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ORIGINAL ARTICLE

A continent-wide study reveals clear relationships between regional abiotic conditions and post-dispersal seed predation

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ABSTRACT

Aim Large-scale patterns linking energy availability, biological productivity and diversity form a central focus of ecology. Despite evidence that the activity and abundance of animals may be limited by climatic variables associated with regional biological productivity (e.g. mean annual precipitation and annual actual evapotranspiration), it is unclear whether plant–granivore interactions are themselves influenced by these climatic factors across broad spatial extents. We evaluated whether climatic conditions that are known to alter the abundance and activity of granivorous animals also affect rates of seed removal.

Location Eleven sites across temperate North America.

Methods We used a common protocol to assess the removal of the same seed species (*Avena sativa*) over a 2-day period. Model selection via the Akaike information criterion was used to determine a set of candidate binomial generalized linear mixed models that evaluated the relationship between local climatic data and post-dispersal seed predation.

Results Annual actual evapotranspiration was the single best predictor of the proportion of seeds removed. Annual actual evapotranspiration and mean annual precipitation were both positively related to mean seed removal and were included in four and three of the top five models, respectively. Annual temperature range was also positively related to seed removal and was an explanatory variable in three of the top four models.

Main conclusions Our work provides the first evidence that energy and precipitation, which are known to affect consumer abundance and activity, also translate to strong, predictable patterns of seed predation across a continent. More generally, these findings suggest that future changes in temperature and precipitation could have widespread consequences for plant species composition in grasslands, through impacts on plant recruitment.

Keywords

Annual actual evapotranspiration, AET, climate, granivory, North America, plant–consumer interactions, precipitation, seed predation.

INTRODUCTION

Because large-scale patterns in abiotic environmental conditions (e.g. energy input and precipitation) may play an important role in affecting the abundance of organisms (Kaspari *et al.*, 2000a,b; Porter *et al.*, 2000; Kaspari, 2001; Brown & Ernest, 2002) and the richness of ecological communities (Kaspari *et al.*, 2000b; Porter *et al.*, 2000; Hawkins *et al.*,

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2003; Clarke & Gaston, 2006; Coops *et al.*, 2009), an important question in ecology concerns the degree to which abiotic conditions provide insight into large-scale patterns in the interactions of ecological communities (Hillebrand *et al.*, 2009; Schemske *et al.*, 2009; Freestone *et al.*, 2011; Moles *et al.*, 2011; Poore *et al.*, 2012; Rodríguez-Castañeda, 2013). Understanding the interplay between abiotic conditions and interactions among species may also be of pragmatic utility for understanding ecological responses to changing climatic conditions (Schemske *et al.*, 2009; Rodríguez-Castañeda, 2013). A recent meta-analysis provides important evidence that climatic variables (e.g. temperature and precipitation) may structure several common trophic interactions, i.e. plant–herbivore interactions and predator–prey interactions (Rodríguez-Castañeda, 2013). However, it is unclear whether other important trophic interactions exhibit similar patterns at large scales. Moreover, while meta-analyses provide a powerful tool for synthesis, their interpretation may be complicated by the synthesis of studies that differ widely in their methods (e.g. variable study durations and different plot sizes) and study taxa (e.g. a focus on arthropods; Rodríguez-Castañeda, 2013). In this study, we utilized a standardized protocol at sites that span temperate North America to evaluate whether a key ecological interaction, granivory, is related to large-scale abiotic gradients in energy and precipitation.

Granivory is an important plant–consumer interaction because the distribution and abundance of plants often hinges on the survival of their seeds (Crawley, 2000; Orrock *et al.*, 2006; Clark *et al.*, 2007; MacDougall & Wilson, 2007; Pearson *et al.*, 2011; Bricker & Maron, 2012; Maron *et al.*, 2012) and granivory can exert a strong influence over the diversity and composition of plant communities (e.g. Crawley, 2000; Howe & Brown, 2001; Pearson *et al.*, 2011; Maron *et al.*, 2012). Much as climate may affect trophic interactions in general (Rodríguez-Castañeda, 2013), geographical variation in seed predation may be related to local climate via several mechanisms that are not necessarily mutually exclusive. Climates that favour increased production of plant biomass may also be environments that support greater abundance and density of individual granivores and granivore species, leading to higher rates of absolute seed consumption. For example, the abundance and diversity of ant, rodent and avian granivores have been linked to energy and precipitation (Kaspari *et al.*, 2000a,b; Kaspari, 2001; Brown & Ernest, 2002; Hawkins *et al.*, 2003; Mönkkönen *et al.*, 2006). Alternately, climates that foster variable production may favour granivory because consumption of storable seeds may be advantageous in systems where resource production can be episodic and unpredictable, such as in arid and semi-arid systems (Mares & Rosenzweig, 1978; Brown *et al.*, 1979; Reichman, 1979; Morton, 1985; Folgarait *et al.*, 1998; Folgarait & Sala, 2002; Kelt *et al.*, 2004).

Previous studies have examined regional patterns of granivory in arid systems (Morton, 1985; Folgarait *et al.*, 1998; Folgarait & Sala, 2002; Kelt *et al.*, 2004), the role of latitude in affecting post-dispersal seed predation (Moles & Westoby, 2003), elevational gradients in seed predation (Hillyer & Silman, 2010) and differences in seed-removal rates as a function of seed species or characteristics (Moles *et al.*, 2003; Hautier *et al.*, 2010; Hillyer & Silman, 2010). Although these studies illuminate general patterns in seed predation, they often rely on comparative approaches that utilize different seed species, different seed-exposure times and/or studies done in different years. These details are important because differences in seed characteristics, seed density and exposure times are all likely to affect rates of granivory (Reichman, 1979; Kerley & Erasmus, 1991; Hautier *et al.*, 2010). Studies that use similar protocols across study sites (Kelt *et al.*, 2004; Hillyer & Silman, 2010) yield important information but are often restricted in their geographical extent (and understandably so).

In this study, we examined seed predation at 11 sites that spanned 15.1° latitude and 41.7° longitude (Fig. 1), thereby capturing a wide range of annual temperature and precipitation regimes. We used seeds of the same plant species and a standardized experimental protocol. With these data, we evaluated whether climatic conditions that are known to alter the abundance and activity of granivorous animals also affect rates of seed removal.

MATERIALS AND METHODS

Study location and design

Our study was conducted in 2009 at 11 grassland sites across North America (Fig. 1) that were part of the Nutrient

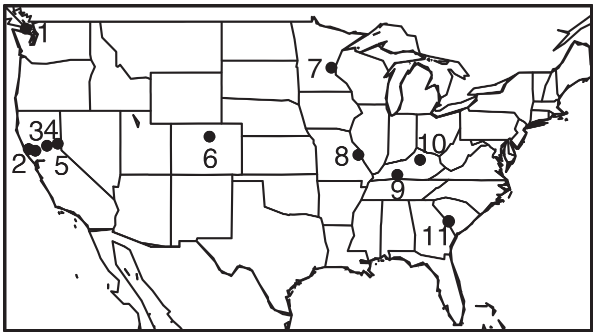

Figure 1 Seed (*Avena sativa*)-removal trials conducted at 11 Nutrient Network (a large-scale experiment examining nutrient and consumer effects on worldwide grasslands) sites across North America. Each of the 11 sites contained between two and four replicate blocks, with one plot (four seed-removal depots) within each block. For additional details, see Appendix S1. The sites were: (1) Cowichan, British Columbia, Canada; (2) Hopland Reserve, California, USA; (3) McLaughlin Reserve, California, USA; (4) Sierra Foothills Reserve, California, USA; (5) Sagehen Reserve, California, USA; (6) Boulder, Colorado, USA; (7) Cedar Creek, Minnesota, USA; (8) Tyson, Missouri, USA; (9) Hall's Prairie, Kentucky, USA; (10) Spindletop, Kentucky, USA; (11) Savannah River Site, South Carolina, USA.

Network (Borer *et al.*, 2014), a large-scale experiment examining nutrient and consumer effects on worldwide grasslands. Each site contained two to four replicate blocks (see Fig. S1 in Appendix S1 in Supporting Information). Each block contained ten 5 m × 5 m plots. Although nutrient addition and consumer-manipulation treatments are part of the Nutrient Network design, our study used data only from the control plots (i.e. the single plot within each block without any nutrient addition or consumer exclusion treatment). The blocks captured a significant portion of spatial variation at each location, e.g. a site with three blocks utilized a minimum area of 750 m^2 and would contain three replicated seed-removal plots across that area (one in each block; see Appendix S1); this spatial extent ensured that replicate seed-removal plots were visited by different individual consumers (e.g. by spanning multiple home ranges of small-mammal granivores and multiple colonies of granivorous ants) and that replicates sampled spatial variation within each study site.

Seed-removal trials were conducted in 2009 using four 1 m × 1 m areas nested within a 5 m × 5 m experimental unit. In the middle of each 1 m × 1 m area, a single seed depot consisting of five oat (*Avena sativa* L.) seeds was placed on the soil surface (see Appendix S1 for additional details). Depots were revisited 2 days after installation (deployment was 3 days at one site but there was no seed removal at this site, so this difference in duration did not affect the observed patterns). This deployment duration was longer than some large-scale seed-removal studies (e.g. Moles *et al.*, 2003), equivalent to some (Morton, 1985) and shorter than others (e.g. Folgarait & Sala, 2002; Kelt *et al.*, 2004; Orrock & Damschen, 2005). Additional data from five sites in our study that included a total of six extended trials confirmed that the duration of deployment was sufficient to capture patterns of seed removal over longer exposure periods. Extending trial duration to approximately six times longer led to no difference in seed removal, i.e. the number of seeds removed during trials extended to a total of 12 ± 1.5 days was no different from the number removed during a 2-day trial (paired *t*-test, $t = 1.62$, 5 d.f., $P = 0.17$). There was also no evidence of a linear trend of greater seed removal with increasing duration of deployment ($r = 0.44$, 4 d.f., $P = 0.38$).

To maximize the comparability of our results, trials were conducted during the growing season and near peak biomass production at each site. This was an important feature of our design, because seed removal may exhibit seasonal variation (Whelan *et al.*, 1991; Mattos *et al.*, 2013). By conducting our removals during a time when dynamics were at a common ecological stage (i.e. when biological productivity was maximum at each of our different grassland systems), we evaluated all sites during the season that was most relevant for understanding the relationship between seed predation and climatic variables that influence productivity.

Study species

Quantifying regional-scale seed removal by using seed species unique to each site hampers among-site comparisons because the available seed pool probably differs in composition, abundance and palatability across sites. To facilitate across-site comparisons, we deployed seeds of *A. sativa* at each site (seed mass = 32.47 ± 1.82 mg, determined from five samples of 10 seeds each; see Appendix S1); the *A. sativa* seeds were obtained from 22.67 kg of seeds purchased in St Louis, Missouri, USA, prior to distribution to the 11 study sites. *Avena sativa* was an optimal species for the study because it is naturalized throughout North America and because seeds of *Avena* spp. are readily consumed by arthropod, avian and small-mammal granivores (e.g. Fordham, 1971; Borchert & Jain, 1978; Westerman *et al.*, 2003; Holmes & Froud-Williams, 2005). To avoid influencing vegetation establishment, seeds were heated to make them non-viable prior to deployment (Appendix S1). Removal of heat-treated seeds was highly correlated with removal of non-treated seeds (Appendix S1). Importantly, additional data from several of our study sites suggested that the removal of *A. sativa* is an effective surrogate for the removal of other species. At three of the study sites, removal of an additional seed species was conducted at the same time as *A. sativa* removal; the rates of removal of these three species did not differ from rates of *A. sativa* removal (Appendix S1). Moreover, additional seed-removal trials conducted at a fourth geographical location found that removal of *A. sativa* seeds was also significantly correlated with removal of seeds of five native prairie species that ranged in size from 1 to 16 mg (Appendix S1), suggesting that the removal of *A. sativa* provided a useful index of removal of other species.

Like other studies of granivory (e.g. Folgarait & Sala, 2002; Moles *et al.*, 2003; Kelt *et al.*, 2004; Hautier *et al.*, 2010; Hillyer & Silman, 2010), our work assumed that seed removal was indicative of seed predation and not secondary seed dispersal. Vander Wall *et al.* (2005) noted that this assumption should be supported with evidence of actual *in situ* seed consumption, as seeds cached by arthropods or mammals may later recruit and play an important role in plant populations. Observations from our study system were in agreement with Hillyer & Silman (2010), who reviewed the literature and concluded that rates of seed recruitment and survival following seed removal are low. In our study, field observations collected at nine sites suggested that seed removal in our study was indicative of seed predation: at the 54 depots where at least one seed was removed, 44% of the depots had signs of direct seed predation (i.e. the presence of seed fragments and shards of seed coats). Furthermore, *Avena* spp. seeds are readily consumed in field settings: the addition of *A. sativa* seeds has been used to elevate rodent populations in field experiments (Fordham, 1971; Taitt, 1981) and rodents alone have been estimated to consume directly 75% of available *Avena fatua* seeds (Borchert & Jain, 1978).

Moreover, *A. sativa* seed removal is probably indicative of seed death, not secondary dispersal, because *Avena* spp. rarely persist in the soil for more than a year even when burial is shallow (Tingey, 1961), and rates of seed loss to rodents are reflected in a 62% reduction in *A. fatua* recruitment (Borchert & Jain, 1978).

Climatic variables and statistical methods

We evaluated the importance of five abiotic variables hypothesized to govern consumer pressure at large scales: mean annual precipitation, mean annual temperature, seasonal extremes in mean annual temperature, the coefficient of variation in inter-annual mean annual precipitation, and annual actual evapotranspiration (hereafter, AET). An additional metric of climatic variability, the intra-annual variation in precipitation regime, was not evaluated in our analyses because we found that it was very strongly correlated with AET in our dataset ($r = -0.88$, $P < 0.001$; Appendix S1; see also Discussion). AET quantifies the amount of water that enters the atmosphere via evaporation from the soil and transpiration through plants. Because AET reflects the availability of water and energy in an environment in a unit of time, it is qualitatively related to vascular plant activity (Rosenzweig, 1968). Both temperature and AET can affect consumer abundance (Kaspari *et al.*, 2000a,b), precipitation and temperature can affect terrestrial trophic interactions (Rodríguez-Castañeda, 2013), and past work in arid systems has shown that productivity, climatic extremes and climatic variance may be related to granivory (Folgarait & Sala, 2002; Kelt *et al.*, 2004).

Because we were interested in understanding how average climatic trends relate to seed predation, we used long-term climate averages rather than climatic conditions during the year when the seed predation trials were conducted. Annual precipitation and temperature data were derived from WorldClim 1.4 release 3, which is a set of interpolated global climate layers at a spatial resolution of approximately 1 km^2 (Hijmans *et al.*, 2005). Where possible, data from these multiple sources were restricted to the period 1950–2000 (Hijmans *et al.*, 2005). Data used for the calculation of inter-annual variation in precipitation were obtained from the National Oceanic and Atmospheric Administration (NOAA). AET was calculated using the method of Thornthwaite & Mather (1957), a common approach in ecological studies (Rosenzweig, 1968; Kaspari *et al.*, 2000a,b). The calculation of AET requires monthly precipitation and temperature data. For all sites except Sierra Foothills, California, USA, and Cowichan, British Columbia, Canada, mean monthly precipitation and temperature data used for the calculation of AET were derived from NOAA monthly climate summaries for the period 1971–2000 from weather stations located as close as possible to the study sites. For Sierra Foothills and Cowichan, data were obtained from a nearby weather station over the period 1989–2000. When possible, the proximity and suitability of weather stations were verified with researchers at each site to ensure that they were representative of the areas where the sites were established.

The utility of these variables for understanding productivity was supported by significant relationships between precipitation, AET and aboveground herbaceous plant biomass at the majority of our sites (Appendix S1). Importantly, we also noted that, because conditions in 2009 were highly correlated with long-term climate data (Appendix S1), the primary conclusions of our work did not differ if 2009 data were used (Appendix S1).

We used generalized linear mixed models with a binomial response distribution for our analyses (Bolker *et al.*, 2009), treating the study site as a random effect and the proportion of removed seeds as the response variable. In addition to being consistent with the data on theoretical grounds, the use of a binomial model also accommodated the slight variation in the number of seed-removal depots among our sites, such that sites with more data logically contributed greater information to the analysis. Seed-removal data were pooled across all depots and blocks to yield the total removal for each site. We utilized this pooled approach because it was consistent with our primary goal of examining between-site variation in seed removal; examining within-site variation in seed removal was not an aim of our study, because we were focused on large-scale variation in seed removal and climate. Preliminary analyses suggested that over-dispersion, although slight, was present in our data. We included site as a random effect in our model because it allowed us to incorporate over-dispersion explicitly in our analyses, rather than adjusting for over-dispersion in a post-hoc fashion (e.g. adjusting estimates using the over-dispersion parameter).

We used a model-comparison approach (Burnham & Anderson, 2002; Johnson & Omland, 2004) to evaluate the importance of abiotic variables associated with granivory. All possible model subsets of the five independent variables (without interaction terms) were created using generalized binomial mixed models, creating candidate models of all possible variable permutations (i.e. each individual model had 1–5 of the independent variables). Models were evaluated with the corrected Akaike information criterion (AIC$_c$), which is preferable when sample sizes are relatively small (Johnson & Omland, 2004). We standardized the independent variables in the model prior to constructing competing models (Grueber *et al.*, 2011) and we considered models within four AIC$_c$ units to be competing models (Burnham & Anderson, 2002; Grueber *et al.*, 2011). We calculated AIC$_c$ weights to characterize the importance of variables in multivariable models (Grueber *et al.*, 2011). Values of R^2 were calculated as described in Nakagawa & Schielzeth (2013). Residuals from our final models were examined to evaluate departure from model assumptions (e.g. lack of independence or heterogeneous variance); correlograms using model residuals were constructed to evaluate whether the data exhibited spatial structure. Analyses were conducted using R 3.0.2 (R Core Team, 2013).

RESULTS

We collected seed-removal data from 135 depots at 11 sites ranging from Vancouver Island, British Columbia, Canada, to near Aiken, South Carolina, USA (Fig. 1, Appendix S1). In general, seed removal was strongly and significantly related to abiotic conditions associated with large-scale climatic factors. The five models in the final model set (Table 1) each explained large amounts of the variation in the original dataset, with conditional R^2_C and marginal R^2_M values ranging from 0.66 to 0.89. Among these models, AET and mean annual precipitation explained significant amounts of variation and occurred in four and three of the five top models, respectively. One model in the best-model set contained a single variable, AET, which accounted for a large proportion of the variation in seed removal (Table 1, Fig. 2). Seed predation increased with annual temperature range, and this climatic variable was included in three of the best-fitting models, although it was only significant in two of those models (Table 1). Mean annual temperature and the coefficient of variation in inter-annual mean annual precipitation were not retained in any of the top models (Table 1). The largest condition index (2.05) among standardized independent variables in the final set of models was below the value of 30, which is indicative of collinearity (Quinn & Keough, 2002). Examination of residuals and correlograms indicated no violation of model assumptions, including no significant spatial signal in model residuals.

DISCUSSION

Although energy availability and climatic conditions are repeatedly found to structure large-scale patterns in the distribution and abundance of species (Hawkins *et al.*, 2003; Clarke & Gaston, 2006), studies that examine the role of energy and climate in affecting biological interactions are rare (Schemske *et al.*, 2009), probably because of the difficulty of using standardized protocols at multiple locations across large scales (Rodríguez-Castañeda, 2013). Using a standardized protocol, our work illustrates that seed predation is strongly associated with energy availability as well as climatic variation across a gradient spanning a large portion of North America. Our experiment, replicated at sites spanning a broad range of climatic regimes, provides empirical support for patterns identified in a recent synthetic meta-analysis, which suggests that global patterns of predator–prey interactions and plant–herbivore interactions may be associated with mean temperature and precipitation (Rodríguez-Castañeda, 2013). Our findings build on this meta-analysis result by finding that interactions between plants and granivores may be predictable at biogeographical scales and that long-term climatic averages, as well as climatic variability, may have an important bearing on plant–granivore interactions.

Abiotic conditions linked to productivity can affect consumer abundance and activity (e.g. Kaspari *et al.*, 2000a,b; Kaspari, 2001; Brown & Ernest, 2002; Coops *et al.*, 2009). Our results show that these same climatic conditions, e.g. AET, are correlated with patterns in granivory (Fig. 2). The strong link we observed between local climate and seed predation may have arisen because consumers are limited by local primary production, because harsh abiotic conditions set limits on the abundance of consumers in temperate regions, or both. It is also possible that the pattern we observed may be created if climatic controls on top-down forces operate in an opposite fashion, e.g. if areas that receive little precipitation are areas where predators, parasites or pathogens of granivores are abundant. In partial support of this hypothesis, a quadratic relationship has been found between the strength of top-down trophic cascades and precipitation and temperature (Rodríguez-Castañeda, 2013). However, because of climatic differences between the current

Table 1 Summary of the best five generalized linear mixed models (binomial distribution) used to describe the proportion of seeds removed from a continent-wide study. All possible model subsets were evaluated; all of the best models shown were within four AIC_c units of the best model. AIC_c indicates the Akaike information criterion corrected for small sample size. Models are ordered starting with the best-fitting model (i.e. the lowest AIC_c). Values of R^2_C represent the conditional coefficient of determination (which includes only fixed effects) and values of R^2_M represent the marginal coefficient of determination (which includes both fixed and random effects), as described in Nakagawa & Schielzeth (2013). For comparison, $AIC_c = 77.28$ and $R^2_C = 0.81$ for an intercept-only model with the same random effect structure. AET indicates annual actual evapotranspiration.

				Model parameters			
Independent variables	Estimate (± SE)	*z*-value	*P*-value	AIC_c	AIC_c weight	R^2_M	R^2_C
1. AET	0.017 ± 0.003	5.88	< 0.001	67.33	0.34	0.66	0.77
2. Annual precipitation	0.017 ± 0.003	5.30	< 0.001	67.49	0.32	0.85	0.89
Annual temperature range	0.468 ± 0.119	3.95	< 0.001				
3. AET	0.009 ± 0.002	4.10	<0.001	68.94	0.15	0.82	0.82
Annual precipitation	0.009 ± 0.003	3.43	<0.001				
Annual temperature range	0.244 ± 0.084	2.92	0.003				
4. AET	0.013 ± 0.003	4.29	<0.001	69.25	0.13	0.69	0.77
Annual precipitation	0.005 ± 0.003	1.76	0.078				
5. AET	0.016 ± 0.003	5.60	<0.001	71.00	0.05	0.66	0.77
Annual temperature range	0.005 ± 0.003	1.19	0.235				

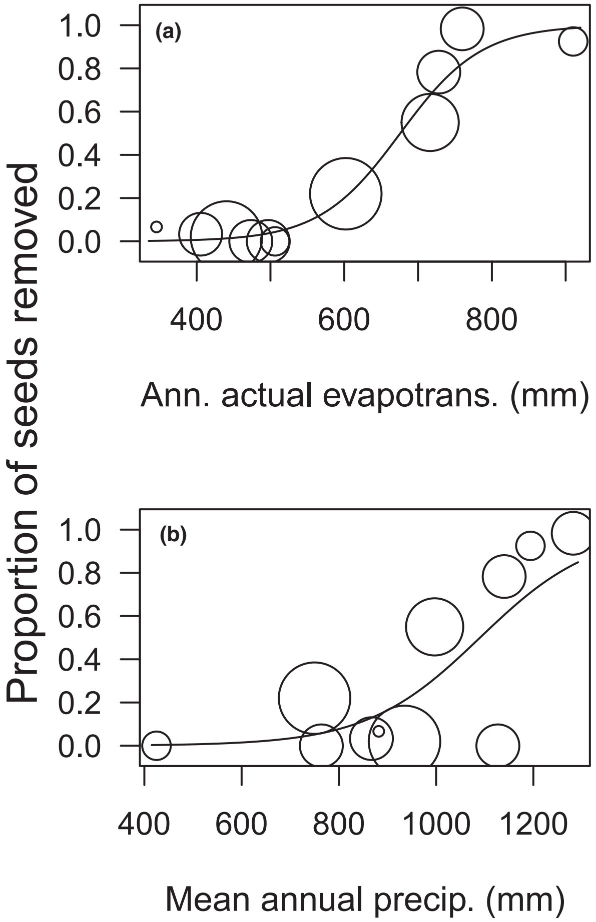

Figure 2 Univariate relationships between seed (*Avena sativa*) removal and climatic conditions at 11 Nutrient Network (a large-scale experiment examining nutrient and consumer effects on worldwide grasslands) sites across North America. (a) Seed removal and annual actual evapotranspiration [$z = 5.345$, $P < 0.001$, corrected Akaike information criterion ($\mathrm{AIC_c}$) = 67.33; see Table 1]; (b) seed removal and mean annual precipitation ($z = 2.921$, $P = 0.003$, $\mathrm{AIC_c} = 72.71$). Trend lines fitted by generalized linear binomial models. The relative size of each data point is proportional to the number of seed-removal depots present at each study site.

study (mean annual precipitation range 425–1282 mm and mean annual temperature range 5.7–17.3 °C) and the studies in the meta-analysis (mean annual precipitation range 100–4500 mm and mean annual temperature range −11 to 28 °C), as well as differences in focal taxa and region (e.g. 88% of the tropical trophic cascade studies were focused on ants; Rodríguez-Castañeda, 2013), future work will be needed to determine whether top-down limitation of granivores generates large-scale patterns of granivory, especially in light of the strong link between the abundance of granivorous animals and climatic conditions in North America (e.g. Brown & Ernest, 2002).

Our work illustrates that thermal climatic variability may also be an important correlate of granivory in temperate systems (Table 1), not just in the arid systems where variability has previously been invoked as an explanation for patterns of granivory (Morton, 1985; Folgarait *et al.*, 1998; Folgarait & Sala, 2002). Our results provide support for the role of thermal extremes in increasing granivory (Table 1) but do not support the role of inter-annual variation in precipitation (Morton, 1985). However, because of the strong relationship between AET and intra-annual variation in precipitation across our study sites (Appendix S1), we cannot fully evaluate the role of precipitation variability in affecting granivory. Future investigation of the independent roles of these two factors for seed predation is warranted.

Climatic conditions that favour biological productivity (e.g. consistent, favourable temperature and precipitation) are often implicated in observed latitudinal gradients in species diversity (see Schemske *et al.*, 2009). Latitudinal gradients in consumer–plant interactions have been documented in a variety of systems (Rodríguez-Castañeda, 2013); however, they have not been found in seed-removal studies (Moles & Westoby, 2003) or in studies of herbivores in marine systems (Poore *et al.*, 2012). Although our study differs from the work of Moles & Westoby (2003) in methodology and latitudinal extent (Fig. 1; our study used sites that were within temperate climates), our work also demonstrates little evidence for a latitudinal pattern in post-dispersal granivory. Rather, we found that large-scale gradients in seed predation in temperate regions were largely related to abiotic gradients that vary with longitude within North America (AET, annual temperature range and inter- and intra-annual variation in mean annual precipitation were correlated with longitude across our study sites; Fig. S1, Appendix S1).

Our findings suggest that the link between climate and consumers may not always travel solely through herbaceous plants, i.e. studies may not always observe a significant relationship between local herbaceous biomass production, climatic variables that indicate productivity and seed predation. One of our sites (Savannah River Site, South Carolina, USA) was a longleaf pine savanna grassland characterized by scattered longleaf pine trees (*Pinus palustris*) in the overstorey. Although this site had high AET, precipitation and seed predation (Appendix S1), biomass production by understorey plants was low, possibly because scattered overstorey trees captured some of the incoming energy and precipitation before it could be captured by understorey plants, or because of soil or nutrient limitation. When local biomass data were examined without this site, there were significant relationships among seed predation, herbaceous biomass and climatic variables (Appendix S1). Notably, the inclusion or exclusion of the savanna grassland site did not alter the importance of climatic variables in affecting seed predation (Appendix S1). This suggests that productivity, although not reflected in the biomass of understorey plants, may nonetheless fuel increases in local consumer pressure (e.g. through the production of seeds for granivores by overstorey trees).

The patterns in seed predation we observed may indicate large-scale differences in the degree to which granivores affect the ecology of plant communities. For example, large-seeded species, such as the one used in our study, are often seed-limited (Clark *et al.*, 2007; Maron *et al.*, 2012), suggesting that the patterns of granivory we observed may yield large-scale differences in the degree to which seed predation, rather than dispersal limitation or microsite limitation, affects the recruitment of some plant species (Orrock *et al.*, 2006; Hillyer & Silman, 2010; Bricker & Maron, 2012; Maron *et al.*, 2012; Germain *et al.*, 2013). An additional implication of our findings is that future changes in climatic conditions may change the strength of plant–granivore interactions. Moreover, changes in climate are likely to have both direct and indirect effects on plants (Parmesan, 2006) that could be dampened or exacerbated by the patterns of seed predation that we have documented. For example, changes in seed survival as a result of climatic variation in local productivity, coupled with decreased seedling survival as a result of temperature or moisture stress, could have additive, detrimental effects on plant population persistence; these effects could be further compounded by other anthropogenic activities (e.g. creation of edge-rich habitats) that also affect seed predation (Tallmon *et al.*, 2003; Orrock & Damschen, 2005; Craig *et al.*, 2011).

Although our work indicates that large-scale climatic variation explains a large amount of the variation in seed predation among sites, our focus on large-scale patterns necessarily ignores variation that might exist within a geographical region or province or within the same area across several years, as well as variation in local processes relating to biotic characteristics (e.g. the composition of the plant community) and landscape context (Craig *et al.*, 2011). For example, it is possible that the relative role of climatic drivers of seed predation, much like drivers of litter dynamics (O'Halloran *et al.*, 2013), vary among geographical provinces: although beyond the capacity of our data to evaluate in a robust manner, if sites with AET < 600 were examined, the relationship between seed predation and AET was no longer positive (Fig. 2). By focusing on a single species, our work provides a strong test of large-scale patterns without the possible confounding of geographical variation in seed traits. However, understanding the role of seed characteristics and geographical variation in the context of large-scale and long-term patterns of granivory may be a particularly informative area for future study (Moles *et al.*, 2003; Moles & Westoby, 2004), especially given the importance of seed traits (Maron *et al.*, 2012) in mediating plant–consumer interactions in terrestrial systems. Moreover, although the timing of our study was during peak plant biomass (and thus probably coincident with peak consumer biomass), future studies should examine how the timing of granivory determines how much it impacts plant populations and communities. In summary, by demonstrating that energy and precipitation can translate into strong, predictable patterns of seed predation across the continent, our work raises an important line of investigation because it suggests that climate change may significantly impact plant species composition in grasslands via impacts on plant recruitment.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 The study data and additional details on study sites, methods, ancillary seed-removal trials and supporting results.

Appendix S2 Information regarding author contributions.

BIOSKETCH

John Orrock studies plant–consumer interactions, large-scale patterns in biological invasion and consumer pressure, and the interface between behavioural ecology and spatial ecology. The research team consists of members of Nutrient Network, a global research collaborative using standardized experiments in grasslands across the world to understand the forces structuring grassland communities (http://www.nutnet.umn.edu/).

Author contributions: J.L.O. conceived the original study concept and design and led the writing of the manuscript; all authors contributed important suggestions during preparation of the final manuscript; D.V.B., A.B.-M., E.T.B., L.A.B., E.I.D., K.F.D., D.S.G., A.D.K., A.S.M., R.L.M., B.A.M., J.L.O., E.W.S. and L.H.Y. collected data; J.L.O. analysed the data; E.T.B., M.J.C., J.F., E.L., B.A.M. and E.W.S. contributed to the analysis; E.T.B., E.W.S. and E.L. coordinated and administered the larger Nutrient Network study, which was essential to the work in this paper; a table describing all authorship contributions is in Appendix S2.

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