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META-ANALYSIS

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Micronutrients enhance macronutrient effects in a meta-analysis of grassland arthropod abundance

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Abstract

Aim: Ongoing alterations to Earth's biogeochemical cycles (e.g., via fertilization, burning of fossil fuels, and pollution) are expected to impact plants, plant consumers and all subsequent trophic levels. While fertilization experiments often reveal arthropod nutrient limitation by nitrogen and phosphorus via effects on plant nutrient density and biomass, these macronutrients are only two of many nutrients important to arthropod fitness. Micronutrients are key to osmoregulation and enzyme function and can interact synergistically with macronutrients to shape the geography of arthropod abundance. We examine arthropod response to macro- and micronutrient fertilization as a function of nutrient type, application amount, duration, frequency, and plant responses to fertilization with the goal of addressing how ongoing alterations to biogeochemical cycles will shape future grassland food webs.

Location: Global.

Time period: 1987–2018.

Major taxa studied: Invertebrates.

Methods: We compiled a database of 62 studies to test the response of six arthropod trophic groups to multiple fertilizer types (compositions of varying macro- and micronutrients), quantities, application frequencies, and application durations. Additionally, we examined the role of plant nutrient content and biomass in mediating arthropod responses to fertilization.

Results: Micronutrients applied alone had no effects on plant biomass or arthropod abundance. However, when added with macronutrients, micronutrients amplified the effect of N, P and K in promoting arthropod abundance, a synergy that did not affect plant biomass. Micronutrients thus catalysed the ability of macronutrients to promote arthropod abundance across all guilds studied.

Main conclusions: In grasslands, the rules governing the abundance of autotrophs and their consumers appear to differ fundamentally in their response to Earth's changing biogeochemistry. By revealing the importance of micronutrients for arthropods using a global dataset, we highlight a stoichiometric mismatch between limits of plants and arthropods for metal cations whose biogeochemistry, along with N and P, are being actively rearranged in the Anthropocene.

Rebecca M. Prather and Karen Castillioni should be considered joint first author.

KEYWORDS

eutrophication, fertilizer, herbivore, insect, invertebrate, nitrogen, NPK, nutrient limitation, prairie, trophic

1 | INTRODUCTION

Arthropod abundance exhibits extreme variation across Earth's ecosystems (Kaspari et al., 2000; Lind et al., 2017). One of the important drivers of this variation is the nutrient content of the plants that support consumers (Awmack & Leather, 2002; Joern et al., 2012). Terrestrial nutrient availability continues to be rearranged in the Anthropocene (Steffen et al., 2015), underscoring the need to understand how nutrients shape ecological communities. While the study of plant nutrient limitation has a long history in the field of ecology, there is a comparatively limited understanding of how the abundances of different consumer trophic groups vary across a spectrum of plant productivity and nutrient content.

Grassland plant productivity is commonly constrained by the macronutrients N and P (Elser et al., 2007; Gruner et al., 2008; Harpole et al., 2011; LeBauer & Treseder, 2008; Zheng et al., 2019). Fertilization experiments across 42 globally distributed grasslands revealed nutrient limitation of plant productivity in 31 sites, primarily by N and P, while a combination of K and micronutrients (henceforth +mN) had little effect on productivity (Fay et al., 2015). Nutrients that promote plant production may be passed up through food webs, increasing the abundance of consumers such as herbivores, their predators, and ultimately, detritivores (Welti, Kuczynski, et al., 2020). While micronutrients, defined here as elements rarer in living tissues (Kaspari & Powers, 2016) such as Na, Ca, Cu, Fe, Mg, Mo, S and Zn, are not commonly limiting to plant growth, they are taken up by plants with repercussions for plant consumers.

There are several reasons why consumer responses to nutrient addition may be different from those of the plants they eat. First, consumer nutritional needs differ from plants in that their growth is more constrained by the availability of metals such as Na, Cu and Zn (Kaspari & Powers, 2016). Consumers may track increases in these micronutrients. For example, gradients of foliar Mg and Na in addition to N, P and K predicted the abundance of prairie grasshoppers (Joern et al., 2012; Welti, Roeder, et al., 2020) while foliar Ca, S and N predicted the abundance of arthropods in Neotropical leaf-litter (Kaspari & Yanoviak, 2009). Second, some micronutrients such as Na are only used by plants under deficiency of other micronutrients (Maathuis, 2014), and at high levels can be toxic to plants but promote higher insect herbivory (Borer et al., 2019). Grassland arthropod abundance increases both with experimental fertilization of macronutrients like N and P (Haddad et al., 2000; Lind et al., 2017; Ritchie, 2000), and micronutrient fertilization (C. M. Prather, Laws, et al., 2018; Welti et al., 2019). However, the role micronutrients may play has received comparatively little attention in studies of insect nutrition.

Here we conduct a meta-analysis to explore how fertilization experiments collectively inform the role of nutrients in limiting the abundance of grassland arthropods, a diverse group that significantly contributes to grassland processes and ecosystem function (Belovsky & Slade, 2000; Meyer et al., 2002; Tscharntke & Greiler, 1995; Whiles & Charlton, 2006). We chose grasslands as our focal ecosystem both due to their importance globally, covering *c*. 37% of Earth's terrestrial surface, and for the practical reason that they have been the location of many fertilization experiments examining arthropod responses (White et al., 2000). Our primary goal was to test for the ubiquity of N, P, K and micronutrient limitation – or some combination of the above – on total arthropod abundance and the abundance of six common feeding guilds: chewing herbivores, sucking herbivores, omnivores, predators, pollinators and detritivores. In addition to examining arthropod abundance responses to fertilizer type, we sought to quantify the magnitude of the response to an added nutrient as a function of (a) total application quantity (Boersma & Elser, 2006; Foy et al., 2003), (b) the number of times nutrients were added (Murphy et al., 2012; Yodzis, 1988), and (c) time passed since fertilizer application (Andrey et al., 2014; Isbell et al., 2013). For the subset of studies that reported plant nutrient concentrations and biomass, we analysed how both plant responses to fertilization and underlying environmental gradients of plant productivity and nutrient content mediated arthropod responses to fertilization.

We predict that arthropod responses to fertilizer addition will vary with fertilizer type (Lind et al., 2017). Arthropod abundance may increase with increasing amount and duration of fertilization or, depending on fertilizer type and application, may decrease as nutrient levels exceed arthropod needs (Andrey et al., 2014; Boersma & Elser, 2006; Murphy et al., 2012). We predict that arthropod abundance will increase as plants become more nutrient rich and produce greater mass in response to fertilization (Lind et al., 2017). Additionally, we expect responses to vary with ecological gradients of plant nutrient content and biomass. We predict decreasing arthropod attraction to N fertilization with increasing background levels of plant %N (in control plots) (Anderson et al., 2018). How underlying gradients of plant biomass may mediate arthropod responses to fertilization is less clear. Dependent on aboveground plant productivity, more habitat structure and food could result in increased arthropod abundance (R. M. Prather & Kaspari, 2019); alternatively, additional plant biomass may dilute nutrient concentrations resulting in dampened arthropod responses to fertilization (Welti, Roeder, et al., 2020).

2 | METHODS

2.1 | Data compilation

We searched for peer-reviewed journal articles published up to 7 February 2020 and catalogued in the ISI Web of Science using the search terms "fertilization" OR "fertilisation" OR "nutrients" OR "nutrient addition" OR "micronutrient" OR "nitrogen" OR "phosphorus" OR "potassium" OR "NPK" AND "arthropods" OR "insects" AND "prairie" OR "grassland" OR "pasture" OR "savannah" OR "savanna" OR "steppe" OR "old field". In total, we found 688 publications. To provide a more adequate representation of fertilization effects and help reduce publication bias, we additionally searched the LTER (Long Term Ecological Research, https://lternet.edu) database for raw experimental data. We then evaluated studies and included only those that were non-cage field experiments in non-agricultural grassland ecosystems (although the experimental area could be mowed, grazed, or have been previously used for agriculture). Additionally, we selected only studies that included both a fertilization treatment and a control (no fertilization) treatment, and from which we were able to obtain either raw arthropod abundances or both means and standard deviations of arthropod abundances in treatment and control plots. In the absence of raw data, we used WebPlotDigitizer (Rohatgi, 2011) to extract data from figures and requested data from authors. If a study included treatments other than fertilization (e.g., water addition), we used only fertilization and control treatment data. From the initial 688 peer-reviewed publications and datasets, 46 publications from experiments on five continents (see Supporting Information Appendix S1: Figure S1) matched our criteria in reporting the response of arthropod abundance to fertilization in tropical and temperate grasslands (Table 1).

Altogether, the 46 publications encompassed 62 separate studies (e.g., the response at a different geographic location; Table 1; see Supporting Information Appendix S1: Figure S1). Fertilization treatments included the macronutrients N, P, K, and the micronutrients Ca, Mg, Mo and Na, alone or in combination. Treatments also included a common micronutrient mix [Scott's Micromax$^{®}$ (BFG Supply Co., Burton, OH, USA) containing Fe, Mn, Zn, Cu, B, Mo, Ca and Ni]. For studies that reported multiple time points of arthropod sampling, only the final time point was included to eliminate temporal pseudoreplication. We considered experiments within the 62 studies independent observations when they differed by fertilization type, fertilizer amount added, arthropod sampling method, and/or plot size. Altogether, this resulted in 278 independent treatment–control pairs (see Supporting Information Appendix S1: Table S1).

For each study, we extracted information on experimental location (site name, geographic coordinates, and continent), fertilization information [type (identity of element or combination of elements), amount of fertilizer added in g/m^2/year, frequency of fertilization, and duration of fertilization in months) and experimental design (arthropod sampling method, plot size, number of control and experimental plots). For any nutrient addition that included N, we recorded whether the N was fast- or slow-release. We extracted the average and standard deviation of arthropod abundance, separated by trophic guild. We divided arthropods into eight trophic guilds, namely: chewing herbivore, sucking herbivore, pollinator, omnivore, predator, parasitoid, detritivore and unknown. When trophic guilds were not defined by authors and taxonomic resolution allowed classification, we assigned trophic guilds based on life history descriptions (Triplehorn & Johnson, 2005); see Supporting Information Appendix S2 for trophic assignments. As arthropod response to fertilization is likely indirectly mediated through the plant responses to fertilization, when available, we also extracted the average and standard deviation of plant biomass, % N, ppm P and ppm K. Several studies reported plant responses in a separate publication; we included these when researchers measured plant responses in the same season and year as arthropod responses. For each of our 62 studies, we calculated the mean and standard deviation of total arthropod abundance, abundance of each arthropod feeding guild, plant biomass, plant %N, and plant P and K tissue concentrations (ppm) in fertilized plots and control plots in order to calculate effect size as Cohen's *d* (Cohen, 1988) of arthropod and plant response to fertilization. We used Egger's regression test in the R package metafor (Viechtbauer, 2010) and a funnel plot to test for publication bias effects (Egger et al., 1997) and found none (Supporting Information Appendix S1: Figure S2).

2.2 | Fertilizer models

To identify which fertilizer predictor variables best estimated arthropod responses to fertilization (effect sizes), we used an Akaike information criterion (AIC) framework (Burnham & Anderson, 2002). Predictor variables included the fixed effects of fertilizer type (e.g., NP), total amount of fertilizer applied as $\log_{10}$ transformed g/m^2/year, frequency of fertilization per year, and duration of fertilization in months. We additionally included $\log_{10}$-transformed plot size (m^2) and sampling method as random effects because they both had significant effects on total arthropod effect size. Continent on which the experiment was conducted did not affect total arthropod effect size ($R^2 = .02$, $F_{(4,274)} = 1.5$, $p = .21$) and thus was not included as a random predictor variable in AIC models. Models with ΔAIC corrected for small sample size (ΔAIC_c) < 2 are considered equally parsimonious top models (Burnham & Anderson, 2002). However, when a non-top model contains one additional parameter and shares a similar log likelihood to the top model, it is not considered competitive; thus we did not report these uninformative models (Arnold, 2010; Burnham & Anderson, 2002; Leroux, 2019). We performed a separate analysis for total arthropods and for the four most abundant trophic guilds (chewing herbivores, sucking herbivores, omnivores, and predators). We conducted AIC_c analysis using the R package MuMIn (Bartoń, 2016), and fitted linear mixed models using the R package lme4 (Bates et al., 2015). As ammonia release from fast release fertilizers can be toxic to arthropods (Warren, 1962), we used a *t*-test to compare the effect of fast versus slow release nitrogen fertilizers on total arthropod abundance.

To visualize arthropod responses to fertilizer type, we plotted effect sizes of total arthropods and individual arthropod feeding guilds for all fertilizer types represented in > 5 studies. While our literature search did not identify ≥ 5 studies with Ca fertilization alone, 6 studies including 21 independent observations conducted fertilizer additions that included Ca (e.g., NCa and NPKCaNa fertilizers). Because Ca is crucial for maintaining physiological function and metabolism in arthropods (Clark, 1958), we included an exploratory analysis of

TABLE 1 Included studies and their location, applied fertilizer type and arthropod sampling method

Study	Number	Latitude	Longitude	Country	Continent	Fertilizer type	Sampling method
Andrey et al. (2014)	1	46.14	7.2	Switzerland	Europe	NPK	Bugvac
Barrios-Garcia et al. (2017); Plant biomass from: Crutsinger et al. (2013)	2	38.32	−123.07	USA	N. America	NPK, C	Bugvac
Boyer et al. (2003)	3	35.32	−92.55	USA	N. America	NPK	Bugvac
Burkle et al. (2013); Plant biomass from: Souza (2010)	4	35.85	−84.18	USA	N. America	N, P, NP	Hand collecting
Callaham et al. (2003); Plant biomass from: Blair and Zeglin (2019)	5	39.08	−96.55	USA	N. America	N, P, NP	Berlese
Chen et al. (2009)	6	27.73	117.95	China	Asia	NPK	Sweep net
Cuesta et al. (2008)	7	43.09	−5.98	Spain	Europe	N	Pitfall
Cuevas-Reyes et al. (2011)	8	−15.93	−47.88	Brazil	S. America	N, P	Hand collecting
Dawes-Gromadzki (2002)	9	−34.1	139.43	Australia	Australia	NPK	Pitfall, sweep net
Dennis et al. (2004)	10	51.95	−3.62	Wales	Europe	N	Pitfall
Dittrich and Helden (2012)	11	52.15	0.16	England	Europe	N	Bugvac
Evans and Sanderson (2018)	12	55.22	−1.68	England	Europe	N, P, K, NPK	Sweep net and pitfall
Everwand et al. (2014)	13	51.44	9.33	Germany	Europe	NPK	Sweep net, pantrap
Fay et al. (1996)	14	39.08	−96.55	USA	N. America	NPK + mN	Sweep net
Fountain et al. (2008)	15	55.47	−2.22	Scotland	Europe	NCa	Pitfall
Haddad et al. (2000)	16	45.4	−93.2	USA	N. America	NPKCaMgS + mN	Sweep net
Hartley et al. (2007)	17	29.23	−95.12	USA	N. America	NPK	Sweep net
Harvey and MacDougall (2015)	18	43.41	−80.47	Canada	N. America	N	Sweep net
Jonas and Joern (2007)	19	39.08	−96.55	USA	N. America	N, P, NP	Sweep net
Kaspari, Roeder, et al. (2017)	20	35.19	−97.45	USA	N. America	NP, Na, NPNa	Bugvac
Kersch and Fonseca (2005)	21	−29.48	−51.1	Brazil	S. America	PKCa	Hand collecting
La Pierre and Smith (2016)	22	40.84	−104.72	USA	USA	N, P, K + mN, NP, NK + mN, PK + mN, NPK + mN	Bugvac
La Pierre and Smith (2016)	23	38.94	−99.3	USA	USA	N, P, K + mN, NP, NK + mN, PK + mN, NPK + mN	Bugvac
La Pierre and Smith (2016)	24	39.08	−96.55	USA	USA	N, P, K + mN, NP, NK + mN, PK + mN, NPK + mN	Bugvac

(Continues)

TABLE 1 (Continued)

Study	Number	Latitude	Longitude	Country	Continent	Fertilizer type	Sampling method
La Pierre et al. (2015)	25	39.08	−96.55	USA	N. America	NPK	Bugvac
Lane (2006)	26	35.97	−84.28	USA	N. America	N, C	Sweep net
Lee et al. (2014)	27	51.51	−0.64	England	Europe	N	Sweep net
Lejeune et al. (2005)	28	39.93	−105.19	USA	N. America	N, P, NP	Hand collecting
Lemanski and Scheu (2015)	29	51.73	9.38	Germany	Europe	NPK	Berlese
Lessard-Therrien et al. (2018)	30	46.14	7.2	Switzerland	Europe	NPK	Pitfall
Lind et al. (2017); Plant P and K from: Anderson et al. (2018)	31	44.28	−121.97	USA	N. America	N, P, K + mN, NP, NK + mN, PK + mN, NPK + mN	Bugvac
Lind et al. (2017); Plant P and K from: Anderson et al. (2018)	32	41.79	−93.43	USA	N. America	N, P, K + mN, NP, NK + mN, PK + mN, NPK + mN	Bugvac
Lind et al. (2017)	33	45.4	−93.2	USA	N. America	N, P, K + mN, NP, NK + mN, PK + mN, NPK + mN	Bugvac
Lind et al. (2017)	34	39	−123.08	USA	N. America	N, P, K + mN, NP, NK + mN, PK + mN, NPK + mN	Bugvac
Lind et al. (2017)	35	39.08	−96.55	USA	N. America	N, P, K + mN, NP, NK + mN, PK + mN, NPK + mN	Bugvac
Lind et al. (2017); Plant P and K from: Anderson et al. (2018)	36	44.21	−122.13	USA	N. America	N, P, K + mN, NP, NK + mN, PK + mN, NPK + mN	Bugvac
Lind et al. (2017); Plant P and K from: Anderson et al. (2018)	37	18.47	−66.48	USA	N. America	N, P, K + mN, NP, NK + mN, PK + mN, NPK + mN	Bugvac
Lind et al. (2017)	38	38.89	−122.42	USA	N. America	N, P, K + mN, NP, NK + mN, PK + mN, NPK + mN	Bugvac
Lind et al. (2017); Plant P and K from: Anderson et al. (2018)	39	39.44	−120.27	USA	N. America	N, P, K + mN, NP, NK + mN, PK + mN, NPK + mN	Bugvac
Lind et al. (2017)	40	38.94	−99.3	USA	N. America	N, P, K + mN, NP, NK + mN, PK + mN, NPK + mN	Bugvac
Lind et al. (2017); Plant P and K from: Anderson et al. (2018)	41	40.84	−104.72	USA	N. America	N, P, K + mN, NP, NK + mN, PK + mN, NPK + mN	Bugvac

(Continues)

TABLE 1 (Continued)

Study	Number	Latitude	Longitude	Country	Continent	Fertilizer type	Sampling method
Lind et al. (2017)	42	39.25	−121.32	USA	N. America	N, P, K + mN, NP, NK + mN, PK + mN, NPK + mN	Bugvac
Lind et al. (2017)	43	35.99	−78.93	USA	N. America	N, P, K + mN, NP, NK + mN, PK + mN, NPK + mN	Bugvac
Loaiza et al. (2011)	44	39.08	−96.55	USA	N. America	N, P, NP	Ring count
Moran and Scheidler (2002)	45	35.06	−92.44	USA	N. America	NPK	Bugvac
Oliver et al. (2003); Oliver et al. (2005)	46	−34.67	148.9	Australia	Australia	Pmo, PCaMo	Pitfall and Berlese
Oliver et al. (2003); Oliver et al. (2005)	47	−34.92	139.03	Australia	Australia	P	Pitfall and Berlese
Patrick et al. (2012); Plant biomass from: Patrick et al. (2008)	48	41.18	−81.65	USA	N. America	NPK	Pitfall
C. M. Prather, Laws, et al. (2018)	49	29.23	−95.11	USA	N. America	Ca, CaNa, K, KCa, KCaNa, KNa, Na, NNa, NP, NPCa, NPCaNa, NPK, NPKCa, NPKCaNa, NPKNa	Sweep net
R. M. Prather and Kaspari (2019)	50	33.89	−96.84	USA	N. America	NPK + mN	Bugvac, pitfall
R. M. Prather and M. Kaspari unpublished	51	33.89	−96.84	USA	N. America	NPK + mN	Bugvac, pitfall
Ribeiro et al. (2014)	52	−21.62	−42.08	Brazil	S. America	PK	Berlese
Ritchie (2000)	53	45.4	−93.2	USA	N. America	N	Sweep net
Ritchie (2018)	54	45.4	−93.2	USA	N. America	N	Sweep net, bugvac
Simons et al. (2016)	55	51.93	11	Germany	Europe	N	Sweep net
Song et al. (2018); Plant biomass from: Song et al. (2012)	56	37.62	101.32	China	Asia	N	Hand collecting
Welti et al. (2019)	57			USA	N. America	NaCl	Bugvac
Williams and Cronin (2004)	58	47.92	−97.32	USA	N. America	Na, N, NNa	Hand collecting
Wilson (2018)	59	45.4	−93.2	USA	N. America	NPKCaMg	Sweep net
Wimp et al. (2010)	60	39.51	−74.32	USA	N. America	NP	Bugvac
Vanwingerden et al. (1992)	61	52.01	5.82	Netherlands	Europe	N	Hand collecting
Woodcock et al. (2009)	62	50.98	−3	England	Europe	NPK	Bugvac, pollard walk

total arthropod and trophic group abundance effect sizes to fertilizers containing Ca in addition to other elements. Additionally, to visualize arthropod responses to fertilizer amount, we examined linear relationships between arthropod effect size and the amount of fertilizer in g/m^2/year for the three most common elements applied – N, P and K – for all experiments adding these either alone or in combination with other elements.

2.3 | Plant models

To test how both the underlying gradients and responses of plant biomass and plant nutrient content to fertilization mediated arthropod response to fertilization we used linear models within an AIC framework. To assess how arthropods responded across environmental gradients of productivity and nutrient limitation, we included the predictors of aboveground plant biomass (g/m^2) and plant %N in control plots. To assess how arthropods responded to plant responses to fertilization, we included the predictor variables of the effect sizes of aboveground plant biomass and plant %N. We assessed responses of total arthropods and the four most abundant trophic guilds (chewing herbivores, sucking herbivores, omnivores, and predators) in separate models. We additionally included herbivore effect size as a predictor variable in the predator model as predators are likely not directly responding to plant nutrient content but rather indirectly tracking plant quality via herbivore responses. Plant biomass was reported in 64% of studies and %N was reported in 44% of studies. Although we extracted information on plant P and K, low replication precluded them from our AIC analysis (11 and 9 studies, respectively; see Supporting Information Appendix S1: Table S2).

To visualize results, we plotted effect sizes of aboveground plant biomass for all fertilizer types represented in > 5 studies. We examined linear relationships between total arthropod effect size and aboveground plant biomass effect size as well as plant N, P and K effect sizes for the most common fertilizer types. We also examined linear relationships between total arthropod effect size and plant biomass in control plots as well as plant N, P and K concentrations in control plots, again using the most common fertilizer types. We ran all analyses in R version 3.6.1 (R Core Team, 2019).

3 | RESULTS

N was added in 71% of studies (added alone in 16% of studies), P was added in 65% of studies (added alone in 10% of studies), while K was added in 57% of studies (added alone in 0.7% of studies). Micronutrients were applied most frequently in combination with NPK and added alone in only six studies (KNa, Na, and Ca + mN; see Supporting Information Appendix S1: Table S1). Aboveground plant biomass response to fertilization varied from no response in the case of K + mN and PK + mN fertilization to a positive response, with NP addition resulting in the greatest increase in plant biomass (effect size: +1.3; Figure 1a). Arthropod abundance varied widely with fertilizer type (Figure 1b), from low abundance with K + mN fertilization (effect size: −0.1) to high abundance with the addition of NPK + mN (effect size: +1.3).

3.1 | K + mN went from inhibiting alone to enhancing arthropod abundance when added with NP

Following the strong positive effect from NPK + mN, NP fertilizers generated the second largest increase in total arthropod abundance (effect size: +0.6), and NPK the third largest increase (effect size: +0.4). In contrast, K + mN fertilization significantly decreased abundance (effect size: −0.1). Thus, micronutrients showed evidence of catalysing the effects of N and P, doubling their effect size, and tripling the capacity of NPK to promote arthropod abundance (Figure 1b). This strong, positive effect of NPK + mN was the only result shared among all six trophic groups, where it yielded the highest average effect size in five of the six guilds (Figure 2).

3.2 | Response to fertilization type, frequency, amount and duration

Fertilizer type was the primary predictor of variation in arthropod abundance across fertilization experiments included in our study (Table 2a). Similar to total arthropods, sucking herbivore response varied with fertilizer type, but increasing frequency of fertilizer application decreased sucking herbivore abundance (Table 2b). Top models predicting the effect sizes of chewing herbivores (Table 2c), omnivores (Table 2d), and predators (Table 2e) included the null model (containing only random effects) and thus were not well explained by our suite of fertilizer variables. With the caveat that responses to Ca addition were examined when Ca was added in conjunction with other nutrients to allow sufficient sample sizes for analysis, fertilizers containing Ca increased arthropod abundance (see Supporting Information Appendix S1: Figure S3).

3.3 | Sucking herbivores profited from more nutrient combinations than chewing herbivores

Chewing herbivores such as grasshoppers increased strongly on only two fertilizer types, both containing N, K and micronutrients (Figure 2a). In contrast, arthropods that get their nutrients from phloem or xylem, like leafhoppers, were able to convert six of the eight added nutrient combinations, most notably including those with P, into abundances higher than control plots (Figure 2b).

3.4 | Response of other arthropod guilds

Pollinator response was only measured at $n \geq 5$ responses on the dominant nutrient addition types (N, NPK, or NPK + mN fertilization) and increased on N and NPK + mN additions (effect sizes: +0.2 and +0.6, respectively; Figure 2c). Surprisingly, omnivores declined when N was applied solo (effect size: −0.3) but increased when N was added in any combination with P (effect sizes: +0.6 to +0.9; Figure 2d). Predators generally tracked the response of lower trophic groups and increased on NPK and NPK + mN treatments (effect sizes: +0.5 and +0.8, respectively; Figure 2e). Finally, while fewer types of fertilization experiments sampled detritivore responses, detritivores consistently increased with fertilization for all measured combinations (Figure 2f).

3.5 | Responses to plant nutrient content and biomass

The underlying environmental gradient of plant %N drove responses of total arthropod abundance to fertilization (Table 3a; see Appendix

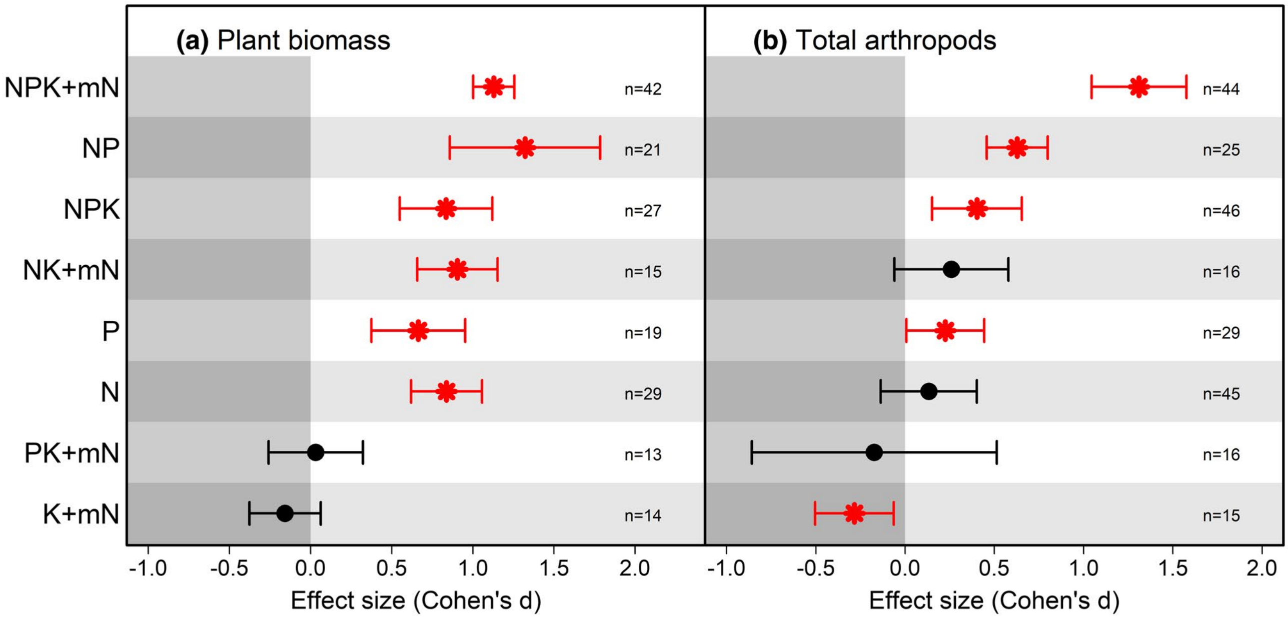

FIGURE 1 Forest plot showing effect sizes (Cohen's *d*) of (a) plant biomass and (b) total arthropod abundances by fertilizer type. Red stars denote significant effect sizes, while black circles indicate non-significant effect sizes. We included fertilizer types used in > 5 studies. The number of replicates provided within the figure refers to the number of experimental responses containing each fertilizer type. Error bars are the standard error of the mean of the effect sizes of individual experiments [Colour figure can be viewed at wileyonlinelibrary.com]

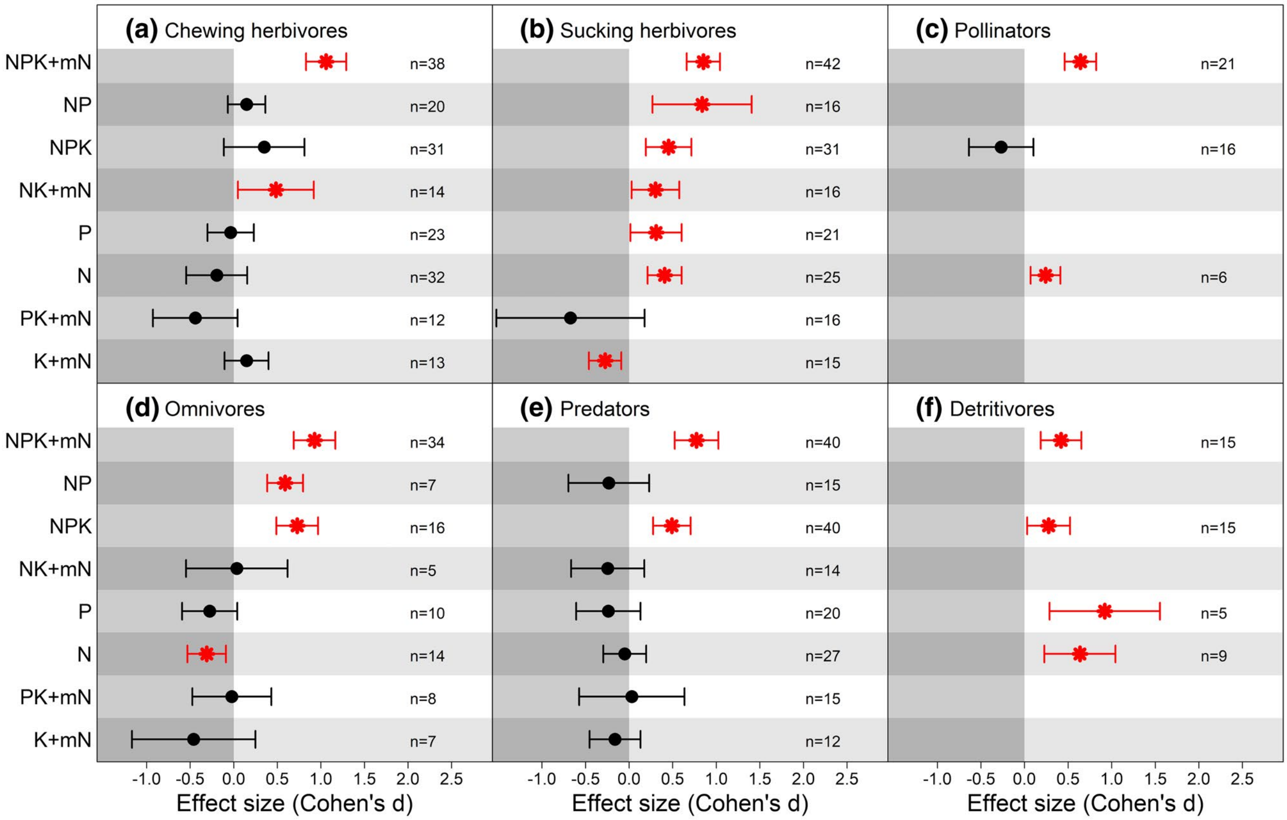

FIGURE 2 Forest plot showing effect sizes (Cohen's *d*) of arthropod trophic group abundances by fertilizer type. Responses are provided for the trophic groups of (a) chewing herbivores, (b) sucking herbivores, (c) pollinators, (d) omnivores, (e) predators, and (f) detritivores. Red stars denote significant effect sizes, while black circles indicate non-significant effect sizes. We included fertilizer types used in ≥ 5 studies. Number of replicates provided within the figure refers to the number of experimental responses containing each fertilizer type and trophic group. Error bars are the standard error of the mean of the effect sizes of individual experiments [Colour figure can be viewed at wileyonlinelibrary.com]

S1: Figures S4 and S5). Both sucking and chewing herbivores had increasing attraction to N-fertilized plots in grasslands with low underlying plant %N (as measured in control plots; Table 3b,c). Chewing herbivores responded negatively to increasing plant biomass effect size (Table 3c). Omnivores and predators had increasing responses to fertilizers at areas of low aboveground plant biomass (Table 3d,e). Additionally, omnivore abundance on fertilized plots increased with plant %N effect size (Table 3d). Besides stronger responses in prairies with less aboveground plant biomass, predator abundance on fertilized plots increased in response to higher herbivore effect size (Table 3e).

3.6 | Variation due to experimental design

Amounts of N, P and K applied (g/m^2/year) varied over 100-fold across the surveyed studies (see Supporting Information Appendix S1: Figure S6). Whereas the quantity of N had no effect on the resulting effect size, there was a small but positive effect of fertilizer quantity on arthropod abundance for both P and K ($R^2 = .03$ and .03, respectively; see Supporting Information Appendix S1: Figure S6). The effect size of total arthropod abundance more than doubled for experiments using slow release compared to quick release forms of nitrogen ($t = -4.03$, $df = 191$, $p < .001$; see Supporting Information Appendix S1: Figure S7). Plot size varied from 1 to 10,000 m^2 in the surveyed studies and effect size decreased with increasing plot size ($R^2 = .04$, $F_{1,277} = 12.3$, $p < .001$; see Supporting Information Appendix S1: Figure S8). Sampling method significantly affected arthropod abundance with the largest effect size resulting from studies using bugvac sampling (i.e., vacuum sampling; effect size: +0.61) while the smallest effect sizes resulted from bugvac combined with pollard walks (effect size: −1.28) and hand collecting (effect size: −0.54; $R^2 = .07$, $F_{9,269} = 2.4$, $p = .01$; see Supporting Information Appendix S1: Figure S9).

4 | DISCUSSION

Fertilization experiments help us to identify key elements that constrain abundance in ecological communities. Our meta-analysis reveals N and P shortfalls commonly limit grassland arthropod abundance. However, unlike plants, a treatment combining K and micronutrients (K + mN) catalyses the effect of N and P; specifically, K + mN is neutral to negative when applied by itself but doubles or triples the effects on arthropod abundance when applied in tandem with N and P. Moreover, this synergistic effect is consistent across the major trophic subsets of arthropod communities. We also show key differences in the response of herbivore feeding guilds with sucking herbivores showing responses to a wider variety of fertilization types than chewing herbivores. In total, our results confirm recent studies showing that nutrient co-limitation in consumer communities is widespread (Gruner et al., 2008; Joern et al., 2012; Kaspari, Bujan, et al., 2017; C. M. Prather, Laws, et al., 2018). The rules translating biogeochemistry to plant biomass in grasslands differ in a fundamental way from those predicting arthropod abundance, highlighting the role of micronutrients in catalysing macronutrients used by consumers but not plants.

4.1 | Micronutrients had synergistic effects with macronutrients

The macronutrients N and P are the primary biogeochemical drivers of global variation in grassland plant production (Elser et al., 2007). We found similar responses among grassland arthropods, with P playing a stronger role in promoting abundance while N applied by itself had no net effect. However, when accounting for nitrogen type, slow release forms increased arthropod abundance. This is probably because slow release fertilizers are less susceptible to nutrient leaching and fast release fertilizers release ammonia, which can be toxic to arthropods (Warren, 1962).

TABLE 2 Akaike information criterion (AIC) models of fertilizer effects on arthropod effect sizes (Cohen's *d*) for each trophic group including (a) total arthropods, (b) sucking herbivores, (c) chewing herbivores, (d) omnivores, and (e) predators

Trophic groups and predictor variables	AIC$_c$	LL	*df*	Marginal R^2	Conditional R^2	ΔAIC$_c$	wi
(a) Total arthropods (*n* = 278)							
type	1,032.9	−478.8	33	.1	.32	0	0.4
(b) Sucking herbivores (*n* = 193)							
type, frequency (−)	732	−347.3	17	.33	.43	0	0.32
(c) Chewing herbivores (*n* = 214)	Null model				.3		
(d) Omnivores (*n* = 131)	Null model				.28		
(e) Predators (*n* = 218)	Null model				.06		

Note: Effects of continuous variables are depicted with (+) and (−). Driver variables in top models include the fixed effects of fertilizer type (type), frequency of fertilization per year (frequency), total fertilizer amount applied (amount) and duration of fertilization (duration). The random effects of plot size and sampling method were included in all models. The number of replicates refers to the number of experimental responses used in analysis. AIC statistics include: AIC$_c$ = AIC statistic corrected for small sample size; LL = log likelihood; *df* = degrees of freedom; marginal R^2 = adjusted regression coefficient considering fixed effects; conditional R^2 = adjusted regression coefficient considering fixed and random effects; ΔAIC$_c$ = AIC$_c$ minus top model AIC$_c$; wi = model weight. An empty model (model with only random variables and no fixed fertilizer-related variables) was included in the top models predicting chewing herbivores, omnivores, and predators; thus, we do not report AIC$_c$ models for these groups. However, we report the conditional R^2 for the model containing only the random effects (plot size and sampling method).

TABLE 3 Akaike information criterion (AIC) models of plant biomass and nutrient effects on arthropod effect sizes (Cohen's *d*) for each trophic group including (a) total arthropods, (b) sucking herbivores, (c) chewing herbivores, (d) omnivores, and (e) predators

Trophic group and predictor variables	AIC$_c$	LL	*df*	R^2	ΔAIC$_c$	wi
(a) Total arthropods (*n* = 89)						
plant N control (–)	337.6	−165.64	3	.05	0.00	0.31
(b) Sucking herbivores (*n* = 74)						
plant N control (–)	225.3	−109.50	3	.18	0.00	0.32
(c) Chewing herbivores (*n* = 82)						
plant N control (–), plant biomass ES (–)	281.3	−136.38	4	.16	0.00	0.34
plant N control (–)	282.8	−138.24	3	.12	1.51	0.16
plant N control (–), plant biomass control (–)	283.2	−137.35	4	.14	1.93	0.13
(d) Omnivores (*n* = 62)						
plant N ES (+), plant biomass control (–)	205.6	−98.43	4	.13	0	0.21
plant N ES (+)	206.3	−99.95	3	.09	0.75	0.15
plant N ES (+), plant biomass ES (+)	207.2	−99.23	4	.11	1.60	0.10
(e) Predators (*n* = 74)						
herbivore ES (+), plant N control (+), plant biomass control (–)	245.5	−117.33	5	.16	0	0.25
herbivore ES (+), plant N control (+)	247.1	−119.25	4	.11	1.56	0.115

Note: Effects of continuous variables are depicted with (+) and (–). Driver variables include the effects of plant biomass in control plots, plant biomass effect size, plant %N in control plots, and plant %N effect size (ES). Herbivore ES was also included as a driver variable for predator effect sizes. The number of replicates refers to the number of experimental responses used in analysis. AIC statistics include: AIC$_c$ = AIC statistic corrected for small sample size; LL = log likelihood; *df* = degrees of freedom; R^2 = adjusted regression coefficient; ΔAIC$_c$ = AICc minus top model AIC$_c$; wi = model weight.

Our most novel result is the strong, synergistic effects of K + mN upon arthropods when added in combination with N and P. Compared to plants, animal tissue generally has higher concentrations of the metals in the micronutrient component of fertilizers, with these metals playing important biological roles as osmoregulators and enzymatic co-factors (Kaspari & Powers, 2016). Moreover, that K + mN has little detectable effect on plant productivity suggests plant biomass does not mediate their effects. This begs the question, which components of the NPK + mN combination drive arthropod responses? There are many candidates, as the micronutrient combination includes 10 elements as cations and anions – that were not often applied individually or separate from K. However, arthropod effect sizes were marginally lower with NPK compared to NP fertilization, suggesting that K is not driving the synergistic effect of K + mN. Moreover, the micronutrients we examined have different soil signatures across geographic gradients (Smith et al., 2014). While we have yet to identify which micronutrients, when added in combination with N, P, and K, are so effective at enhancing arthropod abundance, common garden experiments, field experiments and geographic analysis could be several ways to further study which specific elements enhance arthropod abundance and their mechanisms.

4.2 | Arthropod feeding guilds varied in their response to nutrient additions

Differential arthropod responses among trophic guilds suggest a number of working hypotheses. First, the effect sizes of NPK + mN dropped from *c.* 1.0 standard deviation (*SD*) for herbivores and omnivores to < 1.0 *SD* for predators and detritivores. This suggests that nutrient limitation has the strongest effects on the abundance of herbivores and attenuates up the food chain. This is similar to previous work showing greater Na limitation among plant consumers, versus their predators (Clay et al., 2014). However, pollinators and detritivores had the smallest response to NPK + mN fertilization, potentially because there were fewer observations of these two groups. Many sampling methods such as sweep net and bugvacs – which were common methods in included studies – often do not target pollinators and detritivores and only catch small numbers of these groups.

The group showing the most ubiquitous nutrient limitation – the sucking herbivores – feed on solutions of xylem and phloem. Chewing herbivores get their nutrients from mouthfuls of tissue, with nutrients wrapped in cellulose and lignins and are often deterred by secondary compounds including tannins, phenolics, oxalates (Rosenthal & Berenbaum, 2012). We suggest that sucking herbivores are better able to obtain N and P in soluble form, free from recalcitrant or defensive molecules, and are thus more prone to increase on plots with added N and/or P. Moreover, when added alone, K + mN decreased sucking herbivore abundance. Given that K is a plant osmolyte that promotes water uptake and turgor pressure, sucking herbivores on +K plots may suffer from more dilute xylem and phloem, with a commensurate decrease in the concentrations of amino acids and other nutrients (Butler et al., 2012; Huberty & Denno, 2006).

4.3 | Underlying plant gradients mediate arthropod responses to fertilization

Background level of plant %N was the most important driver of total arthropod response to the application of fertilizers containing N. Arthropods had enhanced attraction to N fertilized plots (increased N limitation) in environments with low background levels of foliar N. This response was driven by the plant consumers, which are the most likely to be N limited. Omnivores and predators increased with application of N-containing fertilizers more in grasslands with lower aboveground plant biomass. While the mechanism for this effect is unclear, omnivores and predators may better track herbivores in less complex habitats with low plant biomass. Alternatively, besides changes in foliar %N and biomass, which we account for in our model, it could be that fertilization affects grassland plants differently across the productivity gradient, such as through changes in habitat heterogeneity (Davies et al., 2007) or plant diversity (Hillebrand et al., 2007) with consequences for trophic structure.

4.4 | Plant responses to fertilization mediate arthropod responses to fertilization

While arthropods responded to fertilizer addition via fertilizer effects on plant biomass and plant %N (as measured by plant effect sizes), this response was not consistent across guilds. Chewing herbivores responded negatively to fertilization-driven increases in plant biomass. While the studies that measured both biomass and plant nutrient content do not provide a large sample size for testing, we speculated that this may be due to increased nutrient dilution in plant tissue with enhanced growth (Welti, Roeder, et al., 2020) and/or increased plant volume creating additional habitat that supported more predators (Post et al., 2000). Alternatively, fertilization may allow plants to produce higher levels of secondary compounds, deterring chewing herbivores (Mur et al., 2016). Omnivores increased both in response to increases in plant biomass and higher plant %N with fertilization. Finally, unlike other trophic guilds, predators had increased responses to fertilization at higher background levels of plant %N. While we did not expect predators to respond to plant %N content, the presence of many predators in a plot may itself enhance plant %N content, as prey increase consumption of carbohydrates relative to protein in the presence of predators (Hawlena & Schmitz, 2010).

4.5 | Experimental design affected arthropod abundance

Ecologists exploring nutrient limitation must make many small decisions regarding the types of nutrients, their amounts, frequency, and the size of plots to use. All can shape the results.

Slow release, and/or frequent small pulses of fertilizer, particularly N, reduces fertilizer loss through run-off (Haynes, 1985), and can enhance plant biomass (Cook & Sanders, 1991; Johnson & Carrow, 1988; Slaton et al., 2002) and plant quality (Haynes, 1985; Neilsen et al., 1995). Accordingly, quick release nitrate fertilizers – susceptible to disappearing both through leaching and through denitrification – yielded half the effect size of slow release urea. Given that urea is the primary form of N in animal urine (Steinauer & Collins, 1995), such applications are also likely more similar to naturally occurring forms of N sources for grassland arthropods.

The amount of fertilizer applied had a small but significant effect on the effect sizes for P and K, but not N. However, compared to fertilizer type, the amount of variance accounted for by fertilizer amount was small. Background variation in nutrient levels across sites results in differential responses to fertilization by arthropod communities, but here we have sufficient data only from plant %N to examine this variation. Additional studies of arthropod responses across gradients of plant and soil chemistry could further elucidate the role of underlying chemistry in driving arthropod abundance. The standard application of 10 g/m^2/year from the globally distributed Nutrient Network experiment (Borer et al., 2017) predominates in grassland nutrient addition experiments. We need more experiments that apply amounts of fertilizer at other levels and gradient studies to understand the future impacts of grasslands to anthropogenic fertilization application and deposition. For example, extremely high levels of Na addition (4,200 g/m^2/year; Williams & Cronin, 2004) significantly decreased arthropod abundance while low levels of Na addition (10 g/m^2/year; Welti et al., 2019) increased arthropod abundance. Experiments with more fertilizer levels will allow researchers to identify any potential tipping points, whereby additional fertilizer application would reduce arthropod abundance. More experiments that test predictions as to how nutrient amount ramifies through food webs are particularly germane in an era of anthropogenic fertilizer application and deposition (Steffen et al., 2015).

Additionally, response to fertilization experiments varied with plot size and sampling method. Small plot sizes had greater responses to fertilizers and thus likely allowed more immigration from outside plots due to increased edge to area ratio. Arthropod sampling method also affected responses, with the largest effect sizes from bugvac, pitfall and sweep net sampling methods relative to bugvac combined with pollard walks or hand collecting. Each sampling method targets different arthropod guilds, body sizes, and dispersal mechanisms (e.g., walking versus flying). As sampling method can impact arthropod abundance results, it is important to take sampling method into account when designing future fertilization experiments. Specifically, future experiments should include sampling methods to target understudied groups such as pollinators and detritivores and use a combination of methods to capture the full response of the arthropod community across body sizes and dispersal abilities.

4.6 | Caveats, conclusions and future directions

Meta-analyses are useful both for synthesizing results across studies and for the gaps they reveal in the literature (Cadotte et al., 2012). More whole food web studies, tracking the nutrients from soil through plants and into consumers (e.g., La Pierre & Smith, 2016; Lind et al., 2017; Welti et al., 2019) are needed to understand these mechanisms. In addition, grasslands in South America, Asia, and Africa make up about 80% of global grasslands (Dixon et al., 2014) but are underrepresented in the global literature. Additionally, researchers and sampling methods tend to target herbivores and predators, leaving pollinators, parasitoids and detritivores poorly studied, despite their potential importance in providing ecosystem services and in food web dynamics. While fertilization can alter production of plant secondary compounds, which also affect herbivore responses, too few studies included in this paper measured plant secondary compounds for analysis of their role in altered herbivory. Clearly, there is much to do and large-scale distributed experiments as well as smaller coordinated collaborative experiments have much to offer in advancing the field. Finally, if micronutrients are key components that regulate consumer abundance, then understanding which elements are important and precisely how they work is paramount. Progress, using simple addition experiments, has been made along those lines for Na, a micronutrient key to animal health and performance (Borer et al., 2019; Kaspari, 2020; Kaspari, Bujan, et al., 2017; C. M. Prather, Laws, et al., 2018; R. M. Prather, Roeder, et al., 2018; Welti et al., 2019). More such experiments are needed to examine the effects of Ca, Mg, Mo and other micronutrients on grassland arthropod guilds (Kaspari & Powers, 2016).

Arthropods contribute significantly to grassland biodiversity, community-level trophic dynamics, and ecosystem function (Belovsky & Slade, 2000; Meyer et al., 2002; Tscharntke & Greiler, 1995; Whiles & Charlton, 2006) and are sensitive to changing environments (Barton & Schmitz, 2009; Di Giulio et al., 2001). Understanding arthropod responses to nutrient addition is important for both conservation and maintaining critical arthropod-provided ecosystem services. Humans have dramatically increased the global availability of reactive N, P, K and other limiting nutrients through fertilizer production and use in the last century (Galloway et al., 2003). Anthropogenic effects on other biogeochemical cycles such as changes in the C and S cycles due to fossil fuel combustion, irrigation with contaminated water, and mining are changing the chemical composition of soils and terrestrial plants (Qadir et al., 2014; Schlesinger & Bernhardt, 2013; Welti, Roeder, et al., 2020). Determining how nutrient addition affects arthropod abundance and trophic groups in grasslands worldwide can improve predictions of arthropod responses to future alterations to Earth's biogeochemistry.

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DATA AVAILABILITY STATEMENT

Effect sizes of invertebrates, plant biomass, and plant chemistry to different fertilization types, amounts and durations are deposited in the Dryad Digital Repository. https://doi.org/10.5061/dryad.s7h44j153.

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SUPPORTING INFORMATION

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

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