



# Predators and rainfall control spatial biogeochemistry in a landscape of fear

Oswald J. Schmitz<sup>a,1</sup>

Scientists have long pondered what the world might have been like during the geological epochs immediately predating the late Pleistocene extinction events, when very large, wild mammals occupied almost every ecosystem on Earth (1–4). By piecing together whatever evidence can be gathered from the fossil record, it is speculated that these megasized species (i.e., species with body masses ranging from as small as tens of kilograms to as large as thousands of kilograms) had profound impacts on ecosystems worldwide. It is thought that, through their foraging and trampling, these herbivores determined the relative abundance of different vegetation types (e.g., woody vs. grassland) across landscapes; through selective feeding, they mediated competition among plant species within vegetation types; and through their behavior (habitat selection and migration) and physiology, they spatially redistributed plant-derived nutrients such as nitrogen (N) and phosphorus (P), thereby having an important hand in shaping the spatial patterning of biogeochemical properties across landscapes (4–6). It is further speculated that the nature and degree of impact depended on the interplay between herbivore body size and biophysical aspects of ecosystems such as soil fertility and amounts of rainfall (5). If only there was a way to experimentally test some of these speculations. In PNAS, le Roux et al. (7) report on a study that does just that, but with an interesting twist.

The study takes advantage of the fact that relic assemblages of large, wild mammalian herbivores, resembling the size range found during the Pleistocene, currently exist within protected areas in African savanna ecosystems (5). Such places offer great testbeds to conduct landscape-scale experiments along soil nutrient and rainfall gradients in order to measure the singular and combined effects of different-sized wild herbivores on the vegetation structure and functioning of ecosystems (5, 8). The interesting twist of the le Roux et al. study is that along a rainfall gradient it further resolves the effects of another important factor determining herbivore impact. It is one that is entertained in discussions about how paleoecosystems functioned (3–5) but not fully considered as part of conventional speculations

about what drives large herbivore impacts on biogeochemistry. That understudied factor is the role of predators. In particular, how shifts in herbivore behavior induced by the mere risk that they may be captured by predators can shape the patterning of biogeochemical properties across landscapes (9). The study resolves a complex interweaving of factors controlling ecosystem functioning to provide a clear picture of the role that predators and herbivores play in shaping variation in biogeochemical properties across landscapes.

The landscape of Hluhluwe-iMfolozi Park in South Africa, where the study was done, is dotted with numerous grazing lawns interspersed among savanna woodlands. Grazing lawns tend to arise in landscape locations with comparatively higher soil nutrient levels (10). These open landscape locations are characterized by large swaths of highly nutritious, short-statured grass species that are kept in this state by frequent, recurrent herbivore grazing that also keeps less nutritious, tall-statured competitor grass species at bay (10). The level of grazing-lawn productivity is generally related to rainfall levels. As well, their high productivity may be sustained by rapid plant uptake of limiting nutrients that are released from herbivores in their dung and urine (10). This herbivore-driven recycling feedback may enhance productivity by circumventing the slower process of nutrient release arising from soil microbial decomposition and mineralization of senescent plant matter (11). However, the general occurrence of fast recycling—especially of N—among grazing lawns is debated (10).

Still, grazing lawns are nutrient hot spots for herbivores, providing them with N for body protein synthesis and P for bone development (10). The demand for N and P, however, varies with herbivore body mass. Larger herbivores require higher amounts of P per unit body mass than do smaller herbivores owing to the need to develop robust skeletons to support their large mass (12). However, they also require disproportionately less N (13). The challenge faced by all herbivores is that the ratios of N and P in their plant resources often do not closely match their demand

<sup>a</sup>School of the Environment, Yale University, New Haven, CT 06511

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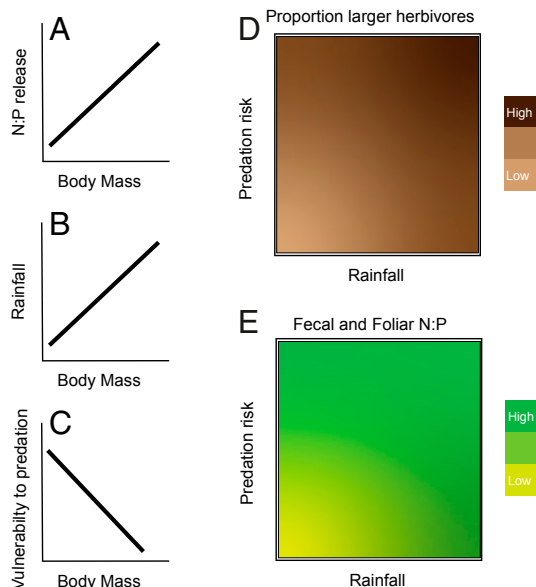
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<sup>1</sup>Email: [oswald.schmitz@yale.edu](mailto:oswald.schmitz@yale.edu).

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**Fig. 1. Animal-driven landscape-scale biogeochemical processes are dependent on the interplay among herbivore nutrient demand and release, rainfall, and vulnerability to predation. The ratio of key nutrients such as nitrogen [N] and phosphorus [P] released in herbivore dung varies with herbivore body mass (A). Varying rainfall levels favor different-sized herbivores (B) through a trade-off in forage production and quality. High rainfall produces large quantities of low-quality forage, which favors large herbivores with high forage demands but that can digest its poorer quality. Lower rainfall leads to lesser amounts of higher-quality forage, which favors smaller herbivores. The vulnerability of herbivores to predation decreases with herbivore body mass (C). Together, the amount of rainfall and level of potential predation risk should create a joint gradient in the sizes of herbivores occurring in different landscape locations (D) and create concomitant gradients in N:P ratios released in herbivore dung and taken up in foliar tissue of forage plants (E). These gradients explain contingency in biogeochemical processes across landscapes.**

(14, 15). Thus, when N:P in resource supply and organismal demand is mismatched, herbivores should respond by releasing the nutrient taken in excess (14, 15). According to these physiological first principles, the nutrient that is released as excess will vary with herbivore body mass. Smaller herbivores, having high N:P demands, should disproportionately release more P (i.e., have dung with low N:P ratios). As P demand increases with herbivore body mass, there should be a concomitant increase in the proportion of N released. Consequently, the ratio of N:P released in herbivore dung should increase with body mass (Fig. 1A).

Rainfall could become a mitigating factor by determining the size range of herbivores that occupy a specific grazing lawn, and accordingly the ratio of N:P that is released there. Rainfall increases the quantity of grass that is produced. However, that grass has poorer quality, making it harder to digest. Larger herbivores stand to disproportionately benefit from this because they require high quantities of forage, plus they have the physiological adaptations to digest poorer-quality forage (16). Smaller herbivores, alternatively, require less quantity, but their digestive adaptations necessitate that they seek high-quality forage (16). Thus, the mean body mass of herbivores present on a given lawn should increase along a gradient of increasing rainfall (Fig. 1B). That is, grazing lawns with lower rainfall (higher forage quality) should be frequented by herbivores from the smaller end of the size range, whereas lawns with higher rainfall (higher forage quantity) should be occupied by herbivores from the larger end of the size range.

Now predators could complicate the matter by further determining which sizes of herbivores occupy a given grazing lawn. In savanna ecosystems, susceptibility of herbivore prey to predation decreases with herbivore body mass (Fig. 1C), with the very largest species even being completely invulnerable to predation (17, 18). Consequently, smaller herbivores should be more fearful than large herbivores, and therefore be more inclined to avoid grazing lawns that pose high risks of being captured by predators. Risky grazing lawns tend to be those surrounded by high vegetation because it hides predators that wait in ambush (19). Hence, more open grazing lawns should attract herbivores from the smaller end of the size range because the greater visibility makes them less risky places to feed (19).

Taken together, the amount of rainfall and level of potential predation risk should create a joint gradient in the sizes of herbivores occupying different grazing lawns, thereby offering a way to explain spatial contingency in biogeochemical properties across landscapes. High-rainfall, high-risk sites should have the highest proportion of large herbivores. That proportion should dwindle as rainfall and risk become lower (Fig. 1D). Such patterning in herbivore size should then determine patterning in associated landscape biogeochemistry (Fig. 1E) due to the size dependence of N:P released in dung. By virtue of fast nutrient recycling, the size dependence of released N:P should be further reflected in the patterning of N:P in grass foliar tissue (Fig. 1E).

le Roux et al. (7) were able to test for such spatially contingent effects using 15 grazing lawns spread across a gradient in rainfall level and the degree to which vegetation obscures herbivore visibility (a proxy for potential predation risk). They continuously monitored the occurrence and numbers of different herbivore species using wildlife cameras as biologging devices set up within designated plots in the middle of each grazing lawn. Camera data on herbivore species composition of a lawn, along with known species mean body masses, enabled the researchers to estimate the overall mean herbivore body mass (and proportion of large herbivores) occurring on a lawn. They further sampled dung that accumulated within the designated plots, noting the mass of dung coming from different species, and measured the N:P content of the different dung samples. To connect the dots further, they sampled the foliar N:P content of grasses within designated plots on each lawn.

Consistent with expectations, they found that the N:P ratio in dung decreased with herbivore body mass. Intriguingly, however, the total biomass of dung on each grazing lawn did not vary with rainfall amount or potential level of risk. However, the mean N:P ratio of the accumulated dung did. le Roux et al. show, again consistent with expectations, that the patterning of N:P release was a consequence of the proportion of larger- vs. smaller-sized herbivores occupying a grazing lawn, which varied with rainfall level and potential predation risk, and this patterning translated into a highly correlated patterning of foliar N:P.

The study affirms the prediction that even if they do not kill their prey, predators can have a decided effect on landscape biogeochemistry by inducing behavioral responses of herbivore prey to perceived predation risk (9). Different structural features among habitats across landscapes can create spatially varying fear responses by vulnerable prey species, a phenomenon that has come to be known as a "landscape of fear" (20). This study reveals that by creating a landscape of fear, predators can intervene in nutrient recycling by filtering which sizes of herbivores occupy a given

landscape location, and thereby can have a decided effect on the ratio of nutrients that are released and taken up by plants. This finding reveals yet another important way in which predators control biogeochemical processes within ecosystems (9). The finding that the proportion of N that is recycled is contingent on herbivore body size, potential predation risk, and rainfall may also help explain where and when N should be rapidly recycled. It thus helps to resolve the debate (10) about the occurrence of rapid N recycling among grazing lawns, and perhaps other ecosystems more generally.

Ecological science has a predilection to seek general understanding of how ecological systems work by seeking trends that can be explained by simple associations between a few key controlling factors. Such approaches often do not lead to tight predictions owing to the blurring effects of residual variation that inevitably arises due to contingent interplay among multiple (often unmeasured) controlling factors among ecosystems (21). The lesson from this study is that a sharper picture of how ecosystems function snaps into focus when deliberately embracing and

systematically resolving the complexity arising from the contingent interplay among multiple, interwoven controlling factors.

There is a certain grandeur in being able to offer deeper understanding into the complexity of these relic ecological systems, to thereby get a glimpse into how similar expansive paleoecosystems once functioned, and importantly to use the modern counterparts to learn what megaspecies extinctions during the Pleistocene did to unravel this complexity and associated functioning. Alas, this understanding comes at a time when even these last relics of the Pleistocene face a similar fate. Human agency is relentlessly constricting where populations of large species are able to occur globally and jeopardizing the ability of species–populations to persist as viable members of modern ecosystems in the remnant spaces where they do occur. As this study shows, we not only stand to lose irreplaceable iconic animal species but more importantly the myriad, tightly woven interdependencies forged by eons of coevolution and the associated ways that biogeochemical processes are controlled across landscapes.

- 1 R. D. Guthrie, Paleocology of the large-mammal community in interior Alaska during the late Pleistocene. *Am. Midl. Nat.* **79**, 346–363 (1968).
- 2 B. J. MacFadden, T. E. Cerling, Mammalian herbivore communities, ancient feeding ecology and carbon isotopes: A 10 million year sequence from the Neogene of Florida. *J. Vertebr. Paleontol.* **16**, 103–115 (1996).
- 3 Y. Malhi et al., Megafauna and ecosystem function from the Pleistocene to the Anthropocene. *Proc. Natl. Acad. Sci. U.S.A.* **113**, 838–846 (2016).
- 4 F. A. Smith et al., Megafauna in the Earth system. *Ecography* **39**, 99–108 (2016).
- 5 E. S. Bakker et al., Combining paleo-data and modern enclosure experiments to assess the impact of megafauna extinctions on woody vegetation. *Proc. Natl. Acad. Sci. U.S.A.* **113**, 847–855 (2016).
- 6 C. E. Doughty et al., Global nutrient transport in a world of giants. *Proc. Natl. Acad. Sci. U.S.A.* **113**, 868–873 (2016).
- 7 E. le Roux, L. S. van Veenhuisen, G. I. H. Kerley, J. P. G. M. Cromsigt, Animal body size distribution influences the ratios of nutrients supplied to plants. *Proc. Natl. Acad. Sci. U.S.A.* **117**, 22256–22263 (2020).
- 8 J. R. Goheen et al., Conservation lessons from large-mammal manipulations in East African savannas: The KLEE, UHURU, and GLADE experiments. *Ann. N. Y. Acad. Sci.* **1429**, 31–49 (2018).
- 9 O. J. Schmitz, D. Hawlena, G. C. Trussell, Predator control of ecosystem nutrient dynamics. *Ecol. Lett.* **13**, 1199–1209 (2010).
- 10 G. P. Hempson et al., Ecology of grazing lawns in Africa. *Biol. Rev. Camb. Philos. Soc.* **90**, 979–994 (2015).
- 11 J. G. Pausas, W. J. Bond, On the three major recycling pathways in terrestrial ecosystems. *Trends Ecol. Evol. (Amst.)*, 10.1016/j.tree.2020.04.004 (2020).
- 12 W. W. Reynolds, Skeletal weight allometry in aquatic and terrestrial vertebrates. *Hydrobiologia* **56**, 35–37 (1977).
- 13 J. Sitters et al., The stoichiometry of nutrient release by terrestrial herbivores and its ecosystem consequences. *Front. Earth Sci.* **5**, 32 (2017).
- 14 D. O. Hessen, G. I. Ågren, T. R. Anderson, J. J. Elser, P. C. de Ruiter, Carbon sequestration in ecosystems: The role of stoichiometry. *Ecology* **85**, 1179–1192 (2004).
- 15 C. L. Meunier et al., From elements to function: Toward unifying ecological stoichiometry and trait-based ecology. *Front. Environ. Sci.* **5**, 18 (2017).
- 16 D. Codron, R. R. Hofmann, M. Clauss, “Morphological and physiological adaptations for browsing and grazing” in *The Ecology of Browsing and Grazing II*, I. J. Gordon, H. H. T. Prins, Eds. (Springer Nature Switzerland AG, Cham, Switzerland, 2019), chap. 4.
- 17 A. R. E. Sinclair, S. Mduma, J. S. Brashares, Patterns of predation in a diverse predator-prey system. *Nature* **425**, 288–290 (2003).
- 18 E. le Roux, G. I. H. Kerley, J. P. G. M. Cromsigt, Megaherbivores modify trophic cascades triggered by fear of predation in an African savanna ecosystem. *Curr. Biol.* **28**, 2493–2499.e3 (2018).
- 19 C. Riginos, Climate and the landscape of fear in an African savanna. *J. Anim. Ecol.* **84**, 124–133 (2015).
- 20 J. W. Laundré et al., The landscape of fear: The missing link to understand top-down and bottom-up controls of prey abundance? *Ecology* **95**, 1141–1152 (2014).
- 21 O. J. Schmitz, *Resolving Ecosystem Complexity* (Princeton University Press, Princeton, 2010).