The seventh macronutrient: how sodium shortfall ramifies through populations, food webs and ecosystems

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Abstract
Of the 25 elements required to build most organisms, sodium has a unique set of characteristics that ramify through terrestrial ecology. In plants, sodium is found in low concentrations and has little metabolic function; in plant consumers, particularly animals, sodium is essential to running costly Na-K ATPases. Here I synthesise a diverse literature from physiology, agronomy and ecology, towards identifying sodium’s place as the ‘7th macronutrient’, one whose shortfall targets two trophic levels – herbivores and detritivores. I propose that sodium also plays a central, though unheralded role in herbivore digestion, via its importance to maintaining microbiomes and denaturing tannins. I highlight how sodium availability is a key determinant of consumer abundance and the geography of herbivory and detritivory. And I propose a re-appraisal of the assumption that, because sodium is metabolically unimportant to most plants, it is of little use. Instead, I suggest that sodium’s critical role in limiting herbivore performance makes it a commodity used by plants to manipulate their herbivores and mutualists, and by consumers like bison and elephants to generate grazing lawns: dependable sources of sodium.

Keywords
Biogeochemistry, biogeography, global change, herbivory, ionomics, plant chemistry, plant–consumer interactions, pollination, sodium, stoichiometry.

INTRODUCTION
Life on Earth shares a recipe of 25 chemical elements (Frausto da Silva & Williams 2001). Much of Life’s stoichiometric variation involves differential investment in C, H and O (land plants are the most carbohydrate rich, followed by aquatic plants, followed by most everything else, Sterner & Elser 2002). The use of light, CO₂ and H₂O by plants to build cellulose skeletons in turn relies on adequate quantities of N and P (which constitute large elemental fractions of cellular machinery) along with K as a critical plant osmolyte (Liebig 1855). Their availability constrains plant quantity and quality with effects that ramify up food webs (Sterner & Elser 2002; Reich & Oleksyn 2016).

Here I focus on another element, sodium (Na), with a long, interesting history in the ecological literature, but one rarely gathered together in one place (but see, Dudley et al. 2012). I review the wonderfully idiosyncratic history of sodium physiology and ecology over the past 50 years. I make the case that sodium is the ‘seventh macronutrient’ (or, arguably, the ninth, if you are a fan of Ca and Mg) because of its paucity in the metabolism of plants compared to that of the fungi and animals that eat plants. In doing so, I hope to spark interest in the broader topic of ‘Ionic Ecology’: the physiology of essential elements like Cl, K, Mg and Ca, that work as ions fluxing across cell membranes. Using Na as a first among equals, I present the case that these ionic elements act in ways different, and complementary to, more constitutive elements like N and P. I show ways that sodium likely regulates a plant consumer’s access to the CHO, N and P in foliage, wood, roots and exudates.

TOWARDS A THEORY OF SODIUM ECOLOGY
In 2014, my colleagues and I (Kaspari et al. 2014) introduced the ‘Sodium Ecosystem Respiration’ hypothesis, built on three assumptions:

(1) Most plants do not require sodium metabolically, whereas it is a vital aspect of metabolism for animals and fungi (Box 1).

(2) Plants tend to have lower tissue concentrations of sodium than their animal and fungi consumers. Thus, plant consumers will have a testable suite of traits and behaviours dedicated to meeting their sodium quota (Box 2). In contrast, predators, which consume a more sodium-rich diet (González et al. 2018), will respond to sodium gradients only indirectly, by following plant consumers.

(3) Sodium has a geography. From mm² to continental scales, sodium fluxes and standing stocks vary predictably (Box 3).

SODIUM AND HERBIVORE FITNESS
Before we can dissect the role of sodium in population interactions and ecological networks, I explore how sodium is used at the cellular level (Box 1), the multiple physiological uses of sodium by herbivores, and how they ultimately help account for survival, growth and reproduction.
## Box 1. What does sodium do? A primer for ecologists.

It is hard for an ecologist scanning the periodic table not to ask a very ecological question: ‘what do all those elements do’? The answer says much about the history of life on Earth (Frausto da Silva & Williams 2001 remains an indispensible resource). Suffice to say that life’s carbon framework accounts for much of the C, O and H. N and S help build most of the machinery. Most of the remaining metals provide active spots on enzymes that make life thermodynamically possible. And P is a general workhorse giving us membranes, DNA and the short-term energy storage of ATP.

Which leaves us with four elements with H orbitals containing only 1 or 2 electrons – Na, K, Mg and Ca. When combined with anions like Cl, these four readily dissociate in water. Moreover, these four – and particularly Na and K – spend most of their organismal existence transporting back and forth across bilipid membranes. This fluxing back and forth – and the resulting changes in the charge of those membranes – generates action potentials that transmit signals. These ‘ionic four’ also work with porters, symporters and ATPases to help move other molecules in and out of cells.

Na-K ATPases (‘Na-K pumps’) play an outsized and expensive role in life’s history. Although Na-K pumps likely originated in prokaryotes (Sáez et al. 2009) it is their proliferation that made possible our animal form of multicellularity.

To see how, consider a basic challenge of life: collecting useful molecules behind a plasma membrane. The more stuff a cell gathers, the stronger and stronger grows the osmotic gradient that would force water into the cell, returning it to a lower entropy and a biologically less interesting equilibrium. To solve this challenge, prokaryotes and plants evolved cell walls to reinforce their bilipid membranes. Protists use organelles like contractile vacuoles as pumps to evacuate this constant leakage of water into the cell.

Multicellular animals – for which the outside of the cell is a kind of shared commons with other cells – evolved a different solution. They (we) studded their bilipid membranes with Na-K pumps that eject 2 Na\(^+\) ions from the cell into the intercellular fluid, and pump in 3 K\(^+\) ions into the cell. By generating this single counter-gradient (in the form of salty solution bathing our cells) Na-K pumps effectively counterbalance the osmotic gradient. Needless to say, ensuring that our cells do not lyse also requires careful monitoring, and the Na set point of an animal is maintained with a high degree of precision, through still more pumps associated with the animal’s excretory system (Blair-West et al. 1968b; Denton 1982). These pumps run constantly at enormous cost to the individual: the Na-K pumps in cell membranes alone account for 25-75% of a cell’s entire ATP budget (Frausto da Silva & Williams 2001). The cost and precision of Na regulation has consequences for the ecological niche of animals, particularly herbivores and detritivores, as predators eat salty flesh and are less likely to experience sodium shortfall (see Box 3, Fig. 2).

Multicellular fungi also accumulate sodium; their mycelial cords and fruiting bodies can be up to 34x saltier than the surrounding forest litter (Cromack et al. 1977). The functional significance of Na to fungal metabolism, however, remains rather a mystery. Scharnagl & colleagues (2017) have suggested sodium’s role as a symporter, maintaining turgor in an organism that is literally a series of wide-ranging tubes. Likewise, the electrical potential of hyphal tips may be regulated by voltage gated Na channels, acting as an ‘inverted neuron’. Their most interesting speculation, given the high levels of sodium found in fungal fruiting bodies, is that sodium acts as an attractant to salt craving animal dispersers, in what Scharnagl and colleagues call the ‘potato chip hypothesis’ (see also Reassessing: do plants manipulate sodium?)

In plants, the metabolic role of Na is limited to a small part in C\(_4\) metabolism (Marschner 1995). K, not Na, is the principle plant osmolyte (universally regulated in the cytoplasm at ca. 200 mmol). However, Na can function as a substitute for its fellow monovalent cation, K\(^+\) (Subbarao et al. 2003). This similarity between K and Na (same size and availability in Earth’s crust) is exploited by halophytes, plants that live in highly saline environments, or have halophytic ancestors, that can substitute Na for many of the functions of K (Subbarao et al. 2003).

Abbreviations for elements on this page: C = Carbon, O = Oxygen, H = Hydrogen, N = Nitrogen, S = Sulphur, Na = Sodium, K = Potassium, Mg = Magnesium, Ca = Calcium.

### Sodium as a constraint on herbivore survival

Both ecological stoichiometry (Redfield 1958; Sterner & Elser 2002) and ionomics (Salt et al. 2008; Jeyasingh et al. 2017) describe how the balance of elements, as much as the amount of a single element, can shape an organism’s performance. Here I give four examples of how an herbivore’s sodium demand changes with the nutrients and toxins in the plants it feeds upon and the microbiomes they use in the process.

#### Na and K in the spring: the danger of temporarily K-rich plants

The osmoregulatory, nervous and motor systems of animals use ATP to transport Na\(^+\), K\(^+\), Ca\(^{++}\) and Mg\(^{++}\) across membranes. Since these fluxes often entail a swap (e.g. Na for K, Box 1) things can go wrong when there is a sizeable imbalance in the availability of either of the pair.

One such case involves the spring flush of new grass in seasonally temperate grasslands (Jones & Hanson 1985). The rapid growth of young foliage allows herbivores (from moose to mouse) access to succulent tissue rich in N, P and K before these macronutrients are diluted by the C-rich cellulose and lignin of mature vegetation. For a few weeks in early spring, herbivores are thus eating K-rich food, without compensatory increases in sodium. Absent sufficient sodium needed to translocate K into cells via Na-K pumps, K can accumulate in blood serum (Denton 1982).

In herbivorous mammals, what happens next is a homeostatic dance involving three ions linked to osmoregulation and motor control. First, they compensate with aldosterone, a
hormone that enhances sodium retention and rids the body of excess K, but also evacuates Mg$^{++}$ in the process. Next, the decreases in serum Mg$^{++}$ (and with it, its ability to relax muscles fibres after a contraction) results in a cascade of ionic imbalances.

The result can be tetany and diarrhoea – and ultimately convulsions and death. This is the seasonal hazard for herbivores, especially in inland, low sodium environments, when the stoichiometric balance of ionic elements is temporarily disturbed (Jones & Hanson 1985). Not surprisingly, browsers like deer tend to be highly selective foragers in spring (when they are also reproducing, see below) seeking out foliage with less K (Swift 1948).

**Sodium as an ecological catalyst: when Na co-limits N and P**

A second way that ionomics informs sodium ecology contrasts Na’s ionic function with that of structural macronutrients like N and P. Shortfall of either commonly constrains plant and plant consumer abundance alike (Haddad et al. 2000; Ritchie 2000; Sterner & Elser 2002; Milton & Kaspari 2007; Kaspari et al. 2008a; Kaspari & Yanoviak 2009; Bishop et al. 2010; Joern et al. 2012; Lind et al. 2014; Fay et al. 2015). If Na shortfall decreases the performance of plant consumers (Box 1, 4), one corollary is that the benefits of N and P to plant consumers will increase along a sodium gradient, as Na catalyses the organism’s ability to use those two macronutrients.

Two grasslands, one inland, and one coastal, allowed a test for such an Na-NP interaction in the limitation of herbivorous insects. In the coastal (and more sodium-rich) grassland, NaCl fertilisation had no effect on insect abundance (Prather et al. 2018a), but enhanced the effect of NP, consistent with ecological catalysis. Farther inland, where Na supplies were lower, both Na and NP fertilisation substantially increased herbivore abundance (≥ 1SD over controls) but did not interact (Kaspari et al. 2016).

One working hypothesis is that in the salty coastal prairie, demand for sodium only increased when NP boosted biomass, effectively diluting the sodium supply in the plant tissue. In the inland grassland, however, sodium availability is a limiting nutrient even in control plots. This interpretation is consistent with detritivore responses in the inland experiment that showed the same pattern as coastal herbivores (Kaspari et al. 2016). As the diets of detritivores like collembola and oribatids frequently include root exudates and Na-rich fungi (Scheu & Simmerling 2004) it is likely that sodium requirements for these taxa are only enhanced when NP fertilisers increase belowground root and exudate production, increasing the demand for enough sodium to process it.

This hypothesis, if true, predicts a synergy in the availability of sodium and macronutrients. A distributed experiment discussed below (Borer et al. 2019), provides further evidence for such nutrient interactions.

**Sodium’s role in dealing with tannins**

Sodium appears to play two other supporting roles, this time in the guts of herbivores.

Tannins are carbon-rich plant molecules that bind to and precipitate proteins (Barbehenn & Constabel 2011). They have
Box 3. The geography of sodium

Sodium is an essential nutrient arrayed in a spatial-temporal ‘template’ (sensu, Southwood 1988). Here I briefly describe some of the major processes that generate these patches and gradients of sodium availability. I focus on terrestrial ecosystems and the first meter or so of topsoil as these are most relevant to the plants that form the foundation of the terrestrial food web.

THE IMPORTANCE OF SOIL.

Sodium constitutes about 3% of Earth’s crust, but not all that sodium is bio-available. Most is locked up in feldspar, an insoluble silicate formed from cooling magma (Anderson & Anderson 2010). Thus geologists typically report soil sodium levels 100–1000 times higher than agronomists (Smith et al. 2014).

Soils are a mix of organic matter, silicates and oxides ranging in size from large round crumbs of sand to stacks of clay microfilms – all periodically inundated by sodium solutions, from rainwater to urine. The surfaces of soil particles tend to be negatively charged, so when a solution of Na⁺ cations and Cl⁻ anions enters the soil the Na⁺ ions tend to adhere to these surfaces. Those ions that do not are washed away. The Cation Exchange Capacity (CEC) reflects a soil’s ability to glom onto positive ions, and is effectively an index of soil surface area – at the microscopic level.

A given volume of clay soil has orders of magnitude more surface area to volume than an equal volume of sand. Likewise, organic matter, rich with carbon and its many charged functional groups, offers other opportunities for soils to glom onto Na⁺. So, when a NaCl solution is introduced into a patch of sandy soil, relatively little will stick, and the rest drains away. A rich organic clay soil with a high CEC, in contrast, will lock down much more of the Na⁺, as well as plant nutrients like Mg²⁺, K⁺, Ca²⁺. The amount of clay and sand in soils has a clear geography (Fig. 1) that sets the stage for the geography of sodium limitation.

Likewise, without water to wash away unbound ions, arid environments should tend to hang onto sodium longer regardless of soil type, with the residence time of a Na⁺ ion in a rainy environment commensurately shorter.

Abiotic inputs of Na occur at large spatial grains

Concentrations of sodium are elevated in alkaline, calcareous soils derived from ancient seabeds. When that rock is deep below the surface, plant transpiration or irrigation that mines water from these aquifers can add sodium to surface soils (Jones & Hanson 1985; Marschner 1995). Vast swaths of interior grasslands and scrublands with low topographical relief can supplement their soils in a similar fashion when seasonal rainfall expands aquifers upward to inundate surface soils (Schofield & Kirkby 2003).

Many local sodium patches, ‘salt licks’, are attractive to wildlife and have been long used by aboriginal communities (North America’s BigBone lick doubles as a fossil bed, Jillson 1936; Jones & Hanson 1985). These sodium-rich gathering places are primarily inland due to another driver of sodium availability: aerosol inputs. Seawater, volatilised by wind and waves, collects in clouds and is deposited in coastal areas as rain (Fig. 1, NADP 2006). Thus, deposition is potentially a significant source of sodium in coastal areas with high rainfall. Twenty percent of terrestrial landmass is within 100 km of the sea and thus receives significant supplements of sodium (Kaspari et al. 2008b; Kaspari et al. 2009).

Hurricanes are a particularly dramatic example of oceanic inputs, importing sodium inland via storm surges (inundation by seawater) and oceanic aerosols (Emanuel 2005). The quantity of Na⁺ (as well as K⁺, Mg²⁺, Ca²⁺ Cl⁻) that hurricanes move inland is proportional to wind speed: in one storm, ion content increased 50-fold as winds increased from 5 to 30 m s⁻¹ (Sakihama & Tokuyama 2005). Windborne dust, too, can transport quantities of Na between continents (Carrillo et al. 2002).

Organisms also generate sodium ‘patches’ by accumulating Na in their tissues, and/or excreting it into the environment (Fig. 2). These patches and gradients tend to occur at much smaller spatial scales than the abiotic processes reviewed here, and often generate patches of higher concentration. They are discussed in the main text.

long been considered anti-herbivory compounds, decreasing the quality of ingested foliage by decreasing its effective protein content (Rosenthal & Janzen 1979). Freeland & colleagues (1985) tested this hypothesis with laboratory mice and indeed found that fat reserves declined when tannins were added to the mouse diet. However, other changes also occurred.

(1) Mice fed tannins began to excrete higher quantities of sodium;
(2) Parotid glands, which secrete sodium-rich saliva, increased in mass by 700%;
(3) Aldosterone levels increased to slow Na excretion.

All three effects returned to normal when mice were supplied ad libitum 0.5% NaCl solution.

Why did mice consume more sodium on a tannin-rich diet? It was not, in fact, to inhibit the tannins. To the contrary, mice with access to NaCl, and hence with more saline stomachs, actually increased the efficiency with which ingested tannin’s bound to proteins in the stomach, enhancing the protein’s undigested passage through the rest of the gut (Freeland et al. 1985). This resulted in a new working hypothesis: that tannins are precipitated – inactivated – in the well-
protected stomach by dietary proteins. As a result, no active
tannins escape the stomach to wreak havoc on the more delic-
ate, filigreed mucosa of the small and large intestine. In sup-
port of this hypothesis, the authors note that tannins, sans
added Na, caused mice intestines to secrete more defensive
mucous, an effect that disappeared when sodium was supplied
ad libitum. Moreover, they noted a doubling of N content in the
faeces when mice were on a tannin-rich diet – not from
undigested food but from breakdown products of intestinal
proteins destroyed by tannins!

This, hypothesis, if true, predicts that herbivore preferences
for tannin-rich foods should track sodium availability and vice
versa. In support, Freeland & colleagues (1985) cite a study of
seasonality in salt craving. Both squirrels and woodchucks
show a springtime peak in attraction to sodium associated
with reproduction (and the risk of grass tetany?, see above,
Weeks Jr & Kirkpatrick 1978). But only squirrels show a
second peak of salt craving in the Fall. They suggest that
while the woodchuck continues its diet of foliage, Fall is when
squirrels switch their diet to tannin-rich acorns, protecting
their GI track from the tannic defences in these protein and
lipid-rich foods. This is yet another way that sodium may act
as an elemental mediator in plant–herbivore interactions (Bar-
behenn & Constabel 2011).

Sodium’s role in maintaining the gut microbiome
(and its need for P)

One way to in increase termite abundance is to add sodium to
the soil and litter (Kaspari et al. 2009; Kaspari et al. 2014).
Like ruminants, and other feeders on live and dead wood, ter-
mites crave sodium and host a microbiome of archaea, bacte-
ria, fungi and protists that convert low quality foliage and
wood into a broad array of macromolecules (Jones & Hanson

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Here I build a working hypothesis that predicts how and why plant consumers with large gut microbiomes demand plentiful sodium. The key is another essential element: Phosphorus.

Phosphorus – as ribosomes, ATP and nucleic acids – makes up ca. 1% of dry mass in consumer tissue, ca. 1/10th less in actively metabolising plant tissue, and even less in wood (Sterner & Elser 2002). Given metabolic scaling, microbiomes swimming in guts have whole body P demands that may be 2x or higher than their host (Gillooly et al. 2005). These P-hungry symbionts exist on a diet rich in carbohydrates and poor in everything else (e.g. Filipiak 2019). So when phosphates enter a termite gut, there are still two challenges to moving them inside the cells of symbionts. First, P is far more abundant in the cytosol, and hence faces a steep osmotic gradient resisting any further transport inside cells. Second both a phosphate anion and the microbe’s cell membrane are negatively charged, producing a further electromagnetic barrier to P absorption.

Enter the Na-P co-transporters. Ubiquitous across the Achaea, Eukarya and Bacteria (Werner & Kinne 2001), Na-P co-transporters are proteins that pair an ion rare outside the cell – and hence difficult to absorb passively – with an ion common outside the cell and hence easier to absorb. In Na-P co-transporters, PO$_4^-$ ions pass from the salty exterior of a cell when they ‘hold hands’ with Na$^+$ ions that rush into the cells less salty interior (and which are then ejected again by Na-K pumps).

Thus the working hypothesis: termites and ruminant guts are packed with P-demanding microbes and thick with bilipid membrane by virtue of surface area to volume scaling. To assure every ingested P-molecule is absorbed by a symbiont and recycled within the microbiome, the host must find and ingest adequate supplies of Na to build and maintain a salty rumen. Only then can its symbionts use Na-P co-transporters to glom onto every ingested phosphate, and build and maintain their P-rich cytosol.

As evidence, termite workers come in two forms, the foragers that harvest plant material and the soldiers that defend the colony. Thus while the cells of forager and soldier termites share cells with similar Na and P demands, the guts of foragers should have larger and more functional microbiomes. On two different colony diets, soldiers did not accumulate Na or P in the gut relative to the rest of the body (Table 1, Yoshimura et al. 2002). However, consistent with our hypothesis, workers had 3x the Na and 5x the P in their guts than in body tissue, concentrations 90x and 450x times higher than their food supply.

Thus, sodium may not only allow herbivores to detoxify plant defences like tannins, it may be key to one of the most successful (by biomass) symbioses on Earth, the herbivores and gut microbes that digest plant carbon. If so, ecosystems with higher Na availability should support higher termite and ruminant populations for a given P supply. In support of this conjecture, and across a survey of tropical forests, those with low P and Na supplies had lower decomposition rates and higher standing dead wood and litter (Kaspari & Yanoviak 2008). One next test would increase the phosphorus content of an herbivore’s food (adding P-rich items like grains is one option). If Na is required to enhance P recycling by the gut microbiome, then P-additions to the diet should decrease Na craving by herbivores with large gut microbiomes, and have little effect with those that do not (like caterpillars, Hammer et al. 2017).

Sodium and herbivore growth and reproduction

Individuals must survive before they can grow, and must grow large enough to reproduce. If sodium is in short supply it

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should thus particularly tax the ability of individuals to both maintain their own sodium supply while building new offspring, each with their own sodium demands.

In the optimised world of agronomy, sodium supplements for pregnant livestock are the norm. Cattle on low-sodium pasture, sans sodium supplements, already excrete urine that is effectively sodium-free (Blair-West et al. 1968a). The added demands of reproduction call for increases in the recommended dietary sodium of 20–40% for pregnant and lactating cattle (NRC 2000, 2005).

Still, much of the evidence for the sodium costs of reproduction come from wild mammal populations – all notably plant consumers – that by definition invest high levels of parental care via lactation1. Squirrels and woodchucks increase their use of Na-impregnated wooden pegs from 4 to 100-fold at the outset of the spring breeding season (Weeks Jr & Kirkpatrick 1978). The added demands of reproduction call for increases in the recommended dietary sodium of 20–40% for pregnant and lactating cattle (NRC 2000, 2005).

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Given the critical nature of ‘on-time’ nutrient supply in developing tissues, even a temporary sodium shortfall can leave a lasting record in the form of a developmental abnormality. This is particularly true in nervous and muscle tissues that concentrate sodium (Box 1). Sodium shortfall during pregnancy can inhibit brain development in humans (Al-Dahan et al. 2002) and rats (Bursey & Watson 1983). Salt cravings in humans peak in adolescence (Leshem 2009) during the brain’s last growth spurt (Giedd et al. 1999).

Caterpillars – herbivores that must accumulate all necessary nutrients before reorganising their body plan – have proven to be model organisms for exploring the developmental effects of sodium (Kaspari 2014). The foliage of *Asclepias*, the host plant of monarch caterpillars, has one of the highest Na concentrations in its prairie habitat (Snell-Rood et al. 2014). Caterpillars feeding on *Asclepias* exposed to road salt maintained six times higher Na levels than controls. Moreover pupating + Na males built bigger thorax muscles, whereas pupating + Na females built bigger eyes (associated with brain

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1Whole cow’s milk is 430mg Na l⁻¹; Gatorade sports drink is 390 mg l⁻¹. (USDA 2019).
Metabolic Rate = $\beta = aM^{0.75}e^{-E/kT}$

Table 1 Termite elemental chemistry from (Yoshimura et al. 2002). Foragers with a large microbiome accumulate sodium and phosphorus

<table>
<thead>
<tr>
<th>Source</th>
<th>Na content (ppm)</th>
<th>P content (ppm)</th>
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<td>Gut</td>
<td>Body</td>
</tr>
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<td>Termite forager</td>
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<td>527</td>
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<tr>
<td>Termite soldier</td>
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<td>1109</td>
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</table>

Sodium and the density and abundance of plant consumers

If plant consumers regularly survive, grow and reproduce better in ecosystems with ample sodium, this should ultimately be reflected in higher population densities, as those consumers avoid, or otherwise suffer, in areas with inadequate sodium.

Natural gradients in sodium availability often act as templates for herbivore abundance. The literature on mineral licks has implicated sodium as an active ingredient driving aggregation of herbivores from ungulates to bats, butterflies to parrots (reviewed in Jones & Hanson 1985; Dudley et al. 2012). An early meta-analysis of the 100-fold range in densities of North American microtine rodents (primarily grass and seed eaters) revealed the highest densities in soils with highest sodium levels (Aumann 1965). A survey of Nebraska grasslands revealed a positive effect of foliar sodium on the local densities of grasshoppers (Joern et al. 2012). Across 54 North American grasslands the abundance of herbivorous insects tracked geographical gradients of increasing plant biomass and plant tissue sodium (Welti et al. in press). Going forward, abundance studies would thus likely benefit from maps of biogeochemistry (e.g. Grossman 2004).

Such gradients can be highly localized. The most concentrated biotic sodium patches (Fig. 2) are also among the most dependable and conspicuous – tears and perspiration. Both are exploited by a variety of invertebrates (Barrows 1974; Bänziger et al. 2009).

The oldest experiments testing for sodium effects on abundance were likely practiced by ranchers that moved cattle among pastures using salt blocks as lures (McDowell 2003). Still larger manipulations involved excavating water holes for elephants in central Africa, who were partial to holes supplemented with salt (Weir 1972).

Still more experiments simulated urine deposits at m² scales and more dilute oceanic aerosol deposits at larger scales. Across 54 North American grasslands, 1-m² plots dosed with 0.5% NaCl hosted 0.5 SD more omnivores/herbivores than those dosed with pure water (Welti et al. 2019); similar small-scale pulse experiments in a Peruvian rainforest had the same effects on detritivores (Clay et al. 2014b). Both experiments generated results after two days. Tropical termites increased sevenfold on sodium pulses in a Peruvian forest (Kaspari et al. 2009) and 17-fold in response to year-long 7x7m plot additions simulating Caribbean rainfall (Kaspari et al. 2014).

Experiments have also been useful at testing the prediction that plant consumers respond to sodium shortfall more strongly than do predators. In pulse experiments in the tropical litter, predator responses lag behind and are smaller in magnitude than those of detritivores (Kaspari et al. 2009; Clay et al. 2014b). A similar pattern exists in grasslands, where the effect sizes of predators and parasitoids are half that of herbivores and omnivores (Welti et al. 2019). These results suggest predators are responding to accumulating prey, not the salt that attracted the prey.

If the reader pauses to wonder about the causality of this relationship (i.e. do rodents enhance soil Na signature or vice versa?) see ‘Turning the tables: herbivores use urine to manipulate plants’ below.
Intermediate between herbivory and carnivory, omnivory – the mixing of dietary plant and animal tissue – was once thought destabilising and rare in food webs, but is now considered pervasive (Winemiller 1996) and a subject worthy of investigation (McCann & Hastings 1997). As flesh is saltier than plant tissue, Clay & colleagues (2017) contrasted 10 pairs of North American ant communities – in salty coastal vs. less saline inland ecosystems – to test the hypothesis that low sodium ecosystems drive omnivore populations to consume more flesh. Decreases in sodium supply – but not Net Primary Productivity nor Nitrogen – accounted for increased omnivory among 20 ant species. More gruesomely, migrating crickets on a low sodium diet will resort to cannibalism (Simpson et al. 2006); lactating prairie dogs – in a part of the life cycle that is particularly sodium stressed (see above) – engage in infanticide (Hoogland 1985).

So, there is growing evidence – experimental and comparative – for the pervasive role of Na as the ‘seventh macronutrient’ (NRC 2005; Kaspari et al. 2009; Clay et al. 2014a; Prather et al. 2018b; Welti et al. 2019), but one whose subsidies promote the fitness of plant consumers. I know of no other element whose supply rate targets two trophic levels – detritivores and herbivores – at the potential expense of others. In the next section I review some of the implications of this elemental asymmetry.

**SODIUM IN ECOLOGICAL NETWORKS**

If plant consumers regularly underperform due to sodium shortfall, then the inverse must be true: herbivores and detritivores, supplemented with sodium, should benefit relative to other parts of the food web – plants, predators and detritus. This is a surmise with relatively little evidence – for or against – thus far.

**Herbivory increases in high sodium ecosystems**

I know of only two experiments bearing on how sodium availability influences the risk of herbivory. In a distributed experiment across 26 grasslands (discussed in greater detail below) plots fertilised with N and P lost their sodium-rich plant species to grazers (Borer et al. 2019). And in an as yet unpublished study Welti and colleagues (Welti et al. In prep) found the dominant grass species on each of four prairies, when fertilised with NaCl, experienced 50% higher levels of herbivory than control plots. Fungal pathogens and leaf miners were the biggest contributors to this pattern.

**Higher decomposition in high sodium ecosystems**

Higher or lower predator abundance in high sodium ecosystems?

Sodium can also limit rates of decomposition, primarily by enhancing the abundance and activity of fungi and invertebrate detritivores. All such studies thus far have come from tropical forests, where the combination of heat and precipitation accelerates basal decomposition rates, further enhancing the ability to detect effects in months instead of years.

In the first experiment, run over two weeks in a Peruvian Amazon forest, sodium pulses simulating urine enhanced litter mass loss by 41% with 7% decreases in lignins – compounds resistant to decomposition (Kaspari et al. 2009). This rapid response was due at least in part to the sevenfold increases in termite densities on + NaCl plots. Similar experiments contrasted a sodium-poor Amazon forest with a Panamanian forest 25 km from two oceans. Wood decomposed twice as fast on + NaCl treatments in the Amazon, with 20-fold increases in termite densities; in a salt-rich Panama rainforest, +NaCl treatments depressed decomposition (Clay et al. 2014a). Decomposers will recruit to sodium patches, and decompose litter there, when sodium is in short supply.

A year-long experiment in inland Ecuador, simulating the dilute inputs of coastal aerosols on 4x4 m plots (Kaspari et al. 2014) revealed similar patterns. Three species of wood, from hardwood to softwood, decomposed 29 to 78% faster on plots with the aerosol inputs of sodium. Termites, again, were implicated as agents, increasing 17-fold on + NaCl plots. A subtropical study that contrasted the effects of urine vs. rainfall concentrations of sodium adds an interesting twist. The higher concentrations were more likely to attract invertebrate microbivores, whereas the lower concentrations enhanced microbial activity (Jia et al. 2015).

Accruing evidence thus suggests that spiking an ecosystem with Na increases both herbivory and decomposition rates – evidence of plant consumers exhibiting ‘top-down’ effects on their ‘prey’. But how should the consumers of the consumers respond?
Box 5. Sodium in the anthropocene

The Anthropocene is delineated by a clear biogeochemical signal that includes increases in CO₂ beyond 400 ppm and a rearrangement of Earth’s elements (Snell-Rood et al. 2015). The story of sodium is intertwined in both.

As we have seen in Box 3, inland ecosystems, particularly those that are more mesic, are pre-disposed to be sodium limited given their lack of oceanic aerosols and the leaching power of rainfall. One consequence is that litter accumulates in large swaths of inland tropical rainforests as decomposition of the forest’s copious NPP is hindered by salt shortage (Kaspari et al. 2009; Kaspari et al. 2014; Clay et al. 2014a). Thus, like arctic peat bogs, considerable carbon remains out of the atmosphere due to conditions slowing decomposer organisms.

Moreover, just as increasing temperatures threaten to decompose ancient peat (Dorrepaal et al. 2009), another positive feedback loop may be in the offing. Tropical storms are common in many parts of the world, and their tracks can move inland 100’s of km’s beyond the coastal zones of aerosol deposition (Boose et al. 1994). As ocean’s warm, stronger and more frequent storms are likely to carry more Na further inland (Emanuel 2005) both creating detritus, and enhancing the conditions by which it is decomposed.

Increases in temperature, particularly in already warm environments, can accelerate demand for sodium by ectotherms, and hence the likelihood of sodium shortfall (Box 4, Prather et al. 2018b). So even as metabolic rates are less constrained when temperatures increase (Gillooly et al. 2001) this may be counteracted by the concomitant decrease in the ability to maintain sodium set points. This is particularly germane to global decomposition rates (Conant et al. 2011), which may be less temperature sensitive because the fungi and termites that do the work are sodium starved (Kaspari et al. 2009).

The Anthropocene highlights a substantial re-arrangement of sodium’s geography. Road salt, applied after freezing precipitation, likely creates a large-scale lattice of NaCl availability throughout many seasonal ecosystems (Fig. 1). In the northeast US, this may mean 68 kg of NaCl for every lane-mile after every freezing precipitation event (Mattson & Godfrey 1994; Massachusetts Department of Roads 2010). Road salt in these areas has already exceeded by fourfold wet deposition in precipitation (Jackson & Jobbagy 2005). The effects of road-salt on plants can extend 10-100 m or more from the point of application (Schonewald-Cox 1988; Forman & Deblinger 2000; Kaspari et al. 2010). Although unquantified, this is a potentially large sodium subsidy to terrestrial ecosystems, one that leaves the sodium in terrestrial food webs while depositing the Cl⁻ as a pollutant in streams and lakes (Jackson & Jobbagy 2005).

Irrigation is a second way to move large quantities of sodium into surface soils. Irrigation water, especially that mined from aquifers, often contains trace quantities of sodium. Arid and semi-arid ecosystems that lack sufficient quantities of precipitation to leach out this sodium are prone to long-term salinisation (Qadir et al. 2014). Estimates vary, but conservatively 20% of irrigated land (Qadir et al. 2014) or 30% of all arable land (NRC 2005) have plant yields diminished by this sodium accumulation. The mechanisms likely include sodium stress on the plants, but it is possible (and testable) that a second driver are the grasshoppers and other herbivores attracted to the sodium-tainted water spraying out of the centre-pivot sprinklers.

(Fig. 2) and the lack of a pervasive role for sodium in plant metabolism (Marschner 1995; Taiz & Zeiger 1998). Even the few cases where micro-additions (< 1 mM) increase growth rate and yield seem limited to crops growing on K-impoverished soils, where the Na ions substitute for K’s osmolytic role (Kronzucker et al. 2013).

A re-evaluation is in order. The first piece of evidence involves the +100-fold variation in sodium concentrations found across plant species (Fig. 2). Across a global suite of 26 grasslands and 201 common herbaceous species, foliar sodium varied five orders of magnitude (Borer et al. 2019). This Na variation scales up to the ecosystem level. Across 54 North American grasslands, plant sodium measured from clip plots varied 100-fold from 8 to 2607 ppm (Welti et al. 2019).

Finally, sodium concentration shows systematic variation in plant parts: Hiebert & Calder (1983) recorded 24- to 40-fold nectar variation in two meadow communities; a survey of pollen loads from 36 plant species yielded a similar 30-fold variation in Na (Somerville & Nicol 2002). What maintains this variation in sodium uptake and standing stocks among plant species and assemblages?

One hypothesis posits that, as related ionic metals, sodium can substitute for K’s osmolytic role when ecosystems are K-poor (Wakeel et al. 2011). Such substitutions likely contribute to the geographical trend of higher plant sodium in sandy soils not far from the ocean (Welti et al. 2019).

In this section I develop a second hypothesis: that plants manipulate their sodium stocks to exploit the sodium cravings of their consumers and mutualists (Kaspari et al. 2019). Variation in plant sodium thus reflects a variety of adaptive solutions by species within communities, and, at the ecosystem scale, adaptive solutions to shared challenges (Subarao et al. 2003).

How would this work? Start with the premise that sodium attracts consumers, and that the intensity of this attraction is inversely related to sodium availability. Next add a cost to the plant of repelling or accumulating sodium, which can be energetic (e.g. root pumps, Subarao et al. 2003) or directly via herbivores shaping a plant’s survival, growth or mortality (Borer et al. 2019). Finally add a benefit to attracting consumers that counterbalances these costs (e.g. plants increase their sodium content to compete for pollinators and seed dispersers; they lower it to repel herbivores). Let us discuss some possible scenarios.

Attracting pollinators with salt

Do pollinator-limited plants spike their nectar with sodium? The bees and ants that pollinate and defend plants void
considerable amounts of water, and with it, electrolytes like sodium (Horn 1985; Prather et al. 2018b). Calder & Hiebert (1983) estimated that 14% of whole body sodium in hummingbirds must be replaced daily. Scale insects (Order: Hemiptera) void exudates consisting of copious sugar water scrubbed of sodium (Horn 1985). One result is that when bees feed on such exudates – like voles feeding on high K grass (Jones & Hanson 1985) – they can exhibit their own form of tetany called ‘acute bee paralysis’ (Horn 1985). Not surprisingly, solutions laced with sodium often are especially attractive to pollinators (Arms et al. 1974; Lau & Nieh 2016) like Apis mellifera, the European honey bee, which shows strong sodium preferences year-round (Bonoan et al. 2017).

Our first hypothesis – that a community’s high-sodium individuals spike their nectar with sodium to better compete for pollinators – begs the question: can plants channel sodium only to parts of the plant where it can do some good – as nectar – while keeping it out of foliage and thus enhancing the risk of herbivory? Or does sodium absorbed through roots or leaves diffuse uniformly through the plant. If the latter, this sets up a potential trade-off – a plant suffers increased herbivory to enhance the dispersal of its pollen. This is a key question but one, for now, unanswered.

The ‘salty nectar’ hypothesis also predicts differing levels of plant sodium among pollination syndromes: plants with animal pollinators should sequester more sodium than clonal or wind-pollinated species. Snell-Rood (2014) found lower leaf tissue concentrations of sodium in wind-pollinated grasses (Panicum oligosanthes, 72 ppm) and oaks (Quercus ellipsoidalis, 51 ppm) compared to insect pollinated mustards (Berteroa incana, 115 ppm) and milkweeds (Asclepias syriaca, 2,065 ppm). If true, the ultimate test of the salty nectar hypothesis would find enhanced seed set in sodium fertilised plants pollinated by animals, but not by the wind. This has yet to be done.

### Weaponising sodium against herbivory

How would sodium be used as a plant defence against herbivores? One method would be to attract bodyguards. Parasitoid wasps and ants are fuelled by sugar and drink the nectar of their host plants (Galetto & Bernardello 1992; Wückers 2004) – spiking nectar with electrolytes like sodium could thus enhance both a plant’s pollination and its defence. Moreover, plants that host ants as defence against herbivores often synthesise specialised food bodies and extra-floral nectaries (Rico-Gray & Oliveira 2007) two more foods to potentially spike with salt. Acacia trees that host their own ant–plant colonies provide food bodies that ‘contain all amino acids and all fatty acids that are considered essential for insects’ (Heil et al. 2004). I know of no such analysis for minerals like sodium.

A second way to avoid sodium-limited herbivores is by being less salty than your neighbours (Arms et al. 1974). If true, then the low end of the interspecific sodium variation within a community (Fig. 2) may reflect strategic investments in root pumps to limit passive absorption of sodium from the soil (Munns & Tester 2008), or switches in life history to wind pollination (Culley et al. 2002), both reducing the possible accumulation of foliar sodium. Freeland & colleagues (1985) proposed that such low tissue sodium is an ‘innate defence’ of plants, one that may be further augmented by evolution of allelochemicals that actively deplete sodium stories in herbivore bodies. For example, as we saw earlier in discussion of sodium tetany, supercharging plant tissue with K simultaneously increases the demand for sodium by its consumer in order to run Na-K pumps. If a plant population invests simultaneously in root pumps to minimise Na and increase K absorption, herbivores and pollinators wishing to avoid tetany may forage elsewhere.

We have seen some evidence above that adding Na to grassland plots can increase herbivory. But do plant species with higher tissue sodium levels pay a cost? Results from a distributed field experiment across 26 grasslands and four continents suggests so (Borer et al. 2019). Some plots were fertilised annually with NPK, which increased plant biomass over that of control plots. Each treatment was further left exposed to, or fenced from, vertebrate herbivores. Borer and colleagues found no discernible change in plant composition on control plots, but on fertilised plots – the ones with more biomass – high-sodium plant species decreased, and low-sodium plants increased. Moreover, the herbivore culling of salty plant species was most pronounced in mesic sites (Borer et al. 2019). Why would vertebrate herbivores – mainly rabbits and deer – cull high sodium plants, but only when biomass was enhanced by NPK fertiliser?

> One possible reason is nutrient dilution (Fan et al. 2008; Welti et al. 2020), the decrease in a plant’s mineral concentration when plant biomass increases, but mineral availability remains the same. Both fertiliser and precipitation are recipes for building more plant tissue, while in turn generating sodium-poor vegetation. Every mouthful of foliage on NPK plots, especially in wet grasslands, would thus be less salty since the same amount of soil sodium would suffice through more plant tissue. This in turn would exacerbate any ongoing sodium limitation of herbivores and spur each to search for, select and consume the saltiest plants in the community. Borer and colleague’s distributed experiment demonstrates the potential role of sodium content in generating risk of herbivory, and the potential advantages to plants that can dilute their sodium content.

### Do plants spike fruits with salt to attract dispersers?

Another place to look for sodium manipulation is in the various contrivances that plants use to attract dispersers. Neotropical bats are a fruitful system to explore this question (Bravo et al. 2010, 2012; Bravo & Harms 2017). Frugivorous bats, particularly pregnant ones, frequent sodium-rich licks and rely on a keystone plant – fig trees – as a year-round source of food (Bravo et al. 2010). The same fig trees also spike their fruits with sodium, though typically at levels lower than those meeting the bat’s metabolic demands (Bravo et al. 2012). When soil sodium supplies increase closer to the coast, sodium concentrations also increase (Bravo & Harms 2017) inching towards levels that meet the bat’s requirements.
Some plants also furnish seeds with eliaosomes with the goal of luring and rewarding ants to disperse the seed far from the parent’s shadow (Rico-Gray & Oliveira 2007). A survey of 15 such plants found their eliaosomes full of low molecular weight amino acids and monosaccharides (Fischer et al. 2008). No data on minerals is presently available, but if sodium is used as a lure, we should expect it to be more effective in low-sodium environments, and at higher levels in species with eliaosomes than species without.

Janzen (1984) suggests a mechanism that links attracting herbivores with more effective seed dispersal. He linked three observations: many grasses (1) tolerate high levels of grazing, (2) are wind pollinated, but (3) produce big inflorescences full of tiny seeds. Janzen proposed that large herbivores like bison are attracted to nutritious vegetation and consume inflorescences along with the foliage. If so, grasses that accumulate sodium, especially late in the season – may pay the price of increased herbivory for the opportunity to send their offspring away in nutrient-rich dung. This is testable, but untested.

Finally, the large ungulates of the grasslands also bring something else to the discussion: urine.

**Turning the tables: herbivores use urine to manipulate plants**

Up to this point, I have been suggesting plausible hypotheses for how plants can manipulate their sodium content to cajole or repel animal associates. But there is growing evidence that herbivores use urine – full of Na, as well as N, Mg and K (Fig. 2) – to manipulate plants. The end result is a dependable sodium source that also tightens the sodium cycle, reducing its loss from the ecosystem.

Known as latrines when used by individuals, and grazing lawns when generated by herds of herbivores, the habit of localising urine deposition is widespread among herbivorous mammals from voles to elephants (Woodroffe et al. 1990; McNaughton et al. 1997; Hempson et al. 2015). Latrines and lawns share a number of features.

1. Urine is deposited on low vegetation, typically grass. Topical application increases foliar sodium more quickly and effectively than relying on roots, especially as roots may have pumps designed to regulate sodium inflow from the soil (Benes et al. 1996). On a variety of African grazing lawns plant foliage, but not soil they grow from, is higher in sodium (Hempson et al. 2015) suggesting it is entering the plant mainly through the foliage.

2. These plants are simultaneously grazed. Herbivores ‘excrete where they eat’.

3. Fertilised by a variety of nutrients, plants on grazing lawns and latrines often regrow lush and green, perhaps enhanced by higher rates of transpiration in clipped vegetation (McNaughton 1984; McNaughton et al. 1997).

4. Grazing lawns and latrines endure, and are revisited, often over multiple years (Woodroffe et al. 1990; McNaughton et al. 1997; Knapp et al. 1999).

5. Grazing lawns and latrines are common in low-Na ecosystems with large ungulates, with their own high sodium requirements.

In sum, latrines and lawns appeared to be engineered by herbivores as dependable nutrient hotspots at spatial grains from cm² to fractions of a ha.

In the North American prairies, herds of bison create and revisit patches and lawns varying from 20 to 400 m², abandoning patches at a rate of 6–7% year⁻¹ (Knapp et al. 1999). Experimental urine patches act as ‘seed crystals’ for bison lawns, enhancing the growth of grasses preferred by bison, which preferentially graze them and, in the process, expand the lawns (Steinauer & Collins 2001).

A variety of African ungulates use grazing lawns and create a novel biogeochemical footprint: 10 of 19 elements were higher in the foliage of grazing lawns, with Na showing the greatest increase (McNaughton 1988). A later study tested the hypothesis that these lawns were repeatedly visited to maintain high nutrient content; grazing exclosures caused nutrient declines only when erected in regularly grazed areas (McNaughton et al. 1997). Hippo grazing lawns in west Africa generate shorter, more digestible grasses that are richer in protein and sodium than those found in exclosures (Verweij et al. 2006). Of course, urine contains many potential nutrients, but Hempson & colleagues (2015) review the evidence and conclude that sodium conservation on grazing lawns was ubiquitous and ‘underestimated’ relative to nitrogen.

On the other end of the size spectrum, water voles are grass eating rodents that maintain core and peripheral territories. Vole latrines are maintained only on the constantly occupied core sites and then, only in breeding season when demand for sodium and other nutrients is high (Woodroffe et al. 1990). The number of latrines rises steadily from early spring through late summer, suggesting a correlation with sexual activity.

**Is sodium this era’s ‘plant secondary metabolite’?**

Sodium is unique in targeting two trophic levels – decomposers and herbivores – in terrestrial food webs, with growing implications for its use by plants to manipulate the behaviour of their associates. This reversal of the assumption – from sodium as a passive, inert ion to sodium as an actively manipulated chemical agent – is not without precedence. It mirrors the gradual realisation, some 50 years ago, that ‘plant secondary metabolites’ like alkaloids and phenolics, were not metabolic by-products, stored out of the way, but active compounds, sequenced as defences against herbivores (Rosenthal & Janzen 1979). This longstanding argument suggests that plants use Na in the same way they use chemical defences, as means of manipulating population interactions. If true, experimental sodium additions, or natural additions via animal urine (Clay et al. 2014a), may have fitness consequences for plants via changing rates of pollination and herbivory with further consequences for the geography of terrestrial food webs.

**CONCLUSION: WHERE DO WE GO FROM HERE?**

I have laid out a research agenda for incorporating sodium as a key biogeochemical driver of everything from individual fitness to the structure of food webs to our atmosphere’s level of CO₂. Allow me to cherry pick four of my favourite sodium opportunities for ecologists going forward.
How are anthropogenic rearrangements of sodium shaping key ecological processes?

In Box 5, I review how humans are irrigating the soil with sodium-tainted water, scattering tons of NaCl on roads and ramping up the tropical storms that carry sodium inland. Where herbivores and decomposers are sodium limited, rates of carbon mineralisation and herbivory should follow these increases.

Do plants actively manipulate their sodium levels to drive population interactions?

This is a two-part question. First, we know that sodium gets into plants from the soil through root channels and pumps (Marschner 1995); and through the leaves via absorption of aerosol-rich rainwater or urine (Benes et al. 1996). Can plants allocate that sodium to different plant parts, spiking nectar, pollen, fruits and seeds with attractive sodium while keeping it out of leaves? If so, then those traits may allow plants to selectively attract pollinators, promoting higher seed set. If not, then the benefits of higher seed set would be traded off against higher rates of herbivory. A second set of compounds – plant defences – may be another player in this trade-off. For example milkweeds (Asclepias) are defended by latex and cardenolides (Züst et al. 2015) yet also accumulate sodium (Snell-Rood et al. 2014) with particularly high concentrations in their flowers (E Welti, unpublished data). Do such defences free plants to exploit the positive effects of sodium, while lessening their otherwise increased vulnerability to herbivores?

Do plant fungal interactions key on sodium?

In contrast to studies of animal models, we remain largely in the dark as to the role of sodium in fungal mycelia and fruiting bodies, save to say they accumulate it (Scharnagl et al. 2017). Fungi can be plant pathogens and mutualists. Does increasing soil sodium promote the health and function of mycorrhizal symbionts? If so, we predict the minerals transported by fungi to plants – like phosphorus – should increase in plant tissue with experimental additions of Na. Likewise, is one cost to increasing sodium inputs higher viability of fungal pathogens?

What is the role of urine in the spatial structure of ecological communities?

Animals – from mites to elephants – create Na hotspots whenever they urinate (Steinauer & Collins 1995, 2001; Clay et al. 2014a). As bladder size scales isometrically (c. $M_0^{0.97}$, Yang et al. 2014) urine patch size declines from 18 l of urine per patch for elephants to a trillionth of that quantity for soil macroinvertebrates. This distribution of patch size and concentration in a given community may be key to promoting coexistence of herbivores (Ritchie & Olff 1999). What is the half-life of an elephant urine dump before soils and plants regain background levels? Migratory animals may move sodium distances proportional to their size (assuming bladders fill at a rate proportional to $M_0^{0.73}$, that bladder size scales as $M_0^{0.97}$, and that velocity of walking animals scales as $M_0^{0.25}$, Peters 1983). Migrating animals can thus be effective generators of Na gradients (Simpson et al. 2006; Doughty et al. 2016). To what extent does the extirpation of megaherbivores leave a lasting signal in an ecosystem’s sodium ecology?

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DATA AVAILABILITY STATEMENT

Data for Fig. 2 of this study are available at Dryad https://doi.org/10.5061/dryad.5735t4b48

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