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FE SPOTLIGHT

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Frugivore zoogeochemistry in tropical forest ecosystems

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Recent progress in the field of zoogeochemistry (sensu Schmitz et al., 2018) has emerged which clearly demonstrates an important role for animals in elemental cycling at local and landscape extents. For example, moose exclosure experiments in North America (Ellis & Leroux, 2017; Pastor et al., 1993) demonstrate that areas with moose browsing and trampling can have much less carbon (C) and nitrogen (N) in the form of plant litter and in soils than areas where moose have been excluded and these impacts may influence the spatial heterogeneity in forest patches and matter at landscape extents (Leroux et al., 2020; Pastor et al., 1997). The majority of zoogeochemical studies focus on antagonistic carnivore or herbivore interactions leaving important gaps in our understanding of other key interactions underlying animal-ecosystem processes.

Frugivory is a form of herbivory where animals feed on the fruits produced by plants (Levey et al., 2002). While consumption by herbivores usually has a negative effect on plant resource fitness, frugivores differ from other herbivores because they can also be important biotic vectors for long-distance dispersal of plant seeds (Jordano et al., 2007). Studies of frugivore ecology have focused on seed consumption, dispersal and germination (see synthesis in Levey et al., 2002), while the ecosystem effects of frugivory have been much less studied (but see Feeley & Terborgh, 2005). Given frugivores are widespread both taxonomically and geographically frugivores may play an important role in zoogeochemical cycles.

Villar et al. (2020) begin to fill the gap in frugivore zoogeochemistry with an experiment of ungulate frugivore effects on elemental cycling in the Atlantic Forest of Brazil. Specifically, the authors report on an 8-year control-exclusion (i.e. frugivores present-frugivores absent) experiment to study the effects of the two largest and most abundant native mammal frugivores in the Atlantic Forest of Brazil, peccaries (family Tayassuidae) and tapirs (genus *Tapirus*) on soil N cycling. The study focused on the *Euterpe edulis* palm dominant forest stands as these are an abundant tree species in the region and a key source of fruit for many animals. The authors used standard methods applied in large herbivore exclusion experiments in grassland and boreal systems for measuring total N, ammonium and nitrate and potential nitrification (i.e. ammonium -> nitrite -> nitrate) and N mineralization (i.e. organic N -> inorganic N) rates.

Villar et al. (2020) observed strong evidence for impacts of frugivores on N cycling in their system. Overall, total N in soil was higher in the presence of frugivores than in the absence of these animals. When looking at N stocks, ammonium was higher in soils in the presence of large frugivores and increased with palm abundance. These findings pertaining to soil N stocks can be interpreted by investigating processes that influence these stocks. Specifically, nitrification rate increased with palm abundance in the presence of frugivores (i.e. controls) but declined with palm abundance in the absence of frugivores (i.e. exclosures). Also, total N in soils was positively correlated with N mineralization potential in controls but not in exclosures. These results constitute some of the first empirical evidence for a strong effect of frugivores on the regulation of N by soil micro-organisms in tropical forests.

The authors also investigated variation in these stocks and rates across sites to uncover interesting landscape-level effects of frugivores on N cycling. This approach is particularly novel and stands out as a major contribution to advancing zoogeochemistry. Specifically, the authors demonstrated that frugivores have a large positive effect on ammonium, nitrate and total N in areas with low background N. These results suggest that frugivores may be reducing the landscape-scale variance in N stocks. The authors used evidence from this experiment to develop the conceptual framework of 'fruiting lawns' for palm-frugivory interactive effects on N cycling in tropical forests. This empirical-based framework is a foundation for developing a priori predictions on the ultimate fate of fruit and frugivore processes (e.g. consumption, trampling, defaecation) on elemental cycling.

Overall, this study elegantly shows that (a) frugivores can be important drivers of N cycling in tropical forests, (b) frugivore effects may be mediated by resource abundance, in this case fruiting palm trees, and (c) frugivore effects can impact spatial patterns of

N stocks across landscapes. This study paves the way for future work to understand how diverse frugivores can impact elemental cycling and the conceptual framework laid out by the authors provides a very useful roadmap.

Most empirical zoogeochemical studies focus on a single or a few abundant species, usually within the same guild thought to have the largest impact on elemental cycling (see review in Schmitz & Leroux, 2020). The study of key modules or interactions has been important for laying the foundation for zoogeochemical inference but future work must place these key interactions within broader ecological networks. This endeavour would parallel progress in community ecology towards scaling modular theory to whole food webs (e.g. Borrelli et al., 2015; Kondoh, 2008) and towards integrating multiple types of interactions to consider a multilayer network of interactions that exist at local and landscape extents (Hutchinson et al., 2019; Pilosof et al., 2017). The use of ecological traits such as body size and feeding mode might be a useful way to bridge the gap between simple modular scales and more complex whole network scales (Kato et al., 2018; Schmitz & Leroux, 2020).

In parallel to adding the above complexity we must continue to develop understanding of specific mechanisms for zoogeochemistry. While some mechanisms may be common across interaction types (e.g. trampling) others may be specific outcomes of one type of interaction (e.g. seed dispersal). Resolving such mechanisms is key for predicting the feedbacks between animals and elemental cycling in the Anthropocene. Indeed, animal management may be part of a portfolio of natural solutions to curb defaunation (Estes et al., 2011), mitigate climate change (Schmitz et al., 2018), and in particular, restore ecosystems (Lundgren et al., 2018) during the current UN decade on restoration.

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