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LETTER

Megagrazer loss drives complex landscape-scale biophysical cascades

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Abstract

Wild animals can modulate ecosystem-climate feedbacks, e.g. through impacts on vegetation and associated carbon dynamics. However, vegetation cover and composition also affect land surface albedo, which is an important component of the global energy budget. We currently know very little about the influence of wild animals on land surface albedo and the resulting climate forcing of these albedo changes. Leveraging a unique, ecosystem-scale, semi-experimental approach, we study how the local removals of the world's largest, terrestrial grazer, white rhinoceros (*Ceratotherium simum*), affected the coupling between fire dynamics, woody encroachment and surface albedo in Hluhluwe–iMfolozi Park (HiP), South Africa. Our path analysis revealed that areas in the park where more rhinos had been removed showed a stronger increase in burnt area and woody encroachment compared to areas with fewer rhinos removed, which were both related to a decrease in surface albedo. Increasing burnt area was further associated with higher rates of woody encroachment, indirectly reinforcing the negative effect of rhino loss on albedo. Our study demonstrates that removals of megagrazers in HiP were related to complex ecosystem-wide cascades with measurable impacts on land cover and surface albedo and consequences on climate forcing. This highlights the importance of restoring functional ecosystems by reinstating trophic processes.

1. Introduction

Natural climate solutions (NCS) are ecosystem conservation and restoration actions that increase carbon storage and/or reduce greenhouse gas emissions (Griscom *et al* 2017). Wild animals are important drivers of ecosystem processes involved in climate regulation (Cromsigt *et al* 2018) and an increasing number of studies highlight the role of wild animals in ecosystem carbon cycling (Schmitz *et al* 2018). This has raised interest in the potential for the restoration and conservation of wild animal populations as a potential NCS (Schmitz *et al* 2023). Although the restoration of animal populations may operate over longer time scales than what is needed for immediate climate mitigation action (Sandom *et al* 2020),

Figure 1. Study area: Hluhluwe–iMfolozi Park.

understanding the role of animals in the climate system has never been more urgent, both for the strategic, long-term stewardship of the climate, and to ensure that the ongoing biodiversity crisis does not exacerbate our climate change mitigation challenges.

In addition to carbon dynamics, recent studies re-emphasize the importance of biophysical feedbacks between ecosystems and the atmosphere, particularly the effects of land cover changes on surface albedo (Hasler *et al* 2024). These studies, together with earlier work on albedo (see for instance Lashof *et al* 1997) suggest that actions that increase the carbon storage of ecosystems (e.g. planting trees) may at the same time reduce surface albedo, which could add to climate warming and reduce, or in some systems even reverse, the carbon removal benefits (Hasler *et al* 2024). When considering the role of wild animals in climate system functioning, it is therefore important to additionally consider their potential effects on biophysical feedbacks, and land cover albedo specifically (Te Beest *et al* 2016, Salisbury *et al* 2023).

Megagrazers (>1000 kg), such as white rhinoceros (*Ceratotherium simum*, rhino from hereon) consume vast quantities of forage per capita, can tolerate low quality grass, and are largely immune to population control by non-human carnivores (Owen-Smith 1988). This allows them to have particularly strong effects on fire regimes and vegetation structure (Hyvarinen *et al* 2021). Megagrazers remove grass biomass, which would otherwise fuel fires, thus limiting fire extent and frequency (Archibald and Hempson 2016). In warm, high rainfall areas with fast growth of grass biomass during the wet season, megagrazers play even larger roles in suppressing fire in the dry season compared to low rainfall areas where grasses grow slower, through their removal of large quantities of potentially flammable biomass (Waldram *et al* 2008, Probert *et al* 2019). Furthermore, they may shape tree–grass ratios, through influencing the fire regime (Smit *et al* 2016, Case and Staver 2017), but also through trampling woody seedlings and through the partial release of trees from grass competition (Riginos and Young 2007).

Tree–grass ratios and fire dynamics are both key determinants of surface albedo. In the short-term, post-fire burn scars have a much lower surface albedo compared to adjacent unburnt grassland, until the burn scar is revegetated (Gatebe *et al* 2014, Dintwe *et al* 2017). In the long-term, however, fires may also strongly affect surface albedo by influencing tree–grass ratios (D'Odorico *et al* 2006). While fire is an important component of open, grassy systems, increasing fire frequency may lead to decreasing fire intensity due to reduced fuel build-up (Rodrigues *et al* 2021). Lower intensity fires that are not able to kill woody seedlings may in fact promote woody plant establishment and recruitment to higher size classes by temporarily reducing grass competition (Walters *et al* 2004). Trees and other woody plants are darker compared to grassy, herbaceous vegetation and heavily-wooded landscapes therefore have a lower surface albedo compared to more open grassy landscapes (Münch *et al* 2019). By affecting fire regimes and tree–grass ratios, we, therefore, hypothesize that megagrazers can have strong effects on surface albedo of the grassland and savanna systems they inhabit.

The last two decades have seen an upsurge in the illegal killing of rhino (Nhleko *et al* 2022) , with significant removal rates in protected areas in South Africa. For this study, we accessed 10 years of spatially-explicit legal and illegal rhino removal data from Hluhluwe–iMfolozi Park (HiP) (figures 1 and 2), creating a fine-scale (1 × 1 km) removal map showing strong spatial contrasts in removal intensities. These intensity contrasts served as a unique natural experiment to study how megagrazer loss influenced changes in woody cover, fire, and surface albedo. We also quantified the albedo-related

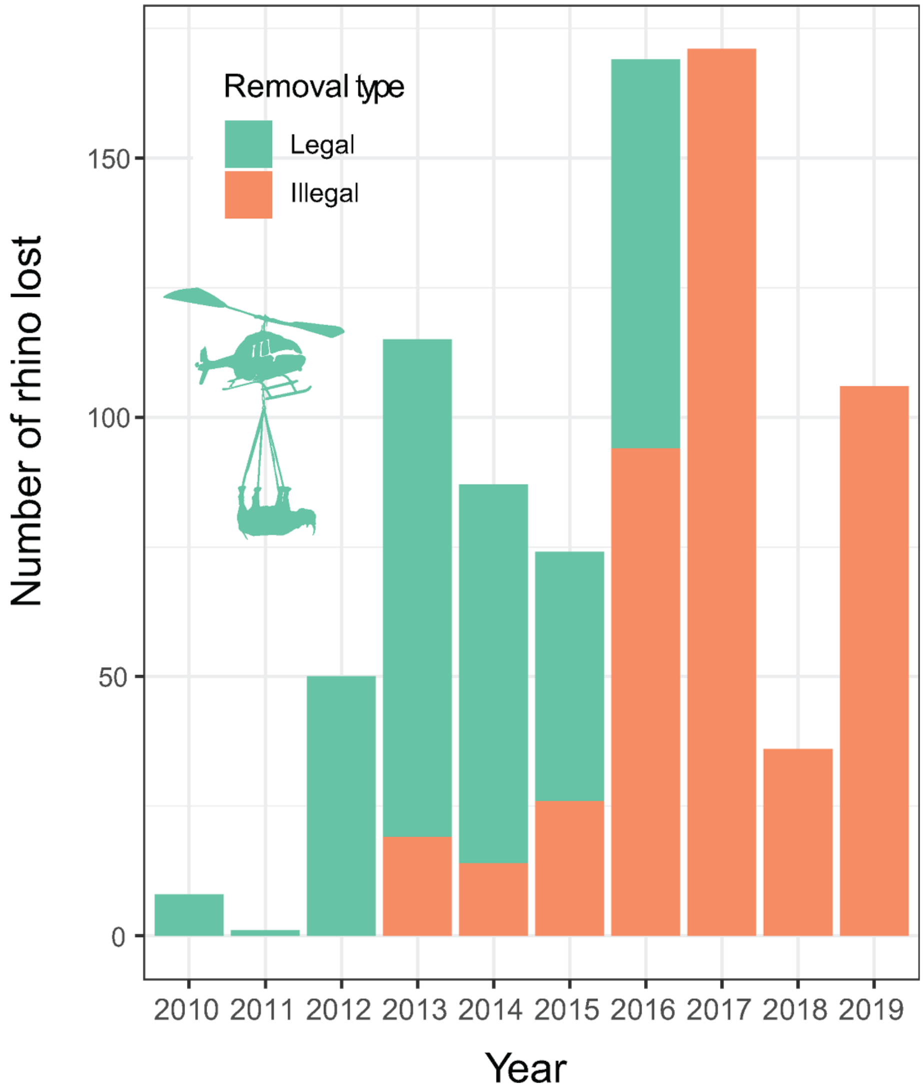

Figure 2. Temporal (2010–2019) patterns of rhino loss in Hluhluwe–iMfolozi Park in South Africa, including legal (management) and illegal (poaching) removals.

climate forcing from these landcover changes. We predicted that rhino loss over the 10 years triggered complex ecosystem-scale responses with strong coupling between woody plant, fire and albedo dynamics. More specifically, we expected (H1): greater burnt area, fire frequency and rate of woody encroachment with more rhino loss, (H2): rhino loss to be associated with woody encroachment directly (through a reduction in trampling) and indirectly through increasing burnt area and fire frequency, (H3): burn scars and woody vegetation to have lower surface albedo compared to unburnt and more open grassland respectively, that (H4): the effects of rhino loss on the fire parameters were stronger in areas with higher rainfall and therefore greater primary productivity, and that (H5): rhino loss-driven increases in burnt area and woody vegetation led to a reduction in surface albedo and a consequent increase in albedo-mediated climate forcing and global warming potential (GWP).

2. Methods

2.1. Study area

HiP, managed by Ezemvelo KZN Wildlife (EKZNW), is a protected area in northeastern South Africa (28.44194°S, 32.22949°E), covering ~960 km^2 with elevations ranging from 45 to 750 m. Annual rainfall ranges from ~490 mm in the southwest to ~910 mm in the northern hills, and most rain falls during summer (figures 3(a) and (b)) (Howison *et al* 2017). Rainfall is considered a good predictor for grass biomass in savanna systems (Deshmukh 1984). While fire is actively managed through prescribed burning, naturally-ignited fires occur regularly, with an average return interval of 2–4 years (Archibald *et al* 2017). Fire extent and intensity are influenced by rainfall and grazing (Archibald *et al* 2017), with higher rainfall areas burning more frequently (Waldram *et al* 2008). The park is dominated by savanna grasslands and woodlands with a varying tree and grass cover,

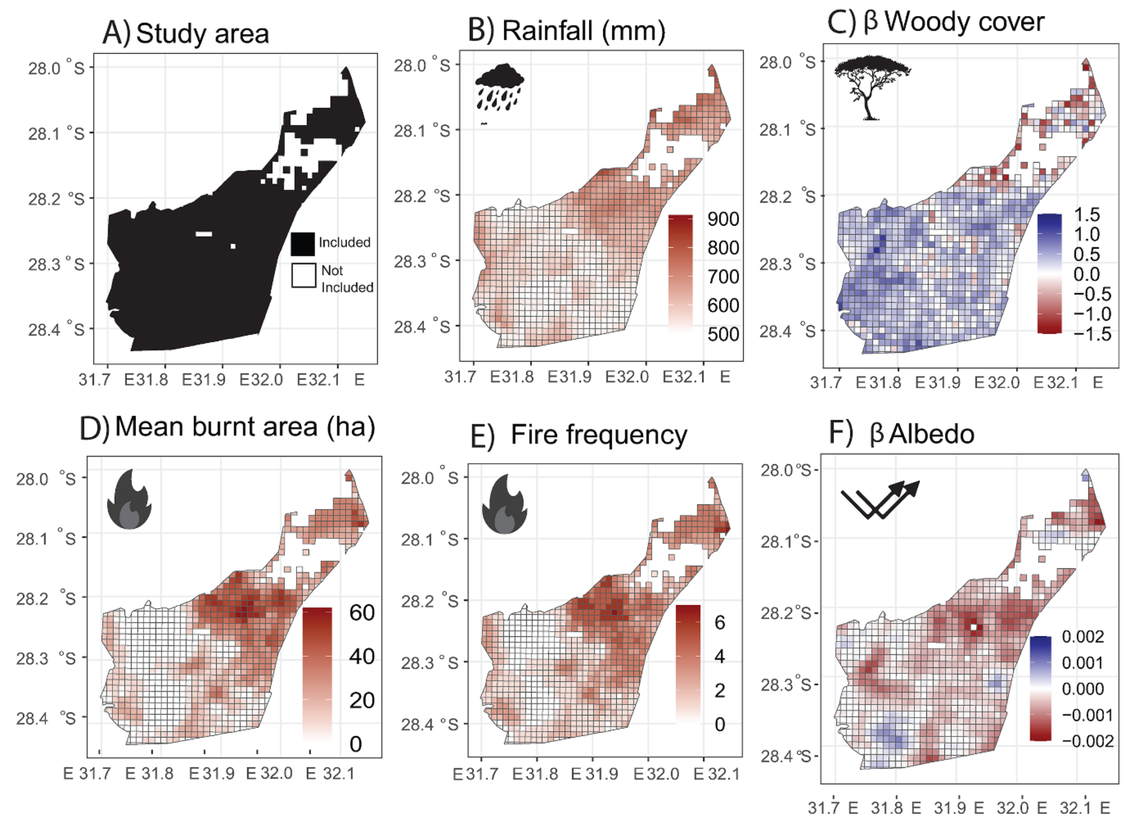

Figure 3. Spatial patterns in (A) the included study area, (B) mean annual rainfall, (C) rate of change in woody encroachment, (D) mean annual burnt area, (E) fire frequency and (F) rate of change in albedo in Hluhluwe–iMfolozi Park in South Africa (2010–2019) in 1 × 1 km grid cells that were used for our analyses.

and patches of heavily grazed ‘grazing lawns’ are distributed throughout the park (Cromsigt *et al* 2017, Cromsigt and Te Beest 2014). For at least four decades, the park has experienced strong woody plant encroachment, where woody shrubs encroach and replace open grass patches (Wigley *et al* 2010, Case and Staver 2017). The park is among the very few places globally that still hosts near-intact mega- and large herbivore and predator communities.

2.2. Rhino removals in HiP

HiP has among the world’s highest white rhino densities (∼2 km^{-2}), which have persisted for several decades. Conservation efforts in the early 20th century increased rhino numbers leading to ∼1500 by the late 1960s. Concerns over high densities of rhino in the park led to legal management relocations, including range expansion (Linklater *et al* 2017). These legal removals fluctuate annually in response to management-determined density limits set for zones within the park. However, since 2013, illegal poaching of rhino surged due to rising demand for rhino horn in Southeast Asia (Wildlife Justice Commission (WJC) 2023). This led to halting of the legal rhino removals in the park in 2016, while illegal poaching continues (figure 2).

2.3. Experimental design

We assessed changes in woody plant, fire and shortwave albedo dynamics along a gradient of rhino loss, including legal and illegal removals at a 1 km^2 spatial scale. Although the average rhino home range often exceeds a single grid cell (0.75–2.6 km^2 for males, 8.9–20.5 km^2 for females (Owen-Smith 1973)), this scale allowed us to assess how localized changes in woody cover, fire, and albedo relate to rhino removal, capturing ecological processes that may be masked at larger scales. To determine the rhino loss gradient, we received permission to use the GPS coordinates for each white rhino removed (legally and illegally) between 2010–2019 (EKZNW Permit number E/5141/02). This permit also allowed us to access rhino aerial counts for the same period for parts of our study area i.e. iMfolozi. Due to sensitivity around rhino poaching, our permit prohibits displaying and sharing spatial data on rhino removals or counts. We overlaid the rhino removal locations and rhino count data on a 1 × 1 km grid and calculated the total number of individuals lost, and mean rhino density for each grid cell over the 10 year period. With only 0.5% of cells showing >10 rhinos lost, we reclassified rhino loss values >10 as 10 to reduce uncertainty from low sample size and high variance at high

Table 1. Summary of the data acquisition for the analysis.

Target variable	Data product	Resolution	Preprocessing	References
Mean annual rainfall (mm yr^{-1})	Long-term mean annual rainfall in HiP.	180 m resolution between 1935 and 2010	Mean annual rainfall data was spatially extrapolated from 17 rainfall stations between 1935 and 2010 using elevation as covariate by Howison *et al* (2017). From this, we derived mean annual rainfall (mm $year^{-1}$) for each 1 × 1 km grid cell.	Howison *et al* 2017
Rate of woody encroachment	MOD44B.006 Terra Vegetation Continuous Fields Yearly Global 250 m accessed with Google Earth Engine	250 m resolution, between 2010 and 2019	We used tree cover estimates from the MODIS product as a proxy for woody plant cover (see figure 2 text S6 for quality check). For each 1 × 1 km grid cell, we derived the mean woody cover across the sampling years (2010–2019), and the rate of change in woody cover as the slope of the linear model with woody cover as the response and year as the predictor.	DiMiceli *et al* 2015, Gorelick *et al* 2017
Mean annual burnt area and fire frequency	FireCCI51: MODIS Fire_cci Burned Area Pixel Product, Version 5.1 accessed with Google Earth Engine	250 m resolution, between 2010 and 2019	We computed the mean annual burnt area for each 1 × 1 km grid cell over the years from 2010 to 2019. We also calculated fire frequency for each grid cell as the number of years that at least one burnt pixel (250 m) intersected the grid cell.	Padilla Parellada 2018, Gorelick *et al* 2017
Rate of change in annual surface albedo	MCD43A3.006 MODIS Albedo Daily 500 m accessed with Google Earth Engine	500 m resolution, between 2010 and 2019	We extracted short-wave white-sky albedo for the entire park for each month between 2010–2019. We eliminated all observations with poor quality. We derived the rate of change in annual albedo for each 1 × 1 km grid cell, as the slope of the linear model with mean monthly albedo as the response and year as the predictor. Here, each grid cell had 12 albedo observations per year (one per month).	Schaaf and Wang 2015, Gorelick *et al* 2017

rhino loss values. We focused on the impacts of rhino loss in grass-dominated savanna, the main white rhino habitat where fire and woody encroachment are most prevalent. Thus, we excluded grid cells dominated by forest or closed-canopy woodland (<25% grass cover between 2015–2019, based on Copernicus Global Land Cover Layers: CGLS-LC100 Collection 3 at 100 m resolution (Buchhorn *et al* 2020)) from further analysis (white areas in figure 3(a)). The same grid was used for all response variables consistently for all years.

2.4. Data collection

We obtained data on mean annual rainfall, burnt area, woody cover and surface albedo across the park between 2010 and 2019. From these products we derived mean annual rainfall, rate of change in woody encroachment, mean annual burnt area, fire frequency and rate of change in annual surface albedo for each 1 × 1 km grid cell (see detailed descriptions in table 1; figures 3(b)–(f)). We included both prescribed and unprescribed fires because we lacked the data to differentiate them. Prescribed fires typically target areas with high grass biomass, which would likely burn naturally. Regardless of ignition source, fire frequency and extent are driven by grass biomass, so we expect both types of fires to respond similarly to rhino loss.

2.5. Statistical analysis

We used piecewise structural equation models (pSEM) in R (package: piecewiseSEM (Lefcheck *et al* 2016)) to test whether rhino loss and its interaction with rainfall influenced woody encroachment directly or indirectly via fire (fire occurrence, burnt area and fire frequency), and whether fire, woody encroachment, and rainfall affected the rate of change in albedo. We built the pSEMs based on *a-priori* hypotheses for each variable and the interactions between the variables (see introduction), such that rhino loss and rainfall were the primary predictors. We first ran the model with fire occurrence (burnt vs. not burnt) and mean burnt area as the fire parameters (pSEM 1 & 2 respectively, see below for difference between 1 and 2), and then with fire frequency as the fire parameter separately (pSEM3).

Each pSEM sub-model was validated independently (see text S1 & S2 for detailed diagnostics for spatial autocorrelation and model assumptions). Submodels with woody encroachment and albedo change as response variables met OLS assumptions and were modeled linearly. However, due to the zero-inflated Gaussian distribution of mean burnt area, we used a hurdle model, separating fire occurrence (presence/-absence) (pSEM1, modeled with a binomial glm in base R) from mean burnt area magnitude (pSEM2, modeled linearly for burnt cells). Both parts of the hurdle model separately met model assumptions. We modeled fire frequency (pSEM3), with a glm specifying Poisson distribution, where no overdispersion was present.

2.6. Quantifying changes in land-cover and albedo driven by rhino loss

For each open to semi-open savanna grid cell (grass cover >25%) that burned and experienced rhino loss over 10 years (26% of all cells analyzed, see table S1), we calculated: (1) change in mean burnt area, and (2) direct change in woody encroachment associated with rhino loss by subtracting observed values from model predictions without rhino loss. This approach allowed us to control for variability between cells and thus to isolate the effect of rhino loss. We also calculated (3) the indirect change in woody encroachment by multiplying the change in mean burnt area (calculation 1 above) by the slope of the mean burnt area term in the pSEM2 submodel where woody encroachment was the response (see text S3 for details). Next, we calculated rhino-associated change in mean annual albedo by multiplying the changes in mean burnt area, direct, and indirect woody encroachment by their respective slopes from the pSEM2 sub-model, where rate of change in albedo was the response (text S3).

2.7. Rhino loss and climate forcing

For each open grid cell, we derived the change in radiative forcing at the top of atmosphere (ΔRF_{TOA}) resulting from the albedo change ($\Delta\alpha$) through the three different pathways (P1- fire, P2- direct woody encroachment and P3 indirect woody encroachment) using the following formula from Chen (2021):

$$\boldsymbol{\Delta RF}_{\mathrm{TOA}} = -\frac{12}{24} \times I_{\mathrm{surface}} \downarrow \times \boldsymbol{\Delta}\alpha_{P1-P3} \times \sqrt{Ta}$$

where $\frac{12}{24}$ refers to the average daylight of 12 h per day, $I_{\mathrm{surface}}{\downarrow}$ = is the mean annual incoming solar radiation at the surface between 2010 and 2019, averaged over the park i.e. 192.5 $\mathrm{Wm^{-2}}$ extracted from LSA SAF (Trigo *et al* 2011), and Ta is the average upwelling transmittance across the park between 2010–2019, i.e. 0.547 (see text S4 for detailed calculations for deriving Ta).

We derived the GWP of the rhino-loss derived albedo changes over the 10 year period for each grid cell that lost rhino through each of the three pathways (P1–P3) expressed in CO_2 equivalents (CO_2e) using the following formula extracted from Zhu *et al* (2024).

$$\boldsymbol{GWP\Delta}\alpha_{\mathrm{P1-P3}} = \frac{S \times \boldsymbol{\Delta RF}_{\mathrm{P1\text{ - }P3}}}{\mathrm{AE} \times \mathbf{AF}} \times \frac{\ln 2 \times M_{\mathrm{CO_2}} \times m_{\mathrm{air}} \times \mathrm{CO_{2}}_{\mathrm{ref}}}{\Delta F_{2x} \times M_{\mathrm{air}}} \times \frac{1}{\mathrm{TH}}$$

where S = area impacted by the albedo change, or the grid cell size (i.e. 1.0×10^6 $\mathrm{m^2}$), AE = the Earth's surface area i.e. 5.1×10^{14} $\mathrm{m^2}$, AF = airborne fraction of CO_2 over 100 years i.e. 0.48, M_{air} and M_{CO2} = molecular weight of air and CO_2 respectively i.e. 28.95 g $\mathrm{mol^{-1}}$ and 44.91 g $\mathrm{mol^{-1}}$, m_{air} = mass of the atmosphere i.e. 5.148 10^{15} Mg, ΔF_{2x} = radiative forcing per doubling of current CO_2 in the atmosphere (W $\mathrm{m^{-2}}$), $CO_{2\mathrm{ref}}$ = the reference partial pressure of CO_2 in the atmosphere i.e. 389 ppm and TH = time horizon i.e. 100 years.

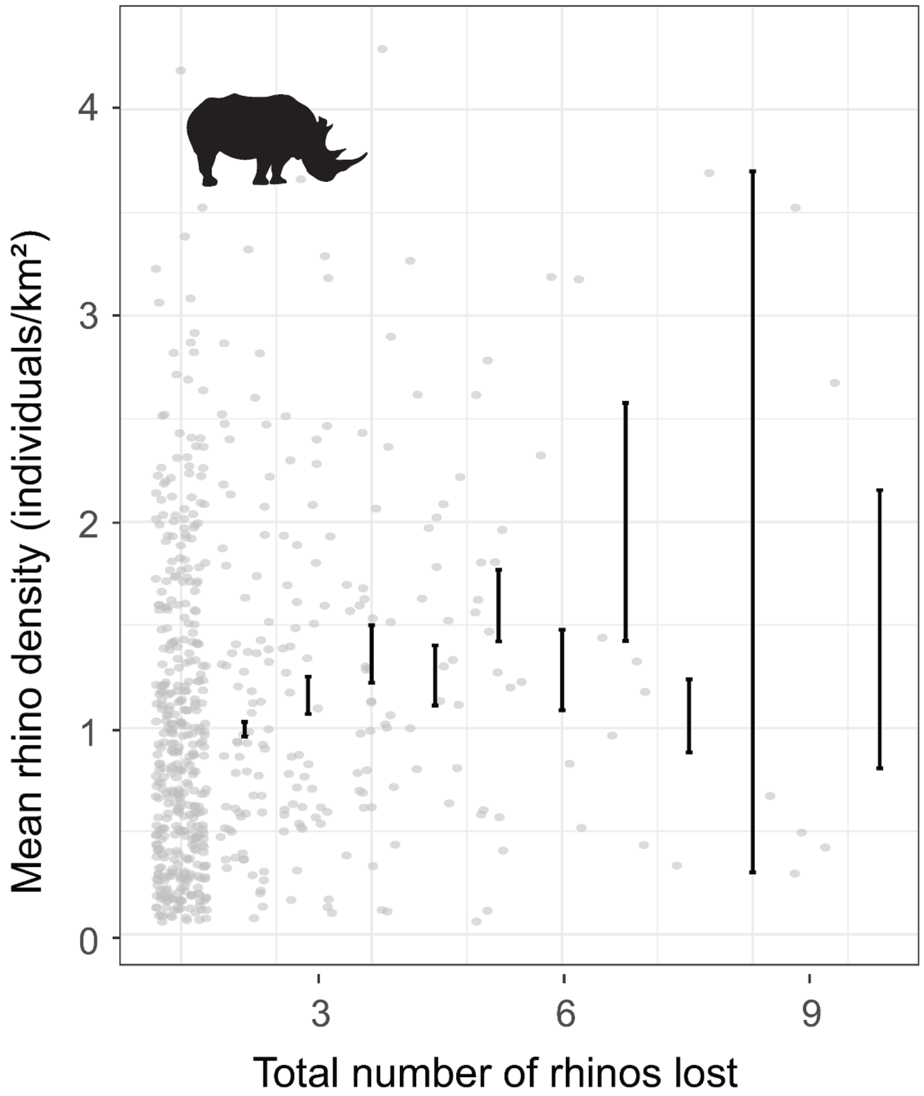

Figure 4. Scatter plot showing the relationship between rhino loss and mean rhino density in the iMfolozi part of Hluhluwe–iMfolozi Park in South Africa (2010–2019) derived for 1 × 1 km grid cells that were used for our analyses. The vertical black lines indicate standard errors for mean rhino density at each rhino loss value.

3. Results

3.1. Rhino loss

The number of legal removals of rhino varied from 8 in 2010 to 75 in 2016, but then stopped, while the number of illegal removals increased from 19 in 2013 to 106 in 2019 (figure 2). Rhino loss took place in 259 out of 886 (29.2%) the open to semi-open savanna grid cells. There was no clear relationship between mean rhino density and rhino loss (figure 4).

3.2. Woody plant cover, fire and albedo

Across the years, mean woody plant cover among the analyzed grid cells varied between 6% and 65% within a grid cell. Woody encroachment (positive rate of change in woody cover) took place in 90% of the open to semi-open savanna grid cells, with the slope (β estimate) ranging between −1.32 and 1.56 with a median of 0.41 ha km^{-2} yr^{-1}. Mean burnt area per grid cell ranged from 0 to 62 ha, averaging 16 ha, and fire frequency ranged from zero to seven, with an average of two fires over 10 years. No fires occurred from 2015 to 2017 likely due to a 2014–2016 drought limiting grass biomass (Mbatha *et al* 2018). Rate of change in albedo varied from 1.0×10^{-3} to -2.2×10^{-3}, with 83% of cells analyzed experiencing a decrease and 17% an increase (see figures 3 and 5).

3.3. Path analysis and biophysical cascades

The effect of rhino loss on burnt area was strongly mediated by rainfall. Specifically, grid cells that lost more rhinos had a larger area burnt at mean annual rainfall >550 mm yr^{-1} rainfall, with 67% of the analyzed cells above this rainfall range. This effect was reversed at very low rainfall levels <550 mm yr^{-1} with just 33% of the cells falling under this rainfall range. Rhino loss was not significantly related to fire occurrence or fire frequency. While cells that burnt had lower rates of woody encroachment compared

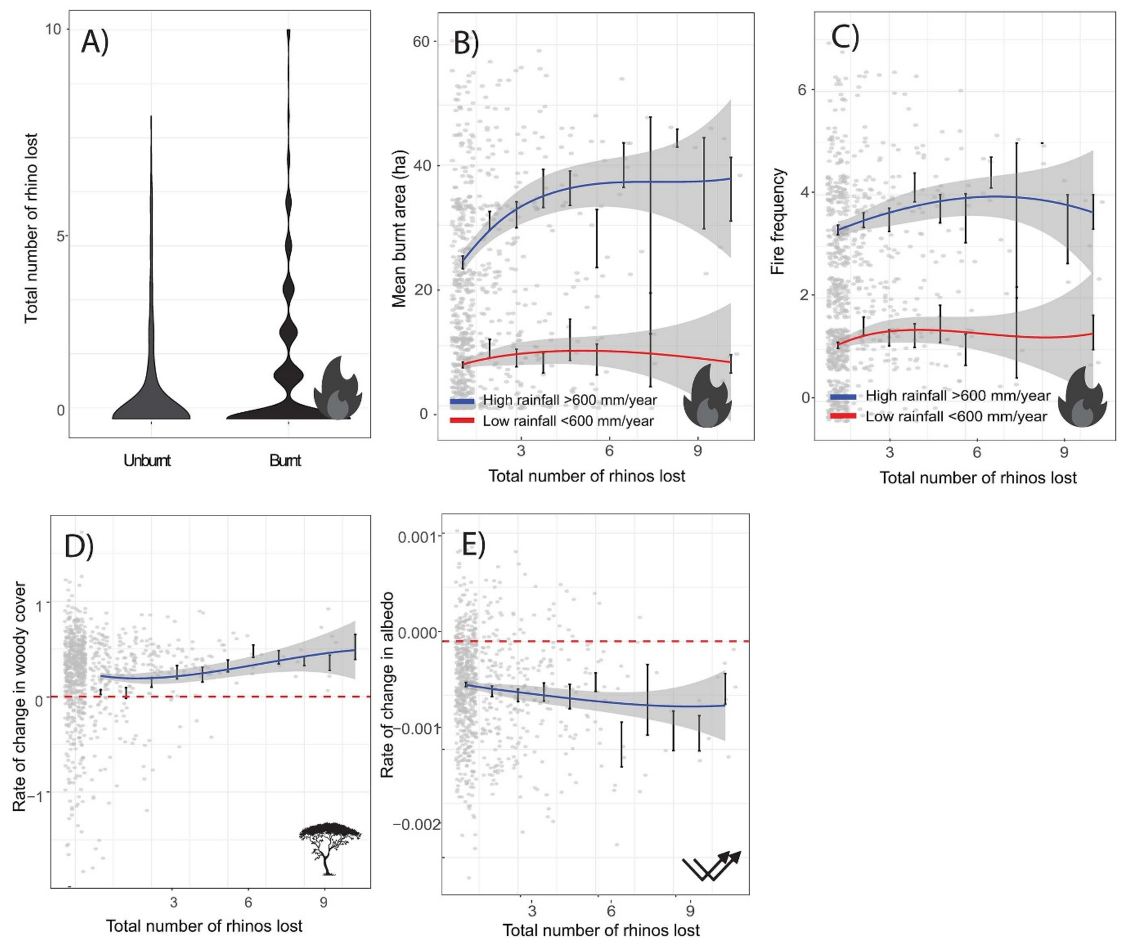

Figure 5. A violin plot and scatterplots showing the relationship between rhino loss and (A) fire occurrence, (B) mean annual burnt area and (C) fire frequency, which are both grouped by rainfall level, (D) rate of change in woody cover and (E) rate of change in annual albedo in Hluhluwe–iMfolozi Park in South Africa (2010–2019) derived for 1 × 1 km grid cells that were used for our analyses, with trendlines fitted using LOESS smoother. The vertical black lines indicate standard errors, and the grey shaded area indicate 95% confidence intervals.

to cells that did not burn, of those cells that burnt, a larger area burnt was associated with higher rates of woody encroachment. Cells with a larger area burnt and more frequent fires and higher rates of woody encroachment experienced greater decrease in albedo (figure 6).

Our model suggests that losing 818 rhinos between 2010 and 2019 across HiP overall accounted for a 8.89 km^2 increase in mean annual burnt area, and at the rate of 0.34 ha km^{-2} yr^{-1} when averaged across the grid cells that lost rhino, 1.49 km^2 (0.06 ha km^{-2} yr^{-1}) direct increase in woody cover and 0.26 km^2 (0.01 ha km^{-2} yr^{-1}) indirect increase in woody cover through fire-related impacts (figure 7).

3.4. Rhino loss and climate forcing

Over the 10 year period at the 1 × 1 km grid scale, rhino loss-driven increase in mean annual burnt area as well as direct and indirect woody encroachment resulted in decreases in mean annual albedo by 3.7×10^{-5}, 8.2×10^{-6} and 1.4×10^{-6} respectively. These changes corresponded to increases in radiative forcing at the top of the atmosphere ($\mathrm{RF_{TOA}}$) by 2.7×10^{-3} Wm^{-2} (with a GWP of 1 845 $\mathrm{tCO_2e}$ km^{-2} yr^{-1}), 5.8×10^{-4} Wm^{-2} (or 2 405 $\mathrm{tCO_2e}$ km^{-2} yr^{-1}) and 1.0×10^{-4} Wm^{-2} (or 2 380 $\mathrm{tCO_2e}$ km^{-2} yr^{-1}) respectively (figures 7 and 8).

4. Discussion

Using a unique semi-experimental approach, our study shows how removals of the world's largest terrestrial grazer were linked to complex ecosystem-wide biophysical cascades. Specifically, we showed that rhino loss was associated with larger area burnt, except where rainfall was low enough to limit grass fuel build up even in the absence of rhino, and higher rates of woody encroachment overall (due both to the direct effect of rhino loss and the indirect effect of larger fires). Larger area burnt and more woody encroachment were both associated with stronger declines in surface albedo, corresponding to increases in climate forcing and GWP.

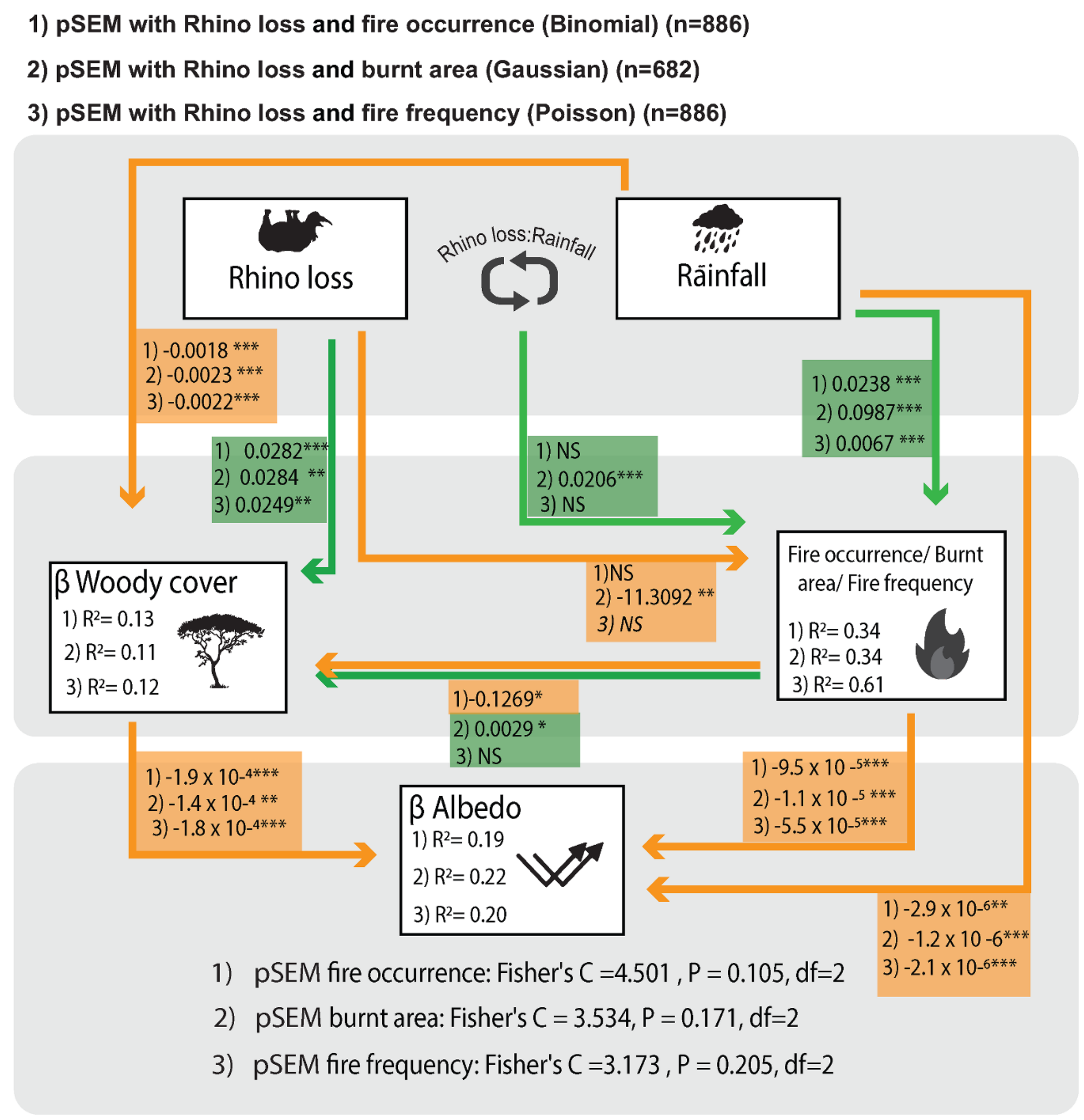

Figure 6. Model output from our piecewise Structural Equations Models where we tested the effects of rhino loss and rainfall on fire, the rate of woody encroachment and rate of change in albedo, and the effects of fire and the rate of woody encroachment on the rate of change in albedo. All open grid cells were used for the pSEM. The figures in the green and orange boxes indicate the sub-model estimates from each three model runs, such that pSEM1 is a model with fire occurrence as a binary variable, pSEM2 is a model with burnt area as a continuous variable (here, we only included cells that burnt) and pSEM3 is a model with fire frequency as the fire parameter. Green arrows indicate positive estimates, orange arrows negative estimates. The significance levels are as follows: $***$ indicates $p < 0.001$, $**$ $p < 0.01$, and $*$ $p < 0.05$. 'NS' indicates a non-significant estimate $p > 0.05$.

4.1. Coupling between megagrazer loss, fire patterns, woody encroachment and land cover albedo

As predicted, rhino loss was associated with an increase in area burnt, but only for grid cells with >550 mm rainfall per year, and higher rates of woody encroachment overall. One mechanism through which rhino influence fire is the creation and maintenance of 'grazing lawns' (Archibald *et al* 2005, Waldram *et al* 2008), a specific community of grazing-tolerant, short-statured grass species that are outcompeted by tall-statured grasses in the absence of grazing. These lawns act as natural fire breaks, reducing the extent and frequency of fires (Hempson *et al* 2015, Johnson *et al* 2018). Another mechanism beyond grazing lawns is the general reduction of tall grass biomass, and thus grass fuel for fire, by grazing (Capozzelli *et al* 2020). For example, Waldram *et al* (2008), found that management-led rhino removal and the subsequent increase in grass biomass accumulation increased fire extent in both low and high rainfall areas of HiP. Similar to our finding, they showed that fire responses to rhino removal were stronger in the higher rainfall Hluhluwe part of the park than in the drier iMfolozi part.

Furthermore, wild and domestic large grazers can limit woody encroachment through grazing-related removal of seedlings and trampling impacts (O'Connor *et al* 2014). Another mechanism,

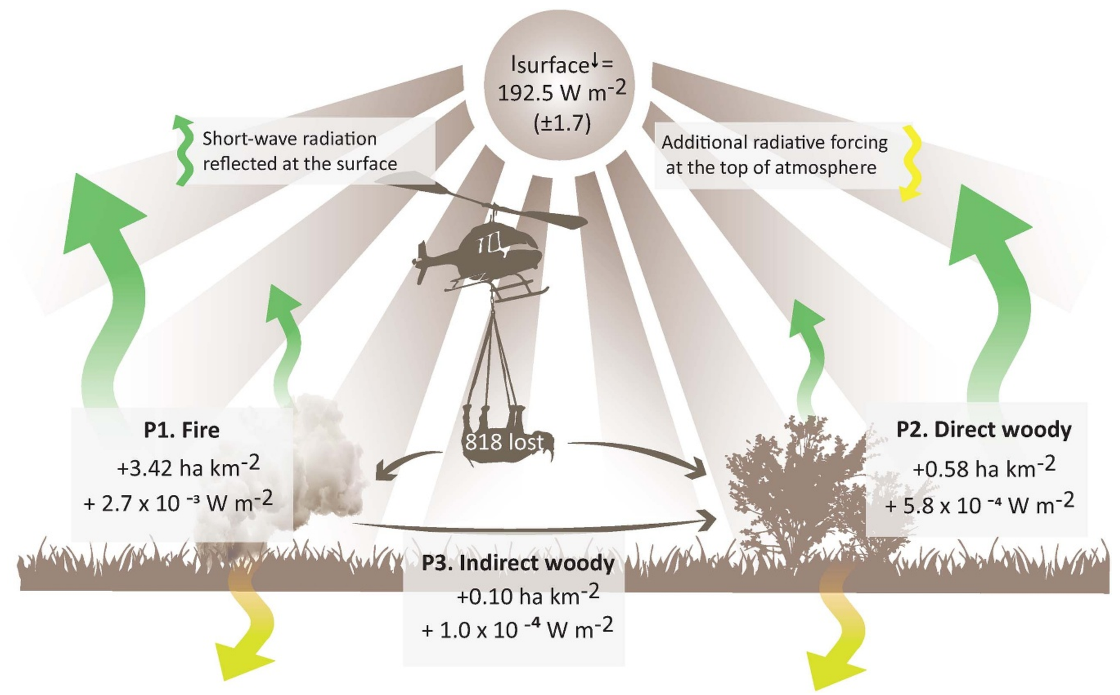

Figure 7. An illustration of the effects of white rhino loss in Hluhluwe–iMfolozi Park (2010–2019) on biophysical climate-vegetation feedbacks through three different pathways. Rhino loss was associated with an increase in burnt area (P1) and an increase in the rate of woody encroachment (P2). Rhino loss-driven increase in burnt area further was associated with an increase in the rate of woody encroachment (P3). Mean annual burnt area and rate of woody encroachment were further associated with stronger decrease in albedo. The radiative forcing values here are presented as radiative forcing at the top of atmosphere i.e. ΔRF_{TOA}.

demonstrated by Voysey *et al* (2021) in HiP, is the concentration of large browsers on rhino-created grazing lawns, which limit woody plant survival nearby the lawns. In addition to these direct effects, we found that rhino loss was associated with more woody encroachment indirectly through changing fire patterns. While burnt area was linked to stronger woody encroachment, fire occurrence (presence or absence of fire) had the opposite effect, meaning cells with fire had a lower rate of encroachment than cells without fire. We speculate that there are two alternative processes at play here. The cells without fire mostly occurred in the drier south western part of the park (figure 3). This region is dominated by short grass, due to heavy grazing pressures, and hence very little grass fuel. We suggest that the lack of fire and heavy grazing in this area of the park promotes woody encroachment (see the mechanisms discussed by Sankaran *et al* 2005, Devine *et al* 2017 for semi-arid savannas). For the cells with fire, a larger burnt area was associated with stronger woody encroachment. Here, we suggest that this is due to the fact that most fires in HiP are relatively cool fires (Cromsigt, personal observations). While intense fires typically reduce woody encroachment by killing plants (Mapiye *et al* 2008, Smit *et al* 2016), low-intensity fires, which do not kill saplings, may encourage woody plant recruitment into fire-tolerant size classes by temporarily reducing grass competition (Walters *et al* 2004, Rodrigues *et al* 2021).

The aerial count data did not show a clear relationship between rhino loss and density (figure 4), as rhino loss was variable across both low and high densities, especially where rhino loss was very high. This made it difficult to separate the effects of rhino loss from density. However, the significant impact of rhino loss on several ecological variables suggests that it affected these variables due to reduced grazing pressure, regardless of density variation. Importantly, removing rhinos from high-density areas may have less effect on grazing pressure than from low-density areas, which could reduce the likelihood of detecting an effect. Despite this potential bias, the presence of an effect in our study supports the robustness of our findings.

4.2. Consequences of rhino-loss-mediated albedo changes for GWP

As expected, landcover changes driven by rhino loss were further associated with reduced surface albedo and increased GWP. Fire-related albedo change had a positive GWP of 1 845 tCO_2e km^{-2} yr^{-1}. This is much higher than the warming from below ground carbon release resulting from increased fire frequencies reported for sub-tropical savanna grasslands i.e. 77.02 tCO2e km^{-2} yr^{-1} (Pellegrini *et al* 2018, Zhou *et al* 2022) (figure 8). Furthermore, the albedo changes from woody encroachment in our study had positive GWPs of 2 380–2 405 tCO2e km^{-2} yr^{-1}, which is more than twice as high

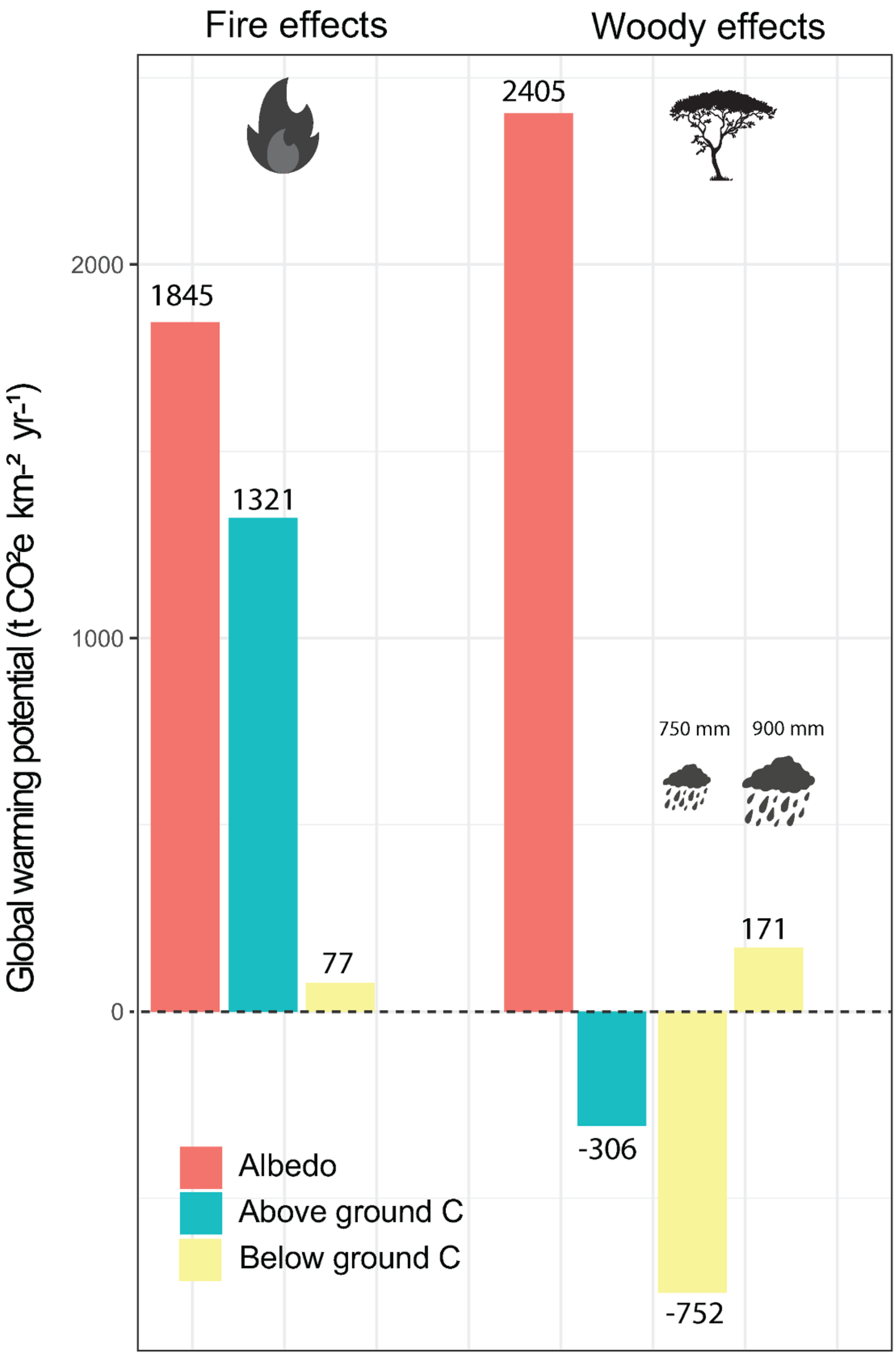

Figure 8. Barplot comparing the global warming potential from albedo vs. carbon impacts (both above ground and below ground) of rhino loss-driven changes in burnt area and woody encroachment. The albedo data are derived from the present study, while the carbon impacts are derived from literature (see text S5 for details).

as the best-case scenario cooling effect from combined above and below ground carbon sequestration. In fact, woody encroachers were reported to sequester from 174.6–305.5 tCO_2e km^{-2} yr^{-1} in their above ground biomass at the 750–900 mm yr^{-1} rainfall areas of HiP, and either sequester up to an additional 752.4 tCO2e km^{-2} yr^{-1} below ground at 750 mm yr^{-1} or release 170.7 tCO2e km^{-2} yr^{-1} from the soil carbon pool at 900 mm yr^{-1} rainfall areas (figure 8) (see text S5 for detailed calculations).

Our albedo-related GWP estimates are consistent with Hasler *et al* (2024), who compared albedo and carbon impacts from tree cover restoration. Our findings suggest that albedo-driven warming from woody encroachment may offset or even reverse the cooling effect of carbon sequestration, especially in high-rainfall areas where soil carbon is reduced. This is important, because many assessments of woody plants on climate often overlook albedo changes, potentially overstating their climate benefits (Griscom *et al* 2017, Roe *et al* 2019).

4.3. Significance and implications of the study for understanding the role of megafauna in the climate system

Importantly, our findings align with those of studies on the consequences of late-Quaternary defaunation, suggesting that this defaunation significantly altered vegetation cover (Gill *et al* 2009, Doughty *et al* 2016, Dantas and Pausas 2022), fire regimes (Gill *et al* 2009, Rule *et al* 2012, Karp *et al* 2021) and surface albedo (Doughty *et al* 2010, Brault *et al* 2013). Furthermore, our findings provide contemporary empirical support for coupling between megafaunal loss, vegetation, fire and climate drivers.

This study advances our understanding of the links between animals and the land-surface climate feedbacks. We show that wild grazers may affect not only carbon dynamics, but also important biophysical climate feedbacks. Our GWP analysis additionally confirms the importance of considering both carbon and albedo when estimating megafauna's net effects on the climate. While we focused on white rhinos, similar mechanisms likely apply to other large wild grazers and livestock in global rangelands, which cover a very large part of the terrestrial surface (UNCCD 2024). We call for further research on the links between grazing, tree–grass ratios, fire, albedo, and climate forcing in rangelands.

4.4. Limitations and future directions

While our study highlighted measurable effects of megafauna-driven landcover changes on the albedo-related climate forcing, the coarse spatial and temporal resolution of our analysis, and various limitations to the data used, mean that our estimated albedo and GWP changes should be considered only ballpark estimates (see further details in text S6). Thus, the emphasis on the interpretation of our findings should be on the relative differences across rhino loss contrasts. To achieve more precise GWP accounting from landcover-related albedo changes, there is a need for data on albedo dynamics at finer spatial and temporal resolution. This is however beyond the capacity of current freely-available satellite data. More suitable tools for such detailed analysis would include handheld or drone-based albedo meters that allow for frequent, high-resolution measurements across space and time (e.g. McGregor *et al* 2024). This approach would advance our understanding of how landcover changes driven by megafauna affect climate through affecting albedo dynamics.

5. Conclusion

The impacts of wild animals on ecosystem carbon uptake and storage have recently gained much interest. However, their potential to regulate biophysical climate-vegetation feedbacks remains largely untested, limiting our understanding of their net effects on the climate system. We demonstrated that the losses of the world's largest terrestrial grazer in HiP between 2010 and 2019 was associated with complex ecosystem-scale biophysical cascades, including changes in burnt area, woody encroachment, and surface albedo, with impacts on climate forcing. This study suggests that large grazer assemblages at natural densities may have substantially impacted climate systems before global human-driven defaunation, and highlights the potential of restoring these processes and the role of wild animals in future Earth and climate system functioning. Finally, these results underscore the urgent need to integrate herbivory into Earth-system models to improve model accuracy and explore herbivore effects under future scenarios.

Data availability statement

The data that support the findings of this study are openly available at the following URL/DOI: https://doi.org/10.5061/dryad.zs7h44jhx.

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References

Archibald S, Bond W J, Stock W D and Fairbanks D H K 2005 Shaping the landscape: fire—grazer interactions in an African savanna *Ecol. Appl.* **15** 96–109

Archibald S and Hempson G P 2016 Competing consumers: contrasting the patterns and impacts of fire and mammalian herbivory in Africa *Phil. Trans. R. Soc.* B **371** 20150309

Archibald S *et al* 2017 10-Interactions between fire and ecosystem processes *Conserving Africa's mega-diversity in the Anthropocene: The Hluhluwe-iMfolozi Park story*, ed J P G M Cromsigt, S Archibald and N Owen-Smith (Cambridge University Press) pp 233–62

Brault M O, Mysak L A, Matthews H D and Simmons C T 2013 Assessing the impact of late Pleistocene megafaunal extinctions on global vegetation and climate *Clim. Past Discuss.* **9** 1761–71

Buchhorn M, Lesiv M, Tsendbazar N E, Herold M, Bertels L and Smets B 2020 Copernicus global land cover layers—collection 2 *Remote Sens.* **12** 1044

Capozzelli J F, Miller J R, Debinski D M and Schacht W H 2020 Restoring the fire–grazing interaction promotes tree–grass coexistence by controlling woody encroachment *Ecosphere* **11** e02993

Case M F and Staver A C 2017 Fire prevents woody encroachment only at higher-than-historical frequencies in a South African savanna *J. Appl. Ecol.* **54** 955–62

Chen J, 2021. Biophysical models and applications in ecosystem analysis (Michigan State University Press) (available at: https://muse.jhu.edu/pub/26/edited_volume/book/82816) (Accessed 20 September 2024)

Cromsigt J P G M and te Beest M 2014 Restoration of a megaherbivore: landscape-level impacts of white rhinoceros in Kruger National Park, South Africa *J. Ecol.* **102** 566–75

Cromsigt J P G M, te Beest M, Kerley G I H, Landman M, le Roux E and Smith F A 2018 Trophic rewilding as a climate change mitigation strategy? *Phil. Trans. R. Soc.* B **373** 20170440

Cromsigt J P G M, Veldhuis M, Stock W, E le Roux, Gosling C and Archibald S 2017 The functional ecology of grazing lawns: How grazers, termites, people and fire shape HiP's savanna grassland mosaic *Conserving Africa's mega-diversity in the Anthropocene: Hluhluwe-iMfolozi Park Story*, ed J P G M Cromsigt, SArchibald and NOwen-Smith (Cambridge University Press) pp 135–60

D'Odorico P, Laio F and Ridolfi L 2006 A probabilistic analysis of fire-induced tree-grass coexistence in savannas *Am. Naturalist* **167** E79–E87

Dantas V L and Pausas J G 2022 The legacy of the extinct Neotropical megafauna on plants and biomes *Nat. Commun.* **13** 129

Deshmukh I K 1984 A common relationship between precipitation and grassland peak biomass for east and southern Africa *Afr. J. Ecol.* **22** 181–6

Devine A P, McDonald R A, Quaife T and Maclean I M 2017 Determinants of woody encroachment and cover in African savannas *Oecologia* **183** 939–51

DiMiceli C, Carroll M, Sohlberg R, Kim D, Kelly M and Townshend J 2015 MOD44B MODIS/Terra vegetation continuous fields yearly L3 Global 250m SIN Grid V006 (NASA EOSDIS Land Processes Distributed Active Archive Center) (https://doi.org/10.5067/MODIS/MOD44B.006) (Accessed 27 May 2024)

Dintwe K, Okin G S and Xue Y 2017 Fire-induced albedo change and surface radiative forcing in sub-Saharan Africa savanna ecosystems: implications for the energy balance *J. Geophys. Res. Atmos.* **122** 6186–201

Doughty C E, Faurby S and Svenning J C 2016 The impact of the megafauna extinctions on savanna woody cover in South America *Ecography* **39** 213–22

Doughty C E, Wolf A and Field C B 2010 Biophysical feedbacks between the Pleistocene megafauna extinction and climate: the first human-induced global warming? *Geophys. Res. Lett.* **37** 15

Gatebe C K, Ichoku C M, Poudyal R, Román M O and Wilcox E 2014 Surface albedo darkening from wildfires in northern sub-Saharan Africa *Environ. Res. Lett.* **9** 065003

Gill J L, Williams J W, Jackson S T, Lininger K B and Robinson G S 2009 Pleistocene megafaunal collapse, novel plant communities, and enhanced fire regimes in North America *Science* **326** 1100–3

Gorelick N, Hancher M, Dixon M, Ilyushchenko S, Thau D and Moore R 2017 Google Earth Engine: planetary-scale geospatial analysis for everyone *Remote Sens. Environ.* **202** 18–27

Griscom B W *et al* 2017 Natural climate solutions *Proc. Natl Acad. Sci.* **114** 11645–50

Hasler N *et al* 2024 Accounting for albedo change to identify climate-positive tree cover restoration *Nat. Commun.* **15** 2275

Hempson G P *et al* 2015 Ecology of grazing lawns in Africa *Biol. Rev.* **90** 979–94

Howison R A, Olff H, Owen-Smith N and Cromsigt J P G M 2017 2 rthe abiotic template for the Hluhluwe-iMfolozi Park's landscape heterogeneity *Conserving Africa's Mega-Diversity in the Anthropocene: The Hluhluwe-iMfolozi Park Story*, ed J P G M Cromsigt, S Archibald and N Owen-Smith (Cambridge University Press) pp 33–55

Hyvarinen O, Te Beest M, le Roux E, Kerley G I H, de Groot E, Vinita R and Cromsigt J P G M 2021 Megaherbivore impacts on ecosystem and Earth system functioning: the current state of the science *Ecography* **44** 1579–94

Johnson C N, Prior L D, Archibald S, Poulos H M, Barton A M, Williamson G J and Bowman D M J S 2018 Can trophic rewilding reduce the impact of fire in a more flammable world? *Phil. Trans. R. Soc.* B **373** 20170443

Karp A T, Faith J T, Marlon J R and Staver A C 2021 Global response of fire activity to late Quaternary grazer extinctions *Science* **374** 1145–8

Lashof D A, DeAngelo B J, Saleska S R and Harte J 1997 Terrestrial ecosystem feedbacks to global climate change *Annu. Rev. Environ. Resour.* **22** 75–118

Lefcheck J S and Freckleton R 2016 piecewiseSEM : Piecewise structural equation modelling in r for ecology, evolution, and systematics *Methods Ecol Evol* **7** 573–9

Linklater W L and Shrader A M (2017). 11 r Rhino Management Challenges: Spatial and Social Ecology for Habitat and Population Management *Conserving Africa's Mega-Diversity in the Anthropocene The Hluhluwe-iMfolozi Park Story*, ed J P G M Cromsigt, S Archibald and N Owen-Smith (Cambridge University Press) p 265

Mapiye C, Mwale M, Chikumba N and Chimonyo M 2008 Fire as a rangeland management tool in the savannas of southern Africa: A review *Tropical and Subtropical Agroecosystems* **8** 115–24

Mbatha N and Xulu S 2018 Time Series Analysis of MODIS-Derived NDVI for the Hluhluwe-Imfolozi Park, South Africa: Impact of Recent Intense Drought *Climate* **6** 95

McGregor S, Cromsigt J P G M, Te Beest M, Chen J, Roy D P, Hawkins H-J and Kerley G I H 2024 Grassland albedo as a nature-based climate prospect—the role of growth form and grazing *Environ. Res. Lett.* **19** 124004

Münch Z, Gibson L and Palmer A 2019 Monitoring effects of land cover change on biophysical drivers in rangelands using albedo *Land* **8** 33

Nhleko Z N, Ahrens R, Ferreira S M and McCleery R A 2022 Poaching is directly and indirectly driving the decline of South Africa's large population of white rhinos *Animal Conservation* **25** 151–63

O'Connor T G, Puttick J R and Hoffman M T 2014 Bush encroachment in southern Africa: changes and causes *Afr. J. Range Forage Sci.* **31** 67–88

Owen-Smith R N 1973 The Behavioural ecology of the white rhinoceros *PhD Dissertation* University of Wisconsin

Owen-Smith R N 1988 *Megaherbivores: The Influence of Very Large Body Size on Ecology* (Cambridge University Press)

Padilla Parellada M 2018 ESA fire climate change initiative (Fire_cci): MODIS Fire_cci burned area pixel product, version 5.1 (Centre for Environmental Data Analysis)

Pellegrini A F A, Ahlström A, Hobbie S E, Reich P B, Nieradzik L P and Staver A C 2018 Fire frequency drives decadal changes in soil carbon and nitrogen and ecosystem productivity *Nature* **553** 194–8

Probert J R *et al* 2019 Anthropogenic modifications to fire regimes in the wider Serengeti-Mara ecosystem *Glob. Change Biol.* **25** 3406–23

Riginos C and Young T P 2007 Positive and negative effects of grass, cattle, and wild herbivores on Acacia saplings in an East African savanna *Oecologia* **153** 985–95

Rodrigues C A, Zirondi H L and Fidelis A 2021 Fire frequency affects fire behavior in open savannas of the Cerrado *For. Ecol. Manage.* **482** 118850

Roe S *et al* 2019 Contribution of the land sector to a 1.5 °C world *Nat. Clim. Change* **9** 817–28

Rule S, Brook B W, Haberle S G, Turney C S, Kershaw A P and Johnson C N 2012 The aftermath of megafaunal extinction: ecosystem transformation in Pleistocene Australia *Science* **335** 1483–6

Salisbury J, Hu X, Speed J D M, Iordan C M, Austrheim G and Cherubini F 2023 Net climate effects of moose browsing in early successional boreal forests by integrating carbon and albedo dynamics *J. Geophys. Res.* **128** e2022JG007279

Sandom C J, Middleton O, Lundgren E, Rowan J, Schowanek S D, Svenning J C and Faurby S 2020 Trophic rewilding presents regionally specific opportunities for mitigating climate change *Phil. Trans. R. Soc.* B **375** 20190125

Sankaran M *et al* 2005 Determinants of woody cover in African savannas *Nature* **438** 846–9

Schaaf C and Wang Z 2015 MCD43A3 MODIS/Terra+Aqua BRDF/Albedo Daily L3 Global—500m V006 (NASA EOSDIS Land Processes Distributed Active Archive Center) (https://doi.org/10.5067/MODIS/MCD43A3.006) (Accessed 27 May 2024)

Schmitz O J *et al* 2023 Trophic rewilding can expand natural climate solutions *Nat. Clim. Change* **13** 324–33

Schmitz O J, Wilmers C C, Leroux S J, Doughty C E, Atwood T B, Galetti M, Davies A B and Goetz S J 2018 Animals and the zoogeochemistry of the carbon cycle *Science* **362** eaar3213

Smit I P J, Asner G P, Govender N, Vaughn N R and van Wilgen B W 2016 An examination of the potential efficacy of high-intensity fires for reversing woody encroachment in savannas *J. Appl. Ecol.* **53** 1623–33

Te Beest M, Sitters J, Ménard C B and Olofsson J 2016 Reindeer grazing increases summer albedo by reducing shrub abundance in Arctic tundra *Environ. Res. Lett.* **11** 125013

Trigo I F, Dacamara C C, Viterbo P, Roujean J L, Olesen F and Barroso C 2011 The satellite application facility for land surface analysis *Int. J. Remote Sens.* **32** 2725–44

UNCCD 2024 GLO rangelands report (available at: www.unccd.int/resources/global-land-outlook/glo-rangelands-report) (Accessed 17 September 2024)

Voysey M D, Archibald S, Bond W J, Donaldson J E, Carla Staver A and Greve M 2021 The role of browsers in maintaining the openness of savanna grazing lawns *J. Ecol.* **109** 913–26

Waldram M S, Bond W J and Stock W D 2008 Ecological engineering by a mega-grazer: white rhino impacts on a South African savanna *Ecosystems* **11** 101–12

Walters M, Midgley J J and Somers M J 2004 Effects of fire and fire intensity on the germination and establishment of *Acacia karroo, Acacia nilotica, Acacia luederitzii* and *Dichrostachys cinerea* in the field *BMC Ecol.* **4** 3

Wigley B J, Bond W J and Hoffman M T 2010 Thicket expansion in a South African savanna under divergent land use: local vs. global drivers? *Glob. Change Biol.* **16** 964–76

Wildlife Justice Commission (WJC) 2023 Rhino horn trafficking as a form of transnational organised crime (available at: https://wildlifejustice.org/rhino-horn-trafficking-report/) (Accessed 7 October 2024)

Zhou Y, Singh J, Butnor J R, Coetsee C, Boucher P B, Case M F, Hockridge E G, Davies A B and Staver A C 2022 Limited increases in savanna carbon stocks over decades of fire suppression *Nature* **603** 445–9

Zhu Q, Chen J, Wu L, Huang Y, Shao C, Dong G, Xu Z and Li X 2024 Changes in albedo and its radiative forcing of grasslands in East Asia drylands *Ecol. Process.* **13** 17