



The Effect of Large Animal Removal or Protection under the Future of Climate Change

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Abstract. Large mammal populations are declining worldwide, yet their impact as biotic drivers of terrestrial carbon and energy exchange with the atmosphere remains poorly represented in ecosystem modelling approaches. Animal processes, like herbivory and predation, shape vegetation structure and composition that governs photosynthetic carbon uptake. This influence is rarely quantified relative to other drivers like climate change and rising CO₂ levels. Here, we apply a generic, process-based, multi-trophic modelling framework that integrates the two models LPJ-GUESS and Madingley. Using this framework, we simulated the impact of large herbivore and carnivore removal across two European and two African biomes, under both constant climate conditions and climate change scenarios.

Under constant climate, the removal of large herbivores increased leaf biomass, a proxy for canopy photosynthetic capacity. However, the impacts of climate change, including changes in atmospheric CO₂ on leaf biomass were much larger. In contrast, the removal of large carnivores reduced leaf biomass, reflecting the release of herbivores from predation and subsequent increases in their abundance. In African biomes, this effects rivals those of a low-warming climate change scenario. To investigate recovery potential, we compared African savanna simulations with and without neighbouring grid cells with modelled trophic structures intact. We found that herbivore biomass could only recover in the vicinity of such protected areas. Our findings underscore the importance of conserving large mammal populations under climate change.

1 Introduction

Animals are impacting key ecological processes in terrestrial ecosystems across the globe (Schmitz et al., 2014, 2018). Through damaging and removing leaf biomass, herbivores are affecting carbon assimilation and plant competition for resources such as light and space. Cascading effects throughout the trophic pyramid can be triggered top-down by apex-predators, or bottom-up by changes in the underlying vegetation layer. Yet in ecosystem modelling the direct and indirect impact of animal populations have been disregarded for a long time (Schmitz et al., 2014). Given the modification and degradation of habitats by humans, as well as calls for habitat restoration and protection (Arneth et al., 2020; Cardinale et al., 2012; Pacifici et al.,



2015), it is necessary to improve our understanding of the often complex interconnections between animals and the underlying vegetation, including determining the role of anthropogenic climate change.

Schmitz et al. (2014) highlighted that the animals' comparably small contribution to global biomass has historically been interpreted as an indicator for a minor role in terrestrial carbon cycling. But this view is not fully compatible with the literature:

35 Edenius et al. (2002) have shown that moose populations are impacting Scots pine and spatial forest heterogeneity by forming and exploiting gaps. Bonan (1992), Kielland and Bryant (1998) and Schmitz et al. (2003) have also reported moose reducing primary productivity of boreal forests. Holdo et al. (2009) investigated the effects of large disease-mediated die-offs in wildebeest populations and hypothesised that future die-offs may increase grass biomass significantly, albeit bolstering fire severity and shifting the ecosystem to a net carbon source. Ultimately, Schmitz et al. (2014) called for the incorporation of
40 animal-mediated carbon cycling dynamics in global carbon budget projections.

The role of large animals is of particular importance. 60% of large herbivores are threatened by extinction (Ripple et al., 2015) whose loss would lead to profound impacts on ecosystem functioning. Wilmers and Schmitz (2016) also emphasized the role of large carnivores and their top-down effects in regulating carbon dynamics. They estimated that wolf predation can either enhance net primary productivity (NPP) and net ecosystem productivity (NEP) by preying upon moose (browsers) in boreal
45 forests, or, in contrast, reduce NPP when preying upon elk (grazers) in the Rocky Mountains.

While field experiments provide valuable information on animals' impacts on nutrient cycling, vegetation dynamics and carbon storage, such studies are often struggling to capture long-term and large-scale effects. Modelling studies have been used as a powerful tool to investigate the broader effects of animals on ecosystems state and functioning. Pachzelt et al. (2015, 2013) integrated a grazer population model into the dynamic global vegetation model (DGVM) LPJ-GUESS. The presence or
50 absence of grazers, on the other hand, substantially impacted tree and grass biomass and thus the areas vulnerability to fire. Berzaghi et al. (2019) reported that selective browsing from large herbivores can put smaller trees at a competitive disadvantage whilst promoting large trees and increase carbon-storage. While these studies all emphasise the importance of incorporating animals in ecological modelling, their approaches are often limited by focussing on a limited range of species and neglect the complexity of the food web, such as top-down control by predators.

55 In Krause et al. (2022), forcing the functional animal population model Madingley with the dynamic global vegetation model LPJ-GUESS improved the predictive power of the Madingley model. Implementing a bi-directional coupling between the two models, resulted in reduced simulated NPP by ~5% in response to herbivory for present-day climate conditions (Krause et al., 2025). The later study also highlighted a large spatial variability in simulated responses; biomes with sparser vegetation experience a greater relative impact from herbivory damage. Inspired by Hoeks et al. (2020), we here employ the model system
60 described in Krause et al. (2025) to investigate ecological impacts of removing large herbivores or carnivores from the trophic pyramid and analyse the ecological responses. To analyse animal-vegetation feedbacks in the light of climate change, we additionally conducted removal experiments under different climatic conditions. As protecting populations of large animals becomes urgent globally, we also simulated the ecosystem's capability to recover from a mass animal removal event with and without the co-existence of protected areas.



65 2 Methods

A brief description of the two coupled models can be found in supplementary material S1. For this study, we chose 21kg as the removal threshold for large mammals (Malhi et al., 2016). Details on the removal process and criteria can be found in supplementary material S2.

We used simulated atmospheric climate data and atmospheric CO₂ from ISIMIP3b MPI-ESM1-2-HR (Gutjahr et al., 2019; 70 Lange and Büchner, 2021) in two different ways. For a recycled climate approach, we repeatedly use detrended historical data from 1850 to 1880 with a constant CO₂ concentration of 283 ppm for the entire simulation. In a climate scenario approach, the same detrended data and CO₂ concentration are used only during the 500-year coupled spin-up phase. Afterwards, historical climate and CO₂ data are applied from 1850 to 2014, followed by RCP 2.6 or RCP 7.0 climate projection data until 2100.

The Madingley model was forced with a monthly average of the climate forcing used by LPJ-GUESS. Its model domain was 75 seeded with 50 cohorts of each functional group, while the maximum number of cohorts allowed per grid cell was set to 500. We carried out three experiments, each across four model domains: two in Europe and two in Africa. For Europe, we chose one region where temperate mixed forest is prominent and a second region representative of boreal ecosystems covered by evergreen forests. The first African model domain represents the tropical rainforest biome in the centre-equatorial region, while the second represents the moist savanna biome at the east of the equatorial region (see Tab. 1).

Domain Tag	Longitudes	Latitudes	Biome Type
EU1	6°E - 37°E	48°N - 53°N	Temperate Mixed Forest
EU2	34°E - 40°E	52°N - 64°N	Boreal Coniferous Forest
AF1	15°E - 28°E	5°S - 5°N	Tropical Rainforest
AF2	28°E - 40°E	5°S - 5°N	Moist Savanna

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Table 1: Detailed list of all four simulation domains across Europe and Africa. All simulations were carried out on a 0.5° grid resolution.

For the first experiment, we used the recycled climate approach. This experiment investigates the isolated effect of animal removal without climate- or CO₂-change-driven responses. After the coupled spin-up phase, either large carnivores or large 85 herbivores (>21kg) are removed for the remainder of the simulations. In the following 200 years, the model system reactions to the removal are analysed. Additional simulations, where no animals are removed, serve as control runs. We highlight shifts in biomass densities of “animal functional types” (AFTs) and carbon mass distributions of “plant functional types” (PFTs) compared to the control runs to visualise the effect of the animal removal.

For the second experiment, we forced the model system with historical climate data, followed by RCP 2.6 and 7.0 climate 90 projections. Carnivores or herbivores are removed consecutively from 1950 onwards and simulations continue until 2100. We compare the PFT leaf carbon mass distribution response to the animal removal under both RCP scenarios to investigate how



animal removal enhances or diminishes the effects of climate change. Also, we highlight responses within the animal populations under the pressure of climate change and animal removal.

For our third experiment, we investigate the ecosystem's potential to recover naturally from the removal of large mammals. In this experiment, we again follow the recycled climate approach. While Madingley simulates large herbivores and carnivores in both the tropical rainforest (AF1) and savannas (AF2), savannas are known in particular to inhabit both very large herbivores and carnivores. Therefore, we chose the AF2 model domains for this experiment. In contrast to experiment one, the continuous animal removal is ended after being applied for 100 years. In the following 200 years, the model can recover from the former animal removal. We present the recovery as herbivore and carnivore biomass density timelines, as well as population dynamics and PFT distribution timelines. Finally, we compared the recovery potential between a simulation where large herbivores were removed from the entire model domain and a simulation where they were preserved in parts of the domain.

3 Results

3.1 Impacts of Large Animal Removal

3.1.1 Animal Biomass Densities

Figures 1 and 2 show the response of overall AFT biomass density and the animals' size distribution during the last time step of the simulation under the 1850-1880 recycled climate conditions. Table 2 shows herbivore, carnivore, omnivore and leaf biomass responses to removing large herbivores or carnivores from the four experiment model domains.

Metric Affected	Response to Herbivore Removal	Response to Carnivore Removal	Metric Affected	Response to Herbivore Removal	Response to Carnivore Removal
Temperate Mixed Forest (EU1)			Boreal Evergreen Forest (EU2)		
Herbivore Biomass	-3.4%	-2.3%	Herbivore Biomass	-43.1%	+7.2%
Omnivore Biomass	-0.2%	+4.0%	Omnivore Biomass	+75.5%	-1.9%
Carnivore Biomass	-0.5%	-4.7%	Carnivore Biomass	-1.4%	-11.0%
Leaf Biomass	+0.7%	+0.5%	Leaf Biomass	+9.7%	-5.9%
Tropical Rainforest (AF1)			Moist Savanna (AF2)		
Herbivore Biomass	-55.8%	+149.3%	Herbivore Biomass	-57.1%	+141.2%
Omnivore Biomass	+23.2%	+101.0%	Omnivore Biomass	+7.2%	+76.8%
Carnivore Biomass	-7.1%	-1.8%	Carnivore Biomass	-4.8%	-10.4%
Leaf Biomass	+4.7%	-19.3%	Leaf Biomass	+6.1%	-19.2%

Table 2: Average large herbivore and carnivore removal effects on biomass densities under constant climate and CO₂. The values reflect data over the final 30 years of the simulation.

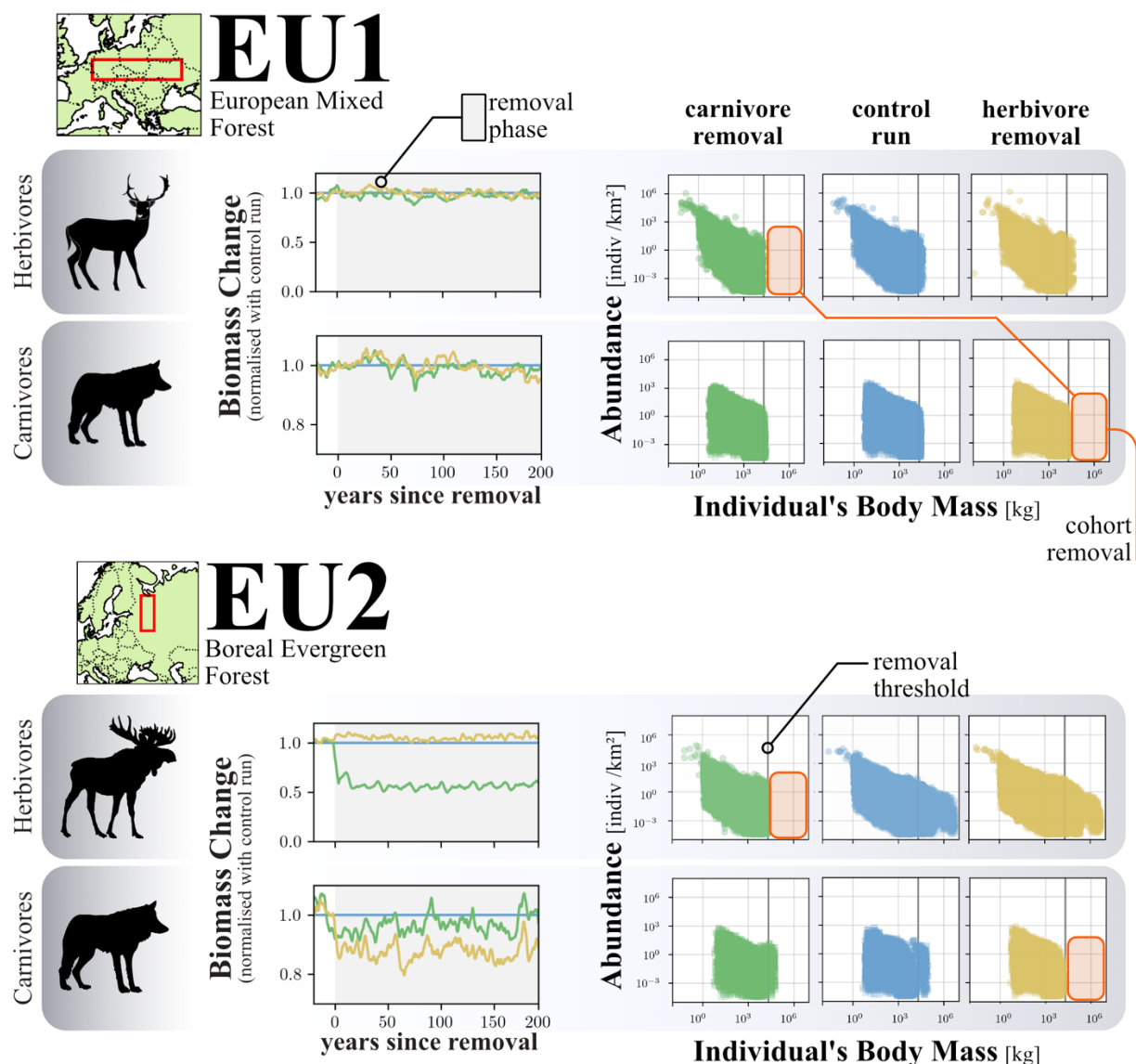


Figure 1: Animal population responses to cohort removal without the impact of climate change (applying recycled, detrended climate conditions) in the two European locations. The left panels depict the domain-averaged biomass of herbivores and carnivores, normalized relative to the control simulation. A five-year moving average was used to smooth annual climate-driven fluctuations while preserving short-term responses. The right panels show the size distribution of animal cohorts. Each point represents one cohort within a location domain during the final timestep of the simulation. A consistent colour coding is used throughout all figures of the study: Blue indicates data from the control simulation without any cohort removal, green indicates data from a simulation where herbivores heavier than 21 kg were removed and yellow indicates data from a simulation where carnivores larger than 21kg have been removed. Grey background shading indicates the active removal window.

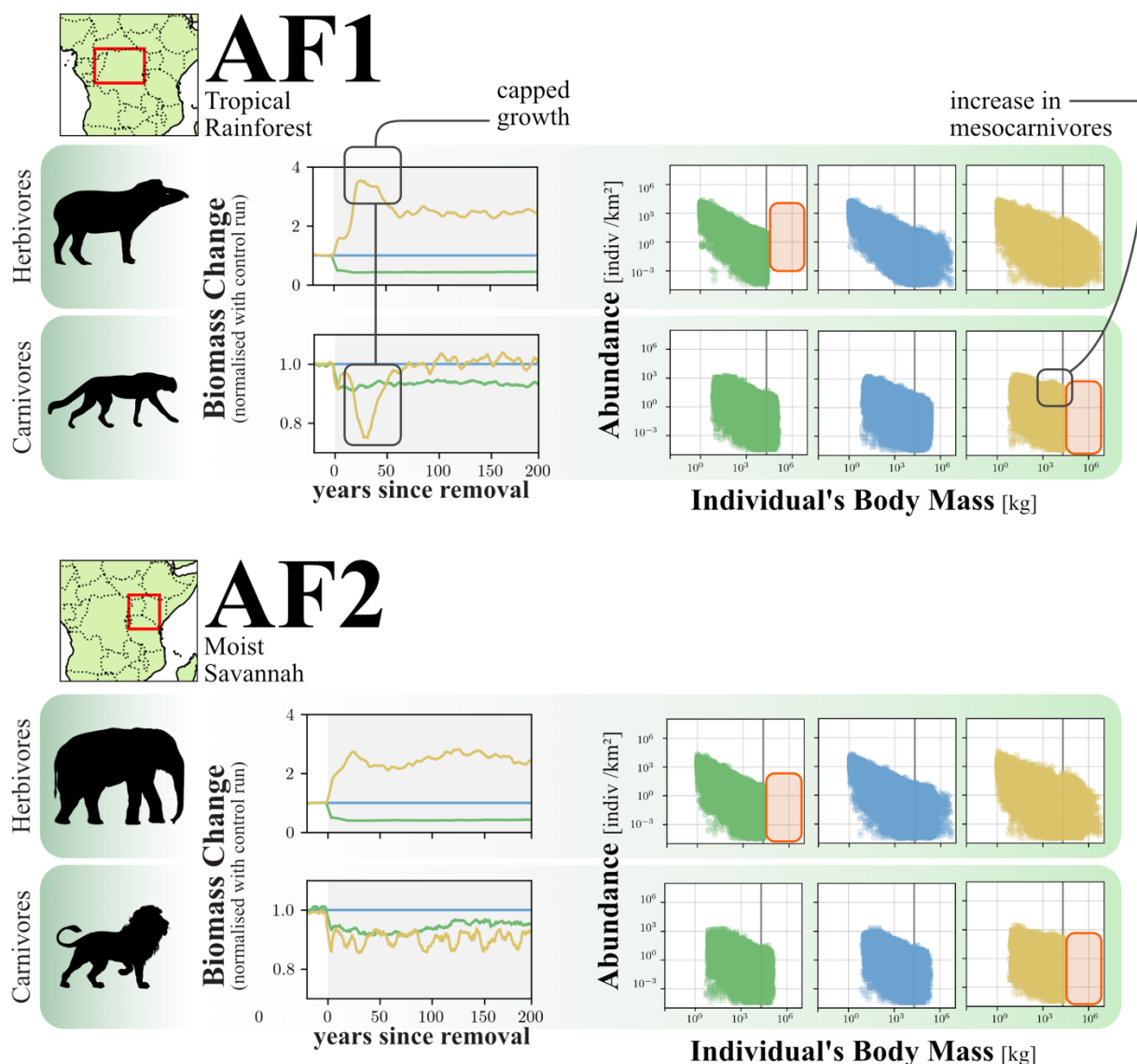


Figure 2: Animal population responses to cohort removal without the impact of climate change (applying recycled, detrended climate conditions) in the two African locations. The figure's arrangement is identical to Fig. 1. In AF1, "capped growth" marks an 'overshoot' of herbivore (and omnivore, not shown) biomass following the removal of large carnivores. We also mark a typical hump that indicates an increase in mesocarnivores in AF1. Consistent colour coding is described in Fig. 1.

In the European mixed forest domain (EU1), the impact of large animal removal is negligible. Madingley simulates only a small population of animals with an adult body mass exceeding 21 kg. As a result, the removal affects only a limited number of individuals, leading to minimal observable differences between the control and removal panels in Fig. 1. In the boreal evergreen forest domain (EU2), the predominantly evergreen vegetation assures that animals have a sufficient supply of



nutrition during winter, which supports a population of large herbivores, although ectothermic (small and mesoscale) herbivores struggle to reach high abundances. Removing large herbivores from EU2 causes a decline in overall herbivore biomass (-43%) while omnivore biomass increases by +76% (Tab. 2). In the undisturbed state omnivores benefit from herbivore removal because, in boreal environments where leaf biomass is the limiting resource, the removal of their primary competitor for this resource outweighs the potential loss of prey density. Removing carnivores from the simulation at the EU2 location only slightly elevates herbivore biomass since the release from predation affects mostly mesoscale herbivores and omnivores (not shown).

While the European animal population responds significantly only within the EU2 domain, primarily to large herbivore removal, the simulated responses in the African grid cells were overall larger, with the strongest response to the removal of carnivores. Differences between the responses in Europe and Africa cannot be explained by the different evergreen-to-deciduous ratios of the model domains. In Madingley, feed quality so far is not yet accounted for, and evergreen and deciduous leaf biomass is treated equally as a source of energy to herbivores and omnivores. In the African tropical rainforest domain (AF1), the removal of large herbivores leads to a substantial reduction in herbivore biomass (-56%) and a moderate decline in carnivore biomass (-7%) (Tab. 2 and Fig. 2). Conversely, omnivore biomass increases significantly (+23%), suggesting a compensatory dynamic within the food web. However, large omnivores cannot completely fill the herbivory consumption gap because they themselves are predators that depend on an abundance of large prey. While facing less competition regarding herbivory, omnivores also experience a shortage of prey after removing large herbivores. A new biomass equilibrium in AF1 is achieved relatively quickly, within approximately 10 years of herbivore removal.

In contrast, removing large carnivores from AF1 results in marked increases in herbivore (+149%) and omnivore (+101%) biomass (Tab. 2 and Fig. 2), aligning with previous findings by Hoeks et al. (2020). However, unlike Hoeks et al. (2020), our study reveals a pronounced transient response within the first 30 years of carnivore removal. During this period, herbivore (and omnivore, not shown) biomass overshoot their eventual equilibrium values, reaching peak increases of +254% (and +236%, respectively). Carnivore biomass exhibits an initial sharp decline (-25%), followed by a rapid recovery that ultimately stabilises at a small net decrease (-2%) (Tab. 2 and Fig. 2). We expect that the overshooting response observed in our experiment to be caused by the bidirectional feedback with the underlying vegetation; the vegetation in Hoeks et al. (2020) was unaffected by herbivory damage, whereas herbivores in our simulations persistently damaged plants.

In the moist savanna domain (AF2), the removal of large herbivores decreases herbivore biomass (-57%) and carnivore biomass (-5%). Similar to AF1, omnivore biomass increases, but only by +7%. The removal of large carnivores from AF2 triggers an initial surge in herbivore biomass similar to AF1, but to a much lesser degree in the open vegetation structure of AF2. After an initial peak 25 years post-removal, herbivore biomass stabilises near the peak level, increasing by +141% (Tab. 2). Omnivore biomass follows a similar trend but with a delay of approximately two years, peaking at +85% (not shown) before stabilising at +77% (Tab. 2). This temporal delay and the close relationship between herbivore and omnivore biomass suggest that large omnivores in AF2 are strongly controlled by large herbivore abundance. In the absence of large carnivores, large omnivores are the sole large predators in this system and play a critical role in regulating herbivore population growth.



165 The body sizes of the largest omnivores in African ecosystems remain unaffected by the removal of either large carnivores or herbivores. While the total biomass of omnivores increases in response to the removal, this increase is driven exclusively by a rise in their population abundance since these ecosystems already support omnivores up to the maximum body size defined by the AFT (200kg).

3.1.2 Canopy Composition

170 Figures 3 and 4 show the impact of the removal on the PFTs on green leaf biomass. In the European mixed forest (EU1, Fig. 3), the low numbers of large mammals in the modelled animal population (as seen in Fig. 1) also result in leaf biomass responses being basically absent. In the European boreal evergreen forest (EU2), however, leaf biomass is reduced by -6% following the removal of large carnivores. By contrast, leaf biomass increases by +10% in response to herbivore removal, but no significant shifts are found in the PFT distribution. In the African model domains (Fig. 4), changes in leaf biomass and PFT
175 composition are visible after removing animals from the simulation. A lasting decline in leaf biomass follows the removal of large carnivores, which is much stronger compared to EU2. The increase in leaf biomass in response to herbivore removal is also visible, but in this case, it is less pronounced than in EU2.

In the tropical rainforest domain (AF1), we find an immediate drop in leaf biomass following the removal of large carnivores as herbivory increases. This reduction is most prominent for the dominant, relatively shade-tolerant tropical broadleaf
180 evergreen (TrBE) trees. Similar to the findings in Krause et al. (2022), shade-intolerant tropical broadleaf evergreen trees are not impacted as strongly. This is partly due to the compensatory effect of increased light reaching the forest floor, combined with the low abundance of shade-intolerant species typical of ecosystems in the late stages of succession. In contrast to tree PFTs, the herbaceous understory benefits from removing large carnivores, which seems contradictory, given the larger pressure from herbivory.

185 In the model system, more light reaching the ground doubles the leaf biomass of grasses in the tropical rainforest until about 50 years after the removal was applied (see Fig. 4), as more photosynthetic active radiation is available for herbaceous photosynthesis (not shown). In response to herbivore removal, an increase in total leaf biomass is visible but less pronounced than in EU2 (+5%). In the moist savanna domain (AF2), the long-term response to carnivore removal is comparable to AF1. However, transient effects are more prominent in AF1. Similarly, the response to large herbivore removal mirrors the herbivore
190 removal response observed in AF1.

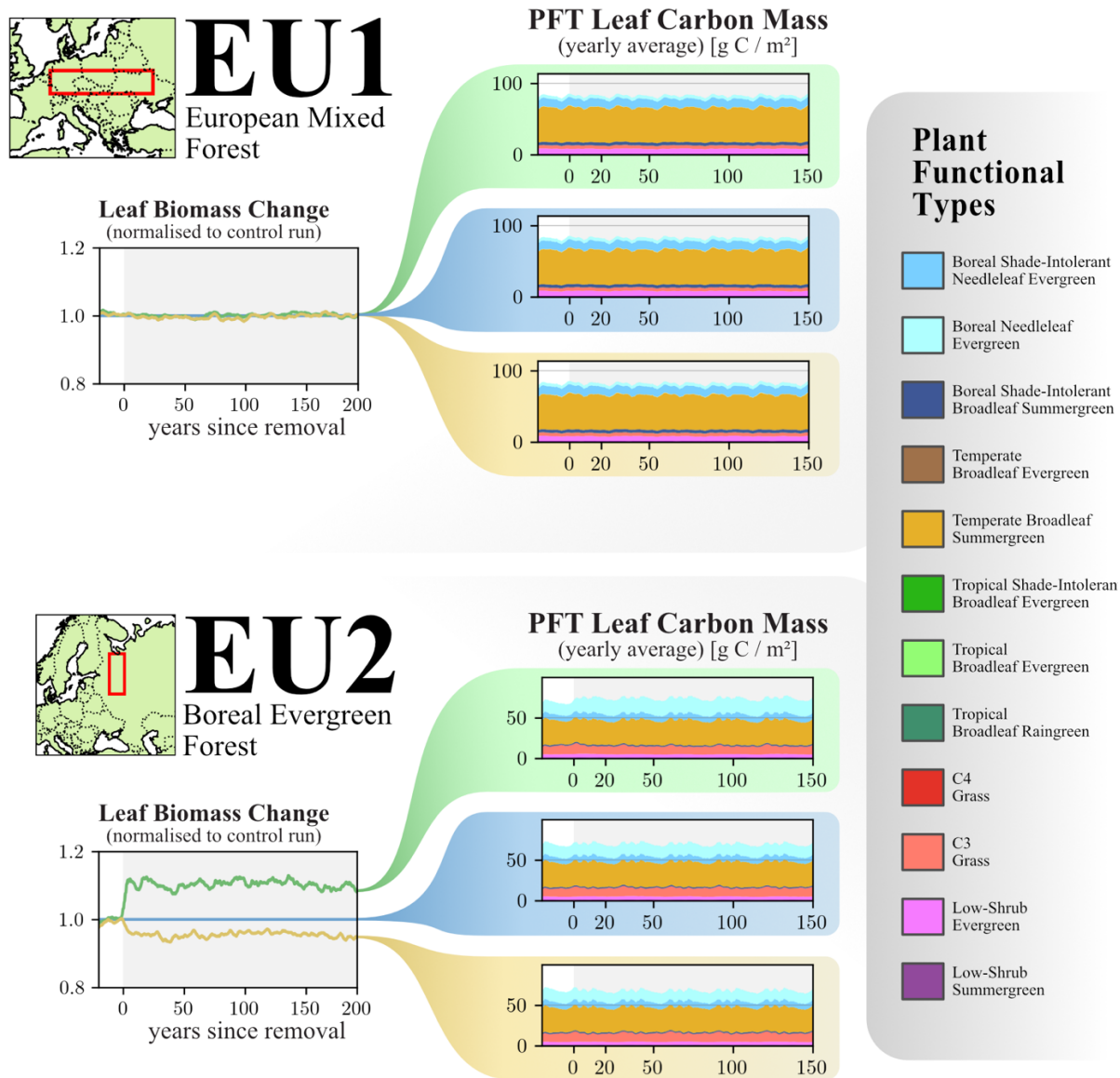


Figure 3: PFT leaf carbon mass responses to cohort removal without the impact of climate change (applying recycled, detrended climate) at the two European locations. The left side of each panel depicts domain-averaged leaf biomass change in response to Madingley’s herbivory, normalized relative to the control simulation. The right side of each panel presents a stacked time series of the different PFTs’ annual average leaf (carbon) biomass. A five-year moving average is used to smooth annual climate-driven fluctuations while preserving short-term responses. Consistent colour coding is described in Fig. 1. PFT colour coding labelled next to the figure.

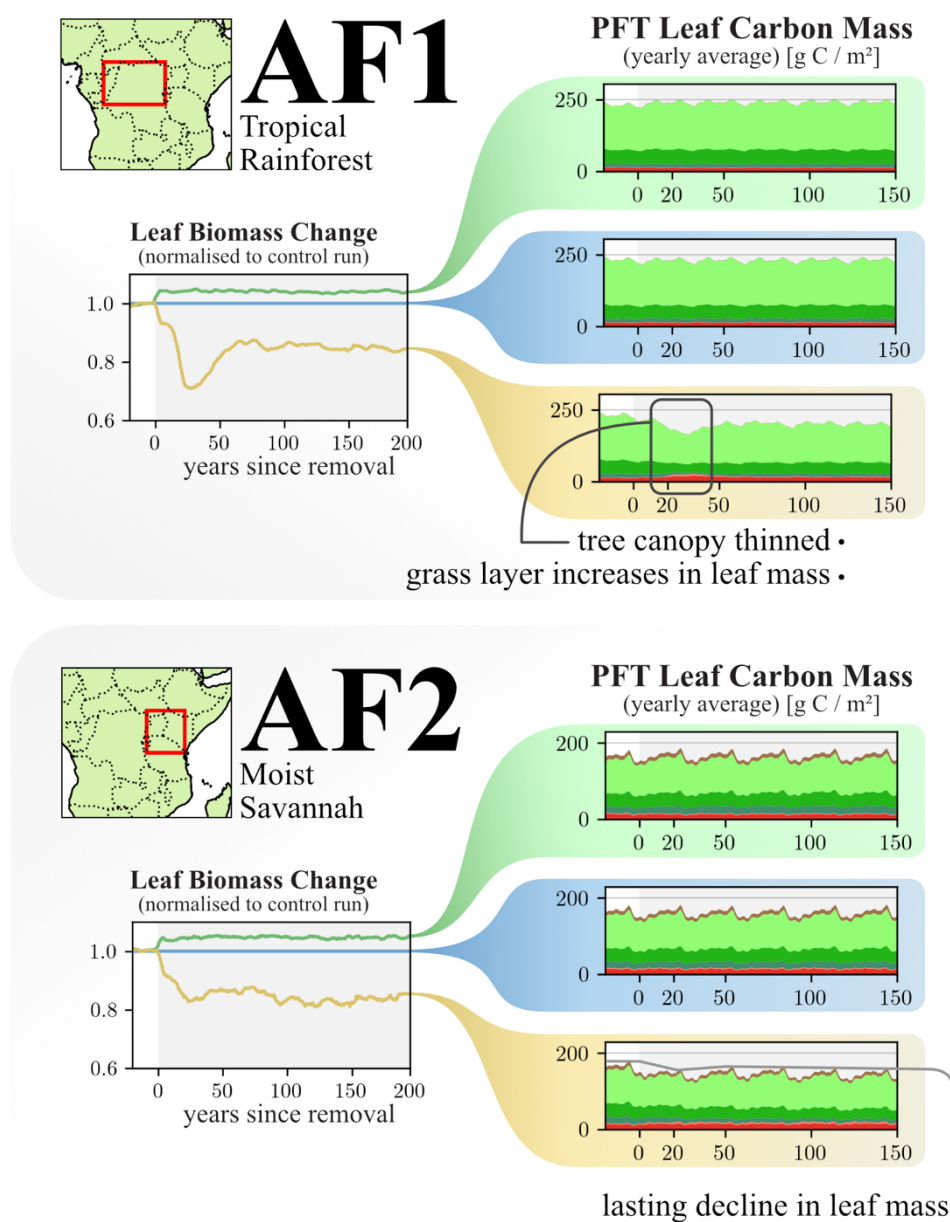


Figure 4: PFT leaf carbon mass responses to cohort removal without the impact of climate change (applying recycled, detrended climate) at the two African locations. The figure's arrangements and colour coding are identical with Fig. 4.

3.2 The Effects of Large Mammal Removal under Climate Change

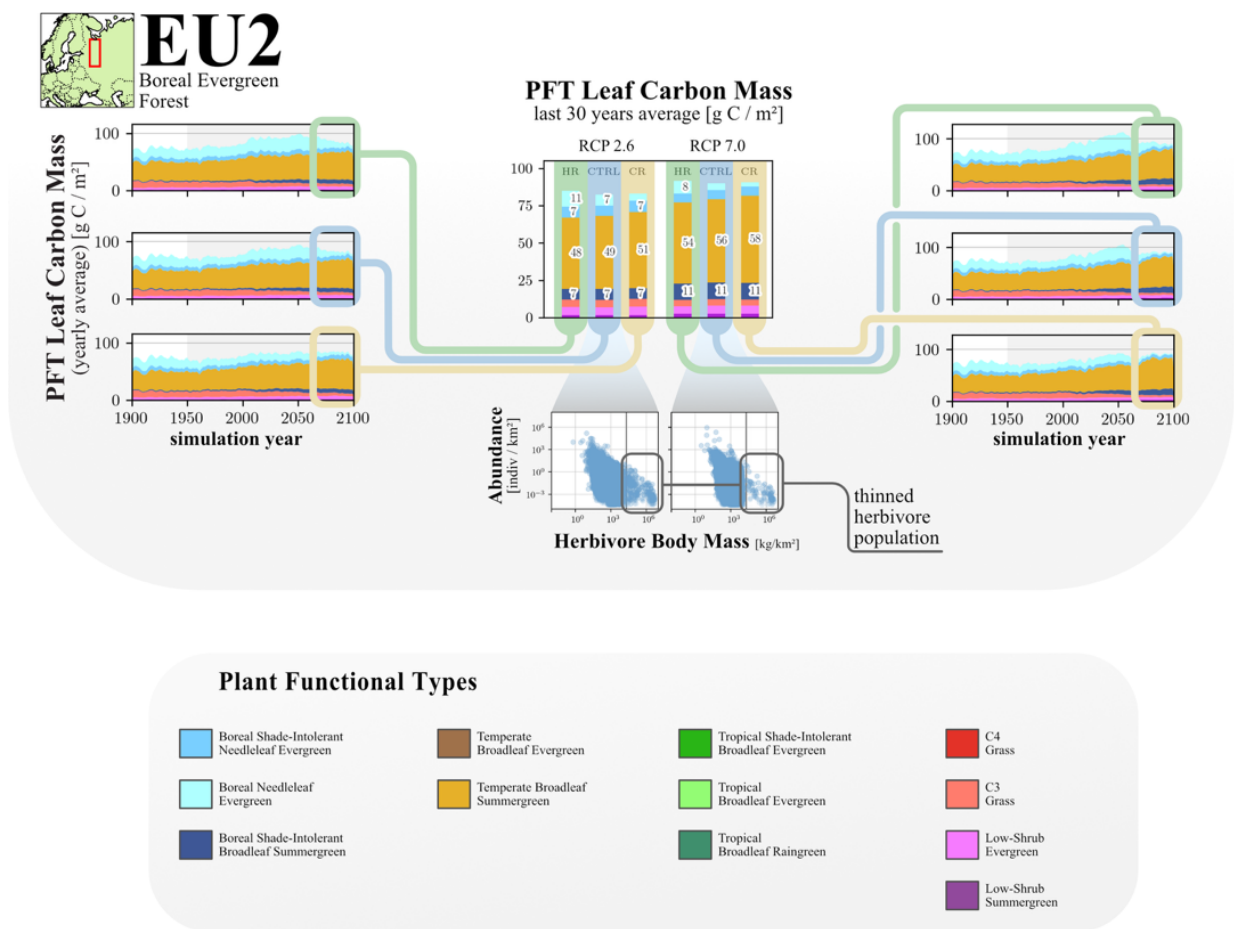


Figure 5: PFT leaf carbon mass responses to cohort removal under RCP 2.6 and 7.0 climate for the EU2 location. The panel shows stacked time series of the different PFTs' annual average leaf (carbon) biomass from 1900-2100. Timeseries to the left show simulations under RCP 2.6 climate, while those to the right show simulations under RCP 7.0 climate. A five-year moving average was used to smooth annual climate-driven fluctuations while preserving short-term responses. The last 30 years of each simulation are averaged and summarised in the middle of each panel. Notable shifts in herbivore populations are presented underneath this central summary for the control simulation in EU2. Consistent colour coding is described in Fig. 1. Consistent PFT colour coding is labelled underneath the figure.

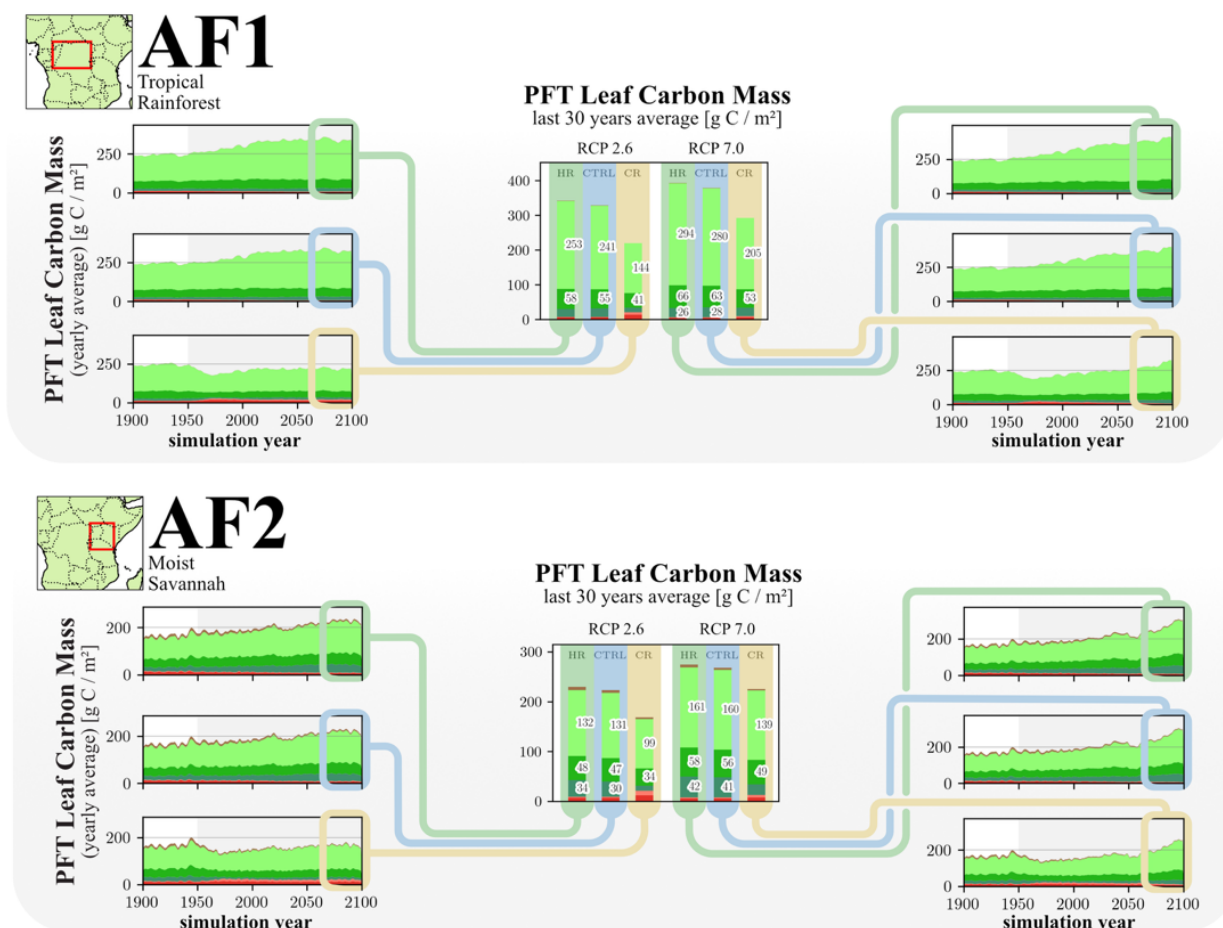


Figure 6: PFT leaf carbon mass responses to cohort removal under RCP 2.6 and 7.0 climate for the AF1 and AF2 location. Consistent colour coding is described in Fig. 1. PFT Colour coding is identical as labelled in Fig. 5.

Figures 5 and 6 illustrate the vegetation's response to cohort removal under climate change. The EU1 domain is excluded from this analysis due to the lack of response to simulated herbivore and carnivore removal (Fig. 1 and 3), as these response patterns did not change during the climate change experiment.

In the absence of animal removal in the boreal evergreen forest domain (EU2), the leaf biomass of boreal needleleaf trees (BNE) increases during the first half of the 21st century (2005–2050). However, from 2050 onward, BNE leaf biomass declines under both climate change scenarios, likely due to warming temperatures. Rising temperatures in both scenarios gradually shift the EU2 domain towards a temperate mixed forest. This effect is more pronounced under the RCP 7.0 high-warming scenario than under the RCP 2.6 low-warming scenario. By the end of the control simulations, the abundance of large herbivore cohorts naturally decreases, particularly under RCP 7.0 (Fig. 5).

The removal of large herbivores in EU2 promotes the growth of BNE trees, especially from around 2000 onwards until approximately 2050. In contrast, the removal of large carnivores results in a reduction of BNE leaf biomass, which remains at



230 near-constant levels from around 2000 until 2050. Beyond 2050, BNE leaf biomass decreases sharply also in the herbivore and carnivore removal experiments, converging to similar levels as in the control run by 2100. In all EU2 simulations under both RCP scenarios, the leaf biomass of temperate broadleaf summergreen (TeBS) trees increases steadily throughout the 1960–2100 period.

In the **tropical rainforest** domain (AF1), without large animal removal, the leaf biomass of tropical broadleaf evergreen (TrBE) trees increases steadily from 1950 onward (Fig. 6). Under RCP 7.0, TrBE leaf biomass continues to rise consistently throughout the 21st century. In contrast, under RCP 2.6, TrBE leaf biomass stabilises around 2070. The leaf biomass of other PFTs remains constant throughout the simulation, making TrBE trees the sole contributors to the overall increase in leaf biomass. Notably, the total leaf biomass is higher under RCP 7.0, driven by a stronger CO₂ fertilisation effect compared to RCP 2.6.

240 The removal of large herbivores in AF1 slightly increases total leaf biomass under both RCP 2.6 and RCP 7.0 scenarios. A much more pronounced response occurs with the removal of large carnivores. The immediate impact on canopy composition closely resembles the response to large carnivore removal in the absence of climate change (Fig. 6), marked by a sharp decline in TrBE leaf biomass and a corresponding increase in C4 grass biomass. Under RCP 2.6, total leaf biomass increases after the initial decline and stabilises after 2010. Large carnivore removal in AF1 promotes the abundance of herbivores (and also omnivores) weighing between 20 to 100 kg, which likely causes the absent (RCP 2.6) and smaller (RCP7.0) leaf biomass increase compared to the control run.

In the **moist savanna** domain (AF2), overall leaf biomass response to climate change is similar to AF1. Under both scenarios, leaf biomass of temperate broadleaf trees - absent in AF1 - declines throughout the simulation due to the expansion of tropical climate zones. The removal of large herbivores or carnivores leads to responses similar to those in AF1.



250 **3.3 Reverting the Effects of Animal Removal**

AFTs Analysed	Simulation State	Top 1	Ø Top 10	Ø Top 5%
Moist Savanna (AF2) under herbivore removal				
Herbivores	pre-removal phase	5.000 kg	4.396 kg	364 kg
	end of removal phase	21 kg	21 kg	21 kg
	post-removal phase	89 kg	78 kg	52 kg
Omnivores	pre-removal phase	200 kg	200 kg	112 kg
	end of removal phase	200 kg	200 kg	113 kg
	post-removal phase	200 kg	200 kg	118 kg
Carnivores	pre-removal phase	205 kg	178 kg	99 kg
	end of removal phase	88 kg	84 kg	63 kg
	post-removal phase	174 kg	173 kg	104 kg
Moist Savanna (AF2) under carnivore removal				
Herbivores	pre-removal phase	5.000 kg	4.396 kg	351 kg
	end of removal phase	5.000 kg	4.666 kg	427 kg
	post-removal phase	4.345 kg	3.744 kg	299 kg
Omnivores	pre-removal phase	200 kg	200 kg	115 kg
	end of removal phase	200 kg	200 kg	157 kg
	post-removal phase	200 kg	200 kg	111 kg
Carnivores	pre-removal phase	209 kg	186 kg	92 kg
	end of removal phase	21 kg	21 kg	21 kg
	post-removal phase	113 kg	109 kg	78 kg

255 **Table 3:** Recovery potential of different AFTs in the moist Savanna biome after ending large herbivore or carnivore removal. The table presents data for endothermic herbivores, omnivores, and carnivores, detailing the weight of the heaviest individual, the average weight of the 10 heaviest individuals, and the average weight of the 95th percentile of individuals. Animal weights are reported for three singular timesteps during the simulations: the undisturbed equilibrium state prior to removal (pre-removal phase), the equilibrium state with the removal employed (removal phase), and the recovering state 200 years after the removal ended (post-removal phase).

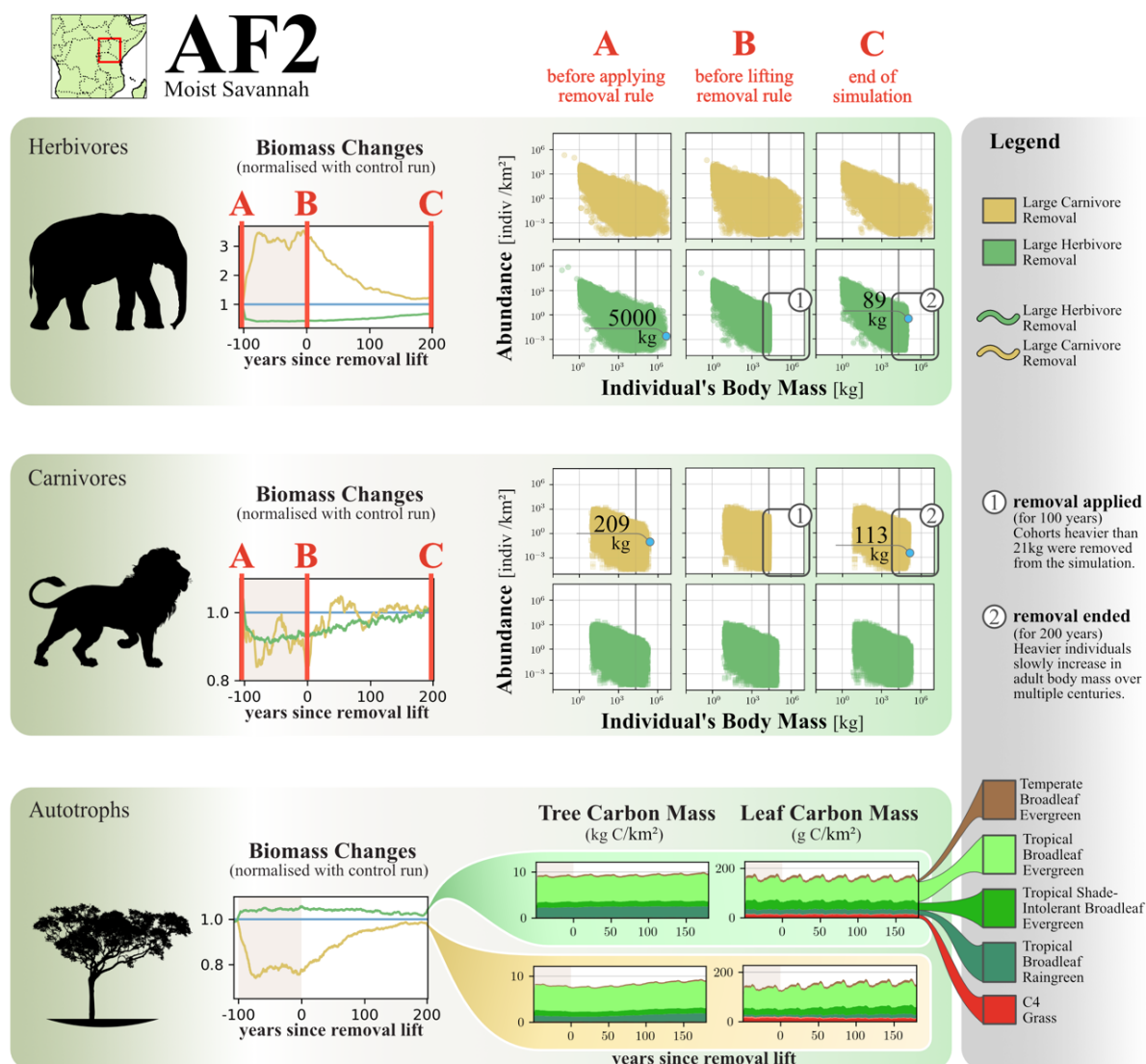


Figure 7: AF2 recovery potential after ending the removal regime (in the absence of climate change). The figure shows responses in three trophic-specific levels (herbivores, carnivores, autotrophs). The left side of each panel depicts the domain-averaged biomass of herbivores (carnivores, autotrophs) normalized relative to the control simulation. The right side of the herbivore and carnivore panel shows the size distribution of animal cohorts at three different simulation stages: (A) undisturbed conditions, (B) after 100 years of consecutive animal removal, (C) after 200 years of recovery. Each data point represents one cohort within a location domain. The right side of the autotroph panels shows a stacked time series of the different PFTs' annual average leaf and tree (carbon) masses. A five-year moving average smooths annual climate-driven fluctuations while preserving short-term responses. In addition to the consistent colour coding is described in Fig. 1, red shading here represents the 100-year removal period. Consistent PFT colour coding is labelled next to the figure.

Figure 7 shows the effect of lifting the otherwise consecutive large carnivore or herbivore removal after 100 years in a simulation without climate change, using AF2 as an example region. After ending the removal of large animals, the size



spectrums of the different AFTs recover over time. Table 3 shows the recovery rates of the endothermic animal size spectrums. When the removal of large herbivores ends, overall herbivore biomass increases slowly until the end of the simulation period. Reinstating the full spectrum of herbivore body masses (i.e. achieving equilibrium biomass) would likely take centuries since large herbivores are overall substantially heavier than carnivores. Two hundred years after stopping removal, the heaviest herbivore found in the model domain weighs 89 kg instead of 5 t in the undisturbed state. Thus, the upper end of the herbivore size spectrum grew 68 kg in 200 years, recovering only 1.4% of the equilibrium size spectrum.

Prior to carnivore removal, the largest carnivore found in the model domain weighs 209 kg. Two hundred years after ending the removal, the largest carnivore living in the model domain weighs 113 kg, reflecting a recovery of 49% of their undisturbed size spectrum. By contrast, two hundred years after ending the large carnivore removal, the herbivore biomass is more or less similar to the undisturbed (pre-removal) state. While the increase in herbivore biomass following carnivore removal is exclusively driven by an increase in the abundance of large herbivores, the subsequent decrease after the removal ends reflects not only a corresponding reduction in large herbivore abundance but also a decline in the maximum body mass of herbivores (Tab. 3). Omnivore biomass levels closely track herbivore biomass trends both during and after the removal of large carnivores. After lifting the removal, the abundance of large and mesoscale omnivores declines, eventually returning to levels simulated prior to the disturbance.

The overall leaf biomass decreases only slowly after ending the removal of large herbivores. After 200 years, leaf biomass levels have hardly changed and are still elevated compared to an undisturbed state. The response of vegetation to carnivore removal and its subsequent reversal is more pronounced. When large carnivores do not act as predators to herbivores, leaf biomass is substantially reduced (Fig. 7). As carnivore biomass increases after ending their removal, herbivore biomass decreases, resulting in a steady increase in leaf biomass towards its undisturbed levels at the end of the simulation period.

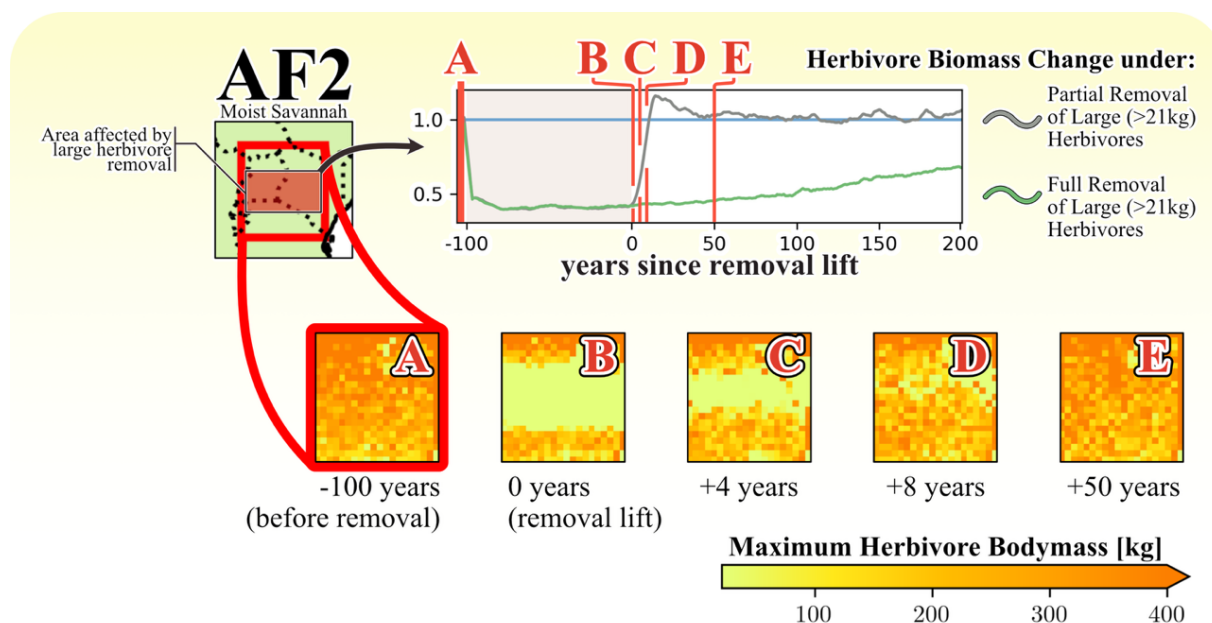


Figure 8: AF2 recovery potential after ending the (partial) removal of large herbivores (in the absence of climate change). The time series depicts the average herbivore biomass in the central domain of the larger AF2 region. All timelines are normalized relative to the control simulation. The green timeline shows herbivore biomass recovery for the simulation, where large herbivores were removed from the entire model domain. The grey timeline shows herbivore biomass recovery from the simulation, where large herbivores were only removed from a central corridor of the model domain. Similar to Fig. 7, red background shading indicates the window in which the removal is active. A five-year moving average was used to smooth annual climate-driven fluctuations while preserving short-term responses. For each grid cell, the largest herbivore inhabiting it is identified. Spatial representations of maximum herbivore biomass across grid cells are plotted in shades of orange and arranged for five different stages of the simulations (A-E).

Figure 8 illustrates the changes in herbivore biomass levels when the removal of large herbivores is only applied partially. Compared to simulations where large herbivores were removed across the entire model domain, herbivore biomass recovers significantly faster after the removal ends. In cases of complete removal, only half of the herbivore biomass recovers within 200 years. In contrast, when large herbivores survive in some parts of the model domain, full herbivore biomass recovery occurs within just 20 years. Moreover, herbivore biomass temporarily overshoots its pre-removal levels before stabilising to similar levels as before the intervention, achieving this equilibrium within 100 years. Figure 8 also shows the spatial distribution of the maximum weight of individual herbivores found in each grid cell. After reallowing large herbivores in the central area of the model domain, the rapid repopulation of large herbivores in this region becomes evident as they migrate from regions where they weren't removed.



4 Discussion

4.1 The Isolated Effect of Animal Removal

We anticipated that **large herbivore removal** results in a shift in vegetation composition, favouring woody biomass as estimated by Bastin et al. (2025) - i.e. a reversal of effects that is supported by paleo-vegetation reconstructions (Pearce et al., 2023). At the EU2 location, the removal of large herbivores results in a slight shift towards a larger proportion of woody leaf biomass, as C3 grass leaf biomass is reduced by -7% (not shown), while overall leaf biomass increases by 10%. In the African model domains, a comparable but less pronounced shift is observed with an increase in overall leaf biomass (+6% AF1) at the expense of leaf biomass from herbaceous PFTs (-5% C3 + C4 grasses, not shown). This result is consistent with recent findings by Nikulina et al. (2025), who described the contribution of megafauna as key factor to vegetation openness.

Empirical animal removal experiments of a scale that allow for comparing our model results to observations are relatively scarce. However, studies in African savannas have demonstrated that herbivore exclusion typically leads to reductions in both tree and grass abundance (-30% and -57%, respectively in a synthesis by Staver et al. (2021)). These experiments differ in their setup (i.e. the size of herbivores excluded), and impacts also depend on the type of herbivory. However, a common response is that in the absence of herbivores, vegetation shifts towards woody cover (Back et al., 2025; Kibet et al., 2021; Levick et al., 2009). Such trends are consistent with other reports of browsers suppressing tree growth (Barnes, 2001; Bond, 2005; Sharam et al., 2006; Staver et al., 2009; Staver and Bond, 2014) and simultaneously releasing grasses. Staver et al. (2021) also highlighted how previous modelling of herbivore impacts in African savannas shows substantially lower effects compared to observations. Our results consistently follow this pattern: The model system does not simulate specific grazer AFTs, which is why we expect the model to underestimate the herbivory pressure on the grass layer.

The proportion of herbivore biomass removed at any experimental location does not result in a corresponding increase in simulated leaf biomass (see Tab. 2). This phenomenon is explained by the underlying competition between herbivores and omnivores. In general, the removal of large herbivores promotes omnivore growth as omnivores have a competitive disadvantage: they are characterised by a lower efficiency at assimilating consumed leaf biomass (68%) compared to herbivores (80%). Omnivores living in environments with sparse vegetation have growth rates that are mainly controlled by leaf biomass supply and hence relatively gain when competition with herbivores is released. In contrast, omnivores living in ecosystems with much denser vegetation do not face regular calorific shortages. Their growth is mainly controlled by predation pressure. Therefore, similar magnitudes of herbivore removal do not elevate omnivore biomasses in Africa as significantly as in Europe, and we cannot expect a similar response of the vegetation's leaf biomass. Ultimately, omnivores and smaller herbivores cannot fill the ecological niche large herbivores inhabit and compensate for their removal. This result is consistent with Pringle et al. (2023), who argued that large herbivore species are not functionally redundant.

In contrast to large herbivores, **large carnivore removal** only eliminates 25% of the overall modelled carnivore biomass. However, the effect of removing these carnivores should not be underestimated due to their lower share of overall animal biomass. Adult carnivores not only control the population of adult herbivores but also place significant pressure on juveniles



of larger herbivores. The offspring of large carnivores compete with adult carnivores of a similar size class for prey. Our results
345 show that removing large carnivores from the simulations decreases the stability of emergent model-wide biomass levels,
which is consistent with previous studies (Hoeks et al., 2020; Miller et al., 2001; Ripple et al., 2014; Van Valkenburgh et al.,
2016).

However, key differences exist between our large carnivore removal experiment and the results reported by Hoeks et al. (2020)
who conducted a similar type of experiment but did not simulate the impact of changing herbivory on plant growth. For
350 Białowieża (Poland), with similar vegetation type to EU1, Hoeks et al. (2020) reported the second-highest response to large
carnivore removal. By contrast, we find that animal-vegetation feedback results in low biomass of large animals at the EU1
site, which consequently minimises the impact of carnivore removal. We elaborate on this model behaviour in the limitations
section (4.4). In our AF2 simulations, large carnivore removal led to a significant increase in herbivore biomass (+141%). By
comparison, Hoeks et al. (2020) reported a much larger increase (+407%) in their corresponding experiment in Serengeti
355 National Park. Here, too, we speculate that these differences originate from missing feedback between animals and vegetation
in the framework used by Hoeks et al. (2020). Incorporating such feedback significantly reduces overall animal biomass levels
by limiting growth rates Krause et al. (2025). This dynamic likely explains why herbivores in Hoeks et al. (2020) were able
to assimilate more biomass following large carnivore removal.

Across all model domains, herbivore responses to carnivore removal followed a similar pattern. Immediately after removing
360 large carnivores, the population of large herbivores and omnivores surges and causes significant damage to the vegetation.
After 20 to 30 years, the vegetation no longer sustains their expanding population. As a result, starvation drives a decline in
herbivore and omnivore abundance. Herbivores tend to suffer more from said starvation, as omnivores are able to adapt to
food shortages. Simultaneously, mesopredators experience a surge due to reduced competition (with juveniles of larger
carnivores) and the increased availability of prey (in the form of juvenile herbivores and omnivores). These dynamics
365 collectively lead to a pronounced rebound effect, significantly reducing the biomass of herbivores and omnivores (Fig. 2). This
rebound effect is most pronounced in AF1, where the rich tropical rainforest vegetation promotes the highest growth rates for
large herbivores and omnivores. However, the rebound effect in AF1 is delayed (compared to AF2) because the abundant leaf
biomass sustains population growth for a longer period. Following the rebound effect, vegetation begins to recover as herbivory
pressure decreases.

Hopcraft et al. (2010) demonstrated that different prey selection strategies, such as specialising on a particular prey body mass
370 (“size-partitioned”) versus adopting a more generalist approach (“size-nested”), can significantly influence the distribution of
predation pressure across the prey body mass spectrum. Carnivory in Madingley follows the “size-partitioned” approach,
which ultimately imposes higher predation pressure on larger animals. However, according to the typology of Hopcraft et al.
(2010), the Serengeti is characterised by a “size-nested” predator-prey pattern. Consequently, the simulated impacts observed
375 for AF2 are likely overestimated, as larger herbivores are probably over-prioritised by carnivores. This hypothesis is supported
by Van Valkenburgh et al. (2016), who argue that elephants – as the largest terrestrial herbivores – are not top-down regulated
by carnivores because of maternal defence of juveniles which greatly reduces predation success rates by modern predators.



More recently, Loft et al. (2025) identified elephants as the main contributor to energy flows across sub-Saharan Africa. Together, these findings strongly suggest that the model system overestimates the impact of large carnivore removal in savanna ecosystems.

However, the overall tendency of large carnivore removal to primarily impact vegetation woody PFTs, resonates with the findings of Ripple and Beschta (2007) who also indicated major impacts on woody vegetation following the removal of large predators. Shade-intolerant or shrubby PFTs are less affected by the increased defoliation, as they benefit from enhanced light availability. Consistent with the conceptual relationship between herbivory pressure and grass growth found in herbivore removal experiments (Staver et al., 2021), increased herbivory pressure (through removing predators) promotes the growth of herbaceous PFTs at the expense of woody PFTs. The herbivore-induced decline in leaf biomass triggers a long-term decrease in whole tree growth and vegetation carbon. These impacts would likely also affect whole ecosystem carbon uptake and pools. Ripple et al. (2014) argued that animals have the potential to cause regional ecosystems to shift from being net CO₂ sinks to sources or vice versa. In our experiment we do not yet explore impacts on total ecosystem productivity, because of crucial missing soil-carbon related processes in Madingley (i.e. CN in animals and their faeces, detritivores).

4.2 Animal Removal under the Effect of Climate Change

While animal-removal is visible under both low-warming (RCP 2.6) and high-warming (RCP 7.0) scenarios the overall impacts of climate change on ecosystems became increasingly dominant towards the end of the simulation, with a concurrent shift in animal populations favouring smaller species. The ecological promotion of lighter individuals (typically ectotherms) reduces the overall influence of large animal removal, rendering their absence less impactful in the evolving ecosystem.

The removal of large animals does not affect ecosystems uniformly when climate change is considered. In the boreal evergreen forests of Europe (EU2), our simulations indicate that removing either large carnivores or herbivores leads to minimal long-term impacts on natural vegetation by the end of the century. Both scenarios show short-term effects, such as increased growth of boreal needleleaf trees following herbivore removal and their suppressed growth with carnivore removal. In the African regions, the influence of large animal removal persists under climate change but varies in magnitude. The effect of large herbivore removal is measurable, but the removal of large carnivores has a far greater impact. In fact, the magnitude of the effects of large carnivore removal is comparable to the effect of climate change on the vegetation (here mainly caused by CO₂ fertilisation). Hooper et al. (2012) have argued that the impact of animals on ecosystems is as large as other (abiotic) drivers of global environmental change. However, given the many processes still absent both in LPJ-GUESS (e.g., drought and heat mortality, herbivore-wildfire interactions, insect outbreaks) and Madingley (e.g., C:N:P stoichiometry, soil-animal biota), it is too early to interpret our results in the light of the synthesis presented by Hooper et al. (2012).

4.3 Reversibility of Animal Removal

Ripple and Beschta (2007) documented the decline of woody vegetation following the removal of grey wolves from Yellowstone National Park. Accompanied by the introduction of livestock, these changes represented an increase in herbivory



410 pressure on the ecosystem. A spatially patchy recovery of woody vegetation was recorded upon a later reintroduction of the
grey wolves (Beschta and Ripple, 2009). The effects said reintroduction were limited by bison that compensated for the losses
in elk abundance but are not hunted by the wolves (Beschta et al., 2020). These observations highlight the complex
interconnections in the food web that are key to assessing reversibility potentials in ecosystems. While the current model
system does not include large herbivores that are excluded from top-down control – like the bison in Yellowstone – and
415 although Yellowstone represents a very different ecosystem, the findings of our study align with the recovery of woody
vegetation patches after carnivore re-introduction.

While Andriuzzi (2025) recently also reported that large carnivore reintroduction alone could not restore ecosystems to their
prior stable state, Pringle et al. (2023) argued that also large herbivores are difficult to replaced functionally. In our simulations,
large herbivores' full recovery takes longer when compared to carnivores because herbivores can potentially achieve much
420 higher maximum body masses. In the coupled model system, this slower growth rate is caused by an increased abundance of
competitors for resources. The large omnivore abundance in the herbivore removal experiment provides food competition for
herbivores. In addition, juvenile herbivores increase prey availability, compensating for the negative effects of competition –
a process that is often upset by maternal defence in nature (Van Valkenburgh et al., 2016) but still missing in the Madingley
model. Together with the potential for higher maximum body mass of large herbivores, recovering their removal would take
425 many centuries in the model system.

In a simulation where large animals are completely wiped out across the whole model domain, the recovery of large animals
depends solely on incremental evolutionary growth and encroachment. However, preserving large animals outside the removal-
affected areas significantly accelerates their reestablishment once the removal regime ends. Similar effects were observed by
Huang et al. (2024), who reported elephants to quickly shift to nearby buffer areas when living conditions change. The
430 effectiveness of this evasive behaviour is directly driven by the connectivity of relatively undisturbed areas. As the Madingley
model assumes vegetation biomass and animals to be well mixed within each grid cell, high levels of connectivity are an
inherent premise of the model. We therefore assume that our simulation results represent the effects of reintroduction in a
landscape, where protected areas are clustered and well connected, as described by Huang et al. (2024). This underscores the
critical importance of protecting large animal species as well as achieving a high effectiveness of protected areas. If large
435 herbivore species go extinct, it may take centuries for natural evolution to produce substitutes, while repopulation through
migration can populate ecological niches much more quickly. This concern is particularly urgent, as approximately 60% of
wild large herbivores are threatened by extinction (Ripple et al., 2015).

4.4 Limitations

4.4.1 The Absence of Large Animals in EU1

440 The EU1 showed limited response to the cohort removal, which can be explained by the interaction of two critical effects.
First, herbivore growth is sensitive to leaf biomass' winter minima, more so than the leaf biomass annual average (Krause et



al., 2022). The high seasonality in boreal environments leads to lower herbivore growth rates compared to ecosystems with more consistent calorific supplies throughout the year. Lowered growth rates extend the time that an individual needs to reach maturity. Such a prolonged youth also exposes juveniles to predation over a longer period, leading to an overall reduced reproduction success rate. This disadvantage counteracts the inherent advantage large animals usually have over smaller ones and puts them at a competitive disadvantage.

A second reason for the observation in EU1 lies in the coupled model's structure. Only one-third of herbivory damage every year is applied to evergreen vegetation, while the full extent of damage affects deciduous vegetation (Krause et al., 2025). This method was chosen to avoid simulating unrealistically large herbivory damage in evergreen PFTs. Thereby, the feedback structure also allows evergreen-dominated ecosystems (like EU2) to sustain larger herbivore populations than deciduous forests with a similar leaf biomass stock (like EU1). As a deciduous forest with high seasonality in leaf biomass, EU1 represents a competition disadvantage for large herbivores and omnivores and, by extension, large carnivores reliant on such prey.

4.4.2 Overestimation of the Maximum Animal Size in the Tropical Rainforest

In our simulations, the largest animals are found in ecosystems with the highest leaf biomass supply. However, this outcome is unrealistic, as we would expect a high abundance of larger animals to thrive in the savannas (AF2) rather than in the rainforests (AF1), where forest elephants are typically rare – even in their natural habitat (Bonnald et al., 2021). This discrepancy between simulation and reality is likely caused by the absence of a vertical feeding structure in Madingley. Unlike in the simulations – where 10% of all leaf biomass is equally accessible for all animals – in actual rainforests, the majority of leaf biomass is located in the canopy, far out of reach for ground-dwelling large animals.

Summary

In this study, we simulated the impact of large animal removal on both the underlying vegetation and the remaining animal population. The removal of large herbivores evidently led to an increase in leaf biomass in boreal biomes (+10%), tropical rainforests (+5%) and moist savannas (+6%). Conversely, removing large carnivores reduced leaf biomass in boreal biomes (-11%), tropical rainforests (-19%) and moist savannas (-19%).

When these effects are compounded by climate change scenarios, general ecosystem shifts caused by climate change overshadowed the effects of large animal removal in the boreal model domain. However, in the African model domains, the suppressing effect of large carnivore removal on productivity proved to be of a similar magnitude as the enhancing effects of CO₂ fertilisation.

Simulations of animal population and ecosystem recovery revealed that the whole system requires centuries to recover from the complete removal of large animals. Ecosystem recovery occurs more rapidly when large animal populations are preserved in unaffected areas. Even though numerous fundamental processes are missing in how vegetation-animal interactions are



represented in the current version of the Madingley/LPJ-GUESS model set-up, these results support the critical role of conserving animal biodiversity in the face of climate change.

Code and data availability

475 The datasets generated during the simulations and the LPJ-GUESS model code are available in the Zenodo repositories published by (Krause, 2026; Krause et al., 2024) under <https://doi.org/10.5281/zenodo.18226328> and <https://doi.org/10.5281/zenodo.11401444>. The original Madingley model code is managed by the UN Environment Programme World Conservation Monitoring Centre (UNEPWCMC) at the University of Cambridge, England. The intellectual property right for the translated version we used in this study is hold by the Radboud University in Nimwegen, Netherlands.

480 Therefore, a public repository link cannot be provided. However, the source can be made available under a collaboration agreement under the acceptance of certain conditions.

Supplement link

The link to the supplement will be included by Copernicus, if applicable.

Author contributions

485 Jens Krause: Conceptualization, Methodology, Writing - Original draft, Visualization.
Peter Anthoni: Software, Validation, Writing - Review & Editing.
Mike Harfoot: Conceptualization, Methodology.
Jens-Christian Svenning: Conceptualization, Writing - Review & Editing.
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490 Competing interests

The authors have no relevant financial or non-financial interests to disclose.

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Financial support

Almut Arneth, Peter Anthoni and Jens Krause acknowledge funding via the Helmholtz Foundation Programme, Changing Earth, Germany. Almut Arneth also acknowledges support by the EU project wilde (GA 101081251). Jens-Christian Svenning was supported by Center for Ecological Dynamics in a Novel Biosphere (ECONOVO), funded by Danish National Research Foundation (grant DNRF173).

Review statement

The review statement will be added by Copernicus Publications listing the handling editor as well as all contributing referees according to their status anonymous or identified.

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