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Community ecology

How and why grasshopper community maturation rates are slowing on a North American tall grass prairie

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Invertebrate growth rates have been changing in the Anthropocene. We examine rates of seasonal maturation in a grasshopper community that has been declining annually greater than 2% a year over 34 years. As this grassland has experienced a 1°C increase in temperature, higher plant biomass and lower nutrient densities, the community is maturing more slowly. Community maturation had a nutritional component: declining in years/watersheds with lower plant nitrogen. The effects of fire frequency were consistent with effects of plant nitrogen. Principal components analysis also suggests associated changes in species composition—declines in the densities of grass feeders were associated with declines in community maturation rates. We conclude that slowed maturation rates—a trend counteracted by frequent burning—likely contribute to long-term decline of this dominant herbivore.

1. Introduction

In temperate climates, insects with annual life cycles have a limited time to convert food into growing bodies and reproductive tissue. Developmental rate is thus a basic component of fitness—one that has shown ubiquitous recent change [1]. In grasshoppers, the phenology of individuals transitioning from egg to adult—like the phenology of plant development [2] and avian migration [3]—responds to a complex of drivers. At the same time, the maturation rate of this dominant herbivore has broad implications for grassland communities by altering the availability of grasshoppers as prey. Here, we analyse a 34-year record of grasshopper community development in a North American prairie toward identifying how trends in temperature, biogeochemistry and management account for changes in a community's developmental age.

For ectotherms, thermal performance curves (TPCs) reflect how activity and growth are unimodal functions of temperature [4–6] generating different responses to warming depending on average temperature and the size and direction of the temperature change [7,8]. The importance of temperature in grasshopper development is reflected in its frequent increase with degree days (number of days above a biologically relevant temperature, [9–11]). Indeed, warming typically results in faster animal development to smaller size [6,12], but see [13], suggesting community temperatures are frequently on the increasing side of the TPC.

A second constraint on development is the availability of the *ca* 25 elements [14,15]—all essential—that, like temperature, vary in time and space [16]. Although the function of elements *in vivo* is still poorly understood [17,18], three elements have consistently been shown to limit grasshopper abundance in the field. Sodium (Na) is an electrolyte that frequently limits the abundance

Table 1. Watersheds were grasshopper sampling occurred. Aboveground plant biomass and plant tissue chemistry was analysed for the three watersheds: 1d, 4b and 20b. U = ungrazed and G = bison grazed. Fire freq refers to the burn interval in years.

watershed	latitude	longitude	grazed	fire freq	start year	end year
1d	39.07865	−96.5626	U	1	1982	2019
20b	39.07255	−96.5775	U	20	1982	2019
2c	39.06966	−96.5626	U	2	1987	2019
2d	39.0786	−96.557	U	2	1984	2019
4b	39.07497	−96.598	U	4	1982	2019
4f	39.07385	−96.5712	U	4	1984	2019
n1a	39.0936	−96.5902	G	1	2002	2018
n1b	39.0813	−96.5714	G	1	2002	2018
n20a	39.0953	−96.5987	G	20	2002	2018
n20b	39.08685	−96.5706	G	20	2002	2018
n4a	39.0803	−96.6059	G	4	2002	2018
n4d	39.07985	−96.5834	G	4	2002	2018

of insect herbivores [19–22]. Phosphorus (P) is a key element limiting growth rates [23] that tends to reach higher tissue levels in smaller, developing organisms [24]. Nitrogen (N) like temperature can have a unimodal effect on grasshopper life history, limiting abundance in experimental studies when added alone [25], see also [26,27] or in conjunction with P [28]. However, reflecting the unimodal relationship between N and fitness, a high ratio of N to carbohydrates can inhibit growth in grasshopper nymphs [29].

Temperature, plant biomass and nutrient density also vary with landscape level processes like grazing and fire. Grazing can have positive effects on grasshopper populations by warming the soil, increasing egg development temperature [9,10], and by enhancing the nutrient content of vegetation through cropping and excretion [30]. Likewise, as plant N content tends to accumulate with time since fire [31], fire frequency can alter grasshopper fitness.

Here, we use a 34-year dataset of grasshopper abundance and age structure + plant biomass and chemistry on a native tallgrass prairie to refine our hypotheses as to the drivers of seasonal community maturity—the weighted distribution of individuals across five growth stages. In this Kansas grassland [32], (1) grasshopper abundance has declined by greater than 2% year over this same period, (2) temperature has increased by *ca* 1°C, (3) precipitation has not, (4) grass biomass has doubled, and, in one watershed, (5) tissue density of N, P and Na in plant samples has declined. We focus on the working hypotheses that both temperature and nutrient density are unimodal drivers, increasing or decreasing based on the state of the system. We do so by first using the longest record on annually burned ungrazed grasslands, then extend those findings to experimentally burned and grazed watersheds, with their own effects on temperature and nutrient density.

2. Methods

(a) Site description

Konza Prairie (KNZ) is a 3487-ha tallgrass prairie and long-term ecological research (LTER) site in northeast Kansas, USA (39°05′ N, 96°35′ W). The site's watersheds are experimentally subjected to crossed design treatments of large-scale fire frequency (1, 2, 4 and 20 year fire return intervals) and grazing (bison grazed and ungrazed). KNZ averaged 12.7°C and 839 mm rain yr^{-1} across the study period (1982–2019). Climate data collected at KNZ headquarters were sourced from [33]. We calculated average temperature and cumulative precipitation annually from January to July (when grasshoppers were sampled) as climate predictors.

(b) Grasshopper sampling

Grasshoppers in the family Acrididae were collected on KNZ from 1982 to 1991 and 1996 to 2019 [34]. Grasshoppers are collected using 38 cm diameter sweep nets in 10 subsamples of 20 sweeps each (totalling 200 sweeps per sample) in two locations per watershed and twice per year (usually mid-July and early August). For consistency, we included only samples collected in July and August and in the watersheds which had no change in land management across sampling periods (table 1). The developmental stage of each grasshopper was recorded in categories of 1st, 2nd–3rd, 4th and 5th instar or adult.

(c) Plant sampling

Aboveground plant biomass is quantified at the end of the growing season on three watersheds (watersheds: 1d, 4b and 20b; all ungrazed, with fire return intervals of 1, 4 and 20 year, respectively); data are available from 1984 to 2015 [35]. All aboveground biomass was clipped from 20 plots per watershed per year in 0.1 m^2 quadrats and sorted into categories of grass, forbs and woody plants before being dried and weighed.

Elemental chemistry was analysed for each plant category for the three watersheds and years with sufficient plant tissue. Per cent N was quantified using combustion analysis while the parts per million (ppm) of P and Na were analysed using hot plate digestion and inductively coupled plasma atomic emission spectroscopy by the Cornell Nutrient Analysis Laboratory (https://cnal.cals.cornell.edu/).

(d) Analysis

For each sample, we calculated a weighted mean of the developmental stage (DSWM) using the formula:

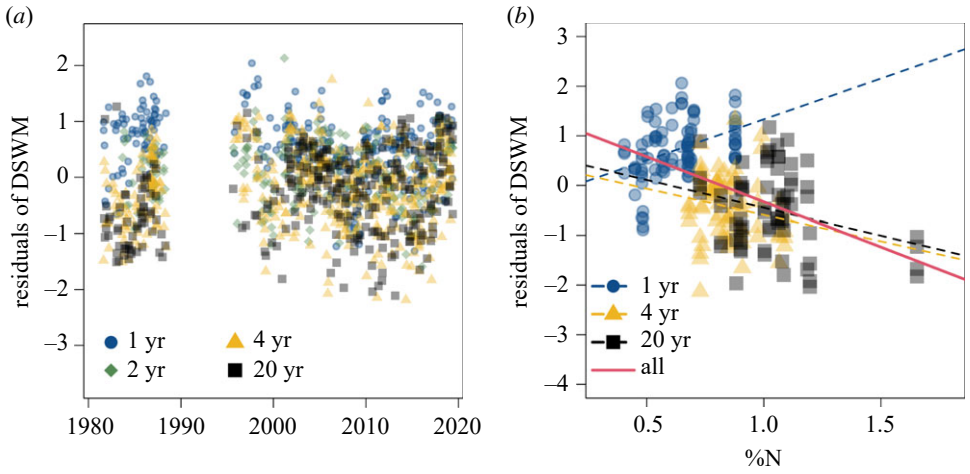

Figure 1. Changes in the residual of grasshopper weighted mean of the developmental stage (DSWM) after accounting for the effect of the DOY over time (*a*) and with concentrations of plant nitrogen for three watersheds (*b*). Points in (*a*) are coloured according to fire frequency and were horizontally jittered to improve visualization.

$$\text{DSWM} = \frac{\text{no. 1st instars} + \text{no. 2nd and 3rd instars} * 2.5 + \text{no. 4th instars} * 4 + \text{no. 5th instars} * 5 + \text{no. adults} * 6}{\text{total abundance}},$$

To test the effects of plant quantity and quality on grasshopper DSWM, we fit generalized least-squares (gls) model using the three watersheds where plant biomass was sampled. These three watersheds were all ungrazed by bison. Independent model terms included total plant biomass, and plant tissue per cent N, ppm Na and ppm P (plant terms), in addition to year, mean temperature and cumulative precipitation of Dec–Aug, fire treatment, the abundance of grasshoppers in the sample (to control for density dependence), the first two axes of a principle component analysis (PCA) of the grasshopper community—using the annual abundance of 52 taxa—to identify changes due to community composition, and the numerical day of year the sample was collected on to control for seasonal period. The model additionally included a correlation structure to group watershed and year of sample.

To test the effects of year, climate and grassland management on grasshopper DSWM, we fit a similar model but with three differences: the model was fit to all 12 watersheds, plant terms were not included, and grazing treatment was included.

Total grasshoppers per sample were $\log_{10}$ transformed and numerical variables were scaled to unit standard deviation prior to analyses. Model selection was conducted by comparing all possible model combinations and using Akaike's information criterion corrected for small sample size (AIC_c) with models with $\Delta AIC_c < 2$ considered equally parsimonious [36]. Gls models were run using the nlme package [37], PCA was conducted using vegan [38], and ΔAICc selection was done using the MuMIn package [39] in program R v. 4.0.5 [40].

3. Results

We draw on a 34-year span of grasshopper data from 84 773 individuals generating 1244 weighted means of a community's developmental stage (DSWM) from 1983 to 2019. DSWM averaged 4.03, s.e.: 0.02 and ranged from 1.3 to 6.

(a) Testing the effects of forage quality and temperature

We first analysed communities from three watersheds that were monitored for plant biomass and ppm N, P and Na. One top model was generated accounting for 53% of the variation in DSWM, with four significant terms (all $p < 0.001$) contributing roughly equally (electronic supplementary material, tables S1–S3). Accounting for sampling date (DSWM increases over the season: Est: 0.34, s.e.: 0.06), grasshopper communities matured more slowly (Est: −0.45, s.e.: 0.09; figure 1*a*) over the same interval during which grass biomass doubled, N, P and Na had declined, and average temperature increased *ca* 1°C [32]. Grasshopper communities also matured more slowly in watersheds and years with higher plant ppm N (Est: −0.26, s.e.: 0.07; figure 1*b*). However, consistent with the unimodal effects of N on fitness, in the annually burned watershed—with the lowest plant N levels—this trend was reversed: more plant N led to faster grasshopper development (figure 1*b*). Notably, temperature did not enter the model.

(b) Testing the effects of land management—burning and grazing

The top model reported seven significant terms (all $p < 0.001$, except precipitation: $p = 0.003$) accounting for 36% of the variation in DWSM. We focus here on the four that account for greater than 1% of the variation in DWSM. After accounting for seasonality (Est: 0.39, s.e.: 0.02; figure 2), grasshoppers again matured more slowly over time (Est: −0.11, s.e.: 0.03). Grasshopper communities matured more slowly in watersheds burned less frequently (Est: −0.21, s.e.: 0.03; figure 2*a*,*b*). Grazing did not enter the model.

(c) Evaluating species composition as a covariate

Finally, in both the forage quality and land management analyses above, the PC2 axis reflecting community composition (electronic supplementary material, tables S1–S3) covaried with DSWM. It accounted for 16% of the variation (Est: 0.73, s.e.: 0.1; correlated ($r > |0.3|$) in the first; and 10% in the second (PC2 Est 0.48, s.e.: 0.04]).

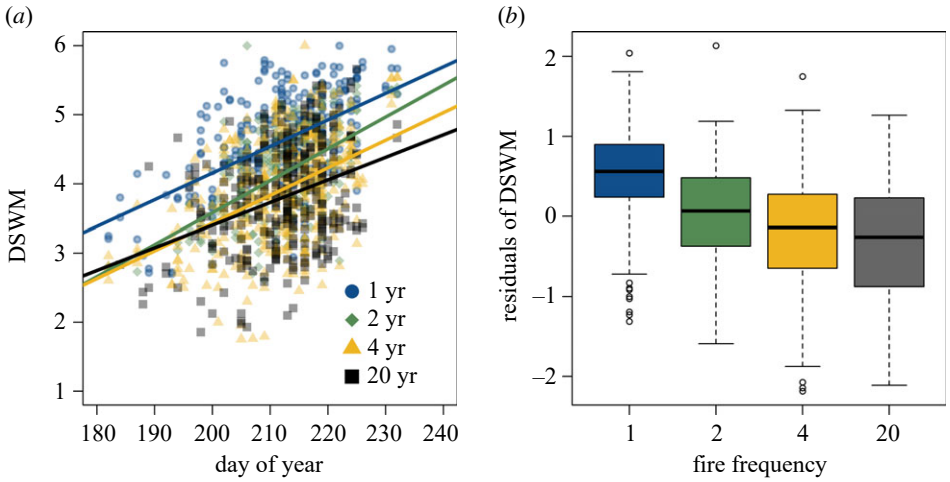

Figure 2. Changes in grasshopper weighted mean of the developmental stage (DSWM) with (*a*) sample date and (*b*) those residuals with fire frequency (years between controlled burns).

4. Discussion

Over the past four decades, the grasshopper communities of a North American tallgrass prairie matured more slowly (i.e. lower DSWM) despite the *ca* 1°C increase in average temperature and the doubling of grass biomass [32]. This slowed rate of community maturation—and the potential decrease in time for adults to build egg mass—likely contributed to the 20+ year grasshopper declines on this grassland preserve [32] and may be an important proximate mechanism for other insect declines (e.g. [41–43]). We found mixed evidence for the direct effects of temperature and plant elemental chemistry on this slowdown in grasshopper community maturation, and evidence that both play a role via a key source of disturbance that maintains tallgrass prairie: burning.

The decrease in maturation rate over a period when temperature increased by 1°C is consistent with a community that crossed the peak and is on the decline side of the thermal performance curve [7], but we found no effect of annual variation in temperature. However, we note that soil temperature, via effects on egg mortality and development [44,45] may be buffered, or even cooled, by enhanced plant biomass, negating the 1°C long-term increase [46,47]. Soil monitoring would clarify the effects of temperature in future studies.

The increases in plant biomass in the ungrazed watersheds can also dilute nutrient concentrations in the grasshopper's host plants as taller plants are increasingly made up of low-nutrient stem tissue (i.e. 'dilution by growth, [48–50]). After accounting for daily and annual changes in DSWM, our best models revealed a unimodal effect of increasing plant N (enhancing maturation in the low-N annually burned grasslands and reducing maturation as burn frequency decreased). Fire frequency may modify this effect. As fires increased from once every 20 years to once every 1 year (generating a gradient of decreasing N, [31]) so did grasshopper community maturation rates, reinforcing evidence for an inhibitory effect of high N when N level was higher, and having the opposite effect when annual fires burns deplete local N supplies.

The contribution of species composition via PC2 suggests a role for species differences on community growth rates. Based on DNA analysis of Konza grasshopper diets [51], the four species whose abundance was most associated with high community growth rates were all grass feeders; those associated with low growth rates were forb feeders. The cause/effect of this association—do grass feeders develop more slowly, or do they perform better in years favouring rapid community development?—deserves further investigation.

It is notable that both temperature and N's hypothesized unimodal effect on grasshopper fitness can generate a diversity of responses to ecosystem change, making broad predictions a challenge. Comparative studies, while vital, cannot unambiguously rule out other interactions caused by, (i) the effects of woody encroachment [52], (ii) shifts in the dietary macromolecules like N-rich proteins and plant defenses, and C-rich carbohydrates, lipids, built by elements [53] and (iii) the effects of increasing plant biomass on predation risk [54] and, via shading, microclimate [46,55]. To this list of interactions, we add the intriguing possibility that decreasing nutrient density of food enhances the herbivore's metabolic rate and decreases its growth rate [56].

Finally, body mass is the third key variable linking abundance and development rate to fitness [6]. When resources are scarce, invertebrate growth rates tend to decrease, and when temperatures increase, size at maturity decreases [12] a pattern that may be reversed as season length declines [13]. Understanding the role of body size in the Konza grasshopper decline is the next step toward understanding the future of grasshopper communities on this tallgrass prairie.

Data accessibility. All but one dataset is publically available via the US LTER network data archives. Climate data: https://doi.org/10.6073/pasta/2483e2420b65d82f23513091956138a7 Grasshopper data: doi:10.6073/pasta/aec67f5d71d14cd39fe8b6b34b4719f4 Plant biomass data: doi:10.6073/pasta/eebbc157d1cf9be85a7327961c89859a.

The plant chemistry data can be found in the Open Science Framework repository: doi:10.17605/OSF.IO/ZSXBP.

The data are provided in the electronic supplementary material [57].

Authors' contributions. M.K.: conceptualization, funding acquisition, project administration, supervision, writing—original draft and writing—review and editing; A.J.: conceptualization, data curation, funding acquisition, investigation, methodology, project administration, supervision and writing—review and editing; E.A.R.W.: conceptualization, data curation, formal analysis, funding acquisition, investigation, validation, visualization and writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Competing interests. We declare we have no competing interests.

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