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Climate change will bring more extremes in temperature and precipitation that will impact productivity and ecosystem resilience throughout agroecosystems worldwide. Historical events can be used to identify drivers that impact future events. A catastrophic drought in the US in the 1930s resulted in an abrupt boundary between areas severely impacted by the Dust Bowl and areas that were less severely affected. Historical primary production data confirmed the location of this boundary at the border between two states (Nebraska and Iowa). Local drivers of weather and soils explained production responses across the boundary before and after the drought (1926–1948). During the drought, however, features at the landscape scale (soil properties and wind velocities) and regional scale (the Missouri River, its floodplain, and the nearby Loess Hills) explained most of the observed variance in primary production. The impact of future extreme events may be affected by land surface properties that either accentuate or ameliorate the effects of these events. Consideration of large-scale geomorphic processes may be necessary to interpret and manage for catastrophic events.

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Extreme climatic events, such as heat waves, droughts, tornadoes, floods, freezes, and hurricanes, are expected to increase in frequency, intensity, or variability as temperatures continue to increase under global warming (IPCC 2018). These events lead to surprising and catastrophic consequences for ecosystems at multiple scales, from landscapes to regions (Allen *et al*. 2010). In addition, interactions between the drivers and ecological processes governing these events can vary through time and space, making their occurrence and ecosystem consequences challenging to predict (Peters *et al*. 2004). Although it is tempting to attribute causal relationships between ecosystem consequences and climate variables, recent events (eg hurricanes, wildfires, drought) are clear indications that data about climate alone are insufficient for predicting consequences, particularly for extreme events that occur across landscape to regional spatial extents and persist for multiple years. However, understanding and predicting ecosystem responses to extreme events across multiple spatial and temporal scales is imperative for natural resource managers and decision makers as both the drivers and landscapes continue to change, either in unison with or interacting and feeding back to the drivers (Briske *et al*. 2015).

In a nutshell:

- Historical data can be used to inform agroecosystem responses to future events
- Agroecosystems are characterized by large-scale drought, which in the US includes the drought event of the 1930s that, in combination with land-use changes, resulted in the Dust Bowl
- We found that analyzing past ecological and agronomic data at small scales was insufficient to explain large-scale patterns in grassland primary production during the drought
- Regional-scale features, such as river basins or fencerows, that affect transport and deposition of sand by wind can overwhelm the local effects of drought, and should be considered in future global-change scenarios

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In grasslands, research on responses to extreme events has generally involved experimental manipulations, simulation analyses, or opportunistic studies conducted after (and sometimes before) an extreme event occurs (eg Peters *et al*. 2010; Wilcox *et al*. 2017; Griffin-Nolan *et al*. 2018). These studies are often conducted at local scales to observe fine-scale heterogeneity (ie plots within landscapes; Smith *et al*. 2015) and multiple levels of biological organization (Smith *et al*. 2011). Conceptual frameworks focus on modifications to either the magnitude or variability of global-change drivers (eg precipitation, temperature, nitrogen) that interact with local ecosystem properties (eg soils, biota) (shown in red in Figure 1; Smith *et al*. 2011; Sala *et al*. 2012, 2015).

However, these studies and conceptual frameworks often do not include ecological phenomena and landscape features that become important as the spatial extent of an extreme event increases beyond plots or quadrats to landscapes and

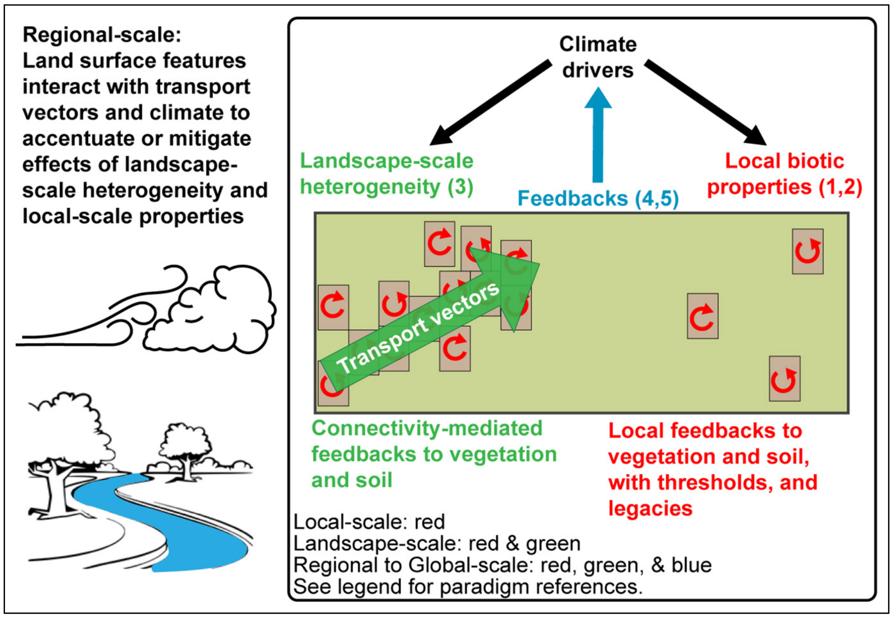

Figure 1. New conceptual model for broad-scale, multi-year, extreme events based on regional-scale land surface features. Climate drivers interact with local properties to govern fine-scale ecosystem patterns and dynamics (red; adapted from [1] Smith *et al.* 2011; [2] Sala *et al.* 2012). As the spatial extent increases to the landscape, transport vectors and the length of connected pathways influence connectivity-mediated feedbacks to the vegetation and soil (green; adapted from [3] Okin *et al.* 2009). At regional to global scales, local-scale patterns can propagate across scales to influence broad spatial extents with feedbacks to climate drivers (blue; from Peters *et al.* [4] 2004, [5] 2008). Although ecologists have developed paradigms for each scale and their interactions (1–5), the importance of regional-scale land surface features, such as rivers, windbreaks, and mountains, have typically been ignored (black).

regions. At the landscape scale, transport of material by wind or water has both direct effects on the redistribution of surface soil and nutrients, and indirect effects on connectivity-mediated feedbacks to ecosystem dynamics (shown in green in Figure 1). Connectivity, in this context, is defined as the ability of material to flow from one location to another on the landscape (Okin *et al.* 2018). Land use, such as cultivation and abandonment, can disturb soils and influence erosive properties and connectivity. In addition, movement of soil from neighboring erosive areas can lead to soil deposition on plants, and subsequent losses of primary production (Okin *et al.* 2018). At the continental to global scale, global-change drivers interact across multiple scales, leading to increases or decreases in connectivity associated with an extreme event (shown in blue in Figure 1; Peters *et al.* 2008, 2014). Although land-use and transport processes have been studied by landscape ecologists, and continental- to global-scale patterns and processes are increasingly studied by macrosystems ecologists, the effects of regional-scale land surface features on connectivity have received little scientific attention. As the spatial extent increases, so too do the occurrences of geomorphic features such as rivers, floodplains, fencerows, and mountain ranges (shown in black along the left-hand side of Figure 1), which can either amplify or mitigate the effects of transport processes to overwhelm local-scale drivers and ecological processes.

Here, we present a new paradigm that includes the importance of regional-scale geomorphic features interacting with landscape-scale transport vectors to influence local-scale agroecosystem responses to extreme events (Figure 1). We sought to explain a pattern that emerged during a well-known extreme event that occurred 80 years ago: the apparent sharp boundary between Dust Bowl-impacted and non-impacted areas (Figure 2, a and b). We expect such explanations will assist land managers in preparing for future events of similar magnitude and extent.

The Dust Bowl – a period when most of the central Great Plains (CGP) experienced drought during the 1930s – was a catastrophic event in US history (Figure 2a). The drought was preceded by cultivation of fields, beginning in the 1870s, of increasingly marginal agricultural land through time. Because modern agriculture only began in the late 1940s, management practices such as irrigation, fertilization, and plant breeding, all of which can alleviate drought effects, were not yet readily available. Consequently, the drought resulted in widespread crop failure and abandonment of fields. The resulting highly connected landscape of bare soil accentuated transport by wind and water, and contributed to the large dust storms that began around 1933 in the western part of the CGP and blew dust eastward across wide swaths of the country (Cook *et al.* 2009).

Maps of the location of the Dust Bowl from different sources typically align with one another to show sharp boundaries between Dust Bowl-impacted and non-impacted areas (Figure 2a). This distinct boundary has been cited extensively (eg Cook *et al.* 2009), although its location has not been questioned and the environmental drivers governing it have not been quantitatively explored. The boundary appears well defined: it separates an area in the west that experienced high wind erosion, sand deposition, and plant mortality, as well as devastating losses in crop production (ie the Dust Bowl-impacted area), from an area in the east that saw reductions in crop production but low plant mortality and little transport of sand (ie Dust Bowl non-impacted area).

Interestingly, a group of ecologists studying the effects of drought on unplowed native grassland in the same region provided another source of information (Weaver and Albertson 1936). Along a 100-km transect between southeastern Nebraska (NE) and southwestern Iowa (IA), numerous quadrats established in native grasslands prior to the drought were re-sampled during and following the drought (Figure 2b; Weaver and Albertson 1936). Quadrats with high plant mortality indicative of Dust Bowl-impacted areas occurred in NE,

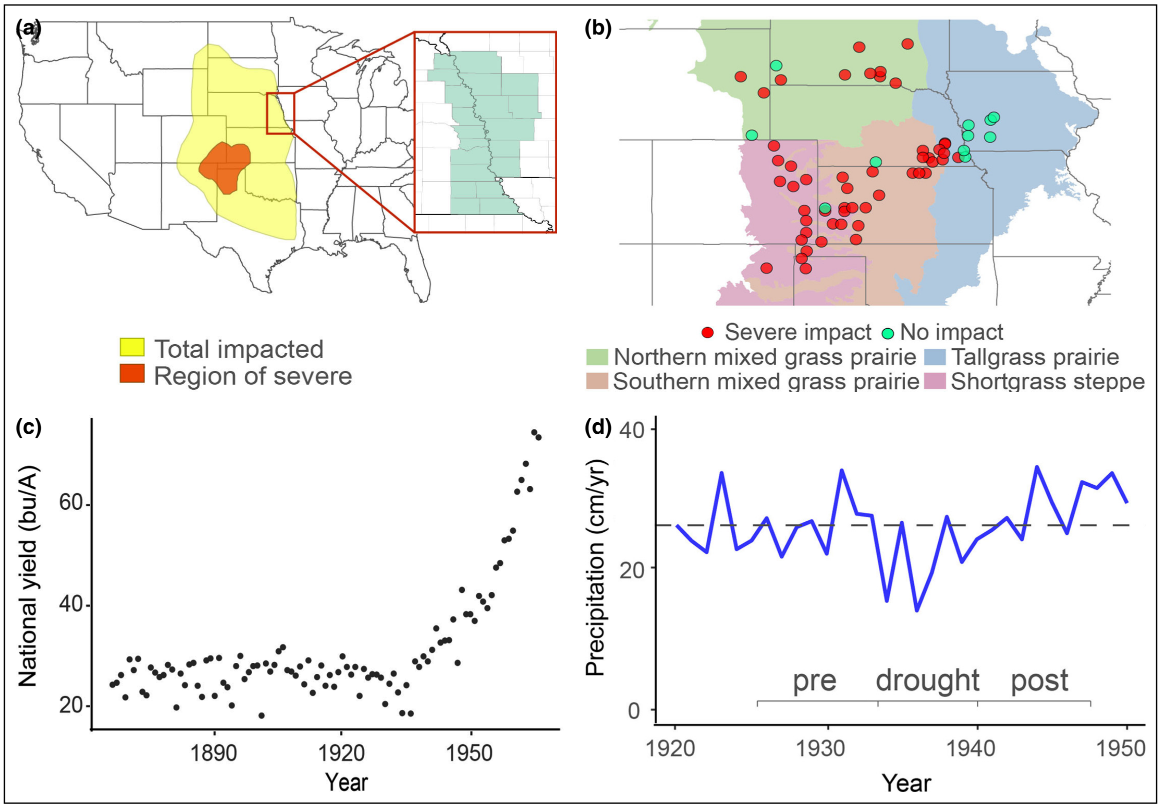

Figure 2. Spatial and temporal variability in Dust Bowl impacts on agroecosystems. (a) Approximate total region of the US impacted by dust storms (yellow) and region of severe damage (red) from 1930 to 1940 (insert shows current 20-county study area). (b) Quadrats sampled by ecologists during the drought showing severe impact (plant mortality; red dots) and no impact (loss of cover only; green dots) (potential vegetation from www.worldwildlife.org/publications/terrestrial-ecoregions-of-the-world; Weaver and Albertson 1936). (c) Total corn yield across the US (bushels per acre; www.nass.usda.gov). (d) Variability in annual precipitation (cm) at Lincoln, Nebraska (NE), represents rainfall pattern in this study region for three time periods: pre-drought (1926–1932), drought (1933–1940), and post-drought (1941–1948).

whereas only loss of cover occurred on quadrats in IA, similar to the boundary on the Dust Bowl map (Figure 2a).

We sought to use contemporary integration approaches (Peters *et al.* 2018) to identify the location of the Dust Bowl boundary between NE and IA where both ecological and agronomic data were available, and to quantify factors governing grass production on both sides of the boundary to test hypotheses from the two paradigms. A large suite of historical data beginning in the 1920s and continuing through the 1940s was available for this NE–IA boundary for synthesis and integration. We tested the following hypotheses: (1) local scales of variability in climate and soil (red text in Figure 1) are sufficient to explain patterns in production (ie the current paradigm), and (2) in addition to local scales of variability, connectivity-mediated feedbacks from landscape- and regional-scale land-surface properties (green and black text in Figure 1) that affect wind erosion and sand deposition are *also* needed to explain patterns in production. We tested these two hypotheses using data collected before, during, and after the drought of the 1930s. These results may help to answer a question that continues to perplex land managers in the present day: how can we be better prepared for these types of catastrophic events (eg www.scientificamerican.com/article/dust-bowl-days-are-here-again)?

A unique, historic, regional-scale experiment within the central Great Plains

In the US prior to the late 1940s, on-farm crop yields were highly variable through time, reflecting variability in weather for rain-fed crops (Figure 2c). Focusing on the 20-county region at the boundary between IA and NE, we selected one crop for analysis (corn; *Zea mays*), which was the dominant plant seeded in each county during the pre- to post-drought period (1926–1948; Figure 2d). Variability in soils (25–70% silt), elevation (239–472 m), mean precipitation (5.1–7.8 cm yr^{-1}), and mean maximum temperature (15.3–18.8°C) occurred over the 23-year period in these counties. Because a proportion of fields in each county was cropped and then abandoned each year, many farmers conducted a similar manipulation (ie plowing followed by planting with corn and no additional amendments, then abandonment or harvesting) across this heterogeneous landscape of 27,432 km^2.

Response variables

Farmers have been reporting yield by farm and crop type to the US government since the 1860s. The values are aggregated to the county level for each crop type before being made publicly available (www.nass.usda.gov). We converted corn grain yield (bushels $acre^{-1}$) to production (grams biomass m^{-2}), a metric more commonly used by ecologists, for each county in each year using a standard conversion (for details see Djaman *et al.* [2013]). Corn production on rainfed fields was assumed to represent an index for annual grass production during three periods: (a) pre-drought (1926–1932) for baseline conditions, (b) drought (1933–1940), and (c) post-drought (1941–1948) for legacy effects (Figure 2d).

Explanatory variables

County-level weather, soil, and land-use data were obtained or derived from original sources (WebTable 1). Eleven variables were selected based on either their expected (1) local-scale effects on grass and corn production or (2) landscape- to regional-scale effects on wind erosion and deposition of sand.

Local-scale variables

Monthly precipitation (cm) and average daily maximum temperature (°C) data were retrieved from PRISM (http://prism.oregonstate.edu/historical), and either summed (precipitation) or averaged (temperature) for the growing season (1 April–31 August) or water year (1 October–30 September), and then averaged across all years within each period. Maximum daily air temperature (°C) data obtained from historical weather stations (www.noaa.gov/climate) were interpolated to a county level using the closest weather station with at least 75% data coverage or with the most complete coverage when multiple stations were available. Missing values were estimated using a multivariate Markov weather model. When no weather station met these criteria, kriging was used to obtain a daily precipitation and maximum temperature surface from which county-level daily data could be obtained. The number of growing season days with maximum daily temperatures higher than 32°C was calculated to account for the deleterious effects of high temperatures on corn growth (Hatfield and Prueger 2015). Soil data from the STATSGO2 database (http://websoilsurvey.nrcs.usda.gov) were summarized by calculating their area-weighted average of soil map units within each county. Patterns in current soil properties were assumed to represent historical soils given that no historical maps are available. Local variables (% silt and % clay in surface horizons) represent effects of soil properties on water available to plants following precipitation events.

Landscape-scale variables

The percentage of very fine sand (particles from 0.10 to >0.05 mm in diameter; measured as both the area-weighted mean and the maximum in the surface horizon) is a soil property easily eroded by wind, and is therefore a proxy for wind erodibility. Threshold velocity ($U^{*}t$; the wind velocity required to initiate soil erosion) is another index of soil erodibility by wind that was calculated for disturbed soils based on % clay in surface horizons (Gillette *et al.* 1980). Both minimum (easy to erode) and maximum (hard to erode) threshold velocities were calculated. Land use was estimated using the acres of abandoned cropland divided by total acres of cropland by county in the closest year of the period when data were available (pre-drought 1929; drought 1934; post-drought 1939; www.agcensus.usda.gov).

Regional-scale variables

The historical locations of the Missouri River between NE and IA, as well as of the flood (alluvial) plain and Loess Hills in western IA, were based on a survey conducted by the US Geological Survey in 1934 (https://ngmdb.usgs.gov/topoview).

Approach

A big data–model integration approach was used to identify a subset of variables for analysis and to test hypotheses about the drivers of production (Peters *et al.* 2018). To predict production across the entire gradient, we used expert knowledge and exploratory analyses to construct a suite of models that prevented inclusion of correlated variables (Pearson $r > 0.70$) in the same model. We then selected the best model using the smallest corrected Akaike information criterion (AICc). Hierarchical partitioning quantified the relative importance of each variable in the model (Chevan and Sutherland 1991; Groemping 2006). Univariate relationships and boxplots between production and each variable identified in the drought model further illustrated differences on each side of the boundary.

Where was the boundary between Dust Bowl-impacted and non-impacted areas?

For the entire time period, a linear rather than a disjunct relationship was found between explanatory variables and production when all data were combined (Figure 3, top and middle panels). However, production values in counties from IA were higher than those in NE, in particular during the drought and post-drought periods (middle panels in Figure 3, b and c). These results suggest that a boundary existed at the border between the two states, which supports published accounts (Figure 2, a and b).

What are the explanations for the Dust Bowl boundary?

Because the same local variables (% silt, precipitation) provided the largest contribution to variance in production in the periods before and after the drought, there was no long-term legacy effect of the Dust Bowl on production, and current paradigms are sufficient to explain patterns in production in these periods (bottom panels in Figure 3, a and c). Spatial variability in temperature was also apparent in the post-drought period, although with a small contribution to variance (<1%).

During the drought, however, two surface soil properties related to transport by wind (very fine sand at two scales of aggregation within each county) and an index of wind erodibility (threshold velocity) were the most important explanatory variables for production, along with a small contribution by a local variable (precipitation; bottom panel in Figure 3b). Patterns in production during the drought could therefore only be explained by including both landscape- and local-scale processes that are commonly included in landscape ecology paradigms. Classifying counties by the boundary between states shows high overlap in values for precipitation and mean sand, whereas maximum sand was higher in NE and maximum threshold wind velocities were highest in IA where soils are the hardest to erode by wind (Figure 4). Production was always similar or higher in the east (IA) than in the west (NE) for the same value of each variable (bottom panel in Figure 4).

Although this analysis provides further support for the location of the Dust Bowl boundary occurring between the two states (Figure 2a), it does not explain *why* the boundary occurs there. The border between the states was formed by the Missouri River, leading to the question: why would the river influence production differently in the two states? Synthesizing additional historical information provides insights to this question and ultimately to our question about the Dust Bowl boundary.

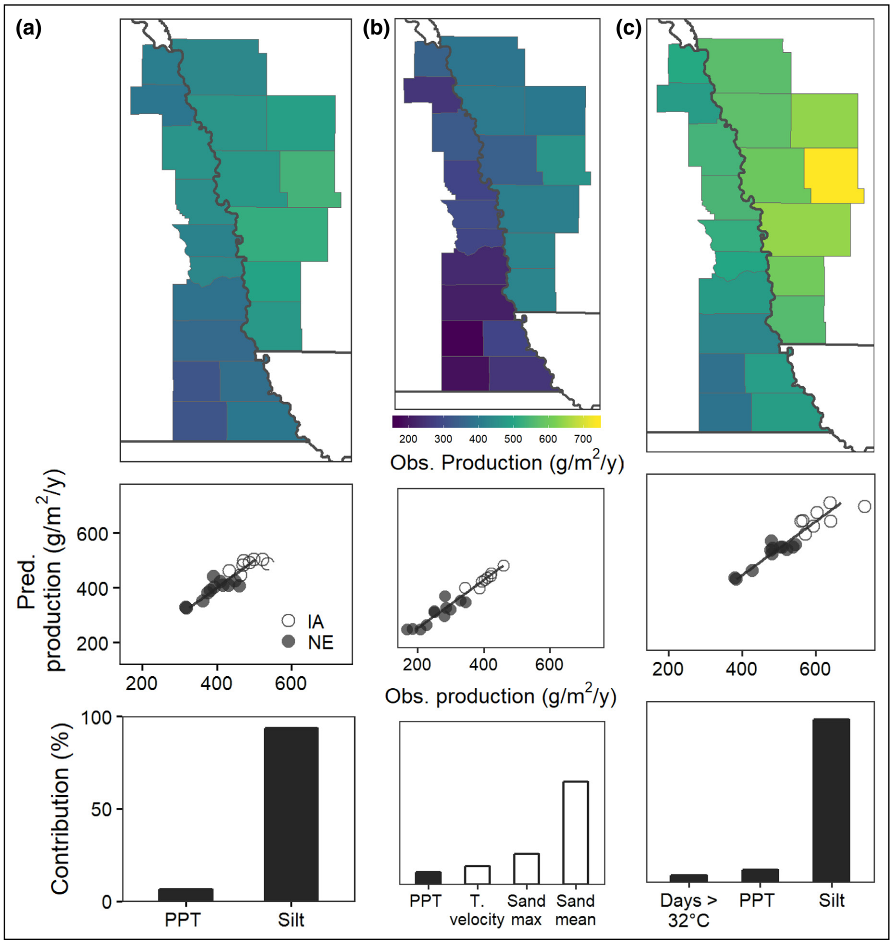

Figure 3. Primary production by county in Nebraska (NE) and Iowa (IA) in three periods: (a) pre-drought, (b) drought, and (c) post-drought. Top panels: spatial patterns by county. Middle panels: predicted production relationships for all counties in NE (filled circles) and IA (open circles). (a) Pre-drought (Prod = –306 + 9.4×silt + 0.26×PPT[wy]), adjusted R^2 = 0.74; AIC_c = 142; ΔAIC_c = 0. (b) Drought (Prod = 172.19 + 0.79×PPT[wy] – 51.16×vfsand_wt_mean – 5.14×vfsand_max + 0.38×$[U^*t]_{max}$), adjusted R^2 = 0.81; AIC_c = 154.25; ΔAIC_c = 3.89. (c) Post-drought (Prod = –725.35 + 13.1×silt + 0.72×PPT[wy] – 66.06×#days > 32°C), adjusted R^2 = 0.79; AIC_c = 154.22; ΔAIC_c = 0. Best model in each period based on a combination of highest adjusted R^2, lowest AIC_c, and a significant univariate regression with a variable and production. Bottom panels: contribution (%) to a regression by each variable in each period. Filled bars are local processes, whereas open bars are landscape processes. Prod = production; PPT(wy) = water year precipitation; vfsand_wt_mean = area-weighted mean of very fine sand; vfsand_max = maximum % very fine sand top layer; U^*t_{max} = maximum wind speed for soil erosion to be initiated; silt = % silt in top layer; #days > 32°C = number of days where maximum temperature was >32°C.

First, in the 1930s, the Missouri River was unmanaged, with frequent flooding occurring throughout its ~10-km-wide floodplain (Figure 5a; Schneiders 1999; NRC 2002). After the initial Pick–Sloan Flood Control Act of 1944, when multiple dams were constructed, additional legislation led to the confinement of the river in a single channel, which currently bears little resemblance to the wild river that existed in the 1930s.

Second, dust storms were a characteristic feature of the Dust Bowl that likely interacted with the Missouri River floodplain to influence production. The abandonment of many agricultural fields during the drought resulted in a highly connected landscape – that is, large areas of bare sand where wind could not only produce dust, which could be transported long distances, but also facilitate the transport of sand over shorter distances (Lee and Gill 2015). The most easily transported sand particles are fine sands. Saltation of these fine sands (ie the transport of particles in a hopping motion) produces dust (silt and clay) through sandblasting that can be transported long distances. In the Dust Bowl, dust from the region was reported as far away as the US East Coast (Figure 5b). Larger sand particles can be moved over short distances to form dunes, which were observed throughout the Dust Bowl region.

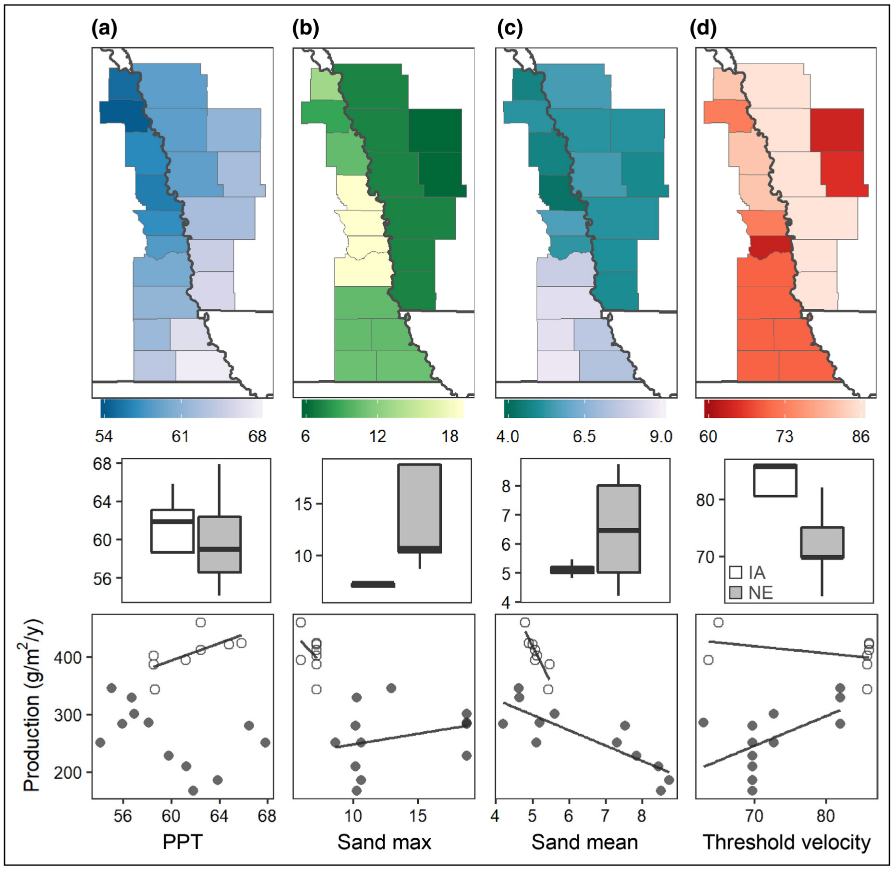

Figure 4. Variables important to production during the drought (from Figure 3b). (a) Water year precipitation [PPT(wy); cm yr^{-1}], (b) very fine sand [vfsand_mean; maximum, %], (c) very fine sand (area-weighted mean, %), and (d) maximum threshold wind velocity (U^*t_{max}; cm s^{-1}). Upper panels: county-level spatial variability in each variable. Middle panels: horizontal lines within boxes depict median values, boxes represent the interquartile range (25th–75th percentiles), and whiskers (vertical lines) represent 1.5×interquartile range; values in IA and NE appear in the white/left and gray/right boxplots, respectively. Bottom panels: production relationships developed by combining all counties in NE (filled circles) or IA (open circles); only significant relationships ($P < 0.1$) are shown. (a) $Prod_{IA} = -60.26 + 0.76 \times PPT(wy)$, $R^2 = 0.76$; (c) $Prod_{IA} = 1050.66 - 126.3 \times$vfsand_mean, $R^2 = 0.78$; $Prod_{NE} = 432.71 - 26.69 \times$vfsand_mean, $R^2 = 0.71$; (d) $Prod_{NE} = -115.27 + 5.16 \times U^*t_{max}$, $R^2 = 0.33$. $Prod_{IA}$ = production in IA; $Prod_{NE}$ = production in NE.

In NE, abandoned fields were prevalent in 1934, which provided a source of sand to be blown by wind, as well as for dune formation and dust storms (Figure 5a). Plants that responded to favorable rainfall and temperature, but were covered or abraded by sand, would have had lower production than would be expected based on precipitation amount (Cleugh *et al.* 1998). However, sand transport across the Missouri River into IA was unlikely because the sand would have been captured by water or deposited on the stable surface of the wide floodplain that occurred in the western counties of IA (Figure 4d). If sand was transported across the floodplain, then it would have likely been deposited on the higher elevation Loess Hills of western IA before reaching croplands. In addition, there were few sand sources in IA based on the high threshold velocities for wind and low sand values (Figure 4, b–d). Because very few croplands were abandoned in IA in the 1930s, there would have been less disturbed land available for erosion, leading to less local transport of sand by wind with less deposition of sand on plants.

Understanding and predicting these landscape- to regional-scale impacts of extreme events therefore requires paradigms that include local- and landscape-scale processes interacting with regional-scale processes associated with land surface features (Figure 1). Support for different processes in NE compared with IA can be found from online archival sources; photographs and news accounts of sand covering crops in NE are common (eg Figure 5, a and b), whereas similar documentation is unavailable for IA.

Conclusions

Large-scale geomorphic features – such as the Missouri River, its floodplain, and the Loess Hills in IA, all three of which likely protected IA grass and crop production from connected sand transport from the west during the drought of the 1930s Dust Bowl – are not typically considered by ecologists in global-change studies. Most ecological studies of extreme events consider local changes in the magnitude and variability in global-change drivers (eg precipitation, temperature, nitrogen). The majority of studies in temperate grasslands focus on extreme events (mostly droughts or wet periods). These ecological studies of localized climatic impacts are used to provide insights to dynamics under future climate scenarios. Ignoring the larger effects of sand transport in NE that was not present in IA during the drought would have either under- or overestimated production for a given value of precipitation using this localized approach.

There is increasing evidence of large-scale, spatial drivers overwhelming fine-scale processes and local inputs in many terrestrial ecosystems, from floods, wildfires, and insect outbreaks in forests to hurricanes in tropical forests and coastal ecosystems (eg Brokaw *et al.* 2012; Seidl *et al.* 2016; Wicherski *et al.* 2017). Because extreme climatic events are increasing in frequency, intensity, and magnitude, there is an urgent need to include larger-scale explanations that require a broader, multidisciplinary perspective (Peters *et al.* 2018). The historical dynamics of our study occurred within a small region that was expected to contain a smooth climatic gradient, yet an abrupt agroecological boundary associated with a geomorphic/topographic feature (the Missouri River floodplain) was observed. While local drivers

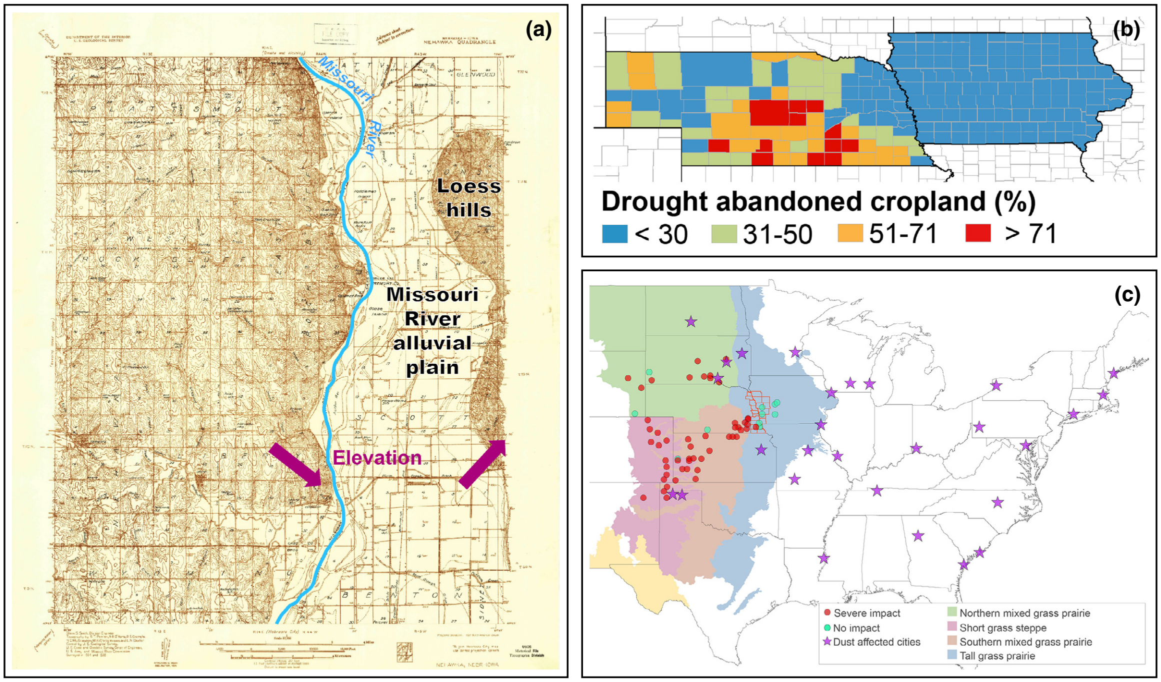

Figure 5. The hypothesized role of the Missouri River floodplain in protecting IA croplands from Dust Bowl impacts. (a) 1930s topographic map for the NE and IA border showing the Missouri River (blue line) and its floodplain prior to dam development and channelization (USGS 1935). (b) In NE counties that border IA, transport from abandoned fields to the west likely deposited sand on grasses, reducing production below that expected from precipitation and soils (Figure 4). In IA counties that border NE, grass production responded to precipitation because the state was protected from sandstorms by the stable soils of the Missouri River floodplain (Figure 4d), and from local dune development by local soil properties (Figure 4c). (c) Dust storms initiated farther west that produced fine dust storms traveling very long distances (purple stars indicate cities where dust was deposited), even as far as the US East Coast, would not have negatively impacted production in either states. Study counties are outlined in red. Red circles indicate severe impact with high plant mortality, and green circles indicate no impact with loss of plant cover only (data sources shown in WebTable 2).

were important to production before and after the drought, managing for these surprising dynamics during a catastrophic drought – even at seemingly fine scales of landscapes – requires a multiscale perspective. Including regional-scale geomorphic features that can either ameliorate or accentuate the cascading effects of extreme events is critical to conceptual models and paradigms for extreme events in order to understand, predict, and manage for the future under changing patterns of climate and land use.

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Supporting Information

Additional, web-only material may be found in the online version of this article at http://onlinelibrary.wiley.com/doi/10.1002/fee.2194/suppinfo