

# The nutritional geography of ants: Gradients of sodium and sugar limitation across North American grasslands

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## Abstract

1. Sugar and sodium are essential nutrients to above- and below-ground consumers. Unlike other properties of ecological communities such as abundance and richness, we know relatively little about nutritional geography—the sources and supply rates of nutrients, and how and why they vary across communities and ecosystems.
2. Towards a remedy, we present a suite of hypotheses for how sodium and sugary exudate availability should vary for a common omnivore—the ants—and test them using a survey of 53 North American grasslands.
3. We do so by running transects of salt and sugar baits and inferring the magnitude of environmental supplies as the inverse of their use as exogenous baits. We then use estimates of potential drivers of the availability of salt and sugary exudates—plant and soil nutrients, and bioclimatic variables—to test the best predictors of sodium and salt use by ant communities.
4. Beyond a baseline of ant activity, salt use increased as an inverse of the amount of sodium in an ecosystem's plant tissue, but not its soils. Plant sodium varied by two orders of magnitude in grasslands across 16° latitude. This suggests that plant exudates are an important source of sodium for grassland consumers. The three drivers that best predict exogenous sugar use by ants all point to factors constraining sugar production: net above-ground productivity, how far the community is into that year's growing season (both reflecting the rates of photosynthesis) and, intriguingly, the potassium content of plant tissue, which is likely linked to exudate production via plant turgor.
5. These data suggest that ants and other consumers across a range of grasslands and climate vary significantly in the demand and supply of sugar and salt. This nutritional geography ultimately arises from gradients of climate and biogeochemistry with implications for the geography of plant–consumer interactions.

## KEYWORDS

ants, biogeography, diet, ecosystems, exudates, omnivore, sodium, sugar

## 1 | INTRODUCTION

A fundamental feature of any community of consumers—including animals, fungi and many protists and bacteria—is what they eat. Consumers are built from and fuelled by a variety of compounds (amino acids, fats, sugars) and minerals (Na, K, Cl; Frausto da Silva & Williams, 2001; Raubenheimer, Simpson, & Mayntz, 2009; Sterner & Elser, 2002). Shortfall in the consumption of these nutrients can limit individual performance, and, collectively, the abundance and activity of populations (Behmer, 2008; Kaspari & Powers, 2016; Simpson, Sibly, Lee, Behmer, & Raubenheimer, 2004; White, 1978). Omnivory—eating plant and animal tissue—is a common way of achieving an optimal mix of nutrients (Digel, Curtsdotter, Riede, Klarner, & Brose, 2014). Just as basic community properties such as abundance and diversity mechanistically track the abiotic template of temperature, precipitation and biogeochemistry (Kaspari, Alonso, & O'Donnell, 2000; Rosenzweig, 1995; Roy, Jablonski, Valentine, & Rosenberg, 1998), there is increasing evidence that the diets of omnivores can vary predictably with the geography of abiotic drivers (Clay, Lehrter, & Kaspari, 2017; Simpson, Sword, Lorch, & Couzin, 2006).

Here, we develop and test a framework for the nutritional geography of sugar and salt. Consumer performance is often limited by shortfalls of sugars and sodium. These nutrients are obtained by consuming soil, microbes, plants (both tissue and exudates) and animals (Bais, Weir, Perry, Gilroy, & Vivanco, 2006; Cook & Behmer, 2010; Cook & Davidson, 2006; Dudley, Kaspari, & Yanoviak, 2012; Galef, 1996; Mayntz, Raubenheimer, Salomon, Toft, & Simpson, 2005; Raubenheimer et al., 2009; Snell-Rood, Espeset, Boser, White, & Smykalski, 2014). Both the supply and demand for sugar and salt likely also vary geographically, as the sugars made available by plants—net primary production ( $\text{gC m}^{-2} \text{year}^{-1}$ )—are constrained by temperature and precipitation (Rosenzweig, 1968) and the availability of sodium tends to increase towards coastlines (as oceanic aerosols) and in clay versus sandy soils (Kaspari & Powers, 2016). Combined, these propositions suggest that a robust understanding of the geography of consumer abundance can start with the geography of essential nutrients that are high in demand relative to supply. Such models are still in their infancy (but see Clay et al., 2017; Simpson et al., 2006). Towards a remedy, we explore how the use of sucrose and NaCl baits (henceforth sugar and salt) by ant communities maps onto potential drivers of both salt and sugary exudates across 53 grasslands in North America.

### 1.1 | Ants as model system to explore nutritional geography of sodium and sugar

Ants (Formicidae) are ecologically diverse and woven into most of Earth's terrestrial food webs (Laakso & Setälä, 2000; Lach, Parr, & Abbott, 2010). Grasslands are widespread, covering ca. 40% of Earth's land surface but often heavily modified (Hoekstra, Boucher, Ricketts, & Roberts, 2005; Wood, Sebastian, & Scherr, 2000). Grassland ant communities are numerically dominated by populations of omnivores whose diets mix plant and animal foods to feed the workers and grow the colony (Wills & Landis, 2018). Ant community

demand for sugar and salt can be quantified by the attraction of ants to artificial baits (in this case, Eppendorf tubes charged with sodium and sugar solution; Kaspari, Yanoviak, & Dudley, 2008). Grassland ants are thus a model system for exploring how salt and sugar demand and supply covary in space.

Sodium is a trace element in most plant tissue (Marschner, 1995; Taiz & Zeiger, 1998). Plant consumers have Na tissue levels 100- to 1,000-fold higher than the plants they eat (Cromack et al., 1977; Frausto da Silva & Williams, 2001) and must find and accumulate Na from a Na-poor diet. Moreover, Na is metabolically expensive (ca. 1/3 of an animal cell's resting metabolism is invested in its Na-K pumps, Frausto da Silva & Williams, 2001) and lacks a stable storage form in the body. A consumer's rate of consumption and excretion must equilibrate at its Na set point, as deviation from that set point causes pathology (NRC, 2005; Prather, Roeder, Sanders, & Kaspari, 2018a).

We posit three primary environmental sodium sources for ants (Table 1).

**Soil Na:** Sodium often accumulates in soil depressions, especially in clay soils, where it exists in solution. These sodium hotspots are distributed non-randomly continentally and within landscapes (Jones & Hanson, 1985; McNaughton, 1988). This hypothesis assumes that ants harvest sodium through geophagy similar to puddling behaviour by butterflies (Arms, Feeny, & Lederhouse, 1974).

**Plant Na:** A second, more speculative hypothesis, builds on the observation that sodium content varies widely among co-occurring plants (Han, Fang, Reich, Ian Woodward, & Wang, 2011;

**TABLE 1** Proposed drivers of sodium and sugar limitation at geographic scales including relevant studies

Driver	Mechanism	Citation
Sodium		
H1: Soil Na	Geophagy or puddling	Arms et al. (1974)
H2: Plant Na	Dissolved in exudates	
H3: Insect Biomass	Consumed in animal tissue	Clay et al. (2017)
Sugars		
H1: NPP	Ultimate constraint on sugar production	Rosenzweig (1968)
H2: %GDD	Plant production capacity increases over the season	
H3: N, P	Macronutrients promote NPP	Harpole et al. (2011)
H4: K	Promotes control of exudates by plants	Carvalhais et al. (2011), Sardans and Peñuelas (2015)
H5: Insect biomass	By releasing ants from NP and Na limitation, increases demand for sugars	Yanoviak and Kaspari (2000), Clay et al. (2017)

Snell-Rood et al., 2014). Ecosystems may thus conceivably vary in the saltiness of their plants. As that sodium can make its way into plant exudates such as nectar (Hiebert & Calder, 1983), it suggests exudate feeders such as ants can obtain Na directly from plants.

**Insect Biomass:** Herbivorous and omnivorous insects often seek out flesh to meet their sodium demands (Simpson et al., 2006). This hypothesis assumes that ecosystems with higher abundances of insect biomass offer more sodium to omnivores such as ants, through living prey or necromass.

In each of the above cases, if ant community use of salt baits decreases along gradients of increasing soil sodium, plant sodium or insect biomass, this would constitute evidence for a geography of limiting sodium supplied by those sources.

Ants invest considerable colony resources harvesting sugars from roots and nectaries of plants directly or via insects that produce honeydew (e.g. Auchenorrhyncha, Blüthgen, Gebauer, & Fiedler, 2003; Davidson, Cook, Snelling, & Chua, 2003; Mayer, Frederickson, McKey, & Blatrix, 2014; Tennant & Porter, 1991; Way, 1963). Access to these sugars has consequences for colony size (Wills et al., 2015), thermal tolerance (Bujan & Kaspari, 2017), competitive ability (Kay, Zumbusch, Heinen, Marsh, & Holway, 2010) and immune function (Kay et al., 2014). However, in contrast, to sodium, we know of no systematic inquiry into the geography of sugary exudates and their subsequent limitation of consumer populations. We hypothesize five basic constraints on plant exudate production in seasonal grasslands (Table 1).

**NPP:** Photosynthesis is the primary source of glucose production in an ecosystem. Net primary production (NPP,  $\text{gC m}^{-2} \text{ year}^{-1}$ ) is the rate that glucose, in its various forms, is made available to an ecosystem's consumers (i.e. the total production minus that respired by the plants themselves). NPP varies over three orders of magnitude geographically and is useful in predicting ant abundance, size and trophic structure (Kaspari, 2001, 2005; Kaspari et al., 2000). It should thus be a fundamental constraint on sugar production.

**GDD:** In seasonal grasslands, photosynthetically active biomass accumulates over the growing season up to the point in autumn when it senesces (Helzer, 2009). The amount of time an ecosystem's plants have had to grow—estimated as %growing degree days (%GDD)—should thus be a second constraint on an ecosystem's ability to generate sugary exudates.

**N and P:** Two macronutrients, N and P, make up a substantial part of a plant's metabolic machinery (Sterner & Elser, 2002). Fertilization experiments regularly limit biomass production in grasslands (Harpole et al., 2011). By the same logic as above, N and P are thus candidates for constraining sugar production.

**K:** Yet another plant macronutrient, K is as an osmolyte, regulating water pressure and hence plant turgor (Chapin, 1980). Since exudate production involves the translocation of sugars from sites of photosynthesis to other parts of the plant,

K shortfalls should thus constrain this movement and hence sugary exudate production (Carvalho et al., 2011; Sardans & Peñuelas, 2015).

**Animal tissue:** Omnivorous ant colonies have a mixed diet of flesh and plant sugars. If these two elements of the diet co-limit a colony's growth, then increasing the supply of one should increase the demand for the other. Clay et al. (2017) posit that such co-limitation should result in higher sugar demands in grasslands with greater abundance of insect prey and necromass.

To sum up, if an ant community's use of sugar baits decreases along gradients of increasing NPP, %GDD, N, P and K (all of which increase sugar production), or increases along gradients of insect biomass (which increases the demand for co-limiting sugar), this would constitute evidence of gradients in sugar limitation.

Here, we use geographically distributed assays of exogenous salt and sugar use to test for evidence that they constrain ant abundance and performance. Specifically, across 53 North America grasslands (spanning 27°–47° latitude, from short to tall grass prairie) we test that the use of salt and sugar—controlling for abundance and activity—should increase as environmental supplies of salt and sugar decrease.

## 2 | MATERIALS AND METHODS

From April to August 2017, we sampled the use of NaCl and sucrose baits in 53 North American grasslands (see Table S1; Figure S1). The sites were chosen to include a range of physiognomy from short grass to tall grass prairie, altitude from sea level to alpine and anthropogenic influence: unploughed to reclaimed, grazed and roadside. To homogenize the stage of the growing season, sampling proceeded from the southern United States (i.e. the states of Texas and Florida) and ended in the northern United States (i.e. South Dakota and Minnesota). In each sample, 100 Eppendorf tubes, stuffed half with cotton and saturated with 1% NaCl or 5% sucrose solution, were dropped 1 m apart in a straight line, and then collected again 1 hr later, along with any ants inside. One hour has become a standard that allows colonies to discover and recruit to baits in a limited microclimate window (Kaspari et al., 2008; Prather, Roeder, Sanders, & Kaspari, 2018b). Most of the grasslands were sampled twice, mid-morning and mid-afternoon (total = 98). The average number of vial hits ( $\text{hr}^{-1}$ )—that is the number of vials containing at least one ant—was our estimate of salt and sugar bait use. Our aim was to analyse the collective use of these two food types by the entire ant community, although species-level differences can also arise (Kaspari et al., 2008).

### 2.1 | Testing hypotheses for environmental drivers of Na use

To control for variation in ant activity and abundance at each site, we used the number of sugar vials hit as a covariate for community activity. We then tested the prediction that residuals in Na use (i.e. high vs. low Na hits relative to sugar hits) decline with three measures of

environmental Na availability: Na concentrations in the soil, Na in plants and the amount of (sodium-enriched) insect biomass (Table 1). To estimate Na availability in plants, we clipped 0.1-m<sup>2</sup> strips from five plots around the ant transect (four plots arranged in a 100 m by 30 m grid and one plot at the midpoint). Plant biomass was dried to constant weight at 50°C and then milled. We excavated soil from each clip plot using four soil cores 5 cm deep. Each site's five plant samples were pooled, as were each site's five soil samples. Na content (ppm) was analysed at the Cornell Nutrient Analysis Laboratory using ICP-AES. One hundred grams of soil air-dried to a stable weight was supplied and was subject to nitric/perchloric acid digestion. To estimate insect biomass at each grassland site, we used four sweep net samples, two on each side of the vial transect, and then separated insects from plant debris. Sweep netting allows for a rapid and spatially extensive sampling of a grassland's large insects (e.g. grasshoppers and lepidoptera larvae) that make up most of a grassland insect biomass (Doxon, Davis, & Fuhlendorf, 2011; Southwood, 1978) and are frequently scavenged by grassland ants (Kaspari and Welts pers. obs.). Each sample consisted of 40 sweeps through the vegetation. Each was dried to stable weight at 50°C and the average of the four used to estimate that grassland insect biomass (g per 40 sweeps).

## 2.2 | Testing hypotheses for environmental drivers of sugar use

To control for variation in ant activity and abundance at each site, we used the number of salt vials hit as a covariate for community activity. We then tested the prediction that residuals in sugar use (i.e. high and low sugar hits relative to salt hits) would *increase* with annual net above-ground productivity, per cent of that sites' growing degree days expended and plant tissues N, P and K, and would *decrease* with insect biomass (Table 1).

Net primary productivity (NPP, gC m<sup>-2</sup> year<sup>-1</sup>) is the ultimate driver of an ecosystem's sugar production. We estimated a 3-year average of each grassland's annual above-ground productivity, NAP, from each site's actual evapotranspiration (AET) via a modified version of Rosenzweig's (1968) regression that converted annualized AET into measures of above-ground productivity (Kaspari et al., 2000). AET estimates were derived from the MODIS/Terra Net Evapotranspiration 8-day 500 m product (MOD16A2 V6). This MODIS product is based on the logic of the Penman-Monteith equation and includes inputs of daily meteorological reanalysis data along with remotely sensed observations (Running, Mu, & Zhao, 2017). This composited product provides the sum of ET for every 8 days at 500 m spatial resolution. Finally, as plant leaf area tends to increase across the growing season, and with it, the capacity to photosynthesize, we calculated how far into the growing season each grassland was at the time of sampling, using the percentage of the growing degree days. The growing degree days were calculated based on the daily minimum and maximum temperature data from the PRISM Climate Group (<http://prism.oregonstate.edu>) with a base of zero. These data are presented as spatial grids at 4 km

spatial resolution, and we selected the gridded value coinciding with each of the ant communities. Plant tissues P and K, and insect biomass were estimated as above; plant N was estimated with an element analyser.

## 2.3 | Statistics

Plant N and plant Na and soil Na were highly right-skewed and varied 100-fold; these variables were log<sub>10</sub>-transformed. We tested the hypotheses from Table 1 in a two-step process. First, we used a stepwise regression (GLMSelect, SAS, 2009) to systematically build the best model account for variation in salt and sugar use. Entry of each variable into the model is constrained by the conservative information index Akaike's information criterion corrected for small sample size (AICc, Burnham & Anderson, 2002). We controlled for baseline ant activity via the use of the alternate bait (i.e. the ant activity baseline for Na use was sugar use and *vice versa*).

Next, we compared this model to all possible models with a  $\Delta\text{AICc} < 2$  and thus considered equally parsimonious by Burnham and Anderson (2002). We used the *dredge* argument and relative importance values (RIVs) for predictor variables using the *importance* argument in the MuMIn package (Bartoń, 2018) in Program R ver. 3.5.3 (R\_Core\_Team, 2019). RIVs were calculated for a given predictor variable as the sum of Akaike weights ( $w_i$ ) of all models containing that predictor (Burnham & Anderson, 2002).

## 3 | RESULTS

Ant activity at baits varied considerably across grassland sites. Sugar bait use (or hits) ranged from 1.5 to 45 vials out of 50 (median = 13); salt hits ranged from 0 to 39 vials out of 50 (median = 13). A total of species recorded can be found in Table S2; here, we focus on the summed behaviour of the entire ant community.

### 3.1 | The geography of NaCl use tracked plant levels of Na

In the top model identified by AICc supervised stepwise regression, over half the variation in salt use by grassland ants was accounted for by three variables. First, on average, one NaCl vial was hit in ant community for every two sugar vials, accounting for about 1/3 of the variation in salt use (Table 2; Figure 1). Next, as predicted by H2: fewer ants were attracted to NaCl baits in grasslands with higher levels of sodium in plant tissue (which ranged nearly 1,000-fold from 8 to 2,606 ppm, median 24). Soil Na ranged only ca. 100-fold (2.7 to 650 ppm, median 36), was *inversely* correlated to plant Na (Pearson  $r = -0.40$ ,  $p = .003$ ) and did not enter the top model.

Finally, contrary to H3, a small, but significant amount of variation in salt use positively covaried with insect biomass (which varied nearly 100-fold from 0.08 to 1.4g/40 sweeps).

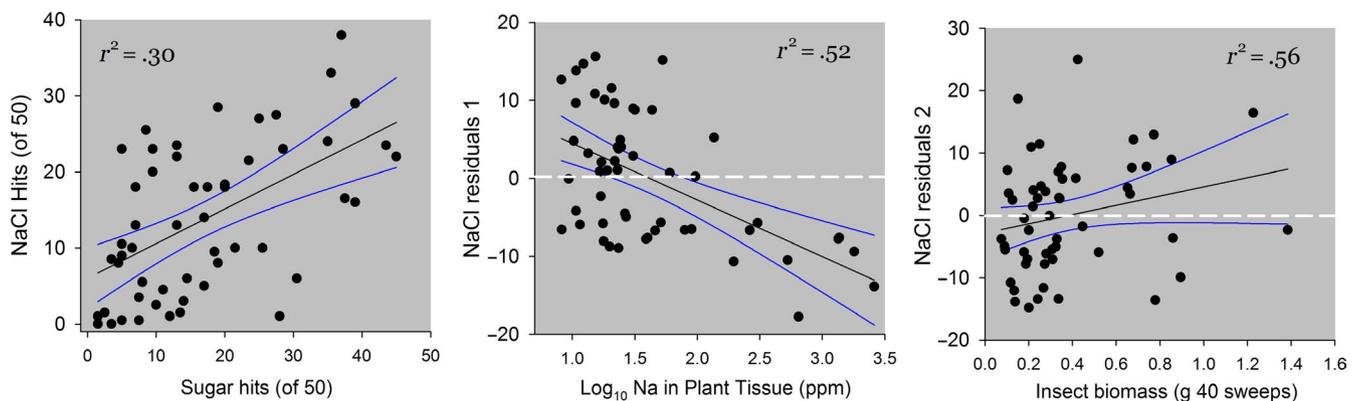
A global AICc analysis identified three top models within two AICc units of each other (Table S3). All three retained the variables

**TABLE 2** Stepwise regression evaluating hypothesized drivers of sugar and salt availability across 53 grassland ant communities, as reflected in the number of baits used  $\text{hr}^{-1}$ , constrained by AICc

NaCl hits (0 of 50)							
Rank	Parameter	Estimate	Error	F value	Pr > F	Model $r^2$	AICc
0	Intercept	13.66	3.28			.00	305.13
1	Sugar hits	0.48	0.07	22.14	<0.0001	.30	288.23
2	$\log_{10}$ plant Na	-6.65	1.51	23.00	<0.0001	.52	270.46
3	Insect biomass	6.99	3.32	4.43	0.0403	.56	268.32
Sugar hits (0 of 50)							
Rank	Parameter	Estimate	SE	F value	Pr > F	Model $r^2$	AICc
0	Intercept	42.06	7.00	6.23		.00	324.98
1	NaCl hits	0.73	0.12	22.14	<0.0001	.30	308.07
2	% GDD	-0.39	0.12	5.78	0.0198	.37	304.60
3	NAP	-0.01	0.004	6.62	0.0131	.41	300.32
4	Plant K	-0.002	0.0004	7.21	0.0099	.52	295.44
5	Plant P	-0.007	0.003	4.39	0.0415	.56	293.38

Note: Rank reflects entry in model.

NAP = net above-ground productivity ( $\text{gC m}^{-2} \text{year}^{-1}$ ), insect biomass = average dry weight of insects from 4 40 sweep samples, plant K = K in tissue (ppm), plant P = P in tissue (ppm), % GDD = % of annual growing degree days at the site a sample occurred;  $\log_{10}$  plant Na = Na in tissue (ppm). PR > F is the probability of a greater F value.



**FIGURE 1** After accounting for gradients in ant activity at sugar baits, the sodium content of plant tissue is the chief environmental driver accounting for geographic variation in the use of NaCl vials by ant communities from 53 North American grasslands. Drivers are arrayed, left to right, reflecting rank entry into model determined by AICc, each accounting for residual variation left by the previous model. Solid dark lines represent OLS regression and blue lines 95% CI; white dashed line separates positive and negative residuals [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

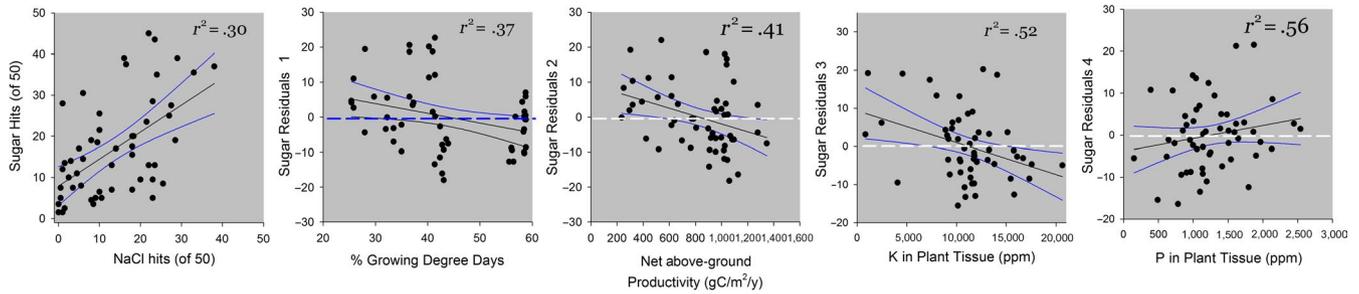
of the model described above. One added a positive effect of plant phosphorus; the other, a positive effect of soil sodium.

### 3.2 | Sugar use tracked NPP, insect biomass, season, and plant K and plant P

In the top model identified by stepwise regression, five variables met the AICc criterion for parsimonious inclusion in a model of sugar use geography (Table 2; Figure 2). As before, the measure of background ant activity was strong with NaCl hits accounting for *ca* 1/3 of the variation in sugar hits. Second, consistent with H2, sugar use declined over the growing season (which varied from 25% to 59%

of growing degree days across the 53 grasslands). Third, consistent with H1, sugar use declined with annual net above-ground productivity (which varied sixfold, 234–1,347  $\text{gC m}^{-2} \text{year}^{-1}$ , across the grasslands). Fourth, consistent with H4, sugar use declined with the quantity of K in plant tissue (which varied 24-fold, 853–20,646 ppm, across the grasslands). Finally, consistent with H3, sugar use increased in grasslands with more plant phosphorus which varied 17-fold (0.8 to 1.4 g dry weight/40 sweeps, median 0.29).

A global AICc model approach identified three top models within the  $\Delta\text{AICc} < 2$  criteria. All three shared the effects of NaCl hits, productivity, season and plant K outlined above, but varied with the residual effects of soil Na and plant P.



**FIGURE 2** After accounting for gradients in ant activity at Na baits, four environmental drivers account for geographic variation in the use of sugar vials by ant communities from 53 North American grasslands. Drivers are arrayed, left to right, reflecting rank entry into the model determined by AICc, each accounting for residual variation left by the previous model. Solid lines represent OLS regression and blue lines 95% CI; white dashed line separates positive and negative residuals

## 4 | DISCUSSION

Nutritional ecology explores (a) how components of a consumer's diet sum to affect fitness and performance and (b) how the demand and supply for nutrients is shaped by an organism's environment. Towards building a nutritional geography, we study sugar and sodium use by grassland ant communities to explore how drivers of sugar and sodium limitation in these communities vary at a continental scale. After taking into account baseline ant activity, we show that supplies of Na (in plant tissue) are the best predictors of an over 100-fold variation in sodium use by ant communities. We also show evidence for a variety of drivers of the availability of sugary exudates—including constraints on plant productivity and K in plant tissue. Combined, our results suggest how the composition of plants exudates—both salty and sweet—may generate gradients of sugar and salt limitation in grassland consumers.

### 4.1 | An unexpected role for plant sodium in regulating grassland consumers

There is growing evidence for the pervasive role of Na as the 'fourth macronutrient' (Clay, Donoso, & Kaspari, 2014; Kaspari, Yanoviak, Dudley, Yuan, & Clay, 2009; NRC, 2005; Prather et al., 2018b; Welti, Sanders, Beurs, & Kaspari, 2019). Our results support these findings, showing that sodium cravings by grassland ant communities declined as sodium availability in plants increased. If true, we would expect sodium additions to enhance consumer abundance in grasslands, and for this effect to strengthen as levels of plant sodium decrease. Consistent with this prediction, across the same North American grasslands, herbivores and omnivores (including ants) increased over controls by ca. 0.7 *SD* on plots salted with 1% NaCl solution after only 2 days, with this effect weakening as plant sodium increased (Welti et al., 2019).

However, despite the relatively low quantity of Na in plant tissue and the lack of a strong role in plant metabolism (Marschner, 1995; Taiz & Zeiger, 1998), two aspects of these results are surprising enough to challenge our simplifying assumption that 'most plants don't need sodium'. The first was our 1,000-fold variation in

sodium content recorded from clip plots. This geographic variation at the ecosystem level, combined with evidence for 100- to 1,000-fold community-level variation in the Na content of both leaf tissue (Snell-Rood et al., 2014) and nectar (Calder & Hiebert, 1983), points to an unexplained suite of factors generating a multi-scale spatial ecology of plant sodium. A second surprise was that across our 53 grasslands, soil Na ranged only ca. 100-fold (2.7 to 650 ppm, median 36) and was *inversely* correlated to plant Na (Pearson  $r = -0.40$ ,  $p = .003$ ). Combined, these results suggest a working hypothesis: that some grasslands and grassland species actively deplete Na from the soil towards some end, generating the wide spectrum of Na concentrations across our 53 sites.

We can think of two hypotheses for this active uptake, neither exclusive. First, in K-poor habitats, plants will substitute Na for K to perform osmotic functions (Wakeel, Farooq, Qadir, & Schubert, 2011). Second, although not a key player in plant metabolism, sodium may still be used by plants to shape interactions with its animal community. For example, the bees and ants that pollinate and defend plants void considerable amounts of water and, with it, electrolytes such as Na (Horn, 1985; Prather et al., 2018b). This Na and K must be replenished. Solutions laced with Na are attractive to pollinators (Arms et al., 1974; Lau & Nieh, 2016), and floral nectars can vary 24-fold in Na concentration within plant communities (Hiebert & Calder, 1983). We suggest the working hypothesis that gives Na a more functional role in plant community ecology, one in which the plants spike nectar and exudates with Na required to attract mutualists and deter enemies. If true, experimental sodium additions, or natural additions via animal urine (Clay et al., 2014), may have fitness consequences for plants via changing rates of pollination and herbivory.

Finally, we assumed that insect biomass would represent a third sodium source and that increasing biomass would thus suppress ant recruitment to exogenous salt baits. We found a weak trend ( $r^2 = .04$ ) in the opposite direction. It is possible that, for a given amount of plant Na in a grassland ecosystem, further increasing animal biomass provides other nutrients such as protein, fat, lipids and minerals that may be co-limiting (Kaspari & de Beurs, 2019). If true, it would suggest that experimentally adding necromass (e.g. dead crickets) to a grassland would enhance activity on salt baits.

## 4.2 | A first attempt to predict drivers of sugar production at a geographic scale

Ant use of sugar baits varied more broadly than that of salt baits; we noticed that sometimes grasslands with ample ant nests often generated relatively little activity on sugar baits. The presence of higher quality sugar exudates was a logical surmise, but surprisingly little was known about the geography of exudate production. The chief models approaching this question focus on the need for plants to lure ants for protection from herbivores (Mayer et al., 2014).

A surprising number of our hypotheses for sugary exudate production were supported within the AICc framework: incrementally contributing to a model that accounted for over half the geographic variation we observed. The best supported drivers focused on plant productivity—both total and seasonal—as a constraint on exudate availability. Orians and Milewski (2007) anticipated our results when they surmised that sugar-fuelled ant–plant symbioses are common in Australia because of its abundant sunshine and poor soils that favour cheap, sugary exudates for defence.

Another novel result was how gradients of increasing plant K appeared to inhibit sugar bait use across our grassland ant communities. Potassium has a number of ecologically relevant functions (Sardans & Peñuelas, 2015), many related to the water economy of the plant. Shortfalls of K can cause maize to release less sugars as exudates into the rhizosphere (Carvalhais et al., 2011). When K was experimentally doubled for *Ricinus communis* (the Castor Bean, which uses elaiosomes to attract ants to disperse its seeds), phloem production and osmotic pressure increased with no decline in sugar concentration (Mengel & Haeder, 1977). Plant exudates—above- and below-ground—fuel a diverse suite of invertebrates (Bais et al., 2006; Cook & Behmer, 2010; Cook & Davidson, 2006; Galef, 1996; Mayntz et al., 2005; Raubenheimer et al., 2009). Fertilization experiments with K at the ecosystem scale and smaller pulses (as both K and Na are ingredients in herbivore urine; Steinauer & Collins, 1995) are worth further exploration.

In conclusion, we find considerable geographic variation in the use of exogenous sodium and sugar by a common insect omnivore—the ants. Towards building a nutritional geography, we find corresponding variation in plant production and elemental content, particularly the ionic elements Na and K, at the ecosystem level. Our geographic ‘Snapshot Experiment’ (sensu Diamond, 1986) suggests future field experiments—supplementing nutrients and quantifying consumer responses—to better understand the role that Na and K play in these grassland food webs.

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## AUTHORS' CONTRIBUTIONS

M.K. and E.A.R.W. conceived the ideas, designed the methodology and collected the field data; K.d.B. provided the bioclimatic data; and M.K. led in writing the MS. All authors contributed critically to the drafts and gave final approval for publication.

## DATA AVAILABILITY STATEMENT

Data are available via <https://doi.org/10.17605/OSF.IO/HU264> on the Open Science Framework (OSF.IO) (Kaspari, Welty, & Beurs, 2019).

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## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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