

USING PLANT ECOPHYSIOLOGY, LONG-TERM COMMUNITY DYNAMICS, AND
EXPERIMENTAL RESTORATION TECHNIQUES TO INFORM RIPARIAN
RESTORATION AND CONSERVATION

by

ISABEL DE SILVA

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Committee Members:

Katharine N. Suding (Chair)

Holly Barnard

Nancy Emery

E. William Schweiger

Timothy Seastedt

de Silva, Isabel (Ph.D., Ecology & Evolutionary Biology)

Using plant ecophysiology, long-term community dynamics, and experimental restoration techniques to inform riparian restoration and conservation

Thesis directed by Professor Katharine N. Suding

ABSTRACT

Over three chapters of my dissertation, I aimed to address drivers of riparian ecosystem change at different scales, ranging from leaf-level plant ecophysiology to long-term plant community dynamics. In my first chapter, I assessed willow water limitation in Rocky Mountain National Park in the context of degraded sites with high ungulate browsing that have also functionally lost beaver-mediated hydrology. I found that, in these degraded contexts, willows were not water-limited compared to more intact reference sites but rather showed responses in association with seasonal drydown. In my second chapter, I assessed decadal turnover trends in riparian wetlands, wet meadows, and fens in Rocky Mountain National Park. I found that riparian ecosystems experienced the greatest compositional change while wet meadows and fen functional group components were relatively stable through time. Further, water balance metrics were the most important determinants of plant community composition and there were only a couple of instances indicating where native functional groups might exclude corresponding non-native functional groups through limiting similarity. In my third chapter, I tested the effectiveness of using a functional trait-based approach to see if functional diversity conferred stability in productivity and reduced invasion by increased niche occupation and complementarity in a riparian restoration project in the Front Range of Colorado. I found some support for a functional diversity oriented approach contributing to the stability of productivity, whereas invasion trends were largely driven by a soil moisture gradient and not biotic contexts. Together, this collection of work provides quantitative assessments for riparian restoration and

conservation trajectories that can be used in adaptive management contexts for decisions about whether to design management strategies to manage drivers of change, enhance adaptive capacity, or enable novel ecosystem configurations.

DEDICATION

This dissertation is dedicated to my mother, Sandra Lee Rayl, who was monumental in inspiring my interest in the natural world and supporting me in my pursuit of higher education, amongst so many other things.

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CHAPTER I

Introduction

Anthropogenic interferences with the earth's natural ecosystems and climate system have caused unprecedented ecosystem changes at a global scale. Noteworthy declines in nature include the loss of biodiversity, species invasions, and ecosystem transformations (Brondizio *et al.* 2019), which together, are often common themes in degraded environments. While deviations from historical ecosystem conditions that occur in multiple ecosystem components over time are usually apparent, they are often not simple to address. This is especially the case in riparian ecosystems and wetlands in general, which on top of environmental change, already have high baseline dynamism, afforded by their inherent connections to hydrology. Informed management of these dynamic systems that provide a multitude of ecosystem functions and services is of great importance as these systems have experienced degradation and habitat loss more rapidly under anthropogenic pressure than other ecosystems (Millennium Ecosystem Assessment 2005), with some estimates showing an 87% percent loss in wetlands globally in the last 300 years (IPBES *et al.* 2018).

Here, I employ methodologies from plant ecophysiology, functional trait-based ecology, and community ecology to assess native species recovery limitations, community trajectories, and novel restoration treatments in the context of riparian ecosystems. This work is unified by the idea that species or functional groups can respond differently to environmental and biotic gradients, and these responses can be assessed at different scales in order to best address management concerns. As part of this aim, some central themes of this work are providing quantitative evidence to help determine whether or not systems are resilient to environmental change or resist invasion. Altogether, this collection of work provides quantitative assessments for riparian restoration and conservation trajectories that can be used in adaptive management contexts for decisions about whether to design management strategies to manage drivers of

change, enhance adaptive capacity, or enable novel ecosystem configurations (*sensu* Dudley *et al.* 2018; Schuurman *et al.* 2022).

In my first chapter, I assess potential willow water limitation in Rocky Mountain National Park in the context of degraded sites with high ungulate browsing that have also functionally lost beaver-mediated hydrology. In sampling sites that spanned a gradient of ecological condition, which I classified as reference (beaver-willow ecosystem state with tall, dense willows), degraded (elk-grassland ecosystem state with short, sparse willows), or those with simulated beaver structures (SBS), I did not find evidence of willow water limitation. Instead, patterns of water use were more strongly associated with seasonal drydown as opposed to site ecological condition, and importantly, did not pass thresholds to cause hydraulic failure.

In my second chapter, I assess decadal turnover trends in riparian wetlands, wet meadows, and fens in Rocky Mountain National Park in order to not only identify biotic and abiotic drivers of change, but also identify potential competitive and facilitative associations amongst functional groups. I show that riparian ecosystems experienced the greatest compositional change while wet meadows and fen functional group components were relatively stable through time. Further, water balance metrics were the most important determinants of plant community composition and there were only a couple of instances indicating where native functional groups might exclude corresponding non-native functional groups through limiting similarity.

In my third chapter, I tested the effectiveness of using a functional trait-based approach to see if functional diversity conferred stability in productivity and reduced invasion by increased niche occupation and complementarity in a riparian restoration project in the Front Range of Colorado. To do this, I designed a factorial experiment to assess riparian restoration outcomes in response to manipulations of water availability (via planform elevation) and plant community types. I found some support for a functional diversity oriented approach contributing to the stability of productivity. Invasion trends, in contrast, were largely driven by a soil moisture gradient and not biotic contexts.

CHAPTER II

Willows are not water-limited in highly browsed, nearly beaver-less montane riparian systems in
Rocky Mountain National Park

By Isabel de Silva, E. William Schweiger, and Katharine N. Suding

Abstract

Some montane riparian systems in the Rocky Mountains (USA) have experienced severe degradation due to missing beaver-mediated hydrology and high browsing pressure. One consequence of this degradation is the loss and lack of recovery of mesic-adapted drought avoidant willow species (*Salix* spp.). Here, we asked if degradation is causing willow species to be water-limited and assessed whether there are nuanced patterns of water use and carbon assimilation that do not follow expected patterns for drought avoidant species or in response to drydown across the growing season. We monitored stem water potential ($\Psi_{MD,PD}$), gas exchange (g_s , A), water use efficiency (foliar $\delta^{13}C$), and stemwater stable isotopes (δD and $\delta^{18}O$) across two years during the three-month summer peak of the growing season in 15 long-term riparian monitoring sites in Rocky Mountain National Park. Sites spanned a gradient of ecological condition and were classified as reference (beaver-willow ecosystem state with tall, dense willows), degraded (elk-grassland ecosystem state with short, sparse willows), or those with simulated beaver structures (SBS). Willow species demonstrated classic drought avoidant (isohydric) behaviors, maintaining high stem water potentials regardless of site condition. Compared to reference sites, willows at degraded sites had higher levels of stomatal conductance without a concurrent gain in photosynthetic rates. Seasonal and diurnal patterns of water use were more strongly associated with seasonal hydrology patterns as opposed to site ecological condition. While we did not find clear evidence of adult willow water-limitation, process-based interventions such as installing beaver mimicry structures to restore hydrology seem promising for accelerating ecosystem recovery.

Introduction

Feedbacks between plants and the hydrologic environment are responsible for important structuring dynamics in a wide range of ecosystems (Busch *et al.*, 1998; Osborne *et al.*, 2004; Huxman *et al.*, 2005; Waddington *et al.*, 2015). Vegetation, through its key role in mediating evapotranspiration (ET, water lost via leaves in the process of photosynthesis), is strongly coupled to various components of the hydrological cycle such as precipitation, soil moisture, groundwater tables, and runoff (Gerten *et al.*, 2004; D’Odorico *et al.*, 2010). These links lead to important feedbacks between hydrologic processes and ecosystem function (Gerten *et al.*, 2004; D’Odorico *et al.*, 2010). For instance, redwood trees help create fog and in turn use fog water to power photosynthesis (Dawson, 1998); grasses in Australia that grow in “fairy” circles facilitate neighboring plant growth by increasing soil moisture (Getzin *et al.*, 2020); and riparian (streamside) plants can favorably aerate otherwise waterlogged soil to the benefit of new seedlings (Ridolfi *et al.*, 2006). While it has been long thought that disturbances such as land degradation, overgrazing, and streamflow diversions can act to decouple these feedbacks (Wilcox *et al.*, 2003; Ridolfi *et al.*, 2006), the consequences of this decoupling on the ecosystem recovery dynamics has been little explored, particularly through the lens of what steps are needed to re-establish feedback dynamics during ecological restoration (Suding *et al.*, 2004).

In montane riparian ecosystems in the Southern Rocky Mountains (U.S.A.), presence of beavers (*Castor canadensis*) and tall dense willows (*Salix* spp.) are commonly used as indicators of ecosystem integrity (Wolf *et al.*, 2007; Schweiger *et al.*, 2016) since beavers and willows have historically sustained positive feedback relationships in many areas. Beavers use willows to build dams (Baker & Hill, 2003) and, in turn, willows benefit from the creation of dams, which raise water table levels and increase flooding duration and magnitude (Westbrook *et al.*, 2006). However, browse pressure from increased ungulate (elk, moose) populations in the recent decades, especially in protected areas where human hunting is controlled, have reduced the spatial extent of beaver-mediated hydrological effects (Peinetti *et al.*, 2002). Ungulate pressure often drives a transition away from a beaver-willow state with tall, dense stands of willows and

high groundwater tables (hereafter ‘reference’) to an elk-grassland state with short, sparse willows and deep groundwater tables (hereafter ‘degraded’) (Wolf *et al.*, 2007). Recovery from the degraded to reference state has been challenged by the difficulties in re-establishing vegetation-hydrology feedbacks, with some success at large scales (wolf reintroduction, Beschta & Ripple, 2016) and smaller scales (beaver mimicry interventions such as simulated beaver structures, SBSs – which are also known as beaver dam analogs, BDAs) (Pollock *et al.*, 2014; Munir & Westbrook, 2021). Yet, recovery is often highly variable with debate about what constraints are key to address in intervention.

Effective means to re-establishing feedbacks depends on specific recovery constraints. Constraints could emerge at dispersal, seedling recruitment, growth or survival stages of population recovery. One common assumption is that slow recovery is due to a threshold shift in plant water relations: water-limitation constrains adult willow growth in the degraded elk-grassland state but not in the beaver-willow reference state. A correlate of this assumption is that drought stress due to climate-related changes in snowmelt-driven runoff and diminished groundwater recharge (Rood *et al.*, 2008; Wieder *et al.*, 2022) could intensify willow water limitation constraints past the realm of possible management interventions. While widely assumed, this assumption has rarely been tested, with most studies and management evaluations instead focusing on either: browsing effects alone (Zeigenfuss & Johnson, 2015), willow performance prior to the last two decades of climate change (Alstad *et al.*, 1999), or hydrology trends alone.

Here, we test the assumption that a key barrier to adult willow regrowth is water limitation in the degraded elk-grassland state by monitoring willow ecophysiology *in situ*. We characterize water limitation and shifts in water use strategies following altered hydrology and browsing across a range of site conditions: reference (beaver-willow), SBS (simulated beaver structure), and degraded (elk-grassland). We first ask if adult willows show water limitation in degraded sites, evidenced by stomatal closure and reduced carbon assimilation in the daytime. Willows and other wetland specialist plant species are generally thought to exhibit drought

avoidance strategies (isohydric responses) by limiting excessive water loss via closing their stomata and more strictly regulating stem water potential in response to water limitation (increasing water use efficiency) at the cost of carbon assimilation (reduced photosynthesis) during dry periods (Attia et al., 2015; Zhao et al., 2021). Thus, if the decoupling of vegetation-hydrological feedbacks in degraded sites results in increased water limitation for these plants, we would expect to see responses limiting water loss in degraded sites but not in reference or SBS sites. Alternatively, willows could exhibit more anisohydric (drought tolerant) responses, maintaining relatively high carbon assimilation even in periods of peak water stress (e.g. midday, near end of growing season) but increasing their susceptibility to hydraulic failure that can lead to dieback or mortality (Tardieu & Simonneau, 1998; McDowell et al., 2008; Skelton et al., 2015). In this case, there may be little decline in carbon assimilation across site types as measured at instantaneous and short-term periods, with longer-term risks of hydraulic failure at degraded sites. In either physiological response scenario, we expect to see stable isotope stemwater signatures indicating reduced access to groundwater and more dependence on surface water at degraded sites.

Second, we examine if there is seasonal or diurnal variation in water relations and carbon assimilation at degraded sites that do not follow expected patterns for isohydric species or in response to drydown across the growing season. We expect willows at degraded sites to have more pronounced isohydricity compared to reference and SBS sites, marked by strict regulation of midday water potential in response to predawn water potential (*sensu* Martínez-Vilalta *et al.*, 2014). Additionally, we expect to see dampened seasonal drydown signals in willow water use at degraded sites, with more homogenous midday water potentials and rates of stomatal conductance across the growing season given our first expectation of water limitation via stomatal regulation at these sites.

Methods

Study sites and species

We sampled 15 riparian study sites in Rocky Mountain National Park (RMNP) that are a part of the National Park Service Rocky Mountain Inventory and Monitoring Network wetland long-term monitoring program (ROMN, Schweiger *et al.*, 2015, 2016, 2019) (**Fig. 2.1, Table 2.1**). These sites are comprised of 10 x 10m plots that are monitored rotationally on an annual basis for vegetation composition, depth to water, ungulate browse, beaver activity, and human disturbance (Schweiger *et al.*, 2015). We selected these sites based on willow cover, depth to water data availability, and beaver and ungulate activity (see last paragraph of this section for more elaboration on site classification). All sites are situated within 2,350-2,800m elevation and were within approximately 19.2 meters of an active perennial stream channel, on average (ranging from 1.3m to 83.4m using site centroids). All sites have a semiarid climate with the majority of precipitation arriving as snow in winter (December-February). Across all sites, mean annual precipitation (calculated as the 1980-2010 historical average) is 619.8mm \pm 48.3 and mean annual temperature is 4.17 C \pm 0.65 (Thornton *et al.*, 2022). During our study period, mean annual precipitation was above the 1980-2010 historical average in 2019 by 12.7mm and below average in 2020 by 157.5mm. Mean annual temperature was above the 1980-2010 historical average by 0.20 C in 2019 and 0.97 C in 2020.

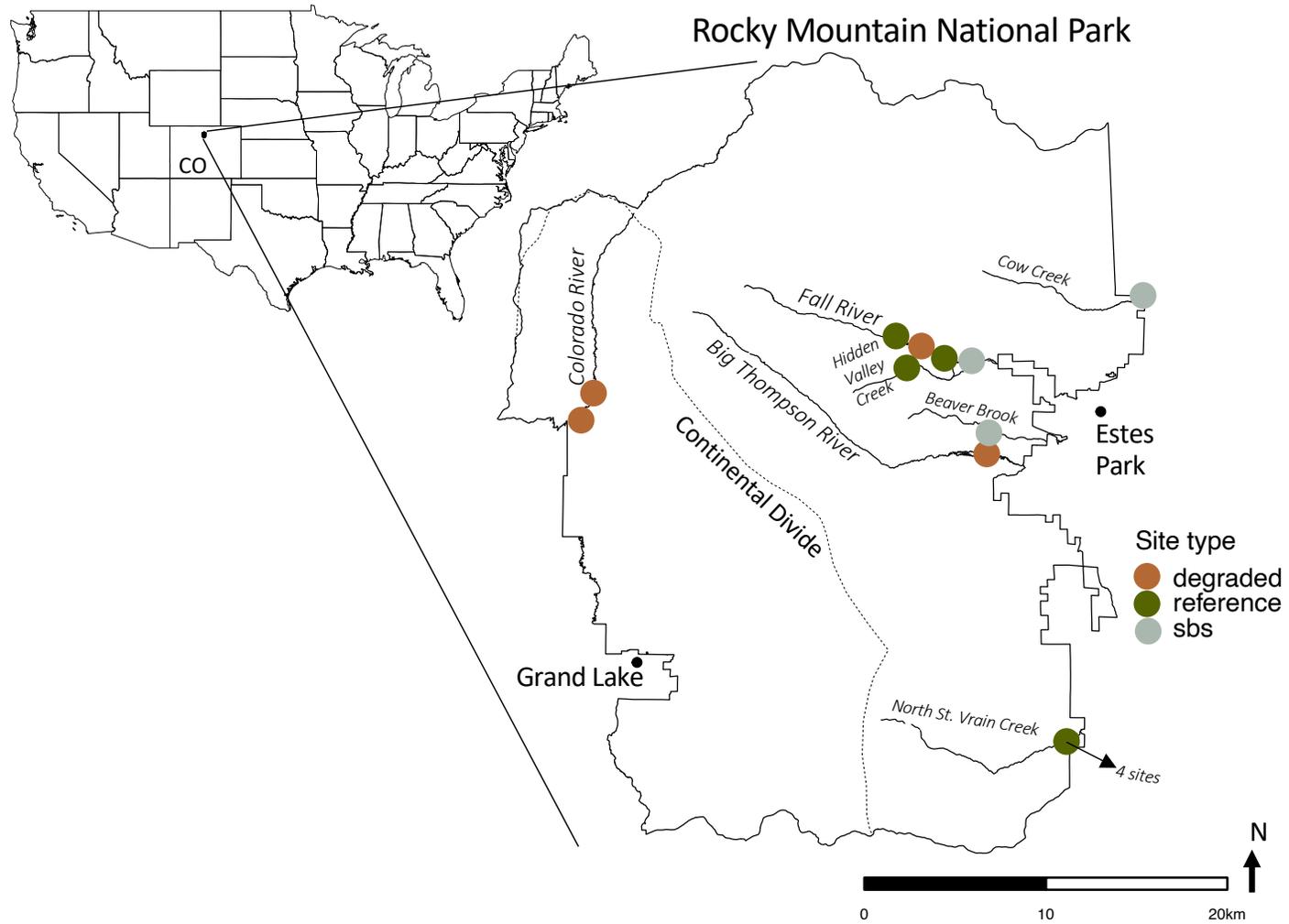


Figure 2.1. Map of study sites located in Rocky Mountain National Park, Colorado, USA. Sites are colored, with degraded sites in burnt orange, reference sites in green, and SBS sites in baby blue.

The dominant willow species (*Salix* spp.) found across our sites include: *S. monticola* Bebb, *S. drummondiana* Barratt ex Hook, *S. geyeriana* Andersson, *S. planifolia* Pursh, *S. bebbiana* Sarg., and *S. eriocephala* Michx. In terms of community composition, willow cover typically ranged from 40-50% across sites (**Table 2.1**) and other dominant genera include: *Alnus* spp., *Betula* spp., *Carex* spp., and Poaceae spp. (RMNP Inventory & Monitoring Network, *unpublished data*). It was not possible to control for *Salix* spp. composition across site types due to natural turnover across these sites.

Table 2.1. Summary site characteristics of our 15 study sites, including focal sites that were intensively sampled in 2020 (bolded entries in ‘NPS I&M WEI Site Names’ column). Mean percent willow cover, willow height, and native woody cover was averaged across sites from the most recent sampling event for each site. Means and standard deviations shown for vegetative cover columns. Asterisks indicate sites that are in exclosures.

Site type	n sites	Willow cover (%)	Willow height (m)	Native Woody (%)	Willow species (ecophysiology)	Beaver activity	NPS I&M WEI Site Names
Reference (beaver-willow)	7	49.5 ± 11.4	1.8 ± 0.18	62.5 ± 6.1	<i>S. bebbiana</i> <i>S. drummondiana</i> <i>S. eriocephala</i> <i>S. geyeriana</i> <i>S. monticola</i> <i>S. planifolia</i>	current - recent	ROMO_: 806 , 807, 809 , 812, N03, N05, WNC07
Degraded (elk-grassland)	4	18.3 ± 9.5	0.91 ± 0.23	20.2 ± 10.6	<i>S. geyeriana</i> <i>S. monticola</i> <i>S. planifolia</i>	historic	ROMO_: 502, 617 , 724 , WC08-R
Simulated Beaver Structure (SBS)	4	39.7 ± 10	1.7 ± 0.26	42.9 ± 10.7	<i>S. bebbiana</i> <i>S. drummondiana</i> <i>S. eriocephala</i> <i>S. geyeriana</i> <i>S. monticola</i> <i>S. planifolia</i>	current (simulated since 2019)	ROMO_: 901* , 904*, 906, 907

Sites were classified *a priori* as degraded or reference based on willow cover, willow height, beaver activity, and ungulate activity from ROMN data. Four sites were designated as SBS sites given this management intervention of the installation of simulated beaver structures in

the fall of 2019. Two of the four SBS sites sampled are also in exclosures. To confirm differences across site type designations, a Nonmetric Multidimensional Scaling (NMDS) and an analysis of similarities (ANOSIM) were performed on relative functional group cover sums and beaver and ungulate use metrics using the most recent ROMN estimates from Schweiger *et al.* (2019; **Fig. 2a**). Functional groups were based on origin and growth habit from ROMN classification as informed by the Colorado Natural Heritage Program species designations. Functional groups were native shrubs (largely comprised of *Salix* spp.), native trees, non-native graminoids, native graminoids, native forbs, and non-native forbs. In addition to the 15 sites we sampled, we included 38 other ROMN riparian monitoring sites for reference in the NMDS. To supplement site classification, depth to groundwater logger-obtained data from the ROMN program as described in Schweiger *et al.* (2015, 2019) is shown to contextualize hydrological differences across site types (**Fig. 2.2b**).

Ecophysiological sampling

Ecophysiological sampling occurred in the months of June, July, and August in 2019 and 2020 across 15 sites (**Table 2.1**). In 2020, more intensive sampling was performed at six of the 15 sites. During each site visit, measurements were taken on six to twelve adult individuals (mean=7.9 across sites) of dominant willow species typical of each site (Schweiger *et al.*, 2016, 2019). Measured individuals were within approximately 10m of the center of each ROMN monitoring plot.

Stem water potential

To estimate soil water availability surrounding root systems, we measured predawn water potential (Ψ_{PD}). A large body of evidence spanning multiple decades and ecological contexts demonstrates how predawn water potential measurements can indicate a plant's access to soil water and serve as a comparative tool to assess population and community level patterns of water use (Pezeshki *et al.*, 1998; Ambrose *et al.*, 2018). Despite this widespread use, it should be noted that using Ψ_{PD} as a proxy for water availability assumes that nighttime transpiration does not occur (or occurs in negligible amounts), thereby allowing plant and soil water potential to

equilibrate (or recharge) given there is no pull from open stomata in the soil-plant-atmosphere continuum (Ritchie & Hinckley, 1975; Richter, 1997). This assumption is reasonable for *Salix* spp., as other studies on congeners have not detected substantial nighttime transpiration (Peng *et al.*, 2015; Bailey *et al.*, 2022).

To compare water stress on seasonal and diurnal scales across site types, we measured stem water potential at midday (Ψ_{MD}), when water stress is maximal. Ψ_{PD} and Ψ_{MD} measurements were paired (taken on the same individual each sampling day). All stem water potential measurements were taken on healthy (i.e. not browned or browsed) terminal canopy shoots receiving full sun during daytime using a Scholander-type pressure chamber (PMS Instrument Company, Corvallis OR, USA). Each shoot sample was collected by hand with a razor blade and immediately covered with wet paper towels, placed in a plastic bag, and contained in a light-proof cooler. To facilitate rapid processing of samples, measurements were always conducted on site, within two minutes of collection. Two to three replicate shoot samples were measured for each individual for each time point for a total of 466 samples across 12 sites in 2019 and a total of 524 samples across 6 sites in 2020. Replicate measurements per individual per sampling point were subsequently averaged prior to plotting and statistical analyses to ensure measurement precision, totaling to 159 measurements in 2019 and 262 measurements in 2020. Predawn (Ψ_{PD}) measurements and midday (Ψ_{MD}) measurements occurred between the hours of 04:00 to 06:30 and 12:00 to 14:00, respectively. For Ψ_{PD} measurements, the sensitivity of pressure chamber couldn't quantify measurements between 0 and -0.0009 MPa, so some measurements were recorded as 0 MPa even though they were in this slightly negative range.

Gas exchange

Gas exchange measurements - stomatal conductance (g_s) and photosynthetic rate (A) - were obtained with a leaf porometer (SC-1; Decagon Devices, Inc., Pullman, Washington) and a portable photosynthesis system (Li-6400; Li-Cor Inc., Lincoln, NE, USA). With both instruments, replicate measurements per individual per sampling point were taken to capture short-term variability in gas exchange rates, and then averaged prior to plotting and statistical

analyses. For measurements taken with the SC-1 leaf porometer, three to six measurements were taken for each individual (on separate leaves) for each time point. For measurements taken with the Li-6400, twelve measurements were taken on each individual (on two leaves, six measurements each). SC-1 porometer measurements totaled to 616 samples across 10 sites in 2019 (94 measurements after replicate averaging) and a total of 1,678 samples across 6 sites in 2020 (503 measurements after replicate averaging). Li-6400 measurements totaled to 2,070 samples across 5 sites in 2020 (345 measurements after replicate averaging). Standard calibration was conducted prior to all measurements for both instruments following manufacturer instruction manuals. All measurements occurred on terminal, sun-exposed leaves. For diurnal sampling events, gas exchange measurements were taken simultaneously (within approximately 15 minutes) to water potential measurements.

Stemwater isotopes

Xylem and source water stable isotopes (δD and $\delta^{18}\text{O}$) were collected on a subset of individuals (115 individuals across 11 sites) in 2019 to identify water sources and functional rooting depths. Samples were collected from terminal, lower-canopy, sun-exposed branches. Stem segments were cut and epidermis and phloem tissue were removed to isolate the xylem. Samples were immediately placed in air-tight vials, which were additionally sealed with Parafilm to ensure samples did not lose water to evaporation. Samples were frozen until processed through a cryogenic distillation system following West *et al.* (2006) at the UC Berkeley Center for Stable Isotope Biogeochemistry (CSIB). Extracted xylem water and source water samples (from ground water from 2m deep wells in each plot and surface water in the closest adjacent stream) were analyzed for δD and $\delta^{18}\text{O}$ values (expressed in ‘per-mil’ or ‰ notation as a function of Vienna Standard Mean Ocean Water, V-SMOW) using an Isotope Ratio Mass Spectrometer. To determine if individuals were using deeper, more depleted water vs. shallower, more evaporatively enriched sources of water, we created a local meteoric water line (LMWL) to characterize local precipitation isotopic composition. We calculated the LMWL by performing a linear regression on monthly isotope data from the Online Isotopes in Precipitation Calculator

(OIPC) (Bowen *et al.*, 2005; Bowen, 2020). Smaller LMWL departure is indicative of use of deeper, depleted surface waters more similar to LMWL precipitation isotopes, whereas larger LMWL departure is indicative of more fractionation following precipitation that commonly occurs in upper soil layers.

Carbon isotopes

Foliar $\delta^{13}\text{C}$ samples across 8 individuals at 6 sites were collected in August 2020, for a total of 48 samples. Samples were immediately dried at 60°C for a minimum of two weeks and were then ground to homogenized powder using liquid nitrogen and a mortar and pestle. Samples were packed in tin and run on an Thermo Delta V Elemental Analyzer at the Earth Systems Stable Isotope Laboratory at the University of Colorado Boulder.

Statistical analyses

Response variables were all normally distributed apart from Ψ_{PD} due to the high prevalence of zeros. Thus, Ψ_{PD} measurements were transformed for statistical analyses by a small incremental addition (0.5) and subsequent cubing.

To address our first question about water limitation across site types, we examined stem water potential (Ψ_{PD} , Ψ_{MD}), gas exchange (A and g_s), and water use efficiency (WUE; $\delta^{13}\text{C}$) in a series of linear mixed effects models (LMMs) with site as a random effect and site type, mean annual precipitation (representing water year, with site by year specific values), and month of sampling (as a factor, when measurements were taken across the growing season) as fixed effects. To test for differences in source water, we ran a LMM with $\delta^{18}\text{O}$ as the predictor, site as a random effect, and site type as a fixed effect. Our prediction of increased water limitation in degraded sites would be supported by decreased g_s , reduced A , increased WUE (less negative $\delta^{13}\text{C}$), and more enriched (more positive) $\delta^{18}\text{O}$ signatures at degraded sites compared to reference and SBS sites.

To address our second question about whether there were differences in the degree of isohydry to anisohydry displayed in willow water use across site types, we followed the approach of Martínez-Vilalta *et al.* (2014). We performed a LMM with Ψ_{MD} as the response to an

interaction between site type and Ψ_{PD} , mean annual precipitation (representing water year), and month of sampling, and with a random effect of site. To discern differences in the timing and magnitude of water use across the growing season (Ψ_{PD} , Ψ_{MD} , gs), LMMs were performed with site as a random effect and site type, mean annual precipitation (representing water year), and an interaction between site type and day of year as fixed effects. Our second hypothesis would be supported by more strict regulation of midday water potential in response to predawn water potential and dampened seasonal drydown signals in willow water use at degraded sites, with more homogenous midday water potentials and rates of stomatal conductance across the growing season.

Due to the uneven sampling from natural variation in *Salix* spp. composition across site types, statistical models were not run with species identity as a fixed effect. To test whether species identity did not change site level trends, all LMMs were repeated with datasets subsetted to *S. monticola* only, which was the most evenly sampled species across all site types.

All statistical analyses were performed in R (R Core Team, 2021). The *vegan* package was used for the ordination and analysis of similarities (ANOSIM) test across site types (Osakanen *et al.*, 2022). All LMMs were run with the *lme4* package (Bates *et al.*, 2015) and the *multcomp* (Hothorn *et al.*, 2022), *MuMIn* (Bartoń, 2022), and *car* (Fox *et al.*, 2022) packages were used for post-hoc multiple comparisons, calculation of R^2 values, and p-value estimates.

Results

Site classification

Degraded sites are distinct from reference and SBS sites in terms of plant community composition, beaver activity, and ungulate activity (**Fig. 2.2a**; ANOSIM $R=0.24$, $p<0.0001$). Degraded sites have lower native shrub (willow) cover, higher ungulate activity, and higher non-native graminoid, native graminoid, and non-native forb cover. Reference and SBS sites have higher native shrub (willow) cover, higher beaver activity, and higher native forb cover. The

SBS sites with the highest willow cover (ROMO_904, highest NMDS2 axis scoring SBS point in **Fig. 2.2**) and highest native forb cover (ROMO_901, lowest NMDS2 axis scoring SBS point in **Fig. 2.2**) are in exclosures. Willow cover and height are highest at reference sites, lowest at degraded sites, and intermediate at SBS sites (**Table 2.1; Fig. A1**). Preliminary evidence indicates that depth to ground water steeply declines in degraded sites lacking beaver activity or SBS features, whereas high water tables and flooded conditions are maintained throughout the growing season in reference and SBS sites that have real or simulated beaver activity (**Fig. 2.2b**).

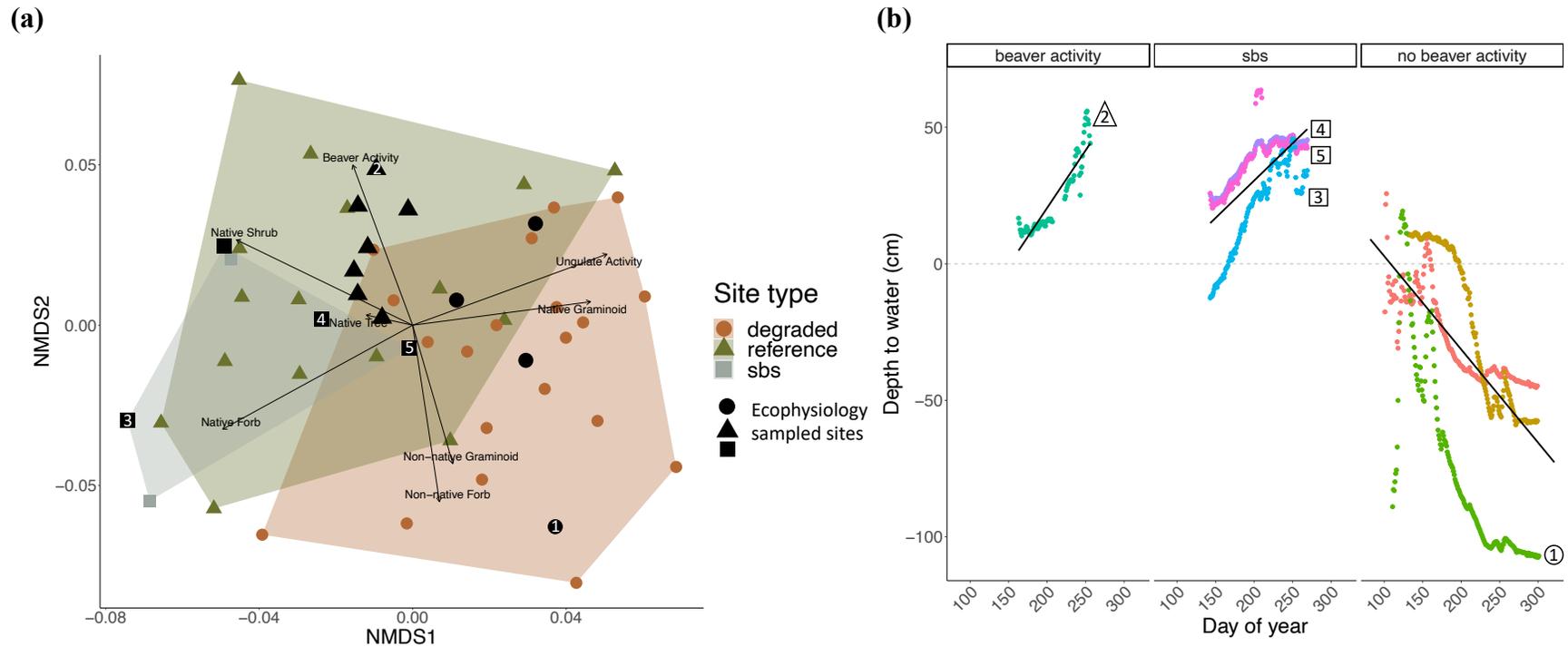


Figure 2.2. NMDS of vegetative cover by origin and growth habit, beaver activity, and ungulate activity (a). Colored polygons and shapes indicate site types, black colored shapes indicate ecophysiology sampled sites, and numbers in shapes correspond to sites in (b), which shows depth to groundwater in 2020 where logger data was available. Degraded sites are distinct from reference and SBS sites in terms of plant community composition, mainly due to low native shrub (willow) cover and high non-native native graminoid, non-native forb, and native graminoid cover (a). Reference and SBS sites, in addition to having high native shrub (willow) cover, have high native forb cover (a). Degraded sites are characterized by high ungulate activity whereas reference sites are characterized by high beaver activity (a). Sites that lack beaver activity or SBS structures, which encompasses degraded sites, had steep declines in water tables in 2020 (b).

Evaluation of water limitation

Ψ_{PD} was generally near 0 MPa and not significantly different across site types ($p > 0.05$) but did significantly differ across water years (mean annual precipitation, $p < 0.01$) ($R^2_{\text{conditional}} = 0.57$) (**Fig. 2.3a**). Ψ_{MD} was also not significantly different across site types ($p > 0.05$), though there was a significant effect of month of sampling ($p < 0.0001$) and water year (mean annual precipitation, $p < 0.0001$), with lower (more negative) Ψ_{MD} later in the growing season, and in the relatively drier year of 2020 ($R^2_{\text{conditional}} = 0.40$) (**Fig. 2.3b**).

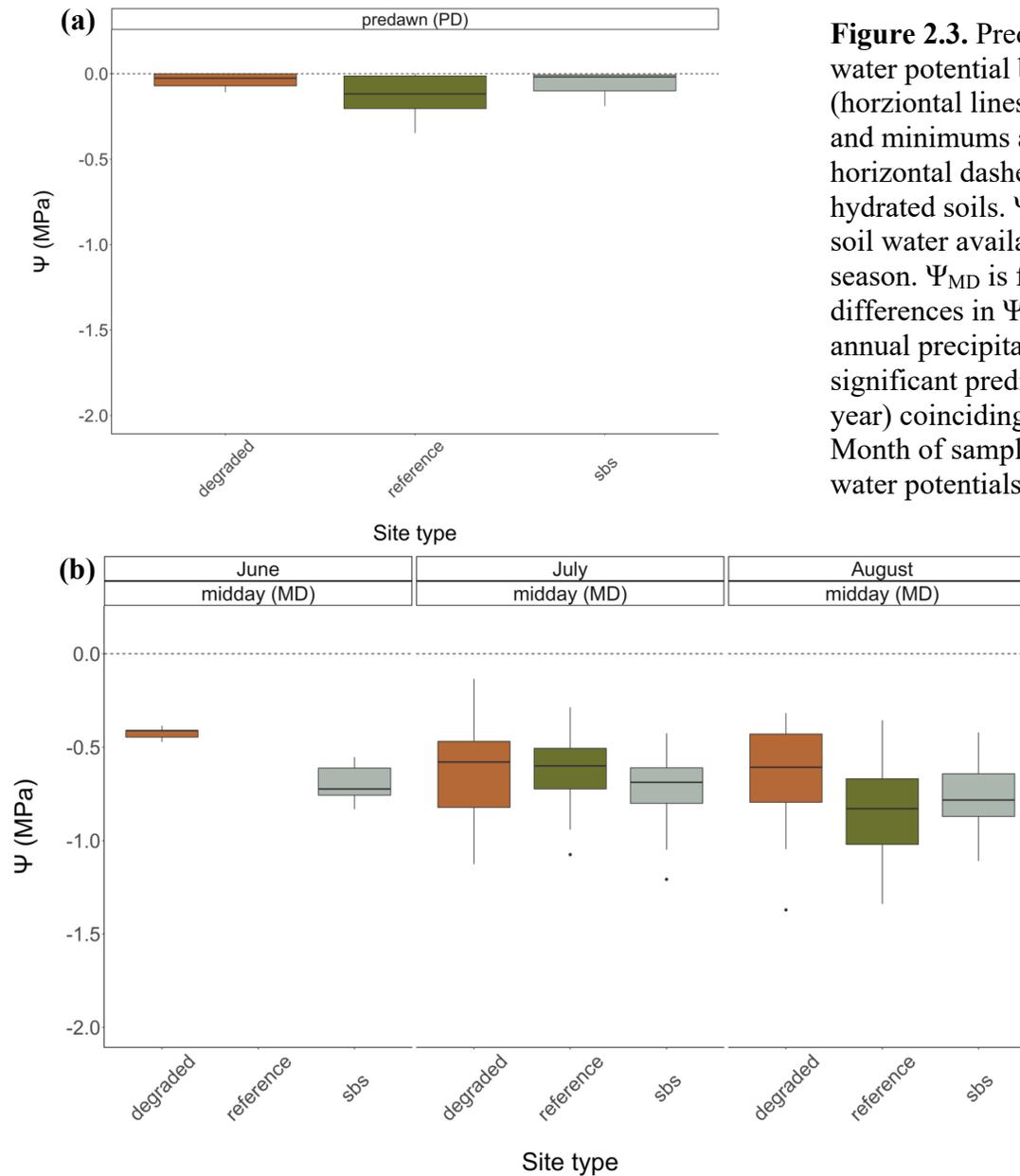


Figure 2.3. Predawn (Ψ_{PD}) (a) and midday (Ψ_{MD}) (b) stem water potential by site type. Boxplots show medians (horizontal lines), interquartile ranges, first and third quartiles, and minimums and maximums. 0 MPa is indicated by the horizontal dashed lines, with near-zero MPa Ψ_{PD} indicating hydrated soils. Ψ_{PD} was mostly sampled in August to assess soil water availability in peak dryness during the growing season. Ψ_{MD} is faceted by month. There were no significant differences in Ψ_{PD} or Ψ_{MD} across site types ($p > 0.05$). Mean annual precipitation (proxy for water year; not shown) was a significant predictor for both Ψ_{PD} and Ψ_{MD} with 2020 (drier year) coinciding with lower water potentials compared to 2019. Month of sampling was significant for Ψ_{MD} , with declining water potentials from June to August ($p < 0.001$).

Midday stomatal conductance (g_s) was highest in degraded sites compared to reference and SBS sites, counter to our predictions (**Fig. 2.4**). Overall, site type ($p=0.01$), month of sampling ($p=0.01$), and water year (mean annual precipitation, $p<0.001$) were significant predictors of g_s ($R^2_{\text{conditional}} = 0.76$).

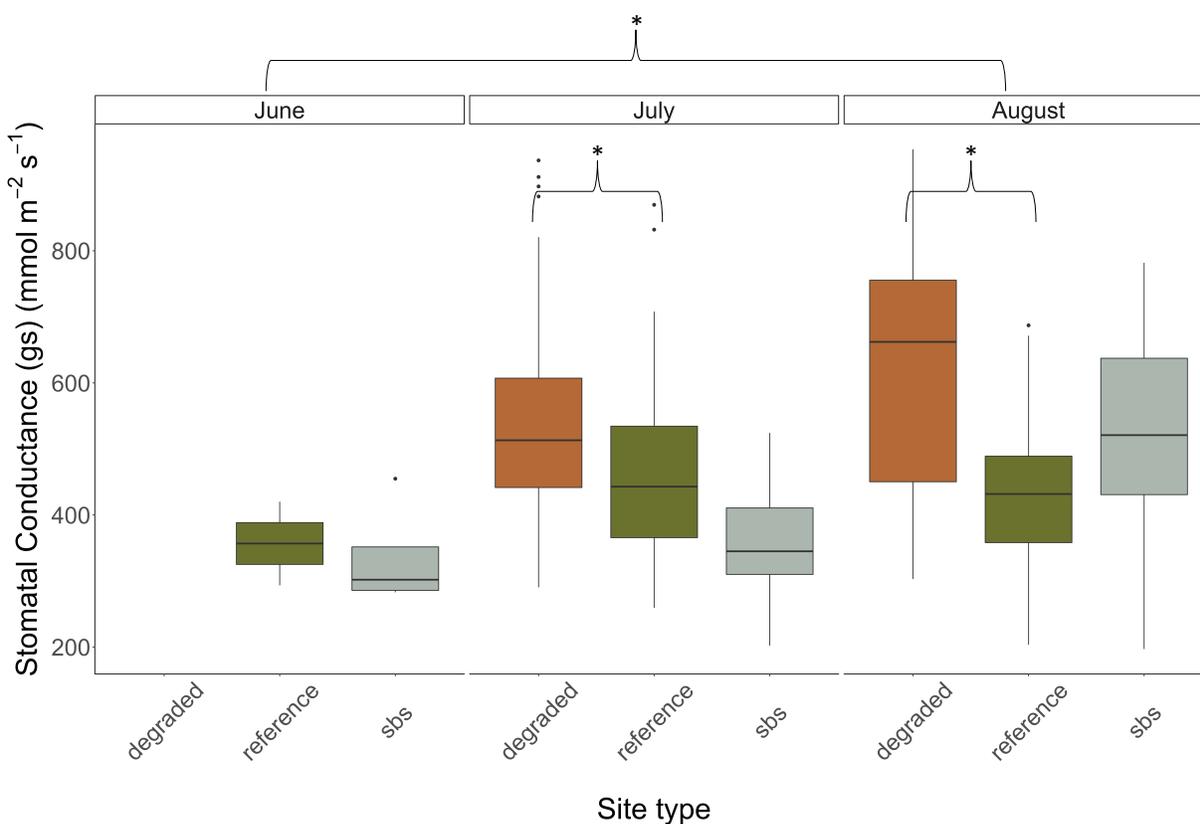


Figure 2.4. Midday stomatal conductance (g_s) across site types. Boxplots show medians (horizontal lines), interquartile ranges, first and third quartiles, and minimums and maximums. There was a significant effect of mean annual precipitation (proxy for water year; not shown), with decreased g_s in 2020 (drier year) compared to 2019 ($p<0.001$). g_s increased from June to August ($p<0.05$), except in reference sites. Degraded sites had significantly higher g_s compared to reference sites in July and August ($p<0.05$).

Photosynthetic rates (A) were similar across site types, opposed to our predictions (**Fig. 2.5**). Degraded sites had slightly higher photosynthetic rates compared to reference and SBS sites, though this was not significant ($p > 0.05$) ($R^2_{\text{conditional}} = 0.33$).

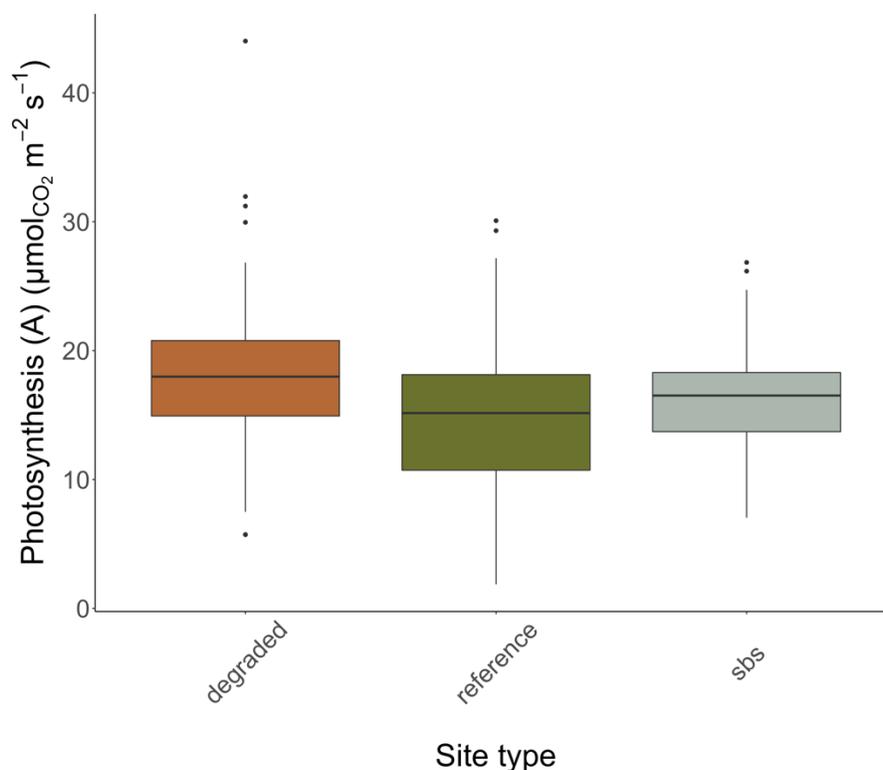


Figure 2.5. Photosynthetic rate (A) across site types. Boxplots show medians (horizontal lines), interquartile ranges, first and third quartiles, and minimums and maximums. There was no significant difference in A across site types ($p > 0.05$) or mean annual precipitation (proxy for water year; not shown) ($p > 0.05$).

Site type was a significant predictor of $\delta^{13}\text{C}$ ($p = 0.046$), while water year (mean annual precipitation) was not ($p > 0.05$) ($R^2_{\text{conditional}} = 0.67$). Degraded sites had the lowest seasonally integrated water use efficiency (most negative foliar $\delta^{13}\text{C}$) compared to reference and SBS sites, counter to our predictions (**Fig. 2.6**).

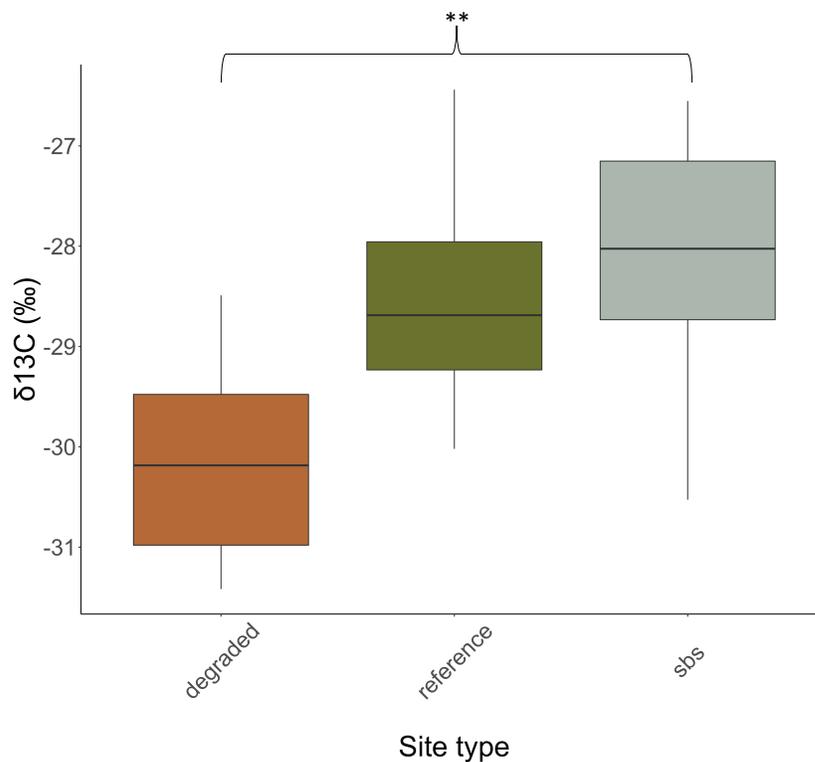


Figure 2.6. Foliar $\delta^{13}\text{C}$ across site types in 2020, with less negative $\delta^{13}\text{C}$ indicating increased water use efficiency (WUE). Boxplots show medians (horizontal lines), interquartile ranges, first and third quartiles, and minimums and maximums. Degraded sites had significantly lower WUE compared to SBS sites ($p < 0.001$).

δHD values ranged from -130.5 to -99.2‰ and $\delta^{18}\text{O}$ values ranged from -17.17 to -12.5‰ for stemwater samples (**Fig. 2.7**). When compared to source water samples from the present study and those measured in Alstad et al. (1999), stemwater $\delta^{18}\text{O}$ values, regardless of site type, are most similar to more perennial water sources such as well (groundwater), snow, and stream water as opposed to summer rain. This is counter to our expectation of increased reliance on enriched surface water at degraded sites.

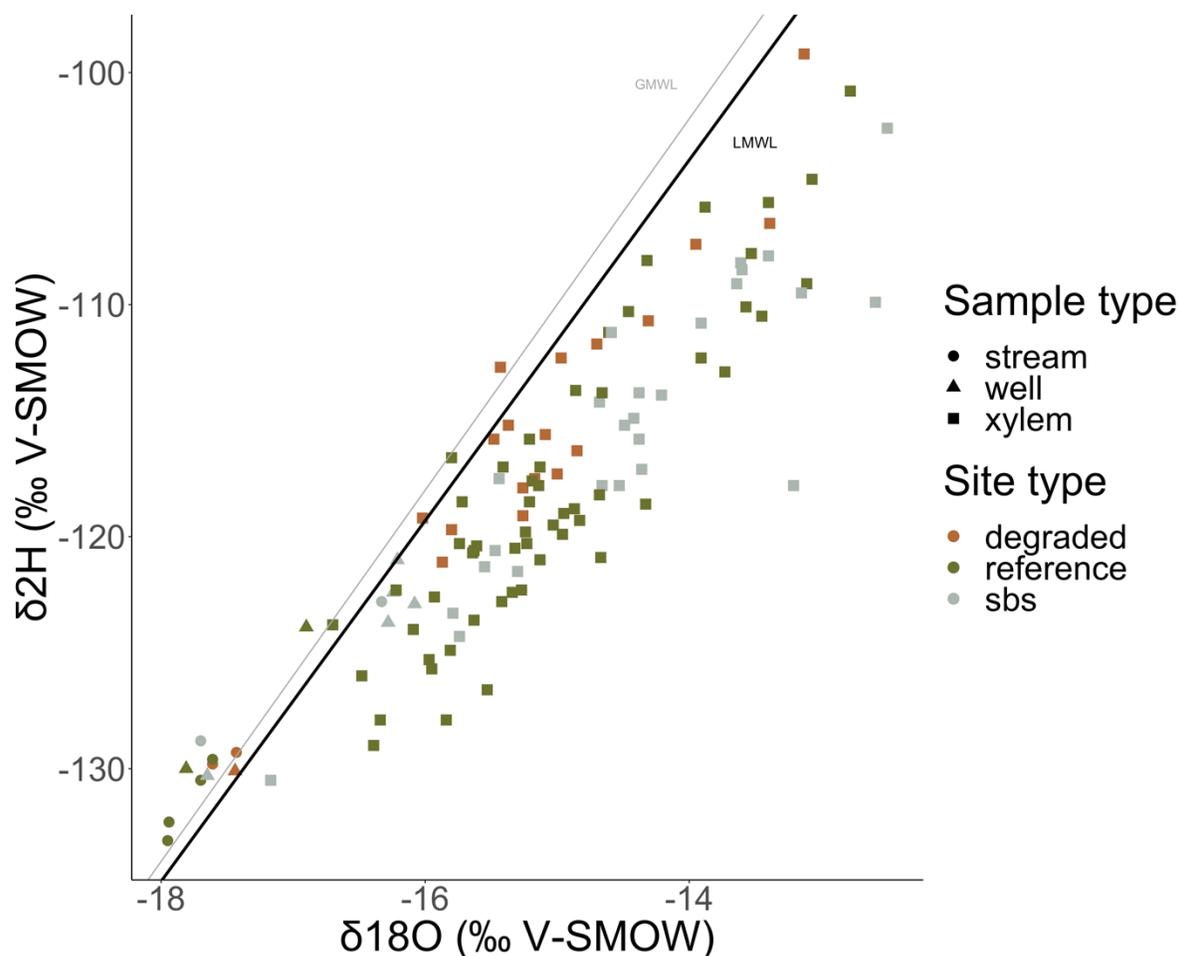


Figure 2.7. Stemwater and source water stable isotope data, with symbols indicating sample type and colors indicating site type. Sample departures from the global meteoric water line (GMWL) and local meteoric water line (LMWL) indicate evaporative enrichment. More negative $\delta^{18}\text{O}$ signatures indicate depleted samples most similar to more stable sources of water (stream, groundwater) compared to enriched summer rain water (not shown, but see Alstad et al. 1999 for mean $\delta^{18}\text{O}$ of approximately -7 ‰).

Temporal variation and the degree of iso/anisohydric behaviors

The linear relationship (slope, σ) between Ψ_{PD} and Ψ_{MD} , characterizing the spectrum of isohydry-anisohydry, did not significantly vary across reference ($\sigma=0.00047$), SBS sites ($\sigma=-0.27$), and more degraded sites ($\sigma=3.13$) ($p>0.05$), largely due to the tight clustering of high (near zero) Ψ_{PD} (Fig. 2.8).

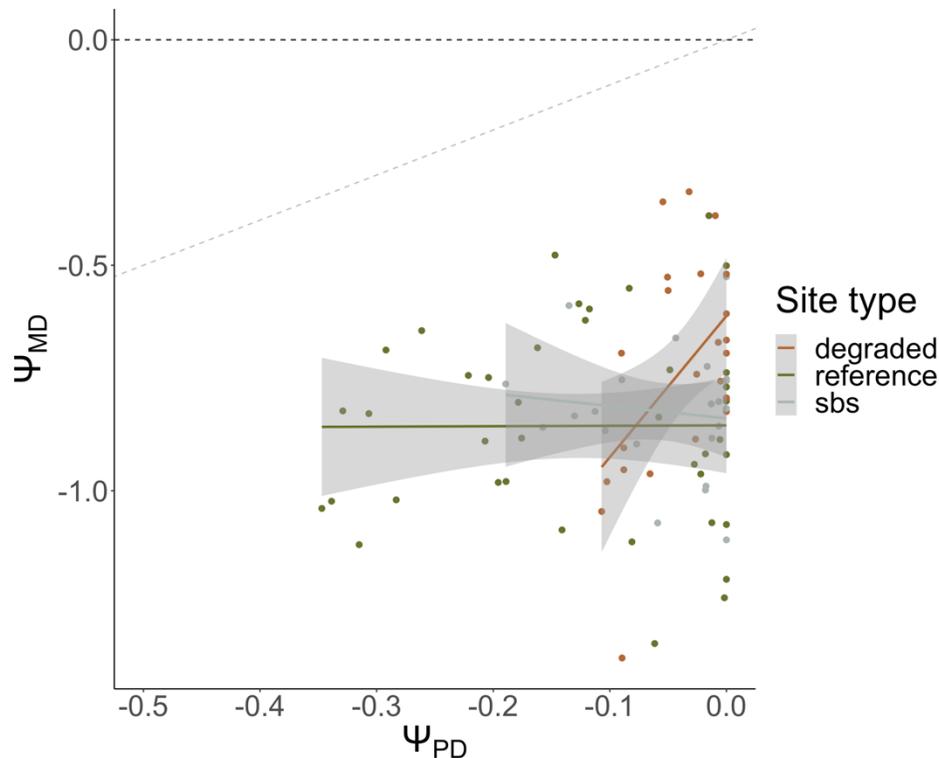


Figure 2.8. Bivariate relationship between Ψ_{PD} and Ψ_{MD} with fit lines and colors by site type. Lower σ (slope) values ($\sigma < 1$) correspond to isohydric behaviors (drought avoidance) and higher σ values ($\sigma > 1$) correspond to anisohydric behaviors (drought tolerance). The dark dashed horizontal line indicates 0 Ψ_{PD} and the light grey diagonal line is the 1:1 line.

Across the course of the growing season, Ψ_{PD} and Ψ_{MD} ranged between 0 to -0.3 MPa, and -0.3 to -1.3 MPa, respectively (**Fig. 2.9a**). As expected with seasonal dry down, midday water potentials declined across the growing season across all site types at similar rates, with the most extreme (negative) Ψ_{MD} measurements observed in August 2020 (significant effect of day of year, $p < 0.001$). There were no significant interactive effects of site type and day of year for Ψ_{PD} and Ψ_{MD} ($p > 0.05$). Both predawn and midday water potentials were lower (more negative) in 2020, though mean annual precipitation was only a significant predictor for Ψ_{MD} ($p < 0.001$). The conditional R^2 for the model was 0.66.

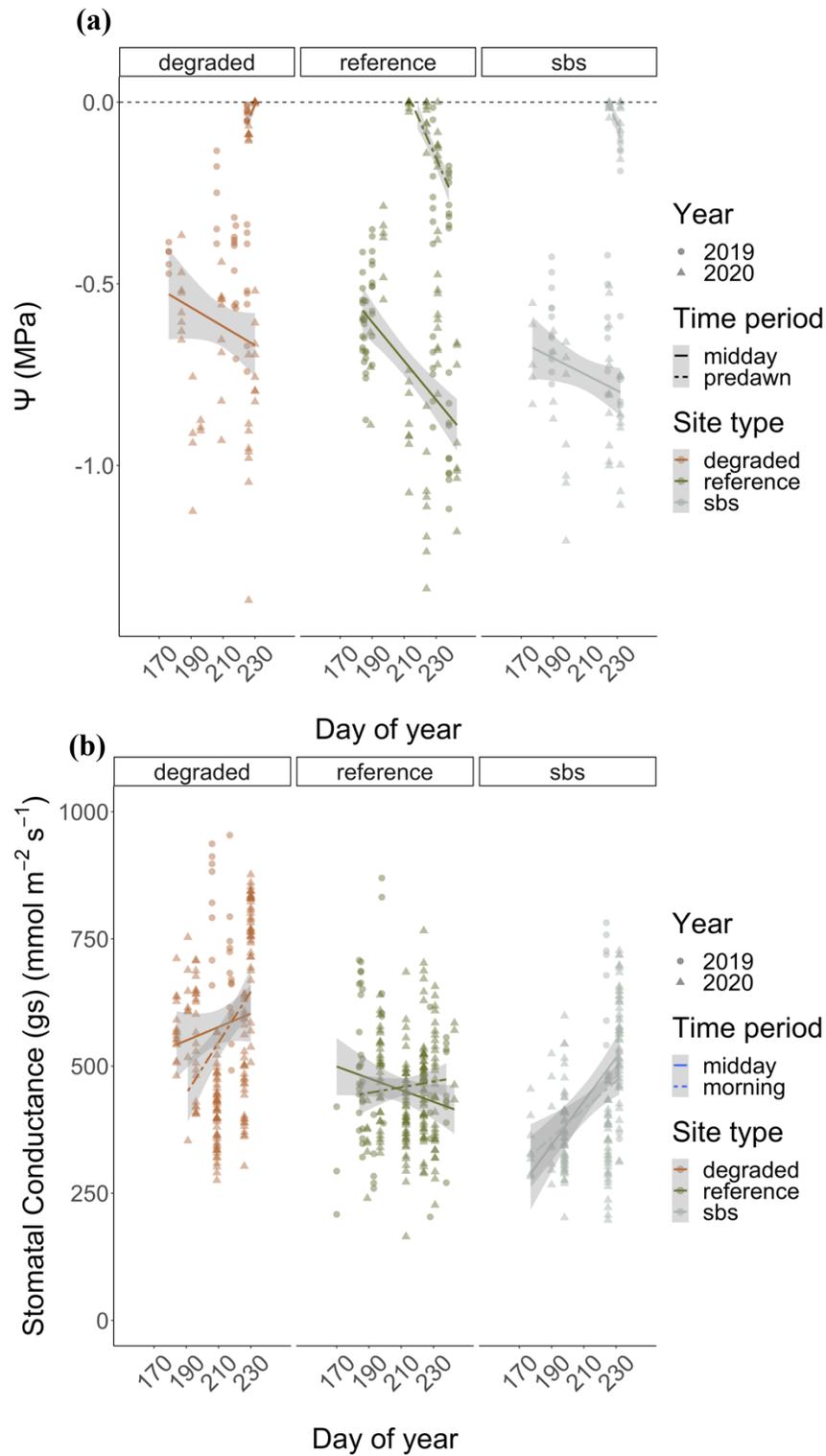


Figure 2.9. Seasonal water potential (Ψ_{PD} , Ψ_{MD}) (a) and stomatal conductance (gs) (b) across years (symbols), time periods (line types), and site types (colors and panels). There were no significant main or interactive effects of site type and day of year (DOY) on Ψ_{PD} ($p > 0.05$),

though Ψ_{PD} was significantly higher in the wetter year of 2019 (main effect of mean annual precipitation) ($p < 0.05$). Ψ_{MD} did significantly decline during the growing season across all sites (main effect of DOY, $p < 0.01$), notably not varying by site type (no interactive effect of site type and DOY; $p > 0.05$). As with Ψ_{PD} , Ψ_{MD} was significantly higher in the wetter year of 2019 (main effect of mean annual precipitation) ($p < 0.001$). There was a significant main effect of DOY and an interactive effect of site type and day of year on g_s ($p < 0.01$). Additionally, g_s was significantly higher in morning vs. afternoon time periods ($p < 0.001$), and also in 2019 (main effect of mean annual precipitation) ($p < 0.001$).

Midday g_s increased across the growing season except at reference sites (**Fig. 2.9b**; significant interactive effect of day of year and site type, $p < 0.01$). Stomatal conductance especially increased during mornings over the growing season at both degraded and reference sites (significant effect of time period, $p < 0.01$). Stomatal conductance was higher in sites that were wetter (significant effect of mean annual precipitation, $p < 0.001$). The conditional R^2 for the model was 0.72.

Supplemental analyses

Species identities generally did not change the site type level trends (**Fig. A3**). When LMMs were repeated with datasets subsetted to *S. monticola*, the most evenly sampled species across all site types, the significance and general overall explanatory importance of predictor variables did not substantially change (**Fig. A2**).

Discussion

We did not find evidence of marked isohydric responses to indicate water limitation in willows at degraded sites as we expected. Instead of regulating stomata more strictly, willows at degraded sites had elevated rates of stomatal conductance and comparable rates of photosynthesis to reference and SBS sites, resulting in low water use efficiency. Further, we observed relatively uniform trends in water potential and stomatal conductance over the course of the growing season across site types. Instead of homogenous midday water potentials across the growing season at degraded sites, the magnitude and rate of midday water potential decline with seasonal drydown was similar across site types. Both degraded and reference sites had

similar trends in stomatal conductance, with high morning stomatal conductance near the end of the growing season. However, while reference sites demonstrated expected tapering of stomatal conductance with seasonal drydown, degraded and SBS sites had increased rates of stomatal conductance later in the growing season.

Climate and physiological contexts

Our study period occurred in one wet water year and one dry water year relative to historical climatic conditions (1980-2010). Given this climatic context, especially for our intensive sampling coinciding with a dry year (2020), our ecophysiological assessments were performed at a relatively suitable time to assess potential water limitation.

On the whole, willow water use was relatively consistent across site types. Instead, abiotic controls on water use and productivity were more evident, as indicated by seasonal trends in water status across site types. Notably, measures of stem water potential were not close to estimates of critical mortality thresholds such as P_{50} , the water potential at which 50% of hydraulic conductivity is lost. Johnston *et al.* (2007) estimated a P_{50} range of -1.57 to -2.13 MPa for *S. geyeriana* and *S. bebbianai*, both of which are included in the present study. Additionally, Savage & Cavender-Bares (2011) documented a range of -0.8 to -1.8 MPa for P_{50} across five *Salix* spp. (mean = -1.2 ± 0.32). To compare these estimates to our data, we found a range of -0.35 to -0.69 MPa and an average of -0.58 MPa in midday water potentials for *S. bebbiana*. Similarly, all *Salix* spp. in our study averaged -0.69 MPa with a range of -0.13 to -1.37 MPa in midday water potentials. This indicates that drought induced mortality is likely not a prevalent phenomenon for *Salix* spp. across our study sites.

Despite variable ecological and hydrological conditions represented at our sites, the relatively homogenous, high midday water potentials we observed over the course of the growing season is consistent with other studies showing that phreatophyte (groundwater dependent) plants have less variable water potential compared to plants that are dependent upon shallow soil water reservoirs (Lin *et al.*, 1996). Alstad *et al.* (1999) found that willows in riparian sites in RMNP (coinciding watersheds with the present study) were consistently dependent upon

stream vs. precipitation inputs over the course of the growing season, even with increasing distance from the stream or variable browse levels, pointing to their consistent access to ground water reservoirs. Similarly, we also found that willows in RMNP across degraded, reference, and simulated beaver structure sites still, 20 years later, have a $\delta^{18}\text{O}$ signature most similar to stream and groundwater sources as opposed to rain water. This ubiquitous access to groundwater is likely reflective of relatively well-developed root systems since we sampled adult willows across all site types. However, it is also possible that willows at degraded sites have experienced some degree of root dieback in response to browsing and hydrologic change (Williams & Cooper, 2005), so while our data indicate willows currently utilize perennial, deeper water sources, this could change in drying environments.

While other studies have found that riparian species often regulate stomata to reduce transpiration in response to reduced water availability (Rood *et al.*, 2003), we did not find evidence of this at our study sites. In contrast, transpiration was higher at degraded sites, both over the course of the growing season, and on diurnal time scales. Johnson *et al.* (2002) also found that experimental water stress alone did not incur significant reduction in willow stomatal conductance. Increased transpiration, in some instances, can be a response to elevated temperatures (Fitter & Hay, 2002), which in our sites could vary with willow cover and the amount of solar radiation a site receives, with tall dense willows providing more shaded and cooled microclimates compared to sites with short sparse willows. However, we did not find strong differences between our simultaneous measures of leaf temperatures and transpiration across site types (**Fig. A4**).

Another plausible explanation for the unexpected elevated stomatal conductance at degraded sites is due to reductions in leaf dimensions and specific leaf area compared to greater leaf dimensions and specific leaf area at reference sites (**Fig. A5**). This phenomenon can cause a thinning of the boundary layer and an increase in stomatal densities, therein causing a reduction of both the boundary layer and stomatal resistances, ultimately resulting in greater water loss in the process of photosynthesis (Fitter & Hay, 2002).

In line with increased transpiration and relatively unchanged photosynthetic rates at degraded sites compared to reference and SBS sites, leaf $\delta^{13}\text{C}$ was lower (more negative/depleted) at degraded sites, showing there was lower water use efficiency at these sites despite drier site conditions. This is in contrast to other studies showing an approximate increase in $\sim +3.5$ mil of $\delta^{13}\text{C}$ in response to experimental water table drawdown (Stella & Battles, 2010) and $+3$ mil of $\delta^{13}\text{C}$ in response to declining groundwater tables *in situ* (Horton & Clark, 2001). Alstad et al. (1999) found upland (vs. streamside) *S. monticola* individuals in RMNP to have relatively similar water use efficiency, though relative instantaneous rates of stomatal conductance could have increased since this study was done (gs was not measured). Overall, our findings indicate that, on average, degraded sites have the lowest seasonally integrated water use efficiency, spending more water without a concurrent gain in rates of productivity.

Two main morphological phenomena occurring over the recent decades could have played key roles in improving *Salix* spp. water status at our study sites. Browsing by ungulates and branch sacrifice (crown dieback) in response to decreased water availability can improve root:shoot ratios, especially for phreatophytic adults with large root systems. Increased root:shoot ratios can alleviate or eliminate water stress by allowing for increased water supply to fewer branches, potentially having a positive effect on growing season productivity by allowing for a longer growing season with maintained access to soil water supply. In fact, Alstad et al. (1999) found that in RMNP, winter elk browsing significantly increased summer *S. monticola* water potentials by approximately 0.2 MPa in a dry year. Additionally, crown dieback or branch sacrifice has been observed in the Salicaceae family (Rood *et al.*, 2000; Horton *et al.*, 2001) and more specifically, in recent decades in RMNP. Between 2007-2011 average Salicaceae dieback was 17.8% across all RMNP I&M WEI monitoring sites (Schweiger *et al.*, 2019). Notably, the lower Kawuneeche Valley, where two of our degraded sites were located, has the highest dieback across RMNP long-term wetland monitoring sites (often greater than 31%), matching observations of marked dieback with many tall (>2m) willows with only live canopy towards the base (**Fig. A6**). Despite our observation of alleviated water potentials at degraded sites which

could possibly be due to increased root:shoot ratios or branch sacrifice, we expect this potential mechanism to not be persistent due to eventual depletion of carbon reserves to support extensive root systems with short, highly browsed aboveground biomass. Carbon-limitation, over time, can eventually lead to carbon starvation and mortality (McDowell et al., 2008), highlighting this as an important consideration for future monitoring.

Implications

In terms of the applicability of our results to assessing willow recovery at a broader scale in the Southern Rocky Mountains, it is important to note that, while our sampling design aimed to quantify trends at reference, degraded, and SBS sites that are representative of gradients in ecological condition more broadly in this region, we likely did not capture the full spectrum of montane riparian ecological condition in the region. For example, there could be areas with even lower water tables, higher browsing pressure, more anthropogenic disturbances (i.e. outside of national park boundaries), or a combination of these factors that could yield different patterns of willow water use. Further, it is important to note that our study was not designed to specifically target both main management interventions – exclosures and simulated beaver structures – to determine whether or not these interventions could be interacting drivers of willow water use.

Overall, despite the lack of evidence to indicate adult willows were water limited or stressed at our degraded study sites, there is other growing conceptual and empirical support indicating that ecosystem recovery is generally accelerated and strengthened with process-based interventions, such as restoring hydrology with beaver mimicry features (Beechie *et al.*, 2010; Higgs *et al.*, 2014; Pollock *et al.*, 2014; Bouwes *et al.*, 2016). Given that *Salix* spp. and wetland species in general have acquisitive traits (Pan *et al.*, 2020) and hydraulic traits vulnerable to drought (Savage & Cavender-Bares, 2011), mesic conditions are likely to benefit the establishment, survival, and growth of these species while limiting the establishment, growth, and survival of more xeric adapted upland species (e.g. non-native grasses) that can become dominant in degraded areas. Further, managing hydrologic conditions in these systems is imperative for ensuring desired ecosystem trajectories with tall willow dominance since willow

regeneration depends on synchronous seed rain and the availability of suitable bare, wet substrate created by fluvial processes (Warner & Hendrix, 1984; Stromberg, 1993; Gage & Cooper, 2004; Cooper *et al.*, 2006).

Given the relatively consistent timing and magnitude of willow water use across site types, other, more frequent monitoring strategies aimed at quantifying willow production might be better suited to assess rates and trajectories of willow recovery. This approach, for instance, would allow for direct assessment of the effects of simulated beaver structures on willows, which did not appear to improve willow water use or carbon assimilation in our assessment. However, this is not surprising as we monitored simulated beaver structure sites less than a year from when beaver mimicry features were installed, before increased water availability could have a substantial effect over multiple growing seasons. Future monitoring to assess the separate and likely synergistic effects of simulated beaver structures and exclosures (*sensu* Marshall *et al.* 2013) on willow recovery is essential.

Conclusions

Ecophysiological assessments, particularly for dynamic systems such as riparian systems, can be highly informative assessments to help quantify and predict ecosystem trajectories in restoration. Here, we applied an ecophysiological approach to better understand the ecological consequences of decoupled beaver-willow feedbacks and high ungulate browsing pressure. While adult willows did not exhibit evidence of water limitation across our degraded, reference, and simulated beaver structure study sites, continued drying trends in montane riparian systems in the Rocky Mountains due to climate change, a continued lack of beaver mediated hydrology, and future flow diversion threats demonstrate the merit of using plant water relations as a periodic ecosystem assessment tool in especially dry years.

CHAPTER III

Partitioning abiotic drivers and biotic associations in decadal wetland plant community turnover
in Rocky Mountain National Park

By Isabel de Silva, E. William Schweiger, and Katharine N. Suding

Abstract

We assessed decadal trends in Rocky Mountain National Park wetlands (Southern Rocky Mountains, Colorado, U.S.A.) to identify key abiotic and biotic factors affecting plant community composition, utilizing *in situ* long-term monitoring data and water balance data. Riparian wetlands, compared to wet meadows and fens, experienced the greatest compositional change, increasing in overall species diversity with a shift towards increasing prevalence of native graminoids, non-native graminoids, and native trees and a decline in native shrubs. Wet meadows and fens, in contrast, had relatively stable functional group components, with increases in native graminoids and native shrubs in wet meadows and increases in native forbs and native shrubs in fens. While wet meadow species diversity was stable, fens had a stark increase in species diversity across the past two decades. Overall, metrics related to water availability were strongest drivers of plant community composition. Specifically, the most sensitive wetlands were those experiencing large changes in mean annual precipitation. Biotic variables, including beaver and ungulate activity, affected compositional turnover in riparian wetlands and wet meadows, but not fens. When looking at associations of functional groups in a joint species distribution modeling framework, we did not find much evidence for limiting similarity, with the exception of limited co-occurrence between non-native graminoids and native graminoids in both riparian wetlands and fens. Altogether, we show how modeling of environmental drivers and associations among functional groups can improve assessments of ecological trajectories, specifically to assess biotic integrity.

Introduction

Wetland and riparian ecosystems are the biodiverse interfaces between upland ecosystems and aquatic habitats. While representing small fractions of land, they host unique and rich species assemblages that, in conjunction with geomorphic and hydrologic attributes, provide numerous essential ecosystem functions and services, including flood mitigation, nutrient cycling, soil retention, habitat provisioning, and human recreational use (Capon *et al.* 2013). Despite providing these essential ecosystem functions and services, these systems have experienced degradation and habitat loss more rapidly under anthropogenic pressure than other ecosystems (Millennium Ecosystem Assessment 2005), with some estimates showing an 87% percent loss in wetlands globally in the last 300 years (IPBES *et al.* 2018). To combat this trend, wetland and riparian restoration efforts have boomed globally across the past 30 years (Bernhardt *et al.* 2005; Palmer *et al.* 2014), and long-term monitoring programs have become much more of a standard in restoration and conservation.

As part of these programs, quantifying the abundance and distribution of wetland indicator species or non-native species at a single time point, or looking at percent cover changes through time, are routine (Lemly, J. & Smith 2014; US EPA 2016; Schweiger *et al.* 2019). Oftentimes, these efforts are undertaken with the assumption that all monitoring sites may be equally vulnerable to change, and further, monitoring programs may not have the resources to incorporate monitoring of other abiotic and biotic factors affecting plant community composition. While these more standard approaches are invaluable for the assessment of many management goal-oriented objectives, there is much to learn about the complexity of and mechanisms behind the biological patterns of these ecosystems. What drives abundance changes in some sites and not others? Do species or functional groups differentially respond (change in abundance or presence) to environmental and biotic drivers? If so, do these changes depend on certain abiotic or biotic factors? Do species or functional group interactions change through time and/or across space? Approaches that consider most or all of these questions will allow for long-

term datasets to more effectively be used to make predictions about future biotic trajectories of ecosystems. In order to predict how wetland systems might be differentially affected by environmental change, it is essential to incorporate underlying hydrology, biotic, and disturbance drivers that vary across different wetland types.

In the Southern Rocky Mountains (U.S.A.), and specifically in Rocky Mountain National Park (RMNP, Colorado, U.S.A.), three dominant wetland types include wet meadows, fens, and riparian wetlands, following classification by Gage & Cooper (2013) and as described by Schweiger *et al.* (2015). Wet meadows have predominately mineral, seasonally saturated soils with high nutrient availability, seasonally declining water tables, and are often dominated by *Juncus*, *Muhlenbergia*, *Scirpus*, *Iris*, *Carex*, and *Eleocharis* species with sometimes sparse *Salix* shrub cover. Fens are characterized by the presence of peat, perennially high groundwater tables that slow or prevent the decomposition of organic matter, and diverse plant communities that are often dominated by *Carex*, *Eleocharis*, *Juncus*, *Salix*, and *Calamagrostis* species. Riparian wetlands, by nature of being adjacent to streams, are physically structured by fluvial processes and their hydrology varies along with seasonal variation in surface water flows, with soil saturation occurring initially early in the growing season. Riparian wetlands are highly variable in terms of vegetative components but are often dominated, particularly at lower elevations, by woody species such as *Salix*, *Alnus*, *Betula* species, and with *Poaceae*, *Carex*, and forb species such as *Senecio*, *Mertensia*, and *Cardamine* at higher elevations.

Two key biotic drivers of these wetland types are beavers and ungulates. Beaver pond formation causes channel migration and/or flooding that can contribute to the wetting and eventual formation of wet meadows (Naiman *et al.* 1994; Westbrook *et al.* 2011). Similarly, abiotic channel migration from changes in snowmelt fed streamflow and/or beaver activity are significant drivers of both the location of riparian wetlands, but also the vegetative components within them, especially dominant woody species as *Salix* (Cooper *et al.* 2006). However, beavers and their hydrologic function have largely been functionally absent from RMNP since the mid-1990s (Peinetti *et al.* 2002; Baker *et al.* 2012). In terms of other biotic factors such as ungulate

browsing activity by elk and moose, meadows are thought to be the most used wetland type given their prevalence and high graminoid (forage) cover (Schweiger *et al.* 2015). However, riparian wetlands, especially shrub species such as *Salix*, are also highly utilized by ungulate populations, which have remained high in the park (Peinetti *et al.* 2002; Baker *et al.* 2005; Zeigenfuss & Johnson 2015).

Lastly, in terms of susceptibility to human disturbance, riparian wetlands are more commonly exposed to anthropogenic disturbances compared to wet meadows and fens in RMNP due to their collocation with roads, their foot traffic use, and since their streamflow inputs can be altered by flow diversions (Woods & Cooper 2005; Woods *et al.* 2006; Schweiger *et al.* 2016).

In addition to quantifying multidimensional environmental factors that can jointly or individually affect wetland plant species composition, incorporation of species interactions within wetland plant communities can improve models to estimate the structure of communities (Ovaskainen *et al.* 2017a; Norberg *et al.* 2019). Though it has been well established that both competitive and facilitative interactions occur within biological communities (Callaway & Walker 1997), analyses of drivers of wetland plant communities have often centered solely on hydrologic or edaphic drivers (Keddy 2003). For long-term monitoring of these systems, it can be important to know if presence of a certain species or functional group can be an indicator of a presence of another species or functional group, or if emerging dominance of a functional group might implicate a decline in another functional group due to limiting similarity. Limiting similarity, specifically through the occupation of niche space in the context of finite resources, has been shown to play a partial role in invasion dynamics in some communities (Price & Pärtel 2013). Fortunately, recent advances in a class of models – joint species distribution models (Pollock *et al.* 2014; Ovaskainen *et al.* 2017b) – allow for explicit modeling of both environmental filtering and biotic associations to harness long-term data towards this aim.

Here, we use *in situ* long-term monitoring data and water balance data to assess decadal trends in Rocky Mountain National Park wetlands to identify key abiotic and biotic factors affecting plant community composition. Given the underlying soil, hydrologic, biotic, and

human disturbance differences across wet meadows, fens, and riparian wetlands in RMNP wetlands, we hypothesized that over the recent decade, wetlands that have experienced the largest change in water balance have undergone largest change in plant community composition. We further hypothesized that abiotic factors related to water availability would be the most important determinant of plant community composition, regardless of wetland type. Lastly, we hypothesized that riparian wetlands are the most susceptible to compositional turnover, particularly in terms of increases in invasion by non-native species not only due to a recent lack of beaver mediated hydrology and high ungulate browse pressure, but due to the presence of non-native species that can establish in disturbed conditions.

Methods

Study sites & sample periods

Our 36 sites are riparian, wet meadow, and fen ecosystems located in Rocky Mountain National Park (RMNP) that are a part of the National Park Service Rocky Mountain Inventory and Monitoring Network wetland long-term monitoring program (ROMN, Schweiger *et al.*, 2015, 2016, 2019; **Fig. 3.1, Table B1**). Of these 36 sites, 12 are riparian wetlands, 14 are wet meadows, and 10 are fens. Wetland types were determined following Gage & Cooper (2013). All sites are situated within 2,440-3,630m elevation and have a semiarid climate with the majority of precipitation arriving as snow in winter (December-February). Across all sites, mean annual precipitation (calculated as the 1980-2010 historical average) was 701.3mm \pm 7.1 and mean annual temperature was 2.5 C \pm 0.64 (Thornton *et al.* 2022).

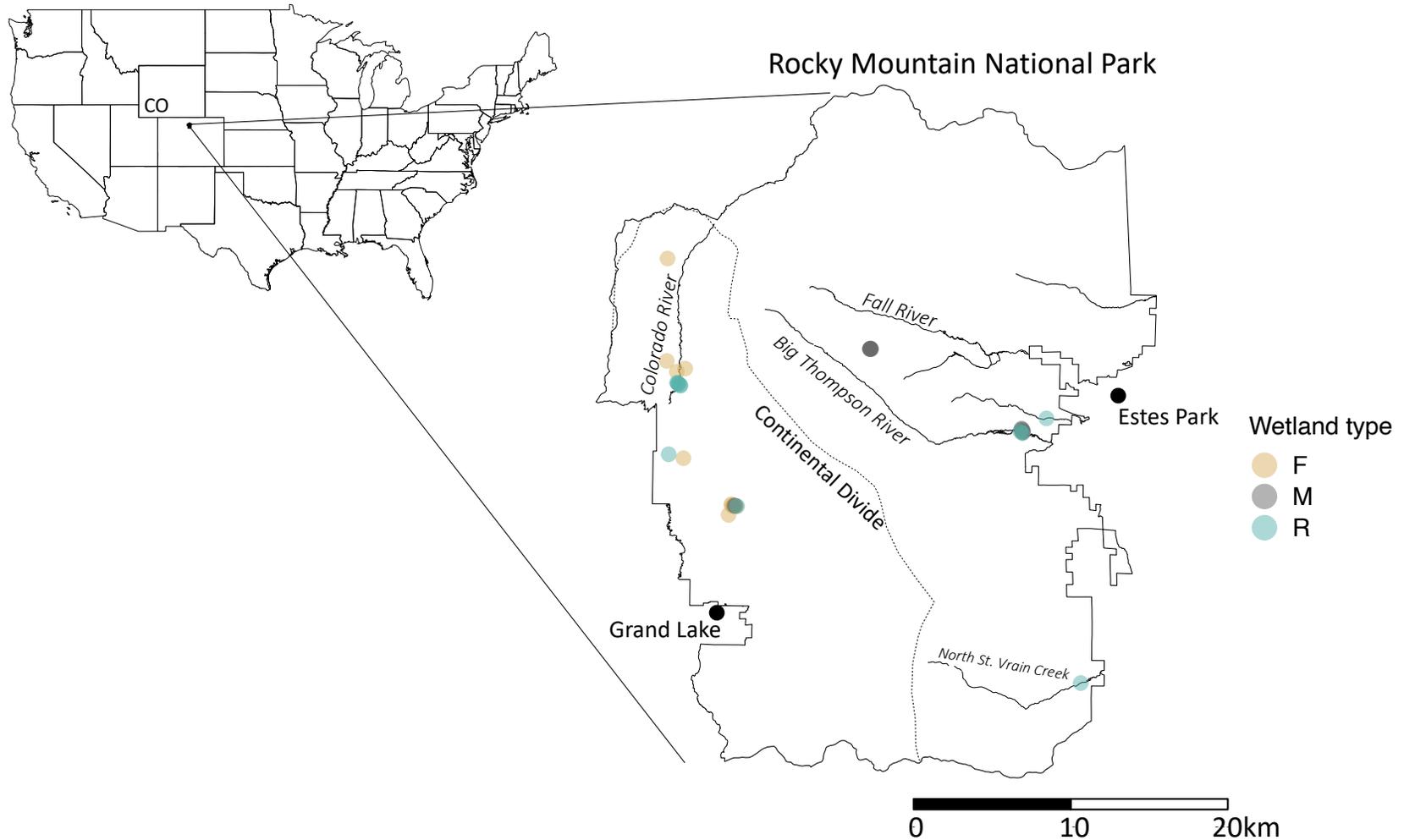


Figure 3.1 Map of study sites located in Rocky Mountain National Park, Colorado, USA. Sites are colored, with fens in yellow, wet meadows in grey, and riparian wetlands in blue. There are clusters of sites in: the southern portion of Colorado River, the Big Meadows region (sites closest to Grand Lake), and the eastern portion of the Big Thompson River within the park boundary.

Because the primary objective of the present study was to assess turnover, we focused on sites with at least three sample events that spanned a minimum of five years (average: 10.2 years, median: 11 years). Since the sample events at each site did not all occur in the same years, in effort to standardize the focal study period across sites, we classified these multiple observations into three periods: ‘early’ occurring between 2007-2010, ‘middle’ (2011-2014), and ‘last’ (2015-2021). If a site was sampled more than three times, the earliest sampling was selected for the early period, the median sampling for the middle period, and/or the latest sampling for the last period.

Plant community composition

Species level percent visual cover estimates for each site and sampling event were obtained by averaging percent visual cover estimates at smaller subplots (four microplots 1m² plots) nested within the larger site 10 x 10 m macroplot (Schweiger *et al.* 2015). Species level data was aggregated to ‘functional group’ level data based on origin and growth habit following ROMN classification as informed by the Colorado Natural Heritage Program species designations. All analyses focus on a total of six functional groups: native trees, native shrubs, native graminoids, non-native graminoids, native forbs, and non-native forbs. **Table 3.1** lists the most dominant species (based on relative cover) in these functional groups across site types.

Table 3.1. Dominant species by wetland type and functional group, listed in order of abundance based on relative cover across all years and sites. The top five species, when available, are listed per wetland-functional type group.

Wetland type	Native shrub	Native tree	Native graminoid	Non-native graminoid	Native forb	Non-native forb
Riparian	<i>Alnus incana</i> ssp. <i>tenuifolia</i> <i>Salix monticola</i> <i>Salix geyeriana</i> <i>Salix planifolia</i> <i>Salix drummondiana</i>	<i>Picea engelmannii</i> var. <i>engelmannii</i> <i>Pinus contorta</i> var. <i>latifolia</i> <i>Populus tremuloides</i> <i>Abies bifolia</i> <i>Pseudotsuga menziesii</i> var. <i>glauca</i>	<i>Carex aquatilis</i> <i>Calamagrostis canadensis</i> <i>Carex utriculata</i> <i>Deschampsia cespitosa</i> <i>Carex simulata</i>	<i>Poa pratensis</i> <i>Phleum pratense</i> <i>Agrostis gigantea</i> <i>Alopecurus pratensis</i> <i>Agrostis stolonifera</i>	<i>Cardamine cordifolia</i> <i>Fragaria vesca</i> <i>Angelica ampla</i> <i>Equisetum arvense</i> <i>Geum macrophyllum</i> var. <i>perincisum</i>	<i>Cirsium arvense</i> <i>Taraxacum officinale</i> <i>Trifolium hybridum</i> <i>Trifolium repens</i> <i>Hieracium aurantiacum</i>
Wet meadow	<i>Salix planifolia</i> <i>Salix petrophila</i> <i>Salix reticulata</i> var. <i>nana</i> <i>Potentilla fruticosa</i> <i>Betula glandulosa</i>	<i>Picea engelmannii</i> var. <i>engelmannii</i>	<i>Carex scopulorum</i> <i>Carex aquatilis</i> <i>Deschampsia cespitosa</i> <i>Carex simulata</i> <i>Carex utriculata</i>	<i>Phleum pratense</i> <i>Poa pratensis</i> <i>Agrostis gigantea</i> <i>Poa compressa</i> <i>Bromus inermis</i>	<i>Bistorta vivipara</i> <i>Artemisia scopulorum</i> <i>Geum rossii</i> var. <i>turbinatum</i> <i>Trifolium parryi</i> <i>Rhodiola rhodantha</i>	<i>Thlaspi arvense</i> <i>Trifolium repens</i> <i>Rumex crispus</i> <i>Taraxacum officinale</i> <i>Nasturtium officinale</i>
Fen	<i>Salix planifolia</i> <i>Salix wolfii</i> <i>Betula glandulosa</i> <i>Pyrola asarifolia</i> <i>Alnus incana</i> ssp. <i>tenuifolia</i>	<i>Picea engelmannii</i> var. <i>engelmannii</i> <i>Populus tremuloides</i> <i>Pinus contorta</i> var. <i>latifolia</i>	<i>Carex aquatilis</i> <i>Carex utriculata</i> <i>Eleocharis pauciflora</i> <i>Calamagrostis canadensis</i> <i>Carex canescens</i> ssp. <i>canescens</i>	<i>Poa pratensis</i> <i>Phleum pratense</i> <i>Alopecurus pratensis</i>	<i>Pedicularis groenlandica</i> <i>Rhodiola rhodantha</i> <i>Viola palustris</i> <i>Equisetum variegatum</i> var. <i>variegatum</i> <i>Swertia perennis</i>	<i>Trifolium repens</i> <i>Cerastium fontanum</i> ssp. <i>vulgare</i> <i>Taraxacum officinale</i>

Beaver and ungulate activity

Beaver activity and ungulate activity were ranked on a scale of 0-10 during site visits (**Table 3.2**), with higher values indicating more activity (Schweiger *et al.* 2015). In this paper, we refer to these variables as ‘biotic drivers’, which are distinct from functional group associations specified later in the joint species distribution modeling approach. Presently, beavers are largely functionally absent from RMNP with less than ten known active dam complexes while ungulate populations (elk and moose) are prevalent across the park.

Table 3.2. Beaver and ungulate use rankings from Schweiger *et al.* (2015).

Indicator	Indicator Value	Criteria
Beaver Use	10	Site/Complex has dams, lodges, beaver chewed stems, beaver slides/runways, beaver tracks. More than one feature(s) and more than once.
	7	Site/Complex has dam, lodge, beaver chewed stem, beaver slide/runway, beaver spoor track. More than one feature.
	3	Site/Complex has dam, lodge, beaver chewed stem, beaver slide/runway, beaver spoor track. One feature only.
	0	Site/Complex has no evidence of beaver use.
Ungulate Use	10	Site/Complex has evidence of native ungulate (see, smell, hear), tracks, feces, browse, or beds. More than one feature(s) and more than once.
	7	Site/Complex has evidence of native ungulate (see, smell, hear), track, feces, browse, or beds. More than one feature.
	3	Site/Complex has evidence of native ungulate (see, smell, hear), track, feces, browse, bed. One feature only.
	0	Site/Complex has no evidence of native ungulate use.

Human disturbance

A composite human disturbance metric was obtained through field and GIS analyses (Schweiger *et al.* 2015, 2019), based on hydrologic alterations and physical and chemical disturbances within buffers surrounding each site (**Table 3.3**).

Table 3.3. Human disturbance index (HDI) metrics from Schweiger et al. (2015, 2019). Most data are field-based, with just four GIS metrics indicated.

Metric Category	Criteria
Alterations within buffers and landscape context	Average Buffer Width (GIS)
	Land Use in 100 m Buffer
	Percentage of Unfragmented Landscape within 1 km (GIS)
	Riparian Corridor Continuity
Hydrological alterations	Hydrological Alterations
	Upstream Surface Water Retention (GIS)
	Upstream/Onsite Water Diversions/Additions (GIS)
	Floodplain Interaction
Physical/chemical disturbances	Substrate/Soil Disturbance
	Onsite Land Use
	Bank Stability
	Algal Blooms
	Invasive Dominance
	Sediment/Turbidity
	Toxics/Heavy Metals

Water balance variables

A Thornthwaite-type water balance model (Tercek *et al.* 2021) with 1km Daymet climate (Thornton *et al.* 2022) and site-level parameters (soil water holding capacity, shade, slope, and aspect) was used to quantify climate and water balance at each site for each sample period (see **Table B2** for descriptions of all water balance metrics). Only three water balance predictors were used in analyses to avoid parameterizing models with highly correlated predictors. These metrics were: mean annual precipitation, mean annual temperature, and climatic water deficit and were first identified by a series of preliminary linear regressions using water balance metrics to predict plant cover, which were then subject to AIC model selection and paired with regressions of water balance predictors together to assess correlation amongst predictors. To show coarse trends in these three variables across sites, simple linear regressions were fit to annual climate data summaries from 1980-2021 (**Fig. 3.1**).

Sensitivity to change

A series of linear regressions were used to assess changes in Shannon diversity and relative cover of functional groups across the sampling period. In each model, an interaction of site by year was specified. Relative cover responses were square root transformed to ensure the data met assumptions of normality. Separate models for Shannon diversity were run for each

wetland type. For relative cover, separate models were run for each functional group-wetland type combination.

To establish that riparian, wet meadow, and fen sites were indeed functionally different, and to visualize the relative changes in functional group composition through time in these sites, an analysis of similarities (ANOSIM) and non-metric multidimensional scaling (NMDS) was used.

Drivers of plant community composition and functional group associations

A series of linear models were run to detect changes in relative cover in response to changes in mean annual precipitation, mean annual temperature, and climatic water deficit throughout the sample period. In each of the three models, a fixed effect of wetland type and an interaction between functional groups and the water balance metric was specified.

To identify the drivers of functional group dynamics with the complete suite of environmental and biotic variables of interest, we applied joint species distribution models via the hierarchical modeling of species communities (HMSC) approach (Ovaskainen *et al.* 2017b). For each wetland type, this entailed first determining functional group responses associated with environmental and biotic drivers and then partition remaining variance due to random effects and discern functional group associations. We fitted the HMSC models assuming the default priors with a normal distribution. We used four replicate MCMC chains, sampling the posterior distribution each with 150,000 iterations after the first 50,000 iterations were discarded. Posterior samples were then thinned by 200 to yield 1,000 posterior samples per chain, yielding 4,000 posterior samples in total.

In all models, we included a random effect of site and year. We also included fixed effects of slope, aspect, elevation, and soil water holding capacity that did not vary over the entire sampling period. Additionally, we included fixed effects of human disturbance, beaver activity, ungulate activity, mean annual precipitation, mean annual temperature, and climatic water deficit that varied with each visit period. For the water balance variables, site specific

means were obtained for each sample period: early (2007-2010), middle (2011-2014), and late (2015-2021).

In terms of the ecological relevance that is less apparent for some of these variables, climatic water deficit and soil water holding capacity are directly related to plant-available water sources, quantifying the amount of water plants could use if it were available and the amount of water soils can retain (Thornwaite & Mather 1955; Tercek *et al.* 2021), related to retention of water throughout the course of seasonal drydown as precipitation becomes more sparse. Slope, although not a direct metric of water availability, serves as a key control on the timing and quantity of drainage in these high elevation wetlands (Gage & Cooper 2013), which are often situated in glaciated valleys.

After functional group occurrences were modeled in response to environmental and biotic drivers, residual variation in each HMSC wetland type model was used to indicate pairwise functional group associations. These associations were evaluated based on 95% credible intervals on posterior support values. Model convergence was assessed by visual assessment of the trace plots and by computing potential scale reduction factors and effective sample sizes. Model predictive performance was assessed by calculating RMSE (root mean square error) and R^2 (coefficient of determination). We utilized the variance partitioning approach from Ovaskainen *et al.* (2017) to distinguish variance explanation from fixed vs. random effects.

All statistical analyses were performed in R (R Core Team 2021). The *vegan* package was used to calculate Shannon Diversity and to ordinate and test for differences in plant community composition and environmental and biotic covariates across wetland types (Oskanen *et al.* 2022). The *car* package (Fox *et al.* 2022) was used to calculate the significance of linear regression predictors. Finally, the *Hmsc* package was used for the joint species distribution models (Tikhonov *et al.* 2022).

Results

Water balance trends

Across 1980-2021, there was a decrease in mean annual precipitation at a rate of 1.7mm per year ($R^2=0.006$, $p=0.001$) and an increase in both mean annual temperature at a rate of 0.04 C per year ($R^2=0.04$, $p<0.0001$) and climatic water deficit at a rate of 1.2 mm per year ($R^2=0.02$, $p<0.0001$) (**Fig. 3.2**; total $N=1,512$, with 42 annual means across 36 sites). Site-level trends through time generally showed the same trends as the cross-site trends (**Fig. B1**).

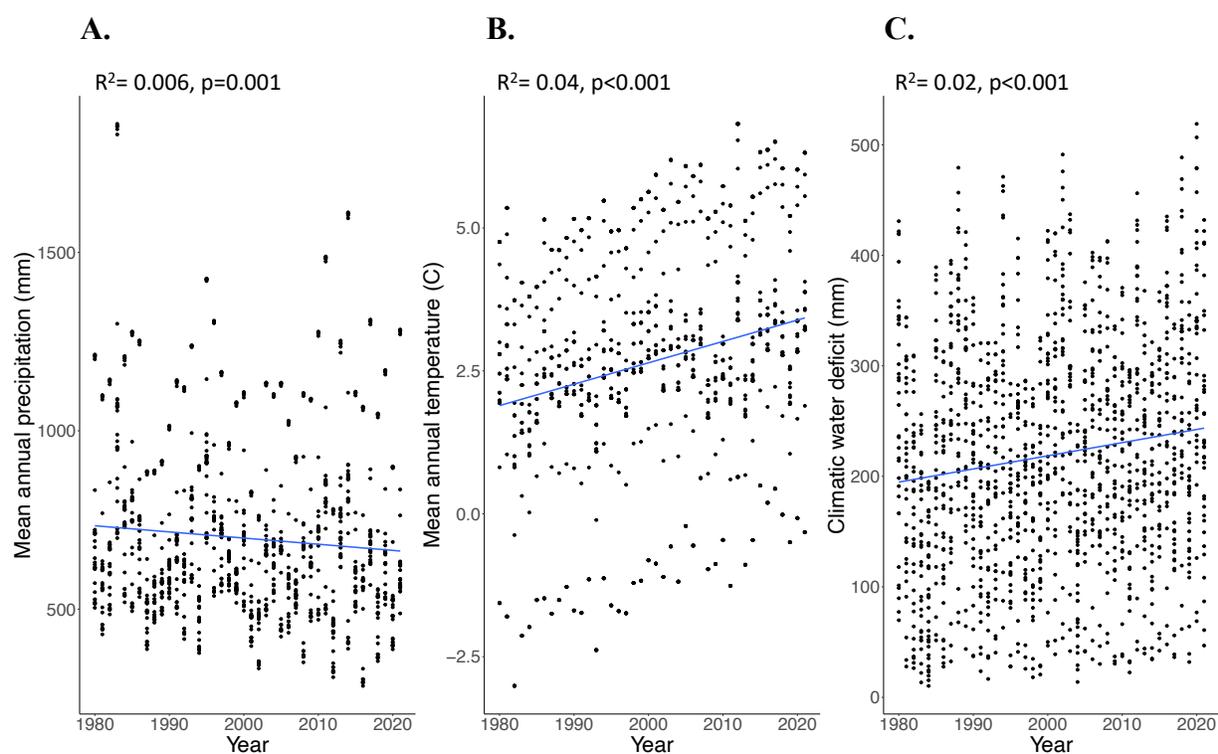


Figure 3.2. Time series of mean annual precipitation (A), mean annual temperature (B), and climatic water deficit (C) across sites. Points represent site-level annual means, with 42 years per site for a total of 1,512 data points given 36 sites.

Sensitivity to change

Across the most recent decade of sampling, out of the eighteen functional group-wetland type combinations, six had relatively stable cover (no significant main effect of year, $p>0.05$), three had no significant changes due to extremely low abundances (no linear models fit), and nine had significant changes in cover (significant main effect of year, $p>0.05$) (**Fig. 3.3**, **Table**

B3 for all model statistics). Notable significant changes in riparian sites, with a significant main effect of year ($p < 0.05$), included an increase in native graminoids, non-native graminoids, and native trees and a decline in native shrubs. Notable significant changes in wet meadow sites, with a significant main effect of year ($p < 0.05$), included an increase in native graminoids and native shrubs. Notable significant changes in fen sites, with a significant main effect of year ($p < 0.05$), included an increase in native shrubs and native forbs. Most models indicated that sites within each functional group-wetland type combination had variable responses in cover, with a significant interaction between site and year in all but seven models. There was high explanatory power in each linear model ($R^2_{\text{average}} = 0.78$, **Table B3** for all model statistics).

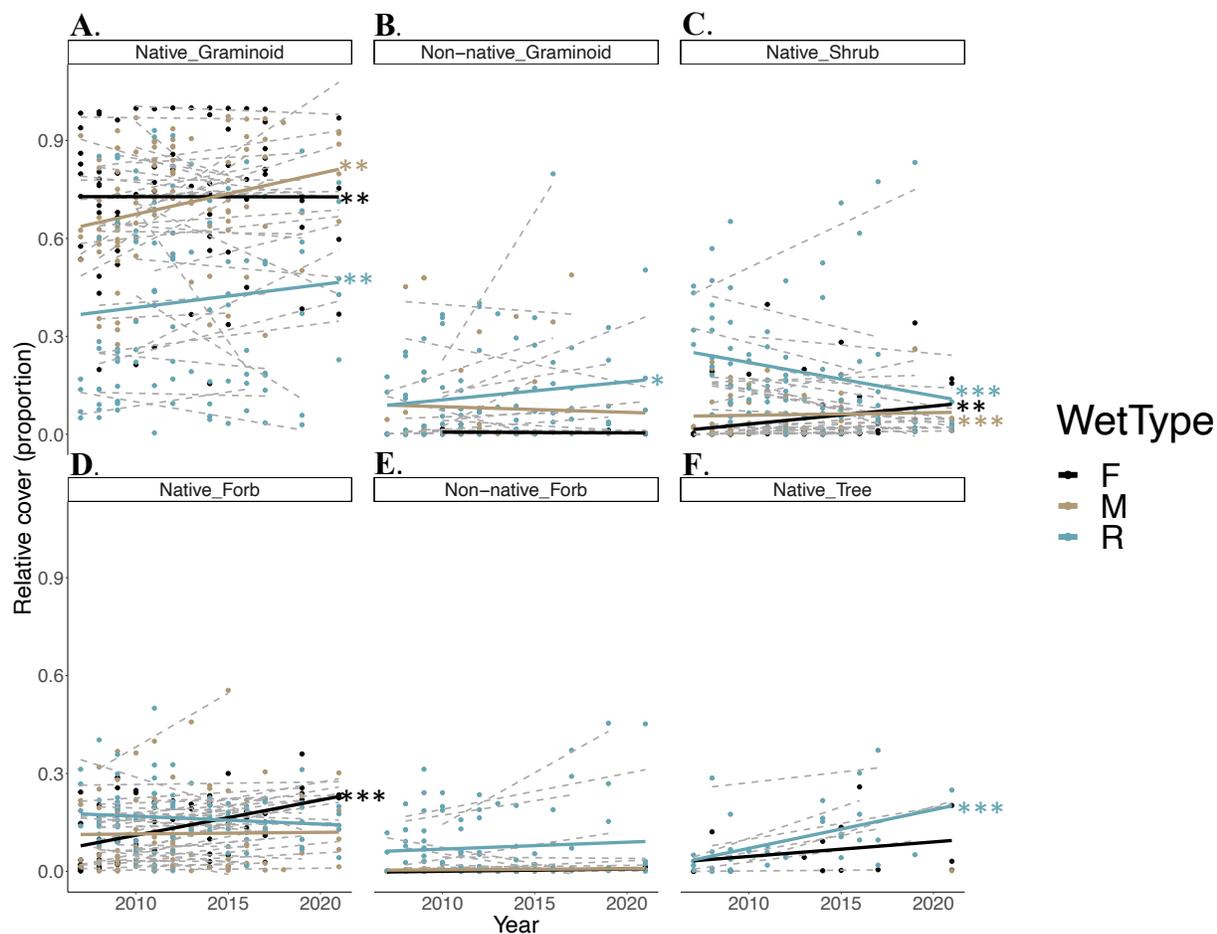


Figure 3.3. Relative cover by functional group (facets) and wetland type (colors) across years (three sampling events per site for a total of 108 events across 36 sites). Colored lines show mean trends across each functional group-wetland type combination, while grey dashed lines show site trends. Asterisks denote significance for a main effect of year where ‘***’ indicates $p=0.001$, ‘**’ indicates $p=0.01$, and ‘*’ indicates $p=0.05$.

Shannon diversity remained relatively stable in riparian ($R^2=0.81$, $p=0.0004$, $\text{slope}_{\text{riparian}}=0.02$) and wet meadow sites ($R^2=0.85$, $p=0.02$, $\text{slope}_{\text{meadow}}=0.05$). Fens, however, had notable increases in Shannon diversity ($R^2=0.88$, $p=0.0002$, $\text{slope}_{\text{fen}}=1.3$) (**Fig. 3.4**). In each of these models, there were no significant site by year interactions ($p>0.05$).

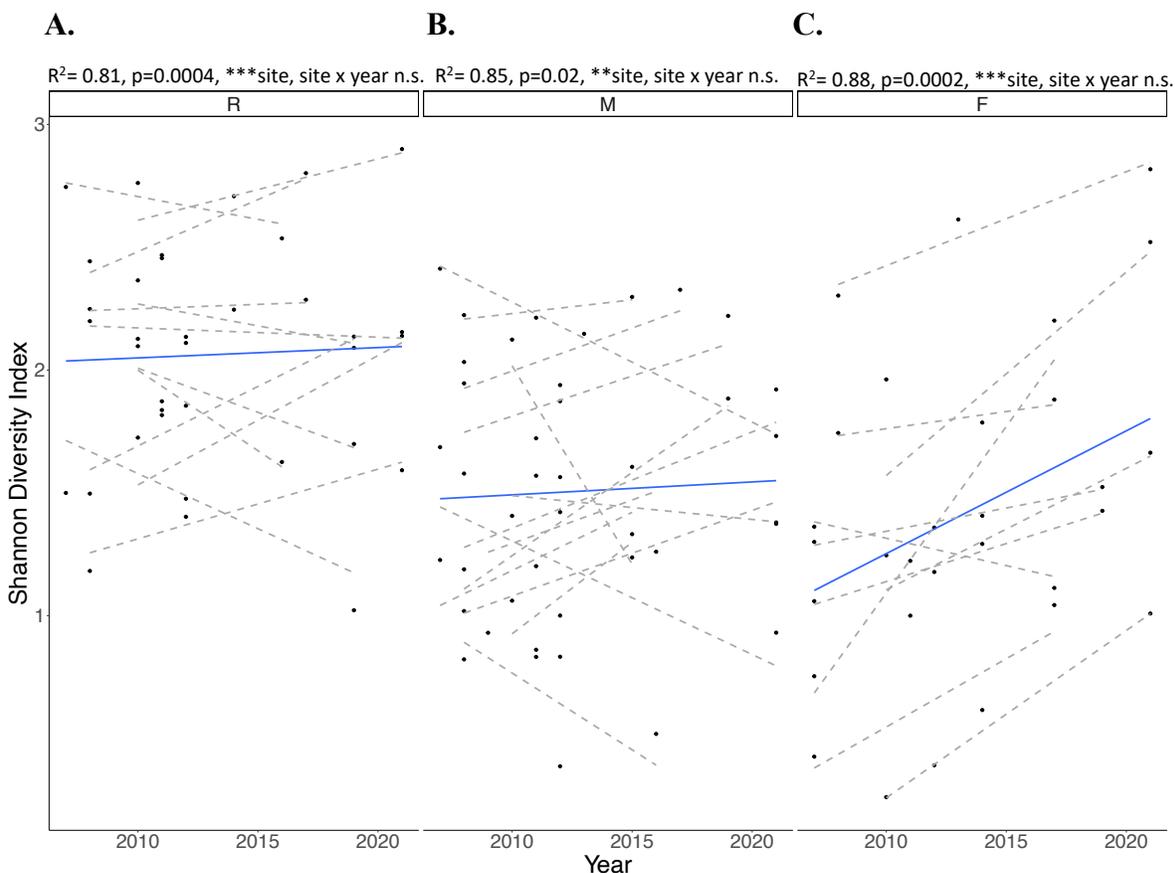


Figure 3.4. Shannon diversity index across wetland types (facets: **A**: riparian, R; **B**: wet meadows, M; **C**: fens, F). Blue lines show mean trends across sites, while grey dashed lines show site trends. While fens had notable increases in Shannon diversity at a rate of 1.3 per year, Shannon diversity in riparian and meadow sites was relatively stable ($\text{slope}_{\text{riparian}} = 0.02$, $\text{slope}_{\text{meadow}} = 0.05$). There were no significant site by year interactions ($p > 0.05$).

The ANOSIM confirmed that riparian, meadow, and fen communities, even despite changes through time, were significantly different from one another (**Fig. 3.5**; $R = 0.17, p < 0.001$; NMDS stress=0.1). Parallel to the previous linear models (**Fig. 3.3**), the greatest functional change across wetland types occurred in riparian sites (**Fig. 3.5**, length of loadings).

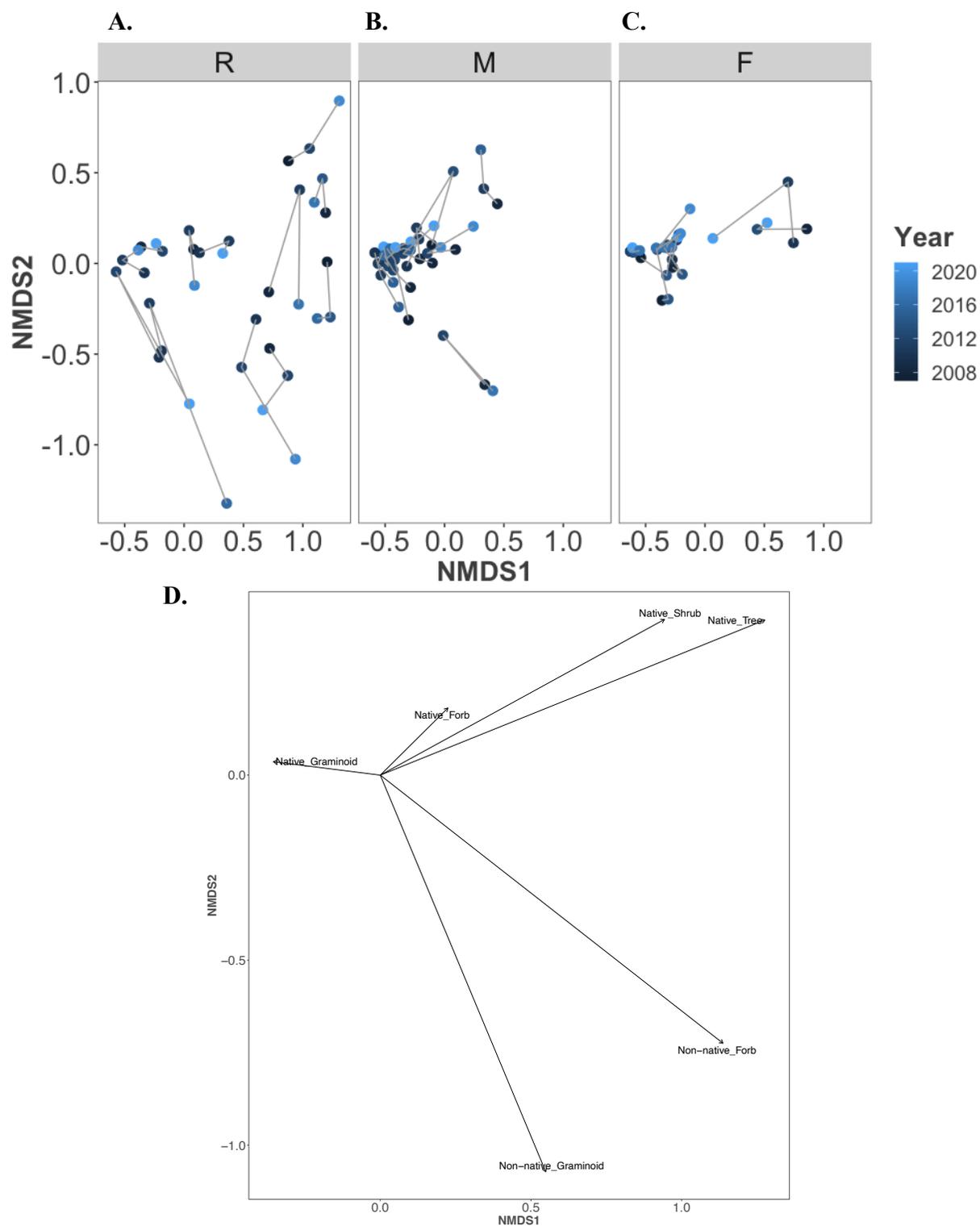


Figure 3.5. Non-metric multidimensional scaling (NMDS) of functional group cover across wetland types (facets: **A:** riparian, R; **B:** wet meadows, M; **C:** fens, F) through time (colors represent years) (NMDS stress=0.1). Lines connect sites through time. Functional groups are plotted as loadings in **D**.

Drivers of plant community composition

While there weren't pronounced changes in relative functional group cover across changes in mean annual temperature and climatic water deficit during the study period, there were more apparent relative cover changes in response to changes in mean annual precipitation (Fig. 3.6, Fig. B3 for all water balance and biotic variables used in HMSC analyses). Namely, there was a marginally significant interaction between functional group change in relative cover and change in precipitation (LMM, $R^2=0.08$, $p=0.09$), mostly driven by native graminoids, the most abundant functional group.

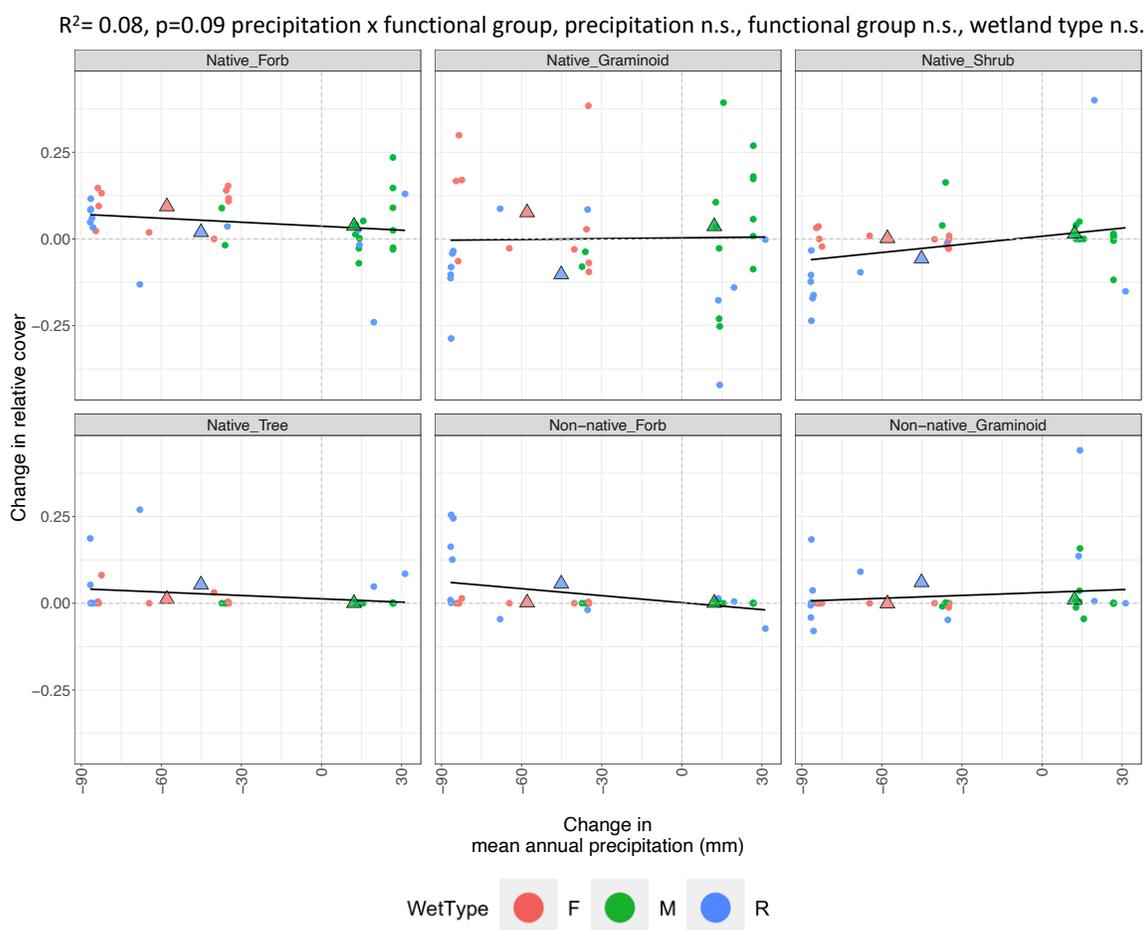


Figure 3.6. Change in relative cover (y-axes) across the change in precipitation (x-axes) by functional groups (panels) and wetland types (colors). Triangle shaped points show functional group means. 0 change values are indicated by horizontal and vertical grey dashed lines. More stark cover changes in association with changes in precipitation occur with steeper linear fits and/or when points have high deviation from 0 along the y-axis (large changes in cover) at the extremes of the x-axis (large decreases or increases in precipitation).

The HMSC models indicated that there were different combinations of environmental controls on functional group distributions across wetland types (**Fig. 3.7, Fig. B3** for raw data). These responses were determined by 95% credible intervals on posterior support values.

In riparian sites, the strongest abiotic driver of plant community composition was slope, with non-native forbs and non-native graminoids showing negative responses to slope, occurring in areas with lower slopes. Most functional groups responded negatively to climatic water deficit and soil water holding capacity, with the exception of native graminoids which occurred in sites with high climatic water deficit and soil water holding capacity. Both non-native graminoids and non-native forbs were associated with southeast aspects and low human disturbance. Non-native forbs were strongly associated with low mean annual temperature, mean annual precipitation, and climatic water deficit. Native trees were associated with northeast and southwest aspects and high mean annual precipitation. Lastly, in terms of biotic drivers, non-native forbs were associated with high ungulate activity. Native shrubs were commonly found in areas low beaver activity and high human disturbance.

In wet meadows, non-native graminoids, native shrubs, native graminoids, and native forbs were associated with low mean annual precipitation. In terms of other predictors related to water availability, native forbs were associated with high soil water holding capacity, while native forbs, non-native forbs, and native trees were associated with lower climatic water deficit. Native graminoids were positive associated with ungulate activity and negatively associated with mean annual temperature and beaver activity. Non-native forbs were also negatively associated with beaver activity.

In fens, non-native graminoids were associated with southeast aspects and had positive responses to human disturbance, mean annual temperature, and soil water holding capacity. Similarly, non-native forbs had positive responses to increasing human disturbance and mean annual temperature. Native shrubs were associated with areas with high human disturbance. Lastly, there were no significant biotic drivers of composition in fens.

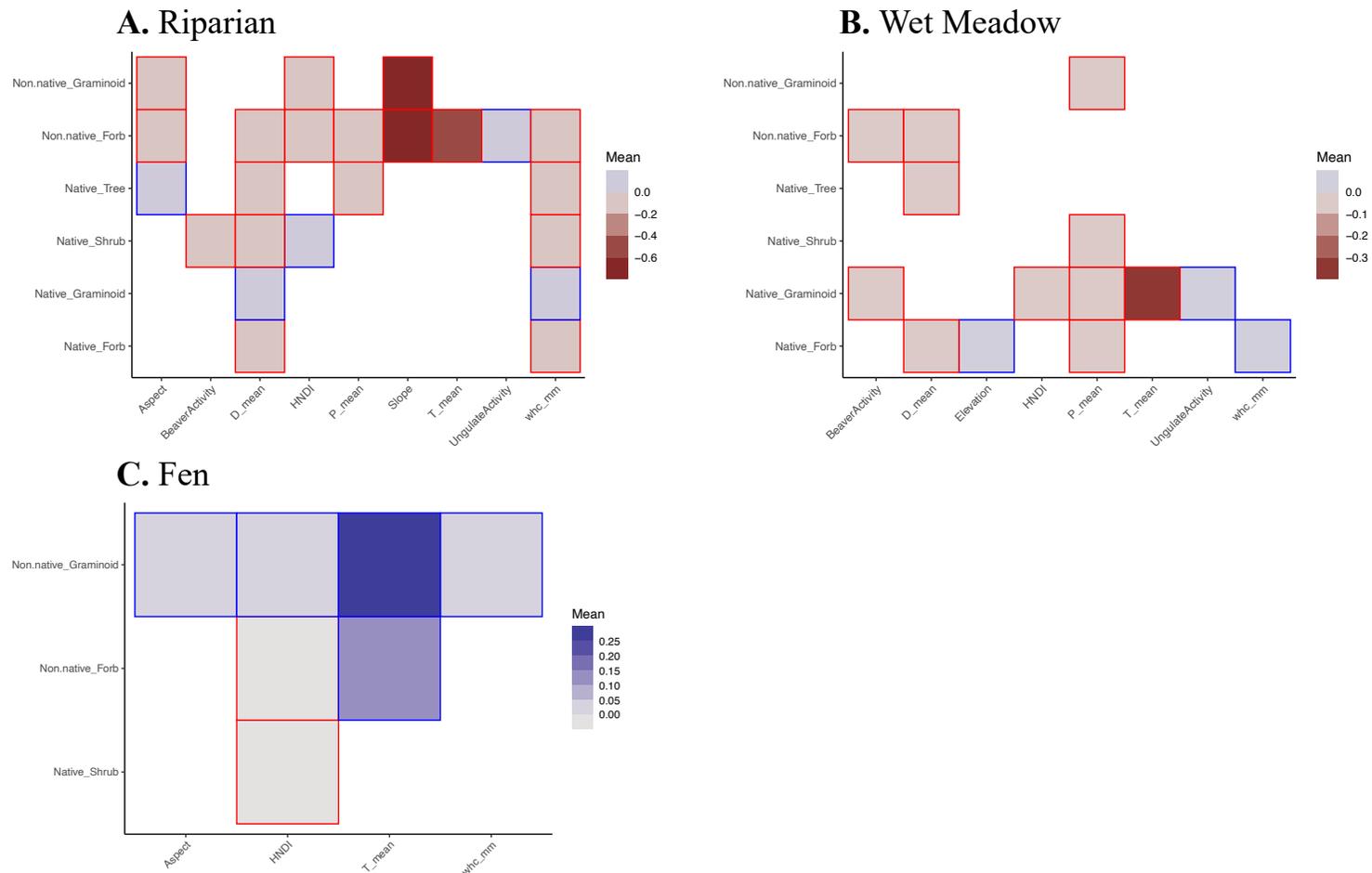


Figure 3.7. Mean effects of biotic and environmental drivers (x-axes) on functional groups (y-axes) across wetland types (facets: **A:** riparian; **B:** wet meadows; **C:** fens), determined by 89% credible intervals. X-axis environmental predictors are: **Aspect**, **BeaverActivity**: beaver activity (following Table 2), **D_mean**: climatic water deficit (mm), **HNDI**: human disturbance index (following Table 3), **P_mean**: mean annual precipitation (mm), **Slope**, **T_mean**: mean annual temperature (C), **UngulateActivity**: ungulate activity (following Table 2), and **whc_mm**: soil water holding capacity (mm). Blue colors indicate positive relationships while red colors indicate negative relationships, with all colors indicating significant ($p < 0.05$) relationships. Associations that are not depicted by colored squares were not significant.

HMSC variance partitioning & model fit

Across functional groups, there was moderate explanatory power in each HMSC model (mean: $R^2_{\text{riparian}}=0.85$, $R^2_{\text{wet meadow}}=0.72$, $R^2_{\text{fen}}=0.86$). Climate and water balance variables across wetland types were consistent top variance predictors (**Table 3.4**, bolded variables), indicating key montane wetland environmental filters. These included soil water holding capacity, mean annual temperature, mean annual precipitation, and climatic water deficit. The two biotic drivers – beaver and ungulate activity – while not yielding as much explanatory power across models, still indicated more of an effect on riparian and fen composition. See **Fig. B2.** for visual representation of variance partitioning.

Table 3.4. Proportion of variance explained by all predictors in all HMSC models. Bolded variables indicate top variance predictors within each wetland type model.

Variable	Proportion of variance, riparian	Proportion of variance, wet meadow	Proportion of variance, fen
Soil water holding capacity	0.27	0.03	0.08
Mean annual temperature	0.09	0.13	0.05
Mean annual precipitation	0.06	0.07	0.14
Climatic water deficit	0.12	0.01	0.13
Elevation	0.06	0.13	0.05
Slope	0.11	0.05	0.03
Aspect	0.06	0.07	0.06
Beaver activity	0.03	0.004	0.02
Ungulate activity	0.01	0.006	0.03
Human disturbance index	0.05	0.03	0.02
<i>Random effect of site</i>	0.11	0.31	0.29
<i>Random effect of year</i>	0.03	0.17	0.09

Functional group associations

There were generally mild associations between functional groups across wetland types, with only a total of nine significant associations across wetland types (**Fig. 3.8**). In riparian sites, there was a significant ($p<0.05$) negative association between native graminoids and non-native

graminoids. In wet meadows, there were significant ($p < 0.05$) negative associations between native graminoids and native forbs and native graminoids and native shrubs. In fens, there was a significant ($p < 0.05$) negative association between native graminoids and three other functional groups: native shrubs, non-native graminoids, and non-native forbs. Additionally, there were positive associations between non-native graminoids and non-native forbs, native shrubs and non-native-graminoids, and native shrubs and non-native forbs in fens.

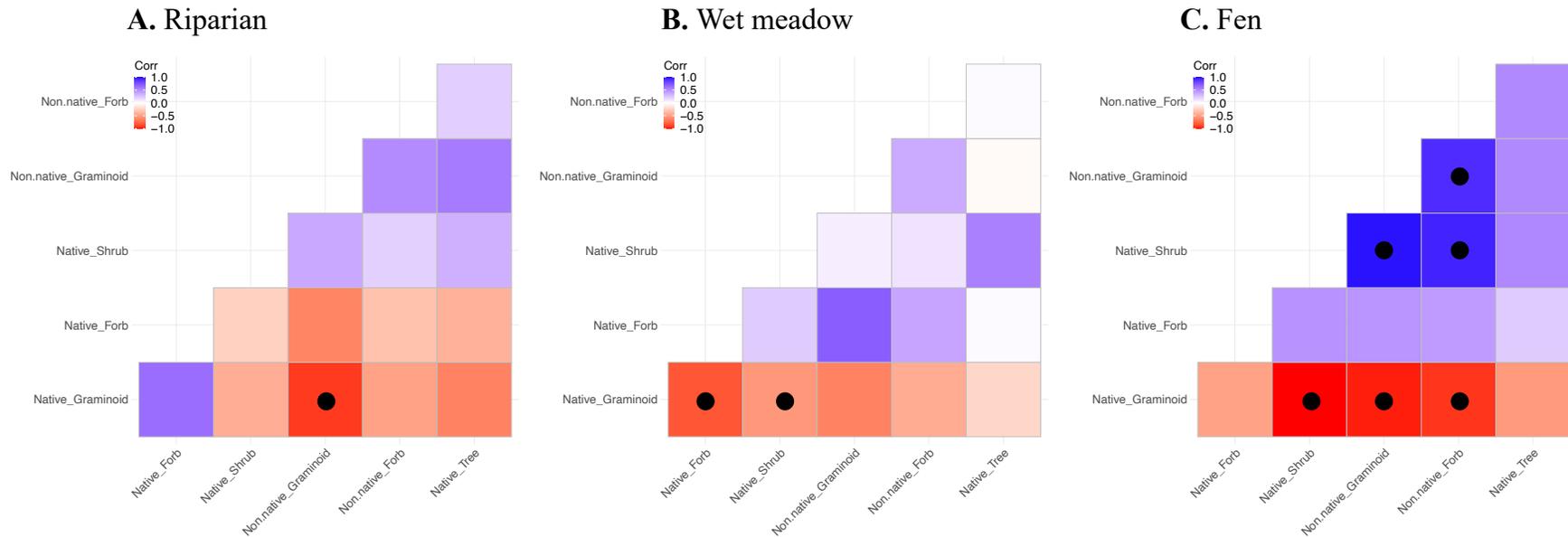


Figure 3.8. Functional group correlation matrices across wetland types (facets: **A:** riparian; **B:** wet meadows; **C:** fens). Each facet represents associations across space (sites) and time. Correlations (species associations) range from -1 (red) to 1 (purple) with darker colors indicating stronger associations. Correlations are shown with a 95% credible interval threshold and were calculated after variance partitioning with environmental drivers. Significant ($p < 0.05$) relationships are indicated by central black dots in correlation plot tiles.

Discussion

Overview

In line with other studies documenting warming and drying trends in the Southern Rocky Mountains (Anderegg & Diffenbaugh 2015; Zhang *et al.* 2021), our sites have experienced a decrease in mean annual precipitation and both an increase in mean annual temperature and climatic water deficit over the past four decades. The high explanatory power of these water balance variables as predictors in our HMSC models indicate that these drivers can have an impact on seasonal productivity, specifically affecting the timing and rates of transpiration and photosynthesis, that ultimately can contribute to changes in wetland plant community composition. This is in line with long-standing research that specifies water balance as a key control on plant productivity (Thornwaite & Mather 1955; Stephenson 1990). Moreover, all HMSC models indicated an environmental or biotic driver that directly or indirectly characterizes water availability, highlighting importance of water availability in structuring wetland plant communities in RMNP. Overall, in terms of assessing the magnitude of change in relative cover across climatic water balance predictors, we found some evidence that changes in precipitation were associated with greater changes in relative cover across the sample period.

Riparian wetlands

As expected, riparian sites had the greatest compositional change, with a shift towards increasing prevalence of native graminoids, non-native graminoids, and native trees and a decline in native shrubs. Species diversity was also the highest yet most stable in riparian sites compared to fens and wet meadows. Beaver and ungulate activity were not top predictors of most functional groups despite beaver, elk, and moose activity being the most concentrated in this wetland type (Schweiger *et al.* 2019). Instead, climatic water deficit and soil water holding capacity were the dominant environmental drivers of functional group composition. The trend of increasing non-native forbs with increasing ungulate activity could be a response to soil compaction, understory disturbance, soil nutrient changes and/or increased light availability with

less abundant overstory (shrub) cover (Kauffman *et al.* 2023). This positive response of non-native forbs with this disturbance is in line with invasion literature showing that invading species are often disturbance opportunists, growing fast and making use of resources after disturbance (Zedler & Kercher 2004; Catford *et al.* 2012; Montesinos 2022), whether disturbance was from the direct removal of native biomass through ungulate browsing, or via indirect effects such as with the trampling of understory flora and/or removal of overstory canopies. While the trend of co-occurrence of native shrubs with high human disturbance is in line with the collocation of riparian sites with roads and foot traffic use, an association between native shrubs and low beaver activity was counterintuitive. This could be partly due to the fact that, by the time the sampling events occurred, beaver activity had been largely lost from most sites, with only 8 of 108 sampling events having some beaver activity. In order to more accurately assess the responses of functional groups to beaver activity, targeted monitoring of sites in the future with either simulated or authentic beaver activity would be required.

Wet meadows

While wet meadows had an increase in native graminoids and native shrubs, they did not undergo much compositional change, remaining dominated by native forb and native graminoids. Additionally, wet meadows had intermediate levels of species diversity that were maintained through time. Non-native graminoids, native shrubs, native graminoids, and native forbs were all associated with low precipitation. The association of native forbs with high soil water holding capacity and low climatic water deficit is opposite of the findings of Schweiger *et al.* (2016), which found that native forbs in these systems were associated with less mesic conditions. This difference could be due to the fact that in our approach, we focused on a subset of sites with high temporal resolution and included more recent years of data. Additionally, we modeled wetland types separately in a different modeling framework (joint species distribution models). Native graminoids were associated with differences in both beaver and ungulate activity, increasing in response to ungulate activity, and decreasing in response to beaver activity. The response to ungulate activity could be associated with sites where native shrub

cover decreased, likely due to ungulate browse, resulting in available resources for graminoid species. The beaver activity trend, however, is likely due to the relatively homogenous lack of any beaver activity described previously with the riparian model outputs.

Fens

Fens, relative to riparian and wet meadow sites, had the least amount of functional change. However, some fen sites did have an increase in native shrubs and native forbs. Additionally, fens in general had a substantial increase in species diversity across time, though fens generally remained less speciose than riparian wetlands and wet meadows. There were variable drivers of non-native graminoid and non-native forb cover in fens even though abundance of non-natives in fens was extremely low. In line with other studies, non-native graminoids and non-native forbs were associated with increased human disturbance and warmer temperatures (Zedler & Kercher 2004; Walther *et al.* 2009). Non-native graminoids were also associated with sites that have high soil water holding capacity. Similar to the riparian model outputs, native shrubs had a positive association with human disturbance, for likely the same reasons stated previously. Lastly, the fact that there were no significant biotic drivers of fen functional groups was not surprising given that fens: a) have very strong hydrologic and edaphic controls resulting from persistently high water tables that retard the decomposition of organic matter, and b) mostly lack anthropogenic and natural disturbances compared to wet meadows and riparian wetlands (Schweiger *et al.* 2015).

Testing for limiting similarity

Functional group associations only indicated two potential instances of limiting similarity, between native graminoids and non-native graminoids in riparian wetlands and fens. However, this is in line with literature showing that empirical examples of limiting similarity are sparse (Symstad 2000; Price & Pärtel 2013; Funk & Wolf 2016). For the most part, functional group associations provided by the HMSC approach indicated that most negative associations between native and non-native functional groups crossed growth form classifications, counter to our expectations. Given this, it is possible that the distribution of plants across these wetland

systems reflects convergences in optimal strategies at the community scale (competitive hierarchies, Herben & Goldberg 2014). However, testing whether limiting similarity or competitive hierarchies structures these communities will require further modeling with trait measurements to quantify and contextualize plant resource use strategies in these communities. Additionally, it is important to note that while associations among functional groups aided in better modeling of community dynamics across these wetland types, these associations cannot be interpreted as definitive species interactions since residual correlations can also emerge from missing environmental covariates (Pollock *et al.* 2014).

Implications

Management of these wetland systems requires quantifying rates and types of ecosystem change in order to prioritize concerns. It is apparent that riparian sites are diverging the most from starting conditions, with notable increases in non-native graminoids that threaten the integrity of the understory plant communities in these systems. Future work to test enclosure and simulated beaver structure interventions in riparian wetlands (e.g., Marshall *et al.* 2013; Zeigenfuss & Johnson 2015), expanding beyond the focus on native shrub recovery to track changes in understory species, would help elucidate functional group responses to improve community-level predictions. Even though wet meadows and fens were relatively stable in terms of functional group composition, it is still essential to continue monitoring these systems, which unlike riparian wetlands, do not currently undergo much active management apart from occasional weed control. Continued monitoring of biotic trajectories with multivariate analyses, as we did with a sample of 36 out of 176 extant wetland monitoring sites in RMNP, can help identify sites more vulnerable to change to help inform management decisions.

Altogether, the HMSC functional group responses to abiotic and biotic drivers and associations across functional groups highlight possible prevalent plant community changes that could be enforced with similar plant responses to directional change in environmental and biotic drivers that have occurred within the study period. It should be noted, however, that although these results elucidate likely community assembly dynamics in a subset of sampled RMNP

wetlands, they should not be interpreted as universal wetland community assembly processes. Repeated analyses with more temporally and spatially comprehensive data would allow for detection of possible threshold shifts in plant community composition due to biotic and environmental drivers or functional group associations. For example, it is possible that climatic water deficit thresholds could be passed in the future to the point where warming temperatures could start to become more important in structuring these communities that seem to currently be predominately structured by water availability. Similarly, there could be instances where repeated years of strong negative functional group negative associations serve as a warning sign for competitive exclusion of a certain functional group at sites.

The multi-faceted approach we took here with linear models, ordination, and HMSC analyses demonstrate a robust toolkit for understanding patterns large spatiotemporal ecological monitoring datasets. With a growing number ecosystems facing degradation pressures (IPBES *et al.* 2018) and with ubiquitous climate change drivers that can outpace plant responses (Loarie *et al.* 2009), it is essential to harness these approaches in a timely manner to identify critical priority areas for wetland conservation and restoration before areas might shift in composition past levels that are easily addressed by conventional management practices.

CHAPTER IV

Testing insurance and niche complementarity concepts in a stage 0 riparian restoration project: Functional diversity improves stability in productivity while soil moisture controls early invasion trends

By Isabel de Silva, Deborah Hummel, Jessica Olson, Yana Sorokin, and Katharine N. Suding

Abstract

Functional resilience to environmental change and functional resistance to invasion, despite being well-developed concepts in ecology, generally lack applied evidence showing that these theories can be operationalized to improve ecological restoration outcomes. In a stage 0 riparian restoration experiment we tested the effectiveness of designing a restoration project using a functional trait-based approach that incorporates insurance and niche complementarity concepts. We experimentally varied water availability (via platform elevation) and plant community types (upland riparian, lowland riparian, and an upland-lowland mixture) to test whether functionally diverse treatments: 1) conferred stability in productivity and 2) reduced invasion by increased niche occupation and complementarity. We found that while our three community types were not very functionally divergent from one another, showing generally acquisitive resource use strategies, lowland communities had higher cover in high water availability treatments (low elevations) while upland communities had marginally higher cover in low water availability treatments (high elevations). We found some supporting evidence of insurance where variability in productivity was reduced with higher levels of functional diversity. In contrast, we did not find support for functional diversity, namely niche overlap with non-native species, as an invasion deterrent. Instead of functional diversity driving invasion trends, we found that the abiotic driver of soil moisture was the most important factor affecting the degree of invasion, with higher invasion in drier conditions. Altogether, this research shows that, in this stage 0 restoration setting, the most desirable treatment outcome, yielding high native

cover and low invasion in the immediate years following restoration, was generated by the combination of planting and seeding lowland specialist species and increasing water availability.

Introduction

In an era of unprecedented climate change, disturbance, and species invasions, land managers face the enormous task of restoring degraded areas using management strategies that consider both historical reference conditions and future trajectories (Millennium Ecosystem Assessment 2005; Suding *et al.* 2015). Although there are many arguments why restoring historical species assemblages might not be an appropriate restoration goal in a changing environment (Hobbs *et al.* 2009; Schuurman *et al.* 2022), there has been little progress in the application of alternatives that still adhere, to some extent, to the fundamental tenants of stewardship and conservation (but see Seastedt *et al.* 2008 for examples). Two key but often unaddressed parts of this include designing management interventions to directly promote both functional resilience to environmental change and functional resistance to invasion challenge (for examples targeting functional resilience or resistance, see Young *et al.* 2009; Laughlin *et al.* 2017).

Restoring ecosystems to promote functional resilience to environmental change often involves a more specific goal of maintaining desired ecosystem functions and services while also allowing the system to track a changing environment (Dudney *et al.* 2018). It has been long thought that biodiversity, be it on the species or functional group level, acts as an insurance mechanism for ecological function because different species respond differently to environmental fluctuations (Gonzalez & Loreau 2009). This phenomenon is based on the idea that compensatory dynamics occur where different species do well in different environmental conditions such that variability in species responses across variable environmental conditions leads to a stabilization of the overall aggregate function of the system (McNaughton *et al.* 1977; Walker 1992; Tilman *et al.* 2006; Loreau *et al.* 2021). One way to translate the insurance concept to restoration projects is to plant a

functionally diverse mixture of species with the expectation that this would result in more stable functioning (lower variability in ecosystem function), as the fluctuations in species abundances will buffer the system across temporal environmental variability.

Niche complementarity is another central tenant in ecology, where coexistence of different species is aided by the partitioning of resources or, in other words, the differentiation of species' resource acquisition strategies. One example of niche complementarity is when species have different rooting depths in a community, leading to utilization of different water sources (Silvertown *et al.* 2015). At the community scale, these types of contrasts in resource use across species can broaden the extent to which different resources are being used (Funk *et al.* 2008). Importantly for restoration, recent work points to the possibility of optimizing niche complementarity (often via functional diversity) as a means to exclude non-native, undesirable plant species from restoration projects (Byun *et al.* 2020, 2023).

While the concepts of insurance and niche complementarity have been well established in theoretical work, we still lack evidence for these dynamics contributing to successful outcomes in applied settings (for exceptions see van Zuidam *et al.* 2019; Lemanski *et al.* 2022). One approach to managing for resilience and resistance in applied settings is to employ functional traits to specifically target desirable response traits and ecosystem functions, and also preempt resources from non-native species (Mwangi *et al.* 2007; Suding *et al.* 2008; Laughlin 2014). For example, in riparian systems susceptible to flood disturbances, a review by Catford & Jansson (2014) highlighted a suite of functional traits that could promote resilience, including: fast growth rates, runner- or rhizome-based lateral spread, and large and persistent seeds in the seedbank. Another example from Price & Pärtel (2013), who conducted a meta-analysis aimed at assessing the effectiveness of using limiting similarity to reduce invasion posited that some successful suppression of invaders they found across studies could be linked to specific traits of the native groups, in this case native forbs having high leaf area. Alternatively, there could be instances where it is not a certain set of species or traits that promote resilience, but instead a diversity of traits that contribute to desired ecosystem functioning (Díaz & Cabido 2001). Further, even though there are instances where an optimal set of resource use

strategies or a diversity of resource use strategies confers resilience or resistance, there are also instances where strong, sometimes interacting abiotic controls mostly dictate ecosystem responses (van der Plas *et al.* 2020).

Here, we test the effectiveness of using a functional trait-based approach that incorporates insurance and niche complementarity concepts into the design of a restoration project. We created a riparian restoration project, experimentally varying: 1) the type of planting (species representative of upland riparian, lowland riparian, or a mixture of both riparian zones) and 2) water availability (via planform elevation) to ask three questions:

Q1 - Traits and Function: How do species functional traits vary along a riparian planform and do these differences relate to function (production) across wet to dry environmental conditions?

Regarding **Q1**, we hypothesized that upland riparian species have more conservative, “slow” traits, typical of resource poor environments, while lower riparian species have more acquisitive, “fast” traits typical of resource rich environments (Grime 1977; Wright *et al.* 2004; Reich 2014; Pan *et al.* 2020). In dry conditions, upland riparian species accumulate the highest relative biomass, while under wet conditions lower riparian species accumulate the highest relative biomass.

Q2 - Insurance: Does geomorphic complexity and the corresponding hydrologic variability across the channel planform, when paired with functional diversity, promote stability in biomass production and productivity?

In terms of **Q2**, we hypothesized that increased functional diversity afforded by mixed community treatments buffers productivity across water availability gradients, with lower variability in both biomass and greenness as a function of variability in water availability compared to lowland and upland riparian community types.

Q3 - Niche Complementary: Does a co-planted, mixed upland-lowland riparian plant community reduce invasion by increased niche occupation and complementarity?

Lastly, in regards to **Q3**, we hypothesized that niche space of non-native species at the field site overlaps most with mixed upland-lower riparian treatments, regardless of water availability, conferring the most invasion resistant restoration strategy. Alternatively, if invasion trends are not

explained by the degree of niche overlap or species or functional diversity, we hypothesized that invasion would be best explained by water availability, with higher invasion in drier conditions.

Methods

Study site

Our study site is located at approximately 1,740m elevation in a plains-foothills transition of the Front Range of Colorado (USA). It sits within a larger stream restoration project area along Left Hand Creek that was designed with the main objective restoring a ~16,982m² area to a stage 0 planform (*sensu* Cluer & Thorne 2014) with anastomosing channels and beaver dam analogs.

Experimental design

Prior to planting, the restoration site underwent grading using excavators to restore historical overflow channels and create new ephemeral channels consistent with a stage 0 planform (**Fig. 4.1**). In the fall of 2019, we established factorial treatments in a blocked design, experimentally varying: 1) plant community (three types of plantings: lowland, upland, and mixed lowland-upland native riparian) and 2) water availability via bench elevation (three elevations: at, below, and above ordinary high water [OHW]). In total, there were 27 plots (12m²/plot) (3 blocks x 3 plant community treatments x 3 bench elevations, **Fig. 4.2**).



Figure 4.1. Photograph of the stage 0 planform, with ephemeral channels and beaver dam analogs in view, and the main channel of Left Hand Creek out of view, towards the mountains.

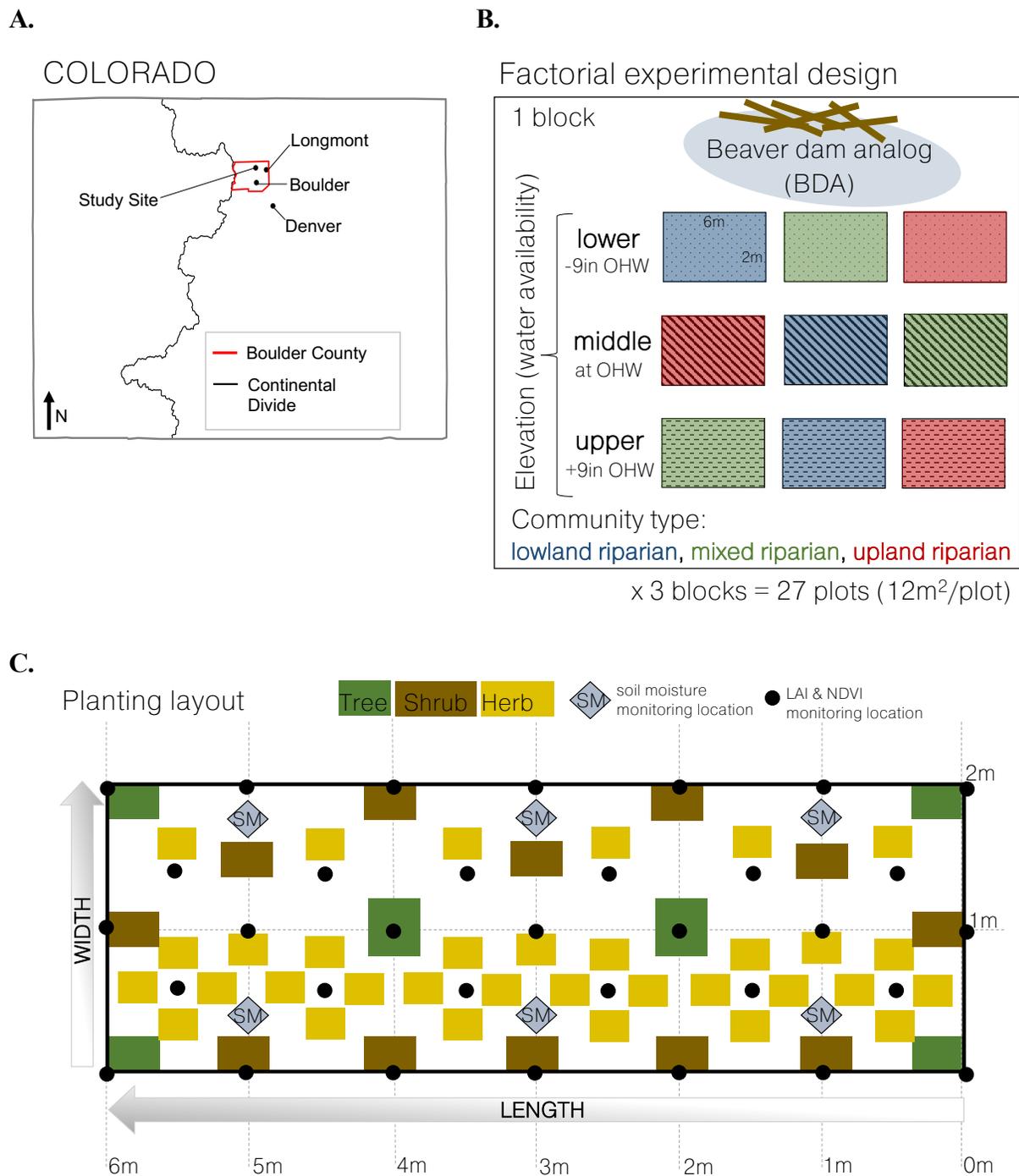


Figure 4.2. A) Map of study site location in Boulder, Colorado. B) Experimental study design showing general layout of one of three replicate blocks. Rows indicate elevation treatments and colors indicate plant community treatments. All blocks are adjacent to a beaver dam analog (BDA). C) Plot layout with trees, shrubs, and herbs indicated by colored squares (spacing not to scale) and soil moisture, NDVI, and LAI monitoring locations indicated by diamonds and black dots, respectively.

The species in the lowland and upland plant community types were selected from species lists made from qualitative observations of local distributions of native species relative to the stream. These plant community types have been used in regional riparian restoration for the last six years, following initial guidance from NRCS Emergency Watershed Protection Program administered through the Colorado Water Conservation Board (Y. Sorokin, *pers comm*). **Table 4.1** details species in each plant community type. Plant material was obtained from a local wetland nursery. Each 12m² plot was planted with a total of six woody species - two tree and four shrub species that were each replicated three times for a total of 18 woody individuals (**Fig. 4.2C**). Additionally, 11 herbaceous species were planted per plot, each replicated three times for a total of 33 herbaceous individuals. Species for each plot were randomly selected from each community type's full species list (**Table 4.1**). A minimum spacing of 2m between trees, 1.3m between shrubs, and 0.3m between herbaceous plants was maintained. Plots were seeded with an average density of 3.6g/m² seed (species lists in **Fig. C1**), corresponding to each community type.

Table 4.1. Species lists for each community type (rows) by growth form (columns).

Community type	Tree	Shrub	Herbaceous
Lowland riparian	<i>Alnus incana</i> <i>Betula occidentalis</i> <i>Cornus sericea</i> <i>Salix amygdaloides</i>	<i>Salix bebbiana</i> <i>Salix exigua</i> <i>Salix irrorata</i>	<i>Asclepias incarnata</i> <i>Calamagrostis canadensis</i> <i>Carex nebrascensis</i> <i>Carex pellita</i> <i>Carex praegracilis</i> <i>Eleocharis palustris</i> <i>Glyceria grandis</i> <i>Helianthus nutallii</i> <i>Iris missouriensis</i> <i>Juncus arcticus</i> <i>Juncus torreyi</i> <i>Panicum virgatum</i> <i>Scirpus microcarpus</i> <i>Verbena hastata</i>
Upland riparian	<i>Acer glabrum</i> <i>Populus angustifolia</i> <i>Populus deltoides</i>	<i>Prunus americana</i> <i>Prunus virginiana</i> <i>Potentilla fruticosa</i> <i>Rhus trilobata</i> <i>Ribes aureum</i> <i>Ribes cereum</i> <i>Rosa woodsii</i> <i>Symphoricarpos occidentalis</i> <i>Artemesia frigida</i>	<i>Carex microptera</i> <i>Carex praegracilis</i> <i>Elymus lanceolatus</i> <i>Erigeron elatior</i> <i>Hesperostipa comata</i> <i>Juncus arcticus</i> <i>Liatris punctata</i> <i>Muhlenbergia montana</i> <i>Pascopyrum smithii</i> <i>Rudbeckia hirta</i> <i>Solidago canadensis</i>

Community composition

Species level percent visual cover estimates for each plot were obtained in June and July of 2021 and 2022 by averaging percent visual cover estimates across smaller subplots (three 2m x 2m subplots) nested within each plot. Total cover of a plot could exceed 100% due to overlapping plant canopies. Due to flooded conditions in the lower bench elevations, compositional surveys took place in August in these plots to allow for understory components to be identified and estimated. Species nomenclature follows Ackerfield (2015). Species origins were determined from the USDA PLANTS Database (USDA, 2022). Native and non-native species lists are in **Tables C2 and C3**.

Climate and soil moisture

Annual climate summaries for planting and sample years (2019-2022) were obtained from NOAA (2023). Soil volumetric water content measurements were measured approximately every two weeks at six locations in each plot (**Fig. 4.2C**) with a modified Campbell Scientific Hydrosense II, following Grinath *et al.* (2019). Since rocky soils prevented the use of conventional soil moisture probes, we installed a set of 12.7cm long galvanized steel nails parallel to one another and flush with the surface of the soil at each of the six monitoring locations within a plot. Steel screws replaced the conventional probes of the handheld sensor and continuous contact with the steel screws and nails was made to take volumetric water content readings. For standing water and saturated readings, the maximum soil moisture measured on site was used (54.3 VWC).

Leaf area index & greenness

Leaf area index (LAI) and greenness (NDVI) were measured every 2-4 weeks at 33 locations in each plot (**Fig. 4.2C**) with a LI-COR LAI-2200c and a Trimble Greenseeker, respectively. Monitoring occurred at every 0.5m plot length increment, with three measurements at whole meter lengths (at 0m, 1m, and 2m widths) and two measurements at half meter lengths (at 0.5m and 1.5m widths). LAI measurements were taken at ground level with a 180° view cap and calibrated according to standard procedure (LI-COR Biosciences 2021). NDVI measurements were collected approximately 4ft above ground level, facing down towards the soil.

Functional traits

Functional trait sampling followed standard protocols from Pérez-Harguindeguy *et al.* (2016) (**Table 4.2** for summary of traits and units). For leaf mass per area (LMA), shoots were clipped, wrapped in a wet paper towel, and placed in a plastic bag within a dark cooler for transport to the lab. Within three hours of collection, 3-6 fresh leaves per sample were separated from stems and measured for leaf area with a flatbed scanner.

Table 4.2. Summary of traits and units. *LMA is the inverse of specific leaf area (SLA).

Abbreviation	Trait	Units
LMA*	leaf mass per area	mg ⁻¹ mm ²
LDMC	leaf dry matter content	mg g ⁻¹
SSD	stem specific density	mg mm ⁻³
C:N	carbon to nitrogen ratio	Unitless
δ ¹³ C	foliar carbon isotope composition	‰
δ ¹⁵ N	foliar nitrogen isotope composition	‰

For leaf dry matter content (LDMC) and stem specific density (SSD), stem segments with leaves were clipped, wrapped in a wet paper towel, and placed in a plastic bag within a dark cooler for transport to the lab. Within two hours of collection, shoot ends were placed in vials with water and covered with a moist plastic sheet in a cool dark room. Shoots were allowed to rehydrate overnight and fresh weights were obtained the following day. For LDMC, 3-6 leaves per sample were weighed. For SSD, the water displacement method was used to measure fresh weights on approximately 3cm long stem segments.

Foliar δ¹³C, δ¹⁵N, and C:N samples were obtained after field collected leaves were dried at 60°C for a minimum of two weeks and then ground to homogenized powder using liquid nitrogen and a mortar and pestle. Samples were packed in tin and analyzed with a CHNOS Elemental Analyzer interfaced to an IsoPrime100 mass spectrometer at the Center for Stable Isotope Biogeochemistry at the University of California Berkeley.

Traits were collected for both native and non-native species that comprised the top 80% of cover on a per plot basis. At each plot, a minimum of two replicates (with samples from different individuals) were collected. Where possible, random species replicates were collected across both elevation treatments and plant community type treatments. In total, 54 species were collected with an average of 14.9 replicates per species for a total of 866 original species by plot replicates. Of these 54 species, there were 9 lowland community species, 20 upland community species, 19 non-native

species that naturally recruited into the plots, and 6 native species that naturally recruited into the plots (i.e. that were not planted as part of community treatments).

When relating functional traits to species abundances based on the idea that dominant species contribute most to production (Grime 1998), community weighted means (CWMs) were calculated following standard protocols (Lavorel *et al.* 2008), where:

$$\text{CWM} = \sum_{i=1}^n p_i \times \text{trait}_i$$

where p_i is the relative contribution of species i to the community (measured at the plot level), and trait_i is the trait value of species i .

Analyses

To establish that bench elevation treatments successfully created a gradient of wetter to drier conditions from lower to upper benches, a linear mixed effects model (LMM) with soil volumetric water content as the response variable was used. In this LMM, and all LMMs described hereafter, a random effect of plot and block was used. Additionally, this soil moisture model was repeated but with Coefficient of Variation (CoV=standard deviation/mean) of soil volumetric water content to assess seasonal variability across elevation treatments.

For **Q1**, to test whether plant community type treatments separated according to predicted acquisitive-conservative trait axes, an analysis of similarities (ANOSIM) on scaled (0-1) species mean traits across elevations and community types (and their interaction) was used. To test whether trait associations in the upland and lowland palettes differently affected total planted cover, another ANOSIM was used, using per plot total cover with community weighted traits. To further assess the influence of planted community type on plant cover across bench elevations, a LMM was used, where higher cover of the lowland community type in lower bench elevations and higher cover of the upland community type in upper bench elevations would support **H1**.

For **Q2**, LMMs were used to compare variability (CoV) in LAI and NDVI across plant community types and elevation (and their interaction) and also in response to functional diversity. **H2** would be supported if either the mixed planting treatment or high functional diversity has significantly lower variability in LAI and NDVI.

For **Q3**, we used a Nonmetric Multidimensional Scaling (NMDS) and convex hull fitting to test for trait niche overlap with non-native plants that recruited into the plots. **H3** would be supported if trait niche overlap with non-native plants is greatest in the mixed communities (combination of lowland and upland communities). **H3** would be further supported if mixed riparian communities have the lowest invasion, supported by a LMM and pairwise community comparisons. Alternative invasion models not involving community type, using a series of LMMs and AIC selection, were also used to assess percent non-native cover responses across species diversity, functional diversity, and soil moisture gradients. Our alternative hypothesis for Q3 will be supported if invasion is highest in dry plots (with low soil moisture).

All statistical analyses were performed in R (R Core Team 2021). The *vegan* package was used to scale trait and percent cover estimates, to calculate species and functional Shannon diversity metrics, and to ordinate and test for differences in plant community trait composition across treatments (Osakanen *et al.* 2022). All LMMs were run with the *lme4* package (Bates *et al.* 2015) and the *multcomp* (Hothorn *et al.* 2022), *MuMIn* (Bartoń 2022), and *car* (Fox *et al.* 2022) packages were used for post-hoc multiple comparisons, calculation of R^2 values, and p-value estimates.

Results

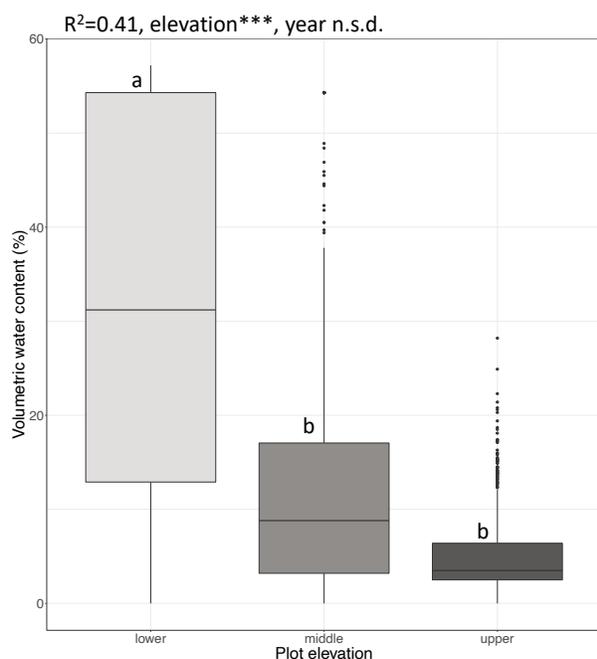
Climate & soil moisture

In 2019, when plots were planted, mean annual precipitation (MAP) was 72.8 mm above the historical norm (1980-2010, MAP= 440.8mm) and mean annual temperature (MAT) was only 0.14 C above the historical norm (1980-2010, MAT= 9.3 C) (Thornton *et al.* 2022). In both sample years,

MAP was similarly below the historical norm, with 32.1mm less MAP in 2021 and 42.0 mm less MAP in 2022. MAT was above the historical norm in both 2021 and 2022 by 1.4 C and 9.7 C, respectively.

Mean soil moisture was significantly higher in lower elevation treatments compared to middle and upper elevation treatments (LMM, $R^2=0.41$; pairwise elevation treatment comparisons $p < 0.05$; **Fig. 4.3A**). The CoV of soil moisture was significantly higher in middle elevation treatments compared to lower and upper elevation treatments ($p < 0.05$) (LMM, $R^2=0.31$; **Fig. 4.3B**).

A.



B.

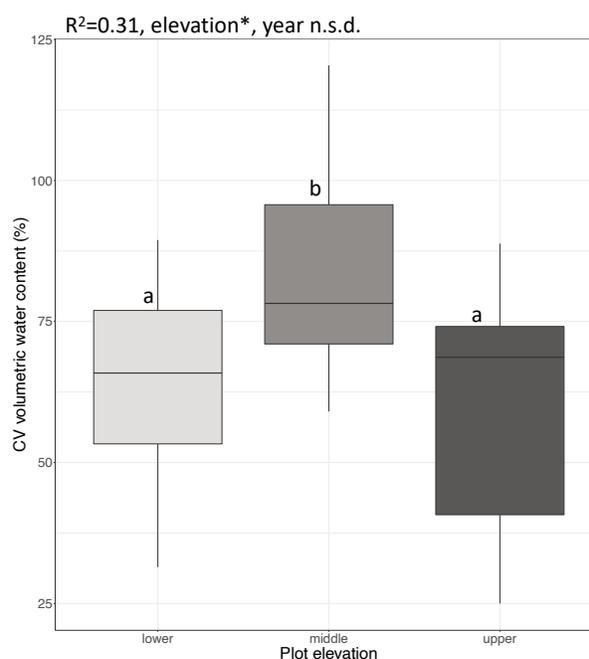


Figure 4.3. Soil volumetric water content (A) and the coefficient of variation of soil volumetric water content (B) across experimental plot elevations. Boxplots show medians (horizontal lines), interquartile ranges, first and third quartiles, and minimums and maximums. Treatments with the same letters do not significantly differ from each other (Tukey's HSD test, $p > 0.05$). Asterisks denote significance where '***' indicates $p=0.001$, '**' indicates $p=0.01$, and '*' indicates $p=0.05$. In total, there were 1,692 observations, with 564 per elevation treatment. The LMMs revealed that volumetric soil water content was significantly different across elevation treatments, with highest soil water content in the lower elevations, intermediate soil water content in the middle elevations, and lowest soil water content in the upper elevations. While variability in soil volumetric water content was consistent between lower and upper elevations, middle elevations had significantly higher variability in soil water content.

Traits & function

There were no significant differences between traits in the lowland and upland community types (ANOSIM $R=0.06$, $p=0.72$; NMDS stress=0.15; **Fig. 4.4**, **Fig. C1**). Instead of seeing classic associations of low $\delta^{15}\text{N}$ and high LMA, LDMC, $\delta^{13}\text{C}$, SSD, and C:N for conservative strategies (and the opposite for acquisitive strategies), all traits were similarly associated across communities, with only marginally higher LMA and lower SSD in the lowland community compared to the upland community.

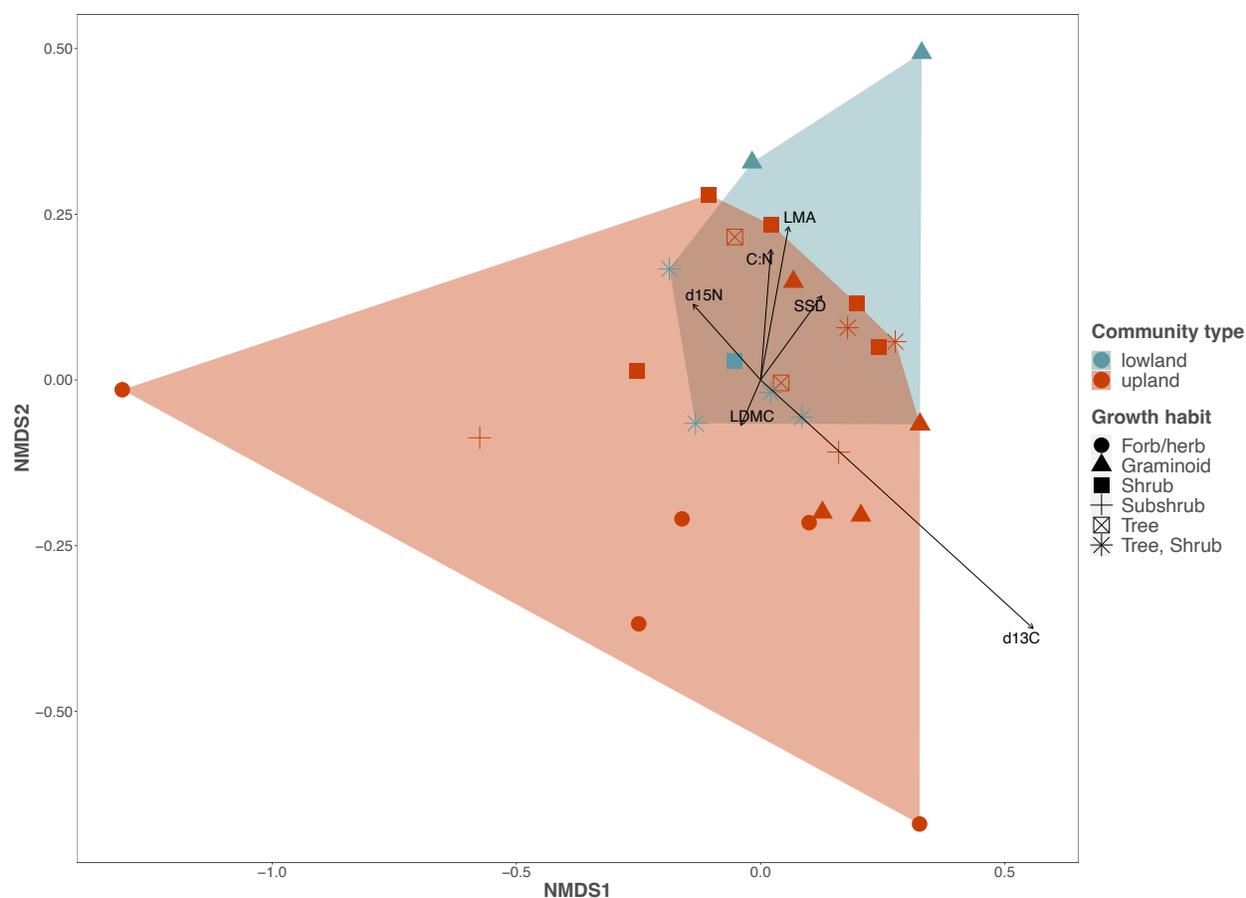


Figure 4.4. NMDS of traits of planted species by community type (colors, hulls) and growth habit (symbols). There were no significant differences between traits in the lowland and upland community types (ANOSIM $R=0.06$, $p=0.72$).

When plot cover was weighted by community traits (CWMs), there were still no significant differences in community types (ANOSIM $R=0.06$, $p=0.91$; NMDS stress=0.019; **Fig. 4.5**).

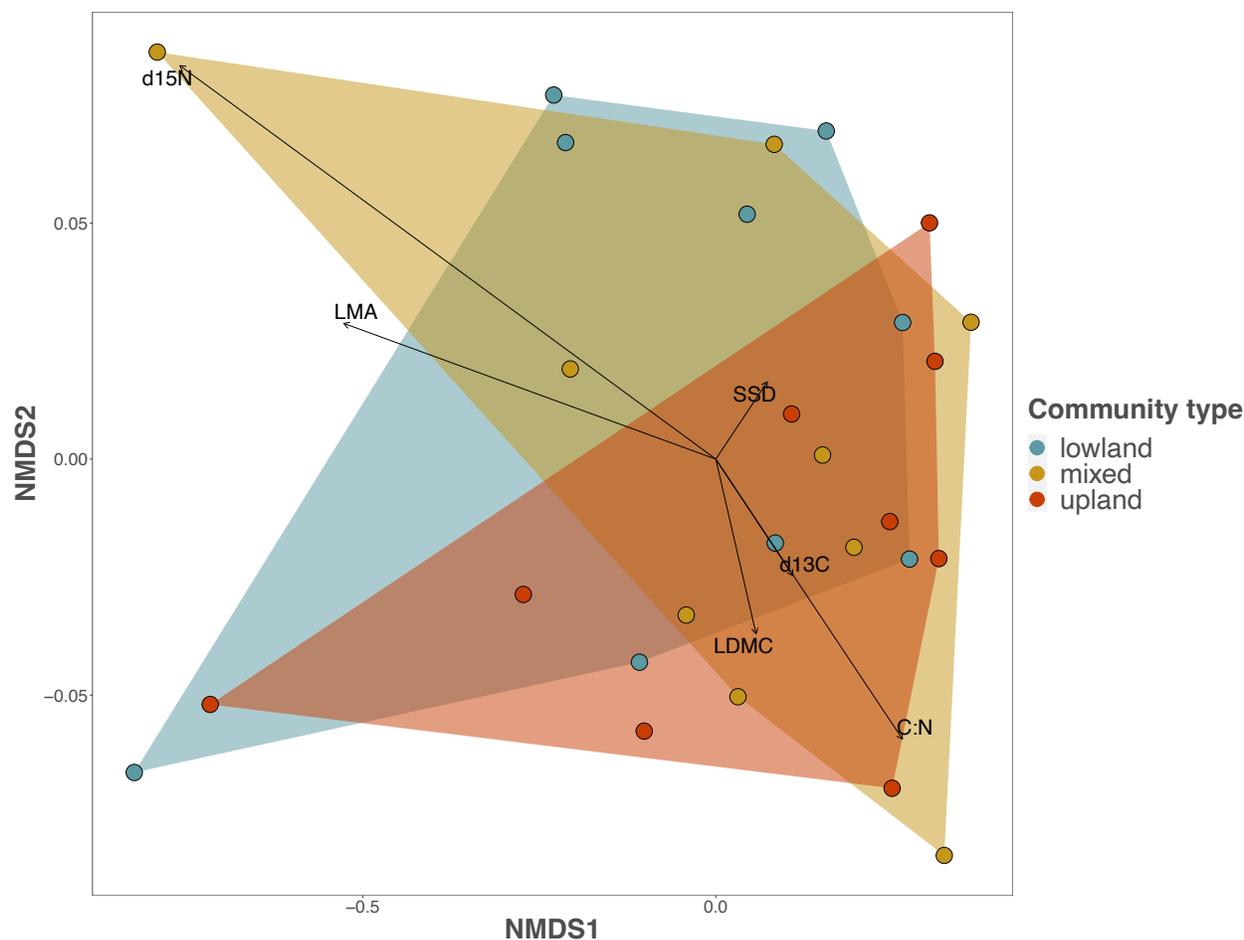


Figure 4.5. NMDS of community weighted mean cover (CWM, by traits) per plot by community type (colors). There were no significant differences across community types (ANOSIM $R=0.06$, $p=0.91$).

There was higher cover of the lowland community in lower elevations ($p < 0.05$) but not significantly higher cover of the upland community in upper elevations ($p > 0.05$) (LMM, $R^2=0.61$; **Fig. 4.6**). Elevation alone was the strongest predictor of total planted community cover, with significantly higher planted cover in lower elevations compared to both middle and upper elevations ($p < 0.05$).

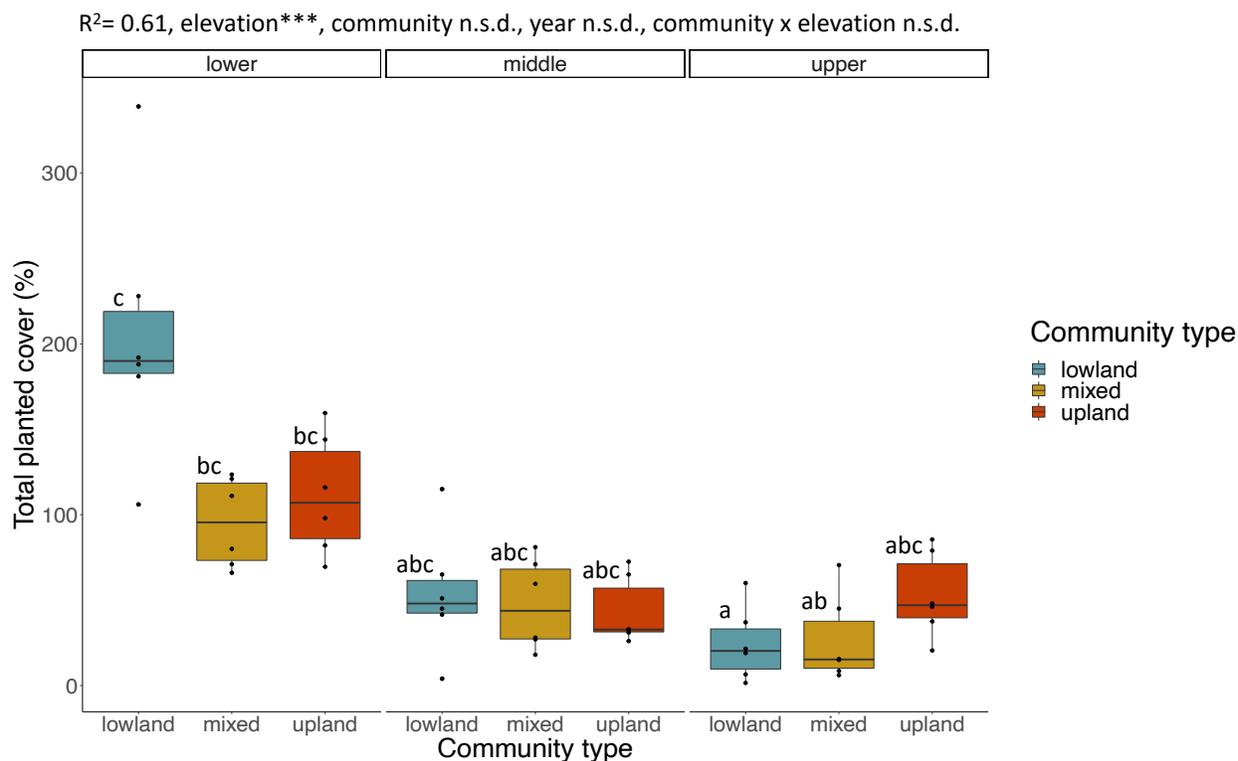


Figure 4.6. Percent planted native community cover across community (x-axes, colors) and elevation treatments (panels). Boxplots show medians (horizontal lines), interquartile ranges, first and third quartiles, and minimums and maximums. Treatments with the same letters do not significantly differ from each other (Tukey’s HSD test, $p > 0.05$). Asterisks denote significance where ‘***’ indicates $p=0.001$, ‘**’ indicates $p=0.01$, and ‘*’ indicates $p=0.05$. Total cover of a plot could exceed 100% due to overlapping plant canopies. The LMM indicated that there was significantly higher cover of the lowland community treatment in the lower elevations, but not significantly higher cover of the upland community in the upper elevations. Additionally, elevation alone was the strongest predictor of total planted community cover, with significantly higher planted cover in lower elevations compared to both middle and upper elevations.

Insurance

The mixed community treatment did not have significantly lower NDVI and LAI variability across bench elevations compared to upland and lowland community treatments (LMM_{NDVI}, $R^2=0.61$, $p > 0.05$; LMM_{LAI}, $R^2=0.13$, $p > 0.05$; **Fig. 4.7**). Overall, only year was a significant predictor of the CoV of LAI (LMM, $R^2=13$, $p=0.01$) and NDVI (LMM, $R^2=61$, $p=0.006$), with lower variability in both LAI and NDVI in 2021.

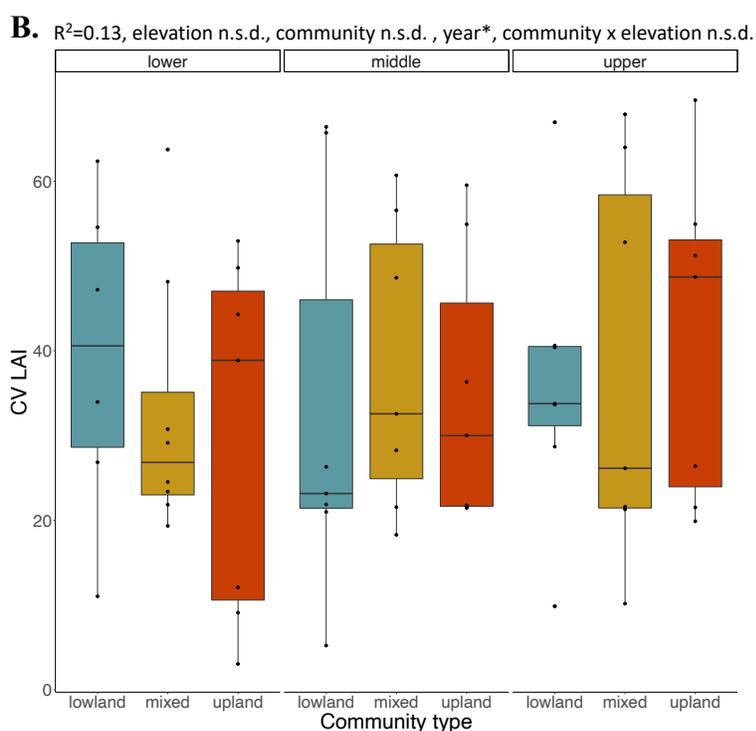
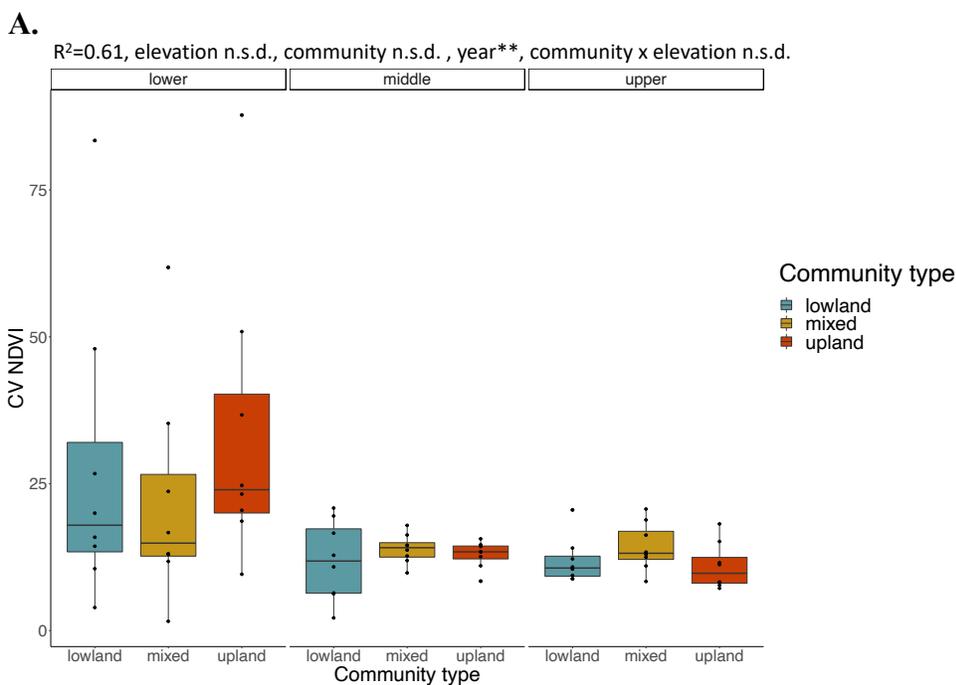


Figure 4.7. Coefficient of variation of NDVI (A) and LAI (B) across community (x-axes, colors) and elevation treatments (panels). Boxplots show medians (horizontal lines), interquartile ranges, first and third quartiles, and minimums and maximums. Asterisks denote significance where ‘***’ indicates $p=0.001$, ‘**’ indicates $p=0.01$, and ‘*’ indicates $p=0.05$. The LMMs indicated that there was not lower variability of NDVI or LAI in mixed community treatments, nor any significant main or interactive effects of community type and elevation.

When comparing variability in NDVI and LAI directly across the range of native species functional diversity in plots, there was a marginally negative relationship with NDVI (LMM, $R^2=0.56$, $p=0.07$), but not LAI (LMM, $R^2=0.09$, $p=0.92$) (Fig. 4.8).

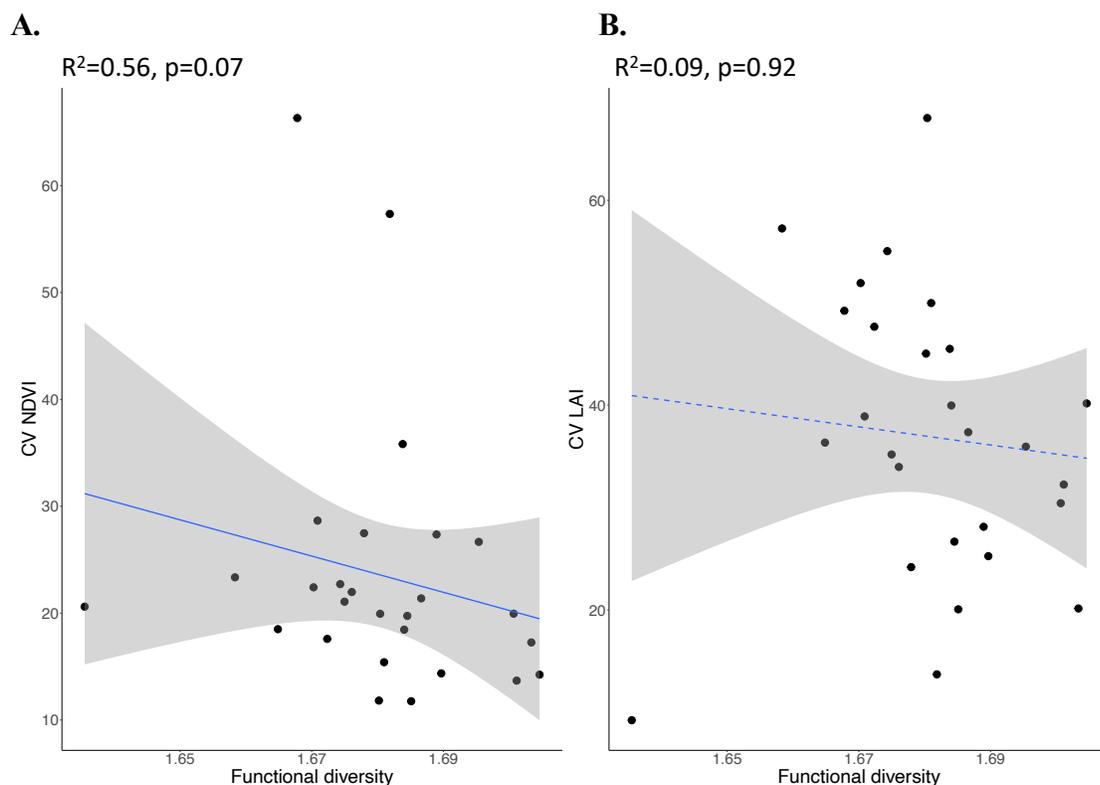


Figure 4.8. Coefficient of variation of NDVI (A) and LAI (B) across native species Shannon functional diversity (x-axes). The LMMs indicated that there was marginally lower variability in NDVI at high levels of functional diversity, but not with LAI.

Niche complementarity & invasion

The mixed planted native community treatment (including upland and lowland riparian communities) did not increase trait niche overlap with non-native species that recruited into the plots (NMDS hull fitting, stress=0.18 Fig. 4.9). Instead, the native upland community alone had the highest trait niche overlap with non-native species.

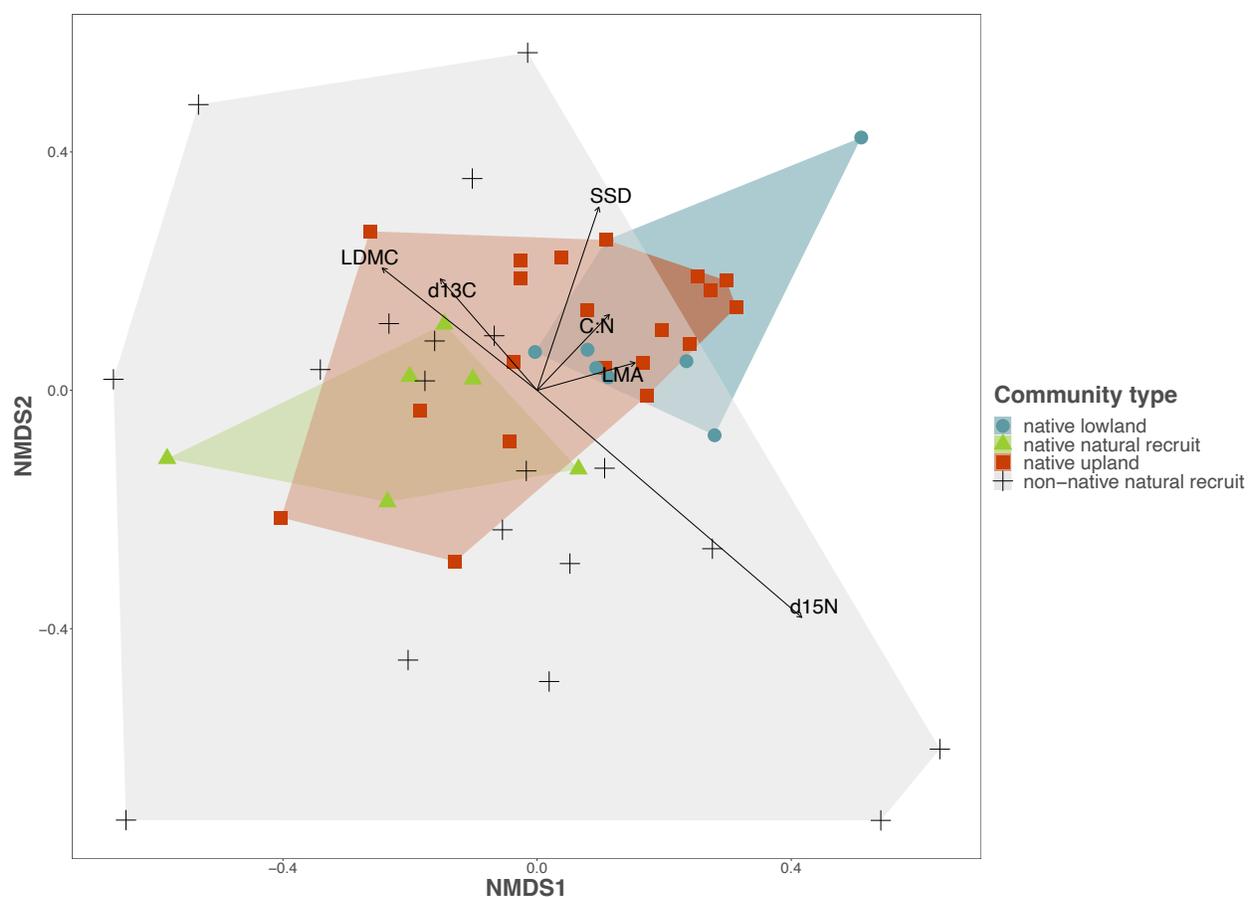


Figure 4.9. NMDS of traits of planted communities and natural recruit species (colors, hulls) showing that the addition of lowland and upland communities (blue and red hulls) approximating mixed community treatments did not increase trait niche overlap with the non-native species (grey hull) that naturally recruited into the plots.

The proportion of non-native cover was significantly lower in lowland community, lower elevation treatments compared to all middle and upper elevations x community treatments ($p < 0.05$; **Fig. 4.10**). The proportion of non-native cover was significantly lower in lower elevations compared to middle and upper elevations (main effect of elevation, $p < 0.05$). There were no significant differences in the proportion of non-native cover across middle and upper elevations and plant community treatments ($p > 0.05$).

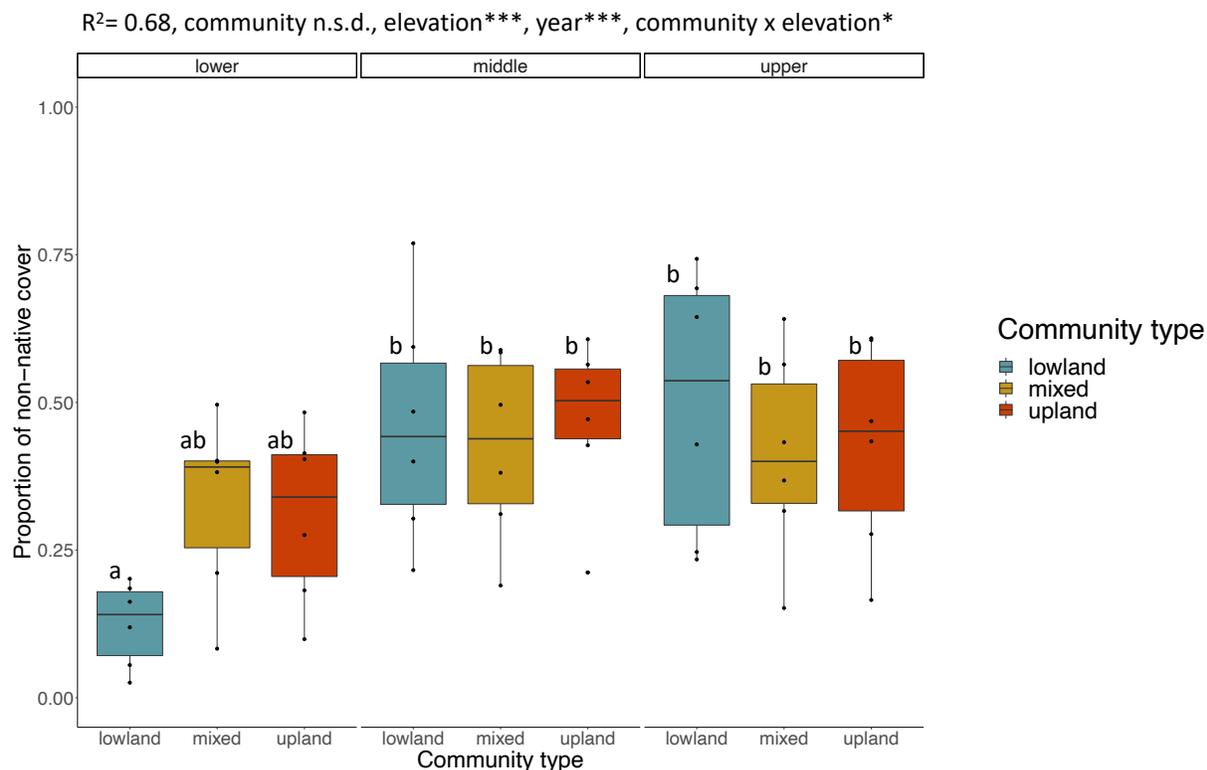


Figure 4.10. Proportion of non-native cover across community (x-axis, colors) and elevation treatments (panels). Boxplots show medians (horizontal lines), interquartile ranges, first and third quartiles, and minimums and maximums. Treatments with the same letters do not significantly differ from each other (Tukey's HSD test, $p > 0.05$). Asterisks denote significance where '***' indicates $p=0.001$, '**' indicates $p=0.01$, and '*' indicates $p=0.05$. A LMM revealed that the proportion of non-native cover was significantly lower in lower elevations compared to middle and upper elevations, with the overall lowest non-native cover in lower elevation, lowland community plots.

AIC selection of LMMs of invasion trends, alternative to assessing the degree of niche overlap or influence of planted community type, using species diversity, functional diversity (based on traits), and soil moisture as fixed effects and a random effect of block indicated that the best model only included soil moisture, with higher invasion in plots with lower soil moisture (LMM, $R^2=0.37$, $p=0.0001$; **Fig. 4.11**).

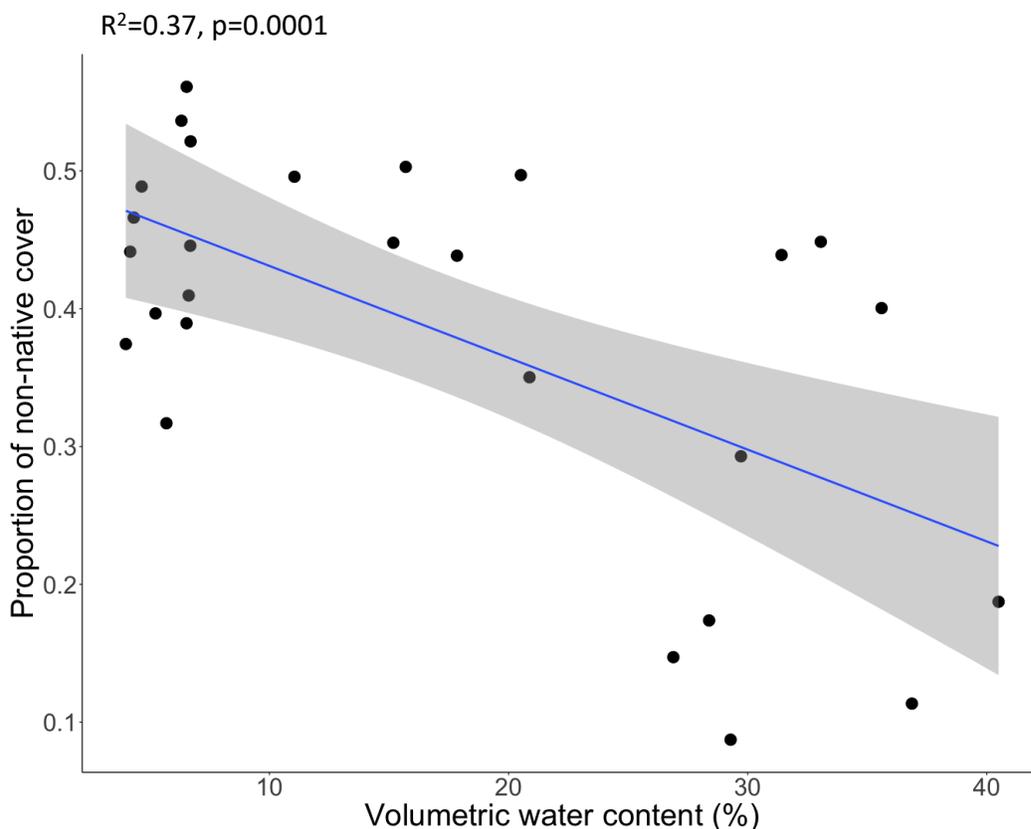


Figure 4.11. Proportion of non-native cover across soil volumetric water content, averaged across both years of sampling per plot (points). A LMM indicated that soil volumetric water content was the sole best predictor of invasion, and inclusion of species diversity or functional diversity (based on traits) did not improve the model.

Discussion

We sought to test the effectiveness of employing a functional trait-based approach that incorporates insurance and niche complementarity concepts into the design of a riparian restoration project. In our manipulations of plant community types, we found that lowland riparian species did not demonstrate more acquisitive strategies compared to upland riparian species in our community treatments. Instead, both communities had relatively acquisitive traits – high $\delta^{15}\text{N}$ and low LMA, LDMC, $\delta^{13}\text{C}$, SSD, and C:N. These acquisitive strategies are typical of many wetland species (Stromberg & Merritt 2016; Pan *et al.* 2020) compared to non-riparian upland species that often occur in much drier environments. One main reason for not seeing even more acquisitive trait values

in our lowland riparian community compared to our upland community could be due to local adaptation to dry conditions in our semi-arid region yielding more slow, conservative strategies to match low resource conditions (Grady *et al.* 2013). After all, our lowland and upland communities are from a shared regional species pool that have shared ecological tolerances, which is thought to increase functional convergence (Cornwell *et al.* 2006; Grime 2006). However, it is important to note that, although we did not find stark differences in trait-based niches across community types, there still could be many other resource use axes of variation not captured by the traits we sampled, specifically in terms of reproductive strategies and belowground investments, that might differentiate species' resource use strategies to yield niche complementarity as we initially expected.

In terms of assessing how community types performed across elevation treatments, we found support to show that the lowland community performed better relative to the mixed and upland community treatments (in terms of higher cover) in lower elevations where there was the highest water availability, even to the extent where these treatments were flooded late spring-early summer in both years of sampling. However, the upland community only had marginally higher cover in the upper elevations with the lowest water availability. This could be because our two study years were not dry enough to elicit stark higher biomass responses of upland communities in upper elevations compared to mixed and lowland community treatments. This is in line with other studies where pronounced declines in biomass, specifically net primary productivity, were only seen in especially dry years (Chen *et al.* 2013; Rudgers *et al.* 2018). Additionally, when assessing temporal variability in productivity to determine if diversity conferred stability in either LAI or NDVI, we found some supporting evidence. While the mixed community treatments did not have lower variability in productivity measures, there was a marginally negative relationship between native functional diversity and NDVI, in line with our initial expectation and supporting literature (Díaz & Cabido 2001).

We did not find clear evidence that planting a functionally diverse species assemblage warded off invaders through increasing functional trait niche overlap or reducing non-native cover, similar to other studies (Hess *et al.* 2019; Yannelli *et al.* 2020). A key reason why we did not find

evidence of limiting similarity could be that there was no delay in invasion after planting. Therefore, planted and seeded native species may have not grown to an extent that would yield priority effects to the detriment of invaders (Hess *et al.* 2019). Larson *et al.* (2013) also found that early establishment of native species was more important than treatments aimed at promoting functional similarity to limit invasion. Although non-native species that naturally recruited into the plots generally had similar traits and presumably resource acquisition strategies to planted native communities, their marginally higher SSD and $\delta^{15}\text{N}$, in addition to unmeasured traits that relate to reproduction and/or rooting ability, could have allowed this group of species to attain a competitive advantage, making quick use of resources after the plots were graded to create a stage 0 planform.

Instead of functional diversity driving invasion trends, we found that the abiotic driver of soil moisture was the most important factor affecting the degree of invasion, with higher invasion in drier conditions. Other studies have also found invasion trends to not be majorly biotically mediated, but rather determined by an abiotic gradient, which can also indirectly affect the degree of competitive or facilitative interactions between resident and invader communities (Byun *et al.* 2015). Consistent with our findings, other studies in riparian systems have shown that invasion is often promoted in periods of low water availability or during times without floods (Decamps *et al.* 1995; Birken & Cooper 2006; Catford *et al.* 2011, 2014).

It is possible, however, that with more time for succession post-restoration that native species diversity and functional diversity conferred by traits could eventually promote invasion resistance through complementarity effects, as other studies have shown (Byun *et al.* 2023). Since the present study only occurred within the first three years since restoration interventions occurred, it is possible that species interactions are not yet strong given that the restored plots are not yet densely vegetated. In addition to this, since our study reach experienced a 100-year flood six years prior to restoration (Moody 2016), it is also possible that disturbance tolerant non-native species were transported and persisted in the seedbank (Catford *et al.* 2014), making for an initial invasion pulse in graded restoration areas that might lessen through time as seedbank reservoirs from the flood are lessened.

Although our expectations of insurance and niche complementarity, mainly with the mixed community treatments were generally not supported, this general approach of using a mixed or functionally diverse community might still be warranted in scenarios where ecosystem change in degraded ecosystems is most suited to being ‘accepted’ or ‘directed’ (*sensu* R-A-D framework) (Schuurman *et al.* 2020). With future climate change predicted to further trends of increased temperature, precipitation variability, and the intensity of droughts in the region (Anderegg & Diefenbaugh 2015; Zhang *et al.* 2021), planting mixed communities that have more conservative, drought adapted species could buffer productivity variability in drought years. Additionally, taking a mixed community approach could be beneficial for other restoration goals such as maintaining high species diversity and for wildlife habitat and food provisioning. Regardless of which of these goals may motivate a restoration, if trait data are available for species in consideration *prior* to the restoration, there are existing tools to help aid picking divergent trait assemblages with different optimization of target ecosystem functions (Laughlin *et al.* 2018).

Overall, our results indicate that, in this stage 0 restoration setting, the most desirable treatment outcome, yielding high native cover and low invasion, was generated by the combination of planting and seeding lowland specialist species and increasing water availability to the degree of temporary early growing season submergence. This outcome provides some support of stage 0 restoration approaches, showing that not only do anastomosing, topographically heterogeneous riparian corridors have desirable geomorphological and hydrological attributes, but that these attributes can also be beneficial for restoring native plant communities.

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APPENDIX A: Supporting Tables & Figures, Chapter II

FIGURES

Fig. A1 Photographic examples of site types (a) and boxplots of mean willow cover (b) and mean willow height (c) across site types.

(a)

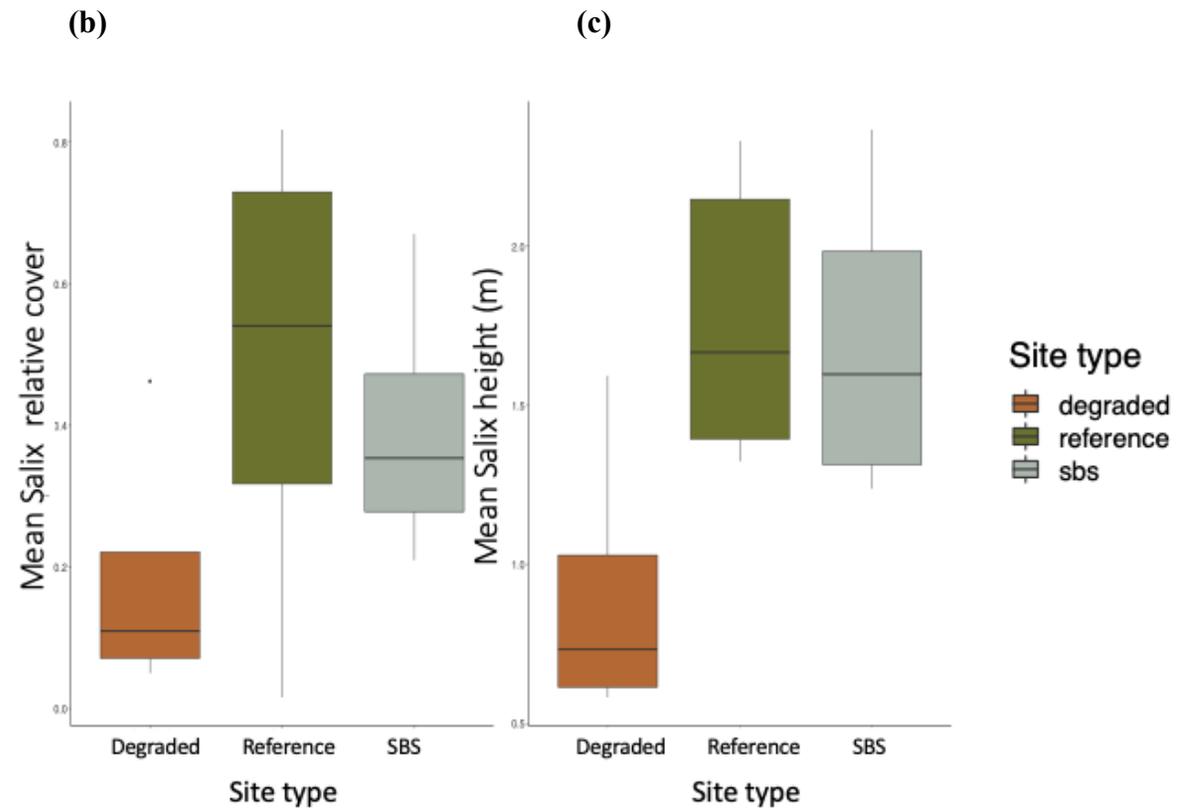
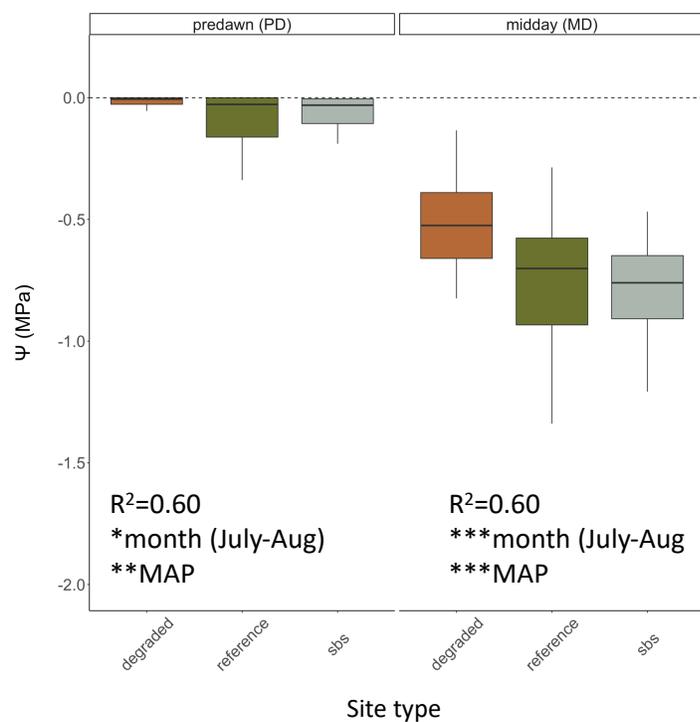
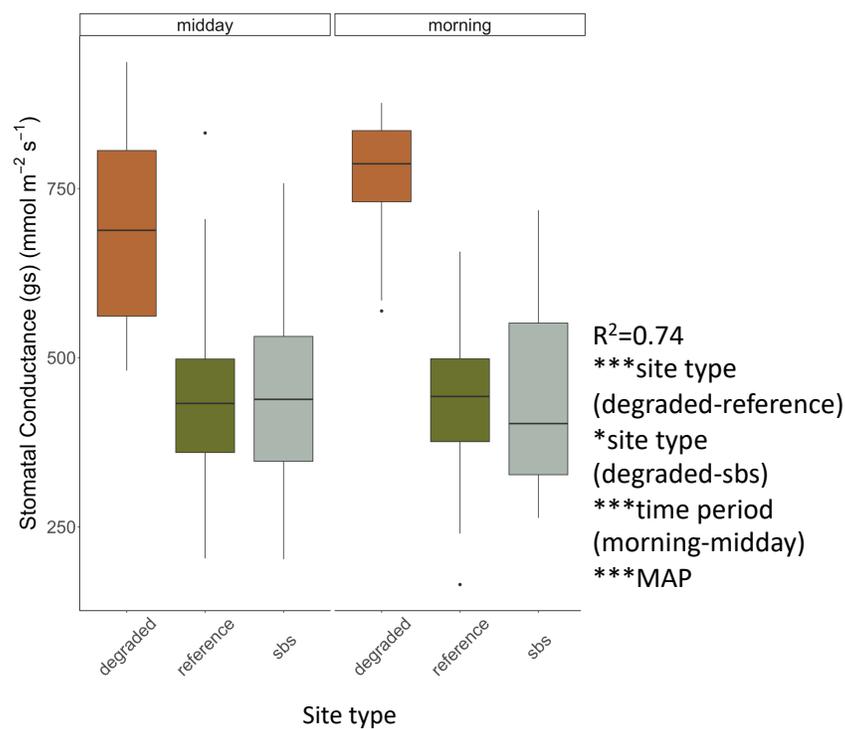


Fig. A2 Subsetted plotting of physiological response variables of *S. monticola* due to its widespread distribution (yielding most even sample size among species) across site types.

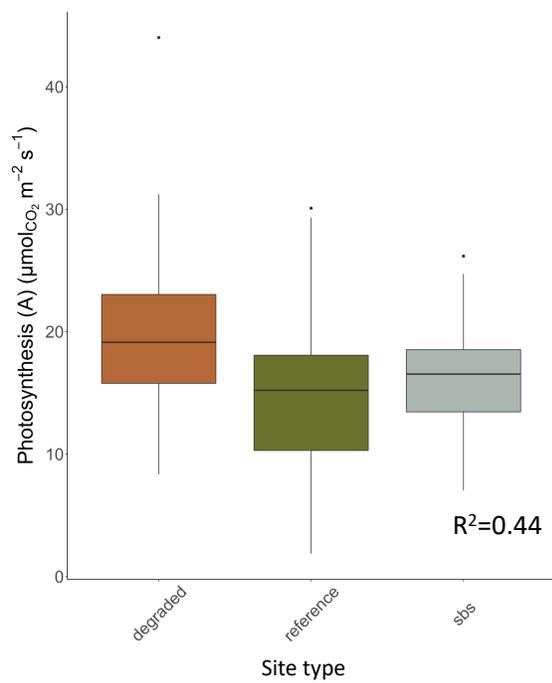
(a)



(b)



(c)



(d)

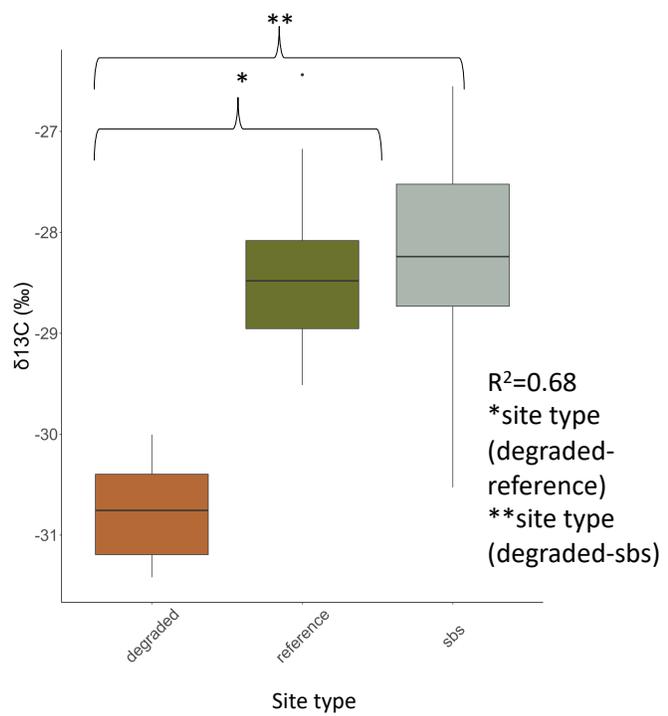
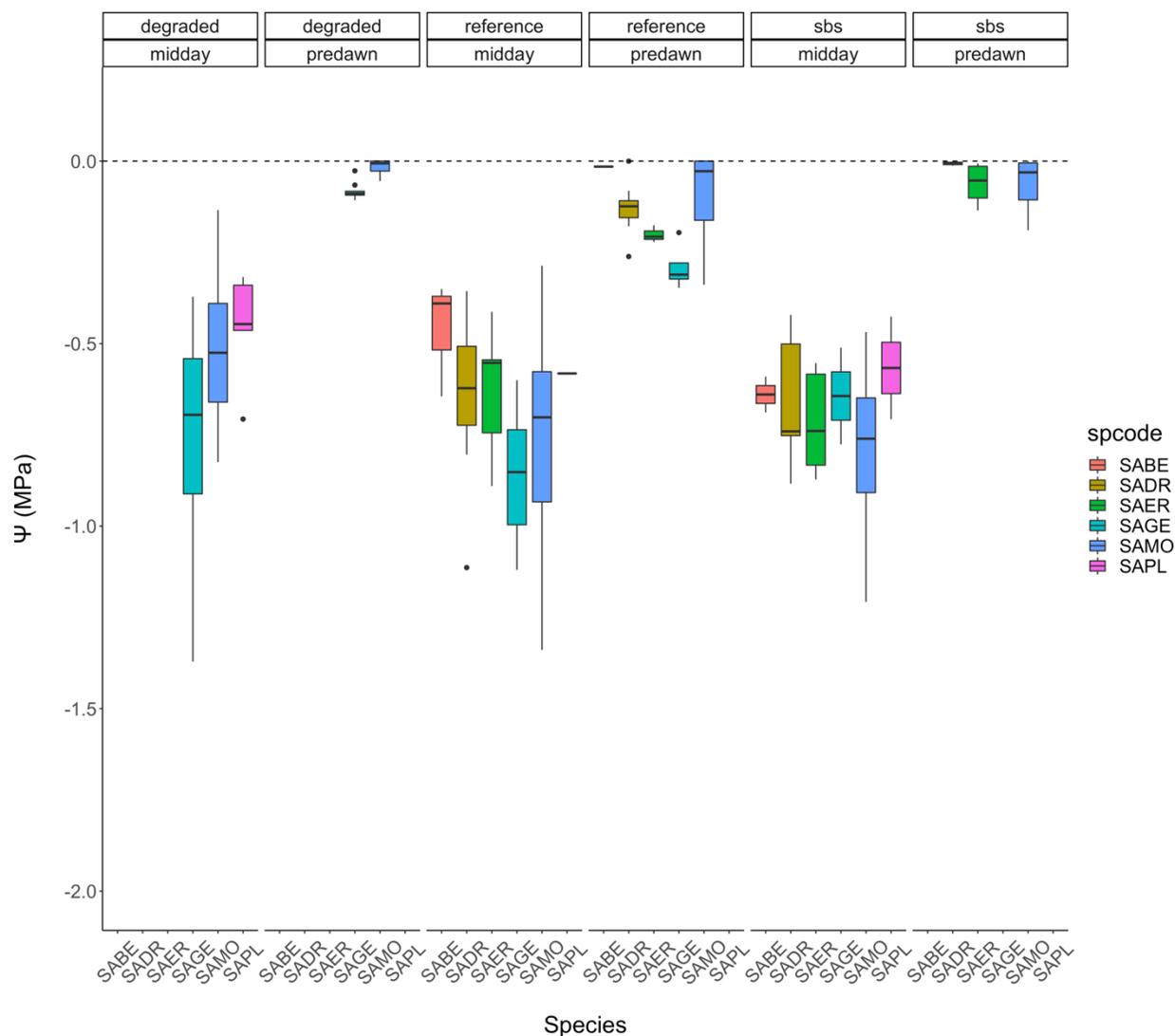
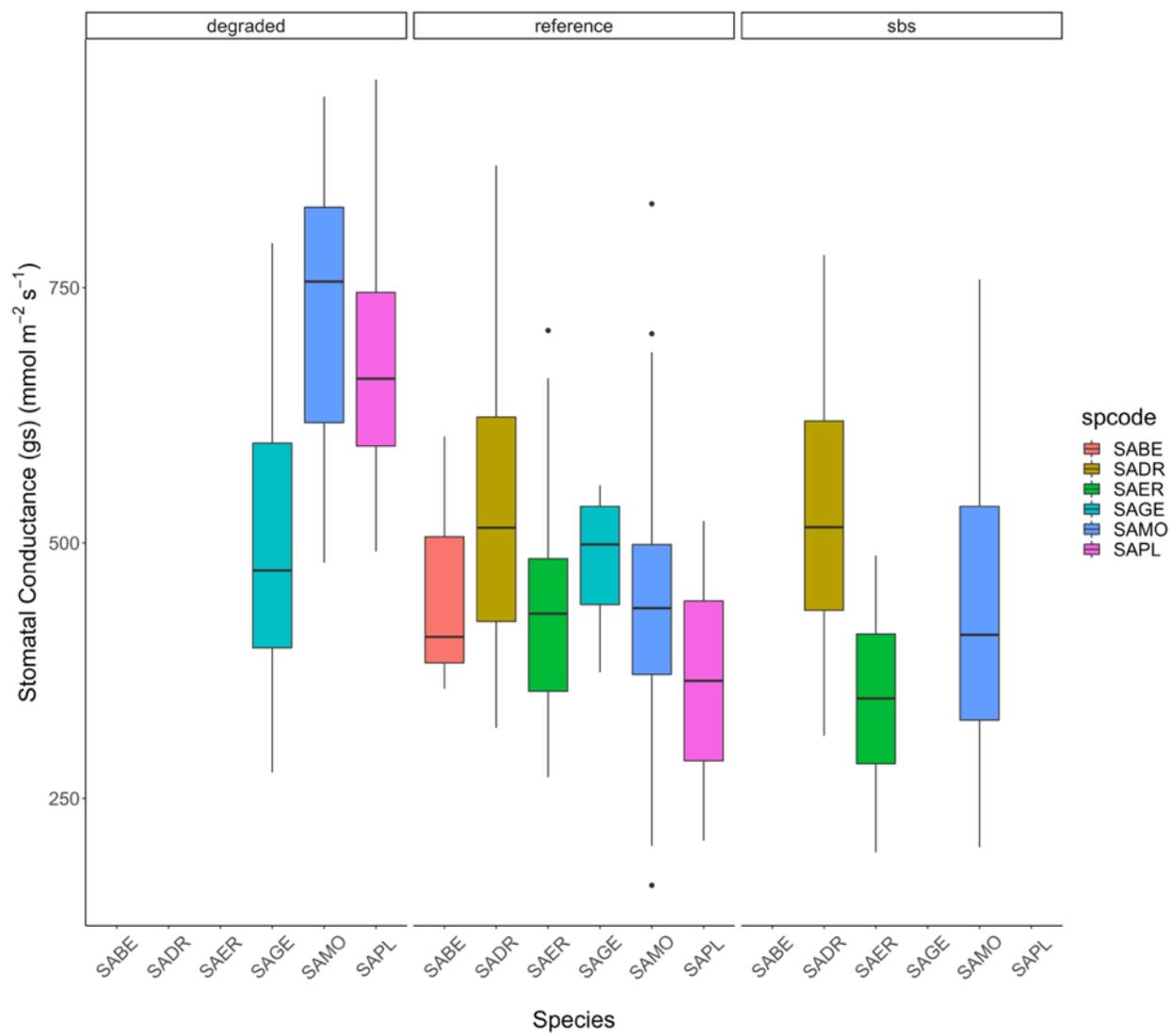


Fig. A3 Species water potential (Ψ) (a), stomatal conductance (gs) (b), photosynthetic rates (A) (c), and foliar $\delta^{13}\text{C}$ (d). Due to natural turnover across site types yielding uneven sample sizes per species, plots are just for visualization and do not have corresponding statistical analyses. Species codes and full scientific names are: SABE, *Salix bebbiana*; SADR, *Salix drummondiana*; SAER, *Salix eriocephala*; SAGE, *Salix geyeriana*; SAMO, *Salix monticola*; SAPL, *Salix planifolia*.

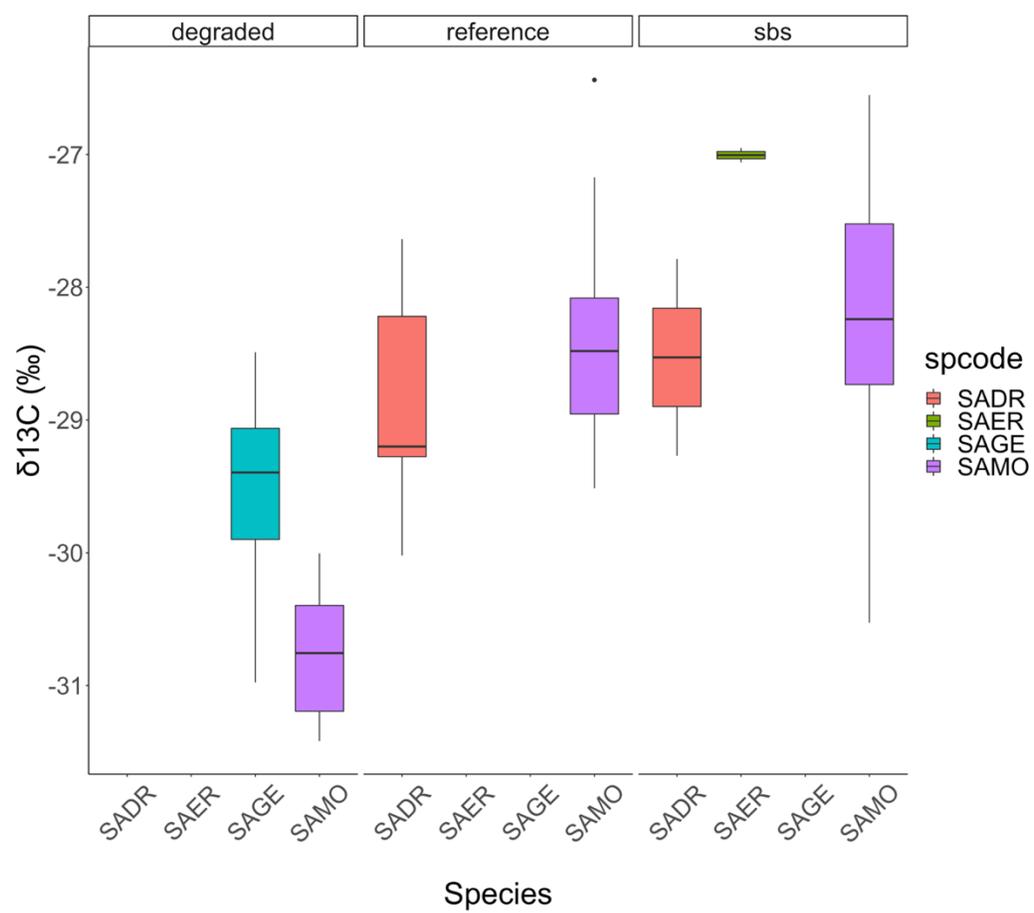
(a)



(b)



(c)



(d)

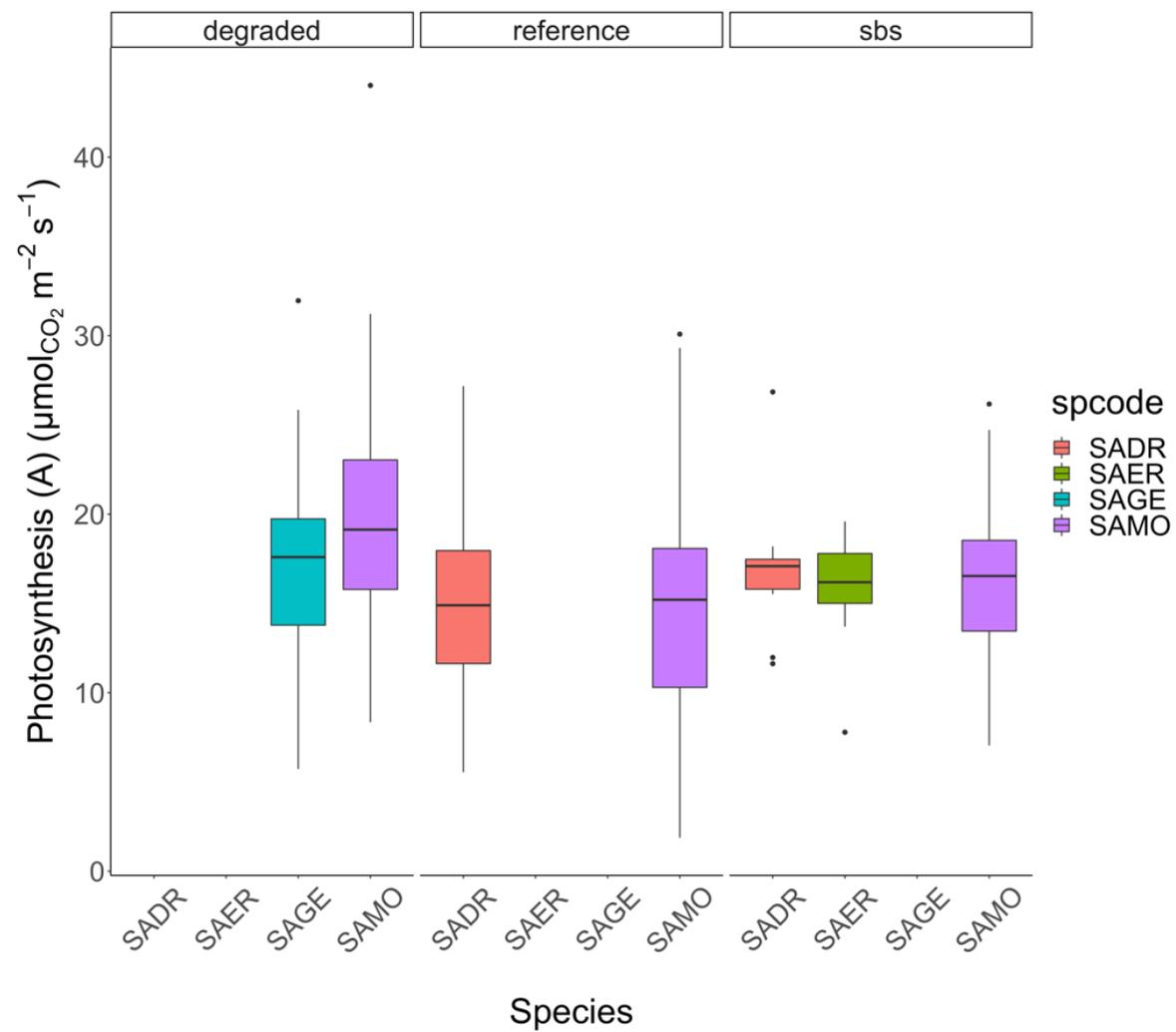


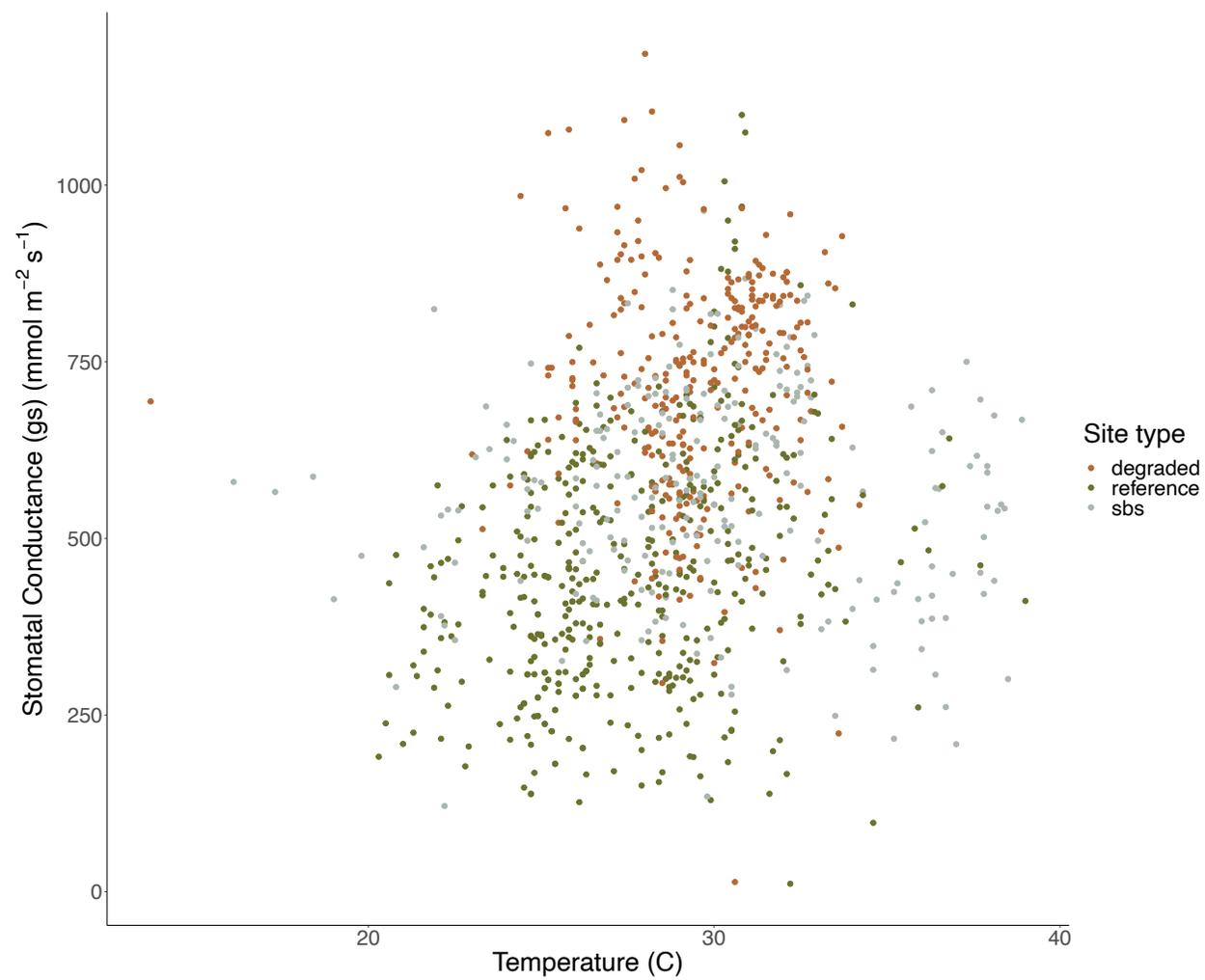
Fig. A4 Stomatal conductance across leaf temperatures.

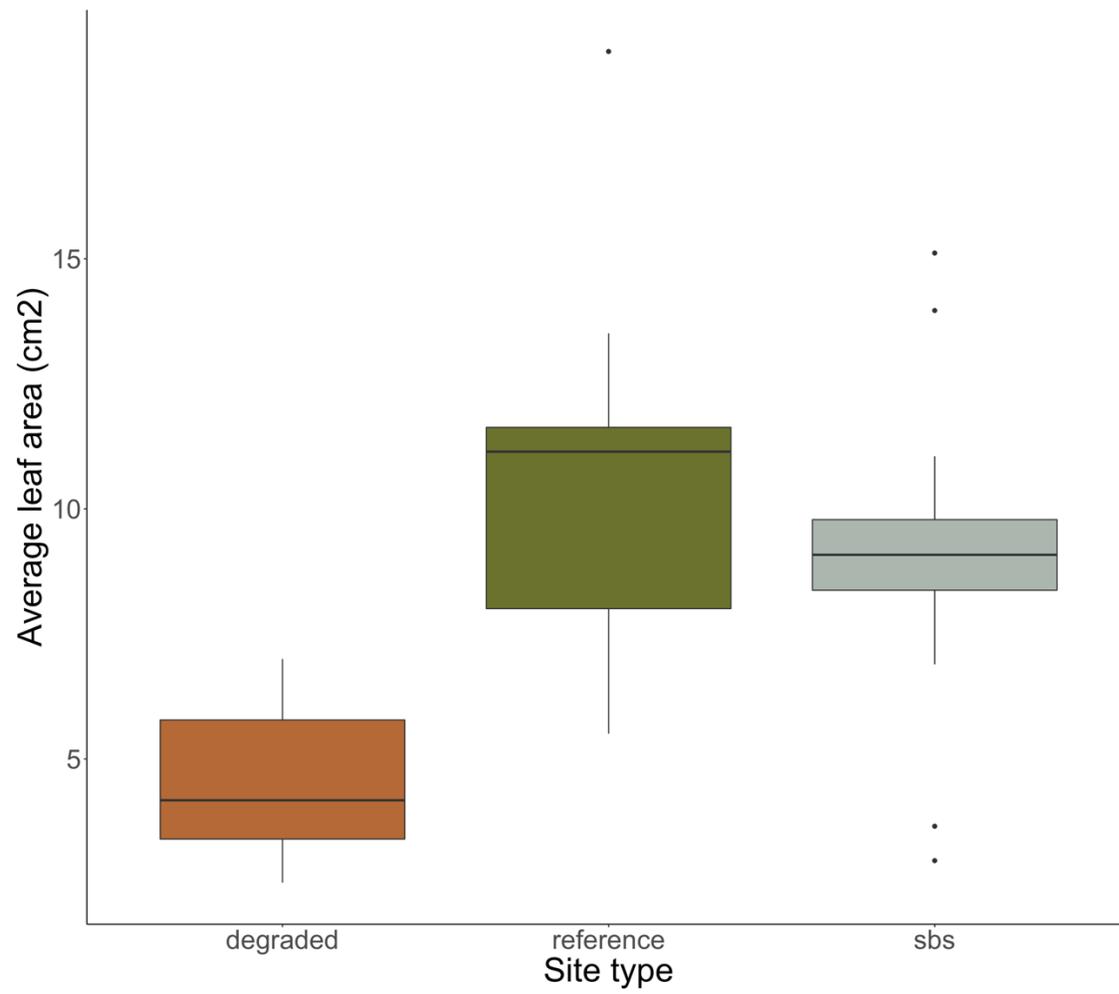
Fig. A5 Average leaf area across site types.

Fig. A6 Example images of crown dieback in the Kawuneeche Valley at a degraded site.
Example images of crown dieback in the Kawuneeche Valley at a degraded site.



METHODS

A1 Leaf area collections and calculations for **Fig. A5**.

Leaf areas were calculated from scanning fresh leaves on the same day of collection, which occurred after full leaf out and development in August 2020 across the six focal sites. Areas were calculated in ImageJ and included the petiole. An average of 6 leaves for 8 individuals at each site were measured for a total of 48 samples.

APPENDIX B: Supporting Tables & Figures, Chapter III

TABLES

Table B1. Study site summary table.

Site	Wetland type	Elevation (m)	Aspect (°)	Slope (°)	Soil water holding capacity (mm)	Latitude	Longitude
ROMO_199	F	2734	129	5	129	40.3900985	-105.85312
ROMO_301	F	2876	181	3	60	40.3082869	-105.81435
ROMO_303	F	2865	174	1	129	40.3131889	-105.81106
ROMO_503	F	2776	235	3	44	40.3406572	-105.84815
ROMO_507	F	2868	160	2	129	40.3139464	-105.81161
ROMO_511	F	2873	137	4	129	40.3142477	-105.81233
ROMO_515	F	2955	131	13	52	40.3962145	-105.86063
ROMO_533	F	3090	26	6	60	40.454723	-105.86005
ROMO_591	F	2743	287	2	129	40.391893	-105.84681
ROMO_802	F	2866	182	2	129	40.3131781	-105.80848
ROMO_505	M	2444	102	1	132	40.3553068	-105.59368
ROMO_506	M	2445	155	1	132	40.3561004	-105.5935
ROMO_551	M	3626	227	6	83	40.4030237	-105.70813
ROMO_589	M	2444	190	1	132	40.3557473	-105.59385
ROMO_590	M	2447	194	3	45	40.3571422	-105.59417
ROMO_604	M	2867	189	1	129	40.3136244	-105.81
ROMO_605	M	3631	232	6	83	40.4029515	-105.70745
ROMO_611	M	3632	221	7	83	40.403367	-105.70779
ROMO_612	M	3628	225	6	83	40.403196	-105.708
ROMO_614	M	2867	193	1	129	40.3134941	-105.80925
ROMO_701	M	2449	192	4	27	40.3575897	-105.59474
ROMO_727	M	2446	177	1	132	40.3564981	-105.59505
ROMO_803	M	3628	222	7	83	40.403277	-105.70808
ROMO_804	M	3623	220	5	83	40.4030465	-105.70847
ROMO_294	R	2722	138	1	129	40.3833132	-105.85211
ROMO_308	R	2867	142	2	129	40.313306	-105.80799
ROMO_522	R	2683	167	0	129	40.3429095	-105.85921
ROMO_530	R	2451	10	6	32	40.3633965	-105.57597
ROMO_553	R	2546	118	2	32	40.2122195	-105.55028
ROMO_615	R	2725	127	3	129	40.3837934	-105.85294
ROMO_616	R	2722	143	1	129	40.3834653	-105.8523
ROMO_617	R	2722	61	0	129	40.3830726	-105.8518
ROMO_618	R	2720	103	1	44	40.3821534	-105.85061
ROMO_725	R	2447	108	1	132	40.355943	-105.59552
ROMO_726	R	2444	135	0	132	40.3549681	-105.59404
ROMO_801	R	2719	114	1	44	40.382315	-105.85033

Table B2. Water balance metrics calculated for all sites through time, with the bolded entries indicating metrics used in joint species distribution models.

Metric	description
Sum of P	Annual sum of precipitation
Average of T	Annual average temperature
Sum of RAIN	Annual sum of precipitation as rain
Sum of SNOW	Annual sum of precipitation as snow water equivalent
Max of PACK	Maximum annual snow pack as snow water equivalent
Sum of MELT	Annual sum of snow melt as water
Sum of W	Sum of melt plus rain reaching soil surface
Sum of PET	Annual sum of potential evapotranspiration
Sum of W	Annual sum of melt plus rain reaching soil surface minus potential evapotranspiration
Average of SOIL	Annual average soil moisture
Sum of AET	Annual sum of actual evapotranspiration
Sum of W-ET- ^SOIL	Annual sum of excess water after available water holding capacity of soil saturated, also called runoff
Sum of D	Annual sum of deficit which is PET-AET
Sum of GDD	Annual sum of growing degree days

Table B3. Linear regression statistics for relative cover trends through time per functional group-wetland type combination. Bolded entries indicate significance ($p < 0.05$).

Wetland type	Functional group	df	R ²	p	Site (p)	Year (p)	Site*Year (p)	Year (beta)
Riparian	Native graminoid	71	0.88	<0.0001	<0.0001	0.02	<0.0001	0.04
	Non-native graminoid	58	0.77	<0.0001	<0.0001	0.03	0.11	0.008
	Native forb	71	0.57	<0.0001	<0.0001	0.85	0.02	0.003
	Non-native forb	68	0.89	<0.0001	<0.0001	0.07	<0.0001	0.03
	Native tree	28	0.67	<0.0001	<0.0001	<0.0001	0.67	0.03
	Native shrub	63	0.89	<0.0001	<0.0001	<0.0001	<0.0001	-0.03
Meadow	Native graminoid	73	0.74	<0.0001	<0.0001	0.001	0.006	0.009
	Non-native graminoid	34	0.85	<0.0001	<0.0001	0.49	0.04	0.01
	Native forb	73	0.82	<0.0001	<0.0001	0.35	0.16	-0.03
	Non-native forb	18	0.33	0.96	0.95	0.84	0.77	-0.0008
	Native tree	-	-	-	-	-	-	-
	Native shrub	49	0.9	<0.0001	<0.0001	0.0003	0.01	0.0007
Fen	Native graminoid	57	0.88	<0.0001	<0.0001	0.002	0.002	0.006
	Non-native graminoid	-	-	-	-	-	-	-
	Native forb	50	0.84	<0.0001	<0.0001	<0.0001	0.23	0.01
	Non-native forb	-	-	-	-	-	-	-
	Native tree	6	0.77	0.01	0.009	0.19	0.65	0.01
	Native shrub	40	0.91	<0.0001	<0.0001	0.006	0.07	0.01

FIGURES

Fig. B1. Climate time series plot (**Fig. 3.1** in main text), with the addition of grey site linear model fits to show site trends generally tracked cross-site climatic trends.

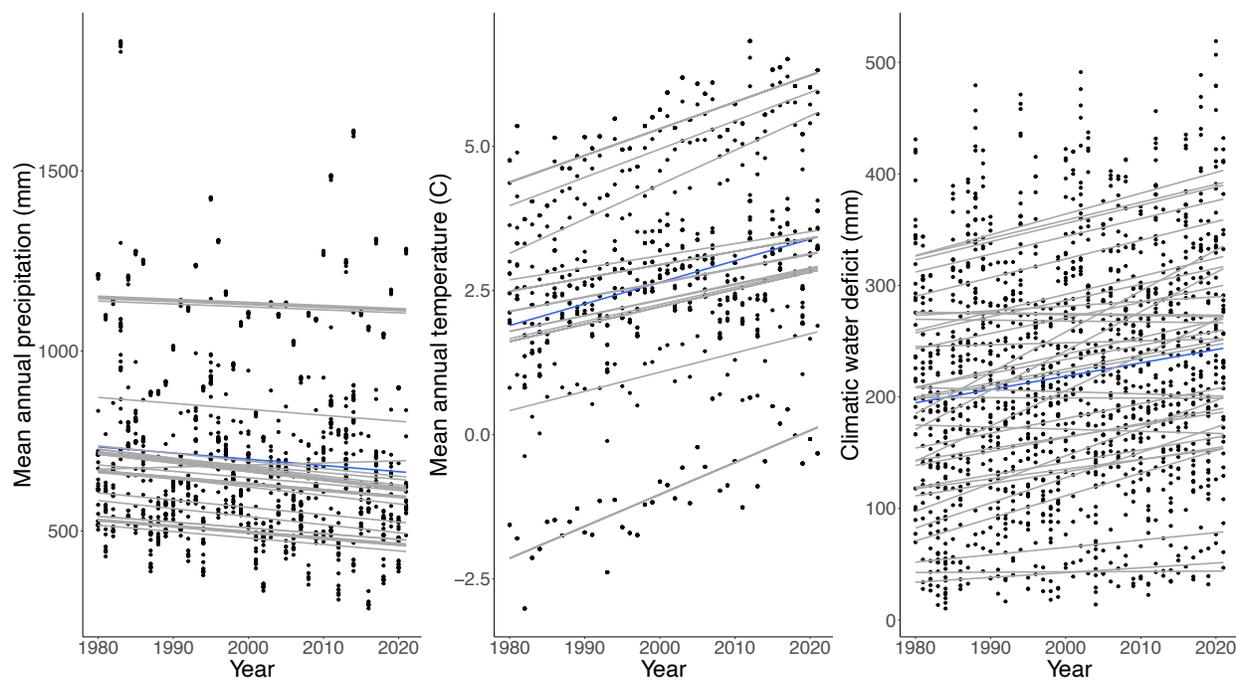


Fig. B2. Proportion of variance explained from each predictor (colors) by wetland type (A,B,C) and functional groups from each HMSC model.

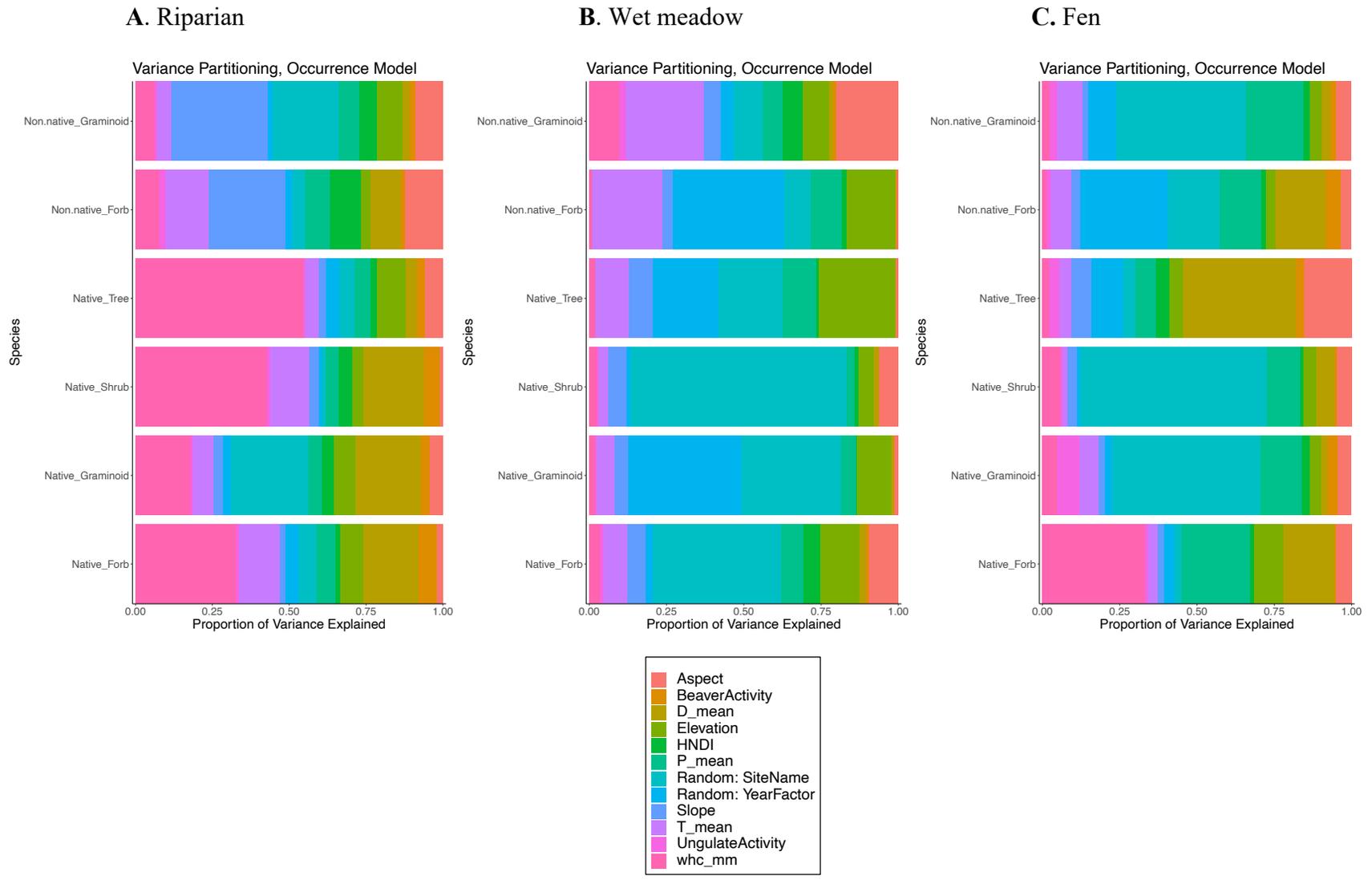
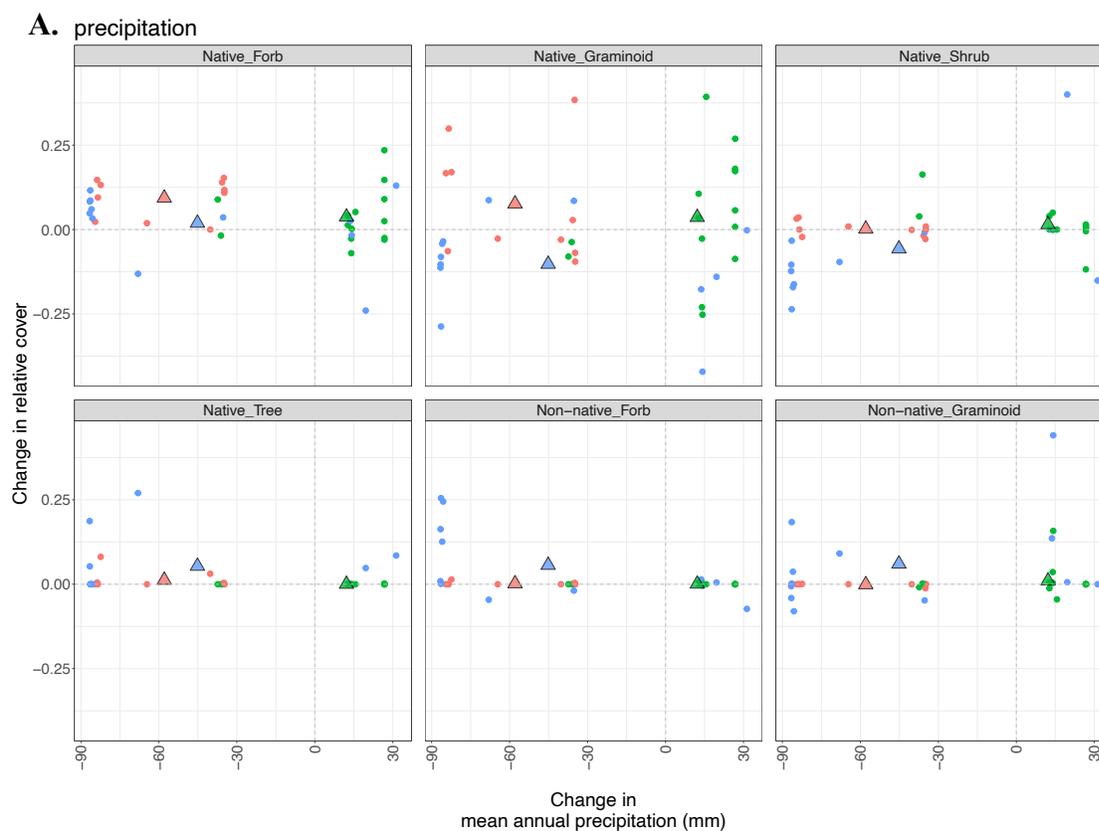
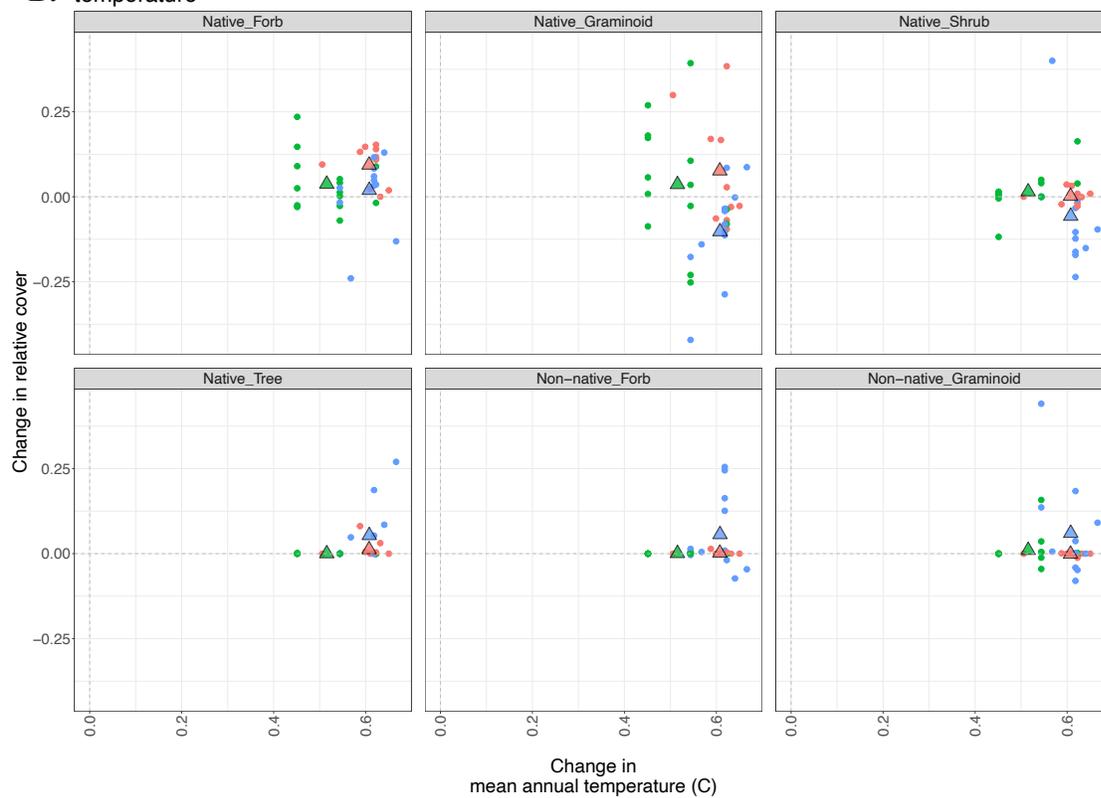
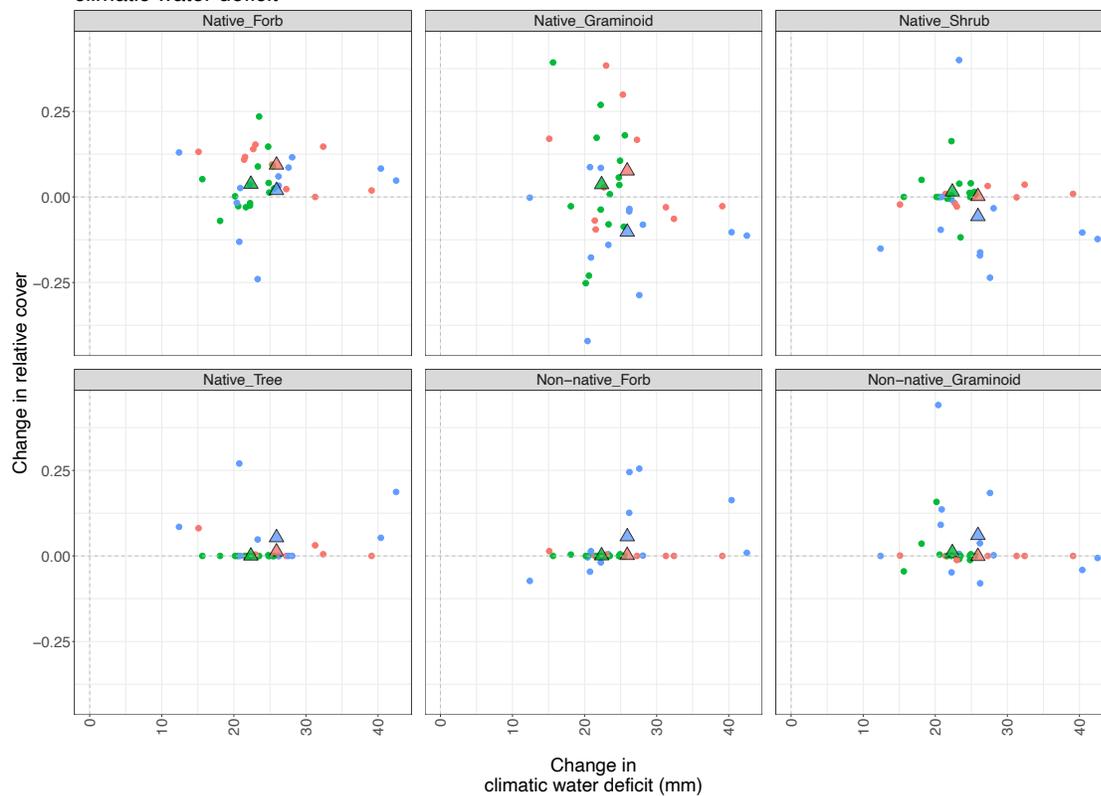
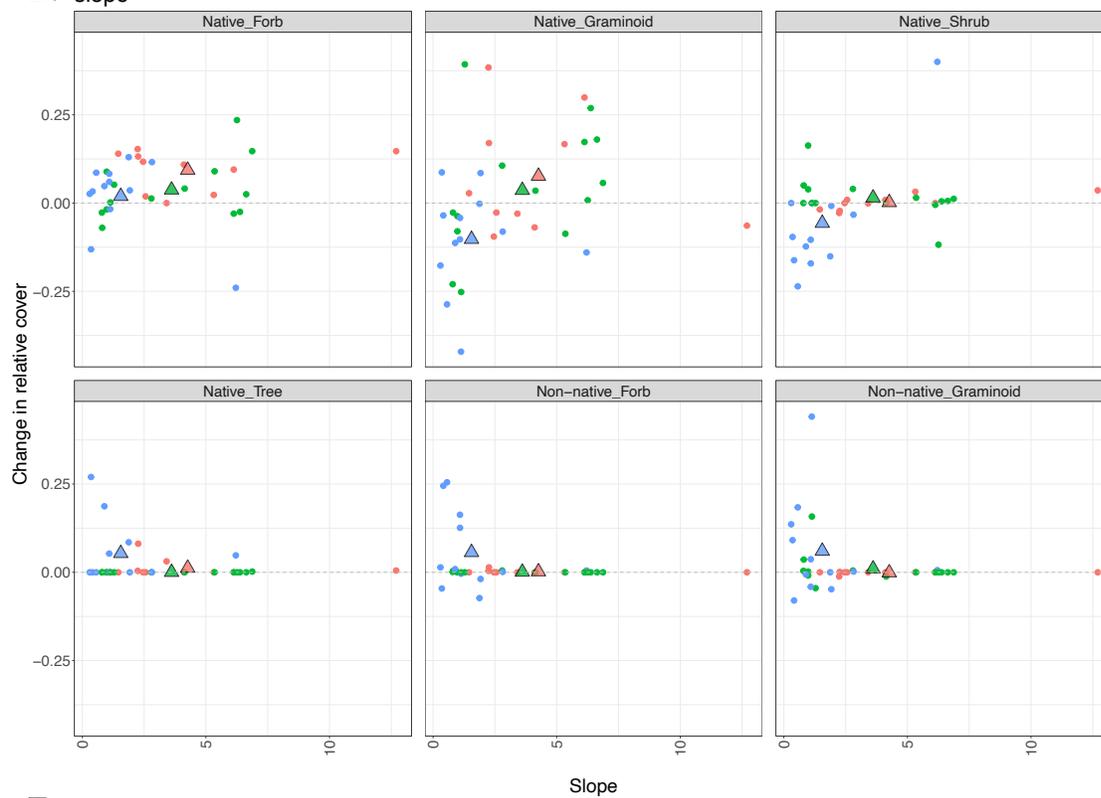
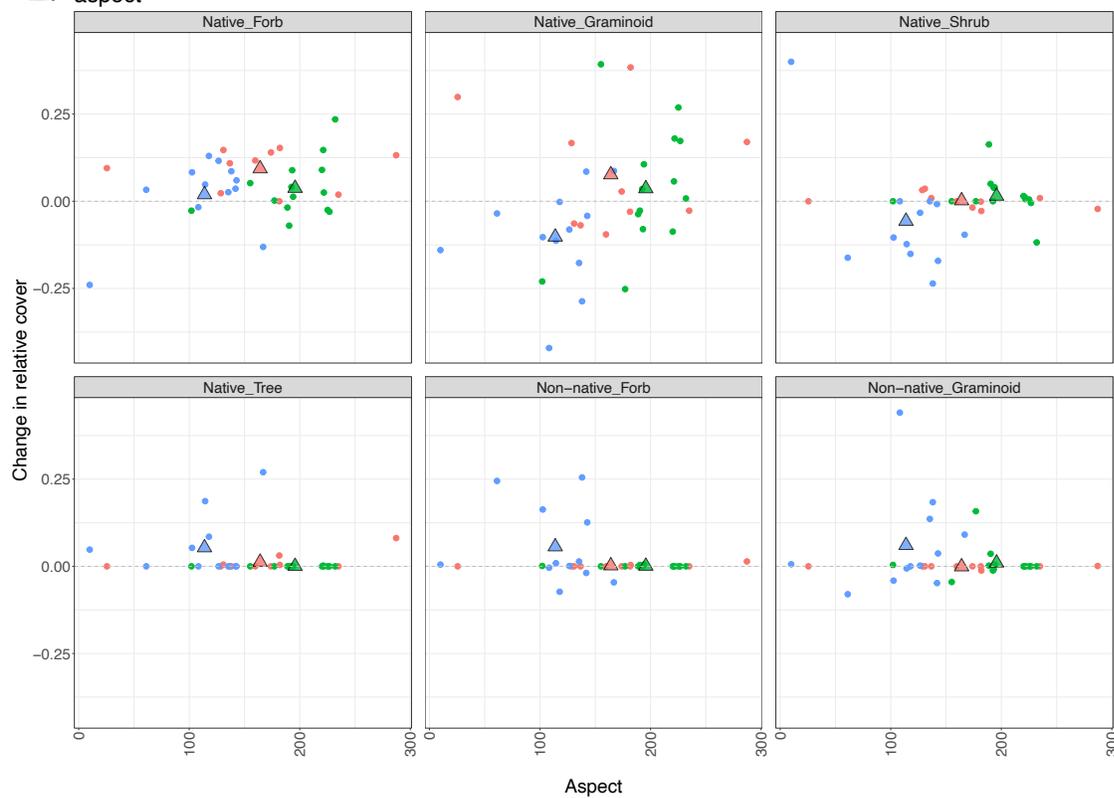


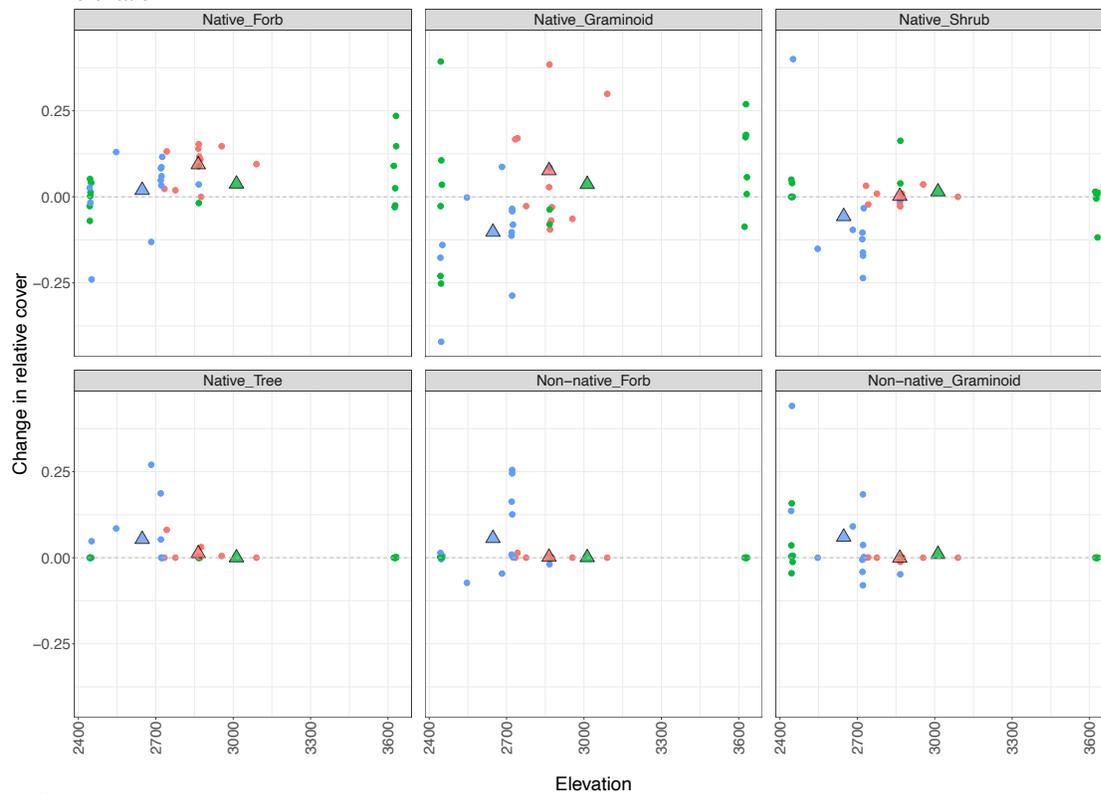
Fig. B3. Change in relative cover (y-axes) across environmental and biotic predictors used in HMSC analyses (y-axes) by functional groups (facets), across wetland types (colors). Changes mean annual precipitation, mean annual temperature, and climatic water deficit (A-C) from the first to last sample event are shown, whereas the last sample event's slope, aspect, elevation, soil water holding capacity, ungulate activity, beaver activity, and human disturbance index (D-J) are shown due to the largely unvarying nature of these variables. Triangle shaped points show functional group means. 0 change values are indicated by horizontal and vertical grey dashed lines.



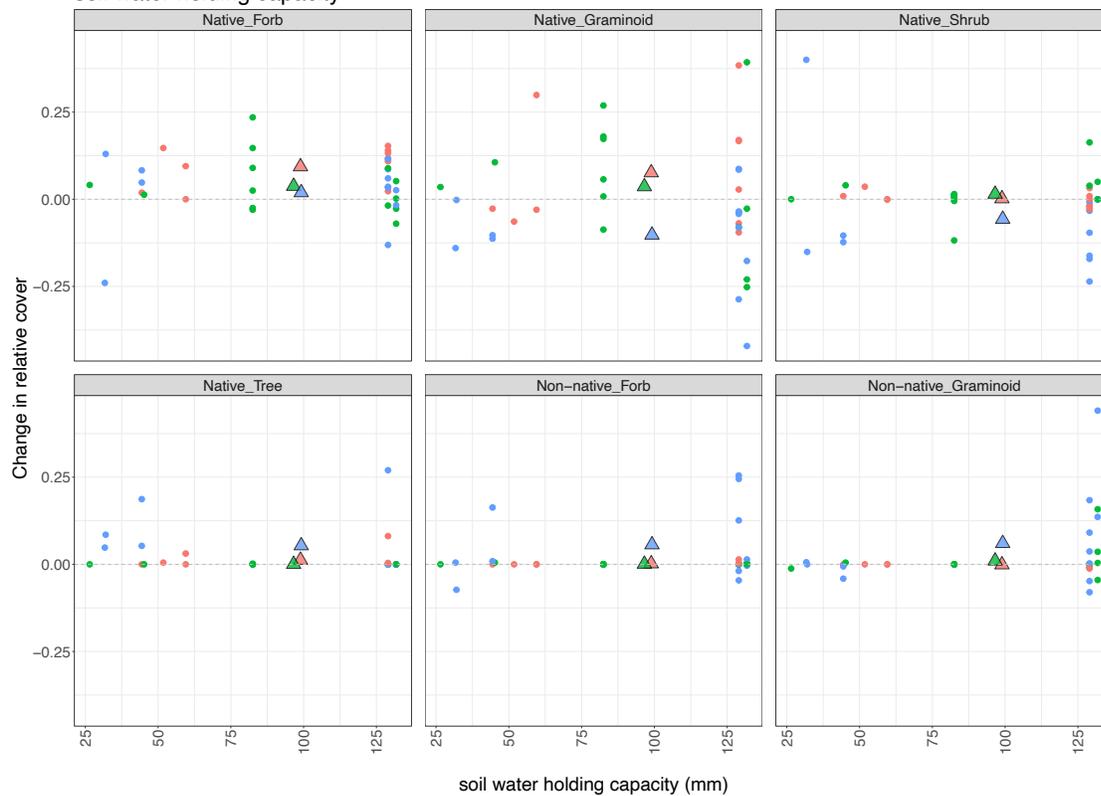
B. temperature**C. climatic water deficit**

D. slope**E. aspect**

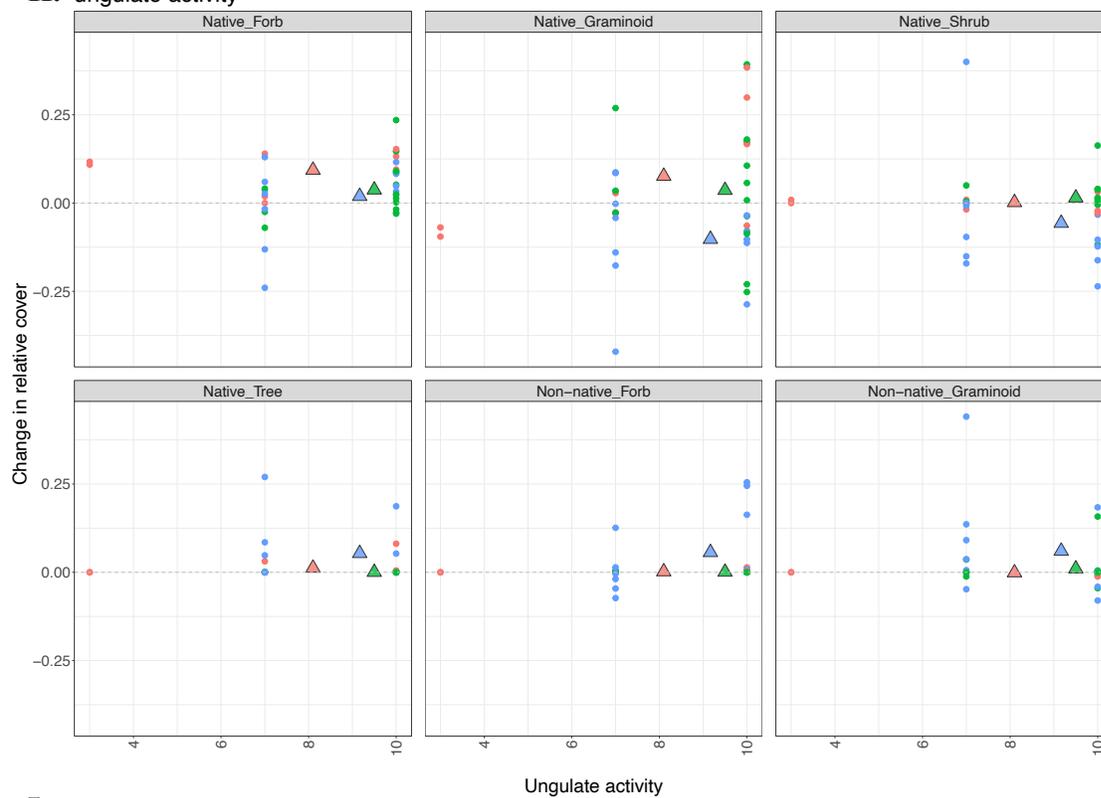
F. elevation



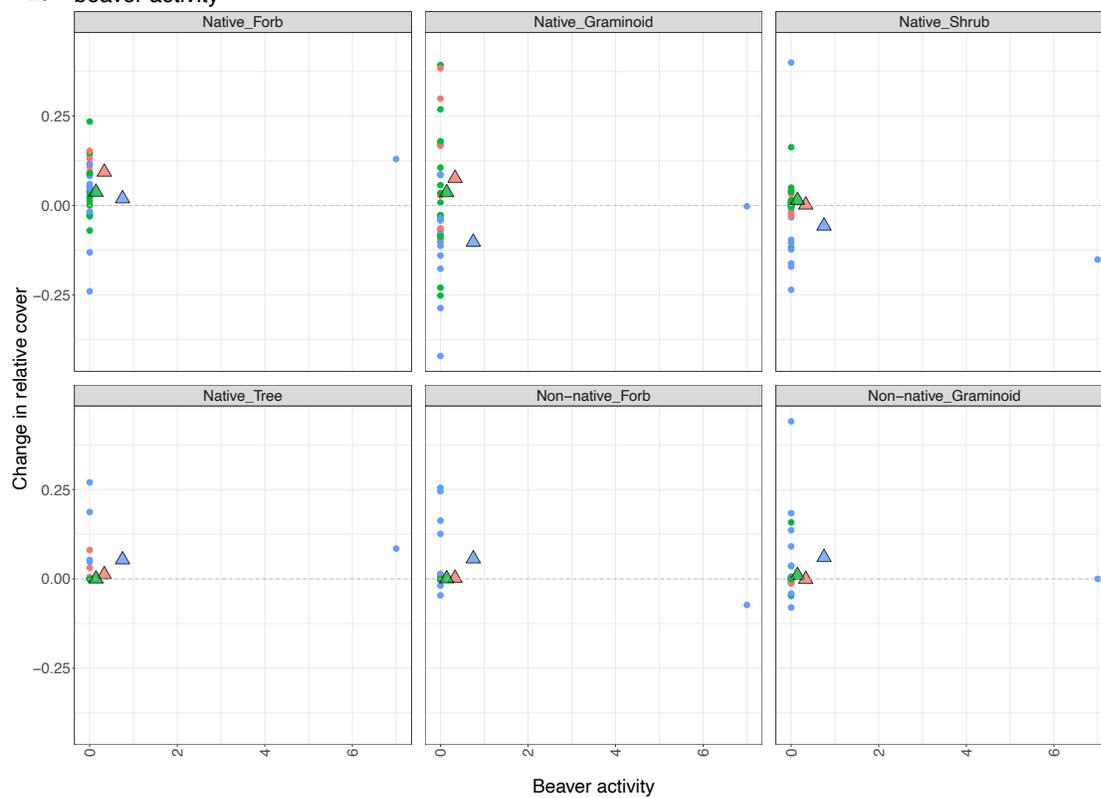
G. soil water holding capacity

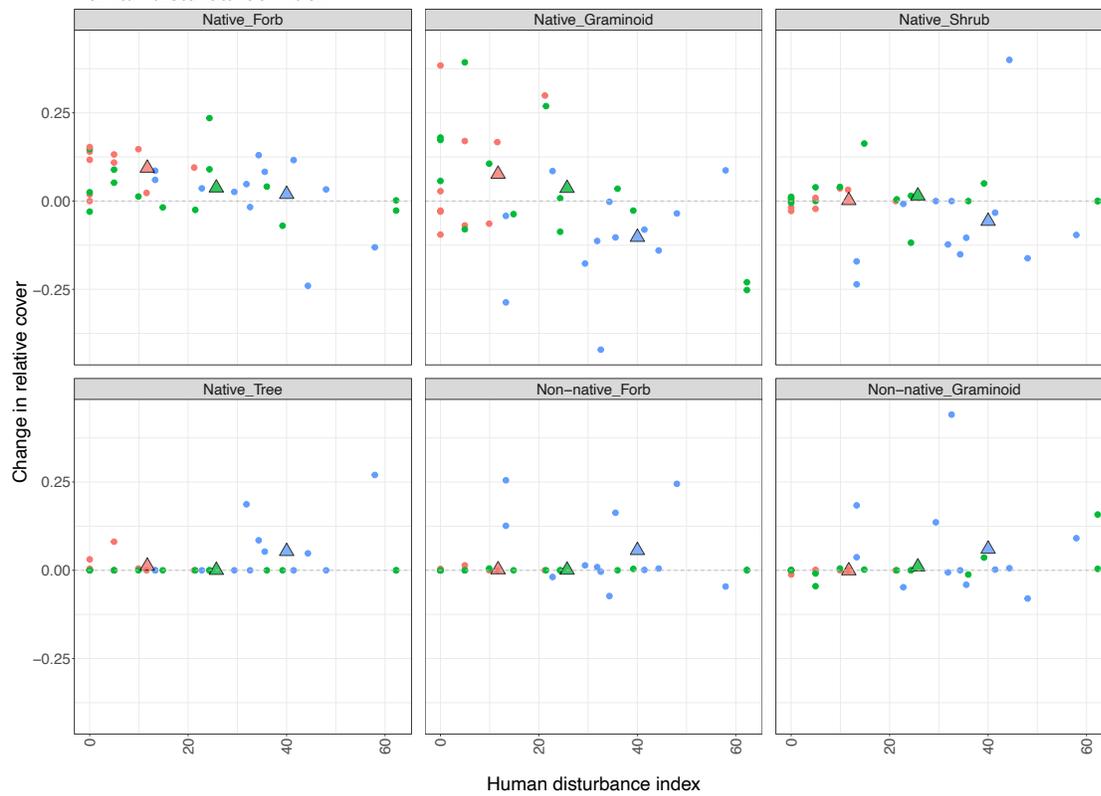


H. ungulate activity



I. beaver activity



J. human disturbance index

APPENDIX C: Supporting Tables and Figures, Chapter IV

TABLES

Table C1. Seeded species by community treatment.

Community	Common name	Scientific name
lowland	switchgrass	<i>Panicum virgatum</i>
	Canada wildrye	<i>Elymus canadensis</i>
	indiangrass	<i>Sorghastrum nutans</i>
	big bluestem	<i>Andropogon gerardii</i>
	alkali bullrush	<i>Bolboschoenus maritimus</i>
	Nebraska sedge	<i>Carex nebraskensis</i>
	prairie cordgrass	<i>Spartina palustris</i>
	common spikerush	<i>Eleocharis palustris</i>
	softstem bullrush	<i>Schoenoplectus tabernaemontani</i>
	clustered field sedge	<i>Carex praegracilis</i>
	baltic rush	<i>Juncus balticus</i>
	small-winged sedge	<i>Carex microptera</i>
upland	sideoats grama	<i>Bouteloua curtipendula</i>
	western wheatgrass	<i>Pascopyrum smithii</i>
	slender wheatgrass	<i>Elymus trachycaulus</i> ssp. <i>trachycaulus</i>
	Mexican hat, red	<i>Ratibida columnifera</i>
	annual sunflower	<i>Helianthus annuus</i>
	purple prairie clover	<i>Dalea purpureum</i> var. <i>purpureum</i>
	yellow prairie coneflower	<i>Ratibida columnifera</i>
	rocky mountain penstemon	<i>Penstemon strictus</i>

indian ricegrass	<i>Achnatherum hymenoides</i>
indiangrass	<i>Sorghastrum nutans</i>
white prairie clover	<i>Dalea candida</i>
bottlebrush squirreltail	<i>Elymus elymoides</i>
big bluestem	<i>Andropogon gerardii</i>
blue gramma	<i>Bouteloua gracilis</i>
green needlegrass	<i>Nassella viridula</i>
sand dropseed	<i>Sporobolus cryptandrus</i>
little bluestem	<i>Schizachyrium scoparium</i>
western yarrow	<i>Achillea millefolium</i> var. <i>occidentalis</i>
black-eyed susan	<i>Rudbeckia hirta</i>
Utah northern sweetvetch	<i>Hedysarum boreale</i>
wild bergamot	<i>Monarda fistulosa</i>

Table C2. Non-native species ordered by abundance across all plots.

USDA Symbol	Scientific name
MEOF	<i>Melilotus officinalis</i>
POCO	<i>Poa compressa</i>
BRTE	<i>Bromus tectorum</i>
VETH	<i>Verbascum thapsus</i>
RUCR	<i>Rumex crispus</i>
AGGI2	<i>Agrostis gigantea</i>
BEIN2	<i>Berteroa incana</i>
LIDA	<i>Linaria dalmatica</i>
AGST2	<i>Agrostis stolonifera</i>
PLLA	<i>Plantago lanceolata</i>
CIIN	<i>Cichorium intybus</i>
MESA	<i>Medicago sativa</i>
BAVU	<i>Barbarea vulgaris</i>

PLMA2	<i>Plantago major</i>
TRPR2	<i>Trifolium pratense</i>
MELU	<i>Medicago lupulina</i>
RUAC3	<i>Rumex acetosella</i>
PHPR3	<i>Phleum pratense</i>
LECA5	<i>Lepidium campestre</i>
CANU4	<i>Carduus nutans</i>
DAGL	<i>Dactylis glomerata</i>
CIAR4	<i>Cirsium arvense</i>
MARE6	<i>Matricaria recutita</i>
LASE	<i>Lactuca serriola</i>
CYOF	<i>Cynoglossum officinale</i>
TAPA6	<i>Tanacetum parthenium</i>
TRRE3	<i>Trifolium repens</i>
DIFU2	<i>Dipsacus fullonum</i>
NECA2	<i>Nepeta cataria</i>
ERCI6	<i>Erodium cicutarium</i>
ONAC	<i>Onopordum acanthium</i>
CEST8	<i>Centaurea stoebe</i>
CIVU	<i>Cirsium vulgare</i>
COAR4	<i>Convolvulus arvensis</i>
SIAL2	<i>Sisymbrium altissimum</i>
HYPE	<i>Hypericum perforatum</i>
TRDU	<i>Tragopogon dubius</i>
CEFO2	<i>Cerastium fontanum</i>
COMA2	<i>Conium maculatum</i>
EUES	<i>Euphorbia esula</i>

Table C3. Native species ordered by abundance across all plots.

USDA Symbol	Scientific name
ACMI2	<i>Achillea millefolium</i>
SAEX	<i>Salix exigua</i>
SAAM2	<i>Salix amygdaloides</i>
ELCA4	<i>Elymus canadensis</i>
SAIR	<i>Salix irrorata</i>
POAN3	<i>Populus angustifolia</i>
SABE2	<i>Salix bebbiana</i>
PODE3	<i>Populus deltoides</i>
POGR9	<i>Potentilla gracilis</i>
RUHI2	<i>Rudbeckia hirta</i>
AMPS	<i>Ambrosia psilostachya</i>
PAVI2	<i>Panicum virgatum</i>
JUAR2	<i>Juncus arcticus</i>
RACO3	<i>Ratibida columnifera</i>
HEMA2	<i>Helianthus maximiliani</i>
COSE16	<i>Cornus sericea</i>
ARFR4	<i>Artemisia frigida</i>
CAPR5	<i>Carex praegracilis</i>
SYPO4	<i>Symphyotrichum porteri</i>
OEVI	<i>Oenothera villosa</i>
JUDU2	<i>Juncus dudleyi</i>
ROWO	<i>Rosa woodsii</i>
PRAM	<i>Prunus americana</i>
GRSQ	<i>Grindelia squarrosa</i>
EPCI	<i>Epilobium ciliatum</i>
PASM	<i>Pascopyrum smithii</i>
ELTR7	<i>Elymus trachycaulus</i>
PRVI	<i>Prunus virginiana</i>
DAPU5	<i>Dalea purpurea</i>

SYOC	<i>Symphoricarpos occidentalis</i>
CAMI7	<i>Carex microptera</i>
RHTR	<i>Rhus trilobata</i>
RICE	<i>Ribes cereum</i>
ELLA3	<i>Elymus lanceolatus</i>
JUTO	<i>Juncus torreyi</i>
BOGR2	<i>Bouteloua gracilis</i>
POPR	<i>Poa pratensis</i>
LUAR3	<i>Lupinus argenteus</i>
VEHA2	<i>Verbena hastata</i>
ELPA3	<i>Eleocharis palustris</i>
CANE2	<i>Carex nebrascensis</i>
CASC11	<i>Carex scoparia</i>
RIAU	<i>Ribes aureum</i>
MUMO	<i>Muhlenbergia montana</i>
SCPUP5	<i>Schoenoplectus pungens</i> var. <i>pungens</i>
EQAR	<i>Equisetum arvense</i>
VEPEX2	<i>Veronica peregrina</i> ssp. <i>xalapensis</i>
SOGI	<i>Solidago gigantea</i>
CAPE42	<i>Carex pellita</i>
JUTE	<i>Juncus tenuis</i>
SCTA2	<i>Schoenoplectus tabernaemontani</i>
PEST2	<i>Penstemon strictus</i>
GLGR	<i>Glyceria grandis</i>
TAOF	<i>Taraxacum officinale</i>
ALINT	<i>Alnus incana</i> ssp. <i>tenuifolia</i>
DACA7	<i>Dalea candida</i>
BEOC2	<i>Betula occidentalis</i>
IRMI	<i>Iris missouriensis</i>
EQHYA	<i>Equisetum hyemale</i> var. <i>affine</i>
ELEL5	<i>Elymus elymoides</i>

HEVI4	<i>Heterotheca villosa</i>
VEAN2	<i>Veronica anagallis-aquatica</i>
ASIN	<i>Asclepias incarnata</i>
COCA5	<i>Conyza canadensis</i>
SCMI2	<i>Scirpus microcarpus</i>
CACA11	<i>Carex canescens</i>
ERFL	<i>Erigeron flagellaris</i>
SYLA3	<i>Symphytotrichum laeve</i>
HENU	<i>Helianthus nuttallii</i>
PHHA	<i>Phacelia hastata</i>
POPA2	<i>Poa palustris</i>
MEAR4	<i>Mentha arvensis</i>
BOCU	<i>Bouteloua curtipendula</i>
TYLA	<i>Typha latifolia</i>
CHSE6	<i>Chamaesyce serpyllifolia</i>
ROPS	<i>Robinia pseudoacacia</i>
CAPA14	<i>Carex pachystachya</i>
ARLU	<i>Artemisia ludoviciana</i>
GEAL3	<i>Geum aleppicum</i>
GLST	<i>Glyceria striata</i>
SAPL2	<i>Salix planifolia</i>
SCPUL4	<i>Schoenoplectus pungens</i> var. <i>longispicatus</i>
VEBR	<i>Verbena bracteata</i>
YUGL	<i>Yucca glauca</i>
SOCAC3	<i>Solidago canadensis</i> var. <i>canadensis</i>
THDI4	<i>Thermopsis divaricarpa</i>
SIAN2	<i>Silene antirrhina</i>
ANAN2	<i>Antennaria anaphaloides</i>
CARO2	<i>Campanula rotundifolia</i>
CAVU2	<i>Carex vulpinoidea</i>

OPPO	<i>Opuntia polyacantha</i>
SIDR	<i>Silene drummondii</i>
GEVI2	<i>Geranium viscosissimum</i>
ACGL	<i>Acer glabrum</i>
ARGL	<i>Arabis glabra</i>
FRVI	<i>Fragaria virginiana</i>
LEVI3	<i>Lepidium virginicum</i>
OXDI2	<i>Oxalis dillenii</i>
ALTE	<i>Allium textile</i>
CEBR3	<i>Cerastium brachypodium</i>
GERI	<i>Geranium richardsonii</i>
MIGU	<i>Mimulus guttatus</i>
PICO	<i>Pinus contorta</i>
DAFR6	<i>Dasiphora fruticosa</i>

FIGURES

Fig. C1. Boxplots of community type (colors, x-axes) traits (panels, y-axes). All traits on the y-axis are arranged from acquisitive to conservative values (the $\delta^{15}\text{N}$ axis was reversed to conform with this format). There were not consistent differences between traits of the lowland and upland community types.

