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_2 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_2-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

As 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_2 and climatic increases in H_2O 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_2 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_2 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_2 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_2—diluting the concentrations in plant tissue of key nutrients which in turn predicted the declines of a dominant herbivore. Nutrient dilution, like CO_2 enrichment, is likely a global phenomenon, posing a challenge to Earth's herbivore populations.

ECOLOGY

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_c (Akaike's Information Criterion corrected for small sample size) model for ungrazed watersheds (spring ENSO + summer NAO − winter PDO; *S1 Appendix*, Table S7A) 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_c model for grazed watersheds (summer NAO − spring PDO;
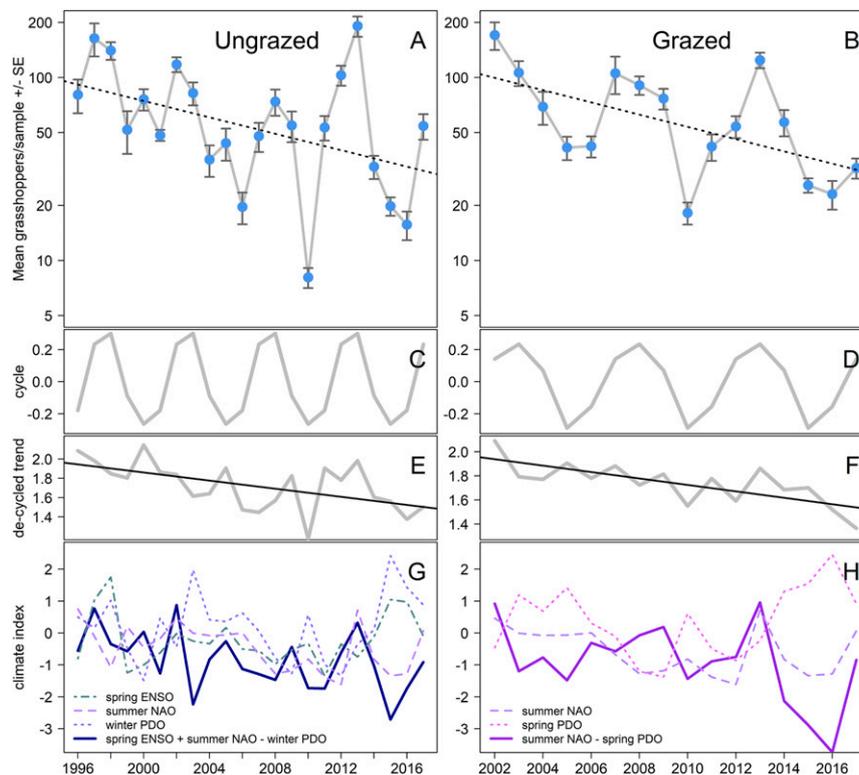

Fig. 1. Mean grasshopper abundance/sample (±SE) exhibited a linear decline from 1996 to 2017 in ungrazed KNZ watersheds (*A*; $F_{(1,20)} = 7.5$, $R^2 = 0.27$, $P = 0.01$, slope = −0.022) and from 2002 to 2017 in bison-grazed KNZ watersheds (*B*; $F_{(1,14)} = 9.7$, $R^2 = 0.41$, $P = 0.008$, slope = −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 (*SI 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*).

Welti et al.

) 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_2 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_4 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_2 favors C_4 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_2 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_2 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_2, 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
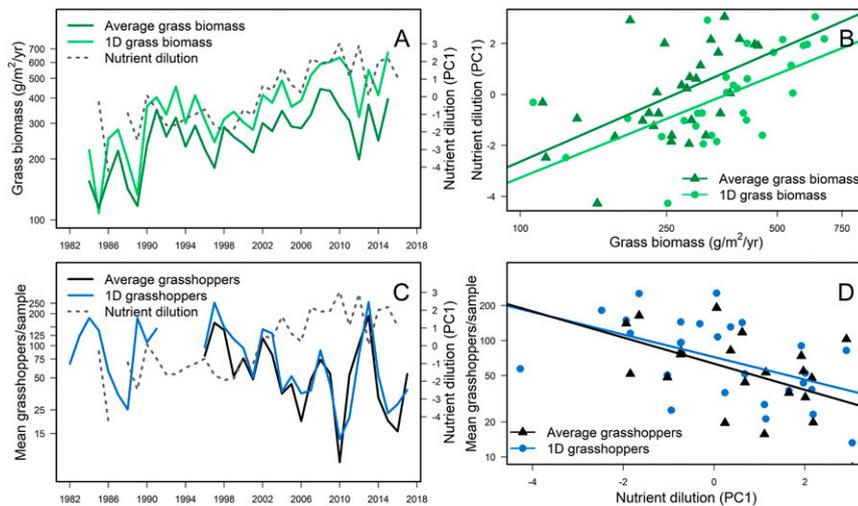

Fig. 2. Both nutrient dilution PC1 and grass biomass increased over time (*A*). Both aboveground grass biomass within watershed 1D ($F_{(1,28)} = 24.1$, $R^2 = 0.46$, $P < 0.001$), where plant chemistry was measured, and the average grass biomass from the three watersheds sampled for plant biomass ($F_{(1,28)} = 13.2$, $R^2 = 0.32$, $P = 0.001$) 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_2—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 AICc 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 *SI 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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