



# Nutrient dilution and climate cycles underlie declines in a dominant insect herbivore

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**Evidence for global insect declines mounts, increasing our need to understand underlying mechanisms. We test the nutrient dilution (ND) hypothesis—the decreasing concentration of essential dietary minerals with increasing plant productivity—that particularly targets insect herbivores. Nutrient dilution can result from increased plant biomass due to climate or CO<sub>2</sub> enrichment. Additionally, when considering long-term trends driven by climate, one must account for large-scale oscillations including El Niño Southern Oscillation (ENSO), North Atlantic Oscillation (NAO), and Pacific Decadal Oscillation (PDO). We combine long-term datasets of grasshopper abundance, climate, plant biomass, and end-of-season foliar elemental content to examine potential drivers of abundance cycles and trends of this dominant herbivore. Annual grasshopper abundances in 16- and 22-y time series from a Kansas prairie revealed both 5-y cycles and declines of 2.1–2.7%/y. Climate cycle indices of spring ENSO, summer NAO, and winter or spring PDO accounted for 40–54% of the variation in grasshopper abundance, mediated by effects of weather and host plants. Consistent with ND, grass biomass doubled and foliar concentrations of N, P, K, and Na—nutrients which limit grasshopper abundance—declined over the same period. The decline in plant nutrients accounted for 25% of the variation in grasshopper abundance over two decades. Thus a warming, wetter, more CO<sub>2</sub>-enriched world will likely contribute to declines in insect herbivores by depleting nutrients from their already nutrient-poor diet. Unlike other potential drivers of insect declines—habitat loss, light and chemical pollution—ND may be widespread in remaining natural areas.**

insect decline | global change | grasshopper | Acrididae | grassland

**A**s studies of insect declines in abundance and diversity accumulate (e.g., refs. 1–5), two challenges are emerging. The first is conclusively measuring the declines, given that data can be noisy (6), are commonly inferred from sites initially selected for high abundances (7), and are often limited to a comparison of two snapshots (e.g., refs. 1, 5, and 8–12) when long time series are needed (13, 14). The second is identifying the drivers of these global declines among candidates such as global heating, light pollution, invasive species, pesticides, pollutants, and habitat loss due to urban expansion and agricultural intensification (15). We address both challenges using a long-term, high-resolution survey of grasshopper abundances in a North American prairie.

A key step in quantifying insect declines is parsing the climate drivers that act at different timescales toward effectively separating cycles from long-term trends. Among these, and particularly germane to the 20–30-y records that dominate the insect decline literature (e.g., refs. 4 and 16–19), are large-scale climate oscillations including the El Niño Southern Oscillation (ENSO), the North Atlantic Oscillation (NAO), and the Pacific Decadal Oscillation (PDO). Climate oscillations control weather patterns (20), indirectly driving primary productivity (21), and varying production of higher trophic levels including fish, mammals, birds, and insects (22–26). Climate cycles can drive insect abundances by influencing the timing and amount of temperature and precipitation, altering plant quantity and quality, including via nutrient dilution (27–29).

In addition to assessing cycles and temporal trends, we examine the nutrient dilution (ND) hypothesis as a potentially potent mechanism for insect declines. ND posits that increased carbohydrate production by primary producers—due to elevated atmospheric CO<sub>2</sub> and climatic increases in H<sub>2</sub>O and temperature—results in increased plant biomass with lower foliar nutrient concentrations, including nitrogen (30, 31) and micronutrients (32) that inhibit insect abundance (33). Prior work on ND has focused on declines in the nutrient content of crops, raising concerns for the future of Earth's human food supply (32, 34). However, a review of meta-analyses of elevated CO<sub>2</sub> experiments and changes in plant elemental nutrient concentrations over the past century reveals this to be a widespread phenomenon (*S1 Appendix, Table S1*). Of the 115 plant responses included in the 24 studies reviewed, 85 (74%) declined in macro- or microelemental nutrient concentrations. Declines occurred for many of the elements essential for animal life, including Ca, Co, Cu, Fe, I, K, Mg, Mn, N, Na, P, S, Se, and Zn. Additionally, all studies found evidence that increasing atmospheric CO<sub>2</sub> decreased noncarbon elemental nutrient concentrations for at least some plant taxa (*S1 Appendix, Table S1*) and nonsignificant results on this topic may be due to low sample sizes (34). Insect herbivores already face the challenge of bioaccumulating essential elements like N, P, and Na that are lower in plant tissue than animal tissue; even incremental decreases in plant nutrients can decrease insect performance (27, 35). Insect herbivores often respond to experimentally elevated CO<sub>2</sub> with increased plant

## Significance

**Parsing variation in long-term patterns underlying insect abundances and assigning mechanisms are critical in light of recent reports of dramatic insect declines. Grasshopper abundances in a North American prairie exhibited both 5-y cycles and >2%/y declines over the past 20 y. Large-scale climate oscillations predicted the cycles in grasshopper abundances. Moreover, plant biomass doubled over the same period—likely due to changes in climate and increasing atmospheric CO<sub>2</sub>—diluting the concentrations in plant tissue of key nutrients which in turn predicted the declines of a dominant herbivore. Nutrient dilution, like CO<sub>2</sub> enrichment, is likely a global phenomenon, posing a challenge to Earth's herbivore populations.**

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The authors declare no competing interest.

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Data deposition: Script for time series analysis is available at Figshare (<https://doi.org/10.6084/m9.figshare.11862483>) and example time series are available at Figshare (<https://doi.org/10.6084/m9.figshare.11862459>).

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consumption but decreased growth and abundance (30, 36), and decreases in pollen %N have been proposed as a driver of pollinator declines (37). However, we know of no studies linking ND of plant foliar tissue to long-term insect declines.

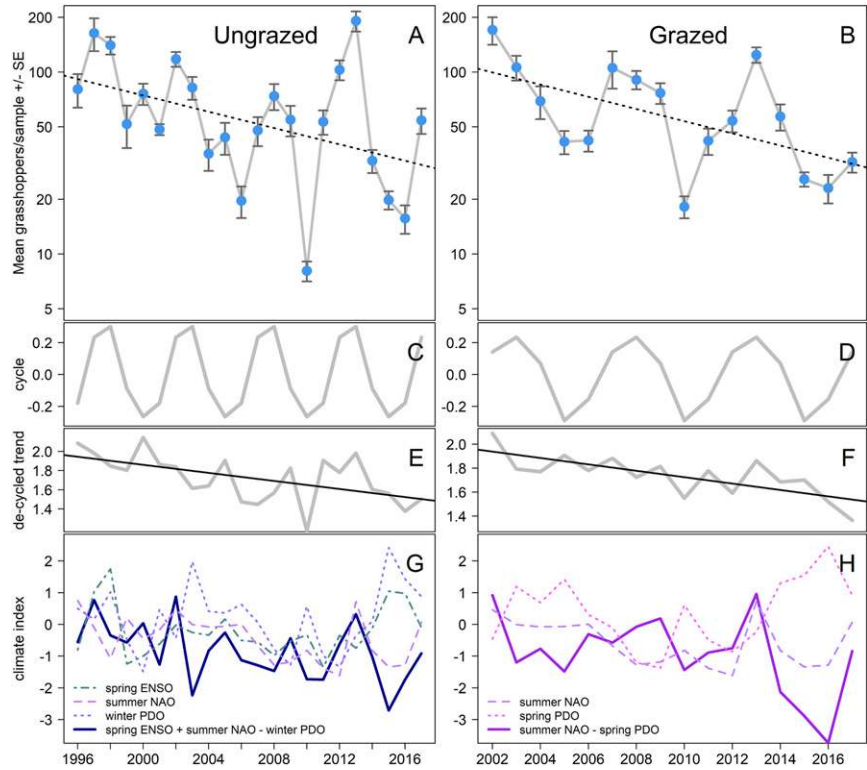
Here we dissect two decades of grasshopper abundance trends and cycles on Konza Prairie (KNZ) in Kansas. This large, native, tallgrass prairie (38) is an unlikely candidate for many alternate proposed drivers of insect decline—it is unaffected by urban expansion and agricultural intensification, and has no known invasive grasshopper species. This allows us to examine grasshopper responses to climate and ND in relative isolation from other drivers of insect decline. To disentangle cycles and temporal trends, we first determine the length of grasshopper abundance cycles using spectral analysis and estimate decycled trends using time series decomposition. Next, we test the predictive consequences of large-scale climate oscillations (ENSO, NAO, and PDO) on grasshopper abundances. Finally, we test the prediction that grasshopper declines track decreasing plant nutrient content (ND).

Results

Extensive sampling of a Kansas prairie (93,551 total grasshoppers, 44 species) revealed both a consistent 5-y cycle and declining overall grasshopper abundance. Grasshopper abundance in all 13 watersheds, feeding guilds, and abundant (>100 sampled

individuals) species exhibited similar trends and cyclicity (S1 Appendix, Figs. S1–S5 and Tables S2–S6). Thus, we focused our analysis on average grasshopper abundances from surveys on ungrazed and bison-grazed watersheds spanning 22 and 16 y, respectively, which we analyzed separately as they covered different time intervals. Grasshopper abundances exhibited one significant frequency in both time series, characterizing a 5- and 5.3-y cycle in ungrazed and grazed watersheds, respectively (S1 Appendix, Fig. S6). When we decomposed the time series into a 5-y cycle and decycled trend, average grasshopper abundance declined by 2.1%/y in ungrazed watersheds and 2.7%/y in grazed watersheds (Fig. 1). Of the 21 abundant species, 11 declined in at least one time series, one increased (*Schistocerca lineata*), and 10 exhibited no temporal trend (S1 Appendix, Tables S4–S6).

**Large-Scale Climate Oscillations as Cause of Cycles.** Large-scale climate oscillations were good predictors of long-term grasshopper abundances. The combined climate index consisting of seasonal indices in the top AIC<sub>c</sub> (Akaike’s Information Criterion corrected for small sample size) model for ungrazed watersheds (spring ENSO + summer NAO – winter PDO; S1 Appendix, Table S74) was positively correlated with grasshopper abundance (Fig. 1 A and G;  $F_{(1,20)} = 15.2$ ,  $R^2 = 0.43$ ,  $P < 0.001$ ). The combined climate index consisting of seasonal indices in the top AIC<sub>c</sub> model for grazed watersheds (summer NAO – spring PDO; S1 Appendix, Table S74) was positively correlated with grasshopper abundance (Fig. 1 B and H;  $F_{(1,14)} = 16.4$ ,  $R^2 = 0.54$ ,  $P = 0.001$ ).



**Fig. 1.** Mean grasshopper abundance/sample ( $\pm$ SE) exhibited a linear decline from 1996 to 2017 in ungrazed KNZ watersheds (A;  $F_{(1,20)} = 7.5$ ,  $R^2 = 0.27$ ,  $P = 0.01$ , slope =  $-0.022$ ) and from 2002 to 2017 in bison-grazed KNZ watersheds (B;  $F_{(1,14)} = 9.7$ ,  $R^2 = 0.41$ ,  $P = 0.008$ , slope =  $-0.033$ ). The time series of grasshopper abundances in ungrazed watersheds was decomposed into a 5-y cycle (C) and decycled (E) trend. The time series of grasshopper abundances in grazed watersheds was decomposed into a 5-y cycle (D) and decycled (F) trend. Black dashed lines indicate linear regression trends of the raw abundances (A and B); solid black lines indicate linear regression of decycled trends (E and F). Declines persisted after removing the cycle for grasshopper abundances in both ungrazed time series (E;  $F_{(1,20)} = 8.9$ ,  $R^2 = 0.31$ ,  $P = 0.007$ , slope =  $-0.021$ ) and grazed time series (F;  $F_{(1,14)} = 16.4$ ,  $R^2 = 0.54$ ,  $P = 0.001$ , slope =  $-0.027$ ). The presence of the 5-y cycle had minimal impact on the slope of grasshopper abundance over time in ungrazed watersheds. In the shorter time series from grazed watersheds, the decomposed estimate of a 2.7% annual decline was ~20% less steep than the raw estimate of a 3.3% annual decline, supporting the axiom that, in a cyclical system, shorter time series increase the likelihood of slope estimation error (S1 Appendix, Fig. S12). Mean grasshopper abundance/sample in ungrazed watersheds (A) was positively correlated with the combined climate index of spring ENSO + summer NAO – winter PDO (G). Mean grasshopper abundance/sample in grazed watersheds (B) was positively correlated with the climate index of summer NAO – spring PDO in grazed watersheds (H).

*S1 Appendix, Table S7B*) was positively correlated with grasshopper abundance (Fig. 1 *B* and *H*;  $F_{(1,14)} = 16.4$ ,  $R^2 = 0.54$ ,  $P = 0.001$ ). Summer NAO, the seasonal climate oscillation appearing in both indices, decreased over time ( $F_{(1,34)} = 12.6$ ,  $R^2 = 0.27$ ,  $P = 0.001$ ), and was negatively correlated with grass biomass (*S1 Appendix, Fig. S7 and Table S8*;  $F_{(1,30)} = 5.7$ ,  $R^2 = 0.16$ ,  $P = 0.02$ ), suggesting changing climate may play a role in driving nutrient dilution.

**Nutrient Dilution as Cause of Grasshopper Declines.** We tested the relationship between plant nutrient dilution and grasshopper abundances using more than three decades of plant biomass and elemental chemistry. Plant biomass increased ( $F_{(1,30)} = 16.3$ ,  $R^2 = 0.35$ ,  $P < 0.001$ ) by 60%, driven by a doubling of grass biomass (*S1 Appendix, Fig. S8*). Over the same period, site mean annual temperature increased whereas cumulative annual precipitation exhibited no temporal trend (*S1 Appendix, Fig. S9*). Consistent with ND, the grass tissue concentrations of four of five elements which limit grasshopper abundance (39) declined. Nitrogen declined 42% from 1985 to 2016, P declined 58%, K declined 54%, and Na declined 90%. Only Mg did not trend over the three decades (*S1 Appendix, Fig. S10*). The five elemental nutrient concentrations were highly correlated and thus were collapsed using principal component analysis into an index of nutrient dilution (*S1 Appendix, Table S9*). Nutrient declines tracked increases in grass biomass (Fig. 2 *A* and *B*). Finally, and as predicted by ND, grasshopper abundances decreased as the nutrient content of grass tissue decreased (Fig. 2 *C* and *D*). Nutrient dilution and climate indices explained grasshopper declines, with a structural equation model of both predictors capturing 44% of the variation in grasshopper abundances in the same watershed sampled for plant chemistry (*S1 Appendix, Fig. S11 and Table S10*).

## Discussion

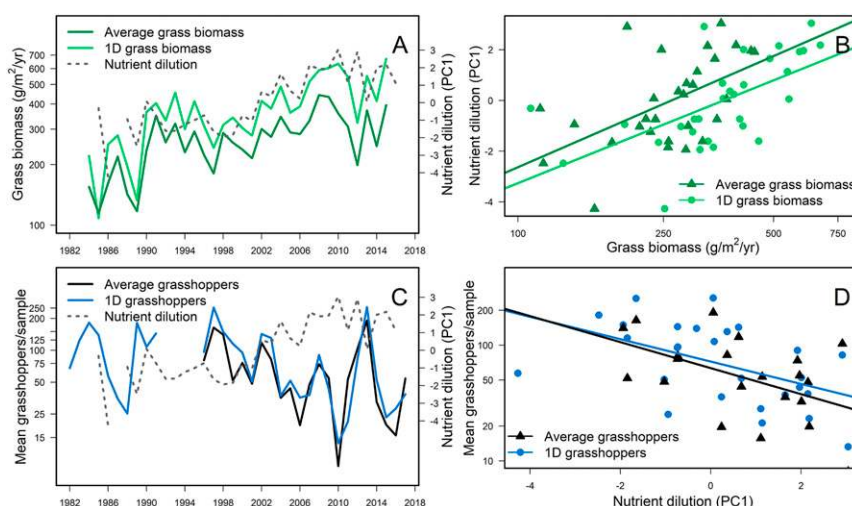
On a large Great Plains preserve, grasshopper abundances declined 36% over 22 y in ungrazed watersheds and 33.7% over 16 y in grazed watersheds after accounting for cyclicity (Fig. 1). The declines correspond to changes predicted by ND: grasshopper abundances decreased with reduced foliage tissue concentrations of N, P, K, and Na, even as the total quantity of the vegetation

increased by 60%. In short, even as the prairie became “greener,” the amount of nutrients per mouthful of plant tissue yielded fewer nutrients. Such declines are expected to continue, with rising CO<sub>2</sub> and climate change models predicting increasing temperatures and growing season precipitation for the Midwestern United States (40, 41).

Here we provide evidence of a direct link between ND and a 2+%/annual decline in a dominant grassland herbivore over two decades. The underlying cause of nutrient dilution that cascaded through this ecosystem is likely, in part, increasing dominance of high-biomass C<sub>4</sub> grasses (42) over the same period. Climate may partially drive changes in grass biomass, as increases were correlated with decreases in summer NAO. Additionally, increasing atmospheric CO<sub>2</sub> favors C<sub>4</sub> grasses (43). While a caveat of our study is that our plant elemental chemistry came from one watershed, declining plant elemental nutrient concentrations with CO<sub>2</sub> enrichment experiments are supported by a review of 19 meta-analyses and five long-term observational studies on this topic (*S1 Appendix, Table S1*), including a decline in grassland plant %N since about 1926 in Kansas (31). This complements work showing that herbivores consume more but grow less with decreased plant nutrient content in CO<sub>2</sub> enrichment experiments (30, 36) and a study of long-term declines in %N content of pollen linked to pollinator declines (37).

The 2%/y decline in grasshopper abundance is a rate shared with four studies of another insect herbivore, butterflies (14). However, unlike transects associated with those studies, which were often intermixed in heavily modified habitat, the KNZ transects were arrayed across 3,487 ha of predominantly unplowed, native tallgrass prairie. While we do not discount the importance of habitat loss and other drivers of insect declines, ND requires only an increase in CO<sub>2</sub>, precipitation, or temperature to enhance ecosystem primary productivity—conditions that are potentially global in scope—and, unlike pesticides, targets herbivores specifically. In that respect, it is notable that a 10-y study of insect declines in 150 European grasslands, while implicating landscape use, found significant declines in abundances of herbivores and omnivores but not carnivores (44).

Grasslands, which constitute ~40% of terrestrial biomes (45), are likely particularly prone to nutrient dilution, given that they



**Fig. 2.** Both nutrient dilution PC1 and grass biomass increased over time (*A*). Both aboveground grass biomass within watershed 1D ( $F_{(1,28)} = 24.1$ ,  $R^2 = 0.46$ ,  $P < 0.001$ ), where plant chemistry was measured, and the average grass biomass from the three watersheds sampled for plant biomass ( $F_{(1,28)} = 13.2$ ,  $R^2 = 0.32$ ,  $P = 0.001$ ) were positively correlated with nutrient dilution PC1 (*B*). Nutrient dilution increased while mean grasshopper abundances per sample decreased over time (*C*). The mean grasshopper abundance in watershed 1D (27 y of overlapping data;  $F_{(1,25)} = 8.1$ ,  $R^2 = 0.25$ ,  $P = 0.009$ ) and the mean grasshopper abundance in all ungrazed watersheds (21 y of overlapping data;  $F_{(1,19)} = 6.2$ ,  $R^2 = 0.25$ ,  $P = 0.02$ ) were negatively correlated with nutrient dilution PC1 (*D*).



show high variation in primary productivity (42). ND may also manifest through interannual patterns in rainfall. Drought conditions, by reducing annual primary productivity, can increase concentrations of plant nutrients, increasing grasshopper abundances (46). This may explain both why grasshopper abundances increase with cycle indices that are negatively correlated with local precipitation, and why grasshopper abundances increased around 2012 (Fig. 1), corresponding to a regional drought (47).

Climate oscillation indices often prove better predictors of animal population size than local weather, likely because they operate over larger temporal and spatial windows (48, 49). Likewise, we found that seasonal measures of ENSO, NAO, and PDO were better predictors of midseason grasshopper abundance than local temperature and precipitation. Climate may have many indirect effects on grasshopper abundance, such as through plant quality, plant quantity, and grasshopper and plant phenology. We showed that both nutrient dilution and climate indices explain variations in grasshopper abundance (*S1 Appendix*, Fig. S11), highlighting such system complexity. For example, while grasshopper abundances positively correlated with climate indices relating to overall cooler temperatures (*S1 Appendix*, Figs. S14–S17), winter temperatures marginally increased abundances in the longer time series (*S1 Appendix*, Fig. S18 and Table S11A), potentially due to increased egg and overwintering nymph survival with less winter freezing (50).

**Future Directions.** Decidedly missing from recent studies reporting insect declines is the decomposition of abundance into trends and cycles. It does not escape our notice that recent literature contains time series of insect abundances with the visual appearance of multiyear cycles, although they remain unanalyzed (e.g., refs. 10, 14, 16, 44, and 51–53). Continuous long-term monitoring and accounting for cyclicity are critical for assessing responses of ecological communities to changing habitats and climate, especially as they are potentially relevant for two mechanisms of insect declines—rising temperatures and nutrient dilution. Documenting abundance and diversity trends is a key first step in this process (54). However, climate, community composition, pesticides, pollutants, and habitat loss often change over time, highlighting the need for experimental studies. Linking patterns to process—that is, simultaneously testing hypothesized drivers—greatly increases our ability to interpret data and propose remedies (55).

Determining drivers affecting insect communities is critical, as insects often have unassessed or high extinction risk (56) and are important providers of ecosystem services (57). Predictive models, such as our joint climate cycle indices, can aid in forecasting future grasshopper abundances for the benefit of integrative pest management models (58). Additionally, this study shows long-term declines in total grasshopper community abundances (24, 59, 60), although more than a quarter of European orthopteran species are listed as threatened (61). Grasshoppers are abundant aboveground herbivores that contribute substantially to turnover of grassland plant biomass (62, 63) and nutrient cycling (64), and they are a food source for many species of conservation concern such as grassland songbirds (65). The importance of grasshoppers for breeding-bird diets is consistent with grassland birds showing the largest absolute declines (53%) of all North American avifauna (66).

Models of long-term changes in insect productivity that contrast the many potential drivers are critical in light of recent studies finding striking declines (3, 4, 10) as well as criticism of this work (7, 15, 67, 68). In that light, if nutrient dilution is

widespread and also drives declines in insect herbivores as we propose, then remedies—particularly reducing atmospheric CO<sub>2</sub>—will be both essential and challenging.

## Materials and Methods

**Site Description and Long-Term Datasets.** KNZ is an NSF LTER site consisting of 3,487 ha of predominantly unplowed, native tallgrass prairie in northeastern Kansas. KNZ consists of a landscape-scale two-way factorial experiment in which watersheds are subjected to different treatments of fire frequency and are ungrazed or grazed by bison (38). Long-term grasshopper (69), plant biomass (70), and weather datasets are available at <http://lter.konza.ksu.edu/>. For full descriptions of these datasets and sampling protocols, see *S1 Appendix*.

**Cycle Detection and Time Series Decomposition.** If insect abundances display temporal cycles, limited sampling intervals and/or the time at which sampling starts and stops in relation to cycle phase can cause error in estimation of long-term temporal abundance trends (*S1 Appendix*, Fig. S12). To identify and correct for cycles in continuous grasshopper time series, we conducted spectral analysis and removed significant cycles using decomposition. We provide details on spectral analysis and decomposition in *S1 Appendix*. The R code for time series analysis is publicly available at Figshare (<https://doi.org/10.6084/m9.figshare.11862483>).

**Climate Signal.** Climate indices that were included in top models compared using AIC<sub>c</sub> and had relative importance values >0.5 were multiplied by the sign (+ or −) of their model estimate and summed to produce a combined predictive climate cycle index. We provide details on AIC models in *S1 Appendix*. We examined relationships between grasshopper abundances and combined climate indices using linear regression. We tested whether seasonal climate cycle indices in the top model for the longer time series predicted grass and forb biomass using one-way ANOVA.

**Plant Nutrients.** To complement LTER datasets, we analyzed elemental composition of grasses collected at the end of the growing season in one ungrazed and annually burned watershed (watershed code: 1D) using dried and ground grass samples collected from the plant biomass dataset (70). We summarized variation in the elements N, P, K, Na, and Mg—those most likely to drive grasshopper abundances (39)—using PCA. PCA (*S1 Appendix*, Fig. S13A) has one significant axis (*S1 Appendix*, Fig. S13B), which is negatively correlated with N, P, K, and Na (*S1 Appendix*, Table S9); thus, we refer to PC1 as nutrient dilution PC1. In order to see if nutritional quality declines with increasing plant biomass, we examined the relationship between grass biomass and nutrient dilution PC1. We tested ND by examining the relationship between nutrient dilution PC1 and grasshopper abundances using linear regression. Additionally, we used a structural equation model (SEM) to examine direct and indirect relationships related to 1D grasshopper abundances. Details on chemical, principal component, and SEM analyses are in *S1 Appendix*.

**Data Availability Statement.** Grasshopper abundance (<https://doi.org/10.6073/pasta/7b2259dcb0e499447e0e11dfb562dc2f>) and plant biomass data (<https://portal.lternet.edu/nis/mapbrowse?packageid=knb-lter-knz.55.12>) are available from the Long-Term Ecological Research (LTER) Data Portal. Plant elemental chemistry are provided in *S1 Appendix*, Table S12. Script for time series analysis is available at Figshare (<https://doi.org/10.6084/m9.figshare.11862483>) and example time series are available at Figshare (<https://doi.org/10.6084/m9.figshare.11862459>).

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1. L. A. Burkle, J. C. Marlin, T. M. Knight, Plant-pollinator interactions over 120 years: Loss of species, co-occurrence, and function. *Science* **339**, 1611–1615 (2013).
2. J. Ollerton, H. Erenler, M. Edwards, R. Crockett, Pollinator declines. Extinctions of aculeate pollinators in Britain and the role of large-scale agricultural changes. *Science* **346**, 1360–1362 (2014).
3. A. Valtonen et al., Long-term species loss and homogenization of moth communities in Central Europe. *J. Anim. Ecol.* **86**, 730–738 (2017).

4. C. A. Hallmann et al., More than 75 percent decline over 27 years in total flying insect biomass in protected areas. *PLoS One* **12**, e0185809 (2017).
5. J. Paukkunen, J. Pöyry, M. Kuussaari, Species traits explain long-term population trends of Finnish cuckoo wasps (Hymenoptera: Chrysididae). *Insect Conserv. Divers.* **11**, 58–71 (2018).
6. C. J. MacGregor, J. Williams, J. Bell, C. Thomas, Moth biomass increases and decreases over 50 years in Britain. *Nat. Ecol. Evol.* **3**, 1645–1649 (2019).

7. A. M. V. Fournier, E. R. White, S. B. Heard, Site-selection bias and apparent population declines in long-term studies. *Conserv. Biol.* **33**, 1370–1379 (2019).
8. J. Bojková, V. Rádková, T. Soldán, S. Zahradkova, Trends in species diversity of lotic stoneflies (Plecoptera) in the Czech Republic over five decades. *Insect Conserv. Divers.* **7**, 252–262 (2014).
9. J. E. Ball-Damerow, L. K. McGonigle, V. H. Resh, Changes in occurrence, richness, and biological traits of dragonflies and damselflies (Odonata) in California and Nevada over the past century. *Biodivers. Conserv.* **23**, 2107–2126 (2014).
10. B. C. Lister, A. Garcia, Climate-driven declines in arthropod abundance restructure a rainforest food web. *Proc. Natl. Acad. Sci. U.S.A.* **115**, E10397–E10406 (2018).
11. J. E. Harris, N. L. Rodenhouse, R. T. Holmes, Decline in beetle abundance and diversity in an intact temperate forest linked to climate warming. *Biol. Conserv.* **240**, 108219 (2019).
12. S. Schuch, J. Bock, B. Krause, K. Wesche, M. Schaefer, Long-term population trends in three grassland insect groups: A comparative analysis of 1951 and 2009. *J. Appl. Entomol.* **136**, 321–331 (2012).
13. E. R. White, Minimum time required to detect population trends: The need for long-term monitoring programs. *Bioscience* **69**, 40–46 (2019).
14. T. Wepprich, J. R. Adrion, L. Ries, J. Wiedmann, N. M. Haddad, Butterfly abundance declines over 20 years of systematic monitoring in Ohio, USA. *PLoS One* **14**, e0216270 (2019).
15. J. C. Habel, M. J. Samways, T. Schmitt, Mitigating the precipitous decline of terrestrial European insects: Requirements for a new strategy. *Biodivers. Conserv.* **28**, 1343–1360 (2019).
16. D. R. Brooks *et al.*, Large carabid beetle declines in a United Kingdom monitoring network increases evidence for a widespread loss in insect biodiversity. *J. Appl. Ecol.* **49**, 1009–1019 (2012).
17. Y. Melero, C. Stefanescu, J. Pino, General declines in Mediterranean butterflies over the last two decades are modulated by species traits. *Biol. Conserv.* **201**, 336–342 (2016).
18. A. B. Swengel, S. R. Swengel, Grass-skipper (Hesperiinae) trends in midwestern USA grasslands during 1988–2013. *J. Insect Conserv.* **19**, 279–292 (2015).
19. C. Shortall *et al.*, Long-term changes in the abundance of flying insects. *Insect Conserv. Divers.* **2**, 251–260 (2009).
20. G. Meehl, J. M. Arblaster, G. Branstator, Mechanisms contributing to the warming hole and the consequent U.S. east-west differential of heat extremes. *J. Clim.* **25**, 6394–6408 (2012).
21. K. M. de Beurs, G. M. Henebry, B. C. Owsley, I. N. Sokolik, Large scale climate oscillation impacts on temperature, precipitation and land surface phenology in Central Asia. *Environ. Res. Lett.* **13**, 065018 (2018).
22. M. D. Hunter, P. W. Price, Cycles in insect populations: Delayed density dependence or exogenous driving variables? *Ecol. Entomol.* **23**, 216–222 (1998).
23. J. L. Jonas, A. Joern, Grasshopper (Orthoptera: Acrididae) communities respond to fire, bison grazing and weather in North American tallgrass prairie: A long-term study. *Oecologia* **153**, 699–711 (2007).
24. J. L. Jonas, W. Wolesensky, A. Joern, Weather affects grasshopper population dynamics in continental grassland over annual and decadal periods. *Rangeland Ecol. Manag.* **68**, 29–39 (2015).
25. N. J. Mantua, S. R. Hare, Y. Zhang, J. M. Wallace, R. C. Francis, A Pacific interdecadal climate oscillation with impacts on salmon production. *Bull. Am. Meteorol. Soc.* **78**, 1069–1079 (1997).
26. N. C. Stenseth *et al.*, Ecological effects of climate fluctuations. *Science* **297**, 1292–1296 (2002).
27. C. M. Prather *et al.*, Invertebrates, ecosystem services and climate change. *Biol. Rev. Camb. Philos. Soc.* **88**, 327–348 (2013).
28. D. E. Lincoln, The influence of plant carbon dioxide and nutrient supply on susceptibility to insect herbivores. *Vegetatio* **104**, 273–280 (1993).
29. E. L. Zvereva, M. V. Kozlov, Consequences of simultaneous elevation of carbon dioxide and temperature for plant–herbivore interactions: A meta-analysis. *Glob. Change Biol.* **12**, 27–41 (2006).
30. E. A. Robinson, G. D. Ryan, J. A. Newman, A meta-analytical review of the effects of elevated CO<sub>2</sub> on plant–arthropod interactions highlights the importance of interacting environmental and biological variables. *New Phytol.* **194**, 321–336 (2012).
31. K. K. McLaughlin, C. J. Ferguson, I. E. Wilson, T. W. Ocheltree, J. M. Craine, Thirteen decades of foliar isotopes indicate declining nitrogen availability in central North American grasslands. *New Phytol.* **187**, 1135–1145 (2010).
32. M.-S. Fan *et al.*, Evidence of decreasing mineral density in wheat grain over the last 160 years. *J. Trace Elem. Med. Biol.* **22**, 315–324 (2008).
33. C. M. Prather *et al.*, Seeking salt: Herbivorous prairie insects can be co-limited by macronutrients and sodium. *Ecol. Lett.* **21**, 1467–1476 (2018).
34. I. Loladze, Hidden shift of the ionome of plants exposed to elevated CO<sub>2</sub> depletes minerals at the base of human nutrition. *eLife* **3**, e02245 (2014).
35. S. T. Behmer, Insect herbivore nutrient regulation. *Annu. Rev. Entomol.* **54**, 165–187 (2009).
36. P. Stiling, T. Cornelissen, How does elevated carbon dioxide (CO<sub>2</sub>) affect plant–herbivore interactions? A field experiment and meta-analysis of CO<sub>2</sub>-mediated changes on plant chemistry and herbivore performance. *Glob. Change Biol.* **13**, 1823–1842 (2007).
37. L. H. Ziska *et al.*, Rising atmospheric CO<sub>2</sub> is reducing the protein concentration of a floral pollen source essential for North American bees. *Proc. Biol. Sci.* **283**, 20160414 (2016).
38. S. L. Collins, L. B. Calabrese, Effects of fire, grazing and topographic variation on vegetation structure in tallgrass prairie. *J. Veg. Sci.* **23**, 563–575 (2012).
39. A. Joern, T. Provin, S. T. Behmer, Not just the usual suspects: Insect herbivore populations and communities are associated with multiple plant nutrients. *Ecology* **93**, 1002–1015 (2012).
40. J. T. Schoof, S. C. Pryor, J. Surprenant, Development of daily precipitation projections for the United States based on probabilistic downscaling. *J. Geophys. Res. Atmos.* **115**, D13106 (2010).
41. USGCRP, “Impacts, risks, and adaptation in the United States” in *Fourth National Climate Assessment*, D. R. Reidmiller *et al.*, Eds. (US Global Change Research Program, 2018), vol. II.
42. K. La Pierre *et al.*, Explaining temporal variation in above-ground productivity in a mesic grassland: The role of climate and flowering. *J. Ecol.* **99**, 1250–1262 (2011).
43. P. B. Reich, S. E. Hobbie, T. D. Lee, M. A. Pastore, Unexpected reversal of C<sub>3</sub> versus C<sub>4</sub> grass response to elevated CO<sub>2</sub> during a 20-year field experiment. *Science* **360**, 317–320 (2018).
44. S. Seibold *et al.*, Arthropod decline in grasslands and forests is associated with landscape-level drivers. *Nature* **574**, 671–674 (2019).
45. J. Hoekstra *et al.*, Confronting a biome crisis: Global disparities of habitat loss and protection. *Ecol. Lett.* **8**, 23–29 (2005).
46. A. Franzke, K. Reinhold, Stressing food plants by altering water availability affects grasshopper performance. *Ecosphere* **2**, 1–13 (2011).
47. M. Hoerling *et al.*, Causes and predictability of the 2012 Great Plains drought. *Bull. Am. Meteorol. Soc.* **95**, 269–282 (2014).
48. T. B. Hallett *et al.*, Why large-scale climate indices seem to predict ecological processes better than local weather. *Nature* **430**, 71–75 (2004).
49. N. C. Stenseth, A. Mysterud, Weather packages: Finding the right scale and composition of climate in ecology. *J. Anim. Ecol.* **74**, 1195–1198 (2005).
50. B.-P. Pang, N. Li, X.-R. Zhou, Supercooling capacity and cold hardness of band-winged grasshopper eggs (Orthoptera: Acrididae). *J. Insect Sci.* **14**, 289 (2014).
51. G. Hu *et al.*, Mass seasonal bioflows of high-flying insect migrants. *Science* **354**, 1584–1587 (2016).
52. K. F. Conrad, M. S. Warren, R. Fox, M. S. Parsons, I. P. Woiwod, Rapid declines of common, widespread British moths provide evidence of an insect biodiversity crisis. *Biol. Conserv.* **132**, 279–291 (2006).
53. S. L. Hermann *et al.*, Thermally moderated firefly activity is delayed by precipitation extremes. *R. Soc. Open Sci.* **3**, 160712 (2016).
54. R. Dirzo *et al.*, Defaunation in the Anthropocene. *Science* **345**, 401–406 (2014).
55. B. J. Cardinale, A. B. Gonzalez, G. R. H. Allington, M. Loreau, Is local biodiversity declining or not? A summary of the debate over analysis of species richness time trends. *Biol. Conserv.* **219**, 175–183 (2018).
56. C. D. Thomas *et al.*, Extinction risk from climate change. *Nature* **427**, 145–148 (2004).
57. Y. Basset, G. P. A. Lamarre, Toward a world that values insects. *Science* **364**, 1230–1231 (2019).
58. D. H. Branson, A. Joern, G. A. Sword, Sustainable management of insect herbivores in grassland ecosystems: New perspectives in grasshopper control. *Bioscience* **56**, 743–755 (2006).
59. E. White, J. Sedcole, A 20-year record of alpine grasshopper abundance, with interpretations for climate change. *N. Z. J. Ecol.* **15**, 139–152 (1991).
60. S. Schuch, J. Bock, C. Leuschner, M. Schaefer, K. Wesche, Minor changes in orthopteran assemblages of Central European protected dry grasslands during the last 40 years. *J. Insect Conserv.* **15**, 811–822 (2011).
61. A. Hochkirch *et al.*, *European Red List of Grasshoppers, Crickets and Bush-Crickets* (Publications Office of the European Union, 2016).
62. A. N. Andersen, J. A. Ludwig, L. M. Lowe, D. C. F. Rentz, Grasshopper biodiversity and bioindicators in Australian tropical savannas: Responses to disturbance in Kakadu National Park. *Austral Ecol.* **26**, 213–222 (2001).
63. A. N. Laws, C. M. Prather, D. H. Branson, S. C. Pennings, Effects of grasshoppers on prairies: Herbivore composition matters more than richness in three grassland ecosystems. *J. Anim. Ecol.* **87**, 1727–1737 (2018).
64. G. E. Belovsky, J. B. Slade, Insect herbivory accelerates nutrient cycling and increases plant production. *Proc. Natl. Acad. Sci. U.S.A.* **97**, 14412–14417 (2000).
65. A. Joern, Context-dependent foraging and enemy-free space: Grasshopper sparrows (*Ammodramus savannarum*) searching for grasshoppers (Acrididae). *Ecoscience* **9**, 231–240 (2002).
66. K. V. Rosenberg *et al.*, Decline of the North American avifauna. *Science* **366**, 120–124 (2019).
67. P. Cardoso, S. R. Leather, Predicting a global insect apocalypse. *Insect Conserv. Divers.* **12**, 263–267 (2019).
68. M. R. Willig *et al.*, Populations are not declining and food webs are not collapsing at the Luquillo Experimental Forest. *Proc. Natl. Acad. Sci. U.S.A.* **116**, 12143–12144 (2019).
69. A. Joern, CGR02 sweep sampling of grasshoppers on Konza Prairie LTER watersheds. <https://doi.org/10.6073/pasta/7b2259dcb0e499447e0e11dfb562dc2f>. Accessed 3 April 2019.
70. J. Blair, J. Nippert, PAB01 aboveground net primary productivity of tallgrass prairie based on accumulated plant biomass on Core LTER watersheds (001d, 004b, 020b). <https://doi.org/10.6073/pasta/38de94ec00e7d553197910b835c37b7d>. Accessed 15 April 2019.