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More salt, please: global patterns, responses, and impacts of foliar sodium in grasslands

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Data information: All data contributors are listed in SI Table 12.

ABSTRACT

Sodium is unique among abundant elemental nutrients, because most plant species do not require it for growth or development, whereas animals physiologically require sodium. Foliar sodium influences consumption rates by animals and can structure herbivores across landscapes. We quantified foliar sodium in 201 locally-abundant, herbaceous species representing 32 families and, at 26 sites on four continents, experimentally manipulated vertebrate herbivores and elemental nutrients to determine their effect on foliar sodium. Foliar sodium varied taxonomically and geographically, spanning five orders of magnitude. Site-level foliar sodium increased most strongly with site aridity and soil sodium; nutrient addition weakened the relationship between aridity and mean foliar sodium. Within sites, high sodium plants declined in abundance with fertilization, whereas low sodium plants increased. Herbivory provided an explanation: herbivores selectively reduced high nutrient, high sodium plants. Thus, interactions among climate, nutrients, and the resulting nutritional value for herbivores determine foliar sodium biogeography in herbaceous-dominated systems.

INTRODUCTION

Sodium is an essential nutrient for herbivores (Michell 1989; Snell-Rood *et al.* 2014) that can determine animal foraging preferences and movement patterns in space and time (McNaughton 1988; Prather *et al.* 2018). In contrast, sodium is not used for physiological function in most plants, and at high concentrations sodium can be toxic for plants (Mäser *et al.* 2002; Pardo & Quintero 2002; Marschner 2011; Maathuis 2014). Because of this key difference in the mineral nutrition of herbivores and the plants they eat, herbivores must use natural salt licks and seek out and efficiently use the sodium present in plants to meet physiological demands for sodium (Michell 1989). In spite of the essential role of plant sodium content for wild herbivores (Seastedt & D. A. Crossley 1981), there is little understanding of the relative importance of the many factors that may control foliar sodium in plants.

For example, abiotic factors including soil sodium content, soil fertility, or climate may determine sodium availability, whereas biotic constraints such as plant species phylogeny and lifeform or palatability to herbivores may determine the capacity for sodium exclusion and whole tissue losses that may occur with preferential herbivory. Further, these factors may interact and operate globally or regionally to influence foliar sodium, and context may determine whether foliar sodium is likely to interact with herbivory to determine the composition of plant communities in future environments.

Plants access sodium through leaf uptake from atmospheric deposition (Benes *et al.* 1996) or root uptake from soil water (Epstein 1973). Because of the similarity of sodium to the potassium ion that is physiologically critical for plants, cation transporters of roots will transport both sodium and potassium across cell membranes (Pardo & Quintero 2002; Maathuis 2014). Although a relatively small group of plants – mostly C_4 grasses – requires sodium (Brownell & Crossland 1972; Furumoto *et al.* 2011), the sodium cation is present in the foliage of many species and can be used for a variety of critical plant functions, including stomatal opening and closing, particularly when potassium is in short supply (Subbarao *et al.* 2003). However, terrestrial sodium is geographically variable (Kaspari *et al.* 2008; Kaspari *et al.* 2009; Wicke *et al.* 2011; Vet *et al.* 2014; Doughty *et al.* 2016) because of mineral acquisition from sources such as ocean spray, terrestrial salinization, or road salting practices (Ramakrishna & Viraraghavan 2005; Vet *et al.* 2014), urine (Kaspari *et al.* 2017), loss from leaching (Vitousek & Sanford 1986), and climatic influences, particularly aridity (Raheja 1966). In spite of these general associations, it remains unclear whether foliar sodium varies predictably among plant taxonomic lineages or biogeographically with e.g., distance to coast or site aridity and whether there are site or plant species characteristics that effectively predict the foliar sodium content of the most abundant plants.

Although plant sodium is often assumed to simply track soil sodium supply, at biogeographic scales, a growing body of evidence suggests that plant sodium content may not be determined solely via soil sodium supply. Like other soil cations, sodium uptake by plants can be reduced in high pH soils (Tyler & Olsson 2001; Bolan & Brennan 2011), and aridity can lead to increased soil pH (Slessarev *et al.* 2016), suggesting that aridity may either increase foliar sodium via increased soil sodium or reduce it via increased soil pH. Evidence also is accumulating that the supply of macronutrients such as nitrogen can reduce the availability of mineral cations to plants (Lucas *et al.* 2011). Thus, anthropogenic activities that are altering soil pH or increasing macronutrient supply to ecosystems (Franklin *et al.* 2016) may interactively alter the sodium content of foliage and quality of foliage for herbivores (Kaspari *et al.* 2017). Furthermore, herbivores may themselves alter the sodium concentration in plant tissue either by promoting the availability of sodium through recycling (McNaughton *et al.* 1997; Doughty *et al.* 2016), by promoting saline soil conditions (McLaren & Jefferies 2004), or selectively consuming plant species with elevated salt levels in their foliage (Seastedt & D. A. Crossley 1981; Welti *et al.* 2019). These conditions may, alternatively, promote plant species with relatively high foliar sodium that have traits, such rapid regrowth, basal meristems, or use of sodium to modify osmotic potential under drought, that are beneficial under both saline soil conditions and high grazing intensity (Coughenour 1985; Veldhuis *et al.* 2014; Griffith *et al.* 2017).

Here, we use existing and experimentally-created environmental gradients to address the following questions (1) *Patterns of foliar sodium*: Which site (10^4 m^2), plot (10^0 m^2), and species characteristics predict foliar sodium content? For example, does foliar sodium vary predictably among plant taxa, with distance to coast, or along a gradient of soil pH or site aridity? (2) *Responses of foliar sodium to a changing environment*: Do selective herbivory or elevated nutrient supply reduce foliar sodium at the local (plot) scale? (3) *Effects of foliar sodium on grassland species composition*: Does a grassland species' foliar sodium content predict changes in the species' relative abundance in response to herbivory or elevated nutrients?

METHODS

Experimental design and locations. Samples for this study were collected at 26 sites that are part of a long-term, nutrient-addition and herbivore-fencing experiment being performed in herbaceous-dominated sites around the world, the Nutrient Network distributed experiment (NutNet, www.nutnet.org). The subset of the NutNet sites that were able to collect tissue samples that comprise the data used in this study spanned Africa, Australia, Europe, and North America (SI Table 1).

Each site had three experimental blocks composed of 10 – 5 x 5 m plots, each assigned randomly to one of 10 unique treatment combinations. Treatments included a factorial addition of N (10 g N m^{-2} yr^{-1} as timed-release urea [$(NH_2)_2CO$]), P (10 g P m^{-2} yr^{-1} as triple-super phosphate [$Ca(H_2PO_4)_2$]), and K (10 g K m^{-2} yr^{-1} as potassium sulphate [K_2SO_4]) plus micronutrients (μ, a mix of Fe (15%), S (14%), Mg (1.5%), Mn (2.5%), Cu (1%), Zn (1%), B (0.2%) and Mo [0.05%]), for a total of 8 plots/block. Importantly, no sodium (Na) was added in any treatment. N, P, and K were applied annually at each site for 2-4 years (SI Table 1); the micronutrient mix, μ, was applied once in the first experimental year to avoid toxicity.

For the focal fence and fertilization experiment, fence treatments were crossed with the control and the all nutrient treatment (N+P+Kμ), adding two fenced plots to each block. Fences were built to exclude medium and large mammals and had been in place for 2-4 years at the time of sampling. Fences were 230 cm tall with four strands of barbless wire suspended at equal vertical distances above the lower 90 cm which was surrounded by 1-cm woven wire mesh with a 30-cm outward-facing flange stapled to the ground. At some sites, logistical considerations required slight modifications of the fence design (Fence exceptions table, SI Table 2). All sampling plots were separated by at least 1 m wide walkways to reduce the impact of treatments on adjacent plots. For additional methods details, see (Borer *et al.* 2014).

Pre-treatment soil collection. Before applying the experimental treatments, three 2.5 x 10cm soil cores were collected from each experimental plot, combined, homogenized into a single sample for each 5 x 5 m plot (roughly 500 g of soil), and dried. Percent soil C and N from each plot were analyzed in a single analytical laboratory using a Costech ECS 4010 CHNSO Analyzer on pulverized soil (Knops lab, University of Nebraska, USA). Extractable soil P, K, and micronutrients, including Na, and pH for every soil sample also were quantified in a single analytical laboratory using standard methods (Borer *et al.* 2014) (A&L Laboratories, Memphis, Tennessee, USA). Across our study sites, plot-level soil sodium ranged from 21 ppm (at Val Mustair in Switzerland) to 150 ppm (at Elliott Chaparral, USA).

Plant abundance and biomass estimation. To determine the most abundant plant species in each plot and the change in cover of species in response to the experimental treatments, the percent areal cover of each species was estimated to the nearest 1 percent for each species within a permanently marked 1-m^2 subplot of each treatment unit.

A metric of site-level net herbivore impact was estimated as the average difference in live mass inside and outside of fences within a block during the first year of the treatment. To estimate this, we clipped the aboveground biomass of all plants rooted within a 0.2 m^2 area of each fenced and control plot. Each sample was divided into growth from the current year and litter from previous years. We used the first year of treatment to estimate herbivore impact on vegetation mass, prior to species-level selection and turnover in response to long-term herbivore exclusion.

Foliar sampling & sodium analysis. Within each plot, the most abundant species were determined as a function of percent cover, and a single healthy leaf was collected from five unique individuals of the species with the greatest cover at the site. Most sites had three to five dominant species present in most plots; however, one site collected 8 different species (Val Mustair), because there were not clearly dominant species. All leaves were transported in a cooler, and then dried at 60°C for 48 hours (Firn *et al.*

157 2019). The collected species represented 5.3% (Val Mustair, Switzerland, a high elevation, highly diverse (25 species/plot) site; this is the site that sampled 8 species) to 52.1% (Saline, KS, USA) of the total plot cover with an average representation of 26% of the total cover across all plots and sites (SI Table 1). All leaves were then sent to Queensland University of Technology (Dr. J. Firn) for sodium analysis. Dried leaves were ground to a fine powder, then analyzed for sodium content with an Agilent 8800 Laser Ablation Inductively Coupled Plasma Mass Spectrometer (LA-ICP-MS), following Duodu et al. (Duodu *et al.* 2015) with two exceptions: C, the most abundant naturally occurring element, was used as a standard, and no additional pulverizing was performed beyond that required for C analysis. The reference material for sodium was NIST SRM 1570a Trace elements in spinach leaves (USA National Institute of Standards and Technology 2014). Elemental quantification followed the method of Longerich et al. (1996), using Iolite, a data reduction software (Paton *et al.* 2010).

<u>Climate data.</u> The WorldClim database provided comparable long-term climate data for all sites (version 1.4; http://www.worldclim.org/bioclim). These global climate data were interpolated at high-resolution from data stations with 10 to 30 years of data (Hijmans *et al.* 2005). We used these data to test whether foliar sodium in the most abundant taxa declined with mean annual precipitation (MAP in mm per year) or increased with a site-level index of aridity (MAP divided by potential evapotranspiration in mm per year)(Barrow 1992). Site-level MAP ranged from 14 at Sheep Station, USA to 1898 mm of annual precipitation at HJ Andrews LTER; Lookout, USA and the index of aridity ranged from 0.2 at Mount Caroline, Western Australia to 2.4 mm at Val Mustair, Switzerland (SI Table 1).

<u>Analyses.</u> We explored the relative importance and interactions among the many factors that we hypothesized to constrain foliar sodium. Many of these factors could covary (e.g., annual precipitation, distance to coast, and soil pH), and it was possible that there could be multiple models that were similarly informative (i.e., had similar AICc values). For this reason, we used a multi-model approach, which does not try to identify a single best model (Grueber *et al.* 2011). This information theoretic

approach starts by calculating all possible subsets of the parameters in the full model, and then uses Akaike's information criterion (AICc) to determine the subset of models sharing similarly high levels of parsimony (Grueber *et al.* 2011). In our case, we included in our high parsimony set all models that fell within 4 AICc units of the model with the lowest AICc value (Grueber *et al.* 2011). Parameter estimates and significance are based on a weighted average of the set of high parsimony models. We present the weighted average parameter value estimate, significance, and the summed AIC weights for all models in which the parameter is included, or *importance*. We used the *dredge* function in the MuMIn R library to calculate the AICc of all possible models and the model.avg function in the MuMIn R library to calculated the weighted parameter and statistics.

All models used a random effect structure with site and species within site treated as random intercepts to account for the hierarchical nature of the sampling. To examine biogeographic predictors of foliar sodium, we examined only control plot values, but for the effects of environmental change, we used data from all experimental plots. Experimental treatments were retained in all models. Because of missing soil data, one site (Mt. Caroline) is excluded from experimental analyses. In addition, to avoid bias from having rare species that were found only in one treatment driving the results, for the analysis of the fence and fertilization experiment (shown in Fig 4), we include species that are present in Control plots and at least two other treatments (e.g., Control, Fence, and Fertilized or Control, Fence, and Fence + Fertilized). Similarly, for analysis of the factorial nutrient experiment (SI Figure 1), we include only species present in Control plots and at least 5 other treatments. Finally, in analyses of abiotic factors associated with foliar sodium, we tested the leverage of two outlier sites. In particular, we examined the role of a single site (Sheep Station, USA) in driving the association of foliar sodium with soil pH and another site (Lancaster, UK) in determining the importance of distance from the coast in foliar sodium content.

204 In addition to assessing foliar sodium, we also used multi-model inference to examine the cover response of each plant for which sodium was measured in each plot as a function of the sodium concentration of that species. For assessing the effects of foliar sodium on plant cover in response to the experimental treatments, species with less than 0.1% cover in a plot were removed (23 out of 1,828 records or 1.3%).

209 All analyses were performed in R (version 3.3; R Foundation for Statistical Computing).

210 RESULTS

211 *Patterns of foliar sodium*

212 Foliar sodium in 201 of the most abundant grassland plant species from 26 sites on four continents, including representatives of 32 plant families, varied across five orders of magnitude among sites and the most abundant plant taxa in unmanipulated plots. Foliar sodium ranged from 0.5 ppm in *Phleum pratense* (Poaceae) to 28,271 ppm in *Epaltes australis* (Asteraceae, SI Table 1), and average site-level plant sodium across the most abundant species ranged from 2.7 ppm (at Konza Prairie in the North American Great Plains) to 9,715 ppm (at Burrawan in southeastern Australia). Foliar sodium of the most abundant species in control plots was similar across grasses with C_4 (463 ± 201 ppm) and C_3 (624 ± 159 ppm) photosynthetic pathways ($P = 0.10$). However, across all taxa in unmanipulated (control) plots, foliar sodium varied spatially both within and among sites (Fig. 1); mean foliar sodium content also varied substantially among plant families (Fig. 1, $P<0.001$, SI Table 3).

222 We found that among sites, mean site-scale foliar sodium in control plots increased with soil sodium (Fig. 2, $P=0.015$; t=2.68), whereas within sites, foliar sodium did not co-vary with plot-scale soil sodium ($P=0.51$; t=0.64). In a model that included multiple candidate predictors (site aridity, distance from coast, soil pH, photosynthetic pathway, and soil sodium), foliar sodium declined with increasing site-level water availability (increasing AI; $P=0.001$) and soil pH (Fig. 3, $P=0.04$, SI Table 4). However, our

model selection criteria did not retain soil sodium or photosynthetic pathway in final models. The decline in foliar sodium was similar across both coastal and inland sites except for a single site in the UK with high precipitation and exceptionally high sodium ion deposition relative to most locations on Earth (Vet *et al.* 2014) (Fig 3b, Lancaster, UK). In contrast, for sites with neutral to acidic soils (all except one in this study, Sheep Station, USA), there was no relationship between foliar sodium and soil pH (Fig. 3). Thus, the biogeographic variation in foliar sodium content is explained, in part, by a combination of local conditions, including soil sodium availability and aridity.

Responses of foliar sodium to a changing environment

Nutrients and herbivory interacted to determine the foliar sodium of the most abundant plants, and the strength of this effect depended on aridity but not soil pH (SI Table 5). In particular, at mesic sites, when herbivores were present, nutrient addition favored abundant plants with high foliar sodium compared to plants in ambient (control) plots (Fig. 4a, SI Table 5). As a result, the addition of the full suite of nutrients (N+P+Kμ, but not Na) outside of fences weakened the negative effect of increasing water availability (increasing AI) on foliar sodium content (Fig. 4b). The factorial nutrient addition experiment clarified that the interaction between aridity and nutrient supply was primarily driven by the effects of potassium and micronutrients (Kμ) and to a lesser extent the effects of nitrogen and phosphorus addition (SI Table 6, SI Fig. 1).

We examined the subset of species that were sampled multiple times among plots and sites to explore the role of intraspecific variability of sodium content in determining these observed responses. Of the 201 species in this experiment, 41 were among the most abundant (and therefore sampled) in plots at more than one site, and 94 were sampled in both control and treatment plots within sites. Models of the subset of species present among sites and in both control and treatment plots were qualitatively similar to models of the larger dataset for both experiments (SI Tables 7 and 8), suggesting that some of the observed variation in foliar chemistry is attributable to intraspecific change in foliar sodium content in response to the biotic and abiotic environment.

Effects of foliar sodium on grassland species composition

The sodium content of foliage and plot-scale nutrient supply contributed to the effects of herbivores on changes in the relative abundance of grassland plant species. Fertilization (with NPKμ) increased the cover of the most abundant species, and in the presence of herbivores, the abundance of species low in foliar sodium increased in response to fertilization, whereas high sodium species became less abundant when fertilized (Fig. 5). However, in the absence of herbivores, fertilization had no consistent effects on species abundances in relation to their foliar sodium concentration (SI Table 9, SI Fig. 2). These effects on foliar sodium were independent of the intensity of herbivory among sites (measured as the site-level log ratio of live biomass inside and outside of herbivore exclusion fences ($P > 0.57$ for all main effects and interactions; importance < 0.40 [model not shown]). The factorial nutrient addition experiment clarified that, in the presence of herbivores, the addition of any elemental nutrient caused dominant plant species with relatively high foliar sodium content to decline more than species with lower foliar sodium (SI Table 10); this effect was greatest in response to fertilization with P (SI Table 10). These results point to selective consumption by herbivores of high nutrient, high sodium plants.

DISCUSSION

This multi-continent, biogeographic study demonstrated that foliar sodium in dominant grassland plants is highly variable among sites and even plots within a site, and there also is significant variation in foliar sodium among families and taxa within families, regardless of geographic location. These patterns likely reflect variation in long-term environmental conditions (e.g., aridity, grazing) that have selected for species with differing strategies for environmental sodium uptake. While there is evidence for phylogenetic conservation of cation transport proteins that can influence sodium uptake (Schachtman &

Liu 1999) with predictable differences across photosynthetic pathways (Brownell & Crossland 1972), photosynthetic pathway was not a predictor of foliar sodium in grasses. Nonetheless, the very highest foliar sodium content recorded in this study was 9% (91,818 ppm) in *Eragrostis curvula* (Poaceae, commonly called African Lovegrass) found at Burrawan, Australia. This species has a C_4 photosynthetic pathway, indicating a physiological requirement for sodium, and this site is among the more arid sites in the experiment, suggesting that both photosynthetic pathway (Brownell & Crossland 1972; Furumoto *et al.* 2011) and aridity (Raheja 1966) can be strongly associated with foliar sodium, in some cases. However, while individual species supported this hypothesis, as a group, C_4 grasses were not consistently high in foliar sodium.

The results of this globally-extensive study demonstrate that the relative abundance of plant species in grasslands is altered by herbivores as a function of sodium content and elemental nutrient supply. In particular, herbivores in grasslands spanning four continents with a variety of herbivore types and densities consistently reduced the cover of plants with high foliar sodium only in high nutrient conditions. The reduction in abundance of sodium-rich plants in fertilized plots is evidence of targeted herbivory of high sodium, protein-rich plants. In particular, herbivores are attracted to plots with elevated nutrients (Mattson 1980), and selective consumption reduces the abundance those species with the highest sodium. These plants are not likely extirpated from the community, since the same species are generally found at higher abundance inside herbivore exclosures, rather they are likely to be in a constant state of regrowth from having their aboveground foliage selectively consumed. Such selective foraging is common in many ecosystems (Belovsky 1981; Jefferies *et al.* 1994; Wallis de Vries & Schippers 1994; Bartolome *et al.* 1998; Doughty *et al.* 2016). Related to this, the impact of herbivores on sodium content of the most abundant plant species was contingent on aridity, with foliar sodium content high and indistinguishable among experimental treatments at arid sites, but declining with increasing water availability. Our arid region results are consistent with previous work that found positive feedbacks generating and maintaining high sodium content grazing lawns because of high evaporation rates under the cropped vegetation (McNaughton 1988). By examining herbivore impacts across a much broader precipitation gradient, we demonstrate that both aridity and herbivory determine foliar sodium biogeography across the world's grasslands, with declining sodium content under increased precipitation and preferential feeding by herbivores.

Our experimental work also demonstrated that the sodium content of locally abundant plants increases with soil sodium at the site-scale; however, when included in models, site aridity was a much more effective predictor of biogeographic variation in foliar sodium than soil sodium. At broad spatial scales, foliar sodium is positively related to soil sodium as has been observed in previous work (Sutcliffe 1959; Epstein 1973; Pardo & Quintero 2002; Maathuis 2014), but foliar sodium was not strongly predicted by distance to coast, a common a surrogate for sodium ion deposition (Vet *et al.* 2014). However, because arid regions are characterized by high evapotranspiration relative to precipitation, these sites tend to accumulate salts over time (Raheja 1966). In contrast, coastal sites may have both high ion input and high precipitation (Vet *et al.* 2014), reducing the environmental pools of ions, including sodium, and causing a mismatch between salt deposition and the location of sodic soils (Wicke *et al.* 2011). In this study, the coastal site with exceptionally high foliar sodium relative to site-scale precipitation (Lancaster, UK) is also situated in a location on Earth with an exceptionally high rate of sodium ion input (Vet *et al.* 2014), suggesting that site aridity combined with direct measures of site-level sodium ion input rate will likely provide even better predictions of site-level foliar sodium in the most abundant plant taxa. In addition, although we found a decline in foliar sodium with increasing soil pH, this pattern was driven by a single, arid site in the intermountain west of the USA. While this pattern is consistent with expectations of reduced cation uptake in higher pH soils (Tyler & Olsson 2001; Bolan & Brennan 2011), we have only a single site with a pH above neutral. Because soil pH is intimately associated with aridity (Slessarev *et al.* 2016), disentangling the roles of soil pH and aridity in determining grassland plant sodium biogeography will require more thorough sampling, particularly at sites with basic soils spanning a range of aridity. Nonetheless, the strong spatial variation in foliar sodium suggests that environmental context is key in determining foliar sodium which, by extension, implies that future environmental changes may alter foliar sodium for herbivores. Given the importance of dietary sodium for herbivores (Seastedt & D. A. Crossley 1981; McNaughton 1988; McNaughton *et al.* 1997; Kaspari *et al.* 2008; Doughty *et al.* 2016), biogeographic patterns of foliar sodium in abundant grassland plants may arise from interactions with wild herbivores, and likely have significant implications for the distribution and impacts of consumers in grassland ecosystems.

The strong difference in the physiological importance of sodium to grassland plants and wild herbivores has gained increasing attention in ecology, with recent calls for a greater understanding of the biogeography of sodium (Kaspari *et al.* 2008). The current study of both patterns and responses to experimental manipulation, performed at 26 sites spanning wide biotic and abiotic gradients, demonstrates that aridity, soil acidity, nutrient supply, and herbivory, interact to influence biogeographic patterns of foliar sodium and its effect on plant abundance. In future environments, climate change is expected to impact global patterns of soil salinity via changes in precipitation and evapotranspiration (Schofield & Kirkby 2003). The current results suggest that the impact of these changes on grassland plant composition will depend on the interactive effects of large-scale changes in aridity and elemental nutrient (N, P) supply and the resulting nutritional value for consumers.

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Code availability R code of all analyses will be made available via GitHub (https://github.com/).

Data availability Data supporting the findings of this study will be made available on Dryad (http://datadryad.org).

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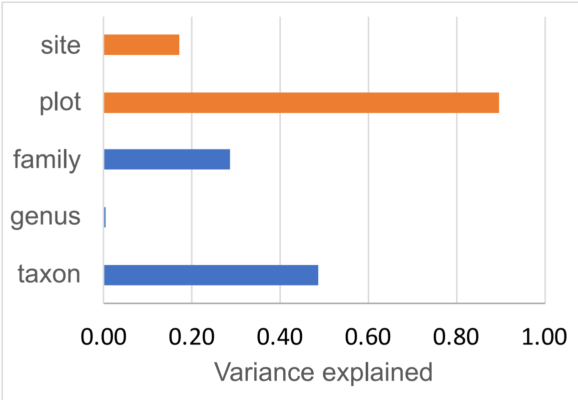

Fig. 1. *Foliar Na variation across taxonomic and spatial scales:* Variance components analysis of foliar sodium in the 85 locally-abundant plant taxa from control plots at 26 sites across nested taxonomic and spatial scales. Foliar sodium for 41 species was measured at two or more sites. Variation in foliar sodium associated with plant location is shown in orange; variation associated with taxonomic groups is shown in blue. Variance explained by genus is extremely small, but non-zero ($<3x10^{-6}$), thus is barely visible in this graph. SI Table 3 provides the full statistical model associated with this figure.

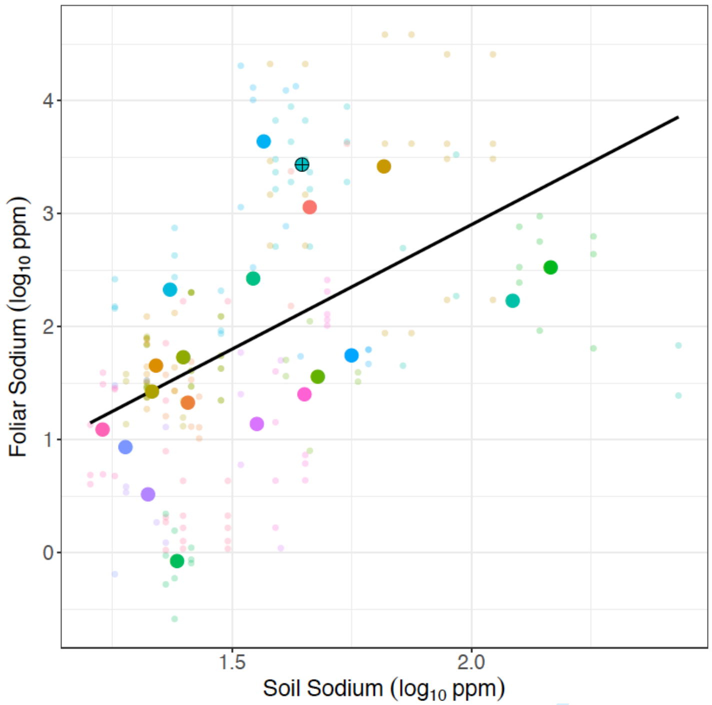

Fig. 2. *Foliar Na and soil Na:* Foliar sodium increases with soil sodium in 85 locally-abundant plant taxa from control plots control plots among sites but not among plots or species within sites. Sites have different colors; site means are shown as large points and small points are species data. Site-level regression is shown as a black line.

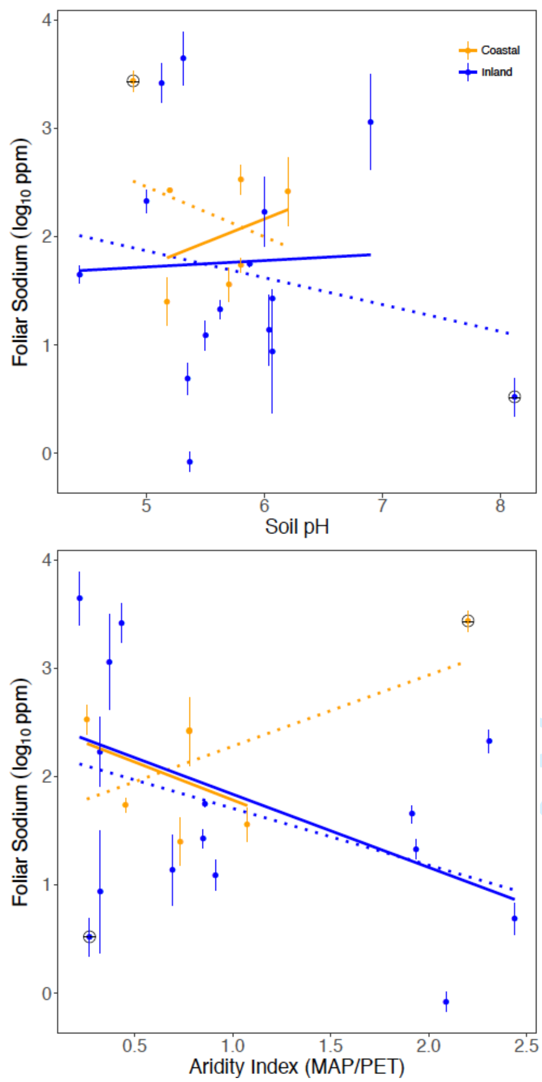

Fig. 3. *Predictors of foliar Na:* The foliar sodium of the most abundant plant species declined across a gradient of plot-scale pH (z=2.03, P=0.04) and site-scale water availability (MAP/PET; z=3.24, P=0.001). Data include the 85 taxa across 22 sites that were growing in control plots. Coastal (orange) and Inland (blue) are divided at 100km from a coast. The dashed yellow line shows the model with all sites included; the solid yellow line shows these relationships without a single site in the UK (Lancaster, orange circled site) with high precipitation and coastal salt input. Similarly, the dashed blue line shows the model with all sites included; the solid blue line shows the relationships without the only site with basic soil pH found in US Intermountain West (Sheep Station, blue circled site). Error bars represent ±SE. SI Table 4 provides the full statistical model associated with the solid lines shown in this figure.

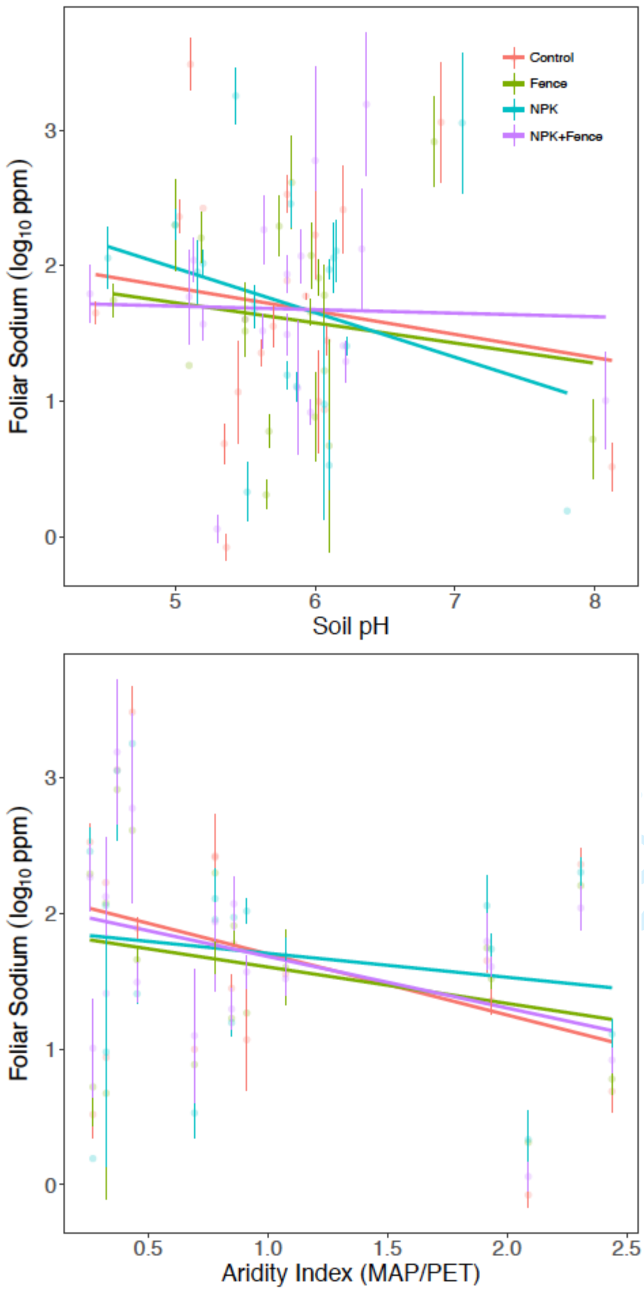

Fig. 4. *Responses of foliar sodium to changes in herbivory and nutrient supply:* Response of foliar Na in 153 locally abundant plants to a factorial combination of fencing to reduce vertebrate herbivory and fertilization by a suite of micro- and macronutrients (not including Na^+) (a) across a gradient in plot-scale pH and (b) across a gradient in site-scale water availability. Foliar sodium is higher than expected from control plots where precipitation is relatively high and nutrients are added ($z=3.49$, $P=0.0005$). Error bars represent ±SE. SI Table 5 provides details of the full statistical model.

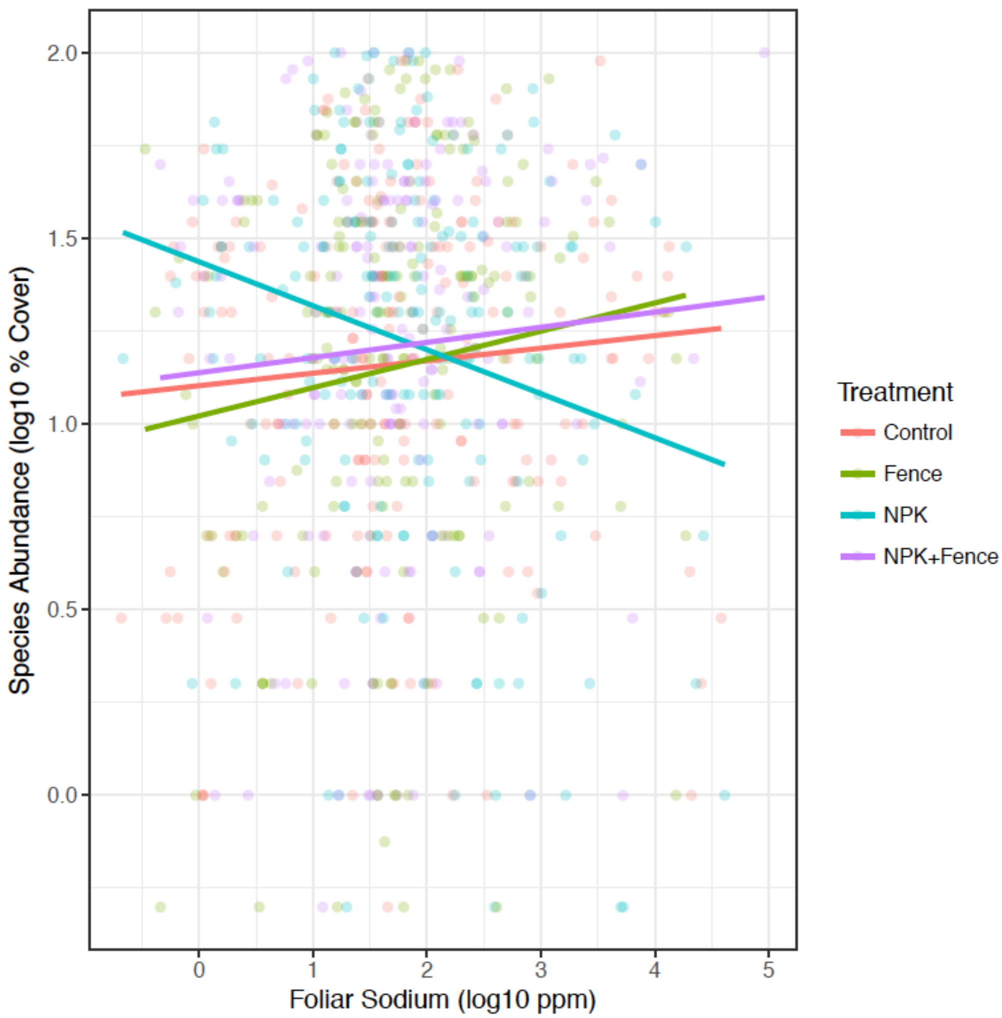

Fig. 5. *Effects of foliar sodium on grassland species composition*: Response of plant abundance to a factorial combination of fencing to reduce vertebrate herbivory and fertilization by a suite macro- and micronutrients (not including Na^+) as function of foliar sodium in 153 grassland plant species. SI Table 9 shows the final model describing species abundance as a function of treatments and foliar sodium content.

557 **SI: DATA AND MODEL TABLES UNDERLYING RESUTS TEXT**

558 **SI Table 1.** Sites, locations, mean annual precipitation (MAP), index of aridity, modeled nitrogen deposition (N Dep.), measured plot-scale soil

559 pH, and measured foliar sodium in each of the most abundant species at the site (leaf Na (ppm).

Site name	Continent	Country	Latitude	Longitude	MAP	AI	Leaf Na (ppm)	Soil pH	Soil Na (ppm)
Mt Gilboa	Africa	ZA	-29.28424	30.29174	943	0.7797	233.13	5.07	35.58
Summerveld	Africa	ZA	-29.81161	30.71573	944	0.7324	125.01	5.15	43.58
Bogong	Australia	AU	-36.874	147.254	1678	1.9159	228.35	4.47	22.10
Burrawan	Australia	AU	-27.734896	151.139517	643	0.4335	9715.51	5.55	59.53
Kinypanial	Australia	AU	-36.2	143.75	408	0.3224	751.22	6.04	148.43
Mt. Caroline	Australia	AU	-31.782138	117.610853	324	0.2186	7628.36	5.29	38.19
Fruebuel	Europe	CH	47.113187	8.541821	1546	2.0892	3.86	5.46	25.50
Val Mustair	Europe	CH	46.631345	10.372252	681	2.4389	38.31	5.66	26.70
Companhia das Lezirias	Europe	PT	38	-8	564	0.4532	65.69	5.93	25.81
Lancaster	Europe	UK	53.9856247	-2.6284176	1522	2.2003	2478.44	4.77	41.56
Cowichan	North America	CA	48.46	-123.38	762	1.0743	112.67	5.63	48.60
Boulder South Campus	North America	US	39.972022	-105.23354	487	0.3701	2358.66	6.82	58.39
Bunchgrass (Andrews LTER)	North America	US	44.2766854	-121.96802	1618	1.9348	38.65	5.54	23.71

Chichaqua Bottoms	North America	US	41.7850667	-93.385383	871	0.849	22.15	6.11	21.94
Duke Forest	North America	US	36.00828	-79.020423	1157	0.9121	70.05	5.27	19.07
Elliott Chaparral	North America	US	32.875	-117.05224	344	0.2565	459.89	5.69	145.46
Hopland REC	North America	US	39.0127534	-123.06031	1065	0.8593	346.67	NA	22.99
Konza LTER	North America	US	39.070856	-96.582821	889	0.7608	2.67	NA	20.56
Lookout (Andrews LTER)	North America	US	44.2051771	-122.12845	1877	2.3085	246.88	5.07	20.83
Mclaughlin UCNRS	North America	US	38.8642721	-122.40641	936	0.6615	316.49	NA	42.48
Sagehen Creek UCNRS	North America	US	39.43	-120.24	831	0.8579	307.13	5.93	63.67
Saline Experimental Range	North America	US	39.05	-99.1	608	0.491	41.99	NA	23.67
Sheep Experimental Station	North America	US	44.242989	-112.19839	246	0.2689	14.02	7.98	23.54
Shortgrass Steppe LTER	North America	US	40.81667	-104.76667	369	0.3244	36.65	6.16	21.88
Sierra Foothills REC	North America	US	39.2355096	-121.2837	936	0.6932	42.19	5.96	36.04
Smith Prairie	North America	US	48.2065807	-122.62475	605	0.7796	421.54	6.09	43.53

SI Table 2. Description of exceptions to the fence design; sites not included in this list have standard design.

Site name	**Fence Type**	**Exception description**
Lancaster	Sheep	Similar to NutNet standard but top strand at 1.2 m
Sheep Experimental Station	Sheep	Similar to NutNet standard but top strand at 1.2 m
Val Mustair	Val Mustair	2.7 m wooden poles (25 cm diameter) driven 70 cm into ground, 3 m apart, covered with 5 cm square mesh to 2 m high and with extra cabling and supports to prevent snow damage. Fences enclose 6 m x 7 m area.

SI Table 3. Patterns of foliar Na: Analysis of spatial and taxonomic variance components in foliar sodium of 85 locally abundant grassland species found in the unmanipulated control plots of 26 sites.

Random effects:

Groups	Name	Variance	Std.Dev.	Number of obs for group
Taxon:(genus:Family)	(Intercept)	2.389e-01	4.888e-01	85
genus:Family	(Intercept)	7.450e-12	2.729e-06	66
plot:site_code	(Intercept)	8.214e-02	2.866e-01	60
site_code	(Intercept)	8.052e-01	8.973e-01	22
Family	(Intercept)	2.924e-02	1.710e-01	17
Residual		4.623e-02	2.150e-01	

SI Table 4. Predictors of foliar Na:

Variation of site-level mean foliar sodium with distance to coast, aridity (MAP/PET), and soil pH for the 85 dominant grassland species found in the control plots of the 26 study sites. Model shows the conditional average estimates of model parameters for all sites except the very high precipitation, very high sodium influx site (Lancaster; see Figure and legend in main text).

	Estimate	Std. Error	Adjusted SE	z value	Pr(>|z|)		Importance	Num models
(Intercept)	1.7957	0.1884	0.1897	9.466	< 2e-16	***		
c.coastal	0.3700	0.4098	0.4125	0.897	0.36975		0.78	6
z.AI	-1.3337	0.4089	0.4116	3.240	0.00119	**	1.00	8
z.pH	-0.4880	0.2392	0.2406	2.028	0.04252	*	1.00	8
c.coastal:z.pH	-1.3458	0.5913	0.5954	2.260	0.02379	*	0.66	4
z.soil.na.lg	0.2049	0.2199	0.2213	0.926	0.35448		0.35	4
c.coastal:z.AI	-0.6275	1.7061	1.7181	0.365	0.71492		0.12	1
c.coastal:z.soil.na.lg	-0.7663	0.5640	0.5677	1.350	0.17712		0.13	2

Signif. codes: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

SI Tables 5 & 6. Responses of foliar sodium to a changing environment:

SI Table 5. Response of foliar sodium in 153 dominant grassland plant species growing in plots with experimental manipulation of herbivores and nutrients. Regression table shows conditional average model results without Lancaster; when this site is included, the results are qualitatively similar but the effect of nutrient addition across the water availability gradient is somewhat weaker due to the extreme outlier. The regression table shows the conditional average values across models in which parameters were included, the number of models in which parameters were included, and their importance in the models.

```
                   Estimate Std. Error Adjusted SE z value Pr(>|z|)     Importance  Num models
(Intercept)        1.6286948  0.1348117   0.1350290  12.062  < 2e-16 ***
z.AI              -0.6601019  0.3111010   0.3116025   2.118 0.034140 *   1.00         5
z.pH              -0.3787517  0.0792799   0.0794058   4.770  1.8e-06 *** 1.00         5
c.Fnc             -0.0144227  0.0345935   0.0346491   0.416 0.677226     1.00         5
c.NPK              0.0816837  0.0347964   0.0348523   2.344 0.019093 *   1.00         5
c.Fnc:c.NPK        0.0006431  0.0686576   0.0687668   0.009 0.992538     1.00         5
c.Fnc:z.AI        -0.0134223  0.0699543   0.0700666   0.192 0.848083     1.00         5
c.NPK:z.AI         0.2581523  0.0739461   0.0740549   3.486 0.000490 *** 1.00         5
c.NPK:z.pH         0.1199696  0.0799398   0.0800687   1.498 0.134047     0.58         3
c.Fnc:c.NPK:z.AI -0.4660938  0.1361232   0.1363347   3.419 0.000629 *** 1.00         5
c.Fnc:z.pH         0.0060036  0.0802725   0.0804007   0.075 0.940477     0.35         3
c.Fnc:c.NPK:z.pH  0.2183428  0.1549416   0.1551920   1.407 0.159451     0.12         1
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Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
```

SI Table 6. Response of foliar sodium in 179 dominant grassland plant species growing in plots treated with a factorial addition of elemental nutrients (but not sodium). Model excludes one site (Lancaster) which was a substantial outlier for AI and pH. Models are qualitatively similar with Lancaster included. The regression table shows the conditional average values across models in which parameters were included; the number of models in which parameters were included are shown below the table.

	Estimate	Std. Error	Adjusted SE	z value	Pr(>|z|)		Importance	Num models
(Intercept)	1.68363	0.13936	0.13947	12.071	< 2e-16	***		
z.AI	-0.64993	0.31441	0.31465	2.066	0.03887	*	1.00	40
z.pH	-0.24259	0.05384	0.05388	4.503	6.7e-06	***	1.00	40
c.K	-0.01129	0.02289	0.02291	0.493	0.62225		1.00	40
c.N	0.06474	0.02302	0.02304	2.810	0.00495	**	1.00	40
c.P	0.02553	0.02282	0.02283	1.118	0.26360		1.00	40
c.K:c.N	0.03479	0.04543	0.04546	0.765	0.44413		0.95	37
c.K:z.AI	0.24490	0.05063	0.05066	4.834	1.3e-06	***	1.00	40
c.K:z.pH	0.10960	0.05034	0.05038	2.176	0.02958	*	0.92	35
c.N:z.AI	0.10176	0.04981	0.04984	2.042	0.04120	*	1.00	40
c.P:z.AI	0.11270	0.04591	0.04595	2.453	0.01417	*	1.00	40
c.K:c.N:z.AI	0.23943	0.09389	0.09396	2.548	0.01083	*	0.95	37
c.N:z.pH	-0.07174	0.05135	0.05139	1.396	0.16272		0.57	24
c.N:c.P	0.05290	0.04522	0.04525	1.169	0.24239		0.45	21
c.K:c.N:z.pH	0.10350	0.09983	0.09990	1.036	0.30019		0.18	9
c.K:c.P	0.03394	0.04511	0.04515	0.752	0.45217		0.33	16

```
c.P:z.pH     -0.01439    0.05017     0.05021   0.287  0.77439      0.18         10
c.K:c.P:z.AI  0.10380    0.08934     0.08941   1.161  0.24564      0.10          5
c.N:c.P:z.AI  0.01774    0.08995     0.09002   0.197  0.84379      0.05          3
c.N:c.P:z.pH -0.12625    0.09267     0.09274   1.361  0.17343      0.03          2
c.K:c.N:c.P  -0.08298    0.09077     0.09084   0.913  0.36103      0.03          2
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Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
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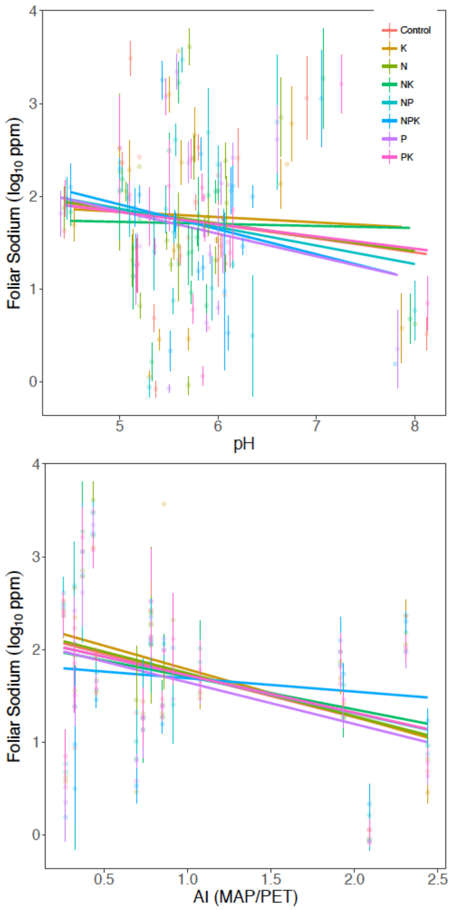
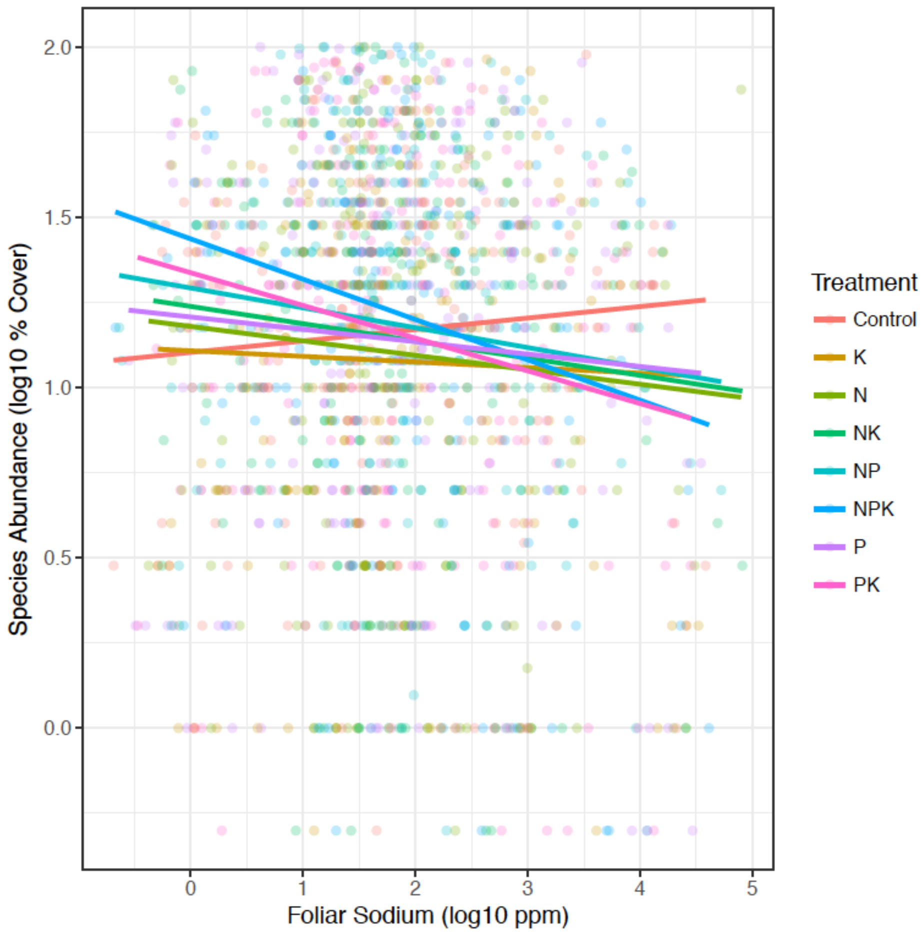


SI Figure 1. Response of foliar sodium in locally abundant plants to a factorial combination of nitrogen, phosphorus, and potassium plus micronutrients (not including Na^+). Plot-scale soil pH and site-scale water availability are significant biogeographic drivers of foliar Na that improve model fit, so are included in all models. This analysis includes 179 species from the factorial nutrient addition experimental plots.



SI Figure 2. Response of plant abundance to a factorial combination of nitrogen, phosphorus, and potassium plus micronutrients (not including Na^{+}) as a function of foliar sodium. This analysis includes 179 species from the factorial nutrient addition experimental plots.

SI Tables 7 and 8. Responses of foliar sodium to a changing environment:

SI Table 7. Response of foliar sodium to experimental manipulation of herbivores and nutrients for the subset of 60 species present in control plots and at least 3 experimentally treated plots of the fence x fertilization experiment. The regression table shows the conditional average values across models, relative importance values are shown below the table.

	Estimate	Std. Error	Adjusted SE	z value	Pr(>|z|)		Importance	Num models
(Intercept)	1.60760	0.15658	0.15690	10.246	< 2e-16	***		
z.AI	-0.90293	0.35730	0.35803	2.522	0.01167	*	1.00	6
z.pH	-0.42239	0.08360	0.08377	5.042	5e-07	***	1.00	6
c.Fnc	-0.01764	0.03728	0.03736	0.472	0.63688		1.00	6
c.NPK	0.09444	0.03743	0.03751	2.518	0.01181	*	1.00	6
c.Fnc:c.NPK	-0.01041	0.07499	0.07514	0.139	0.88984		1.00	6
c.Fnc:z.AI	0.01691	0.07840	0.07856	0.215	0.82958		0.92	5
c.Fnc:z.pH	0.05260	0.08338	0.08354	0.630	0.52896		0.55	4
c.NPK:z.AI	0.28640	0.08119	0.08134	3.521	0.00043	***	1.00	6
c.NPK:z.pH	0.12557	0.08425	0.08442	1.487	0.13690		0.69	4
c.Fnc:c.NPK:z.AI	-0.48307	0.15742	0.15771	3.063	0.00219	**	0.92	5
c.Fnc:c.NPK:z.pH	0.36304	0.17535	0.17566	2.067	0.03876	*	0.34	2

Signif. codes: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

SI Table 8. Response of foliar sodium to a factorial addition of elemental nutrients (but not sodium for the subset of 62 species present in control plots and at least 6 experimentally treated plots in the factorial NPKµ experiment. The regression table shows the conditional average values across models, relative importance values are shown below the table.

	Estimate	Std. Error	Adjusted SE	z value	Pr(>|z|)		Importance	Num models
(Intercept)	1.650418	0.156368	0.156525	10.544	< 2e-16	***		
z.AI	-0.713841	0.363376	0.363740	1.963	0.04970	*	1.00	78
z.pH	-0.258238	0.060821	0.060879	4.242	2.22e-05	***	1.00	78
c.K	-0.006721	0.025683	0.025709	0.261	0.79378		1.00	78
c.N	0.073374	0.025576	0.025601	2.866	0.00416	**	1.00	78
c.P	0.021680	0.025634	0.025660	0.845	0.39818		1.00	78
c.K:c.N	0.044384	0.050890	0.050941	0.871	0.38360		0.76	57
c.K:z.AI	0.303815	0.056138	0.056193	5.407	1.00e-07	***	1.00	78
c.K:z.pH	0.138719	0.056652	0.056708	2.446	0.01444	*	0.99	77
c.N:c.P	0.075999	0.050956	0.051006	1.490	0.13622		0.72	57
c.N:z.AI	0.081498	0.056873	0.056926	1.432	0.15225		0.89	68
c.N:z.pH	-0.112398	0.056589	0.056645	1.984	0.04723	*	0.89	67
c.P:z.AI	0.131357	0.053185	0.053237	2.467	0.01361	*	0.99	77
c.K:c.N:z.AI	0.247463	0.109837	0.109940	2.251	0.02439	*	0.70	50
c.P:z.pH	-0.018531	0.057573	0.057628	0.322	0.74778		0.43	38
c.N:c.P:z.pH	-0.213430	0.106099	0.106205	2.010	0.04447	*	0.31	25

c.K:c.N:z.pH	0.142729	0.113412	0.113525	1.257	0.20866	0.27	20
c.K:c.P	0.051492	0.050758	0.050809	1.013	0.31085	0.40	38
c.N:c.P:z.AI	0.023955	0.112241	0.112340	0.213	0.83115	0.12	12
c.K:c.P:z.AI	0.076209	0.101582	0.101683	0.749	0.45357	0.07	7
c.K:c.N:c.P	-0.051459	0.102002	0.102104	0.504	0.61427	0.03	4
c.K:c.P:z.pH	-0.013211	0.103181	0.103284	0.128	0.89822	0.01	2

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

SI Tables 9 & 10. Effects of foliar sodium on changes in species abundance in response to a changing environment:

SI Table 9. Response of plot scale cover of focal species as a function of foliar sodium in response to experimental manipulation of herbivores and nutrients. (N=153 species).

(conditional average)

	Estimate	Std. Error	Adjusted SE	z value	Pr(>|z|)		Importance	Num models
(Intercept)	1.17346	0.05116	0.05125	22.898	< 2e-16	***		
z.lf.na.lg	-0.02289	0.04719	0.04727	0.484	0.6282		1.00	5
c.Fnc	-0.01806	0.02609	0.02613	0.691	0.4895		1.00	5
c.NPK	0.06037	0.02624	0.02628	2.297	0.0216	*	1.00	5
c.Fnc:c.NPK	-0.06492	0.05079	0.05087	1.276	0.2019		0.61	3

c.Fnc:z.lf.na.lg	0.06108	0.05457	0.05465	1.118	0.2637		0.56	3
c.NPK:z.lf.na.lg	-0.23515	0.05410	0.05418	4.340	1.43e-05	***	1.00	5
c.Fnc:c.NPK:z.lf.na.lg	0.20691	0.10431	0.10448	1.980	0.0477	*	0.30	1

Signif. codes: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

SI Table 10. Response of plot scale cover of focal species as a function of foliar sodium in response to a factorial addition of elemental nutrients (but not sodium). The regression table shows the conditional average values across models. (N=179 species)

(conditional average)

	Estimate	Std. Error	Adjusted SE	z value	Pr(>|z|)		Importance	Num models
(Intercept)	1.11276	0.05274	0.05278	21.083	< 2e-16	***		
z.lf.na.lg	-0.10085	0.03770	0.03773	2.673	0.00752	**	1.00	11
c.K	0.02774	0.01732	0.01734	1.600	0.10951		1.00	11
c.N	0.02403	0.01748	0.01749	1.374	0.16944		1.00	11
c.P	0.03991	0.01723	0.01724	2.315	0.02063	*	1.00	11
c.K:c.P	0.08592	0.03427	0.03429	2.505	0.01223	*	1.00	11
c.K:z.lf.na.lg	-0.06344	0.03453	0.03455	1.836	0.06639	.	0.71	7
c.N:z.lf.na.lg	-0.06115	0.03468	0.03471	1.762	0.07810	.	0.68	7
c.P:z.lf.na.lg	-0.10016	0.03469	0.03471	2.885	0.00391	**	1.00	11
c.K:c.N	0.02331	0.03446	0.03448	0.676	0.49899		0.26	4

```
c.N:c.P          0.01356    0.03428     0.03430   0.395  0.69253          0.23           4
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Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
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SI Table 11. Author contributions and site-level acknowledgments table.

Name	**Contributed samples**	**Developed research question**	**Analyzed data**	**Wrote paper**	**Contributed to paper writing**	**Site coordinator**	**Nutrient Network coordinator**	**Site-level acknowledgments (funding, access, etc)**
Borer, Elizabeth T.	x	x	x	x		x	x	
Lind, Eric M.	x	x	x		x		x	
Seabloom, Eric W.	x		x		x	x	x	
Firn, Jennifer	x				x	x		

Anderson, T. Michael					x	x			
Bakker, Elisabeth S.					x	x			
Biederman, Lori	x				x	x			
La Pierre, Kimberly J	x				x	x			Funding: Konza Prairie LTER
MacDougall, Andrew S	x				x	x			Funding: NSERC Discovery Grant; In-kind site support: Nature Conservancy of Canada; sampling processing: Carly Ziter
Joslin Moore	x				x	x			

Risch, Anita C.	x				x	x		
Schütz, Martin	x				x	x		
Stevens, Carly J.	x				x	x		

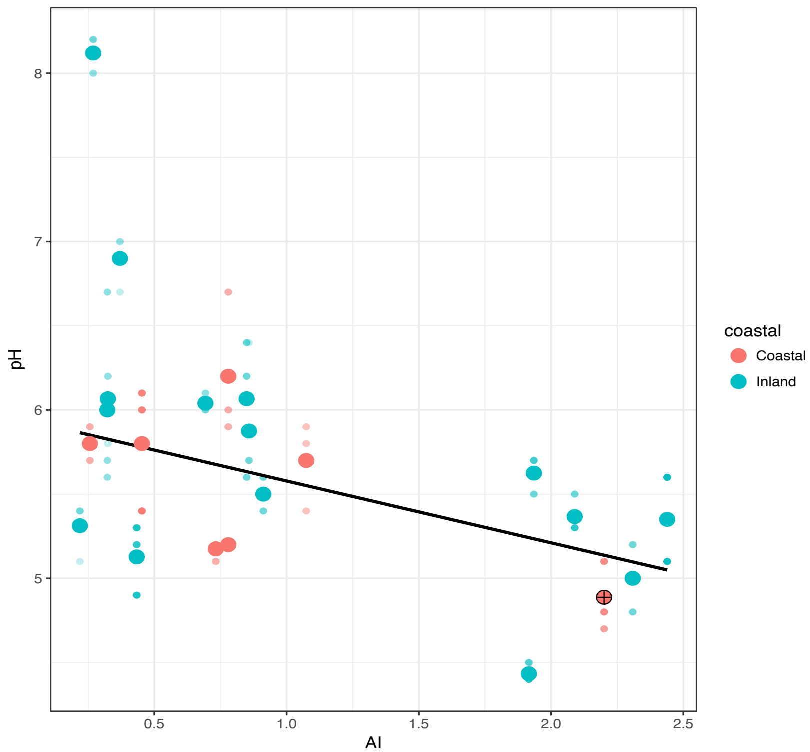
SI Table 12. All data contributors listed by site; site names match those in SI Table 1. Their effort in providing samples was key to this work.

Site PI	Site name(s) from which trait data were contributed
Peter Adler	Sheep Experimental Station
Jonathan Bakker	Smith Prairie
Lori Biederman	Chichaqua Bottoms
Dana Blumenthal	Shortgrass Steppe LTER
Elizabeth Borer	Mclaughlin UCNRS, Bunchgrass (Andrews LTER), Sierra Foothills REC, Hopland REC, Lookout (Andrews LTER)

Cynthia Brown	Shortgrass Steppe LTER
Miguel Bugalho	Companhia das Lezirias
Maria Caldeira	Companhia das Lezirias
Elsa Cleland	Elliott Chaparral
Kendi Davies	Boulder South Campus
Jennifer Firn	Burrawan
Daniel Gruner	Sagehen Creek UCNRS
Sabine Güsewell	Fruebuel
W. Stanley Harpole	Hopland REC, Chichaqua Bottoms, Mclaughlin UCNRS, Sierra Foothills REC
Yann Hautier	Fruebuel
Andy Hector	Fruebuel
Janneke Hille Ris Lambers	Smith Prairie
Kirsten Hofmockel	Chichaqua Bottoms
Julia Klein	Shortgrass Steppe LTER
Alan Knapp	Shortgrass Steppe LTER

Kimberly La Pierre	Konza LTER, Saline Experimental Range
Andrew MacDougall	Cowichan
Brett Melbourne	Boulder South Campus
Charles Mitchell	Duke Forest
Joslin Moore	Bogong
John Morgan	Bogong, Kinypanial
Suzanne Prober	Mt. Caroline
Anita Risch	Val Mustair
Martin Schuetz	Val Mustair
Eric Seabloom	Hopland REC, Lookout (Andrews LTER), Mclaughlin UCNRS, Bunchgrass (Andrews LTER), Sierra Foothills REC
Melinda Smith	Konza LTER, Saline Experimental Range
Carly Stevens	Lancaster
Lauren Sullivan	Chichaqua Bottoms
Peter Wragg	Mt Gilboa, Summerveld

Justin Wright	Duke Forest
Louie Yang	Sagehen Creek UCNRS



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755 **SI Figure 3**. Site-level soil pH declines as a function of site-level water availability (MAP/PET); this relationship does not vary as a function of
756 distance from coast. Coastal and Inland are divided at 100km from a coast. The Lancaster site in the UK, shown with a black circle and cross-hairs
757 in this figure, falls along this line, but has very high coastal sodium influence in its precipitation, leading to exceptionally high site-level sodium
758 (see main text).