

# The impact of the megafauna extinctions on savanna woody cover in South America

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Has land surface cover in South America been impacted by the loss of most large herbivores following the severe Pleistocene and Early Holocene megafauna extinctions on this continent? Here, we estimate how mean savanna woody biomass may have changed in the Americas following these extinctions by creating an empirical model to understand how large herbivores impact savanna woody biomass. To create this empirical model, we combine a large recently published dataset of savanna woody cover from Lehmann et al. (2014) ( $n = 2154$  plots) with estimates of mammals ranges and weights from the IUCN database. We evaluate how variables such as number of megaherbivores (mammal species  $\geq 1000$  kg),  $\log_{10}$  sum species weights, and total number of mammal species predict changes to woody cover by using both ordinary least squares regression analysis (OLS) and simultaneous auto-regressive (SAR) analysis to control for spatial autocorrelation. Both number of megaherbivores and  $\log_{10}$  sum species weights, which both disproportionately weight for megaherbivores, significantly explained much ( $\sim 5\text{--}13\%$ ) variance in woody cover, but the third variable weighting all animals equally, did not. We then combined these biotic variables with abiotic variables such as temperature, precipitation, and fire frequency to create a model predicting 36% of the variance of savanna woody cover. We used this model combined with estimated range maps of extinct South American megafauna to estimate that had those South American megafauna not gone extinct, total savanna woody cover in South America could possibly have decreased by  $\sim 29\%$  and that savannas would likely have been more open like current African savannas.

To what extent do large animals shape their environments and how does this compare to other abiotic inputs such as temperature, rainfall or fire? Trees clearly dominate in very wet ecosystems and grasses dominate in drier ecosystems, but in intermediate ecosystems large animals may play an important role in determining the ratios of grasses versus trees (Bond 2005, Sandom et al. 2014a). Bond (2005) defined such areas as ‘ecosystems uncertain’ on in his ‘brown’ world model, where he hypothesized that such regions may be consumer controlled, with consumers being fire, animals, or both. It is important to understand the drivers of these ecosystems because savannas cover 20% of the global land surface and account for 30% of terrestrial net primary production (NPP) (Field et al. 1998).

Tropical savanna vegetation is dominated by a combination of C4 grasses and disturbance-tolerant woody species (Ratnam et al. 2011), whose distributions can vary over time and space (Sankaran et al. 2005, Murphy et al. 2014). It has been speculated that the processes controlling the presence of these trees are similar throughout the major savanna regions of the world in Africa, Australia, and South America (Knapp et al. 2004, Bond 2008). However, other studies have shown large differences between savannas across continents (Lehmann et al. 2011, Staver et al. 2011). Understanding

the abiotic drivers of savanna woody tree cover was the subject of a recent study where data from 2154 sites in South America, Africa and Australia were aggregated (Lehmann et al. 2014). This study found that increasing moisture availability drives increases in tree basal area, whereas fire reduces tree basal area. However, among continents, the magnitude of these effects varied substantially, so that no single model adequately represented savanna woody biomass across these regions, and South America did not fit well within the model framework.

Why might South America be functionally different than the other regions? South America had a drastic loss of large animals with 59 species of South American megafauna going extinct during the Late Pleistocene and Early Holocene (Sandom et al. 2014b), which was a part of a global loss of large animals between  $\sim 50$  to  $\sim 7$  kybp, with 97 genera of large animals going extinct (Barnosky et al. 2004). Importantly, all South American megaherbivores (herbivores  $\geq 1$  ton in body weight) were lost ( $n = 15$  spp, Owen-Smith 2013) and even most herbivores  $\geq 500$  kg went extinct, with just some species of tapirs (*Tapirus* spp.) surviving to the present day. Africa, in contrast, has maintained a rich fauna of large herbivores until the present-day, albeit some species have experienced massive range losses in recent

decades. How did these prehistoric extinctions affect ecosystem processes? Large herbivores can have major impacts on the vegetation structure, including the balance between trees and grasses. This is, in particular, the case for megaherbivores, which due to their near-immunity to non-human predation on adults (although juveniles may be vulnerable) are not top-down regulated and can attain high densities at which they may radically transform vegetation structure (Owen-Smith 1987). The loss of megafauna could also have had major effects on seed dispersal (Janzen and Martin 1982, Pires et al. 2014) and nutrient biogeochemistry (Zimov et al. 1995, Doughty et al. 2013). Until recently it has been difficult to definitively attribute ecosystem changes to the now extinct megafauna because little that was known about their behaviour. Due to the drastic nature of the extinctions in South America, we would expect to see a larger potential impact on vegetation there than almost anywhere. During the Late Pleistocene, South America had a predominance of very large herbivores, while most of Australia's mammalian herbivores were comparably small and those of Africa were intermediate (Owen-Smith 2013).

There are biogeographical, paleontological and experimental reasons to think that these large-animal extinctions may have impacted savanna woody surface cover. For instance, we can broadly compare savanna tree cover in Africa (with megafauna) to South America (largely without). At a given soil moisture status, Africa has substantially fewer trees than South America (Murphy and Bowman 2012), which could be partially due to the lack of megaherbivores in South America. Paleo-data generally indicates an increase of woody biomass around the time of the megafauna extinctions, but in the past it was difficult to determine whether the increased woody biomass was the cause of the extinctions or an effect of them. The difficulty was compounded because megafauna remains are rare, especially in the lakes that generally archive Late Quaternary pollen records. However, spores of *Sporormiella*, a dung fungus, could be used as a proxy for megafauna abundance because it has been shown that in the lake pollen records, they follow the end-Pleistocene megafauna population decline: they are abundant in late-glacial sediments, rare through the Holocene, and increase in abundance with the historic introduction of domestic grazers (Davis and Shafer 2006). This *Sporormiella* data generally indicate that the extinctions tended to be followed by an increase in tree cover versus vice versa. For instance, vegetation changed drastically in the eastern USA (Gill et al. 2009) following the megafauna extinctions. Another recent study using *Sporormiella* data found that human arrival was correlated with the extinctions of the Australian megafauna, which then caused a major change in vegetation through a combination of reduced herbivory and increased fire (Rule et al. 2012). There are currently no similar studies that we are aware of for South America.

There is also now abundant experimental evidence that large animals may impact land surface cover. Exclosure experiments, experiments that use fences to remove herbivores from ecosystems, show ecosystems with increased tree cover. One of the most comprehensive studies to document this was a recent aircraft campaign that flew over two similar African savanna ecosystems. The only difference between the two was that in one, all animals  $> 5$  kg were excluded, while

in the other, they were included. Woody cover increased  $\sim 9\%$  over  $\sim 36$  years in the system without large herbivores, especially elephants (Asner et al. 2009, Asner and Levick 2012). This study demonstrates that elephants are chiefly responsible for the tree falls, and can uproot up to 1500 trees per elephant per year (Duffy et al. 1999).

What role might herbivores play on woody cover abundance? Here we propose a very simple study to address this question by reanalysing the Lehmann et al. dataset, but incorporating the impact of herbivores in the model (Lehmann et al. 2014). The original study does not analyse the impact of animals because the authors state that “globally, data availability on herbivore abundance is sparse and unreliable”. However, the IUCN database provides a reasonable estimate of animal range and we therefore use this database to estimate herbivory. Likewise, we now have a rough estimate of the ranges of the now extinct megafauna that we can use to estimate how woody surface cover might have changed if those animals still existed (Faurby and Svenning 2015a). We ask the following questions: 1) does adding extant mammal diversity and biomass – and in particular large species – improve empirical global models (OLS and SAR) of woody savanna cover over just abiotic inputs?, 2) based on these results, how might savanna woody surface cover in South America be different if the continent had maintained its rich abundance of Pleistocene megafauna?

## Methods

### Data

We use the recently published dataset from Lehmann et al. (2014) that has data on woody biomass (WB), temperature, effective rainfall, seasonality, drought index, and fire frequency from 2154 plots in South America, Africa and Australia (variables described in Table 1, for any methodological details regarding these variables see Lehmann et al. 2014). We combine this dataset with current ranges for all extant species, based on 43 444 individual range maps (IUCN 2010) and the body masses of these species (Smith et al. 2003, Faurby and Svenning 2015b). For every mammal in the IUCN database we converted its range vectors into rasters (4 pixels per degree) and tested whether each of the coordinates listed in the Lehmann et al. (2014) paper were within this area. However, resolution differences between the two datasets may contribute to error in our analysis.

To understand the impact of animal size on woody biomass, we then divided our animal data into three categories: number of mammals  $> 1000$  kg (current megaherbivore diversity),  $\log_{10}$  sum of average species weight biomass (species richness weighted by biomass), and total number of mammals (current terrestrial mammal diversity) (shown spatially in Fig. 1). We removed all bats (order Chiroptera) from the analysis because they are mammals that will not impact woody surface cover (however, bats are important seed dispersers). We did not use a variable that estimates species density because of the great uncertainty in estimating population densities for extinct megafauna and due to little population density data for existing species. However, population density could potentially provide a more accurate estimate in the future.

Table 1. Detailed descriptions of each of the variables used in the empirical models.

Variable	Description
Current megaherbivore diversity	Number of mammals > 1000 kg from the IUCN database
Species richness weighted by biomass	Log10 of sum of masses of all mammals from the IUCN database
Current terrestrial mammal diversity	Number of all mammals from the IUCN database
Present world with extinct megafauna	Log10 of sum of masses of all mammals from the IUCN database + extinct megafauna from Faurby and Svenning (unpubl.)
Effective rainfall	Effective rainfall defined as the difference between mean annual precipitation (MAP) and mean annual potential evapotranspiration (PET)
Rainfall seasonality	Rainfall seasonality ranges from 0 (all months contribute equally to total annual rainfall) to 100 (all rainfall fell in one month)
Drought index	Foley's Drought Index (Foley 1957) is calculated for each month of each year as actual annual rainfall for three years before every month less the expected (long-term average) rainfall for that period, divided by the MAP
Temperature range	Annual range in mean monthly temperature
Mean annual temperature (MAT)	Mean annual temperature
Fire frequency	Satellite derived fire histories for each region and used the monthly data layers from 2000 to 2010 from the MODIS (MCD45A1) fire product

To estimate the impact of the now extinct megafauna on woody biomass, we created a dataset of the ranges and weights of extinct megafauna based on Faurby and Svenning 2015a and 2015b. The taxonomy for extinct species followed (Faurby and Svenning 2015c). This dataset is based on historical information when available or alternatively based on a method similar to the co-existence approach to infer paleoclimate based on co-occurring taxa (Mosbrugger and Utescher 1997). We combine this with the current IUCN mammal database to estimate mammal distributions as they would have been today been without any extinctions or regional extirpations. In this dataset we include the historical ranges of animals as they would have been prior to human hunting and land use change. For this last variable we also take the log10 sum of average species weight biomass and refer to this variable as present world with extinct megafauna. We therefore divide our data

into present world with extinct megafauna which includes extant species and their historical range (where available) plus extinct species and the other animal variables which only include extant species within their current ranges. There is uncertainty involved in predicting range maps and mean weights of extinct species. For this reason, as a sensitivity study we vary the number and weights of extinct megafauna by  $\pm 20\%$  and show (Fig. 7) under a high and low scenario in Supplementary material Appendix 1 (SOM Fig. 3).

### Data analysis

We used the ordinary least squares (OLS) multiple regression models for our environmental variables (temperature, precipitation and fire, Table 1) alongside our biotic variables to predict woody biomass. Whenever spatial data are

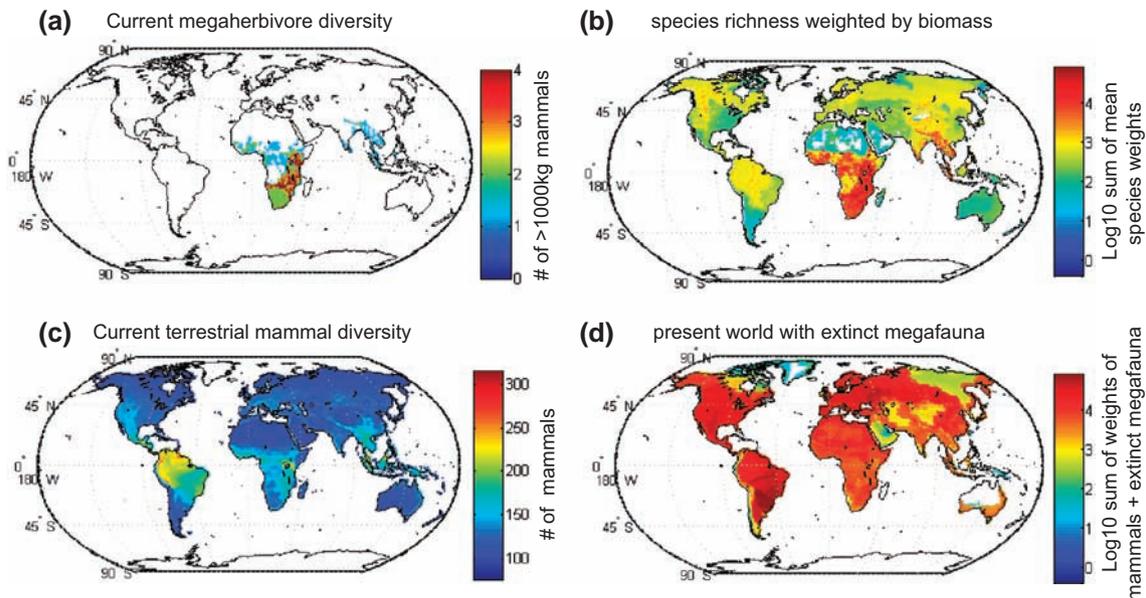


Figure 1. (a) Current megaherbivore diversity or number of mammals > 1000 kg, (b) species richness weighted by biomass or the log10 sum of all mammals combined species weight excluding bats, (c) current terrestrial mammal diversity or all mammals in each pixel excluding bats, and (d) present world with extinct megafauna or the log10 sum of all mammals combined species weight excluding bats but including extinct megafauna.

plotted there is a risk of autocorrelation because plots closer to each other will have more similar signals than plots far from each other. Therefore, we used spatial regression models that takes spatial autocorrelation into account (Dormann et al. 2007) by using Simultaneous Auto-Regressive (SAR) error models (Dormann et al. 2007). To reduce the potential of spatial autocorrelation, we reduced our sample size to 1256 by eliminating all, but one plot within the same quarter of a pixel. We chose these plots in several different ways, but all methods had broadly similar results. Following this reduction of our dataset, our correlogram (Supplementary material Appendix 1, SOM Fig. 1) indicates vastly reduced spatial autocorrelation. SAR models were fit using the R library 'spdep' following Pedersen et al. (2014). We examined possible neighbourhood definitions to determine how effective each was at removing residual autocorrelation from model predictions. For our SAR analyses, the dataset has many close sample points but fewer isolated ones, and we therefore define neighbourhoods by distance to reference point. In our case, we tried distances from 20 km to 100 km and found that Akaike's Information Criterion (AIC) was minimized at 90 km. For model comparison we used AIC, corrected for small sample size, which compares the model explanatory power while compensating for additional model parameters. Therefore, our SAR model assumes that the value of a given cell is a function of the parameter values and the values of the cells within 90 km. By accounting for spatial autocorrelation, the effects estimated by the SAR models may more reflect local effects, while effects estimated by the OLS models may more reflect broad-scale patterns. We estimate the overall model performance (pseudo-R<sup>2</sup>) of the SAR model by calculating the square of the correlation between the predicted (only the predictor and not the spatial parts) and the raw values. We will refer to this as pseudo-R<sup>2</sup> in the paper even though we note that several different estimates of model fit are frequently referred to as pseudo-R<sup>2</sup> (UCLA statistical consulting 2014).

## Results

We predicted woody biomass (WB) using each variable individually with both OLS and SAR analysis (Table 1). Current megaherbivore diversity and species richness weighted by biomass were both highly significant, explaining 6 and 13% of the variance respectively in WB. Current terrestrial mammal diversity, in contrast, was not significant and did not

Table 3. Results of the ordinary-least-squares (OLS) and SAR multiple linear regression models with and without mammals plus environmental predictors to predict woody biomass (WB). \*\*\* =  $p < 0.001$ , \*\* =  $p < 0.01$ , \* =  $p < 0.05$ , unmarked are not significant,  $p > 0.05$ .

Variable	OLS-species richness weighted by biomass	SAR-species richness weighted by biomass
ER	0.02 ± 0.00***	0.03 ± 0.00***
MAT	0.04 ± 0.03	0.065 ± 0.05
Drought	18.60 ± 2.70***	15.35 ± 4.60***
Species richness weighted by biomass	-4.44 ± 0.63***	-3.52 ± 0.91***
Fire	-0.62 ± 0.33	-0.74 ± 0.37*
R <sup>2</sup>	0.36	(pseudo) 0.36
AIC	11563	11328

explain much variance in woody biomass (Table 2). Of the abiotic variables, ER, drought, and MAT were each highly significant and each explained a significant portion of the variance (Table 2).

We then took the significant variables from the individual models (species richness weighted by biomass, ER, drought, and MAT, but also fire because fire has previously been found to predict savanna ecosystem structure (Lehmann et al. 2014)) and combined them to create a stronger model for predicting woody biomass. We used mammal biomass rather than megaherbivore diversity, both because it explained more variance individually and because the 1000 kg cut off was potentially an arbitrary threshold for a process that likely has a continuous relationship with body size. The combined OLS and SAR models both explained 36% of the variance (Table 3). If we remove the animal variables in the multivariate model, the R<sup>2</sup> of both models drop by 0.03. The SAR model was strongly supported by AIC over the OLS model, but the two had broadly similar regression coefficients (Table 3, Fig. 1).

South American plots had much higher woody biomass than African plots and slightly higher WB than Australian plots (Fig. 2a). South American plots had greater effective rainfall and drought index, with lower values in both African and Australian plots (Fig. 2b–c). African and Australian plots also were warmer and more fire prone than South American plots (Fig. 2d–e). African plots averaged 2.7 species > 1000 kg with the other continents both having zero (Fig. 2f). Species richness weighted by biomass is also greatest in African plots, followed by South American and Australian plots (Fig. 2g). In contrast, South American plots had more total extant

Table 2. Results of the ordinary-least-squares (OLS) models and SAR model for each variable separately as a predictor of woody biomass (WB) ranked by smallest AIC. We include slope value and significance, AIC score and percent variance explained. \*\*\* =  $p < 0.001$ , \*\* =  $p < 0.01$ , \* =  $p < 0.05$ , unmarked are not significant,  $p > 0.05$ .

Variable	WB-OLS	WB-SAR	AIC-OLS	AIC-SAR	R <sup>2</sup>
ER	0.03 ± 0.00***	0.03 ± 0.00***	11646	11346	0.31
MAT	-0.27 ± 0.014***	-0.25 ± 0.03***	11805	11398	0.22
Drought	42.30 ± 2.20***	33.50 ± 4.50***	11809	11417	0.22
Species richness weighted by biomass	-9.13 ± 0.65***	-8.56 ± 0.96**	11939	11426	0.13
Current megaherbivore diversity	-5.48 ± 0.68***	-3.70 ± 1.40**	12043	11451	0.05
Current terrestrial mammal diversity	-0.00 ± 0.02	0.05 ± 0.05	12121	11456	0
Fire	-0.23 ± 0.40	-0.71 ± 0.40	12122	11457	0
Temp	-0.01 ± 0.03	-0.09 ± 0.06	12122	11458	0
Season	0.28 ± 0.07***	0.05 ± 0.14	12107	11460	0.01

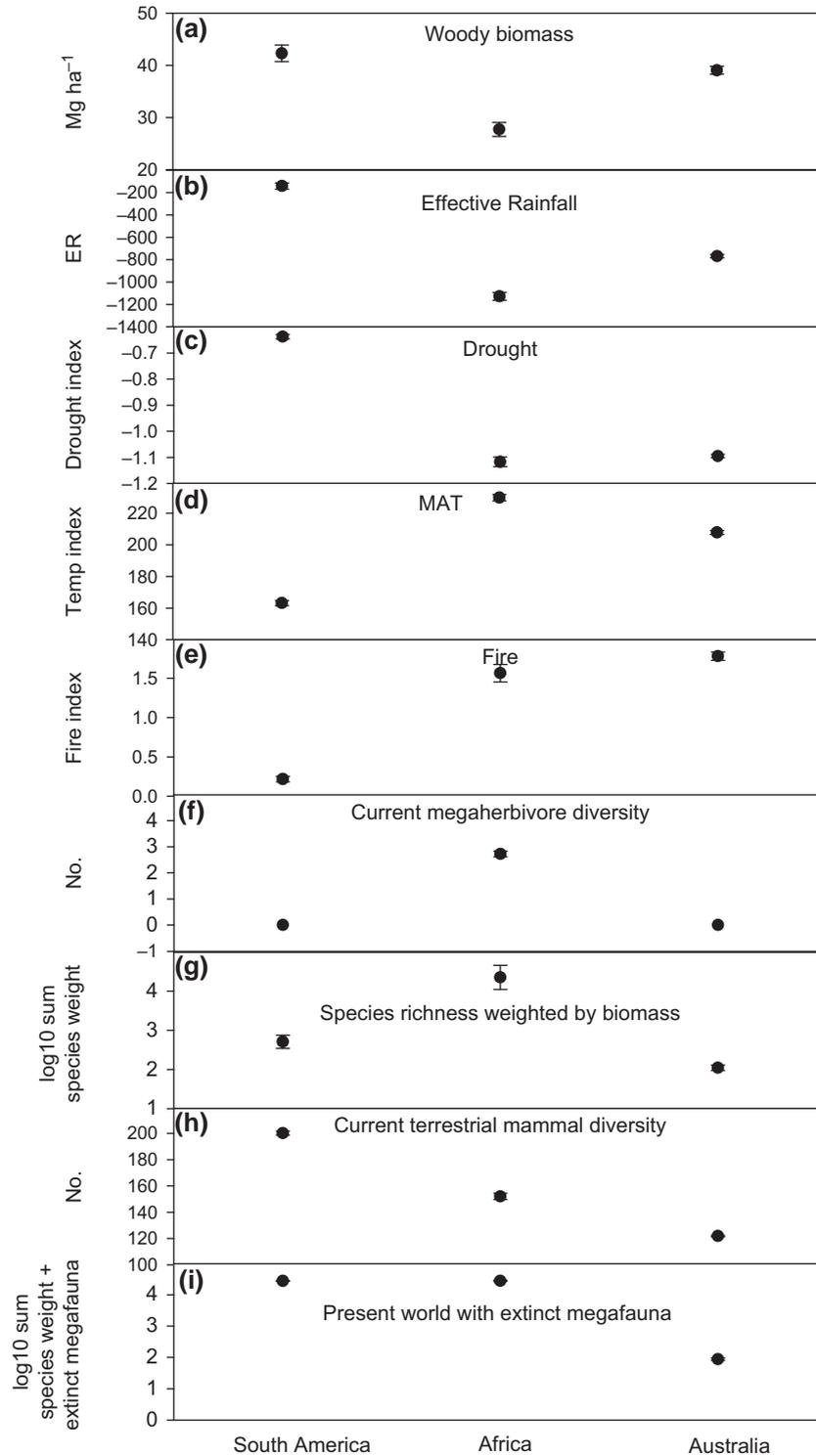


Figure 2. Mean continental values  $\pm$  SE for woody biomass, effective rainfall, drought index, mean annual temperature, current megaherbivore diversity, species richness weighted by biomass, current terrestrial mammal diversity, present world with Late Quaternary extinct megafauna as well for South America, Africa and Australia.

mammal species than either African or Australian plots (Fig. 2h). However, when Late Quaternary extinct as well as locally extirpated species are also included, the mammal biomass is similar in South American and African plots, but lower in Australian plots (Fig. 2i).

Which of the variables in our model are the most important in determining continental variation in woody biomass?

We can estimate the importance of each variable by multiplying its SAR regression coefficient (Table 3) by its mean value for each continent. Effective rainfall has the largest impact on continental variation with a  $\sim 29$  Mg C ha<sup>-1</sup> difference predicted between WB in South America and Africa (Fig. 3). In contrast, fire apparently has very little impact on WB in our model for any of the continents. Drought and

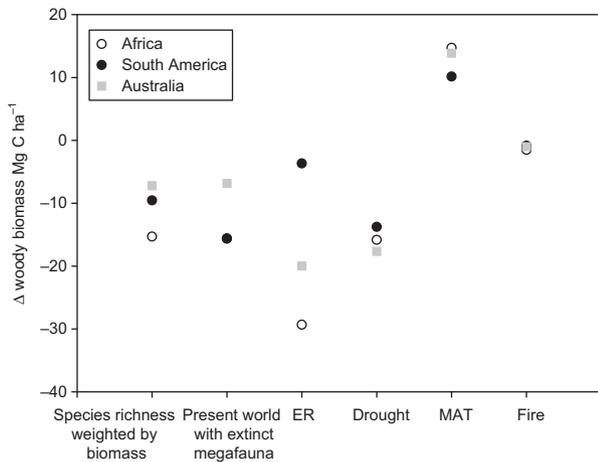


Figure 3. Mean estimated continental impact of each variable (coefficient for SAR from table 3 multiplied by mean continental value) in our model for South America (black), Africa (white), and Australia (grey).

MAT both impact WB by  $\sim 15 \text{ Mg C ha}^{-1}$ , but with opposite signs. Species richness weighted by biomass decreases WB by  $\sim 15 \text{ Mg C ha}^{-1}$  in Africa relative to having no animals due to the larger number of megafauna and by about  $7\text{--}9 \text{ Mg C ha}^{-1}$  in Australia and South America. However, after including the Pleistocene megafauna (present world with extinct megafauna) mammals decreased WB by a similar amount ( $\sim 16 \text{ Mg C ha}^{-1}$ ) in both South America and Africa, but only by  $7 \text{ Mg C ha}^{-1}$  in Australia. Therefore, adding the megafauna back into South America decreased mean WB by  $\sim 7 \text{ Mg C ha}^{-1}$  in our model (Fig. 3).

We estimate WB for each continent and compare this to measured continental average WB values (Fig. 4). The model, while using the variable “species richness weighted by biomass”, greatly underpredicts South America’s WB versus measured values, while slightly overpredicting WB in Africa (Supplementary material Appendix 1,

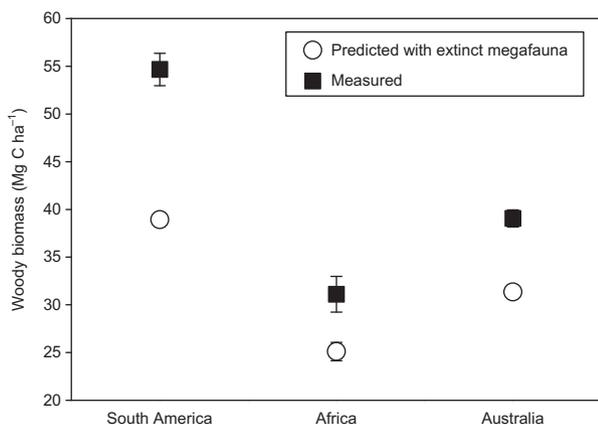


Figure 4. Continental average measured (black) woody biomass versus modelled based on the results of the SAR equations with the now extinct megafauna (present world with extinct megafauna) (white). Error bars are standard error. Residual errors between measured and modelled results were removed from the predicted values. Model coefficients are from the SAR model and listed in column 2, Table 3.

SOM Fig. 2). Therefore, when we use the variable present world with extinct megafauna to predict WB, we correct for the inherent residual continental differences. For instance, the SAR model underpredicts WB in South America by  $\sim 6 \text{ Mg C ha}^{-1}$ , and, thus, we add  $6 \text{ Mg C ha}^{-1}$  to our model results. After this correction, we estimate that woody biomass in savannas in South America has increased by 29% due to the Late Quaternary extinctions and extirpations (Fig. 4). However, there are large regional differences within South America. In Fig. 5a, we show the difference between variables ‘species richness weighted by biomass’ and ‘present world with extinct megafauna’ overlaid with our estimates of changes to WB for each plot (circles) with and without the extinct animals. There is a clear correlation. Where there were many extinctions of large animals, such as in Argentina, there are predictions of increases in WB of greater than  $20 \text{ Mg C ha}^{-1}$  (red circles) following the extinctions. Where there have been large animal extinctions, such as in northern South America, there is very little change in predictions of WB. Therefore, we predict the biggest change in WB would have been in southern Brazil, Uruguay and Argentina (see Figure 6 for artistic depictions of possible species living in these regions). We plot a histogram and find that WB has a median decrease of  $\sim 10 \text{ Mg C ha}^{-1}$ , but with individual plot losses of up to  $80 \text{ Mg C ha}^{-1}$  (Fig. 5b).

Finally, we create a spatially explicit map showing expected percentage decline in woody surface cover from today’s estimated values if the Pleistocene megafauna still existed (Fig. 7). We use maps of ET, drought, MAT, species richness weighted by biomass and fire to estimate percentage woody cover. From this, we subtract the estimated impact of the now extinct megafauna and find that woody cover in most regions would be  $\sim 80\%$  of today’s values. In southern South America, the percentage decline in woody surface cover drops to below 50% in parts. This is a function of the many large, now extinct herbivores that lived in this region as well as lower expected tree cover due to environmental conditions. In other words, in southern South America, our model predicts that the environment reduces almost all the savanna tree cover and the megafauna would have removed what little tree cover remained.

## Discussion

How might South American biogeography have looked without the end-Pleistocene and Early Holocene extinctions? Here, we broadly estimate that the savanna regions would have been more open with, on average  $\sim 29\%$  less woody biomass in the savanna zones, making them more similar to mean tree cover found in African savannas (Fig. 4). Why might megaherbivores have such a large impact on land cover? Owen-Smith originally proposed a ‘keystone herbivore’ hypothesis, where, due to their invulnerability to non-human predation on adults, megaherbivores ( $> 1000 \text{ kg}$ ) attain saturation densities at which they may radically transform vegetation structure and composition. According to the theory, the elimination of megaherbivores elsewhere in the world at the end of the Pleistocene and in the Early Holocene would have drastically changed vegetation structure



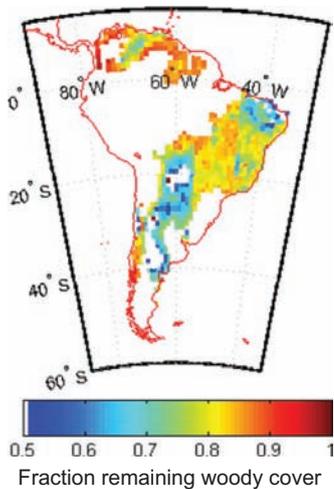


Figure 7. A spatial map of expected percentage decline in woody cover in present day savanna regions if the now extinct South American megafauna still existed. We use variables ER, drought, MAT, fire, and 'species richness weighted by biomass' in our empirical SAR model to predict woody biomass. We then run this model substituting 'present world with extinct megafauna' and show the percent decrease in woody cover.

regions of the planet. In fact, although today we think of Africa as the land of megaherbivores, prior to the extinctions, South America had a higher abundance of megaherbivores, with South America having a predominance of very large herbivores ( $n = 15$ ) (Fig. 6), while most of Australia's mammalian herbivores were relatively small and those of Africa were intermediate (Owen-Smith 2013). Therefore, we might have expected South American megafauna, prior to their extinction, to have had the largest impact on land surface cover.

It does not seem surprising that large mammal herbivores impact savanna tree cover, because there is abundant experimental and paleontological data that demonstrate that animals (and large animals specifically), can play an important role in controlling vegetation cover. For instance, in Kruger National park, when elephants are excluded from a region, there is abundant evidence of a large increase in tree cover (Asner et al. 2009, Asner and Levick 2012). Likewise recent paleontological studies demonstrate that there was an increase in woody surface cover following the extinctions of the Pleistocene megafauna (Gill et al. 2009, Rule et al. 2012, Sandom et al. 2014a). The importance of herbivores was recently highlighted in South American savannas in a recent study that found that grazing and grass competition additively diminished the risk of woody establishment in a wet Argentinian savanna (Maciasa et al. 2014).

How do megaherbivores specifically affect vegetation structure? Megaherbivores, such as elephants, have disproportionate effects on the mortality of adult shrubs, by pulling them out (Pringle et al. 2014), and trees, by pushing them over and breaking them (Asner and Levick 2012) due to their large size and strength. In addition, they also debark trees and feed on saplings (Staver and Bond 2014). Following their extinctions, it is thought that plant matter might accumulate and provide fuel for increased wildfires (Bond 2010).

Grazers may have had a very different effect on woody vegetation than browsers. Therefore, it is important to determine the guild (grazers or browsers) of the extinct animals. This can be done using carbon  $d^{13}$  isotopic data because grasses have a different isotopic signature than do trees and this isotopic signature is incorporated into the fossil remains. A recent comprehensive meta-study on this topic found that region mattered and some species changed between grazers and browsers by region (Franca et al. 2015). This study separated the results into four regions: the Brazilian Intertropical Region where *Equus* was a grazer, *Stegomastodon* and *Toxodon* were mixed-feeders, and *Eremotherium* and *Palaeolama* were browsers. In the Amazon region where *Stegomastodon* and *Toxodon* were browsers. In southern Brazil, Uruguay and northern Argentina where *Equus* and *Toxodon* were grazers while the mixed-feeders included all the other taxa such as *Nothrotherium*, *Stegomastodon*, *Hippidion*, *Scelidodon*, *Scelidothorium*, *Neosclerocalyptus*, *Glyptodon*, *Macrauchenia*, and *Palaeolama*. None of the taxa analyzed in this region were exclusively browsers. In Ecuador and Peru *Equus* was a grazer and *Stegomastodon* was a mixed-feeder (Franca et al. 2015). Therefore, according to this work, the only consistent grazer was the genus *Equus* which we removed from our analysis. This removal had only a very minor impact on our results.

Our model simulations predict that with megafauna, South America's land surface would have been transformed into more open savannas with less abundant woodlands. In practice, what might this mean for the hyper-diverse cerrado regions of Brazil, or the *chiquitano* dry woodlands of Bolivia? We hypothesize that woody encroachment is much greater than it would have otherwise have been, but total levels of biodiversity would likely have been similar or increased with the large animals (Galetti 2004). The more closed woodlands may have increased stress on currently existing animals that co-evolved with the megafauna in the likely more open ecosystems (Owen-Smith 1987). South American savannas are some of the most threatened ecosystems on the planet with rates of clearing often higher than the Amazon forest (Hansen et al. 2013). The extinctions have already transformed and stressed these valuable ecosystems and the results of this study should not be seen as justification for further transformation to agriculture.

Here we predict that savannas likely had less woody biomass and present day dry forests would have been more savannah-like with mega-herbivores. Also, there is evidence that carbon content of forests decreased as large-seeded fruit trees decreased in abundance (Janzen and Martin 1982, Doughty et al. 2015, this issue). At this time it is difficult to access the net carbon impact of the megafauna extinctions on South America? Such land surface changes would also have affected climate beyond just their carbon impact, but would have impacted both albedo and evapotranspiration as well (Doughty et al. 2010, Doughty 2013). Tree cover in the tropics generally leads to cooling while tree cover in high latitude regions generally leads to warming (Bonan 2008) and future studies are necessary to determine the net climate impact of land surface changes on global climate. At this point there are too many uncertain variables to estimate the net climate impact of the extinctions.

Would the ecological roles previously performed by the now extinct megafauna simply have shifted to the

remaining smaller herbivores following the extinctions? This is a highly uncertain issue, but there are a few reasons to think that it would not. The first is simply size. For instance, elephants and other large herbivores have unique impact on forest structure by breaking and knocking down trees that cannot be replicated by smaller animals (Asner et al. 2012). Predation likely would have kept smaller animals from experiencing a population boom following the extinctions. Beetles associated with herbivore dung were better represented during the Last Interglacial (132 000–110 000 y B.P.) than in the Early Holocene (10 000–5 000 y B.P.) (Sandom et al. 2014a). If dung beetles are a proxy for dung quantity, and dung quantity is a proxy for smaller mammal numbers, then this indicates their numbers had not recovered into the Early Holocene. Indeed, jointly with the megafauna extinction South America also experienced extinction of dung beetles associated with their dung (Sánchez et al. 2013). However, there are now significant numbers of domestic cattle, especially in southern South America (Supplementary material Appendix 1, SOM Fig. 4), that may have taken some of the ecological roles of the megafauna (Barnosky 2008).

There is currently an ongoing debate on rewilding or the refaunaation through restoration of extant species to their original geographical distributions (Galetti 2004, Oliveira-Santos and Fernandez 2010). Part of the debate of restoring animals is to restore their ecological function. Here we have shown that this likely includes reducing woody cover in savanna ecosystems. Why might this be important for biodiversity or valuable to humanity? For instance, increased openness in savannas may increase the biodiversity of some savannas (Hoogesteijn and Hoogesteijn 2010, Campos-Krauer and Wisely 2011, Piana and Marsden 2014). Also, currently, in some regions of the world, grasslands are undergoing a rapid shift from herbaceous to woody-plant dominance, possibly due to increased atmospheric concentrations of CO<sub>2</sub> or the reduction of fire events due to conservation initiatives (Archer 1995). One recent study quantified how this increase in woody cover might reduce productivity of pasture land and found a reduction of between 0.6 and 1.6 reproductive cows per square kilometre for each 1% increase in tree cover (Anadon et al. 2014). In a future with more woody encroachment of pastures, could the addition of megaherbivores remove woody cover, making pastures more productive for cattle? In other words, a mixed, biodiverse pasture including megaherbivores could actually be more productive than a monoculture of cattle (Supplementary material Appendix 1, SOM Fig. 4).

This study offers the first evidence that South America's land surface cover may have been drastically transformed following the severe Pleistocene and Early Holocene megafauna extinctions on this continent. However, the statistical methodology used in this paper is simple and the trends we predict might be more accurately predicted using a more mechanistic approach which could be used to help better predict mega-herbivore effects on woody biomass. Overall, the large empirical dataset highlights the potential role of megafauna on reducing woody cover and thus finds evidence for Bond's 'brown world' hypothesis of consumer controlled regions of the planet.

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Supplementary material (Appendix ECOG-01593 at <[www.ecography.org/readers/appendix](http://www.ecography.org/readers/appendix)>) Appendix 1.