RESEARCH ARTICLE

Bottom-up when it is not top-down: Predators and plants control biomass of grassland arthropods

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Abstract

1. We investigate where bottom-up and top-down control regulates ecological communities as a mechanism linking ecological gradients to the geography of consumer abundance and biomass. We use standardized surveys of 54 North American grasslands to test alternate hypotheses predicting 100-fold shifts in the biomass of four common grassland arthropod taxa—Auchenorrhyncha, sucking herbivores, Acrididae, chewing herbivores, Tettigoniidae, omnivores, and Araneae, predators.

2. Bottom-up models predict that consumer biomass tracks plant quantity (e.g. productivity and standing biomass) and quality (nutrient content) and that ectotherm access to food increases with temperature. Each of the focal trophic groups responded differently to these drivers: the biomass of sucking herbivores and omnivores increased with plant biomass; that of chewing herbivores tracked plant quality; and predator biomass did not depend on plant quality, plant quantity or temperature.

3. The Exploitation Ecosystem Hypothesis is a top-down hypothesis that predicts a shift from resource limitation of herbivores when plant production is low, to predator limitation when plant production is high. In grasslands where spider biomass was low, herbivore biomass increased with plant biomass, whereas bottom-up structuring was not evident when spiders were abundant. Furthermore, neither predator biomass nor trophic position (via stable isotope analysis) increased with plant biomass, suggesting predators themselves are top-down limited.

4. Stable isotope analysis revealed that trophic position of the chewing herbivore and omnivore increased significantly with plant biomass, suggesting these groups increased scavenging and meat consumption in grasslands with higher carbohydrate availability.

5. Taken together, our snapshot sampling documents gradients of food web structure across 54 grasslands, consistent with multiple hypotheses of bottom-up and top-down regulation.

KEYWORDS

biomass, Exploitation Ecosystem Hypothesis, grasshopper, insect, katydid, leafhopper, prairie, spider

1 | INTRODUCTION

Examining change in communities across ecological gradients has a long history in ecology (e.g. MacArthur, 1972; Whittaker, 1967). This approach has the advantage of allowing for hypothesis testing while maintaining ecological complexity (Sundqvist et al., 2013). Historically, investigating shifts in communities across ecological gradients has focused on the causes of increasing diversity towards the tropics (Brown, 2014). With the exception of plants, less is known regarding the distribution of biomass across large-scale terrestrial gradients (Andrew & Hughes, 2005) though recent work suggests biomass of higher trophic groups may follow a predictable scaling law (Hatton et al., 2015). Work examining shifts in consumer biomass across productivity gradients has primarily relied on meta-analyses to obtain sufficient data to test for the slope and strength of plant–consumer relationships (Chase, Leibold, Downing, & Shurin, 2000; Schädler, Jung, Auge, & Brandl, 2003).

A long-standing argument in community ecology concerns which mechanisms govern limits on the productivity of trophic levels within food webs (Hairston, Smith, & Slobodkin, 1960; Lindeman, 1942; Oksanen, Fretwell, Arruda, & Niemela, 1981). In this study, we examine four non-mutually exclusive hypotheses about the determinants of consumer biomass of four arthropod taxa in seasonal grasslands (see Table 1).

If food webs are limited by bottom-up processes, then the biomass of consumer trophic levels should increase with increasing primary productivity (Chase, 1996; Fretwell & Lucas, 1970; McNaughton, Oesterheld, Frank, & Williams, 1989). Plant nutrient content poses a bottom-up control on consumers (primarily the macronutrients N, P and K). We test two hypotheses—quantity and quality—of primary producers as regulators of consumer biomass: The biomass of primary producers sets a bottom-up control on the total biomass that can be converted into higher trophic levels (H1), and biomass is limited by biological building blocks so biomass accumulation can be predicted by nutrient availability (H2).

Higher temperatures can increase metabolic rates, and thus promote biomass accumulation rates (Kaspari, 2001; Kaspari, Alonso, & O'Donnell, 2000). Alternatively, high temperature can reduce biomass by causing ectotherms to mature at smaller sizes (Atkinson, 1995) or indirectly reduce arthropod abundance through effects on plants (Welti, Qiu, et al., 2019). We also examine the indirect effects of precipitation through effects on plants, which play a complex role in regulating arthropod populations (Chase, 1996; Jonas, Wolesensky, & Joern, 2015). Thus, local climate conditions, both directly and indirectly through lower trophic levels, affect consumer biomass accumulation (H3).

Models of top-down regulation by predators are more diverse. Hairston et al. (1960) green-world hypothesis (HSS) summarized a world where predators reduced herbivore abundance, decreasing their effect on plants. However, higher trophic levels, cannibalism or social dominance may pose regulations on predators themselves (Arditi & Ginzburg, 1989; Beckmann & Berger, 2003; Getz, 1984; Tallian et al., 2017). A more expansive approach sees the role of top-down regulation as covarying with the primary productivity that maintains the food web (Choquenot & Forsyth, 2013; Letnic & Ripple, 2017; Power, 1992). The Exploitation Ecosystem Hypothesis (EEH) (Oksanen et al., 1981) predicts that the number of trophic levels accumulates along productivity gradients while herbivores alternate between resource limitation and limitation by primary predators with increasing trophic levels. We test a prediction of the EEH that the interaction between plant and primary predator biomass will predict herbivore biomass. Specifically, we predict that herbivore biomass will be limited by primary productivity when primary predator abundance is low and by predation when primary predator abundance is high. We also test the EEH prediction that low plant biomass, through decreasing the amount of primary predators, will lead to weaker regulation by primary predators and stronger regulation by primary productivity on herbivore biomass (H4). Additionally, EEH predicts food chain lengths will increase in more productive systems. We test this prediction by examining the relationship between plant biomass and trophic position of spiders.

We targeted four focal taxa—Auchenorrhyncha, Acrididae, Tettigoniidae and Araneae (from hereon we refer to these groups, respectively, as Auchenorrhyncha, grasshoppers, katydids and spiders)—representing the trophic guilds of sucking herbivore, chewing herbivore, omnivore and predator. These four groups represent a majority (average = 59%) of the biomass of collected invertebrates across the grasslands. We collected and measured biomass of these taxa and above-ground plants using standardized methods across 54 North American grassland sites to explore the effectiveness of alternate bottom-up and top-down models in predicting the geography of arthropod biomass.

TABLE 1 Hypothesized drivers of consumer biomass

	Hypothesis	Prediction
H1	Plant quantity	Plant biomass and productivity sets a bottom-up constraint on arthropod consumer biomass
H2	Plant quality	Plant nutrients concentration sets a bottom-up constraint on arthropod consumer biomass
H3	Climate	Climate can enhance or constrain arthropod consumer biomass directly or via access to plant quality and quantity
H4	Exploitation Ecosystem Hypothesis	1. Increases in plant biomass and productivity allow more carnivory by increasing the amount of available animal tissue 2. Increases in plant biomass and productivity, by increasing the amount of primary predators, increases the likelihood that herbivore biomass is constrained by top-down predator effects

2 | MATERIALS AND METHODS

Sampling occurred between April and August of 2017 across 54 continental North American grassland sites (see Table S1 for list of sites). Sites included native and restored grasslands managed by universities, the US Forest Service, The Nature Conservancy, the USDA, NSF LTER

and the Audubon Society. Above-ground invertebrates were collected with sweepnets between 7:00 a.m. and 04:00 p.m., when wind speeds <25 km/hr and vegetation was dry. At each site, 4–6 samples of invertebrates were collected, with each sample consisting of 40 sweeps along a 40 m transect; all results are given as site means per sample. Invertebrates were freeze-killed and then sorted into five categories: grasshoppers, Auchenorrhyncha, katydids, spiders and other taxa. Samples were dried at 60°C for a minimum of 4 days and then weighed.

2.1 | Plant sampling

At each site, five plots (each 1 m^2) arranged in a 100 m by 30 m grid with one central plot were sampled for above-ground plant biomass. Above-ground plants were clipped from one or two 0.1 m by 1 m clip-strips per plot, dried for 48 hr at 60°C, ground and pooled to produce one composite grass and one composite forb sample per site with the quantity of material coming from each plot being proportional to the amount of dry biomass of the plot out of the combined biomass of the five control plots. Ground plant matter from each site was analysed by Cornell Nutrient Analysis Laboratory for elemental chemistry (Al, As, B, Ba, C, Ca, Cd, Co, Cr, Cu, Fe, H, K, Li, Mg, Mn, Mo, N, Na, Ni, P, Pb, S, Si, Sr, Ti and Zn) using hot plate digestion and inductively coupled plasma atomic emission spectroscopy (https://cnal.cals.cornell.edu/).

2.2 | Climate data

We downloaded the mean monthly temperature and mean monthly precipitation PRISM data (PRISM Climate Group, Oregon State University, http://prism.oregonstate.edu). These datasets are gridded with a spatial resolution of 4 km. The PRISM group produces highly accurate climate data using climate stations, digital elevation data and factors such as location, coastal proximity and topographic position (Daly et al., 2008). They used approximately 13,000 stations for the precipitation interpolation and 10,000 station for the temperature interpolation over the conterminous USA (Daly et al., 2008).

2.3 | Trophic position

To test for shifts in resource use of our representative taxa, we used nitrogen stable isotopes to estimate the relative trophic position of the four taxa (Auchenorrhyncha, grasshoppers, katydids and spiders). To create baseline nitrogen levels at each site, we clipped and sorted plants into graminoids and forbs. We dried plants at 60°C for 48 hr before being ground, weighed to the nearest 0.001 mg and analysed at the Environmental Stable Isotope Lab at the University of Oklahoma for $\delta^{13}C$ and $\delta^{15}N$. We calculated the average vegetation $\delta^{15}N$ value $\left(\delta^{15}N_{base}\right)$ at each site using the formula:

$$\left(\frac{\text{graminoid mass}}{\text{total plant mass}} \times \text{graminoid } \delta^{15}N\right) + \left(\frac{\text{forb mass}}{\text{total plant mass}} \times \text{forb } \delta^{15}N\right).$$

Arthropods were sorted, dried at 60°C, ground and weighed to the nearest 0.001 mg. We analysed arthropods for $\delta^{13}C$ and $\delta^{15}N$ at the UC Davis Stable Isotope Facility and the Environmental Stable Isotope Lab at the University of Oklahoma. The relative trophic position of each of the four taxa was calculated as: $\lambda + \frac{\left(\delta^{15}N_{arthropod} - \delta^{15}N_{base}\right)}{\Delta N}$. We used λ equal to 1, representing autotrophs. We directly measured $\delta^{15}N_{arthropod}$, and $\delta^{15}N_{base}$ was calculated as the average vegetation $\delta^{15}N$ value at each study site (see above). Lastly, ΔN represents the standard enrichment per trophic level of 3.4‰ (Kelly, 2000; Post, 2002; Roeder & Kaspari, 2017).

2.4 | Statistical analyses

As we expected both direct and indirect effects of climate, plant biomass and plant quality on consumer taxa biomass, we used a piecewise structural equation model (*SEM*) to identify effect pathways. Unlike traditional *SEM*, piecewise *SEM* does not assume complete independence of observations, is less constrained by sample size, and is evaluated using a Fisher's *C* statistic and associated *p* value with non-significant *p* values indicating a good model fit (Lefcheck, 2016; Shipley, 2013). We developed an a priori model comprised of the effects of climate (mean annual temperature and cumulative annual precipitation) on plants (biomass and plant quality), their effects on biomass of plant consumer taxa (Auchenorrhyncha, grasshoppers and katydids), the effects of plant consumer biomass on omnivore and predator (katydid and spider) biomass, and effects of omnivore (katydid) on predator (spider) biomass. We additionally included in our model a direct effect of temperature on biomass of arthropod taxa as temperature directly affects metabolism (Gillooly, Brown, West, Savage, & Charnov, 2001). No direct links between precipitation and arthropod taxa were included as we predicted only indirect effects through plant variables and a post hoc model including direct effects of precipitation found no significant direct paths. To quantify plant quality, we conducted a principle component analysis of plant chemistry and used the first axis scores as a plant quality index; the first axis scores are positively correlated with plant concentrations of nitrogen, potassium, magnesium and calcium (Table S3). Biomass of the four consumer taxa (mg) and plant biomass (g) were log transformed to meet normal distribution assumptions. Variance inflation factors (VIF) were calculated for environmental drivers in the final model; no evidence of variance inflation was found (all VIF < 3.5) (Gross, 2003). Piecewise *SEM* was conducted using the piecewiseSEM package (Lefcheck, 2016) in Program R ver. 3.6.1 (R Development Core Team, 2019). To further visualize shifts in the biomass of arthropod taxa across ecological gradients, we use linear regression and plots of biomass of these four focal taxa change over total invertebrate biomass, plant biomass, and temperature and changes in spider biomass over biomass of Auchenorrhyncha, grasshoppers and katydids.

To test the EEH prediction that herbivore biomass is determined by the interaction of predator and primary producer biomasses, we used linear models to test for the interaction of local above-ground plant biomass and spider biomass (continuous) on the biomass of

both herbivore groups (Auchenorrhyncha and grasshoppers). These tests could not be incorporated into one piecewise *SEM* model as they would create a circular path and thus violate directionality assumptions. To visualize results, we categorized sites as 'low spider' (<the median of 20 mg mean spider biomass/sample, *n* = 27) and 'high spider' (≥the median of 20 mg mean spider biomass/sample, *n* = 27). We then used linear regression to examine how Auchenorrhyncha and grasshopper biomass varied with plant biomass when spider biomass is low and when spider biomass is high to test the prediction that herbivore biomass should increase with plant biomass when spider biomass is low but not when spider biomass is high. To assess shifts in resource use, we examined individual linear responses of trophic signal of the four invertebrate taxa across plant biomass. To further assess indirect effects and the EEH prediction of alternating top-down and bottom-up limitation, we include two additional SEMs, one of the high spider sites and one of the low spider sites.

3 | RESULTS

We collected 8,809 arthropods in our four focal taxa (4,634 Auchenorrhyncha, 1,298 grasshoppers, 1,206 katydids and 1,671 spiders) across the 54 grasslands. Total arthropod biomass varied 18-fold across the 54 sites (from 75 mg/sample in central FL to 1,385 mg/sample in a CO meadow, CV = 75). The biomass of all four groups also varied considerably: Auchenorrhyncha (0.25–715.5 mg/sample, CV = 240), grasshoppers (0–665.8 mg/sample, CV = 127), katydids (0–511.8 mg/sample, CV = 173) and spiders (0–100 mg/sample, CV = 85). Orthopterans had the highest biomass, with grasshoppers (the chewing herbivores) yielding a mean dry mass of 29.65 mg ± 4.5 *SE*, the omnivorous katydids with 24.39 mg ± 4.2 *SE*. The predatory spiders had a mean dry mass of 14.95 mg ± 8.4 *SE*, and Auchenorrhyncha (the sucking herbivores) had the lowest average biomass per individual with 9.71 mg ± 4.0 *SE*. As expected, spiders had the highest trophic position, Auchenorrhyncha and grasshoppers had the lowest, and katydid trophic position was intermediate (Figure S1). The spiders, which made up ~9% of the total invertebrate biomass at a site, was the only focal taxon that did not increase with total invertebrate biomass (i.e. the four focal taxa plus 'other', Figure 1a). Additionally, spider biomass tended to increase with prey biomass but the linear relationship was not significant (Figure S2).

Two bottom-up hypotheses (H1, H2) predict that consumer biomass tracks plant quantity and quality. Our a priori piecewise
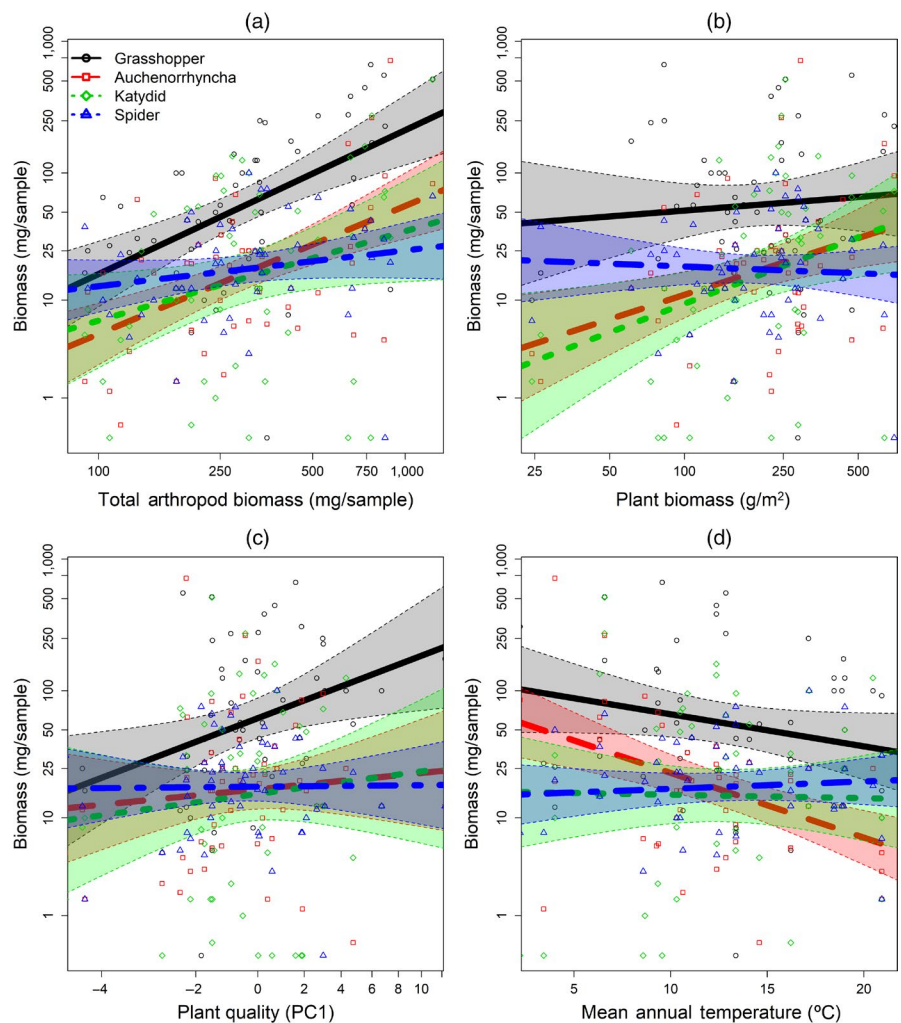

FIGURE 1 Auchenorrhyncha ($F_{1,52}$ = 22.1, R^2 = 0.3, *p* < 0.001), grasshopper ($F_{1,52}$ = 24.8, R^2 = 0.32, *p* < 0.001) and katydid ($F_{1,52}$ = 4.6, R^2 = 0.08, *p* = 0.04), but not spider (*p* = 0.13) biomass increased with total invertebrate biomass (a). Auchenorrhyncha ($F_{1,52}$ = 9.1, R^2 = 0.15, *p* = 0.004) and katydid ($F_{1,52}$ = 6.7, R^2 = 0.11, *p* = 0.01) but not grasshopper (*p* = 0.54) nor spider (*p* = 0.65) biomass increased with total plant biomass (b). Grasshopper ($F_{1,52}$ = 7, R^2 = 0.12, *p* = 0.01) but not Auchenorrhyncha (*p* = 0.49), katydid (*p* = 0.47), nor spider (*p* = 0.93) biomass increased with plant quality as measured by the first axis of a PCA of plant chemistry (c). Auchenorrhyncha ($F_{1,52}$ = 19.5, R^2 = 0.27, *p* < 0.001) but not grasshopper (*p* = 0.08), katydid (*p* = 0.88), nor spider (*p* = 0.56) biomass decreased with mean annual temperature (d)

SEM had a good fit (Fisher's *C* = 13.34, *k* = 16, *p* = 0.647) and accounted for between 10% (spiders) and 29% (Auchenorrhyncha) of the variation in arthropod taxa biomass (Figure 2). Consistent with
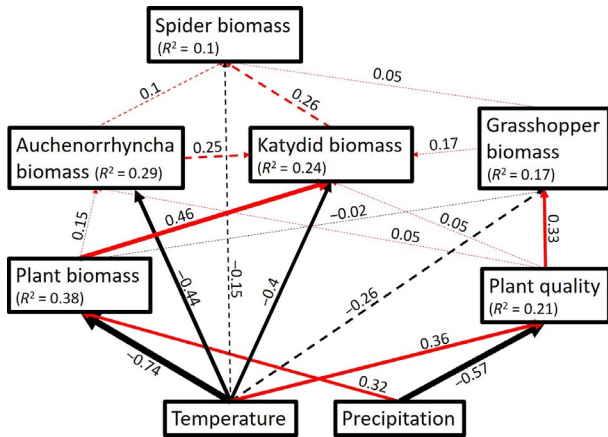

FIGURE 2 Piecewise structural equation model showing direct and indirect drivers of biomass of the four focal taxa. Replication of all variables was at the site level (*n* = 54 sites). Biomass of spiders, katydids, grasshoppers and Auchenorrhyncha is calculated as average mg/sample. Plant biomass is calculated as g/m^2. Plant quality is the first PCA axis of plant chemistry and was positively correlated with many limiting nutrients including nitrogen, potassium, magnesium and calcium (Table S3). The proportion of variance in each predicted variable is given as the R^2 value and standardized path estimates are provided next to each path. Line thickness indicates size of path estimates. Red arrows indicate positive and black arrows indicate negative relationships. Solid lines indicate significant relationships, whereas dashed lines indicate non-significant relationships. Model estimates, standard errors and *p* values are provided in Table S2

H1, plant biomass strongly increased katydid biomass and a weaker positive effect on Auchenorrhyncha biomass (Figures 1b and 2). Consistent with H2, plant quality had the strongest positive effect on grasshopper biomass (Figures 1c and 2). The third bottom-up hypothesis (H3) predicted increased biomass at higher temperatures. After taking into account other relationships between the variables in the *SEM*, gradients of higher mean annual temperature directly decreased Auchenorrhyncha and katydid biomass (Figures 1d and 2).

The EEH hypothesis (H4) predicts that top-down and bottom-up regulation should alternate between trophic levels and 'flip' along a plant productivity gradient. Consistent with the predicted trophic 'flip', the slopes of Auchenorrhyncha and grasshopper responses to plant biomass were steeper in low spider sites compared to high spider sites (Figure 3). The interaction term of plant biomass and spider biomass was significant for grasshopper biomass (Table 2) and trended in the predicted direction for Auchenorrhyncha biomass (Table 3). While few relationships were significant likely in part due to low sample size, the *SEM* of the low spider sites (Figure S3; Table S4) had more positive and strong estimates for relationships between plant variables and herbivore taxa biomass than the *SEM* of the high spider sites (Figure S3; Table S4).

Finally, the trophic positions of the four focal taxa varied systematically with plant biomass, but in different ways. Trophic positions increased with plant biomass for the two Orthoptera, grasshoppers and katydids (Figure 4): these taxa were more carnivorous in environments that are more productive. In contrast, there was no such gradient for the Auchenorrhyncha or spiders (Figure 4).
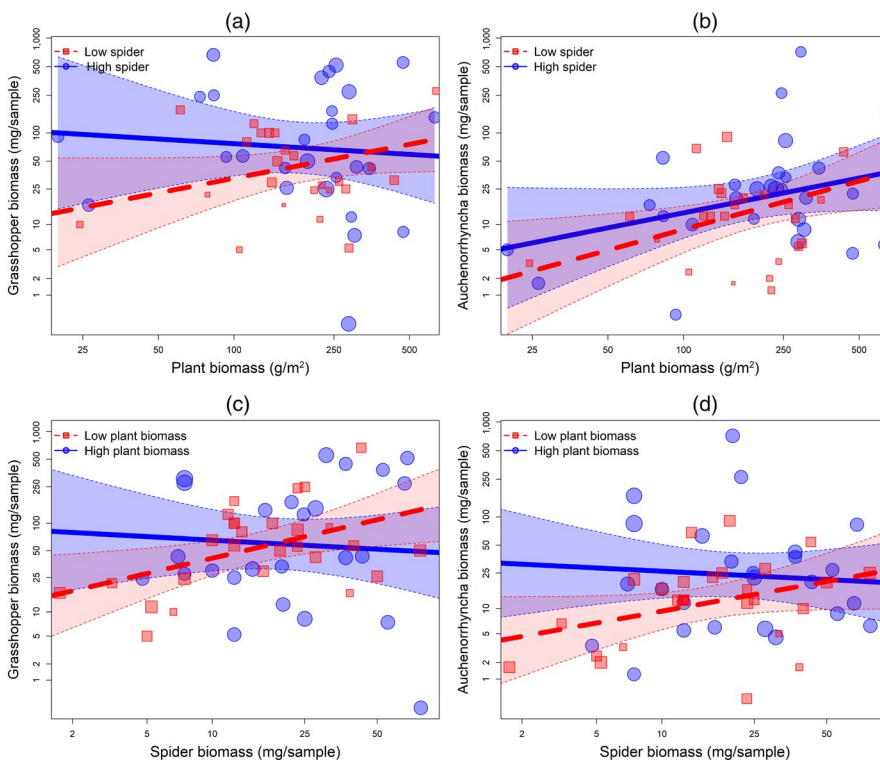

FIGURE 3 Grasshopper biomass did not change across plant biomass for both low ($F_{1,25}$ = 3.6, R^2 = 0.13, *p* = 0.068) and high spider ($F_{1,25}$ = 0.2, R^2 = 0.01, *p* = 0.67) sites (a). Auchenorrhyncha biomass increased with plant biomass for low ($F_{1,25}$ = 6.8, R^2 = 0.21, *p* = 0.015) but not high spider ($F_{1,25}$ = 3, R^2 = 0.11, *p* = 0.091) sites (b). Grasshopper biomass increased with spider biomass in low ($F_{1,25}$ = 7, R^2 = 0.22, *p* = 0.014) but not high plant biomass ($F_{1,25}$ = 0.22, R^2 = 0.009, *p* = 0.65) sites (c). Auchenorrhyncha biomass did not change with spider biomass in low ($F_{1,25}$ = 3.6, R^2 = 0.13, *p* = 0.069) or high plant biomass ($F_{1,25}$ = 0.28, R^2 = 0.009, *p* = 0.63) sites (d). Point size increases with spider biomass (a & b) and plant biomass (c & d)

TABLE 2 The interaction between plant and spider biomass had a significant effect on grasshopper biomass (Figure 3a, c)

	df	SS	F	p
Plant biomass	1	0.13	0.42	0.52
Spider biomass	1	0.22	0.7	0.4
Plant × Araneae biomass	1	1.72	5.47	0.02
Residuals	50	15.71		

TABLE 3 Auchenorrhyncha biomass responses to plant and spider biomass. Auchenorrhyncha biomass increased with plant biomass, while the effect of spider biomass exhibited a trend to dampen this increase (Figure 3b). The relationship between spiders and Auchenorrhyncha switched from positive to flat from sites with low to high plant biomass, respectively (Figure 3d)

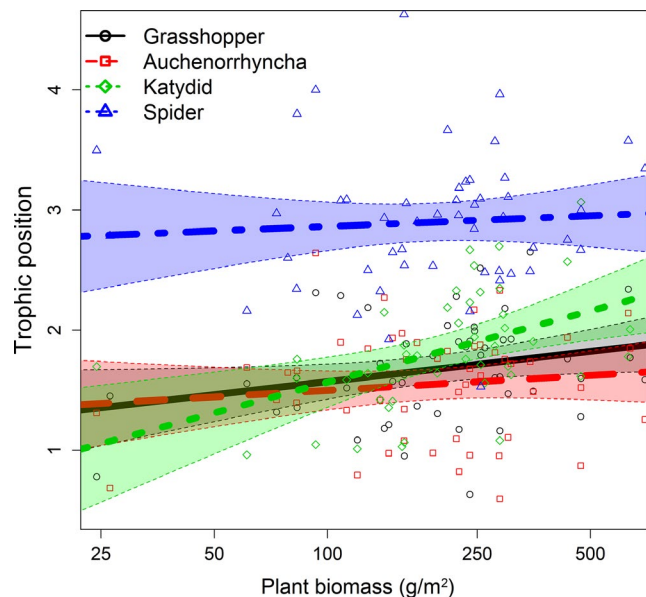|	df	SS	F	p
Plant biomass	1	2.28	9.51	0.003
Spider biomass	1	0.27	1.13	0.29
Plant × Araneae biomass	1	0.73	3.06	0.087
Residuals	50	11.96		

FIGURE 4 Trophic positions increased with plant biomass for grasshoppers ($F_{1,50}$ = 4.6, R^2 = 0.08, p = 0.04) and katydids ($F_{1,41}$ = 11.2, R^2 = 0.21, p = 0.002). Auchenorrhyncha ($F_{1,49}$ = 0.9, R^2 = 0.02, p = 0.34) and spiders ($F_{1,50}$ = 0.2, R^2 = 0.01, p = 0.60) trophic positions had no relationship with standing plant biomass

4 | DISCUSSION

Across North American grasslands, invertebrate biomass varied 18-fold, and all four hypotheses had some predictions supported to account for this variation. Consistent with a bottom-up effect of plant production, both Auchenorrhyncha and katydids increased with plant biomass. The plant quality hypothesis was supported by increasing grasshopper biomass with plant quality. Climate had indirect effects on invertebrate biomass through effects on plants and temperature directly decreased Auchenorrhyncha and katydids. Consistent with the trophic 'flip' predicted by the EEH, herbivores increased faster with plant biomass when spider biomass was low than when spider biomass was high (Letnic & Ripple, 2017; Oksanen et al., 1981). However, spider biomass failed to increase with total invertebrate biomass, and instead acted as if constrained, potentially by their own predators (Sanders & Platner, 2007; Wise, 1993).

4.1 | The geography of trophic biomass

We found evidence that plant biomass controls arthropod biomass. Plant biomass is a useful proxy for primary productivity (Begon, Harper, & Townsend, 1986; although see: Bardgett & Wardle, 2003). This grounding of large-scale gradients of terrestrial consumer biomass in measures of energy availability supports the 'plants have primacy' school of food web ecology (Power, 1992) and is consistent with an energetic approach to trophic ecology (HSS, Kaspari, 2004; Oksanen et al., 1981). This bottom-up underpinning in a well-replicated study of 54 grasslands allows us to detect perhaps our most notable result for trophic ecology: an indication of top-down limitation in systems with higher biomass of spiders, an important primary predator in grassland ecosystems (Barton & Schmitz, 2009; Danner & Joern, 2003).

Spiders failed to track the biomass of insects across the 54 grasslands. One hypothesis is that spiders, which are high in protein and micronutrients (Greenstone, 1979), are themselves constrained by predators via cannibalism and territoriality (Arditi & Ginzburg, 1989; Beckmann & Berger, 2003; Getz, 1984; Tallian et al., 2017), or predation (Purcell & Avilés, 2008). A secondary complementary hypothesis is that the relatively low metabolic rates of spiders (Anderson, 1970) allow them to burn less energy even at warmer temperatures but also allow them to maintain relatively high biomass with few available prey.

Plant quality, the nutrient content per gram of plant tissue, can also constrain insect biomass in grasslands, as revealed by experimental pulse experiments (Gruner & Taylor, 2006; Kaspari, Roeder, Benson, Weiser, & Sanders, 2016; Lind et al., 2017; Welti, Sanders, Beurs, & Kaspari, 2019). Our study, which relies on responses to natural variation in nutrient concentrations, may underestimate nutrient effects relative to experimental additions (Welti, Sanders, et al., 2019), as specific stoichiometric ratios are likely important for biomass accumulation for a given taxon and site (Moe et al., 2005). Nonetheless, grasshopper biomass increased with our index of plant quality, especially in sites with low spider biomass, suggesting a bottom-up nutrient limitation. This is consistent with previous work showing grasshopper abundances increase along a gradient of high biomass tallgrass prairies to high nutrient shortgrass prairies (Craig, Bock, Bennett, & Bock, 1999). Plant quality is likely a better predictor of grasshopper biomass as grasshoppers consume leaf tissue, whereas Auchenorrhyncha are

sap-suckers, and sap contains low proportions of plant macronutrients. Auchenorrhyncha often depend on symbiotic microorganisms to provide them with essential amino acids (McCutcheon & Moran, 2012) and thus their abundances may be less likely to reflect plant quality. Moreover, if plants invest in physical and chemical defences to defend investments in N, P and K, this may further degrade any relationship between plant quality and the abundance of generalist herbivores (Hunter, 2001; Rzanny, Kuu, & Voigt, 2013).

4.2 | The geography of trophic position

Trophic position varied systematically across the 54 grasslands for two of the four taxa. Contrary to EEH, spider trophic position did not increase with plant biomass: grasslands with more plant biomass did not yield longer food chain lengths. Our failure to find an increase in spider biomass with plant biomass suggests that spiders do not generally function as apex predators in these systems and are themselves constrained by higher trophic levels.

However, the omnivorous katydids, and to a lesser extent, the chewing herbivores, grasshoppers, had trophic positions that increased with plant biomass. Auchenorrhyncha, by contrast did not. We suggest that one reason for this dietary flexibility is the chewing mandibles of the Orthoptera, which can easily partake of both plants and meat (Richardson, Reagel, Mitchell, & Whitman, 2012; Simpson, Sword, Lorch, & Couzin, 2006) while the piercing stylet of Auchenorrhyncha is restricted to plant fluids. The switch to a diet with more meat when plant biomass increases likely has two complementary causes. More plants equate to more carbohydrate availability, increasing the relative value of nitrogen-rich animal tissue (Yanoviak & Kaspari, 2000). A simultaneous increase in animal tissue availability, as arthropod biomass tracked plant biomass (Simpson et al., 2006; Whitman & Richardson, 2010), means animal tissue is a ready source nitrogen in grasslands with high plant productivity. This is the second study we know of that has explored the origin and geographical variation in omnivory; Clay et al. (2017) found that sodium shortfall, but not productivity, best predicted the degree of omnivory in ant communities.

4.3 | Caveats and next steps

This study uses the comparative method. We infer process by correlating predicted food web properties to environmental drivers. Moreover, we leave some potential drivers of insect abundance out, including detailed data on plant composition and diversity as well as the actions of possible higher trophic levels: predators/parasitoids of spiders and predators/parasitoids of *that* trophic level. Experiments are the obvious next step to further elucidate the prevalence of top-down versus bottom-up control on productivity of trophic levels (Ford & Goheen, 2015; Letourneau & Dyer, 1998). Interestingly, shifts in biomass distributions across primary productivity gradients often follow patterns predicted by bottom-up limitation while

experimental studies are more likely to support top-down control (Chase et al., 2000; Stoner et al., 2018). This may be due to the difficulty of detecting top-down control in complex food webs compared to the simplicity of experimental designs (e.g. include or exclude a predator from a mesocosm) (Kaunzinger & Morin, 1998). Additionally, experimental studies tend to occur at smaller scales than those across ecological gradients and both spatial and temporal scales are expected to affect the strength of bottom-up and top-down limitation of consumer productivity (Letnic et al., 2011).

Arthropods comprise half of global animal biomass (Bar-On, Phillips, & Milo, 2018) and are dominant competitors for plant biomass with other consumer groups. Grasslands are widespread, covering *c.* 40% of Earth's land surface and in modified form, provide much of the food for human populations (Hoekstra, Boucher, Ricketts, & Roberts, 2005). Our evidence for shifts from bottom-up control to top-down control is thus a potential mechanism accounting for the variation in herbivore damage found along a primary productivity gradient (Schädler et al., 2003). Moreover, given the recent reports of declines in arthropod biomass (i.e. Hallmann et al., 2017; Wepprich, Adrion, Riles, Wiedmann, & Haddad, 2019), understanding the ongoing regulation of insect biomass at continental scales takes on new importance.

AUTHORS' CONTRIBUTIONS
M.K., E.A.R.W. and N.J.S. designed the study; E.A.R.W., M.K. and N.J.S. conducted fieldwork; E.A.R.W. processed plant and arthropod samples and wrote the first draft of the manuscript; R.M.P. conducted stable isotope analyses; K.M.d.B. collected climate data; A grant awarded to M.K. and N.J.S. supported this study. All authors discussed results and substantially contributed to manuscript revisions.

DATA AVAILABILITY STATEMENT
Arthropod biomass, stable isotope and environmental data are deposited in the Dryad Digital Repository: https://doi.org/10.5061/dryad.zw3r2284z (Welti, Prather, Sanders, Beurs, & Kaspari, 2020).

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REFERENCES
Anderson, J. F. (1970). Metabolic rates of spiders. *Comparative Biochemistry and Physiology*, *33*, 51–72. https://doi.org/10.1016/0010-406X(70)90483-4

Andrew, N. R., & Hughes, L. (2005). Arthropod community structure along a latitudinal gradient: Implications for future impacts of climate change. *Austral Ecology*, *30*, 281–297. https://doi.org/10.1111/j.1442-9993.2005.01464.x

Arditi, R., & Ginzburg, L. R. (1989). Coupling in predator-prey dynamics: Ratio dependence. *Journal of Theoretical Biology*, *139*, 311–326. https://doi.org/10.1016/S0022-5193(89)80211-5

Atkinson, D. (1995). Effects of temperature on the size of aquatic ectotherms – Exceptions to the general rule. *Journal of Thermal Biology*, *20*, 61–74. https://doi.org/10.1016/0306-4565(94)00028-H

Bardgett, R. D., & Wardle, D. A. (2003). Herbivore-mediated linkages between aboveground and belowground communities. *Ecology*, *84*, 2258–2268.

Bar-On, Y. M., Phillips, R., & Milo, R. (2018). The biomass distribution on Earth. *Proceedings of the National Academy of Sciences of the United States of America*, *115*, 6506–6511. https://doi.org/10.1073/pnas.1711842115

Barton, B. T., & Schmitz, O. J. (2009). Experimental warming transforms multiple predator effects in a grassland food web. *Ecology Letters*, *12*, 1317–1325. https://doi.org/10.1111/j.1461-0248.2009.01386.x

Beckmann, J. P., & Berger, J. (2003). Using black bears to test ideal-free distribution models experimentally. *Journal of Mammalogy*, *84*, 594–606. https://doi.org/10.1644/1545-1542(2003)084<0594:UBBTTI>2.0.CO;2

Begon, M., Harper, J. L., & Townsend, C. R. (1986). *Ecology: Individuals, populations and communities*. Oxford, UK: Blackwell Scientific Publications.

Brown, J. H. (2014). Why are there so many species in the tropics? *Journal of Biogeography*, *41*, 8–22. https://doi.org/10.1111/jbi.12228

Chase, J. M. (1996). Abiotic controls of trophic cascades in a simple grassland food chain. *Oikos*, *77*, 495–506. https://doi.org/10.2307/3545939

Chase, J. M., Leibold, M. A., Downing, A. L., & Shurin, J. B. (2000). The effects of productivity, herbivory, and plant species turnover in grassland food webs. *Ecology*, *81*, 2485–2497. https://doi.org/10.1890/0012-9658(2000)081[2485:TEOPHA]2.0.CO;2

Choquenot, D., & Forsyth, D. M. (2013). Exploitation ecosystems and trophic cascades in non-equilibrium systems: Pasture - red kangaroo - dingo interactions in arid Australia. *Oikos*, *122*, 1292–1306. https://doi.org/10.1111/j.1600-0706.2012.20976.x

Craig, D. P., Bock, C. E., Bennett, B. C., & Bock, J. H. (1999). Habitat relationships among grasshoppers (Orthoptera: Acrididae) at the western limit of the Great Plains in Colorado. *American Midland Naturalist*, *142*, 314–327. https://doi.org/10.1674/0003-0031(1999)142[0314:HRAGOA]2.0.CO;2

Daly, C., Halbleib, M., Smith, J. I., Gibson, W. P., Doggett, M. K., Taylor, G. H., … Pasteris, P. P. (2008). Physiographically sensitive mapping of climatological temperature and precipitation across the conterminous United States. *International Journal of Climatology*, *28*, 2031–2064. https://doi.org/10.1002/joc.1688

Danner, B. J., & Joern, A. (2003). Resource-mediated impact of spider predation risk on performance in the grasshopper *Ageneotettix deorum* (Orthoptera: Acrididae). *Oecologia*, *137*, 352–359.

Ford, A. T., & Goheen, J. R. (2015). Trophic cascades by large carnivores: A case for strong inference and mechanism. *Trends in Ecology & Evolution*, *30*, 725–735.

Fretwell, S. D., & Lucas, H. L. (1970). On territorial behavior and other factors influencing habitat distribution in birds. *Acta Biotheoretica*, *19*, 16–36.

Getz, W. M. (1984). Population dynamics: A per-capita resource approach. *Journal of Theoretical Biology*, *108*, 623–643. https://doi.org/10.1016/S0022-5193(84)80082-X

Gillooly, J. F., Brown, J. H., West, G. B., Savage, V. M., & Charnov, E. L. (2001). Effects of size and temperature on metabolic rate. *Science*, *293*, 2248–2251. https://doi.org/10.1126/science.1061967

Greenstone, M. H. (1979). Spider feeding behaviour optimises dietary essential amino acid composition. *Nature*, *282*, 501–503. https://doi.org/10.1038/282501a0

Gross, J. (2003). Variation inflation factors. *R News*, *3*, 13–15.

Gruner, D. S., & Taylor, A. D. (2006). Richness and species composition of arboreal arthropods affected by nutrients and predators: A press experiment. *Oecologia*, *147*, 714–724. https://doi.org/10.1007/s00442-005-0337-4

Hairston, N. G., Smith, F. E., & Slobodkin, L. B. (1960). Community structure, population control, and competition. *The American Naturalist*, *94*, 421–425. https://doi.org/10.1086/282146

Hallmann, C. A., Sorg, M., Jongejans, E., Siepel, H., Hofland, N., Schwan, H., … de Kroon, H. (2017). More than 75 percent decline over 27 years in total flying insect biomass in protected areas. *PLoS ONE*, *12*, e0185809.

Hatton, I. A., McCann, K. S., Fryxell, J. M., Davies, T. J., Smerlak, M., Sinclair, A. R. E., & Loreau, M. (2015). The predator–prey power law: Biomass scaling across terrestrial and aquatic biomes. *Science*, *349*, aac6284.

Hoekstra, J. M., Boucher, T. M., Ricketts, T. H., & Roberts, C. (2005). Confronting a biome crisis: Global disparities of habitat loss and protection. *Ecology Letters*, *8*, 23–29. https://doi.org/10.1111/j.1461-0248.2004.00686.x

Hunter, M. D. (2001). Multiple approaches to estimating the relative importance of top-down and bottom-up forces on insect populations: Experiments, life tables, and time-series analysis. *Basic and Applied Ecology*, *2*, 295–309. https://doi.org/10.1078/1439-1791-00068

Jonas, J. L., Wolesensky, W., & Joern, A. (2015). Weather affects grasshopper population dynamics in continental grassland over annual and decadal periods. *Rangeland Ecology & Management*, *68*, 29–39. https://doi.org/10.1016/j.rama.2014.12.011

Kaspari, M. (2001). Taxonomic level, trophic biology, and the regulation of local abundance. *Global Ecology and Biogeography*, *10*, 229–244. https://doi.org/10.1046/j.1466-822X.2001.00214.x

Kaspari, M. (2004). Using the metabolic theory of ecology to predict global patterns of abundance. *Ecology*, *85*, 1800–1802. https://doi.org/10.1890/03-0682

Kaspari, M., Alonso, L., & O'Donnell, S. (2000). Three energy variables predict ant abundance at a geographic scale. *Proceedings of the Royal Society London B*, *267*, 485–490.

Kaspari, M., Roeder, K. A., Benson, B., Weiser, M. D., & Sanders, N. (2016). Sodium co-limits and catalyzes macronutrients in a prairie food web. *Ecology*, *98*, 315–320. https://doi.org/10.1002/ecy.1677

Kaunzinger, C. M. K., & Morin, P. J. (1998). Productivity controls food-chain properties in microbial communities. *Nature*, *395*, 495–497. https://doi.org/10.1038/26741

Kelly, J. F. (2000). Stable isotopes of carbon and nitrogen in the study of avian and mammalian trophic ecology. *Canadian Journal of Zoology*, *78*, 1–27. https://doi.org/10.1139/z99-165

Lefcheck, J. S. (2016). PIECEWISESEM: Piecewise structural equation modelling in R for ecology, evolution, and systematics. *Methods in Ecology and Evolution*, *7*, 573–579.

Letnic, M., & Ripple, W. J. (2017). Large-scale responses of herbivore prey to canid predators and primary productivity. *Global Ecology and Biogeography*, *26*, 860–866. https://doi.org/10.1111/geb.12593

Letnic, M., Story, P., Story, G., Field, J., Brown, O., & Dickman, C. R. (2011). Resource pulses, switching trophic control, and the dynamics of small mammal assemblages in arid Australia. *Journal of Mammalogy*, *92*, 1210–1222. https://doi.org/10.1644/10-MAMM-S-229.1

Letourneau, D. K., & Dyer, L. A. (1998). Experimental manipulations in lowland tropical forest demonstrate top-down cascades through four trophic levels. *Ecology*, *79*, 1678–1687.

Lind, E. M., La Pierre, K. J., Seabloom, E. W., Alberti, J., Iribarne, O., Firn, J., … Borer, E. T. (2017). Increased grassland arthropod production with mammalian herbivory and eutrophication: A test of mediation pathways. *Ecology*, *98*, 3022–3033.

Lindeman, R. L. (1942). The trophic-dynamic aspect of ecology. *Ecology*, *23*, 399–418.

MacArthur, R. H. (1972). *Geographical ecology: Patterns in the distribution of species*. Manhattan, NY: Harper and Row.

McCutcheon, J. P., & Moran, N. A. (2012). Extreme genome reduction in symbiotic bacteria. *Nature Reviews Microbiology*, 10, 13–26. https://doi.org/10.1038/nrmicro2670

McNaughton, S. J., Oesterheld, M., Frank, D. A., & Williams, K. J. (1989). Ecosystem-level patterns of primary productivity and herbivore in terrestrial habitats. *Nature*, 341, 142–144.

Moe, S. J., Stelzer, R. S., Forman, M. R., Harpole, W. S., Daufresne, T., & Yoshida, T. (2005). Recent advances in ecological stoichiometry: Insights for population and community ecology. *Oikos*, 109, 29–39. https://doi.org/10.1111/j.0030-1299.2005.14056.x

Oksanen, L., Fretwell, S. D., Arruda, J., & Niemela, P. (1981). Exploitation ecosystems in gradients of primary productivity. *The American Naturalist*, 118, 240–261. https://doi.org/10.1086/283817

Post, D. M. (2002). Using stable isotopes to estimate trophic position: Models, methods, and assumptions. *Ecology*, 83, 703–718. https://doi.org/10.1890/0012-9658(2002)083[0703:USITET]2.0.CO;2

Power, M. E. (1992). Top-down and bottom-up forces in food webs: Do plants have primacy? *Ecology*, 73, 733–746. https://doi.org/10.2307/1940153

Purcell, J., & Avilés, L. (2008). Gradients of precipitation and ant abundance may contribute to the altitudinal range limit of subsocial spiders: Insights from a transplant experiment. *Proceedings of the Royal Society B: Biological Sciences*, 275, 2617–2625.

R Development Core Team. (2019). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.

Richardson, M. L., Reagel, P. F., Mitchell, R. F., & Whitman, D. W. (2012). Opportunistic carnivory by *Romalea microptera* (Orthoptera: Acrididae). *Annals of the Entomological Society of America*, 105, 28–35. https://doi.org/10.1603/AN11057

Roeder, K. A., & Kaspari, M. (2017). From cryptic herbivore to predator: Stable isotopes reveal consistent variability in trophic levels in an ant population. *Ecology*, 98, 297–303. https://doi.org/10.1002/ecy.1641

Rzanny, M., Kuu, A., & Voigt, W. (2013). Bottom-up and top-down forces structuring consumer communities in an experimental grassland. *Oikos*, 122, 967–976. https://doi.org/10.1111/j.1600-0706.2012.00114.x

Sanders, D., & Platner, C. (2007). Intraguild interactions between spiders and ants and top-down control in a grassland food web. *Oecologia*, 150, 611–624. https://doi.org/10.1007/s00442-006-0538-5

Schädler, M., Jung, G., Auge, H., & Brandl, R. (2003). Does the Fretwell–Oksanen model apply to invertebrates? *Oikos*, 100, 203–207. https://doi.org/10.1034/j.1600-0706.2003.11821.x

Shipley, B. (2013). The AIC model selection method applied to path analytic models compared using a d-separation test. *Ecology*, 94, 560–564.

Simpson, S. J., Sword, G. A., Lorch, P. D., & Couzin, I. D. (2006). Cannibal crickets on a forced march for protein and salt. *Proceedings of the National Academy of Sciences of the United States of America*, 103, 4152–5156. https://doi.org/10.1073/pnas.0508915103

Stoner, D. C., Sexton, J. O., Choate, D. M., Nagol, J., Bernales, H. H., Sims, S. A., … Edwards, T. C. (2018). Climatically driven changes in primary production propagate through trophic levels. *Global Change Biology*, 24, 4453–4463. https://doi.org/10.1111/gcb.14364

Tallian, A., Smith, D. W., Stahler, D. R., Metz, M. C., Wallen, R. L., Geremia, C., … MacNulty, D. R. (2017). Predator foraging response to a resurgent dangerous prey. *Functional Ecology*, 31, 1418–1429. https://doi.org/10.1111/1365-2435.12866

Welti, E. A. R., Prather, R. M., Sanders, N. J., de Beurs, K. M., & Kaspari, M. (2020). Data from: Bottom-up when it is not top-down: Predators and plants control biomass of grassland arthropods. *Dryad Digital Repository*, https://doi.org/10.5061/dryad.zw3r2284z

Welti, E. A. R., Qiu, F., Tetreault, H. M., Ungerer, M., Blair, J., & Joern, A. (2019). Fire, grazing and climate shape plant-grasshopper interactions in a tallgrass prairie. *Functional Ecology*, 33, 735–745. https://doi.org/10.1111/1365-2435.13272

Welti, E. A. R., Sanders, N. J., de Beurs, K. M., & Kaspari, M. (2019). A distributed experiment demonstrates widespread sodium limitation in grassland food webs. *Ecology*, 100, e02600. https://doi.org/10.1002/ecy.2600

Wepprich, T., Adrion, J. R., Riles, L., Wiedmann, J., & Haddad, N. M. (2019). Butterfly abundance declines over 20 years of systematic monitoring in Ohio, USA. *PLoS ONE*, 14, e0216270. https://doi.org/10.1371/journal.pone.0216270

Whitman, D. W., & Richardson, M. L. (2010). Necrophagy in grasshoppers: *Taeniopoda eques* feeds on mammal carrion. *Journal of Orthoptera Research*, 19, 377–381.

Whittaker, R. H. (1967). Gradient analysis of vegetation. *Biological Reviews*, 49, 207–264. https://doi.org/10.1111/j.1469-185X.1967.tb01419.x

Wise, D. H. (1993). *Spiders in ecological webs*. Cambridge, UK: Cambridge University Press.

Yanoviak, S. P., & Kaspari, M. (2000). Community structure and the habitat templet: Ants in the tropical forest canopy and litter. *Oikos*, 89, 259–266. https://doi.org/10.1034/j.1600-0706.2000.890206.x

SUPPORTING INFORMATION

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