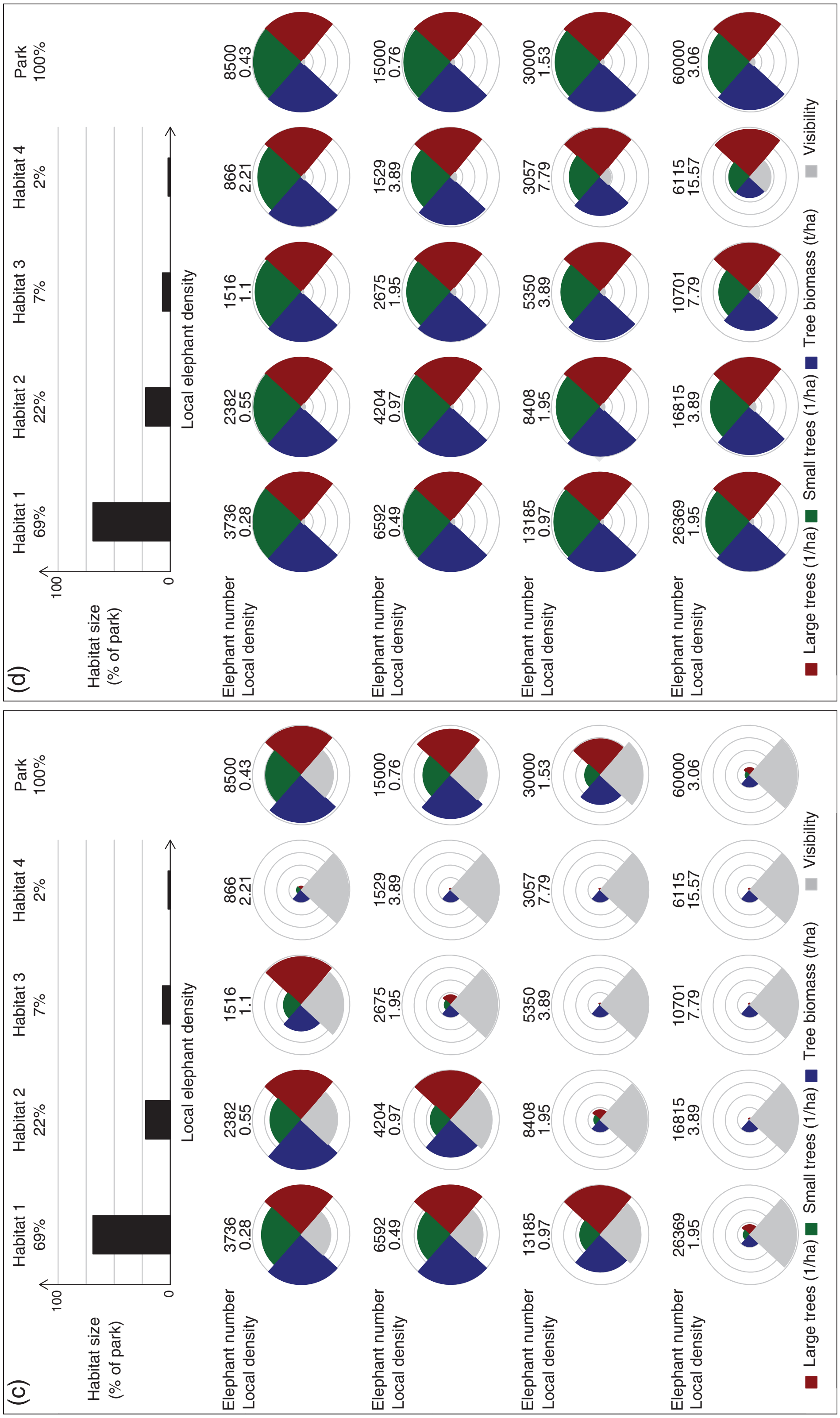

Figure 2 Continued

of elephant habitats and water accessibility. Finally, elevated CO_2 may lead to increases in the C:N ratio of vegetation which may reduce the palatability of vegetation (Stiling & Cornelissen 2007).

A further source of uncertainty is the representation of elephant impacts on vegetation in the model. As some parameters of the elephant impact model are poorly supported by data, we conducted a sensitivity analysis to explore the impact of these parameters on the simulation results. Our findings provide clear guidelines for future empirical work. Specifically, detailed knowledge of how many times elephants visit a site, how long elephants stay at a site, and how much biomass elephants consume per visit and per plant would improve the robustness of our model's projections. This agrees with van Wilgen & Biggs (2011) who argue that elephant impacts rather than elephant numbers should be a priority for empirical work.

Elephants have strong impacts on biodiversity and they can both create and destroy habitats for various plant and animal species. For instance, Pringle (2008) showed that elephants create complex habitats required by lizards. In contrast Ogada *et al.* (2008) observed reduced bird diversity in presence of megaherbivores and Cumming *et al.* (1997) report reduced species richness of birds and ants in Miombo woodlands impacted by elephants. The aDGVM simulates characteristics of habitat structure such as the tree size distribution and a next step would be to link these characteristics with the occurrence of animal species. Such a linkage would allow us to explore how elephant, fire, and climate change impacts on vegetation influence biodiversity surrogates.

In conclusion, this study shows the extent to which the impacts of elephants on vegetation are tolerable and illustrates that management actions that manipulate local elephant densities can be used to shift the ecosystem into desired (low tree cover) states. This first insight is, however, mitigated by the finding that the aDGVM forecasts that elephants will, under future climates, have a limited potential to influence savanna structure. Hence, while elephant impacts might be intense under current climate conditions, under future climates savanna conservation areas could support substantially more elephants, irrespective of how they were distributed within the conservation area. A general implication of our results is that any statement on desired or sustainable densities of herbivores needs to be conditioned on the possible effects of climate and atmospheric change on vegetation.

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Supporting Information

Additional Supporting Information may be found in the online version of this article including Supplementary Methods and References:

Table S1: The table summarises all parameters and variables used in the elephant impact model described in the Methods section. In column "Type", "par" indicates a model parameter which is modified in different simulation runs, "con" indicates a constant that is not changed in simulations and "var" indicates a variable calculated in the simulation runs. For parameters, the default values (column "Value") are given. References for the default values are provided in the text.

Figure S1: Proportion of grass (p_g) and tree (p_t) biomass in the diet of elephants as a function of soil moisture θ (Eqn. 2 and 3). Here, $\alpha = 0.5$ and $\beta = 0.1$.

Figure S2: Utilisation probability of trees ($P_u(H)$) as a function of tree height H for two different uprooting probabilities. These uprooting probabilities represent cows and breeding herds (upper panel, $f = 10\%$) and bulls (lower panel, $f = 90\%$)

Figure S3: Comparison of elephant, fire and climate change impacts on the ecosystem indicators. Here, three different IPCC projections (SRES A1B, A2 and B1) and, for SRES A1B, three different elephant numbers (8500, 14350 and 30000 animals) were used. Note the different scaling of the axes in different panels. The panel with SRES A1B and 14350 elephants is similar to Fig 1b in the main text.

Figure S4: Elephant impacts at the habitat level and the park level for climate projections A2 and B1. See Fig. 2 in the main text for details.

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