Persistence as a target in restoration:  
What can we learn from the storage effect?

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January 16, 2018
Section 1: Abstract. Understanding plant community dynamics over time is a critical but challenging goal for ecological restoration, particularly with growing consensus that communities must be managed for resilience to anticipated environmental changes. We need to better understand how tools that managers can deploy—such as the timing of livestock grazing—can be used to meet management goals in the face of increasing threats from aspects less under their control (e.g., exotic plant invasions and extreme climate events). Storage effect theory posits that population persistence depends on an ability to regenerate (produce seed, recruit) during favorable conditions while storing in a buffered stage (adults or seedbank) during unfavorable conditions. If species’ regeneration and storage responses to fluctuating conditions differ predictably, community diversity could be maintained by managing for species that thrive in different conditions. In this project, I propose to measure demographic responses of species in a mixed prairie over time (3+ years) and in response to direct manipulations of grazing timing and precipitation. I will (1) use species’ traits (e.g., seed, leaf, root, and growth attributes) to predict how changing conditions affect regeneration, storage, and, ultimately, persistence; and (2) ask whether targeted seed addition and grazing treatments are viable tools to reduce regeneration opportunities for exotic species and increase chances of native regeneration—thus enhancing community diversity—under a range of conditions.

Section 2: Introduction. As its name implies, restoration has traditionally been viewed as a means to reset the ecological clock (Jackson and Hobbs 2009). However, due to unprecedented changes in the frequency of extreme climate events, land use, and disturbance (e.g., Dai 2013, Herrero et al. 2013), restoration is also playing a major role in ensuring ecosystem resilience and adaptive capacity to future changes (Folke et al. 2004). A key goal is that an intervention should result in a self-sustaining system, i.e., that management actions reset the ecological trajectory to require little further management, even as climate fluctuates through ‘good’ and ‘bad’ years (Suding et al. 2015). Ensuring that management actions enable species to persist across unfavorable periods
(e.g. climatic or disturbance events) is key to meeting new expectations for restoration.

A well-established theory in ecology, the storage effect (Warner and Chesson 1985, Chesson 2000), posits that persistence of diverse species in a variable environment depends on whether (1) favorable conditions for regeneration occasionally occur and differ among species (unique, periodic windows of opportunity), and (2) species are able to withstand unfavorable periods by being “stored” in a buffering stage such as a dormant seedbank or long-lived adults (Fig. 1). While this theory has wide application to restoration, particularly when goals include enhanced adaptive capacity and ecosystem resilience to changes over time, it has rarely been applied. I propose to address this gap, testing whether managing for persistence through storage effects may be an important but overlooked component to reach a self-sustaining and diverse ecosystem.

In restoration settings, changing conditions could influence plant persistence via effects on regeneration windows or storage, and species will differ in how they respond to fluctuations (e.g., Facelli et al. 2005). If we could identify general indicators of species responses (e.g., traits, Funk et al. 2017, Larson et al. 2015, Larson & Funk 2016, Larson & Funk in review), we could predict species and community responses in fluctuating conditions (Fig. 1, Part 1). By applying restoration strategies that favor native regeneration and storage, community diversity – which often starts high after restoration, then declines with species loss – could be maintained over time (Fig. 1, Part 2).

The proposed study will take place in a mixed prairie managed by City of Boulder Open Space & Mountain Parks (OSMP) in Boulder, CO, USA. The storage effect should be a useful tool.
to understand plant dynamics in this diverse system. Evidence suggests that population sizes in OSMP grasslands can double or triple (or decline by as much) in a single year for a range of species (e.g., Yucca glauca, Dalea purpurea, Artemisia frigida), and that responses vary by site (environment x species interactions) (Keeler 2004). Rapid and variable increases suggest that regeneration windows are as important for species’ persistence and community dynamics in this system as adult survival.

Multiple lines of evidence suggest that soil moisture availability is key in generating “favorable” and “unfavorable” conditions for species persistence. Drought can be a major driver of grassland community dynamics in Colorado’s Front Range—potentially unfavorable for dominant native perennials (Evans et al. 2011). From work in other arid systems, we expect warm, wet early seasons to favor fecundity and recruitment of species that germinate and acquire resources rapidly, competing more successfully, while cooler early seasons favor slow, stress-tolerant species (Angert et al. 2009, Huang et al. 2016). Precipitation may also affect storage capacity in adult plants (with response varying by species, Adler et al. 2006) and seedbanks (although evidence is more limited, Coffin & Lauenroth 1989, Walck et al. 2011). While plant traits have frequently been linked to adult abundance under water stress (e.g., Sandel et al. 2010), less is understood about how traits mediate seedbank responses. However, studies do suggest that seed survival varies by species and climate (e.g., Burnside et al. 1996) and could be related to physiochemical seed traits (Larson et al. 2016).

Additionally, over 60% of OSMP grasslands also support livestock, mostly related to grazing (OSMP 2010). Grazing can directly impact plants via herbivory and trampling, though it is less clear when grazing facilitates native diversity, or has relatively uniform effects on persistence (even equalizing responses driven by precipitation, Swemmer & Knapp 2008). Effects likely depend on grazing regime. For example, in Mediterranean grasslands, early grazing suppressed seedbanks and cover of tall, competitive annual grasses and increased cover of forb seedlings and short annual grasses, which the authors suggest is linked to competition-related regenerative traits such as seed
size and germination fraction (Aboling et al. 2008). In communities with diverse life histories, early or late grazing could also favor regeneration or storage based on phenology. Unlike precipitation, managers have the capacity to alter grazing regimes in light of these effects, and could do so in a way to either suppress/enhance species with particular traits (e.g., graze to inhibit regeneration of early season exotics) or maximize functional diversity by rotating grazing timing to enhance regeneration windows and storage capacities for different species in different years.

If precipitation and grazing differentially impact species’ regeneration and storage on the basis of traits, we could predict how fluctuating conditions affect species persistence, and mitigate potential community-level impacts. Because grazing and drought likely have interactive effects, it is critical to study responses in the context of both. In the proposed study, I address two questions:

Q1) Do species “see” different environmental conditions as favorable (presenting opportunities for regeneration) or unfavorable (requiring storage to persist)? Do traits explain the variation among species (Fig. 1, Part 1)? I propose to experimentally assess species’ demographic responses to drought events and the timing of cattle grazing to test Hypothesis 1: Different environmental conditions will be favorable and unfavorable to species, and variation in regeneration and storage responses is a function of species’ traits.

Q2) Can practical management strategies structured around regeneration events and storage capacities enhance native diversity at the community level (Fig 1, Part 2)? I will experimentally assess whether trait-based seed mixes, combined with grazing, can be used to diversify windows of opportunity for native regeneration while suppressing exotic regeneration and storage. Hypothesis 2: Management strategies designed to target critical storage stages and/or regeneration windows effectively enhance community diversity and productivity.

Section 3: Methods. The proposed project will establish a long-term demography sampling site. In the first three years, I will quantify demographic indicators of plant regeneration and storage
across spatial manipulations of grazing, drought, and seed addition. Over time, demographic data will be used in more rigorous tests of the drivers of plant persistence and diversity.

**Study design.** We have worked with OSMP to identify a suitable mixed-grass prairie site for infrastructure installation (Tracy-Collins property). It is grazed regularly with minimal public access. In spring 2018, we will install a cattle exclosure (160m x 40m) divided into six fenced areas (Fig. 2). Removable exterior walls will allow grazing in different seasons (no grazing, early grazing (Mar-May), late grazing (Jul-Sep), two areas each). Because structures attract cattle (pers. obs.), we should attain effects with 1-2 wk graze events. Within each area, we will establish 12 permanent 2m x 2m plots. Four plots will receive ambient precipitation, four will be covered by 3m x 3m passive shelters (clear slats divert 50% of precipitation), and four will be supplemented with collected runoff (Fig. 2). Shelters will be removed during grazing. We will install soil moisture sensors in at least one plot per treatment combination. Our lab has experience with similar manipulations (e.g., Hallett et al. 2017).

Q1) Do environmental conditions affect storage capacity or regeneration variability
as a function of species’ traits? I will use community-wide demographic data under drought and grazing manipulations to determine how short-term metrics related to regeneration (fecundity, recruitment) or storage (growth/survival or seedbanking) shift with environmental variation, and whether species’ responses are predictable via traits (Fig. 2). Within 2m x 2m plots, I will establish a permanent 1m² plot. I will map the location and size of each individual over the first three years during the growing season, quantifying survival, recruitment (new individuals), and growth (relative basal area per year, short-term fitness metric; Adler et al. 2014). I will assess fecundity via seed traps deployed from spring to fall and sample the seedbank each fall with three 5cm x 2cm soil samples (seed extraction method; ref. collection at Univ. of Col. Herbarium). Analysis. I will use generalized linear mixed models (GLMMs) for each species to calculate fixed effect sizes for changes in growth, survival, recruitment, fecundity and seedbank abundance in response to early or late grazing and dry or wet treatments relative to ambient (grazing block as random effect). For each treatment, I will test overall effects by comparing effect sizes to a null model, then regress species’ traits against effect sizes (Fig. 2) to test whether traits predict regeneration/storage responses.

Q2. Management strategies to enhance native persistence under grazing & drought. In this experiment, I will test the ability of targeted seed addition to enhance native regeneration in the context of grazing, drought, and invasion. I will add two seeding treatments to 0.5m² subplots in each replicate plot and compare to the unseeded control. Seed mixes will be based on regeneration trait data and the goal of creating either diverse or targeted native recruitment windows: 1) a native seed mix maximizing diversity of regeneration traits to increase native recruitment across years and grazing/drought conditions; 2) a native seed mix maximizing regeneration trait similarity to an exotic grass, Bromus japonicus, to suppress invasion via competitive recruitment windows. I will measure native recruitment, diversity and cover, and B japonicus cover to assess treatment effectiveness. Analysis. I will use GLMMs to assess native recruitment responses (total numbers and weighted trait
means of recruits), diversity, and cover, and *B. japonicus* cover as a function of drought, grazing, and seed mix type (grazing block as random effect). For Q1 & Q2, I will also experiment with simulating community responses to temporal climatic variation (e.g., different drought scenarios over time) based on demographic parameters generated from spatial manipulations.

**Table 1** Project schedule. I request support to initiate the project (2018) & will submit a USDA proposal for later support.

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<tr>
<td>Install plots &amp; construct drought structures</td>
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<td>Begin grazing manipulation</td>
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<td>Baseline population sampling (all non-seeded and seeded plots)</td>
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<td>Baseline seedbank &amp; seed trap sampling (all non-seeded plots)</td>
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<td>Year 1 sampling (population, seed rain, and seed bank)</td>
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<td>Year 2 sampling (population, seed rain, and seed bank)</td>
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**Resource Impacts.** To minimize impacts on native population genetics, we will create seed-mixes in collaboration with OSMP to ensure that appropriate species and sources (local seedlots whenever possible). The proposed site is already grazed, and we will work collaboratively with ranchers and OSMP to manipulate the timing of grazing (with relatively flexible windows). To minimize the aesthetic impact and potential vandalism, we have selected a site with minimal public accessibility. The site is a relatively small area (0.64 hectare), minimizing wildlife impacts, and although it is not under official wildlife closure, we will minimize activity during the most significant nesting period (May-Jun) once the site has been installed. We will also coordinate with cultural resources staff during installation and seedbank sampling events to impacts to cultural resources. We will work with OSMP as the project progresses to assess its course and continuation. My ambition is to oversee continued data collection beyond my dissertation work (proposed here), and believe that investment in a long-term drought and grazing manipulation will be mutually beneficial.

**Facilities, Equipment & Resources.** Sample processing (e.g., seed rain, seedbanks) will occur at the Univ. of Colorado, and we have resources for shelter construction. We would like to
partner with OSMP or a contractor to assist with fence installation (see Section 8). Off-road parking of personal vehicles will be required during the growing season (foot traffic only after installation).

**Section 4: Anticipated Results & Discussion.** Forecasting and manipulating plant community responses to climate change, land use, and invasion is a major, complex task for restoration ecology (Folke et al. 2004). Through the lens of storage effect, I expect to characterize a range of persistence responses to drought & grazing—two interacting factors that are essential for realistic forecasting on OSMP lands. I also expect to generate predictions of responses based on functional traits, making this work informative for general, testable hypotheses about when and how storage effect enables species persistence and community stability. In addition to characterizing and predicting demographic responses to precipitation and grazing (Part 1), I will directly test the effectiveness of interactive restoration approaches suggested by storage effect (Part 2) to deliver management recommendations. I will (1) make all data publically accessible to support other progressive work (2) publish Parts 1 & 2 as manuscripts in international journals, and (3) develop and present recommendations for managers (CO Native Plant Society, Natural Areas Conference).

**Section 5: Relationship to Existing Projects.** Over the last two years, I have initiated research in conjunction with OSMP to assess approaches related to adaptive capacity. Initial results from 12 sites across a soil chronosequence suggest that regeneration windows are important, varying by species & environment—recruitment occurred in 0–58% of sites depending on species (n=18). They also suggest that soil moisture dynamics and community composition (both plants and seed bank) vary across spatial environmental gradients in potentially important ways (see also Buckner and Odasz in prep). With data from across the gradient, we can place results from the proposed site in a larger context, comparing patterns observed over space (pre-existing project) to those observed over time (proposed project). Trait data collection is already ongoing (majority completed in 2018).

**Section 6: Project History for Continuing Projects.** N/A
Section 7: References


Buckner D.L. and A.M. Odasz. In prep. Decrease in Species Richness and Invasibility in Big Bluestem (Andropogon gerardii Vitman) Communities along a 2-Million Year Chronosequence in Colorado, USA.


Section 8: Budget. We request scholarship support for Julie Larson for Summer 2018. The support will provide Julie with a stipend over the summer months equivalent to 75% FTE effort for a graduate student (benefits included). We also request funding to support fence construction (estimate provided by OSMP). Costs for other supplies and undergraduate assistants will be covered by other sources (see below). The award will be provided directly to the student, avoiding overhead.

<table>
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<th>Item</th>
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Please list any sources of additional funding including in-kind donations that will support this project (if applicable): Julie has applied for a Garden Club of America graduate fellowship to fund supplies (site installation, drought structures, est. $8,000). Julie has also applied for the Grant A. Harris Fellowship through METER Environmental Instruments to cover the costs of a continuous soil moisture sensor and rain gauge system (est. $8,769), and will apply to the Univ. of Colorado Undergraduate Research Opportunity Program to fund undergraduate assistants for the project (est. $3000). Finally, Julie will apply for two more years of funding (stipend & supplies) for sustained work on the project through the U.S. Dept. of Agriculture pre-doctoral fellowship program in Spring 2018. Julie’s advisor, Katharine Suding, has funding that will enable her to support other costs related to this project, as well as a graduate research assistantship for the 4-month spring semester (including work on initial phases of the proposed project; est. $15,000, including tuition fees). She will also contribute unfunded time to advising and collaborating with Julie on the project.
SECTION 9: PERSONNEL QUALIFICATIONS.

Julie is a second year PhD student in the Department of Ecology and Evolutionary Biology at the University of Colorado Boulder. Julie committed 50% FTE to related OSMP projects in her first academic year and will commit 50% FTE to OSMP-related projects, including the proposed project, in the spring 2018 semester (research assistantships provided by K. Suding). In summer 2018, she will commit 75% FTE to the proposed project and 25% FTE to related OSMP projects.

Katharine Suding is a professor in the department of Ecology and Evolutionary Biology and is Larson’s PhD advisor. She strongly supports the efforts proposed here (her letter follows the CVs) and commits 10% FTE to advise and collaborate on the project.

The CVs of Larson and Suding, as well as Suding’s advisor letter, follow.
EDUCATION
PhD  University of Colorado  Boulder, CO  Ecology & Evolutionary Biology  2016-present
MS  Oregon State University  Corvallis, OR  Environmental Science (Ecology track)  2013
BS  University of Michigan  Ann Arbor, MI  Ecology & Evolutionary Biology; Program in the Environment  2011

PROFESSIONAL/RESEARCH EXPERIENCE
Grad Research/Teaching Asst.  Institute for Arctic & Alpine Research, University of Colorado, Boulder, CO  2016-
Research Associate  Funk Lab (Plant Functional Ecology), Chapman University  Orange, CA  2013-16
Restoration Field Crew Supervisor  Irvine Ranch Conservancy  Irvine, CA  2015
Grad Research Asst.  Oregon State University & USDA-ARS  Corvallis, OR  2011-13
Research Assistant  Cooperative Institute for Limnology and Ecosystem Research / NOAA  Ann Arbor, MI  2010-11
Natural Resource Management Tech  Forest Preserve District of Will County (FPDWC)  Joliet, IL  2008-09

PUBLICATIONS


Boulder Open Space & Mountain Parks Funded Research Program ($10,800) 2017
EBIO Research Grant (Dept of Ecol & Evol Biol, Univ of Colorado; $2490) 2017
Undergraduate Research Opportunity Team Grant (PI K. Suding; $3000) 2017

Principles of Ecology Lab, Univ. of Colorado (0.5 FTE) 2017
Evolution and Diversity of Multicellular Organisms Lab, Chapman Univ. 2015-16
From Molecules to Cells: Evolution of Life on Earth Lab, Chapman Univ. 2015

D. Ewen, K. Ryan, K. Mann, K. Ebinger (Senior thesis) 2017
Research mentor for student projects, CO Science Research Symposium Program 2016-17

LSA Dean’s Scholar, University of Michigan ($80,000) 2007-11
Graham Environmental Sustainability Institute Scholar, Univ. of Michigan ($5,000) 2010
James B. Angell Scholar, University of Michigan 2010-11
Member, Phi Beta Kappa 2011

Undergraduate Outreach Team, Dept. of Ecol & Evo Bio, Univ. of Colorado 2017
Certified Volunteer, Irvine Ranch Conservancy, Irvine, CA. Certification includes 30+ hours of training in stewardship, first aid, public interaction & open lands safety.
Founder & Co-Director, College of Forestry Graduate-Undergraduate Mentorship Program, Oregon State University 2013
Graduate Student Council Member, College of Forestry, Oregon State University 2012-13
Graduate Student Representative, Dept. of Forest Ecosystems & Society, Oregon 2011-13
State Univ.
KATHARINE N. SUDING
Fellow, Institute of Arctic and Alpine Research
Professor, Department of Ecology and Evolutionary Biology
University of Colorado, Boulder

Professional preparation

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<td>University of Michigan</td>
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Appointments

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<td>University of California at Irvine</td>
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Awards and Honors

2017 Web of Science, Highly Cited Researcher, top 1% in Ecology
2016 Fellow, Ecological Society of America
2016 Robert Wilson Lecturer in Botany, Miami University of Ohio
2016 George Lynn Cross Distinguished Speaker, University of Oklahoma.
2014 ESPM Distinguished Research Group Award, UC Berkeley
2008 University Distinguished Assistant Professor Award for Research, UC Irvine
2005 Andrew W. Mellon Foundation, Young Investigator Research Award
2002 Centre National de la Recherche Scientifique Fellow
1998 Rackham Predoctoral Fellow, University of Michigan

Relevant Publications (of over 120)


Recent Professional Activities
Editorial Board, Ecology Letters, 2006-present
Editorial Board, Biological Reviews, 2010-present
Lead Investigator, Niwot Ridge Long-term Ecological Research Site
Board of Directors, Urban Creek Council, 2013-2014.
Board of Directors, California Invasive Plant Council, 2010
Advisor, Resilient Landscape Program, San Francisco Estuary Institute, 2015-present
Eminent Ecologist Award Committee, Ecological Society of America, 2009-2016.
Chair, Whittaker and Forest Shreve Award Committee, Ecological Society of America, 2016-present.
Emerging Issues Conference, Review Committee, Ecological Society of America
Early Career Workshop on Population and Community Ecology at Continental Scales,
Steering committee, sponsored by ESA and NSF
Dear Selection Committee,

I have reviewed Julie Larson’s proposal, “Persistence as a target in restoration: What can we learn from the storage effect?” I approve and support the proposed research. I agree to provide additional assistance needed to complete the project and will be responsible for providing the final report and other deliverables specified in her proposal.

Sincerely,

Dr. Katharine Suding
Professor, Ecology and Evolutionary Biology
Fellow, Institute of Artic and Alpine Research
PI, Niwot Ridge Long-term Ecological Program