FUNCTIONAL STRATEGIES ALONG A SOIL MOISTURE / AGE GRADIENT

Progress Report
November 2017
Prepared for: Lynn Riedel, Plant Ecologist
City of Boulder Open Space & Mountain Parks, Boulder, CO

Julie Larson
Ecology and Evolutionary Biology
University of Colorado at Boulder

Contact Information:
Julie Larson, Campus Box 0450 University of Colorado at Boulder, Boulder, CO 80309
Julie.e.larson@colorado.edu 708-220-7935

Executive summary

- This project was funded by City of Boulder Open Space & Mountain Parks (OSMP) in March 2017 ($10,800). This report describes the status and timeline for completion.
- The purpose of this project is to assess three main research questions
    - Q1: How does water availability differ across a soil gradient in OSMP grasslands?
    - Q2: How does plant functional composition vary with local edaphic variation?
    - Q3: How can management influence adaptive capacity in this system?
- Twelve sites have been established across a 10km stretch of xeric tallgrass prairie with soil surfaces ranging in age from ~5 ka to ~2000 ka yrs. At half of the sites, soil moisture sensors were installed at two depths (10 cm, 30cm) to explore soil water dynamics. At all sites, moisture-related properties are also being assessed. Recruitment success (from a hand-seeded mix) and plant community composition were surveyed at each site in Aug-Sep 2017, and seedbank samples are currently being grown out. These data will be used to assess soil moisture-related differences in the realized (mature plants) and potential (seedbank and seeded) plant communities. Efforts are also underway to develop a seed and plant trait database for ~50 abundant species, which will be used to understand functional mechanisms underlying community responses to the environment.
- Preliminary results (Q1):
    - Soil moisture data suggest that water dynamics likely differ across the surfaces. The youngest soils accumulated moisture at depth relative to the shallow zone beginning in early spring, while the oldest sites exhibit much stronger and rapid accumulation in late spring. The oldest surfaces also exhibited more comparable moisture levels at shallow and deep zones through the growing season. Greenbelt Plateau (age rank 4 of 6) exhibited different dynamics from other surfaces.
    - We found a weak decrease in soil pH with age rank (approx. 0.077 pH units per increasing age class). Other soil properties will be quantified in spring 2018.
- Preliminary results (Q2):
    - Preliminary analyses suggest that soil surfaces do differ in species composition and dispersion based on mature plant composition (data not shown in this report).
    - Once an initial trait database is established (summer 2018), we can assess whether shifts in plant composition across the gradient are explained by species' traits.
- Preliminary results (Q3)
    - Preliminary analyses suggest that first year recruitment rates from a diverse seed mix were low across sites, with the exception of one productive site (youngest soils). We will revisit plots in year two, and given low initial recruitment, may discuss the possibility of future seeding events across years/seasons to determine whether recruitment has an environmental and/or trait-based signature.
    - Once initial trait data are compiled, we will also assess the functional composition and diversity of the seedbank (2018) to explore the capacity of plant communities to respond to changing environments via species turnover.

Abstract

Environmental variation over space and time is one of the strongest drivers of plant community dynamics, and consequently, ecosystem services. Predicting how communities will respond to gradual and fluctuating climatic shifts, and mitigating responses through enhanced resilience, is thus a critical goal for successful land management. However, anticipating community responses may be particularly challenging if the impact of climatic shifts are context-dependent – influenced by local abiotic variation such as edaphic and hydrological properties. In this study, we are exploring how a unique soil age gradient (approx. 5ka to 2000ka years across six surfaces) drives variation in water variability, and relatedly, plant community composition in tallgrass prairie systems. Soil moisture sensor data suggest that surfaces differ in the timing and distribution of water availability in the soil profile, and we expect other soil properties to further elucidate soil-mediated differences in plant water availability. Preliminary analyses of plant community composition data also suggests shifts in composition and dispersion of plant communities across the gradient (data not shown). We have begun compiling a vegetative and seed trait database to understand whether functional traits—historically, powerful predictors of plant environmental responses—are useful in explaining these patterns. Trait-water relationships will be used to anticipate functional strategies that enhance resilience in extreme precipitation events, and therefore, inform community composition targets for management. While most studies overlook recruitment from the seed bank as an important reservoir of functional diversity, we are also using seed bank sampling and seed additions to explore the potential for recruitment from natural or artificial seedbanks, respectively, to manipulate functional composition and enhance the adaptive capacity of this high-value grassland system. While seedbank grow-outs are ongoing, preliminary seed addition results suggest that recruitment may be a limiting factor for community responses on most surfaces and worth further exploration.

Keywords

Adaptive capacity, Environmental gradients, Functional traits, Plant community dynamics, Recruitment, Resilience, Seed bank, Soil age, Soil moisture

Introduction

A key challenge of managing natural ecosystems in the face of climatic changes is the unpredictable nature of such events (Smith 2011). Despite projections of more frequent extreme events (Dai 2013), these occurrences remain highly stochastic, making management to alleviate impacts quite challenging. Natural systems may also vary substantially in resilience to similar climatic events due to variation in local factors such as soils or terrain that influence a system's sensitivity (Scherrer and Korner 2011, Dickinson et al. 2014, Ackerly et al. 2015), and to variation in the adaptive capacity of the vegetation, which has been linked to plant functional composition and diversity (Folke et al. 2004, Houseman and Gross 2011, Fischer et al. 2016) (Fig. 1). While local environmental factors are difficult to control, manipulation of community functional composition may offer a valuable tool to enhance resilience. Here, we explore strategies to increase ecological resilience and recovery by building functional adaptive capacity across a variable landscape (Fig. 1). We are in the process of assessing three research questions:

Q1. How does water availability differ across soil edaphic gradients in Boulder Open Space? Water availability affects plant growth and composition in almost all ecosystems, including those that surround Boulder (Huxman et al. 2004, Evans et al. 2011, Munson 2013, Concilio et al. 2016). The size and timing of rainfall events together with soil organic matter content and soil texture largely control the amount of water stored in soil and the rate of water flow through the soil system (Jenerette and Chatterjee 2012), which in turns governs redox conditions and nutrient availability (Parker and Schimel 2011, Evans and Wallenstein 2012). Our work focuses on a gradient of xeric tallgrass sites that – while receiving similar precipitation – vary in soil age and structure (Buckner and Odasz, in prep). We expect that edaphic variation affects the duration of soil moisture retention following storms, the rate of dry-down as the growing season progresses, and overall water availability for plants.

Q2. How does functional composition of the vegetation vary in relation to these local edaphic controls? Grasslands receiving similar degrees of water deficits can vary strongly in their responses (Biondini et al. 1998, Vermeire et al. 2009), and this ability to respond is often related to the composition of vegetation (Knapp et al. 2015, Wilcox et al. 2016, Witwicki et al. 2016). These studies suggest that functional composition and diversity may be key components of how communities shift in response to drought -- their adaptive capacity (Manning et al. 2006, Yahdjian and Sala 2006, Jentsch et al. 2011). One way to identify functional targets that enhance resilience to drought events over time is to identify traits or diversity metrics associated with drier sites across space. For example, patterns aligning strategies of early, rapid growth with wetter conditions and stress tolerance with drier conditions have been identified over both time (Kimball et al. 2012) and space (Cornwell and Ackerly 2009). We expect that traits related to timing of resource use (e.g., early/late active), tolerance of resource stress, and recruitment ability are key aspects of functional strategy reflected in the variation in species composition across soil gradients.

Q3. How can management influence this adaptive capacity? To date, most efforts have demonstrated that resilience to a climate event such as drought depends on prior functional composition and diversity of the adult community (Hoover et al. 2014, Isbell et al. 2015, Arredondo et al. 2016). However, the functional composition of seedbanks may serve as essential reservoirs of diversity (Ooi et al. 2009), determining whether threatened adult communities have the ability to recover naturally or whether seed addition is required to enhance functional diversity (De Steven et al. 2006, Larios and Suding 2013). While the seed bank defines available functional diversity, recruitment from the seed bank can also act as an important bottleneck restricting the functional expression in the established vegetation (Larson et al. 2015, Larson and Funk 2016). Thus, in addition to the enhancing the adaptive capacity of the established vegetation, we expect that adaptive capacity can also be manipulated by affecting potential recruitment – either in functional diversity stored in the ungerminated seed bank or by addition of native seed.

Methods

Study sites

We established 12 sites in xeric tallgrass prairie grasslands managed by the City of Boulder Open Space & Mountain Parks, spread over 10km of the Colorado Front Range near Boulder, CO, USA (Table 1, Figure 1). Sites span an elevation gradient of approximately 1680m to 1900 m and a soil age gradient of ca $5 \cdot 10^3$ to $2 \cdot 10^6$ years (Table 1), and were selected to align with areas where historic community vegetation data was available for comparison (e.g., Buckner & Odasz, in prep).

Study design

At each site, we established a permanent 50m transect to sample mature plant community composition at the site level. Every 12.5m along each transect we established two 2m^2 plots, starting 2m out from either side of the transect, for total of 10 plots per site. Plots were split into paired 1m^2 recruitment plots and 1m^2 vegetation. In April 2017, we cleared recruitment plots of dead litter and standing dead vegetation (but left live plants intact) and manually roughed the bare soil (to 1-2 cm). We split recruitment plots into two 0.5m^2 subplots – one seeded and one control receiving no additional treatment (non-seeded). Plots were hand-seeded on April 1-3 2017, prior to final spring snowfalls. The seed mix contained 18 native species from local collections to maximize functional group diversity (Table 2). We weighed out approximately 50 filled seeds per species (but increased the smallest-seeded species, *Artemisia frigida,* to 100 seeds). We adjusted target weights by viability estimates if tetrazolium tests or official germination tests indicated ≤80% viability (3 species); however, these test results were only available for 8 of 18 species.

To capture spring cover conditions that could influence recruitment patterns within and among sites, and to measure site differences in the potential effects of clearing litter for seeding, we made visual cover estimates for each recruitment sub-plot (cleared) and vegetation plot (unaltered). For consistency, a single observer estimated percent bare ground, litter (includes detached litter and standing dead), green vegetation, and rock cover in late April 2017. We also estimated the height of litter and standing dead vegetation (cm) in each sub-plot as the average of 3 random measures for each type (6 total replicates per seeded, non-seeded or vegetation plot).

Soil moisture and properties

In Dec 2016, we installed soil moisture sensors at two depths per site (Decagon; 10cm and 30cm depths) to collect hourly volumetric water content and characterize site difference in soil moisture. Data collection is ongoing for the four youngest age classes (Sites A, C, E, G); two dataloggers were lost to cattle grazing in June 2017, limiting data availability at the two oldest sites (Site I, Site K). These may be replaced pending further discussion with OSMP.

To characterize soil properties, we collected 9 replicate soil cores (2cm diam) per site along the 50m transect (at 0m (n=3), 25m (n=3) and 50m (n=3) in April 2017. We sampled to a depth of 10cm where possible, but retained cores approx. 7cm or deeper given high rock content at many sites (as high as 60-80%, Branson et al. 1965). Samples were pooled for site-level analyses at all locations except site A, which exhibited clear edaphic heterogeneity across the 50m transect. At this site, we collected, pooled, and will perform separate analyses on 3 replicate samples at 5 locations along the transect (0m, 12.5m, 25m, 37.5m, 50m). Soil samples were analyzed for pH (pH meter, Mettler Toledo) using a 1:2 mixture of soil to Nanopure™ filtered water (E. Hinckley pers. comm).

Anticipated: Soil samples will be analyzed for texture (ASTM, 1998), organic matter and inorganic C (loss-on-ignition; Wang et al. 2012) in spring 2018. We will discuss the possibility of re-installing damaged sensors and increasing direct inference for soil moisture dynamics with OSMP; in addition to installing more sensors, this may involve plant-based metrics of water availability that were not able to be collected in 2017 (see Results & Discussion Q1, below).

Recruitment and plant community sampling

To characterize the effects of seed addition on community composition, we surveyed 7 to 10 recruitment plots per site (including seeded and non-seeded 0.5m^2 subplots) for species composition in Aug-Sept 2017. We used visual cover estimates for overall composition (taken by a single observer), but also noted presence/absence of species from the seed mix (seedling-juvenile individuals only). To characterize site-level community composition, we also conducted a point-line intercept survey along the established 50m transect at each site. We sampled 2 points on either side of the transect at every meter (100 points per transect) and recorded any additional species present within 1m along either side of the transect (Bunckner and Odasz, in press).

Anticipated: We will re-survey seeded and non-seeded subplots in late summer 2018 to assess second-year recruitment. We may also initiate conversations with OSMP regarding the expansion of seed addition efforts given limited initial recruitment success (see Results & Discussion Q3, below).

Seedbank sampling

To characterize the seedbank, we collected three replicate seedbank samples (6cm diam x 2cm depth) per recruitment plot in April 2017 (i.e. 3 samples x 10 plots = 30 samples per site). Samples were pooled at the plot level, air-dried, sieved (4mm), and spread on top of potting soil at a thickness of 2cm (pots 10cm x10cm x 10cm) in July 2017. Seedbank samples were grown out in the greenhouse and watered 3 times/wk. We monitored weekly seedling emergence for 13 weeks, pulling seedlings as they were identifiable. After 13 weeks, all pots were dried down and stored in a dry, dark outdoor storage unit over winter.

Anticipated: Seedbank samples will be re-wetted in the greenhouse to check for any previously dormant species beginning in January 2018.

Vegetative trait data collection

From Nov 2016 to June 2017, we collected vegetative traits (Table 3) for 40 of the most abundant native and species across local xeric tallgrass prairie communities (Table 2) in the greenhouse at three life stages: emerged (5 d), established (6-8 wks), and mature (16wks)(5 indiv/stage). We collected most seeds for this project locally in 2016 (>90% of species), germinated seeds in petri dishes, then transplanted seedlings into pots (6.4cm diam x 25.4cm length) containing a 1:1:1 mixture of sand:perlite:vermiculite, plus 15mL of locally-collected soil inoculum mixed into the top 3cm. After the determined growth period, plants were removed from pots, cleaned by hand, and leaves and roots were scanned and analyzed for area or length, respectively (total or subsamples of leaves/roots depending on lifestage; WinRhizo software, Regent Instruments, Quebec, CA). Roots, leaves, and shoots were rehydrated for at least 24 hrs, then weighed for fresh mass, dried at 60C, and weighed for dry mass.

Anticipated: In spring 2018, we will finish sample processing and compiling of 2017 vegetative trait data. We will also repeat vegetative trait data collection for at least 11 additional species that were included in the 2017 seed mix (either collected by J.L in 2017, or by OSMP).

Seed trait data collection

To collect seed dormancy and germination traits (Table 3), we made fresh seed collections of three populations for each of 28 species (Table 2) from June-Nov 2017. Because seed processing time was limiting, species that had been included in the seed mix were prioritized for collection. Within two weeks of collection, we conducted germination tests to assess fresh dormancy percentages, imbibition rates, and scarification requirements (dormancy mechanism). Seeds have been storied in dry, outdoor conditions until further testing (see *Anticipated,* below). Within two weeks of seed collection, we also filled 8 nylon mesh bags per population with 30-50 seeds (depending on seed availability; 3 populations * 8 bags = 24 bags per species) and buried them in soil to a depth of 10-15cm. The burial site is an outdoor raised bed (6ft x 30ft) in Boulder, CO that was cleared and tilled prior to burial, and is weeded biweekly during the growing season. Bags were buried into one of 24 blocks, and will be harvested seasonally over a period of 2 years (see below).

Anticipated: Stored seeds from 2017 collections will undergo periodic germination testing with and without artificial dormancy breaks over the next two years, including at least one trial at multiple temperatures and water potentials to assess germination requirements (e.g., thermal time and minimum water potential for germination, Table 3) to characterize some dormancy and germination metrics via controlled tests. To characterize seasonal *in situ* dormancy patterns, buried bags will be harvested seasonally over the next two years (3 blocks per harvest), beginning in Nov 2017 and ending in in Nov 2019. Seeds will be extracted from the bags, rinsed, and germinated in a growth chamber for total germination % and time to 50% germination.

Results & Discussion

Q1: How does water availability differ across soil edaphic gradients in OSMP tallgrass prairies?

Preliminary

Soil moisture data from January-June 2017 suggest that soil moisture dynamics may differ across the surfaces (Figure 3). The youngest sites accumulated moisture at depth (30cm) relative to shallow zone (10cm) in early spring, and tended to stay above 20% volumetric water content (VWC) at depth throughout the growing season. In contrast, older sites exhibited less substantial moisture accumulation in early spring and much stronger accumulation in late spring, when VWC exhibited rapid and sustained increases to field capacity. Furthermore, old sites exhibited comparable soil moisture levels at the shallow and deep zones throughout the growing season, while younger soils were consistently drier at the surface during spring. While maximum saturation levels appeared to be similar across sites and depths (40-47% volumetric water content (VWC)), shallow soils at the youngest surface (site A), never exceeded 25% VWC. This could reflect differences in soil texture (this site was located near an ephemeral drainage bed with coarser soils, pers. obs), which tends to align with soil moisture retention (e.g., Saxton & Rawls, 2006). Texture will be measured as an indicator of soil field capacity—the water content of soil after excess water has drained (2-3 days post-saturation)—in spring 2018 (see below). One soil surface on Greenbelt Plateau (age rank 4 of 6) also appeared to have soil moisture dynamics unique from all other surfaces, perhaps due to unique topography (mesa top).

Linear regression also suggests a weak decrease in soil pH with age rank (approx. 0.077 pH units per increasing age class; $p=0.024$; $R^2 = 0.414$) (Figure 4). This gradual decline of pH over time agrees well with another recent study across this particular soil gradient (Tea, 2014), and matches expectations of changes in soil chemistry over time (e.g., Vidic 1998).

Forthcoming

Forthcoming metrics include soil organic matter, soil texture, and in situ infiltration rate (spring 2018). We plan to use these metrics, along with soil pH, to more fully characterize surficial edaphic properties across the soil age gradient. Soil organic matter and soil texture, in particular, can be useful proxies for soil moisture (Saxton & Rawls, 2006). We will also pursue further analyses with soil moisture to quantify some metrics of soil moisture retention after precipitation events. While soil moisture sensor data provided a direct metric of soil moisture dynamics, we have some limitation in scope of inference based on the lack of replication, and no longer have sensors on the oldest surfaces. We may consider replacing these sensors, if permitted. Furthermore, given the potential difficulties with soil moisture sensor installation and maintenance, coupled with the need to understand differences in soil moisture dynamics at depth, we will likely pursue an additional plant-based metric in 2018 (proposed in 2017 but unable to complete). In this scenario, leaf samples would be harvested from a ubiquitous species across sites (e.g., *Andropogon gerardii*) at a standard time, and assessed for leaf water content and/or C13 isotope analysis to capture site differences in plant water availability (spring/summer 2018).

Once these data are compiled, we will compare sites in multivariate edaphic space, and combine soil data with plant community and trait data to ask whether community composition varies predictably with soil properties, and whether this is mediated by plant traits. Initial results are anticipated as early as summer/fall 2018, but final results may be delayed until the full suite of seed and plant traits is compiled (see Q2, below).

Q2: How does functional composition of the vegetation vary in relation to these local edaphic controls?

Preliminary

Assessing functional composition involves the quantification of a) species functional traits and b) abundance of those species at the site. While we do not yet have final trait databases compiled, species composition data from 2017 suggest that the soil surfaces differ in community composition. We have compiled species composition data from non-seeded recruitment plots (7-10 0.5m^2 plots per site), and conducted preliminary ordinations (non-metric multidimensional scaling, to visualize differences in community composition) and tests of differences in community dispersion (diversity metric, can be used to assess beta diversity) after removing rare species. Data are not shown here, but suggest that sites from the same surfaces do cluster together, but that composition may not turnover linearly with age. For example, while the youngest sites appear to have unique composition and higher dispersion than other surfaces (in agreement with Buckner and Odasz, in prep), Greenbelt Plateau sites (surface age rank 4 of 6) appears most different in terms of species composition, while the two oldest surfaces appear to cluster tightly between these two community types. Greenbelt Plateau also differed with respect to soil moisture dynamics (see above), which could suggest that direct measures of soil properties may be more effective than soil age to anticipate functional turnover in plant communities.

Forthcoming

Site-level composition data (50m transects) is currently being compiled and checked for unknown species, after which plant community composition data will be ready for final assessment. Once trait data is compiled, we will assess functional composition (community-weighted trait means CWM) and functional diversity (several possible indices, including functional dispersion and community-weighed variance) (Spasojevic and Suding 2012, Butterfield and Suding 2013), and compare how these metrics change across edaphic gradient (using environmental measures in Q1). We will also employ a null modelling approach to compare trait diversity to regional pools (after Bernard-Verdier et al. 2012).

Q3: How can management influence this adaptive capacity?

Preliminary

To answer this question, we are assessing the extant seed bank at each site and have conduct a seed addition experiment to determine how and where along the edaphic gradient seed addition may be effective tool to enhance adaptive capacity. While seedbank grow-outs are still in progress, preliminary results from the seed mix addition suggest that recruitment is likely to be an essential process for anticipating potential community change via the seedbank. We recorded the presence/absence of recruits of each species in seeded plots, and found that plots in most sites had no more than 1 or 2 species from the seed mix by the end of summer (and a majority had none; Figure 5A). At least some of the recruitment failure is likely attributable to seedling mortality (based on personal observations earlier in the season), although formal assessments over the growing season were limited by site accessibility. Understanding which components of recruitment are limiting (e.g., germination, seedling emergence or survival) under different environmental factors (e.g., Larson et al. 2015) could be key to assessing and improving adaptive capacity, and represents a potentially important area for future work.

The site with the most recruiting species (site B) appeared to be the most productive in terms of biomass and small-scale (i.e. within-plot) species richness (data not shown). We do not have soil moisture data for this site, but hope to explore the seemingly high potential for recruitment success via other soil properties (e.g., texture, organic matter). Following recruitment into the second year will also be critical to assess realistic establishment potential (see below).

While we observed many of the seed mix species in at least one site (Figure 5B), there were six species that were not documented. Some of these species were challenging to germinate in the lab prior to seeding despite high viability test results (from official tetrazolium (TZ) testing initiated by OSMP; *Erysimum capitatum, Pascopyrium smithii, Sporobolus heterolepis, Verbena hastata*), while others had no official viability test results available but appeared to germinate well (*Andropogon gerardii*) or poorly (*Artemisia frigida*) in the lab prior to seeding. This suggests that there could be a variety of mechanisms explaining lack of recruitment in the first year (dormancy or germination failure, post-germination mortality, or granivory). If we expand this trial seeding effort into a fuller experiment (see *Forthcoming*), it will be critical to have standard TZ tests and germination tests available for all species just prior to seeding (data availability is mixed for the 2017 seed mix), and useful to consider organizing at least one sampling event in late spring to capture seedling emergence prior to summer periods of heat/water stress. Because we are currently collecting a suite of dormancy- and germination-related traits for many of these species (see above), we will also have more power to discriminate between potential mechanisms moving forward, if a seeding experiment is repeated.

Forthcoming

Once seedbank grow-outs are complete and trait data are compiled, we will compare trait distributions in the seedbank to trait distributions in the established adult community across the soil gradient. Effect sizes calculated relative to a model of null assembly will be compared across the environmental gradient to determine where the extent seed bank will likely expand adaptive capacity and where seed addition may be an effective tool. However, a key component in understanding the potential efficacy of seed addition is anticipating recruitment patterns. We could potentially compare functional composition of the seed mix to the community of successful recruits, or compare composition of seeded plots to non-seeded plots for a trait-based understanding of recruitment success. However low initial recruitment rates in 2017 may be a challenge for these analyses. We will continue to follow species composition in recruitment plots for at least one more year (analyses in fall 2018) to see whether recruitment patterns change and there is potential for more rigorous analyses. We also acknowledge that our scope of inference regarding seed addition is limited by the particular conditions of the seeding year and the timing of seeding (April), which could affect dormancy break and susceptibility to granivory. If feasible, we may propose the possibility of a more extensive seeding trial, with seeding occurring at several time-points to see whether seeding seasonality can be used to manipulate recruitment success.

Timeline

By spring 2018, we expect to complete the seedbank grow-out and analyses of soil properties. By summer 2018, we expect to have a final vegetative trait database compiled, and an initial seed trait database compiled (dormancy trials initiated in summer/fall 2017 won't be complete until fall 2019). We will also re-survey seeded and non-seed recruitment plots in summer 2018. By fall 2018, we expect to complete analyses for a final report.

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Tables

Table 1 Soil type classification and age (following Buckner & Odasz, in prep) and site attributes for 12 study sites (see Figure 2).

Site	Soil classification	Parent material age (est. ka)	Transect Origin Lat.	Transect Origin Lon.	Elevation (approx.)
A	Post-piney creek	<5	39.9542	-105.2448	1680
B	Post-piney creek	<5	39.9567	-105.2412	1672
C	Louviers	120-160	39.9585	-105.2438	1677
D	Louviers	120-160	39.9519	-105.2473	1687
E	Slocum	240	39.9590	-105.2485	1689
F	Slocum	240	39.9495	-105.2530	1704
G	Verdos	640	39.9398	-105.2323	1806
H	Verdos	640	39.9323	-105.2337	1809
I	Young Rocky Flats	~1000	39.8823	-105.2450	1908
J	Young Rocky Flats	~1000	39.8774	-105.2477	1920
K	Old Rocky Flats	~2000	39.8681	-105.2432	1907
L	Old Rocky Flats	~2000	39.8765	-105.2426	1909

Table 2 Species that were collected for vegetative and seed trait data (J. Larson collected seedlots in 2016-2017, except for *Sporobolus heterolepis* and *Erysiumum capitatum* [OSMP-collected]) and species that were included in the seed mix (OSMP-collected seedlots from 2012-2017).

Species	Genus	Lifeform	Life history	Origin	Veg traits?	Seed traits?	Seed mix?
Achillea	*lanulosa*	Forb	Perennial	Native	x		
Adenolinum	*lewisii*	Forb	Perennial	Native	2018	x	x
Alyssum	*parviflorum*	Forb	Annual	Non-native	x	x	
Andropogon	*gerardii*	Graminoid	Perennial	Native	x	x	x
Anisantha	*tectorum*	Graminoid	Annual	Non-native	x	x	
Aristida	*purpurea*	Graminoid	Perennial	Native	x	x	
Artemisia	*frigida*	shrub/woody	Perennial	native	2018	x	x
Artemisia	*ludoviciana*	Forb	Perennial	Native	x		
Aster	*porteri*	Forb	Perennial	Native	2018	x	x
Bouteloua	*curtipendula*	Graminoid	Perennial	Native	x		
Breea	*arvensis*	Forb	Perennial	Non-native	x	x	
Bromopsis	*inermis*	Graminoid	Perennial	Non-native	x	x	
Bromus	*japonicus*	Graminoid	Annual	Non-native	x	x	
Chondrosum	*gracile*	Graminoid	Perennial	Native	x		
Cichorium	*intybus*	Forb	Perennial	Non-native	x	x	
Cirsium	*vulgare*	Forb	Biennial	Non-native	x		
Dactylis	*glomerata*	Graminoid	Perennial	Non-native	x		
Dianthus	*armeria*	Forb	Annual	Non-native	x	x	
Elymus	*elymoides*	Graminoid	Perennial	Native	2018	x	x
Elymus	*repens*	Graminoid	Perennial	Non-native	x		
Erysisimum	*capitatum*	Forb	Annual	Native	2018		x
Gaillardia	*aristata*	Forb	Perennial	Native	2018	x	x
Grindelia	*squarrosa*	Forb	Biennial	Native	x		
Helianthus	*rigida*	Forb	Perennial	Native	2018	x	x
Heterotheca	*foliosa*	Forb	Perennial	Native	2018	x	x
Heterotheca	*villosa*	Forb	Perennial	Native	x	x	
Juncus	*arcticus*	Graminoid	Perennial	Native	x		
Lactuca	*serriola*	Forb	Annual	Non-native	x		
Liatris	*punctata*	Forb	Perennial	Native	x	x	x
Lotus	*tenuis*	Forb/Legume	Perennial	Non-native	x		
Lupinus	*argenteus*	Forb/Legume	Perennial	Native	x	x	
Medicago	*sativa*	Forb/Legume	Perennial	Non-native	x		
Oenothera	*villosa*	Forb	Biennial	Native	x		
Oligosporus	*pacificus*	shrub/woody	Perennial	native	x		
Panicum	*virgatum*	Graminoid	Perennial	Native	x	x	x
Pascopyrum	*smithii*	Graminoid	Perennial	Native	2018		x
Phleum	*pratense*	Graminoid	Perennial	Non-native	x		
Plantago	*lanceolata*	Forb	Perennial	Non-native	x		
Poa	*agassizensis*	Graminoid	Perennial	Native	x		
Poa	*compressa*	Graminoid	Perennial	non-native	x	x	
Psoralidium	*tenuiflorum*	Forb/Legume	Perennial	Native	x	x	x
Ratibida	*columnifera*	Forb	Perennial	Native	x	x	x
Schizachyrium	*scoparium*	Graminoid	Perennial	Native	x	x	x
Sorghastrum	*avenaceum*	Graminoid	Perennial	Native	x	x	x
Sporobolus	*asper*	Graminoid	Perennial	Native	x		
Sporobolus	*heterolepis*	Graminoid	Perennial	Native	2018		x
Tragopogon	*dubius*	Forb	Biennial	Non-native	x	x	
Verbascum	*thapsus*	Forb	Biennial	Non-native	x		
Verbena	*hastata*	Forb	Annual	Native	2018	x	x
Vulpia	*octoflora*	Graminoid	Annual	native	x	x	
Yucca	*glauca*	shrub/woody	Perennial	native	x		

Table 3 Trait data currently being compiled in the vegetative phase (at 3 life stages: 5 days/6 wks/16 wks) and in the seed phase (including germination and dormancy metrics). Species for which trait data have or are being collected are given in Table 2.

Type	Trait
Vegetative	Specific leaf area (cm^2 g^{-1})
Vegetative	Relative growth rate (g g^{-1} d-^{1})
Vegetative	Root elongation rate (cm cm^{-1} d^{-1})
Vegetative	Root, leaf, and shoot dry matter content (g dry mass g^{-1} fresh mass)
Vegetative	Root mass ratio (g root g^{-1} total biomass)
Seed	Seed mass
Seed	Imbibition rate (% hr^{-1})
Seed	Thermal time for germination (°C d)
Seed	Minimum water potential for germination (MPa)
Seed	Dormancy type (based on quantitative responses to several artificial dormancy breaking mechanisms)
Seed	Seasonal dormancy type (based on in situ measures)

Figures

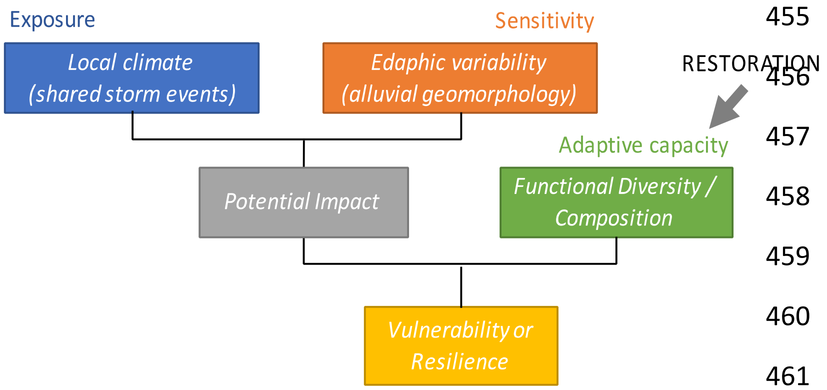

Figure 1 Exposure to climate events (blue) put ecosystems at risk to lose natural, cultural, and economic value. Potential impacts (gray) are expected to vary along environmental gradients due to system sensitivity (orange). Although management practices have little control over climate exposure and environmental sensitivity, they can affect vulnerability or resilience by influencing the adaptive capacity (green) of the local community. This adaptive capacity is likely related, in part, to the functional composition and diversity of the community—a feature which can be manipulated in restoration (e.g., via seed addition or through other practices like targeted timing of grazing). This progress report details our initial efforts to examine this important link in Boulder grassland sites, where exposure to climate is relatively uniform due to their close proximity yet sensitivity can vary greatly due to differences in alluvial geomorphology.

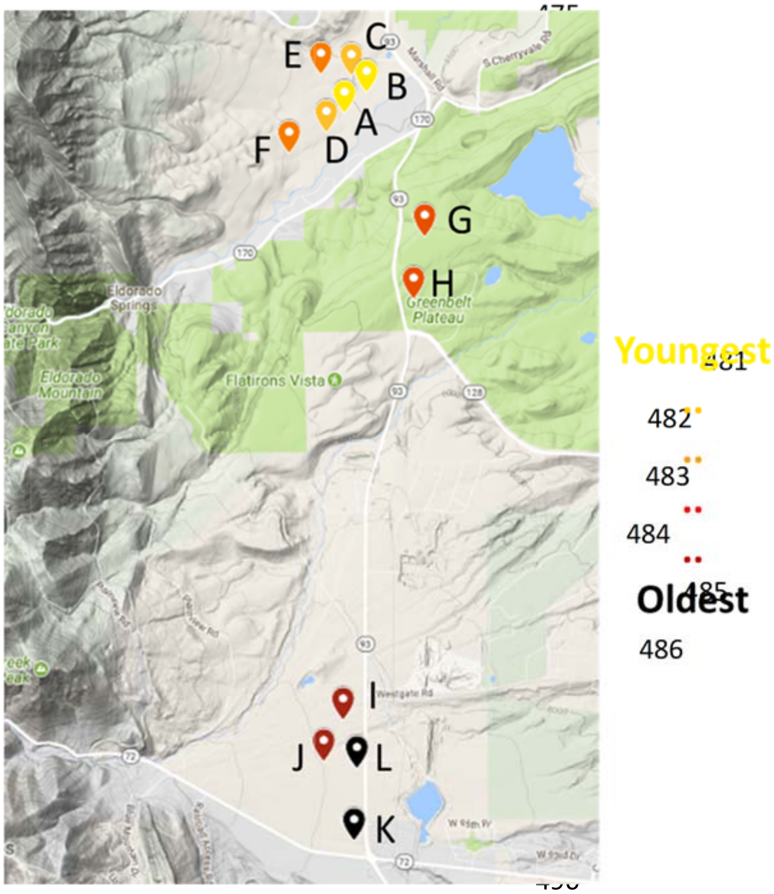

Figure 2 Study sites (n=12) were established in xeric tallgrass prairie systems managed by the City of Boulder Open Space and Mountain Parks. Two sites were established on each of six soil age surfaces (Table 1).

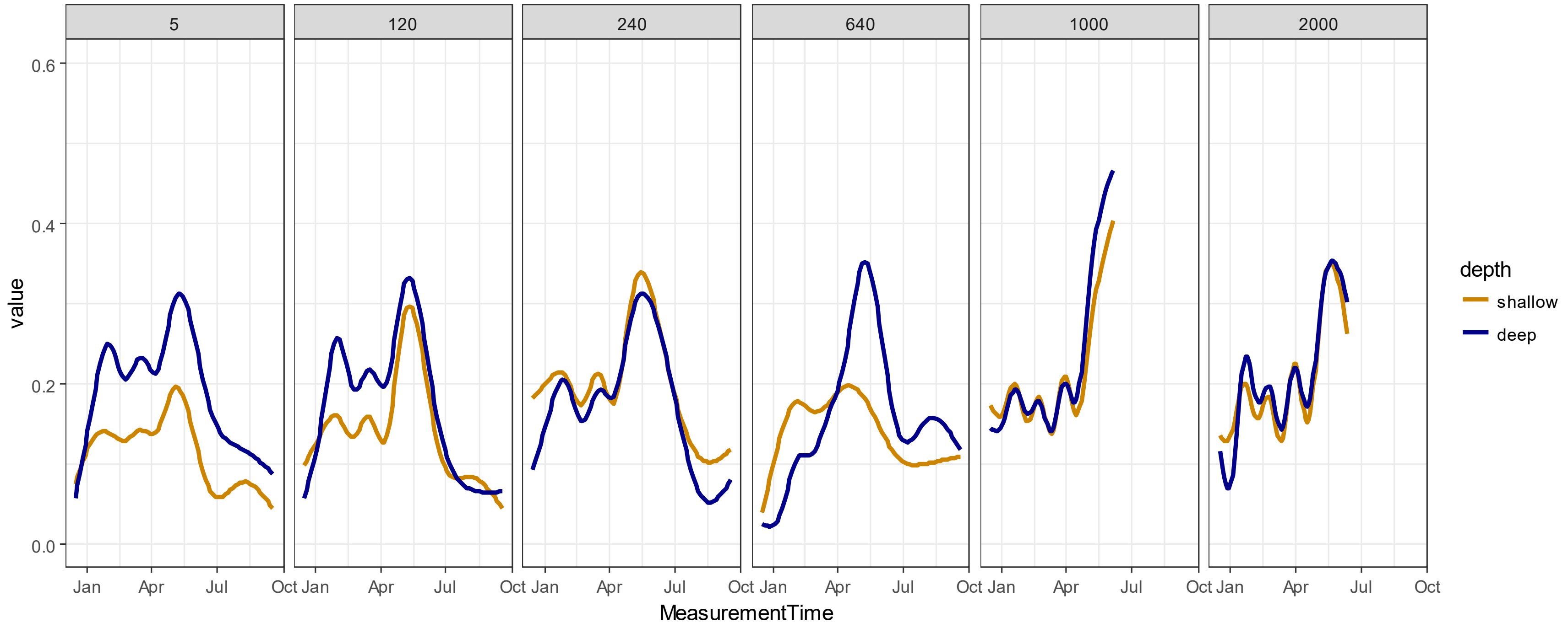

Figure 3 Volumetric water content (cm^3 cm^{-3}, range 0 to 1) from approx.. January 2017 to October 2017 across six soil age surfaces (ranging from 5ka years on left to 2000ka yrs on right) at two depths (shallow, 10cm; deep, 30cm). Soil moisture data ends in June 2017 for 1000ka and 2000ka yr surfaces due to cattle-related damage.

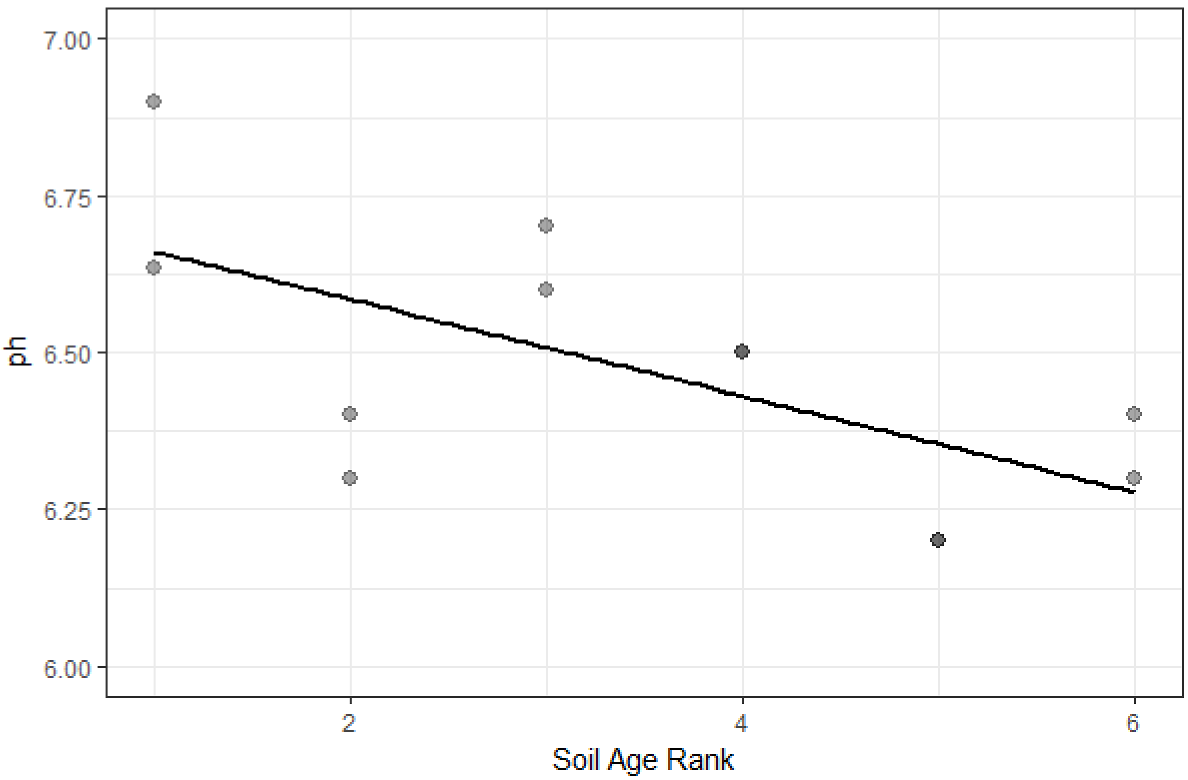

Figure 4 Soil pH as a function of soil age rank (1 to 6) across 12 xeric tallgrass sites (darker points indicating overlapping sites).

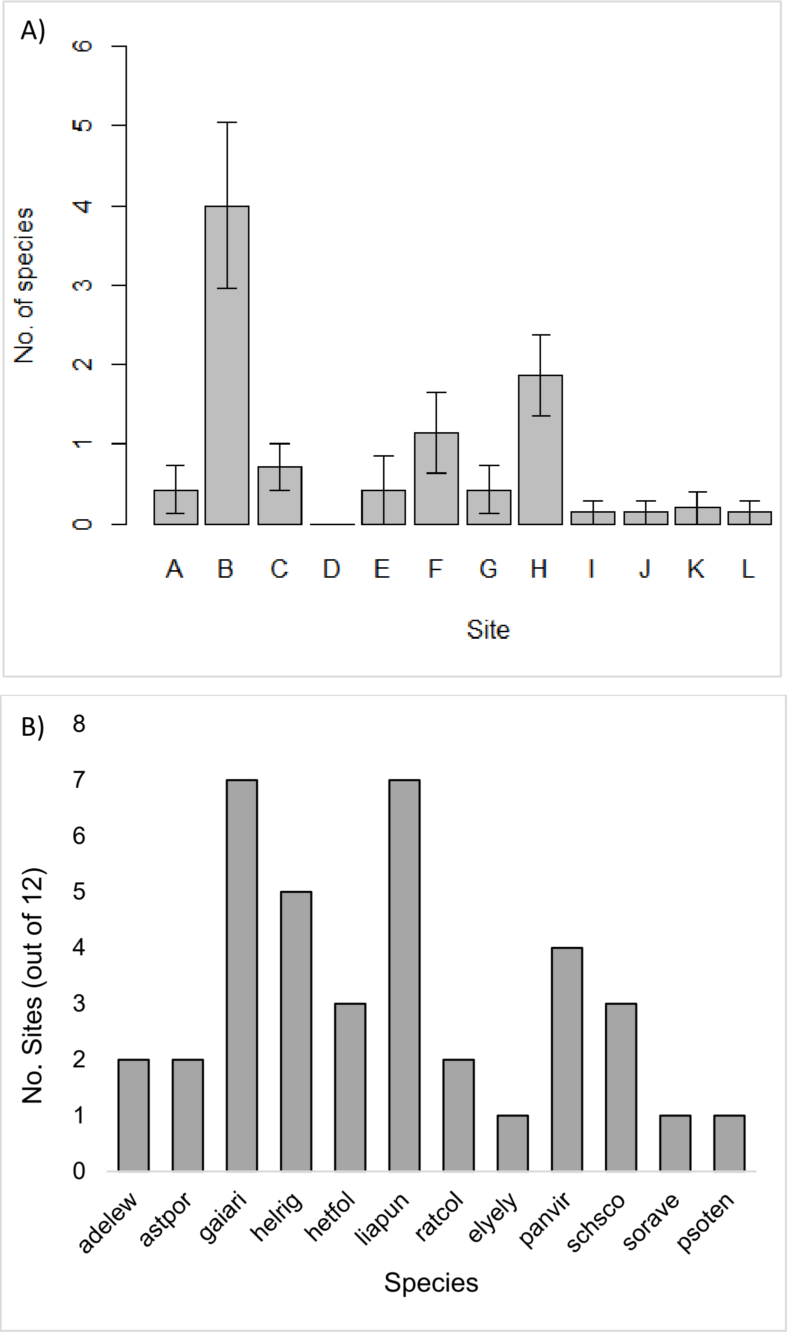

Figure 5 **A)** Site-specific differences in the average number of species observed as new recruits per plot (based only on presence/absence of a species that was in the seed mix). **B)** The number of sites that each species from the seed mix was observed in (at least one recruit in a seeded plot per site). Six species are not shown here because they were not documented at any sites (*Andropogon gerardii, Artemisia frigida, Erysimum capitatum, Pascopyrium smithii, Sporobolus heterolepis, Verbena hastata*).