

## COMMENTARY

# Herbivore size matters for productivity-richness relationships in African savannas: Commentary on Burkepile *et al.* (2017)

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Since the Late Pleistocene, human impact has increasingly resulted in defaunation, or human-caused animal loss, leading to largely impoverished vertebrate communities (Dirzo *et al.* 2014; McCauley *et al.* 2015). These extinctions are not random, but are strongly size-selective with large animals going first. This trend is continuing, with native large herbivores being currently increasingly threatened around the globe (Ripple *et al.* 2015). As a consequence, native herbivore communities both lose their largest members, hence, decreasing in average size, but simultaneously decrease in diversity. This may have strong consequences for the herbivore's impact on biodiversity, ecosystem functioning and landscape structure (Dirzo *et al.* 2014; Bakker *et al.* 2016a). However, field tests of the effect of size-selective loss of vertebrate herbivores remain rare.

Burkepile *et al.* (2017) performed such a test and address the question how the loss of vertebrate herbivores affects plant species richness in African savanna. They incorporated the size-selectivity of herbivore extinctions in their design by using size-selective exclosures to separate the effect of losing only the larger herbivores as elephant, zebra and wildebeest from that of losing all vertebrate herbivores >1 kg together. They subsequently replicated this design across a 10-fold gradient in plant production within Kruger National Park, South Africa.

## Herbivore impact on plant species richness along a productivity gradient

The study design incorporates the notion that herbivores affect plant species richness systematically across a productivity gradient: herbivores reduce plant species richness at low production and increase it at high productivity (Bakker *et al.* 2006; Borer *et al.* 2014). So far, nothing new, as Burkepile *et al.* (2017) confirm this pattern. However, these previous tests worked mostly with presence or absence of herbivores only, whereas the size-selective exclosures give more information on the role of the different herbivores. Although this has been done previously, this was in already severely impoverished herbivore communities as nowadays present in most

of Europe and North-America. Hence, the relationship between plant production and herbivore impact on plant species richness that we know comes from the impact of one or two herbivore species. In contrast, African herbivore communities are species-rich and thus the question is whether this may result in different dynamics and impacts then studying only one or two species. And it does. Although the general patterns hold, the surprising result is that the large herbivores negatively affect plant species richness at low production, whereas the small to medium-sized herbivores affect species richness positively at high production. Although the herbivore community is species rich, the results are predominantly explained by the role of a single species: impala.

Interestingly, the important role of impala affecting savanna vegetation has been found before in suppression woody plant colonization as well as selectively feeding on fruits from woody species, thus contributing strongly to seed dispersal (Sankaran, Augustine & Ratnam 2013; Pringle *et al.* 2014). Burkepile *et al.* (2017) now demonstrate that they can also strongly affect grassland plant diversity.

Impala were the most abundant herbivores in the study sites, which explains part of their strong impact. However, that is only part of the answer as it is the feeding strategy of the impala causing the impact on plant species richness: their diet consists mostly of grasses, hence forbs profit from impala grazing on grasses and subsequent suppression of grass competition. Thus, feeding on the dominant competitor warrants their impact on plant species richness. Although this effect is usually attributed to large bulk grazers, this study shows that medium-sized herbivores may have similar effects.

The finding that density as well as the diet selection of the herbivores are the parameters determining their impact on the vegetation has important implications for the interpretation of other studies on herbivore impact. Many studies investigating the impact of herbivores are set in sites with managed herbivore populations. Native herbivore densities can be kept very low due to hunting (for instance deer), leaving herbivores seemingly functionally unimportant (e.g. Bakker *et al.* 2016a). However, this may just be because the herbivores are managed to avoid them causing impact on vegetation, which is perceived as damage (Morellet *et al.* 2007; Tanentzap *et al.* 2011). Thus, when generalizing herbivore impact on vegetation and ecosystems one should be aware of the role of

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herbivore density and the role of humans managing the herbivore densities.

Furthermore, the study of Burkepile *et al.* (2017) points to the importance of feeding selectivity of the herbivores. Indeed, Burkepile *et al.* (2017) find a strong relation between the dominance of the plant species and the impact of the herbivores on plant species richness: when reducing the dominant, the impacts on species richness are increasingly positive. This sheds new light on the current theory: it is not just a matter of large herbivores being bulk grazers, removing dominant plants at high production, thereby preventing light limitation among the plants and thus promoting species richness (Borer *et al.* 2014). Instead, the role of limiting plant dominance is not just for large herbivores, but also for smaller ones, if present at sufficient densities, and not just at high production, but across the whole productivity gradient, as Burkepile *et al.* (2017) demonstrate. That herbivores regulate plant diversity through their impact on plant dominance is a principle already outlined by Olff & Ritchie (1998), but is not often taken into consideration.

### Towards new approaches to predict herbivore impact

As a consequence, new approaches are needed to predict under what conditions herbivores will preferentially or mainly consume the dominant plant species and when the subordinates. Although light limitation coincides with productivity, herbivore selectivity may not, as plant quality is determined by the resource limitation of the plant, including light, and also water and nutrients. Therefore, plants at high productivity may be very poor or very high in quality, depending on whether nutrients, water or light is limiting their growth (Olff & Ritchie 1998) and similarly for plants at low productivity. Selective herbivore feeding on dominant or subordinate species may depend on which have the best quality, which varies with the type of resource limiting plant growth, and not systematically with production per se.

Furthermore, it may be the traits of the herbivores themselves that allow prediction of their feeding selectivity. The study of Burkepile *et al.* (2017) stresses to take into account herbivore traits to allow prediction of their effects on ecosystems. In that sense, the title is a bit misleading as the authors themselves state: the impact of removing small to medium herbivores had less to do with them being smaller as with impala being a numerically abundant grazer in the wet season with a preference for dominant plants. This illustrates that the classical division of large vs. small to medium herbivores and the classification of them as bulk grazers vs. selective grazers is primitive and in need of revision.

Altogether, revising our current relatively straightforward theory of the impact of large vs. small herbivores on plant species richness along a productivity gradient may seem a big task, which may lead to some discouragement. At least, Burkepile *et al.* (2017) conclude in their synthesis that the impact of herbivore loss on plant diversity will be strongly situation dependent, which may seem to render the results very local

and context specific. However, this is not doing justice to the findings that there are emerging general patterns with respect to the role of herbivore selectivity and plant dominance to predict herbivore impact, but these just need more future elaboration. Several recent developments are very helpful in this respect, which are addressed in the following section.

### Functional grouping of herbivores

Expanding the classical division of herbivores in large vs. small to medium into grouping of herbivores based on their traits would greatly facilitate a better understanding of herbivore impacts in multi-species assemblages. Recently, Hempson, Archibald & Bond (2015) made a functional grouping of savanna herbivores based on their body weight, sociality, diet selection and dependence on water sources. Bakker *et al.* (2016b) grouped large aquatic herbivores based on their aquatic plant dependency and territoriality. This functional approach to vertebrate herbivore communities allows fine-tuning of the predictions of their impact on vegetation and ecosystems. Better knowledge of herbivore diets becomes more and more available due to stable isotope techniques (Codron *et al.* 2007) as well as DNA analyses of plants and herbivores and their faeces (Kartzi- nel *et al.* 2015), which strongly facilitates the functional grouping of vertebrate herbivores.

However, functional grouping of herbivores is one thing, testing their impact another, and in this respect using size-selective or factorial exclosures is a very important tool to study the effect of herbivore diversity (Sankaran, Augustine & Ratnam 2013; Young *et al.* 2013; Keesing & Young 2014). Size-selective or factorial exclosures are designed to not exclude all herbivores in once, but to allow access to different subgroups of the local herbivore community depending on the type of fencing, resulting in different grazing treatments. For instance, the largest herbivores can be excluded with a fence where small herbivores can still pass underneath and both small and large herbivores with a small-mesh fence such as done by Burkepile *et al.* (2017). Furthermore, statistical patterns in large datasets based on monitoring data, may reveal the connection between herbivore diversity and plant diversity (Greve *et al.* 2012). The development of techniques such as LiDAR – a surveying method that measures distance to a target by illuminating that target with a laser light – allows large-scale 3D vegetation mapping either airborne or ground-based, which can be linked to animal behaviour and impact (Davies & Asner 2014). This increasingly allows collection of large amounts of detailed data of on herbivore impacts, which may be species specific. In Kruger, using LiDAR, it was possible to measure the decreasing height of adult trees over time, which set apart the effect of elephants relative to the rest of the herbivore community (Asner *et al.* 2009).

### Outlook

Although these are very exciting developments, more work is needed on the underlying mechanisms of the effect of herbivore diversity. In particular, the question whether there are compensatory or additive effects of different herbivore species

in diverse communities (e.g. Ritchie & Olff 1999) should be investigated. Also very important in this respect are the interactions among the herbivores: does the loss of herbivore species result in lower total herbivore densities or do other species compensate by increasing their abundance? This elaborates on the notion that the effect of herbivore diversity may be modulated strongly by their realized densities (e.g. Bakker *et al.* 2016a).

The findings presented by Burkepile *et al.* (2017) are not just relevant for terrestrial grasslands but apply to a wide range of ecosystems, including aquatic ones (e.g. Burkepile & Hay 2008). Furthermore, the study is very relevant to predict effects of herbivore loss, but also has application in conservation, where herbivore species are added, such as in trophic rewilding, where more complete native large herbivore assemblages are being restored (Seddon *et al.* 2014). Prediction of the impact of rewilding on biodiversity is a topic of ongoing debate. Knowledge of the impact of natural diverse herbivore assemblages as presented in Burkepile *et al.* (2017) can strongly contribute to predict the impacts of diverse vs. impoverished herbivore assemblages (Svenning *et al.* 2016).

## Data accessibility

This paper does not use data.

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