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Salty, mild, and low plant biomass grasslands increase top-heaviness of invertebrate trophic pyramids

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Abstract

Aim: Multiple hypotheses predict how gradients of nutrient availability, plant biomass, and temperature shape trophic pyramids. We aim to disentangle the simultaneous influence of those factors and their indirect effects on trophic structure and individual trophic levels.

Location: United States.

Time period: 2017.

Major taxa studied: Invertebrates.

Methods: To examine differences in trophic pyramid shape and abundance within trophic levels and across ecological gradients, we conducted 54 standardized surveys of invertebrate communities in North American grasslands. We tested for the direct and indirect effects of plant biomass, temperature, sodium (Na), other essential elements (e.g. N, P, and K), and toxic heavy metals, (e.g. Ar and Pb) in plant tissue on both individual trophic levels, and trophic pyramid shape, estimated as the community trophic mean (CTM).

Results: Plant sodium increased CTM, indicating that high plant sodium concentrations are associated with top-heavy invertebrate trophic pyramids. Sites with higher plant biomass had higher proportions of herbivores compared to higher trophic levels. Finally, increasing temperature resulted in more top-heavy trophic pyramids. Overall, plant biomass, temperature, and plant chemistry directly and indirectly affected the abundances within different trophic levels, highlighting the complexity of factors regulating trophic structure.

Main conclusions: Trophic structure of grassland invertebrate communities is strongly influenced by plant sodium, plant biomass, and to a lesser extent, temperature. Grasslands occupy 30% of the Earth's terrestrial surface and are an imperiled ecosystem due to conversion to row crop agriculture. As biogeochemistry and temperature in the Anthropocene are increasingly modified, our results have considerable implications for the trophic structure of future grassland communities.

KEYWORDS
arthropod, ecological gradient, food web, nutrient, prairie, sodium, trophic pyramid, trophic weighted mean

Ellen A. R. Welti and Lucie Kuczynski contributed equally to this study.

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1 | INTRODUCTION

Trophic pyramid shape – the relative biomass of plants, herbivores, and predators – is expected to vary with resource availability (Hatton et al., 2015; Moore et al., 2004; Post, 2002) and climate (Ruiz-Cooley et al., 2017). These drivers, in turn, vary across ecological, geographical, and anthropogenic gradients. While relationships between environmental drivers and species occurrences have been fairly well explored (e.g. Rosenzweig, 1995), variations in species abundance along ecological gradients are less studied (Supriya, Moreau, Sam, & Price, 2019), despite their potential insight for understanding the trophic structure of communities. To remedy this gap and to identify critical drivers of terrestrial food web structure, we sampled abundances of four invertebrate trophic levels using standardized surveys in grasslands across large chemical and climatic gradients in the continental United States (De Frenne et al., 2013).

The shape of animal food webs arises from the interplay between primary resource quality, habitat structure, climate, and the features of the consumers themselves. Food webs can become more top-heavy – increasing predator abundance/biomass relative to prey – with many processes including: greater energy transfer between trophic levels, complex habitat structure providing niche space for predators, increased turn-over rates of lower trophic levels, increased predator mobility, and with increased subsidies to consumers (McCauley et al., 2018). Here we focus on the role of three drivers – plant nutrient quality, plant biomass, and climate – that can influence consumer abundances, and in turn, the trophic structure of communities supported by grassland systems.

Plant quality, quantified here as elemental tissue concentrations, can constrain the abundance of consumer communities when essential elements (e.g. N, P, K, Na) are in short supply (Joern, Provin, & Behmer, 2012; Kaspari & Powers, 2016) or when toxic elements bioaccumulate (Cui, Zhang, Zhang, Liu, & Zhang, 2011; Ouédraogo, Chételat, & Amyot, 2015). The role of sodium in shaping trophic pyramids is relatively unique among the elements in that sodium is an essential element for all animals but is generally not limiting for plants, unlike many other nutrients that are often limiting, such as N, P, and K in terrestrial systems (Kaspari, Welti, & de Beurs, 2020). The amount of sodium found in plant tissue is highly variable (Borer et al., 2019; Han, Fang, Reich, Ian Woodward, & Wang, 2011), resulting in spatial variation in sodium limitation for primary consumers (Prather et al., 2018; Seastedt & Crossley, 1981; Snell-Rood, Espeset, Boser, White, & Smykalski, 2014; Welti, Sanders, Beurs, & Kaspari, 2019), with expected consequences for higher trophic levels that have yet to be explored. By exploiting a continental-scale gradient of element nutrient concentrations, including sodium, across the backdrop of classic environmental drivers (e.g. temperature and plant biomass), we test the prediction that food quality shapes food webs through limiting primary consumer abundance (Kaspari, Clay, Donoso, & Yanoviak, 2014; Welti et al., 2019).

Plant biomass can constrain herbivore abundance, and thus, indirectly, predator abundance (Hutchinson, 1959; Oksanen, Fretwell, Arruda, & Niemela, 1981). In bottom-up systems, biomass production and insect abundance within higher trophic levels should be positively correlated as more energy is required to support viable populations of taxa at higher trophic levels (Kaspari, 2001; Welti, Prather, Sander, de Beurs, & Kaspari, 2020). However, a tendency toward bottom-heavy animal trophic pyramids as biomass of primary producers increases might be the dominant pattern across a wide variety of terrestrial and aquatic food webs, although the mechanism for this pattern is not currently known (Hatton et al., 2015).

Finally, because arthropods are ectotherms, temperature directly constrains their metabolic activity and abundance. Both average temperature and its variability can thus shape trophic pyramids. Higher metabolism due to higher temperatures may result in increased energy use and increased abundance (Twomey et al., 2012) or lead to resource limitation and result in lower abundance (O'Connor, Gilbert, & Brown, 2011). Trophic level-specific responses to temperature are expected (Jonsson et al., 2015) due to different metabolic and heat dissipation rates (Brown, Gillooly, Allen, Savage, & West, 2004). For example, increases in temperature may favour herbivore energy use, increasing herbivore abundance and resulting in trophic pyramids that are more bottom-heavy. Alternatively, increasing temperatures may either reduce herbivore abundance or benefit higher trophic levels, resulting in top-heavy trophic pyramids (Kratina, Greig, Thompson, Carvalho-Pereira, & Shurin, 2012; Shurin, Clasen, Greig, Kratina, & Thompson, 2012). Additionally, unstable climatic conditions may be exploited by more *r*-selected species which tend to occupy lower trophic levels (Dossena et al., 2012; Ledger, Brown, Edwards, Milner, & Woodward, 2013).

To determine the relative importance of direct and indirect effects of plant quality, plant biomass, and temperature on community trophic structure, we investigate three non-exclusive hypotheses (Table 1, Figure 1): (1) We hypothesize that increasing sodium availability will primarily favour plant consumers, and thus as sodium availability increases, trophic pyramids will become more bottom-heavy (Table 1: H1). Additionally, we predict that increasing concentrations of essential elements in plant tissue will increase the trophic pyramid's top-heaviness (Table 1: H1). We conducted an exploratory analysis of variation in trophic pyramid structure with changing concentrations in toxic metals found in plant tissue. As plants passively uptake toxic metals from the soil (Marschner, 1995), we hypothesize a suppressive effect of metals like lead and arsenic on consumer abundance and trophic structure (Table 1: H1). (2) We hypothesize that increases in plant biomass, through increasing the resource base, will benefit herbivores, resulting in more bottom-heavy invertebrate trophic pyramids (Table 1: H2A). Alternatively, if predators can benefit from an increase in herbivore abundance, high plant biomass systems may result in more top-heavy invertebrate trophic pyramids (Table 1: H2B). (3) Finally, depending on metabolic temperature sensitivity across trophic levels, we hypothesize increases in temperature and temperature stability will result in more bottom-heavy trophic pyramids (Table 1: H3A) or more top-heavy trophic pyramids (Table 1: H3B).

Here we surveyed multi-trophic invertebrate communities across North American grasslands. We used identically sampled

TABLE 1 Hypotheses of major drivers of trophic pyramid shape. Hypothesis numbers are referred to both in the main text and Figure 1. Variable abbreviations are provided in the Model variables column. The expected effects of drivers on community trophic mean (CTM) are graphically resented in Figure 1 and observed effects on CTM are provided for significant linear regressions ($\alpha = .05$)

Hypothesis	Prediction	Model variables	References	Expected effect on CTM	Observed effect on CTM
H1. Plant chemistry	Decreases in plant essential elements and increases in plant toxic elements and sodium will make trophic pyramids more bottom-heavy	$PCA_{plant.e}$, $PCA_{plant.t}$, Na_{plant}	Post (2002), Cui et al. (2011), Kaspari et al. (2014), Welti et al. (2019)	Plant essential elements + Plant toxic elements – Plant sodium –	Plant essential elements -NS Plant toxic elements -NS Plant sodium +
H2. Plant Biomass	A) Decreasing plant biomass will make trophic pyramids more bottom-heavy	Plant biomass	Oksanen et al. (1981)	A) –	Negative (–)
	B) Increasing plant biomass will make trophic pyramids more bottom-heavy		Hatton et al. (2015)	B) +	
H3. Temperature	A) Increasing temperature and temperature stability will make trophic pyramids more bottom-heavy	TEMP, StabTEMP	O'Connor et al. (2011)	A) –	Hump-shaped (∩)
	B) Decreasing temperature and temperature stability will make trophic pyramids more bottom-heavy		Pimm and Lawton (1977), Kratina et al. (2012), Shurin et al. (2012)	B) +	

PCA = principal components analysis; $PCA_{plant.e}$ = first Principle Component Axis of plant essential elements; $PCA_{plant.t}$ = first Principle Component Axis of plant toxic elements; Na_{plant} = plant sodium concentration; TEMP = mean annual temperature; StabTEMP = temperature stability.
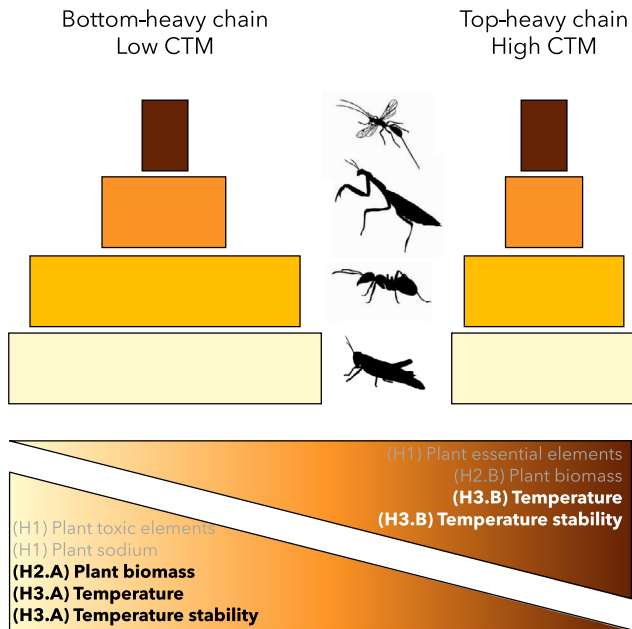
FIGURE 1 Graphical representation of the three hypotheses. Each box represents a trophic level (darker boxes indicate higher trophic levels such as predators and parasitoids). On the left side, herbivores and omnivores (lightest boxes) dominate the system, while on the right side, the system is more balanced, leading to a less bottom-heavy trophic chain. We assume that in our grassland systems, turnover is not high enough to result in an inverted biomass pyramids such as those found in some marine systems. Thus, even the most top-heavy food chains in our system are mostly composed by herbivores and omnivores, although the ratio of top levels to bottom levels is closer to 1 than in bottom-heavy chains. Bottom triangles indicate how different factors can influence the balance between low and high trophic levels in communities. Hypotheses numbers refers to Table 1. Hypotheses in grey were not supported while those in black/white were supported by our results. CTM = community trophic mean. [Colour figure can be viewed at wileyonlinelibrary.com]

communities across ecological gradients to examine how abundance within trophic groups and community trophic mean (CTM) shift along these ecological gradients. By incorporating both the number of trophic groups and abundances within those groups, CTM measures the distribution of individuals across trophic levels. While community structure is often described using a single trophic level (e.g. Srivastava et al., 2009), trophic levels may not track environmental gradients in parallel, suggesting multi-trophic studies will better capture system dynamics (Bruckerhoff et al., 2020; Soliveres et al., 2016).

2 | MATERIALS AND METHODS

2.1 | Study sites

We sampled 54 protected grassland sites across the United States during the 2017 growing season, across many large environmental gradients ranging from Florida and Texas in the south to Minnesota

in the north (Figure 2; for a list and description of all sites, see Supporting Information Appendix S1, Table S1.1). Gradient analysis can expand the magnitude of proposed drivers beyond that of field experiments (Sundqvist, Sanders, & Wardle, 2013). To limit variation in the seasonal timing of sampling, sampling began in the southern-most sites in late April and ended in the northernmost sites in late July.

2.2 | Invertebrate sampling

Aboveground invertebrates and plants were collected from five 1 m^2 (270 total) plots within each 30 m × 100 m site. Plots were located at the four corners and at the centre (arranged like the 'five' side of a die and varying from 28 to 98 m apart). All analyses were conducted at the site level, corresponding to average values across the five plots. We used a G-vac (Stewart & Wright, 1995; Zentane, Quenu, Graham, & Cherrill, 2016) to sample invertebrates by moving it across the vegetation of each plot for 30 s. Most invertebrates were identified to family level and categorized into the trophic levels of herbivore, predator, parasitoid, detritivore, pollinator, omnivore, and unknown (see Welti et al., 2019 for classification table).

2.3 | Plant sampling and laboratory methods

Following the collection of invertebrates, aboveground vegetation within 1 m × 0.1 m strips was clipped from each plot. Graminoid and forb samples from each plot were dried at 60 °C for 36 hr, weighed for dry mass, and ground. To calculate aboveground plant biomass, we summed aboveground dried graminoid and forb weights with each plot, and took the average across each site (hereafter plant biomass). Elemental chemistry of one composite graminoid and one composite forb sample per site was analysed using combustion analysis, hot plate digestion, and inductively coupled plasma atomic emission spectroscopy (ICP-AES) by the Cornell Nutrient Analysis Laboratory (https://cnal.cals.cornell.edu/). To assess the ecosystem nutrient availability, we used global plant elemental chemistry computed as the sum between graminoid and forb elemental concentrations, weighted by relative biomass for each individual site.

2.4 | Plant chemistry

To characterize plant chemistry at each site, we ran two principal components analyses (PCAs): one based on essential nutrients (i.e. B, C, Ca, Co, Cr, Cu, Fe, K, Mg, Mn, Mo, N, P, S, Zn) and a second one based on toxic elements (i.e. Al, As, Ba, Be, Cd, Pb, Sr, Ti, V), hereafter named $PCA_{plant.e}$ and $PCA_{plant.t}$, respectively. All variables were scaled prior to conducting PCAs, by subtracting their mean and dividing by their standard deviation, and only one axis was kept for each PCA. The R package *ade4* was used to run PCAs (Dray & Dufour, 2007, p. 200). The eigenvalues for $PCA_{plant.e}$ and $PCA_{plant.t}$
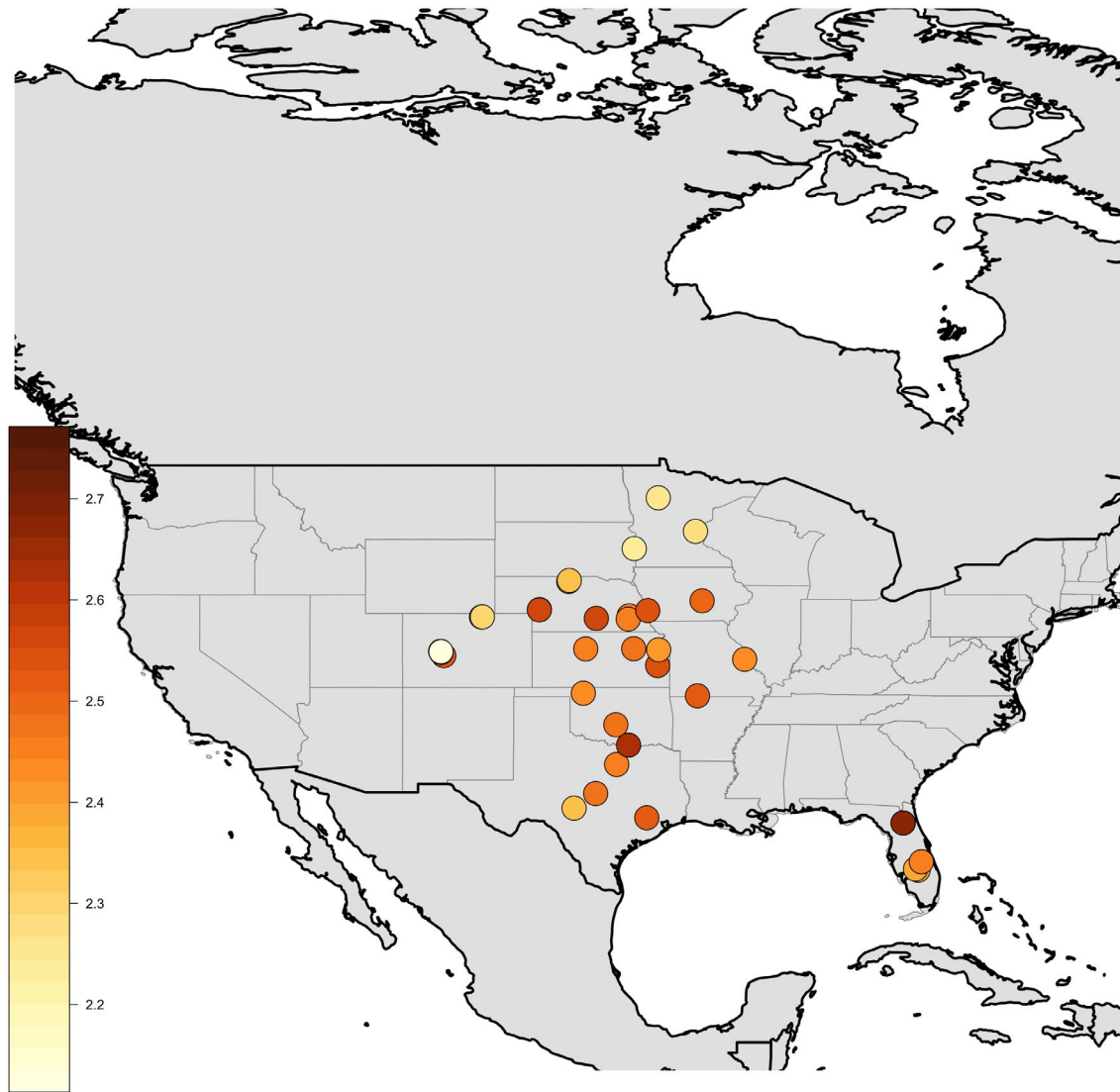
FIGURE 2 Map of studied sites. Light colours indicate lower community trophic mean (CTM) values (bottom-heavy trophic pyramids) while dark colours mean higher CTM values (top-heavy trophic pyramid) [Colour figure can be viewed at wileyonlinelibrary.com]

are both 0.34. PCA$_{plant.e}$ is strongly positively correlated with N, Ca, S, K, Mg, Fe, Zn, Cu, B and Co, and negatively correlated with C (i.e. |correlation| > .6). PCA$_{plant.t}$ is most positively correlated with Al, As and Ti. We left out sodium (Na) in order to examine the role of plant sodium (log-transformed to meet normality assumptions) on invertebrate communities separately.

2.5 | Temperature

In order to collect temperature data from each site, we matched geographical coordinates of the 54 sites to a 4 km × 4 km grid cell using the parameter-elevation regressions on independent slopes model (PRISM) datasets (downloaded winter 2017). We used monthly averages of temperature from 1981 to 2016 for each site to calculate mean annual temperature (TEMP) and temperature stability (StabTEMP) as the inverse of the inter-annual coefficient of

variation. We used averages of the full 36 year climate time series in determine average climatic conditions for each site while reducing the effects of extreme years.

2.6 | Community trophic mean

To describe the trophic structure of communities, we calculated the CTM as the community weighted mean (CWM; Devictor et al., 2008; Kampichler, van Turnhout, Devictor, & van der Jeugd, 2012; Ricotta & Moretti, 2011) using trophic level weighted by abundance:

$$CTM = \frac{1}{P} \sum_i^N p_i \cdot t \quad (1)$$

where P represents the total number of individuals, N the number of species, p_i the abundance of the species i, and t_i its trophic level.

High CTM values indicate top-heaviness (i.e. high trophic levels are the most abundant) while low values mean bottom-heaviness (i.e. low trophic levels are more abundant). We attributed a value to each identified trophic level (herbivores, pollinators, and detritivores = 2, omnivores = 2.5, predators = 3, and parasitoids = 4). Although these values simplify existing biological complexity, they provide information on the structure of the trophic pyramids while also being intuitive. In a prior study across these sites, we found that omnivores had a N isotope determined trophic position intermediate to herbivores and predators tested, supporting our proposed 2.5 trophic position value (Welti et al., 2020). Our classification of taxa into three trophic levels simplifies the natural history of hundreds of North American arthropod taxa, subsuming trophic variation within taxa (e.g. Formicidae are classified as omnivores, whereas ants can vary from herbivores to predators). A high CTM indicates a top-heavy trophic pyramid (e.g. relatively more predators and parasitoids) while a low CTM indicates a bottom-heavy trophic pyramid (e.g. relatively more herbivores, pollinators, and detritivores). Plant biomass was not included in the calculation of CTM as we were interested in examining the effects of plant biomass on invertebrate trophic pyramid shape.

2.7 | Drivers of CTM

To describe the influence of environmental gradients on community trophic structure, we examined the relationship between CTM values and plant chemistry, plant biomass, and temperature using linear regressions. The first CTM model tests plant chemistry drivers (H1) and includes $PCA_{plant.e}$, $PCA_{plant.t}$, and Na as explanatory variables. The second model tests H2 and includes only plant biomass as an explanatory variable of CTM. The third model examines the role of temperature (H3) and includes the explanatory variables TEMP and StabTEMP. The third model incorporated quadratic effects to test for a hump-shaped relationship resulting from an optimal temperature regime favouring more top-heavy trophic pyramids. As the role of plant sodium was potentially masked by a negative correlation with plant biomass [$F_{(1,257)}$ = 19.9, R^2 = .07, p < .001], we visualized the joint effects of plant sodium and biomass on total herbivore abundance using a contour plot.

2.8 | Structural equation model

To examine how a suite of biotic and abiotic factors are related to trophic composition, we first used a piecewise structural equation model (SEM; Lefcheck, 2016) that accounts for both direct and indirect effects. The SEM was built from five models (Figure 3a). The first one contained plant biomass as the response variable and TEMP as the explanatory variable. The second model predicted herbivore abundance using the explanatory variables of TEMP and plant related variables (i.e. $PCA_{plant.e}$, Na_{plant} and plant biomass). The third model used omnivore abundance as the response variable, and herbivore abundance is used as a predictor, together with the environmental

explanatory variables (i.e. $PCA_{plant.e}$, Na_{plant}, plant biomass, TEMP) of the second model. The fourth model explained predator abundance using plant biomass, TEMP, herbivore abundance and omnivore abundance as explanatory variables. Finally, the fifth model examined parasitoid abundance as the response variable and plant biomass, TEMP, and herbivore, omnivore and predator abundances as explanatory variables. Pollinators and detritivores were not included in the SEM as they occurred less frequently and at lower densities across the 54 sites. We used Fisher's C to assess the completeness of our model. The SEM was conducted using the R package *piecewiseSEM* (Lefcheck, 2016).

All analyses were performed using R 3.5.2 (R Core Team, 2019).

3 | RESULTS

In total, we sampled 9,347 invertebrates (averaging 17.5 ± 37.8 SD herbivores/m^2, 4.9 ± 9.3 SD omnivores/m^2, 3.4 ± 3.8 SD predators/m^2, and 1.8 ± 3 SD parasitoids/m^2). The estimated CTM (mean = 2.42 ± SD 0.18), a measure of trophic pyramid shape (theoretically ranging from 2–4), ranged from 2.08, representing the most bottom-heavy trophic pyramid from a Colorado montane meadow, to 2.85, representing the most top-heavy trophic pyramid from the Nebraska Sandhills. Herbivores were present in all invertebrate trophic pyramids and average abundances across all sites decreased with increasing trophic level (Supporting Information Appendix S1, Figure S1.1).

3.1 | Plant chemistry

Across the 54 grasslands, plant sodium and CTM were positively correlated (estimate = .040, p < .05, R^2 = .12), indicating that grassland sites with higher plant sodium concentrations were associated with top-heavy invertebrate trophic pyramids (Figure 4c). Results from the SEM (Fisher's C = 37.56, p < .05; R^2 ranging from .26 to .63) corroborate the important role of plant sodium, with an especially strong positive effect on herbivore abundance (Figure 3b). Additionally, we found an interaction between the effects of plant sodium and plant biomass on herbivore abundance: plant sodium concentration increased herbivore abundances for a given level of plant biomass, especially in the range of 400–800 g dry mass/m^2 (Figure 5). We did not find evidence for effects of other plant essential or toxic elements ($PCA_{plant.e}$, $PCA_{plant.t}$) on trophic structure (Figure 3b).

3.2 | Plant biomass

Plant biomass and CTM were negatively correlated (estimate = −.003, p = .026, R^2 = .1), suggesting that sites with high plant biomass had trophic structures that are more bottom-heavy (Figure 4d). Plant biomass had the strongest direct positive effect on herbivores, but also directly increased parasitoid abundances (Figure 3b).
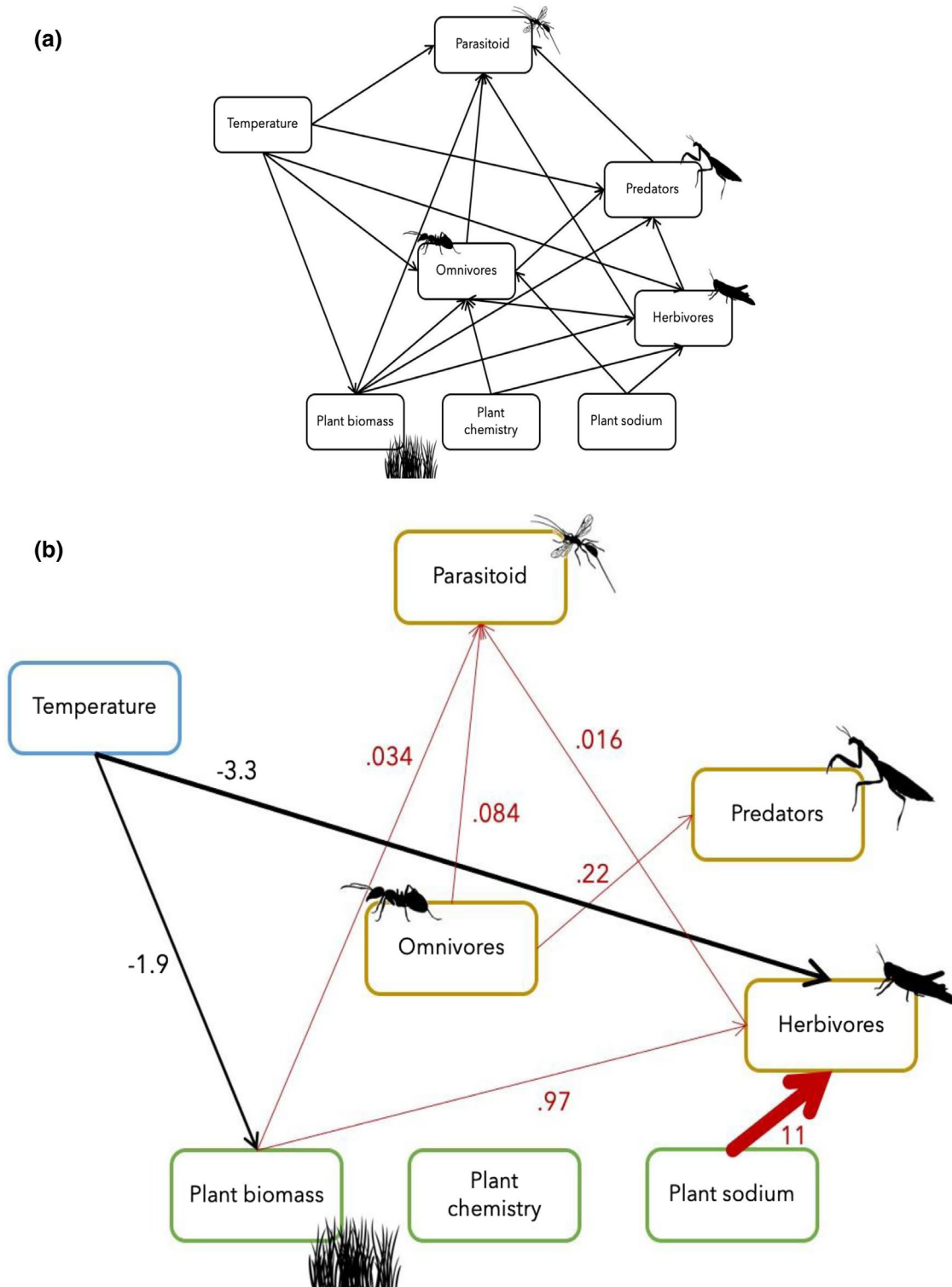
FIGURE 3 Structural equation model (SEM) of drivers affecting abundance of different trophic levels. The upper figure depicts the hypothesized links (a) while the lower figure shows the final SEM (b), including only observed significant links ($p < .05$). Red and black arrows represent significant negative and positive relationships, respectively. Numbers and arrow line thickness indicate standardized coefficients [Colour figure can be viewed at wileyonlinelibrary.com]

3.3 | Temperature

Higher mean annual temperatures (TEMP) and higher inter-annual temperature stability (StabTEMP) both exhibited significant first and second order estimates ($estimate_{TEMP} = .06$, $estimate_{TEMP}^2 =$ $-.002$, $estimate_{StabTEMP} = .03$, $estimate_{StabTEMP}^2 = -.001$, all $p < .01$), indicating more top-heavy trophic pyramids occurred at an optimum along those gradients (Figure 4a,b). In addition, higher temperatures directly decreased plant biomass and herbivore abundance (Figure 3b).

FIGURE 4 Main drivers of trophic structure. Significant relationships between community trophic mean (CTM) and mean annual temperature (TEMP; a), temperature stability (StabTEMP; b), plant sodium concentrations (NA$_{plant}$; c), and aboveground dried plant biomass (plant biomass; d) [Colour figure can be viewed at wileyonlinelibrary.com]
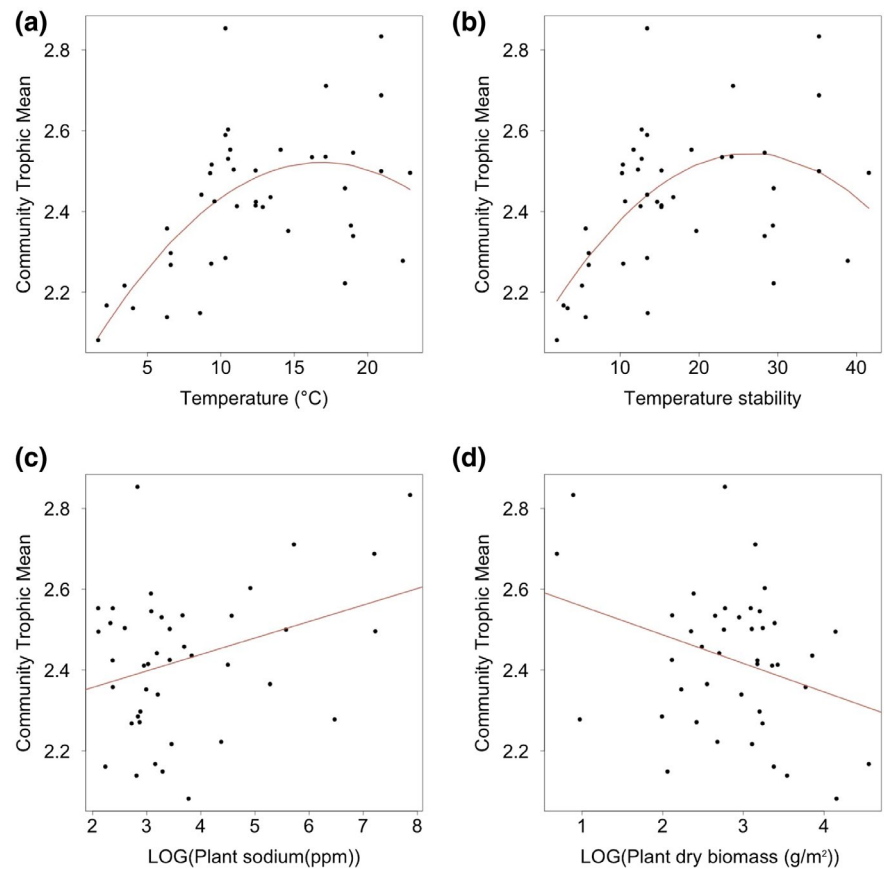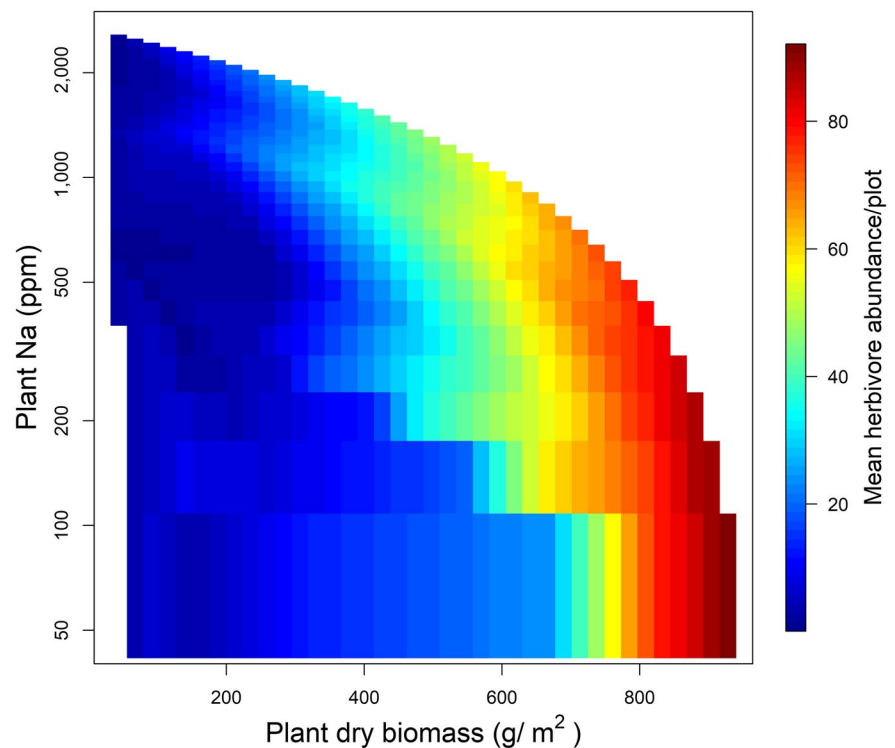

FIGURE 5 Interaction between plant biomass and sodium on herbivores and trophic structure. Contour plot of the interactions between dry plant biomass (g/m^2 clip strip), plant sodium concentration (ppm), and mean herbivore abundance per plot [Colour figure can be viewed at wileyonlinelibrary.com]

4 | DISCUSSION

Despite extensive variation in the abundance of invertebrates and shape of grassland trophic pyramids across North America, our results indicate both can be predicted by plant biomass, plant sodium, and temperature. Higher levels of plant sodium resulted in invertebrate communities with more top-heavy trophic pyramids while higher aboveground plant biomass resulted in more bottom-heavy trophic

structure across 54 North American grasslands. In addition, trophic pyramids were the most top-heavy at intermediate values of temperature and temperature stability (i.e. a hump-shaped relationship). In our study, while plant essential and toxic elements did not influence community trophic structure, plant sodium, an element limiting to herbivores (Welti et al., 2019), strongly increased herbivore abundances, and indirectly led to increased parasitoid abundances. Increases in temperature directly decreased herbivore abundances, also resulting in more top-heavy trophic pyramids. As both the distribution of sodium (Jackson & Jobbagy, 2005; Kaspari, Chang, & Weaver, 2010) and temperature (Bradley, 2001) are changing in the Anthropocene, our results point to potential impacts on consumers in grasslands, one of the Earth's dominant and threatened terrestrial ecosystems (Hoekstra, Boucher, Ricketts, & Roberts, 2005; Ratajczak, Nippert, & Collins, 2012).

In contrast to our prediction that increases in sodium availability would result in more bottom-heavy food webs by benefiting plant consumers, we found an increase in top-heavy food webs with increasing plant sodium. Our logic that herbivores will disproportionately increase relative to higher trophic levels with increasing plant sodium because they are more sodium limited than other trophic levels held; however, higher herbivore abundances supported more parasitoids, resulting in an increasing CTM with plant sodium. Sodium pulses in these same grassland sites were more effective at attracting invertebrate herbivores and omnivores than predators and parasitoids (Welti et al., 2019). Additionally, in a tropical nutrient-limited food web, predator responses to sodium pulses were delayed relative to their detritivore prey (Clay, Yanoviak, & Kaspari, 2014). While both of these studies of sodium pulse attraction were conducted at local spatio-temporal scales (i.e. few m^2 and over days), at larger spatial scales and over decades, higher naturally occurring plant sodium levels, such as here where plots were not manipulated, likely provide an overall larger resource base for invertebrate consumers, resulting in higher CTMs. This suggests a new working hypothesis – of a scale dependent trophic response to variation in sodium availability.

Our exploratory analysis did not detect covariance between CTM and trophic abundance with toxic elements in plants (PCA$_{plant.t}$) nor for essential elements in plants (PCA$_{plants.e}$). The former suggests that naturally occurring levels of Ar and Pb in sites selected to be relatively undisturbed are not high enough to bioaccumulate and inhibit individual performance and hence population size. If so, repeating these studies along a pollution gradient may be more illustrative. However, we also found that PCA$_{plant.t}$ and PCA$_{plants.e}$ were themselves positively correlated (R^2 = .69). This means that at the ecosystem scale, plants rich in toxic elements were also rich in essential elements (e.g. N, P, and K). If and how this covariation persists at the species or individual plant level may be important for understanding the trade-off between avoiding toxins and acquiring sufficient amounts of essential nutrients.

As predicted, we found that as plant biomass decreased among grassland sites, trophic pyramids became more top-heavy (Post, 2002). This negative relationship between plant biomass and top-heaviness contradicts theoretical predictions that increasing plant biomass should increase availability of resources and niche space, resulting in increased abundances of higher trophic levels (McCauley et al., 2018). However, this result is consistent with a recent survey of a variety of aquatic and terrestrial ecosystems, though the mechanism for this pattern has yet to be supplied by the theoretical literature (Hatton et al., 2015). Additionally, consumers feed on resources not examined in this study such as litter (Sauvadet et al., 2016). Plant biomass may be itself be driven by trophic structure, complicating the assessment of this response (Schmitz, Krivan, & Ovadia, 2004). If robust, reduced CTMs with plant biomass suggest similar changes in trophic structure as biomass accumulates from drought to heavy rainfall years, and from early to mid-season in seasonal grasslands (Prather, Castillioni, Welti, Kaspari, & Souza, 2020).

The impact of climatic variation on trophic structure remains challenging to predict (Voigt et al., 2003) partly because both direct and indirect effects need to be considered (e.g. Chen et al., 2018; Kuczynski, Chevalier, Laffaille, Legrand, & Grenouillet, 2017) and because temperature may have trophic level-specific effects. Additionally, systems that are climatically stable over years are predicted to support more diversity (Jackson, Peres-Neto, & Olden, 2001) due to relaxed habitat filtering on species (Weiher & Keddy, 1995). Invertebrate ectotherms can be especially sensitive to temperature (Deutsch et al., 2008; Paaijmans et al., 2013), and primary consumers are expected to be susceptible to changing temperature due to their need to match phenology with that of plants (Thackeray et al., 2016). We document a direct decrease in herbivores but no other trophic levels with increasing temperatures. Changing the proportionate abundance of herbivorous insects is likely to affect ecosystem services, as they are one of the most important groups driving ecosystem function (Soliveres et al., 2016). While our dataset does not allow us to examine changes in species interactions, temperature can have strong effects on interactions, such as through changing attach rates or temporal intervals when species interact (Laws & Joern, 2013). In our study, warmer grasslands indirectly decrease parasitoid abundance, through effects on plant biomass, potentially as plant biomass is a measure of habitat structure for small animals (Coudrain, Schüepp, Herzog, Albrecht, & Entling, 2014). Across all our sites in this geographical snapshot study, invertebrate grassland communities are the most top-heavy structures at intermediate mean annual temperatures and long-term temperature stability (i.e. intermediate thermal disturbance).

4.1 | Conclusion

Our analysis at a continental scale can be viewed as a working hypothesis for the structure of grassland food webs and their future (Gian-Reto, 2010). Due to human activities (e.g. salting winter roads, salinization of irrigation waters), sodium will become much more available in many ecosystems. Sodium supports herbivores that in turn increase the abundance of parasitoids, resulting in top-heavy invertebrate trophic pyramids. In addition, the heightened sensitivity of herbivore abundance to rising temperature suggests future

dominance of higher trophic levels with warming (Allen et al., 2018; Romero, Piccoli, de Omena, & Gonçalves-Souza, 2016). We document a bottom-heavy skew in trophic pyramids occurring in more productive, extreme temperature (coldest and hottest), and less salty sites, while terrestrial ecosystems are predicted to get more productive (Li et al., 2017), but hotter (Bradley, 2001), and more salty (Jamil, Riaz, Ashraf, & Foolad, 2011).

DATA ACCESSIBILITY

Invertebrate abundances by trophic group, CTM, temperature, plant biomass and chemistry data are deposited in the Dryad Digital Repository: https://doi.org/10.5061/dryad.612jm6411.

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SUPPORTING INFORMATION

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