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LETTER

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Grazing herbivores reduce herbaceous biomass and fire activity across African savannas

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Abstract
Fire and herbivory interact to alter ecosystems and carbon cycling. In savannas, herbivores can reduce fire activity by removing grass biomass, but the size of these effects and what regulates them remain uncertain. To examine grazing effects on fuels and fire regimes across African savannas, we combined data from herbivore exclosure experiments with remotely sensed data on fire activity and herbivore density. We show that, broadly across African savannas, grazing herbivores substantially reduce both herbaceous biomass and fire activity. The size of these effects was strongly associated with grazing herbivore densities, and surprisingly, was mostly consistent across different environments. A one-zebra increase in herbivore biomass density (~100 kg/km^2 of metabolic biomass) resulted in a ~53 kg/ha reduction in standing herbaceous biomass and a ~0.43 percentage point reduction in burned area. Our results indicate that fire models can be improved by incorporating grazing effects on grass biomass.

KEYWORDS
burned area, fire, grazing, herbivore exclusion, megafauna, savanna

INTRODUCTION

Grazing herbivores substantially influence terrestrial ecosystem processes (Jia et al., 2018; Pringle et al., 2023; Staver et al., 2021; Trepel et al., 2024), especially in African savannas where wild herbivores can occur at high densities and grass-fuelled fires are frequent (Ripple et al., 2015; van der Werf et al., 2017). Together, these consumer controls not only maintain savannas but also act as critical carbon fluxes in these globally important ecosystems (Archibald & Hempson, 2016; Bond, 2005); savannas account for 30% of terrestrial primary productivity and sequester an estimated 0.39 GtC/yr (Grace et al., 2006). Therefore, balancing global carbon budgets will depend on understanding both direct grazing effects and how they interact with fire (Archibald, 2008;

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Archibald & Hempson, 2016; Waldram et al., 2008) and factors such as rainfall (Johnson et al., 2018; Staver et al., 2021), which strongly constrains both grazing and fire activity across their highly varied range from 300 to 1500 mm/yr (Archibald et al., 2009; Krawchuk & Moritz, 2011; van Wilgen et al., 2000).

A recent synthesis suggested that grazing effects on herbaceous biomass increase with the density of grazing herbivores but could not establish the influences of environmental variables, including rainfall and soil texture (Staver et al., 2021). Rainfall controls trade offs between grass nutrient content and quantity (Coe et al., 1976), while soil texture is related to soil fertility, which may increase the forage quality of herbaceous plants (Bell, 1984), thereby regulating grazing herbivore densities (East, 1984; Hempson, Archibald, & Bond, 2015) and shaping grazing effects indirectly. For example, at the African continental scale, herbivore density peaks at intermediate rainfall and on nutrient-rich soils (East, 1984; Hempson, Archibald, & Bond, 2015). Rainfall and soil nutrients may also influence plant productivity, composition, and traits, which could mediate grazing effects on biomass (Mohanbabu & Ritchie, 2022). For example, in arid and semi-arid savannas (<600 mm/yr), herbaceous productivity and re-growth post-herbivory are moisture-limited and thus strongly correlated with rainfall (Chase et al., 2000; Sala et al., 2012). Several site-specific studies report that grazing effects are dependent on rainfall and soil, but variation in herbivore density across sites is usually not explicitly considered (Anderson et al., 2007; Augustine & McNaughton, 2006; Smit & Archibald, 2019).

It therefore remains unclear whether grazing herbivore impacts depend mainly on grazing herbivore densities or whether their impacts also depend on the direct effects of rainfall and soils on herbivore consumption (top-down) or plant growth (bottom-up) (Ritchie & Olff, 1999). The simplest possibility (H1a) is that grazing impact varies minimally with environmental conditions (Figure 1a,b) because it is mainly determined by grazing herbivore metabolic density (Staver et al., 2021). In this scenario, environmental conditions could still shape grazing effects indirectly via herbivore densities (Hempson, Archibald, & Bond, 2015). Alternatively, environmental conditions may influence per-capita impact of grazing herbivores, with several potential quantitative outcomes. One possibility (H1b) is that grazing effects might be larger at higher rainfall and/or on nutrient-poor soils (Figure 1c,d), if, as some authors have suggested, per-capita consumption increases to compensate where forage quality is poor (Chase et al., 2000; Milchunas & Lauenroth, 1993). Another

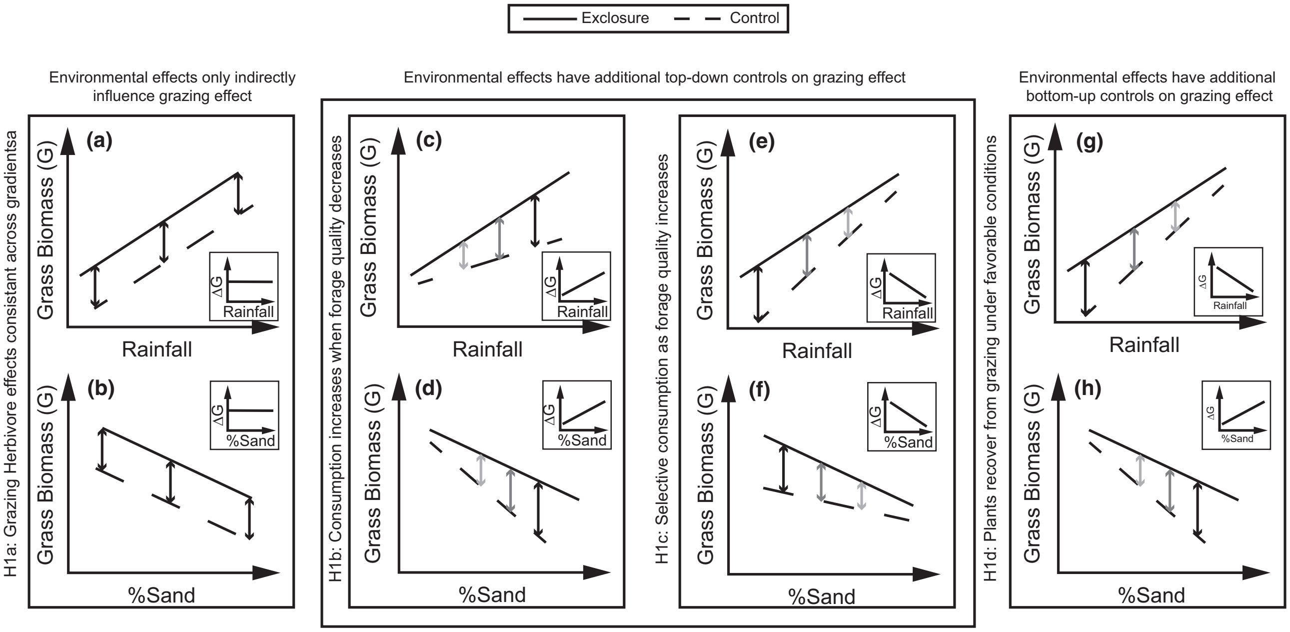

FIGURE 1 Hypothesized environmental controls on grazing effects on grass biomass (G). Grazing effect is measured as the difference between biomass inside exclosures and outside exclosures (control) ($\Delta G = G_{\text{inside}} - G_{\text{outside}}$). Solid lines show the hypothesized relationship between G and environmental variables in exclosure plots and dashed lines show the hypothesized relationship between G and environmental variables outside of exclosure plots (controls). The arrows between the lines represent the difference between exclosure and control plots, which are shown graphically in the sets. a, c, e, g show potential grass biomass and herbivore impact responses to rainfall and b, d, f, h to soil texture. H1a: Rainfall (a) and soil texture (b) may have no effect on grazing effects, resulting in a constant ΔG across the rainfall gradient (if grazer density is overwhelmingly important [Staver et al., 2021]). H1b: Higher rainfall (c) and sandier soils (d) may increase grazing effects (if intake increases as forage quality decreases [Chase et al., 2000; Milchunas & Lauenroth, 1993]). H1c: Higher rainfall (e) and sandier soils (f) may decrease grazing effects (if herbivores preferentially select nutrient rich patches at a finer scale than our herbivore population data capture [Anderson et al., 2007; Borer, 2020]). H1d: Higher rainfall (g) and clayier soils (h) may decrease grazing effects (if grass regrowth at high rainfall and/or on nutrient-rich soils outpaces herbivore consumption [Gurevitch et al., 2000]).

possibility (H1c) is that grazing effects might be larger at lower rainfall and on nutrient-rich soils (Figure 1e,f), if, as others have suggested, per-capita consumption is more efficient and intake higher where forage is more nutritious (Hillebrand et al., 2009; Meyer et al., 2010; van Langevelde et al., 2008). This scenario might also arise for sampling reasons; grazing herbivores sometimes concentrate locally on nutritious, palatable patches (Anderson et al., 2007; Borer, 2020), which can result in higher local densities (e.g., at the site of an exclosure) that are measured at the scale of a reserve. Finally, grazing effects might be larger in all resource-limited settings (H1d; Figure 1g,h); plants' ability to recover from herbivory could contribute to estimates of impact, so any water- and/or nutrient-limitation that decreased plant recovery from grazing might lead to larger herbivore effects (Daskin & Pringle, 2016; Gurevitch et al., 2000).

We tested these hypotheses (Figure 1) using a large dataset (1931 paired measurements from inside and outside exclosures) of herbaceous biomass (grasses and forbs; kg/ha) from eight herbivore exclusion experiments across six savanna sites. This allowed us to evaluate the effects of grazing herbivore metabolic density on grazing impacts across gradients in rainfall, soil texture, and fire frequency on herbaceous biomass. Though most exclosure experiments exclude both browsers and grazers, here we focus our analysis on the effects of grazing herbivore (grazers and mixed feeders) densities specifically because these are the guilds that consume the bulk of herbaceous biomass (Staver et al., 2021). First, we examine which factors impact overall standing herbaceous biomass (G, separately including both 'inside' exclosures and 'outside' controls). We then assessed "grazing impact" via both the difference in herbaceous biomass ($\Delta G = G_{\text{inside}} - G_{\text{outside}}$) and the proportional reduction in herbaceous biomass ($\Delta G / G_{\text{inside}}$). This allowed us to disentangle the effects of environmental variables on the amount of biomass removed by herbivores (the numerator) from the effects of environmental variables on overall herbaceous productivity (the denominator), while also contextualizing past work more fully (Chase et al., 2000; Mohanbabu & Ritchie, 2022; Smit & Archibald, 2019; Staver et al., 2021).

We can also hypothesize how these grazing effects might affect savanna fires. Grazing may influence fire in several different ways. The simplest is that grazing effects may reduce fuel loads and thus the amount of area burned (H2a; Figure 2) (Archibald et al., 2009). However, grazing herbivores can strongly affect the species composition of herbaceous plant communities (Anderson et al., 2007; Koerner et al., 2018; Veblen et al., 2016), favouring plants with higher moisture content and bulk density (Archibald et al., 2019; Simpson et al., 2016, 2022), which are associated with palatability rather than flammability (Hempson et al., 2019), thereby further suppressing fire on 'grazing lawns' (Archibald et al., 2019; McNaughton, 1984) (H2b; Figure 2).

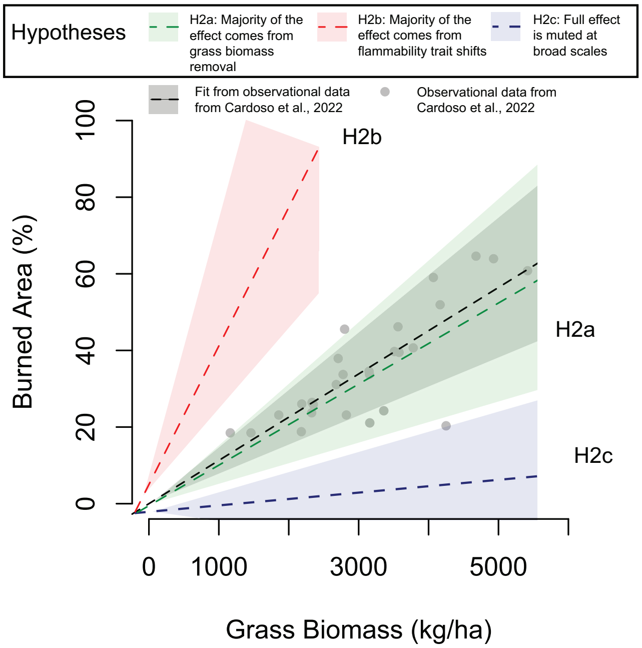

FIGURE 2 Hypotheses for testing the mechanism by which herbivores affect burned area. Grey points and the black best-fit line replotted from data published in Cardoso et al. (2022), with shading representing the 97% confidence interval. Each coloured line represents a hypothesis that would be supported by the comparison of herbivore derived $\Delta BA / \Delta G$ effect. The green line represents support for H2a: grazing herbivores impact burned area mainly by removing fuels. The red line represents support for H2b: grazing herbivores have additional amplifying impacts on fire activity by additionally reducing plant community flammability. The blue line represents support for H2c: some compensating process reduces the effects of grazing herbivore fuel removal on fire regimes or local herbivore effects do not fully scale-up to impact broad-scale burned area. Intercepts were set to zero for plotting, and intercept from the best-fit line of the data from Cardoso et al. (2022) was added to the data to directly compare the slopes and datapoints on the same graph.

Additionally, herbivore reductions in fire may not have the same effect across the rainfall gradient, because fire spread is governed by both fuel load and fuel moisture thresholds (Alvarado et al., 2020; Cardoso et al., 2022). In arid savannas, sparse and patchy fuel loads limit fire spread by reducing fuel connectivity. In contrast, in humid savannas, fuel loads are higher and more continuous, so fire spread is instead limited by high fuel moisture. Given that these dynamics vary across a rainfall gradient, the same magnitude of herbivore reduction in herbaceous biomass may have a greater effect on fire activity in lower rainfall areas, where fuel loads are more limiting to fire spread. To test how environmental conditions moderate herbivore–fire relationships, we evaluated herbivore metabolic density effects on burned area reductions (ΔBA) (see Materials and Methods) using a spatially extended remote-sensing dataset across 31 African reserves, combined with previously published on-the-ground estimates of grazing herbivore metabolic density from Hempson, Archibald, and Bond (2015).

Finally, we combined results from both the herbivore exclusion and fire-reduction analyses to ask whether herbivore effects on fuel loads (ΔG) are sufficient in magnitude to account for observed herbivore effects on burned area (ΔBA). To do this, we calculated the ratio of burned area to grazing effects due to herbivores (ΔBA/ΔG), which we compared with the observed relationship between burned area and grass biomass derived from observations in Kruger National Park (KNP) (Cardoso et al., 2022) (H2a-c; Figure 2).

Together these datasets allow us (1) to quantify the magnitude of grazing effects on herbaceous biomass and fire activity, (2) to test whether these effect sizes varied across environmental gradients, and (3) to evaluate the mechanisms by which grazers act on fire activity broadly across African savannas.

MATERIALS AND METHODS

Herbivore exclusion experiment and spatial data sources

Herbaceous (i.e., grass and forb) standing biomass data were collected from paired exclusion and control plots from eight different exclosure experiments in six African sites, resulting in a total of 1931 paired measurements (Figure 3a). Some of these data were accessed from previous publications (Charles et al., 2017; Jacobs & Naiman, 2008; Mohanbabu & Ritchie, 2022; van Coller et al., 2013), while most were contributed directly by co-authors. Soil texture, fire frequency, and rainfall data were either contributed by co-authors or reported in previously published work where experimental design is described (Anderson et al., 2007; Burkepile et al., 2017; Charles et al., 2017; Craine et al., 2008; Goheen et al., 2018; Jacobs & Naiman, 2008). Herbivore densities were derived from Hempson, Archibald, & Bond (2015) except for Gorongosa, which we extracted from Stalmans et al. (2019) and specified by year because herbivore densities in this recovering system increased substantially during the exclosure experiment (Guyton et al., 2020). We estimated metabolic density by calculating individual body mass as kg^b, where b is the allometric scaling exponent of metabolic rate (Kleiber, 1932), and multiplying by individual density per km^2 of grazers and mixed feeders. For individual body mass, we used species average body mass estimates from Hempson, Archibald, & Bond (2015). To account for potential uncertainty in the metabolic scaling exponent b, we compared three approaches, first using b=0.75 for livestock from Kleiber (1932) and b=0.899 for African wildlife from Lovegrove (2000)

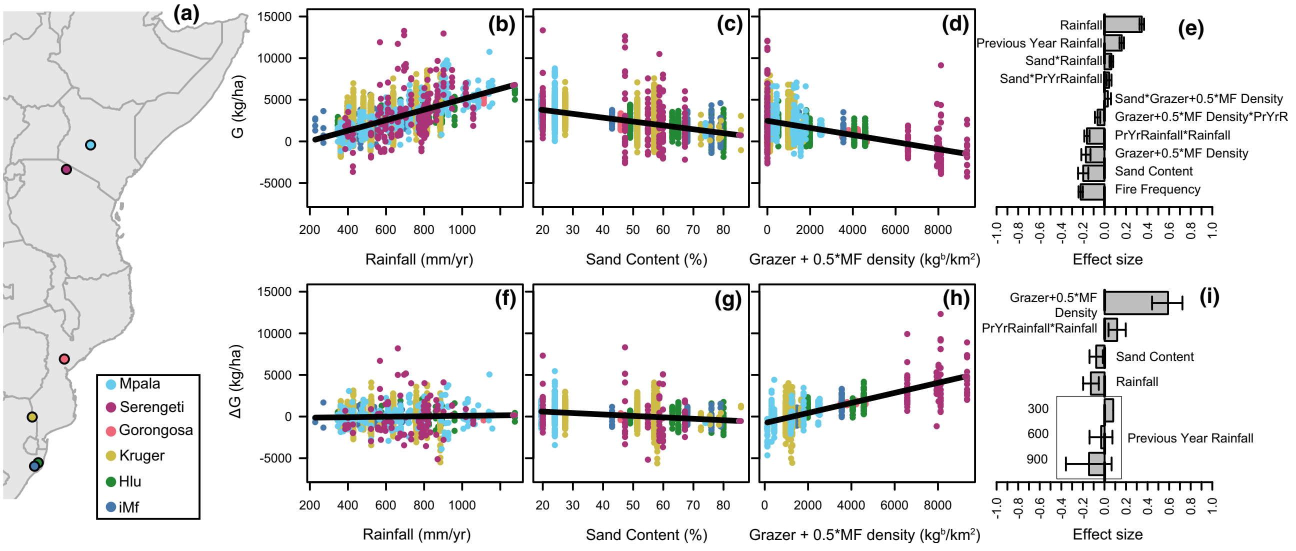

FIGURE 3 The effects of bottom-up and top-down controls on grass biomass (G) and grazing effect ($\Delta G = G_{\text{inside}} - G_{\text{outside}}$) in African savannas. Black lines represent the best-fit models. To visualize the response for single predictor variables (plotted on the x-axis), partial dependences (points plotted on the y-axis) are calculated by holding all variables other constant (b–d; f–h), which causes y-axis values for the same observation to vary across plots. Pr Yr rainfall stands for the previous year rainfall. (a) Map of reserves with herbivore exclusion experiments included in this analysis. (b) Partial dependences of grass biomass (G) for annual rainfall. (c) Partial dependences of grass biomass (G) for soil sand content. (d) Partial dependences of grass biomass (G) for grazing herbivore metabolic density (grazers and one-half of mixed feeders). (e) Scaled effect sizes for fixed predictor variables for best-fit linear mixed-effects model with grass biomass (G) as the response variable. Reserve/plot/treatment were nested random effects. AIC$_c$=8219.641; Conditional R^2=0.81; Marginal R^2=0.23. (f) Partial dependences of herbivore impact (ΔG) for annual rainfall. (g) Partial dependences of herbivore impact (ΔG) for sand content. (h) Partial dependences of herbivore impact (ΔG) for grazing herbivore metabolic density (grazers and one-half of mixed feeders). (i) Scaled fixed effect sizes for predictor variables for best-fit linear mixed-effects model with herbivore impact (ΔG) as the response variable. For quadratic fits (Pr YR Rain and Rain), effect sizes were calculated at discrete rainfall amounts to show the magnitude and direction of the effect size change over the range of rainfall values. Reserve/plot/time since experiment started were nested random effects. AIC$_c$=4954.1; Conditional R^2=0.61; Marginal R^2=0.27.

(following Staver et al., 2021), (2) a taxonomic order-level average (Genoud et al., 2018), and (3) a species-specific value when available, otherwise a taxonomic order-level average (Genoud et al., 2018) (Figures S1 and S2; Table S1). The 'best' method for estimating metabolic biomass density (selected via AICc value for models of ΔG ($G_{\mathrm{inside}} - G_{\mathrm{outside}}$)$\sim$metabolic density; Table S2) was using the order-level b with a halved contribution from mixed feeders. However, ΔG estimates of all three scaling exponents were within error of each other (Z-test, $p \gg 0.05$) (Figure S2a), which indicates that the choice of metabolic exponent is not a significant source of uncertainty in model results (see supplement for more detail).

For analysis of the burned area, we selected 31 African reserves with good-quality herbivore density data from Hempson, Archibald, and Bond (2015). We examined relationships between mean annual burned area (MODIS 6 monthly product; MCD64A1) (Giglio et al., 2015), mean annual rainfall (WorldClim) (Fick & Hijmans, 2017), seasonality (WorldClim) (Fick & Hijmans, 2017), soil texture (SoilGrids) (Poggio et al., 2021), woody cover (Landstat-based rescaled MODIS VCF) (Sexton et al., 2013) and herbivores across these 31 reserves, where we could safely assume that human populations were small and agricultural activities limited (see supplement for more detail).

Statistical modelling

Analysis of grazing effects on herbaceous biomass in herbivore exclusion experiments

All statistical analysis were conducted in R v 4.0.3 (R Core Team, 2020) using the packages 'lme4' (Bates et al., 2015), 'quantreg' (Koenker, 2021), 'MuMIn' (Bartoń, 2020) and 'visreg' (Breheny & Burchett, 2017). We ran linear mixed-effects models with three different response variables: standing herbaceous biomass (G, both inside and outside are included as separate data points in the model), absolute change in herbaceous biomass ($\Delta G = G_{\mathrm{inside}} - \mathrm{G}_{\mathrm{outside}}$), and proportional change in herbaceous biomass ($\Delta G/G_{\mathrm{inside}}$). For each set of models, rainfall, the previous year rainfall, average fire frequency, grazing herbivore density, and sand content were modelled as fixed effects. 'reserve', 'experimental plot', and 'treatment (control/experiment)' were modelled as having nested random intercepts (1|Reserve/Plot/Treatment) for the G model. For ΔG models, 'reserve' and 'experimental plot' were modelled as having nested random intercepts and 'years since start of the experiment' was modelled as having an additional random intercept (1|Reserve/Plot/years since experiment start). Random variable structure listed above was selected by comparing Akaike Information Criterion (with small sample size correction; $\mathrm{AIC_c}$) for nested and non-nested random variable combinations with the full set of fixed-effect variables. We also considered interactive effects between variables. For models with ΔG as the response variable, we explored a quadratic term for 'rainfall' and 'previous year rainfall', because grazing effects are projected to be most intense between 600 and 800 mm/yr (Archibald & Hempson, 2016; Hempson, Archibald, & Bond, 2015; Hempson, Archibald, Bond, Ellis, et al., 2015). Both response and predictor variables were centred to a mean of zero and scaled to standard deviation of one. Models were selected by comparing $\mathrm{AIC_c}$ for all possible model combinations. The simplest model with $\mathrm{AIC_c}$ within two of the smallest $\mathrm{AIC_c}$ was chosen as the 'best' model (Tables S3–S5). Fixed-effect sizes for mixed-effects models were calculated from $\beta_{\mathrm{fixed\ effect}}/\sqrt{(\Sigma\sigma^2_{\mathrm{random\ effects}})}$, where $\beta_{\mathrm{fixed\ effect}}$ is the model estimate for the fixed-effect variable and $\Sigma\sigma^2_{\mathrm{random\ effects}}$ is the sum of the variance for all the random effect variables (Hedges, 2007). Since all variables were scaled for direct comparison of effect sizes, effect sizes, and slopes were back-transformed into meaningful units (Table S6). We also ran a model using the log response ratio as the response variable [$\mathrm{logRR} = \log(G_{\mathrm{inside}}/G_{\mathrm{outside}})$] to check if this commonly used normalization changed our interpretations of the proportional model; the best logRR model included the same predictor variables and estimated generally equivalent effect sizes as the proportional model (Figure S3).

Reserve-level analysis of grazing effects on burned area

First, we constructed quantile regression models ($\tau = 0.5$) for the mean annual burned area (BA) using only environmental conditions as predictors. This type of model predicts specified percentiles of the response variables and thus can provide an estimate of the maximum potential BA. Environmental variables that are known to determine BAs in Africa (Archibald et al., 2009)—tree cover, rainfall, and seasonality—were included in the model. We purposefully excluded grazing herbivore metabolic density at this stage of modelling. We did not examine any anthropogenic variables known to affect fire activity (e.g., population density), since our analyses focused exclusively on reserves where we can reasonably assume a minimal impact of fire suppression. We also included sand content, even though it has less explanatory power than the other variables (Archibald et al., 2009), because it was relevant in predicting herbaceous biomass in the herbivore exclusion dataset. $\mathrm{AIC_c}$ was again used to select predictor variables. Selected predictor variables were used to construct a quantile regression model at the 99th percentile ($\tau = 0.99$) to project the maximum environmental BA potential at 1 km resolution. For ~3.5% of pixels, the model projected >100% and <0% BA. We reassigned pixels with a value of >100% as 100% and those with a value <0% as 0%. The difference in % BA was calculated as the difference between the projected maximum BA and the observed BA at 1 km resolution. We next calculated the average values for the difference in % burned area (ΔBA), mean annual rainfall (MAR), seasonality, tree cover, and sand content for each reserve and used them to construct linear regression models with difference in % burned area (ΔBA) as the response variable and mean grazing herbivore density, MAR, tree cover, seasonality, and sand content as the predictor variables. We used linear models even though the response variable was on a percentage scale because values ranged from 20% to 80% and met the normality assumption. AIC_c was again used to select predictor variables. We checked a linear mixed-effects model with country as a random effect to account for differences in fire management, which had no effect. To check if the size of the herbivore effect on fire reduction was comparable between the ΔBA and BA models, we also ran reserve-level models using the BA product as the response variable.

Examining the mechanism by which herbivores impact burned area

First, we compared the size of herbivore impacts (ΔG) to calculated metabolic demand to assess how well impact matched consumption. We calculated dry matter intake (DMI) using the following equation (Dong et al., 2006): metabolic grazer density (kg^b/km^2) × ($0.0119\ NE_{ma}{}^2 + 0.1938)/NE_{ma}$, where NE_{ma} is the net energy concentration of the herbivore's diet, taken at the default value of 6 MJ/kg dry matter, and metabolic grazer density is calculated using order-level b and halving the contribution of mixed feeders (Staver et al., 2021). DMI is measured in kg $km^{-2}\,day^{-1}$, then multiplied by 365 (days) and 0.01 (km^2/ha) to convert it to kg/ha estimated at the annual scale. We took the average ΔG at each DMI within each park. We then examined the relationship between ΔG~DMI using linear regression with an intercept of zero.

We then took the effects of grazing herbivore densities produced from the herbivore exclusion experiment model (ΔG; kg/ha grass biomass per kg^b/km^2 grazing herbivores) and the reserve-level BA model (ΔBA; % burned area per kg^b/km^2 grazing herbivores) and divided them to estimate the reduction in burned area per unit of grass biomass reduction ($\Delta BA/\Delta G$). We compared this value to the slope of the model of the relationship between grassy fuel loads and burned area quantified from a simple linear model of an empirical dataset from KNP (Cardoso et al., 2022). To test hypotheses (Figure 2), we conducted a Z-test to check if slopes were significantly different from each other.

RESULTS

Herbaceous biomass response to herbivore exclusion

Across both exclosures and control plots, standing herbaceous biomass (G) increased with rainfall (Figure 3b,e), with previous year rainfall, and on soils with less sand (Figure 3c,e). G also decreased with grazing herbivore metabolic density (Figure 3d,e) and fire frequency (Figure 3e). Annual rainfall had the largest effect on G (normalized effect size = 0.35), followed by fire (−0.22), sand content (−0.20), and grazing herbivore metabolic density (−0.17) (Figure 3e). On average, for every 100 kg^b/km^2 (kg^b is metabolic biomass, where b is the scaling exponent of metabolic rate based on order; see Materials and Methods and Supplement) of grazing herbivore metabolic biomass (equivalent to ~1 zebra), herbaceous biomass decreased by 21 kg/ha.

The absolute difference between herbaceous biomass inside and outside exclosures (ΔG) increased with grazing herbivore metabolic biomass density (Figure 3h). Previous year rainfall was best modelled as a quadratic term, with ΔG increasing slightly until 513 mm/yr and then decreasing (Figure S4). To access the effect size of the previous year's rainfall, we took the derivative every 200 mm/yr and found normalized effect sizes were small across the range examined here (Figure 3i; Figure S4). Thus, the normalized effect sizes of previous rainfall (<±0.15), rainfall (−0.08), and soil texture (−0.13) were all much (~4×) smaller than the effects of herbivore metabolic density (0.59) (Figure 3i). The relatively minimal effect of soil and rainfall can be seen graphically in partial dependence plots (Figure 3f,g) We also modelled and plotted G_{inside} and $G_{outside}$ separately and found that the slopes for sand content and rainfall were statistically indistinguishable from each other (Z-test; sand $p = 0.21$; rainfall $p = 0.81$) (Figure 4). Together this suggests that the effects of these drivers on ΔG were relatively small.

The best models of proportional change in herbaceous biomass ($\Delta G/G_{inside}$) included herbivore metabolic density as the largest effect size and also included all the environmental variables that were predictive of herbaceous biomass (G) (Figure S5). The proportional change metric inherently reflects influences on both the numerator (ΔG) and the denominator (G_{inside}); because results from difference models (ΔG) indicate that the top-down effect of herbivore consumption was strong and consistent across environmental conditions (Figure 3), we can attribute the effect of environmental variables to the denominator (G_{inside}) (Figure 4; Figures S5 and S6). The normalized effect sizes of rainfall and sand content for $G_{outside}$ were 4× and 1.5× greater than those of the ΔG model (Table S7), which indicates that bottom-up effects of productivity determine how much consumption matters to overall biomass (Figure 4; Figures S5 and S6).

Burned area associations with herbivore densities

BA was higher at higher MAR, in more seasonal environments, and in areas with lower tree cover,

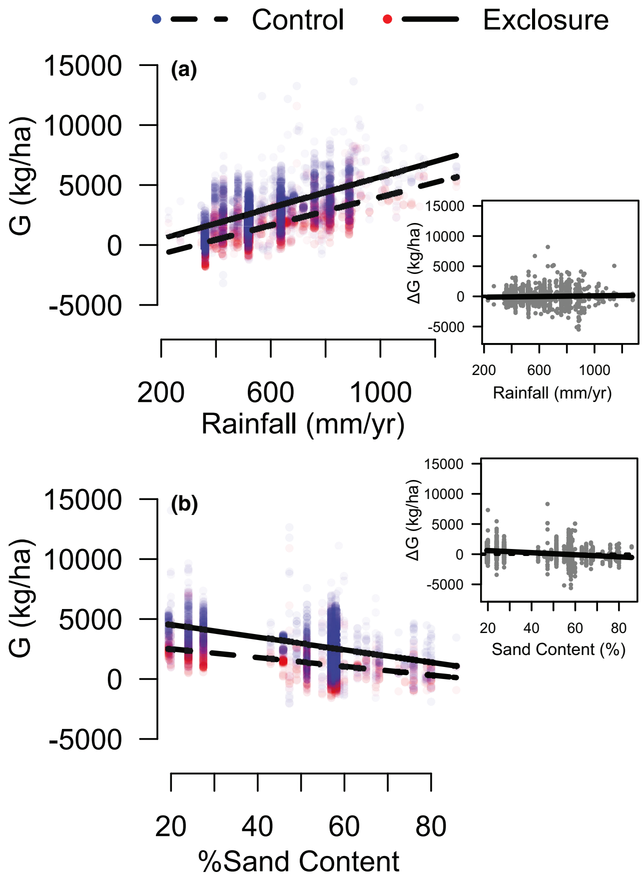

FIGURE 4 Grazing herbivore effects on grass biomass are generally consistent across environmental gradients. Analysis of grass biomass (G) and grazing herbivore impact (ΔG) replotted in the format of hypotheses presented in Figure 1. Grass biomass (G) models were run separately for control and exclosure plots (with grazing herbivore density excluded as a predictor) to generate fitted lines presented in a and b. Slope between for rainfall (Z-test, $p=0.81$) and sand (Z-test, $p=0.21$) were not statistically distinguishable between the models. Partial dependences of G on rainfall (a) and sand (b) are plotted for control plots (red points) and exclosure plots (blue points). Insets are identical to Figure 3f,g. Direction of results shows weak support for H1c (higher rainfall and sandier soils may decrease grazing effects), but the small magnitude of these effects more generally supports H1a (that rainfall [a] and soil texture [b] do not directly affect grazing effects, resulting in a constant ΔG across the rainfall gradient).

especially low-tree-cover areas at higher rainfall (MAR > ~500 mm/yr) and on sandier soils (Table S8). We used these results in a quantile regression model ($\tau=0.99$) to generate the maximum potential BA based on the environment alone (Figure 5a), from which we calculated the difference between the potential BA and observed burned area (ΔBA). The best model of ΔBA included just herbivore metabolic density ($R^2=0.28$, $N=31$, $p=0.001$; Figure 5c; Table S9). On average, for every 100 kg^b/km^2 of grazing herbivore biomass (equivalent to ~1 zebra), the percent BA decreased by 0.43 percentage points. We note that the intercept on the ΔBA model is large (41 percentage points ΔBA), which means variables that we did not account for also reduced BA, potentially including, for example, landscape connectivity and ignitions (Archibald et al., 2012).

To verify that the size of the effect of herbivores on the burned area was reasonable and not an artefact of modelling procedure used to quantify potential burned area, we also ran models with observed BA as the response variable at the reserve scale (including grazing herbivores as a predictor) (Table S10). Effect sizes for herbivore densities were identical for the ΔBA and BA models (0.43 ± 0.12% reduction *v.* −0.39 ± 0.12% BA for 100 kg^b/km^2 grazing herbivore biomass). Over the range of grazing herbivore densities included in this study, grazing herbivores reduced the percent BA by an average of 11 percentage points and a maximum of 35 percentage points, suggesting that herbivores can substantially reduce fire activity at broad scales. We also ran models with a proportional response ($\Delta BA/BA_{potential}$). The best-fit model included both herbivore metabolic density and MAR as significant predictors (Tables S11 and S12; Figure S7). We cannot rule out that BA and herbivore densities co-vary for other reasons, for example, if poachers both set fires and reduce herbivore densities. However, an herbivore-driven reduction in fire is consistent with herbivore-driven fuel reduction observed in the exclusion dataset.

The relationship between herbivore characteristics and environmental variables

To check if environmental conditions indirectly shaped herbivore metabolic densities and communities, we examined correlations between herbivores, rainfall, and soil texture in both the exclosure dataset and across 31 reserves. At exclosure sites, MAR was correlated with herbivore densities ($r=0.39$; $p=0.001$; Figure S8a), but soil texture was not ($r=0.004$; $p=0.97$; Figure S8b) (see SI extended results and discussion). In contrast, we found weak to no correlation between grazing herbivore densities and environmental controls at the reserve scale ($r=0.02$–0.29). We found stronger relationships between environmental factors and shifts in herbivore community characteristics (body size and ruminant vs. non-ruminant) ($r=0.22$–0.64) in both datasets (see SI extended results and discussion; Figures S8 and S9).

Comparing effect sizes across herbivore effects on grass biomass and fire activity

Estimated herbivore consumption (DMI) closely matched observed herbivore reductions of grass

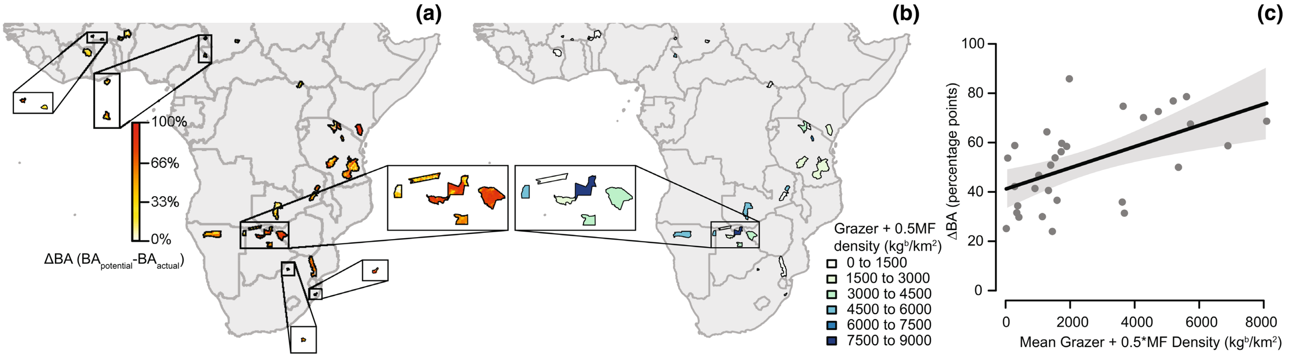

FIGURE 5 The effect of grazing on the reduction in burned area (ΔBA) across African savannas. (a) Difference between maximum projected mean annual burned area and actual mean annual burned area ($\Delta BA = BA_{potential} - BA_{actual}$) across 31 African reserves (1-km resolution). Insets from a and b are magnified by ×100. (b) Grazing herbivore biomass density across 31 African reserves. Grazer density was reported at the reserve level. (c) Partial dependences of ΔBA for grazer density, at the reserve level. Slope is equivalent to a reduction of 0.43 percentage points for every 100 kg^b/km^2. Shaded region in c represents 95% confidence interval on the fit ($R^2 = 0.28$, $p < 0.001$).

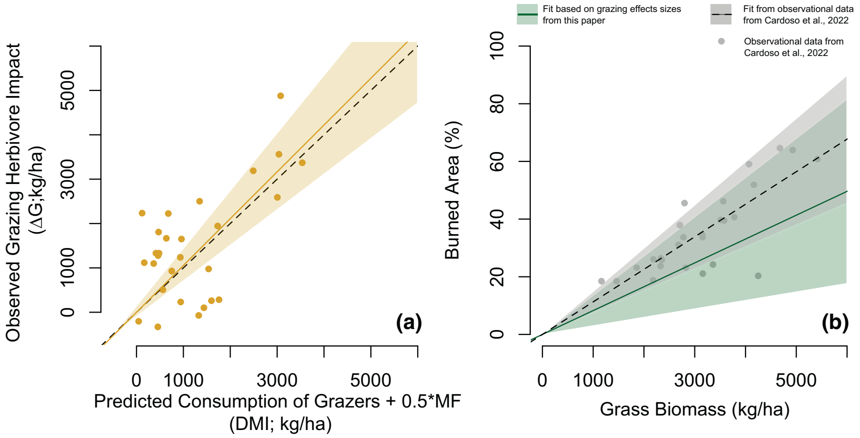

FIGURE 6 Fuel reductions via consumption are the primary mechanism by which grazing herbivores reduce burned area. (a) Comparison of herbivore effects on herbaceous biomass and consumption estimates based on grazing herbivore densities (kg^b/km^2; where b is based on the order average and mixed feeder contribution is halved. Solid gold line is $\Delta G = 1.05 * DMI$, with shading representing the 97% confidence interval. Dotted line is the 1:1 line. (b) Comparison of the empirical relationship between fuel load and burned area and the relationship between fuel load and burned area derived from the herbivore removal effects constrained in this study. Grey points and the black best-fit line replotted from data published by Cardoso et al. (2022), with shading representing the 97% confidence interval. Green line was calculated by dividing the effects of herbivore metabolic densities on ΔBA and ΔG, with shading representing the 97% confidence interval. Slopes were statistically indistinguishable from each other (Z-test, p-value = 0.31), indicating grazing herbivores impact savanna-burned areas mainly by removing herbaceous biomass (Figure 2; H2a). Intercepts were set to zero for plotting both lines and intercept from the best-fit line of the data from Cardoso et al. (2022) was added to the data to directly compare the slopes and datapoints on the same graph.

biomass [$\Delta G = 1.05$ (± 0.12 s.e.) × DMI; $N = 28$, $R^2 = 0.71$, $p \ll 0.001$] (Figure 6a), suggesting that herbivore consumption is sufficient to account for observed reductions in grass biomass in the presence of herbivores. The effect size of fuel load on burned area calculated from the KNP dataset was 0.0113 ± 0.0017 percentage points BA per kg/ha grass biomass (Figures 2 and 6b), and the "herbivore derived" effect size of fuel load on the burned area was 0.0083 ± 0.0025 percentage points BA per kg/ha grass biomass (Figure 6b); these values were statistically indistinguishable from each other (Z-test; $p = 0.31$), which supports the interpretation that grazing herbivores primarily influence burned area via fuel load reductions.

DISCUSSION

Collectively, our results indicate that (1) the magnitude of grazing effects on herbaceous biomass and fire activity is substantial across African savannas, (2) although there was some variation in herbivore effect on grass biomass across environmental gradients, this was minor compared with the effect of herbivore metabolic densities, and (3) grazing reduces fire activity, (4) most likely by consuming fuel loads.

Grazing herbivore density was by far the strongest determinant of the absolute amount of herbaceous biomass removed (ΔG) (Figures 1a,b, 3i and 4), with smaller additional effects of rainfall, previous year rainfall, and sand content (Figure 3i). Grazing herbivores consumed slightly more biomass when soils were less sandy (more nutrient-rich) (Figure 3g) and rainfall was higher (Figure 3f). While the direction of these relationships is consistent with H1c, that herbivore effects are more intense on more palatable forage (Figures 1e and 4) (see also Anderson et al., 2007; Borer, 2020; Mohanbabu & Ritchie, 2022; Smit & Archibald, 2019), the effects were weak, suggesting that these mechanisms are of secondary importance. Many previous studies that documented larger environmental effects relied on proportional response variables (i.e., $\Delta G/G_{\text{inside}}$) (Anderson et al., 2007; Archibald, 2008; Milchunas & Lauenroth, 1993). These proportional response variables mathematically reflect determinants of both the numerator (here, herbivore-induced biomass changes; ΔG) and the denominator (standing biomass without herbivores; G_{inside}) (Figure S5). Similar effects of ratio metrics have been observed in studies examining plant constitutive and induced resistance to herbivory (Morris et al., 2006). We found that G_{inside} increased substantially over resource gradients (Figures 3b–e and 4), which aligns with a large body of literature showing that environmental gradients strongly constrain herbaceous production (Sala et al., 2012), while ΔG changed much less (Figures 3f–i and 4; Figure S5). Together, ratio and absolute value metrics provide complementary biological interpretations of how environmental controls mediate productivity versus consumption (Cebrian & Lartigue, 2004) and suggest that our results most closely align with hypothesis (H1a)—that herbivore densities are the primary determinant of the magnitude of grazing impacts on herbaceous biomass (Figures 1a,b and 4). This interpretation is further supported by a comparison of ΔG with estimated DMI required by the grazing community across sites, which closely match in magnitude (Figure 6a) (see also Staver et al., 2021).

Still, given the large body of work predicting herbivores adjust their consumption based on forage quantity and quality (Chase et al., 2000; Hopcraft et al., 2010; Illius & Gordon, 1992; Meyer et al., 2010; Olff et al., 2002; van Langevelde et al., 2008), the finding that environmental gradients weakly influence the absolute magnitude of grazing effects is surprising. Each community of grazing herbivores certainly adjusts how they use landscape resources based on the environment (Cromsigt & Olff, 2006; McNaughton, 1988). However, fine-scale differences in soil nutrients and topography, which can concentrate grazing effects locally (Young et al., 2013), may have less perceptible effects at larger scales. We found that grazing herbivore communities had consistent effects even at high rainfall and on sandy soils (Figure 4), despite probably lower forage quality, which suggests relatively consistent consumption of the grazing community overall (Figure 6a). Functional turnover in the grazing herbivore community towards larger body sizes and non-ruminants contribute (Figure S8e,f; Hempson, Archibald, & Bond, 2015), perhaps by allowing herbivores to subsist on poorer-quality forage (Illius & Gordon, 1992; Olff et al., 2002). Thus, environmental controls on forage likely do influence grazing effects on grass and fuels, but mostly via indirect effects on the density and/or composition of herbivore populations (Hempson, Archibald, & Bond, 2015; Olff et al., 2002).

Grazing effects on herbaceous biomass translated directly into impacts on fire. Past work showed that reductions in grazing populations result in increased BA and vice versa at local (intra-reserve) scales (Norton-Griffiths, 1979; Smit & Archibald, 2019; Waldram et al., 2008). Here, we showed wild grazing populations may also substantially reduce fires at broad spatial (inter-reserve) scales, supporting the hypothesis that biomass consumption by grazing herbivores and fire are strongly interconnected across African savannas (Archibald & Hempson, 2016). Burned area absolute and proportional reductions (ΔBA and $\Delta \text{BA}/\text{BA}_{\text{potential}}$) increased strongly with grazing herbivore metabolic density (Figure 5c; Figure S7a; Table S12). The proportional model ($\Delta \text{BA}/\text{BA}_{\text{potential}}$) also indicated larger fire reductions at lower rainfall (Figure S7b,c; Table S12), which is consistent with the observation that fuel loads primarily constrain fire spread (Alvarado et al., 2020; Archibald et al., 2009; Waldram et al., 2008) in semi-arid savannas. Even if herbivore consumption of fuels is consistent across rainfall (Figure 3f–i), the same grazing herbivore metabolic density more strongly excludes fire at lower overall grass productivity (Archibald et al., 2009; Smit & Archibald, 2019) (Figure S7). In nutrient-rich, semi-arid systems, herbivores could completely exclude fire by reducing fuel loads below the threshold for fire spread (Cardoso et al., 2022), whereas in humid systems, herbivores might instead reduce, but not completely exclude, fire.

Finally, we found that effect sizes estimated from herbivore impacts on grass biomass and BA were sufficiently large to account for direct estimates of BA responses to grass biomass (Figure 6b). This supports the hypothesis (H2a), that grazing herbivores reduce BA mainly through the removal of fuel loads (Figures 2 and 5a). Interestingly, our results may capture the most important elements of functional turnover between bunch-grass vs. lawn-grass savannas: past work has suggested that the most important trait for grass flammability is above-ground biomass (Simpson et al., 2016) and that grass height and biomass respond most dynamically to heavy grazing (Archibald et al., 2019; Hempson et al., 2019), although we note that the close match between grazing community metabolic demand and ΔG (Figure 6a) is not an obvious outcome of this trait perspective. Regardless, from a practical standpoint, our results mean that the effect of herbivores on fire activity can be quantified in terms of how much fuel they remove.

These findings have implications for how we think about fire dynamics in the past and future, not just the present (Andela et al., 2017). In both the historical and prehistoric past, wild grazing herbivore densities in Africa and globally were much higher than they are today (Faith et al., 2018, 2019; Hempson, Archibald, & Bond, 2015; Ripple et al., 2015; Staver et al., 2021), which suggests that similar environmental conditions may have been associated with less fire activity in the past. Historically, the collapse of wild herbivore populations, especially of migratory grazers with high grazing densities (Harris et al., 2009; Staver et al., 2021), has led to increases in fire activity (Holdo et al., 2009). However, the density of livestock grazers has increased relative to historic densities, which may in part explain observed decreases in BA in Africa (Andela et al., 2017), since livestock can also reduce herbaceous biomass and fire activity.

Currently, few global climate models include dynamic herbivory (but see Pachzelt et al., 2015), and the empirical relationships produced here can be used to parameterize and verify models that incorporate the impacts of grazing herbivores. We note that our focus on wild communities makes these results particularly optimized for historical and paleofire models. To fine-tune applications in present-day models, further work is needed to quantify functional differences between domesticated versus wild (especially non-ruminant) grazing communities (Hempson et al., 2017; Young et al., 2013). Regardless of the time frame, it is clear that including herbivores in models for savanna carbon cycling will be critical both for planning management strategies and for predicting future changes (Charles et al., 2017; Hempson et al., 2017). Finally, our results make it clear that herbivores represent not only an important consumptive carbon flux in savannas but also that including them formally into models could be relatively straightforward from estimates of population density.

AUTHOR CONTRIBUTIONS

ATK and ACS designed research. DMK, LMP, and TPY provided data from the KLEE site at Mpala, Kenya. JRG, TRK, TMP, and RMP provided data from the UHURU site at Mpala, Kenya. SEK, DEB, DIT, and MDS provided data from Kruger National Park, South Africa. ACS and WJB provided data from Hluhluwe iMfolozi Park, South Africa. TMA, NM, and MER provided data from Serengeti, Tanzania. JAG and RMP provided data from Gorongosa National Park, Mozambique. GPH provided herbivore density data. ENF contributed to discussions regarding herbivore metabolic density comparison analysis. ATK analysed data and primarily wrote the paper. All authors reviewed and edited the paper.

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DATA AVAILABILITY STATEMENT

The data that support the finding of this study are openly available on Dryad at http://dio.org/10.5061/dryad.q2bvq83q2.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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