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The geography of grassland plant chemistry and productivity accounts for ant sodium and sugar usage

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Abstract

In Focus: Kaspari, M., Welti, E. A. R., & de Beurs, K. M. (2020). The nutritional geography of ants: Gradients of sodium and sugar limitation across North American grasslands. *Journal of Animal Ecology*, *89*, 276–284. Biologically essential elements and macromolecules impact individuals to ecosystems and vary across space. Predictive frameworks for understanding community patterns across nutritional gradients are increasingly important as the nutritional landscape is continually altered by global change. Grasslands vary in the quantity and quality of essential nutrients that can impact plant consumer abundance, biomass and activity, but causes for variation, particularly across large spatial scales are poorly understood. In 53 North American grasslands spanning 16° latitude, Kaspari et al. (2020) tested three hypotheses for explaining sources of sodium (Na) limitation and five hypotheses for explaining sources of sugar limitation of ants, which are common and ecologically important omnivores that consume both plant- and animal-derived material. For both Na and sugar, over half of the variation in ant bait usage was accounted for by their predictions. Specifically, after accounting for ant activity (ant usage of sugar baits), ant Na-limitation was next best predicted by plant Na content and lastly, insect biomass, while sugar limitation after accounting for activity (ant usage of Na baits) was best predicted by growing season, then ecosystem productivity, plant potassium (K) and phosphorous (P), respectively. Kaspari et al. (2020) demonstrate the importance of plant physiology and chemistry towards a predictive framework for understanding sugar- and Na-limitation and highlights the importance of tackling ecological questions from a geographical perspective. This framework can provide a useful foundation for predicting future patterns in grassland organism nutritional ecology as plant species and physiology are altered with global change.

KEYWORDS
carbohydrate, formicidae, geographic ecology, nutritional ecology, phytochemical landscape, salt, stoichiometry, sugar

Global change is altering plant species composition, biomass, physiology and chemistry (Borer, Grace, Harpole, MacDougall, & Seabloom, 2017; Reich, Hobbie, Lee, & Pastore, 2018), which necessitates increasing our understanding of how the availability of biologically essential elements and macromolecules relative to the requirements of consumers impacts individual behaviour to ecosystem functions (Raubenheimer, Simpson, & Mayntz, 2009; Rosenblatt & Schmitz, 2016; Sterner & Elser, 2002). Historically, when trying to understand how nutrient availability shapes

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ecological patterns and processes, most of the nutritional focus in the literature has been on carbon (C), nitrogen (N) and phosphorous (P) (Stoichiometry; e.g. Sterner & Elser, 2002) or carbohydrates, proteins and lipids (Nutritional Ecology; e.g. Raubenheimer et al., 2009), but plant chemistry varies in other nutritionally relevant variables (Hunter, 2016; Kaspari & Powers, 2016). Currently, the field is expanding to include previously overlooked elements, such as heavy metals and ions, and macromolecules such as sterols and types of carbohydrates (Behmer, 2017; Fischer & Shingleton, 2001; Kaspari & Powers, 2016), and the pairing of nutritionally predictive frameworks with geography, which together seeks to explain how ecological phenomena like organismal activity, community structure and ecosystem functions change across space mediated by nutrient availability (e.g. Borer et al., 2017; Kaspari & Powers, 2016; Wilder, Holway, Suarez, LeBrun, & Eubanks, 2011). Kaspari, Welti, and de Beurs (2020) further expands the breadth of this field using a geographical perspective to test a suite of hypotheses for potential sources of sodium (Na) and sugar and how their availability impacts the activity of temperate grassland ant communities across North America. Ants are ecologically important and widespread omnivores in temperate grasslands that impact ecosystem functions like decomposition, nutrient cycling, productivity and biodiversity (Wills & Landis, 2018). Sodium (Na) is emerging as a major focal nutrient (Clay, Lehrter, & Kaspari, 2017; Kaspari, Yanoviak, & Dudley, 2008; Kaspari, Yanoviak, Dudley, Yuan, & Clay, 2009) and although many studies have considered the ecological importance of sugar (Fischer & Shingleton, 2001; Raubenheimer et al., 2009; Wilder et al., 2011), spatial gradients of sugar quantity and quality and their impacts on community-level processes has remained largely unexplored. Kaspari et al. (2020) supports the hypothesis that gradients in the sweetness and saltiness of plants underlie variation in omnivore nutrient limitation. Future studies could test whether the geography of plant sugar and salt also predict variation in ant biomass and community structure across grasslands.

Nutrient surplus or shortfall impacts on organism physiology to ecosystem functions is a fruitful field in ecology ripe with examples (Behmer, 2017; Kaspari et al., 2008, 2009; NRC, 2005; Swanson et al., 2016). Conversely, the question of how and why

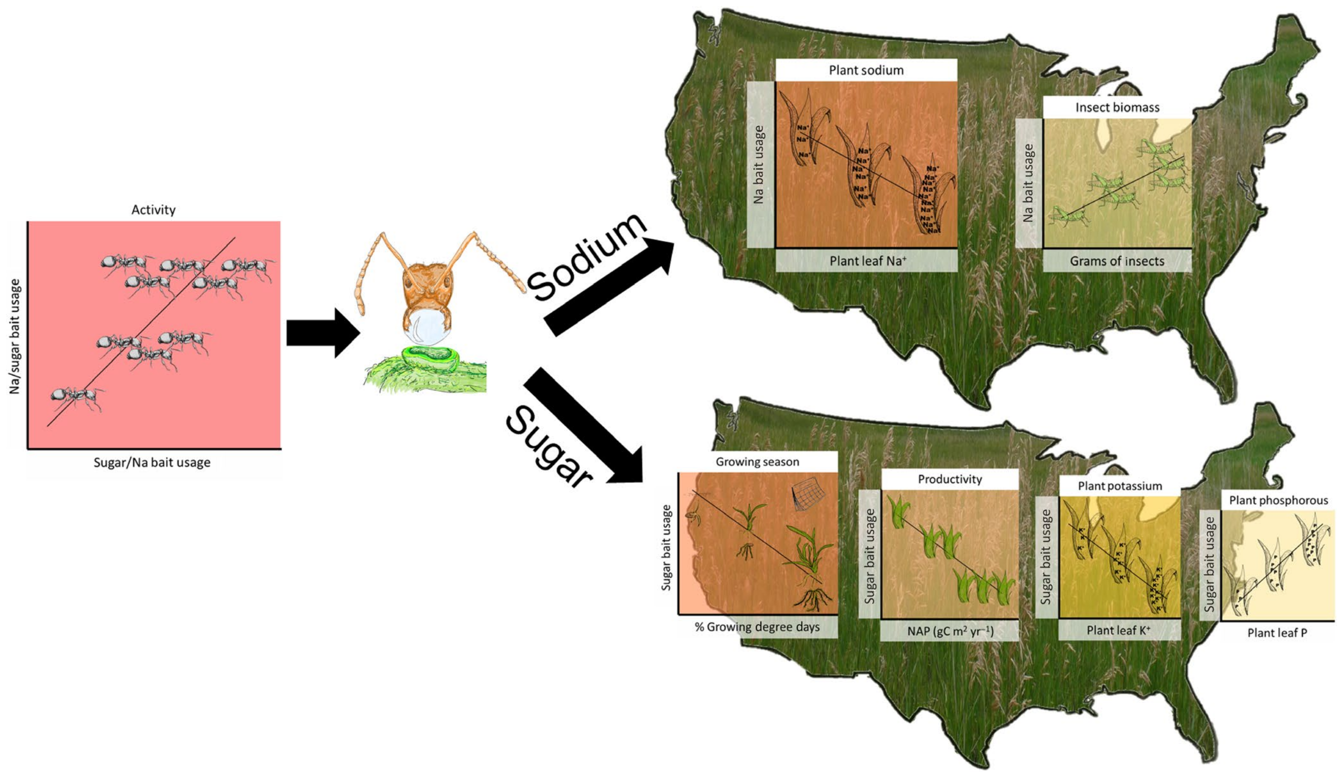

FIGURE 1 The significant predictors of sodium (Na; r^2 = .56) and sugar (r^2 = .56) bait usage by ants in 53 North American grassland sites as determined by stepwise regression and Akaike's information criterion corrected for small sample size (AIC_c; Kaspari et al., 2020). Ant activity (the use of the opposite bait type: sugar or Na) was the best predictor in models for both Na (r^2 = .30) and sugar (r^2 = .30) bait usage. Specifically, the greater the activity on one bait (e.g. Na), the greater the activity on the other bait (e.g. sugar). For sodium, bait usage was next best predicted by plant leaf Na content (r^2 = .22): in grasslands where plant Na was high, ant Na bait usage was low suggesting ants may get their sodium from plants (e.g. exudates). This was followed by insect biomass, where insect biomass increased so did Na bait usage in a weak trend (r^2 = .04) potentially signifying co-limitation of Na and other nutrients (e.g. protein, fats). For sugar, after accounting for activity, bait usage was best predicted by percent degree days into growing season (r^2 = .07) then net primary productivity (r^2 = .04): the further in the season and the more productive the site the lower the bait usage suggesting plants were producing more sugar as season progressed and with more productivity. Next ant sugar bait usage decreased as plant potassium (K) content increased (r^2 = .11) suggesting that K is involved in sugar production. Lastly, sugar bait usage was weakly but positively correlated with plant phosphorous (P) (r^2 = .04). Together, these results suggest a geography of Na and sugar that impacts omnivore trophic ecology in part regulated by plants. Illustrations by Natalie Clay [Colour figure can be viewed at wileyonlinelibrary.com]

essential nutrients and macromolecules vary across space has received less attention. Kaspari et al. (2020) provide a predictive framework towards understanding Na and sugar availability and their usage for ant communities across 53 North American grasslands spanning 16° latitude by laying transects of salt and sugar baits in each grassland and quantifying the number of baits with ants (i.e. activity). They posit three primary environmental Na sources for ants: (a) Soil Na through geophagy or puddling (e.g. Arms, Feeny, & Lederhouse, 1974), (b) plant Na through plant exudates and (c) insect biomass through consumption of animal tissue (e.g. Clay et al., 2017), and five constraints on plant sugar exudate production: (a) Net primary productivity as the ultimate constraint on sugar production (e.g. Rosenzweig, 1968), (b) time into growing season as plant production capacity increases as the season progresses, (c) N and P plant content as these are essential for plant productivity (e.g. Harpole et al., 2011), (d) plant K as it promotes plant control of exudates (Carvalhais et al., 2011; Sardans & Peñuelas, 2015) and (e) insect biomass because increased access to N, P and Na should increase demand for sugars (e.g. Clay et al., 2017; Yanoviak & Kaspari, 2000). For both Na and sugar, their predictions accounted for over half the variation in ant bait usage. Specifically, they found that after accounting for the positive relationship between ant activity and Na bait usage, ant community Na usage was most associated with plant Na content (negative relationship) and a small amount of variation accounted for by insect biomass (positive relationship; Figure 1). For sugar, after accounting for the positive relationship between ant activity and sugar bait usage, ant community sugar usage was most associated with time into the growing season (negative relationship), then in order, net primary productivity (negative relationship), plant K (negative relationship) and plant P (positive relationship; Figure 1). These results generate for the first time a predictive framework towards understanding the geography of sugar availability, support a new hypothesis, which posits that plant exudates are a significant source of Na, and together, illustrate the importance of the phytochemical landscape (e.g. Hunter, 2016) in impacting foraging decisions for both Na and sugar.

Plants are typically considered Na-poor and Na is not considered an essential plant nutrient (Clay et al., 2017; Kaspari et al., 2008, 2009). Kaspari et al. (2020) challenge this notion; they found that grassland plants vary two orders of magnitude in Na content, which suggests that the role of Na for plants may be a salient topic after all (e.g. Subbarao, Ito, Berry, & Wheeler, 2003; Swanson et al., 2016). In support of this, ant Na bait usage was not related to soil Na content, suggesting that ants may indeed be acquiring salt from plants rather than geophagy (Kaspari et al., 2020). Kaspari et al. (2020) suggest that ants may be acquiring a substantial portion of their Na balance from plant exudates. This also leads to two non-exclusive alternative hypotheses: that omnivores like ants acquire Na (a) indirectly via increased Na from plants through honeydew and (b) by consuming Na-enriched herbivorous prey that fed on Na-enriched plants. For example, Downing (1980) found that aphids raised on sea aster grown on sea water had nearly 44-fold and 9-fold increase in Na content of honeydew and haemolymph, respectively, than those raised on sea aster grown on fresh water. This new hypothesis put forth by Kaspari et al. (2020) that plant sugar (e.g. nectar, exudates) may be an important Na source opens a new potential avenue for research and challenges the current dogma that plants are Na-poor and not an important source of Na for plant consumers.

One of the most exciting components of Kaspari et al. (2020)'s paper is their exploration of the nutritional geography of sugar. Sugar is a driving force in ecosystems and is essential for the energy production of animals (Arms et al., 1974; Raubenheimer et al., 2009; Sterner & Elser, 2002; Wilder et al., 2011). Kaspari et al. (2020) demonstrate that sugar availability may have a predictable geography (Figure 1). One of the surprising findings was the strong association between plant K content and sugar bait usage that supported the hypothesis that plant K is important in plant sugar production (e.g. Borer et al., 2017; Carvalhais et al., 2011). Potassium is often an understudied nutrient (Sardans & Peñuelas, 2015), and Kaspari et al. (2020) demonstrate the importance of stepping outside the C, N, P, box to examine other essential elements in shaping ecological phenomena and moving beyond a single-limiting nutrient perspective (Borer et al., 2017; Harpole et al., 2011; Kaspari & Powers, 2016; Raubenheimer et al., 2009). Kaspari et al. (2020)'s paper is also timely as mounting evidence suggests that plants and grasslands are changing. Shifts include changes in the relative abundances and biomass of C_3 and C_4 plants and altered plant quality including sugar content (Borer et al., 2017; Reich et al., 2018; Rosenblatt & Schmitz, 2016). The framework demonstrated by Kaspari et al. (2020) may pave the way for better predictions for how global change will affect the nutritional ecology of grasslands.

Together, the results of Kaspari et al. (2020) demonstrate a variably sweet and salty plant landscape that shapes the nutritional ecology of grassland omnivores. This research provides a launchpad for future experiments that test the specific mechanisms (Figure 1) across space and time and is an important step towards building a predictive nutritional geography.

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