

## **Herbivore size matters for productivity–richness relationships in African savannas**

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### Summary

Productivity and herbivory often interact to shape plant community composition and species richness with levels of production mediating the impact of herbivory. However, differences in herbivore traits such as size, feeding guild and dietary requirements may result in different impacts of diverse herbivore guilds across productivity gradients.

We used size-selective herbivore exclosures to separate the effects of herbivory by larger herbivores, such as elephant, Burchell's zebra and blue wildebeest from those of medium/smaller herbivores, such as impala and warthog, on herbaceous plant communities. These exclosures were established along a 10-fold productivity gradient, ranging from 90 to 950 g m<sup>-2</sup> of standing plant biomass in the Kruger National Park, South Africa.

Exclusion of all herbivores generally increased plant species richness at low productivity, but decreased richness at high productivity. Exclusion of medium/smaller herbivores (e.g. impala, warthog) showed stronger effects on plant richness, particularly loss of forbs, at higher productivity rather than at lower productivity. In contrast, exclusion of larger herbivores had stronger effects on plant richness, typically with increasing forb richness, at low rather than high productivity.

The change in species richness appeared linked to changes in light availability following herbivore exclusion. Strong increases in shading led to declines in species richness while more moderate increases in shading led to increases in species richness, possibly due to amelioration of heat and water stress by modest increases in shading.

Increasing plant dominance, which likely alters multiple mechanisms of plant interactions, was correlated with declines in plant richness following herbivore exclusion. The impact of increasing dominance on plant richness operated independent of productivity, with the exclusion of impala appearing particularly important in driving this relationship.

*Synthesis.* We show that the impact of herbivore losses on plant diversity will be strongly situation dependent and will vary with the herbivores lost (e.g. larger vs. smaller, grazers vs. browsers), plant functional type (e.g. grasses vs. forbs) and environmental context (e.g. productivity). Although larger herbivores are often emphasized for their strong impacts on community dynamics and ecosystem processes, we show that smaller, abundant herbivores can exert strong top-down control on plant communities.